Marine stressor and receptor interactions: A new approach to incorporate multiple stressor impacts into marine spatial management

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Abstract

Soft sediment benthic ecosystems are highly productive habitats which provide humans with a variety of valued resources and ecosystem services globally. However, coastal environments are subject to ongoing and increasing levels of anthropogenic stress which urgently needs to be quantified and strategically managed to balance socioeconomic resource interests. To support a more holistic approach to Marine Spatial Planning and better inform management decisions, spatial assessment approaches are needed which quantify the accumulating impact of multiple stressors on coastal species and habitats. This thesis investigates stressor-induced change in the density and distribution of subtidal benthic invertebrates from two globally pervasive stressors (sedimentation and bottom fishing), to develop spatial assessment tools useful to inform marine spatial management decisions.

For many benthic species, their functional capacity is inherently density-dependent, and environmental stressors can impact population density, hence limiting the functional capacity of species and their ability to contribute to ecosystem processes and overall ecosystem health. A holistic approach to MSP needs to address the ways in which humans can cumulatively use, and also impact the environment, but it is difficult to measure the impact an environmental stressor can cause without first quantifying the current density and distribution of key species that they effect. Furthermore, it can often be challenging to obtain species records measuring abundance, density, or species richness within certain geographical locations, due to data scarcity, even if more data is available over a broader spatial scale. Probability of occurrence, abundance, and density was predicted using Species Distribution Models (SDMs) for seven functionally distinct benthic invertebrates, over two different spatial scales to compare the difference in model performance and usefulness of predictions made using data-rich national scale models compared to data limited regional scale models. Results indicated that neither occurrence nor abundance SDMs performed consistently better at either scale across all taxa models, demonstrating the challenge of working in-data limited environments. Models which achieved the more optimal predictive performance across spatial scales were selected to be combined into a regionally useful density model (i.e., regional data-derived occurrence model * national data-derived abundance model) highlighting the utility of a multi-scalar approach.

Knowledge of how multiple stressors impact marine species and modify habitats over time is critical, to support management and mitigation of anthropogenic stressors. Bottom fishing and sedimentation stress are two globally pervasive coastal stressors. The transportation of terrestrially sourced silt, mud, and clay into the coastal environment from inadequate land management can alter sediment biogeochemistry, and alter macrofaunal community composition, which can lead to the smothering of seafloor communities. Bottom fishing can directly damage and disturb seabed habitats, reducing the abundance of macrofaunal communities, and can lead to homogenisation of the seascape. A spatially explicit model including correlative stressor-response relationships were applied to simulate single and multi-stressor impact scenarios over a temporal period of four-years to predict the change in density, distribution, and recovery for different stressor

combinations and magnitudes. Models focussed on three functionally distinct coastal seafloor invertebrates that varied in stressor response and recovery time. All taxa exhibited different stressor responses in terms of density change, and the spatial distribution pattern of density values was affected, informed through empirically derived stressor-receptor response curves. The greatest modification to taxa density occurred across the shallow coastal environment, near shore, for habitats that were predicted to have high density to begin with. Fishing was the more dominant stressor and overlapping fishing impact year on year resulted in little to no recovery. For sensitive emergent epifauna (*Callyspongia*), sedimentation stress was almost as impactful as fishing, highlighting that greater management consideration should be given to the compound effect of slow-acting, accumulating stressors, even in scenarios where a single stressor is more dominant.

Failure to adequately identify and mitigate the effects of multiple stressors increases the risk of focussing conservation efforts on areas that could become ecologically diminished in the future. To ensure that global biodiversity conservation targets are upheld under ongoing anthropogenic conditions, practitioners must identify robust and ecologically resilient habitats that will persist over time as part of a systematic prioritization approach. A comparative spatial prioritization assessment was performed to test the utility of using density SDMs that had been modified by stressor impacts (stressor-impacted predictions) to drive a spatial prioritization using Zonation, as opposed to using unimpacted density SDMs (the conventional method). Utilising stressor-impacted predictions within the prioritisation assessment increased conservation efficiency, and thus spatial accuracy, to help prioritise high-density areas that showed resilience to stressor impacts over time (from 4 years of successive stress). This analysis highlighted that conventional prioritization approaches may no longer be sufficient and may prioritise habitats that experience density loss under stressed conditions, undermining conservation effectiveness. Incorporating multiple stressor effects that have accrued over time can help identify areas that are likely to retain a higher total density into the future, to support long-term conservation objectives. Incorporation of spatially explicit stressor effects using taxa stressor impacted density predictions helps identify ecologically rich and resilient habitat areas that persist within the broad footprints of stressors, instead of avoidance, which is often promoted by conventional approaches to minimise conservation cost.

Collectively, this thesis demonstrated the utility of novel modelling approaches which integrate the combined and accumulating effects of anthropogenic stressors on coastal species and habitats to help inform MSP decision-making. It also highlighted the range of possible implications to benthic species and coastal ecosystems if anthropogenic stressors are not adequately identified and managed.

Preface

The main body of this Thesis is comprised of three research chapters (Chapters 2 – 4), which have either been published or are in preparation for publication in peer-reviewed scientific journals. As the chapters were written as separate articles there is some crossover in the methods (specifically within Chapters 3 and 4), as outputs created in each chapter were used within the analysis of the subsequent chapter. I have assumed responsibility for all data analysis and writing for this thesis. Unless otherwise referenced, the material produced for this thesis was from my ideas. This work was undertaken under the supervision of Professor Conrad Pilditch and Dr Fabrice Stephenson from the University of Waikato, and Dr Carolyn Lundquist from the National Institute of Water and Atmospheric Research (NIWA).

Chapter 2 has been published in Ocean and Coastal Management (2022) under the title 'Improving predictions of coastal benthic invertebrate occurrence and density using a multi-scalar approach' by Stephanie L. Watson, Fabrice Stephenson, Conrad A. Pilditch and Carolyn J. Lundquist. doi.org/10.1016/j.ocecoaman.2022.106355

Chapter 3 is currently in preparation for publication.

Chapter 4 is currently in preparation for publication.

I also contributed to a publication related to chapter 2 which is not included in this thesis, published by Frontiers in Marine Science (2020) under the title "Development of a seafloor community classification for the New Zealand region using a gradient forest approach'' By F. Stephenson, A. A Rowden, T. Brough, G. Petersen, R.H Bulmer, J.R Leathwick, A. M Lohrer, J. I Ellis, D. A Bowden, S. W Geange, G. A Funnell, D. J Freeman, K.Tunley, P. Tellier, D. E Clark, C. J Lundquist, B. L Greenfield, I. D Tuck, T. L Mouton, K. F Neill, K. A Mackay, M. H Pinkerton, O. F Anderson, R. M Gorman, S. Mills, S. Watson, W. A Nelson, J. E Hewitt doi.10.3389/fmars.2021.792712

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I would also like to thank Fisheries New Zealand for providing me access to trawling data within Tasman and Golden Bay, and for approving use of my outputs created for this thesis and for publication.

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831 forever.

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Glossary of Key Terms

Ecosystem function: The flow of energy and materials through the arrangement of biotic and abiotic components of an ecosystem that allows or could allow natural systems to provide ecosystem services (Mitchell *et al.,* 2015).

Ecosystem service: The benefits and values that humans gain from ecosystems (Gladstone-Gallagher *et al*., 2019)

Biological Trait: Any morphological, physiological, or phenological feature measurable at the individual level (Snelgrove *et al*. 2014).

Functional group / Trait: A grouping of species that share combinations of biological traits that affect ecosystem function in similar ways. Note that this concept could also apply to resource use traits, and depending on the context, grouping species by traits that are associated with their resource use behaviour might be more appropriate to assess their role in the community or ecosystem (Gladstone-Gallagher *et al*., 2019).

Functional Role: The functional role of an individual or species in an ecosystem is expressed through their biological traits (i.e., the functional role of a predatory scavenger is related to both morphology and feeding habit (Bremner, 2008).

Resilience: Resilience is the capacity to retain ecosystem function despite disturbance and is assessed by functional group diversity. Resilience attribute: an attribute (or trait) of an individual species, population, or community that increases the resilience of ecosystem functions (Gladstone-Gallagher *et al*., 2019)..

Recovery: Recovery is an aspect of resilience that is concerned with the ability of species or functions to return to pre-disturbance levels (Gladstone-Gallagher *et al*., 2019).

Disturbance: A force or process that causes a response in the biodiversity and/or ecosystem function (e.g., a reduction in species biomass, abundance, or ability to carry out functions). Whilst many definitions and synonyms of disturbance exist, we characterise disturbances across a continuum of time, space, and intensity (Gladstone-Gallagher *et al*., 2019)

Cumulative impact: Cumulative impacts (also referred to as cumulative effects) can be broadly defined as the combined and incremental impacts from past, present, and future human activities and natural processes which have caused a change to the environment (Clark, 1994). Within an ecological context it can be the cumulative effects of multiple drivers of change that can cause non-linear shifts in ecosystem functions and services, known as tipping points or regime shifts (Gladstone-Gallagher *et al*., 2019).

1. Chapter 1
General Introduction

1.1. Background and Introduction

Allocation of marine space has historically been governed by a sectoral approach, dominated by individual economic domains such as shipping, aquaculture, and mineral extraction (Douvere, 2008; Olsen, Olsen and Schaefer, 2011). An increasing complexity of users, resource requirements and economic interests in the coastal environment has led to the development of Marine Spatial Planning (MSP) to support multi-objective marine management requirements (Kelly *et al.*, 2014). Although MSP supports the spatial allocation of resources and competing uses, the management of ecosystem health and ecological resources required to balance competing socio-economic interests has remained challenging, with many marine ecosystems continuing to experience declining biodiversity (Domínguez-Tejo *et al.*, 2016; Menegon *et al.*, 2018). MSP focuses on regulating human activities in marine areas, and sustainable development of marine resources, it is focussed on the allocation of space and often does not include a comprehensive assessment of stressors and there impacts on ecosystem health (Ehler and Douvre 2009). To account for many of the ecological challenges which have failed to be addressed by conventional spatial management of marine resources, many practitioners aspired to adopt an Ecosystem-Based Management (EBM) approach (Arkema, Abramson and Dewsbury, 2006). At its core, Ecosystem-Based Management is an integrated approach that considers the entire ecosystem with aims to maintain the health, productivity, and resiliency of the oceans and highlights the need to address how humans can impact the environment and the interconnectedness between biological, physical, and socioeconomic elements within the wider ecosystem (Levin and Lubchenco, 2008; Link and Browman, 2014). Several research-oriented barriers to implementation have delayed progress in implementing an EBM approach to MSP (Crowder and Norse, 2008; Domínguez-Tejo *et al.*, 2016; Ehler and Douvere, 2009). The three main research-based barriers which perpetuate lack of understanding of the social and ecological dynamics of coastal and marine systems include: (1) how stressors and receptors interact spatially and temporally; (2) insufficient monitoring of those dynamics particularly monitoring data tied to ecological indicators of stress; (3) and inadequate development of tools that enable learning and adaptive management (Leslie and McLeod 2007; Foley *et al.*, 2017; Stelzenmüller *et al.*, 2020). Below I explore some of the key challenges faced by scientists when trying to develop quantitative approaches to overcome the above research barriers.

Several studies have discussed the paucity of appropriate marine-based environmental and biological data hindering conservation efforts, particularly in comparison to more data-rich terrestrial realms (Bučas *et al.*, 2013; Gorman *et al.*, 2012; Stephenson *et al.*, 2019; Cawardin *et al.*, 2012). However, it is understood that any ecosystem condition assessment will likely be challenged by either missing or imperfect datasets to varying degrees (Halpern and Fujita, 2013), and the development of approaches that can make data more accessible (e.g., the amalgamation of historic data) through transformation into spatial or visual outputs are needed. One of the primary challenges stems from the lack of spatially explicit data, as many historic monitoring plans measured fewer metrics, sampled fewer species, and visited locations infrequently, meaning that available long-term datasets are often lacking key information for modern assessment approaches (Parravicini *et al.*, 2012; Stamoulis and Delevaux, 2015). For example, numerical models (e.g., Species Distribution Models; SDMs) have mostly relied on occurrence records from a combination of research surveys, commercial fishing records and museum records, which often lack measurements of abundance, with many taxa represented at a genus level of taxonomic identification, not species level (Elith and Leathwick, 2009; Guisan and Zimmermann, 2000; Johnston *et al.*, 2015; Watson *et al.*, 2022)**.** Available datasets often contain spatial heterogeneity because of inherent spatial bias in survey data due to physical limitations of survey vessels (e.g., depth, current), resulting in insufficiently sampled regional coastal environments (Chaudhary *et al*., 2016; Costello *et al*., 2015). Furthermore, taxonomic biases also exist towards commercially and recreationally important species resulting in knowledge gaps toward species that perform critical ecological roles (e.g., working of sediments via bioturbation or formation of biogenic structures) which support productivity for higher trophic animals (Hillman *et al*., 2019; Ribo *et al*., 2021). Moreover, direct collection of pertinent spatial data is often outside the scope of MSP practitioners, and obtaining datasets which are consistent across management interest areas is often difficult, particularly for ecological and human use data (Stamoulis and Delevaux, 2015). Although data availability is rapidly improving and many approaches now exist to use data surrogates, marine practitioners cite that the lack of decision-support tools that can integrate current datasets and provide spatial outputs at a useful scale for management as one of the greatest barriers to implementation of multiple stressor effects in practice (Collie *et al.*, 2013; Halpern and Fujita, 2013; Orobko *et al.*, 2022).

The elaborate interaction pathways of stressor and receptor relationships result in inherent difficulty in predicting the stressor impact across space and time, particularly if environmental conditions differ across the spatial prediction area (i.e., the management extent) compared to the location where the stressor relationships were originally defined (Batista *et al.*, 2014; Crain, Kroeker and Halpern, 2008; Pınarbaşı *et al.*, 2017). For example, intertidal benthic invertebrates are unlikely to have the same stressor response to sedimentation as subtidal invertebrates, as sediment regimes and coastal processes vary across depth gradients (Lohrer *et al*., 2004; Thrush *et al*., 2004). Furthermore, several parameters and processes (Figure 1.1) define the interaction relationship, such as stressor magnitude, baseline ecosystem condition, resilience, recovery potential, ecosystem feedback loops, coupled processes, stressor interactions, temporal scale, and spatial scale, many of which are specific to a locale of habitat (Ellis *et al.*, 2017; Foley *et al.*, 2017; Gladstone-Gallagher *et al.*, 2019; Lundquist *et al.*, 2018; Thrush *et al.*, 2014; Crowder and Norse 2008). Studies which investigate the impacts of multiple anthropogenic stressors in a lab, mesocosm or small-scale field experiments (Boyd *et al*., 2018; Hodgson and Halpern, 2019) can inform understanding of the variety and importance of stressor mechanisms and stressor-receptor relationships (McElhany and Busch, 2012). However, there are many limitations when trying to translate stressor relationships obtained from localised empirical studies to broader spatial scales relevant to coastal management (Hunsicker *et al*., 2016), due to the variability in environmental processes, ecological relationships, and species responses across different ecological scales (Gonzalez *et al*., 2020).

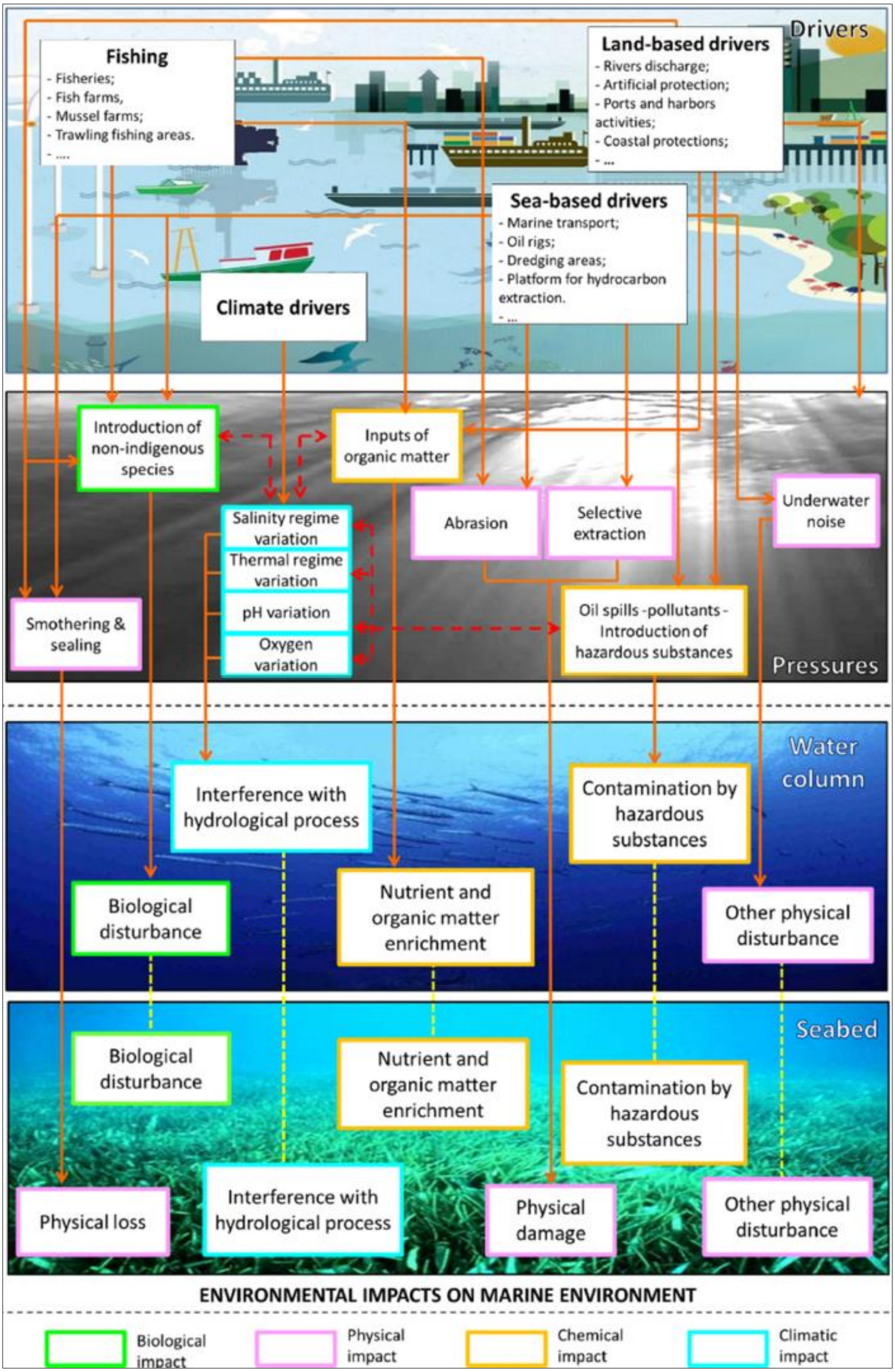


Figure 1.1: Drivers, Pressures, States, Impacts, Responses (DPSIR) based conceptual framework highlighting potential pathways of interaction between selected drivers, pressures, and impacts. Figure 1 adapted from (Furlan et al., 2018).

These key parameters are often easier to determine from localised empirical studies which have conducted in situ stressor assessment or experimentation, (Gladstone-gallagher *et al*., 2021; Thrush *et al*., 2021) but many of these relationships don't hold when extrapolated over wider management areas. Furthermore, literature has shown that changes in biodiversity occur across multiple spatial scales in response to anthropogenic stressors, and quantifying how feedback between ecosystem functioning and biodiversity varies between localised spatial scales to regional scales is a major challenge (Chase *et al*., 2019; Gonzalez *et al*., 2020; Tréguer *et al*., 2017). With a growing reliance on predictive spatial models to inform coastal management decisions, better approaches are required to upscale multiple stressor impacts and stressor-receptor relationships quantified from empirical studies to relevant management scales (Janßen *et al* 2019). To address the challenges of scale and spatial variability, the development of comprehensive spatial tools is required, that not only quantify impacts from multiple stressors but are also transparent and not overly complicated so that they can be understood and accepted by their end users, primarily management practitioners, stakeholders, and policymakers (Hammar *et al*., 2020).

Spatial approaches that account for stressor impacts (often termed threats in terrestrial conservation planning) have been applied to systematic conservation planning in terrestrial realms as early as 1872, and marine conservation efforts are rooted in terrestrial conservation theory and applications (Kirkpatrick, 1983; Margules & Pressey 2000. Marine managers often need spatial outputs at a fine resolution over the management scale that enables them to distinguish high-impact areas with low abundance, from low-impact areas with high abundance within a stressor footprint (i.e., the extent of the stressor impact) to determine the appropriate conservation or management action. Cumulative threat mapping approaches (e.g., see Halpern *et al.*, 2009; Robertson *et al*., 2016; Schafer and Piggott, 2018; Furlan *et al* 2019) provide some estimate of stressor loads that can be used as a proxy for habitat condition. However, these approaches do not quantify the current habitat condition from accumulating stress over time or reveal how functionally important taxa within the community respond directly to multiple stressors. Both elements are crucial for the identification of resilient habitats that still provide ecological value in an increasingly exploited coastal environment. Many empirical studies have measured cause-and-effect relationships between benthic invertebrates and single stressors over single or multiple small experimental sites or under lab conditions (Thrush *et al*., 2004; Hewit and Norkko 2006; Lohrer *et al*., 2004; Cummings *et al*., 2020). However, extrapolation of empirically derived stressor responses over larger spatial extents requires the consideration of additional spatial and temporal dynamics such as: considering historical effects of stressor impacts, the accumulation of stressors over time, and stressor interactions over space and time – to evaluate this level of complexity, spatial modelling approaches are required (Crain *et al*., 2008; Bučas *et al*., 2013; Martin *et al*., 2017).

Soft-sediment macroinvertebrates are considered sensitive indicators of ecosystem health and are regularly used to assess the effects of natural and anthropogenic disturbances (Borja, Franco and Pérez, 2000; Pearson and Rosenberg, 1978; Rodil, Compton and Lastra, 2012; Weisberg *et al.*, 1997). Many benthic invertebrates physically modify their habitat through key ecological functions like bioturbation, filter-feeding, depositing organic matter and biomass production (Lohrer, Thrush and Gibbs, 2004; Rullens *et al.*, 2021), which in turn supports the health of the seafloor ecosystem and provides additional ecosystem services (e.g., food provision, recreation, and tourism). A greater understanding of the distribution, abundance, and anthropogenic impacts on benthic species is vital: as they disproportionately contribute to ecosystem health (Thrush *et al.*, 2021), the critical functions that they provide to support ecosystem health are density-dependent (Lohrer, Thrush and Gibbs, 2004; Spaak *et al.*, 2017), and they are at high risk of functional extinction under increasing rates of physical disturbance (i.e., changes to environmental conditions), particularly from commercial fishing (Hillman *et al.*, 2019; Lundquist *et al.*, 2018; Thrush *et al.*, 2006) and sedimentation (Anderson, 2008; Thrush *et al.*, 2004). Disturbance events which are of a sufficient magnitude can enact a regime shift (i.e., tipping points) by disrupting the state of equilibrium; where critical ecological boundaries are crossed it is often difficult or impossible to recover (Gladstone-Gallagher *et al.*, 2019; Scheffer and Carpenter, 2003; Thrush *et al.*, 2014). The effects of disturbance events from bottom fishing on benthic invertebrates have been well studied (Hiddink *et al.*, 2006; Kaiser *et al.*, 2006; Baird *et al.*, 2015; Lambert *et al.*, 2017; Lundquist *et al.*, 2018), however, literature which quantifies bottom fishing impacts in combination with other stressors is sparse.

1.1.1. Multiple stressors in coastal ecosystems

Anthropogenic stressors are physical, chemical, and biological factors which have exceeded natural limits of variation from human activities that can affect the structure, function, and environmental health of coastal ecosystems (Foley *et al.*, 2017; Sanderson *et al.*, 2002). Coastal ecosystems support highly productive habitats, which in turn provide humans with valued provisioning-based ecosystem services such as the harvesting of food and materials (e.g., sand) and other regulating services (e.g., water quality, coastal stabilisation; Rullens *et al.*, 2019). Approximately 40% of the world's population lives within 100 kilometres of the coast (Creel, 2003). The coastal interface is a highly populated multi-use area subject to a concentration of anthropogenic stressors driven by human socio-economic interests (Batista *et al.*, 2014), hence the growing need to quantify these stressor impacts. Increased population density requires greater coastal development and resource use, which results in habitat modification, toxic pollution, chemical contamination, nutrient loading, sedimentation, and increased fishing effort, amongst others (Batista *et al.*, 2014; Crain, Kroeker and Halpern, 2008; Ellis *et al.*, 2017; Halpern *et al.*, 2008).

Within New Zealand, and many coastal ecosystems globally, sedimentation from terrestrially derived sediments and bottom fishing are two of the most pervasive anthropogenic stressors (Sciberras *et al.*, 2018; Simeoni *et al.*, 2023; Wahlstrom *et al.*, 2022; Willsteed *et al.*, 2018). The term sedimentation refers to the transport of terrestrially sourced silt, mud, clay, and rock material to the coast, which can occur through natural erosion processes, and can also be human-induced by inadequate land management (e.g., deforestation and large-scale intensive agriculture; Sahin *et al.*, 2019). Sedimentation is a stressor to marine environments, resulting in increased input rates of mud (e.g., fine silts and clays) into the coastal environment (Thrush *et al*., 2004). Within New Zealand, transitioning land use toward large-scale pastoral farming has increased sediment runoff, modifying the sediment delivery regime to the sea (Swales *et al.*, 2002; Thrush *et al.*, 2004). Small volumes of increased mud content in coastal environments can alter sediment biogeochemistry by affecting the exchange of solutes, oxygenation, and nutrient processing which in turn can alter macrofaunal community composition (Pratt *et al.*, 2015). Large volumes of mud deposits can smother seafloor communities and alter sediment grain size, affecting benthic community composition by lowering diversity and aiding the dominance of shorter-lived, stressor-tolerant taxa in place of larger and functionally important taxa (Anderson, 2008; Thrush *et al.*, 2004). The effects of sedimentation are particularly damaging in shallow seafloor ecosystems, due to the re-suspension of mud from waves and currents, resulting in increased suspended sediment concentration which can reduce the physiological condition of suspension-feeding animals (Ellis *et al.*, 2002; Newcombe, 2016). As suspended sediment in the water column increases, so does the turbidity (e.g., scattering of light particles) which reduces light penetration essential to microphytobenthic communities to use for photosynthesis (Ruiz and Romero, 2003; Thrush *et al.*, 2004). Many empirical studies have assessed the effects of sedimentation on estuarine and subtidal benthic communities, highlighting that even mud deposits < 1 cm thick can negatively influence community structure and function, and that terrigenous mud deposits reduce the density of macrobenthic communities which are slow to recover if at all (Thrush *et al*., 2004; Lohrer *et al*., 2004; Lohrer *et al*., 2006; Hillman *et al*., 2002; Ellis *et al*., 2002; Douglas *et al*., 2023.

Bottom fishing (i.e., trawling and dredging) directly interacts with vast areas of seabed habitat globally (Kaiser *et al.*, 2006). Both direct and indirect impacts of bottom fishing on benthic habitats are significant (Pikitch, Santora and Babcock, 2004). Direct impacts of bottom fishing range from capturing of bycatch (often caused by the indiscriminate small fishing net mesh capturing non-target species; Pitcher *et al.*, 2016), discarded fish (e.g., undersized, and juvenile fish, low commercial value species and hauls that exceed fishing quotas), and direct damage and disturbance to seabed habitats from gear impacts (e.g., seagrasses, coral reefs, rock gardens; other soft sediment ecosystems; Kaiser *et al.*, 2006; Thrush and Dayton, 2002). The direct physical impacts of bottom fishing can reduce the abundance of macrofaunal communities, change functional community composition and can lead to homogenisation of the seascape (Hiddink *et al.*, 2006; Kaiser *et al.*, 2006; Lundquist *et al.*, 2018; Sciberras *et al.*, 2018). Examples of indirect effects from fishing include sediment resuspension, indirect trophic effects (e.g., changes in population size, growth rate and availability of fish and benthic species, predator-prey relationships) and changes to sediment composition (Hiddink *et al.*, 2011). Although the effects of bottom fishing are well understood, it becomes more difficult when trying to quantify impact spatially over a larger management area, particularly when a variety of gear types (e.g., beam trawl, dredge), and fishery types (e.g., scallop, fin fish) take place simultaneously (Baird *et al*., 2015; Lundquist *et al*., 2018). Furthermore, deciphering the impact on benthic communities across temporal and environmental scales of disturbance is complex, as recovery is conditional on gear type, penetration depth into the sediment,

sediment composition, and baseline habitat condition in addition to community-level responses such as taxa resiliency (Lambert *et al*., 2017; Baird *et al*., 2015; Sciberras *et al*., 2018).

Although some empirical stressor-receptor response relationships for bottom fishing and sedimentation have been quantified (individually), extrapolation of locally derived species-environment relationships across broader spatial scales is challenging due to the environmental heterogeneity and gradients of stress which requires further research via different spatial modelling approaches (Hewitt *et al*., 2007; Lohrer *et al.,* 2015). First, the habitat distribution and abundance of the focal species must be modelled to determine the species-environment relationships over the management area (Guillaumot *et al*., 2020). However, records of abundance are not always available and can be challenging to acquire over broader spatial scales (Johnston *et al.*, 2015; Howard *et al.*, 2014). Secondly, spatial data detailing the footprint and magnitude of the stressor (i.e., percentage of mud in the sediment or turbidity) needs to be quantified either through direct sampling, modelling, or a combination of the two (Hateley *et al*., 2005; Bostock *et al.*, 2018). Thirdly, a suitable computational modelling approach must be developed to scale up the stressor response relationship (if available from empirical studies) across different habitats and gradients of stress (Degraer *et al* 2008; Ellis *et al* 2017; Gonzalez *et al* 2020; Lohrer *et al* 2020; Stephenson *et al*., 2023). Furthermore, the units of measurement or terms used to develop spatial datasets and stressor response relationships often differ between studies making data integration challenging. For example, empirical stressor response relationships may have quantified a localised stressor response as probability of mortality from exposure, but a practitioner may want to determine the reduction in density over the management area. Spatial modelling approaches can be used to apply a variety of conditions in an attempt to predict real-world dynamics of disturbance and recovery, but the usefulness of outputs is contingent on the quality and availability of spatially explicit environmental data, and stressor-response relationships from empirical studies (Stamoulis and Delevaux, 2015; Zurell *et al.*, 2021; Hewit *et al*., 2007).

To quantify the impacts sustained from multiple stressors it is also important to consider recovery processes, which are typically poorly understood (Lambert *et al.*, 2014; Stelzenmüller *et al.*, 2020). Benthic environments are subject to many natural disturbances (e.g., wave action), which are important drivers of function and structure (Stephenson *et al.*, 2019). Over time, varying spatial and temporal scales of disturbance in combination with species interactions and a range of recolonisation abilities, create a mosaic of habitat patches in varying degrees of recovery (Lambert *et al.*, 2014; Sciberras *et al.*, 2018; Sousa, 1987; Thrush *et al.*, 2005). Many studies have aimed to facilitate understanding of disturbance-recovery dynamics that occur at larger spatial and temporal scales, which has provided knowledge on the likely consequences of anthropogenic disturbances (particularly from bottom fishing) and species recovery rates (Ellis, Schneider and Thrush, 2000; Lundquist *et al.*, 2018; Thrush and Dayton, 2002). Nevertheless, quantifying fishing disturbance over a smaller regional management scale with unique trawling effort, and variable stress and environmental gradients remains challenging. Homogenisation of the habitat after a disturbance event may also further inhibit recovery dynamics by disrupting species interactions, diminishing the three-dimensional structure of the benthos, and altering sediment characteristics and biogeochemical processes (Cranfield *et al.*, 2004; Kaiser *et al.*, 2006; Stephenson *et al.*, 2017). Research on seafloor disturbance-recovery dynamics often focuses on changes that occur to easily sampled species (e.g., large bodies or highly visible), or community-wide measures (e.g., species richness; Howarth *et al.*, 2015). However, several studies have highlighted that species loss from disturbance is not random and that species with distinct biological traits (e.g., body shape) can respond and recover differently to variable levels of impact (Sciberras *et al.*, 2018; Thrush *et al.*, 2006). Recovery is dependent on several taxon-specific characteristics such as resiliency (i.e., rebounding to baseline levels after a temporary disturbance), reproductive rate, growth rate, or density. Taxon-specific characteristics can also influence susceptibility to disturbance such as morphology (e.g., size, body shape) and fragility (e.g., hard shell vs. soft body; Gladstone-Gallagher *et al.*, 2019; Stephenson *et al.*, 2019). Analysis via biological traits (also referred to as functional groups) has been used in many studies to predict recovery dynamics of specific species, derive sensitivity to specific stressors, and predict ecosystem functions and services (Ellis *et al.*, 2017; Hewitt, Lundquist and Ellis, 2019; Lundquist *et al.*, 2018). However, many knowledge gaps exist for most soft-sediment macrofauna, therefore quantifying responses to multiple stressors remains challenging (Gladstone-Gallagher *et al.*, 2019; Lambert *et al.*, 2014; Lambert *et al.*, 2017; Stelzenmüller *et al.*, 2020). Marine managers require spatial conservation solutions that can quantify impacts and recovery from multiple stressors to identify ecologically rich and resilient habitat areas for conservation that will persist over time (McLeod *et al*., 2019), even within the footprints of existing stressors which is not currently possible without exploration of new modelling solutions.

Not only are the individual stressor effects from fishing and sedimentation impactful, but they also often overlap spatially and temporally (Davies *et al.*, 2018) resulting in multiple factors of disturbance and recovery where they co-occur (e.g., Figure 1.2). Determining the combined impacts from past, present, and future stressors at a fine resolution over a broad management area for either fishing or sedimentation is challenging (Lundquist *et al*., 2013; Pitcher *et al* 2016; Sciberras *et al* 2018; Lundquist *et al*., 2018; Paradis *et al*., 2021). Consequently, approaches that spatially quantify the combined impact of fishing and sedimentation on the benthic habitats are scarce, and solutions which can be implemented with currently available data are needed.

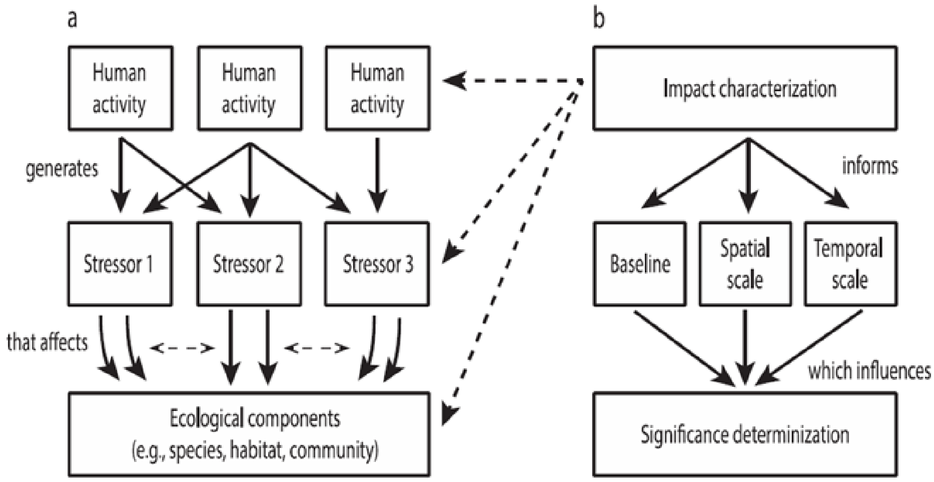


Figure 1.2: (a) Relationship between activities, stressors, and ecological components, illustrating how accumulating impacts are generated via multiple stressors from multiple activities, including the potential for interactive effects (dashed lines between effects arrows); (b) relationship between how impacts are characterized (by activity, by stressor, and/or by ecological components – dashed lines) and baseline selection, spatial scale, temporal scale, and determination of significance. Figure 2 adapted from Foley et al., (2016).

1.1.2. Spatial approaches to modelling multiple stressors

The demand for modelling assessments that quantify multiple stressor effects is rapidly increasing and marine managers need generally applicable tools that can be implemented with currently available data, and with limited resources (Brush and Nixon, 2017; Stelzenmüller *et al.*, 2020). Although highly advanced, biogeochemically complex ecosystem models exist (e.g., the Atlantis model; Hansen, 2016) and Chesapeake Bay Program in the USA (Cerco and Noel, 2004) which can integrate complex empirical relationships and dynamic feedback, the financial cost of developing and calibrating such elaborate models in addition with specialised knowledge requirements creates limitations for researchers and management practitioners (Cerco and Noel, 2004; Hammar *et al.*, 2020). Many studies have highlighted the need to develop "reduced complexity" models to inform coastal management (Duarte, Ribeiro and Paglia, 2016; Ganju *et al.*, 2016; Pace, 2001) leading to the pursuit of alternative modelling approaches such as those that combine empirical and complex mechanistic models (e.g., Brush and Nixon, 2017; Obenour, Michalak and Scavia, 2015). Stressor modelling literature could benefit from a greater understanding of how the combined impact of coastal stressors (e.g., fishing and sedimentation) spatially modify the density and distribution of benthic invertebrates which perform key functional roles to support ecosystem health (Berthelsen *et al.*, 2019). Coastal managers could benefit from the creation of more simplistic, but scientifically robust spatial approaches to better regulate multiple stressor impacts and conservation objectives.

Spatial modelling approaches help to 'bridge the gap' between empirical field experiments and survey data into programming environments that can leverage computational power to spatially analyse and summarise data and create outputs that visually communicate complex analysis and relationships (Guisan and Zimmermann, 2000; Hammar *et al.*, 2020; Schafer and Piggott, 2018). One modelling approach that forms an integral role in conservation planning are Species Distribution Models (SDMs; Guisan *et al.*, 2013; Melo-

Merino, Reyes-Bonilla and Lira-Noriega, 2020). SDMs are spatially integrated tools that can provide information detailing variation in the distribution and abundance of functionally important species and have gained much traction in the marine environment in recent decades (Lundquist *et al.*, 2018; Marshall, Glegg and Howell, 2014; Robinson *et al.*, 2017; Rullens *et al.*, 2021). SDMs use a correlative modelling approach that predicts species distribution patterns by relating known sample locations to a set of spatially explicit environmental predictors (Elith and Leathwick, 2009). These models assist with the spatial integration of ecologically important species distributions into planning frameworks and can inform decision-makers by providing measurable indicators of abundant and functionally healthy ecosystems (Crowder and Norse, 2008; Foley *et al.*, 2010). SDMs provide spatial outputs which aid the visualisation of data and can be used in a variety of management applications from testing hypotheses concerning taxa distribution along environmental gradients (Reiss *et al.*, 2015) to the identification of vulnerable ecosystems to designate protection zones (Georgian, Anderson and Rowden, 2019; Guisan *et al* 2013. SDMs are often used as a complementary approach for multiple stressor analysis (Ellis *et al.*, 2017), or used as input layers into stressor risk assessments (Stelzenmüller *et al.*, 2020). Furthermore, spatial modelling approaches provide a programable solution for predicting species-environmental relationships beyond the sampled space (i.e., beyond the survey area; Guillaumot *et al*., 2020; Brambilla and Saporetti, 2014; Degraer *et al.*, 2008; Hallman and Robinson, 2020).

Early map-based approaches using Graphical Information Systems (GIS) to account for multiple human impacts focussed on spatially mapping the individual footprints of human activities, to identify areas of overlap, and estimate areas of low – high impact based on locations of known ecological habitats (Bryant *et al.*, 1998; Sanderson *et al.*, 2002). At a global scale, Halpern *et al.* (2009) created the first marine-based stressor maps, which summed the additive cumulative impact score across all stressors for multiple anthropogenic drivers, by assigning each driver an impact weight. Further studies over the past decade have applied an approach of a summed cumulative impact score or index, which accounts for stressor impacts in an additive fashion, over various data scales across different coastal habitats (Andersen *et al.*, 2015; Batista *et al.*, 2014; Elliott, Borja and Cormier, 2020; Furlan *et al.*, 2019; Korpinen *et al.*, 2021; Korpinen *et al.*, 2012). For example, Andersen *et al.* (2015) created a pressure index for the Baltic Sea, by additively summing anthropogenic pressure layers to create a cumulative impact score, which was used to inform ecosystem biodiversity status. Although useful, most studies applying a summed index approach recognise their limitations as they do not account for impacts temporally nor do they incorporate empirical species-environmental relationships (Stelzenmüller *et al*., 2020; Ostwald *et al*., 2021). Although standalone GIS-based approaches are useful, there is great difficulty trying to incorporate stressor receptor relationships and other dynamic elements (such as changes in density over time, or sediment transport from coastal processes) without the use of computational modelling power. (Halpern and Fujita, 2013; Thrush *et al.*, 2004; Gissi *et al*., 2017).

MSP and conservation planning practitioners often utilise decision-support tools to implement a structured decision-making process and to assist with the organisation of extensive geospatial datasets which represent marine biodiversity features and associated management boundaries (Guisan *et al*., 2013; Pınarbaşı *et al.*, 2017). Decision-Support Tools (DST) are software-based computer programs with a user interface, that apply different algorithms (e.g., simulated annealing) focussed on achieving the best representation of biodiversity protection for the most cost-efficient option in terms of resource use (Lundquist *et al*., 2020; Leslie *et al*., 2003). Decision-support tools have long considered and planned for the implications of multiple stressors or threats affecting the sustainability of harnessing marine resources, but existing approaches do not necessarily tell decision-makers what they need to know to undertake effective stressor management (Pinarbasi *et al* 2017; Chalastani *et al* 2021; Janßen, Göke and Luttmann, 2019). Examples of knowledge gaps that persist when applying DSTs to marine environments in their current capacity include: how much stressor load is too much?; how do the impacts from the legacy effects of historic stressors influence conservation value?; How do prioritisation values change if more stressor impacts are incorporated? Will areas identified as having high-value habitat now persist into the future under current stressor regimes? One of the primary algorithms (the standard cost trade-off model) common to many decision-support software (e.g., Zonation and Marxan) aims to avoid areas of high conservation cost, thus focussing outside of areas with a high stressor impact (Moilanen *et al*. 2009, Ball *et al*. 2009), making knowledge gaps that pertain to stressor impacts challenging to answer.

Systematic conservation planning can consider stressor impacts either through the use of a direct spatial layer which represents information on the stressor magnitude and location (i.e., fishing trawl tracks) or more often it can be simulated by considering the impact on species records or biodiversity features threat that may occur under different management scenarios (Lundquist *et al.,* 2020; Stock *et al*., 2023). For example, early threat consideration from terrestrial realms focussed on the threats of invasive species, which were determined by predicting their distributions to prioritise management areas and calculating associated costs under different management scenarios (Evans *et al* 2011; Januchowski-Hartley *et al* 2011).

Conservation and restoration actions can be costly (McCarthy *et al*. 2012), and although studies that focus on the cost efficiency of stressor management are important, others have argued that literature should not focus on acquisition costs over biodiversity (Aroponen *et al.,* 2010). Due to calls for threat management actions to explore biodiversity protection and restoration in conjunction with costed and prioritised management actions, some researchers have applied a hybrid analysis approach (Carwadine *et al* 2012; Chambers *et al* 2023). Cattarino *et al.,* 2015, explored the effectiveness of applying alternative management actions to each stressor within a site (e.g., grazing, river flow alteration, buffalo and cane toad), by relating ecological trait information of receptors (freshwater fish) to define species-specific responses to threats assuming that threats would be fully abated by management actions. Linking ecological traits to determine species-specific responses to threats provides greater insight into species-stressor relationships and has been practised in many other marine-based studies (Hewit *et al.,* 2018; Lundquist *et al.,* 2018; Ellis *et al.,* 2017). However, assuming that the implementation of management actions would fully abate stressor impacts is not ecologically realistic and fails to account for the temporal and dynamic effects of stressors.

Climate change adaption has also been assessed in many conservation planning studies (Abrahms *et al* 2017; Chollett *et al.,* 2014; Green *et al.,* 2014), but a recent analysis revealed that 82% of real-world examples within MPA planning focus on coral reefs, highlighting the lack of holistic understanding across wider ecosystems and habitats (Wilson *et al.,* 2020). Some areas of conservation research have advanced to consider how multiple threats from terrestrial sources can influence marine-based conservation efforts, and highlight the important role of decision-support tools in land-sea holistic conservation planning (Alvarez-Romero *et al.,* 2011; Adams *et al.,* 2014). Klein *et al.,* 2010 considered the relative impact (elicitated from expert review) of several terrestrial threats (e.g., nutrient runoff, organic pollution) and marine-based threats (e.g., demersal bycatch, destruction from commercial fishing) to coral reef conservation cost, and found that managing marine-based threats is more cost-effective given a limited budget. Tulloch *et al.,* 2021 considered multiple land-use and climate change threats toward developing a national spatially explicit conservation plan across multiple realms (forests to inshore reefs) and considered linkages between planning units that may not be spatially adjacent, but connected ecologically. Consideration of terrestrial stressor impacts on the marine environment is critical, but approaches should endeavour to account for the accumulation of stress over time as this may affect habitat resiliency, which would influence the conservation value of areas selected (Macleod *et al* 2019; Levin and Lubchenco 2008), and should also aim to use empirically derived stressor relationships to advance upon theoretical assumptions.

In the marine realm bottom fishing is considered one of the most pervasive and destructive stressors to marine biodiversity (Kaiser *et al.,* 2006; Lambert *et al.,* 2017; Tallis *et al.,* 2008; Lundquist 2018).

Within conservation planning, fishing stressor footprints (trawl locations of effort) have been used to consider areas to avoid when selecting marine protected areas (Geange *et al* 2017), to consider the effectiveness of bottom fisheries closures (e.g., Benthic Protection Areas - Leathwick *et al*., 2008), and to inform sustainable fishery options for a system of open and closed areas for bottom trawling which protects vulnerable marine ecosystems (Rowden *et al*., 2019). However, traditional approaches to integrate fishing stress into conservation planning do not utilise empirical species-stressor relationships, nor recovery dynamics, and fail to inform management about biodiversity loss or highlight habitats that retain conservation value within the stressor footprint. Existing spatial approaches applied within MSP and systematic conservation planning often do not quantify impacts dynamically; they fail to address species' environmental relationships. They fail to consider the accumulating impact of stressors over time (past, present or future), or due to lack of spatially explicit data, they have focussed on assessment using low-resolution species data (occurrence only datasets) and approximation of impact from surrogates or estimated impact rather than empirical relationships (Pınarbaşı *et al* 2017; Chalastani *et al* 2021; Janßen, Göke and Luttmann, 2019; Stelzenmüller *et al.,* 2019). However, as demand for marine resources increases, so do the pressures on marine ecosystems and stressor avoidance is no longer feasible.

There are two key numerical modelling approaches which dominate multiple stressor analysis in the marine environment – correlative models, and mechanistic models. Correlative model approaches (also termed regression models) have been used to quantify the relationships between stressors and receptors (Ellis *et al.*, 2017), to examine taxon-specific responses to stressors as indicators of ecosystem health (Berthelsen *et al.*, 2019), and to assess multiple stressor responses on coral reefs (Rullens *et al.*, 2022). Multi-variable linear regression has been used to identify both the direction and magnitude of stressor interactions from model coefficients (Kotta *et al.*, 2016; Ceccarelli *et al.*, 2020). Mechanistic models are based on the fundamental laws of natural sciences and empirical measurements which can be applied mathematically to predictive scenarios to determine broader-scale properties of ecosystems or landscapes (Rastetter *et al.*, 2003). An example of one type of mechanistic model which applies expert knowledge to mechanistic relationships within a probabilistic framework is Bayesian Networks, which have been used to predict multiple pressures on ecosystem recovery (Uusitalo *et al.*, 2016). Other mechanistic models apply empirically established relationships or processes such as dissolved oxygen rates and organic sediment accumulation to quantify interactions and relationships, for example, to determine the risk of estuarine eutrophication (Brush and Nixon, 2017). However, mechanistic models can be constrained by high levels of uncertainty around specific stressor interactions, further exacerbated by a lack of relevant data to drive multiple stressor modelling, particularly with the limited capacity of typical monitoring programs which are not designed to detect early indications of multiple stressor impacts (Hewitt and Norkko, 2007).

Some research has explored the utility of approaches that combine the predictive power of both mechanistic and correlative models to perform a hybrid analysis. Kearney *et al*., 2010 forecasted the distribution of the gliding possum using both correlative and mechanistic models under different climate change scenarios, showing that both SDM types (correlative and mechanistic) can provide reliable and congruent predictions despite being underpinned by different assumptions, which is important when considering the utility of other hybrid modelling approaches to quantify stressors. Gallien *et al*., 2010 also examined the benefits of a hybrid modelling approach combining correlative and mechanistic models to predict the spread and dynamic of invasive species, acknowledging that the aim of hybrid models is not to predict perfectly, but to overcome specific limitations of traditional models. Many challenges (e.g., financial, complexity, scaling, data limitations) hinder spatially explicit multiple stressor assessment, and useful solutions which capture all the complexities of real-world ecosystem dynamics and stressor interactions are unrealistic for now, but perhaps a pragmatic modelling approach focussing on combining the optimal features of existing solutions could provide an effective intermediate solution. Spatial assessments must move beyond the constraints of conventional solutions to successfully account for multiple stressor effects; adopting a combination of different approaches (e.g., correlative studies, manipulative studies, and modelling efforts) can allow for better inference predictions of the combined effects of localised stressors (Gissi *et al.*, 2017) and may help to better integrate empirical data into spatial modelling approaches.

