Interspecific interactions and spatial heterogeneity: using key species to up-scale and map ecosystem functioning

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“*The story is in the variance*”

Abstract

Soft sediments cover most of the ocean seafloor and dominate estuarine and coastal habitats. Most of our current knowledge on the functioning of these ecosystems is derived from experimental studies conducted at scales that are much smaller than those most relevant to society. The results of these experiment can be hard to extrapolate beyond their scope and the outcomes can be affected by the way we scale them. Moreover, heterogeneity and processes interacting across scales of space and time can further hinder our ability to extend the generality of experimental studies. Besides, due to the challenge of extensive sampling marine ecosystems, large scale ecosystem models mainly rely on physical attributes and often overlook the role of the underlying biodiversity.

In this dissertation, I investigate at the existence of species–ecosystem functions relationships in heterogeneous marine landscapes and their persistence across different spatial scales. In particular, I look into the role of key, functionally important infaunal species and of their interactions for sediment biogeochemistry and then up-scale this information to create ecologically nuanced maps of ecosystem functions at the landscape level. After providing a general introduction (Chapter 1), I begin by investigating the interaction between two functionally important but different species (*Macomona liliana* and *Macroclymenella stewartensis*) on sediment biogeochemistry in a laboratory experiment (Chapter 2). I then explore the importance of transitional areas, where the distribution of these two species overlap, for the overall ecosystem functioning and I weight the role of the two key species compared to that of the rest of the community (Chapter 3). Finally, I use this information to create models that relate ecosystem functions rates to key species and extrapolate the models through a high-resolution drone survey of the distribution of those species (Chapter 4). As we then demonstrate, scaling these ecological relationships without adequately taking into account the role of biodiversity and heterogeneity would lead to inaccurate results that are more sensitive to scaling methods chosen than to the ecological characteristics of the system (Chapter 5).

I demonstrated that interspecific interactions and the heterogeneity of processes generate differences of orders of magnitudes in the delivery of functions. Most of these interactions happen in transition areas, where patches of different species overlap, creating ecological boundaries. The contribution of these areas to the overall functioning of heterogeneous systems is significant and needs to be taken into account to accurately estimate functioning at coarse scales. Our findings show how rise in the last decades of new remote sensing technologies and artificial intelligence allows the extrapolation of this complex information to larger extents and the creation of ecologically meaningful maps of ecosystems.

Preface

This thesis contains two chapters that have been published in a peer-reviewed journal (Chapter 2 and Chapter 3). Chapter 4 and Chapter 5 have been submitted to a peer-reviewed journal. These studies are included in the thesis with only very minor modifications. There is therefore some necessary repetition between chapters, which I have done my best to keep to a minimum.

I was the principal contributor and primary author of all chapters presented in this dissertation. My main supervisors – Simon F. Thrush – provided guidance and advice throughout. My co-supervisor – Teri O'Meara – contributed to Chapter 2. Other contributors are recognised in the acknowledgements for each chapter.

Chapter 2 was written in collaboration with Simon F. Thrush and Teri O'Meara. This chapter has been published as: Schenone S, O'Meara TA, Thrush SF (2019). Non-linear effects of macrofauna functional trait interactions on biogeochemical fluxes in marine sediments change with environmental stress. *Marine Ecology Progress Series*; 624: 13–21

Chapter 3 was written with the guidance and support of Simon F. Thrush. This chapter has been published as: Schenone S, Thrush SF. (2020). Unraveling ecosystem functioning in intertidal soft sediments: the role of density-driven interactions. *Sci Rep* 10:11909.

Chapter 4 was written in collaboration with Mihailo Azar, César Adrián Victoria Ramírez, Alfonso Gastelum Strozzi, Patrice Delmas and Simon F. Thrush. It has been submitted for peer-review.

The ideas and study design for Chapter 5 were conceived together with my main supervisor, Simon F. Thrush. This chapter has recently been submitted to a peer-reviewed journal.

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Without the financial support offered by the University of Auckland Doctoral Scholarship it would have not been possible for me to move to New Zealand and complete my degree.

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To my friends (many of whom also fall under the ‘volunteer’ and ‘lab’ categories), thank you for understanding the demands on my time, and for always being there with unconditional love, empathy, and laughter. Your support has meant so much to me.

To my family, my mother, my father and my brother, thank you for the sacrifices you made, financial and emotional. You’ve always supported me, even I moved 18,000 km away. To my partner, Eliana, in particular – thank you. Except for that one time when you claim you broke up with me, your support and the sacrifices you made to be on my side mean a lot to me and made it possible for me to be here and to do my PhD.

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Please indicate the chapter/section/pages of this thesis that are extracted from a co-authored work and give the title and publication details or details of submission of the co-authored work.

Chapter 2

Schenone S, O'Meara T, Thrush S. Non-linear effects on biogeochemical fluxes of macrofauna functional trait interactions in marine sediments change with environmental stress. Mar Ecol Prog Ser 2019. doi:10.3354/meps13041

Nature of contribution by PhD candidate	Experiment, sample analysis, data analysis, manuscript writing
Extent of contribution by PhD candidate (%)	90%

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Simon Thrush	consultancy for experimental design and statistical analysis, revision of the manuscript

Certification by Co-Authors

The undersigned hereby certify that:

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Chapter 3

Unraveling ecosystem functioning in intertidal soft sediments: the role of density-driven interactions

Nature of contribution by PhD candidate	Experiment, sample analysis, data analysis, manuscript writing
Extent of contribution by PhD candidate (%)	95%

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Chapter 4

"Mapping the delivery of ecological functions combining field collected data and Unmanned Aerial Vehicles (UAV)", submitted to Ecological Applications

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César Adrián Victoria Ramírez	Image analysis
Alfonso Gastelum Strozzi	Consultancy for image analysis
Patrice Delmas	Consultancy for image analysis
Simon F. Thrush	Supervision, consultancy for experimental design and statistical analysis, manuscript revision

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Chapter 5

Scaling-up ecosystem functions of coastal heterogeneous sediments: experimenting with high resolution data

Nature of contribution by PhD candidate	Study design, data analysis, manuscript writing
Extent of contribution by PhD candidate (%)	90%

CO-AUTHORS

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Chapter 1 – General introduction

Stefano Schenone

1.1 | A puzzling world

Soft-sediments habitats are the most widespread ecosystem on earth, they cover 70% of the ocean seafloor and dominate estuarine and coastal environments (Snelgrove, 1997). These ecosystems are incredibly complex and dynamic. Yet, sediments are often considered as a homogeneous habitat and far from being as diverse and appealing as algal forests or coral reefs, because much of the spatial complexly and resident organisms are out of sight. However, sediments create a three-dimensional environment where physical, chemical and biological processes interact generating heterogeneity and influencing processes that lead to ecosystem functions (Snelgrove et al., 2014). The continuous exchange of matter and energy across the sediment-water interface boosts biogeochemical fluxes that support most marine ecosystems (Gardner et al., 2006; Savage et al., 2012). Our understanding of these important processes has improved over the years and studies have addressed the role of biodiversity for ecosystem functioning (Dornhoffer et al., 2015; Mermillod-Blondin et al., 2004; Woodin et al., 2016; Zeppilli et al., 2016). The organisms living in sediments, in fact, are known to drive many critical ecosystem functions, in particular the breakdown and transformation of organic material and the associated release of nutrients, facilitating their recycling, dispersion through the sediment-water interface and transfer through food webs (Thrush et al., 2017).

Important questions still remain. To what extent do key species alone drive ecosystem functioning? How much do the interactions between these important and sometimes very different species vary and influence functioning? How does this translate to heterogeneous landscapes, where the mosaic of habitat patches creates important transition zones and what is their contribution to overall ecosystem functioning? What is the net effect of large, functionally important species compared to that of the rest of the community? How do these processes measured at fine scales (< 1 m^2) translate to coarser (> 1 km^2) scales? How much do functions vary across the landscape? How can we use new technologies, like drones and Artificial Intelligence, to benefit landscape ecology research? Despite our efforts to untangle these complicated dynamics, in studies of landscapes at scales that are meaningful to society this dimension of ecological complexity is generally lost. Due to the challenges of extensively sampling marine environments, large scale practices like habitat mapping, ecosystem services assessment and modelling rely on physical parameters and overlook the underlying role of biodiversity and that of patchiness in species distributions and functional performance (Lavorel et al., 2017). This is particularly true for benthic soft-sediment environments where the dominant habitats are coarsely aggregated into sand or mud.

In this thesis, I look at the multi-scale and heterogeneous nature of benthic habitats as an opportunity to address these important gaps (Fig. 1.1). Only through a knowledge of the processes that drive and sustain ecosystems that is well grounded in their ecological roots we are able to get to an accurate estimate of the functions and services they provide. This knowledge offers real-world assessments and a sensitivity to change that ultimately supports us in ecologically sustainable management and prioritize conservation. The biodiversity crisis that affects the world (Smith et al., 2000) adds urgency to bridging these gaps to understand how changes in biodiversity will influence ecosystem function at different scales and the delivery of services that support life and economies.

Fig. 1.1 Soft sediment ecosystems exhibit heterogeneity of structures and processes that can be studied at different scales. Clock-wise from the top left corner: small biogenic structures on the sediment surface; incubation chambers are used to measure biogeochemical fluxes at the sediment-water interface; drones can be used to obtain to sample remotely at different resolutions; spatially explicit information at the landscape level is crucial to manage and protect ecosystems.

1.2 | Heterogeneous landscapes

Environmental heterogeneity is ubiquitous in natural systems and is one of the most important factors to influence population dynamics and community structure (Chesson, 2000; Dutilleul and Legendre, 1993; Oliver et al., 2010; Yang et al., 2015; Zajac et al., 2003). Simplistically, heterogeneity refers to the characteristic of being composed of dissimilar or diverse parts and is different from variability, which refers to the different values of a variable of one kind (Kolasa and Rollo, 1991). Heterogeneity is a complex concept and some distinctions need to be made. The first major distinction is between spatial and temporal heterogeneity. The idea of spatial heterogeneity is relatively straightforward as it evokes visual differences when a quantitative or qualitative of a descriptor, such as vegetation cover, assumes different values at different locations. Temporal heterogeneity is conceptually similar to spatial heterogeneity and it refers from one point in space sampling many points in time (Dutilleul and Legendre, 1993). Most of the landscape ecology research focuses primarily on the role of spatial heterogeneity. Another important distinction is that between functional and measured heterogeneity. The former is referred to as the heterogeneity that influences the organisms, and is not the same for different groups of organisms that live in the same environment, while the latter is the heterogeneity measured by the observer, which may be inadequate to describe all the effects on communities (Kolasa and Rollo, 1991).

In benthic habitats, much of the heterogeneity is generated by the biota and its interaction with the environment. This results in patchy spatial distributions of communities and ecosystem functions across multiple spatial scales. Although this heterogeneity is a powerful indicator of ecological health (Hewitt et al., 2010), it confounds the simple up-scaling of ecosystem function measurements and thus the estimate of ecosystem services at scales most relevant to society (Hewitt et al., 2007). Despite the recognition of the importance of heterogeneity, most ecosystem studies are conducted within a single ecosystem, and homogeneous sites are generally chosen to minimize the complications associated with spatial heterogeneity (Lovett et al., 2005). For example, Canavan et al. (2007) inferred nitrogen cycling of coastal fresh water sediments from measures performed at a single site in a coastal freshwater lake. However, understanding patterns, causes, and consequences of spatial heterogeneity in ecosystem function is crucial to advance our comprehension of the natural world (Chapter 3; Turner and Chapin, 2005). In their book, Lovett et al. (2005) point out that understanding the relationship between spatial heterogeneity and ecosystem processes is especially important i) when it is necessary to know the average rate of a process over an area that is spatially heterogeneous and ii) when one wants to understand or predict the spatial pattern of process rates, using the spatial pattern or spatial scale of variation as a response variable of direct interest. Therefore, rather than a confounding factor to avoid when performing ecological studies, researchers should see heterogeneity an opportunity to investigate and understand the underlying processes that drive ecosystems.

1.3 | The problem of scale

Heterogeneity, like everything else in ecology, is scale-dependent (Wiens, 2000). The concept of scale is intrinsic to ecology and usually refers to the spatial or temporal dimension of a phenomenon. The processes that characterize and impact landscapes occur at many spatial and temporal scales. For example, Kotliar and Wiens (1990) argued the response of organisms to habitat patches changes with scale and developed a hierarchical model to classify patch structure across a range of scales. However, scale is not a property of nature alone but, rather, is something associated with observation and analysis (Allen and Starr, 1982). A simple, yet effective visualization of this concept applied to the recycling of nitrogen is given by Kolasa and Pickett (1991) (Fig. 1.2).

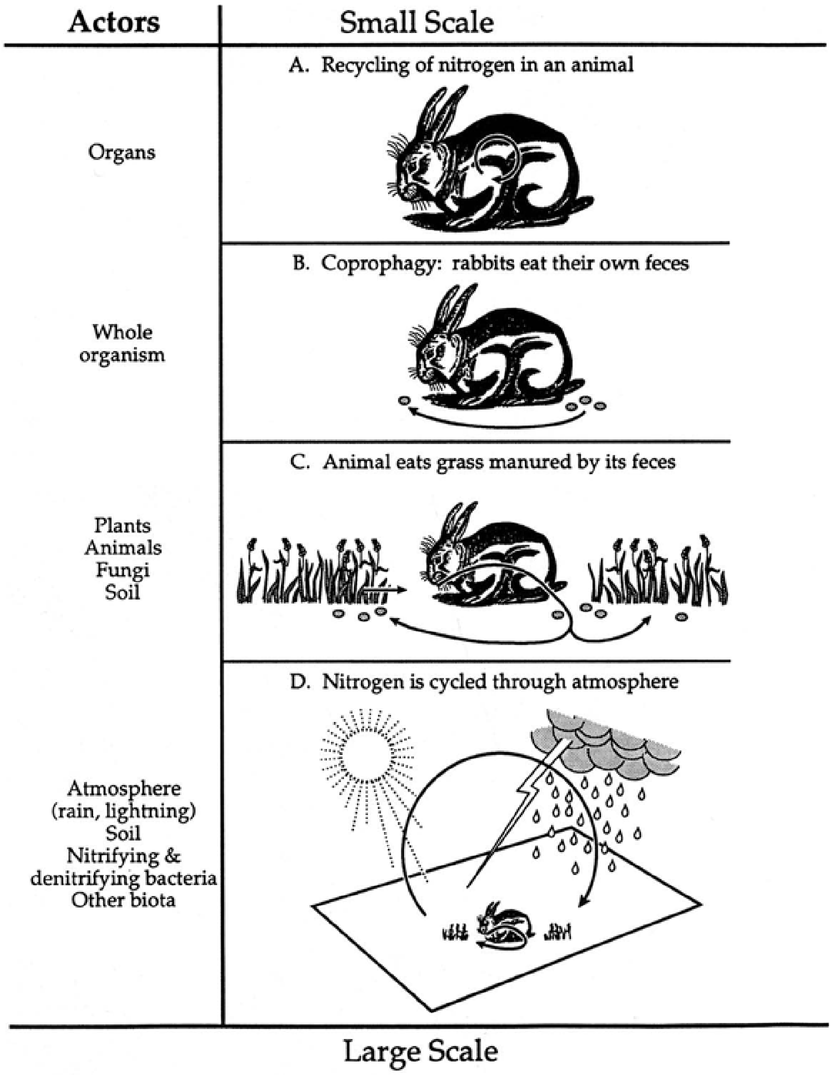

Fig 1.2 The process of nitrogen recycling observed at different scales. From (Allen and Hoekstra, 1991).

In ecology, scale most frequently refers to its basic components that dictate the sampling design of studies: “grain” and “extent”. Grain concerns the level of resolution of a study and determines the smallest and largest entities that can be seen. In contrast, the extent is generally referred to as the total spatial or temporal expanse of a study (Wiens, 1989). The importance of these concepts lies in their influence on empirical ecological studies. The sampling design, in fact, dictates the scale of the processes we can observe and our ability to understand their drivers. Therefore, choosing a scale that is not appropriate to the ecological process in question can limit our ability to accurately hypothesize and determine the underlying causes (De Knegt et al., 2010; Legendre et al., 2002).

Since processes can occur at many spatial and temporal scales and the processes operating at large-scale are not always the same as those operating at small-scale, translating information from one scale to another can be an arduous task. Moreover, environmental heterogeneity is known to increase with scale, complicating this process even further (Hewitt et al., 2007; Lohrer et al., 2015; Peterson, 2000; Snelgrove et al., 2014; Thrush et al., 1997). Nevertheless, developing ways to use the results of small-scale experimental studies to understand larger-scale phenomena (Chapter 4) is essential to predict large-scale effects and has been a central topic of ecology for many decades. Chapter 5 elaborates on the different methods that have been proposed in the literature for the purpose of up-scaling experimental results. There does not appear to be one right way to relate patterns and processes across scales and the choice is dictated by the properties of the system studied. In marine benthic ecosystems, however, heterogeneity has a profound influence on patterns and processes and has to be accounted for in the scaling process (Thrush et al., 1997).

1.4 | The challenges of marine systems

Coastal zones only cover about 8% of the world surface but are estimated to contribute to approximately 43% of the total economic value of global ecosystem service (Costanza et al., 1997). These are highly productive ecosystems that deliver multiple functions that range from the recycling of nutrients and decomposition of organic matter to the sustenance of food webs. For example, continental shelves mineralize more than 50% of the global organic matter, recycling nutrients that fuel ocean primary productivity (Middelburg et al., 1997; Sundbäck et al., 2003). Despite the recognition of their importance, the functions and processes that maintain coastal and marine habitats in general are still poorly understood. The collection of samples in these systems is a costly and time-consuming process and measurements are mainly performed at single points or on transects. For example, Stevens and Connolly (2004) sampled 41 sites in a staggered 5 km spaced array to characterize the habitats of Moreton Bay, Australia. This scarcity of data results in the inadequate knowledge of the distribution of communities and habitats and the ecosystem functions that they provide (Townsend et al., 2014). The use of remote sensing in recent times has enhanced our ability to collect data over large areas in a short period of time. While satellite images and acoustic techniques provide data at relatively coarse resolution, drone and kite aerial photography and underwater tow cameras have the ability to collect data at higher resolution (Bryson et al., 2013). This is particularly important when characterising ecological systems. Currently, large scale benthic habitat characterisation relies primarily on physical attributes and therefore overlooks the role of the underlying biodiversity on ecosystem functioning and ecosystem services. This problem has been referred to as the "lack of biophysical realism" (Lavorel et al., 2017; Seppelt et al., 2011). As I show in Chapter 2 and 3 in fact, species richness and the presence of functionally important species can be strongly related to the ecological functions and the supply of ecosystem services. This notion is supported by the body of literature on ecosystem function (Cardinale et al., 2012; Fourqurean et al., 2012; Ieno et al., 2006; Mermillod-Blondin et al., 2005). Therefore, ecological research and the study of ecosystem services needs to focus on finding ways to close this gap in biophysical realism.

1.5 | Advances in remote sensing and artificial intelligence

In the previous paragraph I mention some of the advantages that the use of remote sensing technologies brings to ecology. The rise of remote sensing techniques and new technological advances, in fact, have revolutionized ecological research by providing both spatial and temporal perspectives on ecological phenomena that could not be achieved otherwise (Anderson and Gaston, 2013). For a long time, satellites have been the most exploited remote sensing platform. However, despite the improvements obtained in recent years, they provide data at relatively coarse spatial resolution, not suitable to study small scale processes. For example, high-resolution satellites can provide resolution of 0.5-10 m per pixel (e.g., QuickBird, IKONOS) (Wang et al., 2010). Freely available satellite images usually have lower resolutions of around 30 m per pixel (e.g., Landsat, MODIS). The advent of unmanned aerial vehicles (UAVs) has emerged as a solution to this problem. UAVs, commonly known as drones, can achieve higher resolution than satellites and occupied aircraft and at the same time reduce costs as well as providing more flexibility (Johnston, 2019; Ridge et al., 2020). The use of drones in environmental research has increased over the last decade and drone imagery has proved successful in a number of studies and habitats, from the mapping of coastal morphology, to the monitoring of coral and oyster reefs (Casella et al., 2017; Long et al., 2016; Ridge et al., 2020).

Another technological advance that has demonstrated potential in addressing important issues of environmental and ecological research is the progress in deep learning architectures. Deep learning is a type of machine learning based on artificial neural networks inspired by the structure and function of the brain. Its aim is to train a computer to perform tasks, such as identifying images, learning by examples (LeCun et al., 2015). An emerging class of algorithms in particular, known as convolutional neural networks (CNNs), have shown breakthrough performance in image classification (Brodrick et al., 2019). Even though training these artificial intelligences may require the classification of thousands of images, their benefit for biodiversity and ecological research is undeniable and they have proven effective in both terrestrial and marine studies (Gray et al., 2019; Ridge et al., 2020; Weinstein, 2018). In Chapter 4, I present a method developed for mapping ecosystem functions that uses drone imagery and machine learning to extrapolate the results of function models, detecting biogenic features in more than 7000 pictures.

1.6 | From Functions to Services

Ecosystem functions occur in the context of biological, physical and chemical properties and the interaction of processes. Ecosystem services (ES), represent the benefits human populations derive, directly or indirectly, from ecosystem functions (Costanza et al., 1997). This drawn attentions attention to biodiversity contributes human wellbeing (de Bello et al., 2010). A common practice for ES research is to use the general definition given by the Millennium Ecosystem Assessment that “ecosystem services are the benefits people obtain from ecosystems” (Millenium Ecosystem Assessment, 2005). However, despite the attention ES have received, understanding of their ecological foundation is still limited, with negative consequences on our ability to target management and conservation efforts (Kremen, 2005). This issue is particularly relevant due to the current threats posed to ecosystems. Due the increasing anthropogenic pressures, in fact, our planet is experiencing a growing loss of biodiversity and changes in the functioning of ecosystems (Smith et al., 2000). Therefore, the sustainable management of ES requires knowledge of the effects that species have on ecosystem functioning at different scales and of the consequences of their loss. Ultimately, our ability to capture the spatial and temporal dynamics of ecosystem functions will influence the assessment of the services that ecosystem provide.

