From ecology to the assessment of multiple ecosystem services; a case study of estuarine bivalves

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Abstract

Estuarine and coastal environments provide a wide range of societal goods and services that need to be strategically managed to ensure sustainable use of resources. Ecosystem service (ES) assessments are transitioning from individual ES to multi-service assessments that consider interactions and grouping of ES (i.e. bundles). This thesis investigates the use of ecological mechanism (i.e. the links between ecological processes, functions, and ES) to derive insights into the associations between multiple ES provided by marine bivalves and the implications for management.

In data-scarce marine environments, conventional spatial methods for assessing ES interactions and bundles are not always feasible. However, advancements can be made by focussing on ecological mechanisms, as for bivalves their ecological role has been extensively studied. The complex links between processes, functions, and ES were identified for bivalves, which were used to derive four ES bundles based on shared underpinning mechanisms. This study provides detailed descriptions of the specific (set of) ecological mechanisms per bundle, thereby gaining insights in how the ES are formed, the interactions between ES (synergies and trade-offs) and the environmental stressors they are prone to.

Quantification of ES remains challenging, and measuring them in functionally similar species in different habitats is rarely considered, although ecological studies indicate differences are likely. I measured *in situ* bivalve contribution to water quality regulation for two functionally similar bivalve species (infaunal suspension-feeders) that dominate different estuarine habitats (subtidal and intertidal). Benthic chambers were used to measure solute fluxes (oxygen and nitrogen) and bed clearance rates as proxies for ES. Empirical findings indicated higher hourly productivity, nitrogen recycling, and water column filtration in the intertidal. However, when converted to daily ES estimates these patterns did not persist, emphasising the unequal contribution to functions and ES by functionally similar species and the non-linear scaling between them.

Many ecological processes and functions are density dependent, hence spatial information on the distribution and density of bivalves is an important prerequisite to estimate ES. Probability of occurrence and density were predicted using Species Distribution Models (SDMs) for two estuarine bivalve species. Fine scale (100 m resolution) predictions showed different spatial patterns depending on habitat association. Species with a narrow distribution displayed good congruence between occurrence and density predictions, whereas species with a wide distribution demonstrated that a high probability of occurrence does not always equate to high density. Simultaneously considering both occurrence and density will improve decision-making and identify areas of greatest ecological value to the species of interest.

Ecological mechanisms can be further applied to advance spatial predictions of multiple ES in marine environments, through process-based models that incorporate ecological principles to derive ES potential and assess natural variability in ES. Four ES (food provision, water quality regulation, nitrogen removal, and sediment stabilisation) were spatially predicted for two bivalve species. Spatial patterns in ES related to the species habitat association, with varying quantities and were driven by environmental conditions. Hotspot analyses on combined ES maps per species identified high-density areas for the provision of multiple ES simultaneously. These models provide a versatile tool to inform current management practices and can be further applied to test management scenarios.

Collectively the results from this thesis demonstrated the utility and effectiveness of ecological mechanisms to determine ES interactions and bundles, and the spatial heterogeneity observed across estuaries. It also highlighted the interconnectedness of marine ES and the implications for their management.

Preface

The main body of this thesis comprises of four research chapters (Chapters 2 to 5), which have been published, or are currently in preparation for publication, in peer reviewed international scientific journals. I have assumed responsibility for the fieldwork, laboratory and data analysis, and for writing this thesis. Unless otherwise referenced, the material produced in this thesis was produced from my own ideas. All work presented was carried out under the supervision and co-authorship of Professor Conrad Pilditch at the University of Waikato, Dr Andrew Lohrer and Dr Fabrice Stephenson from the National Institute of Water and Atmospheric Research Ltd. (NIWA), and Dr Michael Townsend from the Waikato Regional Council.

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I could not have made it this far without the support of those dearest to me, my partner Cameron, and my family: Ben, Anita, Loes, Bart, Jaap and Benna. Cameron, I am so grateful for your support, kindness, and never-ending enthusiasm and optimism. You have filled these last few years with so many adventures, and I am so excited to see what comes next. Loes, Bart, Jaap, and Benna, it is wonderful having you all as my brothers and sisters, and although I keep moving further and further away, I am so glad we stay close. To mom and dad, you have enabled and encouraged me to get to where I am today, and for that I am most grateful. Although I set out on this journey to New Zealand alone, knowing that I would always have a place to return to and that I have your support has meant so much.

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CHAPTER 1
General introduction

1.1 Background and Introduction

1.1.1 Ecosystem services, interactions, and bundles

Within any ecosystem, a wide range of goods and services are generated that link the natural environment to various benefits on which societies rely (Daily 1997). These *ecosystem services* (hereafter ES; see Table 1.1 for definitions used in this thesis) include, for example, the provision of food, material, fresh water, climate regulation, soil formation, cultural heritage, and recreation (MEA 2005). The ES concept was first proposed as a means of linking the natural environment to the benefits and values people derive from them (Costanza et al. 1997, Daily 1997, MEA 2005), and has grown and gained increasing traction as a practical tool to spatially assess ES and their value to inform environmental (resource) management (Egoh et al. 2008, Burkhard et al. 2012, Maes et al. 2012a). ES are underpinned by a complex web of abiotic and biotic interactions, i.e. the ecological *processes* and *ecosystem functions* taking place in the environment (Haines-Young and Potschin 2010), through *ecosystem service providers* (ESP; Kremen 2005, Luck et al. 2009). ES therefore rely on well-functioning, healthy and resilient ecosystems that need to be maintained to ensure sustainable use of all resources and services, and are jeopardized by increasing anthropogenic pressures on the environment (MEA 2005). It is important to recognise that ES are merely the consequence of the natural processes and functions normally performed by ecosystems and the species therein, and are not actively provided as such (Beaumont et al. 2007). However, ecosystem functions require a societal demand for the benefits and values generated to be considered an ES (Haines-Young and Potschin 2010). The ES framework therefore enables interdisciplinary research on the supply and demand of these services from ecological, social, economic, and management perspectives. A common challenge for all disciplines is to gain better understanding on how multiple ES are formed from the same system or ESP, how they interact with each other, and how they can be best managed simultaneously (e.g. Raudsepp-Hearne et al. 2010, Martín-López et al. 2012, Dendoncker et al. 2013, Ament et al. 2017, Baró et al. 2017).

The multitude of ES and their estimated values have long been recognised in many different environments around the world (e.g. Costanza et al. 1997, Barbier et al. 2011), although in the past the majority of studies have focussed on single ES in isolation. However, ES are strongly interconnected and interact in complex, dynamic, and non-linear ways in space and time (Rieb et al. 2017), just like the ecology that generates them. A first typology for ES interactions was proposed by Bennett et al. (2009), and focussed on two different pathways resulting in interactions. These interactions can occur when multiple ES are affected by similar drivers, or by direct interactions amongst ES themselves, in the form of *synergies* or *trade-offs*. Synergies are often considered as ‘win-wins’, as one service positively affects the delivery of another ES and vice versa (Bennett et al. 2009, Maes et al. 2012b, Howe et al. 2014). Trade-offs on the other hand result in one ES increasing at the cost of another, and can result in a loss/decline of ES (Bennett et al. 2009), e.g. *provisioning ES* often conflicts with other ES that rely on the presence of the harvested good/species from the system to contribute to other regulating or supporting processes (Lee and Lautenbach 2016). The interconnectedness of ES is further exemplified in the formation of *ES bundles*, which reflects groups of associated ES (Raudsepp-Hearne et al. 2010). ES bundles provide insights into the multiple ES associated with heterogeneous, multifunctional landscapes and often focusses on the spatial distribution of ES clusters. *Ecosystem multifunctionality* refers to the characteristic of ecosystems to simultaneously perform multiple functions, that may lead to a particular ES bundle (Berry et al. 2016, Manning et al. 2018). Most ES bundle assessments focus on the congruence or co-occurrence of ES in space, thereby reflecting *pattern-based multifunctionality* (Mastrangelo et al. 2014, Spake et al. 2017). *Process-based multifunctionality*, on the other hand, focusses on the mechanistic understanding of the ecological processes driving multiple ES (Mastrangelo et al. 2014), but are much less frequently used for ES bundles assessments.

There are a variety of methods available to assess ES interactions and bundles, mostly derived from terrestrial studies where extensive spatial and land-use data are often available (Burkhard et al. 2012, Martínez-Harms and Balvanera 2012). ES interactions are frequently assessed through pairwise correlation between two ES, where a positive and negative correlation coefficients indicates a synergy and trade-off respectively (Mouchet et al. 2014). Bundles on the other hand are mostly determined using clustering analyses (including k-means or hierarchical clustering) on a regional or municipality scale (Raudsepp-Hearne et al. 2010, Mouchet et al. 2014). These bundles are often consistent with land-use patterns, specific to forests, agricultural or aquatic areas (Raudsepp-Hearne et al. 2010, Queiroz et al. 2015, Depellegrin et al. 2016), and reflect a competition for space (Spake et al. 2017). In

Table 1.1 Definitions of key terminology as used in this thesis.

Term	**Definition**
Ecological mechanism	The mechanistic links between processes, ecosystem functions, and ecosystem services
Ecosystem functions (EF)	An intrinsic ecosystem characteristic related to the set of conditions and processes whereby an ecosystem maintains its integrity, including decomposition, production, and fluxes of nutrients and energy (MEA 2003)
Ecosystem multifunctionality	The characteristic of ecosystems to simultaneous perform multiple functions, that might be able to provide a particular ES bundle (Berry et al. 2016). *Pattern-based multifunctionality* refers to the joint supply of multiple ES in space, whereas *process-based multifunctionality* is defined as the joint supply of ES in space caused by well understood relationships of synergy or complementarity among them (Mastrangelo et al. 2014)
Ecosystem service (ES)	The direct and indirect contributions of ecosystems to human well-being (de Groot et al. 2010a)
- Provisioning ES	- Products obtained from ecosystems (e.g. food, fresh water, fibre, genetic resources)
- Regulating ES	- Benefits obtained from regulation of ecosystem processes (e.g. climate regulation, water regulation)
- Supporting ES	- Services necessary for the production of all other ES (e.g. nutrient cycling, primary production)
- Cultural ES	- Nonmaterial benefits obtained from ecosystems (e.g. recreation, aesthetics, cultural heritage) Definitions and examples of ES categories from the Millennium Ecosystem Assessment (MEA 2005)
Ecosystem Principles Approach (EPA)	A method for simplifying ecological information into management frameworks relevant to the goods and services approach (Townsend et al. 2011)
ES bundle	Sets of associated ES that repeatedly appear together across space or time (Raudsepp-Hearne et al. 2010)
ES provider (ESP)	The component populations, species, functional groups (guilds), food webs or habitat types that collectively produce ecosystem services (Kremen 2005)
Processes	The complex interactions (events, reactions or operations) among biotic and abiotic elements of ecosystems which underlie an ecosystem function, e.g. photosynthesis (Tirri et al. 1998, Harrington et al. 2010)
Synergy	A situation where the use of one ES directly increases the benefits supplied by another ES (Turkelboom et al. 2015)
Trade-off	A situation where the use of one ES directly decreases the benefits supplied by other ES (Turkelboom et al. 2015)

environments where detailed spatial data are scarce, like many marine and coastal ecosystems, applying these methods has not been possible and has resulted in a lag in ES assessments (Maes et al. 2012a, Townsend et al. 2018). A number of models for marine ecosystems have been developed, including for example marine applications in InVEST (Guerry et al. 2012) or studies that apply matrix-based approaches using seascape type or seafloor habitat as an analogue to land cover (e.g. Galparsoro et al. 2014, Potts et al. 2014, Geange et al. 2019). However, studies focussing on specific habitat types often make the assumptions of equal service delivery and disregard landscape heterogeneity (Schröter et al. 2020) and do not account for non-linear scaling between ecosystem functions and ES in relation to habitat size, seasonality, or varying environmental conditions (Barbier et al. 2008, Koch et al. 2009). Recent advancement in marine systems include studies that (spatially) quantified multiple marine or coastal ES (e.g. Townsend et al. 2014, Arkema et al. 2015, Cabral et al. 2015, Geange et al. 2019, Manea et al. 2019, Neumann et al. 2019, Depellegrin et al. 2020), however the assessment of ES interactions and bundles in marine ecosystems remain limited.

When insufficient data are available to assess ES bundles and interactions spatially, information can be derived from underpinning ecological processes to gain insights in the mechanism that drive ES formation and the resulting associations between ES from the same ESP. *Ecological mechanisms*, as the links between processes, ecosystem functions, and ES, can provide insights in process-based multifunctionality and is fundamental to understand the formation of ES bundles. Although research on the contribution of organisms and/or biodiversity to ES is ongoing, their contribution to ecosystem functioning is relatively well established (Luck et al. 2009). The ecosystem-functioning literature established the role species, functional groups, and/or biodiversity (e.g. species richness) play in ecological processes, and are increasingly linked to ES (Hooper et al. 2005, Naeem et al. 2009). For example, plant functional traits were proposed as indicators for ES, as an improvement for pure land-use land-cover approaches, to assess the delivery of multiple ES (de Bello et al. 2010, Lavorel et al. 2011) and have been further applied to study trade-offs and synergies between ES (Lavorel and Grigulis 2012). Ecological mechanisms are increasingly used in marine ES assessments (Snelgrove et al. 2014, Culhane et al. 2018, Broszeit et al. 2019, Armoškaitė et al. 2020) but have not been progressed much past network diagrams. These network diagrams show the numerous and complex links and feedbacks between ecosystem attributes, ecosystem functions and ES, and that there is no one-to-one correspondence, meaning that one function underpins more than one ES. By embracing this complexity, information can be gained on the drivers of and associations between ES through process-based multifunctionality. In this thesis, I focus on bridging the gap in marine ES bundle and interaction assessments by applying ecological mechanisms to assess ES associations, and discuss the implications and benefits for management of multiple ES.

When multiple services are derived from the same ecosystem or species therein, it is important to recognise that management actions and decision for one service may alter the delivery of others. ES are never independent, and hence decision makers must consider multiple ES derived from the same system to avoid unanticipated and undesired consequences of their actions. Sustainable management is of growing importance to ensure the future capacity of systems to provide ES in a world of environmental decline. However, the strong focus on tangible provisioning services of high economic value in the past has led to losses of other (*regulating, cultural, and supporting)* services (Rodríguez et al. 2006). However, multifunctional habitats that provide regulating services tend to increase other ES simultaneously, as well as resilience of the system, and underpin long-term service delivery (Raudsepp-Hearne et al. 2010, Sutherland et al. 2017). For marine ecosystems, the management focus is shifting towards a more holistic Ecosystem Based Management (EBM) approach that emphasises the long term health of coasts and oceans, as well as human well-being (McLeod and Leslie 2009). In contrast to previous management approaches, that were fragmented and often focussed on managing single species or sectors (e.g. fisheries management), EBM focusses on cumulative impacts of multiple sectors and ecosystem connections. Marine Spatial Planning (MSP) is a practical approach to implementing EBM and focusses on organizing the spatial and temporal distribution of human uses of the ocean space, and the interactions between different uses and the environment (Santos et al. 2019). Studies focussing on multiple ES, their interactions, and ES bundles provide great insight for EBM and MSP (e.g. White et al. 2012, Lester et al. 2013), especially when trade-offs between different ES, uses, or pressures need to be balanced (Turkelboom et al. 2018). It can also provide information to help optimise management decisions, by identifying if and where ES can best be utilised, maintained, or increased without negatively affecting other ES in the process. Maintaining the delivery of all ES is a key goal for EBM and MSP, and hence ecological insights in the health, functioning, and resilience of ecosystems are needed to guide management (Crowder and Norse 2008, Foley et al. 2010).

1.1.2 Ecosystem service supply in coastal systems

The majority of the worlds societies are based along the coast and are strongly dependent on the benefits provided by estuarine and coastal regions (Hinrichsen 1999, Small and Nicholls 2003, MEA 2005). Some examples of ES provided by coastal regions include the provision of goods, like food from fisheries, aquaculture, recreational gathering of food, and materials (e.g. seaweed as fertiliser, shell material). Other services provided include regulating ES like nutrient recycling, carbon sequestration, and erosion prevention of shorelines, as well as supporting ES providing habitat and support for species, and coastal ecosystems are hotspots for biodiversity (Barbier et al. 2011). Furthermore, a range of cultural services are provided, including recreation, tourism, aesthetical appreciation and cultural significance (Barbier et al. 2011, Brown and Hausner 2017). The vast number of people living near coastal ecosystems and utilizing the ES provided, has resulted in pressures on resources and negative local anthropogenic impacts on the marine environment. Some of the most concerning local threats to estuaries and coastal ecosystems include overharvesting, urbanization and land-use change, resulting in increased eutrophication, sedimentation and runoff of pollutants and pathogens, reclamation, altered hydrology, invasive species, etc. (Kennish 2002). These stressors combined with global stressors (like sea level rise (SLR), global warming, and ocean acidification) can have cumulative impacts on the health and functioning of coastal and estuarine ecosystems and threaten the long-term supply of ES to society (Halpern et al. 2007, Crain et al. 2008). For example, a global decline in marine biodiversity has resulted in a loss of ES through collapses in fisheries, reduced water quality and reduced resilience of the system to perturbations (Worm et al. 2006). There is an urgent need to improve our understanding of the multiple ES and their bundles provided in coastal and estuarine ecosystems and identify the interactions between services to improve our ability to make informed management decisions. This includes both quantitative and qualitative studies, and improving knowledge on spatial heterogeneity in service supply at a scale appropriate for their management, as well as their vulnerability to environmental stressors.

An example of a key ESP in estuarine and coastal ecosystems is bivalve beds (hereafter more broadly referred to as shellfish beds), which represent an important component of coastal and estuarine ecosystems as many aspects of their functioning link the benthos to the water column. Shellfish habitats are defined as a location where shellfish dominate the benthic biomass, and function as ecosystem engineers (*sensu* Jones et al. 1994). When bivalves occur at high densities, they can create, modify, and maintain habitats that alter the physical state of the environment. Much of the work related to ES delivery by shellfish beds has focussed on epifaunal species, (e.g. oysters and mussels). Overharvesting and eutrophication have resulted in the loss of large proportions of epifaunal bivalve reefs globally (Beck et al. 2011). The first overviews of shellfish ES were targeted at summarizing the benefits that were lost and could be regained by restoring collapsed populations (e.g. Coen et al. 2007, Grabowski and Peterson 2007), including not only the harvesting of bivalves for food, but also their contribution to water quality, shoreline stabilisation, and habitat provision for other species (Coen and Luckenbach 2000, Zu Ermgassen et al. 2020). More recently, a detailed review of the multitude of ES provided by marine bivalves has been published (Smaal et al. 2019) and multiple papers have addressed specific case studies, like ES derived from aquaculture (e.g. Shumway et al. 2003, Alleway et al. 2019, van der Schatte Olivier et al. 2020) or non-commercial bivalve species (Carss et al. 2020).

Despite the attention bivalve reefs have received, the contribution of infaunal bivalves (those living within the sediment) to ES has received much less attention. The ecological role of infaunal bivalves has been studied extensively around the world, and they are known to contribute to a range of similar ES (Carss et al. 2020). However, due to functional differences between infaunal and epifaunal species (e.g. bioturbation or irrigation vs. reef formation, and differences in filtration rates), the findings from ES assessments for epifaunal bivalves may not apply and the contribution to ES may differ in quantity, space, and time. For example, infaunal bivalves will not contribute to habitat provision, sediment stabilisation, and coastal protection to the same extent as epifaunal species. With a lack in ES bundle and interaction assessments, in combination with a strong focus on few well-known species in previous assessments, the shellfish ES literature would benefit from a better understanding of how multiple ES interact for a wider variety of shellfish functional groups. Furthermore, understanding how functionally similar species contribute to ES in different habitats (e.g. intertidal and subtidal estuarine areas) can further our understanding of spatial heterogeneity in ES provision and what may change when habitats shifts, due to for example SLR. This information is crucial for our understanding of the ES shellfish deliver in estuarine and coastal environments, and to establish baselines for the current available ES to which past losses and future changes can be assessed. Moreover, it contributes to effective local-scale management strategies and actions to protect, maintain, and restore these ecologically important species.

1.2 Thesis rationale, aims and objectives

The overall aim for this thesis is to broaden the understanding on how shellfish beds contribute to the provisioning of multiple ES in temperate estuaries, through the ecological mechanisms that underpin interactions between services and the formation of ES bundles. I focus on the ES supplied by bivalves as a case study, as they are key ESP species in estuaries and coastal ecosystems and their ecology is well understood, allowing me to derive the underpinning ecological mechanisms that result in ES provision. My thesis comprises four research chapters, each addressing a key component to further the understanding of ES bundles and interactions between services. These components include identifying conceptual ES bundles (Chapter 2), quantifying EF underpinning ES (Chapter 3), creating reliable bivalve density models at a fine resolution (Chapter 4), and mapping multiple ES across an estuary to assess co-occurrence of services (Chapter 5). Work in Chapters 3 to 5 is conducted in Tauranga Harbour, an ecologically and culturally important estuary in New Zealand, where the impact of two dominant infaunal bivalve species on ES is considered. The intertidal venerid littleneck clam *Austrovenus stutchburyi* and the subtidal mesodesmatid clam *Paphies australis* are chosen to assess the impact of functionally similar species occupying different habitats on ecosystem functioning and ES. The thesis concludes with a general discussion (Chapter 6) where I focus on the variability in ES and the non-linear scaling from ecosystem functions to ES, and the implications for environmental management. The specific aims and objectives for each research chapter are described below.

1.2.1 Chapter 2

This chapter aimed to identify the range of services provided by bivalves and group these services in bundles based on similarities in underpinning ecological mechanism(s). Via a literature review, links between processes, ecosystems functions and services were identified based on the current ecological understanding of the roles bivalves play in estuarine ecosystems. This information can then be used to identify shared mechanism that underpin multiple services, which can be grouped together in bundles of associated ES. This study focused on the synergies and trade-offs between services from a qualitative perspective, and stressors impacting ES bundles. Identifying bundles based on existing literature increases our theoretical understanding of multiple ES supply and their interactions and addresses process-based multifunctionality of ES.

1.2.2 Chapter 3

In this chapter I aimed to empirically quantify ES related to water quality regulation by measuring a number of ecosystem functions that directly underpin this service. To do this, I designed an *in situ* field study to measure functions and quantify services comparing an intertidal and subtidal community dominated by different species of suspension-feeding bivalves. In this study, I quantified the contribution of naturally occurring shellfish beds to EF and ES by studying their effect on nutrient processing, water clarity improvements and primary production. Obtaining measures on the amount of services provided by key species occupying different parts of the estuary helps identify under what circumstances these services are provided and help quantify the contributions to human derived benefits of water quality regulation.

1.2.3 Chapter 4

Many ecosystem functions are density-dependent, and hence having reliable spatial predictions of species density is a key prerequisite for mapping ES in marine environments. The aim of this study was to create spatial predictions of the occurrence and density of two infaunal bivalves in Tauranga Harbour (New Zealand). Species Distribution Models (SDMs) were used to study the links between the environmental conditions under which the species can be present and in what densities, derived from estuary-wide surveys. These models are then used to predict occurrence and density at unsampled locations by interpolating the models on the available environmental data throughout the estuary. In my approach, I focus on *Austrovenus* and *Paphies*, which have contrasting habitat associations, to show the importance of density predictions over those using occurrence alone, and determine uncertainty in model predictions to inform spatial management.

1.2.4 Chapter 5

This chapter focussed on the spatial distribution of services across an estuary, by semi-quantitative modelling of ES, using an *ecosystem principles approach* (EPA). Insufficient data are available to confidently quantify ES in marine environments, and ecosystem function quantification from field studies are often context specific and cannot always be scaled up beyond the relatively small scale of the study. My aim was to provide insight in the locations of relatively high service delivery instead and compare areas of interest and interactions for four ES: provision of food, water quality regulation, nutrient removal, and sediment stabilisation, thereby demonstrating a way of scaling up ecological findings to ES without using time consuming, data intensive numerical modelling. Many underpinning processes and ecosystem functions are density dependent and vary with environmental variables. Services were therefore mapped using the shellfish density maps generated in Chapter 4, and by deriving generalised principles that link ecological mechanisms to density and environmental variables (based on findings in Chapter 2 and 3). Spatial analyses were conducted to assess patterns in individual service supply areas, followed by hotspot analysis to assess overlap and congruence between multiple services. Furthermore, I discussed the effect of species habitat association on heterogeneity in ES provision at a scale appropriate for local management. This furthered our knowledge on spatial interactions between multiple services and contributed in identifying areas of interest for marine spatial management.

Each research chapter contributed to the overall aim of assessing how ecological mechanisms could be applied to further our knowledge of interacting ES in data-scarce environments. Different assessment types (e.g. conceptual, quantitative, and spatial assessments) were applied to determine the versatility of ecological mechanisms as a tool for ES assessments and the variety of information that can be gained. Although different in their approach, the overlapping concepts and focus species (marine bivalves) of the studies in this thesis link the research chapters together (Figure 1.1). Chapter 2 and 3 both focussed on applying the known links between processes and functions to assess ES. Similarly, these mechanisms were at the core of both conceptual bundle formation in Chapter 2, as well as the ecological principles identified in Chapter 5 (see also Appendix 4). Ecological processes and functions are known to be density dependent (Chapter 3 and 4) and vary based on environmental characteristics and context (Chapter 4 and 5) thereby resulting in spatial heterogeneity of ES. Each chapter contributed insights to improved coastal management (EBM and MSP) through the ES framework, which is at the core of my thesis (Figure 1.1).

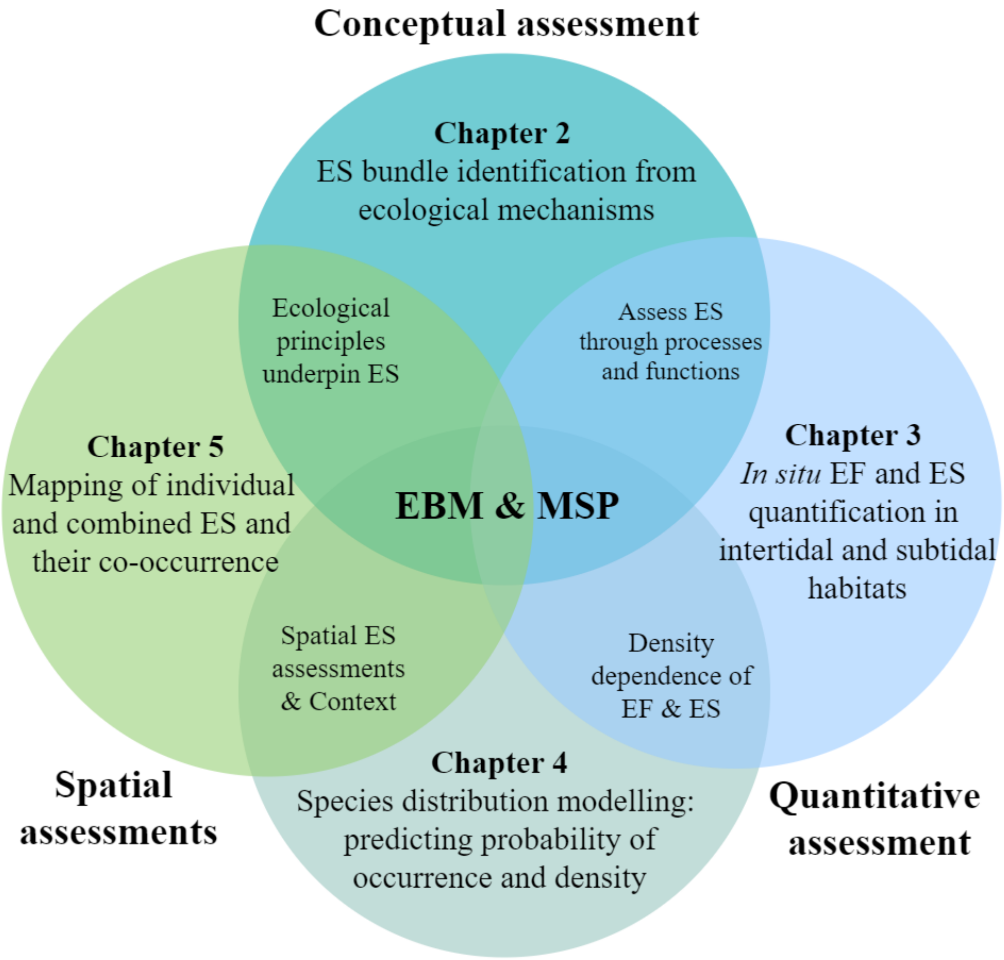

Figure 1.1 Venn diagram of the connections between research chapters focussed on the assessments of ecosystem services (ES) through processes and ecosystem functions (EF). At the core of all research chapters lies their implications for ecosystem-based management (EBM) and marine spatial planning (MSP) in coastal ecosystems.

CHAPTER 2

Ecological mechanisms underpinning ecosystem service bundles in marine environments – a case study for shellfish

2.1 Introduction

Ecosystem services (ES) are a means of linking the natural environment to various benefits that humans are able to extract, utilize or experience (Daily 1997, MEA 2005, De Groot et al. 2010b). This explicit recognition can facilitate improved environmental resource management. To implement this concept, it is important to understand how the structure, processes and functions of ecosystems relate to the generation of different services (Müller and Burkhard 2007, De Groot et al. 2010b, Quintessence 2016, Culhane et al. 2018). These relationships are numerous and complex and do not necessarily show a one-to-one correspondence, as exemplified by Snelgrove et al. (2014) who showed the multiple, complex linkages between biodiversity, processes, functions and services for seafloor environments. On top of this complexity, processes span multiple spatial and temporal scales, which affect where, when, and how services are delivered (Raffaelli and White 2013). Bennett et al. (2009) provided a typology for ecosystem services relationships, including the impact of drivers on multiple ecosystem services as well as the level of interactions, thereby demonstrating the need to study multiple, rather than individual services. Hence, understanding the relationships between services (effectively their inter-dependence and collinearity) has been proven important (Bennett et al. 2009, Lester et al. 2013, Howe et al. 2014) and resulted in the development of the ES bundles concept (Raudsepp-Hearne et al. 2010). Ecosystem services bundles, defined as "sets of associated services that appear together repeatedly across space and/or time" (Raudsepp-Hearne et al. 2010) allow the assessments of trade-offs and synergies among services in complex and changing environments.

Most work to date on ES bundles has focused on terrestrial environments, using cluster methods to identify spatial patterns in service delivery (Raudsepp-Hearne et al. 2010, Turner et al. 2014, Queiroz et al. 2015). However, marine, and especially estuarine and coastal environments, provide ecosystem services that need to be strategically managed to ensure sustainable use (Barbier et al. 2011). Studies in the marine environment are fewer than those of terrestrial systems as a result of data scarcity, and complications arising from system complexity and connectivity, spatial scales and context, and the 3-dimensional use of these environments (Guerry et al. 2012, Townsend et al. 2018). Even though the importance of understanding links between biodiversity, ecosystem function and service delivery is emphasized (Kremen 2005, Haines-Young and Potschin 2010, Nagendra et al. 2013), few studies have been able to incorporate this in ES identification and quantification. In terrestrial systems, functional traits of plants have been used as a way of including ecological mechanisms in determining ecosystem service delivery (de Bello et al. 2010, Lavorel et al. 2011, Lavorel and Grigulis 2012, Lamarque et al. 2014). While research in the marine environment has focused on the links between biodiversity and ecosystem functions (Solan et al. 2006, Stachowicz et al. 2007, Gamfeldt et al. 2015), links to ES and especially bundles of services in this environment remain unclear.

The idea of bundles of services, whether or not ecologically underpinned, is useful for resource managers, policy makers, communities and as an interdisciplinary tool helping stakeholders understand the value of multiple services. Work on individual and multiple ecosystem services in the marine environment can be used to inform Ecosystem Based Management (EBM) and Marine Spatial Planning (MSP) (McLeod and Leslie 2009, Granek et al. 2010, Lester et al. 2013). Application of the ES bundle approach and understanding the underpinning ecology can facilitate sustainable management of resources, a key aspect of current and future marine management to ensure the continuation of the services they provide (Martínez-Harms and Balvanera 2012). It will also contribute to conservation of biodiversity and ecosystem resilience to prevent tipping points in ES provision (Bennett et al. 2009, Maes et al. 2012b). Loss of ecosystem services has been a key motivation for ecological restoration of degraded habitats (Bullock et al. 2011). For example, shellfish beds and reefs have degraded globally (Beck et al. 2011), which has resulted in negative impacts on environmental health (Grabowski and Peterson 2007) and recovering lost ecosystem services has motivated shellfish restoration efforts (Coen and Luckenbach 2000, Cerco and Noel 2007, Coen et al. 2007, Schulte et al. 2009, Beck et al. 2011). Shellfish provide a number of ecosystem services beyond the provision of food, including regulating services like water quality regulation, and sediment or shoreline stabilization, as well as a number of habitat and supporting services, such as habitat provision and increasing biodiversity (Figure 2.1) (Grabowski et al. 2012, van der Schatte Olivier et al. 2020). Thousands of ecological studies world-wide provide insight in the structure and

Figure 2.1 Examples of ecosystem services provided by shellfish; (A) recreational gathering of shellfish for food [NZ Story], (B) mussel (*Perna canaliculas*) aquaculture [Chris Woods], (C) habitat provision by horse mussel (*Atrina zelandica*) beds [Simon Thrush], (D) infaunal shellfish (*Austrovenus stutchburyi*, *Macomona liliana*) as a food source for stingrays on the intertidal sandflat [Helen Cadwallader] (E) sediment and shoreline stabilisation by artificial oyster (*Crassostrea gigas*) reefs [NIOZ, EcoShape] and (F) water clarity improvements and contaminant removal through filter feeding, comparing aquaria with (right) and without (left) shellfish (*Austrovenus stutchburyi*) [Vera Rullens].

processes created and altered by shellfish. However, the multitude of services they provide have not been explicitly linked back to these linkages in underlying functions and processes, nor have interactions between services been studied.

The aim of the current study was to review the ecological mechanisms that underpin service delivery to determine ES bundles, applied to shellfish dominated systems as a case study. Shellfish-associated processes and functions were then linked to ES to investigate the potential for complex interactions. The role of shellfish in estuarine and coastal environments, and how they affect ecosystem functions, has been studied extensively, although our understanding of how services are generated and what drivers or stressors might affect them remains unconsolidated. This work will enable investigations of the interactions between services, including the potential for tradeoffs and synergies within and between bundles. This provides an example of a different approach identifying ES bundles in data-sparse (marine) environments and could be applied to other habitats or key species where sufficient ecological knowledge is available to elucidate these linkages and relationships. The approach is novel as it shifts towards a focus on ecological processes driving services supply, and provides a format useful for ecologists, managers and other stakeholders to translate and generalize ecological knowledge into the ecosystem services framework.

2.2 Methods

2.2.1 Scope of review

To explore the complex linkages and interactions between processes, functions and services, a literature review was conducted to extract the current ecological knowledge on the mechanisms that underpin shellfish service delivery. The aim of this review was on the higher-level ecological mechanisms, with a focus on well-understood, generalizable concepts, and on elucidating the key linkages in service generation. Although there are thousands of peer-reviewed ecological publications that focus on shellfish, we limited our review to studies specifically targeting ecosystem functions and services. In this study, shellfish habitats are defined as a location where shellfish dominate the benthic biomass, and function as ecosystem engineers (*sensu* Jones et al. 1994). Both epifaunal reefs and infaunal shellfish beds are therefore considered, as both can significantly create, modify, and maintain habitats, thereby changing the physical state of the environment, controlling the availability of resources to other species, and affecting the ecosystem functioning of the system at a scale larger than the habitat itself (Jones et al. 1994, Gutiérrez et al. 2003, Bouma et al. 2009). In addition to natural habitats (reefs and beds), studies that focused on highly modified (aquaculture) settings were also included within this review.

2.2.2 Literature review details

This research was based on findings reported in 146 peer-reviewed papers. Papers were derived from a literature search in ISI Web of Science database (December 2017), using combinations of search terms applied to title, themes, and abstracts. The search terms used included combinations of either “Ecosystem service” or “Ecosystem function” with a search term for shellfish, i.e. “Shellfish”, “Bivalve”, “Clam”, etc. In total, 202 papers matched these search criteria, which were then screened for relevance based on title, abstract and/or paper content. Papers were excluded if they were not specific to marine shellfish, did not focus on the links between shellfish and processes that affect functions or service delivery, or were not focused on current studies in estuarine or coastal habitats (i.e. excluding for example paleo-ecological studies, or studies in deep-sea or polar environments).

The resulting 146 papers were reviewed to extract general information on study type (e.g. experimental, observational, review) and provide an overview of what was studied, where and when, the species and environment studied. Specific emphasis was placed on the species type, categorized for ‘epifaunal suspension feeders’, ‘infaunal suspension feeders’, ‘infaunal deposit feeders’ and the more general ‘bivalves’ if not further specified. Emphasis is placed on these distinct groups as they affect ecosystem functioning differently, driven by their feeding mechanisms (suspension vs. deposit) and position in or on the sediment (infaunal vs. epifaunal respectively). The list of presented services was not specified prior to the review but was guided by the literature to ensure all those discussed were included. Shellfish not only provide “final” services that can be directly utilized (Fisher et al. 2009), but also a number of “intermediate” (or supporting) services that contribute to maintaining high-level functioning and resilience of coastal systems, which were included to maintain the nuances found in the reviewed literature. Services indirectly provided by other species or habitats that flow on from the supporting services provided by shellfish were beyond the scope of this paper. This resulted in the inclusion of two provisioning services, five regulating services, and five habitat & supporting services (Table 2.1). To allow comparison with more generalized frameworks, the TEEB classification categories (De Groot et al. 2010b) are included in Table 2.1 for these services. Cultural services were excluded as they are more subjective and context specific, and are

Table 2.1 Overview of the ecosystem services found in the reviewed literature as function of service category. The ecosystem services are aligned to the TEEB categorization (De Groot et al. 2010b) to enable comparison with a more general framework.

Category	**Ecosystem service**	**TEEB category**
Provisioning services	Provision of food	Provision of food
	Provision of material	Provision of raw materials
Regulating services	Water quality regulation	Wastewater treatment
	Nutrient removal	
	Pollutant removal	(Carbon sequestration and storage)
	Pathogen removal	Biological control
	Sediment stabilization	Erosion prevention
	Shoreline stabilization	Moderation of extreme events
Habitat and supporting services	Habitat provision	Habitat for species
	Biodiversity	
	Sediment biogeochemistry alterations	
	Foodweb structure	

strongly underpinned by social variables, like identity, country of origin, ethnicity, religion, and income level (Stephenson 2008, Dickinson and Hobbs 2017), rather than the ecological processes and functions that this review targeted.

The main focus of the review was to establish the links between processes, functions, and services, which were documented for each paper in the review. Most papers discussed only one ecosystem function or service; hence they were documented as one input that described the identified link between process-function-service. A number of studies discussed multiple services and links with processes and functions that needed to be summarized. When studies discussed multiple services resulting from the same underpinning processes and functions, their input was as one, while if they were underpinned by different processes, they were treated separately. For example, if a paper included information on how filter feeding affects both the services of water quality regulation, and nutrient cycling/removal, this was considered one input. However, if they studied two services that were underpinned by different processes, like growth underpinning food provision, and filter feeding underpinning water quality regulation, these were considered as two separate inputs from the same paper. Furthermore, for each paper, the main driver or stressor was noted as well as their impact on service delivery (positive, negative, or neutral) with further explanations.

2.2.3 Bundle identification, cascades, and interactions

The links identified between processes, functions, and services (Appendix 1) formed the basis for bundle identification. Linkages were quantified per service in terms of the number of papers discussing a specific link (Table A1). Links were included if described in three or more papers and if they were well established and understood. If the same linkage was found for more than one service, these services were grouped together to form the initial bundles. Once grouped, all included linkages were examined for similarities in their effects on the services and the services within each group for their co-occurrence to form the four final bundles. Each service was only categorized for one bundle, but underpinning processes or functions could be used more than once, due to the ecological complexity of the system and key processes provided by shellfish. Overlapping processes and/or functions were therefore allowed, if their effects on service delivery differed, for example, biological vs. physical effects. Each of the identified bundles contained two to four services and were underpinned by key processes and functions. To provide more detail about the ecological mechanisms behind each of the bundles, the underpinning processes and functions were mapped and simplified to represent the main links from the literature to the provisioning of the services in cascade diagrams. In the section on ‘ES bundles for shellfish’ below, the four bundles are described, followed by further explanation and examples of the mechanisms generating them.