1.2. Thesis rationale aims and objectives

The overall aim of this thesis is to explore new methods of incorporating the effects of anthropogenic stressors into marine management, by developing a spatially explicit methodological approach to quantify multiple stressor impacts in shallow seafloor ecosystems. I focus on the stressor-induced change in density and distribution of subtidal benthic invertebrates, as they are not only key indicators of ecosystem health, but they also support vital ecosystem processes (e.g., oxygenation of sediments) through their functional roles (e.g., bioturbation, suspension-feeding, creating habitat structure). My thesis is comprised of three research chapters each of which addresses key analysis components in the development of a new approach to quantify stressor impacts (Figure 1.4). The thesis components include the development of reliable benthic invertebrate density models at a fine resolution (Chapter 2), quantifying change in taxa density and distribution from the impact of multiple stressors via a correlative stressor model (Chapter 3) and advancing the spatial prioritisation of marine conservation by incorporating the effects of marine stressors on density into systematic conservation planning (Chapter 4). The analyses conducted in chapters 2 to 4 are focussed on the shallow seafloor ecosystems located within Tasman and Golden Bay and surrounding areas, comprising of habitat with ecological significance to New Zealand (Tonga Island Marine Reserve and Horoirangi Marine Reserve, Figure 1.3), where I consider the spatial and temporal effects of two anthropogenic stressors (bottom fishing and sedimentation). Seven coastal seafloor taxa that vary in habitat usage, functional role, morphology, and distribution were used to examine response effects from multiple stressors. The thesis concludes with a general discussion (Chapter 5) where I explore the ecological implications and spatial variability of stressor effects on shallow seafloor ecosystems and address the implications for coastal management. Below, I describe the specific aims and objectives for each of the research chapters outlined above.

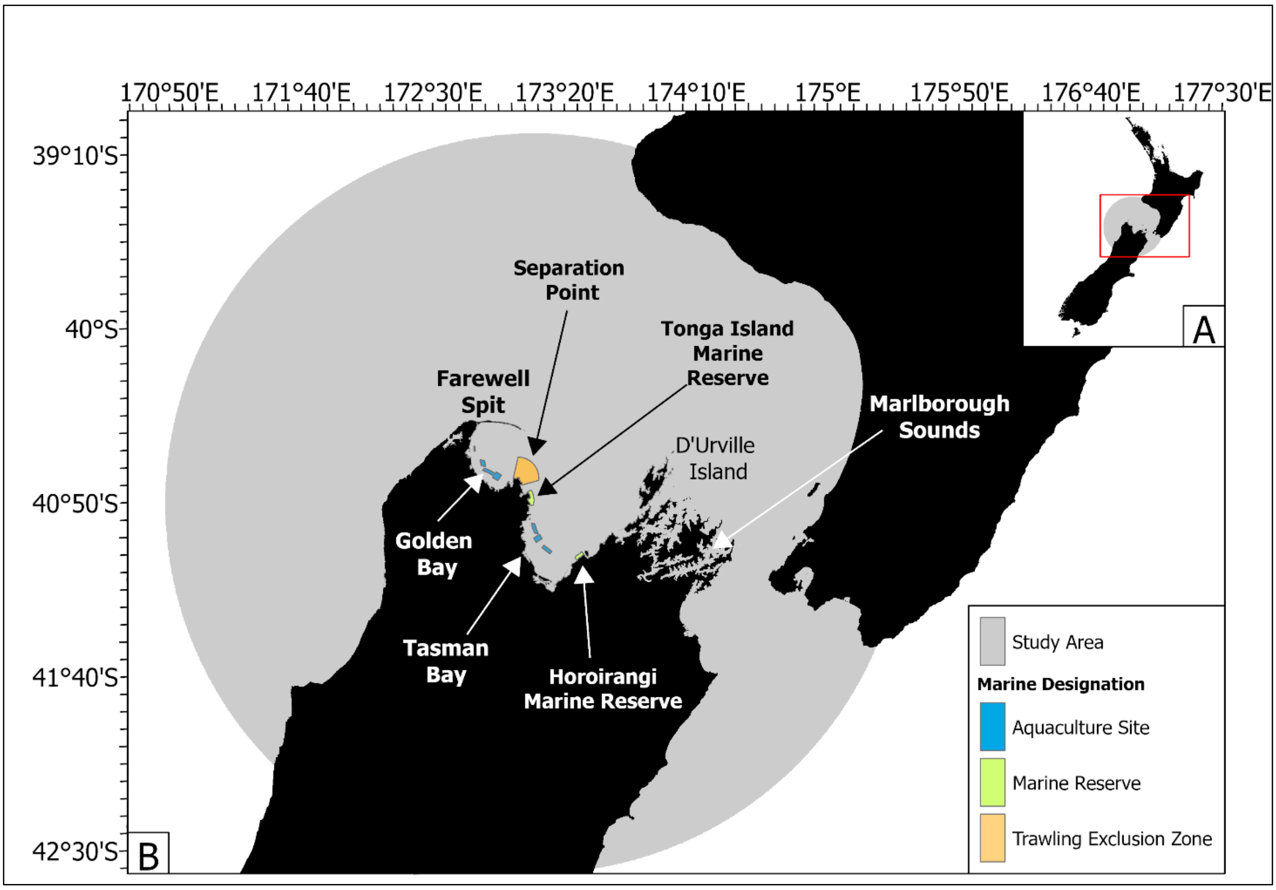


Figure 1.3: Map of the study region, feature names and, marine designation zones (B) with inset map indicating the location within New Zealand (A).

1.3. Study area and focal taxa

This thesis focussed on the coastal environment between the North and South Islands of Aotearoa - New Zealand, encompassing the South Taranaki Bight, Tasman Bay, and Golden Bay (Figure 1.3). This area was identified as part of the Sustainable Seas National Science Challenge and has been used as a case study area for several other research projects related to the challenge, which can be viewed on the interactive map created for Sustainable Seas. The extent of the study area (Figure 1.3) for Chapter 2 of this thesis covered 82,000 km^2, which was later refined to smaller extents in subsequent chapters.

Within the context of this thesis, the study area is representative of a variety of coastal habitats from enclosed bays, exposed coastlines, and high energy straits, and encompasses habitats which reflect gradients of stress from marine protected areas to degraded shallow ecosystems (Newcombe, 2016). The current economy in the area is highly marine-driven, based on fishing, aquaculture, recreation, and tourism. Commercial fishing has a long history within both Tasman and Golden Bay, which have previously supported large populations of mussels (*Perna canaliculus*), scallops (*Pecten novaezelandiae*), and flat oysters (*Tiostrea chilensis*; Handley, 2006). The study area also supported large fin fish stocks, with commercial fishing of snapper dating back to 1945 (Handley, 2006) but many other species (e.g., orange roughy) have been targeted by both inshore and offshore fisheries for several decades (Baird, Hewitt and Wood, 2015). Within the region, three areas exist which are restricted to fishing: Separation Point – commercial trawling and dredging have been prohibited since 1980, and two marine reserves (Tonga Island and Horoirangi) which were designated as no-take reserves in 1993 and 2006 respectively (Lundquist *et al.*, 2013). The surrounding terrestrial habitats have also undergone many land use changes since the 1950s from deforestation, increased intensive agriculture and more recently urbanisation (Handley, 2006), resulting in a near seabed layer of highly turbid water, which is present most of the year, in addition to sediment washed into the bays from the Motueka River after heavy rainfall (Newcombe, 2016). The study area exhibits high variation in fishing effort and high levels of coastal sedimentation, providing both temporal and spatial variability in stressor impacts, which makes it an ideal location for testing model predictions.

The area is affected by multiple overlapping stressors which operate over a variety of spatial and temporal scales, such as the physical disturbance of benthic habitat from trawling and in addition to sediment transport and resuspension of land-derived sediments, nutrients, and contaminants (Newcombe, 2016). Despite these impacts, data available from fisheries trawls and research survey samples indicate that many benthic taxa are still present and have remained resilient to the ongoing stressor impacts (Handley, 2006). Nonetheless, shellfish populations have been steadily declining over the past decade and the southern scallop fishery (SCA 7 – comprised of Tasman Bay, Golden Bay, and the Marlborough Sounds) has been closed to commercial fishing since 2017, and populations have yet to recover to fishable levels (Williams *et al.*, 2021).

Historically the study area has been dominated by "soft bottom fauna," consisting of deposit feeding (e.g., *Echinocardium cordatum*) and suspension feeding (*Pecten novaezelandiae*) benthic invertebrates, (Handley, 2006). The focal taxa in this thesis were selected due to the availability of suitable sample records of occurrence and abundance (number and distribution). Taxa varied in their functional role, including habitat-forming epifauna (*Callyspongia*), mobile surface feeders (*Amalda*), tubeworms that stabilise sediments (*Asychis, Maldane*), bioturbators/burrowers (*Echinocardium*), mobile predators (*Glycera*) and suspension-feeding bivalves (*Pecten)*(Chapter 2, Table 2.1). In addition, as taxa exhibited different functional (biological) traits (e.g., morphology, life history, dispersal characteristics) they provided a range of responses to, and recovery from, anthropogenic stressors which was useful for this analysis.

1.3.1. Chapter 2

Many anthropogenic stressors can modify the density and distribution of benthic invertebrates, hence spatial predictions of taxa density, relevant to the scale of management are required to investigate stressor impacts. This chapter aimed to create ecologically informative Species Distribution Models (SDM) of density, at a fine resolution (250 m), that can provide useful predictions in data-limited environments. This chapter intended to address, how the spatial scale of the model affects the performance and accuracy of predictions concerning the creation of species distribution models? The predictive differences between Species Distribution Models (SDMs) generated across different spatial scales and model types (occurrence vs. abundance), for 7 subtidal benthic invertebrates using data-rich national (Exclusive Economic Zone) models compared to data-limited regional (Tasman and Golden Bay) models were examined. SDM outputs were assessed to determine the differences in predictive performance, and distribution patterns of both occurrence and abundance models to identify the most optimal outputs for each taxa. Optimal models were then combined to create ecologically relevant density SDMs for each taxa. In my approach, I focus on seven invertebrates common in temperate soft-sediment coastal regions globally, varying in habitat usage, distribution, and functional role, to highlight the utility of a multi-scalar approach to creating ecologically informative density models to inform spatial management.

1.3.2. Chapter 3

Understanding how multiple stressors impact coastal environments across space and time is key to supporting effective marine management, and the accumulating impact of multiple stressors is often not quantified spatially. This chapter addressed how the individual, combined and accumulating effects of fishing and sedimentation stress modify the distribution and density of benthic invertebrates over time. This chapter intended to answer, how do the effects of multiple anthropogenic stressors modify the distribution and density of benthic invertebrates over time? I developed a correlative stressor modelling approach to modify taxa density SDMs based on empirically derived stressor-response curves, over 4 years of accumulating stress. This analysis focussed on three functionally distinct seafloor invertebrates that varied in stressor response and recovery time. I focussed on two common coastal stressors (bottom fishing and sedimentation) within Tasman Bay and Golden Bay (New Zealand). Impacts were quantified spatially, and model outputs proved useful to indicate areas of potential interest for marine management (i.e., differentiating between highly impacted, and highly resilient areas).

1.3.3. Chapter 4

Scientific literature has shown that protected areas seldom provide effective biodiversity conservation when not protected from unmitigated environmental impacts. Therefore, effective conservation management must consider stressors that are not addressed by conservation management measures such as MPAs. The objective of this Chapter was to demonstrate the advantages of using stressor-modified density distribution predictions to identify conservation areas which have already shown resiliency to multiple stressors over time. This chapter aimed to answer, how does the inclusion of empirically derived taxa responses to multiple anthropogenic stressors drive changes in areas prioritised for conservation management? This chapter examined the difference in predictive performance, and spatial patterns of prioritised areas between prioritisation scenarios that incorporated multiple stressor impacts, and those that did not. In addition, this analysis also aimed to improve the usefulness of prioritisation outputs by using density distribution data, rather than probability of occurrence, as density is a more ecologically relevant metric to inform the quality of conservation habitats. Prioritisations were performed using stressor-impacted density predictions for seven functionally distinct benthic invertebrates which were ranked to reflect the perceived value they contribute toward the value of the seascape (i.e., habitat formers, bioturbators), to observe how different taxa are represented.

1.3.4. Chapter Interconnectedness

Each research chapter contributed to the overall aim of developing a new methodological approach to spatially quantify how marine stressors and receptors interact in coastal environments. Different assessment types (quantitative and spatial assessments) were applied to determine the breadth of impacts on benthic taxa from coastal stressors. Each chapter applies a different assessment approach, but the objective of quantifying anthropogenic impacts on marine benthic invertebrates links the research chapters together. The density SDMs created in Chapter 2 act as the foundation of the analysis and are utilised in both subsequent chapters; In Chapter 3 stressor response relationships are used to modify the density distributions to create stressor-impacted SDMs. In Chapter 4 the stressor-impacted SDMs are utilised in a spatial prioritisation assessment to reflect areas of high density that persist over time with ongoing stress. Each chapter contributed insights to improve the management of multiple stressors by advancing spatial planning assessment approaches, which is at the core of my thesis (Figure 1.4).

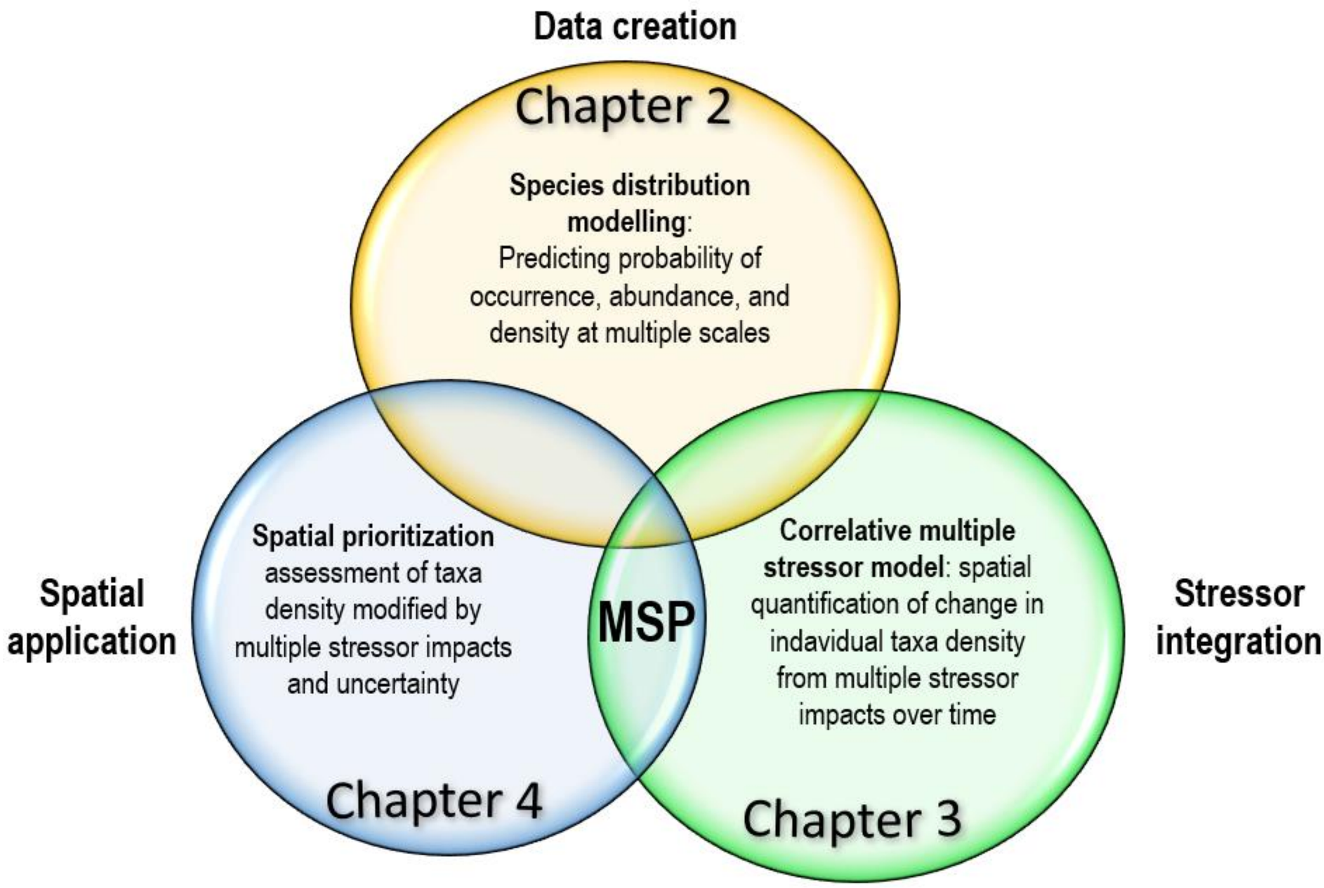


Figure 1.4: Venn diagram showing the interconnectedness between each research chapter, highlighting the novel contribution each chapter makes, and the overlap and relevance to Marine Spatial Planning (MSP).

2. Chapter 2
Improving prediction of coastal benthic invertebrate occurrence and abundance using a multi-scalar approach

2.1. Introduction

Globally, coastal marine ecosystems are subject to ongoing and often increasing anthropogenic stressors resulting in habitat degradation and biodiversity loss. Prolonged changes in species relative and absolute abundance, habitat homogenisation and declines in species richness have been recorded in many marine ecosystems, with associated reductions in functional capacity (Halpern *et al.*, 2019; Hewitt, Thrush and Dayton, 2008; Loreau *et al.*, 2001; Lundquist *et al.*, 2018; Thrush and Dayton, 2002; Thrush *et al.*, 2006). Conservation of essential ecosystem functioning, and management of associated services requires spatial information detailing the variation in the distribution and abundance of functionally important species (Lundquist *et al.*, 2018; Marshall, Glegg and Howell, 2014; Robinson *et al.*, 2017; Rullens *et al.*, 2021). Species distribution models (SDMs) are spatially integrated tools that can provide this information and have gained traction in the marine environment. SDMs use a correlative approach that predicts species distribution patterns by relating known sample locations to a set of spatially explicit environmental predictors (Elith and Leathwick, 2009). These models assist with the spatial integration of ecologically important species distributions into planning frameworks and can inform decision-makers by providing measurable indicators of abundant and functionally healthy ecosystems (Crowder and Norse, 2008; Foley *et al.*, 2010).

Investigating the effects of varying spatial scales on the predictive capacity of SDMs is imperative to account for the changes in species-environmental relationships across ecological scales. The influence of varying ecological scales has been well documented throughout many areas of research, from survey design (Thrush *et al.*, 2000), functional resilience (Gladstone-Gallagher *et al.*, 2019), disturbance effects (Ellis *et al.*, 2008), climate change (Halpern *et al.*, 2019), to fishing disturbance (Lundquist *et al.*, 2018). Accounting for the influence of ecological scale on predictive models (particularly abundance models) is important, as spatial outputs could substantially differ across geographical scales. Changing an SDMs scale is known to influence the extent of predicted suitable habitat and the relative influence of environmental predictors (Basher, Bowden and Costello, 2014; Morán-Ordóñez *et al.*, 2017; Ploton *et al.*, 2020). Furthermore, many environmental predictors (e.g., sea surface temperature) are averaged over large geographical scales. When averaged conditions are applied homogenously over an area, fundamental effects on populations, fine-scale environmental drivers, and non-linear species-environment relationships may go undetected (Bacheler *et al.*, 2009; Bacheler *et al.*, 2012; Puerta *et al.*, 2015). Moreover, ecological processes that drive species patterns over broad spatial scales (e.g., depth, temperature) may not occur at local scales and can be challenging to extrapolate accurately (Arenas-Castro *et al.*, 2018). The effects caused by altering the spatial scale are well known for probability of occurrence models (Arenas-Castro *et al.*, 2018; Basher, Bowden and Costello, 2014; Brambilla and Saporetti, 2014; Degraer *et al.*, 2008; Hallman and Robinson, 2020); however, few studies have focussed on marine-based abundance models (Rodil, Compton and Lastra, 2012). With a growing reliance on SDMs to inform coastal management decisions, practitioners need to ensure that spatial predictions reflect ecological scales relevant to the ecological extent of the management area.

SDMs to inform marine management have significantly increased in recent decades (Robinson *et al.*, 2017), and they have become more commonly used in conservation (Elith *et al.*, 2006; Guisan and Zimmermann, 2000). However, a recent review by Melo-Merino, Reyes-Bonilla and Lira-Noriega (2020) focused on marine SDM applications found that only 11% of the literature concentrated on conservation planning and just 9% incorporated measurements of abundance or density, biomass or species richness, any of which is critical for assessing ecosystem functions and services. Furthermore, levels of uncertainty (standard deviations) in the spatial predictions, which allow confidence in model predictions to be assessed, were often not included (Melo-Merino, Reyes-Bonilla and Lira-Noriega, 2020). Although SDMs show great potential for their use to support conservation planning, there are still many challenges that may impede their usefulness regionally, such as: (1) data scarcity – limited survey data and low abundance data availability; (2) habitat suitability or occurrence only – the majority of available SDMs predict a species probability of occurrence; although useful, they are less ecologically informative than predictions of abundance (count per sample unit) or density (count per km^2); (3) model scale – SDMs that predict over large geographic scales may be representative of broad-scale distribution patterns, but they may not be reflective of localised habitat differentiation; and (4) coarse-resolution – SDMs created at 1 km resolution or greater often lack the spatial detail required for fine-scale management decisions (Marshall, Glegg and Howell, 2014; Melo-Merino, Reyes-Bonilla and Lira-Noriega, 2020; Robinson *et al.*, 2017). Therefore, new modelling approaches are needed to address data and scale limitations and to incorporate abundance measurements.

Historically, coastal invertebrate occurrence models have focussed on long-term niche stability (Brame and Stigall, 2016), diversity and distribution prediction (Gogina and Zettler, 2010), and examination of scale-dependent influences on coastal species (Nyström *et al.*, 2013). However, fewer SDMs predict the abundance of benthic animals due to data representing presence records only, with limited information about abundance (Lohrer, Thrush and Gibbs, 2004; Spaak *et al.*, 2017). A greater understanding of the distribution and abundance of species that are found across seafloor ecosystems globally is vital. Many species disproportionately contribute to ecosystem health (Thrush *et al.*, 2021), their functional capacity is inherently density-dependent (Lohrer, Thrush and Gibbs, 2004; Spaak *et al.*, 2017), and they are at high risk of functional extinction under increasing rates of physical disturbance, particularly from commercial fishing (Hillman *et al.*, 2019; Lohrer *et al.*, 2005; Thrush and Dayton, 2002). The incorporation of abundance data into SDMs, even at a coarse-scale, can enhance distribution predictions (Howard *et al.*, 2014) and improve decision-making because abundance is often a more ecologically relevant metric than occurrence for assessing biodiversity and ecosystem function (Johnston *et al.*, 2015). However, there are limitations when creating abundance SDMs because they are more challenging to model due to data requiring greater pre-processing (Waldock *et al.*,

2021) and often fewer data points inform them. Consequently, abundance models may have a lower predictive capacity for specific species or poorly sampled regions (Johnston *et al.*, 2015). An approach which aims to leverage the strength of individually created occurrence and abundance (count per sample unit) models by combining them into a single spatial output, known as a density (count per km^2) model has been successfully utilised in other marine studies (De Raedemaecker *et al.*, 2012; Dedman *et al.*, 2015; Rullens *et al.*, 2021). Although this approach effectively amalgamates predictions, there is still the need to address the challenges of data scarcity and model scale.

Here, I develop probability of occurrence, abundance, and density models for seven key coastal seafloor invertebrates common in temperate soft-sediment coastal regions globally, varying in habitat usage, distribution, and functional role (e.g., substrate stabilisation, burrowing, scavenging). I also include spatial measurements of uncertainty to understand the variability in model predictions better. I assess the differences in model performance and environmental driver influence of predicted distributions at both regional (e.g., a geographically representative area of coastline - 82,000 km^2) and national (e.g., the whole country and surrounding coastal waters - 4.2 million km^2) scales, across data type (occurrence and abundance), within and between taxa. I investigate whether the creation of regional-scale SDMs can be improved upon by including abundance data, hurdling individual predictions of occurrence and abundance together to make a combined density model, and selecting models from the optimally performing scale. I also explore whether I can utilise information-rich national datasets to inform robust regional-scale models comparable to models created exclusively from regional data. Furthermore, I hypothesise that spatial predictions for functionally important taxa will vary across spatial scales based on their ecological traits and scale-dependent environmental processes affecting species distributions (Robinson *et al.*, 2011). I aim to illustrate the predictive benefits of incorporating abundance data and accounting for model scale when creating SDMs to support regional spatial management decisions.

2.2. Methods

2.2.1. Study area description

The study area focuses on the coastal environment between the North and South Islands of Aotearoa - New Zealand, covering over 82,000 km^2 encompassing the South Taranaki Bight, Tasman Bay, and Golden Bay (Figure 1). National scale environmental predictor datasets at 250 m resolution, extending over 4.2 million km^2 (the full extent of New Zealand's Exclusive Economic Zone (EEZ), were utilised to create SDMs for the study area (Stephenson *et al.*, 2022).

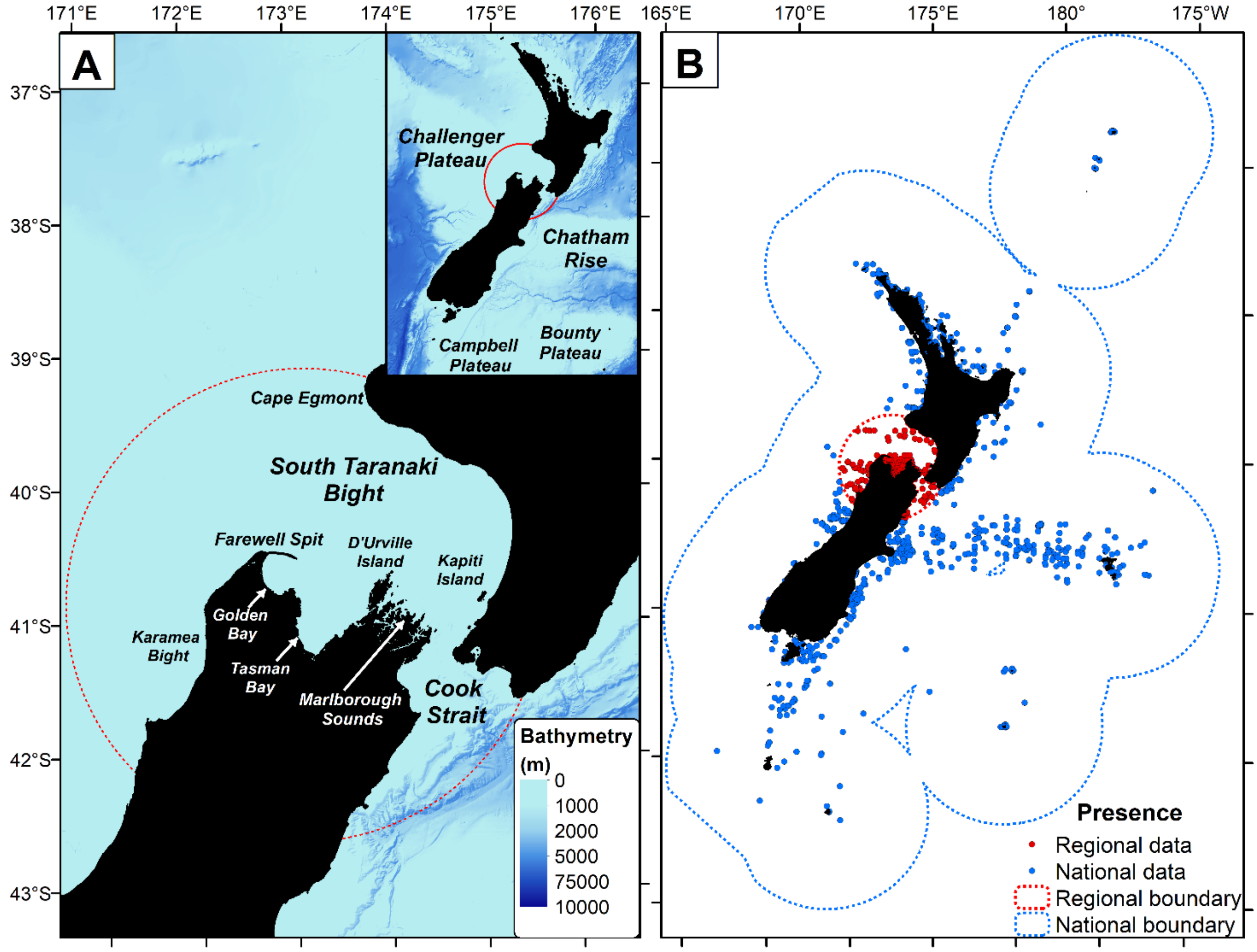


Figure 2.1: Map of the study region. A. Regional study area and bathymetry with the red dashed line indicating the regional model boundary. B. Sampling locations for point records for seven benthic invertebrate taxa. The blue dashed line represents the extent of New Zealand's Exclusive Economic Zone (EEZ).

2.2.2. Data and data processing

Benthic invertebrate occurrence records were collated from multiple databases, including records collected between 1896 and 2020 (Table A1). Seven taxa with sufficient record numbers (occurrence ≥ 60 and abundance ≥ 40) within the national and regional areas were selected to train and fit predictive occurrence and abundance models, with records comprising at least 70% unique locations. To limit the effect of spatial bias on models and to address multiple samples occurring within the same 250 m x 250 m grid cell, each cell was weighted proportionally (1/ [n-1]) by the number of records (Anderson *et al.*, 2016).

Insufficient point records were available to model at the species level; thus, point records were amalgamated *at* the genus level, with each taxon including point records for 2-15 individual species (Table 2.1). Modelled taxa varied in their functional role, including habitat-forming epifauna (*Callyspongia*), mobile surface feeders (*Amalda*), tubeworms that stabilise sediments (*Asychis, Maldane*), bioturbators/burrowers (*Echinocardium*), predators (*Glycera*) and suspension-feeding bivalves (*Pecten* - Table 2.1). The distribution and number of records varied across taxa from 76-210 abundance records and 248-887 occurrence records. The regional dataset contained fewer records as it was a direct sub-sample of the national dataset (Table 2.1).

Taxa records were collected using various equipment, including sleds, trawls, dredges, grabs, boxcores, diver observations and towed video cameras. Sampling gear varied in target organisms, substrate type and spatial extent. To address sample heterogeneity and mixed data scales resulting from gear selectivity, abundance data were standardised to the Swept Area Ratio (SWAR) for each gear type (based on dimensions of research vessel surveying equipment) and average sample distance, as a proportion of each 250 m raster cell (Przeslawski *et al.*, 2018). For each taxon, point records, in the form of count data, were converted to relative abundance ('relative' indications of low to high abundance) by multiplying each record with the corresponding SWAR for each sampling gear type, which circumvents some sample heterogeneity issues among survey data (Pecuchet *et al.*, 2017). I will refer to relative abundance as abundance moving forward.

Boosted Regression Tree (BRT) models were selected due to their robustness to incomplete data coverage, correlated predictor variables and ability to fit complex non-linear relationships (Elith, Leathwick and Hastie, 2008). I created a delta log normal model-(also known as a 'hurdle' model) using a three-step approach (Figure 2.2; 1) fitting a binomial Boosted Regression Tree (BRT) model (Elith *et al.*, 2006) for the probability of occurrence; 2) fitting a separate BRT model with a Gaussian distribution for abundance; and 3) multiplying the occurrence and abundance model outputs together to create a density map (Dedman *et al.*, 2015). All BRT analyses were undertaken in R (R Core Team, 2021) using the “dismo” package (Hijmans and van Etten, 2012). BRT models were run using the “gbm’’ (generalised boosted model) package (Ridgeway, 2007).

Table 2.1: Description of each modelled taxa: taxonomy, functional role, habitat, and available records (at least 70 % unique locations)

Common name	Phylum - Genus	Functional role	Possible species within genus	Description	Presence Records National (Regional)	Abundance Records National (Regional)
Olive shell snail	Mollusca - *Amalda*	Mobile surface grazer/predator	*Amalda australis, A. bathamae, A. benthicola, A. mucronata, A. northlandica, A. novaezelandiae* *Amalda* spp. (n = 6)	Surface burial and disturbance Sandy flats from shallow waters down to ~ 600 m (Powell, 1979; Dell 1956)	213 (64)	126 (57)
Bamboo worm	Annelida - *Asychis*	Tube mat former/Substrate stabiliser	*Asychis amphiglyptus, A. trifilosus* *Asychis* spp. (n = 2)	Large tube forming subsurface worm. Sandy mud habitats from intertidal to deep-sea (Ehlers 1897, Augener 1926)	266 (113)	175 (94)
Colonial tube sponge	Porifera - *Callyspongia*	Habitat-structure forming epifauna	*Callyspongia bathami, C. clavata, C. conica, C. difficilis, C. diffusa, C. fallax, C. fibrosa, C. fistulosa, C. latituba,C. ramosa, C. siphonella, C. stellate, C. vaginalis* *Callsyspongia* spp. (n = 13)	Sessile. Low tide to subtidal down to 50 m, often on boulders, walls and rocky reef habitats (M. Kelly 2015, Hooper & Wiedenmayer, 1994)	390 (98)	128 (67)
Heart urchin	Echinodermata - *Echinocardium*	Bioturbator /Burrower/ Substrate destabiliser	*Echinocardium cordatum, E. lymani, E. pennatifidum* *Echinocardium* spp. (n = 3)	Highly mobile bioturbator. Sandy to sandy/mud sediments - intertidal to subtidal to 200 m (Hill., 2008)	887 (773)	141 (107)
Bloodworm	Annelida - *Glycera*	Predatory scavenger	*Glycera americana, G. benhami, G. capitate, G. kerguelensis, G. knoxi, G. lamelliformis, G. lapidum, G. onomichiensis, G. ovigera, G. russa, G. tesselata* *Glycera* spp. (n = 11)	Mobile, surface-mixing worm, carnivores/detritivores. Sands and sandy to muddy habitats from intertidal to the deep sea (Knox., 1960)	397 (128)	210 (60)
Bamboo worm	Annelida - *Maldane*	Tube mat former/Substrate stabiliser	*Maldane theodori M. sarsi antarctica, M. cristata* *Maldane* spp. (n = 3)	Sedentary, large, tube-forming worm. Sandy and sandy/mudflats from intertidal to the deep sea., areas (Paterson *et al*., 2009)	282 (98)	170 (69)
Scallop	Mollusca - *Pecten*	Suspension feeding surface burrower	*Pecten novaezelandiae, P. raoulensis* *Pecten spp.* (n = 2)	Shallow burying bivalve, highly mobile. Mud to coarse sand, low to moderate energy areas down to over 90 m. Large populations found at depths of 10-25 m. (Morton and Miller, 1973)	248 (116)	76 (44)

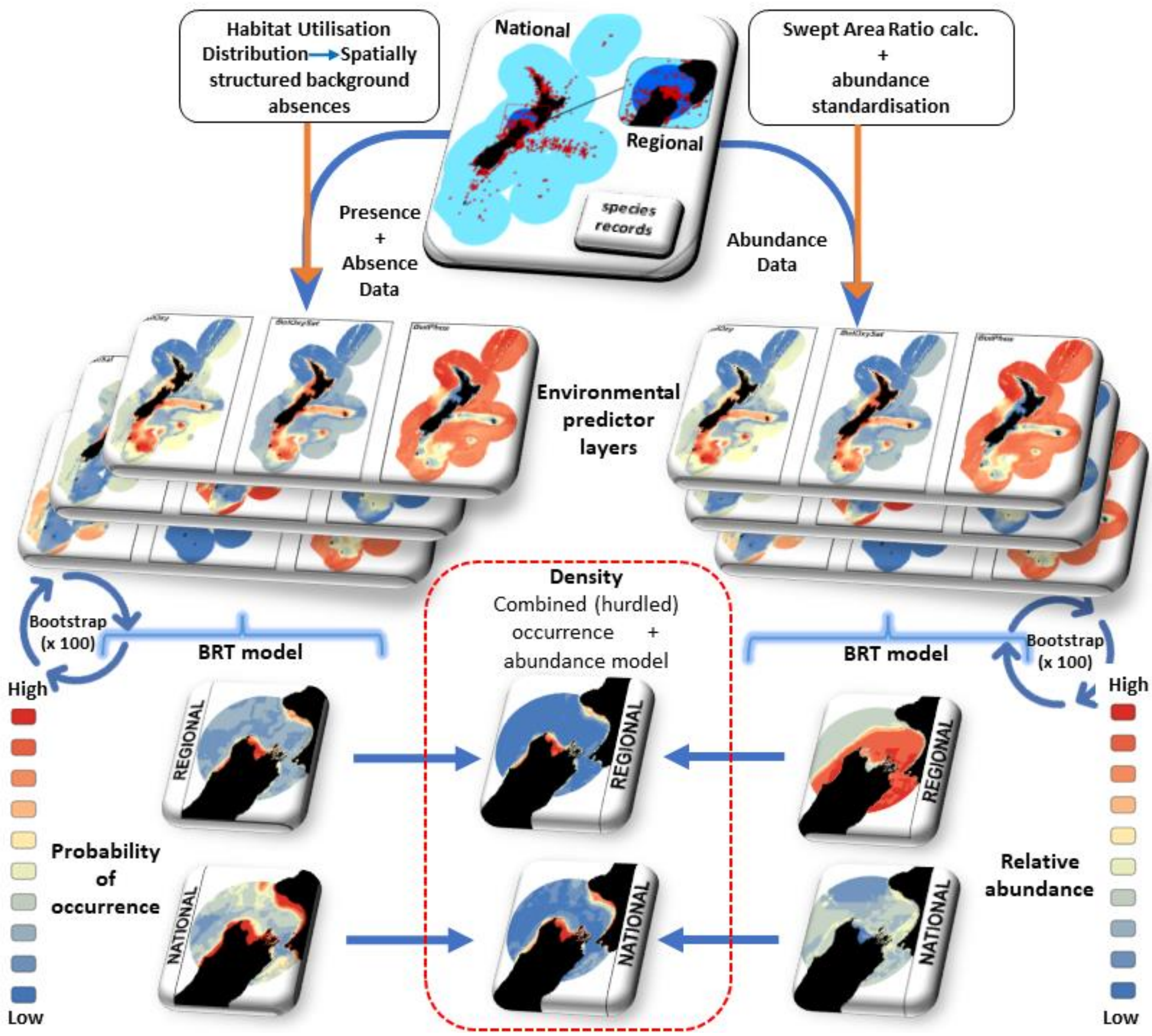


Figure 2.2: Analysis workflow demonstrating model inputs and processes to produce 'hurdled' density model

2.2.3. Environmental variables

Twenty-six chemo-physical environmental predictor variables were available to inform the occurrence and abundance models (descriptions of environmental variables are found in Table A2). Environmental parameters for each of the predictor variables were extracted for all point records (occurrence, abundance, and relative absences) at both regional and national model scales, using the "raster" package in R (Hijmans and van Etten, 2012). Predictor correlation was examined before model fitting for each taxon; a correlation matrix was created for all initial predictor variables and presence locations (Figure A2).

Environmental variables were iteratively reduced to attain model parsimony, achieving the greatest predictive power with the fewest predictor variables, and avoiding overfitting (Elith, Leathwick and Hastie, 2008). Predictors were progressively reduced in two successive phases using the "simplify" function (Elith *et al.*, 2006), broadly analogous to backward selection. First, predictor variables were refined from 26 to 7 for all taxa for national scale models and then independently for regional-scale models. Then, the top seven predictors at each scale were combined (with a maximum of 14 variables for each taxon) and then refined from 14 down to seven predictors using the "simplify" function, so that the top 7 predictors were the same for both national and regional models. These steps were taken so that differences in environmental predictor influence across spatial scales could be evaluated.

2.2.4. Modelling

2.2.4.1. Occurrence Models

To perform occurrence predictions, BRT models require data for locations of known presences (field samples) and locations of absences (a selection of the set of conditions available where the taxon is absent from). The most robust forms of absence data are 'true' absences (i.e., locations where the environment was sampled, and the target taxon was confirmed absent). As true absence data were not available, I created spatially-structured "target-group background" absences by using the presences of other taxa from the same broad taxonomic group, sampled using the same sampling methods, in locations where the target taxon was absent (Georgian, Anderson and Rowden, 2019; Phillips *et al.*, 2009). I refer to target-group background absences as ‘’relative absences’’ (Barbet-Massin *et al.*, 2012). Relative absence data were selected from within a spatial boundary created for each target taxa distribution based on their habitat utilisation distribution (also termed "Home Range"). Home ranges were created by performing a kernel density estimation with the presence records (Figure A1), using the R package 'adehabitatHR' (Calenge, 2006). BRTs for occurrence models were fitted with a Bernoulli error distribution, a tree complexity of 3, a learning rate between 0.01 – 0.0001 (representing between 1,000 and 3,000 trees for each taxa model), a bag fraction of 0.7, and an interaction depth of 2 (to account for pairwise interactions).

2.2.4.2. Density Models

Abundance models were tuned and fitted with the same model parameters as the occurrence models but with a Gaussian error distribution and using the standardised abundance data (count per km^2). Abundance model spatial rasters (250 m) were then multiplied (hurdled) with occurrence spatial rasters (250 m) to create a density prediction. I evaluated model performance based on the metrics from the abundance model, but when I evaluated the spatial predictions, I focused only on the density output. Abundance predictions are conditional on presence locations, and spatial distributions should not be assessed from standalone abundance predictions; therefore, I focus on the density output, which accounts for both occurrence and abundance.

2.3. Model Evaluation

To evaluate the performance of the models, I applied two separate cross-validation approaches. For both approaches, a 5% difference between national and regional scores was used to indicate whether metric scores differed. Here, I present all performance results based on the subset of evaluation data.

The first evaluation approach follows commonly used methods where performance estimates are obtained directly from the model by partitioning data into training (75%) and evaluation (25%) subsets and then extracting evaluation metrics from them. I will refer to this approach as the 'direct evaluation’ method. Direct evaluation of model performance [for occurrence models] was assessed against the randomly selected training data (samples included in each bootstrap run) and the evaluation data (samples omitted from the model at each bootstrap run) separately, using two metrics for the occurrence model: deviance explained, and area under the receiver operating characteristic curve (AUC). The deviance explained provides a measure of the goodness-of-fit for the models between the predicted and raw values, with a higher score indicating a better model fit (Rodil, Compton and Lastra, 2012). The model's ability to correctly distinguish between the presence and relative absence locations was measured by the AUC value, which ranges from 0 – 1, where a score of > 0.7 indicates adequate performance and a score of 0.5 is no better than random chance (Hosmer, Lemeshow and Sturdivant, 2013). For the abundance models, performance was evaluated using Pearson's product-moment correlation coefficient, which estimates the correlation between the predicted values against the sampled values (Puth, Neuhäuser and Ruxton, 2014). Due to limited sample [abundance] records for certain taxa, data were not split into training and evaluation abundance subsets so that 100% of the dataset could be used to support model convergence. Though some taxa had sufficient abundance records to partition the data into training and evaluation subsets, I applied the same methodology across all abundance models to keep evaluation metrics consistent across taxa.

The second approach used for evaluation was spatial cross-validation which accounts for potential spatial biases by partitioning (spatially stratifying) the datasets to achieve an even distribution before extracting statistically independent evaluation metrics. The spatial cross-validation method provides a more representative error estimation in sample data that contains dependence structures (e.g., spatial bias) associated with sampling constraints (Roberts *et al.*, 2017). A 5-fold spatial block cross-validation was performed using R's "block cv" package (Valavi *et al.*, 2018). Spatial blocks were created based on the locations of the occurrence data. Each block was randomly assigned to one of five k-folds (e.g., where data is split into 'k-subsets'). Blocks were created using the 'SpatialBlock' function, based on defined cell sizes, determined with the 'Range Explorer' interactive tool to assess the optimum block size, defined by the minimum size where spatial autocorrelation was no longer present in the environmental variables (Valavi *et al.*, 2018). To ensure that the random selection of relative absences in each spatial block would not skew our evaluation, I applied the same bootstrapping method to the spatial cross-validation, and relative absence data were randomly sampled with replacement to match the number of presences in each iteration. The Spatial Block method partitions the dataset into training (blocks 1-4) data used in the model and evaluation (block 5) data withheld from the model based on the block number. When the spatial block model is run, each model iteration (a total of 4) is assessed against the withheld data from block 5, and this process was bootstrapped 100 times. The extracted performance metrics are the averaged evaluation data from the withheld spatial block. Spatial block number allocation was randomly re-assigned for every bootstrap iteration, and the location of spatial blocks varied between taxa (e.g., Figures A4 & A5). The spatial cross-validation was applied to the occurrence models only. For the more data-limited abundance models (e.g., *Pecten*), there was an insufficient number of records, or distribution of records, to successfully partition the data into five equal spatial blocks throughout the study area, therefore I opted to not perform spatial cross-validation for any abundance models so that available metrics were consistent across taxa. AUC, Sensitivity and Specificity were calculated using the 'pROC' package in R (Robin *et al.*, 2021) to measure model performance. Sensitivity assesses the model's ability to predict presences (true positive rate) accurately, and Specificity assesses the model's ability to predict absences (true negative rate) accurately.

2.3.1. Spatial predictions and uncertainty

BRT models at both scales were predicted spatially at a 250 m resolution within the study area. Bootstrapped predictions were averaged (mean), and spatial uncertainty (standard deviation of the mean) was calculated. To create the predictive uncertainty maps for the density models, I combined the mean and standard deviations from both the occurrence and the abundance models. To account for uncertainty in predictions, a bootstrapping approach was applied to the BRT models (Figure 2). A random sample of the presence records and an equal number of randomly selected relative absences were drawn with replacement which was iterated 100 times for each taxon and over each model scale. Using an equal number of relative absences to presences followed the best practice outlined in Barbet-Massin *et al*. (2012). Spatial predictions were mapped using ArcGIS 10.7, and raster data scales were classified into ten equal 0.1 classification intervals (data bins) for visualisation.

All SDMs were graded and summarised via a semi-objective, qualitative assessment based on performance metrics, spatial outputs and alignment with ecological knowledge as assessed by the authors (Table 2.4). The following criteria were used to determine model grading: Red (not useful) – evaluation metrics low and spatial predictions did not align with expert ecological knowledge; Orange (moderately useful) - evaluation metrics medium or high and spatial predictions mostly align with ecology; Green (useful) - evaluation metrics medium or high and spatial predictions align well with ecological knowledge.

2.4. Results

2.4.1. Model evaluation and cross-validation

The direct evaluation approach indicated that all national scale probability of occurrence models were robust with AUC values ≥ 0.88 (Table 2.2). The regional models produced lower AUC values, though they were above a threshold of 0.7 for 6/7 taxa. AUC values were 13 % higher for the nationally trained occurrence models (national mean AUC 0.93, regional mean 0.80). Standard deviations of mean model performance (AUC) were low for all occurrence models (range 0.01 – 0.03 for national models, 0.01 – 0.12 for regional models), demonstrating that models performed consistently across bootstrap iterations with the national scale predictions achieving greater consistency across most taxa (Table 2.2). With consideration of SD scores, the national scale occurrence models achieved a higher AUC for 4 out of 7 taxa. The direct evaluation deviances explained were higher for national occurrence models (0.32 – 0.63) compared to regional models (0.04 – 0.39) for all taxa apart from *Amalda*. Regional-scale model deviances for *Pecten, Maldane* and *Callyspongia* (≤ 0.1) were substantially lower than for other taxa (≥ 0.18), indicating a poor model fit based on the relationship between the environmental data and limited occurrence records for these taxa.

All national scale abundance models performed well, achieving strong positive correlation scores ≥ 0.79 (Table 2.2). Regional-scale abundance models also achieved strong correlation scores of ≥ 0.83 for 5 of 7 taxa and ≤0.56 for the remaining taxa. Standard deviations of mean model performance (Pearson's r) were low ≤ 0.06 across both model scales. Abundance model deviance explained scores were higher nationally for 3 of 7 taxa, higher regionally for 1 of 7 taxa, and similar at both scales for the remaining three taxa. Regionally, abundance models for *Echinocardium* and *Pecten* performed poorly with AUC values < 0.7 threshold and corresponding low deviance explained. Nationally, the *Pecten* abundance model had the lowest performance, with only 22% of deviance explained, although it still achieved a Pearson's correlation of 0.83. This contrast between scores across evaluation metrics for the same taxon highlights the need to aim for evaluation scores that meet the minimum thresholds for robustness across both metrics.

Table 2.2: Cross-validated estimates of model performance from the direct evaluation method. Occurrence results were extracted directly from the withheld evaluation data for bootstrapped BRT models for seven taxa (100 iterations ± standard deviation). Occurrence performance metrics include the mean deviance explained and mean AUC (area under the receiving operator curve). Abundance results were calculated using the full dataset. Abundance performance metrics include the mean deviance explained and the Pearson's correlation between prediction and training data. Bold values indicate the highest metric value for each taxon if the difference is ≥ 5%. There are no separate evaluation metrics for the Density model as this is post-processing of model outputs by combining the spatial predictions of the individual models below.