In this perspective, ES maps are critically important tools for ecosystems management, particularly since the introduction of Geographic Information System (GIS) (Maes et al., 2012). Maps should support the quantification of service delivery and distribution at different scales. ES maps are a key element to improve the recognition and implementation of ES into institutions and decision-making (Daily and Matson, 2008). Other important features of maps are that they can be used to assess spatial trade-offs and synergies among ES, as well as to prioritize areas that will allow to achieve multiple conservation goals (Martínez-Harms and Balvanera, 2012). Many mapping approaches have been proposed, from the estimate of the value of ES in monetary terms from land-cover or habitat maps (e.g. Kreuter et al., 2001; Troy and Wilson, 2006; Turner et al., 2007), to the quantification of ES in biophysical units, without including monetary valuation (e.g. Egoh et al., 2008; Naidoo et al., 2008; Townsend et al., 2014). In general, however, despite processes and functions being part of biodiversity, most of the efforts into the mapping of ES does not quantify the underlying role of biodiversity in providing services. This problem is even more pronounced in marine habitats, since their complexity and highly dynamic nature, translates into the lack of spatially explicit information. Despite the recognition of this gap, only very few studies have addressed the creation of maps of ecosystem functions in marine systems (e.g., Eyre and Maher, 2011; Gogina et al., 2017; Harborne et al., 2006). Therefore, more research is needed to both understand the link between biodiversity – interpreted not just as biological communities – and ecosystem functioning and create new methods to translate this knowledge to larger scales.

1.7 | Thesis outline

In Chapter 2, I explore the effect of 2 key bioturbators for benthic biogeochemical fluxes. Specifically, I study the tellinid bivalve *Macomona liliana* and the maldanid polychaete *Macroclymenella stewartensis*, two infaunal organisms that dominate patches in New Zealand intertidal flats in terms of both abundance and biomass, but that are functionally very different. In this chapter I focus on the effect of these two species on benthic biogeochemical fluxes when they are incubated in single-species treatments vs their effect when both species are incubated together and interactions occur. The effect of environmental stress is also taken into account

In Chapter 3, I build on the results from Chapter 2 and investigate the role of these two species in the natural environment and of their interactions in transitional areas, at the interface between their patches. The study was performed in the Whangateau Harbour, a pristine estuary where both *M. liliana* and *M. stewartensis* are abundant. I use regression analysis to identify which biotic and abiotic variables drive ecosystem functioning and variance partitioning to tease apart the role of these two key species from that of the rest of the macrofaunal community in driving ecosystem function.

In Chapter 4, I use the information from the previous chapters to develop models that link ecosystem function to the presence and abundance of the biogenic features that key bioturbators leave on the sediment surface. Then, through the images of the sandflats collected in a drone survey, I use the density of such surface features to extrapolate predictions of denitrification, ammonium efflux and organic matter degradation across the whole landscape. This chapter represents the most important outcome of my research and ends with the creation of biologically nuanced maps of ecosystem function of the northern sandflats of the Whangateau Harbour.

Fig 1.3 Picture of the drone as it performs the aerial survey of Whangateau Estuary

In Chapter 4 I combine high resolution information on the spatial patterns of important species with models of functions built from field data to estimate functions at large scale. However, not all landscapes can be extensively mapped for easily quantifiable features and other methods of translating information between scales need to be developed. Therefore, in Chapter 5 I compare the performance of different scaling approaches in estimating large scale ecosystem functioning in heterogeneous landscapes.

Finally, in Chapter 6, I synthesise the research outlined in this thesis, outline conclusions, and offer directions for future research. Together, the research presented in this thesis demonstrates that biodiversity and the interaction between its components drive ecosystem functioning in marine benthic ecosystems and the location where these interactions take place play a significant role in the overall functioning. Given the importance of the biophysical component of ecosystems, estimate of ecosystem services that do not take it into account are inaccurate and lack of realism. Finally, we show how for some ecosystems it is possible create biologically meaningful models and maps of functioning. I hope that my thesis will shed light on some crucial aspects of ecological and landscape research and will create the basis for a better characterization of soft-sediment habitats and the ecosystem services they provide, that reflect their underlying complexity and heterogeneity.

Chapter 2 – Non-linear effects of macrofauna functional trait interactions on biogeochemical fluxes in marine sediments change with environmental stress

Stefano Schenone, Teri O’Meara, Simon F. Thrush

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2.1 | Abstract

Biogeochemical fluxes in marine sediments are profoundly influenced by species that bioturbate and bioirrigate the sediments. However, functional traits associated with these activities encompass a wide range of behaviours that have different consequences for the movement of particles and solutes. Interactions between infaunal species of different functional groups and benthic biogeochemical fluxes may be context-specific, requiring multiple studies; yet, to date these experiments are rare. In a laboratory experiment, we incubated specimens of *Macomona liliana*, a facultative deposit-feeding bivalve, and *Macroclymenella stewartensis*, a head-down conveyor-belt feeding polychaete, both separately and together, and measured fluxes of nutrients and oxygen. Both species are common in New Zealand estuaries and often coexist. The addition of thin surface layers of mud generated 3 treatment levels (0, 3 and 6 mm thickness). The presence of *M. liliana* and *M. stewartensis* enhanced benthic fluxes compared to control treatments. Oxygen uptake and nitrogen cycling stimulation due to their interaction were modelled, based on the results of single-species treatments, and then compared to results of multiple-species treatments with no animals. The effect of the interaction of the 2 organisms proved to be stronger than the additive effect of each species. This study demonstrated the central role of functional trait inter-actions for ecosystem functioning and its non-linear nature, highlighting the importance of testing actual effects against prediction based on trait analysis and the incorporation of these community effects in future research and models of ecosystem function and service delivery across marine habitats.

2.2 | Introduction

Soft sediments cover 70% of the ocean seafloor and dominate estuarine and coastal habitats, where infaunal organisms profoundly influence biogeochemical processes and ecosystem functioning (Snelgrove, 1997; Thrush et al., 2004). These habitats support primary production in coastal seas, and through remineralization can contribute between one-third and half of the nutrients required for primary producers in the water column (Mortazavi et al. 2012). However, the human-induced decline in biodiversity and resulting loss of benthic bioturbators threatens the ecosystem services these habitats provide. Thus, it is critical to understand the role of these species in ecosystem functioning and the mechanisms through which they affect processes. This information is also fundamental to create more realistic mathematical models of biogeochemical processes. These models are often based on general assumptions and lack a real understanding and explanation of the role of the underlying biodiversity, leading to potentially biased results and misleading conclusions (Snelgrove et al., 2018).

The role of macrobenthic organisms' functional traits in marine ecosystem functioning has been addressed in previous studies (Dornhoffer et al., 2015; Mermillod-Blondin et al., 2004; Volkenborn et al., 2012; Woodin et al., 2016). Different bioturbation and bioirrigation modes have been shown to affect ecosystem functions such as carbon mineralization (eg. Banta et al. 1999) and nutrient cycling differently (Mermillod-Blondin et al., 2004; Pelegrí and Blackburn, 1995). Michaud et al. (2005) demonstrated how different species representing 2 functional groups in a *Macoma balthica* community have different effects on the oxygen (O_2) uptake at the sediment−water interface and concluded that future studies should also account for the interactions among these species to fully understand their importance for ecosystem functioning. Despite the importance of the link between functional biodiversity and ecosystem processes, there are few specific and empirical studies. Previous studies have indicated that the effects of functional biodiversity on ecosystem processes are not additive and suggested that functional biodiversity and species-specific traits, rather than species richness per se, can be important in explaining ecosystem processes (Godbold et al., 2009; Harvey et al., 2013; Ieno et al., 2006; Mermillod-Blondin et al., 2005; Norling et al., 2007).

The combination of real-time porewater pressure recording and O_2 imaging has improved our mechanistic knowledge of the behaviour-related hydraulic activity of a number of worms and bivalves (Volkenborn et al. 2010, 2012). The use of this technique has demonstrated the relationship between both positive and negative pressurizations, mostly due to feeding, excretion and burrowing, and the O_2 dynamics in the sediment. However, the link between the functional traits of macrofauna, their behaviours and the biophysical interaction of different species is often overlooked when predicting changes in ecosystem functioning. Direct measurements of ecosystem functions in the presence of different species are especially important where synergistic effects are possible. This may explain the variability observed in field-measured ecosystem processes driven by bioturbation (Woodin et al., 2016) and help untangle the complex relationships between biodiversity and ecosystem functioning.

The aim of this study was to assess how the interaction between different functional traits affects nutrient cycling and ecosystem functioning. We hypothesized that when different functional groups coexist, the results may not be linear due to non-additive effects. Therefore, we chose 2 deposit feeders with very different traits (Fig. 2.1) that co-occur and are abundant in New Zealand intertidal sandflats: the bivalve *Macomona liliana*, a facultative de posit feeder and bio-irrigator, and the polychaete *Macroclymenella stewartensis*, a head-down conveyor-belt feeder. To assess how their interaction enhances biogeochemical processes, we measured nutrient and dissolved gas fluxes. In particular, due to the different mechanisms of bioturbation and bioirrigation exhibited by the 2 organisms, our hypothesis was that the interaction would be synergistic and would enhance benthic fluxes. Moreover, we investigated how the effect of surface mud deposition, one of the most common and important stressors in New Zealand estuaries (Thrush et al. 2004), alters this relationship. Recent studies have demonstrated that thick (>1 cm) deposits can reduce macrofauna-mediated ecosystem functioning (Cummings et al., 2003; Mestdagh et al., 2018) and impact the recovery of the macrobenthos, often leading to completely defaunated sediment and habitat change (Hewitt et al., 2003; Norkko et al., 2002; Thrush et al., 2003). Al though often non-lethal, thinner (<1 cm) deposits also negatively affect macrobenthic community structure and modify the behaviour and functional role of benthic organisms (Cummings et al., 2009; Loher et al., 2004; McCartain et al., 2017; Needham et al., 2010; Woodin et al., 2012). The deposition of thin clay layers on the sediment surface can also impact the diffusion of nutrients and solutes across the sediment−water interface (Berkenbusch et al., 2002; Cummings et al., 2009); furthermore, it occurs with greater frequency and over greater spatial scales than the deposition of thicker layers (Foster and Carter, 1997; Wheatcroft, 2000). Hence, we determined whether the presence of a mud layer can alter the interaction between different species and its effect on benthic fluxes.

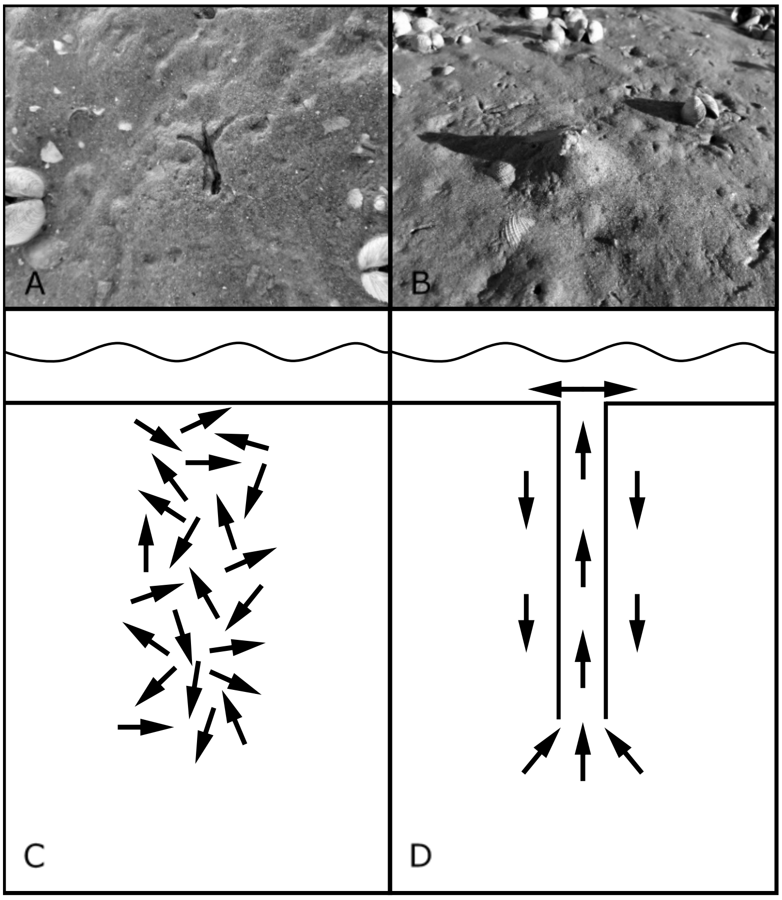

Fig. 2.1 Functional groups of the target species. (A) *Macomona liliana* feeds on the surface through a long inhalant siphon leaving bird-like feeding traces and (C) behaves as a biodiffuser. (B) *Macroclymenella stewartensis* creates volcano-like fecal mounds on the sediment surface and (D) behaves as an upward conveyor (modified from Kristensen et al. 2012)

2.3 | Materials and Methods

Study species

Macomona liliana (tellinid bivalve) is a deposit feeder common in New Zealand intertidal sandflats, where adults live within the sediment to depths of 10 cm (Hewitt et al. 1996). Adult *M. liliana* alter the sediment and its biogeochemical properties, playing an important role in community dynamics and benthic fluxes (Thrush et al. 1992; Woodin et al. 2012). This species feeds through a long inhalant siphon to ingest surface deposits and excretes through an exhalent siphon at depth in the sediment (Pridmore et al. 1991).

The polychaete *Macroclymenella stewartensis* (maldanid) is a conveyor-belt feeder that feeds head-down at depth in the sediment and defecates at the sediment surface. It also irrigates its burrow, pumping in oxygenated water for respiratory purposes. This species is commonly found in New Zealand sandflats, both in subtidal (Thrush et al. 1995; Wong & O'Shea, 2010) and intertidal (Pridmore et al. 1990; Thrush et al. 1989; Turner et al. 1995) habitats and naturally co-occurs with *M. liliana* (authors' pers. obs.).

Specimen collection and preparation

Sediment and target species were collected at low tide in the Whangateau Harbour (36° 18' 40'' S, 174° 46' 42''E), on the north-east coast of New Zealand, between April and May 2017. The sediment at the collection site consists mainly of fine sand (median grain size: 211 µm; fine sand fraction: 50.6%; mud fraction: 3.9%) with an average organic content (% loss on ignition) of 0.71%. Both *M. liliana* and *M. stewartensis* are present and dominate the macrofaunal community. Specimens of both species were hand collected. The sediment was collected on 30 March 2017 and sieved through a 500 µm mesh to remove macrofauna. Sediments were homogenized prior to addition to experimental aquaria. Cylindrical buckets (25 cm diameter, 27 cm deep) were filled to a depth of 13 cm with sieved sediments and left for 4 wk with flow-through seawater to allow for equilibration. Prior to the 4 wk equilibration, the mud layer settled on top of the sediment was removed by feeding the aquaria with a seawater flow higher than the resuspension rate of mud and lower than that of underlying sandy sediment and allowing the mud to overflow for 24 h. This created uniform sediment conditions to which we could add our mud addition treatments (see next sub-section).

Experimental design

We used 4 species treatments: (1) *M. liliana* only; (2) *M. stewartensis* only; (3) a combination of the same density of the two and (4) a control without macrofauna. These animal treatments were crossed with 3 mud layer treatments (surface thickness levels: 0, 3 and 6 mm). The average animal length and wet weight were, respectively, 40 mm and 2.3 g for M. liliana and 103 mm and 0.2 g for M. stewartensis. Species density in the microcosms for both M. liliana and M. stewartensis was 101.9 ind. m^{-2}, which reflects the natural density of the 2 species observed in the ecological monitoring of other intertidal sandflats (Hailes & Hewitt, 2012) and is consistent with density ranges found in previous studies of New Zealand estuaries (e.g. Thrush et al. 1989, Pridmore et al. 1990, Turner et al. 1995). The same density of each species was used in the combined treatment. To create the 3 mud level treatments, 3 and 6 mm mud layers were added to all medium and high mud treatments by adding, respectively, 150 and 300 ml of mud. The chosen thicknesses mimicked field conditions following depositional events, known to alter macrobenthic community structure (Loher et al., 2004). Mud (<63 µm) was obtained by sieving sediment collected at Whangateau Harbour. For the duration of the experiment, microcosms were maintained under the same laboratory conditions (water temperature: 19°C; salinity: 36). Organisms were left for 24 h in the experimental microcosms for acclimation before the first set of measurements was performed. Individuals that did not burrow within 30 min were replaced with new individuals. During 3 consecutive days, we randomly incubated 2 microcosms of each treatment per day (n = 6); all incubations lasted for 4 h in the dark. At the end of the experiment we recorded the wet weight (without shells) of the organisms in each microcosm.

Benthic flux measurements

O_2, N_2, dissolved inorganic nitrogen (DIN; NH_4^+ + NO_2^- + NO_3^-) and dissolved inorganic phosphorus (DIP; PO_4^{3-}) fluxes were measured using dark, dome-shaped plastic incubation chambers (17 cm diameter) placed on the sediment surface. All chambers had Luer stopcock ports for sample collection, and pressure was equilibrated using a vent port open to the surrounding reservoir. Water samples were collected at the beginning of each incubation and after 4 h, following the procedure described by O'Meara et al. (2017). O_2 and N_2 concentrations were determined by membrane-inlet mass spectrometry (MIMS) with a Pfeiffer Vacuum QMS 200 quadrupole mass spectrometer (Kana et al., 1994). Consumption and production rates were calculated from the concentration difference between initial and final samples. DIN and DIP concentrations were determined by flow injection analysis (FIA) with a Lachat Quick-

Chem 8000 automated ion analyser (Thrush et al. 2017). The difference between the concentrations in the final and initial samples was used to calculate net DIN and DIP fluxes.

Data analysis

Preliminary analysis of the data was performed using 2-way ANOVA to investigate the effects of each species and sediment layer and their interaction on measured fluxes. Post hoc pairwise comparisons to identify the source of any significant differences were performed using Sidak's tests.

The effect of the interaction between the 2 species was then modelled based on the results of single-species treatments (hereafter called 'modelled'). To do so, for each sediment composition level (0, 3 and 6 mm surficial mud layer) the per gram (wet weight of animal tissue) rates of O_2, N_2 and DIN change were calculated for the single-species treatments and then summed to match the biomass composition of the multiple-species treatment. A simple additive effect was assumed to represent the modelled interaction with no synergistic or antagonistic effect, which was then compared to the actual results of multiple- species treatments (hereafter called 'real'). Permutational multivariate analysis of variance (PERMANOVA) was used to test for differences between the modelled interaction and the real interaction (source factor, 2 levels), the effect of increasing mud levels (treatment factor, 3 levels) and the interaction between the 2 factors. A post hoc test was then conducted using pairwise permutation MANOVAs to test the effect of the mud layer treatments within modelled and real. All analyses were conducted in R v.3.4.1 (RC Team 2013). Semiparametric tests were calculated using the R packages 'vegan' (Oksanen et al. 2013) and RVAideMemoire (Hervé, 2019). Results were considered significant at $p \leq 0.05$; however, in a few cases we obtained p-values between 0.05 and 0.08.

2.4 | Results

NO_2^-, NO_3^- and PO_4^{3-} levels were close to the detection limit of the instruments and therefore considered to be negligible. For the statistical analysis of DIN fluxes, only NH_4^+ was taken into account. Preliminary analysis indicated that the presence of macrofauna stimulated benthic fluxes compared to control treatments (Fig. 2.2 and the Table A1 in the Appendix A). The presence of a thick mud layer also had a positive effect on fluxes in single-species treatments. NH_4^+ efflux and sediment O_2 uptake were higher with a 6 mm mud layer than with 0 and 3 mm layers. NH_4^+ efflux, however, decreased with the increasing mud layer thickness in the multi-species combination. Denitrification rates were consistent between treatments. Furthermore, when the rates were normalized for biomass, the effect of *Macroclymenella stewartensis* on fluxes was always found to be stronger than that of *Macomona liliana* (Table 2.1).

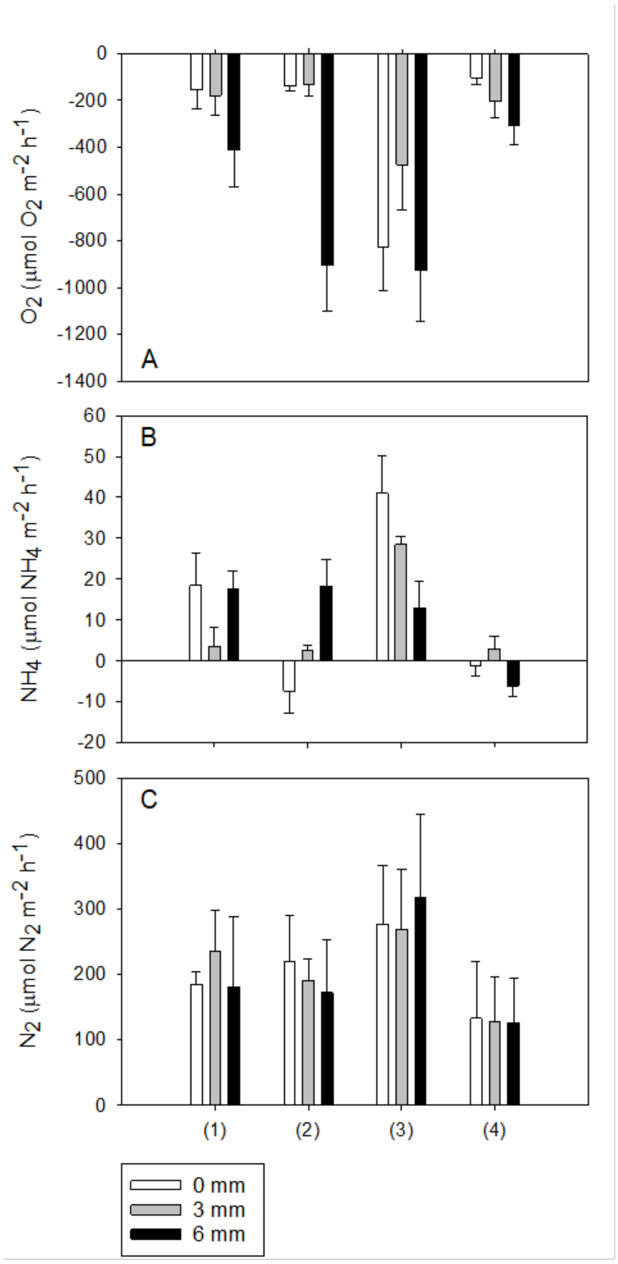

Fig 2.2 Measured rates of benthic processes expressed as mean (±SD) changes in the concentrations of (A) oxygen, (B) ammonium and (C) nitrogen. Numbers on the x-axis correspond to: (1) *Macomona liliana*; (2) *Macroclymenella stewartensis*; (3) combination of both *M. liliana* and *M. stewartensis*; (4) control

Comparison between the modelled and real interaction (source factor) showed differences with sediment composition (Fig. 2.3, Table 2.2). The analysis of variance indicated a significant treatment (p = 0.001) and source × treatment (p = 0.001) effect on sediment O_2 uptake. Pairwise multiple comparison analyses showed that the difference between modelled and real was only significant in the 0 mm treatment (p = 0.037). Source and source × treatment had a significant effect on NH_4^+ efflux (p = 0.003 and p = 0.001 respectively). However, both measured O_2 and NH_4^+ fluxes changed from being higher (in the 0 and 3 mm mud treatments) to being lower (in the 6 mm treatment) than those predicted. Real denitrification rates instead were lower than modelled rates, and the difference was statistically significant (p = 0.07).

