Monitoring Deep-Sea MPAs: Functional and Trait-Based Approaches for Adaptive Management in Changing Oceans

by

Megan A. Davies
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We acknowledge and respect the lək̓ʷəŋən peoples on whose traditional territory the university stands and the Songhees, Esquimalt and W̱SÁNEĆ peoples whose historical relationships with the land continue to this day.

Supervisory Committee

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Dr. Amanda Bates, Supervisor
Department of Biology

Dr. Cherisse Du Preez, Co-Supervisor
Fisheries and Oceans Canada, Department of Biology

Dr. Ana Colaco, Outside Member
University of the Azores

Thesis Abstract

Changing ocean conditions are disrupting marine ecosystems, posing significant challenges for monitoring and managing biodiversity in remote, offshore marine protected areas (MPAs). Effective conservation depends on biological assessment tools that can overcome the logistical constraints of deep-sea monitoring while detecting long-term ecological changes. This thesis evaluates two possible approaches for assessing and monitoring species in offshore MPAs. First, I assess the feasibility of a functional-group monitoring approach, using cold-water corals and sponges (CWCS) in the Northeast Pacific as a case study. I analyze inter- and intra-seamount variability in depth-occupancy patterns using data extracted from remotely operated vehicle (ROV) transects performed by Fisheries and Oceans Canada (Chapter 2). Additionally, I identify potential indicator species that could be used to streamline long-term monitoring efforts. Second, I develop a species-level vulnerability framework using functional traits, with molluscs in the Azores Marine Park as a case study. I conduct a comprehensive literature review to determine which traits are most relevant for assessing vulnerability to climate change. Using species trait data from the FUN Azores Trait Database, I integrate oceanographic models to quantify species-specific exposure, sensitivity, and adaptive capacity to ocean acidification and warming (Chapter 3). My findings show that while functional groups capture broad CWCS distribution patterns, species-level assessments remain necessary for detecting ecological changes and refining monitoring strategies in the NE Pacific. In the Azores, I find that bivalves in northern MPAs are particularly vulnerable due to their high sensitivity and low adaptive capacity, while cephalopods exhibit greater resilience to climate change. Together, these studies highlight the strengths and limitations of biological assessment tools for long-term deep-sea MPA monitoring, offering insights into their role in adaptive conservation strategies. By integrating functional-group and trait-based approaches, this thesis contributes to a more adaptive and effective conservation framework for managing marine species in a changing ocean.

Co-Authorship Statement

I have made the primary intellectual and practical contribution to the work that is reported in this thesis.

Chapter 2

- I, **Megan Davies**, designed and identified the research questions, analyzed the data, prepared the figures and tables (unless otherwise stated), and authored the manuscript.
- **Cherisse Du Preez** contributed the Fisheries and Oceans data used in this chapter and assisted with the conceptualization of the manuscript.
- **Amanda E. Bates** assisted with the conceptualization and editing of the manuscript.

Chapter 3

- I, **Megan Davies**, designed and identified the research questions, analyzed the data, prepared the figures and tables, and authored the manuscript.
- **Ana Colaco** contributed the FUN Azores data used to build the vulnerability framework and assisted with the conceptualization.
- **Amanda E. Bates** assisted with the conceptualization, editing of the manuscript, and assisted with the coding of the vulnerability framework in R.

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Chapter 1 – Introduction

1.1 Background

1.1.1 Marine Protected Areas

Marine Protected Areas (MPAs) cover approximately 8% of the global oceans and are a cornerstone of efforts to safeguard marine biodiversity (ProtectedPlanet, n.d.). Designated by the International Union for Conservation of Nature (IUCN) as clearly defined regions managed through legal or other effective means, MPAs aim to achieve long-term conservation of nature (IUCN, 2017). These areas are associated with ecosystem services and cultural values and are crucial for the protection and preservation of marine habitats and the variety of life they support. The level of protection within these demarcated oceanic zones exists on a large spectrum. In its most strict form, there are MPAs that prohibit all human entry, such as portions of the Seaflower Reserve in the Caribbean (Sanchez-Jabba & Mauricio, 2016). Others are composed of “no-take” areas, which prohibit all extractive activities such as fishing, mining, and oil extraction, or “multiple-use” MPAs where some anthropogenic and/or extractive activities are allowed. The constancy of protection within MPAs can also vary, with some offering year-round protection measures while others are seasonal or rotating. Despite this, all MPAs are designed to offer some degree of protection against harmful activities that could impact the natural and cultural resources therein.