Taxa	**National**	**Regional**	**National**	**Regional**
Occurrence model	deviance explained	deviance explained	AUC	AUC
Amalda	0.44 ± 0.08	0.39 ± 0.10	0.92 ± 0.03	0.90 ± 0.07
Asychis	**0.32 ± 0.05**	0.18 ± 0.05	**0.88 ± 0.03**	0.81 ± 0.05
Callyspongia	**0.46 ± 0.11**	0.10 ± 0.06	**0.92 ± 0.03**	0.75 ± 0.07
Echinocardium	**0.54 ± 0.04**	0.35 ± 0.04	0.96 ± 0.01	0.93 ± 0.01
Glycera	**0.42 ± 0.04**	0.33 ± 0.10	0.90 ± 0.02	0.86 ± 0.05
Maldane	**0.63 ± 0.05**	0.09 ± 0.07	**0.97 ± 0.01**	0.70 ± 0.12
Pecten	**0.57 ± 0.06**	0.04 ± 0.04	**0.94 ± 0.02**	0.64 ± 0.09
Abundance model			**Pearson's r**	**Pearson's r**
Amalda	**0.60 ± 0.05**	0.07 ± 0.04	**0.87** ± 0.03	0.56 ± 0.01
Asychis	0.45 ± 0.05	0.42 ± 0.13	0.83 ± 0.03	**0.96** ± 0.03
Callyspongia	0.47 ± 0.12	0.45 ± 0.12	0.96 ± 0.04	0.96 ± 0.05
Echinocardium	**0.87 ± 0.04**	0.03 ± 0.02	**0.98** ± 0.01	0.45 ± 0.05
Glycera	0.38 ± 0.05	0.41 ± 0.08	0.79 ± 0.04	0.83 ± 0.04
Maldane	**0.54 ± 0.05**	0.46 ± 0.08	0.91 ± 0.02	0.87 ± 0.04
Pecten	0.22 ± 0.12	**0.33 ± 0.07**	0.83 ± 0.06	0.86 ± 0.01

For the spatial cross-validation evaluation, firstly, the AUC metrics are compared; 3 of 7 taxa (*Asychis*, *Callyspongia* and *Pecten*) scored significantly higher nationally, 1 of 7 taxa scored significantly higher regionally (*Echinocardium*), and 3 of 7 taxa perform within ± 4% across both model scales (Table 2.2). For the Sensitivity metric, 3 of 7 taxa (*Pecten, Maldane, Asychis*) scored significantly higher at the national scale, with the remaining 4 of 7 within ± 4% across both scales. For the Specificity metric, 3 of 7 taxa (*Amalda*, *Echinocardium* and *Maldane*) scored significantly higher regionally, 2 of 7 (*Callyspongia* and *Pecten*) scored significantly higher nationally, and the remaining two taxa performed within ± 4% across both scales.

Table 2.3: Cross-validated estimates of model performance from the partial cross-validation method providing area under the receiver operating curve (AUC), True Skills Statistic (TSS), Sensitivity and Specificity for all taxa and model scales for the probability of occurrence models (100 iterations ± standard deviation). Results are the mean value from 100 bootstrap iterations. Bold values indicate the highest metric value for each taxon if the difference is ≥ 5%.

Taxa	Spatial cross-validation evaluation metrics		
National Model	AUC	Sensitivity	Specificity
Amalda	0.77 ± 0.12	0.81 ± 0.21	0.72 ± 0.09
Asychis	**0.72 ± 0.11**	**0.77 ± 0.09**	0.68 ± 0.19
Callyspongia	**0.8 ± 0.04**	0.75 ± 0.09	**0.82 ± 0.04**
Echinocardium	0.69 ± 0.04	0.82 ± 0.15	0.63 ± 0.17
Glycera	0.7 ± 0.06	0.72 ± 0.18	0.68 ± 0.11
Maldane	0.73 ± 0.06	**0.83 ± 0.13**	0.65 ± 0.23
Pecten	**0.81 ± 0.10**	**0.84 ± 0.11**	**0.76 ± 0.10**
Regional Model			
Amalda	0.76 ± 0.12	0.82 ± 0.17	**0.81 ± 0.19**
Asychis	0.66 ± 0.14	0.69 ± 0.24	0.72 ± 0.21
Callyspongia	0.68 ± 0.13	0.73 ± 0.31	0.73 ± 0.10
Echinocardium	**0.76 ± 0.10**	0.81 ± 0.10	**0.69 ± 0.25**
Glycera	0.69 ± 0.11	0.73 ± 0.14	0.7 ± 0.27
Maldane	0.75 ± 0.12	0.77 ± 0.13	**0.76 ± 0.27**
Pecten	0.6 ± 0.09	0.64 ± 0.26	0.67 ± 0.25

In summary, two taxa (e.g., *Callyspongia* and *Pecten*) achieved consistently higher performance scores across all metrics at the national scale. Still, results were mixed for the remaining five taxa, with neither model scale performing consistently better across all metrics or evaluation methods. Performance appeared to be taxon-specific, not scale or metric-specific, indicating the results are heavily influenced by data availability, sample distribution and sampling method. Regional models achieved higher Specificity scores indicating a greater ability to discriminate between relative absences, and national models achieved higher Sensitivity scores indicating a greater ability to discriminate between presences. Overall, the AUC metric reflects model performance well, but the difference in AUC score between national and regional models was far greater for the direct evaluation method (13%) compared to the spatial evaluation method (1%), which indicates the need to address the disparity in the number of sample records when comparing performance at different geographical scales.

2.4.2. Spatially predicted distributions

Individual SDMs for the probability of occurrence, abundance, density, and corresponding uncertainty were predicted at both model scales for all seven taxa (Figures A6 – A11). Prediction patterns and model observations are discussed in the next section and summarised in Table 2.4. Here I present a single taxon (*Callyspongia* spp.) to illustrate some of the observed distribution patterns between model scales and model type and demonstrate a multi-scalar approach's utility. The national scale occurrence model for *Callyspongia* showed little spatial differentiation, with a high probability of occurrence (≥ 0.9) predicted across most of the study area. In contrast, the regional occurrence model was more spatially differentiated, with localised areas of moderate to high occurrence predicted in the coastal marine area (Figure 3). The regional scale SDM predictions align with ecological knowledge of the preferred *Callyspongia* habitat (Table 2.1). They are often found in the shallower subtidal environment down to 50 m, attached to boulders or walls in and around rocky reef habitats (Kelly and Herr, 2015). Furthermore, the regional occurrence predictions align well with the locations of presence data. However, when I examine whether the spatial predictions align with predictive performance, the national scale model outperformed the regional scale model across all evaluation metrics except for Sensitivity (Table 2). This observation of high inshore prediction coupled with high evaluation metrics reflects the model fit from taxon-environmental relationships established from many offshore occurrence records. The model fitted a relationship based on available data, which indicated that nationally, *Callyspongia* is found in the shallow subtidal environment in sediments with higher gravel content or rocky substrates, and the model was able to apply this fitted relationship over most of our study area, hence the higher evaluation scores. Therefore, the evaluation metric scores reflect a good fit when the model compared the training data to the withheld evaluation data. However, applying the model fit from the national taxon-environmental relationships to a shallower inshore coastal region led to reduced differentiation and higher prediction levels inshore than is ecologically likely.

Abundance model predictions at both scales share similar patterns despite the training of the regional model containing fewer (~ 50%) taxa records. This similarity across spatial scales is also reflected by the evaluation metrics, which were the same for Pearson's correlation (0.96) and 0.02 for deviance explained (Table 2.2). Despite contrasting predictions between the occurrence models at each scale, patterns are more aligned when I examine the density model outputs. The contrasting predictions between the two occurrence model scales indicate that the abundance model is the primary driver of the observed density distribution patterns. However, if there were no spatial overlap between the occurrence and abundance model, the observed distribution patterns in the density model would be different, as only the areas that spatially converge between the two are retained in the density output. Thus, I acknowledge that the density predictions are conditional on the presence locations of the occurrence model distribution patterns firstly, and secondly, the abundance model selects a subset of those conditions that support higher abundances displayed within the density output.

Levels of uncertainty were low for both the regional (SD ± 0.07) and national (SD ± 0.03) models. Nationally, the greatest uncertainty was found along the Karamea Bight, which is likely a reflection of the low probability of occurrence predicted along this coastline compared to the abundance model. Regionally, the greatest uncertainty was observed in the inner and outer Tasman Bay.

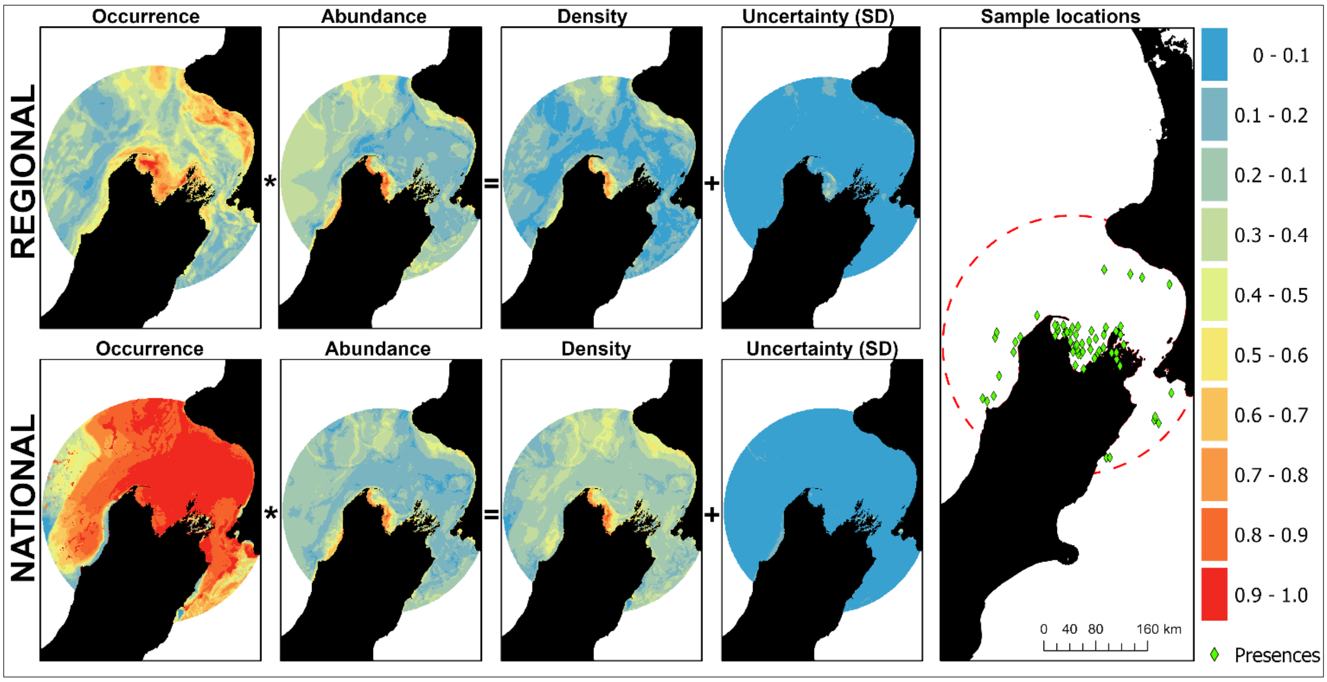


*Figure 2.3: Callyspongia spp. BRT spatial predictions of the study area at regional and national scales: probability of occurrence (presence & relative absence), abundance (abundance), density (occurrence * abundance) and uncertainty (standard deviation of density model). All data has been normalised to be on a scale of 0-1 (right legend).*

2.4.3. Spatial predictions summary

Across all models, common areas of abundant habitat were highlighted (e.g., areas that predicted a high probability of occurrence or density) within the shallower coastal environment, coastal bays, and inlets. For some taxa, national scale models were deemed less useful than regional-scale models. This conclusion was based on poor levels of differentiation and predictions of very high occurrence or abundance over most of the study area (e.g., Figure 2.3 – national occurrence) that did not align with ecological knowledge at a localised scale (Table 2.1). For other taxa, the opposite was true and regional scale models scored lower than national scale models. There was no apparent relationship between the robustness of spatial predictions achieved at each scale and the number of data points used to train the models. For some taxa, spatial predictions were similar across spatial scales (e.g., *Amalda* – Figure A6), and for others, dissimilar (e.g., *Maldane* – Figure A9). I also observed that for certain taxa, when occurrence predictions were alike between national and regional scales, abundance predictions were not, and vice versa. Furthermore, when contrasting predictions were observed (either for occurrence or abundance), the density model produced consistently similar distribution patterns across both scales for 4 of 7 taxa models (*Amalda*, *Asychis*, *Callyspongia* and *Pecten*). Focussing on the occurrence models, for several taxa (e.g., *Callyspongia*, *Glycera* and *Maldane*), primary differences across model scale were contrasting predictions between the deeper offshore waters (in the outer study area) and the shallower coastal waters. For those three taxa, the national scale models indicated that the probability of occurrence was high over most of the study area, whereas in the regional models, it was lower and more differentiated, although the national scale models had higher direct evaluation metrics. Conversely, for

Echinocardium and *Pecten*, the opposite was true, and national models appeared to have a more logical spatial distribution than the regional scale model, but national direct evaluation metrics were still the higher.

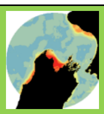
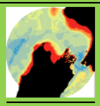
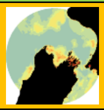
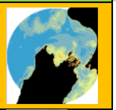
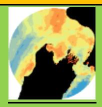
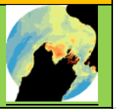
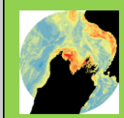
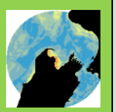
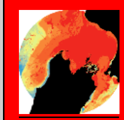
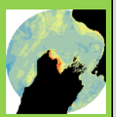
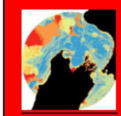
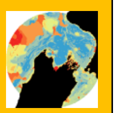
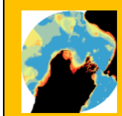
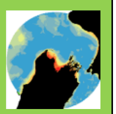
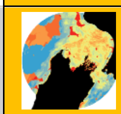
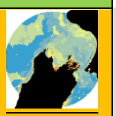
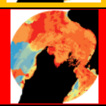
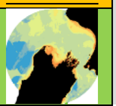
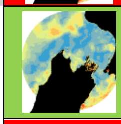
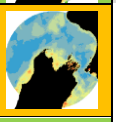
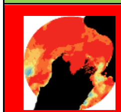
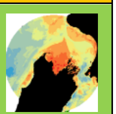
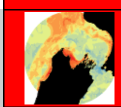
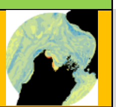
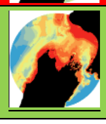
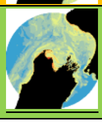
All national scale direct model metrics achieved high scores (mean AUC 0.93, mean deviance explained 0.48), but robust evaluation metrics did not always result in those models producing more ecologically relevant or spatially differentiated predictions. This contrasting relationship between high-performance metric scores and less useful spatial outputs was observed nationally for 4 of 7 taxa (*Callyspongia, Maldane, Asychis* and *Glycera*), regionally for one taxon (*Pecten*), and at both scales for one taxon (*Echinocardium*).

Abundance predictions were more stable across spatial scales in that they often shared similar patterns and differentiation between national and regional models for most taxa. Generally, spatial distribution patterns observed for the density models closely reflected patterns from the abundance models, a result driven by the following process: firstly, only areas that spatially corresponded between both the occurrence and abundance models are retained in the density model, therefore, the distribution patterns are conditional on the presence data locations generated in the probability of occurrence predictions. A clear example of this can be seen in the regional scale models for *Maldane* (Figure A10), where there are predictions of high abundance throughout Tasman and Golden Bay and around Farewell Spit, but these patterns were not emulated in the density output because the same corresponding areas have a low probability of occurrence. Secondly, the abundance model selects a subset of those conditions that support higher abundances, which often correlate with areas of high occurrence, and these are the patterns displayed within the density output. Additionally, the creation of the density model neutralised values that did not correspond between occurrence and abundance models and only retained areas with higher prediction certainty from both models.

Levels of uncertainty were low across all national occurrence models (SD ± 0.01-0.03) and slightly higher regionally (SD ± 0.01-0.12). Abundance model uncertainty was also low, ≤ 0.06 regionally. Higher levels of uncertainty were observed mainly offshore or in poorly sampled regions. The greatest levels of uncertainty were recorded for *Pecten* and *Maldane* regional occurrence models.

All density models (at least one from either scale) were deemed useful (Table 2.4). When comparing performance across all density models (two scales for each taxon), 9 of 14 models were deemed useful (7 national, 2 regional). For the occurrence models, 6 of 14 were deemed useful (3 national, 3 regional). Even when an individual input model was graded medium or low (orange/red), or contrasting predictions were observed between models at different scales, the density model was still able to produce a spatially refined and ecologically useful distribution map for at least one model scale, and more often at the national scale.

Table 2.4: Summary of overall model performance across spatial scale, model type and taxa. Spatial predictions graded from low-high (red-green) based on the visual appearance of spatial maps, alignment with ecological knowledge (Table 2.1) and evaluation metric scores. Model scale indicated by (R) for regional and (N) for national. All map outputs are provided in the appendices, except for Callyspongia (Figure 3) which is presented in the paper. Small pictures of SDMs have been overlaid onto performance colour cells.

Taxa	Occurrence	Density	Performance observations
***Amalda* (R)**			**Occurrence:** Models predicted similar spatial patterns across both spatial scales and aligned well with ecological knowledge (Table 2.1). Both evaluation methods indicated that national and regional models performed similarly with regard to AUC. The regional model did achieve higher Specificity.
***Amalda* (N)**			**Density:** Both model scales achieved similar prediction patterns and were deemed useful. They retained a higher-density core prediction area in the inner bays and shallow coastal areas (Figure A6).
***Asychis* (R)**			**Occurrence:** National scale model aligns best with ecological knowledge (Table 2.1), predicting a wider distribution throughout the study area compared to regional. The national scale model scored higher evaluation metrics across both evaluation methods except for Specificity, which were similar.
***Asychis* (N)**			**Density:** The national scale model aligns best with ecological knowledge and is deemed most useful, predicting moderate to high density over most inner coastal areas (Figure A7).
***Callyspongia* (R)**			**Occurrence:** Regional-scale model aligned best with ecological knowledge (Table 2.1) and displayed greater differentiation. National scale predictions were much higher than ecologically likely and not informative at a regional scale. However, the national scale model achieved higher evaluation metrics across all metrics apart from Sensitivity.
***Callyspongia* (N)**			**Density:** Models predicted similar spatial patterns across both spatial scales reflecting hotspots in the shallow coastal environment and inner bays. A similar spatial distribution was achieved at both scales despite contrasting predictions from the occurrence models (Figure 3).
***Echinocardium* (R)**			**Occurrence:** National and regional models produced poorly representative spatial outputs and did not align well with ecological knowledge (Table 2.1). The national model achieved a higher deviance explained score from the direct model evaluation method, but the spatial cross-validation method indicated that the regional model achieved higher AUC and Specificity.
***Echinocardium* (N)**			**Density:** National scale density model was deemed most useful and achieved high-performance scores. Although the national scale is most useful for a core prediction area of high density, it is likely underpredicting higher abundances in the deeper subtidal environment reflected in the regular abundance model (Figure A8).
***Glycera* (R)**			**Occurrence:** The regional occurrence model produced a somewhat useful spatial output over the central study area but with some erroneous high predictions in the northwest. The national model predicted very high levels throughout the study area with poor differentiation and was deemed not useful at a regional scale. The national model achieved higher deviance explained, but all other metrics were within a similar range.
***Glycer a* (N)**			**Density:** The national scale model was deemed most useful as it aligned best with ecological knowledge predicting high density in the inner bays and moderate density over most of the study area (Figure A9).
***Maldane* (R)**			**Occurrence:** Regional-scale model was deemed most useful. The national scale model was less informative, with poor differentiation predicting much higher levels of probability of occurrence than is ecologically likely. From the direct model metrics, the national model achieved higher AUC and deviance explained, and from the spatial cross-validation, the national model achieved higher Sensitivity and regional higher Specificity.
***Maldane* (N)**			**Density:** National scale density model was considered most useful. The regional density model had a very limited distribution than would be expected based on ecological knowledge (Table 2.1) of this taxon (Figure A10).
***Pecten* (R)**			**Occurrence:** National occurrence model was deemed most useful and aligned well with known ecology. The regional model has some core prediction areas that align with the known distribution of *Pecten* around the inner bays, but the high occurrence was also predicted offshore along the northwest of Karamea Bight up to Cape Egmont, which does not align with the shallow (10-25 m) sandy / muddy habitat where large populations are usually found. The national scale model achieved higher evaluation scores across all metrics.
***Pecten* (N)**			**Density:** The national scale density model was deemed most useful in performance and ecological knowledge alignment (Figure A11).

2.4.4. Environmental drivers of spatial predictions

The relative influence of environmental predictors varied across all taxa, model types and model scales (Figure 2.4). Out of the 26 predictor variables used to train the initial models, 17 were commonly selected between occurrence and abundance models across multiple taxa. The variation in predictor influence (Figure 2.4) across spatial scales may account for predictive differences between national and regional spatial outputs observed for the same taxa.

From the 14 occurrence models (7 taxa at two spatial scales), sediment and productivity predictors were the most influential drivers across all taxa and water chemistry. The most influential occurrence variables were: percent gravel (Gravel - 10 of 14; mean 17%), bottom concentration of phosphate (BotPhos - 10 of 14; mean 14%), and percent mud (Mud - 8 of 14; mean 13%). The highest contributing variable for a single model run was bottom temperature (BotTemp - 42%) which appeared in the national scale model for *Amalda* and can also be correlated with bottom oxygen.

From the 14 abundance models, water chemistry, seafloor terrain and sediment were the most influential drivers across all taxa. The most influential abundance variables were: bottom nitrogen (BotNi - 12 of 14; mean 18%) and mixed layer depth (MLD - 8 of 14; mean of 15%). The highest contributing variable for a single model run was bottom oxygen (BotOxy - 52%) which occurred in the national scale model for *Amalda* and can also be correlated with bottom temperature. These observations highlight that for benthic invertebrates, environmental processes related to water chemistry that occur at depth to maintain oxygen levels and regulate temperature are key drivers of high abundance. Mixed layer depth had a stronger influence at the national scale for 4 of 7 taxa. Mixed layer depth measures the depth gradient at which shallower homogenised mixed water separates from the denser stratified deep water, reflecting the importance of this gradient as a key temperature interface for benthic organisms.

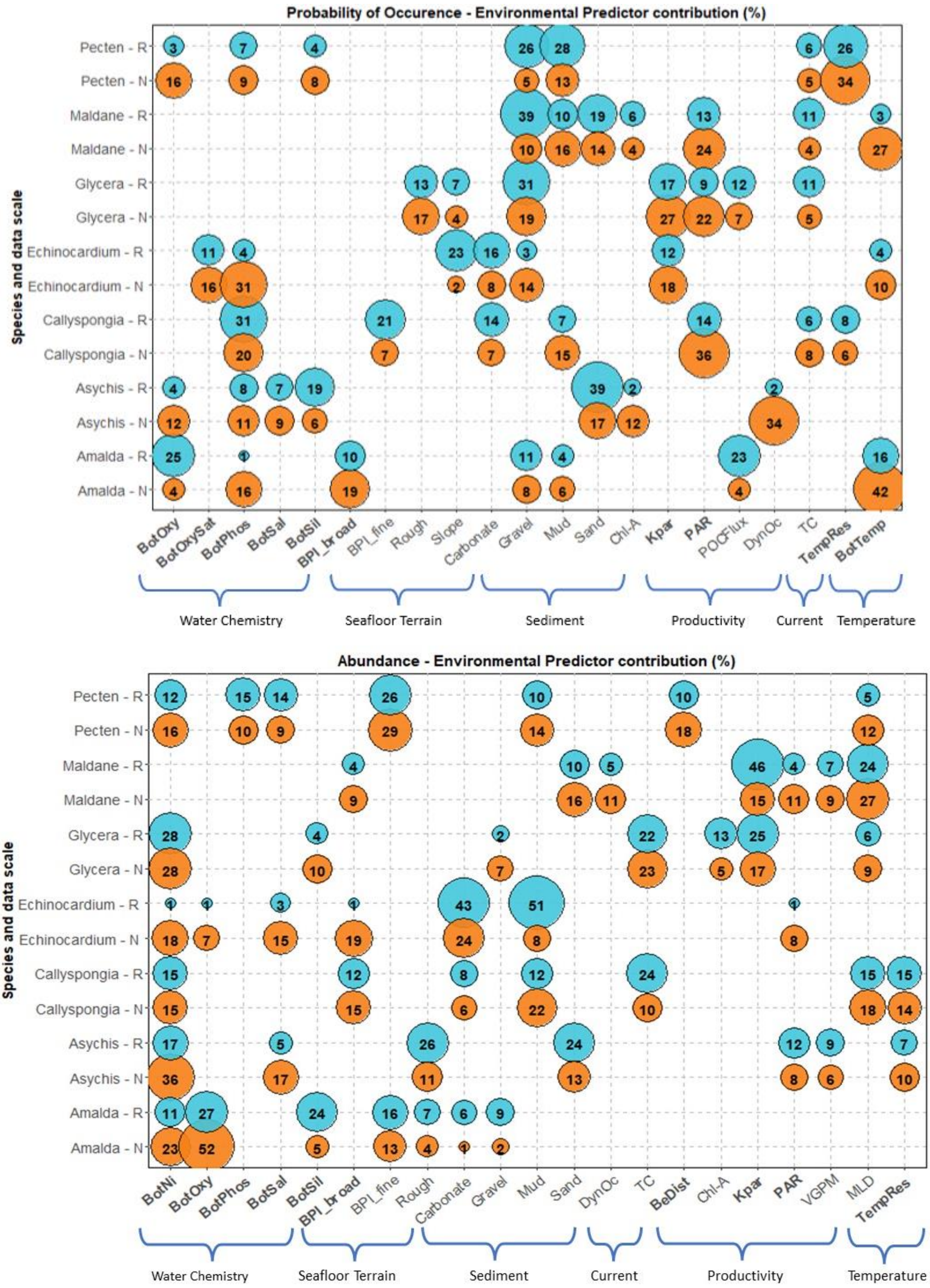


*Figure 2.4: Percentage of predictive influence of environmental predictors for boosted BRT models - Occurrence (top), abundance (bottom), variables formatted by geographical sampling scale: broad-scale variables (**bold**), fine-scale variables (plain). Predictors have also been ordered and grouped by "category". Note: Full names for variable abbreviations, temporal resolution, units and description are provided in Table A2.*

2.5. Discussion

This study demonstrates the functionality of a multi-scalar SDM approach that successfully predicted occurrence and abundance to create combined density maps for a broad range of benthic taxa with different functional ecology and life-history traits common in temperate systems worldwide (Kozloff, 1997; Hayward and Ryland, 1995; Morton and Miller, 1968). To our knowledge, comparing the performance of benthic density models across regional and national spatial scales at fine resolution has not yet been explored. BRT models were used to create predictions for seven key coastal invertebrates, with occurrence models achieving AUC scores on the evaluation data that indicated good performance for all taxa models at the national scale and for most at the regional scale. For the abundance models, there was a high correlation between predicted values and sample data for all taxa models at the national scale and for most at the regional scale (Table 2.2), which was also reflected in the consistency of distribution patterns between national and regional models. Sensitivity scores were higher for a greater number of taxa models at the national scale, and Specificity scores were higher across more taxa at the regional scale highlighting the differences in model strengths at different spatial scales. The qualitative assessment determined that all national scale density models were useful (Table 2.4); however, the quality of spatial outputs for the occurrence models was highly variable across both spatial scales. Even when high evaluation metrics were achieved, some taxon models exhibited higher than likely levels of prediction and poor differentiation, which was also found by Waldock *et al*., (2022). The variability in SDM outputs reflects the effect that utilising different datasets (data-limited vs data abundant) across spatial scales can have on predictive models, which can be challenging for coastal managers to leverage these tools at a localised scale (Nyström *et al.*, 2013).

Model performance varied greatly across model scales for the same taxa, and I found that the relationships between occurrence and abundance estimates were non-linear and also varied across taxa and model scales, a result which has been reported in previous studies (Johnston *et al.*, 2015; Mi *et al.*, 2017; Rullens *et al.*, 2021; Yu, Cooper and Infante, 2020). Neither occurrence nor abundance SDMs performed consistently better at either scale across all taxa, demonstrating the utility of comparing performance across spatial scales when working in data-limited environments. National AUC metrics were higher across all taxa, though the greater number of presence records may have influenced this, at least double, used for national model training compared to regional models (excluding *Echinocardium*), as AUC measures are not robust to large differences in sample size (Hanczar *et al.*, 2010). Overall, regional model performance was poorer across most taxa, which could be due to the number and distribution of regional sample records not covering a large enough range of environmental conditions in which these taxa occur and are abundant (Waldock *et al*., 2022). Furthermore, although I met the minimum criteria regionally for the number of records required to run an occurrence model, I acknowledge that these were not all unique locations (which was addressed by weighting) and could also account for a more limited sample of taxa-environmental relationships available for model training which would likely improve with more regional sample records. Accordingly, data-rich national scale model performance was higher for occurrence and abundance taxa models, predicting well over the regional study area inshore.

One of the aims of this study was to compare the differences in model prediction and performance at different geographical scales. Our models were calibrated at two scales; a geographically representative area of coastline (82 thousand km^2) and at the scale of the EEZ of one country (New Zealand) that has the 4^{th} largest EEZ (4.2 million km^2). Although these scales were appropriate for New Zealand's coastal waters and Exclusive Economic Zone, I acknowledge that the scales may not be relevant for other countries where the spatial extent of the coastal zone may be similar to our regional area (e.g., Europe). Nevertheless, the underlying principle illustrated by this study is still applicable. In other words, to effectively utilise SDMs for marine spatial management and conservation, practitioners need to explore the effect of using geographically limited vs. geographically expansive datasets and to understand how scale influences predictions of SDMs, especially for taxa with different ecological niches. For countries with smaller coastal zones, this would require international collaboration to share environmental knowledge to obtain more geographically expansive species and environmental datasets.

Environmental predictor influence was highly variable between model types demonstrating the differences in ecological drivers of occurrence compared to abundance, a result also found in previous studies that applied the hurdle model approach (Dedman *et al.*, 2015; Rullens *et al.*, 2021). Abundance model performance was more stable over geographical scales for the same taxa than occurrence models, in both predictor influence (e.g., Figure 2.4) and consistency of spatial predictions (e.g., Figure 2.3). I found that for taxa with the same functional role, fitted environment predictors may vary, but there are patterns of similarity in predictor selection across each driver category (e.g., sediment, productivity and temperature). Notably, environmental predictors representing water chemistry properties close to the seafloor (e.g., bottom nitrogen, bottom oxygen), were influential across all models, highlighting their importance as drivers of benthic invertebrate distribution. Interestingly, I observed that regional scale models were more highly influenced by fine-scale environmental predictors (environmental data sampled over a fine geographic scale e.g., sand from sediment cores) and national scale models had greater influence from broad-scale predictors (environmental data sampled over a broad geographic scale e.g., bottom temperature average from satellite data). This observation further highlights differences in scale-dependent environmental processes driving species occurrence and density distribution patterns, even over the same study area, an observation also recorded for blue mussels in the baltic sea (Nyström *et al.*, 2013). Although observation of scale-associated predictor influence is a key finding, I acknowledge that the predictor selection method (utilising the same top seven variables across both regional and national models) may have led to an imbalance in broad-scale or fine-scale predictors for each taxa model and could be improved upon in future applications. When applying the methodology to future model scenarios, it would be advantageous to refine the predictors independently at each comparative scale, likely resulting in an improved and more balanced model performance at each scale and clearer observation of predictor influence.

To leverage the predictive improvements provided by the inclusion of abundance data (Howard *et al.*, 2014), the model extent must include an acceptable species niche range, otherwise, the species response will be curtailed (Austin, 2007; Guisan and Thuiller, 2005), which aligns with our findings. I observed limited occurrence distribution predictions at the regional scale and similar distribution patterns for abundance across both scales, resulting in robust predictions across national scale density models due to the broader extent of the sampled environmental conditions. All modelled taxa are found either on or below the sediment surface but occupy their specific ecological niche and associated functional roles from substrate stabilisation (*Asychis* and *Maldane*) to surface burrowing and grazing (*Pecten* and *Amalda*). Previous studies have noted that probability of occurrence models often predict more accurately for taxa with a narrow ecological niche (Morán-Ordóñez *et al.*, 2017; Reiss *et al.*, 2011; Rullens *et al.*, 2021), but this analysis was unable to identify any such correlation within taxon level models. Rather, the models utilised in this study include species with similar functional traits but often differing across depth and sediment gradients. Other studies that utilised occurrence models as proxies for density found that good correlations are observed for some taxa (observations from fish and arthropods) but not for others (Jiménez-Valverde *et al.*, 2009; Young and Carr, 2015), which aligns well with our findings. Poorer regional spatial predictions were observed for taxa that have a more diffuse distribution (e.g., *Asychis*, *Glycera*, *Maldane*), highlighting that with limited data, the combined density model approach may be more suitable for taxa with colonial or patchy distribution. Other complex interactions between lifestyle traits (Rodil, Compton and Lastra, 2012), recovery from fishing or survey vessels (Thrush and Dayton, 2002), and environmental stress (Gladstone-Gallagher *et al.*, 2019) may also contribute to contrasts between predicted distribution and expected distribution patterns. However, neither influence from environmental stress nor ecological traits were accounted for in this study and our models assume all adult populations are in equilibrium (Evans *et al.*, 2016). The combined model approach can be used to create a spatially refined density model, reflecting a subset of highly abundant habitats, which is useful for marine conservation because a taxon's ecological niche is more spatially restricted than the predicted probability of occurrence extent, in addition to limitations imposed by sample data and methodology applied to predict these patterns (Johnston *et al.*, 2015).

The inclusion of abundance data helps identify key areas of high abundance, which is more helpful to inform management than habitat suitability (Guisan and Thuiller, 2005; Howard *et al.*, 2014). I identified that neither regional nor national scale SDMs provided more robust spatial predictions across all taxa. Therefore, by incorporating abundance data and comparing models across two spatial scales, I can use a combination of expert knowledge, known distribution and qualitative assessment to select the more ecologically representative model, or combinations of models (e.g., regional occurrence, national density), without having to rely on a single model type or model scale. This can be particularly useful when working in data-limited environments or creating SDMs for poorly sampled species (Dedman *et al.*, 2015). Density outputs retained only areas with higher predictive certainty that spatially aligned between both models. For certain taxa, high-density areas often reflected a subset of high-occurrence areas (e.g., *Amalda* – Figure A6), but for other taxa, the degree of intersection was much less (e.g., *Callyspongia* – Figure 2.3). Consequently, the density models produced a more conservative spatial output than occurrence alone, which was also found by Rullens *et al*., (2021). Although identifying spatially refined areas of high abundance is advantageous for regional management, there is also a risk that ecologically important areas may be discarded in the combined density model if they are not adequately identified or spatially conflict with the individual occurrence or abundance models. Therefore, it is important to consult the uncertainty maps when reviewing the density models to ensure key habitat areas are retained in the final output. This mechanism of retaining areas which align between models may be a contributing factor driving national density model performance higher; a greater spatial extent of higher prediction in the national occurrence models provided a wider distribution to be combined with the abundance model, thus retaining a wider and more ecologically representative prediction pattern.

Here, I show evidence that demonstrates the benefit to conservation managers of incorporating measures of both occurrence and density, as well as consideration of spatial scale into regional conservation and management approaches. Our research emphasises scale-dependent relationships driving benthic occurrence and density, which were shown to vary between taxa and model type and are often non-linear (Johnston *et al.*, 2015). When data permits, practitioners should strive to use robust regional data to make ecologically informative and well-differentiated models, and in the absence of well-distributed regional data, national models can achieve good density predictions regionally for many taxa. By assessing the influence of scale and utilising a combined analysis approach, practitioners can avoid dependence on a single analysis method, poorly differentiated occurrence models or structural assumptions providing conservation managers with options based on data availability. Additionally, the inclusion of abundance data can provide a more robust characterisation of spatial variation (Waldock *et al.*, 2021) and thus enhance distribution predictions compared to occurrence models alone (Howard *et al.*, 2014). This multi-scalar approach could be particularly useful for conservation initiatives from MPA design through hotspot analysis (Dedman *et al.*, 2015) or integration into conservation prioritization software such as Marxan or Zonation (Stamoulis and Delevaux, 2015). Our findings emphasise the challenge for practitioners when considering the utilisation of SDMs, which often lack the resolution required for regional-scale management. However, with an increasing reliance on SDMs in the marine environment, it is even more critical to produce robust models and develop adaptive approaches so that poor predictions are not utilised in the decision-making process.

3. Chapter 3
Modelling taxon-specific responses to multiple stressor scenarios in a shallow seafloor ecosystem

3.1. Introduction

The need to understand how multiple stressors impact marine species and habitats is critical, particularly as demands for marine resources and anthropogenic stress in the coastal environment continue to grow. Correlative modelling approaches in the form of Species Distribution Models (SDMs) are often used as a tool by decision-makers to better understand the spatial distribution of important species, but often SDMs are created without the inclusion of stressor effects. Species response relationships to varying magnitudes of stressor exposure have been measured by several small-scale empirical experiments (e.g., sediment loading, nutrient loading, disturbance events, bottom trawling), which provide insight into stressor effects and mechanisms of change (Thrush *et al*., 2004; Lohrer *et al*., 2006; Ellis *et al*., 2017; Gladstone-gallagher *et al*., 2021; Thrush *et al*., 2021; Kaiser *et al*., 2002). To implement better management practices that mitigate or abate stressor impacts, scientists need to be able to quantify changes to species assemblages that result from multiple stressors over broader spatial scales. However, scaling-up locally derived stressor relationships with species and habitats in a dynamic, multi-use environment, with many gradients of stress is complex and remains challenging. Two of the most pervasive and globally impactful stressors in shallow coastal ecosystems are commercial bottom trawling and sedimentation (Davies *et al.*, 2018; Sciberras *et al.*, 2018; Simeoni *et al.*, 2023; Wahlstrom *et al.*, 2022; Willsteed *et al.*, 2018). To support better management of these stressors, new approaches which spatially quantify the combined and accumulating impact of fishing and sedimentation stress are needed. As practitioners hover in the “analysis paralysis” between lack of suitable assessment approaches and inaction from inadequate management (Davies *et al.*, 2020), multiple stressor impacts continue to degrade the marine environment and diminish natural resources upon which humans rely (Foley *et al.*, 2017).

The lack of development of suitable assessment approaches is in part due to the complexity of stressor effects assessment and the lack of spatially explicit data to integrate spatial and temporal dynamics, in addition to quantifying both stressor-specific variables and taxon-specific variables within the analysis. Stressor characteristics for consideration include spatial scale (e.g., local, regional), temporal scale (e.g., six months vs. successive years), temporal variation (e.g., seasonality), overlaps in stressor footprints (co-occurrence), variability of stressor effect across a gradient (e.g., distance from pollutant), and stressor history (e.g., the legacy effects of how long a stressor persists within the environment). Taxon-specific characteristics include identifying the receptor type (e.g., single species, or a whole community), resilience (e.g., ability to recover from or resist perturbations), taxon-specific response to single stressors (e.g., affinity to mud, sensitivity to trawling), and any combinations thereof (Willsteed *et al.*, 2018). Data on seafloor mud content are often available over large geographic areas (e.g., local authority environmental monitoring or satellite data), and this information can be included with other environmental variables to develop species-environmental relationships (Austin, 2007; Bostock *et al.*, 2018; Thrush *et al.*, 2004; Halpern and Fujita, 2013; Hewitt *et al.*, 2014; Parravicini *et al.*, 2012; Stamoulis and Delevaux, 2015; Zurell *et al.*, 2021). Similarly, data on bottom trawling footprints and intensity are also typically available for marine ecosystems (Baird *et al*., 2015). Sciberras *et al.* (2018) undertook a meta-analysis of 122 experiments on the effects of bottom fishing and found that benthic invertebrate abundance was reduced by up to 26% from a single fishing gear pass. This review provides impacts separated across a diverse suite of invertebrate taxonomic and functional groups and quantifies impacts with respect to different fishing gears and different sediment types (Sciberras *et al*. 2018). By using spatial data collected on commercial trawling paths (often collated by regulating agencies), and cross-referencing data with predictions of species density, estimations can be made on the potential levels of impact on benthic invertebrate density based on trawl effort (Austin, 2007; Bostock *et al.*, 2018; Lundquist *et al.*, 2018; Pitcher *et al.*, 2016; Thrush *et al.*, 2004).

The individual effects of bottom fishing and sedimentation on benthic habitats have been widely researched (Reiss *et al* 2009; Hiddink *et al* 2006; Baird *et al*., 2015; Lundquist *et al* 2018; Sciberras *et al* 2018; Robertson *et al* 2016; Thrush *et al* 2004; Lohrer *et al* 2006). Shallow coastal ecosystems experience direct disturbance to the seafloor from fishing gear such as commercial bottom trawling or dredging which can reduce the abundance of macrofaunal communities, change functional community composition, cause habitat destruction and lead to homogenisation of the seascape (Thrush and Dayton, 2002; Hiddink *et al.*, 2006; Kaiser *et al.*, 2006; Lundquist *et al.*, 2018; Sciberras *et al.*, 2018). Sedimentation occurs from the deposition of eroded sediment, usually derived from terrestrial sources resulting from poor land management (Swales *et al*., 2002; Thrush *et al*., 2004). In large volumes, sedimentation can directly impact seafloor communities by smothering, and in lower volumes, it can indirectly cause impact by elevating turbidity and increasing the mud content of sediments when deposited onto sandy substrates (Pratt *et al.*, 2015; Thrush *et al.*, 2004). The effects of sedimentation are particularly damaging in shallow seafloor ecosystems, due to the re-suspension of mud from waves and currents, resulting in increased suspended sediment concentrations which can reduce the physiological condition of suspension-feeding animals (Ellis *et al.*, 2002; Newcombe, 2016). Furthermore, direct contact with fishing gear on the seafloor also results in the re-suspension of fine muddy sediments, increased water column turbidity, and modification to nutrient budgets (Linders *et al*., 2018; Martín *et al*., 2014). Many empirical studies have assessed the effects of sedimentation on estuarine and intertidal benthic communities, highlighting that even mud deposits < 1 cm thick can modify community composition and function, and that terrigenous mud deposits reduce the density of macrobenthic communities, which are slow to recover, if at all (Thrush *et al*., 2004; Hillman *et al*., 2002; Ellis *et al*., 2002; Douglas *et al*., 2023). Previous studies have also linked mud content with sedimentation stress to create response curves from regression-type models to apply them to stressor effects models (Ellis *et al.*, 2017; Norkko *et al.*, 2013; Robertson *et al.*, 2016). However, research that has assessed the effects of sedimentation in subtidal environments is more limited (although see Lohrer *et al*., 2006).

Empirical studies that quantify the combined effects of bottom fishing and sedimentation are limited and are identified as a critical research need (Crain *et al*., 2008; Worm *et al*., 2006). Cumulative threat mapping approaches have been used to create outputs which estimate the combined impact of stressors, by applying an index score (based on the stressor magnitude) over the stressor footprint (or proxies of the stressor) to identify areas with the greatest cumulative stress (e.g., Andersen *et al.*, 2015; Halpern *et al.,* 2008; Halpern *et al.,* 2009; Furlan *et al*., 2019; Korpinen *et al.*, 2021; Korpinen *et al.*, 2012). Cumulative threat mapping approaches are useful for identifying areas most impacted over a broader spatial scale (Halpern *et al*., 2008; Furlan *et al*., 2019) but they fail to differentiate between the effects of individual key stressors and the effects of dominant stressors that may be masked from the inclusion of several stressors of lesser impact. Other approaches aim to integrate the effects of multiple stressors within an environmental risk assessment framework, by applying a qualitative scoring to risk criteria of the stressor (e.g., frequency of impact, magnitude), based on sensitivity of the receptor (e.g., Gimpel *et al*., 201). Risk-based approaches help to communicate areas of high risk to management practitioners to evaluate management effectiveness (Stelzenmüller *et al.*, 2020), but they fail to indicate key ecological management elements (e.g., what levels should stressor magnitudes be limited to?) and few comprehensive spatial approaches can quantify the tolerance thresholds of receptors given specific risk management frameworks (Stelzenmüller *et al.*, 2020). Within the field of systematic conservation planning, a greater number of studies have considered both marine-based threats (e.g., fishing) and land-based threats in combination (e.g., land-to-sea modelling) such as groundwater and nutrient discharge in combination with fishing pressure on coral habitat (Delevaux *et al*., 2018), and land-based pollution and river plumes on marine coastal water quality (Alvarez Romero *et al*., 2015). However, typically conservation planning aims to achieve the most cost-efficient solution for the best conservation outcome (Moilanen *et al*. 2009, Ball *et al*. 2009), focussing outside of areas with high stressor impacts, thus making it challenging to address knowledge gaps that pertain to multiple stressor effects. Therefore, the exploration of modelling approaches which spatially integrate complex stressor-species relationships from key stressors, to quantify individual and combined effects on species in highly stressed coastal habitats are needed.

The limitations and capabilities of conventional numerical modelling approaches have been explored by others (see Austin, 2007; Degraer *et al.*, 2008; Elith and Leathwick, 2009; Reiss *et al.*, 2011), but applying these approaches to model the multiple and accumulating impact of stressors remains challenging (Foley *et al.*, 2017; Gissi *et al.*, 2017; Schafer and Piggott, 2018). Two key modelling approaches dominate marine multiple stressor effects analysis– correlative models (including regression type models), and mechanistic models. Correlative model approaches have been used to quantify the relationships between stressors and receptors (Ellis *et al.*, 2017; Kotta *et al.*, 2016; Ceccarelli *et al.*, 2020), to examine responses to multiple stressors as indicators of ecosystem health (Berthelsen *et al.*, 2019; Magni, 2003) and to assess stressor effects on uncertainty and ecological risk (Rullens *et al.*, 2022). SDMs (also a correlative model) are often used as a complementary approach to multiple stressor analysis and risk assessments (Ellis *et al.*, 2017; Stelzenmüller *et al.*, 2020) but as SDM predictions do not incorporate stressor effects; they likely provide unrealistic predictions based on modern stressor regimes. However, Guisan *et al*., (2013) highlighted that better integration of SDMs can be achieved when decision needs lead to the building of the SDMs, (instead of them being considered retroactive), which provides an opportunity for their usefulness to inform decision-making to be improved by combining the visual communication power of SDMs with the computational power of more complex modelling approaches. Mechanistic models are based on the fundamental laws of natural sciences and have been used to apply empirically established relationships or processes over assessment areas (Rastetter *et al.*, 2003; Brush and Nixon, 2017), but have also been applied to a range of different modelling techniques such as mechanistic niche models (Kearney and Porter, 2009). Gallien *et al*., (2010) explored the benefits of a hybrid modelling approach (mechanistic and correlative) and acknowledged that they do not aim to predict perfectly but enable practitioners to overcome specific limitations of traditional models. To address many of the complex analysis challenges related to quantifying stressor impacts across coastal landscapes, practitioners are further exploring the utility of hybrid modelling approaches to integrate correlative SDM predictions with empirically derived stressor relationships (e.g., Gallien *et al*., (2010); Kearney *et al*., 2010; Stephenson *et al.*, 2023).

Here, I develop a spatially explicit correlative stressor model including empirically derived stressor response relationships for fishing and sedimentation stress as single stressors and in combination. Scenarios were developed for three coastal seafloor invertebrates found commonly in temperate soft-sediment coastal ecosystems, each with different functional stressor responses and recovery times. Soft-sediment macroinvertebrates are considered sensitive indicators of ecosystem health and are regularly used to assess the effects of natural and anthropogenic disturbances (Borja, Franco and Pérez, 2000; Pearson and Rosenberg, 1978; Rodil, Compton and Lastra, 2012; Weisberg *et al.*, 1997). I combine previously developed taxa density SDMs (Watson *et al.*, 2022), with a correlative model to integrate taxon-specific stressor responses. I model environmental stressors as drivers of change in taxa density and distribution and quantify the change in mean density from accumulating impacts over time. I also explore the effects of varying stressor magnitudes (trawl effort and sedimentation rate) and assess differences between recovery and no-recovery scenarios. My objective is to develop a spatially explicit approach that can quantitatively integrate the assessment of multiple stressors, into a modelling platform (SDM) that management practitioners are already familiar with, and many organisations already collect data for, to help simplify complexity and address existing knowledge gaps to help inform coastal management decisions. Through the application of the correlative stressor model approach, I hope to answer, how do bottom fishing and sedimentation stressors modify the spatial distribution and density of benthic invertebrates over time?

3.2. Methods

3.2.1. Study area description

The study area comprises 32,000 km^2 of coastal environment between the North and South Islands of Aotearoa - New Zealand, which is representative of a variety of coastal habitats from enclosed bays, exposed coastlines, and high energy straits (Figure 3.1). The spatial boundary of the study area was selected based on the approximate distance of turbidity plumes from satellite remote sensing (Pinkerton, 2018) to maximise the region of overlapping fishing and sediment stressors. In addition, the availability of data on environmental stressors as well as greater confidence, and lower uncertainty, of modelled species distributions was also considered (Watson *et al.*, 2022). The study area has a long history of commercial fishing impacts in addition to high levels of fine, muddy surface sediment inputs from inadequate land management to prevent sediment erosion (Handley, 2006). Trawling is prohibited in some areas, such as aquaculture sites, marine reserves, and the Separation Point trawl exclusion zone (Figure 3.1, C dark blue zones).