Treatment	O_2 (µmol O_2 g^{-1} h^{-1})	NH_4 (µmol NH_4 g^{-1} h^{-1})	N_2 (µmol N_2 g^{-1} h^{-1})
0 mm			
M. liliana	-12.8 ± 6.5	1.5 ± 0.6	15.2 ± 1.6
M.	-123.5 ±	-6.6 ± 4.8	200 ± 62.4
3 mm			
M. liliana	-15 ± 7.3	0.3 ± 0.4	19.7 ± 5.4
M.	-125.2 ±	2.5 ± 1.1	179.2 ±
6 mm			
M. liliana	-35.5 ±	1.51 ± 0.4	15.7 ± 9.2
M.	-870.4 ±	17.6 ± 6.3	166.4 ± 77

Table 2.1 Mean (±SD) measured fluxes of O_2, NH_4^+ and N_2 in the single-species incubations normalized to faunal biomass (g wet weight, excluding shell material) for the 3 different mud level treatments

Within the modelled interaction, O_2 uptake and NH_4^+ efflux were significantly higher in 6 mm compared to both 0 and 3 mm but no significant differences were observed for denitrification rates. Within the real interaction, however, NH_4^+ efflux followed an opposite path, with rates in the 6 mm treatment significantly lower than those in both 0 and 3 mm. Sediment O_2 uptake and denitrification rates, on the contrary, were not different between treatments.

Factor	df	SS	MS	F.Model	R^2	p-value
(a) O_2						
Source	1	590	589.5	2.406	0.01605	0.138
Treatment	2	20953	10476.3	42.750	0.57030	**0.001**
Source x Treatment	2	7845	3922.7	16.007	0.21654	**0.001**
Res	30	7352	245.1		0.20011	
Total	35	36739			1	
(b) NH_4						
Source	1	1856.6	1865.6	16.278	0.11942	**0.003**
Treatment	2	823.3	411.7	3.609	0.05295	**0.047**
Source x Treatment	2	9445.7	4722.8	41.407	0.60754	**0.001**
Res	30	3421.8	114.1		0.22009	
Total	35	15547.4			1	
(c) N_2						
Source	1	651.45	651.45	8.9466	0.21685	**0.007**
Treatment	2	11.04	5.52	0.0758	0.00368	0.933
Source x Treatment	2	157.2	78.60	1.0794	0.05233	0.355
Res	30	2184.47	72.82		0.72715	
Total	35	3004.15			1	

Table 2.2 Results of the PERMANOVA showing the differences between ‘modelled’ and ‘real’ interactions. Significant results ($p \leq 0.05$) are indicated in **bold**

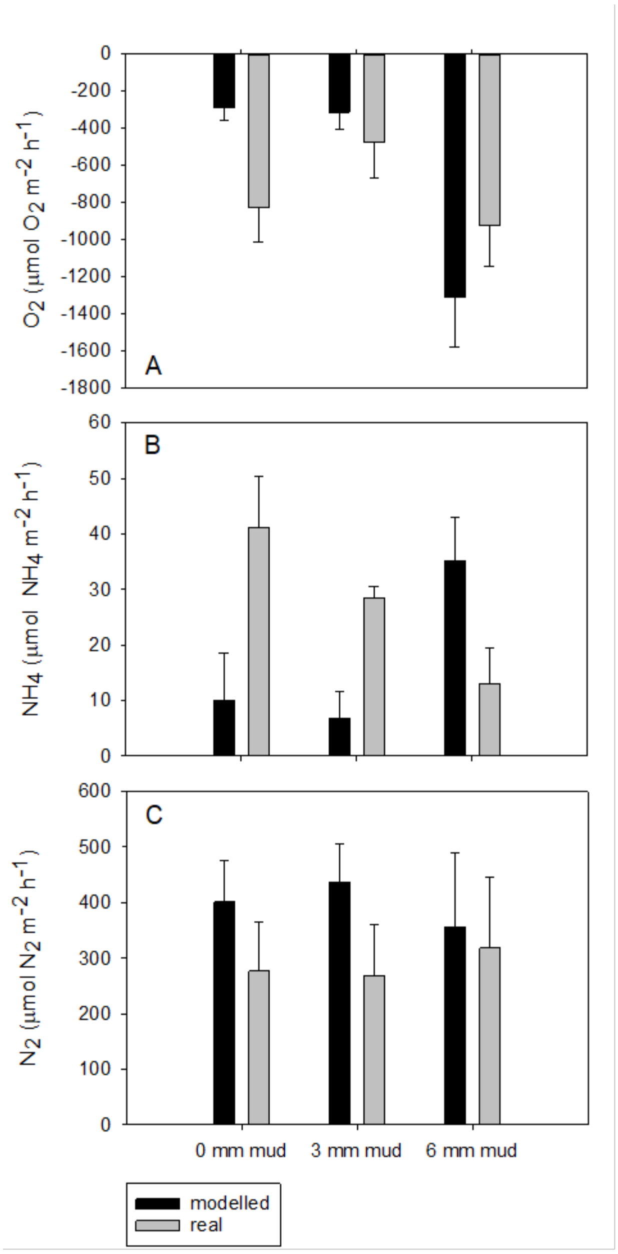

Fig. 2.3 Mean (±SD) rates of change in the concentrations of (A) oxygen, (B) ammonium and (C) nitrogen. Black bars: results from the calculated interaction; grey bars: real interaction. The x-axis refers to the thickness of the added mud layer in the treatment

2.5 | Discussion

Through the manipulation of sediment and macrofauna composition in a controlled laboratory setup, it is possible to detect the effects of single species on benthic fluxes (e.g. Bertics et al. 2010; Bertics et al. 2012; Volkenborn et al. 2007). The present study, however, differed from previous studies in the literature as it directly addressed the interaction between species with different functional traits on biogeochemical fluxes. Although microcosm experiments are a simplified representation of natural conditions and are carried out in a highly controlled setup, they provide a mechanistic understanding of ecosystem functioning, thus being a pivotal tool to untangle the relationship between ecological processes and the underlying biodiversity.

Our study confirmed the well-documented stimulation of sediment biogeochemical processes caused by burrowing infauna. Mermillod-Blondin et al. (2004) compared the influences of bioturbation activities by 3 dominant species of shallow-water habitats on sediment processes and found amphipods and polychaetes had a stronger effect than bivalves, due to the creation of irrigated biogenic structures. Another study (Braeckman et al., 2010), comparing the role of 2 polychaete and 1 bivalve species in biogeochemical fluxes, showed similar results, suggesting that the maldanid polychaetes stimulated benthic respiration, nutrient release and denitrification more than bivalves. In agreement with these findings, our study indicated that the per gram effects of *Macroclymenella stewartensis* on sediment O_2 uptake, denitrification and NH_4^+ efflux were always greater than those of *Macomona liliana*. This difference can be explained by the different behaviours of the 2 organisms. *M. stewartensis* is a tube builder and periodically flushes its burrow with overlaying water. Because of this characteristic, according to Levin et al. (1997) maldanid worms also have the capacity to redistribute labile organic matter deep within the sediment column. The biodiffuser *M. liliana* instead creates oxygenated pockets at depths of around 10 cm in the sediment, bringing oxygenated fluids into contact with suboxic or anoxic sediment and pressurizing the surrounding porewater (Volkenborn et al., 2012). Moreover, based on previous literature (Meyhöfer, 1985; Volkenborn et al. 2010) and the direct observation of the surface features created by the 2 species in our experimental aquaria, *M. stewartensis* is likely to exhibit higher activity rates than M*. liliana*. Observed benthic respiration and denitrification rates are within the range of those observed in other New Zealand estuaries (e.g. Gongol & Savage, 2016) although, to the best of our knowledge, no other studies have directly measured the specific effect of the polychaete M. stewartensis on sediment bio geochemistry. However, literature on nereid polychaetes (eg. Pelegrí & Blackburn, 1995) reported denitrification rates similar to those of M. stewartensis in our study.

The analysis of the interaction between our 2 species produced context-dependent outcomes. The PERMANOVA indicated differences between the modelled (additive) and real interaction for all of the measured variables. Excluding denitrification rates, which seemed to be unaffected by the different mud layers, the 2 sets of data also showed different responses to the increasing mud contents. Modelled rates, predicted from the single-species results, increased greatly in the 6 mm treatment compared to the 0 and 3 mm treatments. The higher input of organic matter due to the higher mud concentration can, in fact, be responsible for the increased O_2 consumption and NH_4^+ efflux rates observed in the modelled interaction (Williams et al. 1985; Provoost et al. 2013); however, this increase was not present in the real interaction. As a result of the interaction, real NH_4^+ efflux decreased with increasing mud content and sediment O_2 uptake did not change. These results support our hypothesis, demonstrating that the nature of the interaction between different functional traits is not additive and thus cannot be predicted from the sum of the components. In agreement with our predictions, this interaction was found to be synergistic, with the exception of denitrification rates, which showed antagonistic effects. This is in contrast to previous studies on the effects of functional biodiversity on ecosystem processes, which reported lower fluxes of both benthic O_2 and nutrients for multiple-species than for additive single-species treatments (Ieno et al., 2006; Mermillod-Blondin et al., 2005; Norling et al., 2007; Waldbusser et al., 2004). Our study, however, not only focused on the interaction between very functionally different organisms, but also demonstrated how the presence of a stressor (the deposition of a mud layer on the sediment surface) can change the nature of the interaction to such an extent as to shift it from synergistic to antagonistic. In addition, our results indicate that the deposition of a mud layer has different effects on processes that occur at different depths in the sediment. While eliciting a strong effect on O_2 uptake in single-species treatments, it had no detectable effect on the multiple-species treatment, leading to the conclusion that the interaction provides some resilience to this stressor. Denitrification rates in both single- and multiple-species treatments, however, were not affected, suggesting that denitrification may not have been carbon-limited during our experiment and that the organic carbon was more rapidly utilized in aerobic processes. Furthermore, we demonstrated that simple additive models of functional trait effects on nitrogen cycling could largely underestimate the processes involved, such as denitrification and remineralization, by not including interactions in the models.

This study was limited to 2 species and constant densities in a highly controlled environment, and it is therefore necessary to use caution when extrapolating the results to explain real-world ecosystem functioning. The nature and the degree of the interactions could be affected both by abiotic factors, such as water flow and sediment grain size and porosity (Biles et al., 2003), and biotic factors, such as the functional traits involved and patchiness of the organisms (McIntosh, 1991). Plasticity in the behaviours of the animals (i.e. switching feeding modes) may also have played an important role. In fact, similar to other tellinid bivalves, *M. liliana* may have the potential to suspension feed under some circumstances. However, this behaviour has not been observed in previous studies—and was not observed in the context of the experiment—and feeding traces on the sediment –water interface highlight the importance of surface deposit feeding. To understand the importance of the interactions between different functional traits at large scales, it is of critical importance to further investigate the role of species density. By controlling the distance between the organisms and therefore the probability and extent of their interaction, species density is likely to control the strength of the effect of the interaction on ecosystem functioning. However, our results provide mechanistic insight into the nature of ecological processes. This information is critical to mathematical models, which often underestimate the role and importance of biodiversity, and to the formulation of new theories and studies that address ecosystem functioning. This may be particularly important for ecological boundaries and habitat transition areas, the contributions of which to overall functioning are still unclear and poorly studied (Cadenasso et al., 2003). Lohrer et al. (2013) demonstrated that habitat transitions influence facilitation in a marine soft-sediment ecosystem and suggested that these areas should be included in future studies rather than avoided. Our findings agree with this concept and support the importance of ecological boundaries and the interaction between functional traits for ecosystem functioning. Moreover, they suggest that the loss of functional diversity can have significant consequences for ecosystem function.

Acknowledgements

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Chapter 3 – Unraveling ecosystem functioning in intertidal soft sediments: the role of density-driven interactions

Stefano Schenone, Simon F. Thrush

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3.1 | Abstract

Although they only occupy a relatively small portion of the surface of the planet, coastal habitats are some of the most productive and valued ecosystems in the world (Barbier et al., 2011). Among these habitats, tidal flats are an important component of many harbours and estuaries, but their deterioration due to human activities poses a serious threat to biodiversity and ecosystem function (Douglas et al., 2017; Edgar and Barrett, 2000). Benthic communities are usually arranged in patches dominated by key species with overlapping distributions. Understanding the ecological consequences of interactions between these species in transition zones where their habitats overlap is necessary in order to quantify their contribution to overall ecosystem functioning and to scale-up and generalize results (Lohrer et al., 2013). Spatial transition in abundance and the interaction of multiple factors that drive ecosystem function are complex processes that require real-world research. Through a multi-site mensurative experiment, we show that transition areas drive non–linear effects on biogeochemical fluxes that have important implications for quantifying overall functioning. In our study the main drivers of ecosystem function were the abundance of two large but functionally very different species rather than biodiversity per se. Furthermore, we demonstrate that the use of the biogenic features created by specific infaunal species at the sediment-water interface is a better predictor of ecosystem functioning than the density of the species per se, making this approach particularly appealing for large scale, mapping and monitoring studies.

3.2 | Introduction

Coastal habitats only occupy about 10% of the ocean's surface area but make a disproportionate contribution to key earth-system processes. Humanity has benefited from and evolved around coastal ecosystems but this has come at a cost of massive exploitation and intense deterioration of these systems. Nevertheless, recent reviews of the global value of estuarine and coastal ecosystems highlight these ecosystems still deliver many critical ecosystem services (Barbier et al., 2011).

The global distribution of tidal flats occupies at least 127,921 km^2 (Murray et al., 2019). These soft sediment environments are complex ecosystems containing strong physical gradients that affect the distribution of species and physico-chemical conditions. These features interact with biology resulting in patchy spatial distributions of communities and ecosystem functions across multiple spatial scales. Such patchiness is often not as apparent as in other ecosystems where above ground structures define patches (e.g. terrestrial and marine forests). This heterogeneity is a powerful indicator of ecological health but confounds the simple up-scaling of ecosystem function measurements and thus the estimate of ecosystem services at scales most relevant to society (Hewitt et al., 2007). When patches dominated by specific community types overlap, they create interface areas where communities and habitat features grade into one another, with largely unexplored consequences for ecological functioning (Cadenasso et al., 2003). These areas of transition between contrasting patches of habitat can lead to interactive effects and emergent properties and therefore cannot be fully characterized by solely characterizing the adjacent patches (Lohrer et al., 2013).

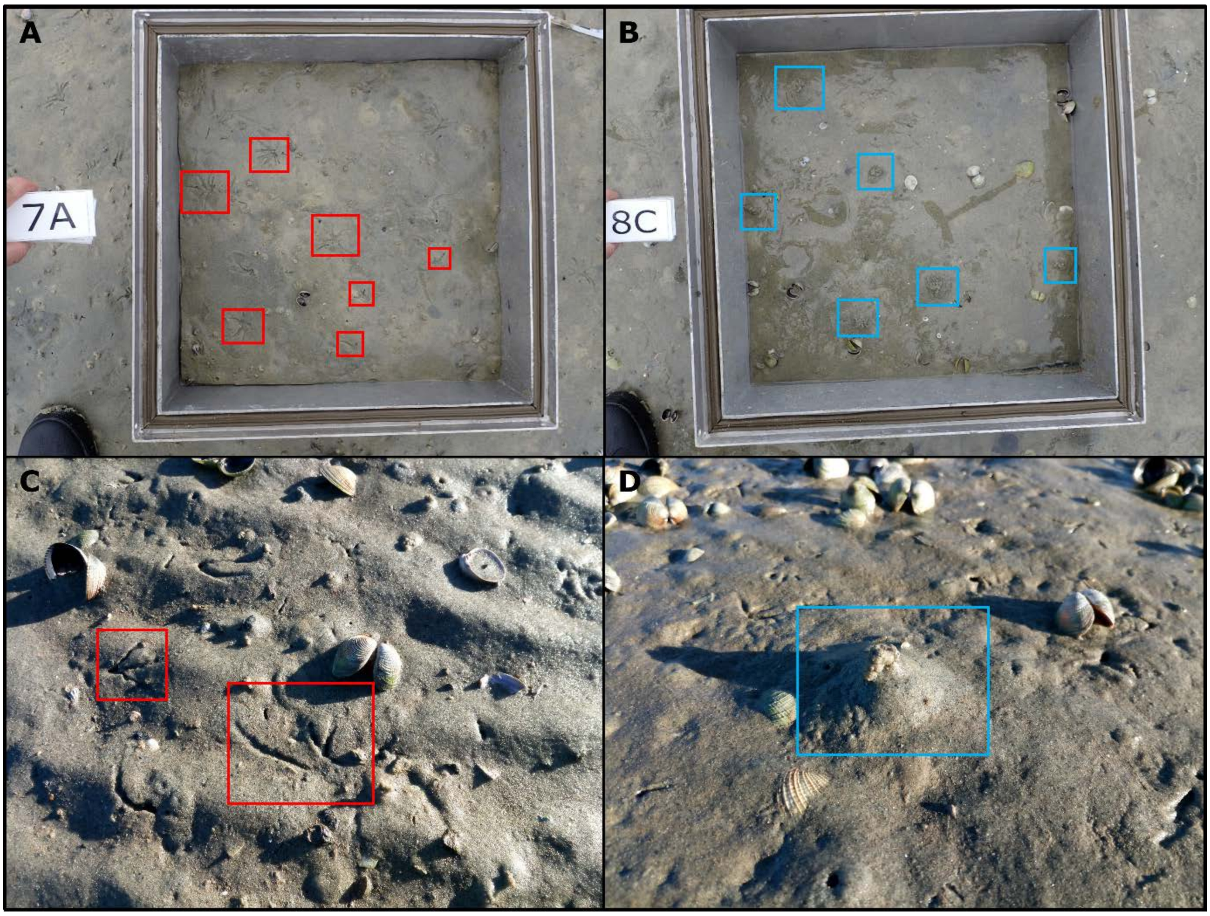

Fig. 3.1 The top panels are examples of pictures of the sediment surface inside the experimental incubation chambers, showing in red the annotation of the feeding tracks of Macomona liliana (A) and in light blue that of the sediment mounds created by Macroclymenella stewartensis (B). In the bottom panels, close-up pictures of the biogenic features of both M. liliana (C) and M. stewartensis (D) are included for reference.

Due to the complexity of interactions involved in driving rates and processes in these heterogeneous marine sediments, empirical measurement is essential, but exceedingly challenging. To resolve this fundamental problem we focused on resolving the shifts in multiple ecosystem functions associated with two co-occurring and functionally important species that differentially influence a variety of sedimentary rates and processes (Schenone et al., 2019;

Chapter 2). Adult *Macomona liliana* (tellinid bivalve) are ecosystem engineers that alter the sediment and its biogeochemical properties, playing an important role in community dynamics and benthic fluxes (Thrush et al., 1992). The polychaete *Macroclymenella stewartensis* (maldanid) is a head–down conveyor belt feeder that feeds at depth in the sediment and defecates at the surface. As a result of their biological activity, both species create distinctive microtopographic features on the sediments surface providing opportunities to quickly assess major changes in abundance and identify how these species partition the habitat in the transition zones (Fig. 3.1). Using in-situ benthic incubation chambers and an organic matter degradation assay we measured the fluxes of dissolved oxygen (O_2) and ammonium (NH_4^+) as well as the organic matter degradation rate at the sediment surface (C_o) and the extinction coefficient of organic matter degradation with sediment depth (k). By quantifying these ecosystem functions at different locations with varying densities of target species, we were able to demonstrate how the co–occurrence of both species at high densities tends to decrease biogeochemical fluxes as compared to patches dominated by either species and how this negative effect changed with the relative density of the two organisms. These sandflat communities are species rich (c 100-150 macrofauna species) and yet, using a methodology originally developed to understand the variation in community data (“variance partitioning”; Borcard et al., 1992), we were able to tease apart the role of these large species that leave signatures on the sediment surface from the role of the community (biodiversity) in driving ecosystem function.

3.3 | Results

Exploring the importance of the single biotic and abiotic components, each ecosystem function was driven by different variables (Table 3.1). However, the presence of *M. liliana* and *M. stewartensis* and their interaction were consistently important predictors, while the environmental variable that was most consistently retained in the models was sediment porosity. Our ecological functions models, except for O_2 consumption and denitrification, identified an important interaction effect.

Factor	**N_2**	**NH_4^+**	**O_2**	**C_o**	**k**
M. liliana	14.78	24.41	10.28	0.14	3.47
M. stewartensis	12.32	0.46		7.75	20.73
M. liliana x *M. stewartensis*		8.51		19.37	24.78
Porosity	7.14	22.62	21.16	17.92	3.05
Mud %		6.82			
Grain size		5.31	12.91		16.65
Organic matter		7.01	2.44		
Total explained	**34.24**	**75.14**	**46.8**	**45.18**	**68.88**

Table 3.1 Important variables for each predictive model – identified by backwards variable selection – and their relative importance (%).

Changes in the relative abundance of *M. liliana* and *M. stewartensis*, measured from the change in the density of their biogenic features, modified the nature of their effect on multiple ecosystem functions (Fig. 3.2). NH_4^+ efflux showed the highest rates when only one of the two species was present at the highest density (i.e., 30 to 45 ind m^{-2} for *M. stewartensis* or 130 to 145 ind m^{-2} for *M. liliana*). Lowest NH_4^+ efflux occurred when both organisms where present at the highest densities. Simultaneous, low densities of both organisms also led to low NH_4^+ efflux. Both organic matter degradation parameters showed a similar response to the interaction, with high C_o and low k present in areas of high densities of *M. liliana* with and low densities of *M. stewartensis* and vice versa, and low C_o and high k when both organisms were present at high density simultaneously. Finally, even though backwards variable selection retained the density of both organisms but not the interaction term in the final statistical model explaining denitrification, we investigated the changes in denitrification rates with changing densities of *M. liliana* and *M. stewartensis*. Denitrification was highest when the densities of *M. liliana* were highest and those of *M. stewartensis* lowest. An increase in *M. stewartensis*, or a decrease in *M. liliana* densities, led to a decrease in net denitrification rates. Net nitrogen fixation was predicted at average to high densities of the polychaete in presence of the lowest densities of the bivalve.