Even when services are bundled, they are not completely independent, as interactions i.e. synergies and trade-offs, between bundles are still possible. Synergies are defined as “a situation where the use of one ES directly increases the benefits supplied by another service”, while trade-offs are defined as “a situation where the use of one ES directly decreases the benefits supplied by another” (Turkelboom et al. 2015). A subset of the data was used to study these interactions, by including those that look at multiple services from different bundles, which could be underpinned by the same process and function, in which case they are considered as ‘interactions’, or those that were treated separately, as explained above. In some cases, a service was mentioned as a driver or stressor of another service, in which case they were also included in the subset looking at interactions. For example, aquaculture was considered as the main driver or stressor of the delivery of other services, whilst not discussing the provisioning benefits generated by aquaculture itself.

2.3 ES bundles for shellfish

2.3.1 Ecosystem services bundles

From the obtained linkages in the literature review, four bundles of services are identified for shellfish (Figure 2.2) based on 21 key linkages (Table A1). The first bundle, *Marine resources*, contains all services related to the provision of goods, including food and shell material. In total, information from 25 papers is included in this bundle, mainly with a focus on the provision of food (24 papers total) from either natural environments (11 papers) or artificially through aquaculture (13 papers). The second bundle, *Coastal health and quality*, includes the effects of shellfish on water quality regulation and the removal of contaminants from the water, including nutrients, pollutants and pathogens. Data from 51 papers supports the linkages for this bundle, with the majority of papers focusing on water quality regulation (27 papers) and/or nutrient cycling/removal (25 papers), while less emphasis is placed on removal of other pollutants (9 papers) and pathogens (4 papers). The *Habitat modification* bundle includes the physical effects shellfish have on the environment, through their role as ecosystem engineers,

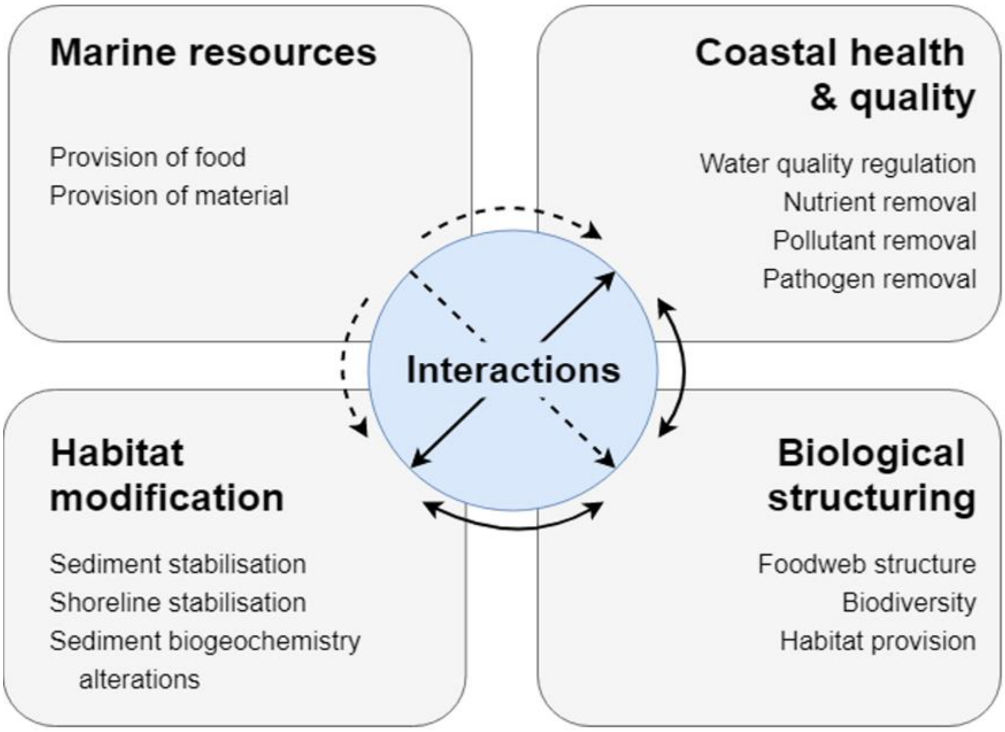

Figure 2.2 Bundles of ecosystem services provided by shellfish. Each box contains the services grouped for the respective bundles. Arrows between bundles in the center of the figure indicate the interactions between bundles either as synergies (black bi-directional arrows) or trade-offs (dashed one-directional arrows).

as discussed in 44 papers. This includes their effect on stabilizing shorelines (6 papers) and sediments (7 papers), and their effect on altering sediment biogeochemistry (25 papers). The final bundle *Biological structuring*, includes the services by which shellfish have biological effects on the environment by supporting other species and communities. This is based on data from 54 papers, that demonstrate shellfish providing habitat (22 papers), altering biodiversity (26 papers) and food web structure (19 papers), which results in and contributes to the intrinsic value and resilience of the system.

2.3.2 Linkages cascades per bundle

Marine resources

The *Marine resources* bundle is underpinned by three main processes: shellfish survival, growth, and recruitment, which determine the amount of biomass generated in the system that can be harvested (Figure 2.3). In the review, 15 papers described the contribution of biomass production to the delivery of goods. Food provision (i.e. the production of edible shellfish biomass) is strongly dependent on the biomass produced in a system and the production yield in a region. Biomass can be harvested through commercial or recreational collection of natural populations, or from artificial (aquaculture) set-ups specifically aimed to grow shellfish as a food source. Aquaculture examples are discussed where shellfish are viewed as being increasingly important for the production of proteins and thereby as an alternative for exploiting natural resources (Kluger et al. 2017), resulting in benefits to local economies and employment (Ferreira and Bricker 2016). In some cases, invasive species are used for aquaculture (Ruesink et al. 2006, Humphreys et al. 2015), where the annual yield generated by these species can exceed the historical landing of native species (Ruesink et al. 2006). Limited information was available in the review on the provision of material, except for some papers discussing shell formation. Shell formation and calcification were discussed in relation to the impact of ocean acidification and thermal stress, which have a negative impact on shell growth and thickness (Hiebenthal et al. 2013, Lacoue-Labarthe et al. 2016), that not only affects the provision of materials but could also impact bivalve fisheries revenues (Marshall et al. 2017).

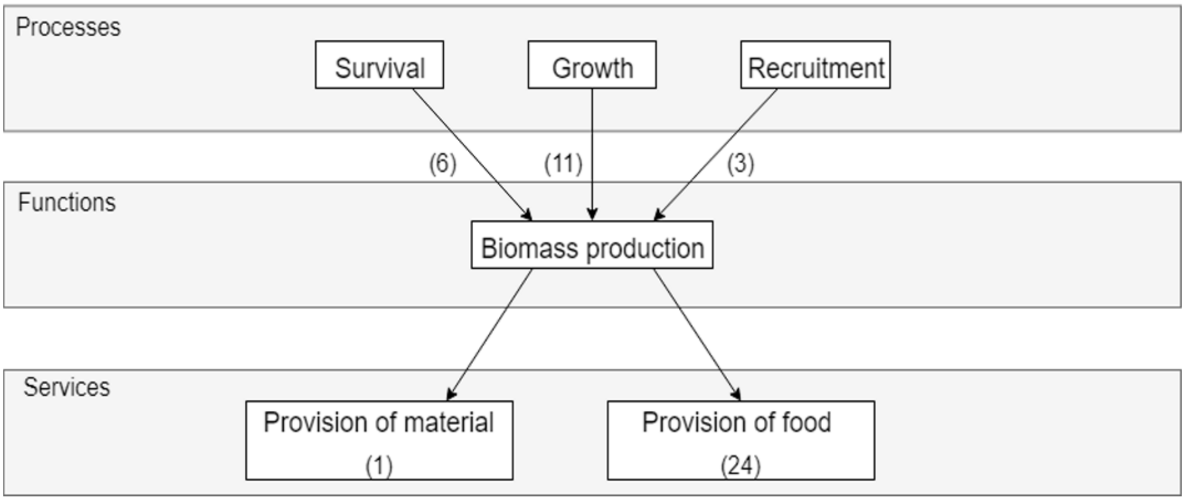

Figure 2.3 Simplified cascade showing the links between processes, functions and services in the *Marine resources* bundle. The number of papers discussing a service is indicated in brackets within the service box, while the number of times links between processes and functions were discussed is indicated in brackets next to the arrows.

The effect of growth was discussed 11 times as the underpinning process for this bundle, where growth rates of shellfish determine how much biomass is generated over time, with higher growth rates resulting in higher service delivery. Growth rates are dependent on environmental variables and can vary temporally (Li et al. 2012) and spatially, as is shown for mussels along the Swedish coast (Bergström et al. 2015) where models and empirical studies were used to spatially determine growth rates over a two-month timeframe. Survival (or mortality) of shellfish affects the amount of biomass available, as discussed in six reviewed papers, where high survival rates result in greater service delivery. Stressors generally have a negative impact on survival rates. For example, emergence of infaunal shellfish from the sediment when stressed by macroalgal blooms or hypoxia, and physical distress from high temperatures can alter mortality rates (Lewis and DeWitt 2017). Disease outbreaks (Wilkie et al. 2013) can affect survival rates of farmed and wild shellfish populations, but also could make them unsafe for harvest and human consumption, thereby resulting in a loss of value. Finally, recruitment of juveniles affects biomass production, particularly in restoration areas (Marsden and Adkins 2010). The methods used for harvesting can also affect recruitment, where Toupoint et al. (2016) show that hand raking, a method of recreational harvesting, inhibited primary recruitment, whereas aquaculture promoted primary recruitment intensity.

Coastal health and quality

The key process underpinning the *Coastal health and quality* bundle is filter feeding by shellfish, as discussed in 38 out of 51 papers for this bundle. Through filter feeding, shellfish act as biofilters, removing suspended particles from the water column, thereby affecting all services in this bundle (Figure 2.4). Water quality regulation is the service most frequently discussed in the scientific literature (27 times), with a strong focus on epifaunal-suspension feeders (e.g. oyster and mussel reefs). By removing phytoplankton and suspended sediments from the water column, filtration improves water clarity by reducing turbidity and increasing light penetration. This, together with the effect shellfish have on the exchange of biomass, energy, or nutrients between the sediment and water column, i.e. benthic-pelagic coupling, results in the service of water quality regulation. Filtration rates are size and density dependent, and depend on a number of variables including phytoplankton, organic matter or seston concentrations (MacDonald and Ward 2009, Galimany et al. 2017b), temperature (Zu Ermgassen et al. 2013a), dissolved oxygen, and turbulence (Li et al. 2012). A number of studies have focused on the effect of oyster reef declines and restoration effort on filtration rates. For example, an 80% decline in filtering capacity was found when comparing past and

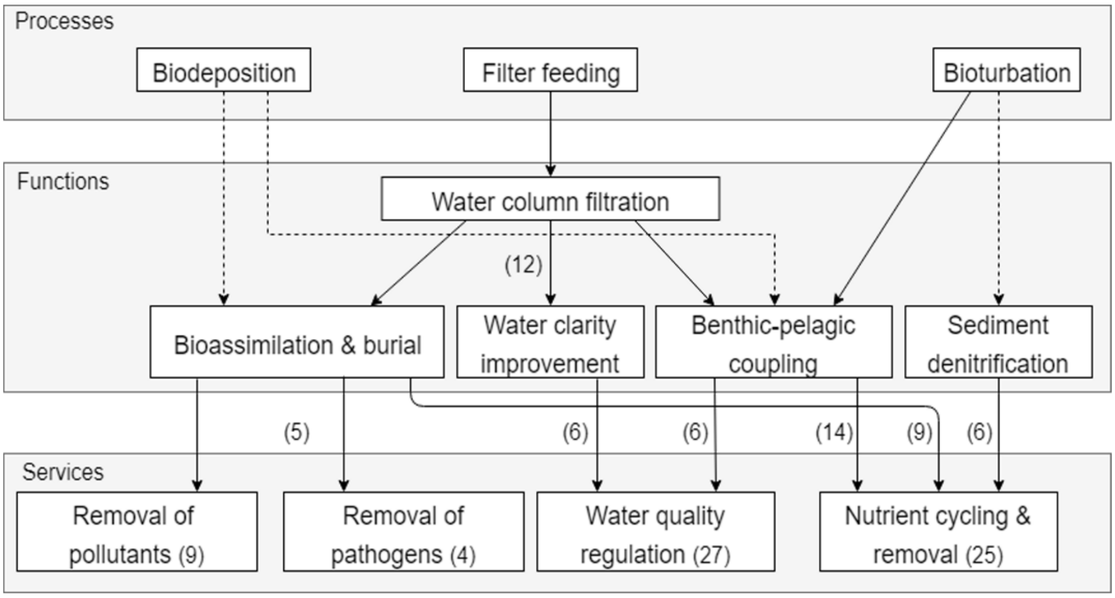

Figure 2.4 Simplified cascade showing the links between processes, functions and services in the *Coastal health and quality* bundle. The number of papers discussing a service is indicated in brackets within the service box, while the number of times links between processes and functions were discussed is indicated in brackets next to the arrows. Dashed lines indicate links that are inferred from expert knowledge.

present situations in Chesapeake Bay (Zu Ermgassen et al. 2013b) and restoration of reefs can help regain lost services (Coen and Luckenbach 2000, Grizzle et al. 2008, Baggett et al. 2015, Milbrandt et al. 2015). Filtration rates for invasive versus native species were compared, where invasive mussels were more efficient than native species that occupied similar niche space (Galimany et al. 2017a) thereby outcompeting them (Ruesink et al. 2006).

Benthic-pelagic coupling drives both water quality regulation, as well as nutrient cycling and removal. Shellfish contribute to benthic-pelagic coupling through filter feeding, by moving particles from the water column to the sediment as biodeposits (Kent et al. 2017a) and can alter pelagic community structure and trophic interactions in the system (Orlova et al. 2006, Sunda et al. 2006, Filgueira et al. 2016). Biodeposition by both suspension and deposit feeders also increases sedimentation rates and modifies the physical, chemical, and bacterial composition properties of settling particles (Karlson et al. 2010, Kanaya 2014) altering rates of nutrient cycling (including denitrification) and burial (Cerco 2015, Kent et al. 2017a). Modifications in the physico-chemical benthic environments, through for example bioturbation, can affect the cycling and removal of nutrients by affecting ammonia fluxes at the sediment water interface (Thrush et al. 2006, Jones et al. 2011a, Filgueira et al. 2016, Lohrer et al. 2016) and denitrification in the sediment that removes bio-available nitrogen from the system to the atmosphere (Kellogg et al. 2013, Cerco 2015, Welsh et al. 2015). Nutrient cycling and removal is also affected by bioassimilation of nutrients in tissue and burial of organic matter, as well as nutrient excretion by shellfish. A number of studies quantify nutrient removal from the system through assimilation in tissue or shell and often in relation to aquaculture settings (Sebastiano et al. 2015, Galimany et al. 2017c). Eutrophication can have direct negative impacts on estuarine ecosystems through phytoplankton blooms, as well as indirect effects on denitrification, some of which could be mitigated by bivalve filter feeding through phytoplankton biomass control and should be considered in management decisions (Ferreira and Bricker 2016).

The removal of pollutants and pathogens from the system is also linked to bioassimilation and burial (Figure 2.4). Bivalves can act as a filter for bacteria and contaminants thereby removing them from the system (Volety et al. 2014, Broszeit et al. 2016). Once ingested, toxins or bacteria can either be assimilated in tissue or discarded in biodeposits that are buried in the sediment. Burge et al. (2016) reviewed the role of filter feeders on pathogen removal through augmentation and reduction, with emphasis on the role of bivalves. Their findings suggested that the effects of filter feeding on pathogen transmission and disease risk can be either positive or negative depending on the bivalve and pathogen specific selectivity or mechanisms. Pathogens can be removed from the system by degradation and released in biodeposits. If pathogens are able to resist degradation and are bioassimilated, this can pose a threat to humans and wildlife upon ingestion through biomagnification. Bivalves can remove a number of pollutants from the system by bioremediation of wastes (Broszeit et al. 2016) and biotransformation of contaminants that alter their bioavailability (Montes et al. 2012). As a result of the bioassimilation in tissue, shellfish are often considered as bioindicators of toxins in estuarine habitats (Chapman et al. 2013, Burge et al. 2016). Carbon sequestration is a form of pollution removal occurring on a much longer temporal scale but is underpinned by the same processes and functions of bioassimilation and burial. A couple of examples were found in the literature showing how shellfish can contribute to carbon removal through burial (Cerco 2015) or through carbon sequestration in shells (Talmage and Gobler 2010, Volety et al. 2014).

Habitat modification

Habitat modification is linked to the role of shellfish as ecosystem engineers, where they modify habitat by interacting with the physical environment around them (Figure 2.5). Infaunal shellfish interact with their environment mostly by bioturbation, thereby reworking the sediment (supported by 9 papers), whereas epifaunal shellfish do so by reef formation (supported by 6 papers). Sediment reworking by infaunal shellfish drives a number of ecosystem functions and the resulting services of sediment biogeochemistry alterations and sediment stabilization (as discussed in 24 and 7 papers respectively). Shellfish alter sediment biogeochemistry through the burial of organic matter to depth (Maire et al. 2006, Sousa et al. 2009, Kanaya 2014), cause changes in benthic metabolism and nutrient fluxes between the sediment-water interface in soft sediment-habitats (Rossi et al. 2008, Sandwell et al. 2009, Lohrer et al. 2010, Lohrer et al. 2012, Norkko et al. 2013, Premo and Tyler 2013) , as well as changes in the Redox Potential Discontinuity Layer depth (Clare et al. 2016). Sediment biogeochemistry alterations are affected by key species composition (Michaud et al. 2009) and density (Sandwell et al. 2009, Clare et al. 2016, Sospedra et al. 2017), predator presence affecting burrowing behaviour (Maire et al. 2010) and feeding behaviour or the availability of food (Maire et al. 2006, Karlson et al. 2010). This supporting service is important in soft sediment habitats as it affects productivity and overall condition of the system but is susceptible to a number of physical stressors. Terrestrial sediment deposits of a couple of mm can have a

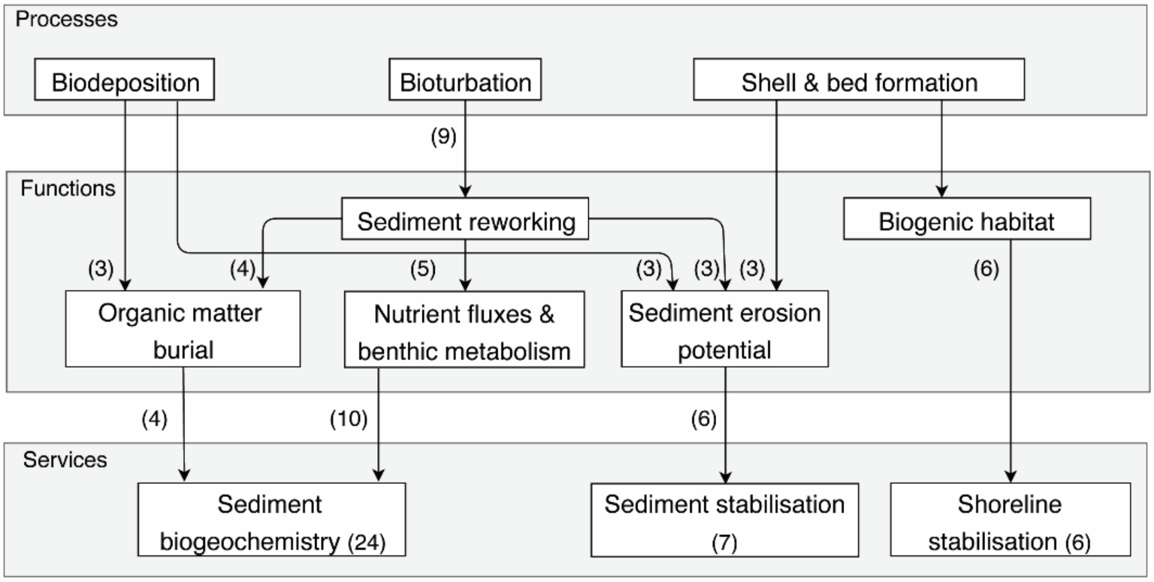

Figure 2.5 Simplified cascade showing the links between processes, functions and services in the *Habitat modification* bundle. The number of papers discussing a service is indicated in brackets within the service box, while the number of times links between processes and functions were discussed is indicated in brackets next to the arrows.

significant effect on this service (Pratt et al. 2014a), as not only will the deposition alter physical properties of the sediment but has also been shown to cause subtle changes in behaviour of adults and juvenile shellfish (Hohaia et al. 2014, McCartain et al. 2017). Similarly, smothering or hypoxia can greatly impair the benthic communities, and in particular shellfish, and their ability to contribute to sediment oxygen and nutrient fluxes (Rossi et al. 2008, Lohrer et al. 2010, Villnas et al. 2012).

Through sediment reworking, the sediment erosion potential is altered by changes in near-bed flow dynamics, sedimentary properties (e.g. grain size distribution, microbial activity) and bottom roughness (Sousa et al. 2009). The effect shellfish have can be either stabilizing or destabilizing, depending on a number of factors, including densities, size distribution, patch scale, etc. Eriksson et al. (2010) show that the effect on sediment stability can be species dependent, where they found a stabilizing effect at high densities of oysters, mussels and cockles in a pre-disturbed scenario, whereas deposit feeders (lugworms) resulted in sediment destabilization in a human disturbed scenario. Similarly, Harris et al. (2015), found differences between juvenile and adult *Macomona liliana* (deposit feeding shellfish), where adults had a stabilizing effect on the sediment, compared to juveniles, indicating a shift in species functioning. Through biodeposition and mucus production, sediment erosion potential can also be reduced (Donadi et al. 2013), as discussed in three papers. Six papers look into the effects epifaunal bivalves have on shoreline stabilization by reef formation, thereby creating biogenic habitat (Brumbaugh and Coen 2009) and form natural breakwaters and reduce wave attenuation. Oysters can be used as living shorelines to improve shoreline protection by reef restoration efforts (Baggett et al. 2015) or through creating artificial breakwaters from oyster shell bags. These breakwaters have been shown to provide similar shoreline stabilizing services, but also create more habitat for other species, compared to other artificial breakwaters (Scyphers et al. 2015).

Biological structuring

Shellfish provide a number of supporting services by biological structuring in estuarine and coastal habitats (Figure 2.6). By supporting and altering species and communities, these services contribute to the intrinsic value of the system and make them more resilient to change. Both infaunal and epifaunal shellfish contribute to habitat alterations and have been shown to be habitat providers, as discussed in 22 papers. Most of this service is attributed to epifaunal shellfish that alter and provide habitat through the formation of reefs (15 papers). Reefs can result in the creation of refuge, feeding, or nursing habitats (Guidetti and Boero 2004, Coen et al. 2007, Volety et al. 2014). Dinesen and Morton (2014) describe the habitat provided by horse mussel reefs, that create 3 layers of habitat, with the first layer residing on the shell debris, the second layer for mobile megafauna and the third layer for mobile or sedentary macrofauna that live in the crevices. Reefs form refuge areas from predation for other bivalves (Glaspie and Seitz 2017) or benthic macroinvertebrate species (Micheli and Peterson 1999) and juvenile fish. An important indirect service resulting from nursery and feeding habitat provided by shellfish is increased secondary production of higher tropic levels, such as fishes and crabs (Coen et al. 2007, Volety et al. 2014), that if harvested, indirectly result in increased food provision (Kent et al. 2017b). Infaunal shellfish also alter and provide habitat (as discussed in four papers) through creating colonizable substrate from shells (Sousa et al. 2009) and by sediment reworking. An example of the latter is the work by (Queiros et al. 2011), showing that the invasive Manila clams can modify the functioning of the invaded system through their effect on sediment reworking by bioturbation. Thereby they can provide variability in habitat characteristics and community composition. These effects can be context dependent, as they can be mediated by structuring vegetation, or sediment granulometry and compaction (Queiros et al. 2011).

As discussed in 11 papers in the review, habitat alterations are crucial for increasing biodiversity (Coen and Luckenbach 2000, Volety et al. 2014, Kasoar et al. 2015, Gittman et al. 2016, Kent et al. 2017b). Shellfish have been shown to have positive effects on biodiversity in the system, by altering both macrofauna and microbial communities. A number of papers (nine) have shown the link between shellfish and community composition alterations in general, showing changes in community assemblages (Kluger et al. 2016), species richness, abundance and biomass (Quan et al. 2012, van der Zee et al. 2015). The majority of the papers focused on the changes in macrofauna (invertebrate) or meiofauna communities or fish population dynamics (Boldina et al. 2014, Winberg and Davis 2014, Van Colen et al. 2015). There are some examples of how shellfish affect microbial communities also, for example, Deng et al. (2015) show that the presence of ark shells resulted in higher archaea diversity in intertidal sediments, and Liu et al. (2009) show that clam culturing systems have an effect on both microbial and macrobenthos biomass and diversity. Stressors can have negative effects on community composition and biodiversity, as is shown for anoxia effects (Riedel et al. 2014) and extreme flooding in a eutrophication recovery site (Cardoso et al. 2008).

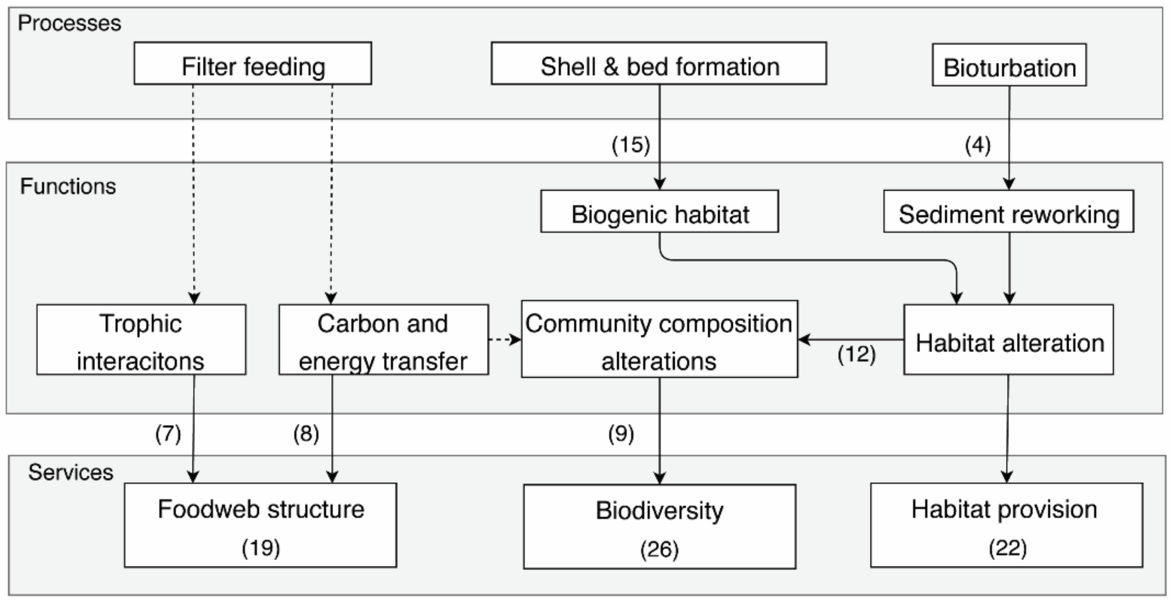

Figure 2.6 Simplified cascade showing the links between processes, functions and services in the *Biological structuring* bundle. The number of papers discussing a service is indicated in brackets within the service box, while the number of times links between processes and functions were discussed is indicated in brackets next to the arrows. Dashed lines indicate links that are inferred from expert knowledge.

Foodweb structure is affected by trophic interactions in the system and the transfer of carbon and energy from primary producers to higher trophic levels. Bivalves are primary consumers and form an important link between primary producers (either phytoplankton or microphytobenthos) and higher trophic levels (Vinagre et al. 2015), as they are an important food source for shorebirds (Caldow et al. 2007), fish and rays, thereby transfer carbon and energy up the foodweb. There are two possible pathways, benthic or pelagic trophic interactions, which can be determined using stable isotope data. Christianen et al. (2017) found that microphytobenthos was the main food source for *Limecola* (*Macoma*) *balthica* (a deposit-feeder), while suspension-feeding cockles had a pelagic food source. Shellfish can have significant impacts on the phytoplankton dynamics through their feeding, which can be affected by hydrodynamics, immersion time, and shellfish density (Grangere et al. 2010). Important also is the transfer of energy to benthic communities by organic matter deposition that can fuel microbial communities (Franzo et al. 2016). Non-consumptive interactions can also cause changes in foodweb dynamics, like mortality events (Long et al. 2014, Jones et al. 2016) or predation (Barrios-O'Neill et al. 2017).

2.4 Interactions

Even though services are bundled, there are still likely interactions between services across bundles which must be considered in their utilization and management. In the review, 37 papers considered interactions and 17 papers discussed multiple services. Understanding the interactions between services is key, which can manifest as either trade-offs or synergies (Figure 2.2) and are highly relevant for coastal management.

2.4.1 Trade-offs

Trade-offs are often found between provisioning and regulating/supporting or cultural services. In our study, this relates to the marine resources bundle, where nine papers looked at multiple services or interactions and an additional 12 papers included either aquaculture or fishing/harvesting as a driver or stressor of other services. The harvesting of biomass for either food or material will result in the loss of other services as shellfish are removed from the system. Furthermore, shellfish harvesting methods can have negative impacts on the delivery of other services. As Toupoint et al. (2016) demonstrated, recreational fishing can reduce primary recruitment intensity and fisheries can negatively affect biodiversity and foodweb structure through the effect on habitat provision. For example, a loss of nursery habitat on rocky reefs can affect fish population dynamics, through the dismantling of rocky substrate by date-mussel fisheries, thereby creating barrens, (Guidetti and Boero 2004), while clam digging can alter nematode and copepods aggregated in spatial structures (Boldina et al. 2014). We trade off the benefits generated for food and the economic value to the delivery of other services in natural systems, so we need to consider what is lost if shellfish disappear or become functionally extinct.

Aquaculture differs from the provision of food, as the active growing of shellfish for food will result in a different mixture blend and differing levels of service provision. Aquaculture is linked to services in the *Coastal health and quality* bundle (discussed in six papers), as their presence in the system will result in water filtration and removing particles, thereby positively contributing to the delivery of the services in this bundle (Grant et al. 2007). For example, Ruesink et al. (2006) discuss the use of invasive species for aquaculture, thereby generating food that exceeds the yield from historic landings and at the same time contributing to water quality regulation through filtration. Nutrient cycling and removal is affected by aquaculture through excretion (Filgueira et al. 2016) and the cycling and removal of nutrients from the system (Saurel et al. 2014). Shellfish from aquaculture can contribute to the mitigation of eutrophication symptoms by removing excess nitrogen (Sebastiano et al. 2015, Ferreira and Bricker 2016). However, these services vary depending on the age and biomass structure of the farmed population, and are only provided when the shellfish are present, and disappear when harvested.

Aquaculture is discussed (seven times) in the context of impacts on habitat provision and biodiversity. By creating new habitat, aquaculture settings can have positive impacts on biodiversity, as compared to open mudflats, with more diverse epibenthic organisms (Ruesink et al. 2006), as well as microbial communities (Liu et al. 2009). However, other examples exist describing negative effect of aquaculture on biodiversity (Bendell 2014), with a drop in primary producers and consumers in a 100-year scenario, resulting in a loss of resilience (Kluger et al. 2017). Another potential downside is that aquaculture may provide habitat or structure for undesirable invasive species or biofouling (Bendell 2014). Additional trade-offs may arise from indirect services that flow on from supporting services. For example, food provision can be increased indirectly through secondary production of harvested fish and crab species (Kent et al. 2017b). This is often a primary driver for shellfish restoration projects, but design considerations can contribute to trade-offs with other services, particularly in the *Habitat* *modification* bundle and water quality outcomes. Habitat provision from complex 3D reefs favor juvenile fish and invertebrate species (Coen et al. 2007) compared to shellfish beds and aggregations that allow for high shellfish densities. However, the exact degree in which habitat provision contributes to secondary production and resulting trade-offs will be dependent on the species present and the shapes or topography of the 3D structure and can vary geographically (Dinesen and Morton 2014).

2.4.2 Synergies

Synergies exist also, where the delivery of services enhances each other. For example, there is a strong link between sediment biogeochemistry alterations and nutrient cycling and removal (discussed in 17 papers). One of the key aspects related to sediment biogeochemistry is the exchange of nutrients across the sediment-water interface, as caused by sediment reworking. In soft sediment habitats, bioturbation by macrofauna enhances the release of ammonium from the sediment and oxygenates the sediment (Rossi et al. 2008, Lohrer et al. 2010, Wrede et al. 2017). A number of studies have looked at the effect of shellfish on nutrient exchange between the sediment and water column and included the effect of bivalve densities (Sandwell et al. 2009, Lohrer et al. 2016, Sospedra et al. 2017), or the effect of large adults by removing them (Thrush et al. 2006, Norkko et al. 2013). Furthermore, sediment denitrification, the function of removing bio-available nitrogen, is often strongly coupled with the oxygenation of the sediment. Through sediment biogeochemistry alterations, including organic matter inputs and sediment oxygenation, shellfish can enhance denitrification (Welsh et al. 2015).

Other key interactions are between biogenic habitat generation and a range of services. Biogenic habitat drives services in the *Habitat modification* bundle, by stabilizing sediments and shorelines, which again result in improved water clarity (as less sediment and particles will be re-suspended) and hence water quality in the *Coastal health and quality* bundle. Through shoreline protection, shellfish habitats can also contribute to the creation of new habitats, like seagrass meadows. One of the key linkages is between biogenic habitat or habitat alterations and biodiversity, as discussed above. Not only is this link discussed in a number of papers (12 times), but also reef restoration is often discussed as one of the key drivers for service delivery (nine times in the interaction subset). Habitat provision and alterations also interact with food web structure, as microbenthic engineering has been shown to help sustain the smaller components of the food web (Braeckman et al. 2011). Foodweb structure and biodiversity are also linked to sediment biogeochemistry alterations (Michaud et al. 2009, Kanaya 2014), nutrient cycling and removal by altering the structure of benthic and planktonic communities (Orlova et al. 2006, Compton et al. 2013), and water quality regulation by shellfish clearance rates (Jones et al. 2016).

2.5 Discussion

Our review provides a new approach in identifying bundles of ecosystem services, focused on the use of key linkages in elucidating the mechanisms underpinning these bundles. As opposed to the majority of work in the bundles literature (Spake et al. 2017, Saidi and Spray 2018), our work does not identify bundles as a spatial representation of where services are being delivered. Instead, its strength lies in providing a generalization of well understood ecological mechanisms resulting in bundle identification, without requiring any spatial or proxy data that is often lacking in marine environments (Guerry et al. 2012, Townsend et al. 2018). We were able to identify associated services, each underpinned by one or two key processes or functions. This information on mutual drivers will result in a better understanding on how services are generated and provide insight in interdependencies between services (Bennett et al. 2009, Wu and Li 2019).

However, as these bundles are never independent, and non-linear relationships are possible, interactions among services between bundles should also be considered (Barbier et al. 2008, Lester et al. 2013). As commonly found, provisioning services in the *Marine resources* bundle tend to generate trade-offs with other services, while synergies are mostly found between regulating and supporting/intermediate services in the other bundles (Lee and Lautenbach 2016). For terrestrial systems, biomass production generates trade-offs with other ecosystem functions, as they are underpinned by different ecosystem attributes (Wu and Li 2019). By including the effect of shellfish on biological structuring and habitat modification, the importance of intermediate services was captured for service supply. These services contribute to biodiversity effects and overall functioning and resilience of the system. Biodiversity has both intrinsic and utilitarian values contributing to human well-being (Haines-Young and Potschin 2010), and overall findings indicate positive, but complex, linkages between biodiversity attributes and ecosystem services (Harrison et al. 2014). Biodiversity loss in ocean ecosystems is reducing the oceans capacity to provide ecosystem services, like food provision and water quality regulation, as well as reduced recovery from perturbations and a loss in resilience (Worm et al. 2006).

Issues often identified for bundle methodology are related to location or context specific findings using clustering methods and a lack of causal understanding (Spake et al. 2017). This complicates cross-study comparisons, as studies are often conducted at different scales, studying different services and using different proxies or indicators for quantification (Grêt-Regamey et al. 2014, Rodríguez-Loinaz et al. 2015). This scale and context specificity could cause mismatches with management, and hence should be taken into consideration when used in decision making processes, as recommendations may be non-transferable or could affect management outcomes (Raudsepp-Hearne and Peterson 2016). Our approach provides an insight in the mechanism resulting in service provision and would therefore be more readily transferable. However, it does not quantify the amount of services generated, nor does it include where these services are being consumed or benefitted from. Flow of services from the place of supply to societal demand is important in marine ecosystems due to connectivity and complexity in structure and flow (through wind, currents, and tides) (Townsend et al. 2018).

Many ecological processes and functions are density and/or size dependent, often in a non-linear manner that have implications for service delivery. Shellfish densities can affect the provision of ecosystem services, where for example, a reduction in water column turbidity can be directly proportional to shellfish abundance (Newell 2004) if there is a linear scaling of filtration capacity, whereas a density threshold is predicted for nitrogen removal, as this service is reliant on the exchange across the oxic-anoxic sediment interface. Burrowing behavior and spacing by benthic macrofauna alters the amount of oxygen in the sediment. When a critical organism density is reached, surface area of the oxic-anoxic boundary is reduced across which exchange processes occur that are necessary for coupled nitrification-denitrification in sediments. Therefore, denitrification potential is highest at moderate densities, with a collapse at extreme densities (Gilbert et al. 2003, Newell 2004). Similarly, (Lohrer et al. 2016) show the complex direct and indirect effects of shellfish density on primary productivity and nutrient cycling in seagrass beds, with highest effect of cockles on primary production at intermediate densities. Shellfish size can also affect service delivery, where for example, the removal of large adults has a negative impact on nutrient and oxygen fluxes and hence affect alterations in sediment biogeochemistry (Thrush et al. 2006, Norkko et al. 2013). Koch et al. (2009) show the effect of non-linearity in wave attenuation by benthic habitats on shoreline stabilization, and the resulting changes in valuation of this service and the impact on coastal management if non-linearity is taken into consideration. Unexpected non-linearity in service delivery as a result of density dependency and dynamic ecosystem processes or functions, can therefore have a significant impact on the assessment of service supply and resulting decision making.

Predicting the delivery of ecosystem services is a key challenge in resource management which may benefit more from a mechanistic understanding of the supply of services rather than a collection of differing, context specific, and non-transferable case studies (Spake et al. 2017). Understanding which processes drive the generation of these service bundles and how they link with environmental variables will help us better predict and quantify service delivery at different spatial and temporal scales. In many cases, models and maps are used as tools to predict ecosystem service delivery to inform management and decision making (Tallis and Polasky 2009, Burkhard et al. 2012, Maes et al. 2012a, Burkhard and Maes 2017), by providing useful insights in where services are likely delivered.

The next step in applying our framework is to move from identification to ecological quantification of linkages and bundles, including shellfish density and size effects, and to consider the implications of interactions for management. When managing for individual services in isolation, interactions can be overlooked and tend to down-weight human perceptions of the total benefits provided (Rodríguez et al. 2006). Ecosystem models are based on ecological principles and processes and could be configured to derive information on interactions between services that would represent a step forward in predicting multiple services delivery. For example, environmental carrying-capacity models predict shellfish growth and clearance rates (e.g. Dame and Prins 1997) that could be used to quantify services in the water quality bundle. In some instances, coupled models may be required, for example carrying-capacity and morphodynamical models (e.g. van Maanen et al. 2015) could be used to predict how shellfish distribution affects sediment and shoreline stability. Such advances would lead to a better understanding of interactions between multiple services and support a more holistic, ecosystem-based management (EBM) approach to marine systems (McLeod and Leslie 2009).

2.6 Conclusion

The ecosystem services and bundles concept have been proposed as a step forward in ecosystem-based management (EBM). Ecological understanding on how bundles are generated will contribute to sustainable management, as it will create a better understanding of what drives the supply of services, how they interact with each other, what stressors they are prone to, and what might be lost if not managed properly. As a result of global shellfish bed degradation, recovery of lost ecosystem services through shellfish bed restoration effort and methods form a large part of the ecosystem services literature on shellfish. Our case study is an example of how we should manage for more than the tangible services that have direct economic gain, as this bundle will often form trade-offs with other services that are generated through different processes. Shellfish, like many other marine organisms and habitats, are prone to multiple and cumulative stressors, and global losses are linked to a loss in service value, reduced habitat quality and affects the functioning of the system. As estuarine and coastal systems are prone to change, maintaining resilience through healthy systems should be a main concern for management. A holistic approach to managing shellfish beds and estuaries in general is in line with EBM and will help maintain resilience and ensure future use of the services they generate. More generally, our approach provides a format to translate ecological knowledge to advice decision makers and spatial planners, without getting caught up in case or location specific details and will help connect ecological knowledge with social science and decision making.