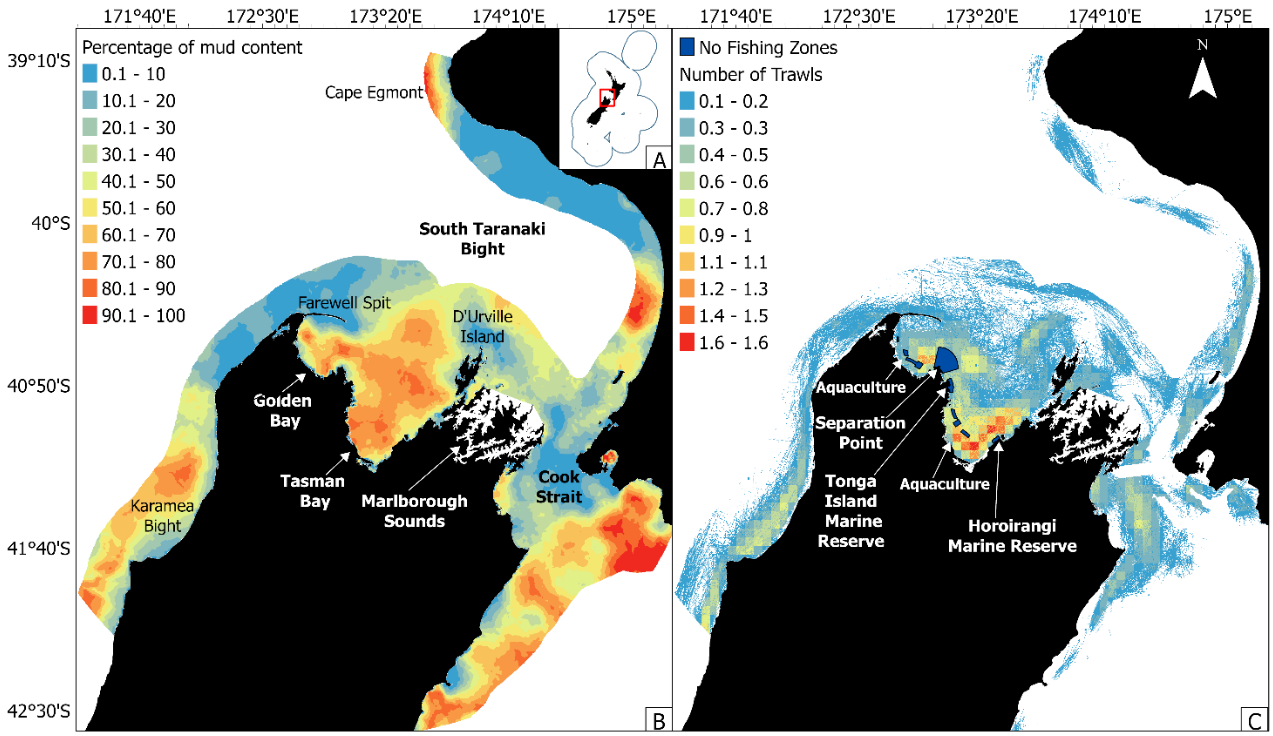


Figure 3.1: Map of the study region, extent of stressor data and feature names used throughout the text. A. Inset map indicating the location of the study area (red line), and the extent of New Zealand's Exclusive Economic Zone (grey line). B. Percentage of mud content (Bostock et al., 2018) recorded in seafloor sediment. C. Mean number of inshore trawls per 250 m x 250 m grid cell for years 2009-2012 (Ministry of Primary Industries), from fishing effort raster with a native data resolution of 5 km x 5 km, with trawling prohibited zones and marine reserves shown as dark blue areas.

Density predictions were generated at 250 m x 250 m grid resolution using species distribution models (SDMs) following methods described in Watson *et al.* (2022) - Chapter 2. Briefly, two SDM models were created for each taxa using Boosted Regression Trees (BRT) – a probability of occurrence model (using a Bernoulli error distribution) and an abundance model (count per sample unit [using a Gaussian error distribution]). To create the final density SDM (count per km^2), individual predictions of both occurrence and abundance were multiplied together using the delta log-normal method or 'hurdle' model (Dedman *et al.*, 2015). All BRT analyses were undertaken in R (R Core Team, 2021) using the "dismo" package (Hijmans *et al.*, 2022). Modelled taxa varied in their functional role, including habitat-forming epifauna (genus *Callyspongia*, phylum Porifera), mobile surface feeders (genus *Amalda*, phylum Mollusca), and bioturbators/burrowers (genus *Echinocardium*, phylum Echinodermata), which allowed for stressor responses to be explored across three taxa with different functional responses to stressor impact (Table 3.1). Models were available at the genus level, with a variable number of species represented in each genera model (*Amalda,* n = 6; *Callyspongia,* n = 13; *Echinocardium,* n = 3, see Table 3.1, Watson *et al*., 2022, Chapter 2). While multiple individual species are represented in the point records used to derive the SDMs, each of the species typically has similar functional traits to allow stressor-response curves to be representative of all species in the genera. Data on bottom fishing effort from 2009-2012 were chosen to represent a typical spatial pattern of fishing effort and intensity in the Tasman and Golden Bays region. Data were based on the number of trawls per 5 km x 5 km grid cells for inshore fishing, provided by Fisheries New Zealand. Thus, my analysis focussed on this temporal period assuming that four years was sufficient to be representative of the typical inter-annual variability in fishing effort in the region.

For this analysis, we discuss changes in the mean density that result from stressor impacts, relative to the starting density predictions, prior to stressor modification which we refer to as the 'baseline' conditions moving forward. The temporal range of species records and environmental variables used to create the density predictions are detailed in Watson *et al*., (2022).

Historically, there have been high levels of fishing pressure within the study area (bottom fishing and dredging) subjecting areas of the seascape to a variety of disturbances from benthic fishing gears (Handley, 2006). The commercial harvest of scallops, oysters, and mussels dates to the mid-1900s in Tasman and Golden Bay, which (Drummond 1994, Bradford-Grieve *et al*., 1994, Handley, 2006) have subsequently collapsed, with the final closure of the scallop fishery (SCA7) occurring in 2017 (Handley and Brown, 2013). Data used in this analysis represents finfish trawling only and omits oyster and scallop dredging which would have been key contributors to seabed disturbance during 2009-2012. But it also represents a temporal period where finfish trawling and shellfish dredging would have occurred together, before fisheries closures.

*Table 3.1: : Description of modelled taxa and stressor parameters: taxonomy, functional role, average annual count of trawls which occur (per 250 m x 250 m grid cell) for all taxa sample records present in each cell within the entire study area (as per Ministry of Primary Industries (MPI) in New Zealand trawling Data from 2009 – 2012, provided by Fisheries New Zealand), percent change in density after a single trawl (Sciberras et al., 2018), time to recover (years) after trawling (Sciberras et al., 2018), and density-mud stressor relationship derived from SDM model fit of probability of occurrence * abundance model, indicating correlation direction.*

Common name (n = point records within the study area)	**Phylum - Genus**	**Functional role** (Lundquist *et al.,* 2018)	**Average annual trawl count per cell for taxa locations** (MPI 2009-2012)	**Change in density (%) per trawl** (Sciberras *et al.*, 2018)	**Recovery time (years)** (Sciberras *et al.*, 2018)	**Mud Relationship (R^2)**
Olive shell snail (n = 58)	Mollusca - *Amalda*	Mobile surface grazer/predator	Min: 0.1 Mean: 0.7 Max: 1.5	+ 4	<1	+ 0.93
Colonial tube sponge (n = 88)	Porifera - *Callyspongia*	Habitat-structure forming epifauna	Min: 0.1 Mean: 0.3 Max: 1.2	-10	> 3	- 0.87
Heart urchin (n = 701)	Echinodermata - *Echinocardium*	Bioturbator/burrower/substrate destabiliser	Min: 0.1 Mean: 0.9 Max: 1.6	-7	< 1	+ 0.35

3.2.2. Stressor response parametrisation

Detailed analysis steps of the correlative stressor model process are outlined in the combined stressor model section below (3.2.2.3). An overview of the methodology for the sediment stressor (3.2.2.1) and the fishing stressor (3.2.2.2) are presented first. Within the context of this analysis, the model is defined as a multiple-stressor correlative model that focuses on the change in taxa density and accounts for the accumulating effects of stressors over time (e.g., accumulating sediment, and repeated impact and recovery from fishing) with a generalised recovery. This approach does not include model terms which measure stressor interactions, nor does it account for population dynamics or environmental feedback. The methodology applied for each stressor individually is the same as for the combined stressor analysis; both steps are integrated sequentially into the combined stressor analysis. A total of 12 stressor scenarios were modelled: 5 single stressor scenarios – fishing (with and without recovery), increasing sedimentation (at 1%, 2%, and 3% mud); and 6 multi-stressor scenarios – fishing & sedimentation combined at each level of mud (1%, 2%, and 3%), both with and without recovery (Figure 3.2, Table 3.2)

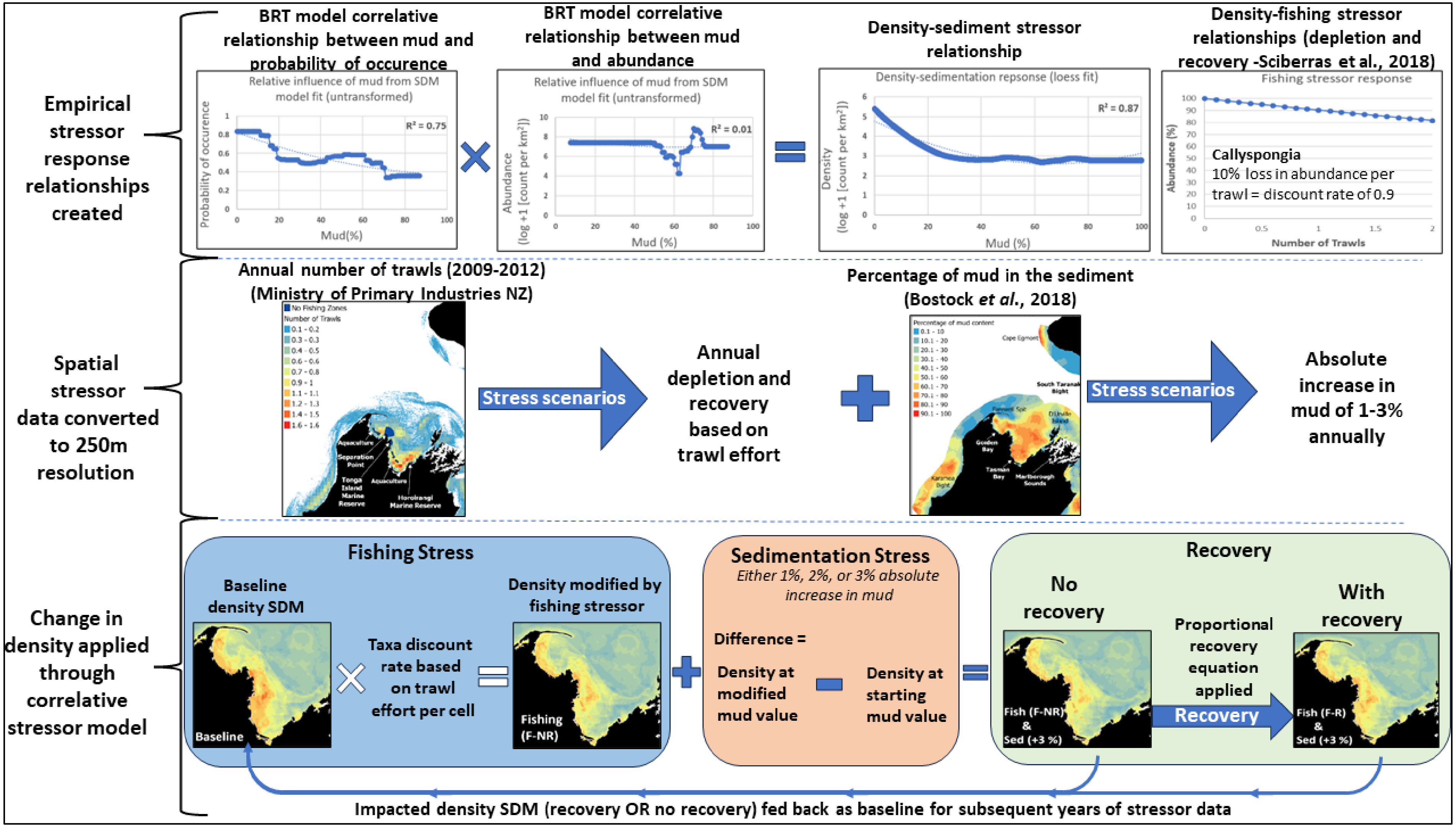


Figure 3.2: Analysis workflow demonstrating stressor model combinations, recovery scenarios and stressor response curve relationships modelled over four years (2009-2012) of consecutive stress. 12 stressor scenarios were modelled: 5 single stressor scenarios – fishing (with and without recovery), sedimentation (at 1%,2%, and 3% mud); and 6 multi-stressor scenarios – Fishing & Sedimentation combined at each level of mud (1%, 2%, and 3%), both with and without recovery. Stressor response curve relationship data was used to modify density values after each year of impact.

3.2.2.1. Single Sediment Stressor

Mud content for the region were developed from over 30,000 sediment samples (collected over 60 years prior to 2008) compiled in dbseabed (Jenkins *et al*. 2008), which were then imported into ArcGIS and interpolated using Inverse Distance Weighting at a 1 km grid (Bostock *et al*. 2018). The percentage of mud content spatial later at 1 km grid was transformed in ArcGIS to 250 m grid by cubic interpolation. The temporal sampling period used to generate the mud spatial layer predates the temporal period of the fishing stressor (2009-2012) and reflects a long-term average of the substrate characteristics (Bostock *et al*. 2018). In the absence of long-term sediment monitoring within the study area (Newcombe, 2016) I assume that the mud data is spatially representative of broad coastal patterns of accretion and deposition that occur from long-term coastal processes within the bay and represents the best available data. I acknowledge that there have likely been changes in the sediment rates and sediment mud content since they were sampled, but general trends of potential sedimentation effects are still relevant even though they are not temporally aligned across both stressors.

Sedimentation stress was simulated by calculating an annual absolute increase in sediment mud content (of 1%, 2%, and 3%), for each cell value, over the study area. This provided a homogenous increase on top of the existing, spatially explicit mud levels from the mud spatial data (Bostock *et al*., 2018). Although sediment deposition does not occur uniformly, this analysis aimed to demonstrate how small annual increases in sediment mud content impact taxa density and distribution over time. Therefore, I acknowledge that the spatial changes in taxa density and distribution predicted via this approach will differ from in situ changes, but the results are still representative of possible changes from small levels of regular sediment loading. An equal increase in sediment mud content will provide a variable spatial impact on the relative density of taxa, based on both the taxa-stressor response curve and the existing levels of sedimentary mud. For example, an increase in sedimentary mud of 1% in an area with high density and low mud content (i.e., sandy /gravelly substrate) will provide a greater relative impact compared to an area with low density and high mud content.

Here, relationships between probability of occurrence and abundance of taxa in response to mud were derived from Boosted Regression Tree (BRT) models (Appendix A2 2). These mud relationships from individual models were multiplied together, to create a density-sedimentation response curve (Figure 3.3). Creating a taxa-specific density-sedimentation response curve ensured that both the stressor spatial layers and the density SDMs were in the same units for direct value manipulation within the correlative model. A LOESS (locally estimated scatterplot smoothing) smoothing function was applied to the response curves to extract a smoother trend line and remove extreme values (Figure 3.3).

Spatially explicit estimates of taxa density were modified (detailed in section 3.2.2.3) based on the density-sedimentation response curves and the spatial distribution of the regional mud data. Three sediment stress scenarios were investigated representing an increase in absolute terms of 1%, 2%, and 3% mud per year, to simulate the effect of small annual incremental increases in coastal mud from regular sediment loading. The model did not consider larger sediment impacts from extreme weather events. Each year, based on the annual density-sedimentation rate (+ 1%, 2%, and 3%), the taxa density SDM was modified to fit a new density layer. This annual change in density represented an accumulation of sediment stress of 4%, 8% and 12% respectively, over the 4 years. The sedimentation stressor impacts were applied additively.

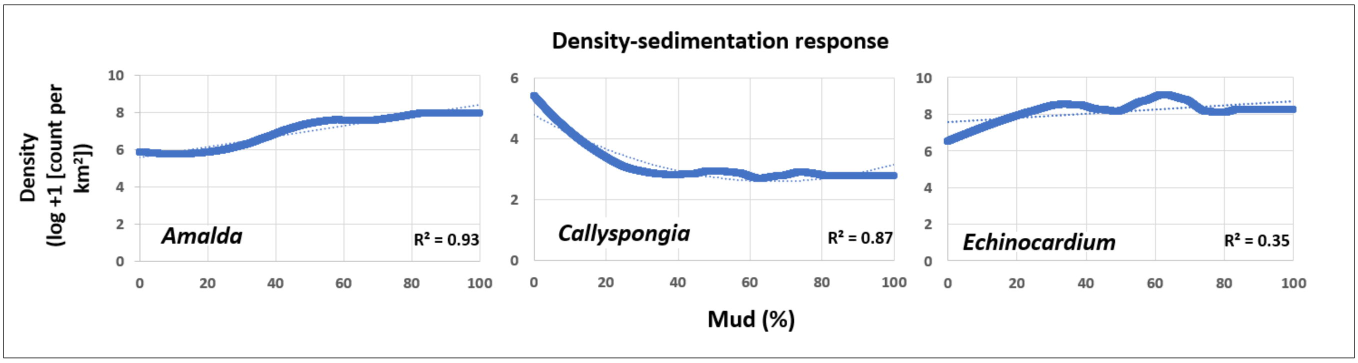


Figure 3.3: Density-sedimentation stressor response curve developed from combining the SDM model fit with mud correlate from probability of occurrence model and abundance models. Response Relationships have a LOESS (locally estimated scatterplot smoothing) smoothing function applied to extract a smoother trend line and remove extreme value. R-squared value represents the goodness of fit for the density-mud relationship for a linear trendline.

3.2.2.2. Single Fishing Stressor

Benthic faunal responses to anthropogenically-induced stress from bottom trawling were obtained from a global meta-analysis which recorded changes in taxa abundance and recovery after bottom trawling (Sciberras *et al.*, 2018). Historically, there have been high levels of fishing pressure within the study area, subjecting areas of the seascape to a variety of benthic fishing gears, including finfish trawling and dredging for shellfish (scallops and oysters; Handley, 2006). Here, I simplify the focus to inshore bottom trawling data and estimate the mean change in abundance based on spatial variability in the trawl footprint. I utilised the mean abundance change from the 'initial response estimates' which are presented on a 'per pass' basis, which were extracted from a global meta-analysis of impacts of bottom trawling on benthic invertebrates (see Tables S17.8 & S17.10 in Sciberras *et al.,* 2018). Otter trawls or bottom trawls using otter boards were determined to be the most prevalent fishing gear used in our study area, by cross-referencing vessel size and target species data (Baird, Hewitt and Wood, 2015) with specific vessel gear information (Przeslawski *et al.*, 2018). We, therefore, used estimates of abundance change for otter trawls and used estimates for phylum Porifera, order Gastropoda and phylum Echinodermata.

Spatial data detailing the annual inshore trawling paths and frequency (Table 3.1) were available for Tasman and Golden Bay and the surrounding coastal areas (Baird, Hewitt and Wood, 2015), provided by the Ministry of Primary Industries (MPI) in New Zealand. Data from 2009 – 2012 were used, assuming they are representative of the typical inter-annual variability in fishing efforts in the region. Trawl paths and frequency varied between years, and each annual dataset was treated as a unique layer. For each year of inshore fishing data, the raster was transformed from its native resolution of 5 km x 5 km to 250 m x 250 m by cubic interpolation, ensuring the number of trawls was scaled to the smaller cell area in ArcGIS Pro 2.9.3. Fishing stressor response curves were created as a linear relationship between taxa density and fishing effort and assumed a starting value of 100% abundance where the corresponding fishing trawl value was 0.

Recognising that recovery between fishing events is likely to influence the quantification of multiple stressor impacts and their effects over time, two fishing recovery approaches were modelled. For the first approach, fishing with no recovery (hereafter F-NR) assumes impacts accumulate over the four-year model period, and taxa do not recover between stressor events. The second approach incorporated a generalised recovery (hereafter F-R) in the taxon-specific response and assumed that the environment in which fishing impact occurs can recover. Trawling recovery time was also based on data from Sciberras *et al.,* (2018) and ranged from less than one year to greater than three years for the modelled taxa (Table 3.1), conditional on sediment type, gear type, penetration depth and disturbance history. In the F-R approach, recovery was quantified as a proportion of fishing effort related to density for the current year, divided by the subsequent year. Calculation of a proportional trawl effort from one year to the next allowed for the identification of cells that would either have less or no trawling in a cell in the following year and allowed the identification of areas with recovery potential. For taxa that would likely recover within 12 months (*Amalda* and *Echinocardium*), the annual proportion was calculated as the number of trawls per cell in a year / the number of trawls per cell in the following year. For slow-recovering taxa (*Callyspongia*) the proportion was calculated in the same way, then divided by 3, to represent recovery occurring at 1/3rd of the annual rate to match the greater than 3-year estimated recovery time (Table 3.1). To account for the broad range of possible taxa responses, and to elucidate possible non-linear effects of stressor responses that could occur or shift under different stressor thresholds, I apply a best-case (F-R) and worst-case (F-NR) recovery scenario over an annual trawling time frame.

3.2.2.3. Combined stressor models

Firstly, the fishing and sedimentation stressor effects were analysed independently via the correlative model as single stressor impacts over four-years (sections 3.2.2.1, 3.2.2.2). Secondly, individual models were combined to develop a multiple-stressor model, to modify baseline density SDM values based on the taxon-specific stressor response curves for each independent stressor. Stressors were applied in the following operational order: fishing stress, sedimentation stress, and then recovery from fishing. This order of model operations seemed most ecologically likely given that sedimentation impacts are often experienced after bottom fishing (due to seabed disturbance and sediment re-suspension), followed by recovery. The following steps were applied within the correlative model to create stressor-impacted SDMs (Figure 3.2):

Step 1. Density modified for Fishing Stressor – The density change rate per trawl (Table 3.1) was used to create an annualised linear discount rate, to modify the density values of the SDM (density multiplied by discount rate), based on the number of annual trawls in each cell. The magnitude of trawl effort and location of trawl tracks varied over each year of data, providing a spatially heterogeneous change in density over the study area after 4 years. After the baseline density values had been modified by the year 1 fishing effort, the results were predicted back to the SDM to fit a new density layer. For example, *Callyspongia*, had a change value of 0.86 for 1.5 trawls in year 1 based on a -10% density reduction rate per trawl, assuming a starting density of 100% (year 1 Fishing stressor impacted density = baseline density x 0.86).

Step 2. Density modified by Sediment Stressor – The new fitted density layer which incorporated the year 1 fishing stress was used as the starting density to apply the sedimentation stress**.** The density-sedimentation response curves were used to calculate a proportional change in taxa density, based on an absolute increase in the mud values in each cell. The new density layer and the spatial mud layer were combined into a raster stack using the "raster" package in R (Hijmans and van Etten, 2012), to allow the values in each layer to be directly compared and sorted in ascending order, so that each range of predicted density for the corresponding percentage of mud could be examined. Firstly, the starting density value was recorded for the corresponding baseline level of mud value in each cell, which we refer to as the reference value. Secondly, the density value was recorded for the corresponding mud value that was 1% greater than the baseline value, which we refer to as the scenario value. The proportional change in density from the 1% change in mud was calculated by subtracting the reference value, from the scenario value (providing a small negative number). For example, starting at 60% mud, the corresponding density for *Callyspongia* was 2.34 (log +1); with an absolute increase in mud of 1% resulting in 61% mud, the corresponding density value was 2.27 (log +1), providing a proportional difference of - 0.07 (log +1), in density for a 1% increase in mud. The proportional difference value was then added back to the density layer, to fit a new density layer.

Step 3. Generalised recovery from fishing assessed – Recovery was calculated as a proportion of fishing effort for each year of the scenarios, using the recorded recovery times (Table 3.1). As I did not have data defining the trawl effort in 2008, recovery was not applied for 2009 fishing stress but was for 2010, 2011 and 2012. Firstly, the recovery potential was calculated as: Recovery potential = current year fishing effort / subsequent year fishing effort (highlighting where fishing effort was lower or greater in the subsequent year, compared to the first year). Secondly, the difference in density between the current year impact values (T1), and the previous impact year density values (T0) were calculated (density difference = T1 – T0). The two previously calculated values (recovery potential and density difference) were used to calculate how much density could recover by: density recovery = density difference – (density difference * recovery potential). Lastly, the density recovery value was added back to the current year's density layer (now fishing and sediment impacted), to fit a new density layer.

Step 4. New Starting Density – At each stage of the model, the starting density values were modified by the corresponding stressor, and a new density layer was fitted. For year 1 impact, the baseline density SDM values were modified by each stressor impact (fishing impact, then sediment impact, then recovery), to provide a stressor-impacted density layer. The stressor-impacted density layer from the current year was then fed back into the model as the new starting density values for the subsequent year of impact and so on. Steps 1 through 4 were repeated for each year of distinct trawl effort data, at each sedimentation rate, over 4 years (Figure 3.2).

The supporting R code for this analysis can be accessed via Github https://github.com/S-L-Watson/multi_stressor_model.

3.2.3. Multiple stressor assessment

Stressor scenario outputs from the correlative model for all taxa were converted into spatial maps and explored visually and statistically to summarise change with increased fishing and sedimentation stress. For the summary statistics, a reverse log was applied to the logged density values to calculate both mean density and the associated percentage change in mean density by applying the formula $e^{(x)-1}$. Mean density per cell was calculated as the sum of density values from each grid cell, divided by the total number of cells in the model.

Taxa densities were mapped using ArcGIS Pro (version 2.9.3). Changes to density distribution patterns were explored by subtracting the stressor scenario density maps from the baseline density SDMs. Changes in the density distributions were explored at two levels of analysis resolution. Broad patterns were examined with violin plots, and detailed patterns were examined with histogram plots of density values that were partitioned into frequency counts of distribution values for each corresponding density interval (density bin size of 1). For each frequency interval, the difference in density from the baseline was calculated as a percent change, by applying the following equation:

$$Percent\ Change = \frac{Scenario\ Frequency - Baseline\ Frequency}{Baseline\ Frequency} * 100$$

Due to the magnitude of difference in the percent changes between density intervals and across stressor scenarios, I converted values to a pseudo-log scale (Candocia, 2020) using the ggplot2 (version 3.4.0) package in R, which used the following transformation:

$$x \ \geq \mathrm{sign}(x) * \ \log(1 + abs(x))$$

3.3. Results

All spatial analyses were performed at a single scale, over the extent of the study area (Figure 3.1). For spatial outputs (Figures 3.4-3.6), I focused the maps on a core area with the highest predicted density in the coastal area around Tasman and Golden Bay, which corresponded to where the greatest stressor effects were observed, and therefore changes in taxon distribution and density were most clearly observed. These figures represent an exact visual subset of the full study area. I have focussed on this core area as multiple maps are presented within the results figure grid, and I aimed to retain a high resolution of detail at this smaller scale whilst presenting all pertinent information.

3.3.1. Sedimentation

Callyspongia was the most sensitive taxa modelled, exhibiting a negative density-sedimentation relationship (R^2 = -0.87) with mud. Density was high with low levels of mud, a declined between 0-40% mud, which levelled off beyond ~50% mud content (Figure 3.3, *Callyspongia*). The mean density for *Callyspongia* was predicted to decrease between 3.4-9.5% over four years under sedimentation stress scenarios (with an absolute increase of 1-3% mud annually) over the entire study area (Table 3.2; see Section 3.3.3). Spatial changes in density and distribution patterns were minor, with small observable density increases offshore, and small density decreases to the east of Tasman Bay (Figure 3.4A-C). The spatial difference map (Figure 3.4D) highlighted bands of density change relative to the baseline density along sediment gradients.

Echinocardium had a slightly positive density-sedimentation response ($R^2 = +0.35$). At low levels of mud content, the response was positive, which levelled off with a high mud content of ~60% (Figure 3.3C, *Echinocardium*). The density-sedimentation relationship showed both positive and negative changes in density depending on the initial percentage of mud. Due to the mixed sedimentation effects across the study area, the mean percentage of density decline (1.1-1.7%) was small (Table 3.2). Spatial changes in density were observed to increase mainly in offshore habitat areas, and a mixture of decreased and increased density was also visible in inner Tasman and Golden Bay (Figure 3.4C). The spatial difference map highlighted bands of density change along sediment gradients similar to those observed for *Callyspongia* (Figure 3.4H).

Amalda was the most tolerant taxa modelled and exhibited a positive density-sedimentation relationship (R^2 +0.93). At low mud content, density was high, which increased further between 15-80% mud, and then plateaued at high mud content (Figure 3.3, *Amalda*). Density was predicted to increase over most of the existing moderate to high-density areas (Figure 3.4J-K), which corresponded to habitat areas with a sediment mud content between 50-70%. Mean density over the study area increased by 10.6 - 34.2% with increasing sedimentation scenarios over the 4-year impact period, indicating that sediment mud content is a key driver for sediment-tolerant taxa distribution. The spatial difference maps highlighted increased density values along sediment gradients which likely follow seabed terrain contours, ranging from the shallow coastal to deeper offshore waters (Figure 3.4L).

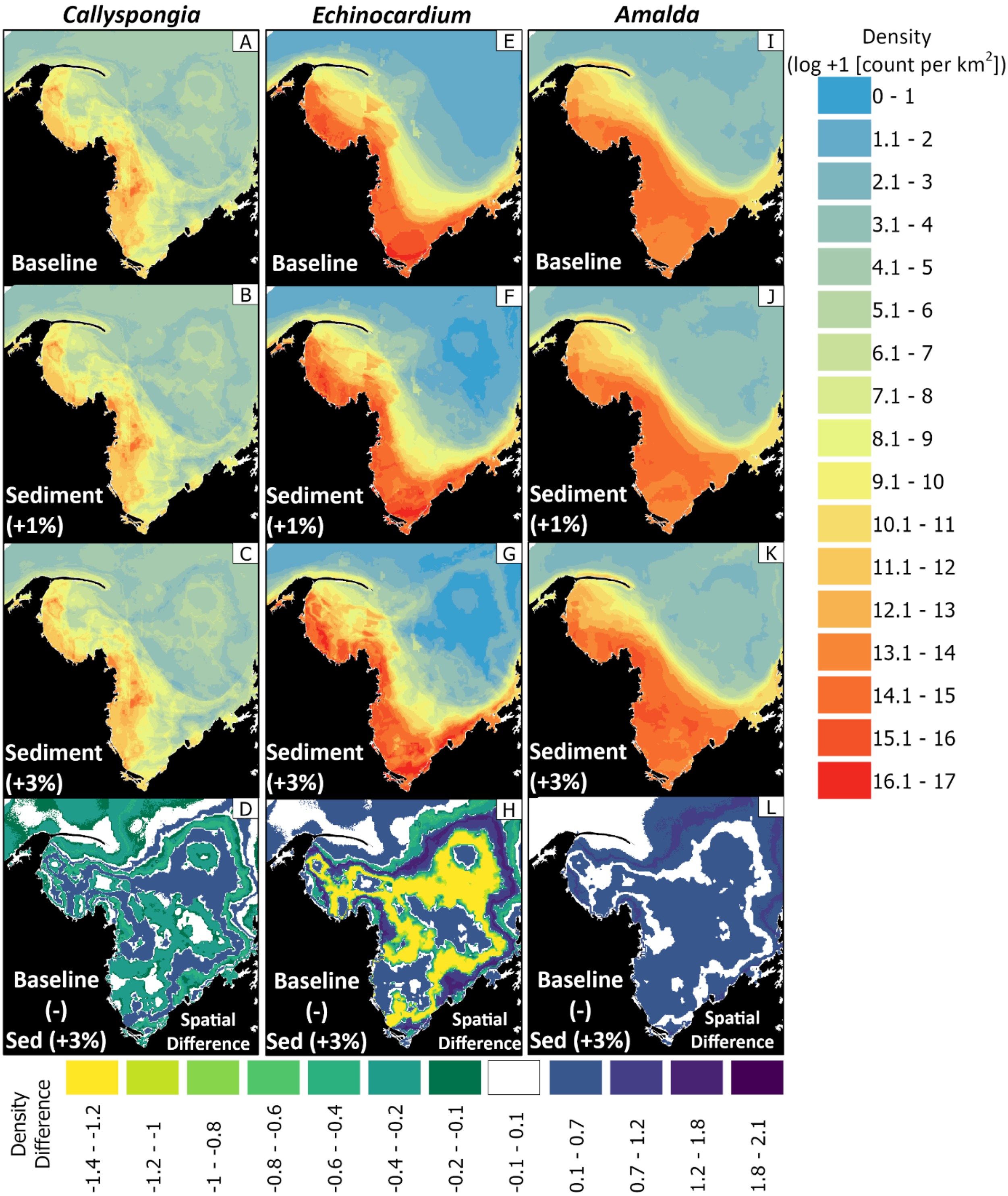


Figure 3.4: Spatial maps from single stressor correlative models detailing the change in density (log +1 [count per km^2]) and distribution from the baseline from sedimentation stress provided by an absolute increase in mud of 3% per year, over four years of cumulative stress (plots A-K). Spatial difference maps (density (log +1 [count per km^2])) highlight the difference in the density value by subtracting the baseline density SDM without stress from the density SDM with stress (Stressor impacted SDM values – baseline SDM values; plots D, H, L). All values in the spatial difference maps that are negative indicate that the baseline density values were greater than the stressor impacted values for the same location (i.e., this is how much the density has decreased after stressor impact). All positive values indicate that the stressor impacted values were greater than the baseline value in the same location. All plots contain density values which are count per km^2 with log +1 transformation.

3.3.2. Fishing

Callyspongia had a predicted decline in mean density of 14.1 % after four years of bottom trawling impacts (Table 3.2), modelled with a -10 % density change per trawl (Table 3.1). Due to the slow recovery period of 3 years for this taxa, there were no predicted differences in mean density or visible spatial differences between recovery scenarios (Figure 3.5B, C). Broad changes in density were observed throughout Tasman and Golden Bay from fishing impact, but most evident in previously mid to high-density habitats in shallower coastal areas (Figure 3.5B). The greatest density declines were predicted in inner Tasman Bay and to the west of Separation Point (Figure 3.5D) which spatially correlated with high fishing effort cells which received 1.2-1.5 trawls annually per 250 m cell (Figure 3.1).

Echinocardium had a predicted decline in mean density of 16% from bottom trawling (Table 3.2), resulting from a -7% density change per trawl (Table 3.1). There was only a 0.1 % difference in density change between scenarios with and without recovery (Table 3.2). Although *Echinocardium* had a shorter recovery time of just 1 year, results indicate that in habitats where the greatest density reduction occurred, mean fishing impact did not decrease year on year, which prevented density from recovering back to baseline levels (i.e., recovery was proportional to fishing effort in each cell). The greatest changes in density were also observed to the west of Separation Point and in inner Tasman Bay (Figure 3.5H), for cells that received 1.2-1.6 trawls annually. Although the fishing-stressor relationship for *Echinocardium* recorded a lesser impact (-7 %) compared to *Callyspongia* (-10%), high trawling effort occurred in areas with the highest predicted density for this taxon (Figure 3.5F), in the shallow coastal habitats, resulting in a greater mean density decline.

As a predatory scavenger, *Amalda* had a recorded positive density change of +4% per trawl (Table 3.1), which resulted in a mean density increase of 10.3% over four years. Recovery for this taxa was modelled as density lowering back to baseline density predictions, as stressor impacts were positive. When recovery was included in scenarios, taxa density still showed an increase above baseline density predictions of 2.5%, which is much lower than scenarios that did not incorporate recovery, which remained 10.3 % higher. The greatest changes in density were observed over a similar stressor footprint as *Callyspongia* and *Echinocardium*, but also to the east of Tasman Bay. Model results indicate that *Amalda* was able to thrive in highly disturbed environments, benefiting as a scavenger but also due to its small size and the robustness of its shell making it more resilient to fishing impact.

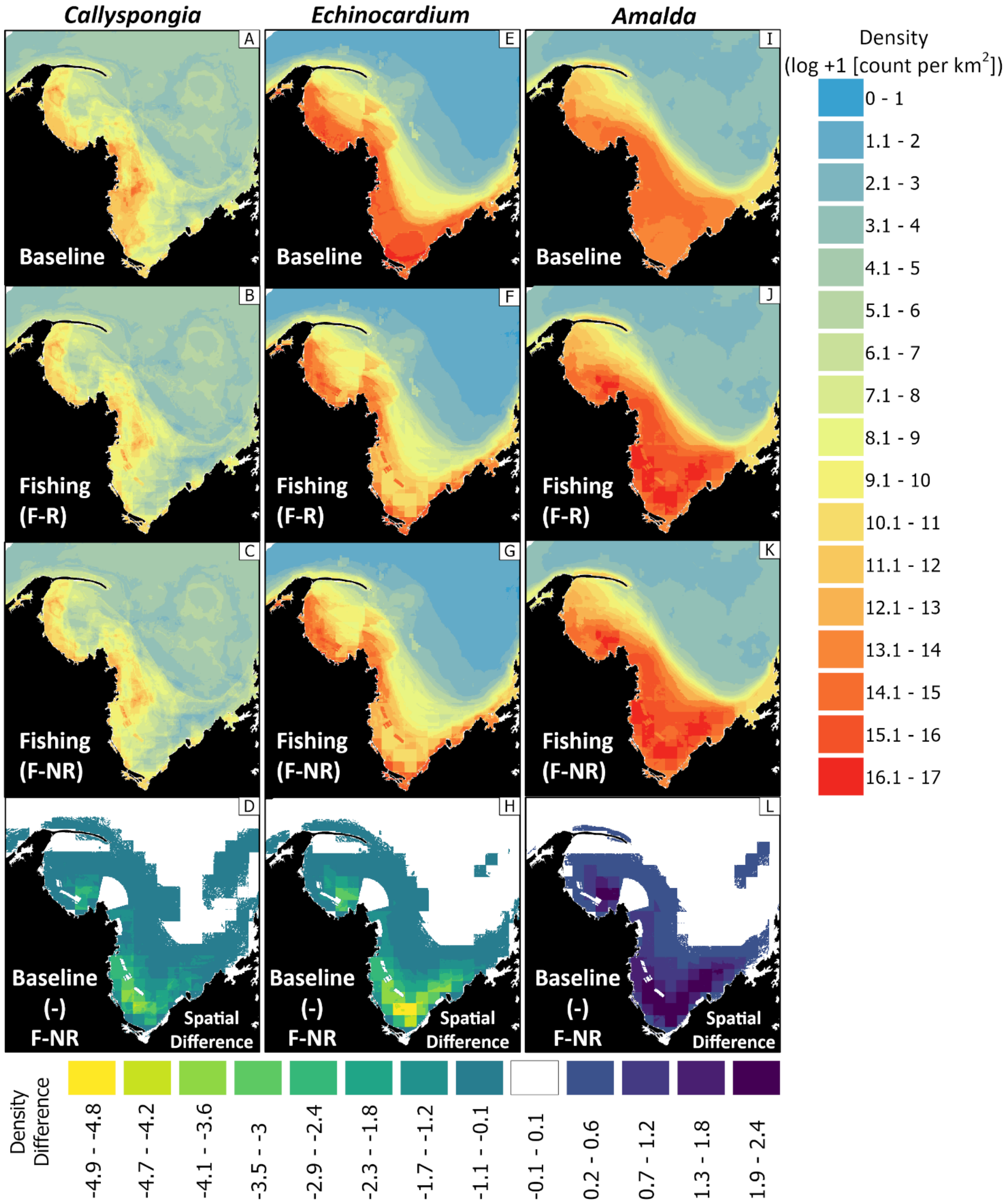


Figure 3.5: Spatial maps from single stressor correlative models detailing the change in density (log +1 [count per km^2]) and distribution from the baseline from fishing stress after for years of cumulative impact (plots A-K). Spatial difference maps (density (log +1 [count per km^2])) highlight the difference in the density value by subtracting the baseline density SDM without stress from the density SDM with stress (Stressor impacted SDM values – baseline SDM values; plots D, H, L). All values in the spatial difference maps that are negative indicate that the baseline density values were greater than the stressor impacted values for the same location (i.e., this is how much the density has decreased by post stress). All positive values indicate that the stressor impacted values were greater than the baseline value in the same location. All plots contain density values which are count per km^2 with log +1 transformation.

3.3.3. Multiple stressor effects

Callyspongia had a predicted decline in mean density (-11.9% to -16.1%) across F-R and sediment combined stressor scenarios (Table 3.2). For F-R scenarios with 1% and 2% annual increases in mud content, the change in mean density was less than fishing alone, indicating that sediment had a slightly positive effect in some areas, acting to reduce the mean impact of the fishing stressor. However, the observed reduction in mean density decline was likely a result of increased density from sedimentation offshore, and around Separation Point (Figure 3.6D) and could be an indication that at optimum sedimentation levels, more suitable habitat conditions are being created. At 3% annual sedimentation (combined with fishing), mean density was lower (-16.1%) than the fishing-only scenario, indicating that as the magnitude of sedimentation increases, any slight density increases offshore are outweighed by the combined stressor impact inshore (a net negative impact), even when impacts are averaged. Declines in mean density were lower in the F-R and sediment combined scenarios (-11.9% to -16.1%) compared to the F-NR and sediment combined scenarios (-17.1% to -19.3%). There was no measurable difference between recovery scenarios for fishing alone, indicating that recovery plays an important role in a multiple-stressor environment. Changes in mid to high-level densities were observed between the multiple stressor recovery scenarios in the shallow coastal environment to the west of Golden Bay and east of Tonga Island marine reserve (Figure 3.6B, C).

Echinocardium had a predicted decline in mean density (-13.5% to -15.6%) from the F-R and sediment combined scenarios (Table 3. 2). Like *Callyspongia*, the mean density decline in the combined F-R scenario for *Echinocardium* was less than fishing alone (Table 3.2). The mean change in density was also influenced by the observed density increases offshore and around Separation Point from the elevated mud levels (Figure 3.6H). However, in the combined F-NR scenario, the impact on density was greater (-18.9% to -19.6%), as no recovery was applied. The difference in mean density between the combined FR and FNR scenario at 3% mud was 6.6%, as observed by the difference in density values inshore (Figure 3.5F, G)

For *Amalda*, density was predicted to increase by 9.7% - 30.0% for the F-R and sediment combined scenarios and increase by 17.6%-27.5% in the FN-R scenarios. Even when recovery from fishing was accounted for (all F-R scenarios), density remained high because of this taxon's positive relationship with sedimentation. The positive effects from sedimentation resulted in larger increases inshore, but small widespread small increases in density over the wider study area and offshore (Figure 3.6L). However, the largest density increases were predicted to occur in areas with high fishing effort (Figure 3.1C), particularly in inner Tasman Bay (Figure 3.6K).

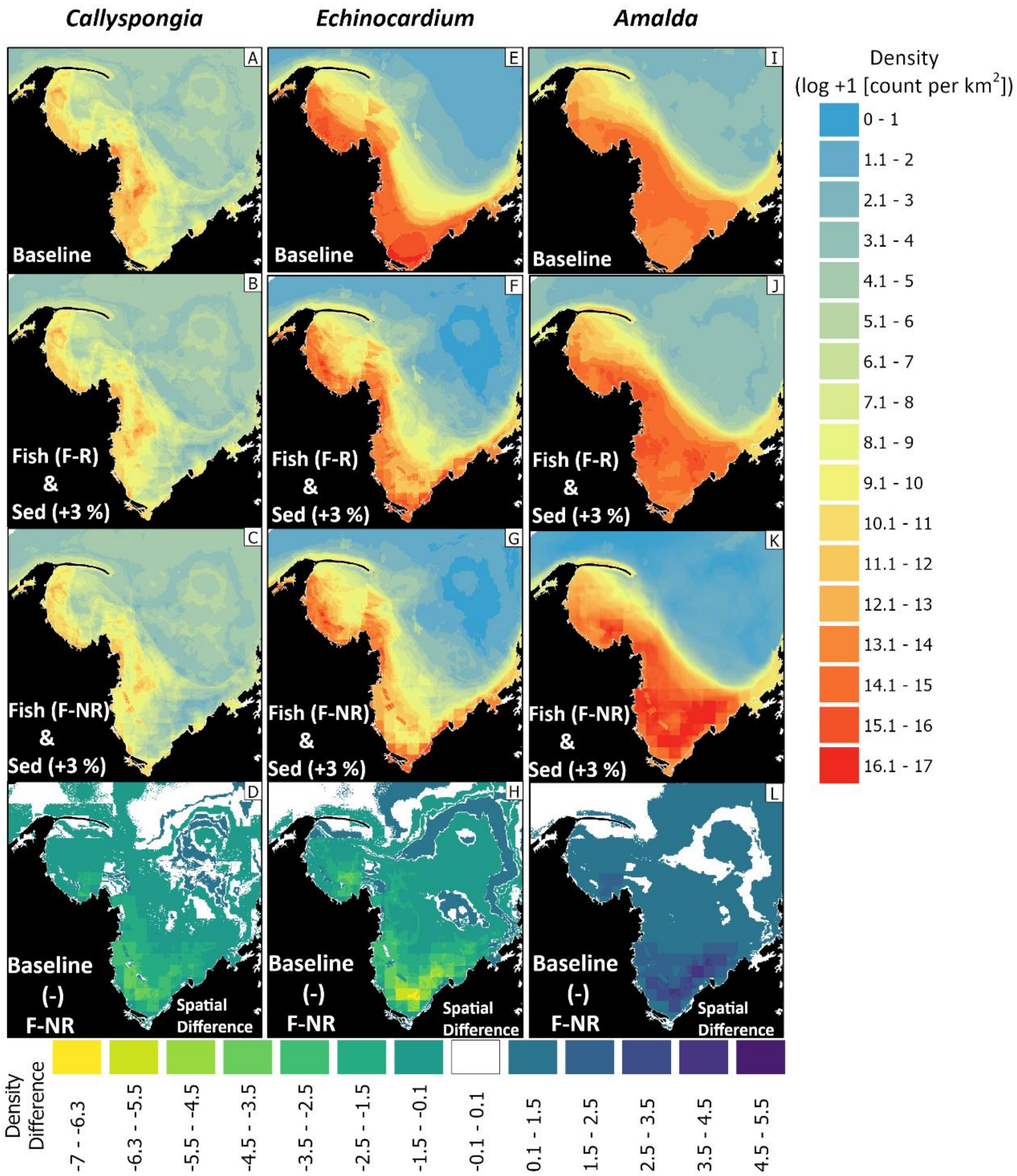


Figure 3.6: Spatial maps from combined stressor correlative models detailing the change in density (log +1 [count per km^2]) and distribution from the baseline from fishing and sedimentation stress after four years of cumulative impact (plots A-K). All scenario maps contain a combination of two stressors, either fishing with recovery (F-R), or fishing without recovery (F-NR), and sedimentation. Sedimentation stress provided by absolute increase in mud of 3% per year, over four years. Spatial difference maps (density (log +1 [count per km^2])) highlight the difference in the density value by subtracting the baseline density SDM without stress, from the density SDM with stress (Stressor impacted SDM values – baseline SDM values; plots D, H, L). All values in the spatial difference maps that are negative indicate that the baseline density values were greater than the stressor-impacted values for the same location (i.e., this is how much the density has decreased following stressor impact). All positive values indicate that the stressor-impacted values were greater than the baseline value in the same location. All density values are count per km^2 with log +1 transformation.

All taxa exhibited different stressor responses in terms of density change, and the spatial distribution pattern of density values effected (Figure 3.6). For negatively affected taxa (*Callyspongia* and *Echinocardium*), combined stressor scenarios that applied recovery (F-R) had lower density impacts than scenarios without recovery (F-NR). The spatial difference maps highlight that most of the density change in the shallow coastal waters occurred within the spatial footprint of the fishing stressor (Figure 3.6D, H, L). However, in areas where there is low or no fishing (including offshore and in protected areas), sedimentation effects are visible. Although sedimentation had a smaller magnitude of impact compared to fishing for some taxa (i.e., *Callyspongia* and *Echinocardium*), changes in density occurred over a broader stressor footprint. Based on taxa-specific response relationships, for sensitive taxa, the effects of sedimentation resulted in a decreased density over most of the study area (e.g., *Callyspongia*), whereas for stress-tolerant taxa (e.g., *Amalda*), large increases in density were observed from the creation of more suitable habitat conditions. Although recovery from fishing can be accounted for in the model, recovery from sedimentation will be limited as this stressor accumulates in the system over time, though it will be subject to localised sediment transport influencing finer scale patterns.

Table 3.2: Change in mean density (count per km²), across all stressor scenarios for each taxa. Difference in mean density provided by subtracting baseline density values from scenario density values. Magnitude of change in density is indicated by gradient of colour, with orange indicating density reduction, and blue indicating density increase.

Taxa	*Callyspongia*	*Callyspongia*	*Echinocardium*	*Echinocardium*	*Amalda*	*Amalda*
Stress Scenario	mean density (count per km²)	Difference in mean density (%) from Baseline	mean density (count per km²)	Difference in mean density (%) from Baseline	mean density (count per km²)	Difference in mean density (%) from Baseline
Single Stressor						
Baseline (without stressors)	144.0	-	59.2	-	195.4	-
Sed (1%)	139.2	-3.4	58.6	-1.1	216.0	10.6
Sed (2%)	134.6	-6.5	58.2	-1.7	238.4	22.0
Sed (3%)	130.4	-9.5	58.4	-1.3	262.2	34.2
Fish (F-R)	123.7	-14.1	49.8	-16.0	200.3	2.5
Fish (F-NR)	123.7	-14.1	49.7	-16.1	215.6	10.3
Multiple Stressors (with recovery)						
Fish & Sed (1%, F-R)	125.2	-13.1	51.2	-13.5	214.3	9.7
Fish & Sed (2%, F-R)	126.9	-11.9	50.0	-15.6	230.8	18.1
Fish & Sed (3%, F-R)	120.9	-16.1	51.5	-13.0	253.9	30.0
Multiple Stressors (without recovery)						
Fish & Sed (1%, F-NR)	119.4	-17.1	48.0	-18.9	229.7	17.6
Fish & Sed (2%, F-NR)	117.7	-18.3	47.8	-19.3	239.3	22.5
Fish & Sed (3%, F-NR)	116.2	-19.3	47.6	-19.6	249.1	27.5

3.3.4. Change in density distribution

All taxa exhibited broad changes to their density distribution with increased stress (Figure 3.7), whether the changes developed from a positive stressor response (e.g., *Amalda*), negative response (e.g., *Callyspongia)* or a combination of the two from either stressor (e.g., *Echinocardium*). The greatest changes were observed in both the lower (0.25 - 0.5) and maximum (> 0.75) quantiles, particularly in the combined F-NR stressor scenarios that did not incorporate recovery. For both *Callyspongia* and *Echinocardium,* the observed density losses in areas most affected by sedimentation stress were always greater than the localised density gains observed in the higher density ranges (Figure 3.8A, B), resulting in a net density loss (Table 3.2). The predicted change in density from baseline levels increased with increasing sedimentation rates (highest at 3% annually) highlighting how the accumulation of sediment will progressively impact density over time.