MPAs are often established in areas recognized as Vulnerable Marine Ecosystems (VMEs) and Ecologically or Biologically Significant Marine Areas (EBSAs). VMEs are typically associated with deep-sea environments and refer to areas that are particularly susceptible to disturbance due to the presence of fragile features or species, such as cold-water corals. These ecosystems often host VME indicator species, which signal the presence of vulnerable marine ecosystems rather than directly reflecting ecosystem health (NAFO, 2015). The concept of VMEs originated from United Nations General Assembly Resolution 61/105, which called for action to minimize the impacts of deep-sea fishing on the high seas (UNGA, 2007). As a result, VMEs are formally recognized by the Food and Agriculture Organization (FAO) and used in international fisheries management to identify areas where bottom-contact fishing should be restricted or avoided (FAO, 2008; Watling & Auster, 2021).

In contrast, EBSAs are identified under both Canada’s domestic marine planning framework and the Convention on Biological Diversity (CBD). These areas are defined based on criteria such as uniqueness, importance for life history stages, vulnerability, biological productivity, and naturalness (Ban et al., 2016; CBD, 2008). While EBSA designation does not trigger formal protection, it is used to guide conservation priorities and inform the development of area-based management measures, including MPAs or other spatial protections. In Canada's Offshore Pacific Bioregion, EBSAs have been identified using expert- and data-driven assessments of seamounts, hydrothermal vents, and continental margins (Ban et al., 2016).

MPAs are often biodiversity hotspots, aimed at encompassing a wide range of taxonomic diversity. By creating refuges from anthropogenic disturbance, MPAs provide opportunities for population recovery and long-term ecosystem resilience. Indeed, the establishment of MPAs has led to notable marine conservation success stories (Rossbach et al., 2023). Species recovery has been observed in large charismatic megafauna such as Hector's dolphins (*Cephalorhynchus hectori*) in New Zealand (Gormley et al., 2012) and reef sharks (e.g., *Carcharhinus amblyrhynchos*) on coral reefs in Western Australia (Speed et al., 2018), where improved survival and increased abundance followed strict protection measures. MPAs have also supported the recovery of seabird and fish species (Aburto-Oropeza et al., 2011; Barbraud et al., 2020; Jackson et al., 2012; Waterhouse et al., 2020), as well as marine invertebrates (Bavestrello et al., 2015; Powers et al., 2009; Rehm et al., 2014), demonstrating their value as effective conservation tools across a range of taxa.

1.1.2 Geological Features of offshore MPAs

Among the diverse environments protected within MPAs, underwater geological features such as seamounts and hydrothermal vents are of particular ecological significance. These features often overlap with designations such as VMEs and EBSAs due to their biodiversity, structural complexity, and the presence of key indicator species.

Seamounts, which are underwater mountains rising at least 1,000 m above the surrounding seafloor, are estimated to cover approximately 2.6% of the global ocean floor (Ramirez-Llodra et al., 2010). Some can exceed 4,000 m in height, rivalling continental mountain ranges. As they rise through the water column, seamounts intersect multiple depth zones – each with distinct physical and chemical conditions– creating a range of habitats from deep-sea environments to, in some cases, comparatively shallower summits. The abrupt topography of seamounts has profound effects on the surrounding oceanographic regime. Their structure disrupts current flow, promoting localized upwelling, turbulence, and nutrient retention, all of which enhance primary productivity (Boehlert & Genin, 1987; Rogers, 2018). These processes support dense aggregations of plankton and higher trophic levels, making seamounts biological hotspots. Consequently, they harbour high biodiversity, including coral gardens, sponge fields, and numerous species or invertebrates and fish (Rogers, 2018). Many migrator species – such as whales, sharks, and tuna –use seamounts as feeding and breeding grounds, emphasizing their ecological importance across broad spatial scales (Rogers, 2018).

Hydrothermal vents, although far smaller in areal extent, are similarly critical for the specialized species they support. Located along tectonic plate boundaries, these features emit superheated, mineral-rich fluids into the deep ocean, creating chemically extreme environments (Ramirez-Llodra et al., 2010). While inhospitable to most marine life, certain extremophiles thrive under these conditions. Instead of relying on sunlight for energy, organisms around vents depend on chemosynthesis –a process where bacteria and archaea convert chemicals such as hydrogen sulphide into organic compounds (Ramirez-Llodra et al., 2010). This contrasts with photosynthesis, which occurs in sunlit waters and uses light energy to convert carbon dioxide and water into organic matter. While many marine ecosystems depend on photosynthesis-driven food webs, hydrothermal vent ecosystems are fuelled entirely by chemosynthesis. These represent two distinct pathways of primary production, each supporting very different biological communities. Chemosynthetic microbes form the base of the food web at vents, supporting complex and highly adapted communities that include giant tube worms, vent crabs, and microbial mats (Ramirez-Llodra et al., 2010).