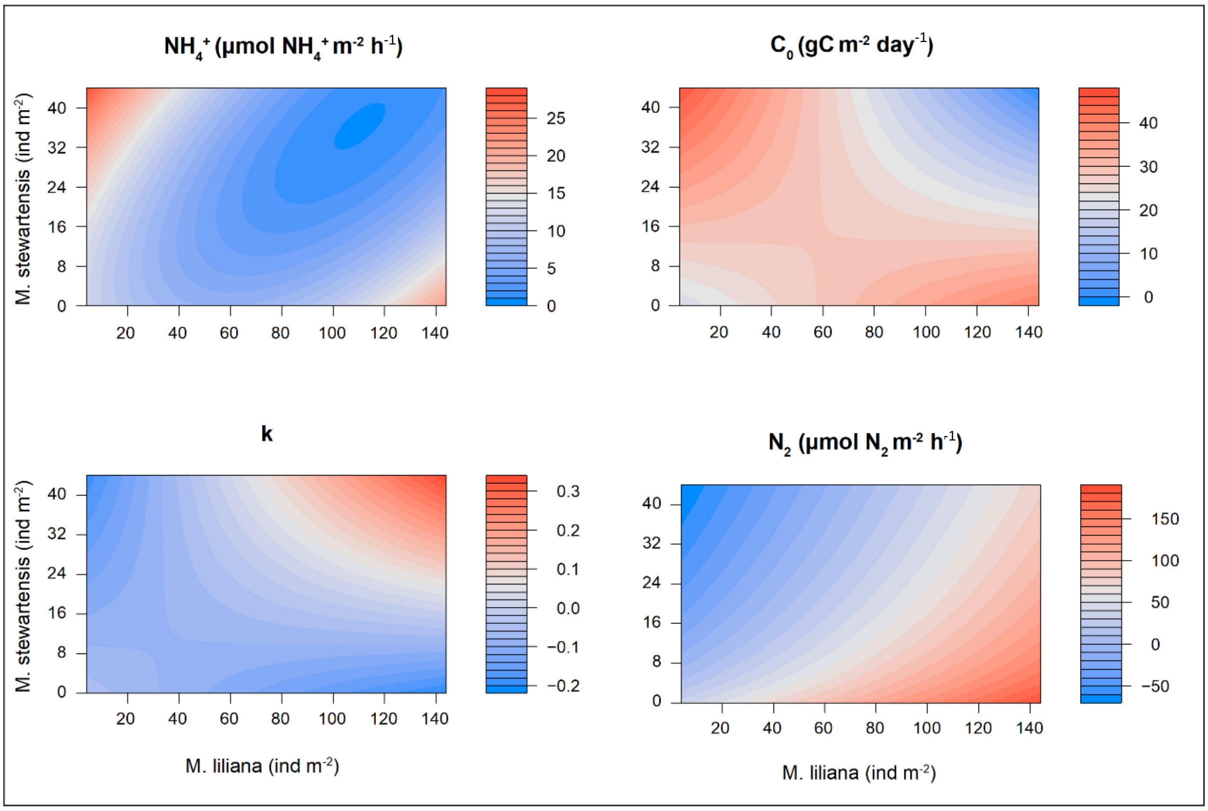

Fig. 3.2 Contour plots showing the modelled effect of the interaction between *M. liliana* and *M. stewartensis* on ecosystem functions as their densities change. Clockwise from upper left: ammonium efflux (NH_4^+), organic matter degradation at the sediment surface (C_o), denitrification (N_2), extinction coefficient of organic matter degradation with sediment depth (k). Note the scale is different for different functions.

Although best results were obtained using untransformed data, all models included significant polynomial terms emphasising non-linear rates across the sandflats. Organic matter degradation seemed to be mainly driven by linear relationships and the only non–linear relationship of organic matter degradation at the sediment surface (C_o) was with porosity (Fig. 3.3). Denitrification, NH_4^+ efflux and O_2 consumption had different non–linear predictors, however *M. stewartensis* showed a non–linear relationship with ecosystem functions more consistently than the other predictors.

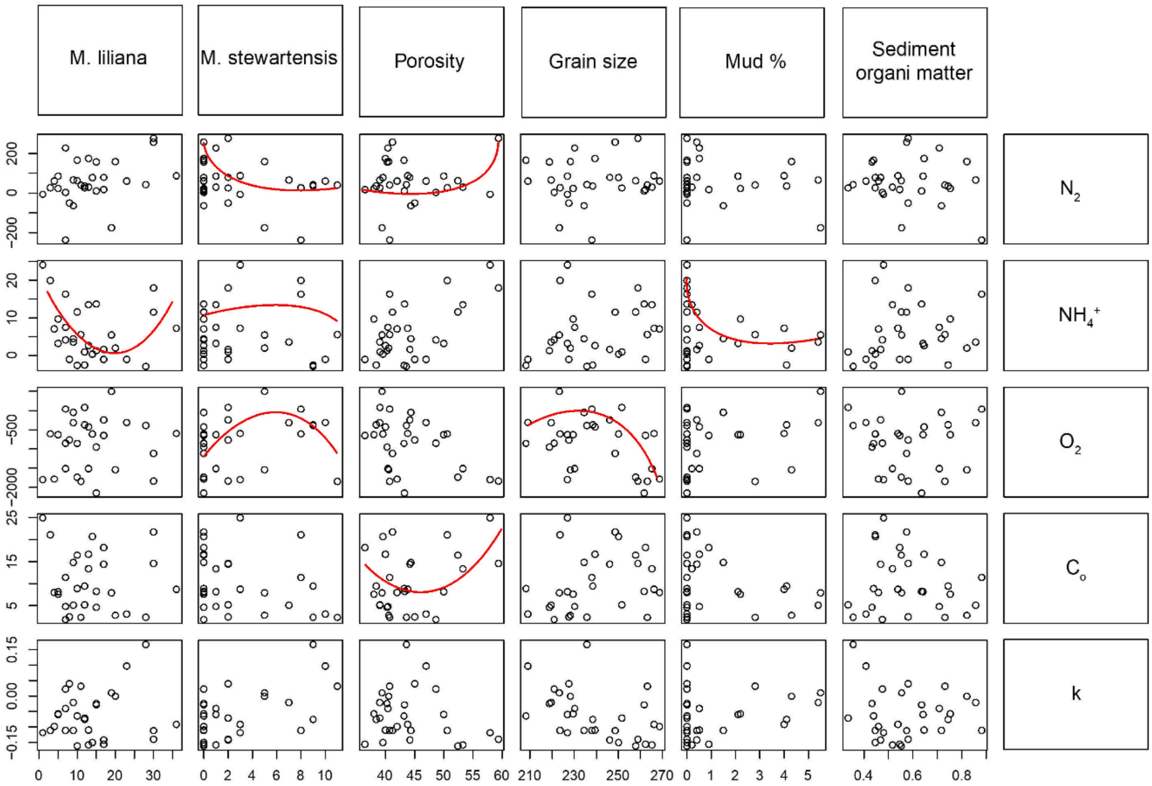

Fig. 3.3 The red lines represent the shape of the non–linear relationships between biological and environmental variables (on the top) and the ecosystem functions (on the right). Where the red line is missing, the relationship was either linear or not significant.

Partitioning the variation in the ecological functions between the biogenic features of *M. liliana* and *M. stewartensis*, the measured environmental variables and the rest of the macrofaunal community showed that biogenic features explained the largest portion (21%, p = 0.001) of variance, followed by the environmental variables (17%, p = 0.008) and macrofauna (11%, p = 0.053) (Fig. 3.4). These biogenic features are signatures on the sediment surface of the activity of Macomona (feeding traces) and Macroclymenella (faecal mounds) and offer an estimate of their abundance and biological activity. However, most of the variation explained by macrofauna was shared with the biogenic features and environmental variables, while the non–shared portion explained purely by macrofauna accounted for only 2% of the total variation (p = 0.346). Consistently, when we analysed the variance partitioning of one function at a time, macrofauna was only important in explaining NH_4^+ efflux, the organic matter extinction coefficient (k) and surface organic matter degradation (C_o) (23, 21 and 16% respectively). The non–shared portion of variance purely attributable to macrofauna was not significant for any of these functions.

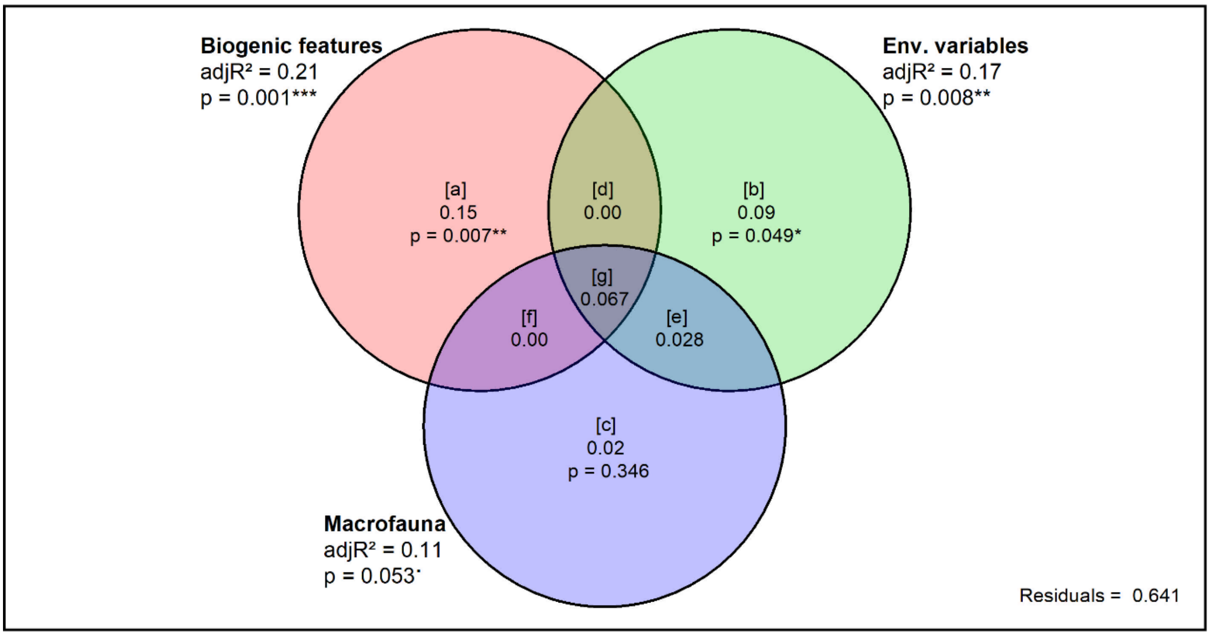

Fig. 3.4 Results of the variance partitioning of the functions data between biogenic features of *M. liliana* and *M. stewartensis*, environmental variables and the rest of the macrofaunal community. [a] is the fraction explained purely by *M. liliana* and *M. stewartensis*, [b] is the fraction explained purely by environmental variables, [c] is the fraction explained purely by the rest of the macrofaunal community and [d], [e], [f], [g] are the fractions of explained variance shared by two or more of the sets of variables. The adjR2 values indicate the total variance explained by a set of variables. Note the size of the circles is not correlated with the variance explained.

3.4 | Conclusions

Our results confirmed the importance of specific, large but functionally different, species for ecosystem functioning and in particular, highlighted the importance of studying transition zones where their interaction can significantly alter benthic fluxes. Looking at the two species individually, our findings were consistent with previous studies on their effect on biogeochemical fluxes (Banta et al., 1999; Braeckman et al., 2010; Dornhoffer et al., 2015; Mermillod-Blondin et al., 2004). However, the presence of non–linear relationships and significant interactions indicates that these effects can change with the density of the organisms. As hypothesized based on our previous mesocosm experiments (Schenone et al., 2019; Chapter 2), the co–occurrence of both species at high densities reduced fluxes. However, this negative effect changed with the relative density of the two organisms and became positive when one of the two species was dominant. Several studies report the positive effects of *M. liliana* on nitrogen fluxes and primary production (Thrush et al., 1992; Woodin et al., 2012, 2016). However, our findings suggest that such effects can be completely negated in transitional areas with high densities of *M. stewartensis*. These transition zones are a common component of the tidal flat landscape and can occupy a vast portion of the ecosystem (Pridmore et al., 1990; Thrush et al., 1989; Turner et al., 1995; Zajac et al., 2003), therefore exerting an important influence on overall ecosystem functioning at large scales. Tellinid bivalves and maldanid worms are cosmopolitan organisms that inhabit intertidal and subtidal marine soft–sediments all over the world (Kobayashi et al., 2018; Volkenborn et al., 2012; Waldbusser et al., 2004; Woodin et al., 2016). Although, different systems are likely to host different sets of key species, with different functional traits, the implications of the results of our experiment are of global importance in linking ecosystem function measurements to the mapping of ecosystem services. The latter is often very coarse scale with little consideration for the spatial or temporal variation in function. Our results, with a 200-fold change in functions across intertidal flats, highlight the need for much quantification of the drivers of ecosystem function.

The unprecedented and pioneering use of variance partitioning in biodiversity–ecosystem functioning research allowed us to distinguish between the impact of the whole macrofaunal community (see Table B1 for complete macrofaunal families list and abundances) and that of our surface feature–forming species. Our findings indicate that even though community composition is important in explaining ecosystem functioning, our two target species held more explanatory power than the rest of the macrofaunal community. This is consistent with the “passengers and drivers” model, which proposes that in most ecosystems certain species have a disproportionate ecological impact (“drivers”) while others have a negligible effect (“passengers”) (Walker, 1992). However, while all the functions that we measured are linked to sediment biogeochemistry, driver and passenger species may be different when the entire multifunctionality of sediments is considered. Our results suggest that the sampling or the entire macrofaunal community is not always necessary. While our models generally identified *M. liliana* and *M. stewartensis* as important variables to explain fluxes, the variance partitioning showed that macrofaunal community only explained a small portion of the variation in ecosystem functions and most of the explained variation was shared with (i.e. already explained by) the other sets of variables. Therefore, the sampling of surface features of key species and a few easily measurable environmental variables can be sufficient to predict ecosystem functioning, which makes this approach particularly appealing for large–scale, mapping and monitoring studies.

In this context, our study also demonstrates the potential of using surface features to scale up ecosystem functioning measurements. The density of the small biogenic surface features, in fact, is not only a good surrogate for species distribution and density but also contains an intrinsic measure of the activity of the infaunal organisms, which in return affects ecosystem functions (Volkenborn et al., 2010). More active (e.g. feeding, excreting) individuals indeed have a bigger impact on sediment biogeochemistry than less active ones and this results in a greater number of biogenic features. Counting biogenic structures is not only non–

invasive and faster than sampling macrofauna but can easily be applied over large scales through remote sensing.

Our analysis opens up new ways to use the information provided by functionally important species and their surface features to up–scale ecological processes measurements and map ecosystem functions at the landscape level. We indeed need more research to focus on the quantification of ecosystem services at scales that are relevant to society and on the underlying role of living organisms in the provision of these services.

3.5 | Methods

Study location and sampling design

Field sampling took place in the intertidal zone of the Whangateau Harbour, New Zealand, in April 2018. The extensive intertidal flats are predominantly composed of medium to coarse grain sand with a relatively low percentage of mud (<6%). The flats are largely mid-intertidal, with little difference in elevation and tidal inundation. Sampling was conducted at four sites in different parts of the harbour (“Tramcar Bay”, 36°18.59' S, 174°46.71' E; “Lews Bay”, 36°18.72' S, 174°46.42' E; “Horseshoe Island”, 36°19.02' S, 174°46.17' E and “Point Wells”, 36°19.21' S, 174°45.59' E). 30 stations distributed across sites to maximise information at different scale were sampled. Sampling covered a wide range of densities of both target species and encompassed patches dominated by each species and transitional areas.

Benthic flux measurements

To measure the changes in the concentration of solutes we used opaque benthic incubation chambers and rapid organic matter assay (ROMA). At each sampling station we deployed one dark benthic chamber as described in (Thrush et al., 2017). The chambers incubated a volume of approximately 30 L of sea water and the incubations lasted for approximately 4h, during high tide. Water was sampled from the chambers at the beginning and the end of the incubation period. We deployed dark, 1 L plastic bottles filled with ambient sea water, secured to the sediment surface in proximity of the chambers. Ambient water external to the chambers was also sampled at the beginning and the end of the incubations. Samples for O_2 and N_2 were transferred into 12 ml glass vials and stored in a portable ice chest until stored in a fridge. Samples for dissolved inorganic nitrogen (DIN; $NH_4^+ + NO_2^- + NO_3^-$) were pressure–filtered through a Whatman GF/C glass fibre filter into 50 ml polyethylene centrifuge tubes and kept on ice prior to freezing. Since NO_2^-, NO_3^- and PO_4^{3-} levels were close to the detection limit of the instruments, only NH_4^+ was used in the statistical analysis of DIN fluxes.

For the ROMA, ten days prior to the incubations one ROMA plate was deployed at each sampling station (see O'Meara et al., 2018 for a description of the methodology). The plates were then incubated in the sediment for ten days prior to the flux measurements, then collected and stored in a portable ice chest until they were analysed on the same day.

Sediment and macrofauna

At low tide, before the incubations, sediment characteristics were sampled next to each chamber. Benthic macrofauna was sampled at each sampling station (1 x 13 cm dia. x 15 cm deep cores), sieved over a 500 µm mesh and preserved in 70% isopropyl alcohol. Specimens of *Austrovenus stutchburyi* and *Paphies australis* in the samples were counted in the field and returned to the sediment alive due to local restrictions on their harvesting. Using a tripod to maintain a constant angle and distance, the sediment surface contained within each chamber base was vertically photographed to count *M. liliana* feeding tracks and *M. stewartensis* sediment mounds. After the incubations the sediment contained in the chambers was excavated to a depth of 15 cm and sieved over an 800 µm mesh to count the total number of *M. liliana* and *M. stewartensis* individuals.

Laboratory analyses

O_2 and N_2 concentrations were determined by membrane–inlet mass spectrometry (MIMS) with a Pfeiffer Vacuum QMS 200 quadrupole mass spectrometer (Kana et al., 1994). DIN concentrations were determined by flow injection analysis (FIA) with a Lachat Quick–Chem 8000 automated ion analyser (Thrush et al., 2017). Sediment porosity and organic matter content were determined from dried (48 h at 60 °C) and ashed (4 h at 500 °C) sediment samples respectively. Sediment grain size was measured with a Malvern Mastersizer–S. Preserved and stained macrofaunal samples were sorted under a dissecting microscope. All organisms were counted and identified to the lowest possible taxonomic level (usually species). Carbon consumption was measured by the change in agar volume in each well on the ROMA plate using an agar–to–carbon conversion factor of 0.026. Using linear regression to analyse the relationship between the natural log of organic matter degradation rate and the depth of the wells, we were able to calculate two parameters: the organic matter degradation rate at the sediment surface (C_o) and the extinction coefficient (k) (O'Meara et al., 2018).

Image analysis

The density of biogenic features within the surface area delimited by the experimental chambers was calculated from the pictures taken before the start of the benthic flux incubations. Features of both *M. liliana* and *M. stewartensis* were manually counted.

Data analysis

The relationship between surface features and actual densities of *M. liliana* and *M. stewartensis* in the sediment was assessed via linear regression. Variance partitioning (Borcard et al., 1992; Legendre and Legendre, 2012) was then computed using the R 'vegan' package to compare the portion of the multivariate functions data explained by the density of surface features and the density of target species respectively. The significance of each portion was tested using Redundancy Analysis (RDA). *M. liliana* and *M. stewartensis* densities were highly correlated with the densities of surface features they produced ($R^2 = 0.74$ and 0.88 respectively). However, using variance partitioning we distinguished between how much of the variation in functioning was explained by the density of biogenic features compared to that explained by the actual density of *M. liliana* and *M. stewartensis* in the sediment. The former explained 21% of the variation in the functions data while the latter only explained 9% (Fig. 3.5). Therefore, we chose the densities of biogenic features produced by *M. liliana* and *M. stewartensis* over their actual densities in our analysis.

The variables were then divided into 3 sets of variables: "biogenic features", (i.e. the density of the surface features of *M. liliana* and *M. stewartensis*); "env. variables", (i.e. all the sampled environmental variables); "macrofauna", (i.e. the information on the macrofaunal community, excluding *M. liliana* and *M. stewartensis*). Using variance partitioning, we calculated how much of the variability in multifunctionality (i.e. the entire set of functions) was explained by each set of variables. To explore the differences in the partitioning of the variation for each single function we then used partial linear regression on denitrification, NH_4^+ efflux, O_2 consumption and organic matter degradation separately.

Generalised linear modeling with incorporated nonlinearities and backwards variable selection was then used to determine which of the biotic and abiotic variables better predicted ecosystem functions. Best models were selected based on the residual by predicted plots, residual normal plots and partial leverage plots. For each model, we determined the relative importance of each predictor variable using the lmg metric in the ‘relaimpo’ R package (Grömping, 2006). When the models identified significant interactions, two–dimensional contour plots were created to investigate the effect of the interaction on the ecosystem function of interest. All statistical analyses were performed with R v3.6.1 (Team, 2013).

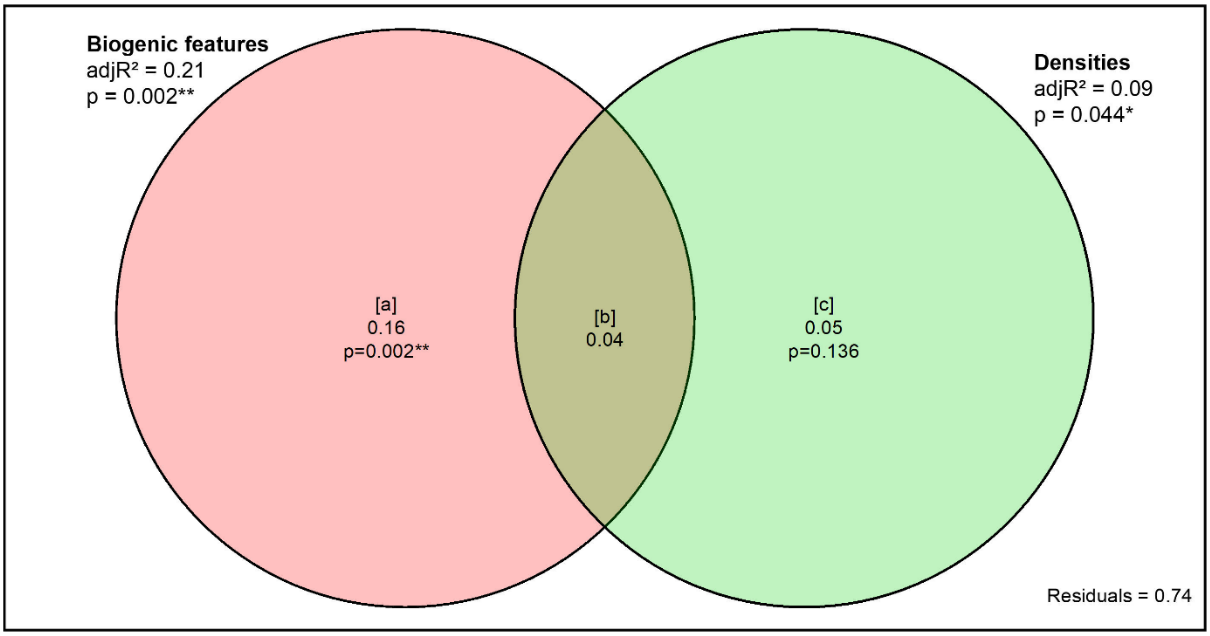

Fig. 3.5 Variance partitioning of the multivariate functions data between the density of surface biogenic features and actual density of *M. liliana* and *M. stewartensis*.