For *Callyspongia*, the differences in mean density between F-NR and F-R scenarios were modest, indicating that even when recovery is included in the scenarios, the impact on density is very similar to no recovery. Stressors impacted high-density value ranges the most across all taxa, with a trend of decreasing density as the stressor magnitude increased for more sensitive taxa (Figure 3.7A, B), and a trend of increasing density for opportunistic taxa (Figure 3.7C). The changes in the high-density value ranges likely result from a combination of stressor aspects: high density was predicted for most taxa in areas with lower mud content, and taxa density decreased for most taxa (*Callyspongia* and *Echinocardium*) as mud content increased due to the stressor response relationship (1), and fishing effort was also higher over broadly the same lower to mid-level mud content habitats (2). The decrease in high-density values represents a reduction in population size within high-value habitats for *Callyspongia* and *Echinocardium* because of increased anthropogenic stress (particularly fishing), whereas the opposite pattern was observed for *Amalda*.

By splitting the range of density values into frequency intervals and calculating the change as a percentage of the baseline levels, I was able to observe in greater detail the trends of impact on high-density values compared to mid or low-density values (Figure 3.8). Density distribution was affected differently for each taxon compared to their baseline density distribution; density interval ranges shifted from higher to lower for *Callyspongia* and shifted from lower to higher for *Amalda*, and the response was variable for *Echinocardium*. The impact of the fishing stressor reduced high-density values for both *Callyspongia* and *Echinocardium* (Figure 3.8A, B). A reduction in high-density values under the fishing stressor scenario represents homogenisation over time as areas of high-density habitat are removed within the fishing stressor footprint. A similar shift in density distribution was also observed for *Amalda*, but high-density value ranges increased (Figure 3.8C), highlighting that as a predatory scavenger, *Amalda* would thrive in highly disturbed environments such as those created from bottom fishing and elevated sedimentation. These results suggest that over time, population increases in predatory scavengers coupled with a reduction of other larger-bodied invertebrates would result in broad changes to the community composition, particularly in areas where stressors overlap. Models predicted that with increased sedimentation (1-3% annually), certain high-level density ranges for *Callyspongia* (13-15, log +1), and *Echinocardium* (16-18, log +1), increased, suggesting that taxa populations which occur in greater density may be more resilient to sedimentation and exposure and it may even be slightly beneficial at tolerable percentages of mud.

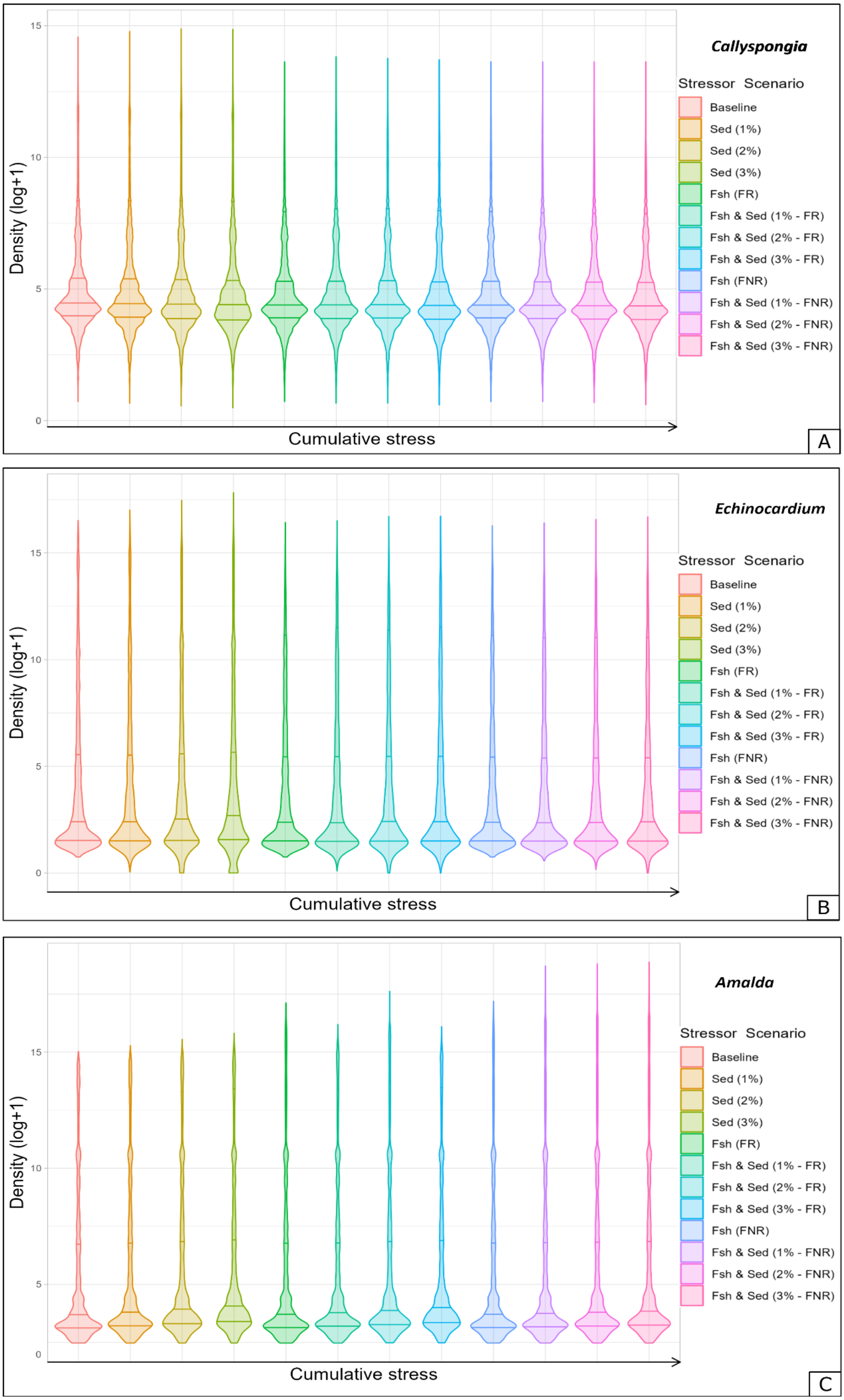


Figure 3.7: Violin diagram of density distributions across single and multiple stressor scenarios for each taxon ordered by increasing levels of stress, displaying quantiles at 0.25, 0.5, 0.75, and 0.95, for Callyspongia (A), Echinocardium (B), and Amalda (C).

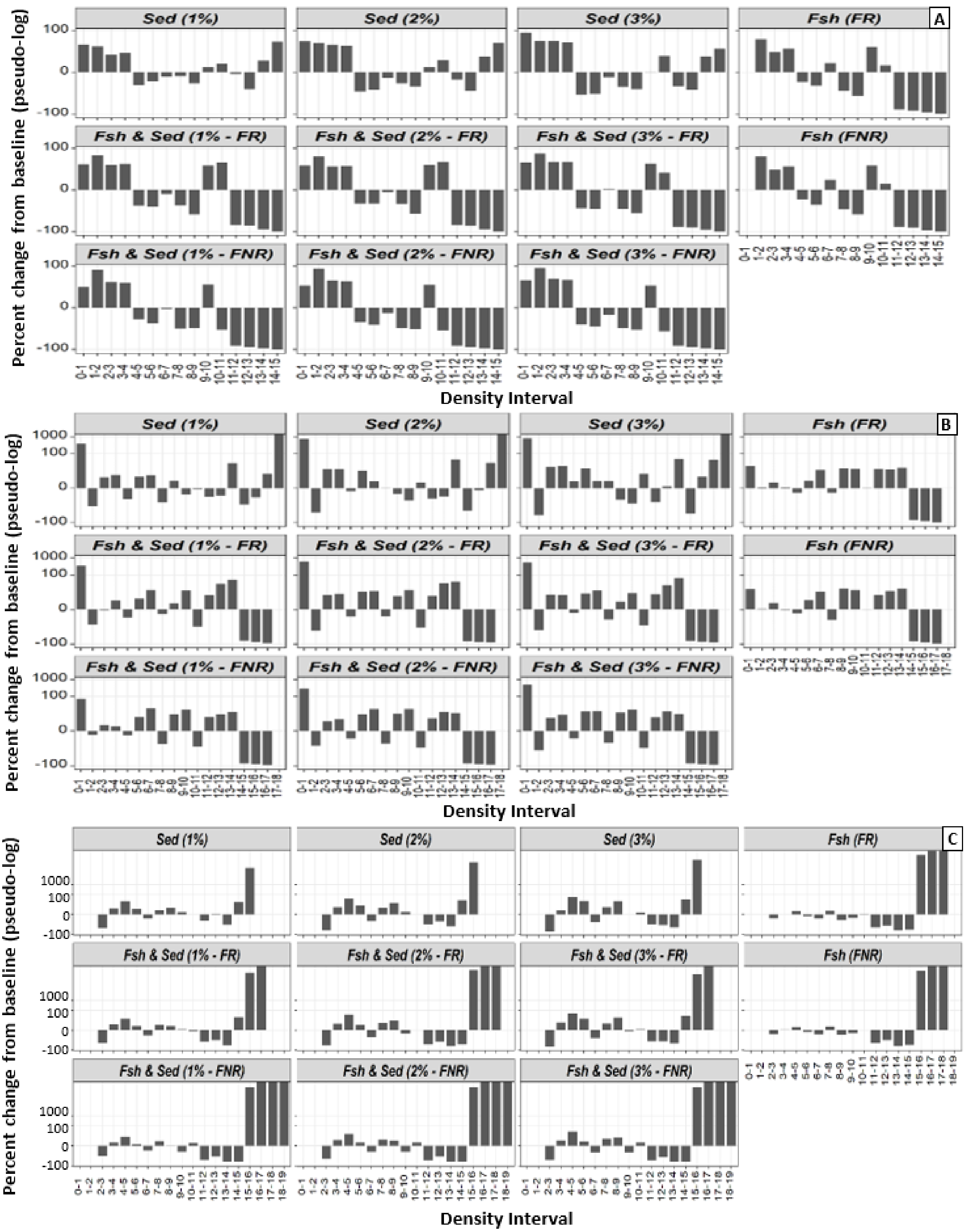


Figure 3.8: Density interval histograms showing the percent change in density across each stressor scenario compared to the baseline scenario for Callyspongia (A), Echinocardium (B), and Amalda (C). Percent change is on a pseudo-log scale showing both positive and negative change on the y-axis, and density split into interval (bin size of 1) ranges on the x-axis.

3.4. Discussion

This study presents a spatially-explicit correlative stressor model to assess the response of key coastal taxa which support ecosystem functioning such as bioturbation, filtration, and habitat formation in benthic environments (Lundquist *et al.*, 2018; Lohrer *et al*., 2004; Gammal *et al*., 2023) to bottom fishing and sedimentation stressors. This analysis revealed that fragile-bodied, shallow burying infauna and emergent epifauna (*Callyspongia* and *Echinocardium*) experienced density decline from both fishing and sedimentation stress, resulting in lower density areas and a patchier distribution. However, highly mobile, small-bodied taxa which act as opportunistic scavengers in disturbed environments were predicted to thrive, demonstrating that anthropogenic stressors are modifying benthic communities and the associated ecosystem functioning they provide over time (Gammal *et al*., 2023; Lundquist *et al*., 2018; Lohrer *et al*., 2010; Norkko *et al*., 2013). This analysis highlights the importance of considering taxon-specific responses to anthropogenic stressors when developing management approaches and helps advance methods to spatially quantify impacts on benthic invertebrate density distribution, and highlights areas most impacted by, and most resilient to, multiple stressors in shallow seafloor ecosystems.

Impacts on density from bottom fishing were less discriminate, as density decline for larger and more fragile taxa were similar between *Callyspongia* (-14.1%) and *Echinocardium* (-16.1%) despite having different functional traits (e.g., living positions in the sediment and mobility), and different recovery times.

Fishing scenario predictions align with previous research recording declines in taxa density (>15%) within the stressor footprint and limited recovery from repeated disturbance events (Sciberras *et al*., 2018; Hiddink *et al* 2017, Baird *et al*., 2015). The predicted declines in benthic invertebrate density are also supported by recorded shellfish fishery closures (dredge oyster and scallop) in Tasman and Golden Bays, which remain closed due to non-viable stock levels and slow recovery (MPI, 2022; MPI, 2008). Repeated trawling disturbance within Tasman and Golden Bay has contributed to a homogenisation of the seascape and reduced benthic density (Lundquist *et al*., 2018; Hanley *et al*., 2020) also reflected by model predictions showing a reduction in larger epifauna and infauna and an increase in small and mobile predatory taxa. Over time these changes modify the community composition and reduce associated ecosystem functioning provided by large macroinvertebrates such as bioturbation (Lohrer *et al*., 2004) and biogenic habitat formation (Bell, 2008; Chin *et al.*, 2020). Historic fishing pressure within Tasman and Golden Bay has likely resulted in a mosaic of unfished, recently fished, and recovering habitats (Sciberras *et al.*, 2018).

Sedimentation scenario predictions align with the findings of others showing changes in benthic taxa distribution and density from increased sedimentary mud and highlight the importance of assessing long-term responses of subtidal faunal communities to habitat change from sedimentation (Anderson *et al*., 2008; Ellis *et al*., 2017; Johnston *et al.,* 2015). Despite the high levels of accumulated sedimentary mud, and known impacts of sedimentation stress, there is no ongoing sediment monitoring within Tasman and Golden Bay, but research indicates that sediment re-suspension may be a greater stressor than new sediment input (Newcombe, 2016;

Newcombe *et al*., 2015). Some intertidal studies have specified mud thresholds can impact ecosystem functioning at 12% (Stephenson *et al*., 2022) and 19.9% mud content (Thrush *et al*., 2012), and others have stated that estuarine locations with >25% mud content support a lower diversity and abundance of macroinvertebrate assemblages (Johnstone *et al*., 2015). Most of the central study area had a high mud content between 20%-80%, which indicates that taxa may have developed a tolerance to high levels of suspended sediment, influenced by adaptation to high levels of near seabed turbidity (Lohrer *et al*., 2006; Cummings *et al*., 2020; Newcombe, 2016). Small positive effects were observed along sediment gradients likely following seabed terrain, where levels of mud became more optimal with slight increases (possibly in sandier habitats), but overall, sedimentation was predicted to have a net negative impact on density (for both *Callyspongia* and *Echinocardium*). These model predictions align with other empirical research in that a gradient response to increasing sediment was observed and that more sediment resulted in greater impacts (Lohrer *et al*., 2006; Thrush *et al*., 2004; Ellis *et al*., 2017). Although deposits of coastal sediment have been shown to be transported offshore by the mechanisms of currents and wave action (Lamarche *et al*., 2008; Strachan *et al*., 2022) environmental problems occur when the rate of sediment deposition increases beyond natural levels and can greatly alter the structure and function of coastal habitats (Thrush *et al*., 2004).

The combined stressor model predicted a greater change in the density distribution of taxa than either single stressor model, reducing the density of *Callyspongia* and *Echinocardium* by up to -19.3% and -19.6% respectively, and increasing the density of *Amalda* by up to +30%. Model predictions indicate that the density and distribution of all modelled taxa would be modified over most of the inner coastal environment, and the magnitude of impact would increase over time. Fishing was the more dominant stressor. For taxa with a mixed response to sedimentation (*Echinocardium*), the combined impact of both stressors was less than fishing alone (when models accounted for recovery), due to the spatial variability of density changes from sedimentation. This observed variability from sedimentation stress is due to a larger relative impact over areas with low mud content, which had higher baseline densities. However, when no recovery was accounted for, the density decline predicted for both *Callyspongia* and *Echinocardium* was greater in the multiple stressor scenarios, particularly where high stressor magnitudes co-occur. These results reinforce that management approaches focusing on single stressor impacts are no longer sufficient (Thrush *et al.*, 2021), and that even in the presence of a dominant stressor (i.e., fishing) other stressors can still provide further impact, particularly those that accumulate over time.

Spatial analysis revealed that when fishing effort was consistent, recovery was restricted for both slow (>3 years) and fast (<1 year) recovering taxa (*Callyspongia* and *Echinocardium*) as the fishing stressor footprint typically spatially overlapped from one year to the next. Although the effort and location of fishing trawls did vary between years, large areas were repeatedly targeted (i.e., fishing grounds), which corresponded to areas with the greatest change in density for all taxa. Model predictions demonstrate that a community's ability to recover after a single disturbance event compared to repeated disturbances diminishes over time, which aligns well with other disturbance and recovery research (Baird *et al*., 2015; Lambert *et al*., 2015; Lundquist *et al*., 2018). Although models did not apply any recovery from sedimentation, differences in density change between the multiple stressor scenarios that accounted for fishing recovery and those that did not were observed (-6.6 to +7.9%), highlighting that the broad spatial pattern of both positive and negative density changes caused by sedimentation (e.g., Figure 3.6D, H) influenced the predictions within the multiple stressor model. Although many empirical studies have explored the effects of coastal sedimentation (Thrush *et al*., 2004; Lohrer *et al*., 2006; Douglas *et al*., 2023; Hateley *et al*., 2005), model outputs demonstrate spatially how the annual accumulation of mud, in addition to existing high levels of sedimentary mud can influence recovery within a multiple stressor context over a longer temporal scale. An increase in mud content of 3% annually resulted in a density decline (-9.5%) comparable to fishing (-14.1%) for *Callyspongia*, highlighting the possible magnitude of impact from slow-acting stressors that accumulate over time. Furthermore, as the spatial footprint of the sedimentation stressor was broad, its effects extend into conservation areas that are restricted to fishing and may impact their effectiveness. Marine management often focuses on more immediately damaging threats (e.g., fishing, pollution) from which there can be recovery potential (not always) over time if the stressor is removed or abated (Stephenson *et al*., 2019; Lambert *et al*., 2014). However, this analysis demonstrates an immediate need to address stressors from which there can be little to no recovery (as sediment mud content remains elevated without effective management).

Steps to validate the performance of correlative and regression-based models (e.g., SDM and habitat suitability models) through evaluation metrics and uncertainty measurements have become common practice (Dormann *et al.*, 2018; Roberts *et al.*, 2017), however, methods to fit novel simulation models to assess predictive performance is considered innovative and rarely done (Zurrell *et al*., 2021). Performance metrics and measurements of uncertainty for the input occurrence and abundance models used to create the density SDMs indicated good performance and were deemed useful, as detailed in Watson *et al*., 2021 (Chapter 2). However, performance metrics were not applied for the correlative stressor model due to a lack of quantified methods for this novel approach; standardisation of evaluation metrics would help assess predictive performance, transferability, and adoption (Yates *et al.,* 2018; Roberts *et al*., 2017). Rather, I applied a robustness test to determine if the order in which the stressors were applied (order of operations) within the model would influence the outcome of the predictions. The results presented in Section 3.3 applied the stressors in the following order: fishing stress, sedimentation stress, and then recovery from fishing. An alternative operational order (fishing stress, then recovery, followed by sedimentation stress) was tested (Appendix A2) and there was no material difference (0.1% - 0.2%) observable in the spatial outputs for negatively impacted taxa (*Callyspongia* and E*chinocardium*), but a range of density differences over the stressor scenarios (0.4% - 7.5%) for positively impacted taxa (*Amalda*). This result emphasises the need to consider the influence of the operational order when assessing the validity of model predictions, which could vary depending on the quantity and sequence of model operations, in addition to taxon-specific responses under each scenario modelled. to each.

Marine managers require highly transferable assessment approaches which can provide predictions over a variety of temporal and spatial boundaries (Yates *et al.*, 2018), but data availability is an ongoing challenge which limits multiple stressor assessment and the predictive ability of models (Stamoulis and Delevaux, 2015; Stelzenmüller *et al.*, 202; Stephenson *et al.*, 2023). The outputs from this modelling approach are highly dependent on the taxa-stressor response curves used to parameterise the stressor relationships. Therefore, the availability of data will limit both the quality and quantity of stressor responses that can be integrated into future applications. Generally, all environmental stressor modelling approaches (existing or potential) could benefit from improvement in long-term (stressor impact-oriented) environmental monitoring efforts (Hewitt *et al.*, 2014; Tremblay *et al.*, 2023). Investment in new surveys (e.g., stock assessment surveys, systematic research surveys, annual sedimentation rates) to collect more reliable datasets, preferably with measures of abundance, would improve model validation and increase confidence in spatial management measures (Lundquist *et al.*, 2020; Stephenson *et al.*, 2023).

Model predictions are likely conservative as they only represent a partial impact prediction in an environment that has multiple gradients of stress from a variety of historic and ongoing threats (Ellis *et al*., 200; Handley, 2006). For example, the fishing stressor only accounted for the impact of one gear type (otter trawls) on taxa density during a timeframe that several other gear types (other bottom trawls such as beam trawls, oyster dredge and scallop dredge) would have been disturbing the benthic environment. Furthermore, it was deemed difficult to incorporate the effects of the other fishing impacts (mainly dredges) due to a combination of factors such as: several fishery closures or reduced fishing effort over the dredge area occurring during 2009-2012 (Drummond 1994, Bradford-Grieve *et al*., 1994; Handley, 2006); and the fisheries report data over broad statistical areas for all fishing methods, averaging trawl effort, although the underlying data used for each fishing method varies and thus the quality of the data also varies (Baird *et al*., 2015; Stephenson *et al*., 2018)

. The predictive models focussed on density decline with a generalised recovery over time and did not quantify other population dynamics. The inclusion of additional model terms which act to regulate population size (e.g., reproduction rate) and better represent real-world equilibriums (e.g., carrying capacity) could be incorporated for more accurate density loss and recovery predictions (Lipcius *et al.*, 2019; Spaak *et al.*, 2017). The impacts of sedimentation on density are also likely conservative as the stressor-taxa relationships did not account for the physiological harm (e.g., diminished filtration from clogging) caused by the build-up of fine sediments (Schönberg, 2015; Thrush *et al.*, 2004). Furthermore, the application of a uniform increase in sediment mud content does not account for the dynamics of sediment transport in shallow coastal systems (Bostock *et al.*, 2018; Hateley *et al*., 2005). Sedimentation stressor predictions could be improved through the incorporation of a catchment model to determine sediment deposition rates from the surrounding landscape (e.g., Delevaux *et al*., 2018; Alvarez-Romero *et al*., 2015). The challenges of additive models to represent the dynamics of stressors in real-world environments have been explored by others (Crain, Kroeker and Halpern, 2008; Folt *et al.*, 1999; Piggott, Townsend and Matthaei, 2015). Although this spatial modelling approach does not elucidate information on stressor interactions provided by other model types (e.g., linear regression, Ellis *et al*., 2017), I can conclude that the predicted additive impacts are not likely to be lesser than the true environmental impact (Stephenson *et al*., 2023), given that predictions are likely conservative, and density reduction estimates align with empirical research (Sciberras *et al*., 2018; Hiddink *et al*., 2017). I can still conclude that the effects were positive, negative, or mixed in addition to the magnitude of density change from bottom fishing and sedimentation stress. When considering ecological risk, combined negative effects present the greatest ecological risk (Rullens *et al*., 2022) irrespective of indeterminate stressor interactions (Stephenson *et al*., 2023).

The demand for modelling assessments that quantify stressor effects is rapidly increasing and marine managers need generally applicable tools that can be implemented with currently available data, and with limited resources (Brush and Nixon, 2017; Stelzenmüller *et al.*, 2020). Some research has indicated that the reason coastal management has failed to address the impacts of multiple stressors is due to a lack of integrated land-sea assessment (Griffiths *et al*., 2020; Tulloch *et al*., 2021). This approach helps advance multiple stressor research by spatially quantifying the location, response type (positive or negative) and the magnitude of the impact on taxa density distribution from a critical marine stressor (fishing) in combination with a terrestrially derived stressor (sedimentation). This analysis revealed that greater consideration should be given to the compound effect of slower impacting, accumulating stressors such as sedimentation which were shown to cause similar rates of density decline for sensitive taxa (e.g., *Callyspongia*) over time compared to the more immediate impacts of bottom fishing. Furthermore, this analysis also addresses a critical research need to assess the impacts of bottom fishing in combination with sedimentation over time need (Crain *et al*., 2008; Worm *et al*., 2006) and makes a novel contribution to advance multiple stressor research by providing a more realistic representation of multiple stressor effects in the coastal environment to inform management decisions. Model predictions indicate that the benthic environment is experiencing a loss of density and associated ecosystem functioning from poorly managed stressors, across spatial and temporal gradients of impact, from which there is little to no recovery and will worsen over time without concerted management reform.

4. Chapter 4
Advancing spatial prioritisation of marine protected areas by integrating multiple stressors

4.1. Introduction

Marine environments are subject to multiple localised and global forms of anthropogenic stress. Over the past several decades, understanding the need to halt declines in biodiversity through conservation measures has gained significant momentum (Brooks *et al.*, 2006; Geange *et al.*, 2017; Leathwick *et al.*, 2010). Biodiversity loss has been addressed in part by conserving ecologically rich habitat 'hotspots' in the marine environment through the implementation of networks of Marine Protected Areas (MPAs; Ban *et al.*, 2014; Fernandes *et al.*, 2005; Mach *et al.*, 2017). Designation of MPAs has origins back to the early 1960s (Humphreys and Clark, 2020), but area-based designations gained momentum after the Rio Earth Summit in 1992, with the Strategic Plan for Biodiversity (Aichi target 11) in 2011, which targeted to protect at least 10 % of global oceans by 2020 (Convention on Biological Diversity, 2010), superseded with a 30 % protection target by 2030 (Target 3; Kunming-Montreal global biodiversity framework, 2022). To implement critical conservation targets and support systematic planning of ocean resources marine managers require spatial assessment approaches that can quantify impacts from multiple anthropogenic stressors which help identify ecologically rich and resilient habitat areas that will persist over time (McLeod *et al*., 2019). To assist with the myriad of tasks involved with fulfilling conservation objectives and to support the management of regional stressors, local governments and marine practitioners often utilise Decision Support Tools (DSTs; Pınarbaşı *et al.*, 2017) to help identify areas with conservation value.

A variety of DSTs have been developed to support planners with essential tasks, such as quantifying spatial boundaries, defining temporal scales based on data availability, identifying use conflicts, scenario design, mapping existing designated and future important areas and prioritising high biodiversity areas (Ehler and Douvere, 2009). Spatial conservation prioritisation is a systematic approach to locate, configure, and implement the most efficient conservation solution whether that be optimisation in terms of financial cost or resource space (Moilanen, Kujala and Leathwick, 2009). Consequently, DSTs have been used to support a variety of national and international MSP and MPA planning assessments to generate and refine suitable options for biodiversity protection and to inform conservation prioritisation processes (Ban *et al.*, 2014; Di Minin *et al.*, 2019; Lu *et al.*, 2004; Lundquist *et al.*, 2020; Virtanen *et al.*, 2018). DSTs help find solutions to complex conservation objectives, particularly within multi-use environments with strong socio-economic drivers, and multiple stakeholder objectives (Stelzenmüller *et al.*, 2020). The utility and functionality of many DSTs have been explored previously (Pınarbaşı *et al.*, 2017; Stelzenmüller *et al.*, 2020), with some tools (e.g., Zonation, Marxan, InVEST ®, and Ecopath with Ecosim (EwE)) more widely used than others (Stamoulis and Delevaux, 2015). Zonation has been used to support systematic spatial conservation projects nationally around New Zealand to explore MPA design (Geange *et al.*, 2017; Leathwick *et al.*, 2008), to evaluate biodiversity protection and potential trawl corridors in the Hauraki Gulf Marine Park (Bennion *et al.*, 2023; Jackson and Lundquist, 2016; Tablada, Geange and Lundquist, 2022), and to support the protection of vulnerable marine ecosystems from trawling impacts (Rowden *et al.*, 2019).

Commonly used datasets to inform systematic conservation planning (also termed spatial prioritisation) in Zonation include predictive species (Species Distribution Models [SDMs]) or habitat distribution models (Lundquist *et al.*, 2020). Model predictions represent environmental relationships derived between sampled occurrence or abundance data and environmental predictor data (e.g., sediment classifications), based on the conditions at locations where species have been observed to occur (Leathwick *et al.*, 2008). Additional biotic datasets (e.g., habitat types, ecosystems, ecosystem services) and abiotic datasets (e.g., aquaculture sites, conservation areas, management boundaries) can also be incorporated into the analysis to synthesise information across a multitude of datasets to identify biologically diverse habitats of conservation value, and to test different management scenarios based on the assessment objectives (Moilanen, Kujala and Leathwick, 2009).

Despite many advances, modelled species-environmental relationships from SDMs do not directly incorporate environmental stressor effects (though they may reflect historical stressor effects such as reduced abundance), therefore they may not be representative of current patterns of distribution given ever-increasing anthropogenic impacts in the coastal environment (Chalastani *et al.*, 2021; Ehler and Douvere, 2009). Furthermore, many conservation planning studies to date have focussed on performing assessments underpinned by binary presence/absence data, highlighted by a recent review on marine SDM applications which found that only 9% of conservation planning literature incorporated measurements of density, biomass, or species richness (Melo-Merino, Reyes-Bonilla and Lira-Noriega, 2020). Reliance on presence/absence point data or habitat suitability layers often stems from a lack of data available to generate predictive models of abundance or species richness (Bennion *et al.*, 2023; Janßen, Göke and Luttmann, 2019). Even when suitable species data is available, high-resolution spatial data detailing environmental stressors are often not readily available or have to undergo extensive processing (Schaffer and Piggott 2017; Stelzenmüller *et al.*, 2020). This shortfall can lead to the use of low-resolution data and stressor proxies, resulting in increased model assumptions and greater uncertainty (Ban *et al*., 2010; Gissi *et al*., 2017; Halpern and Fujita, 2013; Rullens *et al*., 2022). In scenarios where both appropriate species data and spatial stressor data are available, knowledge of species response relationships, tolerance thresholds and recovery time from environmental stressors remain limited, which can make integration of spatial data layers challenging (Berthelson *et al*., 2018; Hewitt *et al*., 2018; Hunsicker *et al*., 2016; Lundquist *et al*., 2018; Stephenson *et al*., 2019; Lambert *et al*., 2014). A recent bibliometric assessment found that only 11% of studies (n = 1323) incorporated quantitative and/ or modelling approaches to directly address MSP (Chalastani *et al*., 2021). Furthermore, Stock and Micheli (2016) demonstrated that model assumptions and data quality influence the results of multiple stressor effects maps, which are highly dependent on the case study region and the data describing it. Consequently, conventional approaches used to tackle systematic conservation planning typically have not incorporated abundance data and often use coarse-resolution data to represent anthropogenic stressors, which may lead to conservation actions being implemented in unsuitable habitats that are either currently under stress or will succumb to stress over time (Geange *et al*., 2017; Tulloch *et al.*, 2021; Stelzenmüller *et al*., 2020; Stephenson *et al*., 2022).

The incorporation of stressors (often termed threats) has been at the core of terrestrial systematic conservation planning for decades. Innovative approaches have focussed on how to plan for threat management whilst considering the spatial co-occurrence of species and threats in addition to recovery from threats under different management scenarios (Leslie, 2005; Evans *et al*., 2011; Gallien *et al*., 2010; Auerbach *et al*., 2015; Catarino *et al*., 2015). Conservation planning has evolved to recognise that a variety of threat-specific conservation actions within the same site may be needed to independently manage the combined impact on species and habitats of conservation value (Cattarino *et al*., 2015; Pressey *et al*., 2007). However, threat management is more challenging to implement in the highly dynamic marine realm (Alvarez-Romero *et al*., 2011). The combined and overlapping effects of multiple stressors and their relationships with species and habitats in the marine environment are difficult to quantify, hindered by data limitations and the technical capacity of existing optimisation approaches (Gissi *et al*., 2021; Orr *et al*., 2020 Tulloch *et al*., 2021; Simeoni *et al*., 2023; Janßen *et al*., 2019). Furthermore, many coastal stressors which originate from terrestrial sources, are often not assessed alongside marine stressors (Adams *et al*., 2014; Álvarez-Romero *et al* 2011). There is growing recognition that threats to biodiversity span multiple realms, leading to increased research on land-to-sea stressor relationships. Examples include terrestrial pollutant loads on coastal water quality (Álvarez-Romero *et al* 2015), the effect of forest conservation on coral reefs (Klein *et al*., 2012), and land-derived run-off of and sediment dispersal on coastal reef ecosystems (Tulloch *et al*., 2021).

Within New Zealand, and many coastal ecosystems globally, sedimentation from terrestrially derived mud and bottom fishing are two of the most pervasive anthropogenic stressors (Sciberras *et al.*, 2018; Simeoni *et al.*, 2023; Wahlstrom *et al.*, 2022; Willsteed *et al.*, 2018), which can be mitigated through more effective management (Davies *et al.*, 2018; Thrush *et al.*, 2004). However, in systematic conservation planning, impacts from these stressors are often assessed separately, and few research examples exist where they are spatially and quantitatively assessed in combination, except for some land-to-sea conservation plans (See, Tulloch *et al*., 2021, Delevaux *et al*., 2018; MacNeil *et al*., 2019).

In an increasingly modified coastal environment, conservation managers need to apply decision-making over time, to maintain ecological systems and their functional capacity into the future (Williams *et al*., 2023). Despite many advances across all realms, certain challenges remain persistent, as outlined by Williams and Brown (2023): 1) prediction of future consequences of management; (2) uncertainty about the system's structure; (3) inability to observe ecological systems fully; and (4) nonstationary system dynamics. To address these challenges and help overcome issues with data scarcity, more researchers are utilising advanced spatial modelling approaches (e.g., correlative models), in combination with DSTs, to optimise management solutions and maximise biodiversity conservation (e.g., Stephenson *et al*., 2023; Ban *et al*., 2014). The aim of hybrid modelling approaches is not to predict perfectly, but to overcome specific limitations of traditional models (Gallien *et al*., 2010). Although environmental stressors have long been considered in systematic conservation planning, the advancement of modelling solutions to provide improved predictions of species distribution, density, and stressor effects at a finer resolution provides an opportunity to progress methodological approaches, particularly for cross-realm stressors.

Here, I investigate how the inclusion of multiple anthropogenic stressors can drive changes in areas prioritised for conservation management when spatial predictions of density are modified by bottom fishing and sedimentation stress. The performance of different prioritisation scenarios was analysed within Zonation, using impacted density predictions that have been modified ('stressor impacted') by a correlative stressor model (Chapter 3), to alter the distribution and density of each taxon based on the individual and combined impact of bottom fishing and sedimentation stress over 4 years. I also incorporate spatially explicit measures of uncertainty to provide more robust predictions. The differences in spatial patterns and efficiency are compared between prioritisations run with unimpacted density predictions (i.e., conventional data inputs), and impacted density predictions for 7 key coastal seafloor invertebrates common in temperate soft-sediment habitats. This analysis aims to demonstrate the advantages of this approach to support marine conservation targets by identifying areas of conservation value which have shown resiliency to multiple stressors over time. The inclusion of stressor-modified density predictions should provide a more spatially differentiated and ecologically representative output, compared to conventional and temporally limited approaches. To demonstrate the utility of this approach and provide insight into how spatially explicit multiple stressor effects can be incorporated into systematic conservation planning, I performed an analysis on a shallow coastal ecosystem in New Zealand which has multiple gradients of stress, near existing conservation areas.

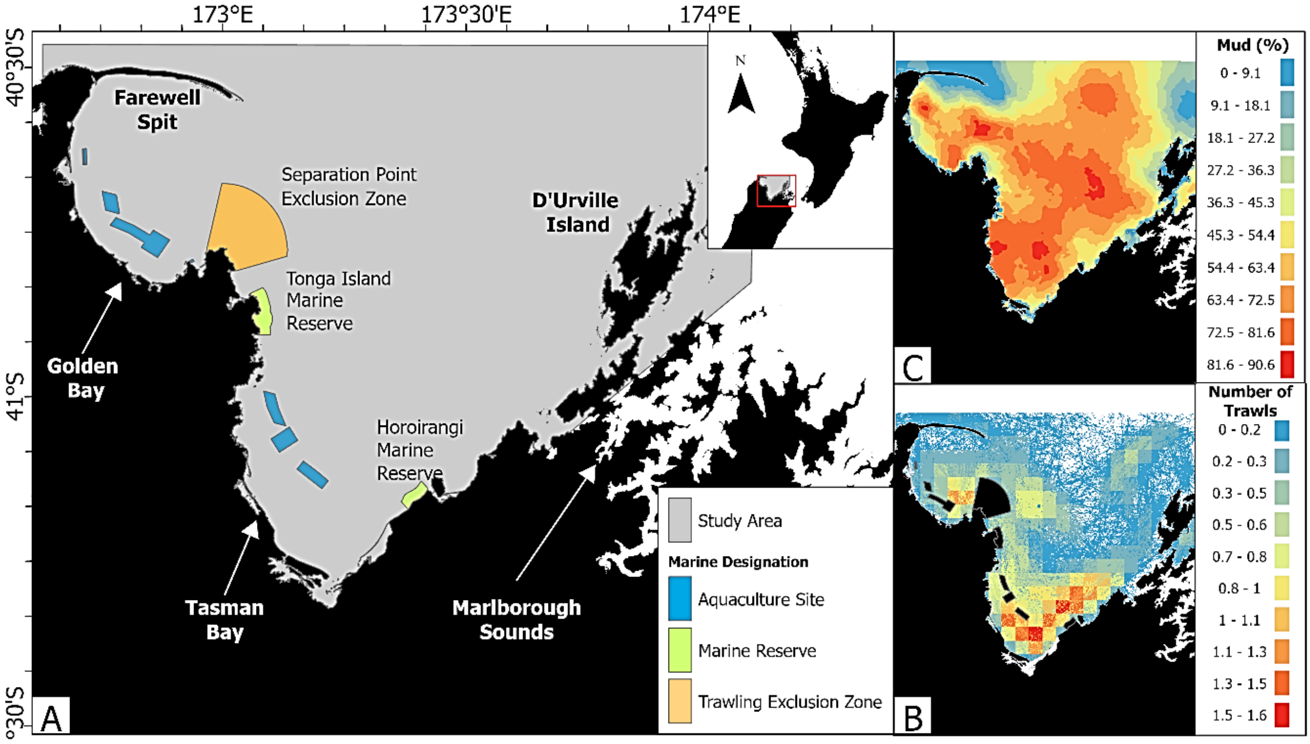


Figure 4.1: Map of the study region and feature names with inset map indicating the location within New Zealand, and extent of stressor data. A. Marine designation zones within the study region. B. Mean number of inshore trawls per 250 m x 250 m grid cell for years 2009-2012 (Ministry for Primary Industries), from fishing effort raster with a native data resolution of 5 km x 5 km. C. Percentage of mud content (Bostock *et al*., 2019) recorded in seafloor sediment.

Spatial predictions of density, uncertainty (Appendix A3, Watson *et al.*, 2022) and stressor-impacted density (Chapter 3) were available for seven taxa across the study area at a 250 m resolution. The seven taxa were selected as they varied in distribution, density, and functional role (Table 4.1). Taxa were modelled at the genus level due to the availability of records. Detailed methods for predicting the spatial distribution of densities and stressor-impacted densities are available (see Watson *et al*. 2022; Chapter 3). Briefly, two SDM models were created for each taxon using Boosted Regression Trees (BRT) – a probability of occurrence model (using a Bernoulli error distribution) and an abundance model (count per sample unit [using a Gaussian error distribution]). To create the final density prediction (count per km^2), individual predictions of both occurrence and abundance were multiplied together (e.g., Dedman *et al.*, 2015). Density uncertainty was created by combining uncertainty (standard deviation of the mean prediction) from both occurrence and abundance models following the same methodology as density predictions to ensure that the output units were comparable. All BRT analyses were undertaken in R (R Core Team, 2021) using the “dismo” package (Hijmans *et al.*, 2022).

Table 4.1: Taxonomy and functional role of each taxon included within the prioritisation assessment.

Common name	*Phylum - Genus*	*Functional role*
Olive shell snail	Mollusca - *Amalda*	Mobile surface grazer/predator
Bamboo worm	Annelida - *Asychis*	Tube mat former/Substrate stabiliser
Colonial tube sponge	Porifera - *Callyspongia*	Habitat-structure forming epifauna
Heart urchin	Echinodermata - *Echinocardium*	Bioturbator/Burrower/Substrate destabiliser
Bloodworm	Annelida - *Glycera*	Predatory scavenger
Bamboo worm	Annelida - *Maldane*	Tube mat former/Substrate stabiliser
Scallop	Mollusca - *Pecten*	Suspension feeding surface burrower

Bottom fishing and sedimentation (increased percentage of mud content in seafloor sediments) stress were applied to the density predictions for each taxon via a correlative approach which successively altered density, based on stressor response curves and spatially explicit environmental stressor data (Chapter 3). Impacts from bottom fishing represent successive stress measured from annual inshore trawl paths over four years (2009-2012). Stressor impacts from sedimentation were represented by an absolute increase in mud of 3% per year, over 4 years, increased annually from a baseline of estimated seafloor mud content (Bostock *et al.*, 2018). After each year of impact, the changes in density were predicted back to the density SDM to modify the values, which were used as the starting density for the subsequent year of modelled stress so that stressor impacts accumulated over time. The effect of recovery or lack thereof from the impact of bottom fishing was also incorporated into the correlative stressor model. No recovery was applied for sedimentation impact as it was assumed that the habitat had already been modified by increased mud and was not able to return to its previous state as mud accumulates in the environment over time (though it is subject to localised movement from waves and tides). After stressor impacts were incorporated over 4 years, the model outputs were used to examine how spatial patterns of density and distribution varied between unimpacted density predictions and impacted density predictions from both single and multiple stressor scenarios for each taxon (Chapter 3).

4.1.1. Spatial prioritisation analyses

This study utilises Zonation software, which was selected due to its previous application to a variety of conservation assessments around New Zealand from benthic protection areas (Leathwick *et al.*, 2008) to evaluation of MPA design (Geange *et al.*, 2017). Zonation applies a hierarchical prioritisation algorithm that successively removes cells of the lowest conservation value first, leaving the highest value cells to last and producing a spatial prioritisation of high-value habitat based on representation across the landscape (Moilanen, Kujala and Leathwick, 2009). This analysis used the 'Core Area Zonation' cell removal rule which prioritises the representativeness of species across all biodiversity features. The highest values are given to the most important locations within each species distribution layer, to prioritise the highest biological values, based on the proportion of proportion of the remaining distribution of a species in each cell. This cell removal approach tries to retain core areas of all species until the end of the cell removal process, increasing representativeness across all species, even for rare and weighted features. All other settings were kept at their defaults.

Zonation produces spatial outputs of the prioritisation with habitat ranked based on the priority value of the cells. The maps show the priority value of the habitat grouped into ranks (Top 2%, Top 2-5%, Top 5-10%, Top 10-25%, 25-50% and below 50%) with the top 2% representing the highest conservation value. The prioritisation rankings are also paired with performance curve values that communicate both the quality and efficiency of the modelled scenario in absolute terms (Moilanen, Leathwick and Quinn, 2011). The proportion of density for each taxon at two priority levels is quantified as a nested sum (the top 10%, and the top 25% of area) and serves as a measure of conservation efficiency. Additionally, the absolute density (mean and total density) at the 10% and 25% priority levels were also calculated. The absolute density values were extracted in ArcGIS Pro v.2.9.3, using the 'Zonal Statistics as Table' tool, which extracted density summary values from the unimpacted density prediction raster for each priority area defined from the Zonation prioritisation.

Biodiversity features in the study area were represented by two different distribution models for each taxon (Figure 4.2): 1) unimpacted density predictions (the baseline without stress), and 2) impacted density predictions (density modified by stressor impacts) which contain a combination of single stressor and multiple stressor impacts. For clarity, in the methods and discussion I refer to the different models as 'unimpacted density' or 'impacted density,' but in the results section, I refer to the different distribution model types by their specific stressor impact name (i.e., 'fishing impacted density') or scenario number (Table 4.2). The stressor model outputs used in this analysis were chosen to provide a cross-comparison of performance between the different data types (impacts vs unimpacted) used in the prioritisation, without the influence of additional model parameters or biodiversity features. A spatially explicit measure of uncertainty (standard deviation of the mean density prediction) was produced for all unimpacted density predictions of all taxa (Appendix A3, see Watson *et al.*, 2022). Spatially explicit uncertainty layers were incorporated by using the 'Info-Gap Analysis' option in Zonation to prioritise areas where predictions had low uncertainty and discount areas that had greater uncertainty (Moilanen, Kujala and Leathwick, 2009), contributing to the certainty of predictions. A discounting weight of 1.0 was applied to the uncertainty layers across all model types.

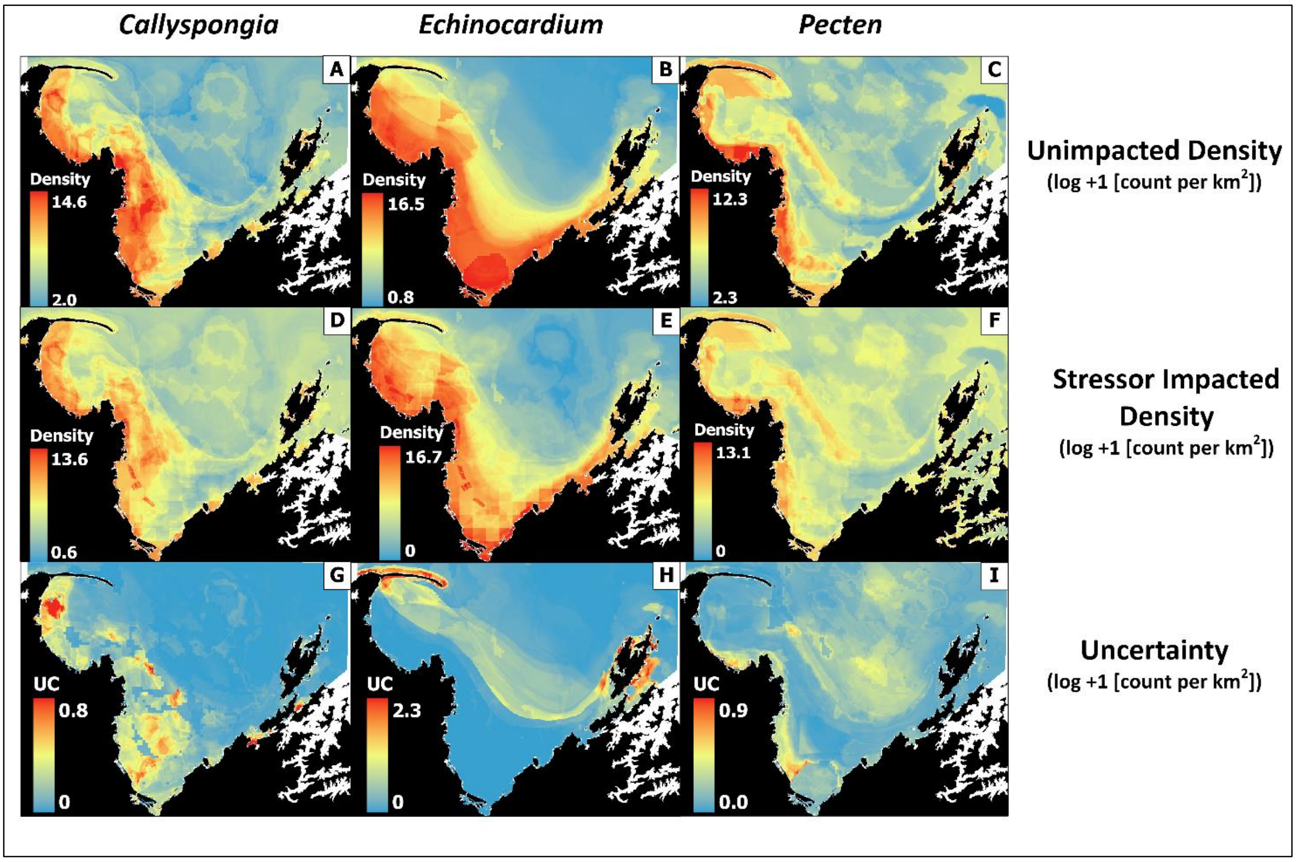


Figure 4.2: Spatially explicit predictions of unimpacted density (baseline conditions), *stressor impacted density (bottom fishing & sedimentation)* and density uncertainty (standard deviation of density) for *Callyspongia* (A, D, G), *Echinocardium* (B, E, H) and *Pecten* (C, F, I). Maps show 3 representative taxa (out of 7), and only the combined stressor impacted density SDM which were used as input layers for the spatial prioritisation analysis.

Taxa can also be ranked to reflect the perceived value that they contribute toward the biodiversity of the seascape (i.e., habitat formers), by applying taxon-specific weights (Table 4.2) to prioritise the habitat most suitable for important taxa. *Callyspongia* was allocated double the weighting (2.0) of other taxa due to their sensitivity to disturbance (Wulff, 2006), and for their value as biogenic habitat creators (i.e., habitats formed by key animal or algal species); the sponge structure provides a three-dimensional space supporting an assemblage of faunal communities (Bell, 2008; Chin *et al.*, 2020). *Echinocardium* was weighted higher (1.5) than other taxa due to its functional role as a large-bodied sediment bioturbator (Lohrer *et al*., 2004). *Pecten* was also weighted at 1.5 due to its value as a commercially harvestable species and its role as an ecosystem health indicator (Stokesbury and Bethoney, 2020). Unimpacted density (i.e., baseline conditions), stressor-impacted density (bottom fishing and sedimentation stress), and density uncertainty maps for these important taxa are presented above (Figure 4.2), and additional figures for the remaining taxa are provided in Appendix A3. *Amalda* was weighted lower than all other taxa (0.5) due to its role as an opportunistic scavenger. The predictive models suggest that the density of *Amalda* increased with increased fishing and sedimentation stress (Chapter 3). All other taxa were weighted equally (1.0). For several scenarios, density prediction layers for some taxa were included in the prioritisation with a weighting of zero. These unweighted layers do not alter or contribute to the spatial prioritisation output, but the proportion of these layers within the priority levels is recorded in the same fashion as the weighted layers (see next section for details).