CHAPTER 3

Variations in ecosystem service provision of two functionally similar bivalve species

3.1 Introduction

Marine and coastal ecosystems provide a wide range of benefits and values to society (MEA 2005, Barbier et al. 2011). A desire to better recognise and protect these tangible and intangible benefits has led to the development of the Ecosystem Services (ES) concept (Costanza et al. 1997, Daily 1997, De Groot et al. 2012). ES link benefits and values to the underpinning biophysical structures, processes and ecosystem functions (hereafter EF) in the environment (Haines-Young and Potschin 2010). Knowing where and in what amount ES are being generated is required if we wish to protect and maintain them, yet quantifying the mechanistic links between ecosystem attributes, functions, and ES to incorporate biophysical realism remains challenging (Luck et al. 2009, Boerema et al. 2017, Lavorel et al. 2017). Furthermore, a lack of quantitative data on all goods and services provided by an ecosystem can create a bias towards more data rich ES (e.g. fisheries and coral-reef eco-tourism in marine ecosystems) (Beaumont et al. 2007). There is an urgent need to quantify ES to test existing theory, however, this is a challenging task due to the complexity of links between processes, EF, and ES (Snelgrove et al. 2014, Hattam et al. 2015a).

Bivalves are an example of an important ES provider in coastal ecosystems contributing to the provision of multiple services (e.g. food provision, water quality regulation, shoreline stabilisation (Smaal et al. 2019)) for which the links between processes, EF, and ES have been defined (Chapter 2). As regulating ES are generally more easily quantified ecologically (Boerema et al. 2017) this study focussed on quantifying a subset of shellfish ES that contribute to regulating water quality. Estuaries are prone to multiple local anthropogenic stressors that impair environmental health and quality, through for example eutrophication, sedimentation, and other pollutants that enter the system (Kennish 2002). Bivalve mediated processes and EF are known to mitigate these effects and thereby provide important ES (Kellogg et al. 2014, Bricker et al. 2018). For example, water clarity is improved by shellfish acting as a biofilter, removing suspended material from the water column when feeding (Newell 2004, Grabowski and Peterson 2007, Cranford et al. 2011). Bivalves impact nutrient cycling through depositing organic material, excreting ammonium (Dame and Kenneth 2011), and alter nutrient fluxes through bioturbation (Laverock et al. 2011, Norkko and Shumway 2011). Nitrogen can be removed from the system through bioassimilation in tissue and shell, burial of biodeposits, and through enhancing denitrification in the sediment (Petersen et al. 2019). Coupled nitrification-denitrification is the only process that permanently removes nitrogen by making it biologically unavailable (Herbert 1999), and is enhanced by bivalves through extra nitrogen sources as well as bioturbation of the sediment (e.g. Pelegri and Blackburn 1995, Newell et al. 2002, Norkko and Shumway 2011). Finally, benthic primary production by microphytobenthos in marine sediments is important for sequestering carbon and oxygenating sediments, whilst simultaneously supporting secondary production and foodwebs (Miller et al. 1996). Shellfish enhance benthic primary production by exerting both top-down (removal of phytoplankton as a consumer) and bottom-up (mobilisation of inorganic nutrients) control, affecting light penetration, nutrient cycling and phytoplankton community structure (Prins et al. 1997, Dame and Kenneth 2011).

Bivalve filter feeding and bioturbation are at the core of these ES (Chapter 2) and vary with biological and environmental controls. Filtration and clearance rates for example, show species specific allometric relationships with size/weight (Møhlenberg and Riisgård 1979, Riisgård and Seerup 2003, Cranford et al. 2011), density (Newell 2004, Jones et al. 2011b), and are controlled by a number of environmental variables like temperature (Riisgård and Seerup 2003), current velocity (Sobral and Widdows 2000, Widdows and Navarro 2007), seston concentration and quality (e.g. Iglesias et al. 1996, Navarro and Widdows 1997, Cranford et al. 2011). Ecosystem functions, like nutrient cycling and oxygen fluxes in benthic habitats, are known to vary with bivalve density (Newell 2004, Sandwell et al. 2009) and presence of large individuals (Thrush et al. 2006, Norkko et al. 2013). Denitrification rates reach an optimum at intermediate bivalve densities by enhancing the oxic-anoxic interface (Gilbert et al. 2003, Newell 2004). EF are likewise affected by environmental and ecosystem level controls, e.g. denitrification is affected by nitrate and oxygen concentration, macrofauna community, residence time (Cornwell et al. 1999), and sediment characteristics like mud or organic matter content and quality (Jones et al. 2011a, Eyre et al. 2013, Douglas et al. 2019). Piehler and Smyth (2011) observed varying levels of denitrification EF and ES, with higher levels in intertidal than subtidal sand and mudflats. As habitat and context-specific results are observed for EF, it is presumed that this will translate to varying ES quantities, thereby creating spatial heterogeneity in ES provision in estuaries.

Much of the work on shellfish ES quantification has focussed on epifaunal species, in particular oysters (Ostreidae) and mussels (Mytilidae), to justify restoration after global declines in reefs (e.g. Coen et al. 2007, Grabowski and Peterson 2007, Beck et al. 2011, Zu Ermgassen et al. 2013b). Infaunal bivalves, although more cryptic, can also form high density beds and contribute to a similar range of ES (Carss et al. 2020). Relative to oysters and mussels, there is very little quantitative data on the ES provision from infaunal shellfish beds, and the differences in ecosystem functioning between species or functional groups are rarely considered. For example, all suspension-feeding bivalves are functionally similar; filtering seston from the water column and depositing (pseudo-)faeces to the sediment. However, other functional differences may translate in varying contribution to ES, e.g. epifaunal and infaunal species have different clearance rate responses to increased suspended sediment concentrations (e.g. Bacon et al. 1998, Hawkins et al. 1998). Furthermore, environmental differences in intertidal and subtidal estuarine habitats (e.g. light climate, sediment characteristics, current velocities) where infaunal bivalves are common, can influence EF and ES (Piehler and Smyth 2011). Collectively these differences are important; a decline/loss of one species and/or habitat (e.g. loss of intertidal area with SLR) may not be compensated by gains elsewhere, impacting ES provision. Through quantifying functional differences for naturally occurring infaunal shellfish beds in different habitats (e.g. intertidal and subtidal), a better understanding can be gained on the implications of changing species/habitat for ES provision.

In this study, I aim to quantify the complex links between processes and EF affected by infaunal bivalves that directly underpin key ES related to coastal health and quality. Measurements of sediment-water column fluxes of dissolved inorganic nutrients, dissolved oxygen, and N_2 gas were used as a proxy for nutrient recycling, primary productivity, and denitrification rates respectively, and clearance rates as a proxy for water clarity improvement over the bed. A comparison is made between a naturally occurring intertidal and subtidal high-density shellfish bed of two New Zealand bivalve species: the intertidal littleneck clam (*Austrovenus stutchburyi*) and pipi (*Paphies australis*), a subtidal clam (hereafter *Austrovenus* and *Paphies* respectively) (Powell 1979). They are functionally similar species belonging to the same functional group (Greenfield et al. 2016), i.e. both suspension-feeding bivalves that live within the top five centimetres of the sediment, yet dominate different parts of the estuary (intertidal versus subtidal habitat). This research aims to fill a critical gap in quantifying the contribution of infaunal shellfish to ES provision in coastal environments and gain insight in spatial heterogeneity of ES provision due to habitat association.

3.2 Materials and methods

3.2.1 Study sites

This study was conducted at two sites in Tauranga Harbour, New Zealand (37° S, 175° E): one site on the intertidal sandflat of Otumoetai peninsula (37°39’54.2” S, 176°09’23.5” E) and one in a nearby shallow (-1.6 m below MSL) subtidal channel (Tilby channel; 37°39’30.3” S, 176°07’28.7” E). The intertidal sampling location is representative of a low to mid intertidal site (at -0.7 m below MSL, 1.5-2 m water depth at high tide) with a 7 h inundation period. Both sites were characterized by presence of naturally occurring high-density shellfish beds, with natural small-scale variations in density. *Austrovenus* was the dominant species in the intertidal site with densities ranging up to 1800 individual m^{-2}. *Paphies* was the dominant clam species in the subtidal channel with densities exceeding 500 individuals m^{-2}, although some small (< 20 mm) *Austrovenus* were also present at this site. Sampling occurred over three days in a two week period in austral autumn sampled one week apart, one day for the intertidal site (7th May 2018), and two consecutive days for the subtidal site (15 and 16th May 2018). The intertidal site was sampled over a mid-day high tide and for consistency in water depth, the subtidal site was sampled over a mid-day low tide (~1.5 m water depth), to encompass the period of highest natural irradiance in both sites.

3.2.2 Field sampling

Sediment-water column fluxes were measured using pairs of light and dark benthic incubations chambers , to distinguish between the presence and absence of photosynthesis. Twelve pairs of incubation chambers (50 x 50 x 15 cm) were placed over the natural shellfish beds, by pressing the chamber bases approximately 8 cm into the sediment, thereby enclosing all fauna present in a 0.25 m^2 surface area. Each chamber was equipped with a dissolved oxygen (DO) logger and some with temperature/light intensity (HOBO) loggers sampling at 1 min intervals. Translucent domes were clamped on to the bases to seal in approximately 30L of seawater at the start of the incubation. Additionally, for the dark chambers a shade cloth was used to cover the chamber to prevent photosynthesis, thereby measuring community respiration only (hereafter referred as sediment oxygen consumption; SOC), whereas net primary production (NPP) was measured in the light chambers, which were exposed to ambient light levels. A pump system recirculated the water within each chamber for 5 s at 20 s intervals. At each site, two pairs of light and dark bottles were incubated at the same time to determine water column processes. Hourly ambient radiation (MJ m^{-2}) were obtained from a nearby weather station (NIWA CliFlo database, cliflo.niwa.co.nz) and converted to PAR (µmol m^{-2} s^{-1}), by first converting hourly rates to Watts (1 Watt = 1 J s^{-1}) and then apply a 2.02 conversion factor for W m^{-2} to PAR (Mavi and Tupper 2004).

Incubations ran for ~4.5 h around high tide at the intertidal site where all 24 chambers were deployed on the same day, and ~2.5-3 h in the subtidal channel on two consecutive days (light and dark chambers separate) around slack low tide as SCUBA was used to deploy and sample chambers. At the start and end of the incubation, 60 ml water samples were collected from each chamber for nutrient concentrations. Nutrient samples were filtered over a 0.45 µm Whatman GF/C glass fibre filters, collecting two 15 ml samples which were stored frozen and in the dark. Additionally, two 60 ml water samples were collected from each chamber using air-tight locks for N_2 fluxes. N_2 samples were stored in air-tight glass vials in triplicate with $ZnCl_2$ added as an antimicrobial agent for storage. At the end of the incubation, chambers were spiked with high concentrations chlorophyll a (Chl *a*) (Reed Shellfish Diet 1800, comprised of *Isochrysis*, *Pavlova*, *Tetraselmis*, *Thalassiosira weissflogii*, and *Thalassiosira pseudonana*, algal size: 4 - 20 microns) at 22 µg L^{-1} (similar to Jones et al. 2011b) compared to ambient concentrations of 0.65 µg L^{-1} in the intertidal and 1.30 µg L^{-1} in the subtidal to measure bed clearance rates. After 30 min, 50 ml water samples were collected from chambers. Two samples were lost in the subtidal light treatment and all remaining samples were filtered over 0.45 µm Whatman GF/C glass fibre filters. Filters were stored in aluminium foil, kept frozen in the dark (-20 °C) until analysed for Chl *a*. For dark chambers in the subtidal site, no clearance rate measurements could be obtained due to weather conditions, and hence data from light chambers of both sites were used as a comparison instead.

Sediment and macrofaunal samples were collected from directly outside the chamber on undisturbed sediment at each site. Macrofauna samples were taken using a large core (13 cm diameter, 15 cm depth) and sieved in situ over a 500 µm mesh sieve and retained material preserved in 70% isopropyl alcohol. Sediment samples were collected by pooling 5 small cores (2.6 cm diameter, 2 cm depth), stored frozen and in the dark for further analysis (including median grain size, Chl *a*, and organic matter). At the end of the incubation period, large shellfish (> 10 mm shell height) were collected from within the chamber bases by hand ploughing the top 8 cm of the sediment. These samples were frozen and analysed later for density, size, and biomass. Shellfish could not be collected from the bases for the dark chambers at the subtidal site, due to early termination of incubations caused by a severe thunderstorm. Densities of large individuals collected from the macrofauna cores corresponded well to the numbers and biomass of hand collected samples (*Austrovenus*: R^2=0.67, and *Paphies* R^2=0.78) and therefore the average of the two macrofauna cores per chamber pair were used to approximate biomass and densities of large *Austrovenus* and *Paphies* for subtidal dark chambers.

3.2.3 Laboratory analyses

In the laboratory, nutrient samples were analysed for NH_4^+ concentrations on a Lachat QuickChem 8000 Series FIA+ (Zellweger Analytics Inc. Milwaukee, Wisconsin, USA) using standard operating procedures for flow injection analysis. N_2 concentrations were determined by Membrane Inlet Mass Spectrometry (MIMS; Bay Instruments, Cambridge, Maryland, USA) using a N_2/Ar method (Kana et al. 1994). Chl *a* samples for clearance rates were analysed by extracting pigments from the filters in 10 ml 90% buffered acetone, samples were seeped overnight and measured before and after acidification (1M hydrochloric acid) using a fluorometer (Turner Designs 10-AU) to differentiate between Chl *a* and phaeopigments. Sediment samples were thawed, homogenized, and subsampled to determine median grain size, Chl *a*, and OM concentrations. Sediment Chl *a* samples were freeze dried to standardize water content then analysed as described above. Grain size was analysed by digesting 10 g of subsample in 10% hydrogen peroxide until all organic matter was removed, followed by analysis on a Malvern Mastersizer 3000. OM concentrations were measured as the weight loss upon ignition of dried samples (> 48 h at 60°C until constant weight) for 4 h at 500°C. Macrofauna samples were stained with Rose Bengal, sorted, and identified to order or species level for eight randomly selected samples per site. All large bivalves collected from the chamber bases and all macrofauna cores were counted, measured for length, height, and width. A subsample from each chamber (up to 10 individuals per species) were used for biomass estimates. Soft tissue was removed from shell, dried to constant weight (>48 h at 60°C) and incinerated at 500°C for 4 h to calculate ash free dry weight (AFDW). Strong relationships (R^2 = 0.88 for *Austrovenus,* and R^2=0.92 for *Paphies*) between length and AFDW allowed estimate of shellfish biomass to be calculated for the chamber.

3.2.4 Data analysis

Differences in the concentrations of DO, NH_4^+ and N_2 at the start and end of the incubation period were used to calculate fluxes across the sediment water interface over time. Fluxes (µmol m^{-2} h^{-1}) were calculated for each chamber and scaled to chamber surface area and adjusted for chamber volume. Water column processes accounted for a small proportion of the solute fluxes, relative to benthic processes (<5% of the chamber fluxes in both light and dark conditions at both site) and were therefore ignored. Gross primary production (GPP) was estimated by correcting the NPP (DO flux in light chamber) by SOC (DO flux in dark chamber) for pairs of chambers. GPP was standardised by sediment Chl *a* content (averaged for light and dark chamber pairs), a proxy for microphytobenthic (MPB) biomass as a measure of photosynthetic efficiency (Pratt et al. 2014b). Similarly, bed clearance rates (L m^{-2} h^{-1}) were calculated from the difference in water column Chl *a* concentration compared to the injected concentration after 30 min, and were corrected for chamber surface area and volume ('Clearance method', adjusted from Riisgård (2001) and Jones et al. (2011b)):

$$\mathrm{Bed\ CR} = \frac{\mathrm{V}}{\mathrm{A\ t}} \ln \left(\frac{\mathrm{C_i}}{\mathrm{C_f}}\right)$$

Where, V = volume of water in the incubation chamber (L), A = area of incubation chamber (m^2), t = time (h), C_i (22 µg L^{-1}) and C_f are the initial and final Chl *a* concentrations, respectively. As final measurements could not be taken for clearance rates due to extreme weather for subtidal dark sampling, data analysis were performed on a subset of the data (from light chambers) for a site comparison.

By integrating hourly light and dark fluxes over 24 h, a better comparison of ES potential between the two shellfish beds can be obtained, accounting for the differences in inundation period between sites. Tauranga Harbour experiences a semi-diurnal tide, with the intertidal study site inundated for approximately 7 h per tidal cycle, e.g. 14 h per day (58% of the time), whereas the subtidal site is continuously inundated. When assuming on average one tidal cycle in the light and dark per day, differences in functioning due to 'cover' can be accounted for. Integrated daily fluxes were calculated as a first estimate of ES, by multiplying observed hourly functions per chamber by inundation period (7 and 12 h per tidal cycle for intertidal and subtidal respectively), separated for light and dark fluxes where possible. The average fluxes over one tidal cycle in the light and dark were then summed as a total daily estimate. Clearance rates were only obtained for light chambers, and hence clearance rates were assumed to be equivalent in the dark for ES estimates. For nitrogen cycling (e.g. ammonium fluxes), nitrogen removal (e.g. denitrification rates), and water clarity (e.g. clearance rates) functioning was assumed to be limited to the time inundated by the tide. Primary production however is known to occur during emersion also in NZ estuaries (Drylie et al. 2018, Mangan et al. 2020b). Therefore, observations from Mangan et al. (2020b) in June 2018 at a nearby intertidal site (‘Omokoroa’) were used as an estimate for daytime primary productivity during low tide (at 1523 µmol O_2 m^{-2} h^{-1}) during emersion (5 h per tidal cycle).

Prior to statistical analysis of the data, data explorations (Zuur et al. 2010) were performed and extreme outliers identified which were removed from the analysis when measurement error were expected (1 outlier detected for DO and 2 for N_2 fluxes). N_2 flux rates less than zero in some duplicate samples were excluded due to potential oxygen contamination of sample (12 samples, Eyre et al. 2002). Student’s t-tests were conducted when analysing significant differences ($\alpha<0.05$) between sites, whereas Analysis of Variance (ANOVA) was used to assess differences between sites and cover (light and dark) where applicable. Assumptions for normality and homogeneity of variance were checked visually and with Shapiro and Levene test, respectively. If the assumption of normality was not met, data were ln transformed (i.e. N_2 fluxes). When homogeneity of variance was not met for t tests, a Welch t-test was used instead. Differences in macrofauna community composition were assessed with PERMANOVA tests with Bray-Curtis resemblance matrices (Anderson 2005). Community structures were visualised with non-metric multi-dimensional scaling (nMDS) ordination (Bray and Curtis 1957). A Simper analysis was then conducted to identify key contributors to the dissimilarities between sites. All statistical analyses were conducted in R (R Core Team 2013) using the vegan package for PERMANOVA and Simper analyses (Oksanen et al. 2007).

3.3 Results

3.3.1 Site characteristics

The comparison between the intertidal and subtidal site characteristics, including sediment characteristics, MPB community, and light regimes, displayed differences between habitats (Table 3.1). Sediment were coarser with lower mud and organic matter content in the subtidal site compared to the intertidal site. Sediments in the subtidal had a median grain size of 365 µm, and a low mud and organic content (1.7% and 1.5% respectively), whereas intertidal sediments had a median grain size of 209 µm, a mud content of 5.7%, and organic content of 2.1%. Chl. *a* and phaeopigment content were on average 1.3 and 1.5 times higher in the intertidal than subtidal site. Photosynthetic active radiation (PAR), as measured in the light chambers, was significantly higher and was more variable for the intertidal site than the subtidal

Table 3.1 Site characteristics during intertidal and subtidal sampling. Means are displayed with standard deviation in parentheses, with n=24 for all characteristics per site, except mean size (light chamber only, n=12 per site), and abundance and species richness (n=8 per site).

	Intertidal	**Subtidal**
Sediment characteristics		
Median grain size (µm)	209 (13)	365 (32)
Mud content (%)	5.7 (1.6)	1.7 (0.8)
Organic content (%)	2.1 (0.3)	1.5 (0.2)
Microphytobenthos		
Chlorophyll a (µg g^{-1}DW)	16.4 (4.1)	12.3 (2.8)
Phaeopigments (µg g^{-1}DW)	9.6 (2.3)	6.3 (2.0)
Light regime		
Seafloor PAR (µMol s^{-1} m^{-2})	135 (77)	10.3 (3.1)
Ambient PAR (µMol s^{-1} m^{-2})	964 (262)	392 (224)
Light attenuation (% ambient PAR at seafloor)	14.0 (7.7)	2.6 (0.7)
Macrofauna community		
Austrovenus stutchburyi (>10mm)		
Density (n 0.25m^{-2})	253 (157)	115 (54)
Biomass (g AFDW 0.25m^{-2})	12.4 (7.6)	3.0 (1.5)
Mean length (mm)	21 (2.3)	16.5 (0.5)
Paphies australis (>10 mm)		
Density (n 0.25m^{-2})	0.7 (0.7)	80 (43)
Biomass (g AFDW 0.25m^{-2})	0.1 (0.2)	7.3 (5.0)
Mean length (mm)	40 (11)	29 (1.6)
Abundance (n core^{-1})	302 (74)	259 (40)
Species richness (n core^{-1})	24 (3)	19 (4)

channel, which had low light intensity in all measured chambers as a result of lower ambient PAR on the day (Table 3.1) and high turbidity in the channel. Blackout treatment in the dark chambers was successful and resulted in a light intensity not significantly different ($p=0.31$) from 0 µMol s^{-1} m^{-2}.

3.3.2 Macrofauna community

Austrovenus was the dominant large bivalve (>10 mm) in the intertidal community with an average biomass of 12.4 g AFDW 0.25 m^{-2}, occurring over a range of natural densities within the bed (Table 3.1, Figure 3.1 A). *Paphies* were rarely found in the intertidal and did not contribute to the biomass of large bivalves (Figure 3.1 B). In the subtidal on the other hand, both *Austrovenus* and *Paphies* were found (Figure 3.1 A & B), and although density of *Paphies* was lower, when converted to biomass they contributed most, at approximately 70%, of the

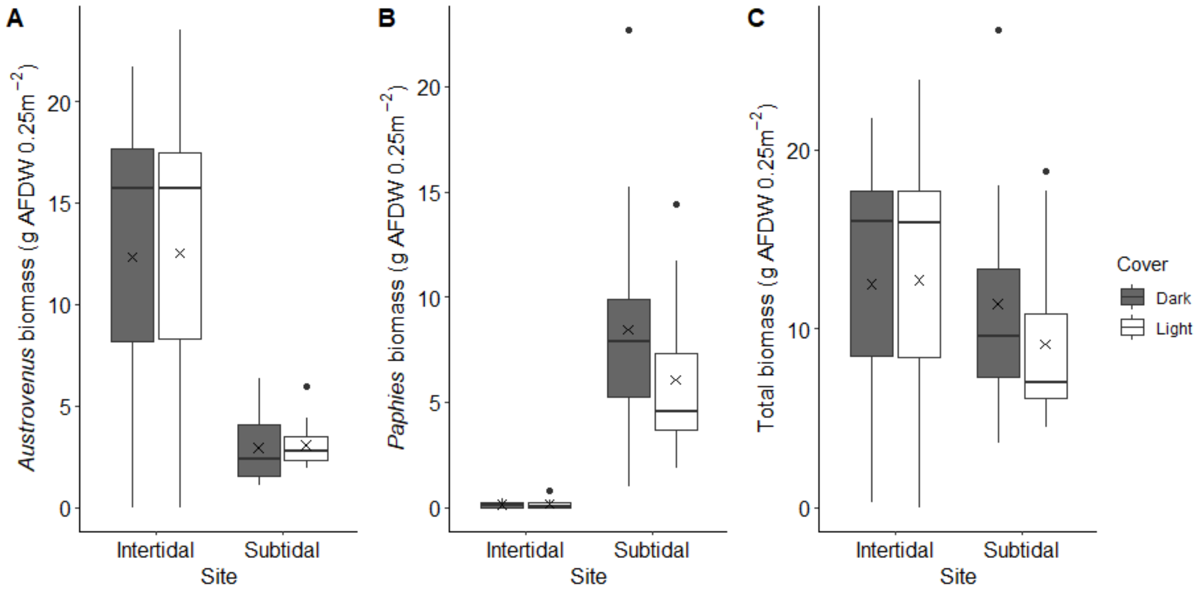

Figure 3.1 Biomass of large bivalves (>10 mm) for A) *Austrovenus stutchburyi*, B) *Paphies australis*, and C) the total biomass of *Austrovenus* and *Paphies* combined, collected for light (white) and dark (grey) chambers. Box limits represent the 25th and 75th percentiles, whiskers indicate the non-outlier range, and circles marking outliers. Median values are displayed with lines intersecting boxes and mean values by crosses within boxes.

Table 3.2 ANOVA results examining the differences in total biomass of large bivalves (*Austrovenus* and *Paphies*), ammonium fluxes (NH_4^+) and denitrification (N_2, ln transformed) between sites (intertidal and subtidal) and cover (light and dark). Significant p-values are indicated in bold.

	df	**MS**	**F value**	**p-value**	
Total biomass					
Site	1	64.47	1.35	0.252	
Cover	1	12.52	0.26	0.611	
Site x Cover	1	18.54	0.39	0.537	
Residuals	44	47.77			
NH_4^+					
Site	1	31501	20.2	**<0.0001**	Intertidal > Subtidal
Cover	1	3384	2.17	0.148	
Site x Cover	1	2920	1.87	0.178	
Residuals	44	1560			
ln N_2					
Site	1	0.586	1.41	0.245	
Cover	1	3.795	9.10	**0.005**	Dark > Light
Site x Cover	1	1.333	3.20	0.084	
Residuals	30	0.417			

total biomass (Table 3.1). The total bivalve biomass between site (intertidal and subtidal) and cover (light and dark) was not significantly different (Table 3.2, Figure 3.1 C). The size-frequency distribution for *Austrovenus* showed a consistent mean length within sites, but with larger individuals in the intertidal than the subtidal (Figure A1). *Paphies* in the subtidal had a consistent mean length around 30 mm (Table 3.1, Figure A1). Small bivalves (<10 mm shell length, identified from macrofauna cores) made up a small fraction of the total shellfish biomass, at <0.2 and <0.01 g AFDW 0.25 m^{-2} for *Austrovenus* and *Paphies* respectively on average over the two sites.

The macrofauna community in the intertidal site had a significantly higher species richness than the subtidal site, but no significant difference in abundance was found. From the total number of species found (n=57), more than half (56%) occurred in both sites which made up 92% of the total abundance over both sites. Although abundance did not differ significantly, nMDS results (Figure A2) show significantly distinct communities in the two sites (PERMANOVA, p(perm)=0.001). When not taking into account the difference in *Austrovenus* and *Paphies* between sites, the SIMPER analysis showed that 71% of the cumulative contribution to dissimilarity between communities is explained by the abundance of 7 species. Oligochaetes, Nereidae, and *Aonides trifida* were more abundant in the subtidal sites, whereas *Heteromastus filiformis*, *Prionospio Aucklandica*, *Linucula hartvigiana*, and *Paradoneis lyra* were more abundant in the intertidal site (Table A2). These species are mostly annelids (soft bodied, deposit-feeders or scavengers) and a small deposit feeding bivalve (*Linucula*) (Greenfield et al. 2016).

3.3.3 Ecosystem functioning in shellfish beds

Dissolved oxygen fluxes in both the intertidal and subtidal sites showed net oxygen production in the light chambers, where primary production exceeded the amount of oxygen used for respiration (Figure 3.2 A). However, NPP was significantly higher in the intertidal site compared to the subtidal site (Table 3.3) and was on average 3 times higher. Similarly SOC, a proxy for respiration or the benthic community metabolism, showed a larger uptake of oxygen in the intertidal than the subtidal site (Figure 3.2 A, Table 3.3). When correcting NPP for respiration (as measured in the paired dark chamber), patterns persisted for GPP and showed a higher total amount of primary productivity in the intertidal (Table 3.3). Similar to NPP, GPP in the intertidal was on average 3 times that in the subtidal (Figure 3.2 B). As the MPB biomass differed between sites (Table 3.1), GPP was corrected for the sediment Chl a content to calculate photosynthetic efficiency. Although MPB biomass was higher in the intertidal site, this did not account for the differences in GPP between sites (Figure 3.2 C) and GPP_{MPB} indicated a significantly higher photosynthetic efficiency in the intertidal site (Table 3.3).

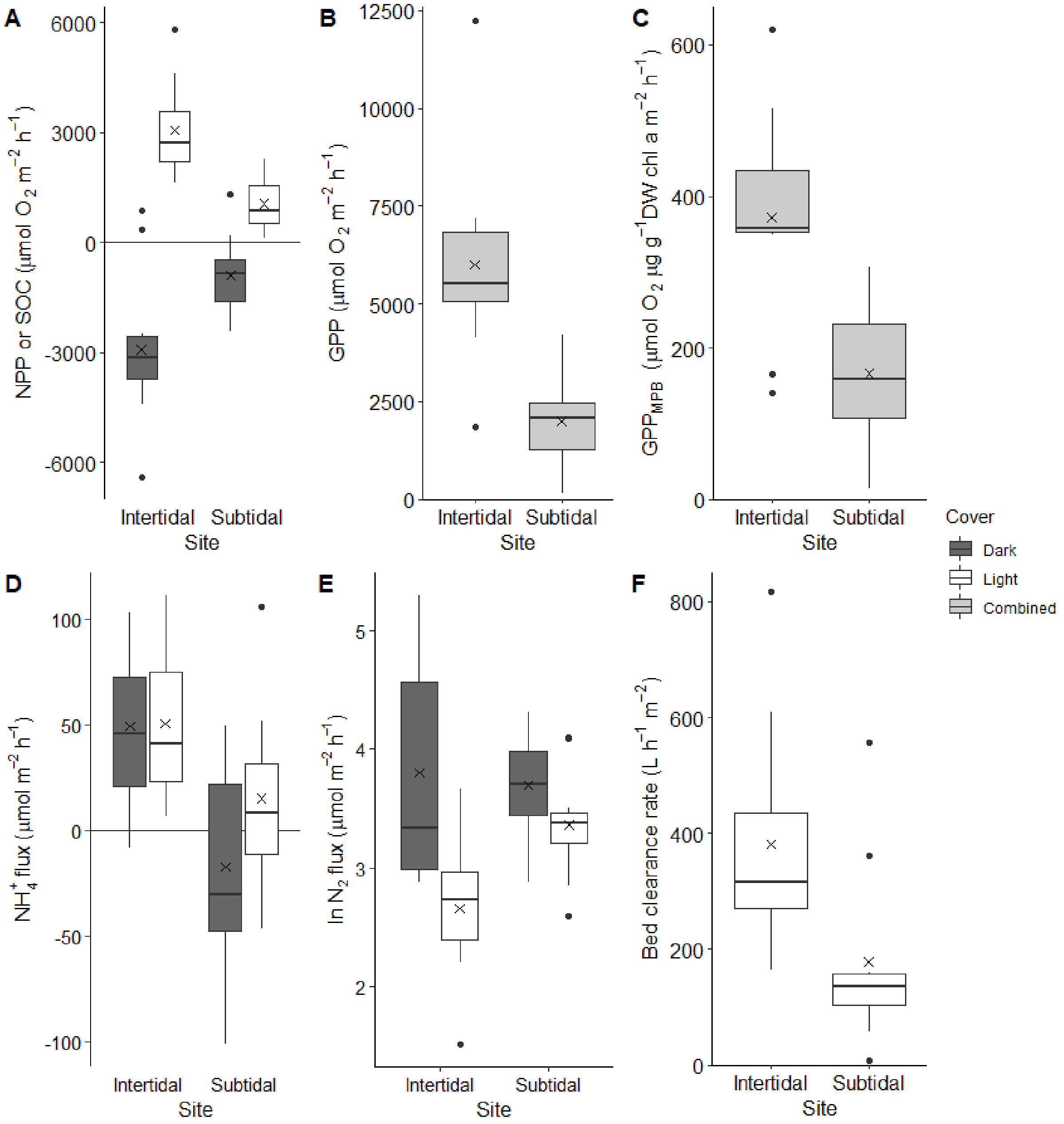

Figure 3.2 Measures of productivity, nutrient fluxes, and clearance rates per site and cover, showing A) Net primary production (NPP; white boxes) and sediment oxygen consumption (SOC; dark grey boxes), B) Gross primary production (GPP), and C) Gross primary production corrected for the microphytobenthos (MPB) biomass, D) Ammonium flux (NH_4^+), E) Denitrification (ln N_2), and F) Bed clearance rates. Box limits represent the 25th and 75th percentiles, whiskers indicate the non-outlier range, and circles marking outliers. Median values are displayed with lines intersecting boxes and mean values by crosses within boxes.

Table 3.3 t-test results examining differences in net primary production (NPP), sediment oxygen consumption (SOC), gross primary production (GPP), and GPP corrected for microphytobenthic biomass (GPP_{MPB}), and bed clearance rates (CR) between sites. Significant p-values are indicated in bold.

	NPP	SOC	GPP	GPP_{MPB}	Bed CR
df	22	21	21	21	20
t	4.78	-3.04	4.81	4.21	2.65
p	**<0.0001**	**0.006**	**<0.0001**	**<0.001**	**0.015**

Differences in nutrient cycling and nitrogen removal were observed between sites and light and dark chambers. For ammonium fluxes across the sediment water interface, a significant differences between sites was observed, but fluxes in light and dark chambers did not differ significantly (Table 3.2). The NH_4^+ efflux was higher in intertidal sites at an average of 50 µmol m^{-2} h^{-1} compared to subtidal measurements, which were lower and showed an uptake of NH_4^+ in the dark chambers (-17 µmol m^{-2} h^{-1}) (Figure 3.2 D). Denitrification rates, measured as the efflux of N_2 into the water column, did not differ significantly between sites (Table 3.2). However, a significant effect of photosynthesis was observed, where denitrification in light chambers was significantly smaller (approximately half) compared to dark N_2 fluxes in both the intertidal and subtidal (Figure 3.2 E). Bed clearance rates, measured in light chambers, were significantly higher in the intertidal, typically double the rates measured at the subtidal site (Table 3.3, Figure 3.2 F).

3.4 Discussion

3.4.1 Differences in functioning between shellfish beds

Results from this study provide valuable insights into the contribution of infaunal bivalves to EF that directly underpin ES. Higher hourly fluxes and rates for almost all measured EF were found in the intertidal site, except for denitrification where no site specific differences were observed, yet a difference between light and dark conditions was found. In this study, bed specific rates (fluxes m^{-2}) were measured to gain insight in how much EF (and ES) is provided in a given area of naturally occurring shellfish bed. The intertidal and subtidal site were dominated by two different bivalves (*Austrovenus* and *Paphies* respectively) in terms of biomass, and had distinctly different macrofauna communities associated with each site. Due to their presence in high numbers and biomass, *Austrovenus* and *Paphies* play a dominant role in ecosystem functioning at these sites, which is in agreement with previous studies in New Zealand soft-sediment ecosystems where large bivalves consistently come up as important predictors for ecosystem functioning (e.g. Thrush et al. 2006, Lohrer et al. 2010, Pratt et al. 2014a, Thrush et al. 2014, Lohrer et al. 2016, Douglas et al. 2017). Although in some cases other macrofauna species are linked to ecosystem functions (e.g. O'Meara et al. 2020), their contribution in this study is likely overshadowed by the large presence of bivalves. Despite the functional similarities between *Austrovenus* and *Paphies*, contribution to EF varied between sites and differences cannot be ascribed to bivalve biomass, which were equivalent between sites and cover. Although previously differences in EF have been observed with density (Sandwell et al. 2009) and size structure (Thomas et al. 2020) (for *Austrovenus*), here differences between sites (e.g. light regime, sediment characteristics, MPB biomass) are discussed to explain variation in EF and ES over existing shellfish beds within estuaries.

Dissolved oxygen fluxes showed marked differences between the intertidal and subtidal shellfish beds, with higher respiration (SOC) of benthic communities as well as higher net and gross primary production in the intertidal. The photosynthetic efficiency equally showed a higher efficiency in the intertidal than the subtidal, indicating that this difference between sites was not caused by the biomass of photosynthesising algae. Bivalves alter DO concentrations directly through respiration in relation to density/biomass (Emerson et al. 1988, Bartoli et al. 2001, Welsh et al. 2015), and indirectly by making nutrients available that stimulate MPB (Newell et al. 2002). The efflux of ammonium in the intertidal indicates nitrogen availability to stimulate MPB, as was also observed by Sandwell et al. (2009), whereas nitrogen limitation was expected in the subtidal site (as evident from ammonium uptake). Furthermore, the two sites experienced different light regimes which influences primary production of MPB, with lower PAR reaching the seafloor in the subtidal site. Measurements were conducted at high and low tide for intertidal and subtidal sites respectively as to allow for comparable water depths between sites during incubations. Although the ambient PAR on the two sampling days was lower for the subtidal, both were within the expected range for Tauranga Harbour (Mangan et al. 2020b). The turbidity of the channel caused a small percentage of the ambient light to reach the sea-floor, creating a light-limited environment.

Organic matter is an important source for nitrogen cycling in marine sediments, and was found to be higher in the intertidal. In high-density (infaunal) shellfish beds, the excretion of ammonium (Smyth et al. 2018), biodeposits (Newell et al. 2002), in combination with reworking of the sediment (Laverock et al. 2011) contribute to increased NH_4^+ concentrations that dissipate to the water column. The NH_4^+ efflux in the intertidal was comparable to results found by Sandwell et al. (2009) for medium to high *Austrovenus* densities. The small rates of ammonium fluxes in the subtidal indicated limited nitrogen sources to support the demand for both primary producers as well as bacterially mediated processes. Uptake of NH_4^+ is likely the result of low porewater ammonium due to coarse sediments low in organic matter content, creating a concentration gradient related influx. Denitrification rates in both the subtidal and intertidal were higher in dark conditions than in the light, a common result (e.g. Andersen et al. 1984, Sundbäck et al. 2000), which can be explained by either an inhibition of dissimilatory nitrate reduction due to MPB O_2 production (Jørgensen and Sørensen 1988) or competition for resources with MPB (Rysgaard et al. 1995). Denitrification rates did not differ significantly between sites, although the variation in the intertidal dark measurements was larger. This contrasts with other studies that found higher denitrification in intertidal sand and mudflats, compared to subtidal habitats, and both were found to be lower than denitrification in epifaunal reefs (Piehler and Smyth 2011, Eyre et al. 2013, Smyth et al. 2013). However, the intertidal and subtidal habitats in these studies were not specific to infaunal shellfish beds and differences were ascribed to OM content and quality (Eyre et al. 2013). Although OM content was higher in the intertidal, from an ecological perspective OM content between sites are relatively comparable and could explain similar denitrification rates between sites (Douglas et al. 2019).

Bed clearance rates from the light chambers showed significantly higher rates in the intertidal than subtidal, and rates measured here for *Austrovenus* were in agreement with earlier laboratory work conducted in an annular flume by Jones et al. (2011b), that observed a similar bed clearance rate (up to ~400 L h^{-1} m^{-2}) at equivalent *Austrovenus* densities. Overall, clearance rates are density and size dependent, with allometric relationships between biomass and individual filtration or clearance rates determined for many species (Møhlenberg and Riisgård 1979, Riisgård and Seerup 2003, Cranford et al. 2011). Bed clearance rates tend to level off with density, caused by intraspecific competition for food (Prins et al. 1997, Newell 2004) or reduced numbers of actively feeding individuals (Dolmer 2000, Strohmeier et al. 2009, Hansen et al. 2011, Jones et al. 2011b). Clearance rates for *Paphies* and *Austrovenus* show peak clearance rates at <100 mg l^{-1} SSC, but *Paphies* are more sensitive to increased suspended sediments resulting in lower clearance rates (Hewitt and Norkko 2007). Clearance rates are furthermore related to current velocity in a unimodal distribution with a decrease at higher current velocities (Sobral and Widdows 2000, Widdows and Navarro 2007). *Paphies* in the subtidal sampling site are normally exposed to higher current velocities and turbidity in the channel, and hence their feeding rates may not be adjusted to more stagnant flow in benthic chambers over the short period of the incubation, thereby resulting in lower rates.