Acknowledgements

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Chapter 4 – Mapping the delivery of ecological functions combining field collected data and Unmanned Aerial Vehicles (UAV)

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This work has been submitted to *Ecosystems* and is currently in review.

4.1 | Abstract

Mapping ecosystem functions and services has gained considerable importance, particularly for its applications in ecosystem management and conservation. While practices for terrestrial ecosystems are well established and mainly rely on land cover, marine ecosystems face challenges that hinder our ability to quantify and understand the distribution of ecosystem services. In particular, soft-sediment marine habitats are complex and heterogeneous but data on the distribution of communities and habitats in these systems in scarce. Mapping relies primarily on the sampling of abiotic variables and physical attributes, easier to obtain at broad scale, and therefore underestimates the role of the underlying biodiversity. In our study, we develop a mapping procedure that can handle situations where only a limited amount of data can be collected. We combined field measurements of species abundance and benthic fluxes to create models and then used data from a drone survey of the distribution of selected sediment microtopographic features linked to specific species to extrapolate these measures. This method quantifies ecosystem functions at broad spatial scales and with high resolution leading to the creation of ecologically nuanced maps that target the underlying mechanisms of ecosystem functioning.

4.2 | Introduction

Coastal ecosystems, found along continental margins around the globe, occupy about 10% of the ocean surface and are regions of remarkable biological productivity (Burke et al., 2001). This has made them centres of human activity for millennia, resulting in the over exploitation and intense deterioration of these habitats. Despite their global decline, estuarine and coastal ecosystems still deliver many critical ecosystem services (Barbier et al., 2011). Mapping benthic habitats and the ecosystem services they provide will allow for better decisions, more sensitive to current environmental status and nuanced to specific management interventions (Carpenter et al., 2009; Huang et al., 2011; Martínez-Harms and Balvanera, 2012). Maps allow us to identify areas of high ecosystem service supply and ecological importance and are a powerful tool to prioritize management and conservation efforts. Given its importance, the mapping of ecosystem services has become popular and there has been an increase in the number of studies that aim to quantify their spatial distribution at landscape and regional scales (Burkhard et al., 2012; Martínez-Harms et al., 2016; Seppelt et al., 2011; Sousa et al., 2016). Maps predominantly rely on land cover data and landscape elements since increasing the amount of ecological complexity expressed by maps requires an increasing amount of data. However, in marine ecosystems this process faces some important challenges that hinder our ability to accurately quantify ecological processes at large scales.

Coastal bioturbated sediments are highly complex systems where the interactions between organisms and their biogeochemical environment affect ecological functions. These interactions and the spatio-temporal variations in a range of physical conditions result in high heterogeneity in the distribution of benthic organisms and ecosystem functions (Brunier et al., 2020). Such heterogeneity, when underestimated, leads to significant errors in extrapolations aimed at upscaling ecosystem functioning. Because heterogeneity of the environment usually increases with scale, extrapolations that do not incorporate this heterogeneity are subject to inaccuracy, particularly in generating maps of the delivery of services at scales relevant to management (Allen and Hoekstra, 1991; Godbold et al., 2011; Hewitt et al., 2007; Needham et al., 2011; Peterson, 2000). The characterisation of the broad scale functioning of an ecosystem, therefore, necessarily requires a good knowledge of processes that happen at different spatial scales and that are often more tractable to measure at small scales (Lohrer et al., 2015).

Due to the challenge of extensively sampling marine ecosystems, large scale benthic habitat mapping relies on physical attributes (Huang et al., 2011; Roff and Taylor, 2000). Sampling of simple abiotic variables, the use of acoustic techniques and remote sensing are common approaches that rely on topographic features and substrate properties to classify habitat types (e.g. Jordan et al. 2005, Lundblad et al. 2006, Wilson et al. 2007). However, species richness and the presence of functionally important species, have been shown to be positively correlated with the ecological functions and the supply of ecosystem services (Cardinale et al., 2012; Fourqurean et al., 2012; Ieno et al., 2006; Mermillod-Blondin et al., 2005; Schenone et al., 2019). Hence, these broad-scale sampling procedures, overlook or underestimate the role of the underlying biodiversity for ecosystem functioning and thereby ecosystem services (Lavorel et al., 2017).

To overcome the challenge of data scarcity, the search for techniques that allow broad scale, high resolution sampling should be pursued in concert with the development of methodologies that can extrapolate information from a limited amount of ecosystem function data with confidence. New developments in remote sensing techniques facilitate cost effective mapping at scales that can capture small biogenic features on intertidal flats, giving to the possibility to collect data over large areas in a short period of time (Anderson and Gaston, 2013). An accurate description of these features and their size, and of the variations in habitat characteristics requires data at fine resolution. While satellite images and acoustic techniques provide data at relatively coarse resolution, drone and kite aerial photography and underwater towed cameras have the ability to collect data at higher resolution (Bryson et al., 2013). However, to date remote sensing mainly provide information on physical and topographic structures, leaving the acquisition of ecological function data to more arduous field measurement.

In our study we sought to map the distribution and rates of denitrification, ammonia efflux and organic matter degradation in the intertidal flats of the Whangateau Estuary. To do so, we combined the information provided by two co-occurring and functionally important species that create distinctive microtopographic features on the sediments surface with measurements of benthic fluxes. Both the tellinid bivalve *Macomona liliana* and the maldanid polychaete *Macroclymenella stewartensis* alter the sediment and its biogeochemical properties and differentially influence a variety of sedimentary rates and processes (Schenone et al., 2019). These two organisms and their interspecific interactions are more important in explaining ecosystem functions than the rest of the macrofaunal community and environmental variables and therefore can be used to predict functioning (Chapter 3). Moreover, the biogenic features that these animals create on the sediment surface are a good surrogate of their abundance and distribution, and a better predictor of ecosystem functioning than the actual density of the organisms because the biogenic features are a better measure of activity (Chapter 3). Here we developed an automated biogenic features detection tool by training a convolutional neural network to count the number of *M. liliana* and *M. stewartensis* sediment features (Fig. 4.1) from drone collected images and combined this information with benthic fluxes models to create our maps.

Fig. 4.1 Biogenic features on the sediment surface. *M. liliana* (left) leaves bird footprint-like feeding tracks and *M. stewartensis* (right) creates volcano-shaped mounds.

4.3 | Methods

Study location. Whangateau Harbour is a sandspit estuary located on the east coast of the North Island of New Zealand (36°18′58″ S, 174°46′11″ E). Considered to be one of the most valued estuaries within the Auckland region, it is made up of a unique mix of high-value, high-quality habitats contained within a relatively small area. The harbour has an area of approximately 750 hectares (~7.5 km^2), with approximately 85.4% of this being intertidal (Kelly, 2009). The extensive intertidal flats are predominantly composed of medium to coarse grain sand with a relatively low percentage of mud (<6%). Both of our target species are abundant in Whangateau and dominate vast patches of the landscape as well as transitional areas where their distributions overlap.

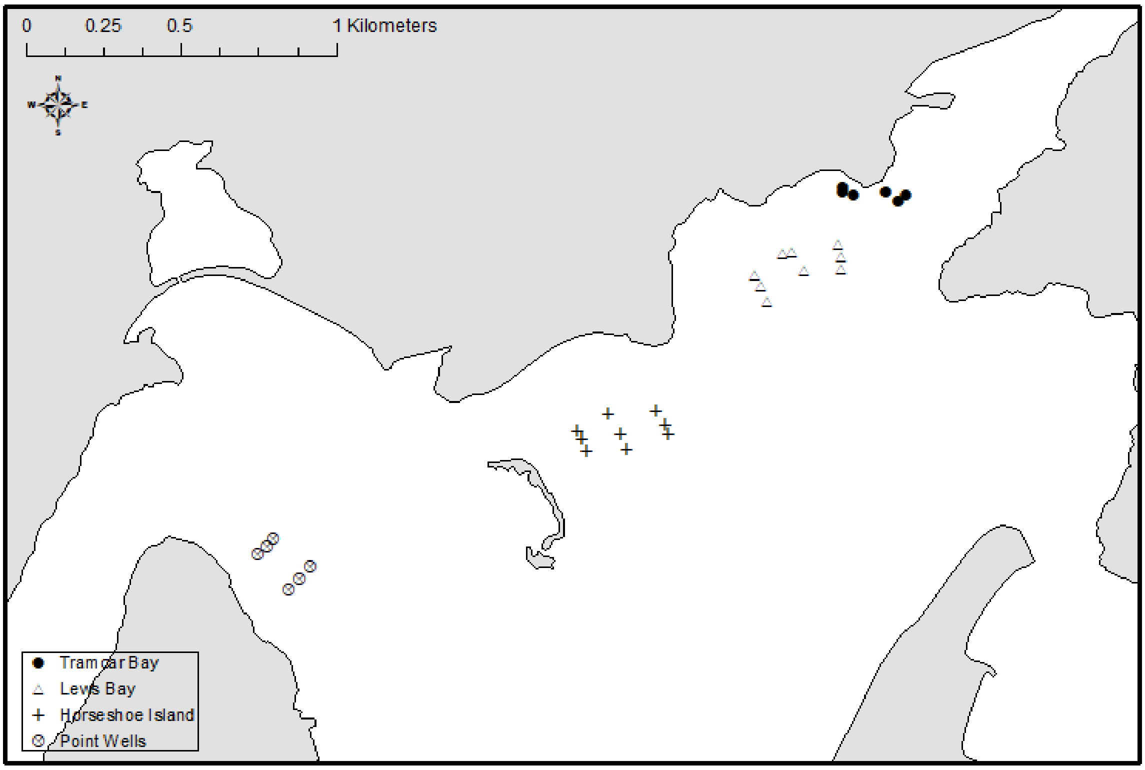

Fig. 4.2 Locations of the sampling of the 2018 experiment in the Whangateau harbour. From the top right to the bottom left corner, the sites are Tramcar Bay (black filled circle), Lews Bay (triangle), Horseshoe Island (plus) and Point Wells (circle cross).

Experimental design. We used data on *M. liliana* and *M. stewartensis*, sediment characteristics, nitrogen and oxygen fluxes and organic matter degradation from a 2018 mensurative experiment in the Whangateau Estuary to quantify the relationships between multiple ecosystem functions and sediment biogenic features (see Chapter 3). Encompassing the heterogeneity in *M. liliana* and *M. stewartensis* distributions, we sampled 30 stations at different locations within the estuary including patches dominated by each species and transitional areas where their distributions overlapped. The sampling strategy was designed to incorporate variation at different spatial scales (Fig. 4.2). At each sampling station, we deployed opaque benthic incubation chambers and rapid organic matter assay (ROMA, O'Meara et al. 2017) plates and measured 4 ecosystem functions: denitrification, ammonia (NH_4^+) efflux, organic matter degradation at the sediment surface (C_o) and the extinction coefficient of organic matter degradation with sediment depth (k). Concurrently, we sampled the sediment characteristics and macrofaunal community, as well as *M. liliana* and *M. stewartensis* surface features at each station.

Modelling Ecosystem Functions. Generalised linear modelling was used to model the relationship between the density of *M. liliana* and *M. stewartensis* biogenic features and each one of the ecological functions measured. The independent variables included in the models where the density of *M. liliana* and *M. stewartensis* surface features and their interaction. Nonlinearities were incorporated into the models using log transformations and polynomial terms. The choice of the independent variables was supported by our previous study (Chapter 3), which demonstrated that in the Whangateau Harbour, the presence of surface features of *M. liliana* and *M. stewartensis* better explains the variation in the ecosystem functions than the rest of the macrofaunal community and the measured environmental variables. Multiple regression models were built from all possible combinations of independent variables. Backwards variable selections was then used to identify variables that could be deleted without a significant loss of fit ($\alpha = 0.15$). To avoid over fitting we restricted polynomials to 2–degrees and then examined the retention of predictor variables within the final models by the Akaike information criterion (AIC) and the Bayes Information Criteria (BIC) (Zuur et al., 2007). Best models were selected based on the residual by predicted plots, residual normal plots and partial leverage plots. All statistical analyses were performed with R v3.6.1(Team, 2013).

Drone survey. We combined the biological, environmental and ecosystem function data with a drone survey of the intertidal sandflats to up–scale these measurements and map functions in the harbour. The survey took place between November and December 2018 and comprised nearly 50 transects, both across and along the shore, generating a total of 7083 pictures (average ground footprint = 5 m^2) (Fig. C1). The survey was carried out within the habitats of *M. liliana* and *M. stewartensis*. A DJI Inspire 1 Pro (SZ DJI Technology Co., Ltd., China) was used with a Zenmuse X5 camera. For flight planning and control we used the open source software Litchi (VC Technology Ltd., UK). Each transect was divided in slow sections, where pictures were recorded, and fast sections, where the drone would fly quickly without recording. In the slow sections, the drone was set to fly at 2m above the ground at a speed of

1.03m s^{-1} and to take pictures every 2 seconds. The resulting image overlap was always ≥ 50%. An integrated GPS recorded the geographical coordinates of each picture.

Image processing & neural network. Convolutional Neural Networks (CNN) are a popular Deep Learning approach in object detection, and in particular as a counting technique when paired with an unmanned aerial vehicle (UAV) (Hong et al., 2019; Kellenberger et al., 2018). An image acquired by a UAV system is fed into the CNN where the output is the image with bounding boxes drawn around the potential biogenic features of interest. The core design of a CNN consists of a series of linked convolutional layers that exist in a hierarchical structure, where at each layer a convolutional kernel (matrices of mathematical weights) passes over an image and creates a feature map (Krizhevsky et al., 2012; LeCun et al., 1998). The training phase of a CNN iteratively adjusts the weights in each layer so a bias is formed towards the desired features for detection, for example; the colour red or a certain shape or edge. The quality of the detection is therefore based on the quality of the training set. To be robust, CNNs require an abundance of data, for animal features counting, this is typically vignettes of the desired animal or feature. For animal classification, Shahinfar et al. (2020) found that 150 - 500 were enough for 70% accuracy, where the features were required to be as unique as possible.

We used RCNN (Girshick et al., 2014), a framework used for object detection and classification, to detect *M. liliana* feeding tracks and *M. stewartensis* faecal mounds, from images gathered by the UAV. Images processed were of 4608 by 2592 pixel resolution and in full colour. Region proposal was performed using Selective Search (Uijlings et al., 2013), and feature extraction the VGG16 CNN architecture (Simonyan and Zisserman, 2015), implemented in Keras. Training was performed on a workstation equipped with two GTX-1080 Ti GPUs. The data set included 1142 *M. liliana* and 296 *M. stewartensis* samples of which the training-test ratio was 80:20 percent. For training, these features were resized to 224 by 224 pixel vignettes. To improve detection rates we used a transfer-learning approach (Shin et al., 2016), where weightings from a VGG16 pretrained model were applied as starting weights and then further modified by during training.

The final trained model was then applied to the test set of data and its accuracy ($F1Score$) was evaluated using the following metrics:

$$Accuracy = \frac{TP + TN}{TP + TN + FP + FN}$$

$$Precision = \frac{TP}{TP + FP}$$

$$Recall = \frac{TP}{TP + FN}$$

$$F1Score = 2 * \frac{Recall * Precision}{Recall + Precision}$$

where TP is the number of true positives, TN is true negatives, FP is false positives and FN is false negatives.

Mapping Ecosystem Functions. The mapping process took place in 2 steps. First, interpolating the abundances of *M. liliana* and *M. stewartensis* calculated with the neural network analysis, to map the distribution and abundance of both species over the range of the estuary intertidal flats; ii) secondly, using the relationships between our target species and ecosystem functions, we combined the two species distribution layers and calculated the predicted ecosystem functions delivery at each point of the map. Given the importance of the interaction between the two species for ecosystem functioning, we also mapped the degree of the overlap in their distribution to better define transition areas and the formula:

$$\mathrm{I} = \left(\frac{\mathrm{Macomona}}{\mathrm{Macomona}_{\mathrm{Max}}}\right) * \left(\frac{\mathrm{Macroclymenella}}{\mathrm{Macroclymenella}_{\mathrm{Max}}}\right)$$

where I is the degree of overlap and takes values between 0 and 1, and $\mathrm{Macomona}_{\mathrm{Max}}$ and $\mathrm{Macroclymenella}_{\mathrm{Max}}$ are the maximum values of density of *M. liliana* and *M. stewartensis* respectively in the data.

All spatial analysis and mapping was performed using ArcMap 10.7.1 software (ESRI, 2019). Spatial autocorrelation was examined via semivariograms using the Geostatistical Wizard tool. First we evaluated the presence and direction of global trends and anisotropy, and then we investigated the species distribution data using the Trend Analysis tool. We investigated the presence of global trends across the whole data, then assessed the presence of local trends by dividing the data into 4 geographical areas and looking at each area individually. Ordinary kriging with 1 x 1 m resolution was then used to interpolate the data and map the distribution of *M. liliana* and *M. stewartensis* based on their biogenic features. Interpolation by kriging allowed us to generate full-coverage standard error maps for each species to show where predicted values were weakest. These two layers where then combined using the Raster Calculator tool based on the ecosystem function models and 4 ecosystem function maps were created.

4.4 | Results

The predictive models explained a minimum of 25% to a maximum of 58% of variance in ecosystem functions (Table C1). The model that explained the biggest amount of variance was organic matter degradation extinction coefficient (k; 58%), followed by ammonium efflux (NH_4^+; 42%), organic matter degradation at the sediment surface (C_o; 32%) and denitrification (N_2; 25%). All models included both response variables (*Macomona liliana* and *Macroclymenella stewartensis*) and their interaction with the exception of N_2, where the interaction was not significant. While C_o and k relationships with *M. liliana* and *M. stewartensis* were linear, N_2 and NH_4^+ showed non-linear relationships. Namely, a negative logarithm of *M. stewartensis* with N_2 and a second degree polynomial of both *M. liliana* and *M. stewartensis* with NH_4^+.

The CNN built to detect *M. liliana* and *M. stewartensis* features on the sediment surface in the drone photographs had an $Accuracy$ of 0.77, a $Precision$ of 0.57 and a $Recall$ of 0.89, resulting in an overall $F1Score$ of 0.69. The resulting species distribution maps for *M. liliana* and *M. stewartensis* didn’t show clear along or across shore trends but revealed the patchy distribution of both species (Fig. 4.3 and Fig. C2). *M. liliana* tended have slightly more homogeneous distribution compared to *M. stewartensis*, particularly in the western portion of the map (Point Wells), with denser patches generally connected by areas of medium density. *M. stewartensis* formed a bigger patch close to the centre of the map (Horseshoe Island) and then smaller patches heterogeneously distributed and poorly connected (see Figure 4.2). However, the plots revealed low densities of both species towards the southern portion of the map. The standard error associated with the predictions was generally between 4 and 34 for *M. liliana* and between 1 and 6 for *M. stewartensis*. However, values greater than respectively 25 for *M. liliana* and 4 for *M. stewartensis* only occurred around the edges of the maps (Fig. C3).

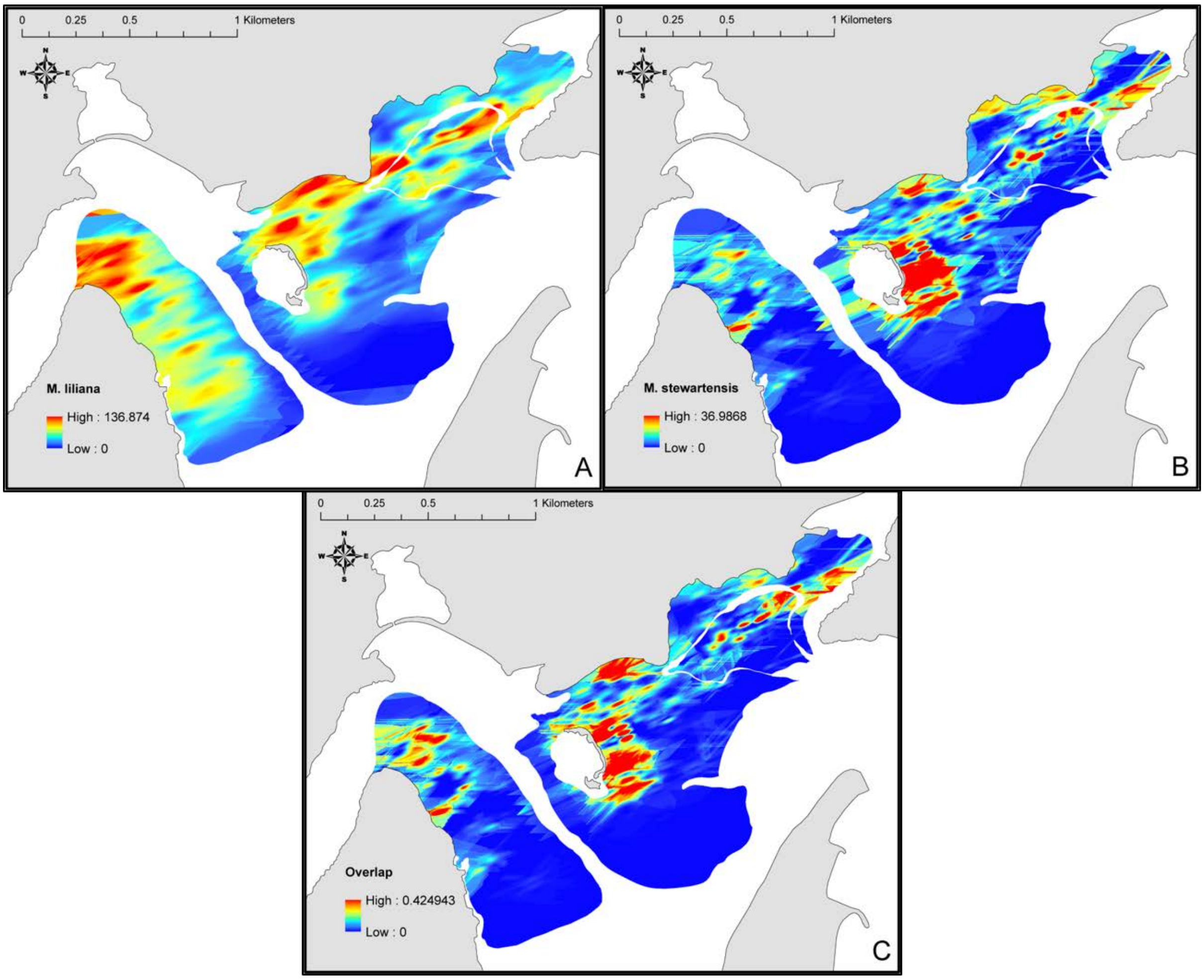

Fig. 4.3 The distribution and density of (A) *M. liliana* and (B) *M. stewartensis* and (C) degree of co-existence in transition areas

Mapping transitional areas revealed that they occupy roughly 40% of the mapped intertidal sandflats of the Whangateau Harbour. In about 80% of these areas, *M. liliana* and *M. stewartensis* coexist at the highest densities. The remaining transitional areas give rise to areas where neither the densities of *M. liliana* or *M. stewartensis* are strongly elevated at the same time. The ecosystem functions maps are tightly related to the distribution of transition areas and to the intensity of the interaction between the two key species (Fig. 4.4).