Table 4.2: Summary of data layers, focal taxa, and conservation weighting applied for each prioritisation scenario. *Taxon abbreviations: AMA = Amalda, ASY = Asychis, CAL = Callyspongia, ECH = Echinocardium, GLY = Glycera, MAL = Maldane, PEC = Pecten*

Scenario	Description of weighted layers	Description of unweighted layers
Scenario 1. Unimpacted **d**ensity (No Stress)	Unimpacted density predictions for 7 benthic taxa with mixed weighting (AMA 0.5, ASY 1.0, CAL 2.0, ECH 1.5, GLY 1.0, MAL 1.0, PEC 1.5); density model uncertainty included for all taxa with weighting set at 1.0.	N/A
Scenario 2. Sediment impacted	Sedimentation impacted density predictions for 7 benthic taxa with mixed weighting (AMA 0.5, ASY 1.0, CAL 2.0, ECH 1.5, GLY 1.0, MAL 1.0, PEC 1.5); density model uncertainty included for all taxa with weighting set at 1.0.	Unimpacted density predictions for 7 benthic taxa with 0 weighting (AMA, ASY, CAL, ECH, GLY, MAL, PEC); density model uncertainty included for all taxa with weighting set at 1.0.
Scenario 3. Fishing impacted	Fishing impacted density predictions for 7 benthic taxa (AMA, ASY, CAL, ECH, GLY, MAL, PEC – all fishing with no recovery [FNR]) with mixed weighting (AMA 0.5, ASY 1.0, CAL 2.0, ECH 1.5, GLY 1.0, MAL 1.0, PEC 1.5); density model uncertainty included for all taxa with weighting set at 1.0.	Unimpacted density predictions for 7 benthic taxa with 0 weighting (AMA, ASY, CAL, ECH, GLY, MAL, PEC); density model uncertainty included for all taxa with weighting set at 1.0.
Scenario 4. Fishing & Sediment impacted (Multiple stressor)	Combined (Fishing and Sedimentation) impacted density predictions for 7 benthic taxa (AMA, ASY, CAL, ECH, GLY, MAL, PEC – all fishing with no recovery [FNR]) with mixed weighting (AMA 0.5, ASY 1.0, CAL 2.0, ECH 1.5, GLY 1.0, MAL 1.0, PEC 1.5); density model uncertainty included for all taxa with weighting set at 1.0.	Unimpacted density predictions for 7 benthic taxa with 0 weighting (AMA, ASY, CAL, ECH, GLY, MAL, PEC); density model uncertainty included for all taxa with weighting set at 1.0.

4.1.2. Zonation Scenarios and Assessment

A variety of scenarios were explored to examine the differences in spatial prioritisations and performance of scenarios in Zonation that incorporated anthropogenic stressor impacts, to those that were unimpacted by stressors (Table 4.2). Final scenarios included: a baseline prioritisation using unimpacted density distributions for all taxa (Scenario 1, Table 4.2); two "single stressor" prioritisations using single stressor impacted density predictions, one accounting for bottom fishing and the other for sedimentation impacts (Scenarios 2 and 3, Table 4.2); and a "multiple stressor" assessment from combined fishing and sedimentation stress. All scenarios represent accumulated impacts over four consecutive years (Scenario 4, Table 4.2).

Each scenario aimed to address a different part of a management problem, yet in combination, contributed to improving the knowledge of where the most and least stressor-impacted areas were, with respect to taxa density, over the prioritisation area. **Scenario 1** acts as a baseline to compare to the stressor-impacted prioritisations, so changes in spatial patterns and magnitude can be identified as stressor-driven. **Scenario 2** integrates a taxon-specific density response to bottom trawling in a subtidal habitat at a fine data resolution (250 m), which improves upon previous approaches which use probability of occurrence SDMs (or point data) and assume fishing impacts more generally and at a coarser resolution of 1 km or greater. This approach should increase the specificity and resolution of the prioritisation outputs for management consideration. **Scenario 3** integrates a taxon-specific density response to sedimentation, which improves upon approaches which model sediment impacts in relation to occurrence data or use coarse-resolution spatial data. Prioritisations run with this scenario provide greater clarity to management of how taxa density has been altered over subsequent years of sedimentation stress. **Scenario 4** provides a taxon-specific density response from both fishing and sedimentation stress in combination, over time, which helps to identify high-density habitats that persist within the footprints of both stressors. This scenario supports conservation management by helping to differentiate between areas of high conservation value, and areas of low conservation value, with consideration of temporal dynamics. Furthermore, stressor scenarios which focus on the inclusion of multiple simultaneous stressors (i.e., Scenario 4) will be more representative of real-world impacts on coastal habitats than single stressor scenarios. Both fishing and sedimentation stressors have been recorded historically, and still occur concurrently within the study area (Handley, 2006).

The analysis was split into two parts, a spatial analysis over all the prioritised habitat areas, and an efficiency analysis that focussed on metrics extracted for the top 10%, and top 25% priority areas. Key data trends for these top priority areas were representative of trends observed over all other priority areas. For the spatial analysis, each prioritisation run produced a spatial raster of priority values ranked over the study area. To highlight differences in spatial patterns of the prioritised habitat between the scenarios, the unimpacted density scenario (Scenario 1) raster was subtracted from each stressor impacted density scenario (Scenarios 2-4) raster using the 'Raster Calculator' tool (ArcGIS Pro v2.9.3), to create a spatial difference map. The resulting raster output highlighted priority values that were greater in the unimpacted density scenario as negative (i.e., the priority value lost), and values that were greater in the impacted stressor scenario as positive, allowing for the effects of the stressor to be delineated over the prioritisation landscape. Two sets of spatial prioritisation outputs were created: one set for each scenario showing the spatial prioritisation ranges over the whole landscape (0-100%), and one set showing the spatial differences between the unimpacted and impacted density predictions for habitat areas ranked within the Top 50% of conservation value. I showcase the spatial differences in the top 50% of conservation areas to highlight the change in prioritisation value in the most important areas with conservation potential.

For the efficiency analysis, I compared prioritisation metrics (mean proportion of density distribution protected [%], mean density and total density [count per km^2) between the unimpacted density prediction scenarios (Scenario 1; Table 4.2) to the impacted density prediction scenarios (Scenarios 2-4; Table 4.2). For each of the scenarios tested, when weighting was applied (Table 4.2), only the weighted spatial layers contributed to the spatial patterns created for the spatial prioritisation (i.e., they drive the scenario). The process of recording both weighted and unweighted layer metrics within each scenario allowed us to compare the differences in conservation efficiency between prioritisations that do and do not include stressor effects. The efficiency metrics also help quantify the differences in spatial patterns of prioritised areas created when using unimpacted density predictions compared to impacted density predictions. Results

4.1.3. Spatial Analysis

4.1.3.1. Single Stressor – Sedimentation (Scenario 2):

There were some large differences observed in the priority values in the bottom 50% of the study area in Scenario 2 (Figure 4.3B), compared to the baseline Scenario 1 (Figure 4.3A), but they were deemed less important as they reflected low-value priority areas for densities in both single stressor scenarios. Focussing on habitat ranked in the Top 50% (blue areas), with increased sedimentation (Figure 4.3B), priority values increased further offshore, and slightly decreased inshore, reflecting the shift in distribution because of sedimentation stress (Figure 4.1C) which altered the priority values when compared to the unimpacted density scenario (Figure 4.3A). There was a reduction in higher-ranked priority areas (top 10%, red/pink) inshore, with an increase in lower-ranked priority areas (top 25–50%, blue) offshore (Figure 4.3B). The change in priority values nearshore (Figure 4.3E) is most prominent to the east of Tasman Bay, at Separation Point, and around Farewell Spit with a reduction in priority values of 11 – 17%. Differences in priority value between the baseline scenario and the scenario accounting for sedimentation impacts were mixed across the study area with primarily small negative (-1 to -2%), or positive (1 to 4%) differences (Figure 4.3E).

4.1.3.2. Single Stressor – Fishing (Scenario 3):

Broad changes to the spatial patterns of the priority values were observed over most of the inner coastal habitat for the fishing-impacted density (Figure 4.3C) compared to the unimpacted density scenario (Figure 4.3A), which reflects the reductions in density from the fishing stressor impact. A reduction in priority values was observed (-16 to -22%; Figure 4.3F), in areas that spatially correlated with areas of high fishing effort (Figure 4.1B). The difference in priority values was most prominent to the east of Golden Bay and inner Tasman Bay (Figure 4.3C), where priority values reduced from the top 10 – 25% (yellow) down to the top 25 – 50% (blue) for the same area, between scenarios. With fishing stress incorporated a reduction in habitat ranked in the top 5% was observed to the west of Tasman Bay, however, this also aligns with areas that had higher uncertainty in certain taxa with higher weightings (i.e., *Callyspongia* and *Pecten*, Figure 4.2G, I), so predictions in this area are less certain. Areas where fishing effort was low, or did not take place (e.g., Separation Point Exclusion Zone and aquaculture sites; Figure 4.1A) became prominent in the spatial difference maps (light green and yellow areas) as habitat in these areas were ranked much higher compared to the surrounding areas which were more greatly impacted by fishing (Figure 4.3F). Like the sedimentation scenario, priority values were shown to increase in the central offshore habitat areas under the fishing scenario (Figure 4.3C), indicating that density remained higher in these areas compared to surrounding habitats due to lower fishing effort.

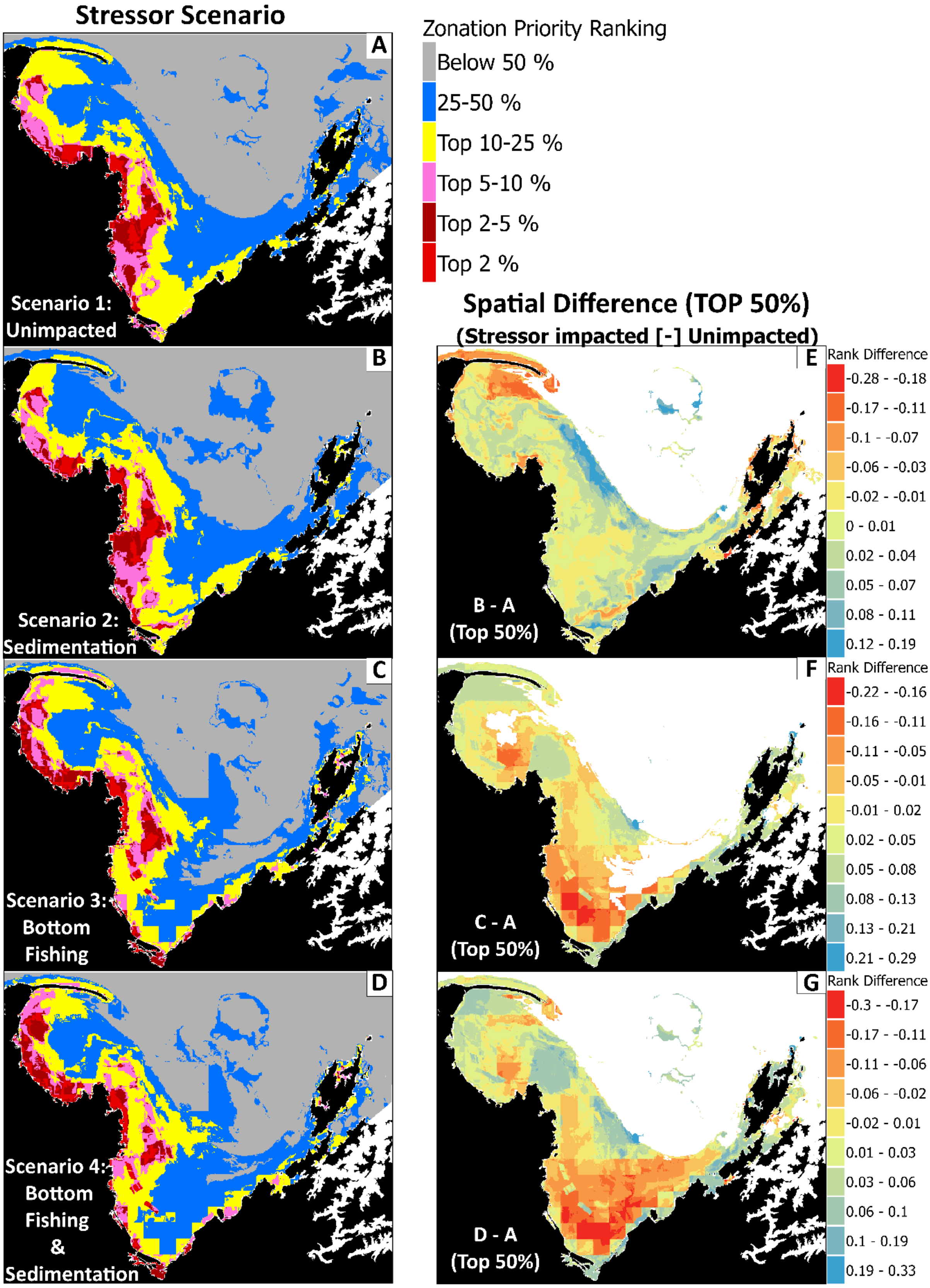


Figure 4.3: Zonation outputs for stressor scenarios (Unimpacted Density & Impacted density predictions; 1.0 weighting of uncertainty; Taxa weighting – *Amalda* [0.5], *Asychis* [1.0], *Callyspongia* [2.0], *Echinocardium* [1.5], *Glycera* [1.0], *Maldane* [1.0], *Pecten* [1.5]) within Tasman and Golden Bay. Panels (A-D) show the priority rankings for Scenarios 1 - 4 (%). Spatial difference maps (E, F, G) highlight the difference in the prioritisation ranking value by subtracting the unimpacted density scenario without stress (Scenario 1), from the impacted density scenario with stress (Impacted scenario – unimpacted scenario; Scenarios 2 - 4). All values in the spatial difference maps that are negative indicate that the prioritisation value in the unimpacted scenario was greater; all values with a positive value indicate that the prioritisation value in the impacted scenario was greater. The Zonation priority ranking indicates the habitat with the top rank for conservation which aims to maximise the inclusion of high-density areas for all taxa, within the given area.

4.1.3.3. Combined Stressor – Fishing and Sedimentation (Scenario 4):

The spatial patterns of priority values in the combined fishing and sedimentation-impacted scenario (Scenario 4; Figure 4.3D) align closely with those observed in the fishing-impacted scenario (Scenario 3; Figure 4.3C). Differences in priority values can be observed to the west of Tasman Bay (to the east of Tonga Island Marine Reserve; Figure 4.1A) where there was a reduction in habitat ranked in the top 5% (pink/red areas). Conversely, priority values in the top 2 – 5% ranked habitat increased to the west of Golden Bay. Both observed changes in priority values are likely a direct result of the sedimentation stressor influencing taxa distribution, but these areas also had greater predictive uncertainty for important taxa (Figure 4.2G, I), which would have caused Zonation to downweight these areas, resulting in the lower priority ranking. Reductions in priority values in the nearshore (-15 to -27%) are easily identified in the spatial difference map (Figure 4.3G). Similarly, for both the sedimentation scenario (Scenario 2) and the fishing scenario (Scenario 3), an increase in priority values in the central offshore area was also observed in the multiple stressor scenario (Figure 4.3G).

4.2. Taxon-specific results of prioritisation

4.2.1. Proportion of taxon-specific density

Prioritisations that utilised the unimpacted density (Scenario 1 - 'Baseline') were efficient across all taxa for both the top 10% and 25% of priority areas (Table 4.3, Scenario 1), protecting up to 18.6% of *Callyspongia* density and 21.6% of *Echinocardium* density within the top 10% of the area. However, these results may be over-optimistic because they do not account for environmental stress (Table 4.3). When the same unimpacted density was used as unweighted layers in prioritisation scenarios that did account for stress, they were less efficient (proportion of density conserved) than the baseline (Scenario 1) for most taxa (Figure 4.3). Prioritisations run using stressor-impacted density (Scenarios 2-4) provided increased conservation efficiency for *Callyspongia* (0.2 – 0.9 %) and *Echinocardium* (0.3 – 0.8%) in the top 10% priority areas (Table 4.3; difference columns).

Overall, small (<5%) efficiency improvements were recorded for the stressor scenario prioritisations (Scenarios 2-4) using the impacted density predictions compared to using unimpacted density for 6 of 7 taxa (all except for *Amalda*) in the top 10% priority areas (Figure 4.4), and 5 of 7 taxa (except *Amalda* and *Echinocardium*) in the top 25% priority areas (Table 4.3). Changes in conservation efficiency also varied between taxa, with the largest conservation improvements in the proportion of density conserved observed for *Maldane, Glycera, and Asychis*.

Table 4.3: Proportion (%) of taxa density (across the entire study area and all density ranges) for all taxa, that would be protected within the top 10% and 25% conservation priority areas across different stressor scenarios. For each of the stressor scenarios defined (Table 4.2), two prioritisation runs were performed: a run with no stress using unimpacted density layers to drive the prioritisation, referred to as the baseline density (Scenario 1) and, a run containing both the unimpacted density layers (unweighted) and the corresponding impacted density layers (weighted) which were used to drive the prioritisation (Scenarios 2-4). The difference column provides the absolute difference in the proportion of density conserved between the stressor-impacted density layers (weighted) and unimpacted density layers (unweighted). *Taxon abbreviations: AMA = Amalda, ASY = Asychis, CAL = Callyspongia, ECH = Echinocardium, GLY = Glycera, MAL = Maldane, PEC = Pecten*

Taxa	**Top 10% Priority Areas**										**Top 25% Priority Areas**									
	Scenario 1 Un-impacted Density	**Scenario 2** Sediment Impacted			**Scenario 3** Fishing Impacted			**Scenario 4** Fishing & Sediment impacted			**Scenario 1** Unimpacted Density	**Scenario 2** Sediment Impacted			**Scenario 3** Fishing Impacted			**Scenario 4** Fishing & Sediment impacted		
	Unimpacted Density (Baseline)	Sediment – unimpacted (unweighted)	Sediment impacted (weighted)	**Difference:** Impacted – unimpacted	Fishing - unimpacted (unweighted)	Fishing impacted (weighted)	**Difference:** Impacted – unimpacted	Fishing & Sediment - unimpacted (unweighted)	Unimpacted Density (Baseline)	Sediment – unimpacted (unweighted)	Sediment impacted (weighted)	**Difference:** Impacted – unimpacted	Fishing - unimpacted (unweighted)	Fishing impacted (weighted)	**Difference:** Impacted – unimpacted	Fishing & Sediment - unimpacted (unweighted)	Unimpacted Density (Baseline)	Sediment – unimpacted (unweighted)	Sediment impacted (weighted)	**Difference:** Impacted – unimpacted
AMA	18.8	18.2	18.5	0.3	18.8	17.8	-1.0	18.7	17.7	-1.0	43.0	43.0	43.7	0.7	44.3	42.5	-1.8	44.0	42.0	-2.0
ASY	10.1	10.1	10.2	0.1	8.0	10.4	2.4	7.6	10.1	2.5	25.0	25.0	25.9	0.9	21.0	24.6	3.6	20.2	24.1	3.9
CAL	18.6	18.4	18.6	0.2	17.4	18.0	0.6	17.2	18.1	0.9	39.6	39.6	39.7	0.1	37.8	38.6	0.8	37.4	38.3	0.9
ECH	21.6	21.6	21.9	0.3	20.9	21.2	0.3	21.0	21.8	0.8	50.4	50.4	50.6	0.2	48.9	48.0	-0.9	49.2	48.3	-0.9
GLY	12.6	12.4	12.7	0.3	10.1	12.5	2.4	9.6	12.2	2.6	30.3	30.3	30.8	0.5	26.0	29.3	3.3	24.8	28.3	3.5
MAL	10.5	10.1	10.3	0.2	8.2	10.1	1.9	7.6	9.8	2.2	25.4	25.4	26.0	0.6	21.2	24.1	2.9	20.2	23.4	3.2
PEC	14.7	14.4	14.5	0.1	13.7	14.3	0.6	13.7	14.3	0.6	33.0	33.0	33.3	0.3	32.2	33.3	1.1	31.9	33.0	1.1

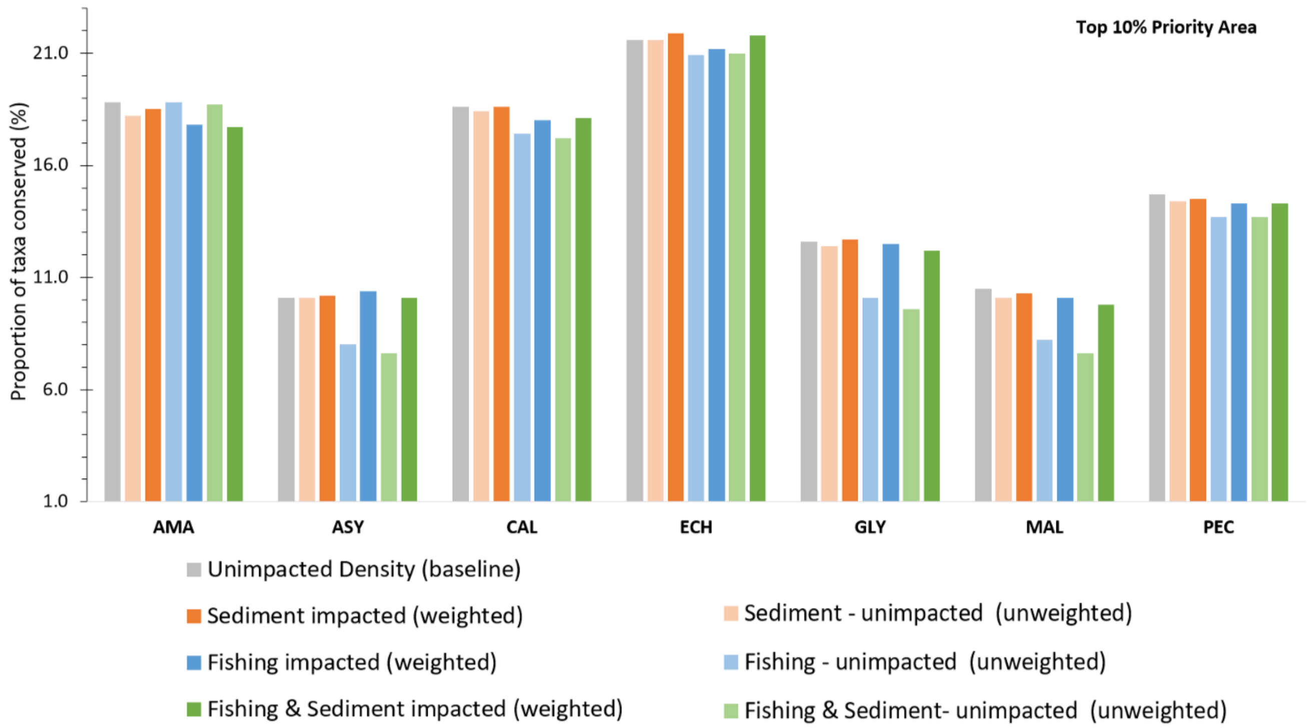


Figure 4.4: Histogram of Proportion (%) of density (across the entire study area and all density ranges) for all taxa that would be protected within the top 10% conservation priority area across different stressor scenarios, from data presented in Table 4.3. Each colour represents the stressor scenario run, with corresponding light-coloured bars (unimpacted density) and dark-coloured bars (impacted density) for each. The baseline scenario run without stress is coloured grey. *Taxon abbreviations: AMA = Amalda, ASY = Asychis, CAL = Callyspongia, ECH = Echinocardium, GLY = Glycera, MAL = Maldane, PEC = Pecten.*

4.2.2. Absolute taxon density

Focussing on mean density metrics (count per km2) between the unimpacted and impacted scenarios did not provide clarity on which scenario was more efficient, as mean density ranges were similar (Table 4.4). However, focussing on the total density conserved metric, prioritisation results revealed large increases in conservation efficiency using the impacted density layers compared to the unimpacted density layers (Scenarios 2-4) for most taxa (all except Glycera – Scenario 2 [Figure 4.5]). For example, in the combined fishing and sediment scenario (Scenario 4), the total density (count per km2) of *Callyspongia* conserved in the top 10% priority areas using unimpacted density was 38,199, which increased by 218% to 121,568, when using impacted density layers (Table 4.4). For all taxa, efficiency increases were observed for Scenario 3 (fishing impacted) and Scenario 4 (fishing and sedimentation impacted) which were often several times greater using impacted density layers, compared to unimpacted density (Figure 4.5).

In summary, small efficiency improvements were recorded over most taxa when stressor impacts were integrated and measured using the proportion of density conserved metric (Table 4.3, Figure 4.4). However, much larger improvements in conservation efficiency were observed when stressor impacts were integrated, revealed by the total density metric (Table 4.4, Figure 4.5). Results were mixed across all scenarios for mean density, indicating that total density may be a more relevant metric when comparing efficiency differences for absolute density.

Table 4.4: Density (mean, and total density [count per km^2]) for all taxa, that would be protected within the top 10% and 25% conservation priority areas across different stressor scenarios. For each of the stressor scenarios defined (Table 4.2), two prioritisation runs were performed: a run with no stress using unimpacted density layers to drive the prioritisation, referred to as the baseline density (Scenario 1) and, a run containing both the unimpacted density layers (unweighted) and the corresponding impacted density layers (weighted) which were used to drive the prioritisation (Scenarios 2-4). *Taxon abbreviations: AMA = Amalda, ASY = Asychis, CAL = Callyspongia, ECH = Echinocardium, GLY = Glycera, MAL = Maldane, PEC = Pecten.*

		Top 10% Conservation Priority Areas							**Top 25% Conservation Priority Areas**						
Taxa	Density	**Scenario 1** Unimpacted Density	**Scenario 2** Sediment Impacted		**Scenario 3** Fishing Impacted		**Scenario 4** Fishing & Sediment impacted		**Scenario 1** Unimpacted Density	**Scenario 2** Sediment Impacted		**Scenario 3** Fishing Impacted		**Scenario 4** Fishing & Sediment impacted	
		Unimpacted Density (Baseline)	Sediment - unimpacted (unweighted)	Sediment impacted (weighted)	Fishing – unimpacted (unweighted)	Fishing impacted (weighted)	Fishing & Sediment – unimpacted (unweighted)	Fishing & Sediment impacted (weighted)	Unimpacted Density (Baseline)	Unimpacted Density (Baseline)	Sediment - unimpacted (unweighted)	Sediment impacted (weighted)	Fishing – unimpacted (unweighted)	Fishing impacted (weighted)	Fishing & Sediment – unimpacted (unweighted)
AMA	Mean density	43.6	42.2	42.1	42.1	40.9	42.3	40.7	56.7	55.3	43.6	55.2	53.2	55.4	53.0
AMA	Total density	154,073	109,246	152,346	59,698	146,252	44,912	146,267	364,477	272,808	362,709	63,043	347,470	51,234	346,434
ASY	Mean density	20.2	29.7	29.7	31.6	31.2	29.4	31.0	27.6	39.5	39.8	41.6	41.3	39.4	41.3
ASY	Total density	71,994	76,759	106,951	44,708	112,162	31,575	111,583	191,147	200,112	271,817	47,272	276,521	36,431	278,630
CAL	Mean density	30.4	36.1	35.5	35.9	34.5	36.0	34.4	38.2	45.2	44.3	46.5	43.4	46.6	43.2
CAL	Total density	106,279	92,326	126,862	50,573	121,630	38,199	121,568	231,469	207,187	271,082	53,295	266,339	43,322	265,335
ECH	Mean density	38.0	37.6	41.6	39.3	40.2	41.5	40.8	49.4	49.7	53.9	53.1	51.9	55.1	52.3
ECH	Total density	134,823	136,914	151,366	60,043	143,055	43,779	144,601	317,902	334,744	353,744	63,598	334,007	50,345	332,107
GLY	Mean density	24.4	41.7	37.8	36.4	36.9	37.8	32.9	54.5	50.1	48.9	49.0	50.1	49.3	24.2
GLY	Total density	86,636	108,499	98,034	51,784	132,801	39,967	133,911	224,568	269,296	251,596	54,985	329,590	45,916	329,203
MAL	Mean density	27.3	44.0	43.9	43.8	42.8	44.2	42.6	37.2	58.4	58.4	57.9	57.2	58.3	57.0
MAL	Total density	96,901	113,666	159,121	62,163	154,170	46,921	153,536	257,296	293,716	396,007	65,771	387,861	53,743	389,249
PEC	Mean density	22.3	23.6	23.3	21.6	23.1	23.9	23.5	28.6	30.1	29.9	29.3	30.0	31.3	30.3
PEC	Total density	77,579	60,748	83,997	30,480	81,814	25,282	83,250	180,018	143,171	192,234	32,461	193,936	28,833	193,500

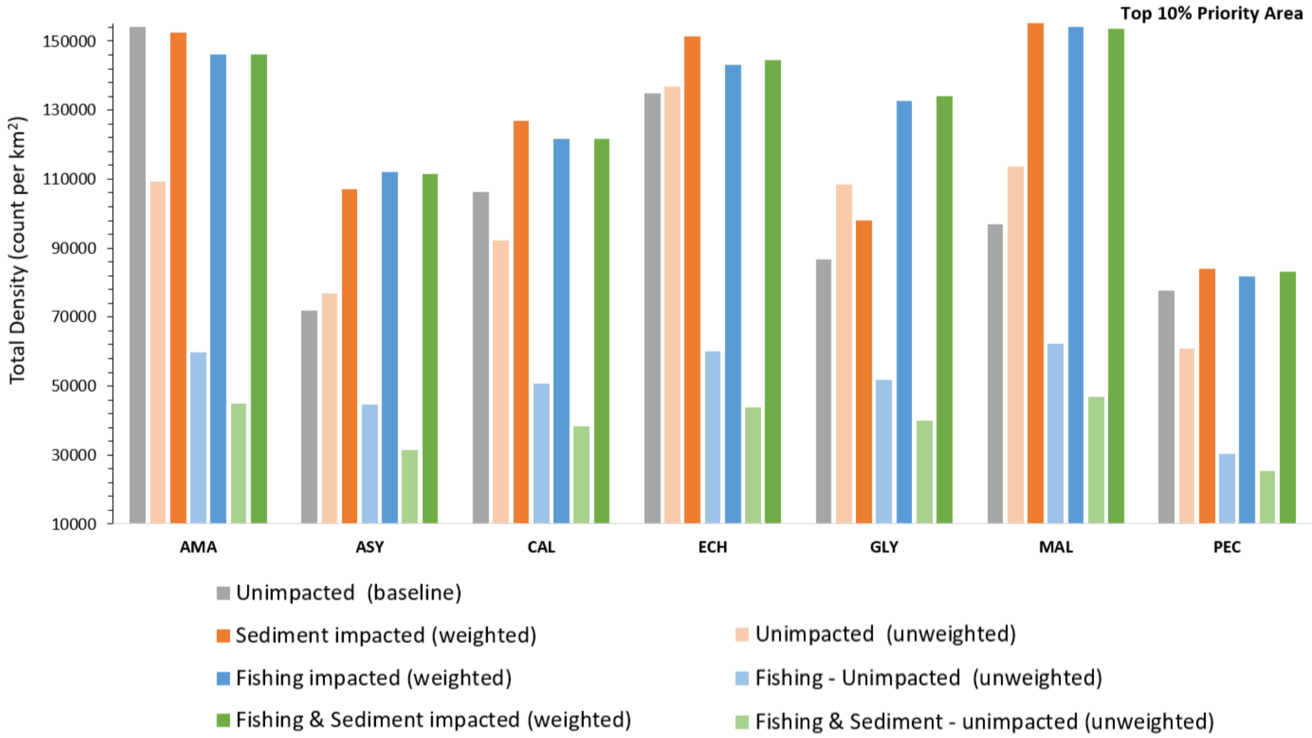


Figure 4.5: Histogram of Total Density (count per km^2) that would be protected within the top 10% conservation priority area across different stressor scenarios, from data presented in Table 4.4. Each colour represents the stressor scenario run, with corresponding light-coloured bars (unimpacted density) and dark-coloured bars (impacted density) for each. The baseline scenario run without stress is coloured grey. *Taxon abbreviations: AMA = Amalda, ASY = Asychis, CAL = Callyspongia, ECH = Echinocardium, GLY = Glycera, MAL = Maldane, PEC = Pecten.*

4.3. Discussion

Scientific literature has shown that protected areas seldom provide effective biodiversity conservation when not protected from unmitigated environmental impacts, land-use changes, weak governance, and climate change (Maxwell *et al.*, 2018; Schulze *et al.*, 2018; Tesfaw *et al.*, 2018). Prior management practices that used qualitative approaches to designate conservation areas may be insufficient for identification and implementation, as they are unlikely to be robust to modern climatic and anthropogenic stress (Di Minin and Moilanen, 2012; Geange *et al.*, 2017; Leathwick *et al.*, 2008). This analysis investigated how the inclusion of multiple anthropogenic stressors (using stressor-impacted density predictions) can drive changes in areas prioritised for conservation management and found key differences in total density conserved and the spatial pattern of prioritised habitats, between scenarios that did, and did not incorporate stressors. This analysis demonstrated that allocation of conservation areas based on high-density values alone, without accounting for stressor impacts, could result in the selection of habitats that are ecologically diminished or could become degraded over time, hence reducing conservation efficiency. In addition, incorporating temporal dynamics into a prioritisation assessment (i.e., stressor effects that have accrued over time) can help identify areas where high density persists, even under stressed environmental conditions. These persistent high-density habitats have shown resilience to multiple stressor impacts, and hold high conservation value, as they are likely to retain a higher total density to support long-term conservation objectives. This analysis helps address, in part, a persistent knowledge gap in conservation planning (non-stationary system dynamics; Williams and Brown, 2023) through the inclusion of at least one (of many) temporal dynamics that could prove useful to support effective longer-term marine conservation.

Quantifying shifts in species distribution from multiple environmental stressors is essential for effective conservation (Ellis *et al.*, 2017; Rullens *et al.*, 2022; Chapter 3), which is supported by the results from this analysis. Prioritisations performed using the impacted density predictions provided less effective protection over the high-density areas identified in the unimpacted scenario, showcasing how the inclusion of stressors reduced emphasis on areas with high stressor loads. The fine resolution of the data layers used in this analysis (250 m) helps to provide greater detail and highlight spatial nuances of the prioritisation distribution that would be more challenging to identify using a coarser data resolution (i.e., > 1km), particularly in the transition zones around the aquaculture sites and existing protected areas. Practitioners have cited that quantifying the combined and overlapping effects of multiple stressors is challenging due to data limitations and the technical capacity of existing optimisation approaches (Gissi *et al*., 2021; Orr *et al*., 2020 Tulloch *et al*., 2021; Simeoni *et al*., 2023; Janßen *et al*., 2019). This analysis approach helps overcome these challenges by integrating the multiple stressor effects into a density SDM via a correlative approach (Chapter 3) so that the prioritisation analysis can be performed within the technical capacity of the existing decision support tool. In addition, Watson *et al*., (2022) demonstrated that SDM data limitations can be overcome in part, by performing predictive modelling over different spatial scales and sample numbers, to select the more optimal model to create ecologically informative density SDMs. Although adopting a combination of different spatial approaches may provide imperfect results and incorporate more model assumptions (Gallien *et al*., 2010; Hodgson and Halpern *et al*., 2019), it can allow for better inference of predictions rather than relying on just a single method (Gissi *et al*., 2017), and help overcome limitations inherent in each approach.

Understanding how both bottom fishing and sedimentation stress impact benthic ecosystems represents a key research gap within conservation planning, as few literature examples spatially quantify their combined impact (although see Tulloch *et al*., 2021, Delevaux *et al*., 2018; MacNeil *et al*., 2019). Given the demonstrated importance of fishing in changing marine ecosystems, researching how fishing interacts with other stressors was identified as a critical research need many years ago (Crain *et al*., 2008; Worm *et al*., 2006), but persists today. This analysis addresses this research need by providing a quantitative spatial approach that integrates both fishing and sedimentation stress into systematic conservation planning. It supports management practitioners with conservation targets by helping differentiate between areas of high conservation value, and areas of low conservation value based on habitat condition (Williams and Brown, 2023). Furthermore, results suggest that accounting for multiple stressor effects via this approach helps increase conservation efficiency compared to analysis that does not include stressors, by highlighting high-density areas that persist over time, even in the presence of multiple stressors (McLeod *et al*., 2019).

Although this approach demonstrated that greater efficiency can be achieved when stressors are accounted for, conservation outcomes are highly dependent on the management strategy (Catarino *et al*., 2015). Strategies for conservation typically focus on the identification and mitigation of threats, or avoidance of threat-impacted areas (Auerbach *et al*., 2015; Cawardine *et al*., 2012). From this application, it could be argued that a hybrid conservation strategy would be most fitting; to avoid areas with the highest disturbance and stressor regime and mitigate threats to a more sustainable level (or full protection) in the remaining high conservation value areas. This approach does not advocate for complete stressor avoidance, rather it highlights that ecologically valuable areas persist even within the footprints of multiple stressors (Chapter 3) which should be considered more, though I acknowledge that these areas often correlate with lower stressor magnitude (particularly trawl effort). Conservation managers need to be able to justify the appropriate level of ecological impact and balance resource needs (Possingham *et al*., 2015; Kuempel *et al*., 2018) as results suggest that lower levels of ongoing stressor exposure can be tolerated, but higher levels should be mitigated to prevent further density decline in an already ecologically stressed environment. Although not explicitly addressed in this analysis, conservation managers need to also consider recovery (Ng *et al*., 2014). Marine management often focuses on addressing more immediately damaging threats (e.g., fishing, pollution) from which there can be recovery potential (not always) if the stressor is removed or abated (Stephenson *et al*., 2019; Lambert *et al*., 2014). However, this analysis highlighted that the effects of sedimentation extend into conservation areas protected from fishing, from which there is little to no recovery (as sedimentary mud levels remain elevated without effective management), and impacts accumulate over time (Thrush *et al*., 2004; Douglas *et al*., 2023). The accumulation of sedimentation stress can be equally impactful to the biogenic structure forming epifauna (e.g., *Callyspongia*) as fishing, which experience comparable reductions in density from these stressors (Chapter 3). Concentrating on only marine-based stressors (just fishing) may still result in continued ecological decline, calling attention to a greater need for land-to-sea assessment of stressors (Klein *et al*., 2010; Álvarez-Romero *et al.,* 2011; Tulloch *et al*., 2021), and legislative reform to require cross realm stressor management in coastal policy plans (Álvarez-Romero *et al.,* 2011; Ban *et al*., 2010).

In addition to the need for increased land-to-sea assessment, this research also highlights that systematic conservation planning should endeavour to be informed by abundance or density data, as it is more informative of ecosystem health than the probability of occurrence. Research has shown that spatial predictions of occurrence and abundance can differ, as drivers of high abundance may not align with those that determine a high probability of occurrence (Howard *et al*., 2014; Rullens *et al*., 2021; Chapter 2). For many species, their functional capacity is inherently density-dependent (Lohrer *et al.*, 2004; Spaak *et al.*, 2017), and environmental stressors impact population density, hence limiting the functional ability of trait behaviour (i.e., sediment mixing from bioturbation) and lowering species contribution to ecosystem processes (Bremner, 2008; Gladstone-Gallagher *et al.*, 2019; Harborne *et al.*, 2017). Therefore, ecosystem health and its resilience to stressors is tied to the abundance and diversity of species assemblages which contribute to critical ecosystem functioning (Gladstone-Gallagher *et al.*, 2019; Thrush *et al.*, 2006).

This analysis also provides a novel contribution with the inclusion of spatially explicit measurements of uncertainty for each taxa density prediction, which allows practitioners to differentiate between areas that are assigned low priority based on high levels of uncertainty, and those based on poor conservation value (from combined stressor and density attributes). For successful transferability to other locations, marine practitioners also need to be able to differentiate between low-accuracy and high-accuracy predictions to ensure that spatial data used to drive management decisions are both useful and environmentally representative (Pınarbaşı *et al.*, 2017; Yates *et al.*, 2018; Zurell *et al.*, 2021). However, these uncertainty estimates only pertain to the unimpacted density predictions (the SDMs), and not the stressor-impacted predictions. Performance and uncertainty metrics were not yet available for the impacted density predictions due to a lack of quantified methods (Zurrell *et al*., 2021) for this approach. However, here I outline some parameters that may contribute to greater uncertainty so that they could be improved upon in future applications of this methodology to provide a more robust prioritisation assessment. Impacts of bottom trawling only accounted for bottom trawls and no other forms of fishing disturbance (such as dredging) have been recorded within the study area (Handley*, 2006*; Baird *et al*., 2015). Therefore, impacts from fishing are likely conservative and future research should attempt to provide a more comprehensive estimate of benthic disturbance from fishing (e.g., Stephenson *et al*., 2023), which could also consider a longer temporal range of annual trawling data. Sedimentation impacts were estimated by increasing sediment mud content annually, in addition to existing levels of mud (Chapter 3). The application of a uniform increase in sediment mud content does not account for the dynamics of sediment transport in shallow coastal systems (Bostock *et al.*, 2018; Hateley *et al.*, 2005), and could be improved through the incorporation of a catchment model to determine sediment deposition rates from the surrounding landscape (e.g., Delevaux *et al*., 2018; Alvarez-Romero *et al*., 2015). Lastly, the impacted density predictions do not include model terms which account for a stressor response based on population dynamics (e.g., reproduction rate), which if included may better represent real-world equilibriums (e.g., carrying capacity) and could be incorporated for more accurate density loss predictions (Lipcius *et al.*, 2019; Spaak *et al.*, 2017).

Incorporation of stressor-impacted density provided modest efficiency improvements over most taxa via the proportion of density conserved metric (0.1-3.9% - Table 4.3), a commonly applied measurement to assess prioritisation performance conventionally applied to prioritisations based on occurrence data (Bennion *et al.*, 2023; Jackson and Lundquist, 2016; Leathwick *et al.*, 2008; Rowden *et al.*, 2019). However, large improvements were recorded over all taxa in the multiple stressor scenarios when measuring total density (stressor impacted), often conserving 2-3 times greater density than unimpacted density layers for the same scenario. The contrast in the efficiency highlights two key findings: (1) when integrating density measurements into a prioritisation assessment, practitioners need to apply a density-specific efficiency metric as conventional approaches do not highlight the extent of these improvements; and (2) areas prioritised without integrating stress often experience large reductions in density when stress is applied. These findings advance knowledge within systematic conservation planning and highlight the need to account for multiple stressor effects to provide a more representative indication of the efficiency (in either cost or biodiversity) of the proposed conservation areas (Simmons *et al.*, 2021; Stephenson *et al.*, 2023; Ellis *et al.*, 2017).

Here, I have demonstrated that the inclusion of multiple anthropogenic stressors does drive changes in areas prioritised for conservation management, and therefore marine managers need to change the way they account for stressor effects in systematic conservation planning. I have presented a new approach aimed at incorporating the combined effects of both bottom fishing and sedimentation over time, with consideration of uncertainty, into spatial prioritisation assessments by applying stressors via a correlative stressor model outside of decision-support software prior to spatial prioritisation. This assessment highlights that perhaps practitioners do not need to re-develop existing DSTs to achieve conservation objectives (Pınarbaşı *et al.*, 2017). Rather, complex non-linear stressor relationships can be incorporated within a more customisable programming environment, and then those outputs can be integrated within the decision-support software. Primarily, this analysis demonstrated that conventional approaches to systematic conservation prioritisation are inefficient as the density and distribution of taxa may change in highly stressed environments (Chapter 3). If marine managers fail to adequately account for multiple stressor effects these negative drivers will undermine conservation effectiveness and areas identified for protection may not be resilient to further stressor impacts and become ecologically diminished in the future (Jones *et al.*, 2016; McLeod *et al.*, 2019; Tulloch *et al.*, 2021). To ensure that conservation targets are upheld under ongoing anthropogenic conditions, marine managers must aim to identify robust and ecologically resilient habitats via contemporary assessment methods.

5. General Discussion

5.1. Summary

Multiple stressor impacts in coastal environments can cause broad-scale changes to coastal ecology by modifying habitats and altering the density and distribution of functionally important benthic invertebrates (Ellis *et al.*, 2017; Thrush *et al*., 2021). Many benthic invertebrates physically modify their habitat through key ecological functions like bioturbation, filter-feeding, depositing organic matter and biomass production (Lohrer *et al*., 2004; Hewit *et al*., 2018), which in turn supports the health of the seafloor ecosystem and provides additional ecosystem services upon which humans rely (e.g., food provision, water quality regulation; Berthelsen *et al.*, 2019; Rullens *et al.*, 2021). Many taxa disproportionately contribute to ecosystem health, their functional capacity is inherently density-dependent, and they are at high risk of functional extinction under increasing rates of physical disturbance (Lohrer, Thrush and Gibbs, 2004; Lundquist *et al.*, 2018; Spaak *et al.*, 2017; Thrush *et al.*, 2006; Thrush *et al.*, 2021).

A greater understanding of the density and distribution of functionally important taxa that are found across shallow seafloor ecosystems is vital so that marine managers can monitor how these patterns may change over time to be able to differentiate between natural environmental change and change induced by poor management and anthropogenic stress. Species Distribution Models (SDMs) are increasingly used to inform marine management and support more complex spatial assessments, however, most existing SDMs only predict the probability of occurrence and not density (Melo-Merino *et al*. 2020). Furthermore, due to data limitations, outputs are often at a coarse resolution (>1 km), and not at a scale (i.e., national scale) useful for regional management. In **Chapter 2** I developed probability of occurrence, abundance, and density models for seven key coastal seafloor invertebrates at a fine resolution useful for management (250m), and investigated the implications of model scale (i.e., regional datasets vs. national datasets), on predictive performance and distribution patterns generated for each model. Neither density (count per km^2) SDMs nor abundance (count per sample unit) SDMs were available within the defined study area (Tasman and Golden Bay), which required new models to be created, and these models were utilised in subsequent stressor models (e.g., Chapter 3). The analysis revealed that while well-performing SDMs were created for all taxa, the predictive performance of SDMs varied across model type and scale, indicating that no singular approach was optimal across all taxa. Models are typically created at a single scale or using a single data type, which often restricts species assessments based on data availability within a restricted geographic area. In this study, I demonstrate the utility of a two-scale approach which aids the selection of the most optimally performing, and spatially representative models across all available data, to address a key research barrier – data scarcity. This analysis contributes new spatial modelling knowledge by demonstrating that SDM performance and accuracy are not defined by the model scale (although they can vary between taxa); rather the stratification of data, distribution of records, and representation of environmental data all have a greater influence. Therefore, marine practitioners can overcome many of the challenges that usually impede the usefulness of regionally restrictive SDMs (e.g., coarse resolution, data scarcity, poor taxa representation in sample data) by exploring solutions over a broader geographical scale to create ecologically informative model outputs at a resolution useful for regional managers (Melo-Merino, Reyes-Bonilla and Lira-Noriega, 2020; Robinson *et al.*, 2017). Broad application of this approach could result in the generation of new density SDMs for many coastal taxa and increase the availability of spatial outputs to be used for decision-making and multiple stressor assessments.

Bottom fishing is considered to be the greatest source of anthropogenic disturbance to benthic communities globally, due to the scale and continuousness of the activities (Dayton *et al.*, 1995; Jennings and Kaiser, 1998; Kaiser *et al.*, 2000). The physical effects of bottom trawling can reduce the abundance of macrofaunal communities, change functional community composition (Lundquist *et al.*, 2018) and can lead to homogenisation of the seascape (Hiddink *et al.*, 2006; Kaiser *et al.*, 2006; Lundquist *et al.*, 2018; Sciberras *et al.*, 2018). Inadequate land management has resulted in increased sedimentation from the deposition of terrestrially sourced mud into the coastal environment, greatly beyond the natural rate of delivery (Davies *et al.,* 2018; Thrush *et al*., 2004). Increased sediment mud content can also alter sediment properties by affecting the exchange of solutes, oxygenation, and nutrient processing which in turn can alter macrofaunal community composition (Pratt *et al*., 2015). The effects of sedimentation are particularly damaging in shallow seafloor ecosystems, due to the re-suspension of mud from waves and currents in addition to re-suspension from bottom trawling which can also increase the turbidity of coastal waters (Newcombe, 2016; Thrush *et al*., 2004). Further contributing to the individual impact of these stressors, fishing and sedimentation often overlap spatially and temporally in coastal environments (Crain *et al*., 2008; Lundquist *et al*., 2013; Leduc *et al*., 2024) resulting in combined gradients of stress where they co-occur. Soft-sediment macroinvertebrates are considered sensitive indicators of ecosystem health and are regularly used to assess the effects of natural and anthropogenic disturbances (Borja, Franco and Pérez, 2000; Pearson and Rosenberg, 1978; Rodil, Compton and Lastra, 2012; Weisberg *et al.*, 1997).

In **Chapter 3** I developed a correlative stressor model to quantify how the impacts of bottom fishing and sedimentation modify the density and distribution of three coastal seafloor invertebrates: by genus – *Amalda, Echinocardium and Callyspongia,* which each have different functional roles (i.e., predatory scavenging gastropod vs substrate destabilising urchin) and vary in stressor response and recovery time. The correlative stressor model spatially modified taxa density SDMs based on empirically derived stressor responses to the stressors (individually and in combination) and magnitudes (+ 1% - 3% mud) over four years of successive (i.e., accumulating) impact. I demonstrated that functionally distinct taxa respond to both individual and multiple stressor exposures differently, resulting in both positive and negative changes to community composition throughout the coastal environment. A key result from this analysis highlighted that although bottom fishing is considered the more dominant stressor, sedimentation stress was almost as impactful on taxa density for sensitive emergent epifauna (e.g., *Callyspongia*), highlighting that greater management consideration should be given to the compound effect of slow-acting, accumulating stressors, from which there is little to no recovery for many taxa. This research fills a key knowledge gap by spatially quantifying the effects of bottom fishing and sedimentation on taxa density in a subtidal environment, as literature which considers the impacts of terrestrially derived stressors in combination with fishing is sparse (Tulloch *et al*., 2021, Delevaux *et al*., 2018; MacNeil *et al*., 2019).