3.4.2 Implications for ES

In the study, distinct differences in levels of EF of infaunal shellfish beds in intertidal and subtidal habitats were measured that directly underpin ES related to the health and quality of the environment, and were used to obtain a first estimates of multiple ES. Integrated daily ES estimates (Table 3.4) showed different patterns between sites than hourly EF fluxes. Nutrient recycling shows a much stronger efflux of ammonium to the water column in the intertidal, compared to the subtidal where daily estimates show a very small net uptake of ammonium from the water column. Although no significant differences were observed between sites for N_2 fluxes (Table 3.2, Figure 3.2), conversion to daily fluxes resulted in lower nitrogen removal in the intertidal due to limited inundation time (Table 3.4). Nitrogen removal remained equivalent in the dark between sites, however in the light, nitrogen removal in the intertidal was only ~30% of the subtidal N removal (Table 3.4). Nutrient recycling and removal is an important ES in estuaries experiencing eutrophication (e.g. Kellogg et al. 2014, Petersen et al. 2016), and can mitigate negative effects of excess nitrogen in the water. Hence, we assumed submersed nutrient recycling and nitrogen removal only to contribute to ES, although some nutrient transformation could occur at low tide (Billerbeck et al. 2006). Nitrogen removal is

Table 3.4 Integrated daily ES estimates, for productivity (DO fluxes, µmol O_2 m^{-2} d^{-1}), nutrient recycling (NH_4^+ flux, µmol N m^{-2} d^{-1}), nitrogen removal (N_2 flux, µmol N m^{-2} d^{-1}), and water clarity improvement (Bed clearance rate, L m^{-2} d^{-1}). EF rates and fluxes were corrected for differences in tidal inundation between intertidal and subtidal sites. Light and dark ES are calculated from respective chamber measurements, and 24 h integrated fluxes by summing the average light and dark flux per day.

	Nutrient cycling (NH_4^+ flux, µmol N m^{-2} d^{-1})	**Nitrogen removal** (N_2 flux, µmol N m^{-2} d^{-1})	**Productivity** (DO flux, µmol O_2 m^{-2} d^{-1})	**Water clarity** (Bed CR, L m^{-2} d^{-1})
Intertidal				
Light (emersed)	356	120	21460 (7615)	2666
Dark	347	489	-20539	(2666)
Daily	**703**	**609**	**8536**	**5332**
Subtidal				
Light	182	380	12619	2395
Dark	-207	531	-10857	(2395)
Daily	**-25**	**911**	**1762**	**4790**

often also assumed through uptake in shellfish tissue and shell (e.g. Higgins et al. 2011, Sebastiano et al. 2015, Reitsma et al. 2017), this however is only a temporary sink unless harvested from the system, whereas denitrification transforms N to a biologically unavailable form (Petersen et al. 2019).

Primary productivity estimates in the beds indicate both habitats produce more oxygen during a 24 h period than is being consumed by the benthic community. However a better light climate resulted in intertidal estimates almost 5 times higher than the subtidal, when accounting for emerged primary production. Low tide productivity has been shown to be important in estuarine environments, especially in turbid locations (Drylie et al. 2018, Mangan et al. 2020a). Although NPP during emersion was lower than submerged NPP in Tauranga Harbour (Mangan et al. 2020b), it accounts for much of the differences between sites. Without accounting for emersed NPP, subtidal productivity would be approximately double the intertidal estimates (921 µmol O_2 m^{-2} d^{-1}). Primary productivity by MPB is an important function leading to carbon sequestration (Heip et al. 1995, Underwood and Kromkamp 1999), and MPB contribute to a number of other ES (e.g. supporting foodwebs, stabilising sediments, (Miller et al. 1996, Hope et al. 2020)). Mangan et al. (2020a) determined that highest sea level rise scenario's (at 1.4 m) in Tauranga Harbour would result in more than 90% loss of intertidal area, with a loss of primary productivity by MPB. Our findings support a loss of productivity when shifting from an intertidal to subtidal dominated shellfish bed, and hence a loss of associated ES.

Finally, the daily amount of water filtration was almost equivalent between the two sites (Table 3.4). For both species we assumed filtration during the time of immersion, although species may not filter the full inundation window. For *Austrovenus*, a 4 h feeding window around high tide was observed (Beentjes and Williams 1986) and in (high-density) beds not all individuals will be feeding simultaneously (Hansen et al. 2011, Jones et al. 2011b). For *Paphies,* such insights in feeding are not available, and hence for both species the full inundation window was assumed to be available for filtration. Similar bed clearance rates between *Paphies* and *Austrovenus* dominated sites indicate an equivalent capacity to contribute to the service, however their contribution will further depend on water residence time (Dame and Prins 1997) and water quality over the bed.

For all EF and ES in this study, findings represent a spatial and temporal snapshot comparing one intertidal and subtidal shellfish bed occurring in close proximity. Fluxes and rates measured here give a first insight and direct comparison between two ecologically and culturally important species in Tauranga Harbour, yet is constrained in its spatial cover. Further spatial heterogeneity in ES provision is expected throughout the harbour and will impact environmental planning and decision making (Crowder and Norse 2008). Increasing the spatial and temporal resolution of empirical studies to cover a wider range of bivalve densities and environmental conditions will further improve ES estimates, which are needed for water quality regulation ES as well as other ES not measured in this study. To obtain estuary wide integrated ES estimates, the spatial heterogeneity in bivalve occurrence and densities, as well as environmental conditions should be considered (see Chapter 4 and 5).

3.5 Conclusion

Infaunal bivalves contribute significantly to ES in estuarine environments and improve water quality by removing suspended solids, recycling and removal of nutrients, and productivity in the system. Although species can be functionally similar, the quantity of EF and ES derived from the same processes can vary greatly depending on environmental conditions or habitat occupied. Measurements of ecosystem functions over naturally occurring *Austrovenus* and *Paphies* beds showed significant differences between habitats (intertidal and subtidal respectively), with higher hourly rates and fluxes in the intertidal for almost all EF. However, when translated to daily rates as an approximation of ES, different patterns emerged due to differences in tidal inundation. ES in this study were specific to water quality regulation, and other services that are less reliant on inundation period may show a different outcome when scaling up EF to ES. By determining EF and ES over naturally occurring shellfish beds, measurements represent realistic amounts for shellfish beds and intact communities. Although more extensive seasonal and spatial studies would provide greater insights into EF in Tauranga Harbour over time, the fluxes and ES conversions here provide a first indications of ES potential of the Harbour's important shellfish beds. Information gained from studying the complex links between processes, functions, and ES can provide valuable insights in how to manage and maintain important ES in estuaries.

CHAPTER 4
Combined species occurrence and density predictions to improve marine spatial management

4.1 Introduction

In coastal marine ecosystems, multiple uses, pressures, and interests must be strategically managed to ensure the delivery of ecosystem goods and services that societies rely on. Marine spatial planning (MSP) can be used to organize the different uses, as well as the interactions among and between users (Santos et al. 2019) and can be combined with other conservation tools (e.g. marine protected areas) to sustainably manage marine environments (Trouillet and Jay 2021). Although progress has been made (Chalastani et al. 2021), MSP is prone to challenges including the need for better governance, management, legislative, and planning structures and processes (Santos et al. 2019). Ecological insights need to be incorporated into decision-making frameworks, as they can guide MSP by recognizing attributes of healthy, functioning ecosystems (Crowder and Norse 2008, Foley et al. 2010). Ecological modelling contributes to a number of information layers used to underpin MSP decision making (Stamoulis and Delevaux 2015, Chalastani et al. 2021), but is complicated in marine systems due to connectivity in a 3D environment, mobility of organisms, and lack of baseline data supporting decision-making (Townsend et al. 2018). Spatial ecological modelling, used to generate information on species distributions, forms an important step in the MSP data analysis process, and provides information required for decision support tools, like Marxan, Ecopath/Ecosim, Zonation, InVest, and many others (Stamoulis and Delevaux 2015).

Spatial information on the distributions and densities of functionally important species and levels of uncertainty in these estimates are required for understanding ecosystem functioning and managing the provision and use of ecosystem services. Species distribution models (SDMs) form an integral part in terrestrial and aquatic conservation planning (Guisan et al. 2013) and are increasingly used in marine environments (Melo-Merino et al. 2020). Recent marine applications of SDMs focused, for example, on the conservation and management of cetaceans (e.g. Stephenson et al. 2020, Putra and Mustika 2021, Sahri et al. 2021) and invasive species (e.g. D'Amen and Azzurro , Koerich et al. 2020, Blanco et al. 2021). SDMs are correlative models that predict the occurrence and/or abundance of species in relation to spatially explicit environmental variables (Elith and Leathwick 2009). According to the review by Melo-Merino et al. (2020), the majority of marine SDM studies examined species' distribution patterns (i.e. occurrence), whereas abundance, density, or biomass was only predicted in 9% of the reviewed literature. Examples of SDM applications with abundance predictions include work on marine protected area design for rays (Dedman et al. 2015), seasonal patterns in density and distribution of cetaceans (Becker et al. 2017), and managing fishery bycatch (Stock et al. 2020), illustrating its utility for conservation and management.

Probability of occurrence predictions from SDMs are affected by species prevalence at the scale of study (Tsoar et al. 2007) and are predicted with higher accuracy for species with narrow ecological niches compared to those with wide distributions (Reiss et al. 2011). For species with a wide distribution, SDM performance may be limited when the species is not restricted by the range of the environmental variables or lacks well-defined thresholds that clearly delineate their environmental niche (Morán - Ordóñez et al. 2017). However, probability of occurrence predictions do not consider the range of environmental conditions under which a species thrives. SDMs derived from abundance data (as opposed to occurrence only) can provide additional information on habitat quality, resulting in better spatial predictions than models trained on presence-absence data alone (Howard et al. 2014). A number of terrestrial and aquatic studies have assessed whether presence-absence models can be used as surrogates for abundance distributions, with contrasting results (e.g. Jiménez-Valverde et al. 2009, Gutiérrez et al. 2013, Young and Carr 2015).

While density is less commonly predicted and assessed in SDMs (Melo-Merino et al. 2020), it provides crucial information for spatial management as ecosystem functions and services are often density-dependent (e.g. Lohrer et al. 2004, Spaak et al. 2017). Bivalves are common in estuarine ecosystems globally, are vital to their functioning, and form biodiversity hotspots (Smaal et al. 2019). The distribution and density of estuarine bivalves are determined by a number of environmental and geographical drivers, like sediment characteristics, tides, currents, temperature and salinity, as well as biotic interactions like competition, predation, and recruitment (reviewed by Dame 2016). Bivalves provide a range of ecosystem services that are underpinned by key ecological functions, like filter feeding, biomass production, and reef formation (reviewed in Chapter 2) and their loss from many estuaries globally (Beck et al. 2011) has led to restoration efforts (Coen et al. 2007, Grabowski and Peterson 2007). Many ecological functions underpinned by bivalves are density-dependent (e.g. Newell 2004, Sandwell et al. 2009), however, only a handful of examples have attempted to predict mollusc abundance or using SDMs, and where done so, at large, regional scales (e.g. Mellin et al. 2012, Fordham et al. 2013, Darr et al. 2014, Vázquez-Luis et al. 2014). For local scale management of estuarine bivalves, high spatial resolution predictions on their distribution and density are required as strong environmental gradients occur over short distances resulting in highly variable and patchy bivalve distributions (e.g. Thrush et al. 1989, Hewitt et al. 2008).

In this study I aim to illustrate the importance of density predictions in SDMs over occurrence predictions alone, and discuss its application for management and restoration. I also emphasise the incorporation of uncertainty measures to provide insight into the robustness of model predictions – information that is crucial for making informed management decisions (Moilanen et al. 2006). Furthermore, I aim to assess how varying habitat associations impact density predictions, as ecological niches are known to affect accuracy of occurrence models. I hypothesise that density predictions will significantly improve the outputs from SDMs for species with a wide spatial distribution, by accounting for the environmental conditions under which a species can thrive, thereby better distinguishing areas important for conservation and management. To do so, my work comprises of SDMs for probability of occurrence and density for two New Zealand bivalve species (*Austrovenus stutchburyi* and *Paphies australis*) with contrasting environmental constraints (one broad, the other narrow) and patterns of dispersion (one highly aggregated, the other diffusely distributed), but otherwise occupying a similar niche (Powell 1979). Model outputs are compared within and between species for their accuracy and contribution to distinguish spatial patterns to inform management.

4.2 Methods

4.2.1 Study area and species

The probability of occurrence and densities of two key infaunal bivalve species were predicted in Tauranga Harbour, located on the north-east coast of the North Island, New Zealand (Figure 4.1). This is a barrier-enclosed, shallow estuary of approximately 200 km^2 of which 66% is intertidal. The intertidal littleneck clam *Austrovenus stutchburyi* and the subtidal clam *Paphies australis* (hereafter *Austrovenus* and *Paphies*) are both infaunal, suspension-feeding bivalve species that live within the top few centimetres of the sediment (Powell 1979). *Austrovenus* has a wide distribution on intertidal sand- and mudflats, from the upper mid-intertidal to the Mean Low Water Springs mark, and can exist in high density beds of up to 2000 ind m^{-2} (Pawley and Smith 2012). Adult *Paphies* (>35 mm shell length) have a narrow ecological niche and are predominantly found in the main channels near the harbour entrance with peak densities of around 1700 ind m^{-2} in Tauranga Harbour (Gouk 2001), whereas juveniles occur on low intertidal sites (Hooker 1995).

4.2.2 Survey and environmental data

Data on bivalve presence/absence, density, and environmental characteristics were available from 192 sites throughout the estuary (Figure 4.1 A). Data were compiled from 5 surveys conducted in different years and seasons (Table 4.1) but with similar methods. For each site, macrofauna cores (13 cm diameter, 15 cm depth) were collected, with all bivalves >1 mm shell length identified and enumerated. The number of cores collected differed across sites (Table 4.1), so average density was used to create occurrence and density data sets for both species.

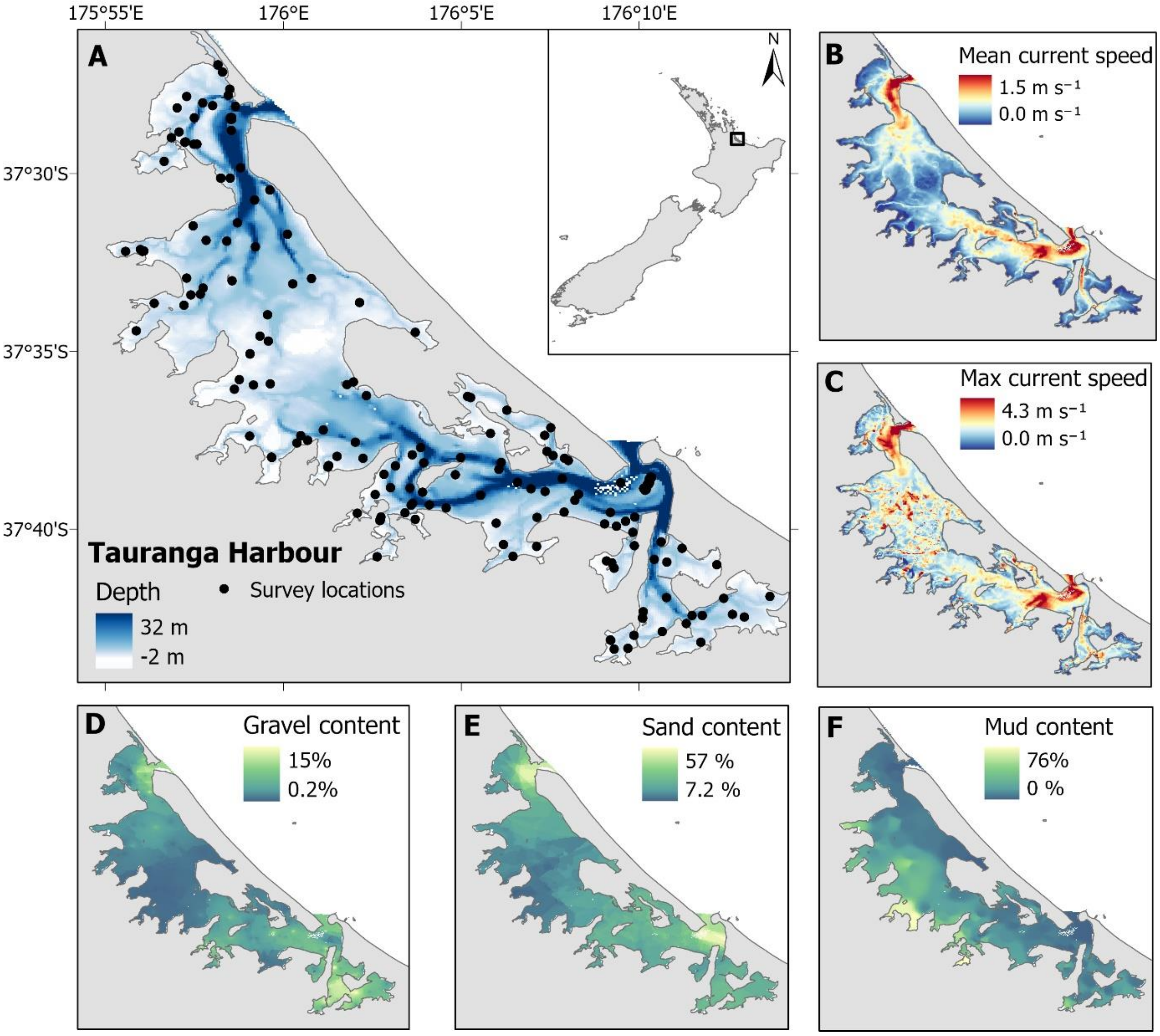

Figure 4.1 Survey locations in Tauranga Harbour, New Zealand and environmental data layers. (A) Location of Tauranga Harbour on the east coast of the North Island (insert) and survey locations. Environmental layers include depth (A), mean and maximum current speed (B & C), and sediment characteristics (gravel (D), sand (E) and mud content (F)).

Table 4.1 Survey information. Data were available from five surveys conducted between 2011 and 2019. For each survey, the species sampled (*Austrovenus* and/or *Paphies*), zone (intertidal and subtidal), year and season of sampling, and number of sites and cores taken at each site are indicated.

Survey	**Species sampled**	**Zone**	**Year**	**Season**	**n sites**	**n cores site-1**	**Reference**
MTA	Paphies	Subtidal	2016	Spring	36	3	(Fairlie et al. 2017)
MTM	Both	Intertidal	2011/2012	Summer	75	10	(Ellis et al. 2013, Berthelsen et al. 2020)
OTOT	Both	Subtidal	2016	Autumn	44	5	(Clark et al. 2018)
	Both	Subtidal	2018	Winter	15	6	Unpublished
UoW	Austrovenus	Intertidal	2019	Summer	22	5	Unpublished

Table 4.2 Overview of environmental variables (and range) used in the boosted regression tree (BRT) models. All layers are used at a 100 x 100 m grid resolution obtained from a hydrodynamic model (Clark et al. 2018) or interpolated from survey data.

Variables		**Unit**	**Range**	**Note**	**Source**
Bathymetry		m	-2 – 32	Corrected to mean sea level	Hydrodynamic model
Current speed	Mean	ms^{-1}	0 – 1.5	Over a tidal cycle	
	Max	ms^{-1}	0 – 4.3		
Sediment characteristics	Gravel	%	0.15 – 14.5	Fraction ≥ 2 mm	Interpolated
	Sand	%	7.2 – 56.6	Fraction ≥ 250, < 500 µm	
	Mud	%	0.02 – 76.4	Fraction < 63 µm	

Paphies and *Austrovenus* were sampled at 170 and 156 locations, respectively (Table 4.1). Estuary-wide environmental variables were available from hydrodynamic models for bathymetry (corrected to mean sea level) and current speed (mean and maximum current velocities over a tidal cycle) (Clark et al. 2018) (Figure 4.1 A-C**,** Table 4.2). Estuary-wide sediment layers were obtained via interpolation of the point data on sediment characteristics collected during the surveys, including percentage gravel, sand, and mud (grams per 100 g dry weight sample) (Figure 4.1 D-F, Table 4.2). For interpolations, inverse distance weighting in the GSTAT package (Pebesma et al. 2019) was used in R (R Core Team 2020) with a 100 x 100 m grid resolution and global search radius.

4.2.3 Species density predictions

Boosted regression tree (BRT) models were used to predict the occurrence and density of *Paphies* and *Austrovenus*. BRT models are a machine learning based approach combining regression trees and boosting (Friedman et al. 2000, Friedman 2001). With this approach a large number of simple regression trees are fitted and then combined using boosting to give a more robust prediction. Boosting is an optimization technique that aims to minimise the models' loss function by iteratively adding new trees that focus specifically on predicting observations that were poorly predicted in the previous trees (Elith et al. 2008). BRT models are a well-established method for SDM studies and have performed well in previous applications in the marine environment (Elith and Graham 2009), with detailed descriptions of the BRT method available in Ridgeway (2007) and Elith et al. (2008). Here we predicted species density using a delta log-normal model (or hurdle model), as bivalve data was highly zero-inflated with a long-tailed distribution. Delta log-normal models firstly fit a binomial model for probability of occurrence, followed by a separate model with a Gaussian distribution to estimate density for locations where presence was recorded (Dedman et al. 2015). The outcomes of these two models are then multiplied to create a final density prediction (hereafter referred to as combined model output), thereby accounting for the likelihood of a species to occur in a location, as well as how suitable the conditions are to support high densities.

An initial full model was run for probability of occurrence for both species to assess the importance of each environmental variable, collection method, and time of sampling. Time of sampling (year and season), zone (subtidal & intertidal) and survey had little contribution to model performance (<5% relative influence on the predictions) and were therefore dropped for the simplified models. The factor 'survey' did contribute for *Austrovenus*, as certain surveys were limited to the subtidal or intertidal zone exclusively, however this was already included as bathymetry. Furthermore, the subtidal zone had on average greater depth, coarser sediment (larger proportion of the sediment as gravel and sand) and stronger current velocities than the intertidal sites (Figure 4.1). Results presented are based on bathymetry, current speed, and sediment characteristics (Table 4.2). All statistical analyses were undertaken in R (R Core Team 2020) using the 'Dismo' package (Hijmans et al. 2017).

A bootstrap approach was used to run all BRT models with 100 bootstrap iterations, in which 75% of the data were partitioned randomly without replacement as the training data set for each bootstrap iteration and the remaining 25% were kept for evaluation (code from Stephenson et al. 2020). BRT models were fitted using the *gbm.step* function from the Dismo package (Hijmans et al. 2017) with a Bernoulli error distribution for the probability of occurrence models, a tree complexity of 3, and learning rate of 0.001 (so as to fit between 1000 and 3000 trees for each species' model), bag fraction was kept to default at 0.75. A random 5-fold cross-validation was used to train the model. The second step was to tune and fit a BRT model for density data (for sites where presence was recorded) using a Gaussian error distribution. Environmental variables and parameter settings were the same as for the occurrence model, but the learning rate was set to 0.002 for the *Austrovenus* density model (to ensure at least 1000 trees were used in each model). Densities were standardised using a ln(Density+1) transformation. The effect of each environmental variable was assessed by calculating its relative influence based on how often it was used to split individual trees, weighted by the squared improvement to the model (Friedman and Meulman 2003). Partial dependence plots were generated which display the predicted response curves across the gradient of the variable of interest when all other variables are held at their means (Elith et al. 2008).

4.2.4 Model evaluation

Model evaluation metrics were obtained from the testing data (the 25% of the withheld data in each bootstrap), which have been postulated to be a more robust and conservative method of evaluating goodness-of-fit of a model than using the same data with which the model was trained (Friedman et al. 2001). For both occurrence and density models, this included the deviance explained; i.e. the proportion of the mean deviance explained by the model to total deviance (Compton et al. 2012). The deviance explained ranges from 0 to 1, with higher values representing a better goodness-of-fit. For the occurrence models, the area under the receiver operating characteristic curve (AUC) was used, where 1 indicates perfect discrimination between presence/absence, and 0.5 indicates no better than random chance (Hanley and McNeil 1982). Sensitivity and specificity (calculated using the pROC package, Robin et al. 2019) were used as measures for accuracy, and reflect the proportion of observed positives or negatives, respectively, that were predicted as such. True Skill Statistics (TSS) was calculated, a measure that includes both omission and commission errors and is independent of the prevalence of a species (Allouche et al. 2006). TSS scores range between -1 and 1, where +1 indicates perfect agreement, whereas scores of 0 or less indicate no better than random chance (Allouche et al. 2006). For the density models, performance was examined as the correlation between predicted values against the known densities in the evaluation dataset, using Pearson’s product-moment correlation coefficient (Puth et al. 2014).

4.2.5 Spatial predictions and uncertainty estimates

For each grid cell, probability of occurrence predictions were made for each of the 100 bootstrap iterations using estuary-wide environmental variables. Predictions were averaged (mean) and prediction intervals (5 to 95% quantiles) calculated (Leathwick et al. 2006). The difference between the mean and the upper and lower bounds, respectively were similar across grid cells and species, and hence the difference between the mean and 5% quantile was used as a measure for ± uncertainty (i.e. reflecting both a plausible lower and upper prediction interval around the mean). Predictions intervals were used as they reflect the range of plausible values predicted by the model (Compton et al. 2012), with small values indicating low variability in predictions (i.e. low uncertainty) and vice versa. For simplicity we refer to this as the 90% prediction interval, which are displayed as ‘Uncertainty’ in maps. Similarly, spatial predictions for density were made throughout the estuary, again providing 100 predictions for each grid cell that were averaged with a 90% prediction interval. Mean density estimates were inverse logged (exponential minus one) to return to original scale, and then multiplied by the mean probability of occurrence to result in the final prediction map for density (combined output). Uncertainty measures for the spatial predictions of density were derived by multiplying the 90% prediction intervals for probability of occurrence and those from the density models.

4.3 Results

4.3.1 Model evaluation

Based on model fit measures from the evaluation data, the probability of occurrence models for both *Austrovenus* and *Paphies* performed well (AUC scores of 0.81 and 0.85 respectively, Table 4.3). Model accuracy was further assessed through several evaluation metrics, including sensitivity, specificity, and TSS scores. For *Paphies,* specificity was slightly higher than sensitivity (86 vs 81%, Table 4.3), indicating a large proportion of observed absences and presences were predicted as such. For *Austrovenus* sensitivity was higher than specificity (82 vs 75%, Table 4.3), indicating more certainty in the predictions where *Austrovenus* were present than where they were absent. Good model performance was also supported by high TSS scores (Table 4.3), indicating performance well above random chance. For both

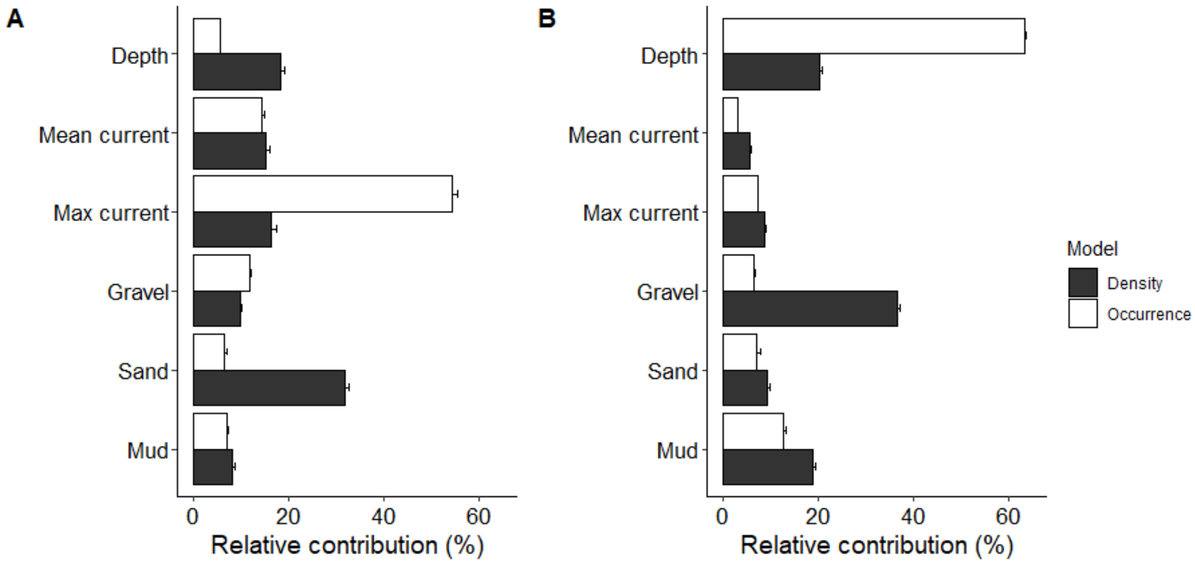

Figure 4.2 Relative contribution of environmental variables for (A) *Paphies* and (B) *Austrovenus* probability of occurrence (white) and density (grey) models. Relative contribution is expressed as average percentage (±1SE) contributed by each environmental variable.

occurrence and density SDMs, models explained between 21% (*Austrovenus* occurrence) and 56% (*Paphies* density) deviance for species occurrence and density (Table 4.3). Correlations between the predicted values and evaluation data were high for *Paphies* (Pearson's r=0.78; p=0.0033) and *Austrovenus* (r=0.58, p=0.014) indicating a good fit of observed and predicted densities. Predicted densities (from combined output) were positively correlated with observed densities (r=0.59, p<0.001, and r=0.67, p<0.001 for *Paphies* and *Austrovenus*, respectively, Figure A3), but densities tended to be under predicted for both species.

4.3.2 *Paphies australis*

Model predictions showed that *Paphies* are likely to occur (in high densities) in fast flowing, shallow channels with a preference for coarse substrates. Probability of occurrence predictions were best explained by mean and maximum current velocities with a relative contribution of 54.5% and 14.3%, respectively (Figure 4.2 A). Partial dependence plots (Figure A4) indicated a positive effect of current speed on occurrence, with a strong increase as the mean current speed increases from 0.2 to 0.6 m s^{-1}. Sediment characteristics had a smaller relative contribution, with the largest contribution of gravel at 11.8%, as *Paphies* were more likely found in locations with coarser sediment. Proportion of mud and sand, as well as depth, had a small contribution at less than 10% each (Figure 4.2 A). For density, the relative contribution of the environmental predictors indicated that the proportion of sand (31.8%), followed by

Table 4.3 Goodness-of-fit metrics for the probability of occurrence and density model of Paphies and Austrovenus. The number of trees (n.trees) in the model, as well as the goodness-of-fit metrics are averaged over 100 iterations (±1 SE). For the probability of occurrence model, metrics include the proportion of deviance explained by the model, the Area Under the Curve (AUC) score, and the Sensitivity, Specificity and True Skill Statistic (TSS) from the evaluation data. For the density models, metrics include the proportion of deviance explained and the Pearson correlation between predictions and evaluation data (including p-values).

		Goodness-of-fit metrics							
Species	**Model**	**n.trees**	**Deviance explained**	**AUC**	**Sensitivity**	**Specificity**	**TSS**	**Pearson correlation**	***p*-value**
Paphies	Occurrence	1609 (±18)	0.30 (±0.007)	0.85 (±0.005)	0.81 (±0.009)	0.86 (±0.008)	0.66 (±0.008)		
	Density	1526 (±81)	0.56 (±0.02)					0.78 (±0.01)	0.003 (±0.001)
Austrovenus	Occurrence	1311 (±37)	0.21 (±0.008)	0.81 (±0.007)	0.82 (±0.01)	0.75 (±0.02)	0.56 (±0.01)		
	Density	1562 (±39)	0.28 (±0.02)					0.58 (±0.01)	0.014 (±0.009)

depth (18.5%) and current velocity (16.5% and 15.3%, mean and max, respectively) were most important (Figure 4.2 A), whereas mud and gravel had relative contributions of <10%. The model predicted higher density with increased proportion of sand, and as water depth increased around 2 to 3 m depth (Figure A4). Current velocities over 0.5 m s^{-1} were positively associated with density (Figure A4).

Spatial predictions for *Paphies* showed high probability of occurrence in the channels of the estuary and areas closer to the estuary entrances (Figure 4.3 A) that were characterised by high current velocities (Figure 4.1). The model predicted low probability of occurrence on the intertidal flats in the centre of the estuary where current speeds were low (Figure 4.3 A). These areas had low prediction uncertainty (Figure 4.3 B), indicating confidence in both presence and absence in these locations. The areas hardest to predict were the intertidal-subtidal transitions, where model uncertainty was highest and probability of occurrence was around 0.5 (Figure 4.3 A & B). An example is just south of the northern estuary entrance (Figure 4.3 A), where probabilities were predicted to be around 0.5, but *Paphies* were not found during surveys (indicated by crosses for absence). Overall, survey data matched well with probability of occurrence in the channels in the southern part of the harbour.

Predicted spatial distribution of *Paphies* densities (combined output) indicated highest densities in the main channels near the mouths of the estuary with densities ranging between 500 – 2500 ind m^{-2} (Figure 4.3 C). These areas were characterised by high mean current velocities and coarse sediments (Figure 4.1), resulting in suitable habitat that can support high densities. Extreme densities were found in a few locations close to the estuary entrances (density >2500 ind m^{-2}, Figure 4.3 C). Although uncertainty was highest in the channels around ±100-500 ind m^{-2} (Figure 4.3 D), these were relatively small compared to predict high densities for these locations. Very low densities were found anywhere in the intertidal area (Figure 4.3 C), where the probability of occurrence was very low and conditions were unsuitable (i.e., low current speeds, higher mud content, Figure 4.1). The predicted densities in areas with higher occurrence uncertainty (i.e. intertidal to subtidal transition) were visually matching better with the observed densities (Figure 4.3 C). These locations, although having a moderate probability of occurrence (0.5-0.6), had unfavourable conditions for high density, and hence the combined result indicated lower densities, matching the observed data.

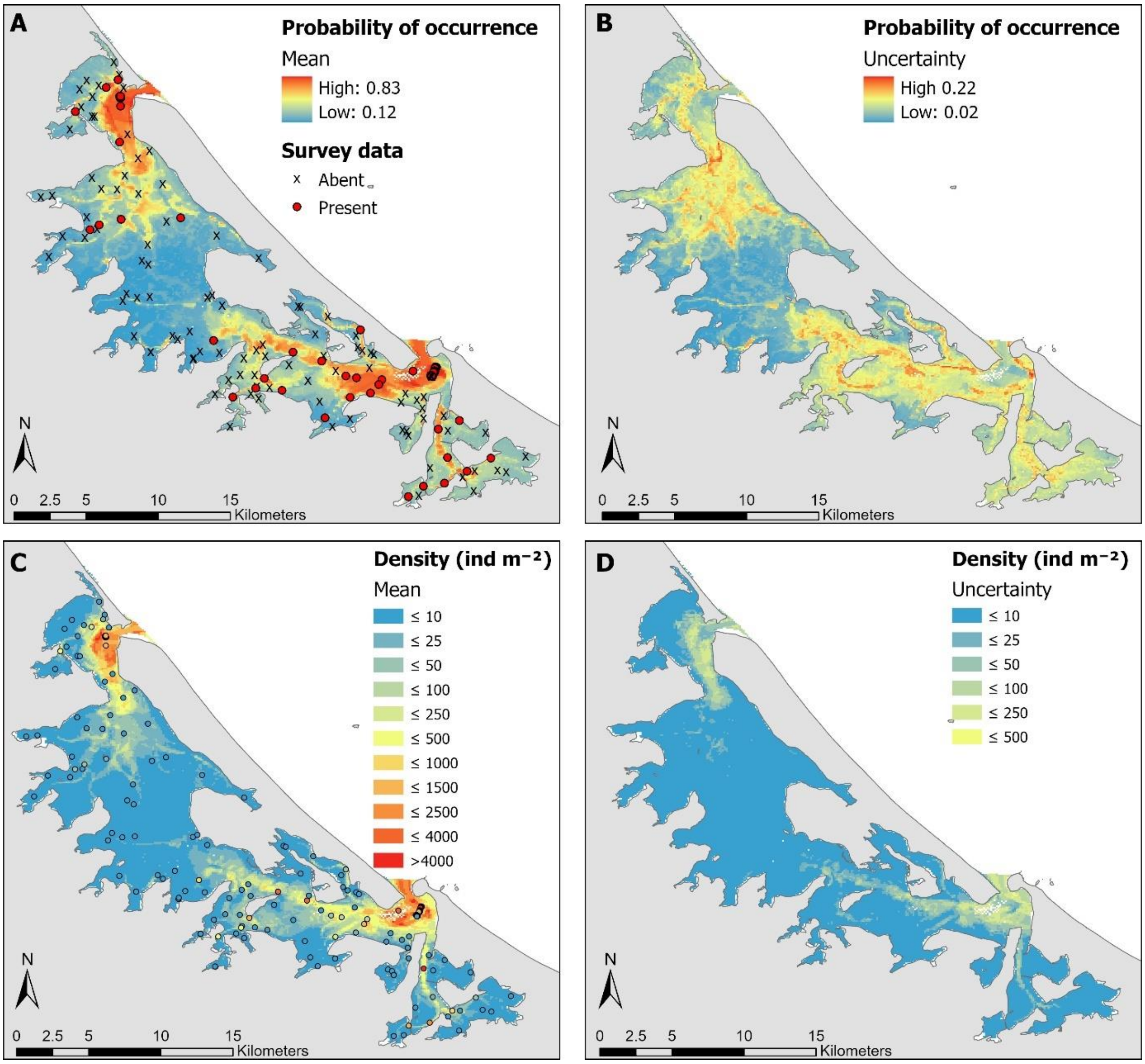

Figure 4.3 Spatial prediction of the probability of occurrence and density of *Paphies* in Tauranga Harbour. Probability of occurrence (A) displays the mean predicted value from 100 bootstrap iterations, and the uncertainty score (90% prediction interval) (B). Mean density (C) is predicted as the probability of occurrence multiplied by the predicted density. Density scales are non-linear. Dots indicate the densities as obtained from the survey data, with colour gradients matching that of the predicted surface. Density uncertainty (D) is measured as the 90% prediction interval and is displayed in the same colour scale as density for comparison, where low values indicate a small range of predicted values around the mean.

4.3.3 *Austrovenus stutchburyi*

From model predictions, *Austrovenus* was found to occur at high densities in intertidal areas with coarser sediments and low sediment mud content. Depth was a very strong predictor for the probability of occurrence, with a relative contribution of 63.3% (Figure 4.2 B). Occurrence was high at shallow depths, dropping quickly below 4 m (Figure A5). There was also a small decline in probability of occurrence with increased mud (Figure A5), which contributed 12.8% to the model predictions (Figure 4.2 B). All other variables had small contributions <10% (Figure 4.2 B) without clear trends (Figure A5). For the density model, gravel and mud had large relative contributions of 36.8% and 19.0%, respectively (Figure 4.2 B). Density was predicted to increase in coarser sediment and lower mud content (Figure A5). Furthermore, density differed along the depth gradient, with a steep decline in predicted density as depth increased from 1 to 2 m. Proportion sand and current speeds contributed <10% to density predictions (Figure 4.2 B).

The combinations of depth and mud content resulted in high probability of occurrence (up to 0.8) in the entire intertidal area and low probabilities in the channels (Figure 4.4 A). Uncertainty predictions were low in most of the intertidal area (Figure 4.4 B), and survey data and predictions matched well (Figure 4.4 A). Since depth was the main driver, most of the intertidal area fell within the shallow zone where probability of occurrence was high. Probability of occurrence was partially reduced in the centre and upper arms of the estuary where the mud content was higher (Figure 4.1 D), locations where uncertainty was also higher (Figure 4.4 B). In these locations the model over predicted presence, and predictions did not match well with the presence/absence survey data. Uncertainty was again highest around the intertidal-subtidal transition in both the northern and southern part of the harbour.

High probability of occurrence was predicted throughout the intertidal area, indicating suitable habitats for *Austrovenus*. However, once the environmental conditions for density were taken into consideration, clear spatial distinctions were found (Figure 4.4 C), with estuary-wide low spatially explicit uncertainty (Figure 4.4 D). Densities were predicted to be low in the subtidal channels (< 50 ind m^{-2}) (Figure 4.4 C), where there was a low probability of occurrence. In the centre and muddy upper arms of the estuary, predicted densities were extremely low (<10 ind m^{-2}) although a moderate probability of occurrence was predicted there initially (Figure 4.4 A). Moderate densities of 500-1000 ind m^{-2} were predicted in the northern and southern most parts of the estuary, and along many of the channels (Figure 4.4 C). The intertidal-subtidal transition had relatively high uncertainty for the probability of occurrence (Figure 4.4 B), which was much reduced in the density predictions (Figure 4.4 D). High densities were found directly opposite both harbour entrances, where densities exceeded 1000 ind m^{-2} (Figure 4.4 C). These areas were relatively exposed and had favourable sediment conditions, e.g. higher percentage gravel and/or sand and low mud content (Figure 4.1).