The ecological significance of both seamounts and hydrothermal vents extends beyond their biodiversity. These features play key roles in global biogeochemical cycles, including carbon sequestration and nutrient cycling. Seamounts influence large-scale ocean circulation by enhancing vertical mixing, affecting broader oceanographic processes (Boehlert & Genin, 1987; Mashayek et al., 2024). Hydrothermal vents facilitate the cycling of elements such as sulphur, iron, and manganese, impacting the chemistry of the deep ocean (Gartman & Findlay, 2020; Sander & Koschinsky, 2016). Protecting these systems is therefore vital for not only conservation but also for maintaining ecosystem functioning in the deep ocean, particularly in the face of increasing anthropogenic impacts and global climate change.

1.1.3 Challenges of MPAs

Management plans of MPAs, including those protecting unique features like seamounts and hydrothermal vents, often focus on the conservation of key taxa, functional groups, or habitat types to maintain ecosystem integrity and biodiversity (e.g., DFO, 2015; DFO, 2019; Du Preez et al., 2024). However, achieving these conservation objectives presents significant challenges, especially in large, remote, or deep-sea environments. Financial and logistical constraints remain major barriers. Many MPAs operate with limited budgets, making it difficult to conduct sustained monitoring, ensure regulatory compliance, or adaptively manage conservation strategies (Gill et al., 2017). Time-intensive data collection and gaps in baseline ecological information further complicate efforts to assess whether conservation objectives are being met. Without adequate temporal coverage and continuity, it becomes difficult to detect ecological change or attribute it to specific stressors, reducing the effectiveness of management interventions.

Although MPAs can provide protection from some local anthropogenic impacts, they are not insulated from the pervasive effects of climate change, which transcend political and spatial boundaries (Bruno et al., 2018). Climate-related stressors—including ocean warming, acidification, deoxygenation, changes to current regimes, and declining particulate organic carbon (POC) flux—are altering marine ecosystems globally. In the Azores, a mid-Atlantic archipelago, climate change is manifesting through warming temperatures, acidification, and reductions in POC, which together threaten food supply and structural integrity for many benthic organisms (Cheng et al., 2022; Gazeau et al., 2013; Ríos et al., 2015). Similarly, in the Pacific, the loss of dissolved oxygen and the expansion of oxygen minimum zones (OMZs) are expected to drive changes in species distributions and community composition, particularly among species with narrow oxygen tolerances (Ross et al., 2020). In addition to oxygen loss, aragonite saturation horizons have been shoaling by 1–2 m per year since the 1980s, further reducing the habitable zone for calcifying organisms. These changes, especially in deep-sea ecosystems that evolved under stable conditions, can have profound consequences for biodiversity and ecosystem functioning.

The environmental changes driven by climate change create a complex and uncertain scenario for marine species. Some may benefit from shifting conditions—for instance, jellyfish are suspected to thrive in warmer waters, with increasing populations and expanding ranges observed in some regions (Boero et al., 2016; Brotz et al., 2012; Purcell, 2005). Others, particularly those with limited physiological plasticity or specialized ecological roles, may face population declines or extinction. Species that rely on stable conditions, such as those forming calcium carbonate shells or skeletons, are especially vulnerable to ocean acidification and warming, which can reduce habitat suitability and weaken structural integrity (Gazeau et al., 2013). Deep-sea taxa, many of which grow slowly, live for decades or centuries, and have narrow environmental tolerances, present a significant source of uncertainty (Paulus, 2021). The deep sea remains one of the least understood environments on the planet, making it difficult to predict how these ecosystems will respond to rapid environmental change.

Climate change is not the only pressure facing MPAs. Many areas continue to experience risks from historical and ongoing bottom-contact fishing, ghost fishing from lost or abandoned gear, and non-compliance with regulatory measures (Du Preez et al., 2020; Du Preez et al., 2024). Additional emerging threats—such as adjacent deep-sea mining, increased shipping traffic, and associated noise pollution—could further alter deep-sea ecosystems in unpredictable ways (Du Preez et al., 2024; Du Preez and Norgard, 2022). While the relative severity of these threats may vary across regions, they contribute to the cumulative stress experienced by benthic communities, particularly in deep, remote environments.

Monitoring efforts must therefore account for a wide range of stressors, including not only climate-related change, but also recovery from historical impacts, compliance with protection measures, and broader environmental variability. Risk-based frameworks, such as the Ecological Risk Assessment Framework applied at SG̲áan K̲ínghlas-Bowie Seamount and Endeavour Hydrothermal Vents MPAs, provide valuable tools to guide the selection of monitoring indicators and management strategies (DFO, 2015). However, the vastness, inaccessibility, and high cost of deep-sea research present major challenges to sustained scientific observation. As a result, managers must rely on efficient and scalable biological assessment tools to track biodiversity patterns, detect ecological change, and support adaptive conservation strategies. Developing and refining these tools is critical to ensuring that deep-sea MPAs remain effective in safeguarding biodiversity, vulnerable marine ecosystems, and the ecological functions they support in the face of growing environmental uncertainty.