As the demands for ocean space and resources grow, marine managers require systematic conservation solutions that spatially integrate impacts from anthropogenic sources to help identify remaining ecologically rich and resilient habitat areas that will persist over time under multiple stressor conditions (McLeod *et al.*, 2019). Due to data scarcity, and the technical limitations of existing optimisation approaches, systematic conservation planning typically has not incorporated measurements of density and often uses coarse-resolution data, or proxies to represent anthropogenic stressors. These technical limitations may lead to conservation actions being implemented in unsuitable habitats that are either currently under stress or will succumb to stress over time (Geange *et al*., 2017; Tulloch *et al.*, 2021; Stelzenmüller *et al*., 2020; Stephenson *et al*., 2022). Furthermore, there is a greater need for research that considers terrestrially-derived threats in addition to marine-based threats to support a more holistic land-to-sea conservation approach (Klein *et al*., 2011; Álvarez-Romero *et al.,* 2011; Tulloch *et al*., 2021).

In **Chapter 4** I investigated how the inclusion of empirically-derived responses to bottom fishing and sedimentation stress can drive changes in areas prioritised for conservation management and could be used to inform management decisions. Conservation efficiency and prioritised areas were compared between scenarios run using unimpacted density predictions (the conventional approach) and taxa density modified via a correlative stressor model (impacted density predictions). I demonstrated that areas prioritised for high conservation value using unimpacted density layers experienced large declines in density when stressors were accounted for, highlighting that if conservation assessments fail to integrate multiple stressor impacts, it may result in the selection of habitats that are ecologically diminished or those that could become degraded in the future. All prioritisations run using stressor-impacted density layers increased conservation efficiency (total density conserved) and identified habitat areas that have shown resiliency to stressors over a temporal scale of 4 years and are more likely to retain a higher total density into the future to support long-term conservation objectives. This analysis approach helped to address some of the persistent knowledge gaps in conservation planning outlined by Williams and Brown (2023), by supporting, in part, the prediction of longer-term impacts of accumulating stressors to help inform future consequences of management, and through the incorporation of spatiotemporal dynamic elements, often missing from conservation planning (William and Brown 2013; Álvarez-Romero *et al.,* 2011. Analyses revealed that failure to adequately account for multiple stressor effects will likely undermine conservation effectiveness, and conservation managers could benefit from the utility of this approach to lower the risk of selecting areas for conservation that may not be resilient to stressor impacts over time (Jones *et al.*, 2016; McLeod *et al.*, 2019; Tulloch *et al.*, 2021).

Collectively, the research chapters comprised in this thesis provide insights into how multiple anthropogenic stressors spatially modify the density and distribution of functionally important benthic invertebrates and in turn compromise the efficacy of marine conservation targets if impacts are not adequately identified or managed. A combination of inadequate assessment approaches, data scarcity, and poor integration leaves coastal managers and practitioners unable to appropriately quantify and mitigate multiple stressor impacts (Simeoni *et al.*, 2023; Orr *et al.*, 2020; Orobko *et al.*, 2022) which continue to degrade the marine environment and diminish natural resources (Davies *et al*., 2020; Foley *et al.*, 2017). The methodologies outlined in this thesis provide novel approaches that can help overcome challenges with data scarcity and help spatially quantify multiple stressor impacts in coastal ecosystems using available data. Results from Chapter 3 indicate that even over a temporal scale of 4 years, benthic assemblages have undergone large declines in density (up to -19.6%), and due to the regular recurrence of stressors, there is little to no recovery, leading to community homogenisation over time. Benthic invertebrates provide key ecological functions which support the health of the seafloor ecosystems (Lohrer, Thrush and Gibbs, 2004; Rullens *et al.*, 2021), and management strategies should focus on conservation, stressor mitigation and better integration of land-to-sea stressor monitoring and assessment (Delevaux *et al*., 2018; Alvarez-Romero *et al*., 2011; Tulloch *et al*., 2021). Results from Chapter 4 emphasised that the identification of conservation areas based on high-density values alone, without accounting for stressor impacts, resulted in inefficient conservation outcomes. Furthermore, failing to adequately account for terrestrially-derived sedimentation undermined the conservation effectiveness of existing conservation areas, and acted in opposition to the management efforts for other stressors. The spatial information generated from Chapters 3 and 4 helps advance conservation management by revealing locations that are most impacted by, and most resilient to, multiple stressor impacts, helping to optimise decision-making.

This research has also reinforced that management approaches focusing on single stressor impacts are likely to be at high risk of exceeding ecological tipping points (Thrush *et al*., 2021; Lundquist *et al*., 2016), and that even in the presence of a dominant stressor (i.e., fishing) other stressor effects can be equally as impactful as they accumulate over time (e.g., sedimentation). Predicting both abrupt and long-term environmental change from anthropogenic stress remains a major challenge (William and Brown 2013) for conservation management. While the improvement of long-term data and environmental monitoring is vital, these actions alone will not be sufficient to create knowledge-driven management actions to prevent continued degradation (Hewitt, Lundquist, and Ellis, 2019; Ratajczak *et al*., 2018). In an era of advancing objectives, shifting baselines, and ongoing challenges with imperfect data (Atmore, Aiken and Furni, 2021; Hodgson and Halpern *et al*., 2019), the development of an all-encompassing multiple-stressor spatial assessment tool remains elusive (Stelzenmüller *et al*., 2020). Conservation practitioners should focus on adopting a combination of empirically-driven spatial modelling approaches, utilising currently available datasets to move forward, not with perfect prediction, but with an interim solution to overcome specific limitations of traditional models and prevent ‘’analysis paralysis’’ (Davies *et al*., 2020; Gissi *et al*., 2017).

5.2. Benthic invertebrate response to stress

The possible pathways for multiple anthropogenic stressors to impact benthic habitats in shallow coastal ecosystems are numerous: directly (e.g., bottom fishing disturbance), indirectly (trophic changes in population size), interactively, through accumulation over time, and any combination thereof (Furlan *et al*., 2018; Hiddink *et al*., 2011; Jennings *et al*., 2001; Willsteed *et al*., 2018). As human population growth continues, so do our insatiable ocean-based resource needs, satisfied in the form of ecosystem services (Rullens *et al*., 2019; Bremner *et al*., 2008; Townsend *et al*., 2018). Growing resource requirements coupled with inadequate management, bear us to witness continued environmental degradation and diminishment of our natural resources (Davies *et al*., 2002; Foley *et al*., 2017; Winship *et al*., 2020). Ongoing decline in benthic organism density across many taxa simultaneously, could lead to a reduction in seafloor biodiversity, a key mediator of ecosystem functioning (Thrush *et al*., 2021; Norkko *et al*., 2013). Despite the functional importance of benthic invertebrates, their roles are often not appreciated, leading to knowledge gaps for species that perform critical ecological roles (e.g., formation of biogenic structures, and sediment mixing (Hillman *et al*., 2019). The role of benthic invertebrates acting as indicators of ecosystem health is central to this thesis as they provide a pathway of understanding to incorporate multiple stressor impacts into marine spatial management (Borja, Franco, and Pérez, 2000; Pearson and Rosenberg, 1978; Rodil, Compton and Lastra, 2012; Weisberg *et al*., 1997). This thesis has demonstrated that benthic invertebrate responses to multiple stressors are taxon and stressor-specific, although general trends of impact were associated with more sensitive or fragile functional traits.

5.2.1. Benthic invertebrate density

For many species, their ability to support ecosystem functions through key roles is inherently density-dependent (Lohrer *et al.*, 2004; Spaak *et al.*, 2017), and environmental stressors can impact population density, hence reduced population size would limit the functional capacity of species and their ability to contribute to ecosystem processes (Bremner, 2008; Gladstone-Gallagher *et al.*, 2019; Harborne *et al.*, 2017). Therefore, ecosystem health and its resilience to stressor impacts are tied to the abundance and diversity of species assemblages which contribute to ecosystem functioning (Gladstone-Gallagher *et al.*, 2019; Thrush *et al.*, 2006). Thus, accurate predictions of density for a representative group of coastal invertebrates were considered essential to model the effects of stressors over the wider coastal environment encompassing Tasman and Golden Bay. Species Distribution Models (Chapter 2) were used to create taxon-specific predictions of density at a fine resolution and to facilitate the correlative multiple stressor models in Chapter 3. Without the consideration of stressor effects, SDMs predicted mid to high levels of density over most of the shallow coastal area for all taxa, reducing in the outer bays over a depth gradient. Although good performance metrics were achieved (Table 2.2), the stark changes observed in taxa densities when stressors were incorporated in Chapter 3 (Figure 3.6) bring into question their usefulness as standalone models given the knowledge of historic and ongoing stressor regimes in the study area (Handley, 2006). Generally, marine managers approximate where the greatest areas of impact are by overlaying occurrence maps (and other biotic and abiotic indices) with static stressor footprints (e.g., Halpern *et al*., 2009). Outputs from Chapter 3 advance knowledge by spatially quantifying the magnitude of density change, in relation to the magnitude of stressor, and identifying which taxa are most and least impacted over time to provide a more realistic representation of real-world conditions.

Prolonged changes in species relative and absolute abundance, habitat homogenisation and declines in species richness have been recorded in many marine ecosystems worldwide, with associated reductions in functional services (e.g., oxygenation of sediments) mediated by key taxa roles (Halpern *et al.*, 2019; Hewitt, Thrush and Dayton, 2008; Loreau *et al.*, 2001; Lundquist *et al.*, 2018; Thrush and Dayton, 2002; Thrush *et al.*, 2004). Reduced densities of large, functionally important taxa (e.g., *Callyspongia, Echinocardium,*) can have more profound impacts on sediment biogeochemistry, environmental regulation, and trophic linkages than smaller species (Thrush *et al.*, 2006). Furthermore, in marine benthic environments, larger individuals play a prominent role in influencing processes related to fluxes of energy and matter (Green, Hewitt and Thrush, 1998; Sandnes *et al.*, 2000). Loss of large suspension feeders (e.g., *Pecten, Callyspongia*) and deposit feeders (e.g., *Echinocardium*) can alter community composition, modify surficial sediment characteristics, and influence oxygen and nitrogen fluxes (Norkko *et al.*, 2013; Thrush *et al.*, 2006). The correlative stressor models predicted greater density reductions for larger-bodied invertebrates (e.g., *Callyspongia, Echinocardium)* than smaller ones (e.g., *Amalda).* Although this analysis did not specifically focus on the intra-specific body size of individuals, disturbance events were recurrent, which can prevent taxa from reaching large sizes therefore reducing (if not removing) the contribution that large individuals make to ecosystem functionality (Norkko *et al*., 2013).

To determine patterns of change in community composition and density, long-term monitoring of benthic macroinvertebrates is essential (Hewitt *et al*., 2014: Tremblay *et al*., 2023). Although benthic monitoring is conducted in New Zealand, it is performed by a range of organisations (e.g., research institutions, universities, regional and central government agencies), and for a variety of purposes, which results in spatially and temporally inconsistent datasets. This lack of coordination presents several challenges: focal species often vary, recording of abundance data is not consistent, benthic invertebrate monitoring occurs primarily in intertidal environments, the resolution of taxonomic identification is not standardised (i.e., species level, genus level), and the sampling frequency is highly variable (though some sites are monitored continuously; Hewitt *et al.*, 2014). Consequently, the development of SDMs also tends to be spatially biased toward the most spatially sampled environments, and towards species with perceived economic (e.g., mussels, oysters) or recreational value resulting in less spatial information and knowledge gaps for species that perform critical ecological roles (e.g., formation of biogenic structures; Hillman *et al*., 2019; Ribo *et al*., 2021; Costello *et al*., 2015). Due to sampling limitations and data scarcity, several adjustments to the approach developed for Chapter 2 had to be made, such as amalgamation and standardisation of records across multiple institutional databases (Table A1: 1), modelling at the genus level instead of species level, and reducing the number focal taxa to ensure that sample record numbers were sufficient for modelling. The disparity in environmental monitoring and lack of sampling in subtidal and coastal environments will make the detection of environmental shifts (i.e., change in density and distribution) from anthropogenic stressors difficult to distinguish from natural variability (Hewitt *et* *al.*, 2014; Tremblay *et al.*, 2023; Pratt *et al.*, 2015) and is an essential step to informing accurate multiple stressor modelling tools.

Declining species abundance also has implications for ecosystem services: provisioning-based services (e.g., seafood/shellfish), functional-based services (e.g., nutrient cycling, sediment oxygenation) and socio-cultural services for indigenous people in New Zealand such as a reduced abundance of 'kaimoana' (seafood) including taonga or treasured species (e.g., Pāua; Bennion *et al.*, 2023). Consequently, managers require spatial tools that allow the impacts upon the density of key seafloor invertebrates to be quantified and predicted over broader spatial scales than usually quantified in empirical studies (Melo-Merino, Reyes-Bonilla and Lira-Noriega, 2020). However, spatial data detailing the density or abundance of benthic invertebrates remain sparse and spatially disproportionate, compared to occurrence data (Howard *et al.*, 2014; Johnston *et al.*, 2015). A recent literature review on marine-based SDM applications revealed that only 9% of studies incorporated measurements of density, biomass, or species richness (Melo-Merino, Reyes-Bonilla and Lira-Noriega, 2020). Benthic invertebrate capacity to support essential ecosystem functioning is density-dependent, and spatial solutions to provide vital knowledge on benthic density and distribution patterns must move forward with available data whilst broader environmental monitoring and sampling efforts adapt to the changing requirements of modern analytical approaches (Hewit *et al.*, 2014; Stephenson *et al.*, 2023). In the absence of well-distributed regional data, national models can achieve good density predictions regionally for many taxa (Chapter 2).

5.2.2. The benefit of taxa-specific stressor response

It is generally well-accepted that the diversity of functional traits within species communities drives several ecological processes (Leitao *et al.*, 2016; Thrush and Dayton, 2002) and there is a growing awareness that the risk of diminished ecosystem functioning caused by a loss in specific processes is increasing under greater levels of anthropogenic stress and biodiversity loss (Naeem, Duffy and Zavaleta, 2012). As many species disproportionately contribute to ecosystem health (Thrush *et al.*, 2021), proactive management of stressor impacts will need to consider the importance of critical ecological processes facilitated by functional roles of key taxa (i.e., functional traits). Functional extinction of species is non-random, and the risk is correlated with functional traits such as living position in the sediment, body size and sensitivity to environmental stressors (Hewitt, Thrush and Dayton, 2008; Lundquist *et al.*, 2018; Solan *et al.*, 2004). An example of this concept would be for stressor management to consider the essential roles of bioturbators, by which certain species alter sediment composition, adding to heterogeneity, thereby altering community composition, and leading to increased oxygenation of sediments (Norkko and Shumway, 2011). Large burrowing spatangoid sea urchins (i.e., *Echinocardium*) likely dominate soft sediment bioturbation and influence sediment biogeochemistry in many locations due to their distinct functional role (Lohrer, Thrush and Gibbs, 2004). Other studies have also acknowledged that certain large-bodied benthic taxa may dominate some functional processes and provide important habitat structuring effects (Norkko *et al.*, 2013; Thrush *et al.*, 2006).

To ensure that critical ecosystem functions provided by key taxa are maintained, approaches to managing anthropogenic threats must consider how specific taxa (or species) respond to individual and multiple stressors. In some instances, the effects of stress and disturbance on benthic environments are easily observed (e.g., direct impacts from fishing gear); in other instances, the effects are more subtle (e.g., the slow accumulation of sediments over time; Pratt *et al.*, 2015; Rodil, Lohrer and Thrush, 2013; Thrush *et al.*, 2004). Recent literature has suggested however, that subtle impacts can lead to larger stressor effects such as breakdowns in feedback loops (e.g., incident light affecting sediment nutrient processing) which can lead to diminished ecosystem functioning, or tipping points from incremental impacts over time (Hastings *et al.*, 2018; Pratt *et al.*, 2015; Thrush *et al.*, 2021; Gladstone-Gallagher *et al.*, 2019). The impacts from small, increments of sedimentary mud were demonstrated in Chapter 3 of this thesis. From a 3% annual increase in mud, models predicted that sediment-sensitive taxa like *Callyspongia* would reduce in density by 9.5%, but that sediment-tolerant taxa such as *Echinocardium* would experience a density decline of only 1.3%, over 4 years. These findings further demonstrate that decisions to manage or mitigate stressor effects must account for taxon-specific responses to stressors, as functional traits have been shown to influence the stressor tolerance threshold of benthic invertebrates (Bremner *et al*., 2008; Ellis *et al*., 2017; Hewit *et al*., 2018). Relationships between fishing disturbance on the abundance of species grouped by functional traits have been explored previously (Hewitt, Thrush and Dayton, 2008; Lundquist *et al.*, 2018), but detection of subtle stressor impacts has been challenging (Hastings *et al.*, 2018). The spatial assessment approaches presented in this thesis help quantify both subtle (i.e., incremental) and distinct changes (both positive and negative based on stressor magnitude) to functionally important taxa and are useful to inform management decisions and help advance the literature in this field.

5.3. Spatial and temporal scales of management

Many experimental studies focussed on benthic ecosystem functioning and macroinvertebrate response to stressors are conducted over relatively small spatial and temporal scales (Lohrer *et al.*, 2015; Snelgrove *et al.*, 2014) due to practical and financial constraints. However empirical relationships need to be scaled up spatially and temporally to obtain generalities that can inform coastal management (Hewitt and Norkko, 2007; Hunsicker *et al.*, 2016). This is important when trying to relate localised empirical stressor responses to predictive species-environmental relationships across larger ecological scales (Arenas-Castro *et al.*, 2018; Thrush *et al.*, 2021). Moreover, ecological processes that drive species distribution patterns over broad spatial scales (e.g., depth, temperature) may not occur at local scales and can be challenging to extrapolate accurately (Arenas-Castro *et al.*, 2018). The effects of spatial scale between regional and national SDMs were investigated in Chapter 2, which revealed that in the absence of spatially distributed regional sample data, national models achieved robust density predictions at a regional scale for many taxa. It was also revealed that neither model scale performed consistently better across all evaluation metrics when comparing both occurrence and abundance SDMs. This is likely due to the spatial variability in the sample data, with unevenly distributed sample records insufficient to represent a large enough range of environmental conditions in which these taxa occur and are abundant (Waldock *et al.*, 2021; Johnston *et al*., 2015). Through applying a multi-scalar approach when creating SDMs, the challenges of spatial disparity and data scarcity can be overcome. However, if these outputs are to be used to support multiple stressor modelling, practitioners should ensure that the SDMs reflect spatial scales relevant to the ecological extent of the management area and that the models are at a resolution sufficient to differentiate stressor responses (i.e., < 1 km grid).

Simmons *et al.* (2021), advocated that multiple stressor research should be refocussed around the targets and scales of ecological impacts, as most studies consider only one scale of ecological organisation. In Chapter 3 the scale of the correlative stressor model was refined from the extent of the regional study area in Chapter 2 (82,000 km^2), to reflect an area best represented by the extent of the stressor footprints (32,000 km^2). Future applications of this methodology could benefit from exploring how focussing on different levels of ecological organisation (i.e., community or ecosystem level) may affect stressor predictions.

The taxa-stressor relationships for mud utilised in Chapter 3 were derived from the regional scale model relationships (Chapter 2), and fishing taxa-stressor relationships were gleaned from a metanalysis covering a mean disturbance area of 0.12 km^2. It would be beneficial to investigate the predictive differences in model outputs across different scales of taxa-stressor relationships, however, this would remain challenging until more robust (stressor impact-oriented) environmental monitoring is conducted (Hewitt *et al.*, 2014).

The temporal and accumulating impact of stressors were modelled over a 4-year scale, which is adequate for fast-recovering taxa (< 1 year) but is likely less representative of longer-term impact and recovery trends for slow-recovering emergent epifauna such as *Callyspongia*. One of the persistent challenges in conservation planning is the lack of ability to predict the future consequences of management outcomes (William and Brown, 2023). With regards to multiple stressor assessment, this stems from a lack of studies which account for dynamic stressor and receptor interactions (Leslie and McLeod 2007). For stressors such as climate change, it is inherent that impacts are predicted for future climatic conditions as we assume that ocean temperatures will increase (Stephenson *et al*., 2023). However, for other stressors, the relationships with receptors are often non-linear, and the dynamic elements of the marine environment (e.g., coastal processes affecting sediment transportation) make this much more challenging (Cotte *et al*., 2016; Welch *et al*., 2019). Although the models in this thesis do not predict future outcomes of taxa density, which have been explored by others (Ehrlén and Morris 2015), they do integrate spatiotemporal dynamics to quantify changes in density distribution over time, helping to address, in part, a key research need. Future research could be improved by extending the temporal scale of the analysis closer to the present day, which would better reflect ongoing real-world ecological impact (i.e., 10 years) and provide more realistic long-term trends of impact and recovery.

5.4. Future Research

In this thesis, I have applied novel approaches focussed on quantifying the impact of multiple stressors on the density and distribution of functionally important taxa within a shallow seafloor ecosystem to develop broadly applicable spatial approaches to inform decision-making and support marine spatial planning. Through my research, I was able to advance my understanding of multiple stressor relationships with species and habitats and there interactions to demonstrate how stressors individually and in combination modify spatial patterns of taxa density to provide insight into how the utility of these approaches are useful to inform decision making. The findings presented in this thesis hold great importance for environmental management, highlighting that the effects of multiple stressors and the compound effect of slowly accumulating stressors must be considered within environmental assessment approaches to ensure that conservation efforts remain robust under present and future conditions. Furthermore, my research has demonstrated that failing to account for multiple stressor effects can generate inefficient and ineffective conservation outcomes.

Within any assessment of ecosystem impact, practitioners will always face the challenge of missing or imperfect data, particularly when trying to quantify multiple stressor impacts that require high-resolution, spatially explicit data over a broad range of ecosystems and historic stressor effects (Halpern and Fujita, 2013). The density SDMs created in Chapter 2 of this thesis served as a critical component throughout as they were utilised for additional analysis in subsequent chapters. The difficulty with a 'follow-on approach' is that results from thesis Chapters 3 and 4 are tied to the predictive accuracy of the SDMs created in Chapter 2. Although identifying spatially refined areas of high density is advantageous for regional management, there is also a risk that ecologically important areas may be discarded in the combined density model if they are not adequately predicted from the initial input models, or if they spatially conflict between the individual occurrence or abundance models. Since other literature has also identified that drivers of abundance and occurrence can differ (Dedman *et al.*, 2015; Rullens *et al.*, 2021), leading to contrasting predictions in some areas between occurrence and abundance, further work should be done to validate the predictive usefulness of the individual spatial outputs before combination into a density prediction. Models were graded using expert knowledge; however, no retroactive work was performed to review possible causes of non-representative predictions or attempts to refine model parameters and re-run the analysis based on feedback. Revisiting analysis steps taken to fit and tune the model, or refinement of the environmental predictors to try and obtain a parsimonious model, may lead to predictive improvements. Furthermore, other modelling approaches such as ensemble models (combining outputs from two different model types) have been used successfully around New Zealand (e.g., Anderson *et al.*, 2022; Stephenson *et al.*, 2021), and internationally (Jones and Cheung, 2015; Winship *et al.*, 2020), which can help to address the spatial disparity in predictions by averaging many model outputs, each of which may differ slightly based on the model parameterisation. It would be useful to compare the predictive outputs from other modelling approaches to the ones created in Chapter 2 (Boosted Regression Trees), which if useful, could be combined into an ensemble model to provide greater environmental representation when dealing with spatially disproportionate data, and thus greater certainty in predictions (Guo *et al.*, 2015).

In Chapter 3 of this thesis, I created a correlative stressor model approach which spatially quantified stressor impacts on receptor density. This approach assumed an additive (linear) interaction between the stressor and receptor defined as the sum of change from two stressors which act independently of others. However, cumulative stressor effects can also manifest from other interaction pathways: antagonistic (non-linear), when the sum of change from two stressors is less than the additive scenario; and synergistic (non-linear) when the sum of change from two stressors is greater than the additive scenario (Folt *et al.*, 1999; Thrush and Dayton, 2002). The application of alternative numerical model types has enabled stressor interactions and the direction of change to be identified (see Ellis *et al*., 2017; Rullens *et al*., 2022). Addressing multiple stressor interactions to spatially quantify stressor effects cumulatively remains challenging in marine science. (Crain *et al*., 2008; Ban *et al*., 2010 Kelly *et al*., 2014; Willsteed *et al*., 2018; Davies *et al*., 2018). Due to the correlative nature of the underlying Boosted Regression Tree models used to predict taxa density, which did not include stressors as environmental predictors, it was not possible to measure or extract interaction data between the stressors. This is why I decided early into the analysis to focus on a correlative approach and use empirical relationships to quantify the stressor and receptor response curves. For future analysis, it would be useful to explore other numerical models such as multiple linear regression, to examine the prevalence and nature of fishing and sedimentation stressor interactions (Ellis *et al*., 2017). Although this could not directly inform change in density from the predictive SDMs, it could be used to create an additional spatial layer which indicates the possible interaction state, based on spatial information of the stressor magnitude over the stressor footprint.

In Chapter 4 of this thesis, my research focused on determining if using stressor-impacted SDMs (from Chapter 3) could improve the efficiency and incorporation of multiple stressor effects into prioritisation conservation assessments. To measure the difference in efficiency, I compared metrics from unimpacted density scenarios to stressor-impacted density scenarios. In Chapter 4 I discuss the benefits of this novel approach, which focuses on the method of integrating stressor impacts via numerical modelling outside of the prioritisation software, a method which has also been successfully utilised by a few key studies to incorporate other stressor complexities (Leathwick *et al.*, 2008; Stephenson *et al.*, 2023; Summers *et al.*, 2012). Although this novel approach provided improved efficiency, it would be useful to compare these results to an assessment performed directly in Zonation using the unimpacted (i.e., baseline) density SDMs as the primary biodiversity features. This would provide a greater perspective to the differences in the spatial prioritisation patterns and efficiency metrics achievable between the newly developed approach presented in this thesis and more conventional approaches.

5.4.1. Predictive models for marine management

For successful model transferability, marine practitioners need to be able to differentiate between low-accuracy and high-accuracy predictive models to ensure that spatial data used to drive management decisions are both useful and environmentally representative (Pınarbaşı *et al.*, 2017; Yates *et al.*, 2018; Zurell *et al.*, 2021). Evaluation metrics which provide measures of predictive accuracy and cross-validation of results (e.g., deviance explained, sensitivity) can be used to quantify performance differences and help justify model outputs used for decision-making (Shabani, Kumar and Ahmadi, 2016). In Chapter 2 of this thesis, I applied two different model evaluation methods to determine if measurements of performance would vary between the two approaches, especially when using spatially disproportionate data between national (data rich) and regional (data poor) model scales. Evaluation metrics varied between the two assessment approaches indicating that more traditional assessment methods may no longer be suitable for alternative modelling approaches or when creating spatial models in data-limited environments. Practitioners may need to utilise advanced evaluation approaches such as spatial block cross-validation (tested in Chapter 2), which can test predictive accuracy over different spatial environments and help overcome challenges caused by spatially stratified datasets, such as spatial autocorrelation (Roberts *et al.*, 2017; Valavi *et al.*, 2018). Increased reliance on advanced modelling approaches will need to be accompanied by greater awareness of appropriate evaluation methods to compare and quantify model performance when applying environmental modelling to inform policy reform and decision-making (Zurrell *et al*., 2022).

Performance metrics are often accompanied by maps of model uncertainty (e.g., standard deviation from the mean prediction), which provide information on areas where models achieved the highest and lowest predictive certainty, to consider in conjunction with predictive maps (Elith and Leathwick 2009). All models contain different degrees of uncertainty, which can be challenging to identify, quantify and communicate when utilising environmental modelling to inform management decisions (Gissi *et al.*, 2017). In Chapter 2 of this thesis, I was able to create uncertainty maps to accompany the density SDMs, which were also utilised in Chapter 4, to represent spatial uncertainty for the systematic conservation assessment. Steps to validate the performance of correlative models (e.g., SDM and habitat suitability models) through evaluation metrics and uncertainty measurements have become common practice (Dormann *et al.*, 2018; Roberts *et al.*, 2017), however, methods to fit novel simulation models to assess predictive performance is considered innovative and rarely done (Zurrell *et al* 2021). Consequently, performance metrics were not applied for the correlative stressor model due to a lack of quantified methods for this novel approach; standardisation of evaluation metrics would help assess predictive performance, transferability, and adoption (Yates *et al.,* 2018; Roberts *et al*., 2017) for future replication. To adequately guide model usefulness and predictive accuracy under global change, greater effort is needed to develop more routine model performance protocols so that models are transferable, and results can be justified when used to support management decisions (Petchey *et al.*, 2015; Yates *et al.*, 2018).

5.5. Concluding Remarks

Investigating how multiple and overlapping stressors impact benthic ecosystems over space and time is a driving knowledge need in marine spatial planning, so that managers and practitioners can try to prevent or mitigate their effects (Foley *et al.*, 2017; Stelzenmüller *et al.*, 2020). The outcomes of this thesis and the extrapolation of their findings contribute toward advancing knowledge and spatial assessment methodology in a challenging field of analysis. This thesis highlighted two key findings that support the advancement of multiple stressor effects into MSP: (1) slow-acting, accumulating stressors (e.g., sedimentation) cause comparable levels of density decline to sensitive and easily disturbed taxa as immediate, high-impact stressors (e.g., bottom fishing), and, (2) focusing management efforts on dominant marine stressors without addressing terrestrially derived stressors can undermine conservation effectiveness (even inside marine reserves).

Proactive management against the effects of localised stressors will result in increased benthic ecosystem health and resilience to provide the greatest defence against the intangible impacts of globally pervasive stressors (Trembley *et al*., 2023; Brown *et al*., 2014; Gissi *et al*., 2021; Willsteed *et al*., 2018. This is especially important in this decade, as climate change impacts are predicted to cause the same magnitude of environmental degradation as all current pressures to date combined (Wahlstrom *et al.*, 2022). If the effects of multiple stressors are not addressed, mankind will be forced to experience a future with far fewer ecosystem services that we rely upon (Rullens *et al*., 2019). As stressor impacts continue to diminish the functional capacity of benthic ecosystems, tipping points will ensue (Davies *et al.*, 2018; Foley *et al.*, 2017; Gladstone-Gallagher *et al.*, 2019; Thrush *et al.*, 2021). Increasing the availability of spatially explicit data through improved environmental monitoring approaches and increased conservation efforts in conjunction with novel research to further understanding, as presented in this thesis, will support the identification of robust and ecologically resilient habitats that can persevere in an ever-changing world.

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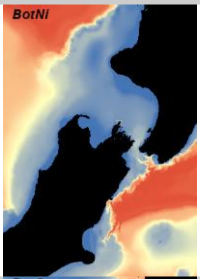
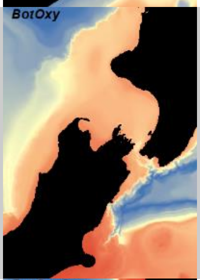
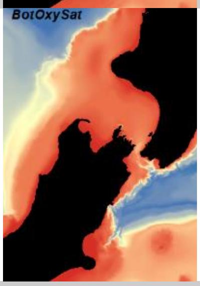
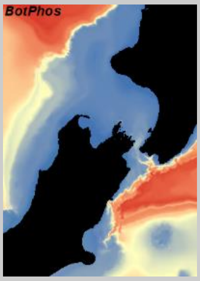
Appendices

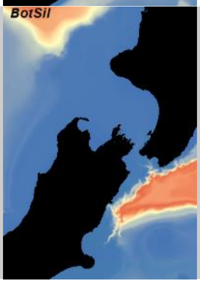
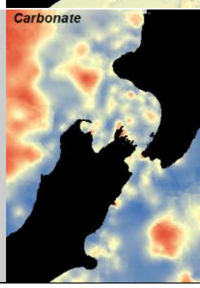
Appendix 1
Species distribution model outputs – Chapter 2

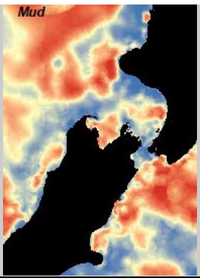
Table A1 1: Summary of all sample data surveyed from various databases.

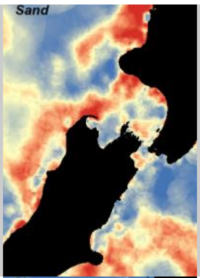
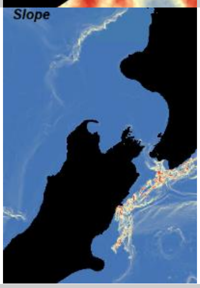
Database	Sources	Records
NIWA invert database	National Institute of Water and Atmospheric Research (NIWA)	3305
TRAWL database	Held by NIWA on behalf of Fisheries New Zealand (FNZ)	249
New Zealand Aquatic Environment and Biodiversity Report No. 118 (2013) - MPI project ZBD200925	Ministry of Primary Industries (MPI)	366
New Zealand Aquatic Environment and Biodiversity Report No. 178 (2017) – MPI Project BEN200701	NIWA & MPI	
Benthic Invertebrates	Auckland Museum	130
Benthic Invertebrates	Te Papa Museum	19

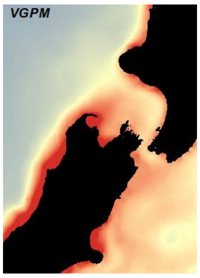
Table A1 2: Environmental variables used as predictors in Boosted Regression Tree Analysis 'adapted from Stephenson et al., 2021' – All variable images captured from GIS using a stretched layer symbology of low to high.

Variable abbreviation	Variable name	Temporal resolution	Unit	Description	Source	Variable Image
BedDist	Benthic sediment disturbance	1/7/2017-30/6/2018	ms-1	One-year mean value of friction velocity derived from (1) hourly estimates of surface wave statistics (significant wave height, peak wave period) from outputs of the NZWAVE_NZLAM wave forecast, at 8-km resolution, (2) median grain size (d50), at 250 m resolution, (3) water depth, at 25-m resolution. Benthic sediment disturbance from wave action was assumed to be zero where depth ≥ 200m.	Leathwick *et al*. (2012)	
BotNi	Bottom nitrate	Static	umol l-1	Annual average water nitrate concentration at the seafloor (using NZ bathymetry layer) based on methods from Dunn *et al*. 2002. Oceanographic data from CARS2009 (2011).	NIWA, unpublished	
BotOxy	Dissolved oxygen at depth	Static	ml l-1	Annual average water oxygen concentration at the seafloor (using NZ bathymetry layer) based on methods from Dunn *et al*. 2002. Oceanographic data from CARS2009 (2011).	NIWA, unpublished	
BotOxySat *	Oxygen saturation at depth	Static	umol l-1	Annual average oxygen saturation at the depths	NIWA, unpublished	
BotPhos	Bottom phosphate	Static	umol l-1	Annual average water phosphate concentration at the seafloor (using NZ bathymetry layer) based on methods from Dunn *et al*. 2002. Oceanographic data from CARS2009 (2011).	NIWA, unpublished	

BotSal	Salinity at depth	Static	psu	Annual average water salinity concentration at the seafloor (using NZ bathymetry layer) based on methods from Dunn *et al*. 2002. Oceanographic data from CARS2009 (2011).	NIWA, unpublished	
BotSil	Bottom silicate	Static	umol l-1	Annual average water silicate concentration at the seafloor (using NZ bathymetry layer) based on methods from Dunn *et al*. 2002. Oceanographic data from CARS2009 (2011).	NIWA, unpublished	
BotTemp	Temperature at depth	Static	°C km-1	Annual average water temperature at the seafloor (using NZ bathymetry layer) based on methods from Ridgway *et al*. (2002). The oceanographic data used to te these climatological maps were computed by objective analysis of all scientifically quality-controlled historical data from the Commonwealth Scientific and Industrial Research Organisation (CSIRO) Atlas of Regional Seas database (CARS2009).	NIWA, unpublished	
BPI_broad	BPI_broad	Static	m	Terrain metrics were calculated using an inner annulus of 12 km and a radius of 62 km using the NIWA bathymetry layer in the Benthic Terrain Modeler in ArcGIS 10.3.1.1 (Wright *et al*. 2012). Bathymetric Position Index (BPI) is a measure of where a referenced location is relative to the locations surrounding it.	NIWA, unpublished	
BPI_fine	BPI_fine	Static	m	Terrain metrics were calculated using an inner annulus of 2 km and a radius of 12 km using the NIWA bathymetry layer in the Benthic Terrain Modeler in ArcGIS 10.3.1.1 (Wright *et al*. 2012). Bathymetric Position Index (BPI) is a measure of where a referenced location is relative to the locations surrounding it.	NIWA, unpublished	
carbonate	Percent gravel	Static	%	The percent carbonate layers for the region were developed from >30,000 raw sediment sample data compiled in dbseabed (Jenkins *et al*. 1997), which were then imported into ArcGIS and interpolated using Inverse Distance Weighting (Bostock *et al*. 2018)	H Bostock *et al*., 2018	

Chl-A	Chlorophyll-a concentration	July 2002 – March 2019	mg m^{-3}	A proxy for the biomass of phytoplankton present in the surface ocean (to ~30 m). Blended from a coastal Chl-a estimate (quasi-analytic algorithm (QAA), local a_{ph}*(555) and the default open-ocean chl-a value from MODIS-Aqua (v2018.0).	NIWA unpublished; Based on processing described in Pinkerton *et al*. (2018) and updated in Pinkerton *et al*. (2020). QAA algorithm detailed in Lee *et al*., 2002, v5 update, Lee *et al*. 2009	
DynOc	Dynamic oceanography		m	Mean of the 1993-1999 period sea surface above geoid, corrected from geophysical effects taken for the NZ region. This broadly corresponds to mean surface velocity recorded from drifters in the NZ region (Hadfield pers comm).	NIWA, unpublished	
Gravel	Percent gravel	Static	%	The percent gravel layers for the region were developed from >30,000 raw sediment sample data compiled in dbseabed (Jenkins *et al*. 1997), which were then imported into ArcGIS and interpolated using Inverse Distance Weighting (Bostock, pers comm)	H Bostock *et al*., 2018	
K_{par}	Diffuse downwelling attenuation	July 2002 – March 2019	m^{-1}	vertical attenuation of diffuse, downwelling broadband irradiance (Photosynthetically Available Radiation, PAR, 400–700 nm). Merged coastal and open-ocean product based on MODIS-Aqua data. Coastal: estimated from inherent optical properties (QAA). Ocean: estimated from K_{490} using Morel *et al*. (2007)	NIWA unpublished; Based on processing described in Pinkerton *et al*. (2018)	
MLD	Mixed layer depth	July 2002 – March 2019	m	The depth that separates the homogenised mixed water above from the denser stratified water below. Based on GLBu0.08 hindcast results using a potential density difference of 0.030 kg m^{-3} from the surface. Models used are: (1) hycom: from day 265 (2008) to present; (2) fnmoc: from day 169 (2005) to present; (3) soda: from day 249 (1997) to end of 2004; (4) tops: from day 001 (2005) to 225 (2010).	Metzger *et al*. (2007); Chassignet *et al*. (2007); Wallcraft *et al*. (2009). Data: orca.science.oregonstate.edu	
Mud	Percent mud	Static	%	The percent mud layers for the region were developed from >30,000 raw sediment sample data compiled in dbseabed (Jenkins *et al*. 1997), which were then imported into ArcGIS and interpolated using Inverse Distance Weighting (Bostock, pers comm)	H Bostock *et al*., 2018	

PAR	Photo-synthetically active radiation	July 2002 – March 2019	Einsteins m^{-2} d^{-1}	Daily-integrated, broadband, incident irradiance at the sea-surface based on day length, solar elevation and measurements of cloud cover from ocean colour satellites (Frouin *et al.*, 2012).	Frouin *et al.* (2012)	
POCFlux	Downward vertical flux of particulate organic matter at the seabed	July 2002 – March 2019	mgC m-2 d-1	Net primary production in the surface mixed layer estimated as the VGPM model (Behrenfeld & Falkowski 1997); this Table). Export fraction and flux attenuation factor with depth estimated by re-fitting sediment trap and thorium-based measurements to environmental data (VGPM, SST) as Lutz *et al.* (2002), Pinkerton *et al.* (2016) and using data from Cael *et al.* (2017).	NIWA unpublished, updated in 2020. Based on processing described in Pinkerton M *et al.* (2016) with new data from Cael *et al.* (2018).	
Rough	Roughness	Static	m	Roughness of the seafloor calculated as the standard deviation of depths in a surrounding 3 x 3 km neighbourhood (Leathwick *et al.*, 2012). Terrain Ruggedness (VRM) as the variation in three-dimensional orientation of grid cells within a neighbourhood. Vector analysis is used to calculate the dispersion of vectors normal (orthogonal) to grid cells within the specified neighbourhood	Leathwick *et al.* (2012)	
Sand	sand	Static	%	The percent sand layers for the region were developed from >30,000 raw sediment sample data compiled in dbseabed (Jenkins *et al.* 1997), which were then imported into ArcGIS and interpolated using Inverse Distance Weighting (Bostock, pers comm)	H Bostock *et al.*, 2018	
Slope	Slope	Static	Degree	Bathymetric slope was calculated from bathymetric depth and is the degree change from one depth value to the next.	NIWA, unpublished	
SST	Sea surface temperature	1981-2018 (ocean) 2002-2018 (coastal)	°C	Blended from OI-SST (Reynolds *et al.*, 2002) ocean product and MODIS-Aqua SST coastal product. Long-term (2002–2017) average values at 250 m resolution.	NIWA unpublished; Coastal based on processing described in Pinkerton *et al.* (2018). Ocean: Reynolds *et al.*, (2002)	

TC	Tidal Current speed	N/A	ms-1	Maximum depth-averaged (NZ bathymetry) flows from tidal currents calculated from a tidal model for New Zealand waters (Walters *et al*., 2001)	Walters, R.A., Goring, D.G., Bell, R.G. (2001) Ocean tides around New Zealand. New Zealand Journal of Marine and Freshwater Research, 35: 567-579.	
TempRes	Temperature residuals		°C	Residuals from a GLM relating temperature to depth using natural splines – this highlights areas where average temperature is higher or lower than would be expected for any given depth	Leathwick *et al*. (2006)	
VGPM	Net primary production by the vertically-generalised production model	July 2002 – March 2019	mgC/ m^2/d	Daily production of organic matter by the growth of phytoplankton in the surface mixed layer, net of phytoplankton respiration. Estimated at monthly resolution based on satellite observations of chl-a, PAR and SST, and model-derived estimates of mixed-layer depth, using the vertically-generalised production model (Behrenfeld & Falkowski, 1997).	Behrenfeld & Falkowski (1997)	

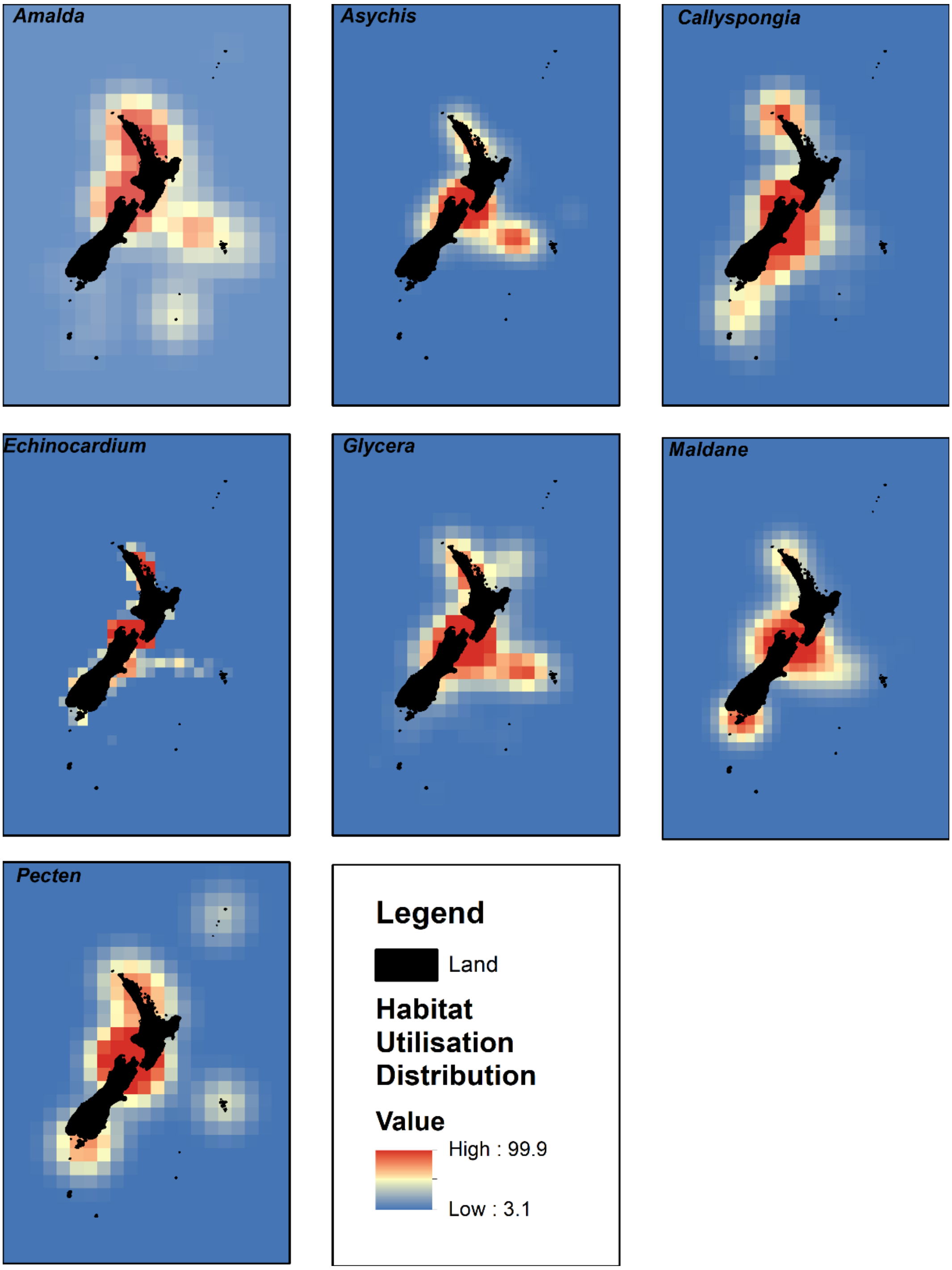


Figure A1: Habitat Utilisation Distribution maps generated in R using the 'adehabitatHR' package. Distribution and use of space described by the bivariate probability density function and based on presence records. The bandwidths (or focal areas) were automatically calculated by the package from the presence records, which defined a default search radius to apply the kernel density function within. Outputs vary in cell size due to automatic calculation of cell size based on location and number of presence records.

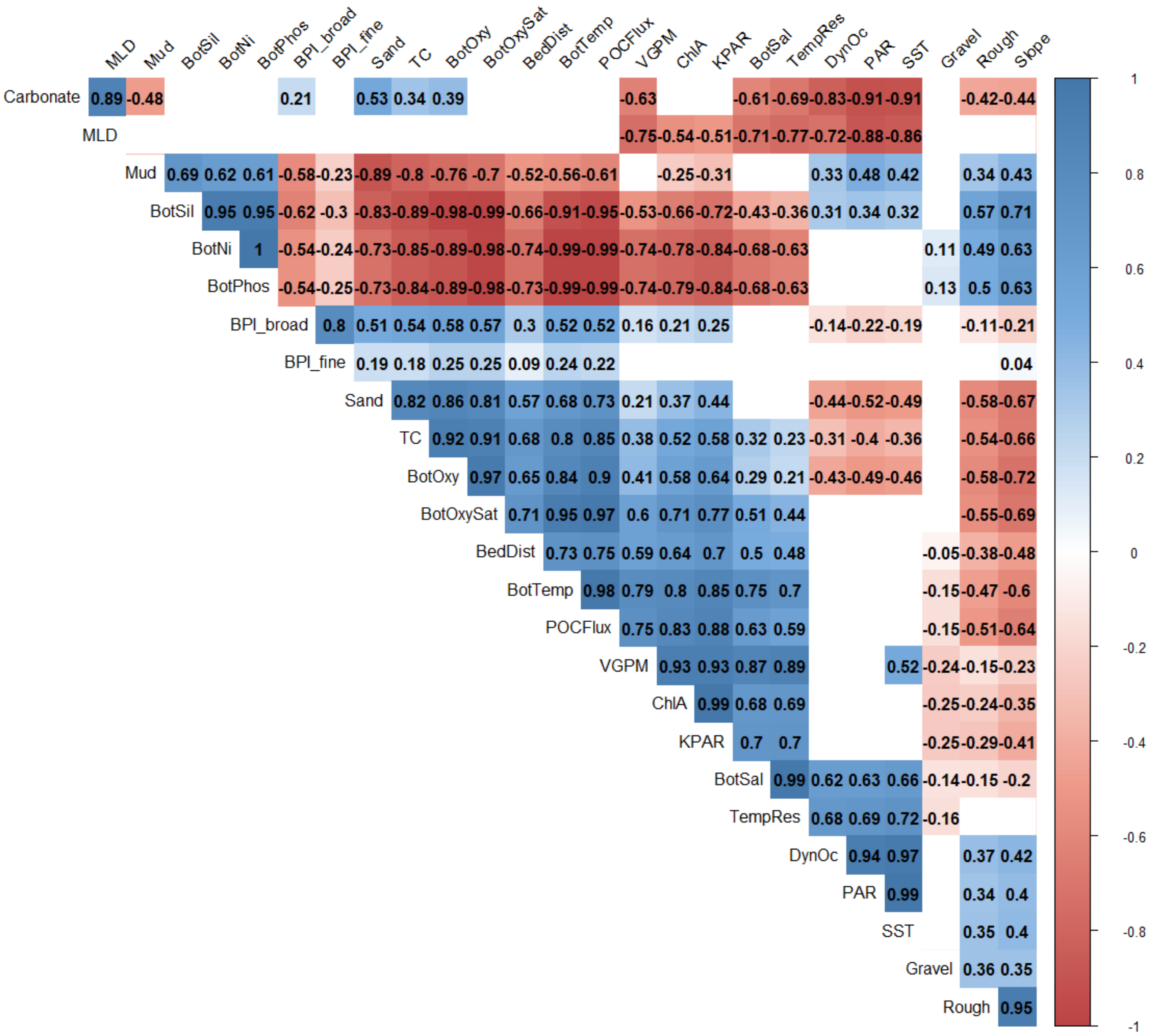


Figure A2 Correlation matrix of all environmental predictors (p-value of 0.5) for the national scale models. Non-significant correlations are shown in white.

