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**Protecting the deep:
The combined impact of climate change
and bottom trawling on VME indicator taxa in
New Zealand and implications for management**

A thesis

submitted in fulfilment

of the requirements for the degree

of

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by

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Foreword

The core of this thesis consists of three research chapters (Chapters 2, 3 & 4), which have been published, are under review, or are being prepared for submission to peer-reviewed scientific journals. I was responsible for the research idea and led the design, data analysis, and manuscript preparation. Unless cited otherwise, the content of this thesis stems from my original ideas, with all work conducted under the guidance and oversight of my academic supervisors.

Scientific work originated from this PhD research project:

Chapter 2 (published in *Journal of Environmental Management*)

Zelli, E., Ellis, J., Pilditch, C., Rowden, A. A., Anderson, O. F., Geange, S. W., ... & Stephenson, F. (2025). Identifying climate refugia for vulnerable marine ecosystem indicator taxa under future climate change scenarios. *Journal of Environmental Management*, 373, 122635.

Publication available here:

<https://www.sciencedirect.com/science/article/pii/S0301479724026215>

Chapter 3 (under review with minor revision with *Ocean and Coastal Management*)

Zelli, E., Ellis, J., Pilditch, C., Rowden, A. A., Anderson, O. F., Geange, S., ... & Stephenson, F. Bottom-Trawling Affects the Viability of Climate Refugia for Vulnerable Marine Ecosystem Indicator Taxa. *Available at SSRN 5084099*.

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https://papers.ssrn.com/sol3/papers.cfm?abstract_id=5084099

Chapter 4 (being prepared for submission)

Further scientific works related to this thesis I contributed to:

“Quantification of bottom trawling impacts in the New Zealand region suggests losses of Vulnerable Marine Ecosystems at ecologically relevant scales” (being prepared for submission in Nature Communication)

Abstract

The deep sea remains one of the least explored ecosystems on the planet, with 95% still uncharted. From what is known, it harbours critical habitat-forming species like cold-water corals and sponges that sustain extraordinary biodiversity and provide key ecosystem services, including supporting fisheries. These fragile ecosystems face escalating threats from climate change and bottom trawling, yet the extent of their impacts remains poorly understood. This PhD addresses these gaps by examining how these stressors influence Vulnerable Marine Ecosystem (VME) indicator taxa in New Zealand's Exclusive Economic Zone and explores implications for conservation. The research explores (i) climate change impacts and potential refugia, (ii) the added pressure of bottom trawling, and (iii) management strategies with policymakers and fishery regulators to fast-track spatial protection measures in the New Zealand region.

In Chapter 2, species distribution models were used to predict the spatial distribution of density for several deep-water VME indicator taxa under present-day environmental conditions and two future climate scenarios (SSP2-4.5 and SSP3-7.0) projected by the end of the 21st century. Results showed a significant decline in both the density (54%) and spatial extent (61%) of all assessed taxa under future conditions compared to the current day. However, the models also identified potential climate refugia: areas where certain taxa may persist despite changing environmental pressures, representing crucial conservation targets. This and previous research, however, indicate that existing spatial management measures with respect to bottom trawling may be insufficient to protect VME indicator taxa now and into the future. This suggests that present-day densities, even within potential climate refugia areas, may have already declined due to this activity.

Chapter 3 examines the impact of bottom trawling by estimating the density loss of VME indicator taxa in high-density areas, particularly climate refugia, in New Zealand waters over the past 30 years. Bottom trawling was predicted to have reduced the current density of all assessed taxa across the study region, with the most pronounced reductions in taxon density and habitat extent (up to 10% loss) occurring in areas predicted to be climate refugia. Such declines may undermine the ability of taxa to form ecologically functional habitats in the future if these impacts persist.

The interplay between climate change and bottom trawling presents a complex multi-stressor scenario for VMEs and their indicator taxa. Addressing these cumulative impacts requires integrated approaches that simultaneously consider ecological and social dimensions to provide the scientific knowledge required to support management decisions.

Chapter 4 introduces a social-ecological perspective by combining density-based spatial analysis of VME indicator taxa distributions under multiple stressors (e.g., climate change and bottom trawling) with participatory methods, including interviews and group elicitation with policy regulators and fishery experts. This approach aimed to assess risk perceptions, inform potential management actions, and identify barriers and solutions for effective conservation in the New Zealand region. Findings revealed that presenting additional scientific evidence and engaging a diverse group of stakeholders in discussions enhanced their risk perceptions and confidence about the impacts of climate change and bottom trawling on VME indicator taxa. Additionally, stakeholder engagement helped refine potential strategies for implementing spatial management measures.

By adopting a social-ecological approach, this PhD thesis integrated ecological modelling, spatial impact analysis, and participatory methods to provide insights into the multiple effects of climate change and bottom trawling on VME indicator taxa and their effective management. The findings that originated from this work can contribute to the development of climate-resilient marine spatial planning strategies aimed at strengthening the long-term protection of deep-sea VMEs as well as from additional impacts such as bottom trawling. Moreover, the thesis identifies key scientific knowledge gaps, including the need for connectivity analyses and recovery following disturbance from local stressors such as bottom trawling. This information can be useful to enhance the predictive power of species distribution models and the importance of broader stakeholder involvement—particularly the fishing industry—to facilitate the implementation of management initiatives in a socially just and equitable manner.

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Chapter 1

General Introduction

1.1 Vulnerable Marine Ecosystems: Ecological relevance and challenges stemming from multiple pressures

Marine ecosystems face mounting challenges due to multiple human-induced stressors and activities, with an escalating degradation of ocean health, ecosystem services and associated societal goods and benefits (Borja et al., 2024; Hewitt et al., 2016; Hoegh-Guldberg & Bruno, 2010; Solé Figueras et al., 2024). Fisheries and climate change are widely recognised as major contributors to global marine habitat deterioration and biodiversity decline, with impacts extending across marine ecosystems (Beddington et al., 2005; Doney et al., 2012; Kaiser & Williams, 2011; Sumaila & Tai, 2020; Williamson & Guinder, 2021), including the deep seas (Benn et al., 2010; Fosså et al., 2002; Ramirez-Llodra et al., 2011). Deep seas are defined as water and sea floor areas below 200 m, representing 90% of the oceans by volume and the largest ecosystem on the planet (Jobstvogt et al., 2014; Tyler, 2003). This ecosystem is also thought to be one of the most diverse ecosystems in the world, with diversity levels that rival those found in the tropical rainforest (Dover, 2021; Freiwald et al., 2004; Grassle & Maciolek, 1992). The deep-sea supplies society with valuable ecosystem services, including nutrient cycling, biogeochemical regulation and carbon sequestration. It also provides important provisioning services, including food that sustains fishery activities (Armstrong et al., 2010, 2012; Jobstvogt et al., 2014).

Global fisheries have expanded in recent decades across tropical, temperate and polar marine environments (Moore & Jennings, 2008; Valdimarsson & James, 2001). Concerns have grown over the sustainability of both target (Worm et al., 2006) and non-target catch (Kelleher, 2005), and their impacts on habitat and community structures as well as biodiversity loss (Beddington et al., 2005; Caddy, 1999). Given the depletion of many inshore stocks and the improvements in fishing technology, which now operate at depths reaching 2000 m (Sissenwine & Mace, 2007), many fishing grounds have reached deep-sea ecosystems (Probert et al., 1997). This exploitation is advancing faster than scientific efforts to understand deep-sea ecosystems' ecological functions and broader significance

to both natural and human systems. Consequently, the impacts on deep-sea habitats and communities could likely be underappreciated (Benn et al., 2010; Tyler, 2003).

Fishing activities, particularly those operating towed bottom-fishing gear (e.g., bottom trawling and dredging), can have significant and long-lasting direct and indirect effects on benthic species richness and community diversity, structure and productivity (Hiddink et al., 2006; Jennings & Kaiser, 1998; Mazor et al., 2021). Bottom trawling, in particular, is widely regarded as the primary threat to benthic ecosystems, particularly deep-seafloor ecosystems (Halpern et al., 2007; Levin et al., 2019; Ramirez-Llodra et al., 2011; Reed et al., 2007; Watson & Morato, 2013). Direct impacts on benthic ecosystems are severe, encompassing the physical removal of organisms, the extirpation of vulnerable species and the reduction of habitat complexity (Clark et al., 2016; Dayton et al., 1995; Hiddink et al., 2006; Kaiser et al., 2002). Indirect effects include sediment resuspension, habitat fragmentation and consequent loss of population connectivity, exacerbating the risk associated with this activity (Clark et al., 2016; Dayton et al., 1995). These disturbances can lead to significant declines in abundance and species composition, resulting in long-term effects on ecological functions and structures, which can take decades or centuries to recover (Clark et al., 2016; McConnaughey et al., 2020; Sciberras et al., 2018). In addition, bottom-contact fishing gear disproportionately impacts habitat-forming taxa such as corals and sponges being particularly vulnerable due to their fragile structures, erect growth forms, long lifespans, and slow growth rates (Bensch et al., 2009; Clark et al., 2016; Goode et al., 2020; Gros et al., 2023a; Morato et al., 2006).

Based on growing concern about the adverse ecosystem impacts of fishing on the high seas, the 2006 United Nations General Assembly Resolution 61/105 called “upon States to take action immediately, individually and through regional fisheries management organisations and arrangements, and consistent with the precautionary approach and ecosystem approaches, to sustainably manage fish stocks and protect vulnerable marine ecosystems (VMEs), including seamounts, hydrothermal vents and cold water corals, from destructive fishing practices, recognizing the immense importance and value of deep-sea ecosystems and the biodiversity they contain” (Auster et al., 2011; UNGA Resolution 65/38, 2010). Moreover, the UN resolution required that States and Regional Fishery Management Organizations (RFMOs) manage fisheries to prevent significant adverse impacts to areas identified as VMEs (Auster et al., 2011; UNGA Resolution 65/38,

2010). Specific criteria for the identification of VMEs are presented in paragraph 42 of the FAO Guidelines, including uniqueness or rarity, functional significance, fragility, life history traits that contribute to slow recovery, and areas of structural complexity (FAO, 2009). Only one of these criteria needs to be met for a site to be designated as a VME (FAO, 2009).

Examples of VMEs include cold-water coral reefs and sponge beds. Ecologically significant taxa that form these ecosystems, such as certain cold-water corals (e.g., Scleractinian corals, Antipatharia, Gorgoniidae) hydrozoans (e.g., Stylasteridae), or sponges (e.g., Demospongiae) are classified as VME indicator taxa, as their presence is often indicative of a VME (FAO, 2009; Gros et al., 2023a; Parker & Bowden, 2010). VME indicator taxa are characterized by habitat-forming species that are both ecologically significant—as they support local biodiversity by providing nursery, feeding and refugia areas to associated species—but also highly sensitive to the impacts of bottom trawling (Roberts et al., 2006; Roberts & Hirshfield, 2004; Rossi et al., 2017; Thurber et al., 2014). However, while VME indicator taxa were conceptualized to protect critical ecosystems and species from bottom fishing, they are also increasingly vulnerable to the impacts of climate change (Gammon et al., 2018; Levin et al., 2019; Ramirez-Llodra et al., 2011; Sweetman et al., 2017).

Climate change is impacting the marine environment globally (Doney et al., 2012; Worm & Lotze, 2021), with the deep-sea ecosystems also affected (Levin et al., 2019; Ramirez-Llodra et al., 2011; Smith et al., 2008; Sweetman et al., 2017). Global ocean surface temperature has increased by 0.88 °C from 1850–1900 to 2011–2020 and is projected to increase by approximately 1–4 °C by the end of the century, with intensity depending on future emissions scenario (Collins et al., 2013; IPCC, 2023). Higher temperatures will intensify water column stratification, reducing oxygenation in deeper waters, with oxygen levels predicted to decline by 1–7% over the same period (Keeling et al., 2010; Stramma et al., 2010). Reduced vertical mixing will limit the availability of particulate organic carbon (POC), a crucial nutrient source for benthic organisms (Levin et al., 2019). In addition, ocean acidification, driven by increased CO₂ uptake, has already lowered seawater pH by 0.1 units since the early 1900s, with further reductions of 0.4–0.5 units expected by 2100 (Sabine et al., 2004; Smith et al., 2008). Ocean acidification is more intense in the deep sea and Southern Ocean due to higher CO₂ solubility in cold water.

Increasing pressure further dissolves calcium carbonate, reducing aragonite and calcite saturation (Figuerola et al., 2021; J. C. Orr et al., 2005).

Such climate-related alteration of environmental conditions is expected to negatively affect the physiological and metabolic processes of deep-sea calcified organisms, such as cold-water corals (Figuerola et al., 2021; Levin et al., 2019; Ramirez-Llodra et al., 2011; Sweetman et al., 2017). Cold-water corals are highly vulnerable to ocean acidification because it reduces calcium carbonate availability required to build skeletons, impairing calcification and reef-building processes (Figuerola et al., 2021; Georgian et al., 2019; Lunden et al., 2013; Turley et al., 2007). Sponges may also suffer reduced feeding efficiency and homeostasis processes under these conditions (Carballo & Bell, 2017; Liu et al., 2021). These environmental stressors result in a more fragile skeleton structure and, therefore, a higher sensitivity to additional disturbances like bottom trawling (Clark et al., 2016). Moreover, changing environmental conditions are projected to drive shifts in species distributions across coral reef ecosystems globally, including warm, cold, shallow, and deep waters. These changes may lead to habitat loss and increased extinction risk in tropical and northern temperate regions while potentially increasing species suitability and range expansions in boreal regions (Chaudhary et al., 2023). Further studies focusing on the deep sea found that climate-related changes in deep waters (e.g., warming, acidification and deoxygenation) are likely to affect the distributions and diversity of deep-sea corals, thereby compromising key ecosystem services (Morato et al., 2020a). Understanding how future environmental conditions can affect the distribution of deep-sea species, including foundation species like cold-water corals, is essential for developing climate-resilient management strategies that support biodiversity conservation and species adaptation to climate change (Morato et al., 2020a; Tittensor et al., 2009, 2010).

Forecasting the effects of climate change on the spatial distribution of species and habitats under future climate scenarios can reveal areas where species and habitats are most likely to experience tolerable or favourable climatic conditions, thereby highlighting high-priority locations for protection (Moilanen & Wintle, 2006; Morelli et al., 2016). These locations, where species and habitats can persist or expand despite changing climate conditions, are commonly referred to as 'climate refugia' (Graham et al., 2019; Keppel et al., 2012; Lancaster & Hildrew, 1993). Climate refugia are considered resilient biological components of natural systems, vital for maintaining ecological functions against

changing environmental conditions and, therefore, their protection is becoming a commonly prioritized target for future and spatial planning efforts (Graham et al., 2019; Keppel et al., 2012; Lancaster & Hildrew, 1993). However, while some studies have investigated the potential impacts of climate change on deep-water coral distributions and pinpointed potential climate refugia at a global scale (Morato et al., 2020a; Tittensor et al., 2010), less work has been conducted at regional scales, including in areas considered hotspots for deep-water corals, such as New Zealand waters (Anderson et al., 2022).

1.2 New Zealand: A biodiversity hotspot for VME indicator taxa and the role of spatial protection measures

Cold-water corals—defined as VME indicator taxa (Parker et al., 2009)—are key components of deep-sea bottom ecosystems and constitute major habitats (Roberts & Hirshfield, 2004). Deep-water coral communities are a highly diverse group and can form large, highly complex biogenic structures that provide habitat, refuge, sanctuary, and nursery areas for a broader set of benthic communities supporting high levels of biodiversity (Buhl-Mortensen & Mortensen, 2005; D’Onghia et al., 2010; Krieger & Wing, 2002; Rogers, 1999; Rossi et al., 2017). New Zealand’s waters, in particular, are globally recognised as a biodiversity hotspot for cold-water corals, with up to 110 deep-water coral species thought to occur (Tracey & Hjørvarsdóttir, 2019). This represents about one-sixth of the world’s described species—with the Gorgonian octocoral assemblage being among the most diverse worldwide (Sánchez & Rowden, 2006; Tracey & Hjørvarsdóttir, 2019). These corals form critical deep-sea habitats, supporting large aggregations of invertebrates and fish (Tracey et al., 2011), including commercially important species and are therefore likely to host numerous VMEs (Tracey & Hjørvarsdóttir, 2019).

Despite the uncertainties surrounding direct ecological links between fish and corals due to little knowledge of coral and fish distribution, evidence of interactions between fishing operations and coral ecosystems in the New Zealand region is provided by bycatch records (Blom et al., 2009; Tracey et al., 2019) along with numerous studies documenting the impacts of bottom trawling on coral ecosystems. These impacts are particularly pronounced on extensive bathyal plateaux, such as the Chatham Rise and Campbell Plateau, as well as on seamounts, highlighting these areas as especially vulnerable to fishing pressure (Brodie & Clark, 2003; Clark et al., 2010; Clark, Bowden, et al., 2022,

2022; Goode et al., 2020). As a result, key taxa, including stony corals (Scleractinia), black corals (Antipatharia), gorgonian corals (Gorgoniidae), and hydrocorals (Stylasteridae) are protected under the New Zealand Wildlife Act (1953), and listed in New Zealand's threatened species classification (Funnell et al., 2023). In addition, marine spatial protection measures were established primarily to protect these taxa from bottom-contact fishing activities, including bottom trawling and dredging (Brodie & Clark, 2003; Helson et al., 2010).

The establishment of spatial closures such as benthic protection areas (BPAs), established in 2007, prohibit bottom trawling and dredging and restrict midwater trawling across approximately 30% of the New Zealand Exclusive Economic Zone (EEZ). Additionally, seamount closure areas (SCAs) and large no-take marine reserves (LMRs) around offshore islands have been introduced, partly to protect functionally important VME indicator taxa from bottom-contact fishing activities (Brodie & Clark, 2003; Helson et al., 2010). However, recent studies highlight these spatial protection measures appear to not provide enough levels of protection for VME indicator taxa from bottom trawling activities, nor do they account for potential shifts in taxa distributions driven by climate change (Anderson et al., 2022; Stephenson et al., 2023a; Zelli et al., 2025). Consequently, the extent of habitats covered by marine spatial measures in New Zealand remains unknown.

1.3 Addressing knowledge gaps on the impact of climate change and bottom trawling on VME indicator taxa in the deep water of New Zealand

The deep sea remains one of the least studied and understood ecosystems due to its inaccessibility and the high cost of exploration and research. For example, approximately two-thirds of all known coral species inhabit deep, cold, and light-limited waters. However, due to the challenges associated with studying these organisms in their natural environment their distribution, biology, ecology, and functional roles remain poorly understood (Roberts & Hirshfield, 2004). Accurate knowledge of species distributions is, therefore, a critical first step toward understanding ecosystem functioning and forecasting future changes (Anderson et al., 2022; Vierod et al., 2014). Species distribution models (SDMs) are numerical tools that integrate observations of species occurrence or abundance with environmental variables and are now widely applied in terrestrial,

freshwater, and marine ecosystems (Elith & Leathwick, 2009; Guisan & Zimmermann, 2000). They are used to gain ecological insights and to extrapolate species distributions across space and time and are particularly useful for characterizing the distribution of species or habitats across unsampled areas or difficult-to-reach environments such as the deep-sea (Elith & Leathwick, 2009; Weber et al., 2017). The main advantage of using such models is the ability to predict the distribution of species over wide geographic regions and project changes under future climate scenarios (Cheung et al., 2009; Hijmans & Graham, 2006). For these reasons, these models are increasingly recognised as an important tool to inform management and spatial planning (Elith & Leathwick, 2009; Guisan & Thuiller, 2005; Mazar et al., 2021).

In New Zealand, SDMs have been extensively applied to estimate the occurrence of VME indicator taxa, including cold-water corals under present-day environmental conditions over broad regions of the Exclusive Economic Zone (EEZ) (Anderson et al., 2016, 2014; Bennion et al., 2024; Stephenson et al., 2023b, 2021b; Tracey et al., 2011). as well as in several other studies that developed predictive models and spatial management options for the protection of VMEs in the South Pacific Ocean region (Anderson et al., 2016; Bennion et al., 2024; Georgian et al., 2019; Rowden et al., 2014). Utilising predictions of future marine climatic conditions from Earth System Models, these modelling tools were also applied to help identify potential future refuges for deep-water corals (Anderson et al., 2022, 2015). However, while abundance is critical for understanding ecosystem functions and provides more valuable information for management, as many ecosystem services are density-dependent, it is less frequently incorporated into SDMs (Gaston & Fuller, 2008; Melo-Merino et al., 2020; Spaak et al., 2017). In addition, predicting the distribution of VME indicator taxa using abundance-based data is often sought to identify a VME, rather than simply the occurrence of an indicator taxon that may or may not, represent a VME (Howell et al., 2011). As a result, recent studies have investigated the abundance distribution of VME indicator taxa in the South Pacific (Bennion et al., 2025) and in New Zealand (Bowden et al., 2021; Stephenson et al., 2024a). Nevertheless, there remains a significant knowledge gap regarding the density distribution of these taxa, particularly in the context of climate change. Therefore, to enhance the protection of functionally important VME indicator taxa and the ecosystem services they provide, it is essential to generate present and future density-based spatial predictions of their distribution (Dijkstra et al., 2021; Rullens et al., 2021).

In Chapter 2, SDMs were used to model the spatial distribution of density for deep-water VME indicator taxa under both current and future environmental conditions within the New Zealand Territorial Sea and Exclusive Economic Zone (100–1500 m water depth) to evaluate potential loss and distribution shifts of density of these taxa by the end of the 21st century.

Spatial predictions of future taxa density offer a robust approach to identifying future climate refugia (Zelli et al., 2025). However, the realization of these refugia depends on several factors, including adequate abundance and high-density levels of taxa at present-day, which are critical for sustaining functional habitats in the future (Carr et al., 2017; Morelli et al., 2017). Given the extensive impacts of bottom trawling on deep-sea ecosystems, it is likely that not all deep-sea areas remain pristine, and regions that once supported VME species and habitats may now exhibit significantly reduced densities (Ardron et al., 2014). Consequently, spatial models that do not account for historical bottom trawling may overestimate the extent of future refugia, particularly in areas with a long history of intense fishing pressure, such as the New Zealand region. Ensuring the viability of these refugia requires assessing their current exposure to local stressors, particularly bottom trawling, which could compromise their ability to function as future refugia (Anderson et al., 2022; Stephenson et al., 2023a; Zelli et al., 2025). This is a key consideration for management, as spatial protection measures should prioritize ecologically significant regions, such as those with high species density and richness. Thus, in addition to mapping the distribution of climate refugia, it is crucial to quantify their spatial overlap with historical fishing efforts and adjust predictions by accounting for potential density declines. This approach enhances the reliability of spatial planning and ensures that conservation measures are effectively targeted (Ardron et al., 2014; Fragkopoulou et al., 2021; Georges et al., 2024; Stephenson et al., 2023a).

Various spatially explicit methods have been developed to assess the impact of bottom fishing, incorporating factors such as historical fishing effort, gear type, habitat vulnerability, and taxa distributions (Eigaard et al., 2016; Pitcher, 2014; Rijnsdorp et al., 2016). For instance, Sharp et al., (2009) assessed longline fishing impacts based on gear deployment and species vulnerability although did not directly integrate benthic taxa distributions. Mormede et al., (2017) introduced a benthic risk assessment using spatial population models to evaluate fishing effects on indicator species, providing insights into ecosystem status. Pitcher et al., (2017) developed a quantitative method for assessing the

risks to benthic habitats by towed bottom-fishing gears using a relative benthic status (RBS) metric that accounts for trawl intensity and taxa sensitivity. Another statistical approach to estimating the impact of bottom trawling on benthic habitats and taxa distributions is the *dynamic* Relative Benthic Status (dRBS) assessment, developed by Pitcher et al., (2015). This method quantifies taxa-specific depletion and recovery rates, offering a more refined estimation of fishing impacts over time. It accounts for fluctuations in fishing intensity, tracks temporal changes, and incorporates seabed recovery during periods of reduced trawling activity, making it particularly valuable for management applications (Pitcher et al., 2015; Stephenson et al., in review).

In New Zealand, the spatial extent of bottom trawling by inshore and deepwater fisheries has been mapped in detail (Baird et al., 2015; Ford et al., 2017; Jones, 1992) including its impacts on deep-water corals (Rowden et al., 2014). However, understanding the effects of bottom fishing on benthic communities remains complex, requiring assessments of actual impacts on specific taxa (Rowden et al., 2014). Penney & Guinotte, (2013) evaluated bottom trawling risks for deep-water corals within the South Pacific Regional Fisheries Management Organisation (SPRFMO) area, including New Zealand waters, using occurrence-based predictive habitat suitability models. Their findings suggest that current spatial closures to bottom trawling within the New Zealand SPRFMO area are suboptimal for protecting VMEs. Moreover, they do not account for future distribution under climate change scenarios or the potential impacts of bottom trawling on predicted climate refugia.

Despite their ecological significance, the vulnerability of climate refugia to bottom fishing remains largely unexplored. Previous studies have estimated the potential overlap between bottom trawling and the distribution of refugia areas for crustose coralline algae (Fragkopoulou et al., 2021) and a deep-water coral species in the Mediterranean Sea (Georges et al., 2024). However, no research has explicitly examined the spatial overlap between historical bottom trawling and density-based climate refugia predictions for VME indicator taxa in New Zealand and the South Pacific. A refined understanding of these spatial interactions is crucial for informing conservation strategies and mitigating potential fishing impacts on climate refugia. To achieve this, comprehensive spatial analysis of the distribution and density of VME indicator taxa, along with their exposure to historical fishing efforts, is essential.

Chapter 3 employed the dRBS approach to estimate the impact of 30-year-period bottom trawling activities on the current density distribution of VME indicator taxa, particularly focusing on areas predicted to serve as climate refugia under future climate change scenarios.

Identifying and assessing the effects of multiple impacts (e.g., climate change and bottom trawling) on both current and future ecologically relevant habitats (e.g., high-density, high-richness, high-biodiverse zones) is crucial for guiding future spatial planning (Hewitt et al., 2016; Stephenson et al., 2023a). Management strategies should particularly prioritise ecologically significant areas such as climate refugia as they represent the sole habitats where VME indicator taxa may persist or expand under future climatic conditions (Graham et al., 2019; Keppel et al., 2012). Protecting these habitats is essential to reducing local extinction risk, preserving biodiversity and maintaining ecosystem functionality (Keppel et al., 2015, 2024; Stephenson et al., 2023a). However, the potential overlap between climate refugia and fishing grounds may suggest the economic importance of these areas for the fishing industry. Effective management must, therefore, consider not only the ecological value of climate refugia but also their socio-economic significance, ensuring that conservation strategies balance biodiversity protection with sustainable resource use. Achieving conservation objectives while ensuring the sustainability of fisheries will require integrating ecological and socio-economic considerations through structured stakeholder engagement and evidence-based decision-making within existing governance frameworks.

1.4 Toward a social-ecological research approach: Engaging with experts to inform future marine spatial planning

The interplay between climate change and bottom trawling constitutes a complex multi-stressor scenario for VMEs and VME indicator taxa (Ban et al., 2014; Hewitt et al., 2016). From a management perspective, addressing these multiple impacts requires integrated approaches that consider ecological, social, and economic dimensions. In this context, risk assessment plays a pivotal role in driving effective decision-making (Treffny & Beilin, 2011; Xu et al., 2015). Risk assessment evaluates the likelihood and consequences of stressors on ecological and social systems, helping prioritize management actions and trade-offs (Harwood, 2000; Holsman et al., 2017). This method has been used to estimate the impacts of climate change on marine ecosystems (Halpern, McLeod, et al., 2008;

Magris et al., 2018a), and fisheries on marine resources (Fletcher, 2005; Halpern, Longo, et al., 2012). While traditional risk assessments focused on single pressures, recent advances consider multiple stressors' interactions between local and global stressors and their importance for cumulative impacts. Such an approach can provide a more comprehensive understanding of marine risks (Brown et al., 2013, 2014; Maxwell et al., 2013) and facilitate the establishment of direct science-policy links to achieve effective management (Côté et al., 2016; Stelzenmüller et al., 2018, 2020). This shift is significant for understanding the interconnectedness of stressors, such as climate change and fisheries, and their combined effects on marine ecosystems. Assessing risk in this way helps decision-makers prioritize interventions, protect vulnerable ecosystems, and ensure the long-term sustainability of marine resources (Adger, 2006; Holsman et al., 2017; Magris et al., 2018a).

Spatial conservation tools (e.g., SDMs) are widely used in spatial planning tools (conservation planning tools) or spatially explicit decision support tools because they provide crucial insights into the taxa and habitats distribution, helping identify the most vulnerable (Elith & Leathwick, 2009; Guisan & Thuiller, 2005; Ramirez-Reyes et al., 2021). These tools facilitate the evaluation of multiple disturbances and help balance conservation goals with socio-economic considerations (Klein et al., 2008; Lester et al., 2018; Mazor et al., 2014; Moilanen et al., 2009; Peterson et al., 2013). The management of the marine environment is therefore also a matter of societal commitment that involves a decision-making process for the allocation of three-dimensional marine spaces to specific uses to achieve stated ecological, economic and social objectives. People play a central role in this process, acting as key drivers of change (Pomeroy & Douvère, 2008). As such, stakeholder engagement and involvement is integral to the success of marine spatial planning—defined as a means of enhancing decision-making and delivering an ecosystem-based approach to managing human activities in the marine environment (Ehler & Douvère, 2009). Stakeholders' involvement should therefore be extended in future research to increase the likelihood that spatial management decisions result from a consensus or are supported by as many stakeholders as possible (Rowden et al., 2019).

This underscores that inclusive, adaptive science-policy frameworks are needed to foster collaboration among scientists, policymakers, and communities, integrating diverse perspectives into decision-making (Davis, 2008; Hartley & Robertson, 2006; Kitts et al.,

2007; Martin-Smith et al., 2004; Sen & Raakjaer Nielsen, 1996; Verheij et al., 2004). Stakeholder engagement and participatory methods, such as expert elicitation, are valuable tools for assessing risks and impacts in environmental management and supporting decision-making (Martin et al., 2012; Morgan, 2014; Singh et al., 2017). Group elicitation, for instance, enables participants to discuss and refine their views on specific issues, fostering deeper understanding and collaboration (Burgman et al., 2011; Kandlikar et al., 2005; Sutherland & Burgman, 2015). This approach helps balance conservation goals with socio-economic considerations, addressing trade-offs in social-ecological systems (Davis, 2008; Kitts et al., 2007). Consequently, group elicitation is regarded as an effective way to expedite decision-making and prioritize management strategies and conservation actions (Hartley & Robertson, 2006; Verheij et al., 2004).

Previous studies in the New Zealand SPRFMO region have employed participatory approaches, including expert-driven workshops, to develop guidelines for the effective conservation of VMEs. The framework proposed revolved around several steps such as (i) identifying the distribution of VME indicator taxa, (ii) establishing ecological thresholds (e.g., density of VME indicator species, spatial extent of associated habitats), (iii) assessing known or potential fishing impacts, and (iv) conducting management strategy evaluations to generate trade-off scenarios (Ardron et al., 2014). However, no research has explicitly integrated density-based predictions of VME indicator taxa distributions under multiple stressors (i.e., climate change and bottom trawling) with participatory approaches to evaluate expert-driven risk perceptions and inform potential management actions in the New Zealand region.

Chapter 4 aimed to assess and compare experts' perception of risk related to the impacts of multiple stressors on VME indicator taxa and associated management strategies priorities. The analysis was based on data collected before (through individual interviews) and after participatory methods (during a workshop) that involved the presentation of novel scientific insights and group elicitation.

This last chapter aims to bridge the gap between science and management by integrating perspectives from both scientific and policy sectors, demonstrating the value of science-based participatory approaches in supporting informed decision-making for marine conservation. By providing data on the density distribution of VME indicator taxa, with

a specific focus on climate refugia and the impacts of historical bottom trawling, this study seeks to contribute to the development of more resilient and adaptive strategies for the long-term protection of VMEs.

1.5 Research goals and contribution

This research aims to address key knowledge gaps and advance our understanding of (1) the spatial distribution of climate refugia in the New Zealand region under present environmental conditions and potential alteration under future climate change scenarios and (2) the potential additional damage caused by the overlap of taxa distribution and bottom trawling grounds. By assessing these factors, this work seeks to (3) engage with local experts to ultimately inform future conservation and management decisions. Specifically, the objectives of this thesis were to:

1. Predict the density distribution of VME indicator taxa under present-day and identify regions of potential climate refugia under future climate change scenarios that follow different Shared Socioeconomic Pathways (SSP2-4.5 and SSP3-7.0) using density-based SDMs (Chapter 2).
2. Estimate the impacts of historical bottom trawling on present-day distributions of VME indicator taxa density within predicted current and future (i.e., climate refugia) habitats employing the dRBS approach (Chapter 3).
3. Evaluate how integrating novel scientific insights (from Chapters 2 and 3) with participatory methods (e.g., individual interviews and group elicitation) influences experts' risk perception regarding multiple stressors and shapes their prioritization of management strategies to mitigate these risks (Chapter 4).

By adopting an interdisciplinary approach that integrates ecological modelling, spatial impact analysis, and participatory methods, this research provides critical insights to support the development of effective and resilient marine spatial planning frameworks. These frameworks aim to enhance the protection of deep-sea VMEs and VME indicator taxa, along with the associated biodiversity and ecosystem services, in the face of global and local stressors.