1.2 Thesis overview and objectives

Given the vast, remote, and deep-sea nature of many MPAs, monitoring efforts must balance scientific rigor with logistical feasibility. Traditional species-level assessments can be time-intensive and costly, while broad ecological indicators may lack the resolution needed to detect meaningful changes. This thesis explores how different biological assessment tools can support long-term monitoring and adaptive management of deep-sea MPAs, ensuring that conservation objectives are met despite these challenges.

This thesis examines different biological assessment tools for long-term monitoring and management of deep-sea MPAs, specifically: (1) A functional-group monitoring approach, using cold water coral and sponges (CWCS) in the Northeast Pacific as a case study, to assess spatial patterns and identify potential indicator species for long-term monitoring; and (2) A species-level vulnerability assessment using functional traits, with molluscs in the Azores as a case study, to evaluate species susceptibility to climate change and inform conservation strategies (Figure 1.1). By applying these tools to two recently monitored offshore MPAs, this research explores how biological data can be used to refine monitoring strategies and support adaptive management in deep-sea ecosystems.

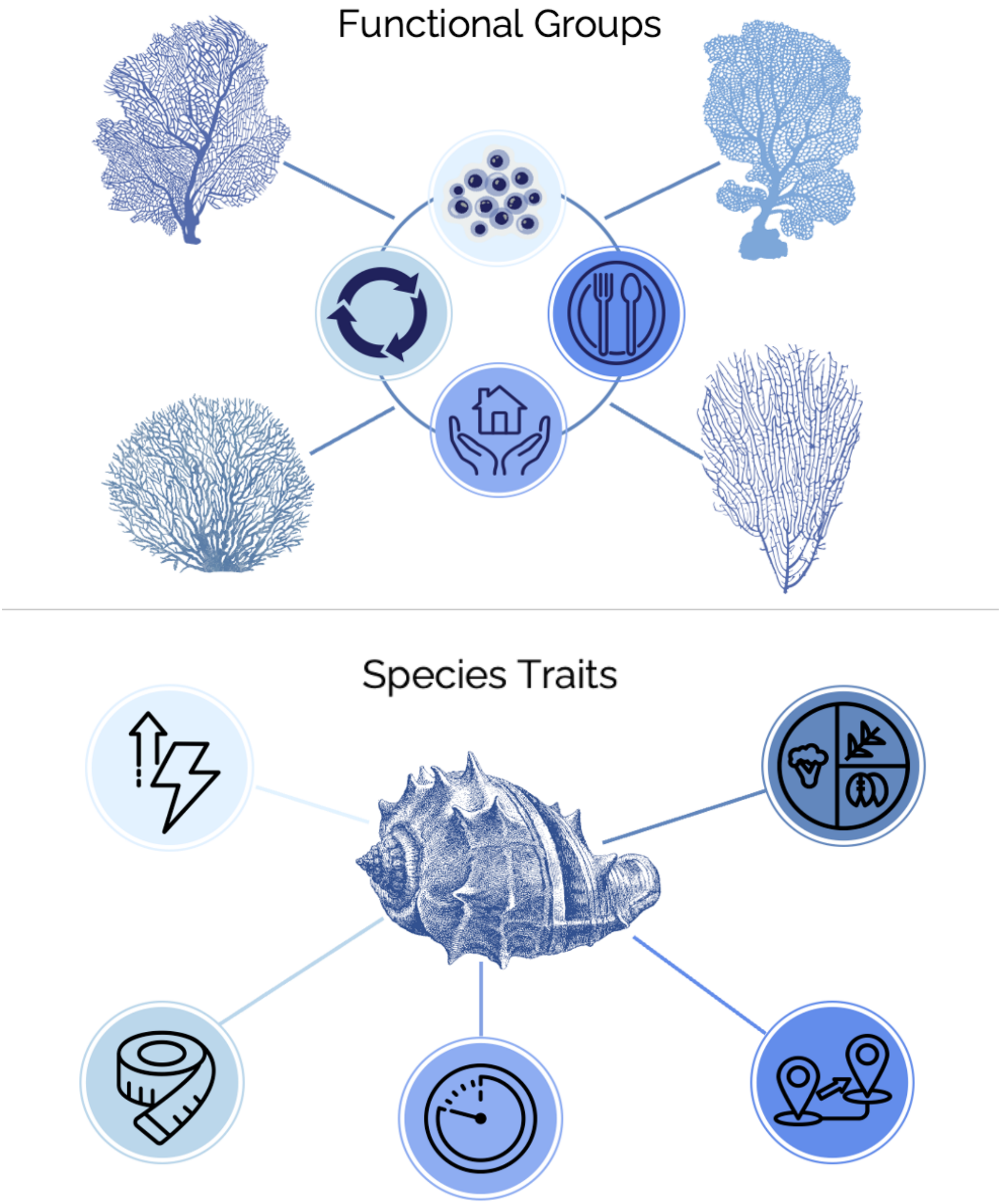

Figure 1.1. Conceptual illustration of the two monitoring approaches explored in this thesis: functional groups (top) and species traits (bottom). The top panel represents the functional group approach used in Chapter 2, where species are grouped based on shared ecological roles and ecosystem functions, regardless of taxonomic relatedness. Different fanned coral species, despite morphological differences, are grouped together because they provide similar functions, including nursery habitat (eggs), nutrient cycling (circular arrows), habitat provisioning (house and hands), and food provisioning (fork and spoon). The bottom panel represents the species traits approach used in Chapter 3, where biological, physiological, life-history, and behavioural traits are assessed to evaluate species vulnerability. The icons represent example traits such as metabolism (lightning bolt and arrow), body size (measuring tape), lifespan (clock), migratory ability (location markers), and diet (food icon).

1.2.1 Chapter 2 – Evaluating Functional Group Monitoring of Cold-Water Coral and Sponges in Northeast Pacific MPAs

1.2.1.1 Objectives

1. To quantify inter-seamount variability in CWCS predicted occupancy across depth gradients to determine whether seamounts in the Offshore Pacific Bioregion exhibit comparable spatial patterns. I predict that CWCS functional group distributions will exhibit depth-related trends, but the depth range and peak occupancy will vary among seamounts due to species-specific preferences and environmental conditions.

2. To examine intra-seamount variability in CWCS occupancy trends across different flanks of the same seamount, using Dellwood and Union seamounts as case studies. I predict that occupancy patterns will differ between flanks due to fine-scale variations in environmental conditions, influencing where CWCS establish and persist.

3. To identify key indicator species that exhibit reliable spatial and depth-related patterns across seamounts, providing a basis for more efficient long-term monitoring and adaptive management of these ecosystems.

1.2.1.2 Main Findings

- CWCS functional groups exhibited distinct depth-occupancy patterns, with predicted occupancy peaks concentrated within the severely hypoxic region (800-1200 m) of the naturally occurring oxygen minimum zone (OMZ).