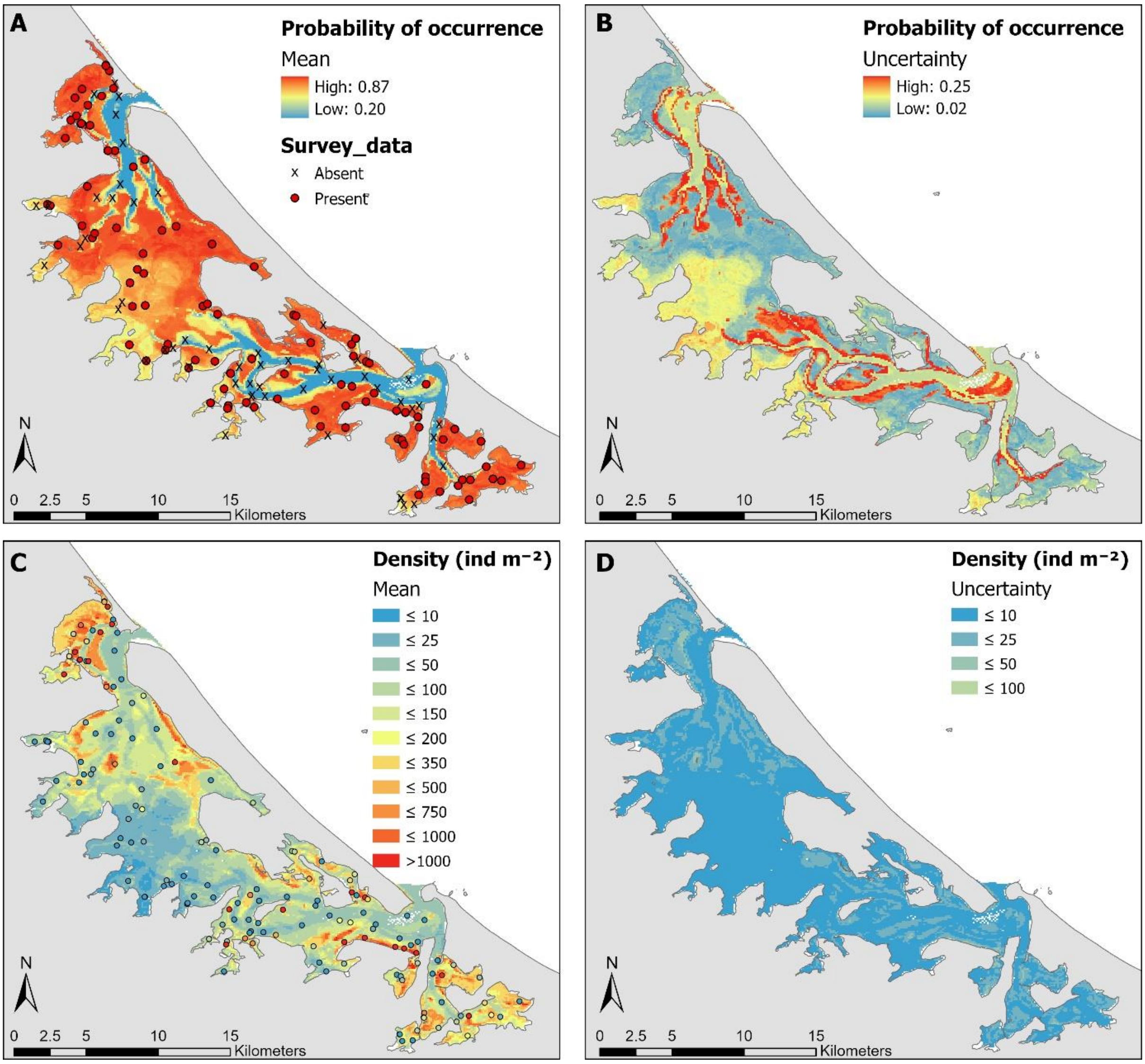

Figure 4.4 Spatial prediction of the probability of occurrence and density of *Austrovenus* in Tauranga Harbour. Probability of occurrence (A) displays the mean predicted value from 100 bootstrap iterations, and the uncertainty score (90% prediction interval) (B). Mean density (C) is predicted as the probability of occurrence multiplied by the predicted density. Density scales are non-linear. Dots indicate the densities as obtained from the survey data, with colour gradients matching that of the predicted surface. Density uncertainty (D) is measured as 90% prediction interval and is displayed in the same colour scale as density for comparison, where low values indicate a small range of predicted values around the mean.

4.4 Discussion

In this study, delta-log normal BRT models were used to predict the occurrence and density of two infaunal bivalve species. Probability of occurrence models for *Austrovenus* and *Paphies* had AUC scores on the evaluation data that indicated strong performance (Table 3) and outputs useful for management (Elith et al. 2008). Accuracy and TSS scores were highest for *Paphies* and indicated better model performance, which was in line with previous observations that species with narrower ecological niches are easier to model accurately when predicting occurrence (Tsoar et al. 2007, Reiss et al. 2011). For the density models, comparison between observed and predicted densities matched well and were significantly correlated for both species, although estimates were somewhat conservative (i.e., density values were underestimated). Good model performance was likely due, at least in part, to the comprehensive spatial coverage of the survey data (Figure 4.1), including environmental variables in the system. Density variations were observed at the fine resolution of this study, and clearly reflected patterns, such as variability in small channels and steep gradients from intertidal to subtidal, that would be lost at coarser resolutions. Furthermore, occurrence uncertainty was relatively high for both species in the intertidal-subtidal transition area. This uncertainty was much reduced when modelling density, resulting in predictions that matched the survey data.

Comparisons between observed and predicted densities indicated densities were underestimated for both species in the combined model outputs (Figure A3), especially towards the higher densities. Overestimating lower values and underestimating higher values is a common issue with regression models (Calabrese et al. 2014). Here the underestimated densities (in particular for *Paphies*) may be generated by some survey points with extremely high densities that the model did not predict. Such survey points had very high numbers of juvenile *Paphies* and can be commonly found at the harbour entrances or on the lower intertidal (Hooker 1995). Areas with high juvenile abundances are often transient or sink populations, whereas adult populations in the subtidal are often well established. Size or life stage could therefore be important in these SDMs and the resulting spatial predictions, as was also shown by Compton et al. (2012) looking at the ontogenetic habitat associations of a demersal fish (*Pagrus auratus*). These population parameters were not modelled here, and SDM predictions assume a population in equilibrium (Evans et al. 2016).

SDMs provided insight into the relative importance of environmental variables associated with occurrence, density, and distribution of the two bivalve species. *Paphies* occurrence was associated with high current velocities, whereas *Austrovenus* was strongly associated with shallow depths. Depth is often a proxy rather than having a true effect on species distribution, as many environmental and biological variables are related to depth, such as temperature, light penetration, oxygen concentration, and predation intensity, and could be the underlying attributes affecting distribution. Similarly, for *Paphies*, the favoured deeper channel habitats near the mouth may have a better food supply (Norkko et al. 2006). As environmental variables often represented proxies and resulted in accurate occurrence and density predictions, caution is needed when extrapolating these models to other areas.

Density models were associated with multiple environmental variables each contributing small-to-medium proportions (~15-40%) in explaining the observed densities. Sediment characteristics were important for predicting the density of both species, matching empirical evidence (Thrush et al. 2005, Anderson 2008). Higher densities of *Paphies* were linked to sandy substrates, and occurrence to higher percentage gravel. Anderson (2008) demonstrated that *Paphies* are most abundant in sandy substrates and have a low tolerance for mud, reaching optimum density in sediments with 3.4% mud content. *Austrovenus* has a wide sand-mud tolerance (Ellis et al. 2006), but density is expected to drop if mud content exceeds 11% (Anderson 2008). Furthermore, these findings are supported by previous observations showing density of *Austrovenus* has a strong negative association with sediment mud content, whereas the probability of occurrence of *Austrovenus* is not sensitive to sediment mud content at a large scale (Thrush et al. 2003, Thrush et al. 2005). The SDMs indicate that the species occupy different areas in the estuary, as little overlap is predicted when comparing patterns of the two combined density maps, and this is in agreement with known habitat preferences (Powell 1979). There are some restricted areas where both species can be found at low or intermediate densities (see Figure 4.3Figure 4.4); for example, juvenile *Paphies* and *Austrovenus* can be found in the low intertidal (Hooker 1995).

Although all models performed well, clear differences were observed in their ability to distinguish spatial patterns in habitat suitability. The probability of occurrence model had a large contribution in distinguishing spatial patterns in habitats suitable for *Paphies* to occur, and those areas almost always had environmental conditions suitable for medium to high densities. However, for *Austrovenus*, probability of occurrence was less important for distinguishing patterns in suitable habitats for shellfish beds, as probability of occurrence was high throughout the intertidal (shallow) areas of the estuary. That is, the patterns did not reflect areas where the species thrives. The density model instead provided more insight into habitat quality and the areas that can sustain high densities, which had a relatively large contribution in distinguishing spatial patterns for *Austrovenus*, confirming our hypothesis. Our findings are in line with previous studies noting that probability of occurrence models tend to create more accurate predictions for species with a narrow ecological niche (e.g. Tsoar et al. 2007, Reiss et al. 2011, Morán ‐ Ordóñez et al. 2017). Furthermore, results indicate that for species with a narrow ecological niche occurrence and density predictions correlate well, whereas this is not necessarily the case for species with a wide distribution. This aligns with conflicting outcomes from previous studies that focussed on the use of occurrence models as surrogates for density (e.g. Pearce and Ferrier 2001, Jiménez-Valverde et al. 2009, Gutiérrez et al. 2013, Young and Carr 2015), and build on these by showing the added value of combining occurrence and density predictions. For example, Gutiérrez et al. (2013) found a good overlap between occurrence and abundance predictions for a rare mountain butterfly. On the other hand, for fish (Young and Carr 2015) and arthropods (Jiménez-Valverde et al. 2009) good correlations were found for some species but not others, corresponding to our findings that high occurrence does not necessarily equate to high density.

Spatial predictions, including uncertainty estimates, and a better understanding of conditions under which species occur and thrive are crucial for spatial management. SDM outcomes can be used for restoration initiatives (Heuner et al. 2016) by informing managers on where to pursue restoration, by targeting those areas predicted to have favourable environmental conditions to support high densities with high certainty and avoiding sites with low habitat quality and high certainty (Moilanen et al. 2006). An interest lies in identifying locations with high predicted densities and high uncertainty or discrepancies with observed numbers, to determine the cause (e.g. overharvesting, allee effects, or missing environmental stressor) and potential management strategies. Shellfish beds are known to be biodiversity hotspots (Craeymeersch and Jansen 2019), hence information on the location and extent of dense beds can be an indicator of biological diversity for significant conservation areas (Asaad et al. 2017). SDM outputs provide spatial information for MSP, which can be applied to strategically plan use for maximum benefits and minimized disruption. For example, models from this study could be used to identify changes in densities as a result of anthropogenic stressors or activities in the case study area, like terrestrial sediment input affecting sediment mud content (Thrush et al. 2004) or harbour dredging affecting bathymetry and current velocity (Healy et al. 1997).

Furthermore, both studied species are important food sources in the area, hence prioritising locations with high density beds for managing wastewater discharges and testing for toxins can help maximize benefits from this ecosystem service.

This study emphasizes the value in including predictions for both density and probability of occurrence in conservation and management applications. This is because high probability of occurrence (which is much more commonly predicted using SDMs at present) does not necessarily equate to high density, as was observed for *Austrovenus*. Comparing two species with contrasting habitat associations allowed us to evaluate the generality of the approach, which is applicable beyond bivalves and estuarine environments. Spatial predictions could be implemented in geospatial tools to inform MSP like Seasketch, Zonation, or Marxan, for marine reserve design, or InVEST for ecosystem services (Janßen et al. 2019). My findings illustrate an important challenge in conservation planning and management, as SDM studies used to inform management often consider occurrence only (Rondinini et al. 2006). Yet, drivers of abundance can be different from those for occurrence for some species. Hence, management that simultaneously considers both density and occurrence probabilities will enable targeted protection of areas that are of greatest ecological value to species of interest.

CHAPTER 5

Applying ecological principles to predict the spatial distribution of multiple shellfish-generated ecosystem services

5.1 Introduction

Ecosystems worldwide are subjected to growing pressures (reviewed in Sanderson et al. 2002, Halpern et al. 2007) that affect their health, functioning and ability to provide benefits utilised by society (i.e. ecosystem services; ES) (MEA 2005). A holistic management approach like Ecosystem-Based Management (EBM) is needed to address the cumulative effects of multiple human uses and pressures, and to safeguard environmental resources while allowing sustainable use (McLeod and Leslie 2009, Delacámara et al. 2020). A key challenge in environmental management is determining how to manage multiple ES simultaneously (Tallis and Polasky 2011) in an efficient and coordinated approach to result in better outcomes for people and nature (Arkema et al. 2015). The analysis of spatial patterns of multiple ES improves our understanding of the distribution of services in an ecosystem, whether interactions (e.g. synergies and trade-offs) among services might occur (Qiu and Turner 2013), and can help prioritise areas for conservation (Naidoo et al. 2008). Spatial information on ES has improved decision making through EBM or Marine Spatial Planning (MSP) (McKenzie et al. 2014, Veidemane et al. 2017, Verutes et al. 2017), including testing different management scenarios (Guerry et al. 2012, Arkema et al. 2015), conservation strategies (Rees et al. 2012, Chung et al. 2015) and ES vulnerability to stressors (Cabral et al. 2015, Farella et al. 2020).

Mapping ES can be challenging as the spatially explicit models used for assessments are often complex, time-consuming, and/or data-intensive (Fulton et al. 2011, Martínez-López et al. 2019). Spatially relevant data is often a limiting factor in marine environments (Townsend et al. 2018) and has resulted in a lag in spatially explicit assessments of marine ES supply (Maes et al. 2012a, Townsend et al. 2014). Overcoming these challenges is particularly important in data-scarce environments where ES supply and demand is high, like estuarine and coastal systems (Barbier et al. 2011). ES are underpinned by processes and functions in a system (Haines-Young and Potschin 2010), and supply is related to presence and abundance of ecosystem service providers (ESP; Kremen 2005, Luck et al. 2009). ES supply maps that are not based on ecological knowledge can miss critical information, especially when not considering functional variation within habitats or between key service providers (Kremen 2005, Barbier et al. 2008), heterogeneity in (marine) environments (Crowder and Norse 2008) and the connectivity between them (Townsend et al. 2018). ES are not generated uniformly across landscapes (Koch et al. 2009), and even within habitats that seem superficially homogenous (e.g. sandflats, water column, etc.), complexity in ecosystem functioning exists (Snelgrove et al. 2014). To successfully manage ES on a local scale, assessments should consider these nuances in ways that account for ecological complexity and heterogeneity that underpin ES, yet balanced against the preferred simplicity and downsides of intensive data and modelling requirements to provide a pragmatic step forward in holistic management of data-scarce environments.

Ecological complexity can be incorporated through existing ecological knowledge to provide a first assessment of important areas for ES provision. Examples of methods used in marine systems include ecological indicators (e.g. Hattam et al. 2015b, Hooper et al. 2017, Manea et al. 2019) and matrix approaches (e.g. Geange et al. 2019, Neumann et al. 2019) using proxies and expert based look-up tables, respectively (Burkhard et al. 2012). Drawbacks from these approaches include assumptions around equal scoring per habitat or ESP and a lack of mechanistic information on the formation of ES (Martínez-Harms and Balvanera 2012). Mechanistic information available from ecological studies can be used to link ecosystem processes and functions relevant to service supply (Petter et al. 2013), and assess feedbacks in complex systems (Broszeit et al. 2019). The ecosystem principle approach (EPA; Townsend et al. 2011) provides a means of linking ecosystem services to well understood ecological principles to provide a semi-quantitative assessment of ES potential. This approach was used to map three ES in a New Zealand case study (Townsend et al. 2014), which were validated with empirical data supporting the validity of the approach (Townsend and Lohrer 2019). Other examples in marine environments using a similar approach come from the deep-sea (Jobstvogt et al. 2014, Turner et al. 2019) and UK marine waters (Broszeit et al. 2019), which identified principles but did not map services. This approach has not yet been applied to spatially assess ES multifunctionality or multi-species assessments of services, nor assess their interactions, which is critical for EBM.

Estuarine and coastal management efforts are focussed on preserving ecosystem functioning and to conserve, restore, and rehabilitate ecosystems (Weinstein 2008). For example, efforts are made to restore degraded shellfish beds and reefs in estuaries around the world (Beck et al.

2011) to regain lost services (Coen et al. 2007; Grabowski & Peterson 2007). Hence, gaining insights in important locations for multi-service potential for different shellfish species can help both current management of existing resources, as well as guide restoration efforts. A strong focus exists on restoring single species communities, particularly reef forming species like oysters or mussels (Fitzsimons et al. 2020). Soft sediment habitats, in contrast, are sometimes construed as 'barren' or homogenous, ignoring the small scale heterogeneity of infaunal communities, bivalve densities and the functions and services they provide (Thrush et al. 1989, Boldina and Beninger 2013). Bivalves are well-studied estuarine organisms, and inter-species variations in their contributions to ecosystem functioning have been observed, like varying responses of clearance rates to increases in turbidity of infaunal versus epifaunal species (e.g. Bacon et al. 1998, Hawkins et al. 1998). Hence service potential will depend on species specific attributes related to their ecology (density, habitat, life-history etc.). Here, we focus on predicting ES potential spatially for two bivalve species with similar ecology (infaunal, suspension-feeding) but distinctly different habitat associations (subtidal vs. intertidal, and spatially restricted or wide distribution), and discuss implications for spatial management.

Infaunal bivalves contribute to a range of ES (Carss et al. 2020) and in this study we focussed on a subset of four ES that are relevant to management and for which literature is available on which to base ecological principles. Bivalves are a food source ('*Food provision ES*') that can be commercially or recreationally harvested, act as a biofilter thereby improve water clarity ('*Water quality regulation ES*'), contribute to removing excess nutrients from the system ('*Nitrogen removal ES*'), and beds and reefs can mitigate erosion of shorelines by stabilising sediments ('*Sediment stabilisation ES*') (Table 5.1) (Smaal et al. 2019). These services are representative of three out of four ES bundles identified for shellfish and are each underpinned by key ecological mechanism, including biomass production, filter feeding, bioturbation, and habitat provision, respectively (Chapter 2). In this study, the ecosystem principles approach to mapping shellfish-generated ES potential is applied to identify areas of relative individual ES potential within an estuary, determine their co-occurrence, and assess hotspots of multiple service delivery, for two bivalve species with varying habitat associations. Our approach explicitly incorporates the known effects of variations in shellfish density on ecosystem processes and functions (Newell 2004, Sandwell et al. 2009), which often vary along environmental gradients in estuaries (Pratt et al. 2014a). Although applied to shellfish, insights from this study extend beyond estuaries and coasts, and provide an approach applicable to other data-scarce habitats or those that are considered superficially homogenous in their service provision.

5.2 Methods

A semi-quantitative approach to mapping ES potential (Townsend et al. 2011, Townsend et al. 2014) was applied to a case study on infaunal bivalves in Tauranga Harbour, New Zealand. The system is representative of many estuaries, and consists of a semi-enclosed barrier harbour (220 km^2) with approximately 66% intertidal area exposed on low tide (Figure 5.1). The city of Tauranga is located at the southern part of the harbour, with a population exceeding 150,000 in 2020 (Statistics New Zealand 2020). The city has one of New Zealand's largest ports and the harbour is culturally important for the local indigenous community and is used for varied recreational activities (fishing, paddling, shell collecting, bird watching, etc.). Within the harbour, infaunal bivalves form a large proportion of the benthic community biomass and are key species in providing ecosystem processes and the resulting ES. The two species under example are *Austrovenus stutchburyi* and *Paphies australis* (*Austrovenus* and *Paphies* hereafter), which are both infaunal, suspension feeding bivalves, living within the top few centimetres of the sediment (Powell 1979). *Austrovenus* is found on the intertidal sand and mudflats with a wide distribution, whereas *Paphies* is predominantly found in subtidal channels near the harbour entrances (Chapter 4). In Tauranga Harbour, these species are important for cultural and recreational gathering, and although not commercially fished, they are elsewhere in the country (Marsden and Adkins 2010, Pawley et al. 2013).

5.2.1 Ecological principle definitions

In this study, the capacity of *Austrovenus* and *Paphies* to contribute to four ES in Tauranga Harbour was assessed, including food provision, water quality regulation, nitrogen removal, and sediment stabilisation (see Appendix 4 for a detailed description). The contribution of bivalves to these ES is a subset of the total for the estuary, and other ESP may contribute to these ES also, but are not the focus of this study. For each ES, a specific set of principles was designed that described and generalised the known links between biological and environmental variables and ES potential (see Townsend et al. 2011 for detailed methodology). Principles were designed to reflect shellfish effects on ES potential, based on 'best knowledge to date' from scientific literature and expert opinion, and can be updated as new links are found. As

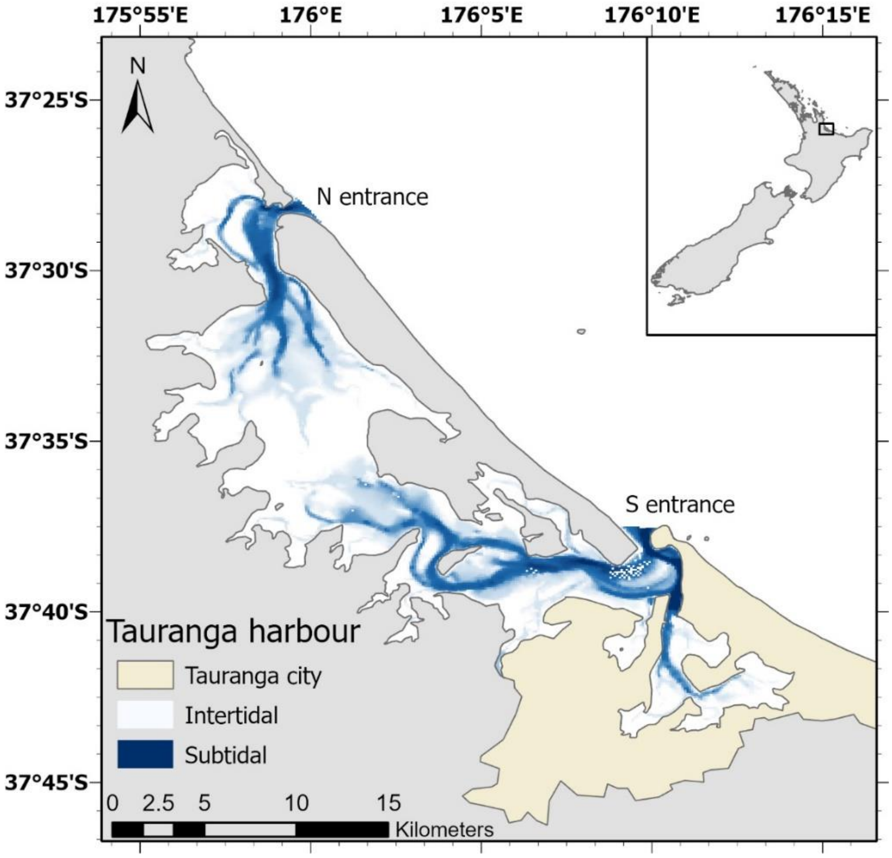

Figure 5.1 Map of Tauranga Harbour located along the east coast of the North island of New Zealand (top-right panel) showing the northern (N) and southern (S) entrances, subtidal (blue) and intertidal (white) area in the harbour, and the urbanised area (Tauranga city).

shellfish capacity to contribute to ES was assessed, presence-absence of the species is a first consideration for all ES. In previous work, *Austrovenus* and *Paphie*s probability of occurrence and densities were spatially predicted in the study area using species distribution models, based on environmental variables and extensive surveys (Chapter 4). Based on these 100 m x 100 m grid-scale predictions, shellfish were considered absent and unlikely to affect ES provision if the probability of occurrence is low (less than 0.3) or predicted density is less than 20 ind m^{-2}, referred to herein as functionally absent.

For the locations where shellfish were predicted to be present in sufficient densities, the ecological principles defined for that service were applied (see Table 5.1 and Appendix 4 for detailed description of all principles). For example, the potential for food provision from shellfish through recreational gathering is related to a) the density of desirable (large) individuals in a location (Hartill et al. 2005), b) accessibility which reflects the likeliness of people gathering in that location (Tinlin-Mackenzie et al. 2019), and c) can be negatively affected if contamination render the shellfish less desirable or unsuitable for consumption

Table 5.1 Description of the four ecosystem services (ES) and principles (P) and their relative weighting (out of 10 per ES) and the basic aligned data used to generate a value (-1 to 1) for each principle. A detailed description of all principles cited literature underpinning justification, and the aligned data are provided in Appendix 4 and 5, respectively.

Principle description		**Weighting**	**Aligned data**
ES1	Food provision		
P1.1	Large bivalves are more desirable for consumption, hence for sites with high densities of large individuals, service value will be higher.	5x	Density of large individuals
P1.2	Easily accessible locations provide higher service potential, which is reduced if more effort is required to access the shellfish bed. Locations within walking distance and on the intertidal/shallow subtidal are scored higher.	3x	Distance to access point & bathymetry
P1.3	High contamination levels can render shellfish less desirable or unsuitable for consumption and can decrease food provision potential in contaminated sites.	2x	Sediment heavy metal levels
ES2	Water quality regulation		
P2.1	Shellfish bed capacity for water clearance is a function of density and current velocity. A density threshold is reached after which bed clearance rate does not increase. Clearance rates generally show an optimum at flow speed around 10-20 cm s^{-1} and decreasing values at higher flow speeds.	5x	Density & mean current velocity
P2.2	Water filtration by shellfish beds on the intertidal is restricted by the time the site is submerged. *Austrovenus* feeding window is 4 h around high tide, hence intertidal sites with shorter inundation period are providing less service.	2x	Tidal inundation
P2.3	Infaunal bivalves reduce filtration rate when suspended sediment concentrations (SSC) exceed their particle processing capacity. An optimum is found for both species with *Paphies* more sensitive to SSC than *Austrovenus*.	3x	Relative turbidity
ES3	Nitrogen removal		
P3.1	Shellfish density promotes denitrification up to moderate/high densities due to increased bioturbation. At extreme densities denitrification can be reduced due to high sediment oxygen demand.	4x	Density
P3.2	Organic matter provides a nitrogen source for nitrification-denitrification and therefore positively affects nitrogen removal.	3x	Organic matter
P3.3	Shellfish are expected to have a larger contribution to increasing denitrification at sites with medium mud content. At sites with a high mud content, denitrification is limited by diffusion of solutes and possible competition with microphytobenthos for the same N source. At sites with very coarse sediments (low mud content), denitrification is limited by physical advection of solutes.	2x	Mud content
P3.4	Denitrification in intertidal sediments is restricted by the time the site is submerged, especially sites that are higher up the shore.	1x	Tidal inundation

Table 5.1 Continued

Principle description		Weighting	Aligned data
ES4	Sediment stabilisation		
P4.1	In muddy sediments (>30% mud), infaunal bivalves often destabilise the sediment through bioturbation. In sandy sediments, bivalves can potentially stabilise the sediment through bed armouring.	4x	Mud content
P4.2	At high densities, shellfish provide a high potential for bed armouring, whereas no effect is expected at low densities. The effects can be highly context specific, here we focus on where shellfish can have a stabilising effect (sandy sediments).	3x	Density
P4.3	Flow induced shear stress affects sediment stability. The potential effect of shellfish is low if current velocity is below a critical erosion velocity and no erosion occurs, or at very high current velocities, when shellfish activity cannot counteract the erosive power of currents. Optimum at intermediate velocities when shellfish can have the largest contribution to sediment stability.	3x	Mean current velocity

(Gagnon et al. 2004) (Table 5.1, Appendix 4). For each principle, appropriate, available spatial data were used reflecting the inherently spatial nature of the (set of) conditions described (Table A4, Figure A10). In the example of food provision, data was available on the density and size distribution of the two species, accessibility was reflected through distance to access points and bathymetry, and contamination data was available as heavy metal concentrations in the sediment (Table A4, Figure A10).

5.2.2 ES mapping

A scoring structure per principle was used to indicate the form of the relationship between that principle and its contribution to an ES, with assigned values normalised (ranging from -1 to 1) allowing all principles to be assessed on the same scale (Appendix 4) (Townsend et al. 2014). Positive values indicated areas suitable for high service potential, whereas negative values were used to down weight locations where service potential was negatively affected by environmental conditions. A value of zero indicated no effect or influence under the conditions specified in the principle. For example, the scoring structure for accessibility is derived from distance to access points and water depth, with relatively high scores (principle score = 1) in areas that are close to shore (< 0.5 km) in the intertidal, and lowest scores in deep subtidal channels (principle score = 0). Each principle was then weighted based on its importance to service potential (Townsend et al. 2014), and were tested using a sensitivity analysis (see below). Weightings ranged from 1 to 5 per principle and all weightings per ES added up to 10.

Thereby a total score out of 10 was generated, which reflected the principles' relative importance to each other, but no distinctions were made between services (i.e. all services had the same potential maximum score of 10). In the food provision example the weightings were divided as follows: density 5x, accessibility 3x, and contamination 2x (Table 5.1).

For each service, the biological and environmental variables aligned to the principles (Table 5.1) were used to create a data layer per principle, by applying the scoring function and multiplying by the assigned weighting (Table 5.1, Appendix 4). Functionally absent cells were not assigned ES scores. For grid-cells where shellfish were predicted to be present, all scored layers applying to a service were combined in an additive model, resulting in four ecosystem service maps per species. Combined, the principles indicate areas with relatively high or low service potential, where the ES score for service *i* in gridcell *j* ($ES_{i,j}$) is calculated as follows:

$$ES_{i,j} = \mathrm{w}_1\mathrm{P}_{1,j} + \mathrm{w}_2\mathrm{P}_{2,j} + \ldots + \mathrm{w}_n\mathrm{P}_{n,j} \quad (1)$$

Where $\mathrm{P}_{n,j}$ is the n^{th} principle score for grid-cell j, multiplied by the associated weighting for principle *n* (w_n) that apply to ES i. $\mathrm{ES}_{i,j}$ scores could range from 0 (i.e. no service potential) to 10 (i.e. maximum service potential).

5.2.3 Spatial analysis of ES maps

Resulting service maps were analysed for spatial patterns of individual ES and ES co-occurrence for both species. A threshold approach was applied to assess patterns and visualise individual ES maps for medium and high ES potential for all services in Esri ArcGIS Pro (v. 2.8.0). All following spatial analyses focus on the area where shellfish can contribute to service potential, by conducting analyses on the areas where shellfish are present only. First, the area (km^2) and proportion of total presence area (%) of medium (ES score > 5) and high service scores (ES score >8) were calculated. Because scores are relative, applying a threshold approach enabled the calculation of area and proportion of medium and high ES potential comparable between ES that is not based on the distribution of ES over the grid-cells (Schröter and Remme 2016). Spatial autocorrelation was assessed using a Global Moran's I (Cliff and Ord 1973), and statistical significance (pseudo p-value) of these scores was assessed using a Monte Carlo permutation test (number of permutations = 999) for Moran's I statistics in R (R Core Team 2013) using the 'spdep' package (Bivand et al. 2015).

Co-occurrence of ES were examined through pairwise Pearson correlations of ES pairs (Mouchet et al. 2014). Here, positive correlations indicate the capacity to contribute to both services under the same conditions. Spatial autocorrelation in ES maps can affect correlation assessments (Willemen et al. 2010, Gos and Lavorel 2012), where the value of the correlation coefficient is not affected, however, p-values tend to be very low (“significant”) simply due to the very large sample size (19980 grid-cells in the map domain) (Cliff and Ord 1973). Therefore, correlation analyses were conducted on a 5 and 10% random sample (without replacement) of the ES maps (*Austrovenus* and *Paphies* respectively to correct for the difference in presence area size), repeated 10,000 times, to calculate an average Pearson correlation coefficient (R).

Following the individual ES assessment, intensity and richness analyses were conducted on combined ES maps (Schröter and Remme 2016). As all maps were equally weighted (scores from 0-10), individual map scores for service *i* were summed for all four individual ES maps per species to calculate intensity per grid-cell *j*:

$$\text{Intensity} = \sum_{i=1} \text{ES}_{i,j} \qquad (2)$$

For richness calculations, all continuous service maps were converted to binary presence/absence scores (PA) by applying a threshold approach (Schröter and Remme 2016). A score of 5 was chosen as a threshold, as it reflects all medium to high (relative) scoring categories, and the average mean score from all 8 maps was 4.7. Richness is calculated as the sum of the binary presence/absence scores per ES *i* per gridcell *j* ($\text{PA}_{i,j}$):

$$\text{Richness} = \sum_{i=1} \text{PA}_{i,j}$$

To determine statically significant areas of high service potential (hotspots) and low service potential (coldspots) for intensity multiplied by richness data, the ‘Hotspot analysis (Getis-Ord GI*)’ tool in ARCGIS PRO was used. This tool determines whether a grid-cell and its surrounding grid-cells (the neighbourhood) are significantly different from the average of the study area, using Gretis Ord Gi* statistics (Getis and Ord 1992). Raster values were rounded to the nearest numbers and aggregated in polygons for grid cells with equal values. For both the ‘Hotspot analysis’ and Global Moran’s I calculations, a k-nearest neighbour (k=8) approach was used, as to ensure each feature was assessed within the context of its closest neighbours.

5.2.4 Sensitivity analysis

A sensitivity analysis was conducted to determine whether small changes in the weighting of each principle would result in large changes in service potential scoring (Townsend et al. 2014).

Individual weightings were increased or decreased by one unit sequentially, whilst keeping the total weighting out of 10. Each possible combination of 1 point change in weighting were considered for the multiple principles per service, yet no principle was allowed to have a weighting of 0. For each iteration in the sensitivity analysis, the residuals between the scores derived from the original weighting and new predictions were calculated. The square root of the averaged squared residuals were considered as a measure of prediction uncertainty (similar to standard deviation):

$$\mathrm{Uncertainty}_{i,j} = \sqrt{\frac{\sum_{\mathrm{k}=1}^{\mathrm{N}}\left(\mathrm{ES}_{i,j} - \mathrm{ES}_{k,j}\right)^2}{\mathrm{N}}} \qquad (4)$$

Where $\mathrm{Uncertainty}_{i,j}$ is the uncertainty score for ES i in gridcell j, $\mathrm{ES}_{i,j}$ is the ES score i in gridcell j with original weighting, $\mathrm{ES}_{k,j}$ the ES score in gridcell j derived for the kth iteration in the sensitivity analysis, and N the total number of iterations in the sensitivity analysis.

5.3 Results

5.3.1 Spatial patterns of individual ES

ES scores generated through the summing of weighted principles resulted in maps reflecting clear spatial patterns of ES potential for food provision, water quality regulation, nitrogen removal, and sediment stabilisation by *Austrovenus* and *Paphies* (Figure 5.2). The relative importance of principles was determined by their assigned weighting and the robustness of model outputs to small changes in these weightings was assessed through a sensitivity analysis in which combinations of small changes in principle layer weightings (± 1) were compared against the predicted ES scores. These uncertainty estimates showed low average variation around the predicted ES scores, with average variation ranging from 0.36 to 0.75 points, and a highest predicted maximum uncertainty of 1.63 points for *Austrovenus* food provision (Table 5.2). Model outputs were largely robust against minor errors in weighting, which did not alter the general patterns observed in ES predictions. All service maps displayed strong, statistically significant spatial aggregations (expressed as the Moran's I value, Table 5.2), indicating that high values were clustered together. For gridcells where species were functionally present, the average service values varied widely between services, ranging from 2.0 to 7.0, and not all services reached the maximum potential score out of 10 (Table 5.2).

Table 5.2 Overview of individual ES scores, spatial structure of ES and results of a sensitivity analysis. Overview ES scores include the average, median and maximum as well as the standard deviation for the areas where bivalves are present. Global Moran's I was used to indicate whether ES scores were significantly clustered, with values range from -1 (fully dispersed) to +1 (fully clustered). Statistical significance (pseudo p-values) for these scores were assessed using a Monte Carlo permutation test for Moran's I statistics (permutations = 999). Uncertainty scores (mean and maximum for the study area) were derived from the sensitivity analysis on the weightings applied to the principles, and reflect the variation around the original mean ES scores (varied by ± uncertainty score).

Species	**ES**	**Overview ES scores**				**Clustering**		**Uncertainty**	
		Mean	**Median**	**Max**	**SD**	**I**	**pseudo p-value**	**Mean**	**Max**
Austrovenus	Food provision	2.0	1.1	10	2.4	0.87	0.001	0.73	1.63
	Water quality	5.1	5.0	10	1.5	0.73	0.001	0.59	0.82
	Nitrogen removal	5.8	5.9	8.9	0.8	0.84	0.001	0.36	0.75
	Sediment stability	4.8	4.7	10	1.7	0.93	0.001	0.64	0.98
Paphies	Food provision	2.6	1.8	8.8	2.6	0.93	0.001	0.60	1.42
	Water quality	4.7	4.7	7.2	0.6	0.78	0.001	0.67	0.80
	Nitrogen removal	5.7	5.5	8.3	0.9	0.85	0.001	0.38	0.62
	Sediment stability	7.0	7.0	10	1.2	0.74	0.001	0.75	1.09

Table 5.3 Area of medium (>5) and high (>8) service scores, expressed as area (km^2) and proportion of the total bivalve presence area per service.

Species	**ES**	**Medium scores (>5)**		**High scores (>8)**	
		Area (km^2)	**Proportion (%)**	**Area (km^2)**	**Proportion (%)**
Austrovenus	Food provision	21	13	8.1	5.1
	Water quality	76	48	10.0	6.3
	Nitrogen removal	133	84	1.3	0.8
	Sediment stability	71	45	2.1	1.3
Paphies	Food provision	12	21	1.2	2.2
	Water quality	15	27	0.0	0.0
	Nitrogen removal	42	73	0.6	1.1
	Sediment stability	53	94	9.4	16

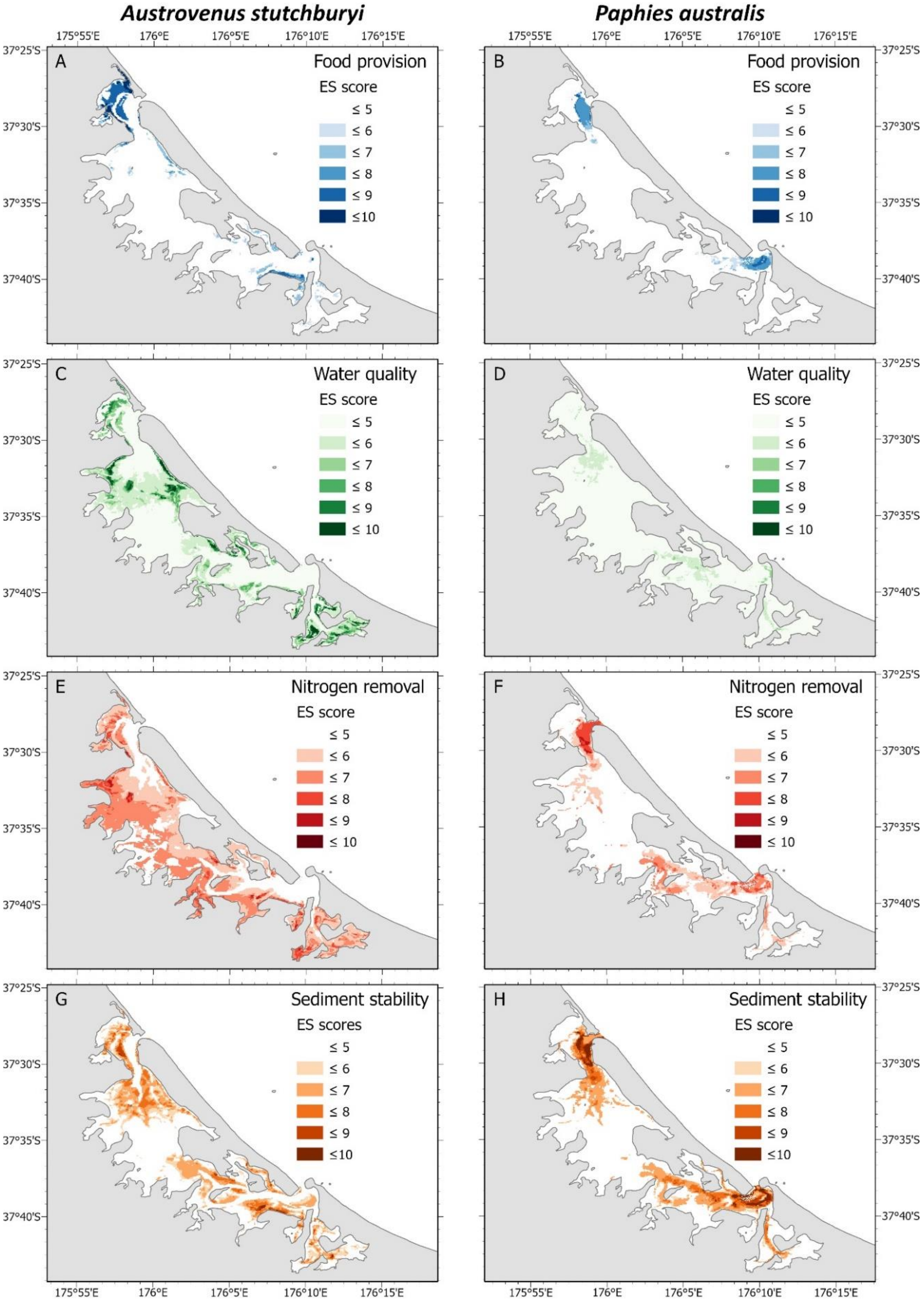

Figure 5.2 Ecosystem services maps for *Austrovenus stutchburyi* (left column) and *Paphies australis* (right column). Maps display ES scores binned per score point for the five highest categories, and all low scores (≤5) are binned together. Maps are displayed per service: food provision = A & B, water quality regulation = C & D, nitrogen removal = E & F, and sediment stability = G & H.