Chapter 2

Identifying climate refugia for vulnerable marine ecosystem indicator taxa under future climate change scenarios

2.1 Introduction

Habitat-forming taxa, including, amongst others, cold-water corals, represent some of the most ecologically significant benthic fauna and are considered key components of deep-sea benthic ecosystems (Cairns, 2007; McFadden et al., 2022; Roberts et al., 2006; Roberts & Hirshfield, 2004). The three-dimensional structure of these taxa modifies the local environmental conditions (Roberts et al., 2006; Rossi et al., 2017) and provides nursery, refugia, and feeding areas for a large number of associated commercially and ecologically important species (Henderson et al., 2020; Jones et al., 2018; Miller et al., 2012; Rowden et al., 2020). As a result, these taxa support high biodiversity and provide other ecosystem services, including provisioning services (i.e., fisheries) (Roberts & Hirshfield, 2004; Thurber et al., 2014). These habitat-forming taxa are, however, susceptible to a variety of human-induced stressors particularly bottom trawling activities (Levin et al., 2019; Sweetman et al., 2017). Vulnerable Marine Ecosystem (VME) is a term adopted by the United Nations General Assembly Resolution 61/105 (UNGA Resolution 65/38, 2010) based on growing concern about the adverse ecosystem impacts of fishing on the High Seas (Auster et al., 2011). International Guidelines for the Management of Deep-sea Fisheries in the High Seas have been developed to prevent significant adverse impacts on VMEs while allowing for sustainable fisheries (FAO, 2009). The FAO guidelines indicate that one of the following criteria; (i) uniqueness or rarity, (ii) functional significance, (iii) fragility, (iv) life history traits that contribute to slow recovery, and (v) structural complexity, can be used to identify VMEs (FAO, 2009). Ecosystems characterized by both high susceptibility to disturbance and protracted recovery times, potentially leading to irreversibility or non-recovery, are the most vulnerable. Examples of VMEs include cold-water coral reefs and sponge beds, which rely on habitat-forming taxa (FAO, 2009). VMEs are not exclusively confined to the High Seas (areas beyond national jurisdictions) but can also occur within areas of national jurisdiction. Here we use the VME concept to demonstrate the broader international

applicability of our study, including reference to VME indicator taxa. That is taxa that have one of the FAO guideline characteristics indicated above, whose occurrence could potentially indicate the presence of a VME (Gros et al., 2023a; Parker & Bowden, 2010).

The New Zealand region is a global biodiversity hotspot for cold-water corals, including habitat-forming taxa (Tracey & Hjørvarsdóttir, 2019). In this area, cold-water corals are widely distributed and are particularly diverse, representing about one-sixth of the world's described species, including several endemic species (Cairns, 2007, 2016, 2012; Sánchez & Rowden, 2006; Tracey & Hjørvarsdóttir, 2019). A significant number of coral taxa, including all stony corals (Scleractinia), black corals (Antipatharia), gorgonian corals (Gorgoniidae) and hydrocorals (Stylasteridae), are protected by the New Zealand Wildlife Act (1953) and are considered VME indicator taxa in the South Pacific (Parker et al., 2009; *SPRFMO*, 2023). Some of the species within these taxa are included in New Zealand's threatened species classification list (Funnell et al., 2023). The establishment of seamount closures and benthic protection areas to mitigate the effects of bottom-contacting fishing activities such as bottom trawling and dredging was in part based on protecting these functionally important species (Brodie & Clark, 2003; Helson et al., 2010). Some large no-take marine reserves around offshore islands, which encompass deep-sea environments, also protect VME indicator taxa. However, current marine spatial measures do not afford high levels of protection for these taxa nor do they account for their vulnerability to future climatic conditions (Anderson et al., 2022; Stephenson et al., 2023a). Therefore, knowledge of the distribution of regionally identified VME indicator taxa, especially under future altered environmental conditions, is pivotal to ensuring the protection of VMEs in the future (Stephenson et al., 2023a).

VME indicator taxa can be negatively impacted by acute or chronic disturbances derived not only from bottom trawling activities but also from those driven by climate change (Gammon et al., 2018; Levin et al., 2019; Ramirez-Llodra et al., 2011; Sweetman et al., 2017). Altered environmental conditions such as changing temperature regimes (Noaa, 2019), seawater pH (Sabine et al., 2004; Smith et al., 2008), quality and quantity of particulate organic carbon (POC) (Levin et al., 2019), and oxygen saturation levels (Keeling et al., 2010; Stramma et al., 2010) are expected to modify VME indicator taxa's physiological and metabolic processes (Dodds et al., 2007). For cold-water corals, for example, these changes are thought to have direct consequences, especially on growth

and calcification rates, resulting in reduced reef-creation capacity (Georgian et al., 2016; Lunden et al., 2013; Turley et al., 2007) and ability to recover from physical disturbance (Clark et al., 2016). Furthermore, recent studies on cold-water corals suggest that climate-driven environmental changes will lead to alterations in their distribution, at both global (Chaudhary et al., 2023) and regional scales (Anderson et al., 2022).

Knowledge of the severity of climate change threat to VME indicator taxa is hampered by our limited understanding of their distribution and habitat requirements. However, obtaining sufficient data to inform conservation actions is particularly difficult in the deep sea. VME indicator taxa have been found on continental shelves, canyons, and seamounts in deep seas across the globe (Freiwald et al., 2004), yet their full extent is unknown. In such a hard to reach environment, field surveys are challenging and logistically difficult to carry out, resulting in data paucity which constrains the adequate representation of taxa distribution (Anderson et al., 2022; Stephenson et al., 2021b; Vierod et al., 2014). Habitat suitability models, including Species Distribution Models (SDMs), are one statistical tool that enables the prediction of distributions of occurrence and/or abundance based on relationships between biological records and spatially explicit environmental variables (Elith & Leathwick, 2009; Guisan & Zimmermann, 2000). SDMs are increasingly recognised as an important tool in resource management and conservation biology (Mazor et al., 2021; Stephenson et al., 2022b). These models are particularly useful for characterizing the distribution of species or habitats and providing surrogate data for knowledge gaps, especially in difficult-to-reach environments such as the deep sea (Elith & Leathwick, 2009; Weber et al., 2017).

Several studies in the New Zealand region have employed an SDM approach to provide occurrence estimates (the probability of the taxa being present) of deep-sea invertebrate benthic taxa, especially cold-water corals for present environmental conditions (Anderson et al., 2016, 2016b, 2015, 2020; Baird et al., 2013; Compton et al., 2013; Georgian et al., 2019; Rowden et al., 2017; Stephenson et al., 2024b, 2021b; Tracey et al., 2011). These studies provided critical knowledge about the environmental drivers influencing the distribution of these species/communities/habitats, identifying depth, temperature, seabed slope and roughness, and the concentrations of dissolved oxygen and aragonite/calcite as the most important predictors. Further studies in the region concentrated on the distribution of cold-water corals under both present and future climate change scenarios

(Anderson et al., 2022). Models from this habitat suitability study predicted a significant decline in both the occurrence and spatial extent of deep-water corals by the end of the 21st century. Nonetheless, the presence or the predicted presence of a species does not necessarily serve as a reliable indicator of the occurrence of a VME, particularly in cases involving habitat-forming taxa, e.g., *Goniocorella dumosa* or *Solenosmilia variabilis* (Rowden et al., 2020), nor does it offer insights into its population abundance (Rullens et al., 2021). Despite the role of abundance in sustaining ecosystem functions being described both qualitatively (Gaston & Fuller, 2008) and empirically (Spaak et al., 2017), it is notably less frequently assessed in SDMs (Melo-Merino et al., 2020). Furthermore, for species with wide distributions, like VME indicator taxa, SDMs trained on abundance, in addition to occurrence data, provide additional information about high-quality habitats, potentially resulting in more accurate and ecologically relevant spatial predictions than models trained solely on presence-absence (occurrence) data (Howard et al., 2014; Rullens et al., 2021). Additionally, abundance plays a pivotal role in informing spatial management strategies as many ecosystem functions and services are often density-dependent (Melo-Merino et al., 2020; Spaak et al., 2017).

VME indicator taxa that occur in high abundance can mediate important ecological processes that shape community dynamics, including habitat productivity and nutrient cycling (Rossi et al., 2017). Consequently, gaining information on VME indicator taxa density, as a measure of abundance, and its geographical distribution becomes paramount when assessing the impact on VME-associated functionality and ecosystem services. Noteworthy, examples of density-based SDMs encompass research on designing marine protected areas for rays (Dedman et al., 2015), studying the distribution patterns of cetaceans (Becker et al., 2017), managing fishery bycatch (Stock et al., 2020), and identifying important conservation areas for estuarine bivalves (Rullens et al., 2021). Recent studies in the New Zealand region incorporated density data for a broad spectrum of benthic taxa, including cold-water corals (Anderson et al., 2014; Bowden et al., 2019; Stephenson et al., 2021a) but they do not account for species/habitat distributions under evolving climate conditions. Therefore, to inform effective future marine spatial planning actions, spatial information on both the distribution and density of functionally important VME indicator taxa that accounts for future climate change is required (Dijkstra et al., 2021). Regions that remain relatively buffered from contemporary climate change over

time and enable the persistence of valued physical, ecological, and sociocultural resources, might serve as climate refugia (Lancaster & Hildrew, 1993). Here we refer to climate refugia as areas within a taxon's current distribution that are expected to persist under future climatic conditions (herein referred to as “internal climate refugia”) as well as areas outside the taxon's current distribution that are predicted to provide suitable conditions for the taxon in the future (herein referred to as “external climate refugia”) (Graham et al., 2019). Both internal and external climate refugia are important regions for resilience to climate change under both present-day and future climatic conditions.

In this study, we use recently developed Earth System Models (Kawamiya et al., 2020) tailored to the New Zealand region (Behrens et al., 2020), and the classification and regression algorithm Random Forest (RF) (Breiman, 2001), to produce SDMs that predict distributions of density for 14 deep-sea habitat-forming VME indicator taxa (10 cold-water coral, 2 hydrozoan, and 2 sponge taxa) under both present climatic conditions and different future climate change scenarios. We selected these taxa due to their ecological importance, potential vulnerability to anthropogenic impacts, and the availability of data. The investigated future climate change scenarios follow the Shared Socioeconomic Pathways SSP2-4.5 (4.5 W m^{-2}) moderate increase trajectory, and the SSP3-7.0 (7.0 W m^{-2}) strong increase trajectory (Behrens et al., 2020; Williams et al., 2016). This study is the first to apply SDMs to assess changes in the distribution of density of VME indicator taxa under future environmental scenarios within New Zealand waters. Model outcomes were used to identify regions where VME indicator taxa are predicted to decline due to climate change and areas that could serve as climate refugia. Our findings are discussed in light of their implications for ecosystem functions and services, and their significance for future spatial management and conservation efforts in New Zealand. While this approach is presented with VME indicator taxa in New Zealand, it can be broadly applied to other marine taxa and regions.

2.2 Materials and Methods

2.2.1 Study area

The study area encompasses water depths of 100–1500 m within the Territorial Sea and Exclusive Economic Zone (EEZ) of New Zealand. This depth range represents the habitat where most records used in this study have been obtained for the studied VME indicator

taxa (Figure 1). Furthermore, these specific depth ranges delineate regions with the highest probability of intersection between the presence of VME indicator taxa and anthropogenic activities, including potential impacts from climate change and bottom trawling (Stephenson et al., 2023a). The spatial resolution of predictions was 1 km² to match the resolution of available environmental predictor data as well as the approximate scale of the main sampling methods used to collect the underlying data – i.e., the length of the seafloor video transects from which the biological data were compiled (see below for further detail) (Bowden et al., 2021).

2.2.2 Biological data

The biological dataset was derived from 798 sampling sites from scientific surveys (Anderson et al., 2023; Bowden et al., 2019, 2021) which employed the Deep Towed Imaging System (DTIS) camera platform that recorded continuous high-definition video of the seafloor and high-resolution still images at regular intervals (Bowden & Jones, 2016; Hill, 2009). VME indicator taxa suitable for modelling have been selected from the dataset based on: (1) their biological traits as a proxy for their ecological and functional relevance (i.e., habitat-forming VME indicator taxa); (2) their sensitivity to climate change-driven impacts and vulnerability to seafloor disturbances by bottom trawling (i.e., their mineralogy and structure, respectively); (3) their conservation status; and (iv) a sufficient number of taxa occurrence records to build robust predictive (Georgian et al., 2019; Morato et al., 2020b; Stephenson et al., 2021b). We selected 14 taxa for modelling: reef-forming scleractinian corals (*Goniocorella dumosa*, *Solenosmilia variabilis*, *Enallopsammia rostrata*, *Madrepora oculata*), black corals (Antipatharia), primnoid (Primnoidae), sea-fans, sea-whips (Gorgoniidae), sea-pens (Pennatuloidae), bamboo corals (Keratoisididae/Mopseidae), golden corals (*Radicipes* spp.) – collectively referred to as the taxonomic group ‘Cold-water corals’; Hydrozoa (Stylasteridae, and other hydrozoans) – referred to as ‘Hydrozoans’; and Porifera (Hexatinellida and Demospongiae) – referred to as ‘Sponges’ (Table 1).

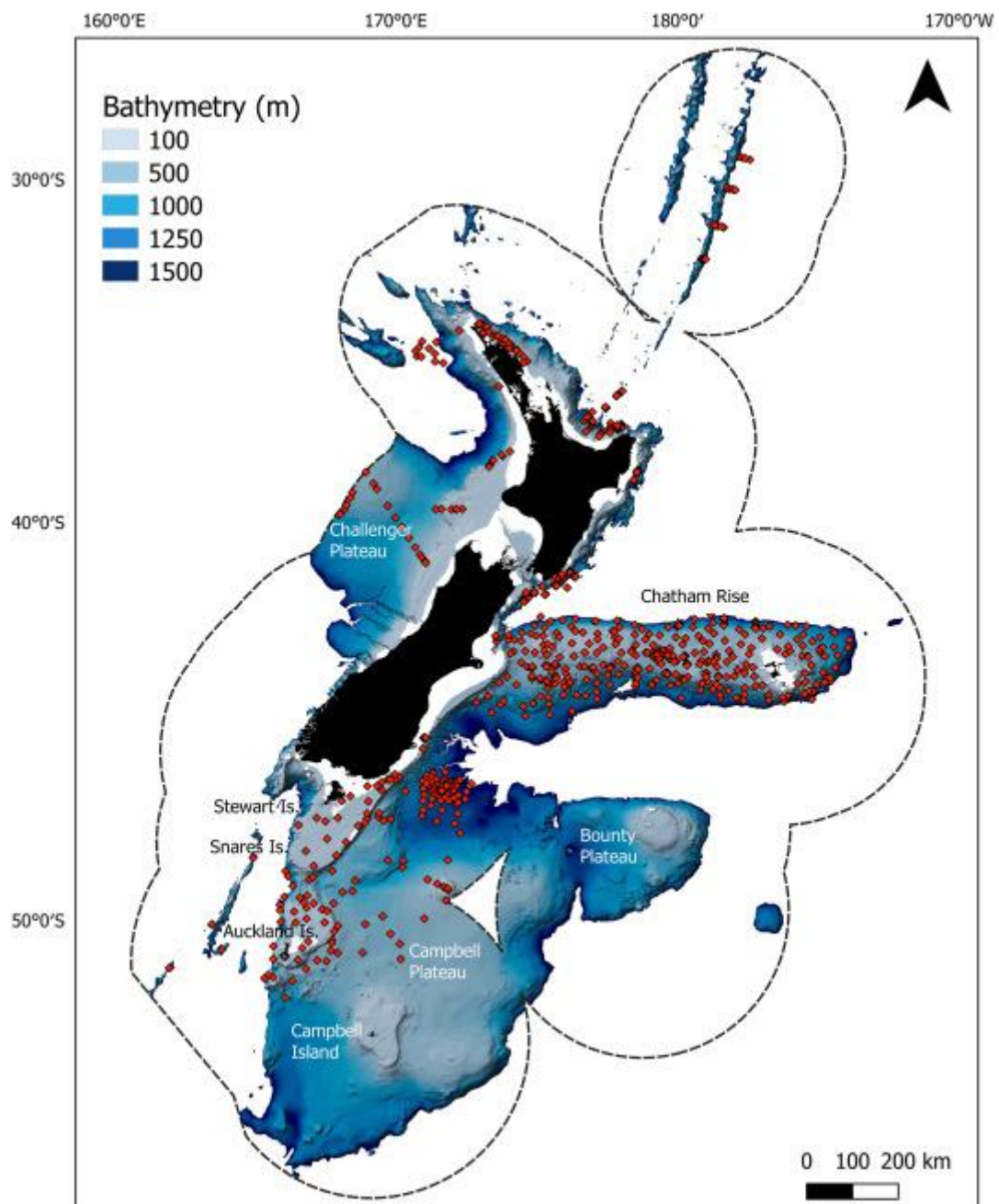


Figure 1. Location of sampling sites (red dots) overlain on the bathymetry of the study area (100–1500 m water depth within the New Zealand Exclusive Economic Zone), and labels of seafloor features mentioned in the text (black dashed line marks the outer limit of New Zealand Exclusive Economic Zone). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

Table 1. Taxa eligible for modelling, along with the categorization (Group) used through the text including Cold-water corals, Hydrozoans and Sponges taxa; their morphological traits (with details on taxa mineralogy and structure characteristics as indication of their sensitivity to climate change (CC) and bottom trawling (BT)); and the relative number of occurrence records within the study area. Taxa denoted with asterisks indicate those aggregated and modelled as a group for multiple-resolution models. Specifically, *Goniocorella dumosa*, *Solenosmilia variabilis*, *Enallopsammia rostrata*, and *Madrepora oculata* have been collectively modelled as a “Scleractinia”. Taxa without asterisks have been modelled individually. Notably, in the case of *G. dumosa*, this taxon has been modelled both individually and as part of the broader "Scleractinia" group. For further taxonomic information about the modelled taxa refer to McFadden et al., (2022). For further details on biological mineralogy refer to Bostock et al., (2015); Farfan et al., (2018); and Thresher et al., (2011).

Phylum	Sub-phylum	Class	Subclass	Order	Superfamily	Family	Genus	Species	Common names	Group	Morphological traits		Occurrence records
											Mineralogy (Sensitivity to CC)	Structure (Sensitivity to BT)	
Cnidaria	Anthozoa	Hexacorallia		Scleractinia		Caryophylliidae	<i>Goniocorella</i>	<i>Goniocorella dumosa*</i>	Stony coral	<i>Goniocorella dumosa</i>	Carbonatic (Aragonite)	Hard, erect, fragile	71
							<i>Solenosmilia*</i>	<i>Solenosmilia variabilis</i>	Stony coral	Cold-water corals	Carbonatic (Aragonite)	Hard, erect, fragile	13
						Dendrophylliidae	<i>Enallopsammia*</i>	<i>Enallopsammia rostrata</i>	Stony coral	Cold-water corals	Carbonatic (Aragonite)	Hard, erect, fragile	21
						Madreporidae	<i>Madrepora*</i>	<i>Madrepora oculata</i>	Stony coral	Cold-water corals	Carbonatic (Aragonite)	Hard, erect, fragile	12
				Antipatharia				Black coral	Cold-water corals	Proteinaceous (Chitin)	Flexible, erect	163	
Cnidaria	Anthozoa	Octocorallia		Scleractinia		Chrysogorgiidae	<i>Radicipes</i>	<i>Radicipes</i> sp.	Golden coral	Cold-water corals	Carbonatic (Calcite)	Flexible, erect	109
						Pennatulioidea			Sea-pens	Cold-water corals	Carbonatic (Calcite)	Flexible, erect	366
						Primnoidae			Primnoids	Cold-water corals	Carbonatic (Calcite)	Flexible, erect	151
				Malacalcyonacea	Gorgoniidae			Sea-fans	Cold-water corals	Proteinaceous (Gorgonin)	Flexible, erect	310	
					Isididae			Bamboo coral	Cold-water corals	Proteinaceous (Gorgonin)	Flexible, erect	124	
Cnidaria		Hydrozoa						Hydrozoans	Hydrozoans	Carbonatic (Aragonite)	Hard, erect, fragile	456	
				Hydroidolina	Anthoathecata		Stylasteridae			Hydrocorals	Hydrozoans	Carbonatic (Aragonite)	Hard, erect, fragile
Porifera		Demospongiae						Demosponges	Sponges	Spicules (Spongin/Silica)	Soft, erect, fragile	543	
		Hexactinellida						Glass-sponges	Sponges	Spicules (Silica)	Hard, erect, fragile	342	

Standardized taxon density estimates (number of individuals per 1000 m² of seabed) were derived from the observation data, using seafloor areas calculated as the product of transect length and average image frame width for the video (see Bowden et al., 2019 for details) and summed areas of all individual images for still photographs (Bowden et al., 2021). Furthermore, VME indicator taxa observations were recorded at varying taxonomic levels to ensure consistent recording of taxa that matched those used in the previous works and because the high taxonomic resolution identification was not always possible. In the case data availability was limited, taxa with comparable ecological functions (e.g., habitat-forming taxa) and biological traits (e.g., sensitivity to increasingly acidified water), such as the reef-building taxa, including *G. dumosa*, *S. variabilis*, *E. rostrata*, *M. oculata* were aggregated and modelled as a single group called “Scleractinia”. However, when sufficient data was available to build robust models, taxon-individual models were generated (see Table 1 for more detail). Furthermore, the taxonomic details at which the biological records were collected, and the availability of occurrence records resulted in the production of models with different taxonomic resolution: (i) single models for one taxon (i.e., for *G. dumosa* and *Radicipes* spp.) (ii) single models for multiple taxa (i.e., for Antipatharia, Primnoidae, Gorgoniidae, Pennatuloidae, Keratoisididae/Mopseidae, Hydrozoa, Stylasteridae, Hexactinellida, Demospongiae), or (iii) aggregated model (i.e., Scleractinia).

2.2.3 Environmental predictor variables

The environmental variables used in the models consisted of a combination of temporally fixed and temporally dynamic variables which are thought to drive VME indicator taxa distribution (Anderson et al., 2022; Georgian et al., 2019). We use an environmental dataset from , which included dynamic variables derived from the New Zealand Earth System Model (NZESM) model (Behrens et al., 2020). Variable selection was guided by previous studies, which identified carbonate ions and dissolved oxygen as key drivers (Anderson et al., 2022). Consequently, we omitted correlated variables such as bottom temperature, as it was found to be highly correlated with both salinity and oxygen (Anderson et al., 2022). Fixed variables included seabed depth, slope, and aspects of seabed shape (fine-scale and broad-scale benthic position index, and roughness [standard deviation of slope]) as well as substrate type (e.g., sand, mud, rubble, rock) which is relevant for larval settlement (Freiwald, 2003; Rogers, 1999; Rowden et al., 2010). Dynamic variables included those that are affected by environmental fluctuations such as

seafloor temperature, salinity, detrital flux, dissolved oxygen, and aragonite/calcite saturation (especially for habitat-forming taxa such as scleractinian corals which rely on dissolved calcium and carbonate ions for biomineralization processes (Falini et al., 2015). These dynamic variables were derived from the NZESM – a regional model which provides a highly complex model of the climate system tuned to the New Zealand region by combining component models of ocean biogeochemistry, biology, and chemistry (Behrens et al., 2020; Williams et al., 2016). Currently, the NZESM can project environmental conditions ranging between the years 1850 and 2100. For this study, we selected three predicted conditions for two time periods: one corresponding to historical conditions approximating the period of sample collection (1995–2014) and a future period (2080–2099) for the end of the 21st century (Anderson et al., 2022). The predictions for the future period were based on “Moderate” (SSP2-4.5) and “Strong” (SSP3-7.0) increases in greenhouse gas concentration trajectories, reflecting respectively a modest or a more limited action to mitigate carbon emissions and adapt to climate change (Anderson et al., 2022; Fricko et al., 2017; O’Neill et al., 2016). Initially, all the above-mentioned environmental predictor variables (at a 1 km² grid resolution) were considered in the present study. However, a high number of predictor variables generally provides minimal improvement in predictive accuracy, which may lead to model overfitting and complicate model interpretability (Leathwick et al., 2006). Consequently, to ensure parsimonious models, a further selection of environmental predictor variables was made to avoid the presence of highly correlated variables. We thus selected only a subset of the initial predictor variables based on two methods: collinearity calculation and analysis of variables' relative influence. We used pairwise relationship correlation (Pearson's correlation coefficient, *r*) to assess the strength of collinearity among predictors (Benesty et al., 2009; Jouffray et al., 2019). All levels of collinearity between predictor variables <0.9 were considered acceptable for tree-based machine learning methods (Elith et al., 2010; Stephenson et al., 2021a, 2021b). In addition, the relative influence of variables was derived from the number of times a variable was selected for splitting weighted by the squared improvement to the model (see next section for details) as a result of each split, using in-bag data (Sapatinas, 2004). Only predictor variables with a relative influence >5% were retained (Jouffray et al., 2019; Müller et al., 2013). Final models were created by refitting the previous ones, but this time with a reduced variables subset specific for each taxon. The final set of predictor variables made available to the models are listed in Table 2.

Table 2. Final set of environmental predictor variables considered for the species distribution models (for more information about the predictor environmental variables see Anderson et al., 2022). Measurements within the water column were taken at different depths, indicating three-dimensional [3-D] data, whereas measurements at the benthic (sea floor) level were taken exclusively, representing two-dimensional [2-D] data.

Variables	Description	Units	Reference
Dynamic variables			
Aragonite	Aragonite	Ω Aragonite	NZESM
Calcite	Calcite saturation	Ω Calcite	NZESM
Oxygen	Dissolved oxygen at	mmol/m ³	NZESM
Nitrogen	Benthic Nitrogen at	mmol/m ²	NZESM
Detrital flux	Total detrital flux to	mmol/m ³	NZESM
Salinity	Seafloor salinity	psu	NZESM
Fixed variables			
Bathymetry	Seabed depth	m	Mitchell et al.,
BPI-broad	Benthic Position	–	Stephenson et al., (2022)
BPI-fine	Benthic Position	–	Stephenson et al., (2022)
Prof-curvature	Profile curvature	–	Stephenson et al., (2022)
Slope-percent	Seabed slope	in %	Stephenson et al., (2022)

2.2.4 Species distribution models

The relationships between the occurrence and density of VME indicator taxa and environmental variables were investigated using a Random Forest (RF) machine learning algorithm. RF is a classification and regression tree-based algorithm that builds large numbers of trees using random subsets of input data and averages out the results (Breiman, 2001). RF is increasingly being used in ecology (Bradter et al., 2013; Chapman et al., 2010) including for SDMs (Valavi et al., 2021) due to its good performance as a classifier (Cutler et al., 2007) and its ability to produce regression estimates of abundance (Hill et al., 2017). Moreover, RF is valued for its robustness, especially in situations where the number of predictors is high relative to the number of data points (Bradter et al., 2013). RF has been successfully applied to spatially predict the distribution of benthic invertebrates in previous works in the New Zealand region (Anderson et al., 2016b; Georgian et al., 2019; Rowden et al., 2017; Stephenson et al., 2023b) including outperforming other modelling approaches (Stephenson et al., 2021b). RF models were built by choosing a random selection of predictor values at each split and employed a

bagging technique to produce many individual trees and aggregate the models' outputs. Models were built using the *randomForest* package (Liaw & Wiener, 2002) in RStudio (version 4.2.2). The *tuneRF* function, in the R package *caret* (Kuhn et al., 2023) was used to select optimal values for complexity parameters including *mtry* which determines the number of predictor variables selected at each tree split and *ntrees* to set the number of classification trees to grow. This process allowed the best combination of parameters that achieves minimum predictive error to be identified (out of bag (OOB) error). To model the distribution of density, a two-part hurdle model (or Delta model) was used (e.g., Dedman et al., 2015). In this procedure, a binomial model was initially used to predict the distribution of occurrence (using presence and absence data), followed by a separate (second) model with a suitable distribution (here a Gaussian distribution following log-transformation) to estimate density (conditional on presence), both of which are multiplied together to produce spatial estimates of density (i.e., density expressed as individuals per km²). We acknowledge that some studies hurdle a discretised binomial layer, however, the approach we employ here (where the layer is not discretised) is considered a standard approach (e.g., Dedman et al., 2015).

2.2.5 Spatial predictions and estimation of uncertainty

For each taxon, maps showing the probability of occurrence, and the predicted density were generated by applying RF models to a spatially explicit grid of taxon-specific environmental variables relative to present and both future climate change scenarios (SSP2-4.5 and SSP3-7.0). Spatial predictions were made for the study area using the 'predict' functions in the *randomForest* package. Spatial predictions for occurrence models represent the predicted probability of occurrence ranging from 0 to 1, with higher values indicating more suitable environmental conditions and a higher probability of finding the target taxa. Spatial predictions for density represent the predicted number of individuals per unit area (density) at locations of taxon presence (Stephenson et al., 2021a). To incorporate uncertainty in predictions across the model extent, a bootstrap technique was used to produce spatially explicit uncertainty measures (Leathwick et al., 2006). Bootstrapping involves a random selection (with replacement) of a 'training' sample, of the same sample size as the full occurrence and density dataset, running the model with this random sample, and then repeating the process a number of times. Occurrence and density records excluded from the random selection were set aside for independent assessment of model performance ("evaluation" data). This process was

repeated 150 times for each model. Each bootstrap model was fitted to the predictor variables, and geographical predictions were made on the 1 km² grid for depths between 100 m and 1500 m. The mean probability of occurrence and density conditional on presence was calculated for each grid cell using the 150 bootstrapped layers for models. Overall estimates were calculated for each grid cell by multiplying the spatial estimate of the probability of occurrence and the density estimate at each bootstrap and were upscaled to match the scale of the environmental variables (from individuals per 1000 m² of seafloor to individuals per km²) (Stephenson et al., 2021b). Final spatial predictions reflect the mean density the spatially explicit measure of uncertainty (SD of the mean) calculated across the 150 bootstraps. To explore the relationship of density across environmental gradients, partial dependence plots were generated (Friedman & Meulman, 2003; Sapatinas, 2004). Partial dependence plots provide a visualization of the relationships between the most influential predictor variables and the response while keeping all other variables at their mean (Friedman & Meulman, 2003).

The uncertainty estimates from tree-based models decrease in areas of extrapolation outside of the domain of the environmental predictors (Liu et al., 2020). That is, in parts of the study areas which have environmental conditions that are not well represented by the available DTIS samples, the model predictions may be less reliable. However, this uncertainty is not captured by the bootstrapping estimates. To address and quantify the uncertainty associated with model extrapolation, we provide an additional estimate of uncertainty – “sample coverage of the environmental space”. The “environmental space” represents the multidimensional space produced by considering each of the environmental variables as a dimension. We modelled variation in sampling density within the environmental space by combining our DTIS samples, assigned as “presences”, with randomly sampled values from the environmental space assigned as “absences” using a presence/absence RF model (Smith et al., 2013; Stephenson et al., 2020, 2021b). Using the predicted environmental variables, the model was then used to spatially predict environmental coverage (ranging from 0 to 1), where high values represent those areas with environmental conditions similar to those already sampled and low values represent those areas with environmental conditions not well represented within our samples. Environmental coverage was calculated for both present-day and future climate scenarios. It is important to note that model reliability under future scenarios is based on predicted environmental variables, which introduces higher uncertainty due to the unpredictability

of future scenarios (SSP2-4.5 and SSP3-7.0). Also, based on previous studies estimating the coverage of environmental space for the prediction of species distribution in New Zealand, we use threshold of 0.05 to represent areas with ‘adequate’ environmental coverage (Stephenson et al., 2020). Areas with values below this threshold indicate limited understanding of the environmental space, making predictions of species' distributions less certain. In these poorly covered areas, geographic predictions from species occurrence models should be treated with greater caution (Elith & Leathwick, 2009).

2.2.6 Model validation

RF model performance was evaluated using metrics calculated from withheld evaluation data (the samples not used in each bootstrap) and averaged across bootstraps. Occurrence models (using presence/absence data) were evaluated using AUC (area under the receiver operator characteristic curve) and TSS (True Skill Statistic). AUC is a robust indicator of model performance and provides a threshold-independent measure of accuracy. AUC score ranges between 0 and 1 where higher values indicate better predictions. A score of 0.5 indicates performance equivalent to random guessing, while a score of 0.8 or above denotes “excellent” performance (Hosmer et al., 2013). In contrast, the TSS is a threshold-dependent measure of accuracy that remains unaffected by prevalence. TSS considers both specificity and sensitivity, yielding an index that ranges from -1 to $+1$, where values of 1 are in perfect agreement and values of less than or equal to 0 indicate a performance no better than random or a systematically incorrect prediction (Allouche et al., 2006). Model fit metrics were calculated using both the ‘training’ dataset and the ‘evaluation’ dataset. Testing the evaluation dataset is regarded as a more robust and conservative approach for assessing the model's goodness-of-fit compared to using the training dataset alone (Hastie et al., 2001). Density models (using density conditional on presence data) were evaluated by using Pearson's correlation (r) a statistical metric that measures the strength and direction of a linear relationship between the predicted and the observed (density) values. Values range between -1 and 1 , with values > 0 reflecting a positive correlation (Pearson & Henrici, 1997).

2.2.7 Density changes in region of primary habitats

Focusing on taxa density, rather than mere occurrence, is crucial as high densities are more indicative of the presence of a VME thereby offering better insights into the effects

on VMEs functionality and their response to environmental impacts. Hence, we set a threshold at the 98th percentile of the taxa density estimates across all grid cells under current climatic conditions to identify areas above this cut-off, that is with the highest density. We refer to these areas as “primary habitats”, a concept described by Anderson et al., (2022) and (Stephenson et al., 2024a). While these studies focused on occurrence and used a 95th percentile cut-off, we opted for a more conservative threshold given our focus on density. This approach ensures that we identify only the areas with the highest densities, which are likely to have a greater capacity for providing ecosystem services.

In this context, a primary habitat is, therefore, defined as a habitat where the density is sufficiently elevated to most likely represent “physical structures created by significant concentrations of biotic [and abiotic] features” or “structuring organisms” (FAO, 2009) and therefore to provide essential ecosystem services associated with each taxon. To ensure consistency in the comparisons across periods, the density threshold identified under current climatic conditions was also used to identify primary habitats under both future climatic conditions. Changes in the extent and density within primary habitats were compared between current and future climatic conditions for each taxon (e.g., Present vs SSP2-4.5 and Present vs SSP3-7.0).

Changes in taxon density are reported as either “total density” (sum of the taxon density across all cells in the study area, averaged across all bootstraps) or “density within primary habitats” (sum of the taxon density across all cells, averaged across all bootstraps within areas defined as primary habitats). Changes in taxon extent are reported as “Contraction areas” – reflecting a predicted loss in primary habitats under future climate change scenarios; “Internal refugia (present-day)” – reflecting predicted current-day primary habitats; Internal refugia (future) – reflecting predicted primary habitats under future climate change scenarios; “External refugia” – reflecting a predicted gain in primary habitats under future climate change scenarios. In the following section we show model outputs for *G. dumosa* and an average for all VME indicator taxa. Maps of all modelled taxa are reported in Supplementary files (see Supplementary Materials, “Density distribution (overall and within primary habitats)” and “Primary habitat overlaps” sections).