- Both inter- and intra-seamount variability were observed in CWCS depth-occupancy trends, with some seamounts displaying consistent patterns across flanks, while others exhibited significant variability.
- Certain species exhibited consistent occupancy across multiple seamounts and thus have potential value as indicator taxa for long-term monitoring.
- While functional groups capture broad distribution trends, species-level assessments remain necessary for detecting ecological changes and refining monitoring strategies.

1.2.2 Chapter 3 – Assessing Climate Vulnerability of Molluscs in the Azores Marine Park Using a Trait-Based Framework

1.2.2.1 Objectives

1. To evaluate key traits that can be used to assess the vulnerability of molluscan species to climate change, refining trait classifications and addressing knowledge gaps;

2. To develop a trait-based vulnerability framework that quantifies species' exposure, sensitivity, and adaptive capacity to climate change stressors;

3. To identify spatial patterns of exposure across MPAs in the Azores Marine Park by integrating species trait data with oceanographic models.

1.2.2.2 Main Findings

- Bivalves exhibited the highest vulnerability due to their combination of high sensitivity (e.g., aragonite-based exoskeletons, filter-feeding) and low adaptive capacity (e.g., sessile adult lifestyles, narrow depth ranges).
- Cephalopods had the lowest vulnerability due to their greater adaptive capacity, characterized by high motility, broad depth distributions, and oceanic dispersal potential.
- Gastropods had wide range of vulnerabilities, with vent-endemic species showing lower sensitivity due to physiological adaptations, while non-vent species were more vulnerable, particularly those with aragonite shells and restricted depth distributions.
- Northern MPAs were more susceptible to acidification, while southern MPAs faced greater warming exposure, shaping species-specific vulnerabilities across the Azores Marine Park.

Chapter 2 – Evaluating Functional Group Monitoring of Cold-Water Coral and Sponges in Northeast Pacific MPAs

Abstract

Seamount ecosystems support diverse cold-water coral and sponge (CWCS) communities that play a foundational role in deep-sea biodiversity. In the Northeast Pacific, Canada's marine protected areas (MPAs) prioritize the conservation of these species, yet effective long-term monitoring remains challenging due to the vast spatial scale and logistical constraints of deep-sea research. This study assesses CWCS distribution patterns across multiple seamounts within the SG̲áan K̲ínghlas-Bowie Seamount MPA and Tang.ɢ̲wan – ḥačxwiqak – Tsig̲is MPA to evaluate whether functional group-based monitoring can serve as a scalable alternative to species-level assessments. Using benthic imagery, I analyzed inter-seamount variability in predicted occupancy trends with depth and examined intra-seamount variability across different flanks. Results revealed that CWCS functional groups exhibit distinct occupancy patterns, with mid-layer habitats (800–1200 m) showing the highest concentrations of predicted occupancy across most taxa. However, substantial variability in distribution patterns was observed both within and between seamounts. The identification of key indicator species suggests that targeted monitoring could enhance the efficiency of conservation efforts. These findings highlight the application of adaptive, functional group-based monitoring frameworks that can account for ecological heterogeneity while maintaining feasibility. This study contributes to the development of robust, long-term conservation approaches for deep-sea MPAs.