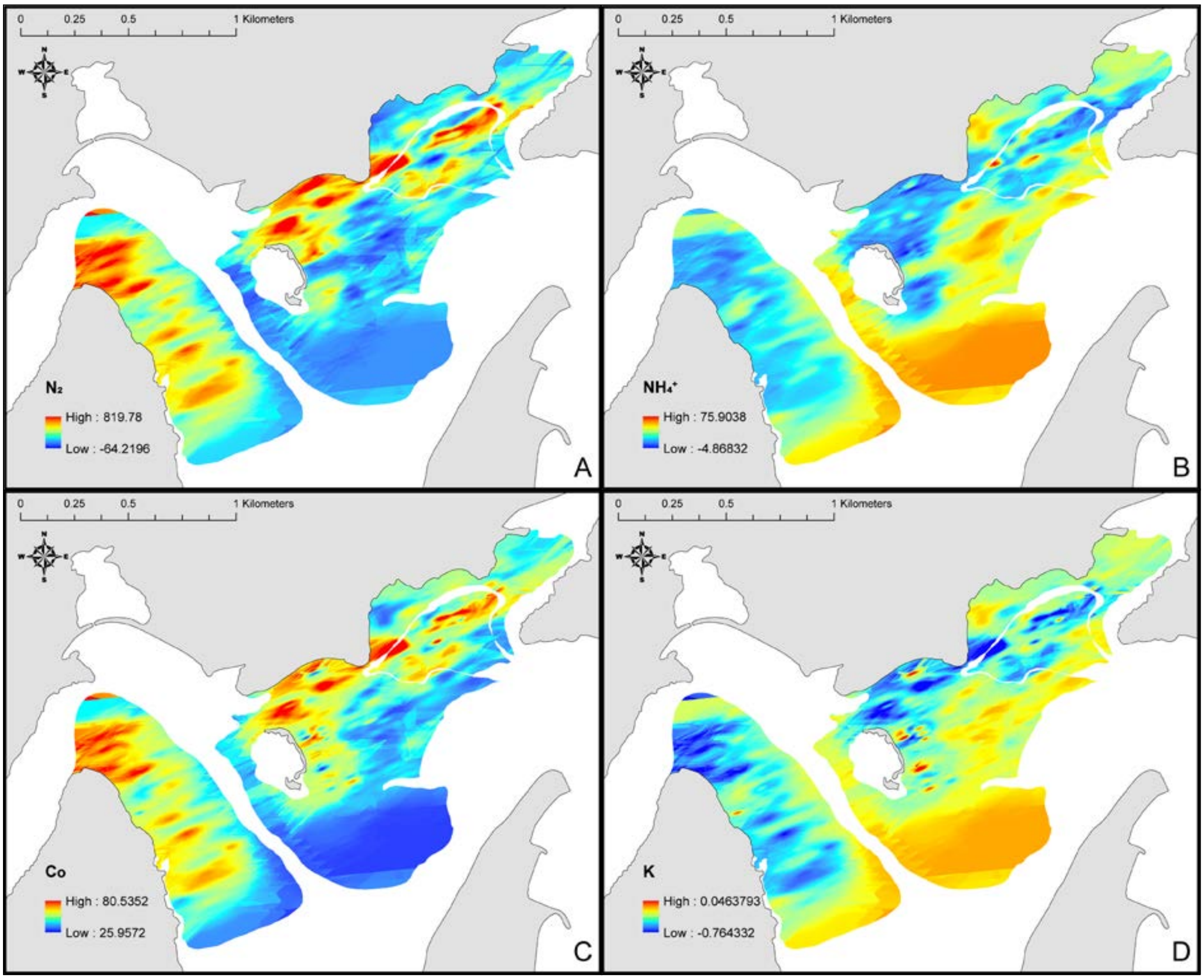

Fig. 4.4 Distribution and delivery of the modelled ecosystem functions. On the top, A shows the denitrification expressed as the N_2 flux in µmol N_2 m^{-2} h^{-1} and B show the efflux of NH_4^+ in µmol NH_4^+ m^{-2} h^{-1}; On the bottom the maps show two different parameters of the organic matter degradation: C_o in g C m^{-2} day^{-1} (C) and k (D).

Areas with the highest density of *M. liliana* promoted high rates of denitrification while areas of low *M. liliana* density or low overlap (*M. stewartensis* present at density > 20 m^{-2} but *M. liliana* present density < 40 m^{-2}) lead to nitrogen fixation. While denitrification happens throughout the whole mapped portion of the estuary, 35% of the surface area delivered almost 60% of the function. NH_4^+ efflux exhibits reverse geographical patterns, where areas of overlapping distribution with high densities of both *M. liliana* and *M. stewartensis* show a pronounced negative effect on NH_4^+ efflux. Organic matter degradation, both in terms of degradation at the sediment surface (C_o) and degradation extinction coefficients (k), are highly influenced by the interaction between our target species and its distribution matches with that of transition areas with high overlap and areas of high density of *M. liliana*. The same areas showed low degradation extinction coefficients values. This indicates that these regions exhibit very high carbon turnover rates in the first few centimetres of the sediment and that these rates don't decay quickly with sediment depth. Conversely, areas with low densities of both organism produces lower rates of carbon degradation at the sediment surface and higher degradation extinction coefficients, which indicates less carbon is consumed and up to a smaller depth in the sediment.

4.5 | Discussion

The combination of data on density of key species, ecosystem function measurements and drone imagery provided a detailed understanding of the distribution and quantification of important ecological functions that underpin critical ecosystem services at the landscape scale. Through our models we were able to identify areas of the estuary that are hot spots of different ecological processes and areas that contribute less. To our knowledge, to date only one other study has addressed the patchiness in functional performance and the location of functional hot and cold spots across heterogeneous landscapes (Thrush et al., 2017). While the areas of greater N_2 and NH_4^+ efflux mainly seem to coincide, these same areas exhibit the lowest rates of organic matter degradation. In particular, hotspots of denitrification are associated with high densities of *M. liliana*, while NH_4^+ efflux shows a stronger negative effect of the presence high densities of *M. stewartensis*. Conversely, hotspots of organic matter degradation, both in terms of its rates at the surface and its persistence with sediment depth, occur where the overlap between the distribution of the two species is minimum. This information can be used to target management and conservation actions. For example, the aim of maintaining denitrification, a regulating ecosystem services that is particularly important in New Zealand, could be achieved prioritizing areas that, due to the high densities of *M. liliana*, show high rates of this process. The procedure used in our study allowed us to collect relevant measurements of ecological functions and combine them with an extensive distribution/activity data with minimum effort and cost. This allowed us to overcome one of the main problems associated with mapping marine ecosystem services, namely the lack of high-resolution spatial information for habitat and species distribution (Lavorel et al., 2017). The use of drones to acquire information on species distribution can be easily adjusted to meet the needs of the experimental design by changing parameters such as height, sampling effort etc.

Another problem that we addressed is the lack of biophysical realism, which results in the inadequate integration in ecosystem models of the role of biodiversity for ecosystem functioning and ecosystem services (Seppelt et al., 2011). Although the positive relationship between biodiversity and ecosystem functioning is recognized, these relationships are still poorly understood and most large scale marine ecosystem services mapping relies primarily on physical attributes (Bergström et al., 2015; Huang et al., 2011; Roff and Taylor, 2000). Our study provides a guideline for future ecosystem services studies. First, it shows the potential of combining field collected data and remote sensing to create combined functioning models. Secondly, it guides future research toward the selection of variables that not only are easy to collect, but also add meaningful biological information to ecosystem models and maps, filling the gap in biophysical realism. Although our models only explain a part of the variation and our maps have a degree of uncertainty associated with their estimates, the quantification of the distribution and delivery of ecosystem functions that they provide represent an important improvement in our understanding of ecosystem services. Our maps succeed in their purpose of detecting spatial changes in ecosystem functions delivery at scales relevant to management and conservation and providing a much more ecologically relevant broad-scale quantification of ecosystem functioning than previously achieved.

Remote sensing has the clear advantage of collecting a high amount of data with minimum effort and in a snapshot of time. Moreover, drone photogrammetry can be tailored to collect data at resolutions sufficient to capture small (cm-scale) biogenic features on intertidal flats. Although being the ideal measure, direct sampling of the benthic communities and their ecological functions would be impractical. Therefore, the choice of surrogate measure that can provide information on the distribution of key species and on the ecological functions that they perform is crucial. The use of biogenic surface features as a surrogate for species density has two main advantages. On the one hand it provides a faithful estimate of the real density of the organisms that generated them. On the other hand it increases the explanatory power of ecosystem functioning models due to an intrinsic measure of their rate of activity (Chapter 3). One of the limits of maps it that they are a static representation of the spatial patterns of species and functions distribution. The distribution and density of both target species of our study are likely to incur in seasonal variations (Thrush et al., 1994; Turner et al., 1995). Similarly, disturbance events can alter benthic communities (Hinchey et al., 2006; Norkko et al., 2002; Thrush and Dayton, 2002). However, given the relationships between key species density and ecosystem functions, drone photogrammetry can be easily applied to monitor changes over time or the response to disturbance, adding a temporal component to our maps.

The successful management of ecosystems is inherently data intensive and requires detailed information on a variety of aspects of an ecosystem. The need for ecological knowledge and good relevant data, together with the increased anthropogenic pressures on the marine environment and the potential for multiple-use conflicts, have led to an increased interest in marine spatial planning (Douvere and Ehler, 2009). Different studies, both in terrestrial and marine ecosystems, suggest how estimating ecosystem services can inform spatial planning decisions (Arkema et al., 2015; Bateman et al., 2013; Birch et al., 2010;

Goldstein et al., 2012). At the landscape level, the main challenge is how to decide on the optimal allocation and management of the many different land use options. Ecosystem functions and services have become an important concept in policy making, as decision makers have to deal with an explicit demand for services from a broad range of stakeholders (Bills and Gross, 2005; de Groot et al., 2010; Hein et al., 2005). A precise quantification and understanding of the distribution of natural communities and of the ecosystem services they provide is therefore crucial to make informed decisions and to accurately estimate their value. The methodology that we propose and the maps that we created provide tools to support marine spatial planning efforts and ecological research, incorporating a true understanding of the underlying ecological mechanisms instead of relying on less informative physical attributes. Moreover, our mapping procedure is feasible in a variety of coastal environments and can be easily tailored to meet the requirements of different systems. The approach we have developed is directly relevant to assessing the ecosystem services of intertidal flats, which currently collectively cover 127,921 km^2 of our planet (Murray et al., 2019). The basic approach could also be applied to subtidal habitats, exploiting incubation chambers or remote sampling techniques to quantify ecosystem functions and video surveys or autonomous underwater vehicles to upscale the measurements.

Chapter 5 – Scaling-up ecosystem functions of coastal heterogeneous sediments: experimenting with high resolution data

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This work has been submitted to *Landscape Ecology* and is currently in review.

5.1 | Abstract

Context Scaling up experimental results to large scale-natural systems that are most relevant to society is one of the most pressing problems in ecology. Different techniques have been proposed, from the simple multiplication of the small-scale average to the use of scaling factors to the investigation of the spatial patterns in the data. These techniques have proved useful for scaling studies in fields such as biology, physiology, physics and economics. However, the use of scaling in ecology is less common and hindered by its intrinsic heterogeneous nature.

Objectives We aimed to demonstrate that the use of different scaling approaches leads to considerably different results and that not accounting for heterogeneity decreases our ability to accurately extrapolate measurements of ecosystem functions.

Methods We used high resolution data on the distribution and quantification of a set of ecosystem functions in a 1,695,158 m^2 area of the Whangateau Estuary, New Zealand. Experimenting with the data, we compared the performance of three different scaling approaches: direct scaling, spatial allometry and semivariogram/kriging.

Results Our analysis shows that the different methods can lead to results that differ by an order of magnitude: direct scaling underestimated functions while allometry overestimated them. The use of structure functions and kriging produced more accurate results.

Conclusions Our work demonstrates the effectiveness using models that link ecosystem functioning to biological attributes that can be measured remotely to accurately study heterogeneous landscapes and the weakness of ignoring spatial heterogeneity within landscapes. Integrating measures of heterogeneity through the spatial structure of the data, although data intensive, leads to results that are more realistic and relevant to resource management.

5.2 | Introduction

Some of the most pressing problems in ecology exist at large spatial and temporal scales. However, predicting the effects of broad scale anthropogenic impacts on ecosystem functions is hindered by the need to scale-up processes that are more tractable to measure at small scales (Hewitt et al., 2007). Our knowledge of the functioning of marine ecosystems, in fact, mainly derives from small scale laboratory and field studies. Extrapolating the results of these experiments is not a trivial task because they may not apply to larger scales that are most relevant to society. Moreover, environmental heterogeneity is known to increase with scale, making extrapolations that do not incorporate heterogeneity prone to inaccuracy (Hewitt et al., 2007; Lohrer et al., 2015; Peterson, 2000; Snelgrove et al., 2014; Thrush et al., 1997).

Scaling is defined as the process of translating information between or across spatial and temporal scales or organizational levels. Although the importance of scaling in ecology has been recognized in recent decades, how to conduct scaling across heterogeneous ecosystems remains a challenging question (Wu et al., 2006). In marine environments, the high heterogeneity and the lack of high resolution data due to the challenges related to extensively sample marine ecosystems further complicate this process. One of the simplest ways to transfer information between two scales is to assume that the broader–scale system behaves like the average value of the finer-scale system. In this case, scaling is obtained simply by multiplying the sample–scale average with the total study area. This process is often referred to as “lumping” or “direct scaling” and assumes that the relationship describing the system is linear (King, 1991; Miller et al., 2004). As a consequence of the oversimplifying assumptions however, this simple upscaling procedure could produce large scaling errors.

Allometric scaling is one of the most common approaches found in scaling literature. Allometry is based on the underlying concept of incomplete similarity or fractality, which implies that the fundamental features of a system exhibit an invariant, hierarchical organization that holds over a wide range of spatial scales (Barenblatt, 1996; Brown et al., 2002; Li, 2000). One of the main advantages of this approach is that it is characterized by relatively simple mathematical or statistical scaling functions, generally in the form of a power law. Nevertheless, the underlying ecological processes may be complex. A common example is the relationship between the metabolic rate of organisms, I, and their body mass, which can be expressed by the equation: $I = I_0 M^b$, where M is body mass, I_0 is a taxon dependent normalization, and b = 3/4 for animals and plants (Brown et al., 2004). Although most of the allometric equations do not directly address the problem of spatial scaling, space can be incorporated into a scaling relationship through, for example, population density or home range (Wu et al., 2006). In particular, allometry as a general method can be applied to spatial scaling when the independent variable is spatial scale instead of body mass (“spatial allometry”; Schneider, 2001). While the benefit of using allometric scaling is recognized for a variety of fields, from physiology to economics, these simple power law may not be adequate to describe the upscaling of ecosystem functions (Brock, 1999; Marquet et al., 2005). Moreover, in seafloor landscapes heterogeneity and non–linear processes can be hard to measure and take into account and can greatly hinder the scaling process.

Most ecological data are inherently composed of several levels of spatial structure: large-scale trends (species responses to climate conditions, migrations, etc.), multi scale patterns or patchiness (physical conditions, dispersal mechanisms, facilitation, etc.), and errors (Klopatek and Gardner, 1999). Structure functions attempt to describe spatial structures in the data and allow us to quantify spatial dependence and partition it amongst distance classes (Legendre and Legendre, 2012). For example, previous work has demonstrated the feasibility of variograms to quantify spatial heterogeneity and explore spatial patterns and describe phenomenon as a function of space (Garrigues et al., 2006; Lausch et al., 2013). Successively, geostatistical techniques, such as kriging, that employ knowledge of the spatial covariance (as contained in the variogram) can then be used to produce a spatial model (Klopatek and Gardner, 1999). To be able to accurately describe these structure and incorporate as much heterogeneity as possible, a high amount of data is usually necessary. Such high-resolution information on the spatial arrangement of the data, however, provides information about patterns at different scales. While spatial analysis deals with the problems associated with spatial heterogeneity, synergistic effects arising from the interaction between species with different functionalities are also likely to confound the upscaling of ecological processes (Chapter 3).

Another complication posed to scaling in marine systems consists in the difficulty of extensively sampling marine environments and the consequent scarcity of data (Townsend et al., 2014). To accurately describe the relationship of a variable to changes in scale in these complex systems often requires more data than it is practical to obtain. In our study, we addressed the issue of whether various methods successfully used to scale up metabolic, ecophysiological and other ecological relationships are suitable to upscale species–ecosystem function relationships in heterogeneous marine landscapes, where the data available is usually limited (Table 5.1). We used a high–resolution map of ecosystem functions to compare the use of different scaling approaches (direct scaling, allometric scaling, variogram/kriging). While such high resolution maps can be used to estimate ecosystem functions at scale, the ability to identify scaling relationships is crucial to help design and estimates across landscapes that cannot otherwise be extensively mapped. The performance of each approach in predicting ecosystem functioning for the landscape was compared to actual values obtained by summing contributions to function across the map (Chapter 4). We hypothesized that in coastal bioturbated landscapes traditional scaling approaches, that fail to take into account the effect of heterogeneity and the functional interactions between different organisms, would produce a poor representation of broad-scale ecosystem functioning.

Approach	**Complexity**	**Data intensity**	**Underpinning theory**	**Scaling function**
Direct scaling	Very low	Low	Geometric similarity	Linear
Spatial allometry	Low	Low	Incomplete self-similarity/fractality	Power law
Variogram/kriging	High	High	Autocorrelation/covariance	Variable

Table 5.1 Characteristics of the scaling methods used in this study

5.3 | Methods

Experimental design. For this study, we used data from a 2018 mensurative experiment that we carried out in the Whangateau Estuary (New Zealand) to quantify the relationships between multiple ecosystem functions and the density of two key species: *Macomona liliana* and *Macroclymenella stewartensis*. Both *M. liliana* (tellinid bivalve) and *M. stewartensis* (maldanid polychaete) are ecosystem engineers that alter the sediment and its biogeochemical properties and differentially influence a various sedimentary rates and processes; details of the sites and the sampling design are presented in Chapter 3. Briefly, to measure fluxes, we deployed opaque benthic incubation chambers and rapid organic matter assay (ROMA, O'Meara et al. 2017) plates. Concurrently, we sampled the sediment characteristics and macrofaunal community, as well as *M. liliana* and *M. stewartensis* surface features at each station. Surface features of *M. liliana* and *M. stewartensis* have been proven to be a reliable proxy of their density and to explain more variance in ecosystem functioning than their density itself (Chapter 3). Finally, we combined ecosystem functioning models that explained the relationship between field measured biogeochemical fluxes and the density of key species, with a drone survey of the distribution of those species in the estuary to map the delivery of ecosystem functions at a 1 x 1 m resolution (Chapter 4). In the present study, we sampled these high resolution raster datasets as described below to build the different scaling relationships.

Study location. Whangateau Harbour is a sandspit estuary located on the east coast of the North Island of New Zealand. Considered to be one of the most valued estuaries within the Auckland region, it is made up of a unique mix of high-value, high-quality habitats contained within a relatively small area. The harbour has an area of approximately 750 hectares (~7.5 km^2), with approximately 85.4% of this being intertidal (Kelly, 2009). The extensive intertidal flats are composed of predominantly medium to coarse grain sand with a relatively low percentage of mud (< 6%). Both our target species are abundant in Whangateau and dominate vast patches of the landscape as well as transitional areas where their distributions overlap. A map of the habitats of Whangateau was first developed in 2000 and successively updated in 2010 (Hartill et al., 2000; Townsend et al., 2010). These maps show that our study area is entirely covered by sandflat habitat (Fig. 5.1). The extent of the study covers the intertidal sandflats of the northern Whangateau Estuary and coincides with the area of the estuary mapped in our 2018 study (Chapter 4).

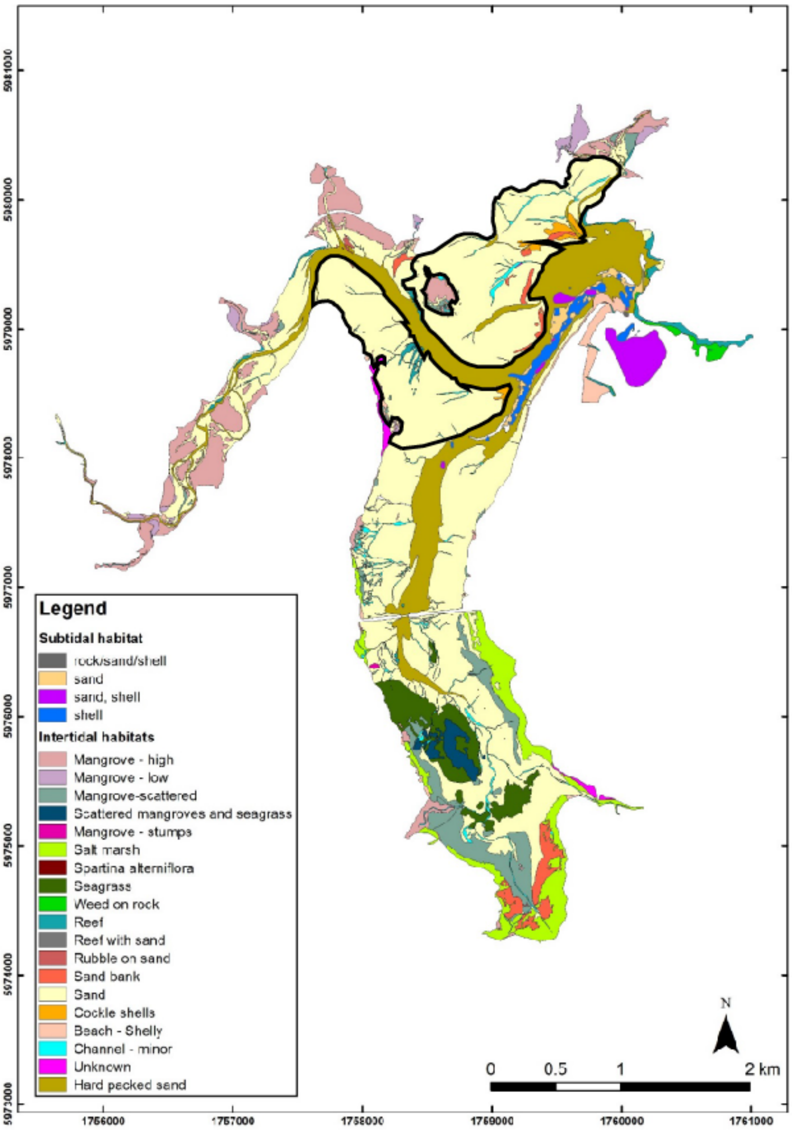

Fig. 5.1 Habitat map of the Whangateau estuary (modified from Townsend et al., 2010). The black contours highlight our study area.