2.3 Results

In this section we present model-generated results depicting the spatial prediction of VME indicator taxa density and the associated changes under future climatic conditions (SSP2-4.5 and SSP3-7.0) across the study area. These results encompass the entire modelled taxonomic groups, with a specific focus on *G. dumosa* as an illustrative example, given its recognised significance as a habitat-forming VME indicator taxon in the New Zealand region (Dawson, 1984; Mackay et al., 2014; Squires, 1965).

2.3.1 Model performance

Overall, both the occurrence and density RF models performed well for all modelled taxa (Table 3). For occurrence models, the mean AUC and TSS scores using the evaluation data suggested good model performance (mean AUC = 0.82; mean TSS = 0.56). AUC and TSS show similar model performance (Table 3). The best and the lowest performance evaluation metrics scores were found for *G. dumosa* (mean AUC = 0.92; mean TSS = 0.75) and Hydrozoa (mean AUC = 0.74; mean TSS = 0.37), respectively (Table 3). For density models, the mean Pearson's correlation was relatively high (mean $r = 0.40$) with Hexactinellida being the highest (mean $r = 0.61$) and Keratoisididae/Mopseidae being the lowest (mean $r = 0.08$).

Table 3. Mean bootstrapped estimates of model performance for occurrence models (AUC and TSS) and density models (Pearson's correlation, r), with relative standard deviation (SD) when assessed using the (withheld) evaluation data for each taxa.

Modelled taxon	Occurrence		Density			
	AUC	SD	TSS	SD	r	SD
<i>G. dumosa</i>	0.92	0.03	0.75	0.05	0.39	0.13
Scleractinia	0.88	0.03	0.70	0.06	0.39	0.12
Antipatharia	0.87	0.02	0.64	0.05	0.46	0.09
<i>Radicipes</i> spp.	0.76	0.04	0.43	0.05	0.39	0.13
Pennatulioidea	0.77	0.02	0.50	0.04	0.45	0.07
Gorgoniidae	0.82	0.03	0.53	0.04	0.34	0.10
Primnoidae	0.81	0.02	0.53	0.04	0.18	0.08
Keratoisididae/Mopseidae	0.84	0.02	0.60	0.04	0.08	0.15
Hydrozoa	0.74	0.02	0.37	0.04	0.45	0.06
Stylasteridae	0.86	0.02	0.62	0.03	0.51	0.09
Demospongiae	0.78	0.02	0.50	0.04	0.56	0.04
Hexactinellida	0.78	0.02	0.50	0.04	0.61	0.06
Mean across all taxa	0.82	0.02	0.56	0.04	0.40	0.09

Environmental coverage values, based on sample locations for all taxa and present environmental conditions, were highest on the Chatham Rise region (0.8–1) (Figure S98). Coverage was moderate around Stewart Island and the Snares Islands, as well as along the southeast and northeast continental shelves (0.3–0.6) and was lowest on the Bounty Plateau and Auckland Island (<0.3). Predictions of taxa' distributions are less certain for those areas with lower environmental coverage. Predictions of environmental coverage under future climate change scenarios (SSP2-4.5 and SSP3-7.0) were similar to those for present-day environmental conditions (Figure S98).

2.3.2 Importance of environmental variables

Aragonite saturation, dissolved oxygen concentration, and detrital flux were the most influential dynamic variables driving the distribution and density of *G. dumosa* (Figure 2). Specifically, there was a positive relationship between *G. dumosa* density and dissolved aragonite saturation ($\Omega_{\text{Aragonite}} \sim 1.5$). Dissolved oxygen concentration was also identified as a significant driver of *G. dumosa* density with a peak in density at approximately 225 mmol/m³, but lower densities at lower and higher concentration levels (Figure 2). Lastly, detrital flux concentration at ca. 0.25 mmol/m³ exhibited strong association between high *G. dumosa* density, albeit with diminishing strength as concentrations increased (Figure 2).

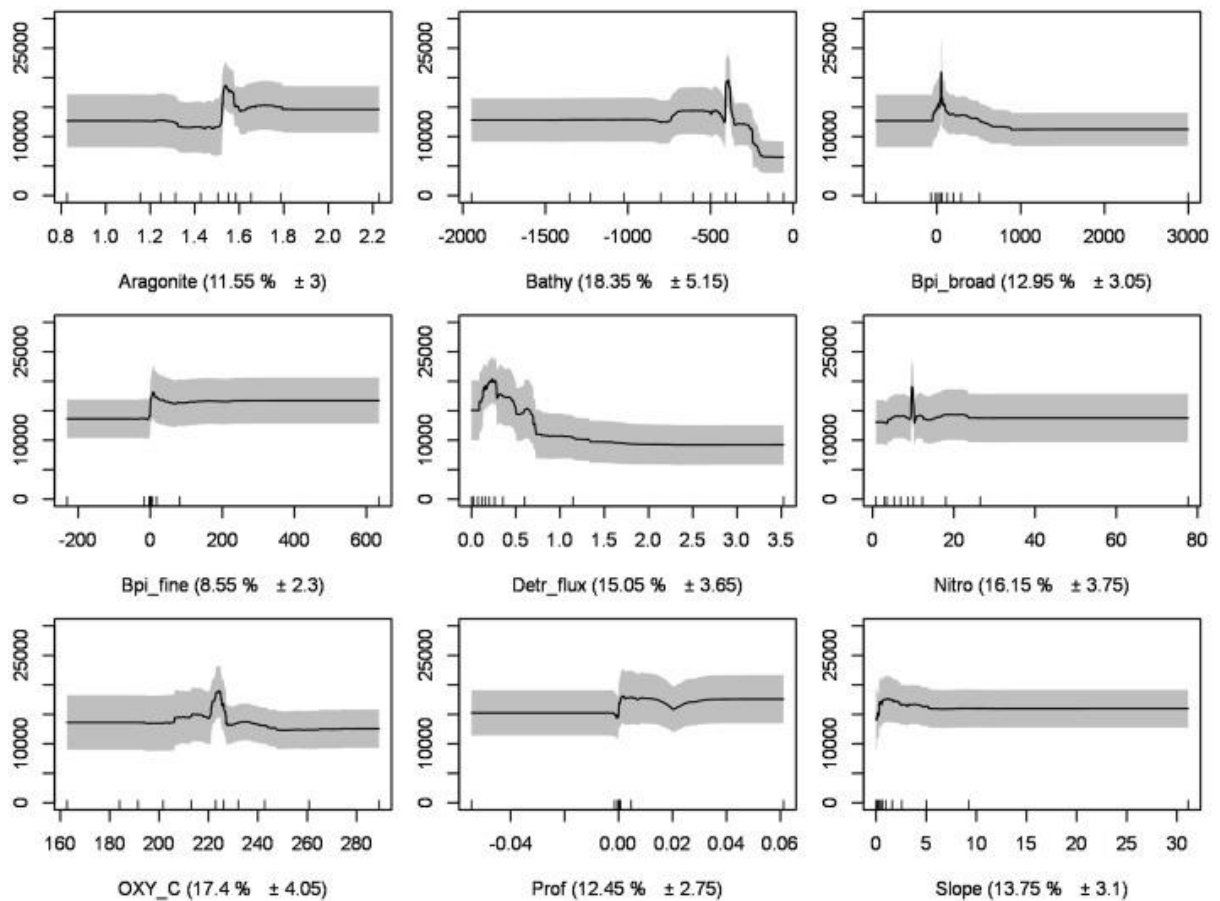


Figure 2. Partial dependence plots showing the relationships between environmental variables (“X” axis) and density (individuals km^{-2}) of *Goniocorella dumosa* (“Y” axis) modelled using bootstrapped Random Forest models. Black lines represent the mean of 150 bootstrap predictions and shaded areas represent 95% prediction interval. Deciles of the distribution of biological samples across the range of each environmental predictor are shown as ticks on the x-axis. Relative mean (\pm SD) percentage contribution of variables is provided in parentheses. See Table 2 for explanation of abbreviations and units.

Across all taxa, the most important dynamic environmental variables affecting the taxa distribution of density were aragonite/calcite saturation. The relationships were similar with aragonite being important for scleractinian taxa (e.g., for *G. dumosa*, Figure 2) and calcite for octocoral taxa, indicating a general correlation between taxon density and carbonate ion concentration (refer to Table 1 for details on which taxa were modelled using aragonite or calcite and see Supplementary Materials, Figure S40; S45; S50; S55; S60 for more details). Seafloor oxygen levels, detrital fluxes, and nitrogen concentration also emerged as relevant environmental predictors driving density and distribution of VME indicator taxa across the modelled area (see Supplementary Materials “Partial Dependence Plots” sections). Noteworthy, significant fluctuations in aragonite/calcite

saturation and oxygen levels were identified across the future climate scenarios. In comparison to present-day conditions, a decline in aragonite/calcite concentration and oxygen levels was predicted throughout the modelled area under both future climate conditions, especially the SSP3-7.0 scenario (Figs. S6–7; S12-13; S18–19 and S8; S14; S20).

2.3.3 Spatial predictions of density

Overall, the uncertainty associated with the spatial predictions of density was generally moderate for all modelled taxa (see Supplementary Materials S86-S98). The spatial patterns in predicted density for *G. dumosa* were similar across the predictions under current and future climatic conditions (Figure 3). However, density was predicted to be higher under present conditions (Figure 3, panel (i)) when compared to future climatic conditions (SSP2-4.5. and SSP3-7.0; see Figure 3, panel (ii) and (iii) respectively).

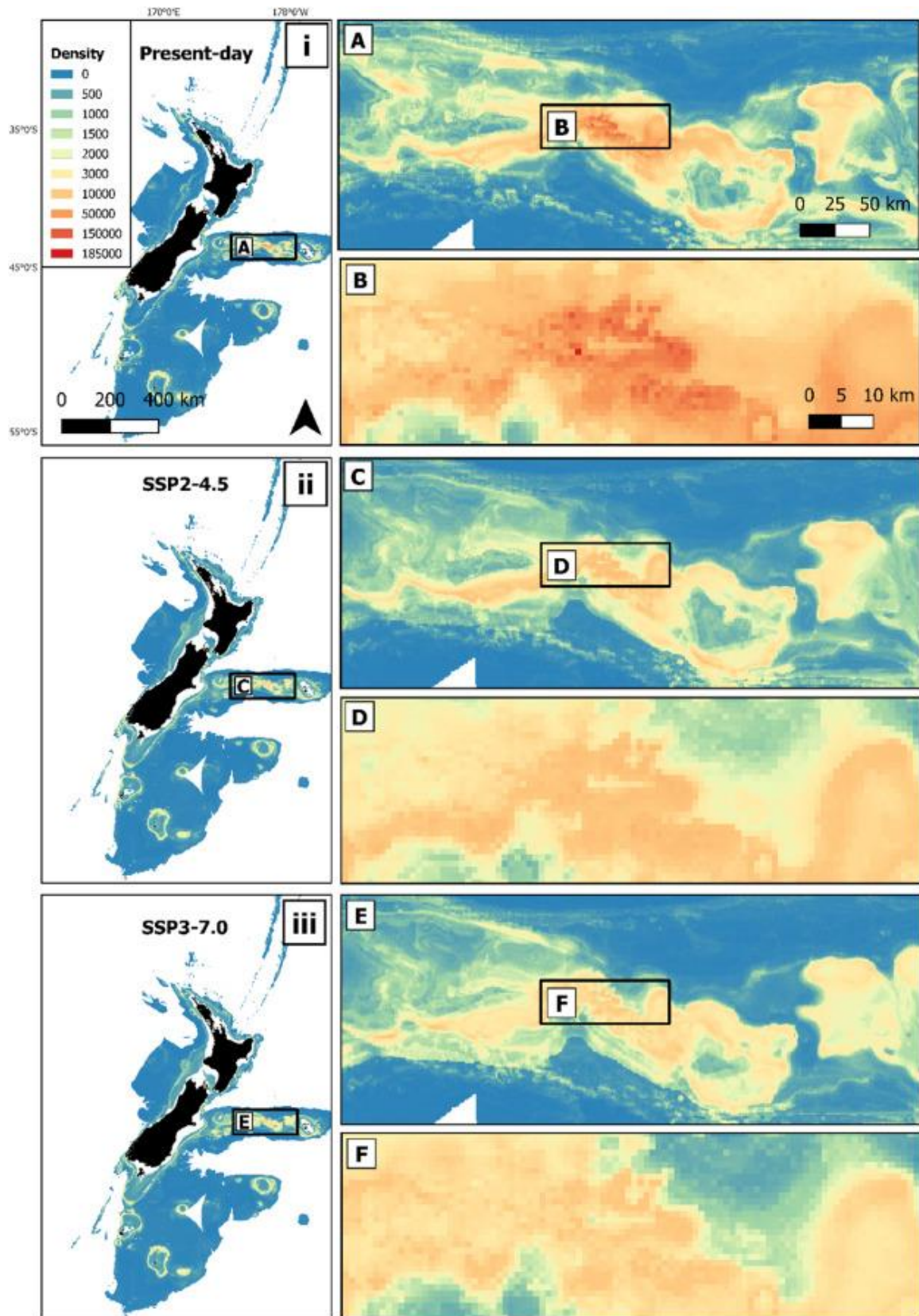


Figure 3. Predicted density (individuals km^{-2}) for the reef-building coral *Goniocorella dumosa* under present-day environmental conditions (panel i); future SSP2-4.5 scenario (panel ii); and SSP3-7.0 scenario (panel iii) for the New Zealand region. The inset (A, C, E) highlights the Chatham Rise region and (B, D, F) the area encompassing most primary habitats (≥ 3000 individuals km^{-2}).

Total density in the study area for *G. dumosa* was reduced by approximately 12% under both future climatic conditions (SSP2-4.5 and SSP3-7.0 scenarios) when compared to present conditions (Table 4). Similarly, when primary habitats (for *G. dumosa*, ≥ 3000 individuals km^{-2}) are considered, we observed a substantial decline in density. Relative to present environmental conditions, total density for *G. dumosa* within primary habitats was reduced by more than half (54%) under both future scenarios, while mean density was reduced by 28% and 35% for SSP2-4.5 and SSP3-7.0 scenarios, respectively (Table 4). Within primary habitats, density estimates for *G. dumosa* were highest in the Chatham Rise region where they reached a predicted maximum of ca. 182,700 individuals km^{-2} under present environmental conditions. The predicted maximum density within primary habitats decreased to ca. 25,600 individuals km^{-2} under the SSP2-4.5 scenario (approximately 86% decrease) and decreased to ca. 22,400 individuals km^{-2} (approximately 88% decrease) under the SSP3-7.0 scenario (Table 4).

Table 4. Summary of the modelled densities (expressed as the number of individuals per km^2) in the study area and within primary habitats (98th density percentile) for *Goniocorella dumosa*, Cold-water corals, Hydrozoans, and Sponges calculated across different future climate scenarios. See Supplementary Materials, Table S1 for more details.

Modelled taxon	Scenarios	Study area		Primary habitats					
		Total	Change	Total	Change	Mean	Change	Max	Change
<i>Goniocorella dumosa</i>	Present	6.2e+8		2.2e+8		6.7e+3		1.8e+5	
	SSP2-4.5	5.5e+8	-12%	1.0e+8	-54%	4.8e+3	-28%	2.6e+4	-86%
	SSP3-7.0	5.5e+8	-12%	1.0e+8	-54%	4.3e+3	-35%	2.2e+4	-88%
Cold-water corals	Present	1.1e+10		1.9e+9		5.7e+4		1.3e+6	
	SSP2-4.5	1.4e+10	+23%	1.5e+9	-28%	4.7e+4	-18%	2.6e+5	-82%
	SSP3-7.0	1.5e+10	+33%	1.5e+9	-28%	4.5e+4	-21%	1.7e+5	-86%
Hydrozoans	Present	6.1e+9		1.2e+9		3.6e+4		1.1e+6	
	SSP2-4.5	7.1e+9	+17%	1.1e+9	-35%	3.5e+4	-7%	5.0e+5	-56%
	SSP3-7.0	7.7e+9	+28%	1.1e+9	-35%	3.5e+4	-10%	4.1e+5	-74%
Sponges	Present	1.6e+10		4.0e+9		1.1e+5		4.0e+5	
	SSP2-4.5	1.4e+10	-12%	2.0e+7	-99%	8.5e+4	-27%	1.1e+5	-39%
	SSP3-7.0	1.3e+10	-15%	2.2e+6	-100%	4.0e+4	-60%	4.8e+4	-93%
All VME indicator taxa	Present	1.1e+10		2.4e+9		7.0e+4		9.5e+5	
	SSP2-4.5	1.2e+10	+9%	8.9e+8	-54%	5.5e+4	-17%	2.9e+5	-60%
	SSP3-7.0	1.2e+10	+15%	9.1e+8	-54%	4.0e+4	-30%	2.1e+5	-84%

Across all VME indicator taxa, total density (on average) in the study area increased by approximately 12% from current conditions to future climatic conditions (Table 4). In particular, total density (on average) of all Cold-water corals (*Scleractinia*, *Antipatharia*, *Radicipes* spp., *Pennatulioidea*, *Primnoidae*, *Gorgoniidae*, *Keratoisididae*/*Mopseidae*) is predicted to increase by approximately 23% under the SSP2-4.5 scenario, and by approximately 33% under the SSP3-7.0 scenario, when compared to present conditions (Table 4). Similar trends were observed for Hydrozoans (*Stylasteridae* and other hydrozoans) whose total density (on average) is predicted to increase by 17% and 28% for the SSP2-4.5 and SSP3-7.0 scenario, respectively. In contrast, total density of Sponges (*Demospongiae* and *Hexactinellida*) is predicted to decrease (on average) by around 12% under the SSP2-4.5 scenario, and about 15% under the SSP3-7.0 scenario, compared to current conditions (Table 4).

Within primary habitats, all VME indicator taxa density (on average) was predicted to decrease by approximately 54% for both future scenarios in comparison to present conditions (Table 4). Mean density (across all taxa) within primary habitats is predicted to reduce by 17% and 30% for the SSP2-4.5 and SSP3-7.0 scenario, respectively (Table 4). Maximum density (on average) within primary habitats is predicted to reduce by approximately 60% and 84% for the SSP2-4.5 and SSP3-7.0 scenarios, respectively (Table 4). Specifically, the total density of Cold-water corals (on average) within primary habitats is predicted to decrease by approximately 28% for both the future scenarios in comparison to present conditions. The mean density (on average) of Cold-water corals within primary habitats is predicted to decrease by 18% and 21% for SSP2-4.5 and SSP3-7.0 scenarios, respectively. Maximum density (on average) of Cold-water corals within primary habitats is also predicted to decrease, by 82% and 86% under the SSP2-4.5 and SSP3-7.0 scenarios, respectively (Table 4). For Hydrozoans total density (on average) within primary habitats, is predicted to reduce by approximately 35% for both future scenarios compared to present conditions. Mean density (on average) of Hydrozoans within primary habitats is predicted to reduce by 7% and 10% for the SSP2-4.5 and SSP3-7.0 scenarios, respectively. Maximum density (on average) of Hydrozoans within primary habitats is predicted to reduce by 56% and 74% under the SSP2-4.5 and SSP3-7.0 scenarios, respectively (Table 4). For Sponges, total density (on average) within primary habitats, is predicted to decline even more, up to approximately 100% for both future scenarios compared to present conditions. Mean density (on average) of Sponges within

primary habitats is predicted to decline by 27% and 60% for the SSP2-4.5 and SSP3-7.0 scenarios, respectively. Maximum density (on average) of Sponges within primary habitats is also significantly predicted to decline by 39% and 93% under the SSP2-4.5 and SSP3-7.0 scenarios, respectively (Table 4). Spatial prediction maps for all the modelled taxa as well as the reported values are shown in the Supplementary files (see Supplementary Materials, “Density distribution (overall and within primary habitats)” sections and Table S1).

2.3.4 Spatial changes in primary habitats under future climatic conditions

For *G. dumosa*, when primary habitats for present conditions are spatially overlapped with those under future climatic conditions (SSP2-4.5 and SSP3-7.0), we observed areas of net habitat loss (contraction), areas expected to maintain high densities both under current and future climatic scenarios (i.e., internal refugia), and areas of net habitat gain, where previously unoccupied locations are predicted to be more favourable for taxa colonization under future conditions (i.e., external refugia) (Figure 4, Figure 5). These trends vary across different regions of the modelled area and exhibit different patterns across future scenarios. Contraction areas were found to be larger than external refugia areas under both future climatic scenarios (Figure 4, Figure 5, Table 5). In addition, although some areas are predicted to be and remain primary habitat, these regions may still exhibit alterations in density estimates (Table 5). The most significant changes in primary habitat distribution are predicted to occur across the Chatham Rise region (Figure 4, Figure 5, A and B). The greatest net loss (at localized scales) is predicted to occur around the Campbell Plateau and Bounty Plateau, and the greatest predicted net gain along the continental margin to the east of Stewart Island, the Snares and Auckland Islands (See Figure 1 for location reference).

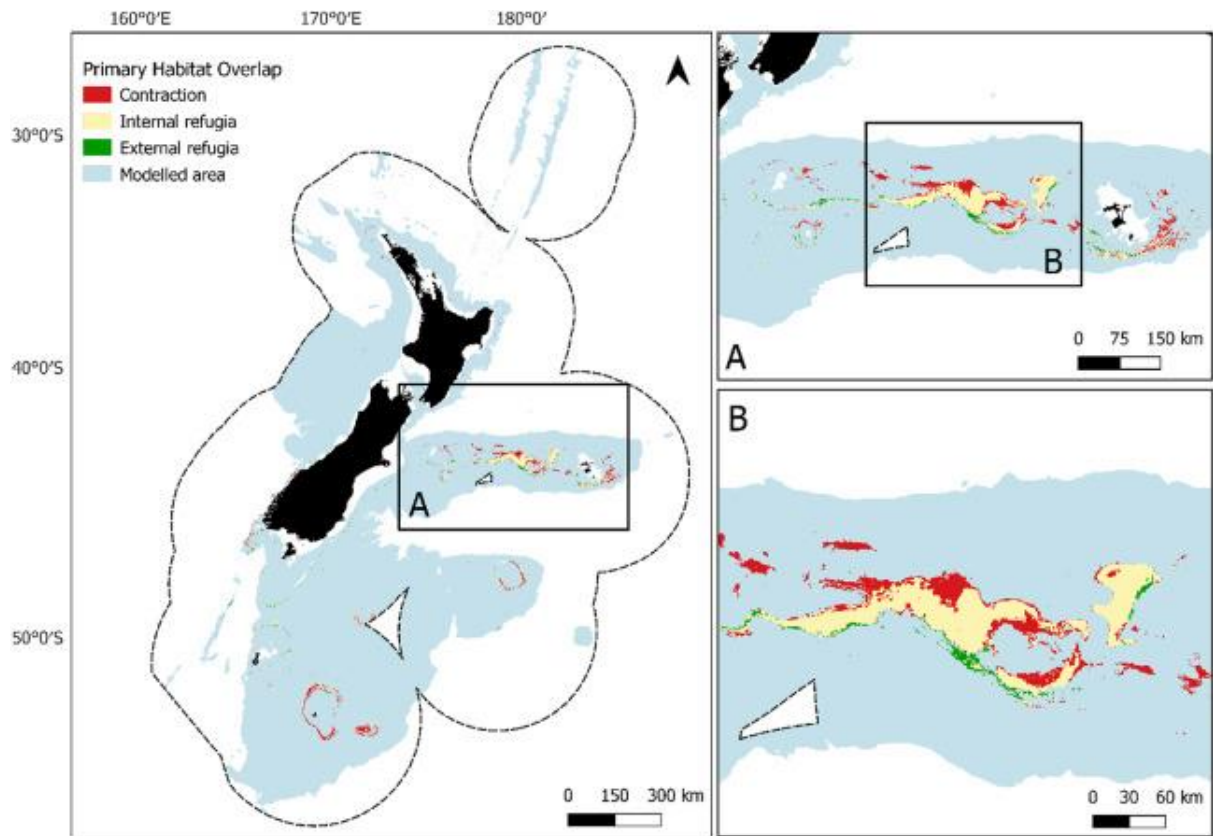


Figure 4. Changes in the distribution of *Goniocorella dumosa* primary habitat (≥ 3000 individuals km^{-2}) from the present to the future under the SSP2-4.5 climate scenario. Insert (A) highlights the Chatham Rise region and (B) the area where most of the current primary habitat for this species occurs. Contraction represents areas where primary habitat is lost, internal climate refugia represent areas where primary habitat is maintained and external climate refugia represent areas where primary habitat becomes available, contingent on source populations being able to colonize expansion areas.

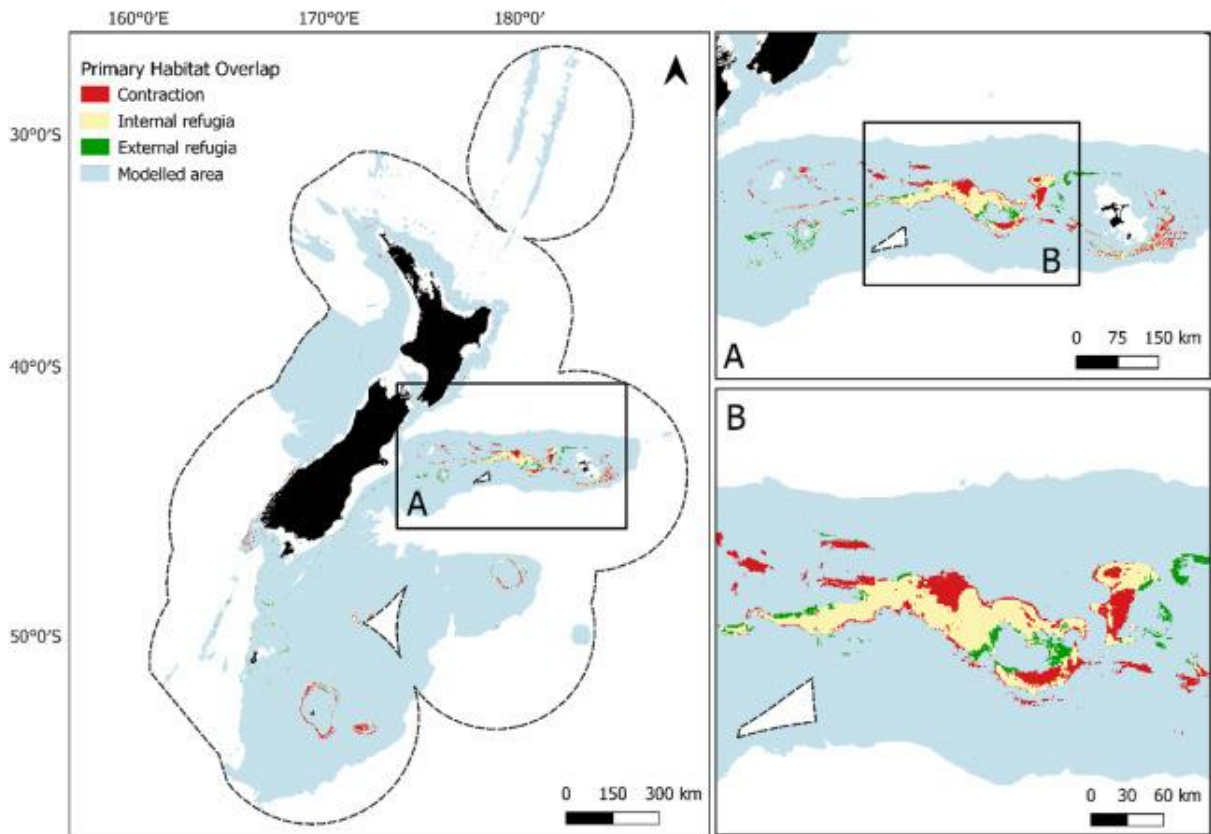


Figure 5. Change in the distribution of *Goniocorella dumosa* primary habitat (≥ 3000 individuals km^{-2}) from the present to the future under the SSP3-7.0 climate scenario. Insert (A) highlights the Chatham Rise region and (B) the area where most of the current primary habitat for this species occurs. Contraction represents areas where primary habitat is lost, internal climate refugia represent areas where primary habitat is maintained and external climate refugia represent areas where primary habitat becomes available, contingent on source populations being able to colonize expansion areas.

Table 5. Summary of spatial variation within primary habitat areas reported as changes in extent (km^2), mean and maximum density (individuals km^{-2}) for *Goniocorella dumosa*, Cold-water corals, Hydrozoans, Sponges, and all VME indicator taxa when future climatic conditions (SSP2-4.5 and SSP3-7.0) are compared to present conditions. The columns represent (i) “Contraction areas”: which reflect the primary habitat extent and density loss predicted under future climate scenarios; (ii) “Internal refugia (present-day)”: which reflects the predicted primary habitat extent and density as it is predicted for current day environmental conditions; (iii) “Internal refugia (future)”: which reflects the predicted primary habitat extent and density as it is predicted under future environmental conditions; (iv) “External refugia”: which reflects the primary habitat extent and density gain predicted under future environmental conditions. See Supplementary Materials, Table S2 for more details.

	Scenarios		Contraction	Internal	Internal	External
<i>Goniocorella dumosa</i>	Present vs SSP2-4.5	Extent	1.5e4	1.8e4	1.8e4	3.4e3
		Mean	4.0e3	9.1e3	5.1e3	3.4e3

Scenarios			Contraction	Internal	Internal	External
	Present vs SSP3-7.0	Max	1.5e4	1.8e5	2.5e4	6.4e3
		Extent	1.5e4	1.7e4	1.7e4	5.7e3
		Mean	4.1e3	9.0e3	4.6e3	3.5e3
		Max	2.3e4	1.8e5	2.2e4	8.7e3
Cold-water corals	Present vs SSP2-4.5	Extent	1.3e5	1.3e5	1.3e5	9.7e4
		Mean	5.7e3	7.7e3	6.4e3	5.2e3
		Max	1.9e4	1.6e5	3.2e4	1.1e4
		Extent	1.4e5	1.2e5	1.2e5	1.2e5
	Present vs SSP3-7.0	Mean	5.8e3	8.7e3	6.0e3	5.2e3
		Max	2.4e4	1.6e5	2.1e4	1.1e4
		Extent	3.4e4	3.2e4	3.2e4	1.1e4
		Mean	1.2e4	2.1e4	1.9e4	1.0e4
Hydrozoans	Present vs SSP2-4.5	Max	1.0e5	5.6e5	2.5e5	3.0e4
		Extent	3.6e4	3.0e4	3.0e4	1.2e4
		Mean	1.2e4	2.1e4	1.9e4	1.2e4
		Max	1.5e5	5.6e5	2.0e5	7.3e4
	Present vs SSP3-7.0	Extent	6.6e4	3.5e2	3.5e2	1.2e2
		Mean	5.8e4	6.0e4	4.3e4	4.3e4
		Max	1.9e5	2.1e5	6.3e4	5.0e4
		Extent	6.7e4	5.4e1	5.4e1	1.0e1
Sponges	Present vs SSP3-7.0	Mean	5.8e4	4.7e4	2.0e4	1.8e4
		Max	2.2e5	1.7e5	2.4e4	1.8e4
		Extent	2.4e5	1.6e5	1.6e5	1.0e5
		Mean	1.5e4	1.8e4	1.4e4	1.2e4
All VME indicator taxa	Present vs SSP2-4.5	Max	6.2e4	2.4e5	7.5e4	2.1e4
		Extent	2.5e5	1.5e5	1.5e5	1.3e5
		Mean	1.5e4	1.7e4	1.0e4	8.7e3
		Max	7.8e4	2.3e5	5.2e4	2.3e4

When present conditions are compared to future SSP2-4.5 scenario, there was a predicted ‘contraction’ (loss of primary habitat) for *G. dumosa* of over 15,550 km², within which a predicted mean density loss estimate of ca. 4000 individuals km⁻² and a maximum predicted density loss estimate of ca. 15,500 individuals km⁻² (Table 5). However, the internal climate refugia areas (maintenance of primary habitat) encompass around 18,000 km², yet the mean density within these regions is projected to decrease from ca. 9100 individuals km⁻² at present conditions to ca. 5000 individuals km⁻² in the future SSP2-4.5 scenario, with the maximum density experiencing a significant decline from ca.

182,700 individuals km⁻² to ca. 25,600 individuals km⁻² (Table 5). Within external refugia (gain of primary habitat) there was only a predicted increased extent of ca. 3400 km² with a smaller mean density gain estimate of ca. 3400 individuals km⁻² and a maximum density estimate of ca. 6400 individuals km⁻² (Table 5). Similarly, when present conditions are compared to future SSP3-7.0 scenario for *G. dumosa*, there was a predicted contraction of ca. 15,000 km², within which a predicted mean density loss estimate of ca. 4100 individuals km⁻² and a maximum density loss estimate of ca. 23,500 individuals km⁻² (Table 5). Nevertheless, the internal climate refugia areas encompass ca. 17,900 km², however, the mean density within these regions is projected to decrease from ca. 9000 individuals km⁻² at present conditions to ca. 4600 individuals km⁻² in the future SSP3-7.0 scenario, with the maximum density experiencing a significant decline from ca. 182,600 individuals km⁻² to ca. 22,300 individuals km⁻² (Table 5). In areas of external climate refugia, density extent increases by ca. 5700 km², with a mean density gain estimate of over 3500 individuals km⁻² and a maximum density estimate of over 8700 individuals km⁻² (Table 5).

Overall, for all the modelled VME indicator taxa in this study, the total extent of contraction areas (61%) was larger than the extent of future internal and external climate refugia areas predicted under both climatic scenarios (Table 5). Notably, mean and maximum density values for all VME indicator taxa were predicted to be lower under future environmental conditions, especially under the SSP3-7.0 scenario (Table 5). Moreover, the extent of internal climate refugia regions showed similar declining trends across taxa when mean and maximum density were compared between present and future scenarios, with the SSP3-7.0 scenarios displaying the most significant reduction.