2.1 Introduction

Understanding and managing environmental change requires long-term ecological monitoring, which provides critical insights into ecosystem dynamics and informs conservation strategies (Havstad & Herrick, 2003; Lindenmayer & Likens, 2010; Vaughan et al., 2001). In both terrestrial and marine ecosystems, monitoring frameworks are essential for detecting shifts in biodiversity, assessing ecosystem resilience, and supporting adaptive management (Addison et al., 2015; Vos et al., 2000). However, designing and implementing long-term monitoring programs that are both scientifically rigorous and logistically feasible presents challenges, particularly in remote ecosystems (Addison et al., 2015; Lindenmayer & Likens, 2010). In marine environments, where large-scale assessments are often constrained by accessibility and cost, improving efficiency while maintaining ecological accuracy remains a key challenge (Fox et al., 2014; Grorud-Colvert et al., 2021).

Marine protected areas (MPAs) are established to protect biodiversity and ecosystem function, yet long-term assessments are often hindered by the scale of protected regions and the complexity of the ecosystems they encompass (Grorud-Colvert et al., 2021). Deep-sea MPAs, in particular, present unique challenges due to their remote locations, limited accessibility, and the high costs of conducting surveys at depth (McLean et al., 2020). Traditionally, ecological surveys rely on methods such as remotely operated vehicle (ROV) and video transects, as well as identifying taxa down to the lowest possible taxonomic level (McGeady et al., 2023; McLean et al., 2020; Smith & Hughes, 2008)l. However, these approaches are time-intensive and resource-demanding (McGeady et al., 2023; McLean et al., 2020). Given these constraints, optimizing monitoring frameworks to balance scientific robustness with logistical feasibility is a pressing priority for deep-sea conservation.

Among deep-sea habitats, seamounts present distinct monitoring challenges due to their steep bathymetric gradients, heterogeneous substrates, and dynamic oceanographic conditions (Azevedo et al., 2024; Goode et al., 2021; Watling & Auster, 2017). These physical characteristics create diverse microhabitats that sustain high functional and taxonomic diversity, supporting a range of habitat-forming species such as cold-water corals and sponges (CWCS, Azevedo et al., 2024; Goode et al., 2021; Watling & Auster, 2017). As foundation species, CWCS enhance biodiversity by providing structural habitat for associated invertebrates and fish (Bell, 2008). Given their ecological importance, many seamounts have been incorporated into MPAs to protect vulnerable marine ecosystems (VMEs) and maintain structurally complex, biodiversity-supporting habitats (DFO, 2019; Wagner et al., 2020). However, the environmental complexity that supports diverse biological communities also complicates conservation efforts, as spatial variability, hydrodynamic conditions, and habitat heterogeneity result in highly dynamic species distributions, making it difficult to establish standardized monitoring protocols and long-term management strategies (Kuhnz et al., 2014; McClain et al., 2009; Thresher et al., 2014).

Canada has prioritized the protection of offshore seamount ecosystems within MPAs, including the SG̲áan K̲ínghlas-Bowie (SK̲-B) MPA and Tang.ɢwan — ḥačxwiqak — Tsig̲is (TḥT) MPA, which together encompass over 65 seamounts (DFO, 2024; DFO, 2019). The SK̲-B MPA, co-managed with the Haida Nation, represents an important collaboration integrating Indigenous stewardship with marine conservation (DFO, 2019). The TḥT MPA, covering over 133,000 km^2, is Canada’s largest MPA, designed to safeguard the ecological integrity of these remote ecosystems (DFO, 2024). Both MPAs host diverse CWCS communities, which serve as keystone habitat-forming species and play critical roles in supporting deep-sea biodiversity (DFO, 2024; DFO, 2019). One of the defining ecological features of these MPAs is the naturally occurring oxygen minimum zone (OMZ), which intersects multiple seamounts. This zone represents an important depth range for benthic communities, yet remains particularly vulnerable to climate-driven deoxygenation (Ross et al., 2020). The ecological significance of CWCS within these MPAs underscores the need for effective monitoring strategies to track population trends, detect environmental shifts, and inform adaptive management.