Austrovenus contributed to all four ecosystem services in Tauranga Harbour, yet there was spatial variation in magnitude across the Harbour (Figure 5.2). In general, food provision tended to be high (ES score > 8) in 5.1% of the area where *Austrovenus* is found (Table 5.3), particularly at the harbour entrances with highest values in the northern harbour and directly opposite the southern harbour entrance (Table 5.2 A). Service potential was reduced in the areas nearby the city (southernmost part of the harbour, Figure 5.1) due to higher levels of contamination. *Austrovenus* contribution to water quality service potential was highest in the centre of the northern harbour, and further up the reaches in the southern part (Figure 5.2 C), and contributed to high scores in 10 km^2 of the estuary (Table 5.3). Medium contribution (ES score > 5) of *Austrovenus* to nitrogen removal was found throughout the harbour (Figure 5.2 E, Table 5.3). Many locations had conditions suitable for nitrogen removal to take place with the presence of mud and organic matter content (in 84% of the area *Austrovenus* was present), yet there were only few locations that were identified as high (0.8% or 1.33 km^2 with scores > 8) (Figure 5.2 E, Table 5.3). Sediment stabilisation mostly occurred in areas around the main channels, yet no service delivery was predicted in the central part of the estuary (due to lower principle scoring associated with higher mud content) (Figure 5.2 G). High service delivery associated with *Austrovenus* was expected to be limited to small patches, mostly opposite the harbour entrances.

Paphies' contribution to the four ecosystem services depended on its predicted density. Food provision potential was predicted to be high at both harbour entrances where large individuals were found in high density. This covered approximately 1.2 km^2 (Figure 5.2 B, Table 5.3). Since *Paphies* is predominantly a subtidal species, accessibility was the main factor limiting its collection as a food resource and resulted in scores ≤8.8 (Table 5.2). *Paphies* did not contribute substantially to water quality regulation, and only showed scores up to 7.2 in the more central parts of the harbour (Figure 5.2 D), and nowhere exceeded a score of 8 (Table 5.3). The main *Paphies* beds were found at the harbour entrances where water is clear due to exchange with the open ocean. Under these conditions, high current velocities limit the capacity of shellfish to filter the large volume of overlying water. Nitrogen removal had large areas of medium service potential in most of the channels where *Paphies* can be found (73% with scores > 5), yet high scores can only be found in 1.1% of the presence area (Figure 5.2 F, Table 5.3). *Paphies* consistently contributed to sediment stabilisation and provided a medium service potential (score >5) in 94% of the area they occupy; of which 16.4% were scores > 8 (Table 5.3). There were large areas where sediment stabilisation occurred in the main channels at the entrances with high current velocities and high densities in sandy substrates to armour the seafloor (Figure 5.2 H).

5.3.2 ES co-occurrence

Co-occurrence of services were assessed as the mean from the randomly resampled Pearson correlation between each service pair per species. Many pairs of services were significantly correlated, however, small correlation coefficients (e.g. < 0.2) in some cases indicated weak relationships. Most correlations between services were positive, indicating congruence of high service potential under the same conditions (Figure 5.3). For *Paphies*, there were positive correlations between sediment stability, food provision, and nitrogen removal (Figure 5.3). High scores for each of these ES coincided spatially with the high-density beds at the harbour entrances **(**Figure 5.2). Water quality regulation showed a weaker negative correlation with food provision and negligible (non-significant) correlations to nitrogen removal and sediment stability. For *Austrovenus*, the strongest positive correlation was found between water quality and nitrogen removal (R = 0.53), followed by food provision and sediment stability (R = 0.41), and sediment stability and water quality regulation (R = 0.3). All other correlations were small or non-significant (Figure 5.3).

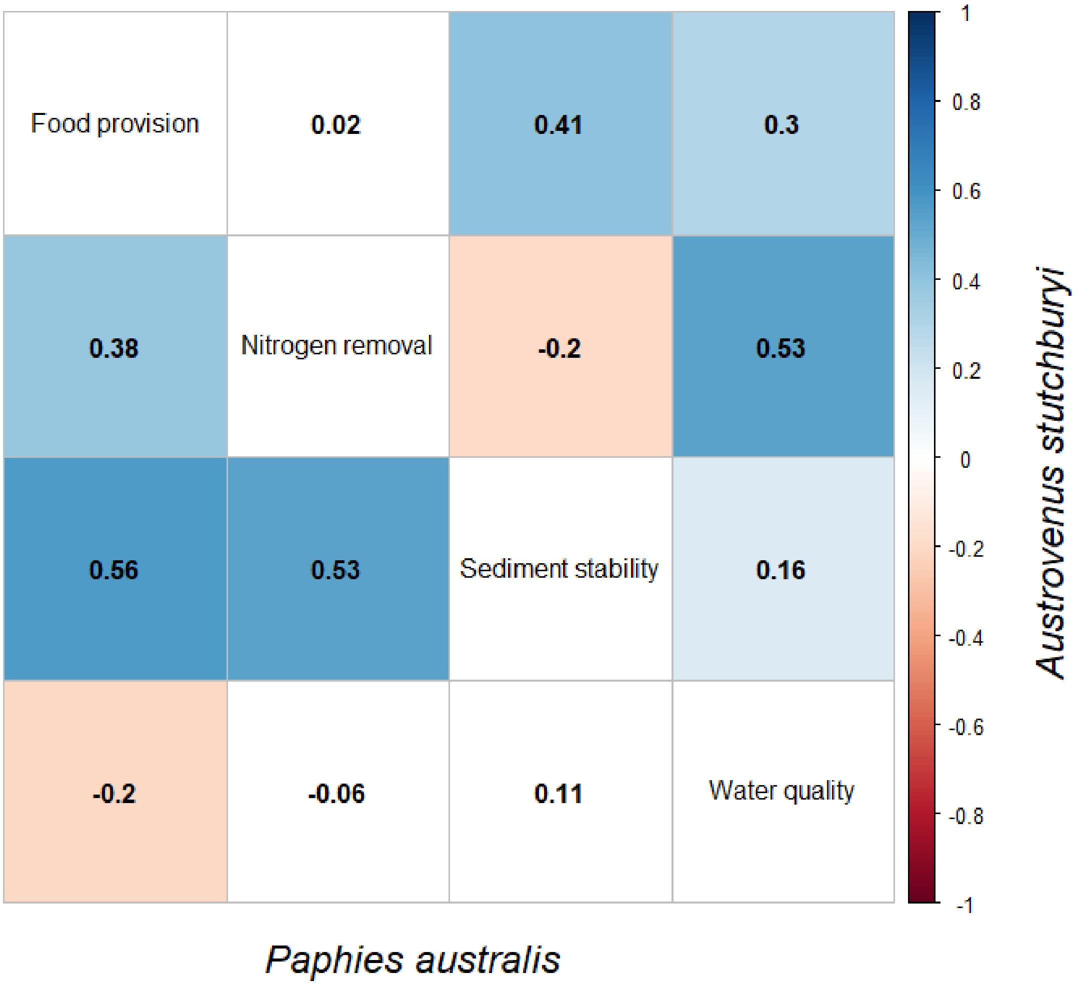

Figure 5.3 Co-occurrence of ecosystem services for *Austrovenus* (top right diagonal) and *Paphies* (bottom left diagonal). Correlation plot with Pearson R values and colour gradient for statistically significant correlations (p<0.05) (and blanks for those not significant).

5.3.3 Multi-service hotspots and richness

For both *Austrovenus* and *Paphies* intensity and richness scores show distinct spatial patterns, with hotspots identified as areas of significantly higher combined richness and intensity (multiplied) than the average for the study area (Figure 5.4). The intensity scores indicated areas where multiple services can be provided simultaneously (Figure 5.4 A & B) with a mean intensity of 17.8 (*Austrovenus*) and 20.0 (*Paphies*), yet nowhere in the estuary are all 4 services provided to maximum capacity (40). Richness (based on a presence score threshold of 5) indicated the number of services provided in a medium to high capacity, with categorical scores between 0 to 4 for both species (Figure 5.4 C & D). For *Austrovenus*, 18.4% and 7.6% of the presence area had an ES richness score of 3 and 4, respectively, making up approximately 41 km^2 in the estuary. Hotspots are predominantly found at the harbour entrances and some smaller patches further up the estuary (Figure 5.4 E). For *Paphies*, areas with high intensity (Figure 5.4 B) reflect the high density areas at the harbour entrances where food provision, nitrogen removal, and sediment stabilisation spatially coincide (with a richness of 3 and scores around 25 to 30), which made up a significant proportion of the presence area at 31%. These areas were identified as the main hotspots for ES potential (Figure 5.4 F). On the other hand, only a small area (2 km^2) had contributions of all 4 service, however intensity scores were not noticeably higher than areas with a richness of 3 (Figure 5.5).

Patterns in multiple services were also reflected when looking at the distribution of intensity values per richness category, displaying the expected trend that with increasing richness, intensity will be higher for both species (Figure 5.5). However, the increase in intensity with richness was not always linear and intensity for some richness categories do not distinctly differ. For example, the average intensity for richness category 0 and 1 for *Austrovenus* are similar (14.3 and 14.7 respectively) and the differences in average intensity reflect a more exponential increase with higher richness categories (Figure 5.5 A). For *Paphies* intensity remains fairly low on average for richness categories 0-2 (at 15.3, 17.3 and 18.4 respectively), yet a sharper increase is seen towards the higher categories, particularly between richness category 2 and 3 (Figure 5.5 B). The intensity score for richness category 3 varied widely for *Paphies*, compared to the other categories. Outliers (reflected as dots in Figure 5.5) were mostly seen for richness category 1 and 2 for both species, indicating areas with much higher (or lower service potential) than expected for the richness category.

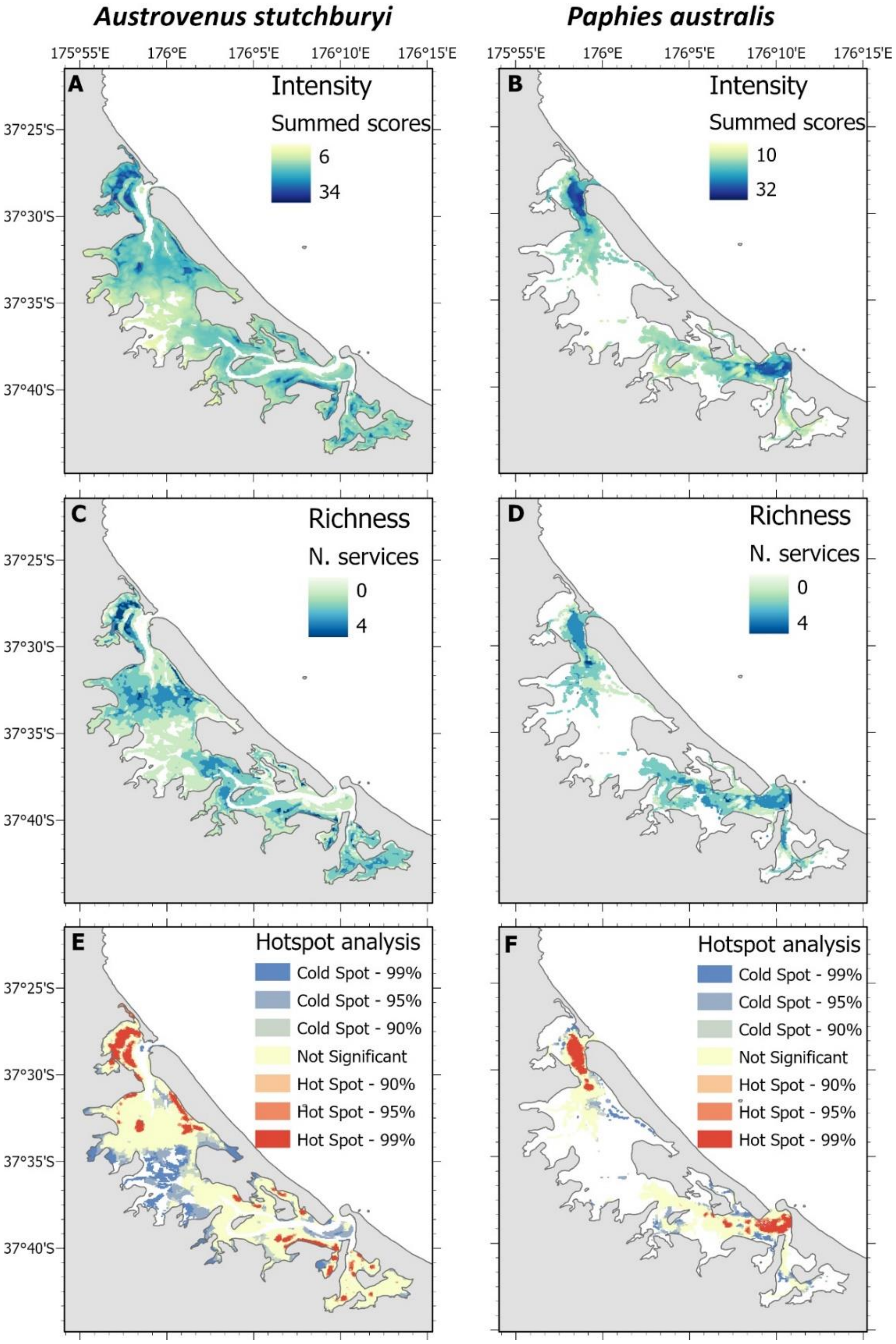

Figure 5.4 Combined ES maps for *Austrovenus* (left) and *Paphies* (right). Intensity (A & B) reflects the summed service scores per species (score out of 40) and richness (C & D) reflects the number of services present (exceeding threshold score of 5). Hotspot analysis (E & F) indicate areas of significant clustering of high (hot spot) and low (cold spot) values of Intensity x Richness scores with confidence levels of 90, 95, and 99%.

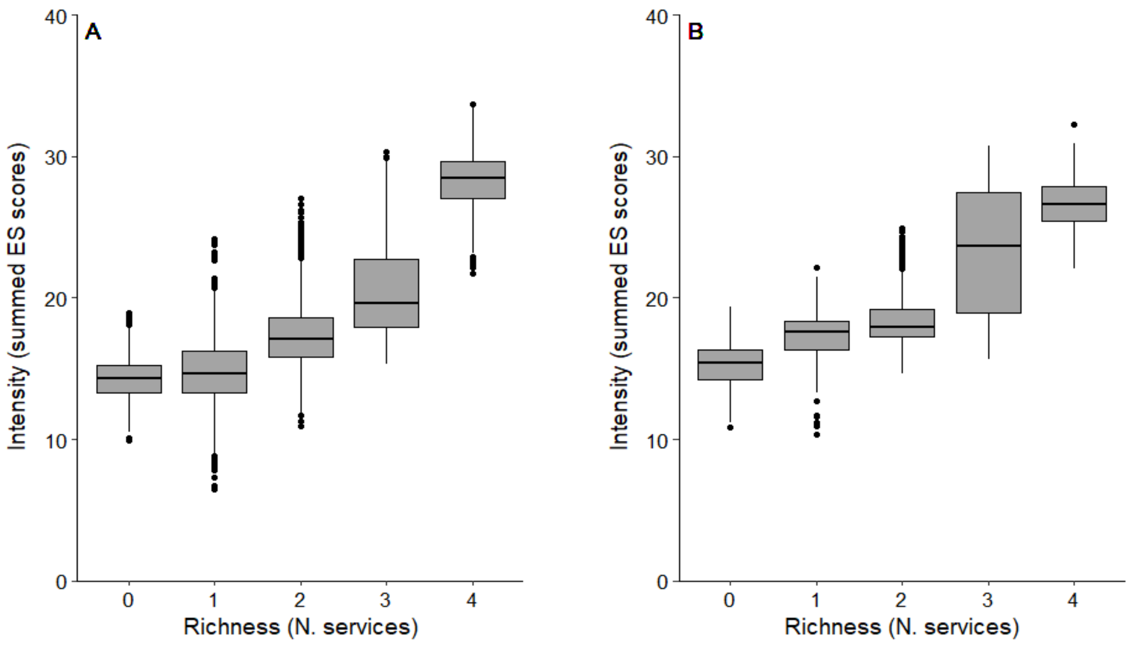

Figure 5.5 Boxplots for intensity scores per richness category from combined maps for *Austrovenus* (A) and *Paphies* (B). For each gridcell, the richness category (number of services that exceed a score of 5) and intensity (sum of all ES scores, without threshold).

5.4 Discussion

5.4.1 Inter- and intra-species comparison

Using an ecosystem principles approach, four ecosystem services were spatially assessed for two bivalve species with slightly overlapping but contrasting use of habitat. The EPA provides benefits for ES assessments as it balances ecological complexity to modelling and data intensity (Townsend et al. 2014). However, the approach had not yet been applied to assess ES multifunctionality or multi-species assessment. Inter- and intra-species comparisons of ES maps displayed contrasting patterns related to species habitat association and are context specific, information which is missed in other approaches that ascribe equal ES value per ecosystem service provider (e.g. habitat type, species, or other indicators) (Lavorel et al. 2017). In our example, *Paphies* provided varying levels of service potential with spatial coincidence between 3 out of 4 services, reflecting *Paphies* spatially restricted distribution in the estuary (Hooker 1995). *Austrovenus* on the other hand has a wide distribution (Powell 1979) and is found to contribute to all services, but with varying strength in different parts of the estuary.

Density was chosen as an important principle for all four services, where functional responses reflect an increase in ES with increasing density, which tend to level off at higher densities (see

Appendix 4). Bivalve size and/or biomass could add additional information to ES predictions, by distinguishing the contribution of large and small individuals to functions (Thrush et al. 2006, Norkko et al. 2013, Thomas et al. 2020) and services (see Smaal et al. 2019). A downside of adding bivalve size/biomass would be an increase in modelling complexity and data requirements to create accurate population models. The EPA balances simplicity and generality of principles vs. complexity in real world systems, and hence density was chosen here that will best reflect general patterns. Some common overlap in ES is expected as all four services are linked to density, however the low to moderate correlation between multiple ES (Figure 5.3) indicated that bivalve occurrence or density alone is not a good proxy for ES on a local scale. Instead, the environmental context in which high-density bivalve beds are found is important for determining high service potential areas, especially for species with a wide distribution. These results align to known heterogeneity in ecosystem functions and habitat or context specific results found in ecological studies (Hewitt et al. 2008, Rossi et al. 2008, Piehler and Smyth 2011, Queiros et al. 2011), and provide insights that cannot be obtained from ES assessments lacking understanding of ecological drivers.

The congruence of services, which reflect the potential for services to be provided in the same location and under the same conditions, raises questions around interactions between services (e.g. synergies and trade-offs; Bennett et al. 2009). Often spatial coincidence in service supply or demand is considered for analysing synergies and trade-offs in ES, particularly in terrestrial studies (e.g. Raudsepp-Hearne et al. 2010, Willemen et al. 2010, Turner et al. 2014). Although service potential can show similar spatial patterns, whether or not these cause synergies or trade-offs will depend on how they are utilised. For example, *Paphies* show spatial coincidence between food provision, nitrogen removal, and sediment stabilisation, indicating high multi-service potential in the same locations. However, there will be trade-offs between ES if used, for example, when shellfish are harvested for food, they will no longer contribute to the other services. In contrast, *Austrovenus* contribution to water quality regulation and nitrogen removal are synergistic because both contribute to improving ecosystem health and quality (Chapter 2). Studies often find trade-offs between provisioning service to other ES, and synergies among regulating and supporting services (Howe et al. 2014, Lee and Lautenbach 2016). Additionally, we show that this will be more pronounced for species with narrow ranges, which therefore require more careful and measured management approaches to ensure balanced resource usage.

The EPA provides valuable insights into important areas for relative ES potential and management, and instead of being paralysed by complex models and a lack of spatial data, environmental decisions can be informed by available knowledge and expert opinion. The principles defined are transferable to other systems, yet thresholds and weightings can be adjusted to reflect conditions specific to other study areas. For example, in Tauranga Harbour, heavy metal contamination in the sediment falls well within guidelines (ANZECC 2000, Ellis et al. 2013), and hence principle 1.3 (Table 5.1) had a relatively low weighting. In heavily contaminated systems, this principle may be more important in determining where shellfish can be harvested for food consumption (Fang et al. 2001), and local experts should be consulted. To inform decision making, uncertainty in the model predictions should be carefully considered (Bryant et al. 2018), though it is not often included in ES assessments (Hamel and Bryant 2017). Here we show that uncertainty from weightings is low (on average less than 1 point difference for all 8 layers). Uncertainty derived from data layers should be acknowledged also, as in some instances approximations had to be made (e.g. relative turbidity, size distributions, see Table A4) that were checked against available data to confirm that the assumptions were valid. A benefit to this approach is that principles and data layers can be easily updated to include new findings or when new data are collected that supports these models.

5.4.2 Application for conservation and management

Implementing ES assessments in environmental management and conservation is deemed increasingly important in frameworks like EBM and marine spatial planning (MSP) (McLeod and Leslie 2009, White et al. 2012, Drakou et al. 2017), in particular through providing spatial information on ES and testing different management scenario's (e.g. Guerry et al. 2012, Galparsoro et al. 2014, Arkema et al. 2015). By focussing on ES hotspots (where many ES are being delivered at high intensities), representativeness, and complementarity (Kati et al. 2004), managers may optimize efforts and prioritize important areas (Egoh et al. 2008, Schröter and Remme 2016), similar to biodiversity hotspots in conservation strategies (Myers et al. 2000). Density is a key driver for ecosystem processes and functions, and combined service maps reflect that high density areas are important for multi-service delivery (richness and intensity). Yet density alone is not the answer to guarantee important areas for individual ecosystem services to be maintained, as demonstrated by the co-occurrence analysis (Figure 5.3). Instead, a targeted management approach requires inclusion of environmental context (Foley et al. 2010), whilst being aware of possible interactions between services and their drivers (Cord et al. 2017, Dade et al. 2019). For example, balancing trade-offs of food provision against other services can be accomplished through sustainable harvesting pressure, that allows the high density stock to persist, thereby maintaining other functions/services (e.g. Lester et al. 2013).

Spatially identifying hotspots of function and services may help to manage resource use by either refining limits or introducing protected areas. Furthermore, size of hotspots and intensity are argued to be important aspects to consider when selecting areas for conservation, when the total amount of ES conserved or connectivity matters for the long-term provision of a service (Moilanen et al. 2011, Schröter and Remme 2016). Based on both individual and multi-service assessments, we argue that redundancy in high service potential should also be considered when identifying key areas for management. In this study, little redundancy in high service potential for nitrogen removal is observed as only small pockets of high scoring areas were predicted (Figure 5.2, Table 5.3) as opposed to large areas of medium score. For *Austrovenus* nitrogen removal, these do not coincide well with the larger hotspot areas (Figure 5.4) and failure to include these areas as high priority management considerations could result in the loss of a key ES in the Harbour.

A key restoration priority worldwide is to restore habitats of ES provisioning species, such as shellfish, to regain lost services (Coen et al. 2007, Grabowski and Peterson 2007). Finding strategic locations for restoration should be based on suitable environmental conditions for species to thrive, as well as locations where service delivery can be optimized (Theuerkauf et al. 2019). Location selection for restoration projects should consider the intention to increase either a particular individual service or the best outcome for multiple services and/or biodiversity (Bullock et al. 2011), which has been shown here to be affected by the service providers ecology or habitat associations. For shellfish reef restorations for example, Coen and Luckenbach (2000) note the importance of linking success criteria to specific goals by identifying realistic ecological milestones as well as how local conditions and habitat traits affect restoration strategies. The models used in this study can be configured to provide insights into areas most suitable for restoration by running scenarios, where the density can be increased in areas to reflect restoration efforts and assess the predicted change in service potential. This can provide novel insights in whether or not density is the limiting factor for service delivery in a location, or that it is the environmental conditions that prevent higher service potential.

The models developed in this study can provide a tool to simulate management scenarios and thereby assess the impact of activities and/or stressors on ES potential in the Harbour. Human activities and environmental stressors can alter occurrence and densities of bivalves, as well as the conditions in the harbour that alter ES potential. For example, dredging of channels for shipping can alter bathymetry, currents, and turbidity in the harbour that may alter or disrupt ES provision by bivalves (Healy et al. 1997). The impact of anthropogenic stressors on ES provision is not well understood (Mach et al. 2015), whereas stressor impacts on processes and ecosystem functions have been better assessed in ecological studies (Crain et al. 2008). These studies can provide valuable insights into susceptibility of services to different stressors, e.g. sedimentation will impact bivalves filter feeding and hence water quality regulation (Norkko et al. 2006), whereas food provision is prone to overharvesting (Beck et al. 2011). Applying ecological principles in the EPA provides an opportunity to simulate human activities and stressor impacts to predict their effect on service potential. They can thereby identify vulnerable areas and a possible shift or loss of services if stressors or activities are not managed well. Overall, the approach provides a versatile tool to inform both current management and conservation, and restoration efforts to guide sustainable use of resources.

5.5 Conclusion

The ecosystem principles approach provides a relatively simple means of balancing ecological complexity and model simplicity, as it is based on well understood ecological mechanisms and requires mostly available data. Our study shows the importance of including ecological complexity to identify key areas of service potential for multiple ES per species and that the relative contributions of species to particular ES can be distinguished. This information will allow managers to set conservation priorities based on more than just occurrence or species densities alone. It offers a means of including context and environmental conditions when planning and managing for individual ES. Detailed mapping can distinguish variation in ES distribution for functionally similar species and distinguish heterogeneity in habitats often considered to be homogenous. These findings are important for other habitats or key service providers, where homogeneity in service provision per land use or habitat is assumed, especially when mapped on a local scale. The approach supports early management actions in data-scarce environments, based on best available knowledge, and can be easily updated to include new findings, providing managers with a versatile new tool for use in spatial conservation planning.

CHAPTER 6
General discussion

Estuarine and coastal ecosystems and the species therein provide valuable benefits to society through the goods and service they generate. A key challenge in environmental management is determining how to manage multiple ecosystem services simultaneously, yet this is fundamental for ensuring efficient and sustainable use of the environment and its resources. In this thesis, I have investigated the use of ecological mechanisms to assess multiple ES provided by marine bivalves, studying the interactions and formation of ES bundles. A variety of methods were considered to assess the application of ecological mechanisms, including conceptual ES bundle formation derived from the literature, *in situ* empirical measurements of ecosystem functions (EF) and ES quantification, and the spatial assessments of bivalve densities and ES distribution in a New Zealand estuary.

6.1 Summary

ES bundles are an important step forward in the transition from single service assessments to studying the interactions and interconnectedness of multiple ES provided in a system (Raudsepp-Hearne et al. 2010, Berry et al. 2016, Saidi and Spray 2018). However, they have so far rarely been applied in marine environments, but would provide valuable insights for holistic EBM and MSP that accounts for the different uses and pressures on the environment (Crowder and Norse 2008, Foley et al. 2010). The methods applied to determine ES bundles in terrestrial ecosystems cannot be easily applied in marine systems, due to data scarcity, complexity and connectivity in a three dimensional environment (Townsend et al. 2018) and has resulted in a lag in ES bundles assessment. In Chapter 2, I applied ecological mechanisms to derive ES bundles, by focussing on process-based multifunctionality to determine associations between bivalve ES. From an extensive literature review, the links between shellfish-mediated processes, EF and ES were determined. Based on the co-occurrence of ES and shared underpinning links between multiple ES identified in the review, four groups of associated ES were defined, including *Marine resources*, *Coastal health and quality*, *Habitat modification*, and *Biological structuring*, with all services within a bundle underpinned by a specific (set of) ecological mechanisms. This novel approach provides great mechanistic insight into the formation of bundles, how ES interact (e.g. the synergies and trade-offs between services), and the implications for management and decision-making. Trade-offs were considered mostly for ES in the *Marine resources* bundle as the harvest of shellfish from the system for food or material could result in loss for other ES that rely on the presence of bivalves in the system, as is often observed for provisioning ES (Raudsepp-Hearne et al. 2010, Turner et al. 2014, Lee and Lautenbach 2016). Synergies were mostly observed between the regulating (and supporting) services in the other bundles, for example between sediment stabilisation and water quality regulation both reducing suspended particle concentrations.

Quantification of ES remains challenging, and can result in biases towards more data rich ES in management and decision making that are easily quantified economically (Beaumont et al. 2007, Boerema et al. 2017). For infaunal bivalves (as opposed to reef-forming species), little quantitative data is available on the ES they provide, and rarely the differences between functionally similar species in different habitats are considered. In Chapter 3 I aimed to determine *in situ* bivalves contribution to water quality regulation through quantifying the complex links between processes, EF, and ES for two infaunal species; *Paphies australis* and *Austrovenus stutchburyi*, that are functionally similar (i.e. infaunal suspension-feeding bivalves) yet differ in their habitat association (subtidal and intertidal respectively). To this end, I measured sediment-water column fluxes and bed clearance rates over a naturally occurring intertidal *Austrovenus* and subtidal *Paphies* bed, as a proxy for ES. I demonstrated that the intertidal site had higher hourly fluxes and rates for almost all measured ecosystem functions than the subtidal site, indicating higher hourly productivity, nitrogen recycling, and filtration of the overlying water. These differences were attributed to environmental differences between habitats (e.g. light regime, sediment characteristics, dominant bivalve species) rather than differences in bivalve biomass, which were equivalent between sites. However, these patterns changed when scaling up EF to daily ES estimates, due to differences in inundation period that restrict water quality regulating services in the intertidal. These findings show that although species can be functionally similar, the quantity of EF and ES derived from the same processes can vary greatly depending on the conditions in which shellfish beds are found.

Spatial information on the distribution and densities of key species is an important prerequisite for understanding ecosystem functioning and management of ecosystem services. Species Distribution Models (SDMs) are increasingly used in marine environments to assist with spatial management; however, most SDMs only predict occurrence and not density (Melo-Merino et al. 2020). In Chapter 4, I used SDMs to predict probability of occurrence and density of two estuarine bivalve species (*Austrovenus* and *Paphies*) that differ in habitat usage and distribution, to gain insight into the utility of these methods for management. Boosted regression trees were used to predict occurrence, density, and uncertainty at a fine spatial scale (100 m resolution). Results showed high probability of occurrence for *Paphies* near the estuary mouth, where high densities were also predicted. For *Austrovenus*, predicted occurrence was high throughout the intertidal area, with no clear spatial patterns. However, areas where the species can thrive were identified once environmental conditions supporting high densities were incorporated. Spatially explicit uncertainty was low throughout the estuary for both species. In this study I demonstrated that a high probability of occurrence does not necessarily equate to high density and illustrates the need for the transition to more informative species density models. Management that simultaneously considers both density and occurrence probabilities will enable targeted protection of areas that are of greatest ecological value to species of interest.

In marine environments, the spatial assessment of ES is lagging as a result of data-scarcity and modelling complexity (Maes et al. 2012a, Townsend et al. 2018). Applying process-based models that incorporate ecological knowledge to assess areas of high ES potential can bridge this gap and enable the assessment of natural variability (heterogeneity) in ES. In Chapter 5, I applied an ecosystem principles approach (Townsend et al. 2011, Townsend et al. 2014) to assess ES potential for food provision, water quality regulation, nitrogen removal, and sediment stabilisation, provided by *Austrovenus* and *Paphies*. Through differences in the spatial distribution of these species, I gained insight into the utility of these models for local-scale management. Maps of individual ES displayed differing spatial patterns related to habitat associations of the species providing them, with varying ES quantities and locations of importance. Combined maps (i.e. the number and summed value of multiple ES layers per species) and hotspot analyses were used to identify significant areas of importance for multiple ES. Combined service maps suggest that areas of high shellfish density are important for multi-service potential (number of services present and their intensity). Yet density alone will not guarantee protection of important areas for individual ecosystem services. Instead, a targeted management approach that includes environmental context is required. The approach provides a versatile tool to inform current management and conservation, and could be applied to identify suitable locations for restoration and assess vulnerability to environmental stressors.

Collectively, the four research chapters in this thesis demonstrated the insights and benefits that can be gained by applying ecological mechanisms to study interconnected ES and the interactions between them. When synergies or trade-offs between ES are not well understood, management strategies or actions can result in undesired or unanticipated consequences (Bennett et al. 2009, Howe et al. 2014). The synergies and trade-offs identified for ES bundles were again reflected in the ES maps. They indicated that the (short-term) benefits from food provision should be carefully balanced against the benefits from regulating and supporting processes, that often create synergies, ensure ES diversity, and long-term health and resilience in ecosystems. Bivalve are important species in estuarine and coastal ecosystems and management strategies should focus on conservation, restoration and maintaining shellfish beds to reduce any further loss of shellfish ES. The spatial information derived from Chapters 4 and 5 can help optimize decision making by identifying locations for targeted management of multiple ES or restoration of populations. Results emphasised that a focus on the presence of (high-density) shellfish beds alone does not guarantee effective management for the variety of ES that are generated. Although applied to shellfish, tools and insights from the research extend beyond estuaries and coasts, and are applicable to other data-scarce habitats that are lagging in ES assessments. For bivalves, variation in EF and ES were observed throughout this thesis, and were attributed to a number of factors, including functional differences between species, bivalve density, environmental context (i.e. habitat association and environmental conditions), and the scale of study, which impacts the scaling from EF to ES.

6.2 Variability and scaling of EF and ES

The numerous links between processes, ecosystem functions, and ecosystem services exemplify the complexity in ecological mechanisms that underpin ES (Snelgrove et al. 2014), and are increasingly used as an ecosystem service assessment tool in marine environments (Culhane et al. 2018, Broszeit et al. 2019, Armoškaitė et al. 2020). Although it is generally accepted that ecosystem functioning is spatially and temporally variable (e.g. Hooper et al. 2005, Brose and Hillebrand 2016, Isbell et al. 2018, Gonzalez et al. 2020), a major assumption for ES quantification is the linear scaling with EF or habitat, that is not supported by findings in the literature (Barbier et al. 2008, Koch et al. 2009). This assumption is predominantly applied in studies that use land use and land cover (in terrestrial systems) or habitat type and ESP in matrix approaches as a proxy for ES (e.g. Galparsoro et al. 2014, Potts et al. 2014, Cabral et al. 2015, Geange et al. 2019), for which equal ES provision is assumed regardless of habitat size, seasonality, species interactions, or environmental conditions (Koch et al. 2009, Schröter et al. 2020). Ecological mechanisms are central in this thesis and provide an avenue to explore the non-linear relationships and variability in EF and ES for different bivalve species.

6.2.1 Functional differences between species

For bivalves, functional differences between species can impact EF and the services they provide. The main distinction between bivalves functional groups relates to their feeding mode (suspension or deposit-feeders) and position (infaunal or epifaunal). Extensive literature on the ecology of these different types of bivalves is available, which were combined in Chapter 2 to identify general patterns for bivalve ES bundles, with differences between functional groups noted and detailed in the bundle explanations. In particular, differences between infaunal and epifaunal bivalves were prominent in their contribution in the *Habitat modification* and *Biological structuring* bundles. The 3D-biogenic habitat from epifaunal bivalve reefs is particularly important for shoreline stabilization (Brumbaugh and Coen 2009, Baggett et al. 2015) and are often used as natural breakwaters that simultaneously create habitats for other species, by creating refuge, feeding and nursery habitats (e.g. Guidetti and Boero 2004, Coen et al. 2007, Volety et al. 2014). Infaunal bivalves effect on sediment stabilisation is substrate dependent, and can be destabilising in muddy cohesive sediments, yet stabilising in coarse sediments (e.g. Ciutat et al. 2007, Donadi et al. 2013). Through bioturbation or bioirrigation, they alter the physical environment and add heterogeneity to sediments, thereby alter community composition and increase sediment oxygenation and solute transport (Norkko and Shumway 2011).

Differences in feeding mode between bivalve species has a significant impact on a variety of ecosystem services, in particular in the *Coastal health and quality* bundle, which is underpinned mainly by water column filtration, as well as biodeposition. In general, reef forming suspension feeders contribute most to water column filtration and biodeposition, through their continuous high filtration rates even at high food (Tenore and Dunstan 1973) and suspended sediment concentrations (e.g. Bacon et al. 1998, Hawkins et al. 1998). These rates are lower for infaunal suspension feeders that reduce their clearance rates and biodeposition at higher suspended particle concentrations (e.g. Tenore and Dunstan 1973, Bacon et al. 1998, Hawkins et al. 1998). Infaunal deposit feeders do add to biodeposition, yet do not filter the overlying water column (Black 1980, Ward and Shumway 2004). Even within functional groups, different species may not contribute equally to EF and ES, as was observed for infaunal suspension-feeders in Chapter 3 and Chapter 5 of this thesis, and was attributed to differences in bivalve density and/or environmental context.

6.2.2 Bivalve density

Variation in bivalve ecology, and processes and functions are often attributed to differences in abundance (density and/or biomass) (Dame and Kenneth 2011). However, not all processes or functions scale linearly with density. For example, Newell (2004) reviewed ecosystem influences of bivalve filter feeding and predicted non-linear effects of shellfish especially once moderate densities were passed. Extreme densities (often associated with bivalve aquaculture) were predicted to result in reduced sediment oxygen content, denitrification potential and increased inter and intra-specific competition for food. Bivalve density can directly and indirectly alter EF, including nutrient cycling and productivity (e.g. Sandwell et al. 2009, Welsh et al. 2015, Lohrer et al. 2016), sediment stability and/or biodeposition (e.g. Widdows et al. 1998, Ciutat et al. 2007, Jones et al. 2011b). Field measurements in Chapter 3 were conducted on two existing shellfish beds with equivalent biomass, and hence could not be used to establish relationships between biomass and EF/ES, although existing literature on *Austrovenus* in particular identified density dependent relationships (e.g. Sandwell et al. 2009, Jones et al. 2011b) in New Zealand estuaries.

Besides density dependent relationships, size matters for many processes and functions, which can impact ES provision by shellfish. In general, large individuals are considered to have a larger contribution to ES than small individuals, in particular for food provision and water quality regulation ES as examples from this thesis. Large bivalves are more desirable for food consumption, which is reflected in both commercial and recreational gathering (Hartill et al. 2005). Filter feeding has known relationships with bivalve size, as discussed throughout this thesis, with higher clearance rates by large individuals (Møhlenberg and Riisgård 1979, Riisgård and Seerup 2003, Cranford et al. 2011). Changes in population size structure can impact EF, as a loss of functioning is often associated with a loss in large bivalves (Thrush et al. 2006, Norkko et al. 2013). Thomas et al. (2020) observed size specific differences in EF for *Austrovenus*, with small clams increasing primary productivity in the system, whereas large clams doubled microbial enzyme activity. Including size effects (population size structure or biomass) could provide further nuances in spatial heterogeneity in EF and ES, additional to the general patterns observed from density. Size effects were outside the scope for this thesis, except for the consideration of large bivalves for food provision in Chapter 5, and require substantial improvements in data availability for spatial predictions in the study area.

Accurate density predictions of *Austrovenus* and *Paphies* were therefore considered essential to scale ecological mechanisms on an estuary wide scale. Species Distribution Models (Chapter 4) were used to derive density predictions at a fine resolution to accommodate ES mapping in Chapter 5. Within Tauranga Harbour, strong gradients in bivalve densities were observed, that were predicted with high accuracy for both species (Table 4.3). Presence/absence and density patterns were strongly linked to environmental conditions under which the species can occur and thrive. For both species, probability of occurrence was mostly explained by a single environmental driver (relative influence >50%, Figure 4.2), namely current speed for *Paphies* and bathymetry for *Austrovenus* (distinguishing mostly the intertidal from subtidal areas). However, whether a species can thrive in the estuary did not always match the location or the conditions where they can occur, and displayed more complex sets of conditions that collectively explained density predictions (Figure 4.2, Appendix 3), including sediment characteristics and depth. These findings were in accordance with known habitat preferences (Morton and Miller 1973, Powell 1979) and empirical findings (Thrush et al. 2005, Ellis et al. 2006, Anderson 2008). Density layers were an essential component of ES mapping in Chapter 5, as density was an underpinning ecological principle reflecting the often non-linear relationships between density and EF/ES (Appendix 4). As a result, hotspots in combined ES potential for Tauranga Harbour (Figure 5.4) corresponded well with high density areas (Figure 4.3, Figure 4.4). Interestingly, individual ES were less driven by density than originally anticipated. If all individual ES would be strongly related to density, the correlations between ES (Figure 5.3) would have been much stronger. Instead, weak to moderate correlations indicate that the conditions under which (high-density) shellfish beds are found drive the individual ES potential.