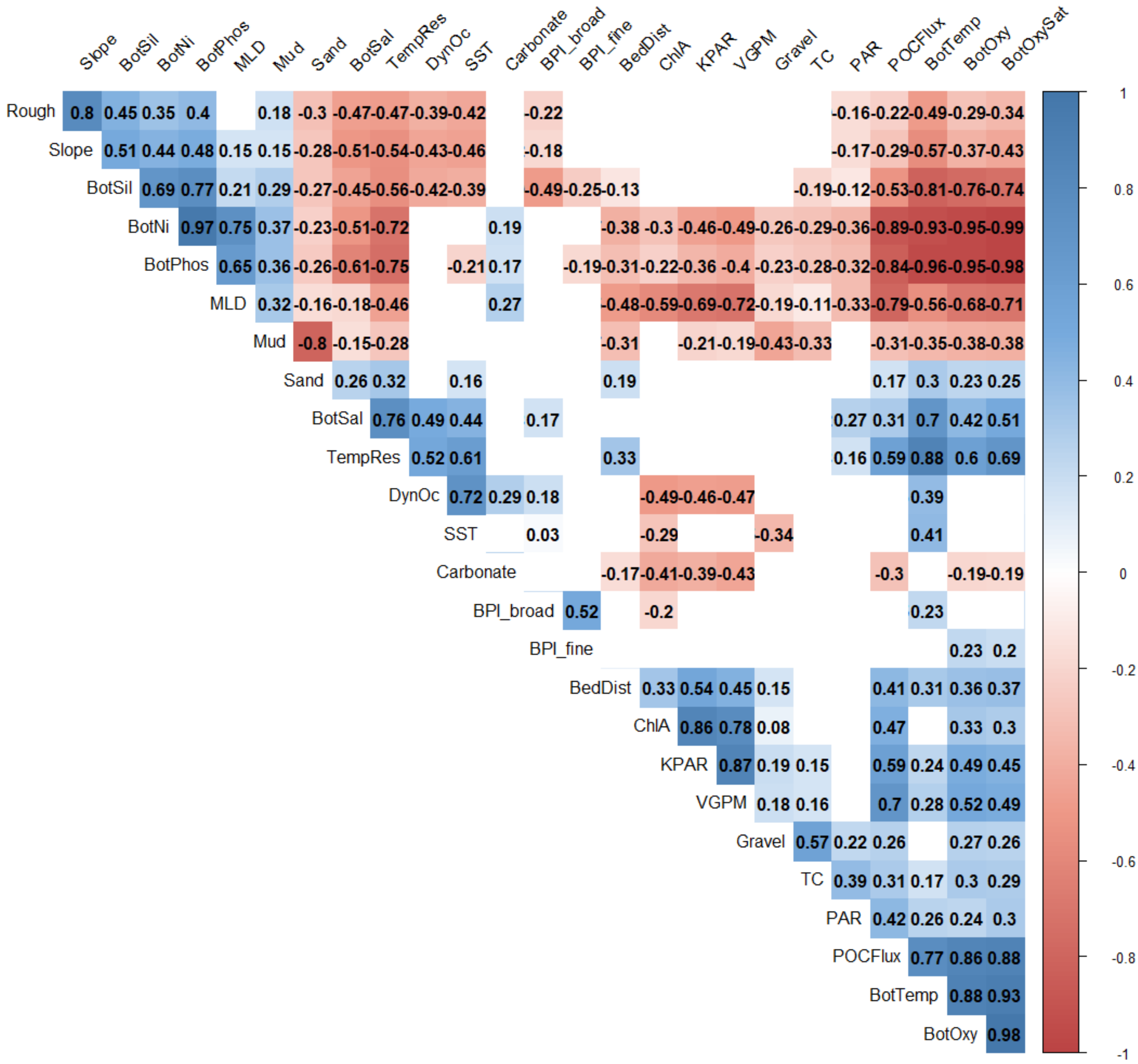


Figure A3 Correlation matrix of all environmental predictors (p-value of 0.5) for the regional scale models. Non-significant correlations are shown in white.

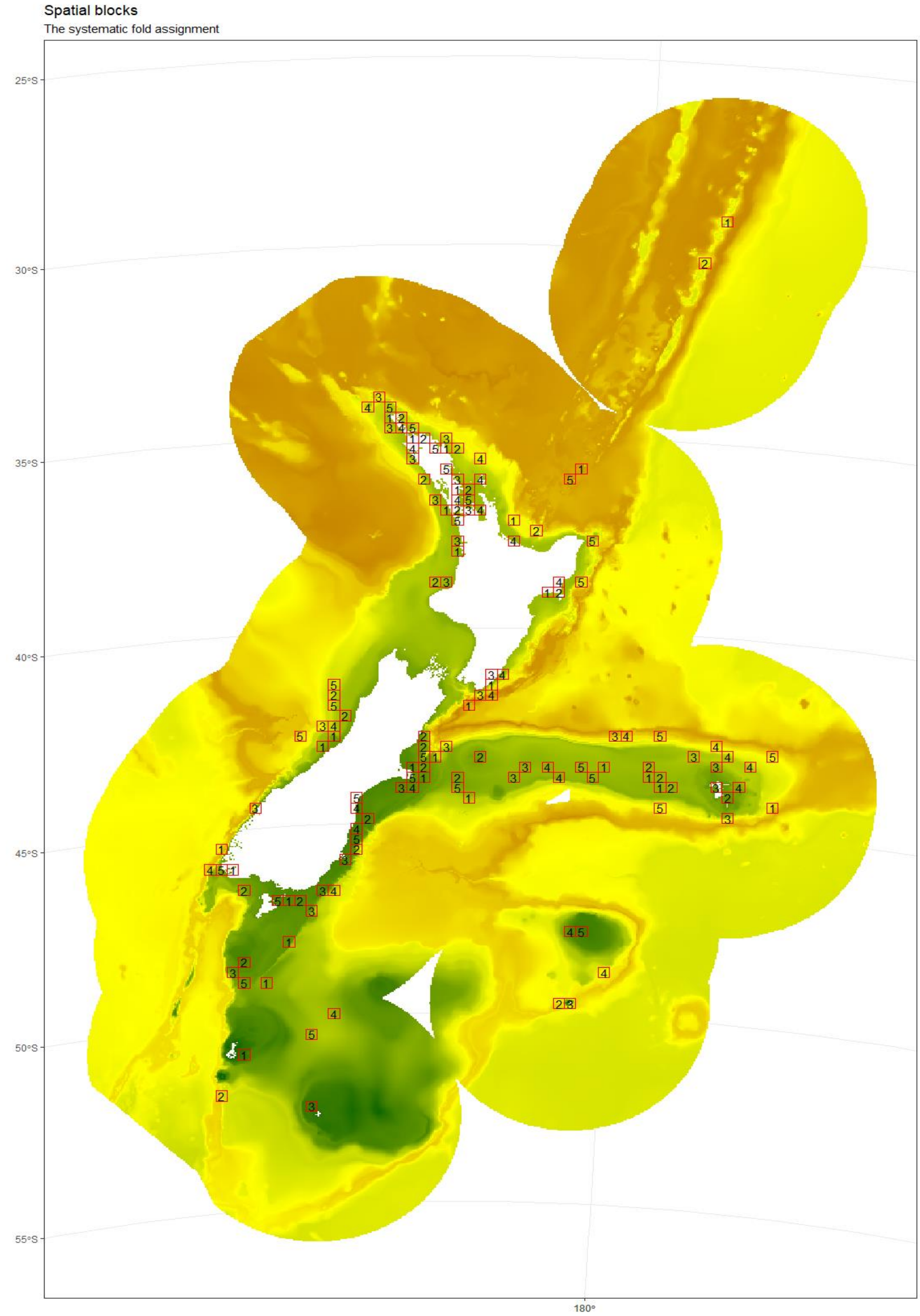


Figure A4: National scale spatial blocks created for Amalda using the national scale dataset exclusively (excluding data directly within the study area /regional dataset) created using the block C.V package in R. Spatial blocks are randomly numbered 1-5 to correspond to number of Spatial Blocks. Blocks created using the 'spatialBlock' function based on defined cell size (the range) of 30 km^{2}. - a cell of ~5.5km x 5.5km. Cell size defined through using the built in 'Range Explorer' interactive tool, to visually assess a suitable spatial block size based on the distribution of data. Spatial block assignment, locations and cell size varied between taxa based on sample data.

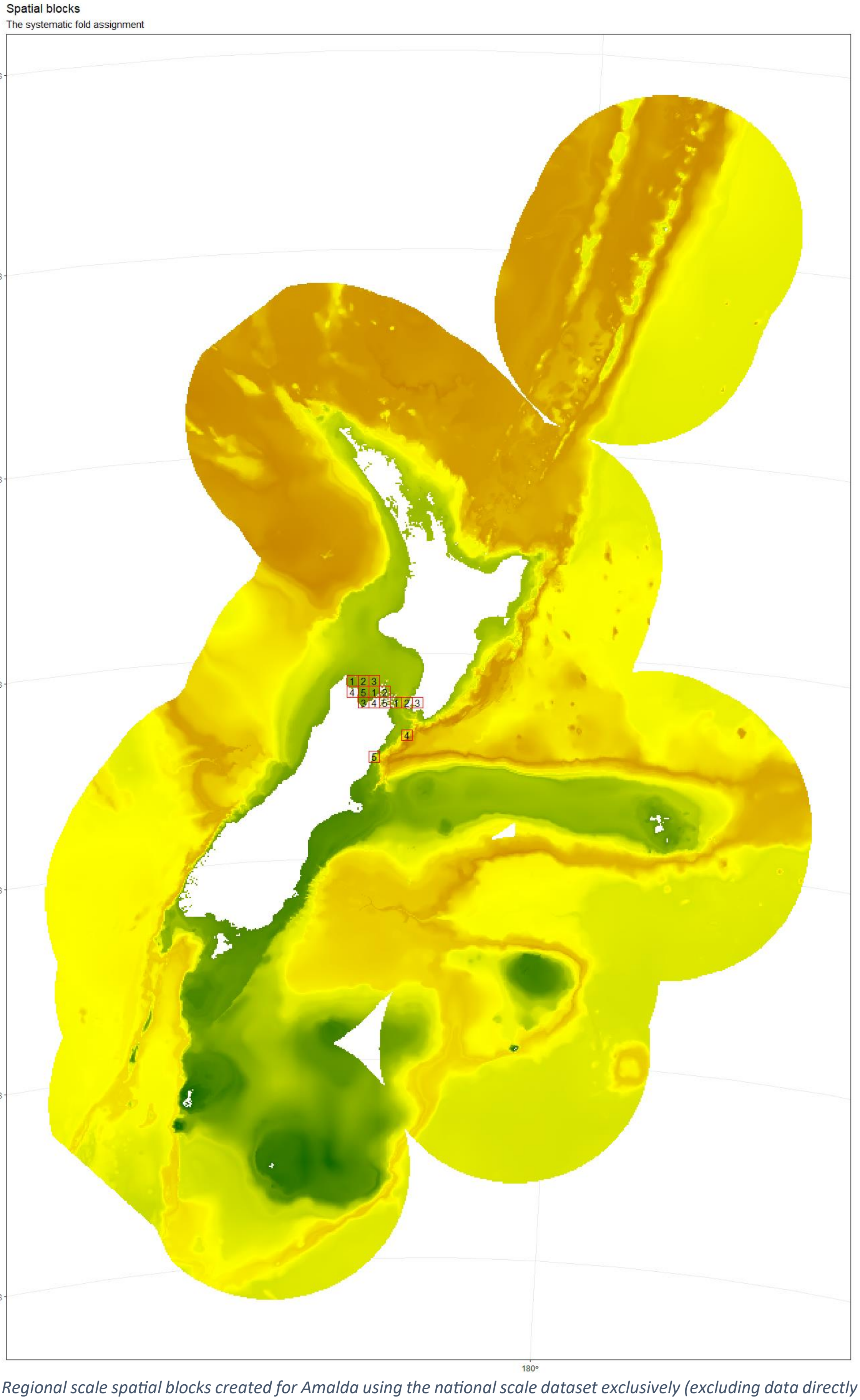


Figure A5: Regional scale spatial blocks created for Amalda using the national scale dataset exclusively (excluding data directly within the study area /regional dataset) created using the block C.V package in R. Spatial blocks are randomly numbered 1-5 to correspond to number of Spatial Blocks. Blocks created using the 'spatialBlock' function based on defined cell size (the range) of 30 km^{2}. - a cell of ~5.5km x 5.5km. Cell size defined through using the built in 'Range Explorer' interactive tool, to visually assess a suitable spatial block size based on the distribution of data. Spatial block assignment, locations and cell size varied between taxa based on sample data.

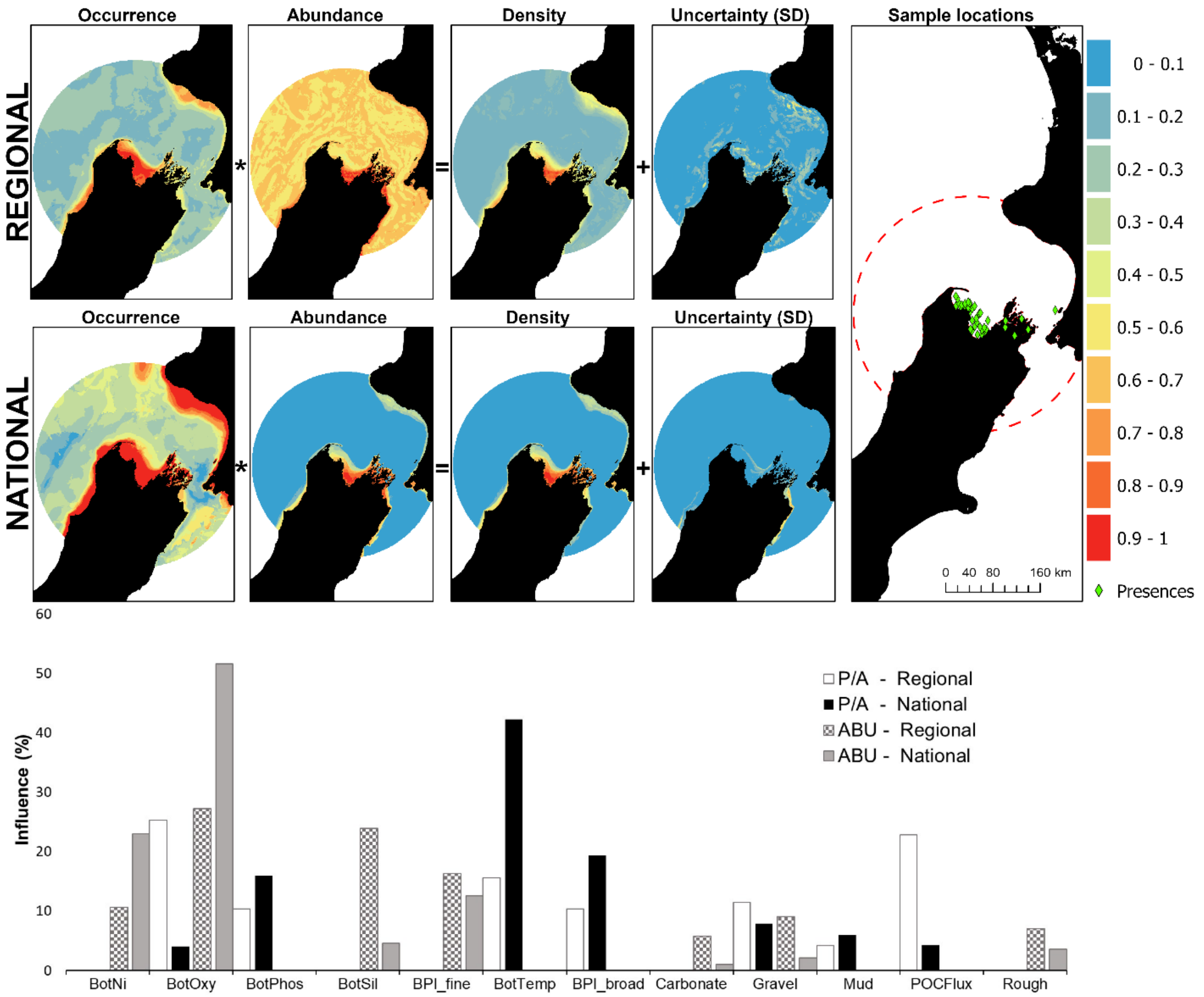


*Figure A6: Amalda spp. BRT spatial predictions of the study area at regional and national scales: probability of occurrence (presence & relative absence), abundance (abundance), density (occurrence * abundance) and uncertainty (standard deviation of density model). All data has been normalised to be on a scale of 0-1 (right legend). Lower histogram displays percentage of predictive influence for corresponding environmental predictors.*

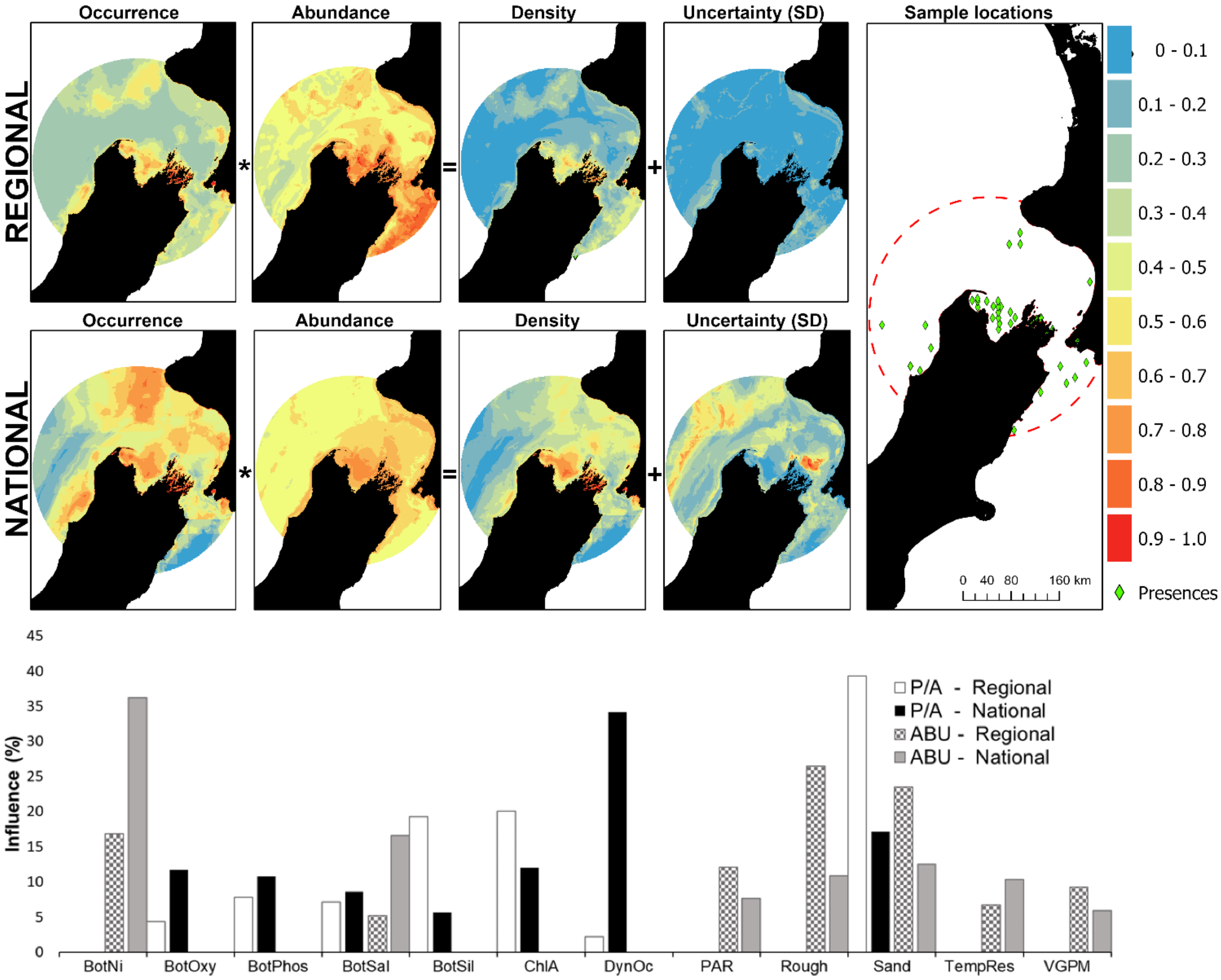


*Figure A7: Asychis spp. BRT spatial predictions of the study area at regional and national scales: probability of occurrence (presence & relative absence), abundance (abundance), density (occurrence * abundance) and uncertainty (standard deviation of density model). All data has been normalised to be on a scale of 0-1 (right legend). Lower histogram displays percentage of predictive influence for corresponding environmental predictors.*

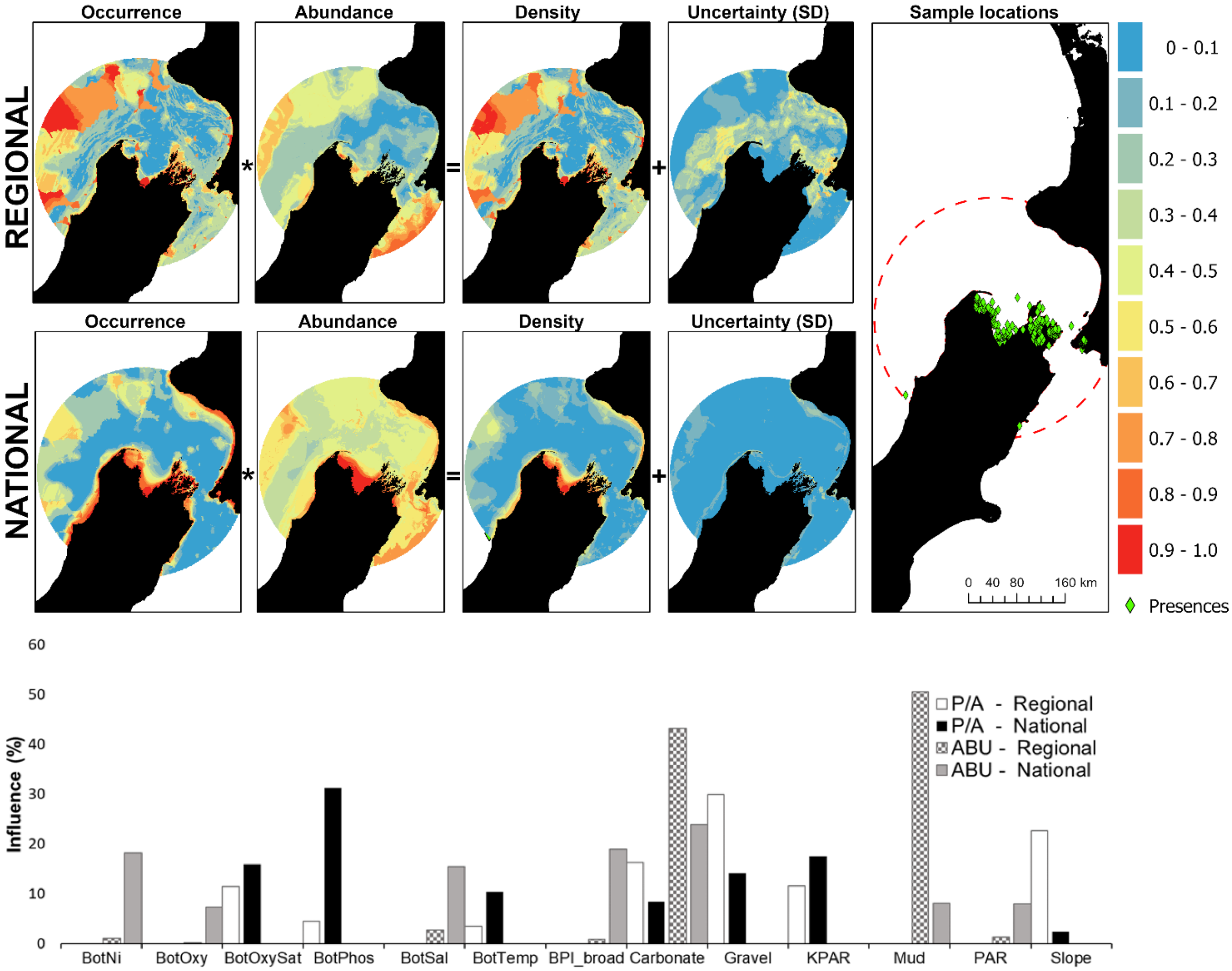


*Figure A8: Echinocardium spp BRT spatial predictions of the study area at regional and national scales: probability of occurrence (presence & relative absence), abundance (abundance), density (occurrence * abundance) and uncertainty (standard deviation of density model). All data has been normalised to be on a scale of 0-1 (right legend). Lower histogram displays percentage of predictive influence for corresponding environmental predictors.*

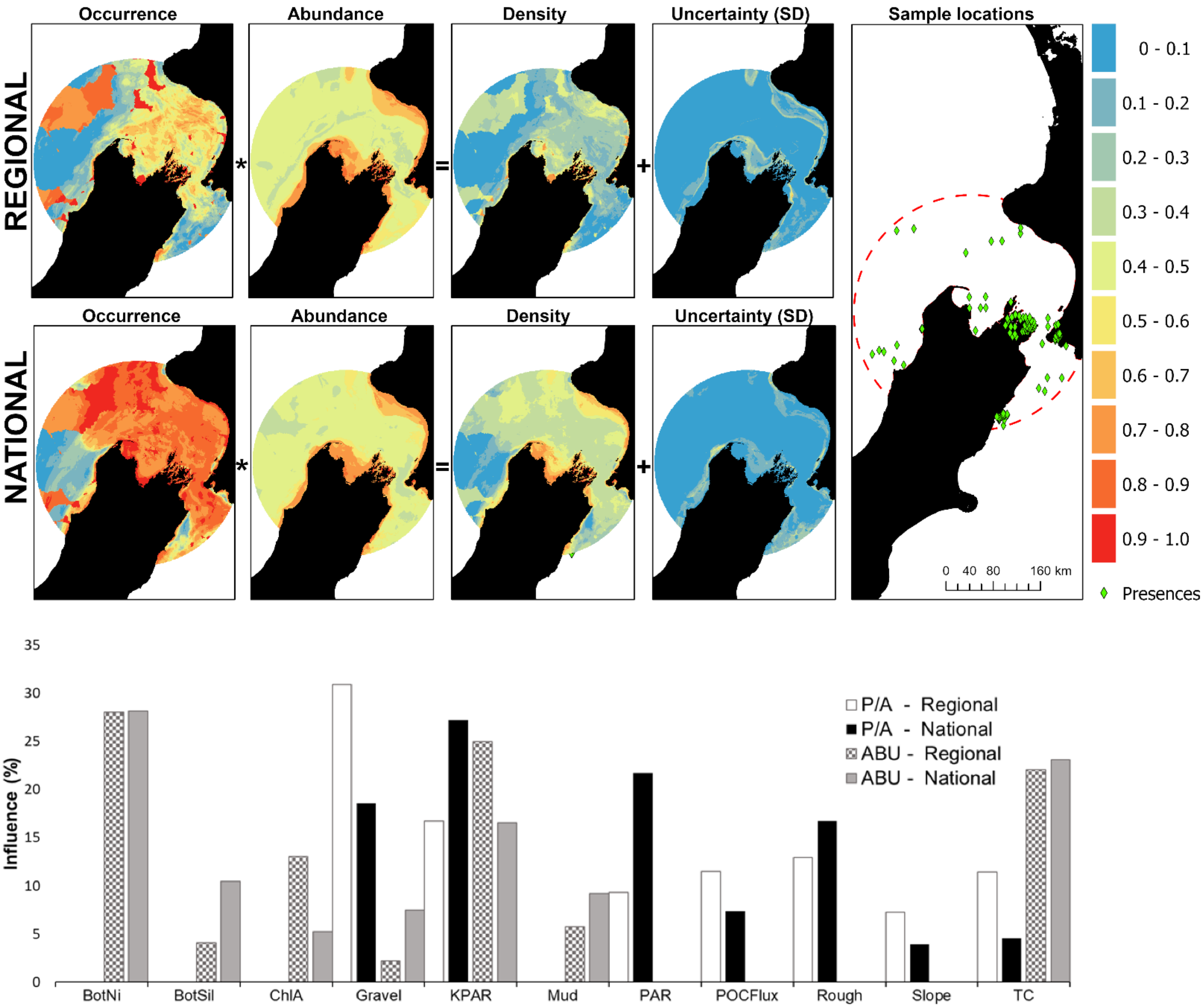


*Figure A9: Glycera spp BRT spatial predictions of the study area at regional and national scales: probability of occurrence (presence & relative absence), abundance (abundance), density (occurrence * abundance) and uncertainty (standard deviation of density model). All data has been normalised to be on a scale of 0-1 (right legend). Lower histogram displays percentage of predictive influence for corresponding environmental predictors.*

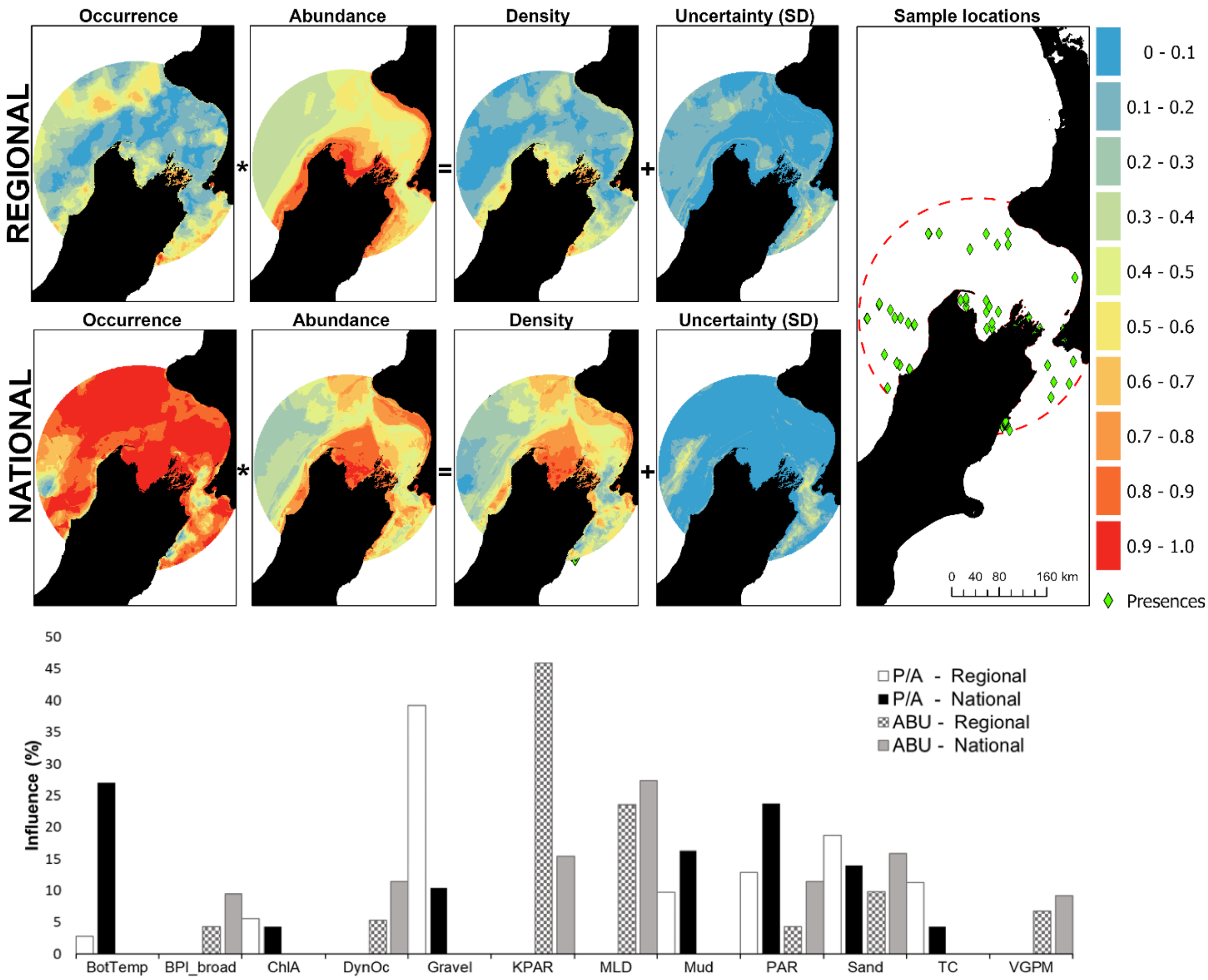


*Figure A10: Maldane spp. BRT spatial predictions of the study area at regional and national scales: probability of occurrence (presence & relative absence), abundance (abundance), density (occurrence * abundance) and uncertainty (standard deviation of density model). All data has been normalised to be on a scale of 0-1 (right legend). Lower histogram displays percentage of predictive influence for corresponding environmental predictors.*

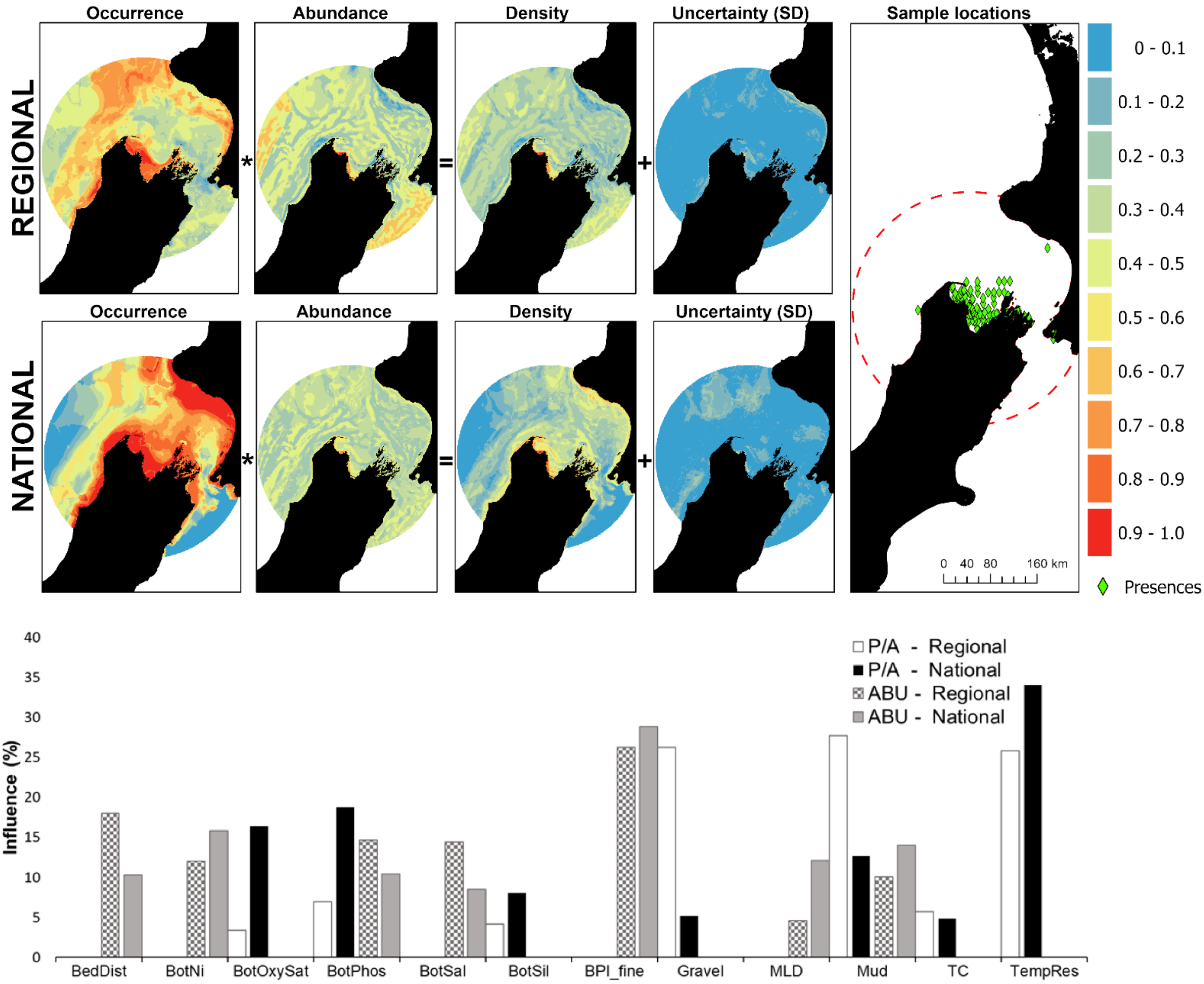


*Figure A11: Pecten spp. BRT spatial predictions of the study area at regional and national scales: probability of occurrence (presence & relative absence), abundance (abundance), density (occurrence * abundance) and uncertainty (standard deviation of density model). All data has been normalised to be on a scale of 0-1 (right legend). Lower histogram displays percentage of predictive influence for corresponding environmental predictors.*

Appendix 2
Correlative stressor model outputs – Chapter 3

*Table A2 1: Change in mean density (count per km²), across all stressor scenarios for each taxa. Difference in mean density provided by subtracting baseline density values from scenario density values. Magnitude of change in density is indicated by gradient of colour, with orange indicating density reduction, and blue indicating density increase. **Alternative stressor order of operations**: Fishing impact, Recovery, Sediment impact*

Taxa	*Callyspongia*	*Callyspongia*	*Echinocardium*	*Echinocardium*	*Amalda*	*Amalda*
Stress Scenario	mean density (count per km²)	Difference in mean density (%) from Baseline	mean density (count per km²)	Difference in mean density (%) from Baseline	mean density (count per km²)	Difference in mean density (%) from Baseline
Single Stressor						
Baseline (without stressors)	144.0	-	59.2	-	195.4	-
Sed (1%)	139.2	-3.4	58.6	-1.1	216.0	10.6
Sed (2%)	134.6	-6.5	58.2	-1.7	238.4	22.0
Sed (3%)	130.4	-9.5	58.4	-1.3	262.2	34.2
Fish (F-R)	123.7	-14.1	49.8	-16.0	195.4	10.3
Fish (F-NR)	123.7	-14.1	49.7	-16.1	195.4	10.3
Multiple Stressors (with recovery)						
Fish & Sed (1%, F-R)	125.5	-12.9	51.1	-13.6	220.6	12.9
Fish & Sed (2%, F-R)	127.1	-11.7	49.9	-15.7	245.4	25.6
Fish & Sed (3%, F-R)	121.1	-15.9	51.7	-12.8	253.2	29.6
Multiple Stressors (without recovery)						
Fish & Sed (1%, F-NR)	119.4	-17.1	48.0	-18.9	229.7	17.6
Fish & Sed (2%, F-NR)	117.7	-18.3	47.8	-19.3	239.33	22.5
Fish & Sed (3%, F-NR)	116.2	-19.3	47.6	-19.6	249.13	27.5

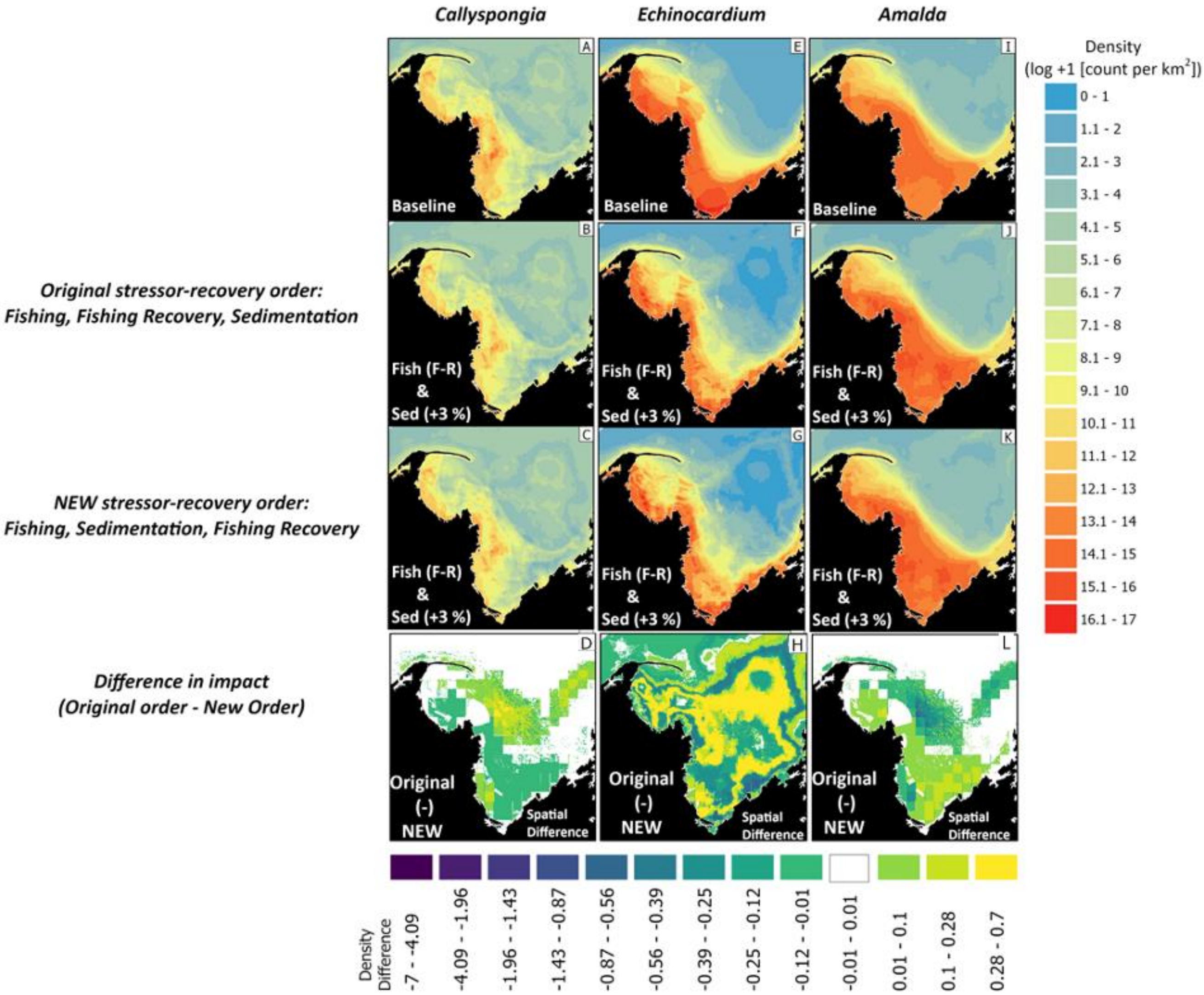


Figure A2 1: Spatial maps from combined stressor correlative models detailing the change in density (log +1 [count per km²]) and distribution from the baseline from fishing and sedimentation stress after four years of accumulating impact (plots A-K). All scenario maps contain a combination of two stressors, showing fishing with recovery (F-R). The plots B,F,J show the original /first stressor order tested, and associated change in density. Plots C,G,K show a second / newer stressor order tested and associated change in density. And, plots D,H,L show the spatial difference between the two scenarios tested.

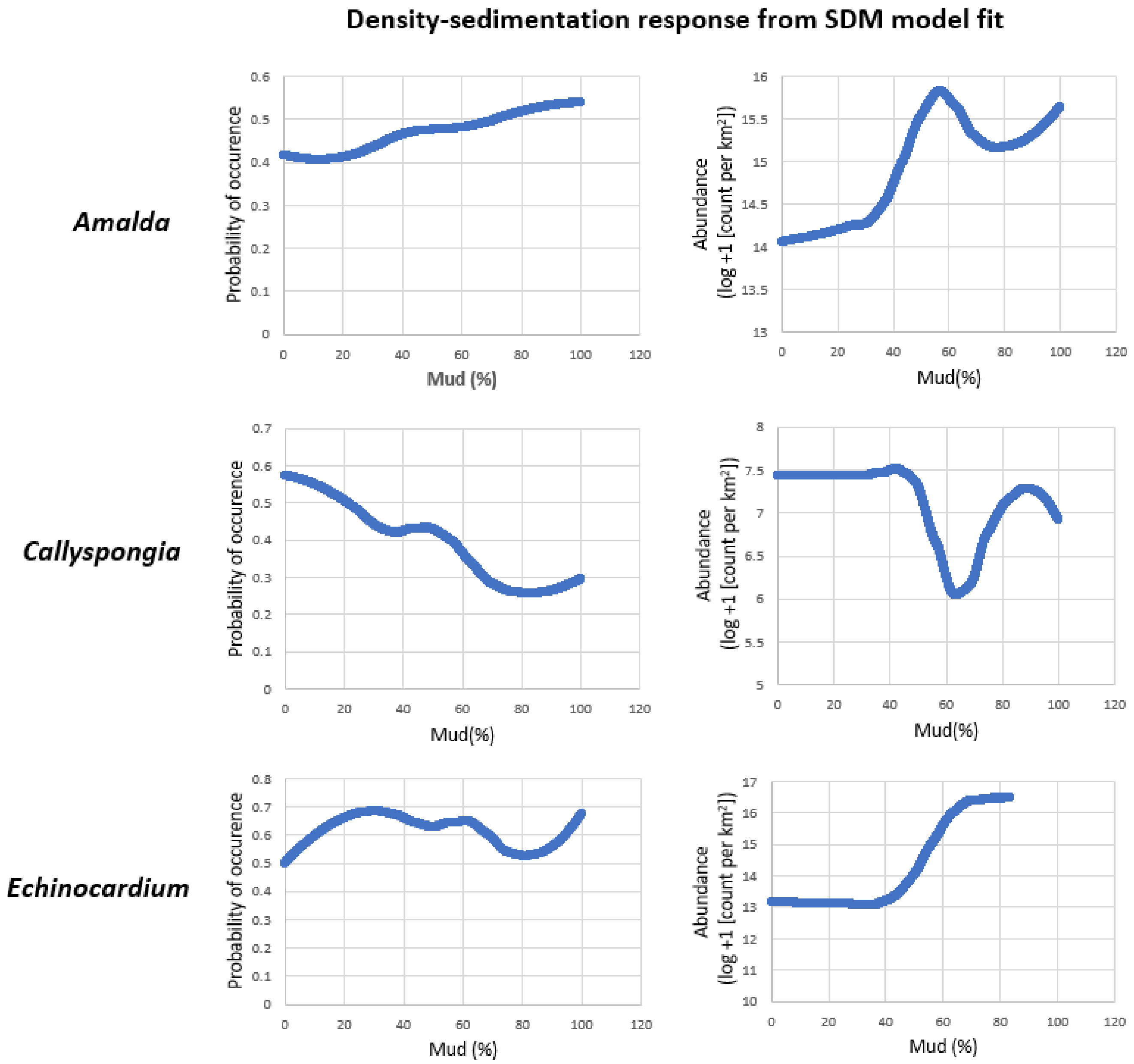
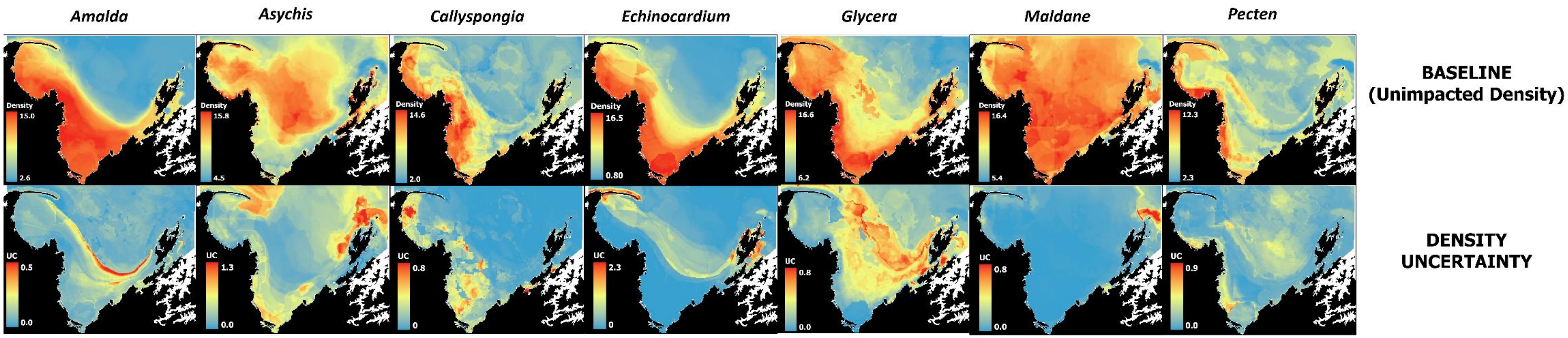


Figure A2 2: Sedimentation response curves from SDM model fit for probability of occurrence and abundance models for each taxa. Individual response curves were multiplied together to provide the density-sedimentation response relationship used in the correlative stressor model.

Appendix 3

Spatial prioritisation assessment outputs – Chapter 4



Appendix 3 1: Spatial predictions of density *(log +1 [count per km^2])* and uncertainty (standard deviation of density) for all Taxa (unimpacted density) that were used as input layers for the spatial prioritisation analysis