When present conditions are contrasted to the SSP2-4.5 scenario the total contraction area for all VME indicator taxa covered approximately 240,000 km² with a predicted mean density loss of over 15,500 individuals km⁻² and a maximum predicted density loss of over 62,000 individuals km⁻² (Table 5). On the other hand, the total internal climate refugia areas encompassed ca. 163,000 km², with a mean density predicted to decrease from over 18,600 individuals km⁻² at present conditions to approximately 14,700 individuals km⁻² in the future SSP2-4.5 scenario, with the maximum density experiencing a significant decline from ca. 242,200 individuals km⁻² to ca. 75,000 individuals km⁻² (Table 5). The total external climate refugia area spanned approximately

108,700 km², with an estimated mean density gain of ca. 12,500 individuals km⁻² and an estimated maximum density gain of ca. 21,000 individuals km⁻² (Table 5). Similarly, when comparing present conditions to the SSP3-7.0 scenario for all VME indicator taxa the total contraction area was over 250,000 km², with a predicted mean density loss of over 15,700 individuals km⁻² and a maximum predicted density loss of over 78,400 individuals km⁻² (Table 5). On the other hand, the total internal climate refugia areas encompass ca. 152,700 km², with a mean density predicted to decrease from ca. 17,400 individuals km⁻² at present conditions to ca. 10,600 individuals km⁻² in the future SSP3-7.0 scenario, with the maximum density experiencing a significant decline from ca. 235,700 individuals km⁻² to ca. 52,800 individuals km⁻² (Table 5). The external climate refugia area spanned ca. 133,600 km², with an estimated mean density gain of ca. 8700 individuals km⁻² and a predicted maximum density gain of ca. 23,000 individuals km⁻² (Table 5).

Overall, we predicted a notable declining trend in specific Cold-water coral taxa (Antipatharia, Primnoidae, Keratoisididae/Mopseidae) and Hydrozoans, and a nearly complete loss of primary habitat for Sponges taxa (Demospongiae and Hexactinellida) under both future climatic scenarios when compared to present day conditions (see Supplementary Materials, Figs. S77–78; S82-83). Furthermore, our predictions indicate that future primary habitats for other cold-water corals (i.e., Gorgoniidae and Pennatulioidea) may undergo increased fragmentation and dispersion across various locations within the study area with potential separation of primary habitats extending up to tens or hundreds of km from their current locations. The maps showing the spatial extent change in primary habitat across different temporal scenarios, as well as the table reporting the values for all the modelled taxa, are reported in the Supplementary files (see Supplementary Materials, ‘Primary habitat overlaps’ sections and Table S2). In addition, in line with previous studies in the study region (Anderson et al., 2022), the predicted primary habitat for most taxa, under both present and future climatic conditions, was primarily located within areas of moderate to high environmental coverage (>0.05, particularly on the Chatham Rise) reflecting that these primary habitats were more certain than if they were derived by extrapolating model prediction into unsampled environmental conditions.

2.4 Discussion

In this study, we used a spatially extensive occurrence and density dataset of 14 habitat-forming taxa which can be considered VME indicator taxa, including cold-water corals, hydrozoans, and sponges. We combined this biological dataset with oceanographic models for both current and future climatic conditions (SSP2-4.5 and SSP3-7.0) tailored to the New Zealand region to predict changes in the taxa density and extent within the whole study area and across those regions considered primary habitats (where density is calculated at the 98th percentile) by the end of the 21st century. Our results build on previous predictions in the same area (Anderson et al., 2022) but offer a significant advancement by providing spatial predictions of taxon density rather than just occurrence. Understanding the density distribution of VME indicator taxa in both present and future conditions is vital for conservation, spatial planning, and resource allocation. Notably, this work helps identify areas at risk of significant habitat loss while highlighting regions that may support vibrant VME communities that sustain ecosystem services in future climates, serving as potential climate refugia.

Despite our study identifying possible areas of primary habitats under present conditions, not all of these areas will maintain high taxon densities under future climate scenarios. We predicted a substantial and consistent decline in density and extent, along with changes in the location of primary habitat regions for all evaluated VME indicator taxa by the end of the 21st century, with the most significant reductions occurring under the high-emission SSP3-7.0 scenario. Nonetheless, our models also identified current primary habitat areas that will persist under future climatic scenarios, potentially serving as internal refugia. However, these areas are predicted to experience large density reductions, especially under the high-emission SSP3-7.0 scenario, when compared to present-day densities. Model results also predicted the expansion of primary habitats into new locations that could act as external climate refugia. This study highlights the vulnerability of deep-sea VME indicator taxa under future climate conditions, with impacts likely worsened by local pressures like bottom trawling.

2.4.1 The effect of climate change on taxa primary habitats

To gain a deeper understanding of spatial variations of ecologically relevant VME indicator taxa, we focussed on the changes occurring within the areas with the highest density (primary habitats). Within primary habitat areas, our models predicted an average

54% decline in the density of the investigated VME indicator taxa, along with a reduction in the extent of primary habitats by approximately 245,000 km², under both future climatic scenarios (SSP2-4.5 and SSP3-7.0) compared to present conditions. Among all the assessed VME indicator taxa, cold-water corals (particularly *G. dumosa*) and sponges (Demospongiae and Hexactinellida) were predicted to be the most severely affected by future climate change. These findings align with previous predictions of reduction in suitable habitats for similar habitat-forming VME indicator taxa, including deep-water corals and hydrozoans (Anderson et al., 2022; Morato et al., 2020b) as well as sponges (Liu et al., 2021) under future climate change in the South Pacific and in the North Atlantic. The predicted reduction in primary habitat extent and density of these ecologically significant taxa is expected to impact habitat structure and ecosystem function. As habitat provision capacity declines, the ability of VME indicator taxa to support biodiversity and density-related ecosystem services may be compromised.

Additionally, severe habitat loss or fragmentation may lead to reduced population connectivity potential and recovery capacity following disturbances (Munday et al., 2009), significantly impacting the functionality of VMEs on both local and regional scales. In addition, recent studies in the New Zealand region also highlight that the combination between the predicted shifts in VME indicator taxa location and the decreases in their extent with the impacts from additional disturbances – e.g., bottom trawling – put such VME indicator taxa at high risk of local extinctions (Stephenson et al., 2023a).

As shown in other studies, declines in the density of the assessed VME indicator taxa by the end of the 21st century may be mainly linked to decreasing levels of seafloor concentrations of carbonate ion saturation levels and dissolved oxygen, which has been predicted by modelling worldwide (Byrne et al., 2010; Purkey & Johnson, 2010; Stramma et al., 2010; Sweetman et al., 2017). In line with previous studies, including those done in the New Zealand region, we found that the main drivers of the predicted changes in suitable habitat for the investigated taxa were future decreases in the seafloor concentration of dissolved oxygen, carbonate ion saturation levels and an increase in nitrogen concentration (Anderson et al., 2022; Bostock et al., 2015b). Our findings are not only consistent with the results of these studies but also provide details about the potential spatial heterogeneity of this effect. Notably, aragonite or calcite (depending on

the taxon, e.g., scleractinian corals typically use aragonite, while octocorals usually use calcite for their skeletons) were the most important predictors affecting the spatial distribution of density of most VME indicator taxa, especially cold-water corals. As an example, experimental and empirical evidence suggests that a decrease in the aragonite saturation state at depth, following the aragonite shoaling (Negrete-García et al., 2019), may affect the distribution of those taxa that particularly rely on aragonite to build their skeleton as it will cause a shallowing of the depth of aragonite saturation horizon (Guinotte et al., 2006; Maier et al., 2009; J. C. Orr et al., 2005). This correlation suggests the likelihood of a future increase in habitat suitability, particularly in shallower regions where aragonite/calcite concentrations are currently well above saturation levels and oxygen concentration is closer to their optimum (Anderson et al., 2022; Farfan et al., 2018).

Decreased oxygen levels can affect essential physiological processes such as productivity, respiration, and calcification and often play a role in the outcome of interactions between corals and other organisms, as found from previous studies on coral reefs (Nelson & Altieri, 2019). Moreover, despite studies on cold-water corals being scarce, the predicted future reduction in the dissolved oxygen concentration (Sweetman et al., 2017) seems also to exert control on cold-water corals' biogeographic distribution, as also found in other reef-forming scleractinian species such as *Desmophyllum pertusum* in the North Atlantic (Tittensor et al., 2010). These observations are corroborated by laboratory experiments, revealing that *D. pertusum* individuals were unable to maintain normal aerobic functions at low oxygen levels (Dodds et al., 2007; Lunden et al., 2014) suggesting that oxygen level may be a limiting factor in the distribution of the investigated cold-water corals.

In addition, numerous field observations and laboratory simulations have demonstrated the adverse effects of nitrogen enrichment on coral growth and calcification (Silbiger et al., 2018) as well as on the resilience to environmental change of individual coral species (Hall et al., 2018). Given the projected increase in nitrogen levels in oceans and seas (Zhao et al., 2021) it is possible that these effects could be exacerbated in the future. Moreover, although future nitrogen loading predictions for the New Zealand region remain uncertain, recent studies on the South Pacific Ocean and Antarctic region suggest that changes in ocean currents, and a consequent reduction in mixed layer depth and

current velocity, could impact nitrogen availability at depths (Li et al., 2023; Luo & Rothstein, 2011). If the Antarctic overturning circulation slows down – due to the increasing freshwater volumes making nearby waters less salty and dense – nutrient-rich seawater could accumulate on the seafloor and become stagnant. This stagnation could significantly alter the amount of nutrients available for both deep and shallow marine ecosystems (Li et al., 2023). Nonetheless, regional-scale model predictions are needed to better understand how the quantity and distribution of individual environmental variables (e.g., oxygen, carbon ions, and nutrients) affect changes in benthic composition under a changing climate.

Sponge taxa were also found to experience significant density declines under future scenarios. While ocean acidification and the consequent reduction of water pH may not affect the siliceous sponge populations as directly as marine taxa that are heavily dependent on carbonate – e.g., such cold-water corals – they could, however, suffer detrimental effects by reducing the feeding efficiency and homeostasis processes (Carballo & Bell, 2017; Liu et al., 2021). In addition, the reduction of primary productivity and dissolved oxygen availability in bottom waters could also explain the decline in the density of Hexatinellida and Demospongiae observed in our study, as also suggested in previous studies for these taxa (Conway et al., 2017; Strand et al., 2017).

Finally, hydrocoral taxa, while showing a strong correlation with both oxygen and nitrogen concentrations, appeared to be more robust to environmental changes. They exhibited less reduction in density, likely because they are primarily influenced by fixed variables (e.g., bathymetry, profile curvature and fine-scale Benthic Position Index) rather than dynamic variables. As a result, minimal changes are predicted in their future suitable habitat, consistent with findings from previous research (Anderson et al., 2022).

2.4.2 Potential for climate refugia?

Despite a predicted reduction in primary habitat extent and density of VME indicator taxa within the study area under both future climatic conditions, model outputs also reveal areas where some taxa may retain high densities in the future in places where they are already predicted to be present (internal refugia, approximately 158,000 km²). However, future densities are predicted to be lower than current-day predictions. Moreover, our predictions highlight regions of habitat gain (external refugia, approximately

121,000 km²) occurring across different locations by the end of the 21st century under both climate change scenarios. These future gains in primary habitats are therefore predicted to have higher overall mean and maximum density compared to the current day across the same areas. Such variation in the spatial distribution might be linked to higher environmental suitability, in both future scenarios, to changing aragonite/calcite saturation states over shallower areas, potentially providing novel conditions for the emergence of new favourable habitats. Previous studies have also suggested the potential for climate change to facilitate the creation of new habitats in shallower areas (Tittensor et al., 2010), including in the New Zealand region (Bostock et al., 2015b). Nonetheless, it is likely that a multitude of other environmental factors (e.g., oxygen saturation levels) influenced by climate change will similarly exert a notable influence on the spatial distribution and depth range of these VME indicator taxa (Bostock et al., 2015b).

For some VME indicator taxa (e.g., scleractinian corals) the location of external refugia is contiguous with internal refugia (e.g., *G. dumosa*, Figure 4, Figure 5 and S32-33 of the Supplementary Materials). Therefore, if supported by the direction of the prevalent currents, the colonization of these taxa in expansion areas under future scenarios may be more likely as they potentially represent ecologically connected VMEs (Hilário et al., 2015). Consequently, the predicted future primary habitats for these taxa might represent climate refugia areas able to provide ecosystem services as VME indicator taxa reach and maintain high densities (internal refugia) and are close enough to establish new areas (external refugia). Such areas could provide shelter in which these populations may persist (Bongaerts et al., 2010), and from which they would subsequently expand (Oliveira et al., 2019), and potentially recover in previously degraded areas (Costantini et al., 2016). In such scenarios, the identification and protection of internal and external refugia, particularly where they are contiguous, should become a priority for conservation (Ashcroft, 2010).

However, the potential for external refugia is not the case for all taxa modelled, for which large areas of future primary habitats are predicted to be substantially distant from internal refugia. Our predictions indicate that future primary habitats for many VME indicator taxa, including some cold-water corals, may become increasingly fragmented across various locations in the study area. Therefore, external refugia that are distant from internal refugia, may be too far for propagules from present populations to allow the

establishment of future populations, especially if dispersal potential for larvae is limited (as is the case for *G. dumosa*, Beaumont et al., 2023). Furthermore, for certain cold-water coral taxa (Antipatharia, Primnoidae, Keratoisididae/Mopseidae) as well as hydrozoan and sponge taxa (Demospongiae and Hexactinellida), our predictions anticipate a substantial loss of primary habitats in future climatic scenarios, which likely prevents the potential for external refugia in the first place (see Supplementary Materials, Figs. S37–38; S52-53; S62-63; S67-68; S72-73; S77-78; S82-83).

2.4.3 Accounting for uncertainty

Model performance may vary based on taxonomic resolution, with predictions at the species-level (e.g., Figure S86) generally being more accurate than those at the group-level (e.g., Figure S87) because group-level predictions are more likely to represent multiple (and sometimes very different) environmental preferences (Stephenson et al., 2021a). Ideally, future SDMs should be conducted at the species level to maximize predictive power (Bowden et al., 2021). However, given current constraints on the available sample number and taxonomic resolution of these samples, grouping taxa for modelling remains a pragmatic approach which may still offer valuable insights into species' distribution patterns and ecological dynamics. Moreover, in this study, we accounted for different sources of uncertainty, that is the uncertainty associated with the spatial prediction of density through bootstrapping and the uncertainty associated with the distribution of biological samples by assessing the environmental coverage. Overall, the spatially explicit uncertainty associated with the SDMs tended to be generally moderate for all evaluated VME indicator taxa and the environmental coverage was low for many areas of deep water but reasonably high for parts of the study area where we predicted climate refugia for both current-day and future environmental conditions.

2.4.4 Implication for management

Overall, the results of our analysis illustrate a substantial loss of primary habitats for all of the VME indicator taxa under future climatic conditions, suggesting severe threats to the maintenance of the functionality and ecosystem services they provide. Nevertheless, our models also identified areas where primary habitats for VME indicator taxa are predicted to persist or expand under future climatic scenarios, offering hope for the formation of both internal and external climate refugia by the end of the 21st century. However, most of the predicted distribution of those primary habitats seems to fall outside

of the existing spatial protection measures in New Zealand waters (Figure 6). This finding raises concerns about the effectiveness of protection measures currently in place to be able to protect VME indicator taxa from the combination of future climate change effects and potential additional pressures, including bottom trawling activities. These concerns align with the results from previous research in the region (Anderson et al., 2022; Stephenson et al., 2023a).

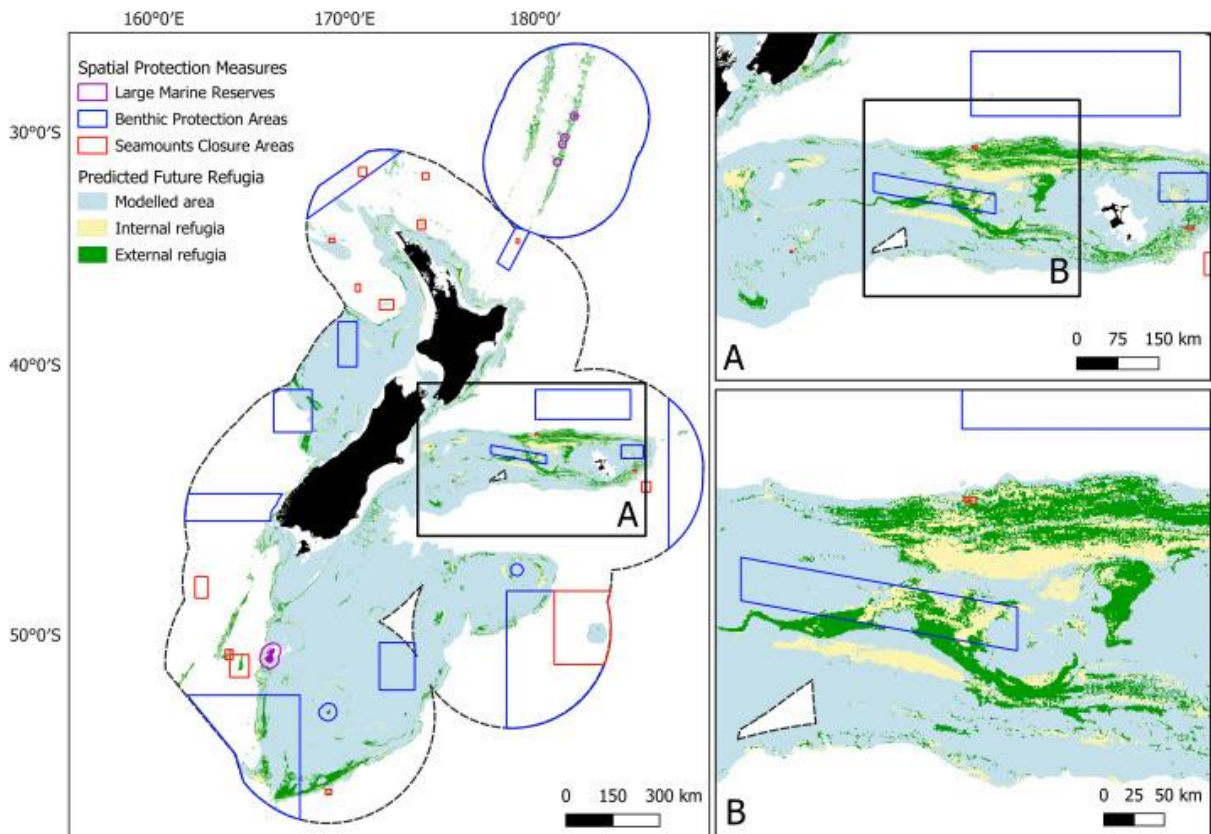


Figure 6. Distribution of primary habitats, corresponding to predicted internal and external climate refugia regions, of all modelled VME indicator taxa combined under the SSP2-4.5 climate scenario. Insert (A) highlights the Chatham Rise region and (B) the area where most of the primary habitat areas occur. Purple polygons indicate Large Marine Reserves in the Territorial Sea, red polygons indicate Seamount Closure Areas, and blue polygons indicate Benthic Protection Areas. See Supplementary Materials (Figure S85) for the distribution of primary habitats under the SSP3-7.0 scenario. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

From a management perspective, internal climate refugia offer the best candidates for inclusion in future marine spatial protection measures that account for climate change effects, especially for taxa with poor dispersal capabilities. However, internal refugia will also need to be both large and dense enough to support a viable number of individuals if

the population contracts from its former range. Including external refugia within spatial protection measures is also challenging. For example, natural colonization of external refugia might not be possible for species with poor dispersal capabilities, those that are restricted to fragmented habitats and/or have range-shift routes blocked by physical barriers. Colonization is more likely where internal and external refugia are contiguous, and therefore areas with such contiguous refugia would make good candidates for future protection. Overall, there are several challenges for conservation planning to maximize the persistence of species through time in both internal and external refugia. To better understand the potential benefits of including external refugia in future spatial protection measures, we recommend work to assess larval dispersal and connectivity dynamics for VME indicator taxa within the region (e.g., Kenchington et al., 2019) as such information will provide spatial planners with the necessary knowledge to effectively prioritize the selection of these potential conservation areas.

The identification of effective climate refugia is required in order to incorporate them into conservation plans and to identify specific management actions that could protect (or restore) priority refugia. The exclusion of such refugia from the current marine spatial protection measures may leave those relevant areas potentially vulnerable to the impacts of additional localised activities such as bottom trawling and/or seabed mining. Here we do not account for such stressors and their potential interaction with areas that are predicted to become climate refugia in the future. However, we acknowledge that investigating both global and local stressors is essential for better understanding the escalating threats to VMEs and for guiding effective conservation planning initiatives (Huges et al., 2017; Stephenson et al., 2023a). Further studies are underway exploring how bottom trawling may affect refugia viability and the effectiveness of conservation areas to prevent impacts on habitats predicted to be critical in the future. This information will further help determine if adjustments are required to improve the effectiveness of existing marine spatial protection measures in the face of multiple stressors. In conclusion, the utilization of density models emerges as an impactful tool for identifying ecologically relevant areas under both present and future climatic scenarios therefore offering crucial information that could guide decisions in marine spatial planning – e.g., enhancing marine areas protection and resource allocation. The significance of this study extends beyond New Zealand, offering useful tools for global applications amidst the challenges of climate change adaptation and necessary conservation actions.

Chapter 3

Bottom-trawling affects the viability of climate refugia for vulnerable marine ecosystem indicator taxa

3.1 Introduction

The global marine environment faces multiple challenges stemming from human-induced pressures, which can detrimentally affect ecosystem health and functioning (Rocha et al., 2015). The impacts of climate change and fisheries on marine ecosystems are responsible for much of the observed global habitat degradation and biodiversity loss (Beddington et al., 2005; Doney et al., 2012; Sumaila & Tai, 2020; Williamson & Guinder, 2021). In particular, bottom trawl fisheries are considered the primary threat to deep-seafloor ecosystems (Halpern et al., 2007; Levin et al., 2019; Puig et al., 2012; Ramirez-Llodra et al., 2011; Reed et al., 2007; Watson & Morato, 2013). Bottom-contacting fishing gears particularly affect erect (rather than encrusting), fragile/brittle (rather than flexible), long-lived (rather than short-lived), and slow-growing (rather than fast) organisms (Bensch et al., 2009; Clark et al., 2016; Goode et al., 2020; Gros et al., 2023b; Morato et al., 2006). Direct impacts include the physical removal of organisms, leading to declines in abundance, biomass, and diversity. Additionally, indirect effects such as habitat fragmentation, loss of population connectivity, and alteration of physical properties of substrate surface and water quality also occur (Clark et al., 2016; Dayton et al., 1995). These impacts can lead to widespread and long-lasting detrimental effects on the structural and functional integrity of ecological assemblages, overall habitat quality and, ultimately, species resilience and adaptive capacity (Clark et al., 2016; McConnaughey et al., 2020; Pusceddu et al., 2014; Sciberras et al., 2018).

Based on growing concern about the adverse ecosystem impacts of fishing on the High Seas, the United Nations General Assembly Resolution 61/105 (UNGA), adopted the term Vulnerable Marine Ecosystems (VMEs) to identify benthic species groups/communities/habitats characterised by both high conservation importance and susceptibility to bottom trawling disturbance (Auster et al., 2011; FAO, 2009). Although

VME is a term primarily associated with application in the High Seas, from an ecological and conceptual point of view, the concept of VME extends to all seafloor habitats, including areas within national jurisdictions (Stephenson et al., 2024a). Various VME indicator taxa, i.e., taxa that indicate the potential presence of VMEs (e.g., Parker et al., 2009), occur in the New Zealand marine region, especially cold-water corals (Tracey & Hjørvarsdóttir, 2019). New Zealand also has a significant bottom trawl fishery (Williams et al., 2017) accounting for approximately 70% (nearly 250,000 tonnes) of the volume of all fish caught commercially (MPI, 2023). In 2021, the trawl footprint within New Zealand's exclusive economic zone (EEZ) was 74,500 km². The total area trawled between 1990 to 2021 was 462,643 km² (MPI, 2023) and in some cases was concentrated in productive areas that may support VMEs (Clark et al., 2016; Clark & Rowden, 2009; Fosså et al., 2002). Many VME indicator taxa in New Zealand are included in the domestic threatened species classification (Freeman et al., 2013; Funnell et al., 2023), and some (including most corals) are listed as protected species in a schedule to New Zealand's Wildlife Act (1953). Additionally, the creation of Seamount Closure Areas and Benthic Protection Areas, as well as some large no-take marine reserves around offshore islands, has been partially driven by the need to protect cold-water corals and other species listed as VME indicator taxa from bottom-contact fishing activities like trawling and dredging (Brodie & Clark, 2003; Helson et al., 2010). However, existing spatial protection in New Zealand is inadequate and does not encompass or comprehensively protect VMEs from bottom trawling activities in the present day, nor do they account for potential declines or shifts in VME distribution due to climate change (Anderson et al., 2022; Stephenson et al., 2023a; Zelli et al., 2025).

Recent regional studies have examined the impact of different climate change scenarios on VME indicator taxa, predicting significant declines in their occurrence (Anderson et al., 2022) and density (Zelli et al., 2025) by the end of the 21st century. This decline is predicted across New Zealand's EEZ, including in regions where taxa were predicted to have particularly high densities or "primary habitats" (i.e., predicted densities are > 98th percentile; by Zelli et al., (2025) and therefore more likely to form VMEs and support ecosystem services (Zelli et al., 2025) also identified potential regions of "internal refugia" to climate change, where some VME indicator taxa were predicted to retain their current high densities—and new areas where these taxa are expected to expand their high-

density range ("external refugia") by the end of the century (Graham et al., 2019; Keppel et al., 2015).

Both internal and external climate refugia are considered to be potentially important for long-term persistence of VME indicator taxa, offering critical resilience to climate change under current and future climatic conditions (Graham et al., 2019; Keppel et al., 2015). These areas are especially valuable as they may be the only regions where taxa can sustain high densities in response to future climatic shifts (Ban et al., 2014; Chollett & Mumby, 2013; Magris et al., 2015; Zelli et al., 2025). Climate refugia are expected to play a key role in supporting essential ecosystem functions and services while mitigating the impacts of climate change (Graham et al., 2019; Lancaster & Hildrew, 1993; Zelli et al., 2025). However, the realisation of climate refugia depends on several factors, including adequate abundance and high-density levels of taxa to sustain internal refugia, and the presence of favourable connectivity pathways to enable the formation of external refugia under projected climate change scenarios (Carr et al., 2017; Morelli et al., 2017). A lack of management for refugia could leave them vulnerable to additional local stressors, such as bottom trawling. As a consequence of exposure to such activities, current density within predicted climate refugia could be impacted, hindering their viability in the future (Anderson et al., 2022; Stephenson et al., 2023a; Zelli et al., 2025). Therefore, spatial information on the predicted future distribution of taxa alongside the impacts of historical/ongoing fishing efforts is required to guide effective, long-term marine spatial planning.

The exploration of the ecological effects of multiple stressors – that is two or more co-occurring or sequential stressors on an ecosystem (J. A. Orr et al., 2020) – constitutes a growing area of scientific research (Ban et al., 2014; Côté et al., 2016; Crain et al., 2008; Hewitt et al., 2016; Pinheiro et al., 2023; Thrush et al., 2021), including accounting for multiple stressors in marine conservation planning (e.g., Kujala et al., 2013; Levy & Ban, 2013; Magris et al., 2015; Sala et al., 2021). It has been argued that multiple stressors should be considered to future-proof marine protected areas for cold-water corals (Jackson et al., 2014, Stephenson et al., 2023), yet little progress on this consideration has been made in practice. While a recent study in New Zealand did assess the combined impacts of bottom trawling and climate change on the distribution of suitable habitats for cold-water corals, it did not explicitly quantify the overlap of fishing with the spatial

distribution of taxa under climate change scenarios. Rather, the study examined the combined effects by identifying areas of current and future importance for cold-water corals using a systematic conservation planning approach (Stephenson et al., 2023a). Moreover, the approach used by Stephenson et al., (2023) does not allow for any recovery over time, therefore it may overestimate the impact of bottom trawling. Evaluating recovery from trawling impacts is crucial for identifying areas with higher resilience, as these areas may have the potential to reverse impacts if left undisturbed. The speed of recovery depends on the connectivity levels across populations (Bevilacqua et al., 2023; Thrush et al., 2013) and the growth rates of affected taxa, with slower recovery observed in slow-growing species such as deep-water corals (Baco et al., 2020; Clark et al., 2019).

In this study, we use a temporally dynamic Relative Benthic Status (dRBS) approach (Pitcher et al., 2015) which incorporates recovery to assess the impact of a 30-year period of historical bottom trawling activity on 10 deep-sea VME indicator taxa. This analysis spans the entire New Zealand EEZ and Territorial Sea (TS) and includes regions previously identified as primary habitats and climate refugia by the end of the 21st century *sensu* (Zelli et al., 2025). Given that the predicted distribution of habitats under both current and future conditions largely falls outside the existing areas closed to bottom trawling, we posit that bottom trawling is likely to overlap with both the distribution of VME indicator taxa in current ecologically relevant habitats (e.g., primary habitats), and in areas expected to become equally important for these taxa under future climate change (e.g., climate refugia). This could potentially limit the ability of these areas to provide critical resilience to climate change under current and future climatic conditions.

3.2 Material and Methods

3.2.1 Study area

The study area spans water depths ranging from 100 m to 1500 m within the EEZ and TS of New Zealand (Figure 1). The selected depth reflects the sampling depths of the biological data (Bowden et al., 2021) used to generate the spatial predictions of density for the 10 VME indicator taxa (Zelli et al., 2025).

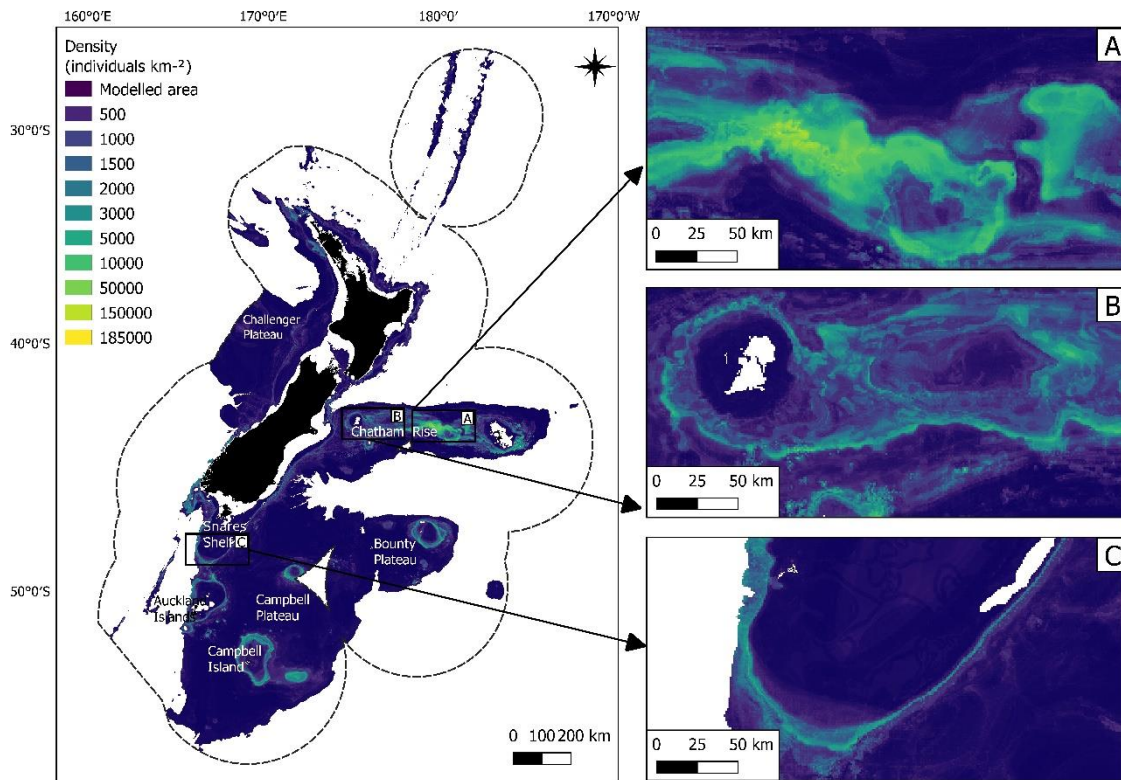


Figure 1. The New Zealand Exclusive Economic Zone and Territorial Sea with the predicted current density (expressed as individual live coral heads per km²) of the reef-building cold-water coral *Goniocorella dumosa* (from Zelli et al., 2025)). White areas are outside the modelled area (100 – 1500 m). Inset maps: A) West Chatham Rise, B) East Chatham Rise, C) Snares Shelf. The density distribution of this taxa is an illustrative example, selected due to its recognized importance as a habitat-forming taxon for coral reef VME in the New Zealand region (Dawson, 1984; Mackay et al., 2014). The predicted distribution of current density for the other nine individual taxa is provided in the Supplementary Materials (see “Overall study area and primary habitats (Present-day)” sections).

3.2.2 Spatial predictions of density

Spatial density predictions for 10 VME indicator taxa, primarily based on data collected from non-fished areas, were obtained from Zelli et al., (2025). These spatial predictions were generated using species distribution models (SDMs) for two time periods: one reflecting current-day conditions, approximating the sample collection period (1995-2014), and the other projecting future conditions for the end of the 21st century (2080-2099) (*sensu*, Anderson et al., 2022). Future taxa distributions were developed under two end-of-century climate change scenarios, corresponding to the SSP2-4.5 (4.5 W m²) moderate greenhouse gas concentration trajectory and the SSP3-7.0 (7.0 W m²) strong greenhouse gas concentration trajectory. The environmental conditions for these future

scenarios were produced by the New Zealand Earth System Model (Behrens et al., 2020; Williams et al., 2016). The modelled VME indicator taxa (Zelli et al., 2025) included reef-forming scleractinian corals *Goniocorella dumosa*, *Solenosmilia variabilis*, *Enallopsammia rostrata*, and *Madrepora oculata*. (here considered as *Goniocorella dumosa*, plus all species together as Scleractinia), black corals (Antipatharia), hydrocorals (Stylasteridae), “Alcyonacea” octocorals - primnoids (Primnoidae), sea-fans (Gorgoniidae), golden corals (*Radicipes* spp.) and sea-pens (Pennatuloidae), collectively referred to as ‘cold-water corals’ (see Roberts, 2009). Modelled taxa also included Porifera (Hexactinellidae and Demospongiae) referred to collectively as ‘sponges’. The selection of these representative VME indicator taxa was based on the following criteria: (i) biological traits, serving as proxies for ecological and functional relevance, especially for habitat-forming organisms; (ii) vulnerability to seafloor disturbances including bottom trawling (iii) conservation status; and (iv) the availability of a sufficient number of taxa occurrence records to construct robust predictive models (Anderson et al., 2016).