Given the challenges of species-level monitoring, functional group-based approaches offer a promising alternative for detecting ecological trends. A functional group refers to a collection of species that perform similar ecological roles or functions within an ecosystem, regardless of their taxonomic relationship (Azevedo et al., 2024; Goode et al., 2021). This approach enables the assessment of broader ecosystem patterns without requiring extensive taxonomic resolution. The use of biological traits in conservation strategies has gained traction as a way to incorporate ecological functioning into monitoring frameworks, improving the ability to assess vulnerability and detect ecosystem change (Miatta et al., 2021). By grouping species based on shared traits such as growth form, substrate preference, or feeding strategy, functional group-based monitoring may provide a more pragmatic tool for assessing community dynamics and tracking ecological shifts (Miatta et al., 2021). This method has been successfully applied in shallow-water and aquatic ecosystems, demonstrating its potential for tracking biodiversity shifts and ecosystem health (e.g., Frainer et al., 2017; Peng et al., 2013). In deep-sea environments, where surveys are infrequent and taxonomic identification is challenging, functional group monitoring could provide a scalable and cost-effective solution. While this approach has been applied in some deep-sea settings (e.g., Boschen-Rose et al., 2021; Danovaro et al., 2020), its applicability to spatially complex features like seamounts, where environmental gradients and species distributions vary at fine scales, requires further evaluation (Kuhnz et al., 2020; Smith & Hughes, 2008). Moreover, although CWCS are often grouped together as habitat-forming taxa because of their structural similarities, differences in morphology, skeleton composition, and microhabitat use can affect their ability to trap sediments, support associated species, and respond to disturbance. This highlights the importance of recognizing functional diversity within groups when interpreting monitoring results. Species that occupy consistent depth zones across multiple seamounts provide reliable baselines for detecting ecological shifts, as their distributions are less likely to fluctuate with small environmental variations.

This study applies a functional group-based approach to Northeast Pacific seamounts to evaluate its effectiveness for long-term monitoring. Specifically, this study aims to: (1) quantify inter-seamount variability in CWCS occupancy across depth gradients to determine whether seamounts in the Offshore Pacific Bioregion exhibit comparable spatial patterns; (2) examine intra-seamount variability in CWCS occupancy trends across different flanks of the same seamount, using Dellwood and Union seamounts as case studies, to assess whether monitoring efforts need to account for fine-scale spatial differences; and (3) identify key indicator species that could be used to streamline monitoring efforts. By addressing these objectives, this research quantifies CWCS occupancy patterns to evaluate the feasibility of functional group-based monitoring and optimize long-term conservation efforts in remote MPAs.

2.2 Methods

Data Collection and Annotation

Benthic ecology data were collected during two research expeditions led by Fisheries and Oceans Canada (DFO) in 2017 and 2018. The 2017 expedition (DFO-Pac2017-036) aboard the *CCGS John P. Tully* surveyed Union, Dellwood, Unnamed (UN) 16, and UN 18 seamounts. Transects were performed using the *Bathyal Ocean Observation and Televideo System* (BOOTS), a DFO drop camera system equipped with a forward-facing HD Minizeus video camera and 10 cm scaling lasers.

The 2018 expedition (DFO-Pac2018-103 & NA097) was conducted aboard the *EV Nautilus* in collaboration with the Council of the Haida Nation, Oceana Canada, and Ocean Networks Canada. Ten scientific dives were completed on six seamounts, including Dellwood, Dellwood South, SG̱áan Ḵínghlas-Bowie, Explorer, Hodgkins, and Pierce/Davidson. Dive transects were informed by multibeam bathymetry and proceeded upslope, capturing seamount communities from base to summit. The dives were conducted using the ROV *Hercules*, equipped with a high-definition video system and multiple still and environmental cameras. The ROV *Argus* was deployed in tandem to provide stable lighting and wide-angle overview footage. Continuous video footage and annotation logs were generated throughout each transect.

All video annotation work was conducted by the Deep-Sea Ecology team at DFO. For the 2017 expedition, annotations were originally compiled in a Microsoft Access database. These annotations were provided to me, and I subsequently cleaned and processed the associated navigational metadata. Navigation data were obtained from Ocean Networks Canada (ONC), who had previously cleaned and synchronized the navigation files with the video footage on a per-second basis. I used this matched video-navigation dataset to validate image locations, extract depth, latitude, and longitude, and remove non-target observations. For the 2018 expedition, annotations were also provided directly by DFO and were conducted using the online annotation platform Biigle (https://biigle.de).

To ensure data quality and consistency across years, a rigorous quality assurance and control (QA/QC) process was applied. Images taken during descent, ascent, or periods of poor visibility were excluded, along with duplicate and overlapping frames to prevent pseudoreplication. Taxonomic names and functional group classifications were standardized across datasets. Spatial metadata were validated using synchronized navigation files, and date and time stamps were cross-checked with dive logs to ensure temporal accuracy. This process resulted in the correction of over 600 entry errors in the 2017 dataset.