6.2.3 Environmental context

Estuarine and coastal habitats are highly heterogenous and multiple habitats (e.g. seagrass beds, salt marshes, oyster reefs, sand- or mudflats, subtidal channels) occur in close proximity. EF and ES are known to vary between these habitats and changes in habitat size can therefore impact system-wide delivery of ES. For example, nutrient cycling and removal EF are known to be highest in structured habitats, followed by intertidal sand- or mudflats, and lowest in subtidal channels (Eyre et al. 2011, Piehler and Smyth 2011). The difference in habitat association between *Austrovenus* and *Paphies*, resulted in varying contribution to EF and ES (Chapter 3) and spatial patterns observed for SDM (Chapter 4) and ES predictions (Chapter 5).

Through *in situ* quantification I determined that intertidal *Austrovenus* EF was significantly higher than those of a subtidal *Paphies* bed. When converted to daily ES, EF did not scale linearly to ES, which is in accordance with findings by Barbier et al. (2008) and Koch et al. (2009). This was further confirmed by the non-linear scaling of ecological principles to spatial ES estimates. The heterogeneity observed in ES maps for individual and multiple ES contradicts the assumption that a habitat type or ESP contributes equally within a system. Although for *Paphies* the high density beds at the harbour entrance were hotspots for ES, this assumption is particularly problematic for species with a wide distribution that thrive under a range of environmental conditions that impact ES potential.

In this thesis, a number of environmental variables were identified that contribute to differences in EF and spatial differences between bivalve ES. Subtidal channels in Tauranga Harbour are characterised by coarser sediments with lower mud and organic matter content, higher mean and maximum current velocities, lower light availability and higher turbidity. Many of these environmental characteristics have been linked to functioning of *Austrovenus* or benthic communities in New Zealand estuaries, especially in intertidal areas. For example, *Austrovenus* had a positive impact on EF like dissolved oxygen fluxes, nutrient cycling or denitrification potential (Jones et al. 2011a, Pratt et al. 2014a), particularly in sandy estuarine habitats in summer (Jones et al. 2011a). In general, denitrification potential was related to mud and organic content in New Zealand estuaries (Douglas et al. 2019, Lohrer et al. 2020). Structural equation models were used to distinguish breaking points in environmental variables and EF, and display different roles of large bivalves or bioturbating fauna when passing breaking points in mud or chlorophyll a content (Thrush et al. 2014, Douglas et al. 2019), and light climate (PAR as a proxy for turbidity) (Thrush et al. 2020). Structural equation models display the complexity of biogeochemical interactions between ecosystem components, including marine bivalves, and multiple processes and/or EF, and could be used to identify breakpoints for their role in ES provision. This was accomplished in Chapter 5 by linking ecological principles to environmental variables that impact ES potential and designing functional relationships for ES scores. Variables included were bathymetry, current velocity, tidal inundation, turbidity, sediment characteristics (organic matter and mud content) (Appendix 5) and create the nuances in ES potential that cannot be obtained by considering bivalve presence/absence or density alone. Findings from Chapter 5 demonstrate that patterns of individual ES potential relate not only to areas of high bivalve densities, but the conditions in which these high-density beds are found matters for the ES they can provide.

6.2.4 Spatial and temporal scale

Many experimental studies are conducted over relatively small spatial and temporal scales, including assessments of benthic ecosystem functioning (Snelgrove et al. 2014, Lohrer et al. 2015). Small scale studies are generally more practical, but scaling up findings to larger and more realistic spatial and temporal scales is required to obtain generalities (Hewitt et al. 2007). This is particularly needed for ES assessments where non-linear scaling between EF to ES may complicate matters (Barbier et al. 2008, Koch et al. 2009), and scales at which ES operate and need to be managed are much larger than most experimental or surveys studies allow (Grêt-Regamey et al. 2014, Snelgrove et al. 2014, Birkhofer et al. 2015, Raudsepp-Hearne and Peterson 2016). Results from Chapter 3 were obtained from a small spatial scale, and would greatly benefit from more extensive spatial and temporal assessments. It does however form an important first step in obtaining estimates of EF and ES over naturally occurring infaunal bivalve beds, and provide value in ES assessments as such. In Chapter 5, ES were scaled up for Tauranga Harbour, allowing density and environmental conditions to drive small-scale spatial heterogeneity in ES estimates. These ES predictions are static, and do not incorporate temporal variability, like seasonal patterns, that could impact the ecological principles described. For example, bivalve processes and functioning are known to vary with temperature (e.g. feeding and growth), salinity (e.g. respiration), currents (e.g. feeding) (reviewed in Dame and Kenneth 2011), that often vary temporally and spatially in estuarine habitats, including Tauranga Harbour (Tay et al. 2013). Furthermore, the impact of filter feeding of bivalves on water quality regulation does not only depend on tidal inundation, but also on water residence time (Dame and Prins 1997).

Although ES maps were static (Chapter 5), they provide great insight into the relative ES potential and the small-scale heterogeneity that was observed. ES maps are a simplification of the real world, and require a balance between generality and complexity to accurately reflect ES as well as be practical and applicable for management (Rieb et al. 2017). The issue of scale in ES research is complex due to social and ecological processes occurring over a range of spatial and temporal scales, as is environmental management that often occurs over multiple scales (Scholes et al. 2013, Raudsepp-Hearne and Peterson 2016). Most ES studies are conducted at regional, followed by national scales driven by data availability (Martínez-Harms and Balvanera 2012), however, the fine-scale processes that drive ES might not be represented at these scales (Spake et al. 2017). The level of complexity that ES models incorporate should reflect the intended scale of study and management. For larger scale studies, e.g. on national or international scales, the fine details that are obtained by including (ecological) complexity will be lost against the resolution and extent of the study (Costanza et al. 1997, Schulp et al. 2014). However, for local/regional scale studies that aim to inform local management strategies, higher level of details in spatial and or temporal differences will be more pronounced and can better inform management incentives.

6.3 Future directions

In this thesis I have applied novel approaches focussed on ecological mechanisms to identify ES bundles, as well as *in situ* and spatial quantification of ES. In doing so, I was able to advance current understanding of how bivalve underpinned ES are formed, how ES interact, and gained insight for environmental management. Interactions between ES can result in win-win situations (synergies), or in the loss or decline of particular ES when trade-offs are not well understood (Bennett et al. 2009, Howe et al. 2014). These insights are of particular importance for environmental management, as discussed throughout the thesis chapters, to ensure well-informed decisions are made that do not only account for the (short-term) benefits, but also by creating awareness of what may be lost. Spatial heterogeneity of ES can impact local-scale strategies by considering where ES interact, to obtain a better balance between ES, in particular harvesting species balanced against the provision of regulating, supporting, and cultural ES.

Cultural ES are not represented in this thesis, as they are predominantly driven by social, rather than ecological, factors like identity, ethnicity, income, and religion (Stephenson 2008, Dickinson and Hobbs 2017), which are not captured in ecological mechanisms. Assessments of cultural ES through social studies and indigenous knowledge (Mātauranga Māori) and the ecological approach suggested here are complementary, and provide an avenue for future collaborative research as findings can enhance the knowledge of ecological and social aspects of sustainable management. Future research should also prioritise the development of this approach by obtaining *in situ* measurements on other bivalve mediated ES (not assessed in Chapter 3) and increase the spatial and temporal resolution of *in situ* quantification to gain a better understanding of spatial heterogeneity in ES. Furthermore, to improve the management application of the spatial tools developed in this thesis, future work should focus the assessment of uncertainty in ES predictions, and the applicability of the tool for risk assessments and scenario testing, including finding optimal locations for shellfish restoration initiatives as well as testing scenario's for environmental stressors that may jeopardise long-term ES potential.

6.3.1 ES quantification

To gain a better understanding of the spatial heterogeneity in ES, more quantitative data must be collected for bivalve EF and ES. Results from Chapter 3 demonstrated different contribution of *Austrovenus* and *Paphies* to water quality regulation, explained by differences in habitat characteristics, but were spatially constrained to two existing beds. Conducting further studies on bivalve EF and ES on larger spatial (and temporal) scales, covering a range of environmental conditions and natural bivalve densities and size structures, will overcome this limitations and enable further assessment of how habitat and context-specific differences in functioning will affect ES potential. Furthermore, *in situ* quantification of other ES not assessed here would be recommended. The water quality regulation ES in particular are affected by inundation period, as removing pollutants from the water column will only occur at high tide on intertidal flats. Inundation period may be less important for scaling up other bivalve mediated ES, and therefore the observed trends may not be generalisable to other ES. For example, *Austrovenus* are an important link in foodwebs and contribute to energy transfer in New Zealand estuaries to birds and marine species, like fish and rays (Thrush et al. 1991, Thrush et al. 1994, Alfaro et al. 2006, Jones et al. 2016), and will contribute to this supporting ES during both high and low tide.

Although this thesis focussed on bivalves, the need for more large-scale quantitative data extends beyond bivalves, to assess the contribution of other species and/or communities to ES. Bivalves tend to be a main contributor to EF and ES in New Zealand estuaries, due to their occurrence in high numbers and biomass often dominating the system. Nevertheless, their contribution is a subset of the total contribution of ES in an area and other ESP may contribute also. The approach described in this thesis can be applied to other ESP for which substantial ecological information is available to define the ecological mechanisms and principles on which this approach relies. For a community based assessment, a combination with other methods may be considered. For example, biological or functional traits has been proven an effective method to study ES in terrestrial ecosystems (de Bello et al. 2010, Lavorel et al. 2011) and are more recently being used in marine studies on ES (e.g. Siwicka and Thrush 2020, Gundersen et al. 2021). However, more (large-scale) quantitative data for a wide range of ES and ESP is needed and would vastly improve our understanding of spatial heterogeneity in ES and help validate spatial ES assessments.

6.3.2 Models and maps as tools for management

All models are inherently uncertain, but this can be difficult to identify, quantify, and communicate when applying environmental modelling in policy and decision making (Cardwell and Ellis 1996, Hellström 1996, Ruckelshaus et al. 2015). Uncertainty assessments and validation of ES predictions remain understudied (e.g. Seppelt et al. 2011, Schulp et al. 2014, Hamel and Bryant 2017), which can limit their applicability in decision making. Townsend and Lohrer (2019) validated the ecosystem principles approach for biogenic habitat provision ES and determined the model outputs were accurate when compared to empirical data. In this thesis, I have determined the uncertainty in species distribution modelling, as well as the uncertainty derived from expert-based weighting of ecological principles. To advance the use of the ecosystem principles tool, further work should focus on other types of uncertainty in the models, including data and parameter uncertainty for ES scoring (Appendix 4). Data uncertainty can be determined by obtaining more spatial data on layers for which assumptions had to be made (e.g. relative turbidity and bivalve size structure), and assessing the difference in ES predictions between original and updated data layers. Parameters and thresholds were chosen based on the best available information from literature and expert opinion, and can be easily updated when new studies or information become available. Until then, a sensitivity analysis for parameter and threshold settings could provide insight in the impact of subtle changes in settings for model outputs. A combined uncertainty score could be obtained that accounts for all these different types of modelling uncertainty, that can be used to assess the relative contribution of each type and identify spatial uncertainty patterns (Grêt-Regamey et al. 2013) and inform risk-assessments.

Finally, the SDM and ecosystem principle tools could be further applied to test different management scenarios to improve conservation, restoration, and protection of bivalve beds by identifying locations suitable for shellfish restoration or by assessing the possible impact of human activities, as well as single and cumulative stressors that may harm bivalves and reduce the ES they provide. Location selection for restoration should focus on identifying areas with suitable environmental conditions (from SDM) to sustain a larger population than currently present (Heuner et al. 2016). Restoration and conservation of *Austrovenus* in New Zealand is mostly achieved through fisheries closures (e.g. Rāhui, temporary closures to restrict access to and use of natural resources) or transplanting adults (Marsden and Adkins 2010) and success is related to seeding densities (Cummings et al. 2007) and is context-dependent (Hewitt and Cummings 2013). These outcomes can be combined with hydrodynamic models of

Austrovenus larval dispersal (Lundquist et al. 2009), to identify suitable habitats that can be self-maintaining in the future. Locations for shellfish restoration can be considered through ES maps (through simulating restoration in the density layer, Chapter 5), thereby assessing the potential for ES improvements if shellfish density is a limiting factor. Optimal locations can be determined that consider good habitat suitability and potential to increase one or multiple ES.

ES maps enable testing management or conservation strategies (Guerry et al. 2012, Rees et al. 2012, Arkema et al. 2015, Chung et al. 2015), as well as the impact of stressors on ES (Cabral et al. 2015, Farella et al. 2020). Marine environments are impacted by multiple cumulative stressors (Crain et al. 2008, Halpern et al. 2008) that may impact the ability of bivalves to thrive and provide ES. Local estuarine stressor include eutrophication, sedimentation, pollutant and pathogen run-off, overharvesting, urban development, etc. (Kennish 2002) that are experienced against a backdrop of global stressors, particularly related to climate change, e.g. global warming, sea-level rise, ocean acidification, and storm events (Doney et al. 2011, Hewitt et al. 2016). Knowledge of stressor impact on ES is limited, yet more information is available on the ecological consequences of one or more stressors (Crain et al. 2008). Ecological mechanisms could therefore provide much insight in the consequences of stressors on ES potential, and could be considered spatially in the ecosystem principles tool through cumulative risk assessments (Callahan and Sexton 2007, Fox et al. 2017). Stressor impact that could be simulated in the models from Chapter 5 include overharvesting, sea level rise, sedimentation, (heavy metal) contamination, either individually or in combination. Overall, the SDM and ES mapping tools provide multiple avenues to explore to inform environmental management under current and future scenarios.

6.4 Concluding remarks

By applying ecological mechanisms in ES assessments, great insight has been gained in the interconnectedness of ES in estuarine environments, advancing an area of research that has fallen far behind its terrestrial counterpart. I proposed and designed novel tools to assess ES in data-scarce environments, which were applied to marine bivalves to demonstrate the utility and effectiveness of ecological mechanisms in determining bundles and ES interactions, and the implications for ecosystem-based management and marine spatial planning. A drawback from the many spatial based assessments of ES bundles and interactions that exists is their reliance on pattern-based multifunctionality. These patterns, based on spatial congruence of ES, often reflect competition for space and do not imply causality between ES and their ecological or social drivers, which can only be obtained through process-based assessments (Spake et al. 2017). Mechanistic insights further benefit transferability of findings and management recommendations outside the study area (Birkhofer et al. 2015, Spake et al. 2017). A shift to more holistic EBM and MSP that accounts for the different uses, benefits and pressures in marine and coastal ecosystems benefits from understanding the synergies and trade-offs between ES in the system (e.g. McLeod and Leslie 2009, Granek et al. 2010, Turkelboom et al. 2018).

In this thesis, I identified four bundles that indicate which ES are closely associated and can be best managed simultaneously, as their benefits and value are underpinned by the same processes and prone to similar stressors. Particularly interesting where the interactions identified in Chapter 2 and how this translated to synergies and trade-offs spatially in Chapter 5. The co-occurrence of ES potential for provisioning and regulating or supporting services indicated that particular care should be taken when managing ES in Tauranga Harbour, as the harvest of shellfish for food should be carefully balanced against the loss of other important services. Throughout the research chapters of this thesis, the implications of findings and approaches have been discussed in the context of environmental management, emphasising the importance of not just considering where shellfish are present in high densities, but to also consider the small scale heterogeneity due to environmental context for local-scale management. Often, multiple stakeholders are involved in environmental management (Reed 2008), and the tools derived in this thesis focus on simplifying and communicating complex ecology to support decision making. I believe that ecological insights in ES and their interactions are paramount for maintaining healthy, resilient, and dynamic ecosystems that support a wide variety of ES, which is essential to safeguard their long-term supply in a world of environmental decline.

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Appendices

Appendix 1

Literature review findings – Chapter 2

Table A1 Explanation of the linkages discussed in the text for each bundle, including processes, functions, and/or services. Processes between brackets indicate a link inferred from expert knowledge rather than the review, to complete the set of linkages. The paper column indicates the number of papers discussing a service, which can be split further in the explanation for services (number between brackets). When linkages include links between two functions, they are indicated in the function column with arrows →. For original data and full literature list, see supplementary material.

Bundle	Process	Function	Service	Papers	Explanation
Marine resources	Growth	Biomass production	Provision of food, material, and aquaculture	11	Growth of shellfish affects biomass production, resulting in all three services: food provision (6 papers), aquaculture (6 papers), and provision of material (1 paper).
	Survival	Biomass production	Provision of food and aquaculture	6	Survival or mortality affects the amount of available biomass, which affects food provision (5 papers) and aquaculture (2 papers).
	Recruitment	Biomass production	Provision of food and aquaculture	3	Recruitment of juveniles affects the amount of biomass production, which affects food provision (2 papers) and aquaculture (1 papers).
Coastal health and quality	Filter feeding	Water column filtration	-	12	This link captures all studies looking at filtration or clearance rates from shellfish, removing phytoplankton and/or other particles from the water column. This is the main underpinning link for all services in this bundle.
	Filter feeding	Water column filtration → Water clarity improvement	Water quality regulation	6	This link includes all papers describing the improvement of water clarity through turbidity reduction, phytoplankton/seston removal.

Table A1 continued

Bundle	Process	Function	Service	Papers	Explanation
Coastal health and quality (cont.)	Filter feeding	Water column filtration → Benthic-pelagic coupling	Water quality regulation	6	Shellfish also contribute to water quality regulation through benthic pelagic coupling (6 papers), through the exchange of biomass, energy, or nutrients between the water column and sediment.
	Filter feeding	Water column filtration → Bioassimilation & burial	Nutrient cycling and removal	9	Includes the way shellfish can remove nutrients by bioassimilation in tissue or shell, or burial of OM, this is derived through filter feeding as the main process.
	Filter feeding, bioturbation	Benthic-pelagic coupling	Nutrient cycling and removal	14	Benthic-pelagic coupling strongly affects nutrient cycling and removal (14 papers) and can either be driven by filter feeding (10 papers) or through bioturbation (5 papers).
	(Bioturbation)	Denitrification	Nutrient cycling and removal	6	Denitrification is shown to remove nutrients from the system. This is not directly affected by shellfish, but can be attributed to processes they affect, either through providing the resources (nutrient transfer through biodeposits) or by altering the oxic/anoxic boundary (bioturbation).
	Filter feeding	Water column filtration → Bioassimilation & burial	Removal of pollutants & pathogens	11	Through bioassimilation and burial, pollutants (9 papers) and pathogens (4 papers) can be removed from the water column. Pollutant removal includes removal of contaminants, heavy metals, etc. (6 papers), as well as CO_2 sequestration (3 papers) that happens over longer temporal scales.

Table A1 continued

Bundle	Process	Function	Service	Papers	Explanation
Habitat modification	Bioturbation	Sediment reworking	-	9	Infaunal shellfish can rework the sediment by bioturbation, which is linked to changes in sediment biogeochemistry and sediment stability.
	Bioturbation, biodeposition	Organic matter burial	Sediment biogeochemistry alterations	4	Sediment biogeochemistry is affected by the burial of organic matter, which is affected by either the sediment reworking (4 papers), or OM biodeposition (3 papers).
	Bioturbation	Sediment reworking → Nutrient fluxes and benthic metabolism	Sediment biogeochemistry alterations	10	Through sediment reworking shellfish can cause fluxes of nutrients between the sediment and water column (5 papers), and alter benthic metabolism, altering nutrient and oxygen in the sediment, and hence sediment biogeochemistry (10 papers).
	Bioturbation, biodeposition	Sediment erosion potential	Sediment stabilisation	6	Sediment stabilisation is affected by processes altering the sediment erosion potential, including shellfish reef/bed formation (3 papers), sediment reworking (through bioturbation) (3 papers), and the deposition of OM and mucus production creating more cohesive sediments (3 papers).
	Shell and bed formation	Biogenic habitat engineering	Shoreline stabilisation	6	This service is provided by shellfish providing biogenic habitats through reef/bed formation (4 papers) and shell production (2 papers).

Table A1 continued

Bundle	**Process**	**Function**	**Service**	**Papers**	**Explanation**
Biological structuring	Shell & bed formation	Biogenic habitat → Habitat alterations	Habitat provision	15	Habitat provision is provided by both infaunal and epifaunal shellfish through the generation of beds/reefs that result in refuge/nursery/feeding areas, or through shells creating colonisable substrate.
	Bioturbation	Sediment reworking → Habitat alterations	Habitat provision	4	Infaunal shellfish can alter the habitat through sediment reworking, thereby creating niches for other species to occupy.
	-	Community composition alterations	Biodiversity	9	In general, shellfish are linked to increases in biodiversity, as their presence can influence the community composition of macrofauna and microbial communities as well as pelagic fish.

Appendix 2

Macrofauna community figures – Chapter 3

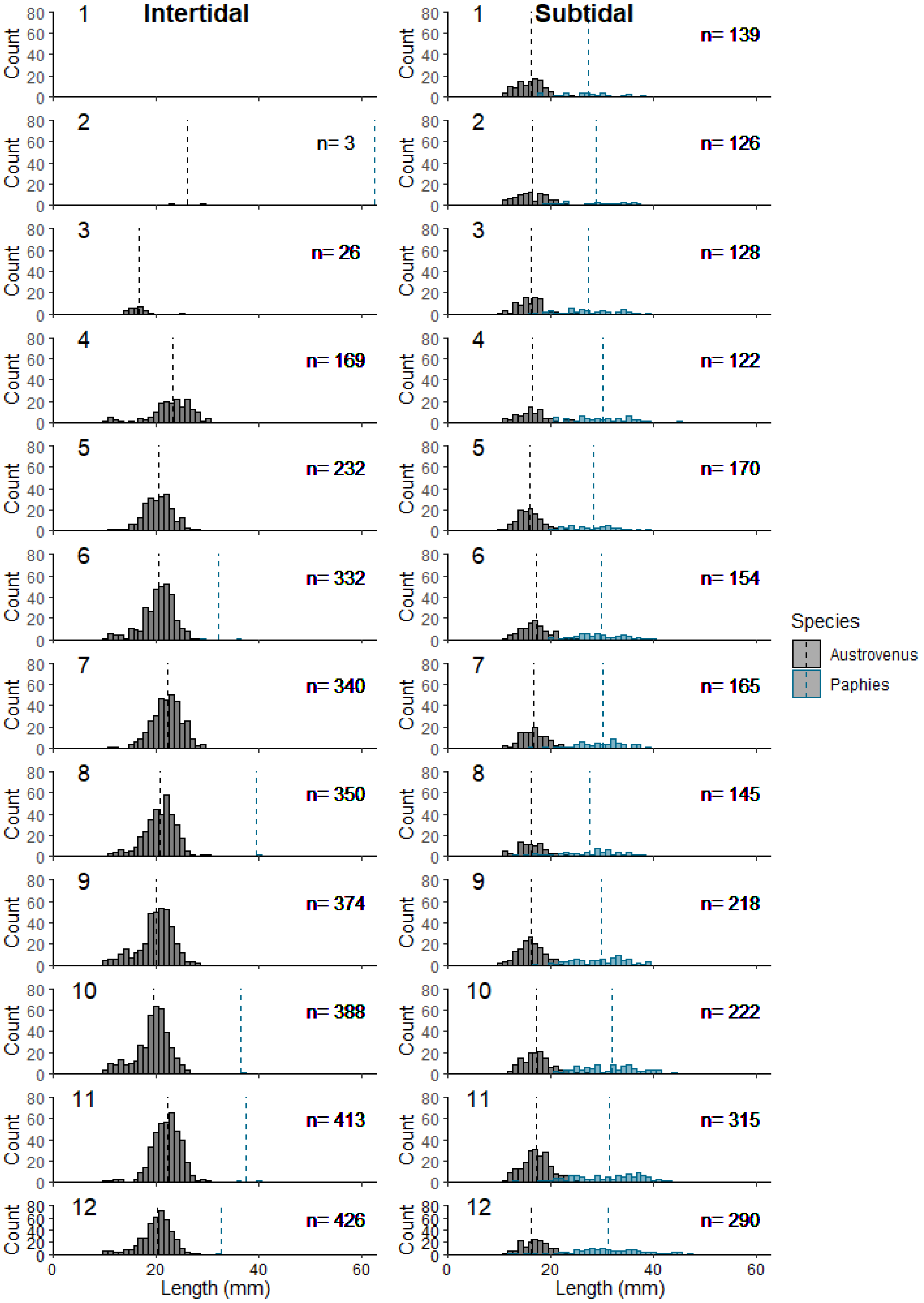

Figure A1 Size-frequency distribution of bivalve population dynamics in the intertidal (left) and subtidal (right) site per chamber (data from light chambers) for *Austrovenus* (black) and *Paphies* (blue). Mean length is indicated per species by a vertical dashed line, and the total number of bivalves exceeding 10 mm (i.e. density (ind 0.25m^{-2})) is displayed in the top right corners.

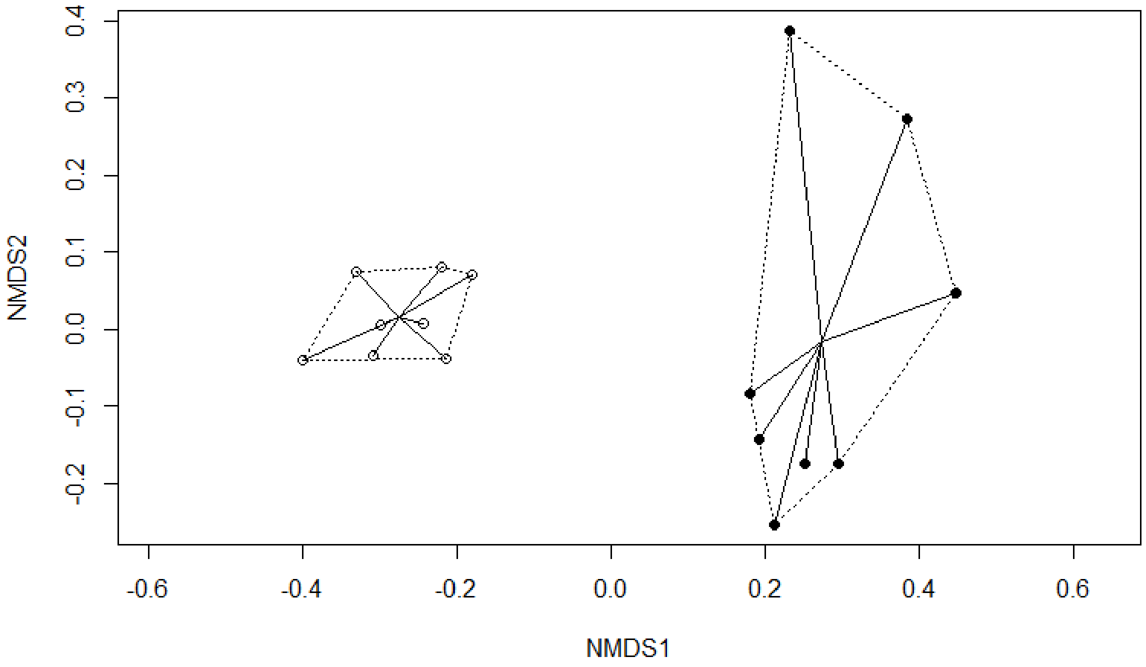

Figure A2 nMDS plot for macrofauna communities. Open circles (○) reflect the subtidal samples, and closed circles (●) are the intertidal sites, with each point representing data from one macrofauna core, for which the assumption of homogeneity was met. The distance to the centroid per group is shown by lines and the hull (dotted line) confines the two communities.

Table A2 Overview table from SIMPER analysis showing the contribution of species to the dissimilarity between the subtidal and intertidal community composition. Columns provide information on the average contribution to dissimilarity between subtidal and intertidal sites ('Average'), the standard deviation (SD), and the ratio between the Average and SD. The average abundance per species in each of the two sites ('Mean subtidal' and 'Mean intertidal', respectively) are given, as well as the cumulative proportion of dissimilarity explained ('Cumulative sum').

Species	**Average**	**SD**	**Ratio**	**Mean subtidal**	**Mean intertidal**	**Cumulative sum**
Oligochaetes	0.154	0.073	2.110	86.3	9.1	0.216
Nereididae	0.078	0.052	1.516	49.6	10.4	0.327
Heteromastus filiformis	0.069	0.101	0.685	11.0	49.8	0.424
Prionospio aucklandica	0.063	0.046	1.373	33.8	64.3	0.512
Linicula hartvigiana	0.058	0.042	1.384	0.1	27.0	0.594
Aonides trifida	0.049	0.019	2.654	25.5	1.3	0.663
Paradoneis lyra	0.031	0.057	0.541	1.4	17.1	0.707
Pseudopolydora paucibranchial	0.029	0.052	0.555	0.0	17.1	0.748
Zeacumantus subcarinatus	0.027	0.021	1.256	0.1	12.6	0.786
Colorostylis lenurum	0.025	0.020	1.280	2.4	14.5	0.821
Sphaeosyllis semiverrucosa	0.019	0.006	2.991	0.0	10.1	0.849
Paracalliope novizealandiae	0.013	0.007	1.771	1.1	7.1	0.867
Scoloplos cylindrifes	0.013	0.007	1.724	7.1	0.9	0.885
Notoacmea scapha	0.010	0.007	1.355	5.9	1.1	0.899
Capitella	0.010	0.006	1.608	5.6	1.0	0.912
Phoxocephalidae	0.009	0.010	0.876	0.5	4.1	0.925
Paravireia	0.008	0.005	1.525	4.0	0.0	0.937
Magalona dakini	0.008	0.013	0.631	0.0	4.8	0.948
Microspio maori	0.004	0.005	0.904	2.1	0.3	0.954
Cominella glandiformis	0.003	0.002	1.974	0.3	1.9	0.958
Nemertea sp.	0.003	0.003	1.197	0.1	1.6	0.962
Zeacumantus lutulentus	0.003	0.003	0.841	0.9	1.1	0.966
Aricidea	0.002	0.003	0.651	0.0	1.3	0.969
Macroclymenella stewartensis	0.002	0.002	1.176	0.0	1.1	0.972
Diloma subrostrata	0.002	0.003	0.744	0.8	0.4	0.975
Austrominius modestus	0.002	0.002	0.854	0.4	0.8	0.977
Corophium	0.002	0.002	0.927	0.0	1.0	0.980
Orbinia papillosa	0.002	0.003	0.527	0.3	0.8	0.982
Torridoharpinia hurlyei	0.001	0.002	0.786	0.3	0.5	0.984
Artritica bifurca	0.001	0.002	0.575	0.5	0.1	0.986
Syllinae bc	0.001	0.002	0.484	0.4	0.1	0.987
Paramoera chevreuxi	0.001	0.002	0.617	0.3	0.3	0.988
Boccardia syrtis	0.001	0.001	0.805	0.1	0.4	0.990

Table A2 continued

Owinea petersonae	0.001	0.001	0.755	0.0	0.4	0.991
Isocladus	0.001	0.001	0.515	0.0	0.4	0.992
Halicarcinus whitei	0.001	0.001	0.657	0.1	0.3	0.993
Patriella	0.001	0.002	0.374	0.0	0.3	0.993
Austrohelice crassa	0.001	0.001	0.562	0.3	0.0	0.994
Barantolla lepte	0.001	0.001	0.557	0.0	0.3	0.995
Pseudopolydora	0.000	0.001	0.568	0.0	0.3	0.995
Cyclapsis thomsoni	0.000	0.001	0.570	0.0	0.3	0.996
Phoronida	0.000	0.001	0.570	0.0	0.3	0.997
Anthopleura aureoradiata	0.000	0.001	0.515	0.1	0.1	0.997
Exogoniae	0.000	0.001	0.521	0.1	0.1	0.998
Levinsenia gracilis	0.000	0.001	0.369	0.1	0.0	0.998
Armandia	0.000	0.001	0.374	0.0	0.1	0.999
Chiton	0.000	0.001	0.374	0.0	0.1	0.999
Eurylana arcuatula	0.000	0.001	0.374	0.0	0.1	0.999
Hiatula siliquens	0.000	0.001	0.374	0.0	0.1	0.999
Amalda australis	0.000	0.001	0.374	0.0	0.1	1.000
Glycera ovigera	0.000	0.001	0.374	0.0	0.1	1.000

Appendix 3

Species distribution model outputs – Chapter 4

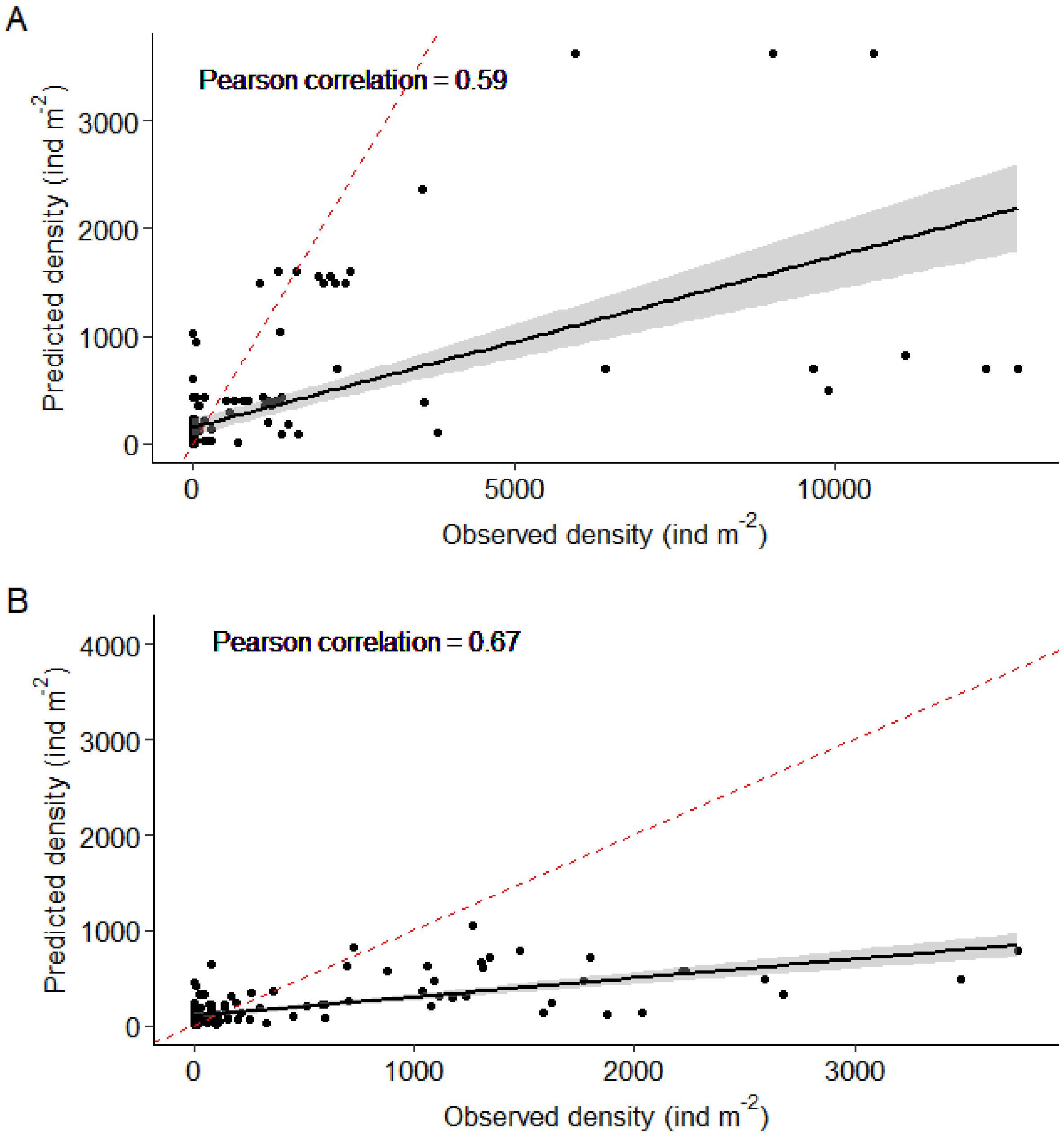

Figure A3 Correlation between observed and predicted values (and 95% confidence interval) for (A) *Paphies* , and (B) *Austrovenus* (including all data (i.e. zeros), extracted from combined maps). Red dashed line shows a 1:1 relationship.

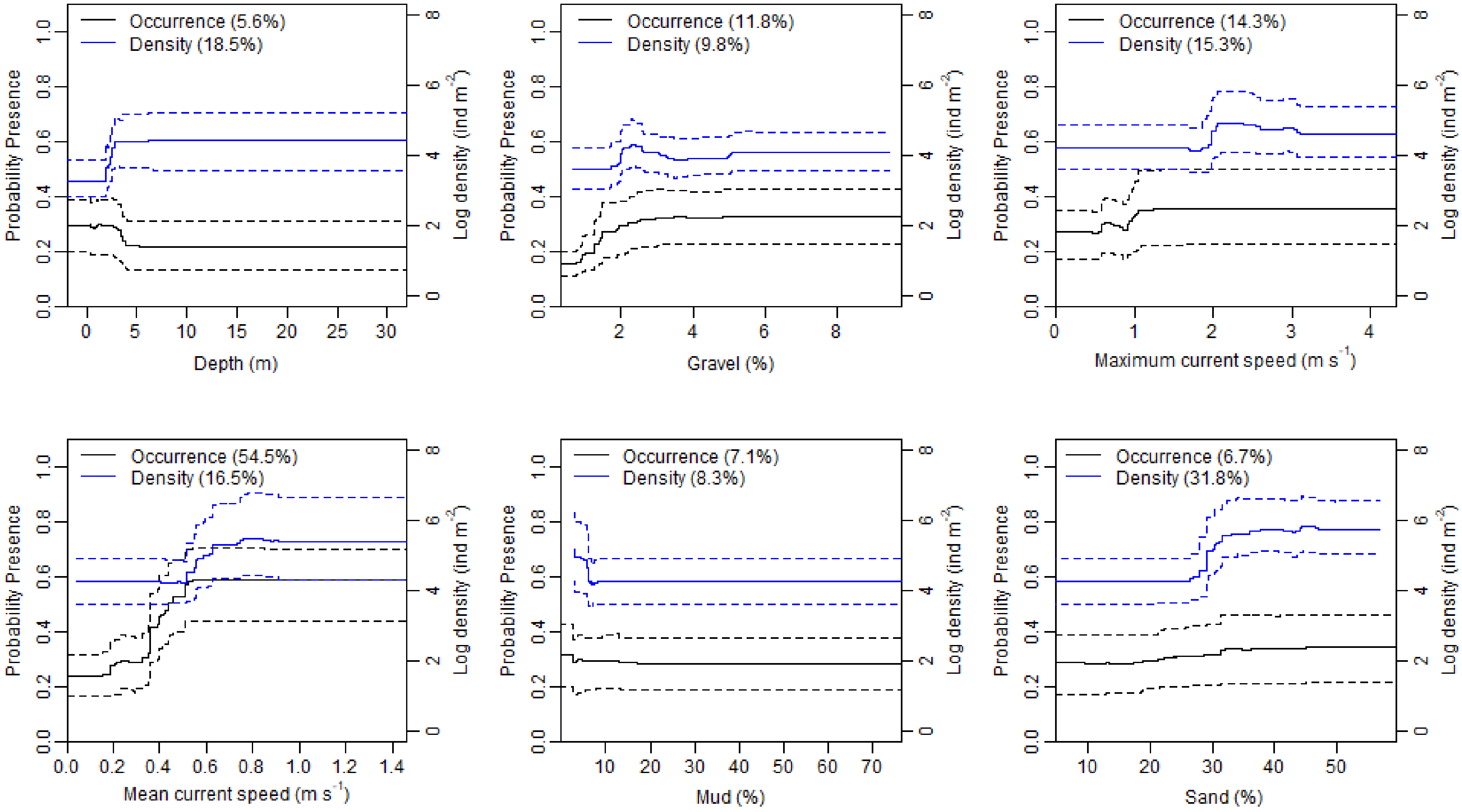

Figure A4 Partial dependence plots for mean probability of occurrence and density of *Paphies* with 95% confidence intervals (dashed lines). Relative influence of the environmental predictor for each model is indicated in brackets.