3.2.3 Estimating the fishing impact on current density predictions

Here, the predicted impact of bottom trawling on species’ distributions followed the approach outlined in Pitcher et al., (2015) which requires data on taxon-specific spatial distribution, depletion and recovery rates from bottom trawling, and the spatial distribution of bottom trawling intensity. A later simplification of the approach, Relative Benthic Status (RBS) (Pitcher et al., 2017), uses a single mean bottom trawling intensity distribution (and is temporally static), allowing it to be applied in data-limited contexts which has resulted in the widespread application of this approach (e.g., Pitcher et al., 2022; Szostek et al., 2022). However, the original approach, termed here, dynamic Relative Benthic Status (dRBS) (Pitcher et al., 2015), is temporally dynamic and utilizes a time series of bottom trawling intensity, making it well-suited for tracking changes over time and accounting for seabed recovery during non-trawling periods. Both approaches yield similar impact estimates in areas where long-established trawling effort is relatively consistent over time (Rowden et al., 2024). However, the dRBS provides added temporal nuances, making it particularly valuable for managers seeking a detailed assessment of fishing impacts that arise when fishing is intense for just a few years rather than remaining consistent over time, and without making assumptions about the distribution of fishing under future conditions.

In this study, we apply the dRBS approach to evaluate the impact of bottom trawling fisheries on the predicted density distribution of taxa under present-day environmental conditions. Annual bottom trawling intensity is measured as the swept area ratio (SAR; Figure 2), which reflects the historical footprint and intensity of the fishery each year over 30 years (1989–90 to 2018–19). SAR is calculated by dividing the total cumulative area affected by bottom trawling within a specific seabed region by the size of that region over time. Typically, assessment regions are gridded, and calculations are applied within every cell, assuming that the taxa in each grid cell respond independently to trawling. Higher SAR values indicate greater trawling activity. For example, SAR < 1 means the trawled area is smaller than the target region, SAR = 1 indicates the trawling occurs all over the region's extent, and SAR > 1 signifies the region has been trawled multiple times over time. The impact of bottom trawling is derived from the degree of spatial overlap between the trawled area and associated trawling intensity and the taxon's distribution and further adjusted by the taxon-specific sensitivity to bottom-contacting gears and recovery capacity (see next section).

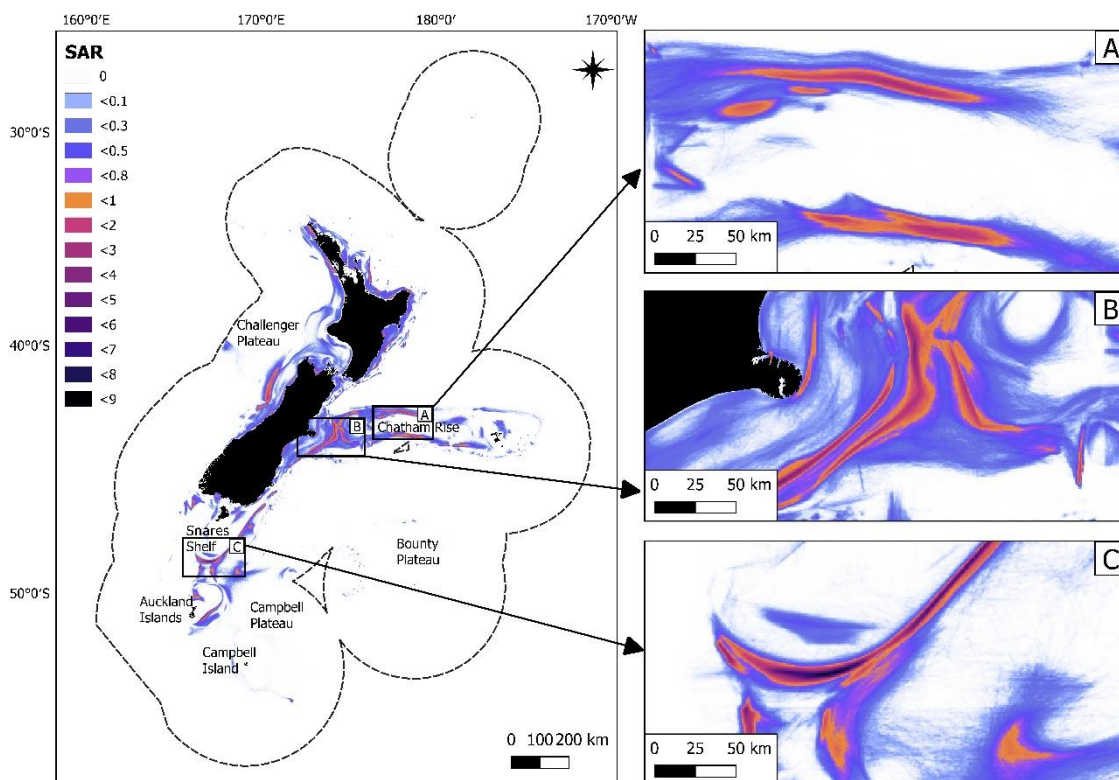


Figure 2. The mean swept area ratio (SAR) for all bottom trawl gear from 1989–90 to 2018–19. Insets A, B, and C highlight regions where the seafloor was subject to higher fishing effort. Data source: Fisheries New Zealand.

3.2.4 Depletion and Recovery data

The impact of fisheries on VME indicator taxa depends on taxon-specific depletion (D) and recovery (R) rates, as well as fishing intensity and occurrence. D and R values were derived primarily from meta-analysis of studies on otter trawling and values published in three studies (Mormede et al., 2017; Pitcher et al., 2017; Welsford et al., 2014), then adapted to VME indicator taxa in the High Seas through expert opinion and re-analysis of some of the raw input data (Anderson et al., 2024; Rowden et al., 2024). The associated uncertainty around these estimates resulted in three scenarios: ‘base-case,’ ‘worst-case,’ and ‘best-case’ (Table 1). The impact of fisheries is ultimately determined by the balance between depletion (D) and recovery (R) rates: taxa with higher depletion and lower recovery are more susceptible to fishing pressure. These taxa typically possess traits such as being erect, fragile, slow-growing, and long-lived. For example, fragile stony corals like *G. dumosa* exhibit high depletion rates and low recovery rates, highlighting their increased vulnerability. Therefore, outputs for dRBS were estimated using the most reliable estimates of D and R, termed here as the ‘base case’ status (e.g., *G. dumosa*, D = 0.67 and R = 0.2, Table 1), along with two alternative scenarios: a ‘best-case’ state, where fishing impact is predicted to be lower and recovery faster than the base case (e.g., *G. dumosa*, D = 0.52 and R = 0.25, Table 1), and a ‘worst-case’ status, where fishing impact is expected to be higher and recovery slower than the base case (e.g., *G. dumosa*, D = 0.82 and R = 0.15, Table 1).

Table 1. Bottom trawl fishing depletion (D) and recovery (R) rates for the ten VME indicator taxa modelled, with sensitivities for the uncertainties in these values (low and high) as used in the calculation of dRBS.

Taxon	Common names	Depletion			Recovery		
		D – low	D	D – high	R – low	R	R – high
<i>Goniocorella dumosa</i>	Stony coral	0.52	0.67	0.82	0.15	0.20	0.25
Scleractinia	Stony coral	0.52	0.67	0.82	0.15	0.20	0.25
Antipatharia	Black coral	0.39	0.50	0.61	0.20	0.33	0.30
<i>Radicipes</i> spp.	Golden coral	0.27	0.34	0.41	0.20	0.25	0.30
Pennatulioidea	Sea-pens	0.26	0.34	0.42	0.29	0.39	0.49
Gorgoniidae	Sea-fans; Sea whips	0.39	0.50	0.61	0.20	0.27	0.34
Primnoidae	Primnoids	0.28	0.50	0.42	0.20	0.25	0.30
Stylasteridae	Hydrozoans	0.32	0.41	0.50	0.25	0.33	0.41
Hexactinellida	Glass sponge	0.30	0.38	0.46	0.18	0.24	0.30
Demospongiae	Sponge	0.30	0.38	0.46	0.18	0.24	0.30

3.2.5 Computing dRBS

Population dynamics are assumed to be described by a Schaefer (1954) type logistic growth equation (Schaefer, 1991). An additional term is included to describe the direct impacts of bottom trawling and the recovery capacity each year. The rates of depletion and recovery for each year were calculated as follows (Pitcher et al., 2015):

$$\delta B/\delta t = R \cdot B (1 - B/K) - D \cdot F \cdot B$$

Where $\delta B/\delta t$ is the rate of change in B (biomass or abundance; here density) in time t for a taxon; R (recovery) represents the proportional recovery rate per year; K is carrying capacity; D (depletion) is proportional depletion rate; and F (fishery) reflects the bottom trawling effort during time t, expressed as the SAR, (Pitcher et al., 2015). Values of dRBS were calculated across different spatial scales, including the overall study area, primary habitat regions, and predicted climate refugia (Zelli et al., 2025). Depletion and recovery estimates were computed sequentially for each year with available fishing data across the 30 years. The final density (dRBS output) reflects the density distribution of each taxon within target areas, following the effects of bottom trawling accounting for taxon-specific depletion and recovery rates. The dRBS calculations were performed in RStudio (version 4.2.2).

3.3 Results

The effects of historical bottom trawling on predicted current-day densities for 10 VME indicator taxa across the entire study area, primary habitats, and climate refugia for ‘base-case’ dRBS are presented in the following sections. Here we illustrate the results for *G. dumosa* as an example due to its recognised importance as a habitat-forming taxon for coral reef VME in the New Zealand region (Dawson, 1984; Mackay et al., 2014; Squires, 1965). Outputs for the nine other VME indicator taxa showing density distribution across the overall study area, primary habitats and climate refugia are provided in the Supplementary Materials.

3.3.1 Impact of historical bottom trawl fishing on predicted density of VME indicator taxa

3.3.1.1. Study area and primary habitats

Accounting for the historical impact of bottom trawling resulted in decreases in predicted current-day density for all VME indicator taxa across the whole study area as well as within the regions of primary habitats (Table 2). For *G. dumosa*, when fishing-impacted areas were compared to baseline conditions, the total density across the entire study area was predicted to decrease by 15.3% (range 12–19%) (Table 2). Within primary habitats, *G. dumosa* density estimates were predicted to be reduced by 7% (range 5–10%) due to bottom trawl impacts (Figure 3; Table 2). Across all VME indicator taxa, total density (on average) in the study area was predicted to decrease by 6.7% (range 5–9%), whereas in primary habitats density was predicted to decrease by 5.5% (range 4–7%) (Table 2).

Overall, scleractinian corals and Demospongiae were predicted to be the most impacted at the study area scale, with predicted losses of up to 10% (range 7–13%) and 11% (range 8–14%), respectively, when compared to their baseline distribution. In contrast, Antipatharia, Hexactinellida, Primnoidae and Stylasteridae were predicted to be less impacted, with density losses ranging from 2% to 5% (range 3–6% on average). Within primary habitats, Pennatuloidae and *Radicipes* spp. were predicted to be most affected by fishing pressure, with predicted density losses of up to approximately 29% (range 20–39%) and 20% (range 14–26%) respectively followed by *G. dumosa* and Scleractinia with predicted density losses of 7% (range 5–10%) and approximately 10% (range 6–15%) (Table 2). Primary habitats of other modelled taxa (e.g., Antipatharia, Hexactinellida, Primnoidae and Stylasteridae) appear to show reduced overlap with fishing pressure and, therefore, were predicted to be less impacted with density losses ranging from 0% to 3% (range 0–5% on average).

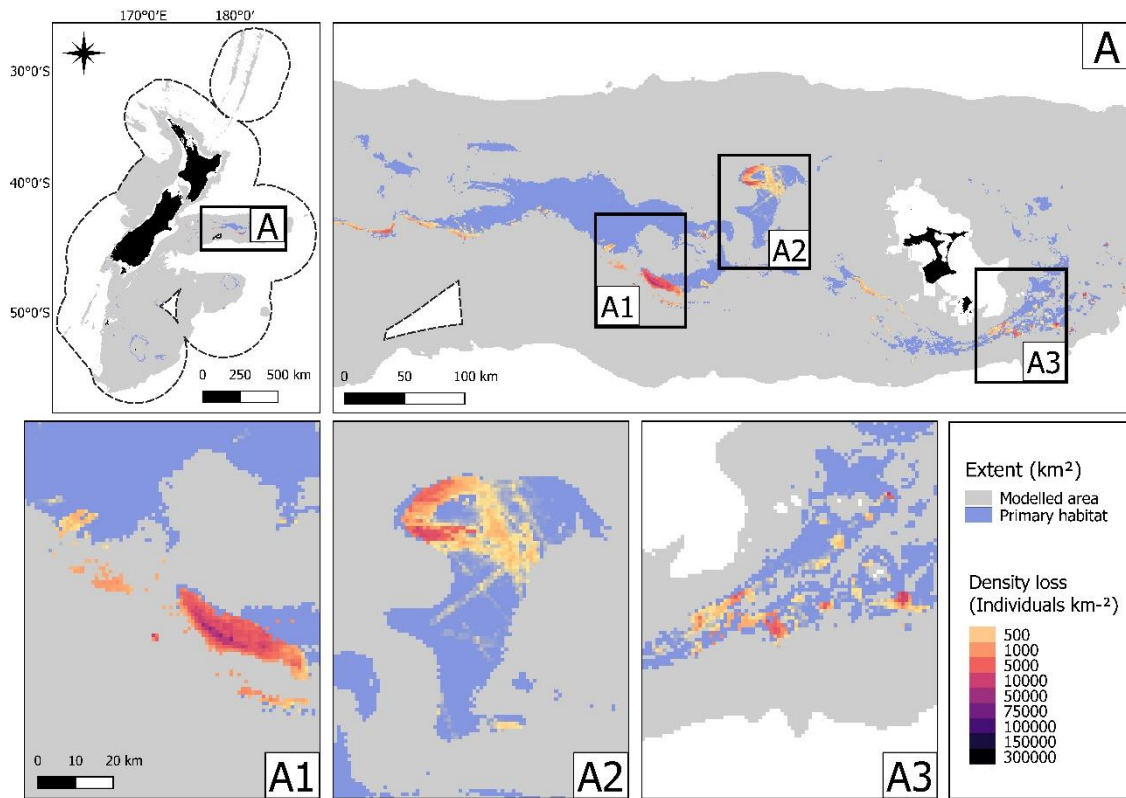


Figure 3. (A) Predicted distribution of density loss (expressed as individual live coral heads per km²) for *Goniocorella dumosa* within primary habitats (light purple) across the Chatham Rise region. Insets A1, A2 and A3 illustrate hotspots of taxa density loss following the impact of historical bottom trawling activity.

Table 2. Predicted VME indicator taxa density (total individuals) under baseline conditions (no fishery impact) and following estimated fishery impact and subsequent recovery using dRBS approach. The results are provided for the overall study area and current primary habitats. The percentage difference between the baseline and dRBS scenarios is provided for the base-case, along with uncertainty expressed as a range reflecting worst- and best-case status.

Taxon	Common names	OVERALL AREA				PRIMARY HABITATS			
		Present-day		Present-day		Present-day		Present-day	
		baseline	dRBS	% loss		baseline	dRBS	% loss	
			Base-case	range	km ²	km ²	Base-case	range	
<i>G. dumosa</i>	Stony coral	6.2E+08	5.3E+08	15.3	12-19	2.3E+08	2.1E+08	7.0	5-10
Scleractinia	Stony coral	1.6E+09	1.4E+09	10.2	7-13	3.9E+08	3.5E+08	9.8	6-15
Antipatharia	Black coral	1.5E+09	1.4E+09	5.2	5-8	4.5E+08	4.5E+08	0.6	1-1
<i>Racidipes</i> spp.	Golden coral	7.5E+08	6.8E+08	9.0	7-12	1.3E+08	1.0E+08	20.1	14-26
Pennatuloidae	Sea-pens	1.9E+09	1.7E+09	7.3	5-10	2.0E+08	1.4E+08	28.6	20-39
Gorgoniidae	Sea-fans; Sea whips	2.1E+09	2.0E+09	6.3	4-8	2.6E+08	2.6E+08	3.0	2-4
Primnoidae	Primnoids	2.1E+09	2.0E+09	4.9	3-5	2.2E+08	2.1E+08	2.9	1-3
Stylasteridae	Hydrozoans	2.9E+09	2.8E+09	4.4	3-7	9.1E+08	8.8E+08	3.0	2-5
Hexactinellidae	Glass sponge	7.8E+09	7.6E+09	1.8	1-2	2.3E+09	2.3E+09	0.1	0-0.1
Demospongiae	Sponge	8.6E+09	7.6E+09	11.2	8-14	1.7E+09	1.5E+09	11.2	8-14
mean		3.0E+09	2.8E+09	6.7	5-9	6.7E+08	6.4E+08	5.5	4-7

3.3.1.2. Climate refugia regions

Internal refugia. The current-day density of *G. dumosa* within internal refugia regions was predicted to decline by 6.0% and 6.8% (range 4–9% on average) for SSP3-7.0 and SSP2-4.5 scenarios, respectively (Figure 4, Table 3). The total density loss was predicted to be over 10 million individuals, with a mean predicted density loss of approximately 900 individuals per km² and a maximum density loss of 28,000 individuals per km² (Table 4). The habitat extent of *G. dumosa* was predicted to decrease by approximately 12% (range 8–15% on average) under both climate change scenarios from c.a. 18,000 km² at baseline conditions to c.a. 16,000 km² (Table 3; Figure 4).

Across all VME indicator taxa, total density (on average) within internal refugia was projected to decrease by an average of approximately 8.1% (range 6–11%) and 7.3% (range 5–10%) under the SSP2-4.5 and the SSP3-7.0 scenarios, respectively (Table 3). The mean predicted density loss amounted to approximately 4,000 individuals per km², and the maximum density loss was almost 90,000 individuals per km² under both climatic scenarios (Table 4). The habitat extent of overall VME indicator taxa within internal refugia decreased by 10.9% (range 7–15%), from over 14,000 km² at baseline conditions to c.a. 12,000 km² under the SSP2-4.5 scenario and by 9.6 (range 6–14%), from over 13,000 km² at baseline conditions to c.a. 12,000 km² under the SSP3-7.0 scenario (Table 3).

External refugia. The density of *G. dumosa* within external refugia regions was predicted to decline due to bottom fishing impacts by 32% (range 26–39%) and 24.8% (range 20–30%) for SSP2-4.5 and SSP3-7.0 climatic scenarios, respectively (Figure 4, Table 3). The predicted total loss of individuals was over 2 million, the mean density loss was almost 800 individuals per km², and the maximum density loss reached almost 3,000 individuals per km² under both climate change scenarios (Table 4). Bottom fishing impacts were predicted to decrease the habitat extent of *G. dumosa* within external refugia by 15% (range 11–18%), from c.a. 3,400 km² at baseline conditions to less than 3,000 km² under the SSP2-4.5 scenario, and by 10.4% (range 7–15%) from c.a. 5,700 km² at baseline conditions to c.a. 5,000 km² under the SSP3-7.0 (Table 3; Figure 4).

Across all VME indicator taxa, total density (on average) was predicted to decline due to bottom fishing impacts by 9% (range 7–12%) and 10% (range 8–13%) within external

refugia (Table 3). The mean density loss amounted to approximately 500 individuals per km², and the maximum density loss reached over 4,000 individuals per km² under both climatic scenarios (Table 4). The total extent of habitat contraction within external refugia resulting from the impact of bottom trawling is relatively low as it leads to an area loss of 3.2% (range 2–5%) and 4.8% (range 3–7%) for the SSP2-4.5 and SSP3-7.0 scenarios, respectively (Table 3).

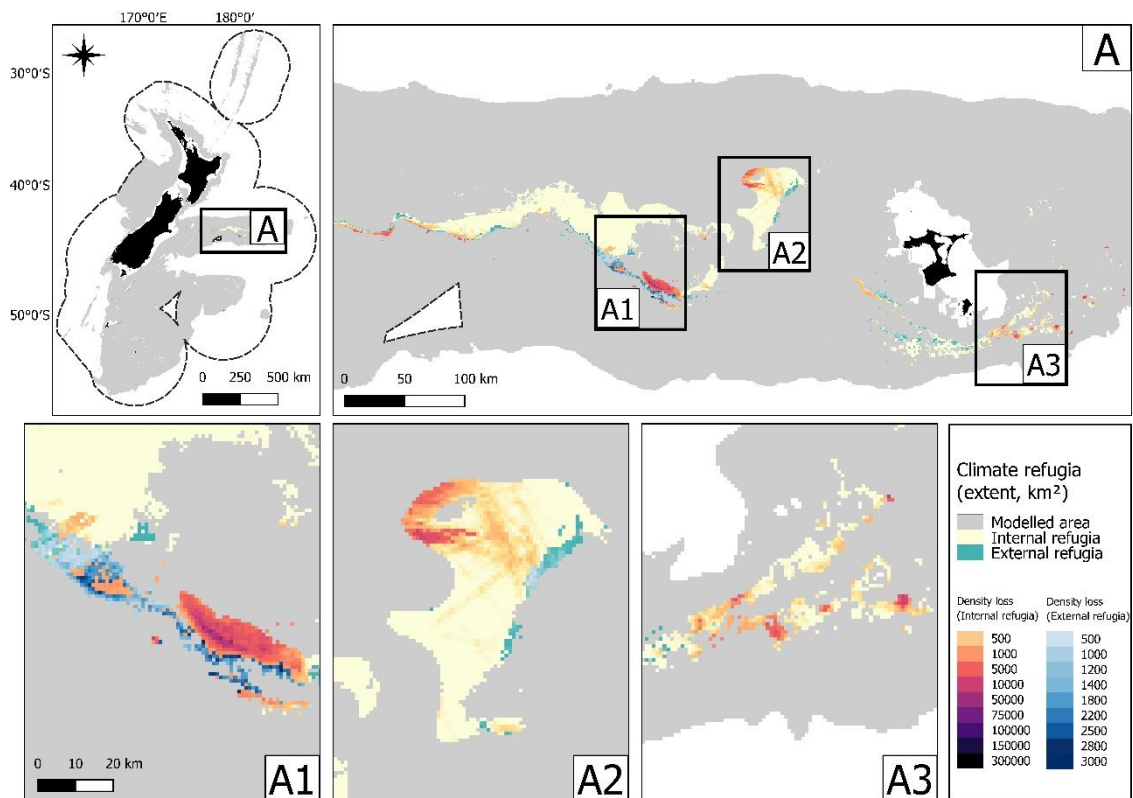


Figure 4. (A) Predicted distribution of density loss (expressed as individual live coral heads per km²) within predicted climate refugia (internal, light yellow and external, light green) for *Goniocorella dumosa* under the SSP2-4.5 scenario across the Chatham Rise region. Insets A1, A2 and A3 illustrate hotspots following the impact of historical bottom trawling activity for internal (density loss showed in the red palette) and external (density loss showed in the blue palette) refugia regions separately. The map for the SSP3-7.0 scenario is provided in the Supplementary Materials (Figure S4).

Table 3. Summary of percentage of (A) total individuals and (B) spatial extent loss for the predicted internal and external refugia for all assessed VME indicator taxa under both SSP2-4.5 and SSP3-7.0 scenarios. Percentage losses are reported for the “base” status and as a “range” reflecting the optimistic (-best) and pessimistic (-worst) status relative to the lowest/highest D and R rates. Values of density estimates (expressed as total individuals) and extent (expressed as km²) are provided in the Supplementary materials (Table S1).

(A) INDIVIDUAL LOSS (%)		INTERNAL REFUGIA				EXTERNAL REFUGIA			
		SSP2-4.5		SSP3-7.0		SSP2-4.5		SSP3-7.0	
<i>Taxon</i>	Common names	<i>base</i>	<i>range</i>	<i>base</i>	<i>range</i>	<i>base</i>	<i>range</i>	<i>base</i>	<i>range</i>
<i>G. dumosa</i>	Stony coral	6.8	4.7-9.1	6.0	4.2-8.2	32.0	26.0-38.8	24.8	19.5-30.1
Scleractinia	Stony coral	10.5	6.7-15.6	10.4	6.6-15.5	9.0	6.4-12.1	10.9	7.9-14.4
Antipatharia	Black coral	0.4	0.3-0.8	0.6	0.5-1.6	3.4	3.1-4.7	1.5	1.4-2.8
<i>Racidipes</i> spp.	Golden coral	23.5	15.4-32.1	23.7	15.4-32.3	40.1	30.9-46.9	44.3	35.9-50.5
Pennatulioidea	Sea-pens	32.4	22.8-44.1	35.8	24.4-49.9	12.0	7.7-17.4	14.6	9.4-21.5
Gorgoniidae	Sea-fans; Sea whips	2.7	1.9-3.7	2.3	1.6-3.2	2.0	1.2-3.2	2.0	1.2-3.2
Primnoidae	Primnoids	2.3	1.0-2.3	2.5	1.1-2.6	3.0	1.2-3.3	4.3	1.9-4.6
Stylasteridae	Hydrozoans	3.3	2.1-4.9	3.2	2.1-4.8	9.5	7.8-11.6	9.7	7.9-12.0
Hexactinellidae	Glass sponge	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Demospongiae	Sponge	31.6	26.5-35.3	8.9	7.4-10.2	0.0	0.0-0.1	0.1	0.0-0.4
mean		8.1	5.5-11.4	7.3	4.8-10.4	8.9	6.5-11.8	10.2	7.5-13.4

(B) EXTENT LOSS (%)		SSP2-4.5		SSP3-7.0		SSP2-4.5		SSP3-7.0	
		<i>base</i>	<i>range</i>	<i>base</i>	<i>range</i>	<i>base</i>	<i>range</i>	<i>base</i>	<i>range</i>
<i>Taxon</i>	Common names	<i>base</i>	<i>range</i>	<i>base</i>	<i>range</i>	<i>base</i>	<i>range</i>	<i>base</i>	<i>range</i>
<i>G. dumosa</i>	Stony coral	13.0	9.4-16.7	10.9	7.8-14.2	15.0	11.2-17.8	10.4	7.0-14.5
Scleractinia	Stony coral	10.1	6.3-15.6	9.6	5.9-15.0	2.6	1.7-3.7	4.7	3.2-6.3
Antipatharia	Black coral	0.2	0.1-0.4	0.5	0.4-4.8	1.6	1.6-1.6	0.8	0.8-0.8
<i>Racidipes</i> spp.	Golden coral	21.7	14.1-30.0	22.1	14.5-30.5	11.0	4.6-18.9	15.6	7.2-23.1
Pennatulioidea	Sea-pens	23.7	15.9-32.8	24.7	16.2-35.2	2.5	1.7-4.2	2.1	1.3-3.7
Gorgoniidae	Sea-fans; Sea whips	4.0	2.8-5.7	3.4	2.4-4.9	0.5	0.3-0.7	0.6	0.4-0.9
Primnoidae	Primnoids	3.3	1.4-3.5	4.0	1.5-4.2	0.3	0.0-0.3	0.5	0.1-0.5
Stylasteridae	Hydrozoans	3.5	2.3-4.7	3.2	2.2-4.3	7.2	5.9-8.2	6.9	5.5-8.1
Hexactinellidae	Glass sponge	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Demospongiae	Sponge	35.9	32.0-36.9	13.0	13.0-13.0	0.0	0.0	0.0	0.0
mean		10.9	7.2-15.1	9.6	6.3-13.8	3.2	2.2-4.5	4.8	3.1-6.6

Table 4. Summary of the sum (total individual live coral heads), mean and maximum current density loss (expressed as individual live coral heads per km²) following the predicted impact of historical bottom trawling activity and potential taxa recovery (dRBS) across the modelled VME indicator taxa within internal and external refugia for both the SSP2-4.5 and SSP3-7.0 climatic scenarios. Values of density loss for the overall study areas and primary habitats are provided in the Supplementary materials (Table S2).

DENSITY LOSS		INTERNAL REFUGIA			EXTERNAL REFUGIA		
SSP2-4.5	Common names	sum	mean	max	sum	mean	max
<i>G. dumosa</i>	Stony coral	1.1E+07	9.2E+02	2.8E+04	2.6E+06	8.6E+02	3.0E+03
Scleractinia	Stony coral	3.7E+07	2.5E+03	8.6E+04	1.6E+07	6.9E+02	6.2E+03
Antipatharia	Black coral	1.2E+05	3.0E+02	3.0E+04	2.9E+04	3.9E+02	5.4E+03
<i>Racidipes</i> spp.	Golden coral	1.7E+07	1.3E+03	5.9E+04	1.4E+06	4.9E+02	2.0E+03
Pennatuloidae	Sea-pens	4.5E+07	3.0E+03	1.4E+05	4.8E+06	4.0E+02	3.6E+03
Gorgoniidae	Sea-fans; Sea whips	5.6E+06	1.0E+03	4.7E+04	1.2E+06	2.4E+02	5.9E+03
Primnoidae	Primnoids	9.7E+05	4.8E+02	1.9E+04	7.1E+04	1.7E+02	4.6E+03
Stylasteridae	Hydrozoans	2.7E+07	2.5E+03	2.8E+05	6.3E+06	1.9E+03	1.2E+04
Hexactinellidae	Glass sponge	9.5E+00	1.6E+00	1.8E+00	3.9E+01	3.9E+00	6.3E+00
Demospongiae	Sponge	6.9E+06	3.1E+04	2.4E+05	1.1E+02	5.5E+01	6.3E+01
mean		1.5E+08	4.3E+03	9.4E+04	3.2E+07	5.1E+02	4.2E+03
SSP3-7.0	Common names	sum	mean	max	total	mean	max
<i>G. dumosa</i>	Stony coral	9.8E+06	8.5E+02	2.8E+04	3.0E+06	6.4E+02	3.0E+03
Scleractinia	Stony coral	3.6E+07	2.5E+03	8.6E+04	2.1E+07	6.8E+02	6.2E+03
Antipatharia	Black coral	5.0E+05	3.3E+02	3.0E+04	3.3E+04	1.5E+02	5.4E+03
<i>Racidipes</i> spp.	Golden coral	1.7E+07	1.3E+03	5.9E+04	2.8E+06	4.7E+02	2.0E+03
Pennatuloidae	Sea-pens	3.7E+07	3.7E+03	1.4E+05	4.5E+06	3.7E+02	3.6E+03
Gorgoniidae	Sea-fans; Sea whips	4.7E+06	9.4E+02	4.7E+04	1.4E+06	2.2E+02	5.9E+03
Primnoidae	Primnoids	6.6E+05	5.3E+02	1.9E+04	2.0E+05	2.3E+02	4.5E+03
Stylasteridae	Hydrozoans	2.6E+07	2.5E+03	2.8E+05	7.9E+06	1.7E+03	1.2E+04
Hexactinellidae	Glass sponge	0	0	0	0	0	0
Demospongiae	Sponge	4.6E+05	2.0E+04	5.9E+04	4.8E+01	4.8E+01	4.8E+01
mean		1.3E+07	3.6E+03	8.4E+04	4.0E+07	5.0E+02	4.7E+03

3.4 Discussion

In this study, we examined whether historical bottom trawling fisheries activity over a 30-year period has likely impacted the density and distribution of primary habitats for VME indicator taxa across the New Zealand TS and EEZ, and areas predicted as climate refugia by the end of the 21st century. Our findings highlight the overall likely negative impact of bottom trawling on important habitat-forming taxa, including cold-water corals and sponges, particularly in regions expected to function as future climate refugia. These results corroborate recent studies in the New Zealand region, that found scleractinian corals amongst the most vulnerable taxa when both climate change and bottom trawling impacts are considered (Stephenson et al., 2023a). Additionally, the results also align with recent research in the Mediterranean Sea, which predicted that climate refugia for cold-water corals overlap with active fishing grounds (Georges et al., 2024). Our findings

underscore the importance of protection measures that consider both global and localised stressors and highlight the necessity of incorporating multiple stressor scenarios on present and future habitats (e.g., climate refugia) in future conservation decisions (Stephenson et al., 2023a).

To date, the impact of multiple stressors on VME indicator taxa (e.g., cold-water corals) has been undertaken using only occurrence-based models (Stephenson et al., 2023). Modelling density responses to multiple pressures can offer deeper insights into habitat quality and ecosystem functioning. This approach may yield more ecologically relevant spatial predictions and provide more accurate estimates of potential impacts on ecosystems compared to analyses based solely on presence-absence data (Howard et al., 2014; Rullens et al., 2021; Zelli et al., 2025). Density plays a pivotal role in informing spatial management strategies as many valuable ecosystem services are often density-dependent (Melo-Merino et al., 2020; Spaak et al., 2017). For instance, VME indicator taxa found in high densities can drive community dynamics, such as habitat productivity and nutrient cycling (Rossi et al., 2017). Consequently, spatial data on the distribution and density of functionally important VME indicator taxa—especially those accounting for future climate scenarios—are essential for assessing impacts on VME-associated functionality and ecosystem services. This information is therefore critical for informing conservation efforts, guiding spatial planning, and optimizing resource allocation (Dijkstra et al., 2021; Zelli et al., 2025).

In the New Zealand region, the existing spatial management measures appear to be inadequate in providing sufficient protection to both current-day primary habitat areas and future climate refugia as part of the predicted distribution of these regions for VME indicator taxa largely falls outside the existing protection measures as stressed by previous works (Anderson et al., 2022; Stephenson et al., 2023a; Zelli et al., 2025). By employing the dRBS approach, here we show that the lack of protection is already impacting the current-day density and extent of selected VME indicator taxa across all the investigated regions, and particularly in areas predicted to serve as refugia, potentially preventing them from becoming effective refugia in the future.

3.4.1 The impacts of bottom fishing across taxa and regions

The dRBS results show that, across the entire study area, bottom trawling was predicted to have the greatest impact on scleractinian corals (e.g., *G. dumosa*) followed by sponges (e.g., Demospongiae). In primary habitat regions, scleractinian corals and sponges, along with octocorals (especially *Radicipes* spp.) and sea pens (i.e., Pennatuloidae), were also identified as highly affected taxa. When focusing on areas of climate refugia, these taxa were predicted to face more substantial losses. The heightened vulnerability of these taxa to bottom trawling impacts compared to other taxa likely stems from the higher overlap between their density distributions and the distribution of bottom fishing effort (i.e., greater exposure to bottom fishing), biological traits resulting in bottom fishing impacts being larger (i.e., greater sensitivity to bottom fishing impacts) and slower growth rate limiting recovery potential (i.e., lower adaptive capacity to bottom fishing impacts).