Scaling. To test our hypothesis, we compared the performance of different scaling approaches and assessed their results against those originally obtained in the survey of the estuary. We considered the rates of 3 ecosystem functions: denitrification (expressed as the release of N_2 from the sediment), ammonia (NH_4^+) efflux and organic matter degradation at the sediment surface (C_o). These functions are the result of important biogeochemical sedimentary processes and underpin crucial supporting and regulating ecosystem services, such as the cycling of nutrients and organic matter. Respectively, we tested i) a linear model that uses the plot average value to calculate the value at the target scale just by means of multiplication (direct scaling); ii) a power law model based on the notion of self-similarity (allometric scaling); iii) a model based on the spatial structure of the data (variogram/kriging).

Direct scaling. To upscale and calculate the delivery of each ecosystem function at the scale of interest we first calculated the plot average of each function and then multiplied it by the extent of the study (1,695,158 m^2). Initially, since the study covered and area that has been classified as one habitat type – sandflat habitat (Fig 5.1) – one average for each function was produced using all data. Then, to produce a more accurate calculation, the data was divided into 4 sites based on the variability highlighted in the maps and the total upscaled value of each function was calculated by the sum of the site average multiplied by the area of the site.

Allometric scaling. We tested the presence of fractal-like relationships in the form of the power law equation:

$$Y = Y_0 A^b$$

$$\log Y = \log Y_0 + b \log A$$

where Y is the ecosystem function of interest, Y_0 is a scaling constant equal to the plot average value of the function, A is space in m^2, and b is the scaling exponent.

To do so, we sampled the raster data from the ecosystem function maps and calculated fluxes across 10 squared surfaces of different sizes that shared the same centroid. The areas of the squares were respectively 1 m^2, 625 m^2, 2500 m^2, 5625 m^2, 10000 m^2, 15625 m^2, 22500 m^2, 30625 m^2, 40000 m^2 and 50625 m^2. Four replicates were calculated in random haphazardly chosen locations. The average values from the 4 replicates for each surface size were plotted against the surface area to check for the presence of disjunctions that could indicate multi-fractality. The allometric model was then fitted to the data and was evaluated graphically and by means of the r^2 value. Finally, using the scaling exponent calculated from the model, we estimated the value of each function at the extent scale from the plot–average value.

Variogram/kriging. To understand whether the use of information about the special structure of ecosystem functions would help improving their upscaling and accuracy and prediction, we used a systematic sampling design and calculated functions in 50 evenly distributed points on the maps. First, we checked for the presence of global trends and anisotropy in the data. Then, for each function we calculated the empirical semivariogram. Finally we used anisotropic kriging to interpolate and extrapolate the data to the study area. The kriging results were used to calculate the up-scaled values of the functions.

The geostatistical processing was performed using ArcMap 10.7.1 software (ESRI, 2019). All other statistical analyses were performed with R v3.6.1 (Team RC 2013).

5.4 | Results

Approach	**N_2 (kg h^{-1})**	**NH_4^+ (kg h^{-1})**	**C_o (tonnes h^{-1})**
Direct scaling	2.07	0.18	7.51
Direct scaling with 4 sites	3.23	0.36	13.5
Spatial allometry	2.36	32.06	11,567.5
Variogram/kriging	14.94	1.54	80.26
Mapped estimate	**13.02**	**1.19**	**77.22**

Table 5.2 Summary of the results of the different scaling methods and comparison with the values calculated from the map of functions in Chapter 4.

Direct scaling underestimated the delivery of all ecosystem functions and allometry underestimated denitrification but overestimated ammonium (NH_4^+) efflux and organic matter degradation (Table 5.2 and Fig. 5.2). Direct scaling predicted 6.3 times less denitrification than the expected value, 6.7 times less NH_4^+ efflux and 10.3 times less organic matter degradation (C_o) across the sandflat habitat. Dividing the habitat into 4 sites and calculating the sum of the predicted value for each site provided a slightly better estimate of functions but still underestimated the functional contribution of the sandflat (4 times less denitrification, 3.3 times less NH_4^+ efflux and 5.7 times less organic matter degradation).

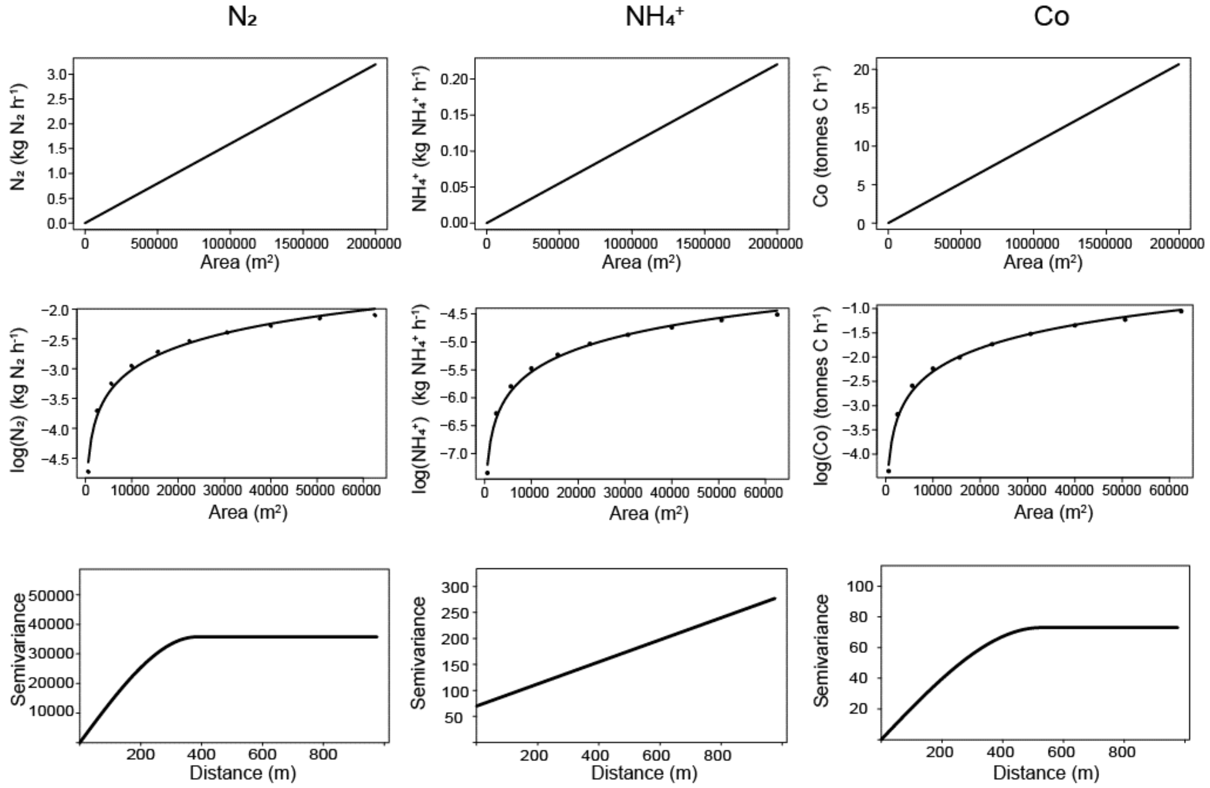

Fig. 5.2 Comparison of the scaling approaches. The top 3 panels show the relationship between spatial scale and, from left to right, denitrification, ammonia efflux and organic matter degradation obtained through direct scaling. The middle panels show the power law relationships between area and the logarithm of the functions obtained through allometric scaling. The bottom panels show the models used for kriging.

Allometric scaling calculated denitrification was 2.5 times lower than the expected value. NH_4^+ efflux was instead 26.5 times higher and C_o was 149.8 times higher. No multi-fractality was observed and all 3 functions showed very similar scaling exponents, respectively 1.18, 1.35 and 1.2.

The use of structure functions and kriging provided a much more accurate estimate of functions. This method was able to detect and account for anisotropy in the data and predicted a total flux of 14.94 kg of N_2 h^{-1}, 1.54 kg of NH_4^+ h^{-1} and 80.26 tonnes of C h^{-1}. The actual values calculated from the results of Chapter 4 were respectively 13.02 kg of N_2 h^{-1}, 1.19 kg of NH_4^+ h^{-1} and 77.22 tonnes of C h^{-1}.

5.5 | Discussion

Experimenting with extensive, high–resolution data on the spatial distribution and delivery of ecosystem functions allowed us to compare the performance of different scaling methods in predicting those functions. Our results show that different methods can lead to differences in the estimates of functions of an order of magnitude. Direct scaling, one of the simplest scaling methods, showed very poor performance and underestimated all functions by more than 80%. This approach merely consists in the multiplication of the plot-scale average with the total study area (King 1991, Miller et al. 2004). By doing so, it assumes that the relationships describing the system are linear and it can lead to considerable bias because it does not account for additional variability and ignores nonlinear changes that often occurs with changes in scale (Rastetter et al., 1992; Turner and Gardner, 2015). For it to provide a more accurate estimate of function would require an excessive amount of sampling and prior knowledge of the system studied to tailor the sampling strategy. To improve the prediction and incorporate some measure of heterogeneity it is possible to divide the study area into a tractable number of discrete elements based on some characteristics, for example land use or different habit type (Turner and Gardner, 2015). However, when we applied this concept to our study, the predictions only improved by 2-5%.

Sampling the three functions at different scales showed the emergence of allometric relationships, with similar scaling exponents of 1.18, 1.35 and 1.2 for respectively denitrification, ammonium efflux and organic matter degradation, suggesting a common pattern in the relationship between ecosystem functioning and scale. Allometric scaling still fails to accurately predict functioning at larger scales and results in underestimated denitrification and overestimated ammonium efflux and organic matter degradation estimates. However, the fluxes measured across polygons of increasing area showed a clear allometric gowth and the fitted models always had $r^2 > 0.9$. This may indicate the presence of multi-fractality at scales bigger than those measured. For several decades allometry has focused primarily on the body size (or mass) of organisms as the fundamental variable (e.g. Calder, 1983; McMahon et al., 1983; Schmidt-Nielsen, 1984; Taylor et al., 1982). In biology, allometric studies have proved successful scaling up metabolic and physiological relationships (e.g. Brown et al., 2000; Labarbera, 1989; Schmid et al., 2000). However, the effect of scale on ecosystem functions is still poorly understood and fractal theory has never been applied to biodiversity–ecosystem functioning research in marine systems. The reason why the estimates of functions from allometric scaling still differ from the actual estimates can be sought in the lack of measures of heterogeneity and in the oversimplification. This approach, in fact, aims to describe the complex nature of these habitats with a rather simple mathematical function. Although this simplification represent one of the limits of the method, it is also its major appeal due to the need to find easy ways to describe complex phenomena, which would otherwise be impossible to describe when the data is scarce.

The approach that led to the most accurate estimates of ecosystem functions was the investigation of spatial structures through variograms/kriging. Spatial statistics are increasingly being used in the context of extrapolation, and they have great potential to improve the accuracy of predictive models (Miller et al., 2004). Probably one of the most commonly used methods in this context, kriging relies on autocorrelation functions to generate spatially explicit predictions (Webster and Oliver, 2001). Although it resulted in rather accurate results, this process requires a larger amount of data compared to the other methods. A good estimation of the parameters of the variogram, in fact, is crucial for the subsequent kriging steps (Fortin, 1999). Therefore, estimating functions at the landscape scale would typically require that at least ~50 sites are sampled. However, when prior knowledge on the study area is available or can be easily obtained (trough remote sensing for example), it can be used to tailor the sampling design. Other methods are available to scale up the results of experiments and can be applied to spatial ecology (Klopatek and Gardner, 1999; Wu et al., 2006). Most approaches, however, are derived from and very similar to those used in this study. Therefore, when applied to heterogeneous systems, such as coastal landscapes, similar differences in estimates can be expected.

Soft sediment habitats are often considered to be homogeneous but are in fact highly complex ecosystems and contain strong physical gradients that affect the distribution of species and functional performance. This results in the patchy spatial distributions of communities and ecosystem functions across multiple spatial scales. Such patchiness is often not as apparent as in other ecosystems where above ground structures define patches (e.g. terrestrial and marine forests). Moreover, ecosystem functioning is driven by the biological activity of species and by their interactions. If we fail to sample the spatial heterogeneity of these systems and to include the role of the underlying biodiversity in the scaling process, we end up miscalculating the results of important ecological processes that support critical ecosystem services.

Scaling ecosystem functions can allow the quantification of the ecosystem services they underpin. The choice of the scaling method therefore can deeply influence the assessment of their ecological, cultural or economic value. For example, the value of Nitrogen removal via denitrification in U.S. dollars has been estimated between \$13/kg N and \$98.70/kg N (Piehler and Smyth, 2011; Watanabe and Ortega, 2011). Using the more conservative value of \$13/kg N, the estimate of the annual cost to replace the removal of N through denitrification in our study site would be of \$US 1,701,367 using kriging to up-scale and \$US 235,731 using direct scaling. If the only way we can value seafloor ecosystems is to monetise their services, this analysis shows substantive value for resource managers in gathering good ecological data, addressing scale, and understanding ecological complexity. Although these are just approximate calculations that do not take into account changes in rates due for example to seasonal changes, they provide a useful indication that the inappropriate use of scaling can lead to differences of more than \$US 1,000,000 in the estimate of ecosystem services. Coastal ecosystems are dynamic and change is often driven by multiple stressors and cumulative anthropogenic effects. Therefore, the way we estimate functioning and service delivery needs to be sensitive to such changes. A map of a sandflat based on purely sedimentological features will not change even if we kill all of the resident macrofauna. A habitat characterisation that recognises the important scales of ecological variability is essential for effective management.

The data used in this study was obtained from maps of ecosystem functions with a 1 x 1 m resolution and therefore relies on their accuracy (Chapter 4). Such maps were created combining high resolution remote sensing data on the distribution of key species and ecosystem functioning models that relate functions to the abundance of those species and measures of uncertainty were provided. Our findings support the importance of the methodology we developed to create these biologically nuanced ecosystem functioning maps to overcome the challenge of integrating ecological variability in habitat description. The use of empirical and theoretical models that link ecosystem functioning to biological attributes that can be measured remotely over large areas will in fact improve our understanding of heterogeneous landscape and overcome the problems associated with extensive sampling. However, we showed that, since not all landscapes can be extensively mapped and linked to easily quantifiable features, the ability to properly identify and use scaling relationships is crucial to landscape ecology.

Chapter 6 – Conclusions

Stefano Schenone

6.1 | Synthesis

In this thesis I used a mix of controlled laboratory experiments, mensurative field studies, large scale surveys and modelling to investigate how key species living in intertidal soft-sediments drive ecosystem functions at multiple scales and how to use this information to map the delivery of these functions. In Chapter 2, I showed that key burrowing infaunal species have the ability to enhance and drive biogeochemical fluxes at the sediment-water interface. How and to what extent depends on the nature of their functional traits. This is consistent with previous literature on the effect of biodiversity on ecosystem functions (Bertics et al., 2010; Mermillod-Blondin et al., 2004; Volkenborn et al., 2007; Woodin et al., 2016). I also showed that their individual effects on biogeochemical processes interact synergistically and furthermore that these effects change with environmental stress (mud deposition). Overlooking these synergistic effects can lead to significant errors when extrapolating the results of experiments on ecosystem functioning. These findings led me to hypothesise that transition areas between patches dominated by specific species play an important role in the overall functioning of heterogeneous benthic ecosystems. This hypothesis was supported by previous studies on the effect of transition zones on populations and functions (Lohrer et al., 2013; Zajac et al., 2003). However, it is still too common for ecologists to avoid patch transition areas in the design of experiments and the inference they draw from them. In Chapter 3, I built on the results from the previous chapter and demonstrated that in the intertidal sandflats of Whangateau harbour the key species *Macomona liliana* and *Macroclymenella stewartensis* are much more important for ecosystem functioning the rest of the macrofaunal community and environmental variables. I also showed that in patch transition areas, where the distribution of these species overlap, fluxes are different from patches dominated by either species. The functioning of these transition areas changes with the density of two species, which controls their interactions. This implies that across the sandflat landscape transition areas play an important role in the balance of ecosystems functioning that because of the synergistic interactions cannot be assumed from studies in patches where individual species dominate (Fig. 3.2). This allowed me to develop ecosystem function models based on the density of key species that explained up to 70% of the variation in function. At the same time, I was able to link the density of these species to the biogenic features that they produce on the sediment surface as a result of their activity. My results showed that the biogenic traces left by Macomona and Macroclymenella are not merely surrogates for animal density but actually better measures because they reflect activity rates. These findings have important implications for ecological studies. Sampling surface features of key species – and potentially some easily measurable environmental variables – can be used to extrapolate the results of experiments to larger scales. Chapter 4 is the natural development of this idea. Combining species-functions models with the survey of the distribution of biogenic features, I was able to up-scale and map ecosystem function over the extensive sandflats of the estuary (1,695,158m^2). These high-resolution maps are well grounded in the underlying ecology and give spatially explicit information on ecosystem functioning that can be used to assess the delivery of ecosystem services. They offer the opportunity to distinguish between areas of high delivery of functions and to identify hotspots of multiple functions. Finally in Chapter 5, I recognized that scaling information across spatial scales can be a complicated process, but it is incredibly important to gain an understanding of ecosystem functioning across scales. Moreover, it is not always possible to extensively map habitats and obtain high resolution spatial information and therefore it is necessary to determine which methods are more useful in scaling up the results of experiments. However, there does not appear to be one right way relate functions across scales. The choice of the approach has to be driven by the ecosystem under study. Simply multiplying the results obtained at small scale (< 1 m^2), although still commonly applied, leads to significant aggregation errors in heterogeneous systems (Attard et al., 2019; Boerema et al., 2016; Ewers Lewis et al., 2018). Heterogeneity increases with scale and extrapolations that do not incorporate measures of heterogeneity lead to results that can be inaccurate by multiple orders of magnitude. Although geostatistical methods give more reliable results, their use requires a large amount of data. Spatial allometry, based on the fractal theory, shows the emergence of some interesting features in the relationship between functions and scale and has the potential to reveal common patterns in the relationship between ecosystem functioning and scale (see Chapter 5). My results help untangling the complex spatial dynamics that drive ecosystem functioning and proposes new ways of bridging the gap between large-scale landscape ecology and functional ecology.

6.2 | Limitations

In this thesis I focused my attention on one estuary and two of the most functionally important organisms that are found in the sandflats: the tellinid bivalve *Macomona liliana* and the maldanid polychaete *Macroclymenella stewartensis*. While the effect of *M. liliana* on sediment biogeochemistry had been studied before, my work is to my knowledge the first published study on the effect of *M. stewartensis*. However, its functioning and consequences on the sediment are consistent with those observed in studies of other maldanid worms (e.g., Dobbs and Whitlatch 1982; Levin et al. 1997). Although my work demonstrated the key role of these two species, other estuaries and other habitats are likely to host different key species and their effects on ecosystem functions will depend on their functional traits and environmental setting. While other species, or in fact measures of biodiversity, may play dominant functional roles in other systems, this does not undermine the validity of the framework I proposed and will not stop other researchers from applying it to their ecosystems of interest.

The ecosystem function models I developed to link the biogenic features of *M. liliana* and *M. stewartensis* to the delivery of functions do not explain 100% of the variability in the data. The models explained on average 50% of the variance with the best model – the ammonium efflux model – explaining up to 75% of variation. This means that, on average, 50% of the variation was due to factors that were measured and included in the model or can be attributed to error. Other studies have shown similar levels of variance explained for ecosystem functions of soft sediments, using combinations of variables related to different aspects of biodiversity and habitat characteristics (e.g., Thrush et al. 2017). While my explanation of functioning was not complete, it still represents a jump forward into a characterization of these habitats that is based on a few tractable variables of their underlying biodiversity that can be measured across large scales, rather than sets of physical parameters. Moreover, since there is no guarantee that all habitats show characteristic biogenic features that can be used for mapping, Chapter 5 deals with the implementation of approaches that can overcome this constraint and shows that autocorrelation and geostatistical methods, although require more data than simpler methods, can lead to accurate estimates of functions over large scales from limited measurements.

6.3 | Future directions and applications

The framework I developed can be further expanded to include temporal scales. The use of drones and artificial intelligence technologies make it cost-effective to measure changes in the estuaries through time and create dynamic mapping that is sensitive to seasonal variations and can be used to monitor temporal changes in species activity levels, patch structure and model functional contributions. However, this will need further verification and testing. It could also be used to assess long-term changes in ecosystem functioning due to major stress events and anthropogenic impacts. Another interesting feature to investigate is the addition to the ecosystem functioning models of more biogenic structure forming species and to link the morphology of the structures to the functional traits of the organisms that generated them. The shape of these structures could also be linked to their specific interaction with hydrodynamics. This trait-feature-function relationship would help investigate those habitats where a thorough empirical sampling of macrofauna is impractical. Finally, information on different functions could be synthetized to create maps of multifunctionality, combining the value of different functions that are potentially divergent into one indicator (e.g., linked to bioturbation vs sediment stability). Such maps would give further insights into the contributions of different patches of habitats to ecosystem services and would strongly benefit the sustainable management of natural resources and space.

Coastal and estuarine ecosystems, at the transition between land and sea, are some of the most productive and heavily used natural systems in the world (Barbier et al., 2011). The ecosystem services derived from these habitats range from food production and contaminant processing to recreational used and cultural identity. This wide range of benefits and the number of people that live near and impact them, make them particularly valuable. Ecosystem management needs to ensure the sustainable exploitation of marine resources as well as the protection of habitats, taking account of potential multiple-use conflicts and impacts over large spatial scales to preserve their ability to deliver functions. This is the foundation of ecosystem-based management (McLeod and Leslie, 2009; Thrush and Dayton, 2010). To be successful, management requires spatially explicit information at all important ecological levels, which has led to an increased interest in marine spatial planning (Douvere and Ehler, 2009). In this thesis, I developed ideas and methodologies that incorporate a true understanding of the underlying ecological mechanisms and spatial arrangement of species, functions and services to support marine spatial planning efforts and ecological research. Precise quantification and understanding of the distribution of natural communities and of the ecosystem services they provide, in fact, is crucial to make informed decisions and to accurately estimate their value to support sustainable management.