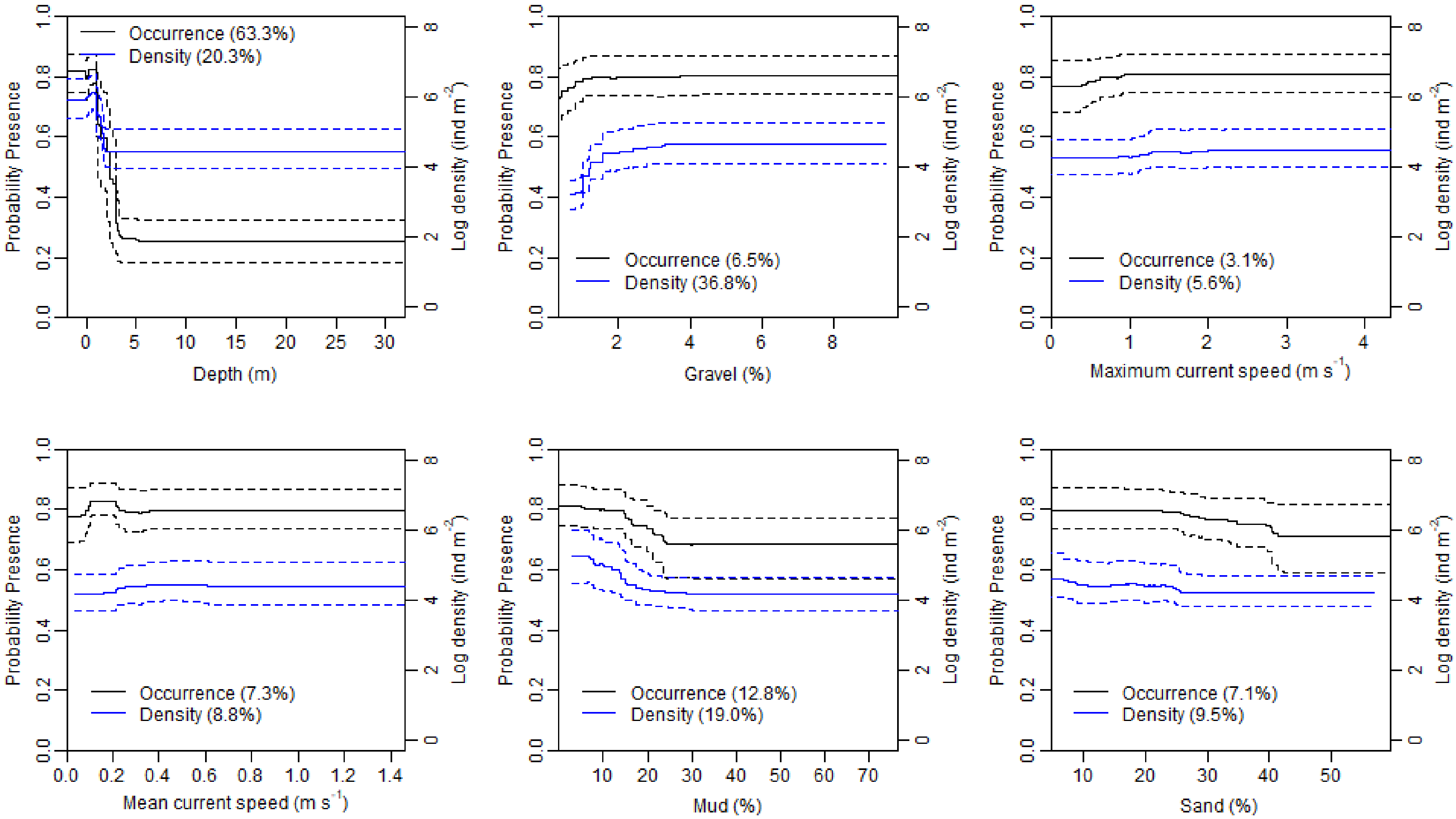

Figure A5 Partial dependence plots for mean probability of occurrence and density of *Austrovenus* with 95% confidence intervals (dashed lines). Relative influence of the environmental predictor for each model is indicated in brackets.

Appendix 4
Ecological principles definitions – Chapter 5

Below I document in detail the rules and scoring structure applied in the ecosystem service maps, with weighting scores in parentheses. The reasoning behind each rule is described and references to supporting literature are provided, as well as our justification for separating high to low contributions to services. These rules were applied to areas where shellfish are present only (probability of occurrence > 0.3 or density > 20 ind m^{-2}). Threshold values for rules were set based on values obtained from literature or based on expert opinion, as well as the range and distribution of the (environmental) variables in Tauranga harbour.

ES1 Food provision service

Bivalves provide a food source to humans, which is underpinned by the amount of biomass available for harvest (Chapter 2). In Tauranga harbour, *Austrovenus* and *Paphies* are harvested recreationally and customary only, but are harvested commercially elsewhere in the country (Marsden and Adkins 2010, Pawley et al. 2013) and equivalents can be found around the world (e.g. Carss et al. 2020).

P1.1 Density of large individuals (5x)

The amount of service provided is strongly dependent on the density of edible (large) individuals, as gathering effort goes down when large individuals are present at high densities (Figure A6 A). A survey on non-commercial gathering in urban intertidal areas showed a strong preference for large individuals in known high density beds (Hartill et al. 2005). This is in line with optimal foraging theory and reflects a type 2 functional response (Holling 1959, Staddon 1983). Size distribution of *Austrovenus* is related to inundation period, distance to harbour entrance, and sediment grain size, with the larger individuals (>20 mm) found in the low intertidal and shallow subtidal close to the harbour entrance in sediments with low mud content (Stephenson 1981, Park and Donald 1994, Jones et al. 2011). Large beds of *Paphies* are predominantly found near the harbour entrances in coarse sediments where the proportion of large individuals (>40 mm) is high (Hooker 1995). Juveniles can be found either directly at the entrance of the estuary, and steadily increase further upstream and on the low intertidal (Hooker 1995). A linear increase in service value is expected as density increases from 0 to 200 large ind m^{-2} and then levels of at high densities (Figure A6 A).

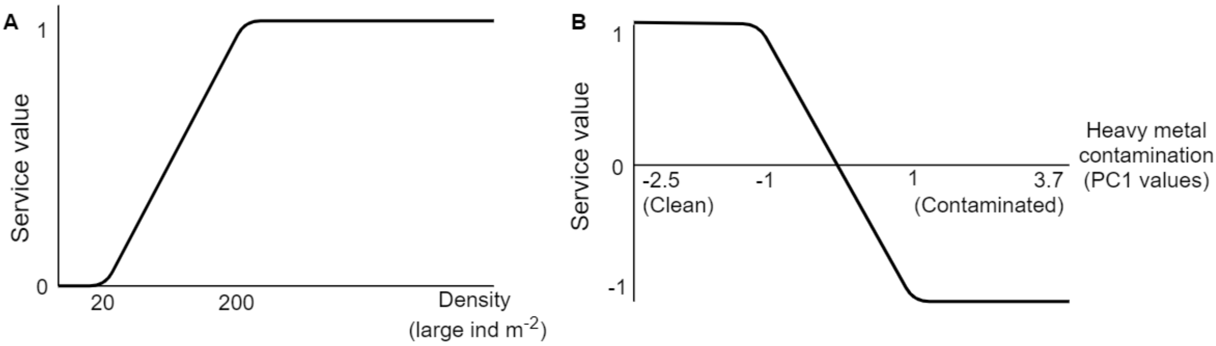

Figure A6 Scoring structure for food provision service, including A) Density of large individual scoring and B) Contamination scoring were derived from a principle component analysis (PCA) of sediment lead, copper, and zinc concentrations (see Appendix 5).

P1.2 Accessibility (3x)

Accessibility is a social driver, as recreational food provision is assumed to be higher in locations that are easily accessible. For estuaries, this means that people can access the shellfish bed by foot on low tide (<0.76 m below MSL for Tauranga Harbour), or shellfish are present in the shallow subtidal (<1.5m below MSL for Tauranga Harbour). Access points have been shown to affect gathering on intertidal areas, with more gathering on the intertidal closer to access points like car parks, walkways, etc. (Tinlin-Mackenzie et al. 2019). Accessibility was categorically determined as a combination of bathymetry (depth around MSL) and distance to access points, like carparks, public toilets, boat ramps, and walk- & cycle ways within 200m from shore (Table A3). Accessibility was limited (score = 0) in main channels (>10m below MSL) that are used for shipping and recreational boating activities, and are subjected to strong currents making it hazardous for shellfish collection.

Table A3 Accessibility scoring.

Distance to access point (km)		Depth (m below MSL)	Score
< 0.5		< 0.76	1.0
< 0.5		< 1.5	0.8
< 1		< 1.5	0.6
< 2		< 1.5	0.4
> 2	OR	> 1.5	0.2
		> 10	0

P1.3 Contamination (2x)

Food provision can be vulnerable to pollution if pollutants accumulate in shellfish and cause illness (e.g. bacterial or algal) to people if eaten (Gagnon et al. 2004). Heavy metals can negatively impact macrobenthic fauna in estuaries (Dauvin 2008), and together with bioaccumulation (Baudrimont et al. 2005, Fukunaga and Anderson 2011) can cause contaminated areas to be less suitable for consumption compared to uncontaminated sites (Figure A6 B). Heavy metals (e.g., lead, copper, and zinc) in the sediment reflect contamination from different terrestrial sources, including industrial and municipal discharge and some agricultural run-off (Birch and Taylor 1999, Herngren et al. 2005, Tang et al. 2010), and is therefore used as a proxy for contamination in this study reflecting the different catchment uses. Heavy metal data from Tauranga harbour show a gradient from low contaminated sites at the harbour entrances to more contaminated sites in the inner harbour, although all values were below those that trigger negative ecological consequences in sediments (ANZECC 2000, Fukunaga and Anderson 2011). However, the bioaccumulation of heavy metals in shellfish could be concerning for food uptake of bivalves (ANZECC 2000), hence the PCA scores were used to reflect the gradient from contaminated to clean for service values.

ES2 Water quality regulation service

Urbanization and land use change has negatively impacted estuarine ecosystems and reduced water quality through increased sedimentation, eutrophication, and runoff of pollutants and pathogens (Freeman et al. 2019). For this service, we focussed specifically on the top-down effect of bivalves through suspension feeding, thereby reducing turbidity and improving water clarity (Newell 2004).

P2.1 Density and mean current velocity (5x)

The capacity of bivalves to filter the water column and remove particles is primarily driven by their density and flow conditions. At extreme densities, however, increases in clearance rates can be reduced due to re-filtration of water and overlap in feeding zone of individuals (Du Clos et al. 2017). Results from Jones et al. (2011) indicated a levelling off in bed clearance rate with densities over 500 ind m^{-2} for *Austrovenus* which is affected by current velocities and indicated highest bed clearance rate at higher current speeds (up to 15 cm s^{-1}). Multiple studies (e.g. Sobral and Widdows 2000, Widdows and Navarro 2007) found a reduction in clearance rate past the optimum with clearance rates declining at higher current velocities (up to 45 cm s^{-1}).

Furthermore, clearance rate can cease at current velocities that cause sediment erosion thresholds to be exceeded (Nielsen and Vismann 2014). We therefore predict a combined effect of density and current velocity to derive bed clearance rates for *Austrovenus* and *Paphies*, with a linear increase and levelling off with density and an optimum at mean current velocity of 10-20 cm s^{-1}, with a drop in clearance rate at higher flow speeds (Figure A7 A). At highest and lowest current velocities (<5 or >45 cm s^{-1}), filtration by bivalves cannot be excluded as mean current velocities are used as the aligned data (e.g. shellfish could filter around slack tides) and hence service values were set to ‘low’ instead of zero, except when no shellfish are present.

P2.2 Inundation period (2x)

Inundation period was considered for this service, as shellfish are only able to contribute to water quality regulation when covered by the tide. Shellfish beds in the subtidal were not limited by tidal inundation, whereas individuals in the intertidal are limited by the time submerged (Vismann et al. 2016). Beentjes and Williams (1986) showed that *Austrovenus* filters at a 4 h window around high tide. Hence, beds on the intertidal inundated for >4 hours will not be limited, but individuals progressively further away and covered for shorter periods and in shallower water will be limited (Figure A7 B) .

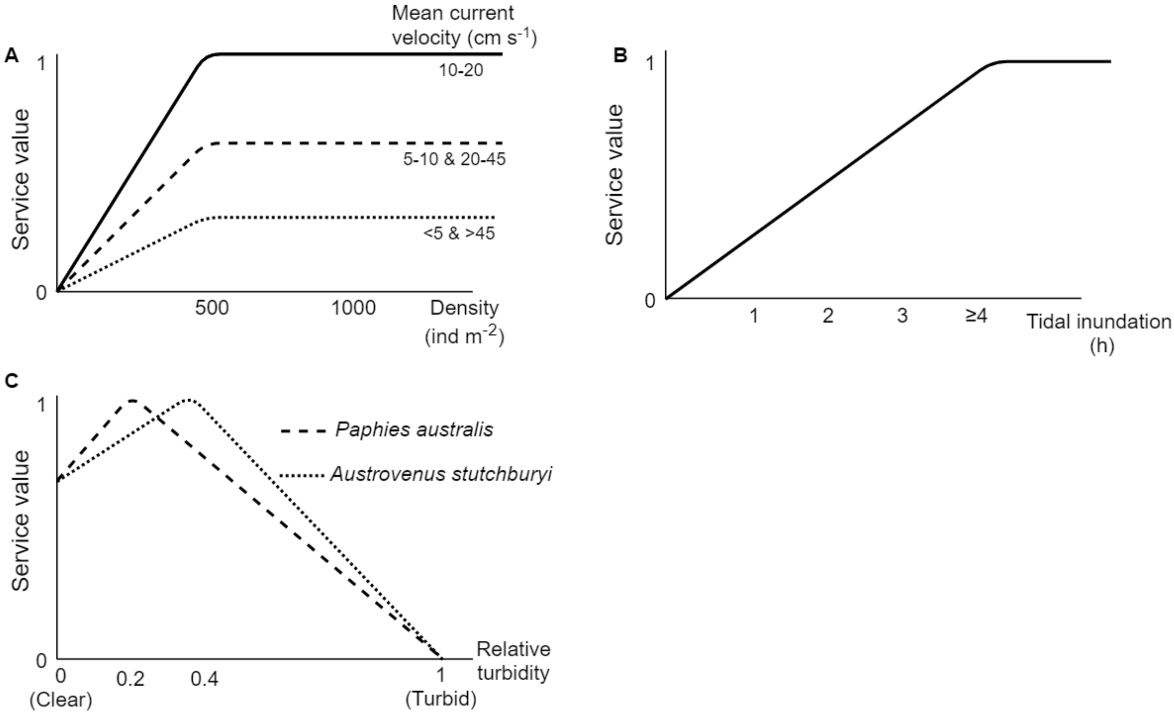

Figure A7 Scoring structure for Water quality regulation service, including A) density and current velocity scoring, B) inundation period scoring, and C) turbidity scoring, based on relative turbidity in the estuary (ranging from clear to turbid).

P2.3 Turbidity (3x)

The amount of suspended sediment concentrations (SSC) or suspended particulate matter (SPM) in the water column have been shown to impact water quality regulation. Clearance rates are shown to vary under different levels of SSC/SPM, with reduced clearance under high particle concentrations for infaunal species, thereby reducing the beds capacity to contribute to water quality improvement (Hawkins et al. 1998) (Figure A7 C) *Austrovenus* clearance rates were high below 100 mg l^{-1} SSC and were optimal at ~60-80 mg l^{-1}. *Paphies* clearance rates were optimal at SSC of 30-50 mg l^{-1} and filtration rates levelled off at concentrations exceeding 100 mg l^{-1} for both species (Hewitt and Norkko 2007, Cussioli 2018). *Paphies* is more sensitive to suspended sediments, but both species show a similar response to increased suspended particles, with an initial increase in clearance rate, followed by a quick drop in clearance rate once the optimal SSC concentration is exceeded (Hewitt and Norkko 2007). Furthermore, at lowest turbidity (e.g. clear water), there is reduced capacity for shellfish to provide to the service as little can be gained by removing particles in already clear water, hence service values <1 for lowest turbidity conditions.

ES3 Nitrogen removal service

Denitrification in marine sediments is one of the primary mechanisms by which biologically active nitrogen can be removed from the system permanently. Denitrification is the microbially mediated process in which inorganic N (NH_4^+, NO_3^-) is converted to N_2 gas that is lost to the atmosphere (Knowles 1982). In healthy estuarine sediments, nitrification (the conversion of NH_4^+ to NO_3^-) and denitrification are often coupled (Jenkins and Kemp 1984), and require both oxic sediments (for nitrification) and anoxic sediments (for denitrification). Denitrification can vary spatially depending on available N sources and is influenced by multiple biotic and abiotic variables (see Cornwell et al. 1999)

P3.1 Density (4x)

Shellfish are considered to have a positive effect on sediment denitrification rates compared to bare sediments or reference sites (without shellfish) (Pelegri and Blackburn 1995, Humphries et al. 2016, Smyth et al. 2018). Infaunal shellfish promote denitrification through the addition and reworking of organic material (N source) into the sediment and by bioturbation, thereby enhancing oxygenation of the sediment and the amount of oxic-anoxic interface needed for coupled nitrification-denitrification to occur. With increased shellfish numbers to moderate-high densities, the effect on denitrification is positive (Welsh et al. 2015), but this effect can collapse as densities reach extreme numbers (Newell 2004). In this case, sediments can become anoxic from the degradation of large amounts of organic rich biodeposits and is strongly related to sediment oxygen demand (SOD) (Cornwell et al. 1999, Eyre et al. 2013) and losses of the 3D structure of the oxic-anoxic boundary layer (Gilbert et al. 2003, Eyre and Ferguson 2009). This collapse at high densities is less likely to be an issue in our example due to high flow and intertidal exposure, yet we modelled a small drop at extreme densities (Figure A8 A).

P3.2 Organic matter (3x)

Initially, organic matter (OM) is expected to positively affect denitrification (Douglas et al. 2018, Smyth et al. 2018) as it provides a bioreactive nitrogen source (Murphy et al. 2019), and shows a gradual (linear) effect on denitrification potential when OM content ranges between 0 and 3% (Lohrer et al. 2020). As available nitrogen becomes less limiting, scores will level-off at higher OM concentrations (Figure A8 B).

P3.3 Mud content (2x)

Sediment grainsize and porosity can affect denitrification potential in estuaries (Douglas et al. 2019) by affecting the transport of solutes across the oxic-anoxic interface. In coarse sediments (with low mud content) the rate of denitrification is affected by physical advection of solutes, whereas in muddy sediments that are not diffuse, the importance of animal-mediated solute transport is high (O'Meara et al. 2020). Therefore, we expected an optimum in service value at intermediate sediment mud contents, with lower and upper limits reflecting limitations by physical advection in coarse sediments, and reduced solute transport at higher mud content (Figure A8 C).

P3.4 Inundation period (1x)

Denitrification rates are habitat specific and tend to be lower in subtidal as compared to intertidal flats (Piehler and Smyth 2011). Measurements of N_2 fluxes over the sediment water interface in Tauranga harbour showed no significant differences between beds dominated by *Austrovenus* in the intertidal and *Paphies* in the subtidal (Chapter 3). However tidal emersion restricted this service value over a full tidal cycle in the intertidal to the time it is inundated, whereas subtidal sites do not have this limitation (Figure A8 D).

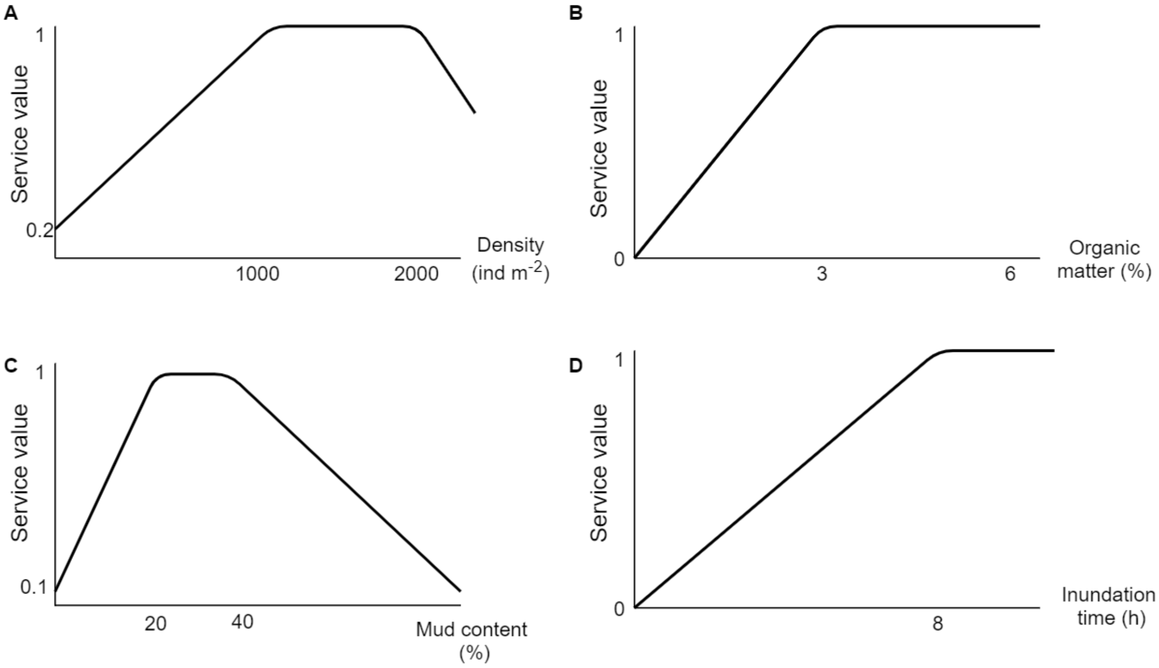

Figure A8 Scoring structure for nitrogen removal service, including A) density scoring, B) organic matter content scoring, C) scoring for mud content, and D) scoring for inundation time.

ES4 Sediment stabilisation service

In estuarine and coastal systems, sediment dynamics are affected by complex interactions of physical, chemical, and biological processes and properties (reviewed by Le Hir et al. (2007)). Hydrodynamic processes affecting bottom shear stress in estuaries include tidal currents and wind generated waves and erodibility is affected by sediment properties like grain size, mud- and organic content and exposure to air. Biological factors can alter sediment dynamics and can have either a stabilising or destabilising effect, which can be density and context dependent. For example, algal biofilms, mussel reefs, and salt marshes tend to have a stabilising effects, whereas biota can cause sediment destabilisation through bioturbation, increasing bed roughness and altering fluxes to the sediment through feeding and biodeposition (Le Hir et al. 2007). Through their presence, bivalves create beds or reefs that can contribute to shoreline and/or sediment stabilisation (Grabowski and Peterson 2007).

P4.1 Mud content (4x)

The effect of infaunal bivalves on sediment stabilisation may be positive or negative, but are more generally considered to make muddy sediment less resistant to erosion by reworking it with their activity. In laboratory flume studies on cohesive (muddy) sediments, both suspension- and deposit feeding bivalves are often considered to be sediment destabilisers (e.g.

Widdows et al. 1998, Sgro et al. 2005, Ciutat et al. 2007). Recently, field studies have focussed on *in situ* or correlative field measurements, where indirect effects and important ecosystem interactions and feedbacks can be considered. Under field conditions in sandy substrates, high abundances of infaunal bivalves may stabilise the sediment (‘armouring’ the bed) by providing a network of physical structures with their shells and mucus production that immobilizes the sediment surface (Donadi et al. 2014). Below approximately 30% mud, sediments are considered non-cohesive whereas above 30% mud sediments start behaving like a cohesive sediment-matrix (Mitchener and Torfs 1996, Van Ledden et al. 2004). Therefore, a stabilising effect is predicted in very coarse sediments (<10% mud content), and a negative effect is expected under muddy conditions (>50% mud content), with a linear decrease reflecting the change in potential (Figure A9 A).

P4.1 Density (3x)

The potential for infaunal bivalves to contribute to sediment stability can occur under high densities in coarse sediments, where bivalves have been found to ‘armour’ the bed and raise sediment level by a few centimetre. This ‘armouring’ of the sediment at high densities, was described by Eriksson et al. (2017) and Donadi et al. (2014), who observed sediment accumulation at high *Cerastoderma edule* addition to a sandy site. Effects of shellfish may be indirect, as they can facilitate the development of biofilms by 1) stabilising the sediment and decreasing sediment erosion, creating low-stress environments for microphytobenthos (MPB)

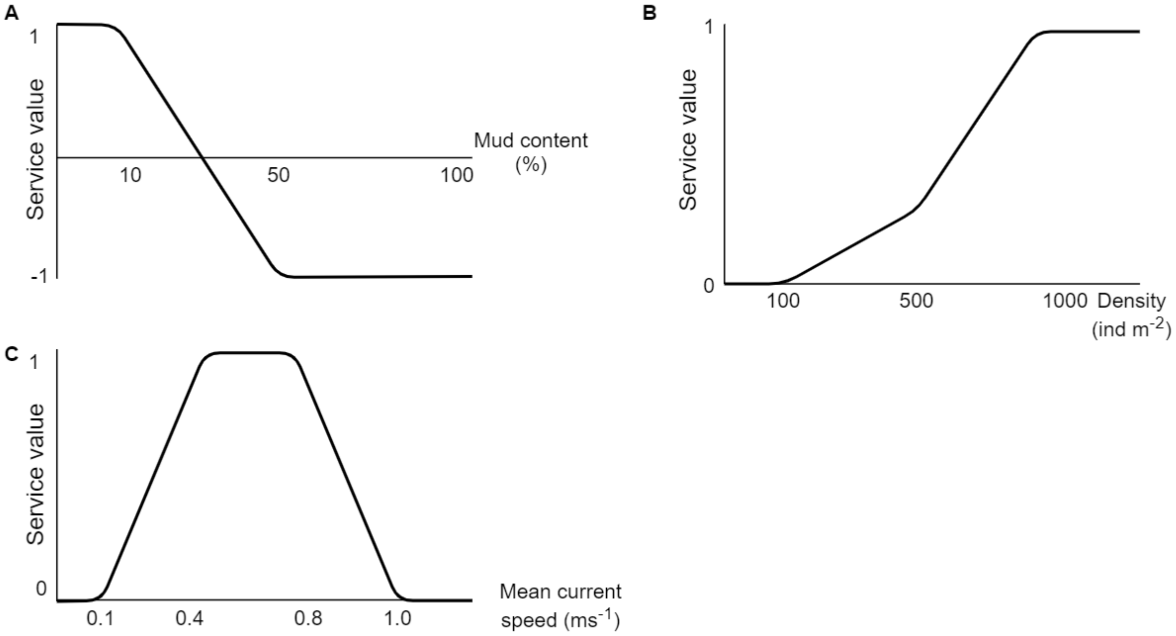

Figure A9 Scoring structures for sediment stabilisation service, including scoring for A) Mud content, B) bivalve density, and C) mean current speed.

(Donadi et al. 2013), and 2) providing additional nutrients needed for MPB (Sandwell et al. 2009). At low densities, this effect will not occur, and therefore service value will be zero for densities <100 ind m^{-2}, and a stepwise increase in service value is used at 500 ind m^{-2} at service value of 0.4 (Figure A9 B).

P4.3 Mean current velocity (3x)

Flow induced shear stress affects sediment stability. If current velocity is below a critical erosion velocity (U_{crit}), no erosion will take place. U_{crit} generally ranges from 0.10 - 0.20 m s^{-1} (e.g. Jie et al. 2001, Lundkvist et al. 2007, Soares and Sobral 2009), here we chose a conservative estimate under which no erosion would take place. The potential effect of shellfish is also expected be low at very high current velocities when shellfish cannot counteract the erosive power of currents (here set at current velocities > 1.0 ms^{-1}). Service value is expected to be optimum at intermediate current velocities where shellfish activities (indirect or direct stabilisation of sediments) can have the largest affect in changing the erosion thresholds (Figure A9 C).

Appendix 5

Data layers for ES mapping – Chapter 5

Table A4 Data layers used for ES mapping. For each data layer, the method used to derive the data layer are identified and examples are shown in Figure A10. Tauranga surveys as mentioned in the 'Data' column include work by Manaaki Taha Moana (MTM) and Oranga Taiao Oranga Tangata (OTOT) projects (Ellis et al. 2013, Clark et al. 2018), Manaaki Te Awanui (MTA) (Fairlie et al. 2017), and University of Waikato (UoW) (unpublished).

Data layer	Method	Data	Map example
Presence-absence Density	Species distribution model – probability of occurrence Species distribution model – bivalve density (ind m^{-2}) (see results Chapter 4)	Predicted probability of occurrence and density maps	Figure A10 A&B
Density of large individuals	Proportion of large individuals x Density Proportion of large individuals (>20mm for *Austrovenus* and >40mm for *Paphies*) relates to the distance to harbour entrance, depth, and sediment characteristics. *Austrovenus:* highest in the lower intertidal/shallow subtidal with low mud content and close to harbour entrance. - Mud: ideal 0-5%, declining 5-20% - Depth: ideal 0-0.7m, increasing from -0.3-0m, declining 0.7-2m depth - Distance: ideal 0-3.5km, declining 3.5-12km *Paphies*: highest close to harbour entrance and decreases further upstream and directly at harbour entrance. - Sand: ideal >50%, increasing: 10-50% - Depth: ideal 0.5-5m, increasing 0-0.5m, declining from 5-31m	Size data: Tauranga surveys (MTM, MTA, UoW) Bathymetry: Hydrodynamic model (see below) Distance to entrance (categorical at 500m intervals from northern and southern harbour entrances) Sediment characteristic (mud or sand content, see below)	Figure A10 C&D

Table A4 continued

Data layer	Method	Data	Map example
Density of large individuals cont.	Distance: ideal: 2-5km, increasing 1-2km, declining 5-15 km Assumptions checked against data points with known size classes in the harbour from surveys. Significant positive correlation between observed and predicted values of 0.62 and 0.59 (Pearson R for *Austrovenus* and *Paphies*, respectively).		
Bathymetry	Depth (m) corrected to mean sea level (MSL)	Hydrodynamic model	Figure A10 E
Mean current velocity	Average current speed (ms^{-1}) over a tidal cycle		Figure A10 F
Tidal inundation	Approximated the semi-diurnal spring tidal curve with sine function, where H is the height (around MSL) and t is time (h) $H(t) = 1.0 \times \sin\left(\frac{\pi}{6.2} t\right)$ - Exposed: inundation = 0 hours - Subtidal: inundation = 12.4 hours - Intertidal: calculate interval for t with the tidal curve function based on the height on shore (around MSL)	NIWA tide forecast Height (inverse bathymetry)	Figure A10 G
Distance to access point	Spatial data on access points (car parks, public toilets, walkways, boat ramps within 200m from shore) that were buffered at 200m, 500m, 1km, 2km, 2+km intervals to create raster layer	Data portals of two district councils (Tauranga City and Western Bay of Plenty Council)	Figure A10 H
Sediment mud content	Inverse distance weighted (IDW) interpolation of survey points (192 points in Tauranga harbour) - Mud content (fraction < 63 μm) - Sand content (fraction ≥ 250, < 500 μm)	Tauranga surveys (MTM, OTOT, MTA, and/or UoW)	Figure A10 I

Table A4 continued

Data layer	Method	Data	Map example
Organic matter content	IDW interpolation of 141 survey points in Tauranga harbour: - Percentage organic matter content as the weight loss on ignition (g/100g ash-free dry weight)	Tauranga surveys (MTM, OTOT, MTA, and/or UoW)	Figure A10 J
Heavy metal contamination	Heavy metal contamination derived from 170 points with data for Pb, Zn, Cu. All heavy metals showed similar patterns and a PCA allowed for the combination of all 3 metals into 1 measure for contamination. PCA axis 1 explained ~89% of the variance and the values from this axis were therefore used to represent heavy metals. Values for data points were then interpolated (IDW) to derive a spatial layer based on PCA axis 1. Low values (-2.5) indicate clean sites, whereas high values (+3.6) indicate contaminated sites.		Figure A10 K
Turbidity	Relative turbidity data (clear vs. turbid) was used as no reliable SSC concentrations were available for the entire harbour. A spatial layer for relative turbidity is based on general trends observed from 19 sampling locations throughout the harbour that reflect low turbidity close to harbour entrance in fast flowing channels (high flushing), with an increase in turbidity further away from the entrance and in areas with low current velocities (reflecting more stagnant water). Relative turbidity is calculated by multiplying distance to entrance (normalised from 0-1) with inverse mean current speed (normalised from 0-1). The observed and predicted relative values in turbidity showed a significant positive Pearson correlation of 0.63.	Suspended sediment concentrations (Scholes 2015, Cussioli et al. 2019)	Figure A10 L

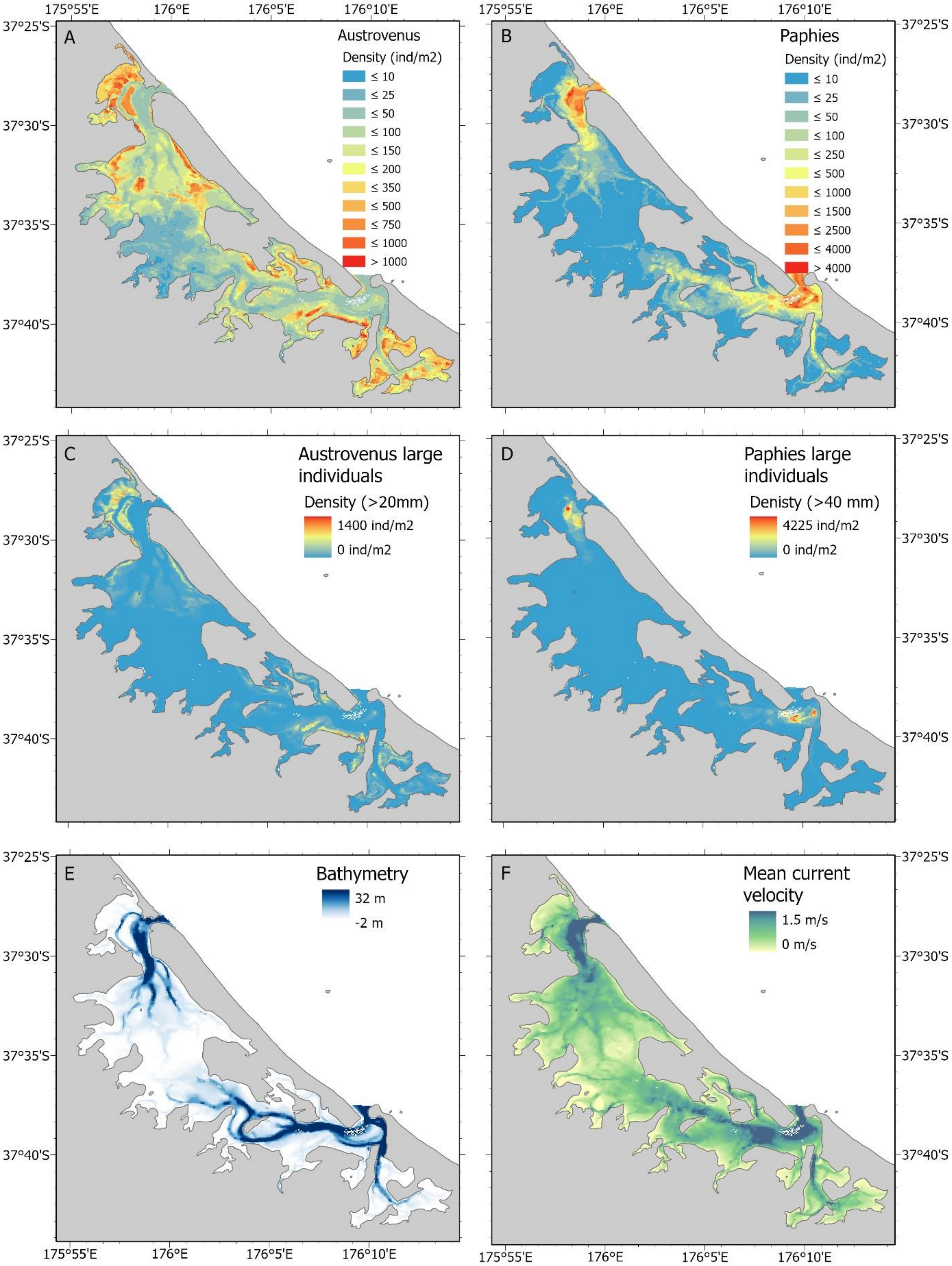

Figure A10 Maps of data layers underpinning ecological principles for ES mapping. including A & B) density of *Austrovenus stutchburyi* and *Paphies* australis, C & D) density of large individuals (>20mm for *Austrovenus* and >40 mm for *Paphies*), E) Bathymetry, F) Mean current velocity, G) Tidal inundation, H) Distance to access point, I) Mud content, J) OM content, K) heavy metal contamination (relative scores from principle component analysis), and L) Relative turbidity. For detailed description of all data layers, see Table A2.

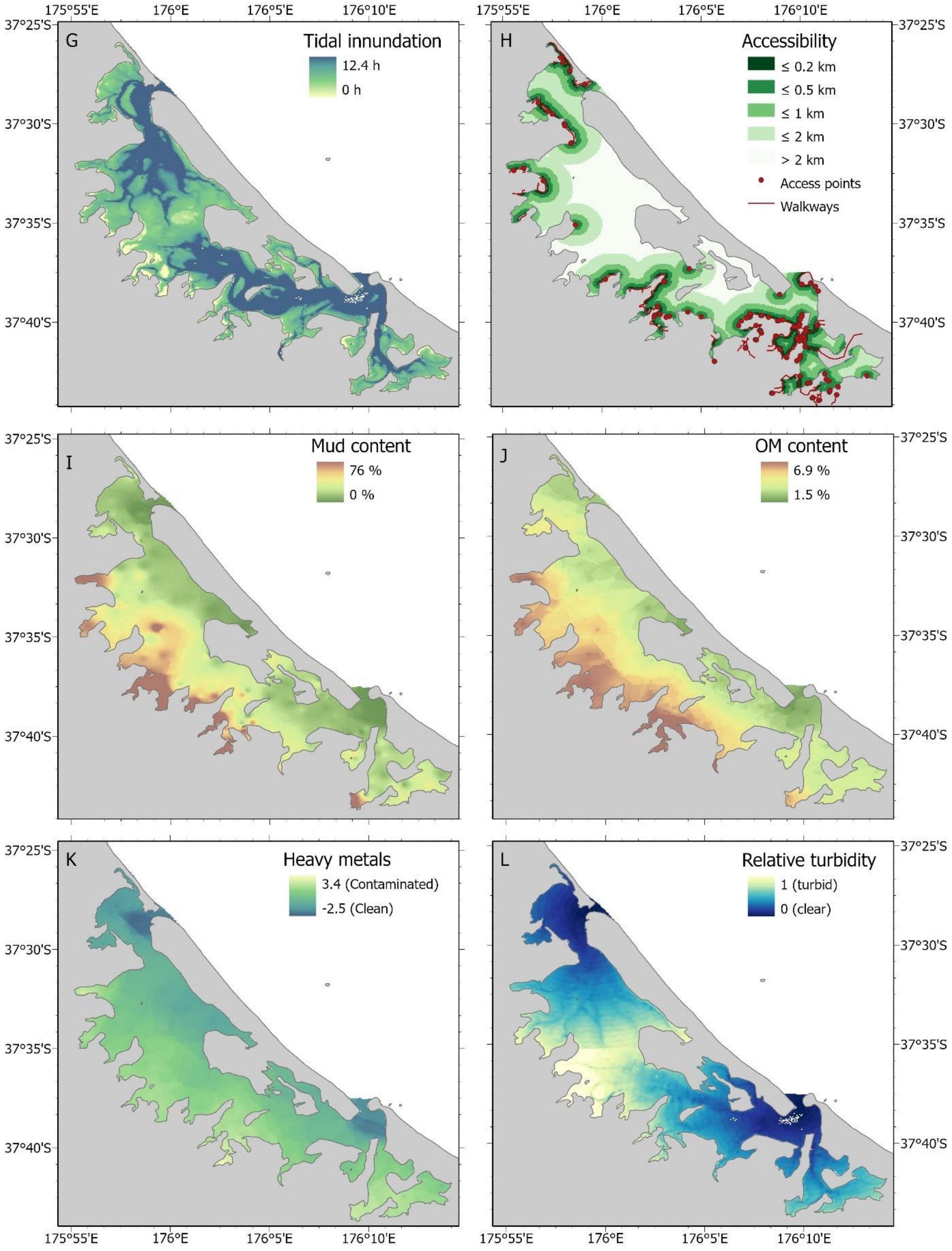

Figure A10 Continued

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