In contrast, taxa such as Gorgoniidae, Primnoidae, and Stylasteridae were predicted to experience less impact on their future distributions from bottom trawling. This reduced vulnerability was likely due to their lower exposure to fishing, combined with lower sensitivity to bottom-contacting gears and faster recovery rates, which collectively reduce the overall impact on these taxa compared to more fragile taxa like scleractinian corals. Additionally, taxa such as Antipatharia and Hexactinellida, appear less affected by fisheries within refugia areas. However, this finding is likely not due to higher resilience to bottom-trawling impacts but rather to the limited extent of their refugia as predicted by Zelli et al., (2025). This limited refugia area reduces the spatial overlap with fishing activities, thereby lowering their exposure. These findings emphasize that certain taxa (e.g., Scleractinia, Pennatuloidae, and Demospongiae) may be at greater risk than others (e.g., Gorgoniidae, Primnoidae, and Stylasteridae), indicating that these vulnerable groups may require higher prioritization in conservation strategies. Disparate rates of predicted density and habitat extent loss between internal and external refugia and amongst taxa require consideration of taxon-by-taxon and area-dependent spatial planning. Future conservation planning could benefit from a nuanced approach, focusing additional protections on the more sensitive and slower-recovering taxa, which are less capable of withstanding or adapting to multiple stressors.

The predicted decrease in the current-day density and extent of VME indicator taxa, particularly within primary habitat and climate refugia regions, as found in this study,

may negatively affect the density-related ecosystem capacity to provide functions and services, including their ability to provide habitat and support biodiversity (Gaston & Fuller, 2008; Melo-Merino et al., 2020; Rossi et al., 2017; Spaak et al., 2017). In addition, significant habitat loss or fragmentation may diminish the population connectivity potential and thereby their capacity to colonize new areas as well as their recovery following disturbances (Munday et al., 2009). This impact might ultimately affect VME indicator taxa at both local and regional scales and expose them to the risk of local extinction.

3.4.2 Implication for Marine Spatial Planning

Multiple anthropogenic activities, including climate change and fishing, can affect the marine environment concertedly. However, current management strategies usually address these activities in isolation (Halpern, McLeod, et al., 2008). Transitioning to a more integrated approach, as highlighted by the recent focus on ecosystem-based management, necessitates methods to evaluate their multiple effects (Gissi et al., 2021; Halpern, McLeod, et al., 2008). Recognising the urgency of accounting for multiple stressors in conservation planning, it is imperative to mitigate the impacts of global and local pressures on vulnerable species, communities, habitats, and ecosystems (Gissi et al., 2021; Halpern, McLeod, et al., 2008). This action is critical to futureproof conservation measures that are implemented now, prioritising areas that are more ecologically relevant (e.g., have high densities) and may facilitate recovery and restoration—e.g., through connectivity—in the future (Moilanen et al., 2011a).

Predicted climate refugia potentially represent the sole habitats where these VME indicator taxa may persist (i.e., internal refugia) or expand (i.e., external refugia) under future climatic conditions, offering hope for the preservation of deep-sea biodiversity and associated ecosystem services. However, it is important to note that these refugia have been predicted based on current-day taxa density; these may not actualise if there are insufficient taxa densities to act as sources, for example, if reduced due to the impact of bottom trawling. Previous research has shown a decline and shift in the distribution of habitat occurrence (Anderson et al., 2022) and density (Zelli et al., 2025), particularly within primary habitat areas for the investigated VME indicator taxa under future climate change. This study further highlights the density and extent reductions predicted within climate refugia regions due to historical fishing, underscoring concerns about the limited coverage provided by existing spatial protection measures in the New Zealand marine

region. Our results highlight the considerable risks of further taxa density declines and potential local extinction if bottom trawling persists and comprehensive strategies that account for future taxa distribution (e.g., climate refugia) and multiple impacts are not implemented (Clark & Dunn, 2012; Sala et al., 2021; Stephenson et al., 2023a).

3.4.3 What to protect?

From a management perspective, internal climate refugia emerge as prime candidates for incorporation into spatial protection measures to address the impacts of climate change and bottom trawling, particularly for taxa with limited dispersal capabilities. This emphasis on protecting internal refugia is because they are predicted to maintain high density, relevant for sustaining viable population numbers and the maintenance of ecosystem services, both at present and in the future (Zelli et al., 2025). The protection of internal refugia can only be one conservation approach. External refugia, on the other hand, should also be considered relevant for conservation as they represent areas where taxa are not particularly abundant currently but are predicted to become more abundant in the future. This information is crucial for managers to consider in spatial planning, as reducing impact in areas that may become important under future scenarios could facilitate climate mitigation and offset local extinction risk (Graham et al., 2019; Keppel et al., 2015). However, we found some relevant taxa, including *G. dumosa* and *Radicipes* spp. experiencing significant density declines within external refugia areas if compared to internal refugia regions.

Managing external refugia within spatial protection measures presents challenges, as their future viability—intended as the formation of high-density regions—depends not only on maintaining current densities that may increase over time but also on ensuring connectivity with internal refugia. Poor dispersal abilities, fragmented habitats, or physical barriers may hinder the natural colonization of external refugia (Carr et al., 2017; Magris et al., 2014, 2018a; Morelli et al., 2017). Connectivity between contiguous refugia increases colonization potential, making such areas promising candidates for protection, especially for taxa like reef-forming corals. As such, to enhance conservation planning, studies on larval dispersal and connectivity for VME indicator taxa are needed (e.g., Kenchington et al., 2019). Conservation should prioritise ecologically valuable unimpacted areas with high-density estimates while considering historically impacted sites that could recover if pressures are mitigated (Stephenson et al., 2023a). Therefore,

conservation priorities should balance areas resistant to climate change and those with recovery potential.

Insights from the areas and taxa that are more vulnerable to the effect of bottom trawling or that have high recovery potential as well as connectivity information will equip spatial planners with valuable information to identify candidate areas for conservation (e.g., allocating resources to protect internal refugia, external refugia, or both) as well as the capacity to calibrate their decisions across taxa. This prioritisation and calibration would ultimately allow the development of a network of spatial protection measures able to provide increased resilience against multiple stressors, both current-day and in the future (Anderson et al., 2022; Zelli et al., 2025). Given the inevitability of short-term climate change (Santos et al., 2016) and the urgent need to address its multifaceted effects (Halpern, McLeod, et al., 2008), identifying and protecting climatic refugia emerges as a promising strategy for effective conservation planning, as highlighted in previous studies (Frazão Santos et al., 2020; Keppel et al., 2015; Rilov et al., 2020) while supporting fish stocks (Ainsworth et al., 2008; Pinsky & Mantua, 2014).

Effective protection measures for potential climate refugia are required to ensure the continuity of essential ecosystem functioning and prevent future local extinction. This finding holds particular relevance in light of Target 3 of the Kunming-Montreal Global Biodiversity Framework, which calls for the effective conservation and management of at least 30% of coastal and marine areas, especially areas of significant importance for biodiversity and ecosystem functions and services. To achieve this goal, spatial planning processes must incorporate multiple stressor scenarios that also account for future species distributions and primary habitats, ensuring the implementation of protected areas that encompass ecologically relevant areas both currently and in the future (e.g., climate refugia). Given the relevance these areas play for the fishing industry (Clark, Wood, et al., 2022), we reiterate that future spatial planning must effectively incorporate areas for sustainable use while providing for the long-term persistence of VMEs. Achieving this goal will require a collaborative approach involving local stakeholders, fishery managers, and scientific advisors working together to assess both ecological and socio-economic priorities (Clark & Dunn, 2012; Rowden et al., 2019; Stephenson et al., 2023a).

3.5 Conclusion

Our findings indicate that bottom trawling is likely to adversely impact all modelled VME indicator taxa across the investigated regions, with particularly pronounced effects within predicted refugia areas. These refugia are identified as regions potentially resilient to climate change (Zelli et al., 2025); yet they remain vulnerable to bottom-trawling impacts which were predicted to reduce the VME indicator taxa density and spatial extent. Such declines may hinder the successful establishment of these refugia, threatening the long-term maintenance of ecosystem service provision and increasing the risk of local extinctions. The trends vary across taxa and regions, underscoring the need for targeted conservation efforts in these crucial refugia zones. Conservation strategies should prioritize ecologically significant areas (e.g., high-density, high-biodiverse and high-connectivity zones) and consider the socio-economic importance of areas expected to function as climate refugia. Achieving conservation outcomes while allowing for sustainable fishing will require active stakeholder engagement and decision-making within the current legal and socio-ecological framework.

Chapter 4

Navigating risk and management: a social-ecological system approach to improve protection for vulnerable marine ecosystems

4.1 Introduction

Multiple anthropogenic stressors and activities impose significant pressures on marine ecosystems, and the risk of sudden nonlinear transformations is increasing (Borja et al., 2024; Hewitt et al., 2016; Hoegh-Guldberg & Bruno, 2010; Solé Figueras et al., 2024). Climate change and fisheries, for example, are considered responsible for much of the observed global habitat degradation and biodiversity loss (Beddington et al., 2005; Doney et al., 2012; Sumaila & Tai, 2020; Williamson & Guinder, 2021). Climate change is driving decreased ocean productivity, disrupted food webs, shifting species distributions, and declining abundance, resulting in diminished habitat complexity and ecosystem functionality (Borja et al., 2024; Elliott, 2023; Hoegh-Guldberg & Bruno, 2010). Furthermore, it poses a significant threat to foundation and habitat-forming species, such as corals, along with the ecosystem services they support in both shallow (Hoegh-Guldberg et al., 2007; Huges et al., 2017; Wernberg et al., 2024) and deep waters (Gammon et al., 2018; Levin et al., 2019; Ramirez-Llodra et al., 2011; Sweetman et al., 2017). In addition, fisheries, particularly those that use bottom-contacting gears are considered the primary threat to benthic ecosystems (Halpern et al., 2007; Levin et al., 2019; Puig et al., 2012; Ramirez-Llodra et al., 2011; Reed et al., 2007; Watson & Morato, 2013). Bottom trawling physically removes organisms, reduces species abundance and diversity, and alters water quality through sediment resuspension, causing extensive and long-lasting impacts on ecosystem structure, function, and habitat quality (Clark et al., 2016; McConnaughey et al., 2020; Pusceddu et al., 2014; Sciberras et al., 2018). As a consequence, the United Nations has passed resolutions to protect Vulnerable Marine Ecosystems (VMEs), defined as benthic invertebrate species/communities/habitats that form fragile, ecologically relevant biogenic structures, from significant adverse impacts of bottom fishing (Auster et al., 2011; FAO, 2009).

The New Zealand marine region hosts several deep-water VME indicator taxa, notably taxa that indicate the potential presence of VMEs, particularly cold-water corals (CWCs) (Tracey & Hjørvarsdóttir, 2019). At the same time, it is also considered a hotspot for climate change (Law et al., 2018; Lundquist et al., 2011) as well as being subjected to significant bottom trawl fishery activities (MPI, 2023; Williams et al., 2017). However, assessing the full extent of anthropogenic impacts (e.g., climate change and bottom trawling) on these taxa remains challenging due to limited knowledge of their spatial distribution in remote and difficult-to-access and data-poor environments such as the deep sea (Vierod et al., 2014). Species distribution models (SDMs) are numerical tools that combine observations of species occurrence or abundance with environmental estimates that offer a robust statistical approach to predict species or habitat distributions under current and future environmental conditions (Elith & Leathwick, 2009; Weber et al., 2017). SDMs are increasingly recognized for their ability to identify ecologically significant areas, facilitating conservation prioritization and spatial management decisions. Consequently, they have become integral to biodiversity conservation and resource management (Elith & Leathwick, 2009; Guisan & Thuiller, 2005; Mazon et al., 2021; Weber et al., 2017).

Recent studies have used spatial modelling approaches, including SDMs, to investigate the effects of climate change on several VME indicator taxa within the New Zealand region. These studies highlighted important areas of habitat loss by the end of the 21st century across the New Zealand Exclusive Economic Zone (EEZ) and Territorial Sea (TS) (Anderson et al., 2022; Zelli et al., 2025). These studies, however, also identified areas that might serve as climate refugia defined as areas predicted to persist or expand under future climatic conditions (Anderson et al., 2022; Zelli et al., 2025). These refugia habitats represent potential "hope spots" for the preservation of biodiversity and associated ecosystem services under unfolding climate change and should therefore represent a conservation priority (Anderson et al., 2022; Graham et al., 2019; Keppel et al., 2015; Zelli et al., 2025). Nevertheless, further studies revealed that bottom trawling has likely affected select VME indicator taxa, with the greatest reductions in density and habitat extent predicted in areas expected to become climate refugia, thereby threatening their future viability (Zelli et al., under review). Therefore, climate refugia hold significant conservation value due to their ecological importance under future climate change and their predicted decline from bottom trawling, highlighting the need for their consideration in conservation planning to ensure protected areas remain suitable (Georges

et al., 2024; Stephenson et al., 2023a). These findings hold particular importance for conservation initiatives as they highlight the importance of implementing effective and climate-resilient protection measures as current marine spatial measures appear insufficient to address multiple challenges effectively (Anderson et al., 2022; Stephenson et al., 2023a; Zelli et al., 2025).

The spatial overlap between climate refugia and fishery areas, however, underscores their dual ecological and economic significance, presenting potential management challenges. Effectively addressing these challenges requires a coordinated, collaborative, and comprehensive ocean planning approach that balances biodiversity conservation with the socio-economic interests (e.g., from the fishing industry), ensuring protection measures support both ecological resilience and sustainable resource use (Hutton & Leader-Williams, 2003; Young et al., 2006). Marine spatial planning (MSP) is a holistic process that aims to assess and guide the spatial and temporal distribution of ocean uses to balance ecological, economic, and social objectives (Ehler et al., 2019; Ehler & Douvère, 2009). In other words, MSP strives to identify conflicts among uses and threats that use may pose to ecosystem health, and develops mechanisms to reduce the conflicts and manage the threats through improved policies, management measures, and governance ensuring that efforts to realize economic interests do not damage already fragile ecosystems (Collie et al., 2013; Halpern, Diamond, et al., 2012; Reimer et al., 2023a). While MSP is gaining traction globally (Foley et al., 2010; Lubchenco & Grorud-Colvert, 2015), its ability to support the long-term sustainability of the marine space depends on effectively bridging the gap between theory and implementation (Trouillet, 2020).

While previous studies have used decision-support tools to estimate the costs of expanding protection for the fishing sector, their integration into MSP remains theoretical and lacks stakeholder engagement (Stephenson et al., 2023a). Moreover, the lack of clear guiding principles for achieving multiple objectives or trade-offs for specific social-ecological systems poses a significant challenge to effective management (Boemare et al., 2023; Rowden et al., 2019; Thiault et al., 2020). This highlights the need for inclusive and adaptive science-policy frameworks that foster collaboration among scientists, regulators, and local communities through stakeholder engagement processes that integrate diverse perspectives into decision-making (Davis, 2008; Hartley & Robertson, 2006; Kitts et al., 2007; Martin-Smith et al., 2004; Sen & Raakjaer Nielsen, 1996; Verheij et al., 2004).

Effective decision-making should also quantify potential risks and associated uncertainty (Treffny & Beilin, 2011; Xu et al., 2015). Risk assessment is intended as the probability and the consequence of single or multiple stressors on various components of ecological and social systems (e.g., individual species, habitats, food webs, human communities) and it is used to prioritize management interventions and assess trade-offs (Burgman, 2005; Harwood, 2000; Holsman et al., 2017). As an example, risk assessments were applied to evaluate the impacts of climate change on coastal human communities (Cinner et al., 2012; Himes-Cornell & Kasperski, 2015; Morzaria-Luna et al., 2014), marine and coastal ecosystems (Halpern, Walbridge, et al., 2008; Magris et al., 2018b; Samhoury & Levin, 2012) or a fishery on marine resources (Fletcher, 2005; Halpern, Longo, et al., 2012; Hare et al., 2016; Hobday et al., 2011). Traditionally, marine risk assessments focused on singular pressure-response relationships, but recent advancements have shifted the central objective towards the assessments of impacts associated with one or more pressures of interest (Adger, 2006; Holsman et al., 2017; Magris et al., 2018b; Maxwell et al., 2013). Additionally, due to environmental conditions changing due to climate change, the nature and magnitude of risks are also likely to evolve (Adger et al., 2018; Simpson et al., 2021). Climate change poses significant challenges to society and decision-making, driving cascading risks across physical systems, ecosystems, economies, and societies (Adger et al., 2018; Simpson et al., 2021). At the same time, policymakers are under pressure to make decisions on climate change which intersect with many other policy domains. Consequently, effective risk assessments must incorporate the potential impacts of climate change to provide a more comprehensive and adaptive framework under future scenarios (Adger et al., 2018; Simpson et al., 2021).

The elicitation of experts' judgment is an important tool for the assessment of risks and impacts in environmental management contexts and for supporting decision-making (Martin et al., 2012; Morgan, 2014; Singh et al., 2017). Expert elicitation is defined as a structured heuristic process used to obtain expert opinions, expressed through qualitative or quantitative means such as descriptive language, numerical estimates, visual representations, or graphical models (Ayyub, 2001). Group elicitation offers opportunities for experts to challenge and refine each other's ideas, clarify ambiguous terms, and reassess confidence in their estimates (Burgman et al., 2011; Kandlikar et al., 2005; Sutherland & Burgman, 2015). However, expert judgments are influenced by various cognitive and motivational biases, as well as the expert's specific context and personal experiences (Hanea & Nane, 2019; Montibeller & von Winterfeldt, 2015).

Group settings can enhance or reduce understanding biases, depending on the group dynamics (Kerr & Tindale, 2004). Structured approaches, such as modified Delphi methods, help address these challenges by minimising dominant voices and encouraging fair and balanced participation (Burgman et al., 2011; McBride & Burgman, 2012). Diverse expert groups (e.g., experts from different backgrounds or belonging to different institutions) are particularly effective in reducing in-group biases, fostering critical discussions and promoting more robust judgements (Kandlikar et al., 2005). For elicitation processes to generate reliable estimates, they must include diverse participants and encourage critical reassessment of initial judgments alongside mitigating the risks of groupthink (or group polarization) where biases can arise when dominant personalities steer discussions, suppress dissent, or when participants amplify confidence due to group corroboration (Burgman et al., 2011; Fish et al., 2009; Sunstein & Hastie, 2015).

The group-discussion effect has been studied in contexts where experts provide quantitative estimates under clearly defined parameters (Fischhoff & Morgan, 2011). However, in addressing multiple impacts, managers face the added complexity of identifying and prioritizing risks before evaluating their severity and formulating solutions. This two-phase approach can exacerbate challenges due to the inherent complexity of tasks (MacDonald, 2000). In such cases, SDMs serve as a valuable resource, offering spatially and temporally explicit predictions of the impacts of specific activities or stressors (e.g., climate change and bottom trawling) on taxa or habitats, thereby supporting informed decision-making in risk and impact assessments (Elith & Leathwick, 2009; Guisan & Thuiller, 2005; Ramirez-Reyes et al., 2021). Elicitation processes were employed to assess the most significant risks posed by multiple stressors and their impacts on coastal ecosystem services in New Zealand (Singh et al., 2017). Specifically, this study examined how group deliberation influenced expert consistency, variation, and subjective uncertainty by comparing individual responses before and after a workshop with a diverse group of experts. One study explored the use of group elicitation and highlighted that elicitation techniques are an invaluable tool in the context of multiple impacts. Notably, the study found that risk estimates differed before and after the workshop, with group elicitation increasing the consistency of risk rankings and impact estimates, while also introducing greater uncertainty among experts when addressing key impacts on ecosystem services in coastal New Zealand (Singh et al., 2017).

Building on Singh et al., (2017), we carried out a social-ecological study in which we assessed expert-driven perceptions of risks and related management actions from various human activities and stressors on 10 VME indicator taxa within the New Zealand EEZ and TS. However, our study takes a novel step forward by integrating spatially explicit tools into the risk assessment process, allowing participants to prioritize management strategies more effectively. To our knowledge, this is the first study to combine future species distribution-based data with participative processes that involve conservation and fishery experts. This approach allowed a more efficient exploration of the perception of risk for VME indicator taxa and then identifying those management actions that are likely to be most effective at mitigating the risk.

We investigated these aspects at two different points in time: during individual semi-structured interviews (SSIs) (hereafter referred to as “individual interviews”) and during a dedicated workshop that involved focus group elicitation activities where participants were presented with quantitative findings from prior studies on the impacts of climate change (Zelli et al., 2025) and historical bottom trawling activity (Zelli et al., under review) on selected VME indicator taxa and the study area. This study addresses a two-phase problem by comparing expert responses before and after introducing spatial conservation tools during the group elicitation process. We hypothesized that, after the workshop where participants reviewed novel scientific findings from spatial modelling tools, they would more consistently identify prominent risks to VME indicator taxa, assigning higher risk priorities and impact scores to climate change and bottom trawling compared to their initial assessments. Additionally, we anticipated greater consensus on the management strategies necessary to mitigate these major risks as a result of the elicitation process. However, given the expertise and prior knowledge of the participants, we expected these shifts in perception to be incremental rather than abrupt. In addition, as the participants were primarily engaged in marine policy and management rather than resource utilisation, therefore, we expected a greater level of consensus and agreement across participants.

4.2 Materials and Methods

This study employed three key methodological steps designed to train and guide experts through the problem context and data collection process: (1) Expert identification: We used a systematic approach to identify and select participants, ensuring balanced

representation from relevant New Zealand conservation and research institutions, including Ministry of Primary Industries (MPI), New Zealand Department of Conservation (DOC), Ministry for the Environment (MfE), Environmental Protection Agency (EPA), and National Institute of Water and Atmospheric Research (NIWA); (2) Individual interviews: Each expert participated in an individual interview, during which they shared their perceptions of risks to VME indicator taxa posed by various human-driven stressors/activities and provided a ranking of management strategies to address these risks and (3) Delphi-like group workshop: All previously interviewed experts took part in a Delphi-like group workshop, where they re-assessed their risk perceptions and rankings of management strategies after being presented with novel scientific insights on the predicted impact of climate change and bottom trawling on target VME indicator taxa as well as the regions that potentially serve as climate refugia under future climatic projections obtained with SDMs (*sensu* Zelli et al., 2025). This study received approval from the University of Waikato Research Ethics Board (No HREC(HECS)2024#47). We direct the reader to the Supplementary Materials for a detailed account of the methodology, stages, and supporting information underpinning this study.

4.2.1 Study area

The study area spans water depths ranging from 100 m to 1500 m within the EEZ and TS of New Zealand (See supplementary Materials; Figure S1). This depth range was based on the spatial distribution of taxa density obtained by Zelli et al., (2025). The selected depth reflects the habitat where most recorded biological VME indicator taxa are observed (Bowden et al., 2021).

4.2.2 VMEs indicator taxa and spatial prediction of density

We asked participants to evaluate their risk perception and management strategies for 10 VME indicator taxa, including reef-forming scleractinian corals (*Goniocorella dumosa*, *Solenosmilia variabilis*, *Enallopsammia rostrata*, *Madrepora oculata*), black corals (Antipatharia), primnoid (Primnoidae), sea-fans, sea-whips (Gorgoniidae), sea-pens (Pennatuloidae), bamboo corals (Keratoisididae/Mopseidae), golden corals (*Radicipes* spp.) – collectively referred to as the taxonomic group ‘Cold-water corals (CWCs)’; Hydrozoa (Stylasteridae) – referred to as ‘hydrozoans’; and Porifera (Hexatinellida and Demospongiae) – referred to as ‘Sponges’. We utilized previously generated spatial density predictions for these taxa, as modelled by Zelli et al., (2025). This included spatial predictions of VME indicator taxa abundance for the entire study area, primary habitat

regions, and predicted climate refugia (both internal (within existing high-density areas) and external (new areas of predicted high density due to climate change)). Predictions were made for present conditions (1995–2014) and future projections (2080–2099) under moderate (SSP2-4.5) and high (SSP3-7.0) greenhouse gas trajectories. For detailed methodology, see Zelli et al., (2025) and Stephenson et al., (under review, dRBS paper) (See Supplementary Materials for more details about spatial prediction outputs).

4.2.3 Identification of experts, data collection and analysis

The group of participants consisted of sixteen representatives from key research, advisory, and policy institutions in New Zealand. Participants were individually invited to join the study, with six attending in person and ten participating online. The group included five representatives from MPI, including senior scientists, a principal advisor, and a senior fisheries analyst. Four participants were science advisors from DOC, three were fishery experts and benthic ecologists from NIWA, and three were policy advisors from EPA. Additionally, the group included a senior analyst from MfE and an environmental lawyer from academia. We evaluated potential changes in participants' perceptions of risks to VME indicator taxa from a specified list of activities/stressors by comparing data collected during individual interviews with data gathered after the group workshop (see next sections). The pre-defined list consisted of 9 activities and stressors (Table 1), which are considered the most relevant threats to deep-sea ecosystems and particularly VME indicator taxa from global and regional studies (Clark et al., 2016; Halpern et al., 2007; Levin et al., 2019; Ramirez-Llodra et al., 2011; Sweetman et al., 2017; Thiel & Schrieffer, 1993; Watson & Morato, 2013). Some of these stressors represent subsets of broader categories; for example, "Climate change-induced physical alteration" is a subset of "Climate change", or "Bottom trawling" is a subset of "Commercial fishery". This distinction is essential to allow experts to select stressors at different levels of specificity based on their knowledge of the potential impacts these stressors may have on VME indicator taxa.

Each expert was asked to rank up to five activities/stressors they regarded as threatening for the investigated taxa groups (i.e., CWCs, hydrozoa, sponges, and overall). They were given a list of activities/stressors (and associated descriptions) to choose from, with the option of adding others not indicated (Table 1). The analysis involved two main components: (1) Risk Assessment, which consisted of creating Probability Distribution Functions (PDFs) to capture and compare participants' perceptions of risk before and

after the workshop and (2) management strategy rankings, which consisted of experts identifying and explaining up to five most relevant management strategies to reduce the risk associated with the most relevant pressures identified by each participant.

Table 1. List of pre-defined global and local activities and stressors provided to experts for ranking and scoring their risk to VME indicator taxa.

Activity/Stressors	Definition
Climate change	A significant alteration in global or regional environmental patterns due to increased greenhouse gases. It can have an impact at the species or ecosystem level.
Ocean acidification	The process of increasing atmospheric CO ₂ levels results in higher carbonic acid levels in ocean waters, lowering pH. This phenomenon adversely affects calcifying organisms such as corals which are vital for maintaining healthy marine ecosystems. It can also lead to changes in species distributions.
Climate change-induced physical alteration	Modification of environmental parameters such as dissolved oxygen level, nitrogen, aragonite/calcite, pH, temperature, Particulate Organic Carbon (POC).
Commercial fisheries	The sector involved in harvesting fish and other marine organisms for consumption and trade. Unsustainable fishing practices can deplete fish stocks, disrupt food webs, and damage habitats, leading to long-term ecological consequences.
Bottom trawling fishery	A fishing method that involves dragging heavy nets across the ocean floor. This practice can severely damage sensitive habitats like coral reefs and disrupt benthic ecosystems by jeopardizing habitats and limiting connectivity dynamics.
Sedimentation	The process of sediment accumulation in marine environments, resulting from land runoff or trawling activities. High sedimentation rates can affect the fitness of benthic organisms.
Seafloor Mining	The extraction of minerals and resources from the ocean floor, including metals and fossil fuels. This activity can impact benthic habitats affecting local biodiversity.
Marine litter	Refers to waste materials (e.g., plastics or fishing nets) that can accumulate in the water column and the seafloor affecting wildlife and benthic ecosystems.
Nutrient input	The introduction/alteration of nutrients into marine ecosystems due to direct (e.g., runoff or sewage) or indirect sources (e.g., alteration of water currents due to climate change). Excessive nutrient input leads to the formation of dead zones and the alteration of physiological mechanisms.

4.2.4 Risk assessment

To assess risk perception of the investigated taxa groups across a list of activities and stressors, we employed a multi-metric approach to create PDFs, or risk curves. These PDFs represent expert-derived estimates of risk and were built by combining three different metrics: (1) The *impact score*, ranging from 0 to 1, indicates the perceived

strength of impact, where “0” is no impact and “1” is complete depletion; (2) the *confidence* level associated to the impact scores, expressed as a percentage, reflect the certainty of participants estimates; and (3) the *skewness* associated to the impact score, with values between -1 and +1, it represents an additional measure of uncertainty. Negative skewness suggests that the perceived impact leans toward lower impact score values (indicating lower risk), while positive skewness indicates a perception leaning toward impact score higher values (indicating greater risk) (See Supplementary Materials for more details on the metrics used). The latter two steps encouraged experts to reevaluate their values, ensuring more accurate risk estimates.

Participants independently completed tables assigning impact metrics to each VME indicator taxa group—CWCs, sponges, and hydrozoa—for the top five activities or stressors they identified during three sessions: (1) individual interviews (also referred to here as “baseline”), (2) following a presentation on climate change impacts, and (3) after reviewing combined effects of climate change and bottom trawling on VME indicator taxa from previous studies (Zelli et al., 2025, under review) (See Supplementary Materials for more details about the table used). Session 1 was carried out during the interview process with the main objective of assessing the preliminary state of knowledge of an individual (subjective opinion). Sessions 2 and 3 were conducted during the workshop with the objective of evaluating potential shifts in baseline risk perception following the introduction of new insights and peer interactions. After each session, participants also provided hand-drawn PDFs for each taxa group and selected stressors. The hand-drawn risk curves complemented the metric scores by offering a visual representation of perceived impacts for each ranked stressor or activity facilitating a clearer interpretation of experts' perceptions, particularly regarding uncertainty metrics such as confidence and skewness. The metric-based tables, together with the hand-drawn curves, were submitted to facilitators at the end of each session. These inputs were then digitized to generate PDFs in RStudio (version 4.2.2). This methodology was derived from a previous study conducted in the New Zealand region, which explored perceptions of risk from various anthropogenic stressors affecting coastal ecosystem services (Singh et al., 2017).

4.2.5 Management strategies ranking

The ranking of management strategies involved experts listing up to five approaches they considered necessary to address the impact of a specific activity and its associated risk. Experts were also asked to identify potential challenges to implementing these strategies and propose solutions to overcome them. The completed tables, which included the top five management strategies, challenges, and solutions, were collected during both the individual interviews and after the group workshop (see Supplementary Materials for more details on the supporting materials used). This approach allowed for evaluating how management priorities, as well as the associated challenges and solutions, might have evolved before and after the workshop. To facilitate the analysis of the identified management approaches, the strategies mentioned by the experts were grouped into broader categories (e.g., “Marine Spatial Planning,” “Climate Change Mitigation,” “Fishery Management,” etc.). Unlike the predefined list of activities and stressors (Table 1), participants were not provided with definitions of these categories to avoid biasing their decisions. To ensure accurate categorization, participants were required to explain each strategy they mentioned, confirming that each strategy was clearly understood and appropriately classified. Each strategy mentioned by a participant was assigned a category-specific code to reflect the category it represented. For example, strategies like “spatial closures,” “marine reserves,” and “marine protected areas” were assigned the same code (e.g., MSP) as they fall under the “Marine Spatial Planning” category. Similarly, strategies such as “de-carbonisation” or “carbon emissions reduction” were assigned the same code (e.g., CM) and included in the same “Climate Mitigation” category. The final ranking was determined by the total number of “citations” across management categories. A citation was counted each time a strategy within a specific category was mentioned. From the previous example: “Marine Spatial Planning” received three citations, while “Climate Change Mitigation” received two.

4.2.6 Individual Semi-Structured Interviews

Individual interviews were performed using Semi-Structured Interviews (SSI). SSI is a data collection method in which an interviewer asks the respondents questions, face-to-face, by telephone or online. It is commonly used to gather information on a specific topic and can include both open-ended and closed-ended questions (Adeoye-Olatunde & Olenik, 2021, 2021; Clifford et al., 2016). Individual interviews with each selected expert were conducted over three weeks, from late September to mid-October 2024. Each

session lasted approximately one hour and was held either online or in person. The aims of these interviews were: (1) Familiarization and training: Participants were introduced to key terminology, including VMEs, VME indicator taxa, and species distribution models, and were trained in the methodologies used in the study. This ensured participants understood the framework and could provide informed input in the subsequent stages; and (2) Assessment of initial risk: Experts shared their initial perceptions of the risks posed by human activities or stressors to the VME indicator taxa. Participants were allowed to use the pre-defined list of activity/stressors (Table 1) and visualize previously obtained species distribution data across New Zealand's EEZ, as modelled by Zelli et al., (2025). Risk was then assessed using the three metrics (impact score, confidence level, and skewness) that were used to generate initial risk curves.

Additionally, participants were asked to rank five management strategies, identify associated challenges in implementing them, and suggest potential solutions. Both steps (1) and (2) remained neutral and exclusively focused on the description of the methodological approach and the presentation of the present-day distribution of taxa density to avoid introducing any bias related to the sensitivity of specific VME indicator taxa (e.g., cold-water corals) towards specific activity or stressors (such as climate change and bottom trawling fishery). The collection of baseline risk curves during the individual interviews was propaedeutic for the workshop activity, where these profiles were reassessed after participants were presented with updated scientific data on species distribution and density under projected climate change projections, as well as the impacts of historical bottom trawling activities (see next section).

4.2.7 Group Workshop

Following the interviews, a three-hour workshop with the same experts from the interviews was held in Wellington, New Zealand, at the end of October 2024. The goal of the workshop was to explore whether the re-evaluation of impact scores collected during the individual SSIs and the identified management strategies would differ once experts were presented with additional model results on the impacts of climate change and bottom trawling on VME indicator taxa and following a group elicitation process. The workshop comprised three sessions comprehending two individual activities and one group activity:

(1) Session one consisted of the presentation of new scientific results on the future predicted distribution of VME indicator taxa under climate change projections (SSP2-4.5; SSP3-7.0) and re-evaluation of impact scores. Findings from this previous work showed substantial habitat loss (up to 54% loss in density and 64% in extent) but also identified regions identified as climate refugia, where high taxa densities were either maintained (internal refugia) or expanded into new areas (external refugia) (see Zelli et al., 2025).