Knowledge of the drivers and location of functions is necessary to predict the consequences of anthropogenic pressures and environmental change on ecosystems. One of the consequences of human impacts on both terrestrial and marine ecosystems is landscape homogenisation (Hewitt et al., 2010; Thrush and Dayton, 2002; Western, 2001). In particular, homogenisation of benthic soft-sediment habitats is caused by physical destruction, removal of species and smothering by terrigenous deposits. This phenomenon is predicted to affect biodiversity by reducing species richness and heterogeneity, leading to potential regime shifts (Hewitt et al., 2010; Thrush et al., 2006). Under these scenarios, the complexity that supports the healthy functioning of benthic habitats is endangered and we could expect a shift towards a more homogeneous distribution of ecosystem functions across the landscape and the consequent loss of functional hotspots. Studies that incorporate various degrees of heterogeneity help predict the long term consequences of species loss and habitat homogenisation. Detailed knowledge on the location of functions can therefore inform conservation efforts targeted at preserving the diversity and functioning of ecosystems.

6.5 | Concluding remarks: portraying the hidden diversity

Soft sediments cover most of the ocean seafloor and dominate estuarine and coastal habitats (Snelgrove, 1997). Given the vast extent that these habitats occupy, sampling and characterizing them individually is impractical. Therefore, the use of maps and models has gained importance and popularity (Huang et al., 2011; Raineault et al., 2012). Unlike their terrestrial counterparts, coastal soft sediment habitats are most frequently characterized by their physical and topographic attributes rather than the underlying species and biodiversity and are often coarsely aggregated into just sand or mud habitat categories (Hillman et al., 2020). Seppelt et al. (2011) defined this problem as the “lack of biophysical realism”. Mapping and modelling must evolve in order to describe these incredibly complex and functionally important habitats, where features are often not visually easy to detect and patch boundaries are fuzzy (see Evrard et al. 2008). Furthermore, the current biodiversity crisis and habitat loss that most coastal ecosystems are experiencing, highlights the critical urgency in investigating drivers of ecosystem functionality at different scales. In this thesis, I demonstrated that even within a single habitat, the heterogeneity of processes generates differences of orders of magnitudes in the delivery of functions, which is totally overlooked in traditional habitat characterization, and I open the way to closing the biophysical realism gap. Closing the gap between our fine-scale knowledge of these habitats and their coarse-scale characterization is possible and should be pursued. Integrating different research approaches and extending empirical research across multiple scales, as I have done here, is challenging, but critical if we are to better understand and protect soft-sediment habitats for the generations to come.

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Appendix A: Supplementary materials for Chapter 2

Supplementary tables

Table A1. Results of the 2 way ANOVA showing the preliminary analysis of effects of each species and sediment layer on measured fluxes. Significant results are indicated in bold text ($^{\cdot}p < 0.1$, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$). N_2 flux data was log-transformed prior to analysis.

Factor	df	SS	MS	F.Model	p-value
(a) O_2					
Species	3	12845.941	4281.980	30.267	**<0.001*****
Treatment	2	8496.382	4248.191	30.028	**<0.001*****
Species x Treatment	6	5093.557	848.926	6.001	**<0.001*****
Res	36	5093.019	141.473		
Total	47	31528.899	670.828		
Pairwise comparison (Holm-Sidak)			Diff of Means	t	p-value
Species within 0mm					
(1) vs. (3)			51.963	6.178	**<0.001*****
(2) vs. (3)			53.475	6.358	**<0.001*****
(4) vs. (3)			56.062	6.666	**<0.001*****
(1) vs. (2)			1.512	0.180	0.858
(1) vs. (4)			4.099	0.487	0.949
(2) vs. (4)			2.586	0.308	0.943
Species within 3mm					
(1) vs. (3)			22.968	2.731	**0.048***
(2) vs. (3)			26.481	3.149	**0.020***
(4) vs. (3)			21.033	2.501	**0.067˙**
(1) vs. (2)			3.513	0.418	0.897
(1) vs. (4)			1.934	0.230	0.819
(2) vs. (4)			5.448	0.648	0.890
Species within 6mm					
(1) vs. (3)			39.946	4.750	**<0.001*****
(2) vs. (3)			1.932	0.230	0.820
(4) vs. (3)			47.796	5.683	**<0.001*****
(1) vs. (2)			38.015	4.520	**<0.001*****
(1) vs. (4)			7.850	0.933	0.586
(2) vs. (4)			45.864	5.453	**<0.001*****
Treatment within (1)					
0mm vs. 3mm			1.734	0.206	0.838
0mm vs. 6mm			19.758	2.349	**0.071˙**
3mm vs. 6mm			18.024	2.143	**0.076˙**
Treatment within (2)					
0mm vs. 3mm			0.267	0.0318	0.975
0mm vs. 6mm			59.285	7.049	**<0.001*****
3mm vs. 6mm			59.553	7.081	**<0.001*****
Treatment within (3)					
0mm vs. 3mm			27.262	3.241	**0.005****
0mm vs. 6mm			7.742	0.920	0.363
3mm vs. 6mm			35.003	4.162	**<0.001*****
Treatment within (4)					
0mm vs. 3mm			7.767	0.923	0.362
0mm vs. 6mm			16.008	1.903	0.183
3mm vs. 6mm			8.241	0.980	0.556
Factor	df	SS	MS	F.Model	p-value
(b) NH_4^+					
Species	3	11121.266	3707.089	52.311	**<0.001*****
Treatment	2	173.169	86.585	1.222	0.307
Species x Treatment	6	6890.554	1148.426	16.205	**<0.001*****

Res	36	2551.195	70.867		
Total	47	20736.185	441.195		
Pairwise comparison (Holm-Sidak)			Diff of Means	t	p-value
Species within 0mm					
(1) vs. (3)			31.538	5.298	**<0.001*** **
(2) vs. (3)			67.580	11.353	**<0.001*** **
(4) vs. (3)			58.968	9.906	**<0.001*** **
(1) vs. (2)			36.043	6.055	**<0.001*** **
(1) vs. (4)			27.430	4.608	**<0.001*** **
(2) vs. (4)			8.613	1.447	0.157
Species within 3mm					
(1) vs. (3)			34.748	5.837	**<0.001*** **
(2) vs. (3)			36.105	6.065	**<0.001*** **
(4) vs. (3)			35.638	5.987	**<0.001*** **
(1) vs. (2)			1.358	0.228	0.994
(1) vs. (4)			0.890	0.150	0.986
(2) vs. (4)			0.468	0.0785	0.938
Species within 6mm					
(1) vs. (3)			6.273	1.054	0.509
(2) vs. (3)			7.235	1.215	0.547
(4) vs. (3)			26.802	4.503	**<0.001*** **
(1) vs. (2)			0.962	0.162	0.872
(1) vs. (4)			33.075	5.556	**<0.001*** **
(2) vs. (4)			34.037	5.718	**<0.001*** **
Treatment within (1)					
0mm vs. 3mm			20.700	3.477	**0.004** **
0mm vs. 6mm			1.335	0.224	0.824
3mm vs. 6mm			19.365	3.253	**0.005** **
Treatment within (2)					
0mm vs. 3mm			13.985	2.349	**0.024***
0mm vs. 6mm			35.670	5.992	**<0.001*** **
3mm vs. 6mm			21.685	3.643	**0.002** **
Treatment within (3)					
0mm vs. 3mm			17.490	2.938	**0.006** **
0mm vs. 6mm			39.145	6.576	**<0.001*** **
3mm vs. 6mm			21.655	3.638	**0.002** **
Treatment within (4)					
0mm vs. 3mm			5.840	0.981	0.333
0mm vs. 6mm			6.980	1.173	0.435
3mm vs. 6mm			12.820	2.154	0.110
Factor	df	SS	MS	F.Model	p-value
(c) N_2					
Species	3	2.523	0.841	0.803	0.500
Treatment	2	0.192	0.0962	0.0919	0.912
Species x Treatment	6	0.835	0.139	0.133	0.991
Res	36	37.679	1.047		
Total	47	41.229	0.877		

Appendix B: Supplementary materials for Chapter 3

Supplementary tables

Table B1. Macrobenthic families and their abundance in the core at each of the 30 sampling stations.

Taxa	Sampling station														
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
Trochidae	6	7	5	7	3	4	3	3	3	2	4	3	3	2	0
Buccinidae	2	3	1	1	2	2	1	3	2	2	2	1	1	1	0
Nassaridae	3	4	2	4	2	2	3	2	2	2	3	3	2	1	3
Batillariidae	84	61	43	52	43	39	37	40	31	26	23	22	28	24	21
Veneridae	5	6	8	3	10	9	9	17	18	46	38	38	32	36	27
Tellinidae	3	5	4	2	2	4	3	6	5	3	2	5	2	4	5
Nuculidae	5	4	9	5	4	6	6	11	8	6	8	15	10	21	28
Actinidae	5	6	5	4	10	5	16	25	27	72	48	35	43	19	1
Nereididae	14	12	10	12	7	9	11	8	8	6	7	11	9	15	16
Spionidae	15	13	17	18	12	14	12	20	18	63	31	35	42	29	24
Paraonidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sabellidae	3	1	0	1	0	0	0	0	0	0	2	0	0	0	0
Lysianassidae	2	4	3	6	4	9	3	7	6	6	4	3	2	2	0
Epitoniidae	2	1	0	0	0	0	1	0	0	0	0	0	0	0	0
Hymenosomatida	0	0	0	0	1	1	0	1	2	0	0	1	0	0	0
Capitellidae	0	0	1	0	2	0	0	3	1	0	0	2	0	1	4
Maldanidae	0	0	0	1	0	0	0	1	1	1	1	1	1	3	2
Haminoeidae	0	0	0	0	1	0	0	2	0	0	0	1	0	0	0
Lottiidae	0	1	2	0	2	1	0	1	1	3	2	2	0	3	2
Ostracoda	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0
Chitonidae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Orbiniidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Sphaeromatidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mesodesmatidae	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0

Taxa	Sampling station														
	16	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**
Trochidae	3	7	1	0	0	0	1	0	1	4	7	8	2	1	1
Buccinidae	2	1	0	0	1	0	1	2	0	2	4	3	2	2	1
Nassaridae	2	3	2	0	1	0	0	1	2	0	2	1	2	0	0
Batillariidae	19	15	17	0	1	1	2	4	7	19	21	25	23	16	14
Veneridae	34	28	26	4	3	1	6	3	3	25	24	19	28	32	24
Tellinidae	3	4	6	2	0	1	2	3	2	2	3	5	1	3	2
Nuculidae	19	26	25	0	1	0	0	0	2	2	5	6	0	0	2
Actinidae	18	13	11	5	5	1	7	4	3	36	28	29	39	24	18
Nereididae	11	18	14	15	11	12	17	12	9	11	13	8	18	17	10
Spionidae	38	35	30	0	1	0	0	0	0	16	22	21	20	28	22
Paraonidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sabellidae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Lysianassidae	3	1	1	0	0	1	0	0	1	0	1	1	0	0	0
Epitoniidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hymenosomatida	0	0	0	0	0	0	0	0	1	2	0	1	1	1	0

Capitellidae	1	3	3	0	1	0	0	0	0	1	5	4	1	3	2
Maldanidae	0	2	1	0	0	1	0	0	0	0	1	0	0	1	2
Haminoeidae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Lottiidae	2	3	2	0	0	1	0	2	0	1	0	1	0	0	0
Ostracoda	1	0		1	0	0	1	0	0	0	1	0	0	3	2
Chitonidae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Orbiniidae	0	0	0	2	0	1	0	0	1	0	1	2	0	0	1
Sphaeromatidea	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0
Mesodesmatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix C: Supplementary materials for Chapter 4

Supplementary tables

Table C1. Summary of the statistics of our four ecosystem functions models

Function	AIC	BIC	R^2	P	Variables	Coefficients	P
N_2	365.17	370.78	0.25	0.02	Intercept	64.275	0.182
					M. liliana	5.141	0.022*
					Log(M. stewartensis)	-56.774	0.043*
NH_4^+	197.03	206.84	0.47	0.006	Intercept	10.619	0.001***
					M. liliana	9.060	0.296
					M. liliana^2	18.185	0.005**
					M. stewartensis	26.64	0.037*
					M. stewartensis^2	-2.489	0.683
					M. liliana x M. stewartensis	-0.102	0.015*
C_o	196.20	203.21	0.35	0.015	Intercept	7.036	0.015*
					M. liliana	0.383	0.044*
					M. stewartensis	1.106	0.085
					M. liliana x M. stewartensis	-0.119	0.005**
k	-83.97	-76.97	0.58	0.001	Intercept	-0.036	0.159
					M. liliana	-0.004	0.013*
					M. stewartensis	-0.012	0.05*
					M. liliana x M. stewartensis	0.002	0.001***

Supplementary figures

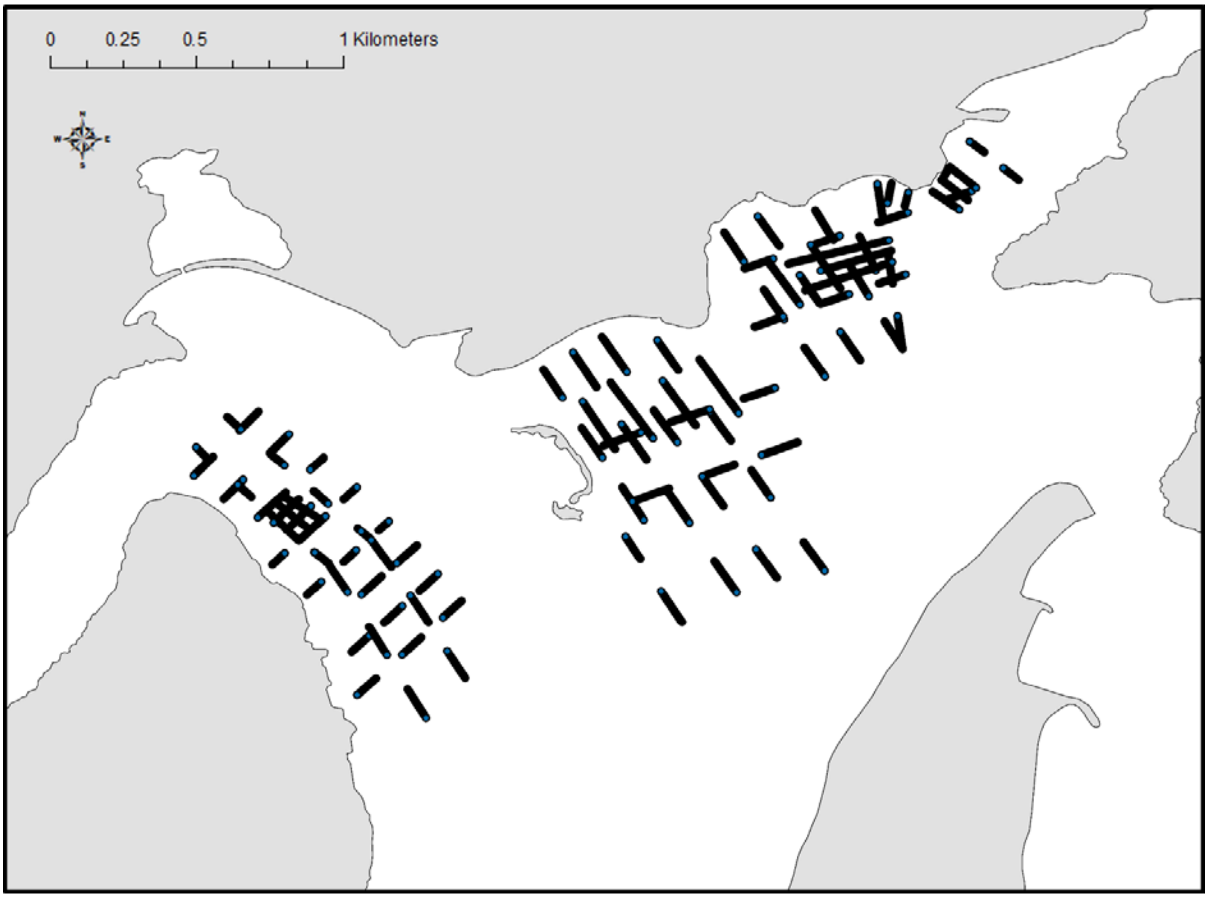

Fig C1. Location of the drone transects conducted to video sediment surface features related to *M. liliana* and *M. stewartensis*. The black lines represent the tracks followed by the drone.

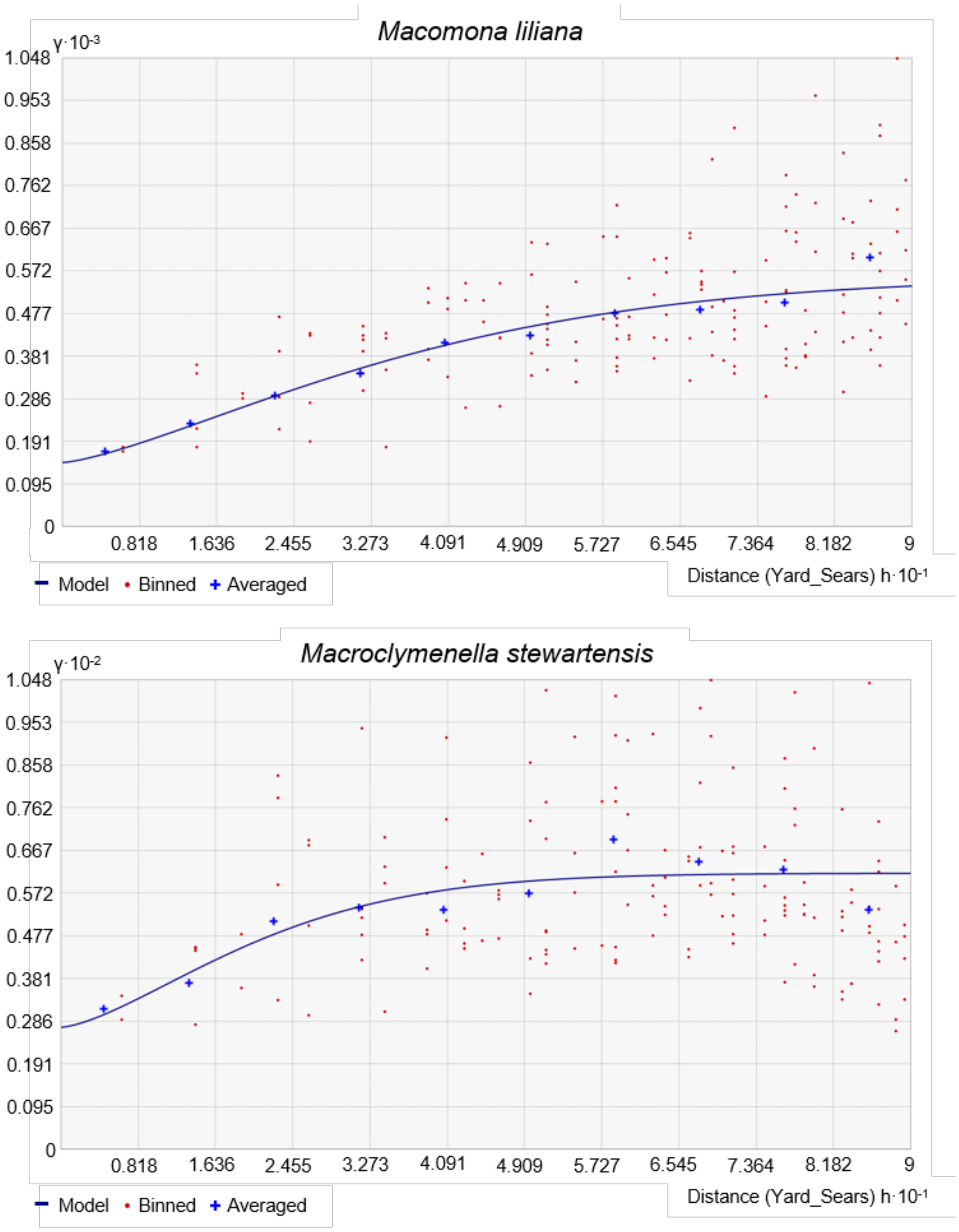

Fig C2. The semivariogram models of the data on *M. liliana* (top) and *M. stewartensis* (bottom). The models were used for kriging.

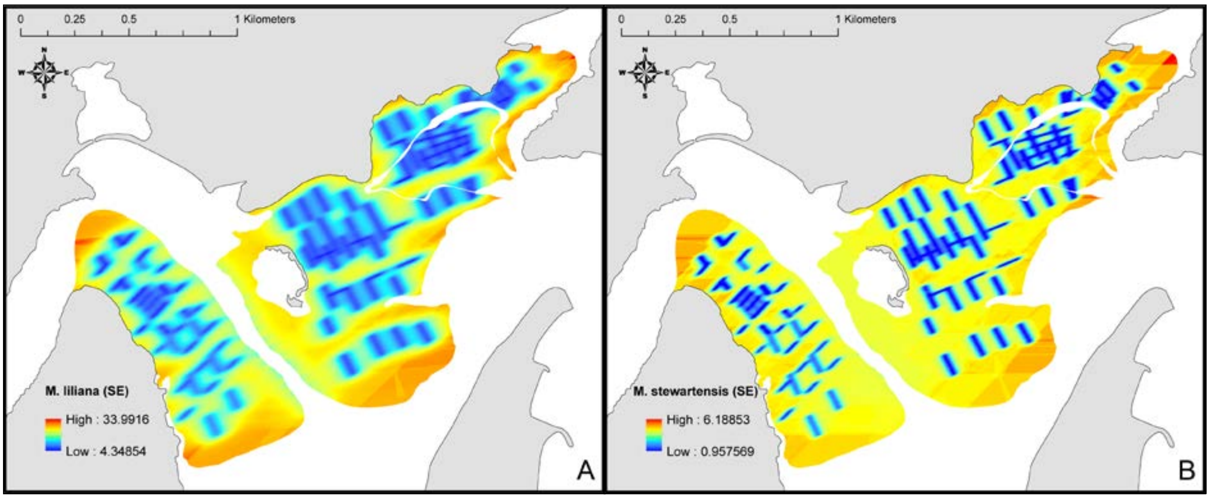

Fig C3. Standard error maps of the predictions of the density of *M. liliana* (A) and *M. stewartensis* (B) generated with kriging.

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