(2) Session two consisted of the presentation of follow-up research on the impact of 30 years of bottom trawling on predicted taxa densities in ecologically important regions, under both present-day and future climate conditions and re-evaluation of impact scores. Findings from this second study showed that bottom trawling caused density losses of about 6% in primary habitats and 7-10% in climate refugia (internal and external) (see Zelli et al., under review). After the first two sessions, participants individually confirmed or changed their previous risk metrics (impact score, confidence and skewness) based on the new results by Zelli et al., (2025) and under review).

(3) Session three encompassed a group activity for the reassessment of management strategies. This last session required participants to engage in a group elicitation process focused on group deliberations and collective ranking of management strategies, challenges, and solutions, followed by reflections and outlining the next steps for the New Zealand EEZ (Clifford et al., 2016; Singh et al., 2017). To ensure a balanced representation across institutions, career stages, and gender, while also fostering diverse perspectives in the decision-making process, experts were divided into four mixed groups (Group "A", "B", "C" and "D"). To elicit prioritization preferences, participants also engaged in a "token allocation" exercise. Token allocation is particularly valuable in social science research as it quantifies group preferences and priorities, providing insights into the relative weight participants assign to different options. It also highlights areas of consensus or divergence among stakeholders, offering a structured yet flexible approach to decision-making in complex, multi-objective scenarios (Collewet & Koster, 2023).

This method not only captures individual and group preferences but also encourages meaningful discussion, negotiation, and justification of choices, thereby enriching the collective evaluation process (Collewet & Koster, 2023). This method has also been used in other disciplines including psychology (Comrey, 1950), marketing (Silk & Urban,

1978) and human health studies (Skedgel et al., 2015). In this exercise, each of the four groups was tasked with distributing a total of 10 tokens among up to the top five management strategies previously chosen by each group. The number of tokens assigned to each strategy represented its perceived priority or significance, reflecting the participants' collective judgment on how resources should be allocated. By requiring the total token allocation to equal 10, the exercise emphasized trade-offs and forced participants to critically evaluate the relative importance of each strategy within a constrained decision-making framework. At the end of the workshop, each group submitted a document with their updated rankings, and each group's moderator shared the top three strategies and associated challenges with all participants.

4.3 Results

This section compares participants' overall risk perception for 10 VME indicator taxa, initially assessed during individual interviews (baseline) and re-evaluated after a group workshop. During the workshop, participants were presented with additional information on the effects of climate change (hereafter “Scenario 1”) and its combined impact with bottom trawling (hereafter “Scenario 2”) on the same taxa. They also engaged in group discussions to prioritize management strategies for implementation.

4.3.1 Rankings of most impactful activities/stressors

When comparing participants' rankings of the top three most impactful activities and stressors on VME indicator taxa, an increase in agreement was observed following the group workshop compared to the individual interviews (Table 2). During the individual interviews, the majority of experts (7 out of 16, or 44%) ranked bottom trawling as the most impactful activity, while 6 out of 16 (38%) ranked it second. Sedimentation and seafloor mining were equally placed as the third most impactful stressors (4 out of 16, or 25% each). However, following the group workshop, participants exhibited more aligned perceptions. After the presentation of preliminary results on the impact of climate change (Scenario 1) on VME indicator taxa (Zelli et al., 2025), half of the experts (8 out of 16, or 50%) ranked climate change as the most significant stressor (Table 2). Bottom trawling was identified as the second most impactful activity by 9 out of 16 participants (56%), followed by seafloor mining, which was ranked third by 5 out of 16 participants (31%) (Table 2). Furthermore, after the presentation of additional results on the effects of climate change and bottom trawling combined (Scenario 2) on the current and future distribution

of density within primary habitats, experts maintained the same ranking order but demonstrated increased agreement across participants. The majority (9 out of 16, or 56%) continued to rank climate change as the most important stressor, followed by bottom trawling (10 out of 16, or 63%) and seafloor mining (5 out of 16, or 31%) (Table 2).

Table 2. List of activities/stressors along with the corresponding number of participants who ranked them as the 1st, 2nd, or 3rd most impactful stressors. The intensity of the colours reflects the ranking of the most impactful activity/stressors according to most of the experts.

Participants engagement	Baseline (Individual interviews)						Following Climate Change Insights (Workshop)						Following Climate Change and Bottom trawling insights (Workshop)					
	1st most impactful		2nd most impactful		3rd most impactful		1st most impactful		2nd most impactful		3rd most impactful		1st most impactful		2nd most impactful		3rd most impactful	
	#People voting	%	#People voting	%	#People voting	%	#People voting	%	#People voting	%	#People voting	%	#People voting	%	#People voting	%	#People voting	%
Climate change	5/16	31	2/16	13	1/16	6	8/16	50	2/16	13	1/16	6	9/16	56	1/16	6	1/16	6
Ocean acid.	1/16	6	4/16	25	2/16	13	2/16	13	4/16	25	2/16	13	2/16	13	3/16	19	3/16	19
CC-induced physical alteration	1/16	6	2/16	13	2/16	13	1/16	6	1/16	6	3/16	19	1/16	6	1/16	6	3/16	19
Fisheries	1/16	6	0/16	0	0/16	0	1/16	6	0/16	0	0/16	0	0/16	0	0/16	0	0/16	0
Bottom trawling	7/16	44	6/16	38	2/16	13	3/16	19	9/16	56	2/16	13	4/16	25	10/16	63	1/16	6
Sedimentation	0/16	0	0/16	0	4/16	25	0/16	0	0/16	0	3/16	19	0/16	0	0/16	0	3/16	19
Marine litter	0/16	0	0/16	0	0/16	0	0/16	0	0/16	0	0/16	0	0/16	0	0/16	0	0/16	0
Seafloor Mining	1/16	6	2/16	13	4/16	25	1/16	6	0/16	0	5/16	31	0/16	0	1/16	6	5/16	31
Nutrient input	0/16	0	0/16	0	1/16	6	0/16	0	0/16	0	0/16	0	0/16	0	0/16	0	0/16	0

4.3.2 Risk curves

This section summarizes the overall perceived impacts of various activities and stressors on VME indicator taxa (CWCs, sponges, and hydrozoa) across three contexts: “baseline”; “Scenario 1” and “Scenario 2”. Although statistical analyses did not indicate significant differences, the risk assessment evaluation following the workshop (where results on climate change and bottom trawling combined were presented) showed a consistently increasing trend in perceived risk, (i.e., higher impact scores and confidence levels), compared to the baseline conditions for seven out of the nine assessed activities and stressors (Figure 2; Table 3). This was particularly evident for the categories "Climate Change", "Ocean Acidification", "Climate Change-induced alteration of environmental variables", "Fishery", "Bottom trawling", and "Seafloor mining" with varied trends across taxa groups.

For example, for “*Climate change*”, the overall impact score increased from 0.62 (baseline) to 0.69 following the presentation of scientific insights on the impacts of climate change (Scenario 1) and to 0.67 under climate change and bottom trawling combined (Scenario 2). Among taxa groups, sponges exhibited the most significant change, with impact scores increasing from 0.58 to 0.76 under Scenario 1 (Figure 2; Table 3). For “*Ocean acidification*”, the overall impact increased from 0.624 (baseline) to 0.67 under both Scenario 1 and 2. Sponges experienced the largest change, with their impact score increasing from 0.56 to 0.63 under Scenario 1 (Figure 2; Table 3). For “*Climate change-induced physical alterations*”, the overall impact score rose from 0.62 (baseline) to 0.69 under both Scenario 1 and 2. CWCs demonstrated the greatest change, with impact scores increasing from 0.62 to 0.71 under Scenario 2 (Figure 2; Table 3). For “*Bottom trawling*”, the overall impact score increased slightly from 0.61 (baseline) to 0.62 under Scenario 2. CWCs exhibited the largest change, with their impact score rising from 0.66 to 0.67 under Scenario 2 (Figure 2; Table 3). For “*Seafloor mining*”, the overall impact score increased from 0.36 (baseline) to 0.40 under Scenario 2. CWCs showed a rise in impact score from 0.46 to 0.50 under Scenario 2 (Figure 2; Table 3).

Overall, “*Climate Change*”, “*Climate change-induced physical alteration*”, and “*Bottom trawling*” were identified as the most impactful stressors or activities (Figure 2; Table 3). These stressors resulted in higher impact scores, greater confidence levels, and increased skewness across all taxa groups on average. CWCs emerged as the taxa group most significantly affected across all activities/stressors. Sponges, however, were ranked as having the most pronounced sensitivity to the “*Climate change*” stressor, underscoring their heightened vulnerability under future climatic conditions. In contrast, sedimentation, marine litter, and nutrient input were consistently ranked as less impactful, with minimal changes in perceived risk observed before and after the workshop (Figure 2; Table 3).

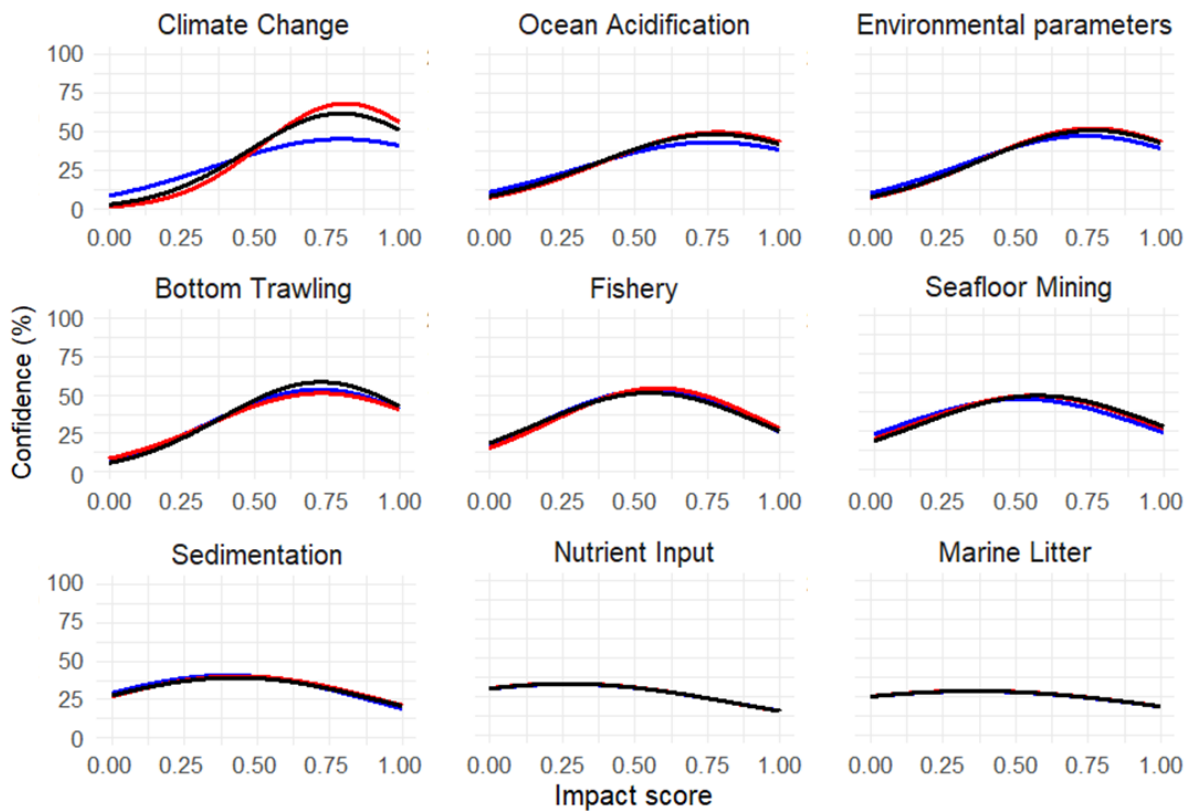


Figure 1. Probability distribution functions (PDFs, or risk curves) illustrating expert risk estimates for VME indicator taxa. Curves show assessments from: baseline individual interviews (blue), after receiving information on climate change (Scenario 1, red), and under combined climate change and bottom trawling impacts (Scenario 2, black). The plots display: (i) impact scores (0–1), indicating the severity of a given stressor; (ii) confidence (%), reflecting participants’ certainty in their assessments; and (iii) skewness (–1 to +1), representing uncertainty in rating impact scores. Skewness is visible in the asymmetry of the curves: right-skewed distributions extend toward lower impact scores, while left-skewed distributions extend toward higher impact scores.

Table 3. Summary of the participants' average impact scores (ranging from 0 to 1), including associated confidence levels and skewness as additional measures of uncertainty, for VME indicator taxa as a group. Scores were assessed against specified activities/stressors during individual interviews under baseline conditions and re-evaluated after the group workshop, which incorporated scientific insights on the impacts of climate change (Scenario 1) and its combination with bottom trawling (Scenario 2) on VME indicator taxa.

<i>VMEs ind. taxa</i>		<i>Cold-water corals</i>			<i>Sponges</i>			<i>Hydrozoa</i>			<i>Overall</i>		
<i>Activity/stressors</i>		<i>Impact score</i>	<i>Confid ence</i>	<i>Skewn ess</i>	<i>Impact score</i>	<i>Confid ence</i>	<i>Skewn ess</i>	<i>Impact score</i>	<i>Confid ence</i>	<i>Skewn ess</i>	<i>Impact score</i>	<i>Confid ence</i>	<i>Skewn ess</i>
<i>Climate Change</i>	Baseline	0.63	52	0.53	0.58	51	0.38	0.53	47	0.37	0.62	52	0.56
	Scenario 1	0.64	68	0.59	0.76	65	0.56	0.56	64	0.54	0.69	68	0.59
	Scenario 2	0.65	65	0.53	0.74	63	0.52	0.56	61	0.47	0.67	65	0.55
<i>Ocean Acidification</i>	Baseline	0.70	57	0.11	0.56	49	0.25	0.56	45	0.27	0.64	52	0.36
	Scenario 1	0.65	63	0.25	0.63	59	0.29	0.60	52	0.26	0.67	57	0.38
	Scenario 2	0.65	62	0.27	0.62	59	0.23	0.60	52	0.28	0.67	57	0.37
Baseline		0.62	59	0.38	0.52	57	0.07	0.57	49	0.19	0.62	56	0.37

<i>CC-induced env. alteration</i>	Scenario 1	0.69	63	0.28	0.65	57	0.14	0.56	53	0.29	0.69	61	0.25
	Scenario 2	0.71	62	0.28	0.66	57	0.14	0.58	53	0.29	0.69	61	0.25
<i>Fishery</i>	Baseline	0.52	61	-0.17	0.48	58	-0.08	0.45	61	-0.15	0.50	62	0.17
	Scenario 1	0.53	61	-0.17	0.52	58	0.08	0.47	63	0.02	0.53	63	0.17
	Scenario 2	0.52	56	-0.10	0.50	59	0.14	0.44	59	-0.08	0.52	61	0.10
<i>Bottom trawling</i>	Baseline	0.66	67	0.37	0.55	59	0.17	0.53	53	0.12	0.61	61	0.40
	Scenario 1	0.65	66	0.37	0.55	58	0.30	0.51	53	0.19	0.61	59	0.41
	Scenario 2	0.67	70	0.41	0.52	61	0.36	0.53	59	0.27	0.62	64	0.42
<i>Sedimentation</i>	Baseline	0.34	53	0.23	0.38	53	0.05	0.35	46	0.14	0.38	51	0.05
	Scenario 1	0.34	53	0.23	0.41	52	0.05	0.35	46	0.24	0.38	50	0.15
	Scenario 2	0.33	51	0.19	0.42	52	0.02	0.35	44	0.19	0.38	49	0.11
<i>Marine litter</i>	Baseline	0.3	30	0.0	0.3	34	0.1	0.3	28	0.1	0.3	31	0.1
	Scenario 1	0.3	30	0.0	0.3	34	0.1	0.3	28	0.1	0.3	31	0.1
	Scenario 2	0.3	30	0.0	0.3	34	0.1	0.3	28	0.1	0.3	31	0.1
<i>Seafloor mining</i>	Baseline	0.46	53	0.51	0.35	53	0.26	0.30	53	0.39	0.36	54	0.45
	Scenario 1	0.47	54	0.51	0.36	54	0.45	0.31	47	0.48	0.38	55	0.55
	Scenario 2	0.50	54	0.52	0.36	54	0.45	0.30	47	0.48	0.40	54	0.55
<i>Nutrient input</i>	Baseline	0.33	40	0.00	0.27	33	0.07	0.23	50	-0.17	0.28	40	-0.03
	Scenario 1	0.33	40	0.00	0.27	33	0.07	0.23	50	-0.17	0.28	40	-0.03
	Scenario 2	0.33	40	0.00	0.27	33	0.07	0.23	50	-0.17	0.28	40	-0.03

4.3.3 Management strategies

In this section, we present the findings derived from the expert interviews and workshops, which aimed to identify effective marine management strategies, their associated challenges, and potential solutions. These results have been obtained by comparing expert perspectives before and after additional scientific insights on the impact of climate change and bottom trawling provided during the workshop. Although no substantial shifts were observed regarding the prioritization of management strategies, 9 out of 16 participants provided either new perspectives or more insights into the challenges associated with their implementation and the potential solutions to these challenges following the workshop. The main strategies, challenges, and solutions identified by the experts following the presentation of scientific insights during the group workshop are summarized in Table 4 in order of priority. Overall, experts ranked Marine Spatial Planning as the most relevant management strategy, with 18 citations out of 66, followed by Fishing Activity Management (12 citations), which includes Fishing Gear Modification (4 citations). The third most important strategy identified was Legislation/Policy (8 citations). Rounding out the fourth and fifth ranks were strategies such as Ban Trawling, Climate Change Mitigation, Research, and Ecosystem-Based Management.

Table 4. Summary of management strategies, challenges, and solutions individually identified by experts for marine conservation and fisheries management following the workshop.

Categories	Expert Description	
Marine Spatial Planning (18/66 citations)	Management strategies	Spatial closures; Marine reserves; Dynamic area-based protection (marine spatial planning, other effective area-based conservation measures (OEFMs) (e.g., Area-based gear restrictions), Indigenous-led management); Targeted closures for key habitats; Fully closed areas; Species action plans (e.g., corals); Precautionary approach; Marine Protected Areas (MPAs), including seamounts and hotspots.
	Challenges	Potentially large impacts on fisheries utilization; Political resistance to extensive closures; Difficulty in balancing conservation with sustainable use; Stakeholder reluctance to adopt new spatial management measures.
	Solutions	Balanced approach to closures to protect benthic ecosystems while allowing sustainable use; Investment in stakeholder engagement and supporting science; Cross-party support for effective legislation; Use of scientific models to define priority areas for closure.
Fishing Activity Management (12/66 citations)	Management strategies	Fisheries management (e.g., temporary closures to fishery activities; gear specifications); Move-on rules; Effort control; Fishery output controls (total allowable catch, catch limits); Breaks between activities for ecosystem recovery.
	Challenges	Limits on utilization of fisheries resources; Resistance from the fishing industry due to economic losses; Uncertainty in the effectiveness of management measures; Challenges with enforcement and compliance.
	Solutions	Design fisheries management measures that allow sustainable use while protecting ecosystems; Engage with stakeholders to adapt strategies to industry needs.
Fishing Gear Modifications (4/66 citations)	Management strategies	Gear restrictions; Trawl modifications to reduce bottom contact; Mitigation of sediment resuspension by trawling; Technology-driven fishing gear improvements.
	Challenges	Industry resistance to adopting new gear; High upfront costs for modification; Uncertainty about the effectiveness of new gear modifications; Need for independent testing.
	Solutions	Engage with the fishing industry to co-design modifications; Provide government funding for the research and independent testing of new gear; Share success stories of improved gear to encourage industry adoption.
Adaptive management & policy (8/66 citations)	Management strategies	Encounter protocols; Science-based decision making; Legislation (e.g., regulations for marine protection); Consenting regimes for marine conservation; Political commitment to reduce emissions and mitigate marine climate change effects.
	Challenges	Fragmented regulatory frameworks; Lack of political will to enforce and implement policies; Resistance from industries focused on short-term economic benefits; Challenges with ensuring compliance.
	Solutions	Streamline regulatory frameworks to facilitate marine conservation; Increase political will through public pressure and industry engagement; Develop strong enforcement mechanisms and provide education on the long-term benefits of conservation.
Management strategies	Full ban on bottom trawling; Restrict seabed mining; Freezing footprints (fishing and mineral extraction);	

Ban Trawling Activities (7/66 citations)		Prohibition of mining activities in sensitive marine areas (e.g., near seamounts).
	Challenges	Resistance from the fishing and mining industries; Economic displacement for workers in affected industries; Legal and political challenges; Difficulty in establishing widespread industry support.
	Solutions	Implement industry buy-in strategies to encourage voluntary bans; Provide compensation for impacted industries and workers; Strengthen legislation and regulatory frameworks to enforce bans.
Climate Change Mitigation (7/66 citations)	Management strategies	De-carbonisation; Carbon emissions reduction (including blue carbon); Climate change adaptation/mitigation; Ocean fertilization; Biogeochemical engineering to mitigate acidification; Mitigation of climate impacts.
	Challenges	High financial and technological costs; Limited political will for rapid climate action; Difficulty in achieving global emission reduction targets; Uncertainty surrounding the effectiveness of some mitigation strategies.
	Solutions	Increase investment in renewable energy technologies; Enforce stricter emission regulations for industries; Foster international agreements on climate change; Invest in scientific research to validate and improve climate mitigation techniques.
Research (7/66 citations)	Management strategies	Impact assessments; Research reform (e.g., SDM improvements, stressor footprints); Ground-truth information on VMEs; Forecasting future shifts in fishing activity.
	Challenges	High costs of conducting extensive research; Insufficient baseline data for accurate modelling; Limited access to scientific data; Fragmented research efforts across organizations.
	Solutions	Increase funding for marine research, particularly in underexplored areas; Facilitate collaboration between research organizations to ensure efficient use of resources; Develop comprehensive databases and models to support informed decision-making.
Ecosystem-Based Management (3/66 citations)	Management strategies	Ecosystem-based management (EBM); Ecosystem-based fisheries management (EBFM); Holistic ecosystem management, considering multiple environmental and anthropogenic impacts.
	Challenges	Complexity in integrating multiple environmental factors; Resource-intensive; Difficulty in balancing ecological needs with economic demands; Lack of comprehensive data on ecosystem interactions.
	Solutions	Engage stakeholders across sectors to address multiple impacts; Develop and apply ecosystem models to improve understanding of ecological dynamics.

4.3.4 Group elicitation: deliberation on management strategies, challenges and solutions

Following the group discussions, spatial management emerged as the most consistently prioritized strategy, ranking first with the highest token allocation (16/40). This category encompassed approaches such as marine protected areas, spatial closures, and area-based protections, reflecting strong agreement among participants (Table 5). Other strategies ranked second and third included climate change mitigation and emissions reduction (6.5/40 tokens), reducing the impact of bottom trawling (5/40 tokens), scientific research (3/40 tokens), Ecosystem-Based Management (EBM) (3/40 tokens) and adaptive management, including measures such as shifting to midwater trawling and gears modification (2/40 tokens). Lower-ranked strategies, including improving aquaculture technologies, reducing pollution inputs, science-based decision-making, emphasizing Ecosystem-Based Fisheries Management (EBFM), adopting a precautionary approach, and prioritizing refuge areas, were allocated approximately 1 token each, placing them in the fourth and fifth positions in the rankings.

Table 5. Ranking and token allocation (indicating the level of importance assigned) for the management strategies identified by participants during the elicitation process, shown for each of the four groups (A, B, C, and D).

Ranking	Group A		Group B		Group C		Group D	
	Management Strategies	Tokens	Management Strategies	Tokens	Management Strategies	Tokens	Management Strategies	Tokens
1	Spatial management	4	Area-based protection	3	Spatial management	5	Spatial closures	4
2	Scientific Research	3	Climate change mitigation/management	2.5	EBM	3	Ban all extractive industries	1
3	Reduce CO ₂ emissions	1	Reduce bottom trawling impacts	2	Adaptive management	2	Reduce CO ₂ emissions	3
4	Aquaculture and improved harvest strategies/technologies	1	Science-based decision-making	1.5	—	—	EBFM	1
5	Reduce pollution inputs	1	Precautionary approach	1	—	—	Seed refuge areas	1

During the elicitation process, participants highlighted several key challenges and potential solutions to the mentioned management strategies. For example, for spatial management, they emphasized difficulties such as bureaucratic delays, budget constraints, and resistance from stakeholders. They suggested streamlining the process of establishing MPAs, collaborating with local communities, fostering political

commitment, and ensuring funding for long-term monitoring. When addressing climate change management, participants recognized global reliance on fossil fuels, limited local impact, and political reluctance as major obstacles. To overcome these, they proposed meeting emissions targets, banning fossil fuel exploration, promoting sustainable industries to gain societal buy-in, and applying EBM for a comprehensive approach. Reducing the impacts of bottom trawling was seen as challenging due to technological and economic barriers and opposition from the fishing industry. Participants recommended shifting to midwater trawling, adopting innovative gear modifications or fishing approaches, and investing in stakeholder forums. Scientific research was acknowledged as being hindered by high costs, and limited data access. Participants suggested implementing levies on industries, fostering collaboration among government agencies and international entities, and establishing open-access data repositories to address these gaps. For EBM and adaptive management, participants pointed to the prevalence of single-sector management, lack of mature legislative/policy support, stakeholder resistance, and lack of agreed policies and objectives as key issues. Proposed solutions included enhancing stakeholder engagement, creating legal frameworks for ocean governance, and funding adaptive management initiatives through industry contributions. Finally, lower-priority strategies, such as improving aquaculture technologies, reducing pollution, and adopting precautionary measures, were constrained by infrastructural needs, political resistance, and a lack of clear objectives. Participants recommended targeted research, end-use legislation, and public education to advance these approaches.

4.4 Discussion

This study highlights how the combination of empirical and expert data provides a better social-ecological framework for informing risk assessment and narrowing down decisions to improve current protection levels for VME indicator taxa in New Zealand EEZ. In particular, spatial explicit predictions of multiple anthropogenic impacts (i.e., climate change and bottom trawling) on 10 VME indicator taxa distributions of density were used in combination with expert elicitation to assess expert-driven perceptions of risk and identify effective management strategies relevant to addressing these risks. Data were collected at two stages: during individual interviews and a subsequent workshop where participants were presented with new scientific insights and engaged in an elicitation process. This approach allowed to evaluate and compare the changes in expert

perception of risk and management action priorities before and after participants were exposed to updated scientific results and involved in group discussions.

Our findings suggest that providing additional scientific insights on the impacts of climate change and bottom trawling influenced participants' risk perception and confidence, leading to these stressors being perceived as more impactful. Furthermore, while the workshop did not substantially alter the prioritization of management strategies among participants, it expanded the range of identified challenges and solutions, underscoring the complexities surrounding marine conservation. This section explores how risk perceptions and management priorities evolved after participants were exposed to novel scientific findings and engaged in the group elicitation process.

4.4.1 Risk assessment

Overall, our findings reveal that while experts' perspectives on the prioritization of stressors did not change substantially, impact scores and confidence generally increased after the workshop when compared to individual interviews (Table 3). This suggests that experts perceive higher risks (and they were more confident about it) following the presentation of insights on the effects of climate change and its combination with bottom trawling. Consistent with the findings of Zelli et al., (2025), which were shared during the workshop, cold-water corals and sponges emerged as the taxa most affected by multiple stressors, particularly climate change and associated environmental alterations such as reductions in aragonite/calcite concentrations, pH, and oxygen levels (Table 3). Moreover, experts reported elevated perceived risks related to fisheries and bottom trawling, aligning with findings from Zelli et al. (under review). These studies identified bottom trawling as a major driver of density reductions in VME indicator taxa, especially within climate refugia regions. However, the increase in perceived risk for bottom trawling was less pronounced compared to climate change and climate change-associated impacts. Nevertheless, confidence in this perception increased substantially. This may indicate that experts were already familiar with the negative impacts of bottom trawling on benthic ecosystems prior to the workshop, but less aware of the effects of climate change on VME indicator taxa. Indeed, while numerous studies have assessed the impact of bottom trawling on VME indicator taxa, including cold-water corals (Clark et al., 2016; Clark & Rowden, 2009; Fosså et al., 2002) fewer have explored the effects of climate change scenarios in New Zealand (Anderson et al., 2022; Zelli et al., 2025).

4.4.2 Management priorities

The benefits of incorporating expert knowledge into decision-making processes are well-established and widely recognized, as it ensures that critical, specialized information is accurately captured and integrated into the decision framework (Burgman et al., 2011; Martin et al., 2012; Morgan, 2014). In our study, the elicitation process played a key role in refining the experts' perspectives and enhancing the clarity of their recommendations. Although the prioritization of management strategies remained largely consistent before and after the workshop, the process of elicitation following the presentation of new scientific insights contributed to fostering a more focused and cohesive vision among participants. By allowing experts to reflect on and reassess their initial judgments in light of updated data, the elicitation process helped to align their views more effectively. This approach enabled participants to consistently identify the most relevant activities/stressors affecting VMEs indicator taxa in line with recent scientific findings as well as strengthening the overall consensus on the most appropriate management strategies. This iterative exchange not only encouraged a deeper understanding of the issue at hand but also ensured that the decision-making process was both informed and robust, with a clearer direction for future action.

The workshop discussions, informed by scientific insights from previous studies (Zelli et al., 2025; under review), led to a more consistent focus on MSP in line with international studies that consider MSP a key process for managing the marine environment under scenarios of increasing demand of space for different uses (Flannery, 2023; Rafael et al., 2024). Participants highlighted MSP as a key tool for mitigating climate change impacts, reducing bottom-trawling pressures, and enhancing ecosystem resilience. They also stressed the need for complementary measures to address climate change (e.g., decarbonization, emissions reductions, and climate adaptation) and mitigate bottom-trawling impacts (e.g., gear modifications and legislative reforms). Experts also underscored the need for research-driven decision-making, advocating for improved data collection, risk modeling, connectivity analysis, and multi-impact assessments to support adaptive management frameworks. The token allocation exercise provided further insights into how experts prioritized resources and perceived the feasibility of strategies. MSP received the highest allocation, underscoring its critical role in addressing multiple stressors, particularly in protecting climate refugia and minimizing bottom trawling impacts. Strategies focused on modifying fishing methods and gear received moderate

attention, reflecting their importance but also the perceived challenges of their implementation.

Overall, MSP emerged as the top-ranked strategy, with strong consensus on its pivotal role in creating adaptive, strategic and participatory actions to safeguard VMEs by limiting fishing activity in areas (i.e., climate refugia) that are predicted to provide resilience to climate change. Following the workshop, participants highlighted the urgent need to protect refugia areas from additional stressors, particularly bottom trawling. This prioritization underscores the importance of managing fishing activities through spatial and temporal closures or gear-specific restrictions. Experts emphasized that tackling multiple impacts in complex social-ecological systems requires innovative approaches. In this context, adaptive management and ecosystem-based management (EBM), including ecosystem-based fishery management (EBFM), are essential for effective MSP. Particularly, the term ‘adaptive management’ refers to the continuous need to adapt to a changing world (Hilborn & Sibert, 1988); it is regarded as a flexible decision-making process that refines strategies based on new scientific data and stakeholder input (Folke et al., 2005; National Research Council, 2004; Rist et al., 2013). It is particularly relevant for addressing the uncertainties of climate change and fisheries management, guiding adaptation and mitigation efforts (Bahri et al., 2021; Hilborn & Sibert, 1988; Marmorek et al., 2019; McCook et al., 2010; Tompkins & Adger, 2004). By monitoring outcomes and adjusting actions accordingly, adaptive management enhances ecosystem resilience, sustains biodiversity (Walters & Holling, 1990) and fosters stakeholder collaboration, ensuring management measures are both scientifically informed and socially accepted (Armitage et al., 2009). Moreover, adaptive management can be used to achieve sustainable development by balancing conservation with socio-economic needs, e.g., where fisheries grounds intersect with biodiversity protection (Lee, 1993).

In addition, EBM is a holistic approach to managing marine and coastal ecosystems that considers the entire ecosystem, including ecological, social, and economic components, rather than focusing on single species or sectors in isolation (Arkema et al., 2006; Levin & Lubchenco, 2008). EBM aims to maintain ecosystem health, resilience, and services while balancing conservation with sustainable resource use. When ‘resource use’ refers to fishery EBFM is increasingly being adopted as a new direction for fishery management as it aims to sustain healthy marine ecosystems and the fisheries they support by preventing ecosystem degradation, minimizing risks of irreversible changes, ensuring

long-term socio-economic benefits, and enhance understanding of ecosystem processes to inform management decisions (Brodziak & Link, 2002; Fogarty, 2014; Pikitch et al., 2004). By incorporating scientific knowledge and stakeholder input, EBM and EBFM, alongside adaptive management, strengthen MSP to manage marine environments under growing environmental and socio-economic pressures effectively (Arkema et al., 2006; McLeod et al., 2005).

4.4.3 Challenges to effective implementation of management strategies and suggested solutions

Experts' perspectives largely remained consistent after the group discussion, as anticipated. However, new scientific insights shared during the workshop and elicitation process led participants to identify a broader range of challenges and potential solutions more consistently. The discussion highlighted the complexity of addressing global climate change issues and the challenges of designing and enforcing spatial protections against additional impacts such as bottom trawling. Key barriers identified include a lack of political commitment, industry resistance to restrictions (e.g., spatial fishery closures and gear modifications) due to economic concerns, and limited understanding of ecosystem processes, risks, and impacts. Incorporating comprehensive conservation principles such as EBM, EBFM, and adaptive management into existing policies and marine spatial planning, while fostering scientific research, were seen as possible solutions to effectively address these challenges. The discussion mainly revolved around the following topics:

(i) *Climate change adaptation and mitigation*

Experts highlighted that addressing climate change requires international cooperation, long-term commitments, and policy alignment, which are difficult to achieve due to competing national interests and economic dependence on carbon-intensive industries (Gattuso et al., 2018). They also stressed the relevance of respecting international agreements including the Paris Agreement to invest in renewable energy technologies and enforce stricter carbon emission regulations for high-emission industries (UNFCCC, 2015; Yuan et al., 2022). Nevertheless, given the wicked nature of global climate change, experts also stressed the urgency to adopt climate adaptation strategies in marine management, such as spatial protection of future relevant habitats such as climate refugia, which can buffer ecosystems' resilience against climate-related stressors (Duarte et al., 2020; Graham et al., 2019; Keppel et al., 2012, 2024).

(ii) *Multiple impacts of climate change and fishery*

The assessment of climate-driven shifts in the distribution of relevant habitats and the identification of refugia areas as found in previous studies (Zelli et al., 2025) underscore their relevance for conservation and the urgency of including such areas within protection measures, especially if they overlap with fishing grounds (Zelli et al., under review). The implementation of such protection measures however is controversial as it implies limiting fishing activities raising conflicts with the industry. Experts identified the fishery industry's resistance to extensive or permanent closures to trawling activities and the adoption of new fishing gears due to perceived economic losses as a main barrier to the establishment of marine protected areas. This tension underscores the complex interplay between conservation and resource use (Hutton & Leader-Williams, 2003; Young et al., 2006). The difficulty of balancing commercial interests with conservation goals often leads to conflicts between local communities, industry representatives, and governmental agencies (Davis, 2008; Kitts et al., 2007). Addressing these challenges requires bringing diverse perspectives into decision-making and implementing comprehensive approaches (e.g., adaptive management, EBS, EBFM) that combine science with stakeholder engagement, and policy (Arkema et al., 2006; Ehler et al., 2019; Ellis et al., 2025; Marmorek et al., 2019; Pikitch et al., 2004).

(iii) *Fishery management*

Experts emphasized that effective fisheries management strategies, such as temporary closures, move-on rules, and gear specifications, depend on the active involvement of stakeholders—including fishery industry representatives, policymakers, and researchers—in decision-making processes to ensure that regulations are both realistic and enforceable, in line with previous studies (Degnbol & Mccay, 2007; Hilborn & Sibert, 1988; Pikitch et al., 2004). Aligning management measures with industry needs can reduce resistance and enhance compliance, especially when economic incentives or co-management schemes are introduced (Gutiérrez et al., 2011). Resistance to fishing gear modifications is often driven by high upfront costs and uncertainty about their effectiveness. A potential solution is to engage the fishing industry in co-designing and testing new gear innovations, ensuring that they improve efficiency while reducing environmental impact (Eigaard et al., 2016; Isaacs, 2016). Government-funded research and independent testing programs can accelerate adoption by demonstrating the economic and ecological benefits of these technologies (Charter et al., 2020). Sharing successful case studies, such as the adoption of selective nets to reduce bycatch, can also help

overcome scepticism and promote widespread uptake (Broadhurst et al., 2007). In terms of bottom trawling bans, experts suggested voluntary phase-out programs supported by incentives for transitioning to less destructive fishing practices as well as compensation schemes for affected industries and workers could ease economic hard and improve policy acceptance (Nyavor et al., 2023; Wu et al., 2023).

(iv) Relevance of scientific research

The limited understanding of the cumulative impacts of climate change and fisheries on VMEs and VME indicator taxa further complicates effective management. Experts noted that limited scientific knowledge and uncertainty are significant obstacles to science-based decision-making, making it difficult to assess ecosystem conditions and human impacts (Mora et al., 2009; Ruckelshaus et al., 2008). Increasing research collaboration and funding for projects focused on ecosystem recovery and connectivity—particularly in underexplored areas like mesophotic and deep-sea ecosystems—was considered crucial for filling critical knowledge gaps and guiding management decisions with greater scientific accuracy (Halpern, Diamond, et al., 2012; Levin et al., 2019). Experts suggested that where scientific information is scarce or highly uncertain, precautionary principles should be applied to ensure responsible management in the face of uncertainty.

(v) Improving marine legislation and policy

Experts highlight the lack of communication across governmental institutions slows down processes to establish spatial protections which need to be streamlined. Furthermore, governance frameworks are often sector-specific and lack mechanisms for holistic management, highlighting the need for structural reforms and improved institutional cooperation (Levin & Lubchenco, 2008; Pikitch et al., 2004). Integrated governance frameworks have been shown to improve regulatory effectiveness and facilitate policy implementation (Fletcher, 2005; Fletcher et al., 2010; Kearney et al., 2007). Enhanced cross-sectoral collaboration, improved communication between regulators and the public, and engagement with Regional Fisheries Management Organizations (RFMOs) and NGOs were proposed as strategies to overcome fragmented governance and accelerate decision-making.

4.5 Conclusion

This study aimed to integrate diverse perspectives from the scientific, management, and policy sectors to assess the risks posed by multiple stressors on VME indicator taxa and to inform future management strategies, identify implementation challenges, and explore potential solutions. The findings underscore the critical need to bridge the gap between science and management while demonstrating the value of participatory methods—such as interviews and expert elicitation—in generating actionable insights that can enhance decision-making around spatial planning in New Zealand and address scientific research gaps in marine conservation. Exposure to novel scientific evidence on climate change and bottom trawling during the workshop heightened participants' risk perception and confidence in their assessments. Notably, climate change was perceived as the most significant risk when risk perception was re-evaluated after the workshop. While bottom trawling was already recognized as a major threat, the discussions reinforced and further clarified its severity. This highlights the substantial risks these stressors and activities pose to VME indicator taxa and the urgent need to strengthen protections for ecologically significant habitats, particularly climate refugia.

Although management strategy priorities did not shift significantly between individual and group assessments, there was a notable increase in consensus on the importance of MSP as a key approach to preventing future climate refugia from being impacted by bottom trawling. Additionally, alongside targeted fishery management actions, climate change adaptation and mitigation emerged as essential components of comprehensive and sustainable conservation strategies. These priorities align with the principles of adaptive management and EBM—indicated by experts as relevant approaches to addressing the complexities around marine ecosystem protection. Despite existing challenges, this study underscores the potential of innovative, collaborative, and science-driven approaches to strengthen VMEs protection and resilience. As current spatial planning frameworks may no longer provide sufficient safeguard (Anderson et al., 2022; Stephenson et al., 2023a; Zelli et al., 2025), our findings support the development of more adaptive strategies to mitigate the impacts of multiple stressors now and in the future. While this study was centred on a regional context in New Zealand, the approach we applied is broadly transferable to other social-ecological contexts.

Chapter 5

General Discussion

The overarching goal of this thesis was to integrate ecological modelling, spatial analysis, and expert engagement to enhance understanding of how climate change and bottom trawling impact habitat-forming VME indicator taxa within New Zealand's Exclusive Economic Zone and Territorial Sea and to assess the implications for conservation. This section synthesizes key findings from Chapters 2, 3, and 4, which are discussed in relation to the effectiveness of current spatial management measures in safeguarding VMEs under multiple climate change and bottom trawling pressures. The chapters build upon one another to advance scientific understanding of cumulative stressors on VMEs. Chapter 2 quantified density and spatial extent loss due to climate change while identifying climate refugia, regions projected to remain suitable under future conditions. However, these refugia require sufficient present-day densities to maintain ecosystem functionality and support future population persistence. To assess whether these regions retain the necessary density levels, Chapter 3 examined the impact of historical bottom trawling on areas predicted to serve as climate refugia. The analysis revealed significant density declines within these zones, potentially compromising their future viability as conservation priorities. Findings from Chapters 2 and 3 underscore the urgent need for spatial management actions to protect these areas. Effective conservation requires bridging the science-policy gap and improving the communication of ecological findings to decision-makers. To address this, Chapter 4 extended the research beyond ecological and impact assessments by examining the social dimensions of spatial conservation measures. Through expert engagement with conservation and fisheries stakeholders, this chapter explored key risks to VMEs and refined decision-making processes, ensuring that scientific insights inform management strategies for more effective protection.

5.1. Climate change drives loss and shifts in VME indicator taxa density

Chapter 2 employed SDMs to predict the distribution of density of several VME indicator taxa under present and future climate scenarios predicted by the end of the 21st century. *The results projected a significant decline in both the density and spatial extent of all assessed taxa when comparing present distributions with future environmental*

conditions. However, the models also identified areas of potential resilience and habitat expansion—termed climate refugia—where certain taxa may persist despite changing environmental pressures.

Mapping the current and future distribution of VME indicator taxa is essential for effective conservation, yet deep-sea data remain scarce (Elith & Leathwick, 2009; Mazor et al., 2021; Weber et al., 2017). Chapter 2 addresses this knowledge gap using density-based SDMs under two climate scenarios (SSP2-4.5 and SSP3-7.0). Unlike occurrence-based models, this approach focuses on density as a measure of abundance, improving the identification of ecologically relevant areas and informing conservation strategies. This approach yields valuable insights that can inform spatial management strategies for the conservation of potential VMEs (Melo-Merino et al., 2020; Spaak et al., 2017).

Findings revealed that under future climate scenarios, the density and spatial extent of primary habitats for the investigated taxa are expected to decline by 54% and 62%, respectively, if compared to current-day predictions. Reductions in critical environmental variables such as carbonate ion saturation and dissolved oxygen are projected to have profound impacts, as also found by previous studies in the region (Anderson et al., 2022). Cold-water corals and sponges were particularly vulnerable, with density reductions of 21–60%, driven by declining carbonate ion saturation and dissolved oxygen. Despite these losses, the study identified climate refugia—areas where taxa may persist—classified as internal refugia (158,000 km², where high-density habitats are expected to persist) and external refugia (121,000 km², potential new high-density habitats).

However, the viability of both internal and external refugia also depends on maintaining sufficient population densities and abundance levels today to support the development of highly dense areas in the future (Carr et al., 2017; Morelli et al., 2017). Without proper management, VME indicator taxa remain vulnerable to local stressors, such as bottom trawling, a major industrial activity in New Zealand which can reduce taxa densities, degrade habitats, and compromise refugia viability (Clark et al., 2016; McConnaughey et al., 2020; Sciberras et al., 2018). Given the potential impacts on taxa distributions resulting from decades of bottom trawling disturbance, incorporating impact-adjusted species distribution layers into spatial planning processes is essential (Moilanen et al., 2011b; Stephenson et al., 2023a). This approach minimizes the risk of designing ineffective conservation measures that prioritize areas based on historical abundances rather than their current ecological value, which may have been diminished due to

anthropogenic pressures such as bottom trawling (Rowden et al., 2019). Furthermore, a comprehensive assessment of the current status of VME taxa is critical for evaluating potential threats to predicted climate refugia. This knowledge is necessary to inform targeted protection measures that mitigate these impacts and enhance the long-term viability of these ecologically significant areas.

5.2. Bottom trawling impacts on predicted climate refugia

Chapter 3 builds on the findings from Chapter 2, addressing the intersection of predicted current VME indicator taxa density distributions and historical bottom fishing efforts within New Zealand waters over the past 30 years. *Findings revealed that bottom trawling has likely impacted all assessed taxa across the study region, with particularly severe reductions within climate refugia region.*

Climate refugia areas were heavily impacted by bottom trawling, experiencing the largest reductions in taxon density and habitat extent, averaging up to 10% loss under both climate change scenarios combined. Cold-water corals and sponges emerged as the most affected taxa, owing to their biological traits (e.g., sessile, erect, fragile taxa) and the extent of the overlap between their distribution and trawling activities. These findings corroborated previous results from Chapter 2 that found these taxa as the most impacted by climate change. These taxa, characterized by slow growth rates and limited recovery potential, are especially susceptible to physical disturbances from bottom-contact fishing gears. Conversely, taxa such as gorgonians and hydrozoans appeared less impacted by bottom trawling, probably due to their lower overlap with fishing efforts and faster growing and recovery rates.

The reduced density could impair the ability of taxa to establish ecologically functional habitats capable of supporting long-term ecosystem services if the impact persists. Furthermore, habitat fragmentation, as a consequence of habitat extent reduction, threatens the connectivity between internal and external refugia, affecting habitat resilience capacity and exacerbating the risk of biodiversity loss, especially for taxa with restricted larval dispersal capabilities (Clark et al., 2016; Munday et al., 2009). Effective management strategies should prioritize the protection of internal refugia, where high-density populations can serve as reservoirs of biodiversity and ecosystem functionality. At the same time, external refugia require protection to ensure their future viability should connectivity with internal refugia occur. These findings corroborate previous research in

New Zealand and highlight critical gaps in current marine spatial protection measures in providing enough coverage for ecologically important taxa (e.g., cold-water corals) (Anderson et al., 2022; Stephenson et al., 2023a; Zelli et al., 2025). This suggests that spatial measures may be insufficient to safeguard VME indicator taxa from bottom trawling activities either in the present or the future especially for climate refugia. Quantifying climate refugia extent into marine spatial protection measures is therefore essential to mitigate extinction risks and ensure the long-term persistence of these ecosystems and their associated services.

5.3. Protection gaps in current spatial measures in New Zealand

Results from the first two chapters suggest that the pressure from climate change and bottom trawling places VME indicator taxa at increased risk of local extinction and loss of ecological functions. This underscores the risk for these habitats to face further density and extent declines if bottom-contacting activities are not halted or escalate in the future, undermining their potential to serve as climate refugia.

Understanding the proportion of protected versus unprotected habitats is essential to providing spatial managers with critical insights for prioritizing conservation efforts. Moreover, identifying unprotected areas sheds light on ecologically relevant regions (e.g., climate refugia) at risk of anthropogenic pressures such as bottom trawling and seabed mining. However, no prior studies have quantified the extent of VME indicator taxa habitats concerning current spatial protection measures. This section addresses this gap by presenting novel results on the spatial coverage of both current primary habitats and predicted climate refugia within or outside New Zealand's existing protection measures. Spatial predictions from Chapter 2, further refined by discounting areas impacted by bottom trawling as quantified in Chapter 3, were overlaid with the distribution of BPAs, SCAs, and LMRs combined.

Results indicate that significant portions of these critical habitats remain unprotected, leaving them vulnerable to further anthropogenic impacts, e.g., bottom trawling (Figure 1). Overall, the combined proportion of habitats excluded from protection across all SPMs (BPAs, SCAs, and LMRs combined) was 80% for current primary habitats, and 83% and 84% under SSP-4.5 and SSP4-7.0 scenarios, underscoring the critical vulnerability of these ecosystems to additional local pressures as well as the increasing risks under climate change (Table 1).

Table 1. Percentage of bottom trawling impact-adjusted current primary habitats (98th density percentile) and climate refugia that currently sit outside the existing spatial protection measures (SPMs) in New Zealand, including benthic protection areas (BPAs), seamounts closure areas (SCAs), and large marine reserves (LMRs). See supplementary materials (Table S1 and S2) for values across each SPM.

VME indicator taxa outside SPMs	Primary habitats		Climate refugia			
	Present-day		SSP2-4.5		SSP3-7.0	
	<i>km</i> ²	%	<i>km</i> ²	%	<i>km</i> ²	%
<i>Goncorella dumosa</i>	2.72E+04	83.4	1.63E+04	80.5	1.79E+04	79.8
Scleractinia	2.35E+04	71.0	6.27E+04	72.0	6.94E+04	73.9
Antipatharia	2.38E+04	70.8	1.32E+03	77.0	4.23E+03	79.5
<i>Radicipes</i> spp.	2.86E+04	91.2	1.57E+04	96.2	1.85E+04	98.1
Pennatuloidea	3.14E+04	98.0	3.37E+04	99.2	2.62E+04	99.4
Primnoidea	2.59E+04	77.6	4.58E+03	85.3	3.75E+03	89.5
Gorgoniidae	1.64E+04	49.3	2.34E+04	60.0	2.43E+04	59.7
Stylasteridae	2.44E+04	73.7	2.50E+04	70.2	2.54E+04	66.1
Demospongiae	2.81E+04	85.9	2.37E+02	91.2	5.00E+01	98.0
Hectanillida	3.15E+04	93.9	1.55E+02	100	0.00E+00	100
<i>mean</i>	<i>2.61E+04</i>	<i>80</i>	<i>1.83E+04</i>	<i>83</i>	<i>1.90E+04</i>	<i>84</i>

For climate refugia (internal and external refugia combined), the lack of protection was even more pronounced: approximately 82% of CWCs, 68% of Hydrozoa, and 97% of sponges were left unprotected. These findings shed light on the limitation of current spatial protection measures in New Zealand to provide protection for taxa such as cold-water corals, hydrozoans, and sponges as only a small fraction of current primary habitats and climate refugia sit within spatial protection measures. These results are also corroborated by similar studies in the New Zealand region but used less informative presence/absence estimates as opposed to the density estimates generated here (Anderson et al., 2022; Stephenson et al., 2023a).

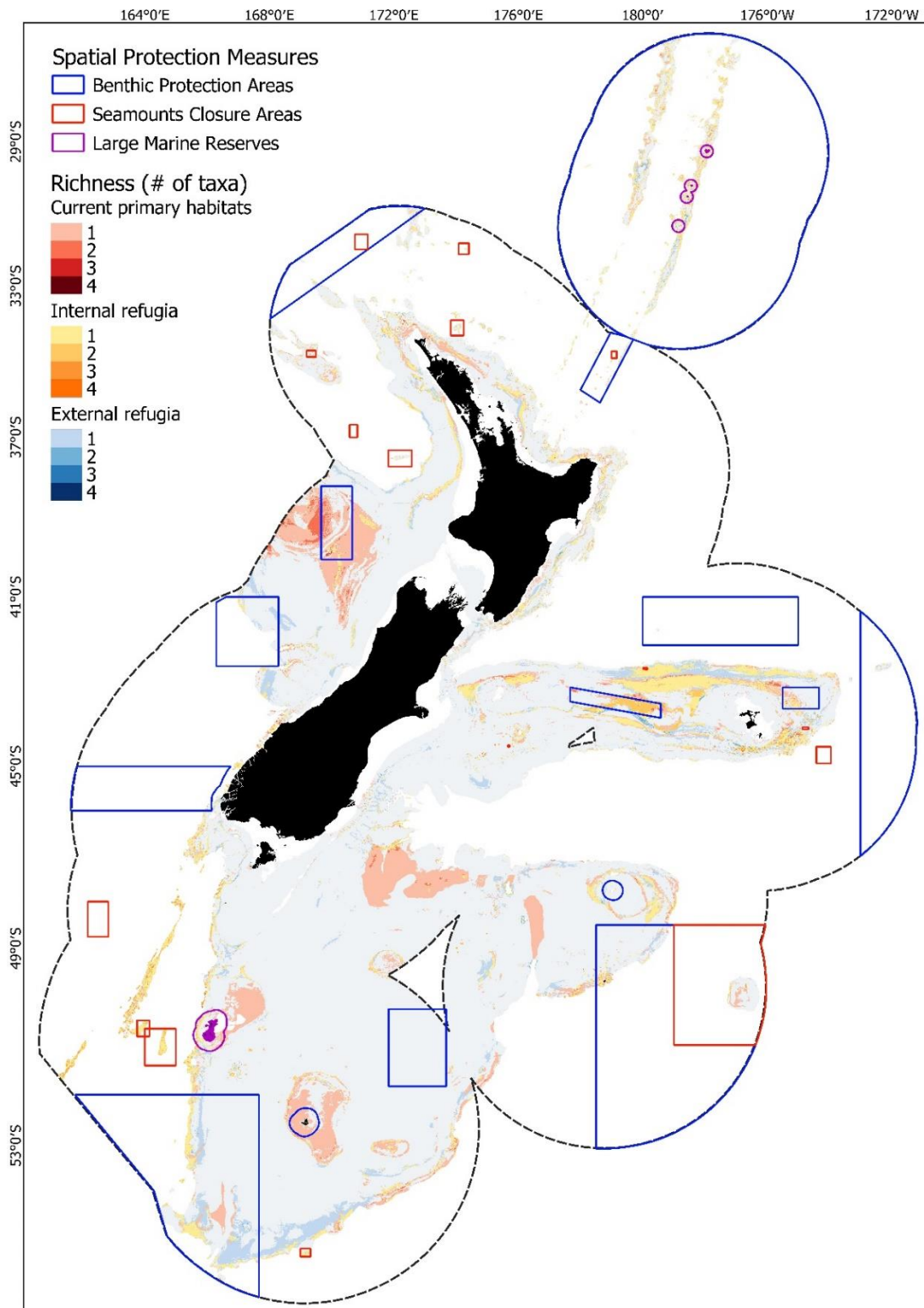


Figure 1. Extent of predicted bottom trawling impact-adjusted current primary habitats and climate refugia (internal and external) under the SSP2-4.5 scenario that sits inside or outside the current marine Spatial Protection Measures (SPMs) in New Zealand. Purple polygons denote Large Marine Reserves (LMRs) within the Territorial Sea, red polygons indicate Seamount Closure Areas (SCAs), and blue polygons represent Benthic Protection Areas (BPAs). The black dashed line marks the outer limit of New Zealand's Exclusive Economic Zone. Plots for the SSP3-7.0 scenario are provided in the Supplementary Materials.

5.4. Implication for conservation

This research underpins the need to better understand the key drivers of biodiversity loss (e.g., climate change, bottom trawling) and pinpoint areas of significant ecological value, required under international frameworks (Kunming-Montreal Global Biodiversity Framework, 2024). This PhD research quantified the loss of ecologically critical habitats due to climate change and projected shifts in their distribution under future climate scenarios, identifying potential climate refugia (Chapter 2). It also revealed that bottom trawling further reduces these habitats, heightening biodiversity loss (Chapter 3). These findings emphasize the urgent need for robust conservation strategies that prioritize biodiversity and mitigate ecosystem degradation and species extinction (Palumbi et al., 2009).

Such conservation objectives align with the goals of the Convention on Biological Diversity Kunming-Montreal Global Biodiversity Framework (GBF) which requires all areas within a country to be under Participatory, Integrated, and Biodiversity-Inclusive Spatial Planning (PI-BISP). PI-BISP is a systematic, holistic and inclusive approach to spatial planning, that identifies the spatial actions necessary to address the drivers of biodiversity loss across ecosystems. PI-BISP guides coordinated spatial interventions through different targets that aim to manage, protect, and restore areas for improved biodiversity outcomes and avoid potential negative impacts on biodiversity. Target 1 of PI-BISP is “*to bring the loss of areas of high biodiversity importance and ecosystems of high ecological integrity close to zero by 2030 while respecting the rights of Indigenous peoples and local communities*”(Kunming-Montreal Global Biodiversity Framework, 2024).

A key headline indicator for Target 1 is the quantification of the percentage of land and seas covered by biodiversity-inclusive spatial plans. Yet, no comprehensive and uniform data sources have been identified for this objective, highlighting the need for their development. This research contributed to addressing this knowledge gap and quantified the extent of ecologically significant habitats left unprotected under current spatial protection measures in New Zealand. Our results showed that only 20% of primary habitats are inside protected areas under current environmental conditions, decreasing to approximately 15% under future climate scenarios. These findings represent a critical first step toward systematically identifying and prioritizing unprotected yet ecologically vital habitats. Addressing these protection gaps contributes to efficient spatial planning

that determines the optimal allocation of conservation efforts and resources across space and time to protect biodiversity while mitigating and minimizing adverse impacts (Brown et al., 2015; Kunming-Montreal Global Biodiversity Framework, 2024; Tallis et al., 2021). Furthermore, the quantification of the percentage included or excluded from protection also aligns with other targets of GBF, such as Target 3, also known as the seeking to effectively conserve and manage 30% of terrestrial, inland water, and coastal and marine areas by 2030 (*Convention on Biological Diversity*, 2022).

Expanding or enhancing spatial protection measures to effectively cover ecologically relevant habitats, particularly those identified as potential future refugia, is crucial to mitigating habitat loss and supporting resilience in the face of environmental change and ongoing local pressures (Alabia et al., 2021; Assis et al., 2016; Lancaster & Hildrew, 1993). However, the overlap between climate refugia and fishery areas, as found in Chapter 3, indicated potential management challenges, as it requires balancing the needs of biodiversity conservation with the socio-economic importance of fisheries (e.g., protecting target marine regions might imply closing active fishing grounds). Yet, the absence of clear guiding principles for navigating trade-offs within specific social-ecological systems poses challenges to effective management (Boemare et al., 2023; Reimer et al., 2023b; Thiault et al., 2020).

Addressing these challenges necessitates an integrated approach that accounts for the interplay between ecological and socio-economic factors (Davis, 2008; Hartley & Robertson, 2006; Kitts et al., 2007; Martin-Smith et al., 2004; Sen & Raakjaer Nielsen, 1996; Verheij et al., 2004). This can be achieved by combining quantitative and qualitative research, drawing on both ecological and social methodologies and insights. Decision-support tools that integrate social and ecological data can help stakeholders make informed and strategic decisions (Ban et al., 2013). This approach would enable more informed and comprehensive risk assessments and guide the development of adaptive management strategies more effectively. This should be undertaken as part of an open stakeholder engagement process to ensure management solutions are both sustainable and feasible.

5.5. Engaging with experts to assess risk perception and inform future marine spatial planning

Chapter 4 explored socio-ecological aspects by engaging with policy and fishery experts and regulators to assess their perception of risk for select VME indicator taxa against multiple human activities and stressors and potential management strategies to mitigate these risks. *Findings showed that presenting additional scientific insights on the impacts of climate change and bottom trawling increased participants' risk perceptions and confidence, with these stressors deemed increasingly impactful. Additionally, the elicitation process proved useful in refining expert perspectives and clarifying the direction of their recommendations.*

This chapter employed a novel approach that combined expert opinions with spatial conservation tools. In particular, individual interviews with experts to establish baseline perceptions of risk and management priorities were performed. Then, a stakeholder consultation workshop was carried out to provide the participants with new scientific insights on the impacts of climate change and bottom trawling, drawn from previous chapters, and re-evaluated risks and management strategies through a group elicitation process.

Following the illustration of scientific findings experts identified climate change and bottom trawling as major risks for VME indicator taxa, particularly for cold-water corals and sponges more consistently. While after the group elicitation fostered a more cohesive vision by allowing participants to reflect on and reassess their initial judgments collectively and in light of updated data. It enabled experts to consistently target key management strategies, carefully weighted through a token allocation methodology reflecting real-world resource allocation processes, particularly marine spatial planning. Marine spatial planning emerged as the top-ranked management strategy, with strong consensus on its critical role in protecting potential VMEs under both present and future climatic scenarios. This was followed by climate mitigation and adaptation actions and fishery management strategies, such as banning, monitoring, and modifying fishing gear. Moreover, the presentation of novel scientific findings and the elicitation process broadened the scope of identified challenges and solutions, underscoring the complexities of marine conservation. The main challenges included political resistance to stricter regulations, industry reluctance due to economic concerns, and the intricacies of

designing and implementing spatial management strategies. However, innovative solutions and actions also emerged, such as speeding up the process that leads to establishing protection measures that also account for climate refugia, applying precautionary principles in uncertain scenarios, strengthening stakeholder collaboration, and increasing research funding oriented on ecosystem recovery and connectivity studies. Moreover, to achieve Biodiversity-Inclusive conservation a holistic approach that balances trade-offs between conservation goals and human activities is essential for designing practical and achievable conservation strategies (Kunming-Montreal Global Biodiversity Framework, 2024). This approach identifies where regions of conservation (i.e., portions of land or sea that have conservation and economic value) are likely to occur and where conservation interventions are most urgently needed to prevent biodiversity loss and mitigate potential negative impacts on people (Neugarten et al., 2024; Oakleaf et al., 2024).

5.6. Conclusions and future research directions

This PhD research employed an interdisciplinary and methodologically innovative approach to advance understanding of the multiple impacts of climate change and bottom trawling on VME indicator taxa, with a strong emphasis on management implications. The findings underscore the critical role of science-driven, collaborative conservation approaches in safeguarding VMEs and highlight the urgent need for adaptive spatial management strategies to mitigate pressures from both climate change and anthropogenic activities such as bottom trawling.

In particular, this research:

- 1. Quantified habitat loss and identified climate refugia, regions capable of sustaining ecosystem functionality and providing essential services under projected climate change scenarios.*
- 2. Assessed the impacts of bottom trawling on these refugia, revealing significant threats to their long-term viability.*
- 3. Integrated ecological findings with stakeholder engagement to explore risks and future management strategies, identifying key barriers and solutions necessary to strengthen the protection of VME habitats.*

The identification of climate refugia and the assessment of the effect of bottom trawling on them provide a strategic framework for future conservation initiatives, guiding the

protection of deep-sea biodiversity and associated ecosystem services against global and local stressors. Nevertheless, more research can be done to improve the reliability of model outputs and inform management actions for effective protection of climate refugia. Specifically, improvements in the predictive performance of broad-scale models, including robust field validation, improved data sets, advanced modelling techniques, and ecological understanding, are necessary to ensure meaningful predictions, especially when applied to biodiversity conservation and climate change adaptation.

SDMs generate correlative spatial predictions by statistically correlating observed species distribution to environmental variables, but their reliability decreases when extrapolating into unsampled areas or future scenarios (Elith & Leathwick, 2009; Guisan & Zimmermann, 2000). Independent field validation, such as systematic visual surveys or direct habitat assessments, is critical for assessing the accuracy of model predictions and refining their performance (Anderson et al., 2016b; Guinotte & Davies, 2014; Tittensor et al., 2009). This validation process is especially crucial in data-deficient regions that also support commercial activities, such as deep-sea habitats exploited by commercial fisheries (Anderson et al., 2016b). In the absence of field validation, broad-scale predictive models should be applied cautiously to avoid ineffective or misinformed management decisions (Anderson et al., 2016b).

In addition, since SDMs depend on environmental and species occurrence or abundance data, increasing sampling efforts through comprehensive and representative field surveys can reduce uncertainty and enhance prediction reliability (Phillips et al., 2006). Moreover, species distributions are shaped not only by environmental gradients but also by biotic positive (e.g., facilitation) and negative interactions (e.g., competition and predation), which can expand or constrict their fundamental niche. Although challenging to quantify, integrating biotic interactions—such as through joint SDMs (jSDMs)—can improve predictions by accounting for multiple species interactions, environmental covariates, species traits, and phylogenetic relationships (Ovaskainen et al., 2017; Stephenson et al., 2022a). Moreover, enhancing predictive confidence using ensemble modelling approaches—that is, the combination of multiple machine-learning algorithms such as Random Forest, Maxent, or Boosted Regression Trees—limits dependence on a single model type or structural assumption (which varies among the model types used) resulting in better performance and uncertainty reduction (Araújo & New, 2007; Lo Iacono et al., 2018; Robert et al., 2016; Rooper et al., 2017).

Furthermore, to reduce prediction uncertainty and ensure meaningful resource allocation for effective spatial planning, understanding ecological dynamics is pivotal for improving SDM predictions and interpretation. A key research gap lies in integrating SDMs with connectivity analyses and species-specific physiological data from laboratory studies. Future research should focus on larval dispersal and connectivity dynamics (Almany et al., 2009; Ani et al., 2024; Hilário et al., 2015). Connectivity analysis is crucial for understanding the feasibility of colonisation, especially for taxa reliant on larval dispersal for colonising new areas (e.g., cold water corals) (Andrello et al., 2015; Baco et al., 2016; Hilário et al., 2015). Such information is essential for identifying refugia within the range of colonization, enabling spatial planners to effectively prioritize these areas for conservation (Kenchington et al., 2019; Moilanen & Wintle, 2006; Wang et al., 2021).

In addition, incorporating physiological thresholds (e.g., temperature, pH, oxygen) from experimental research can enhance SDM ecological accuracy. Defining species' tolerance limits under controlled conditions would refine model parameters and improve predictions of habitat suitability under climate change (Martínez et al., 2015; Rodríguez et al., 2019). Furthermore, physiological data on direct (e.g., gear interactions) and indirect (e.g., sedimentation) trawling effects, as well as reproductive traits such as larval settlement and recruitment, could improve impact assessments and refine predictions of bottom fishing impacts (Beaumont et al., 2023; Mobilia et al., 2023).

Beyond enhancing predictive models' capacities, greater efforts are needed to bridge the gap between science and management. While this study engaged conservation and fisheries experts and regulators, these groups alone do not fully represent the diverse range of individuals and communities who are affected by or have a stake in marine ecosystem management. Future research should aim to include a broader spectrum of perspectives, such as industry representatives (e.g., the fishing community) and indigenous knowledge holders, to ensure that diverse perspectives are considered in marine spatial planning (Ritchie & Ellis, 2010). Policymakers also play a pivotal role in shaping and enacting regulations that influence conservation outcomes; their involvement is crucial for translating research findings into actionable policies (Olsen et al., 2014). Additionally, providing policymakers with clear, accessible briefings or workshops grounded in rigorous scientific evidence could facilitate the adoption of evidence-based conservation strategies (Foley et al., 2010; Sivas & Caldwell, 2008).

Incorporating diverse stakeholder perspectives helps align conservation objectives with the realities of those directly impacted by management decisions, facilitating the co-production of knowledge and the implementation of policies that promote sustainable economic practices in a socially just and equitable manner (Bennett et al., 2021). These can include the creation of economic incentive structures, such as subsidies for sustainable fishing practices or payments for ecosystem services, aligning conservation goals with economic interests (Gutiérrez et al., 2011; Nyavor et al., 2023; Wu et al., 2023).

Moreover, integrating additional decision-support tools beyond SDMs can further enhance the robustness and adaptability of conservation strategies. Tools such as Zonation (Moilanen, 2007) and Marxan (Ball & Possingham, 2000) can be utilized to explore possible levels of spatial marine protection and spatial prioritization scenarios. These tools offer probabilistic decision frameworks that account for multiple stressors, uncertainties, and competing resource uses, enabling the identification of spatial management options that offer high conservation value while minimizing resource use conflicts (Rowden et al., 2019).

In conclusion, to achieve comprehensive and integrated marine management, future research should further incorporate the complex social-ecological dynamics shaping marine ecosystems. This can be facilitated through ecosystem-based marine spatial planning, which integrates ecological principles with sustainable ecological and social considerations. While this PhD research addresses some of these aspects, additional studies are needed to establish a robust scientific foundation that can be effectively integrated with socioeconomic and governance frameworks. Moreover, by expanding stakeholder participation and incorporating spatial and decision-support tools, future studies can enhance the robustness and reliability of risk perception assessments, ultimately leading to more informed and consensus-driven management strategies. Such an approach is essential to ensuring biodiversity conservation, sustainable ocean resource use, and the continued provision of critical ecosystem services for future generations (Douvere, 2008; Foley et al., 2010). Finally, although this study focuses on the New Zealand region, the methodologies and insights presented have broader applicability across diverse social-ecological systems, highlighting the global relevance of combining numerical modelling with stakeholder engagement in marine conservation planning.

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