Observations containing *NA* or *NaN* values were removed. Where depth, latitude, or longitude values were missing, they were interpolated using a custom R script. This script identified consecutive missing values and linearly interpolated them using the nearest valid observations before and after the gap. This approach ensured spatial continuity and completeness of the data across each transect. Where applicable, the flank side of each seamount (e.g., northeast, southwest) was also recorded to support spatial comparisons in subsequent analyses.

Each row in the cleaned dataset represented a unique image frame annotated for the presence or absence of each functional group. These records also included corresponding metadata such as depth, latitude, longitude, and transect identifiers. These image-level records served as the sampling units (*n*) in subsequent statistical models.

Substrate type was also recorded during both expeditions and was initially explored as a potential environmental variable. The 2017 annotations included a wide range of specific substrate categories such as Pea Gravel, Sand, Cobble, Boulders, and Gravel, while the 2018 data used a smaller but still detailed set including Boulders, Bedrock (creviced or smooth), Cobble, and Gravel. However, inconsistencies in how substrates were categorized between years created challenges for integration. These issues became especially apparent during data standardization and 10 m depth binning, where multiple substrate types were sometimes recorded with equal frequency in a given bin. This led to the creation of hybrid categories like Cobble/Mud, PeaGravel/Sand, and Boulders/Gravel. To reduce complexity and allow for comparisons across years, all substrate types were collapsed into three broader categories: Rock, Mixed, and Soft. Despite these efforts, substrate type did not show any meaningful relationship with species or functional group patterns and was excluded from the final dataset and analyses.

Each observed taxon was assigned to one of nine functional groups, reflecting similarities in taxonomy, morphology, and ecological function. These groupings followed the framework proposed by Neves et al. in the 2021 Canadian Science Advisory Secretariat Science Advisory Report (DFO, 2021) and refined in a forthcoming document (Neves et al., in prep). Group assignments were made using a reference table developed for this project and validated by regional experts familiar with Northeast Pacific deep-sea fauna.

Taxa were matched to functional groups based on known morphology (e.g., fan-shaped, solitary, or reef-forming), phylogenetic relationships, and ecological traits such as growth form and skeleton composition. Where taxonomic resolution was limited, assignments were made conservatively to the group that best represented the available ecological and taxonomic information. A summary of the functional groups is provided in Table 2.1, and a complete list of taxa with their group assignments is presented in Appendix A.

Table 2.1. Functional groups assigned to observed taxa based on shared taxonomic characteristics and ecological roles, following the framework proposed by Neves et al. (DFO, 2021; Neves et al., in prep). Example taxa representative of species observed in the Northeast Pacific Bioregion are provided for each group to illustrate typical members.

Functional Group	Example Taxa	Description
Black Corals	*Bathypathes* spp.	Corals in the order Antipatharia; proteinaceous skeletons with whip or feather-like morphology.
Cup Corals	*Desmophyllum dianthus*	Solitary, small corals in the order Scleractinia with calcium carbonate skeletons
Glass Reef Sponges	*Farrea* spp.	Reef-building sponges that form large bioherms
Hydrocorals	*Stylaster* spp.	Order Anthoathecata; branching or encrusting corals with calcium carbonate skeletons.
Large Gorgonians	*Primnoa pacifica, Isidella tentaculum*	Order Alcyonacea; large arborescent or fan-shaped corals, growing to heights >2 m
Other Sponges	*Chonelasma oreia*	Mostly demosponges that do not belong to the other specified sponge groups
Sea Pens	*Anthoptilum grandiflorum, Umbellula lindahli*	Corals in the order Pennatulacea; characterized by a feather-like shape
Small Gorgonians	*Swiftia cf. pacifica*	Differentiated from Large Gorgonains by having smaller adult stages (<30 cm)
Soft Corals	*Gersemia sp., Anthomastus* sp.	Corals in the order Alcyonacea; lacking an inner axis, relying on a hydrostatic skeleton

Transect Selection

The preparation and filtering of the dataset culminated in the selection of specific transects and depth ranges to support quantitative analyses of both inter- and intra-seamount variability.

For the analysis of inter-seamount variability, five eastern-flank transects were selected across seamounts located within both MPAs: Dellwood (B028), Dellwood South (H1690), Hodgkins (H1685), SG̱aan Kinghlas–Bowie (H1687), and Union (B025) (Figure 2.1). Transects were chosen based on two key criteria: (1) all were conducted on the eastern side of their respective seamounts to minimize the potential influence of flank-specific environmental differences, and (2) each covered a consistent depth range of 600–1400 m, allowing for standardized comparisons across sites.

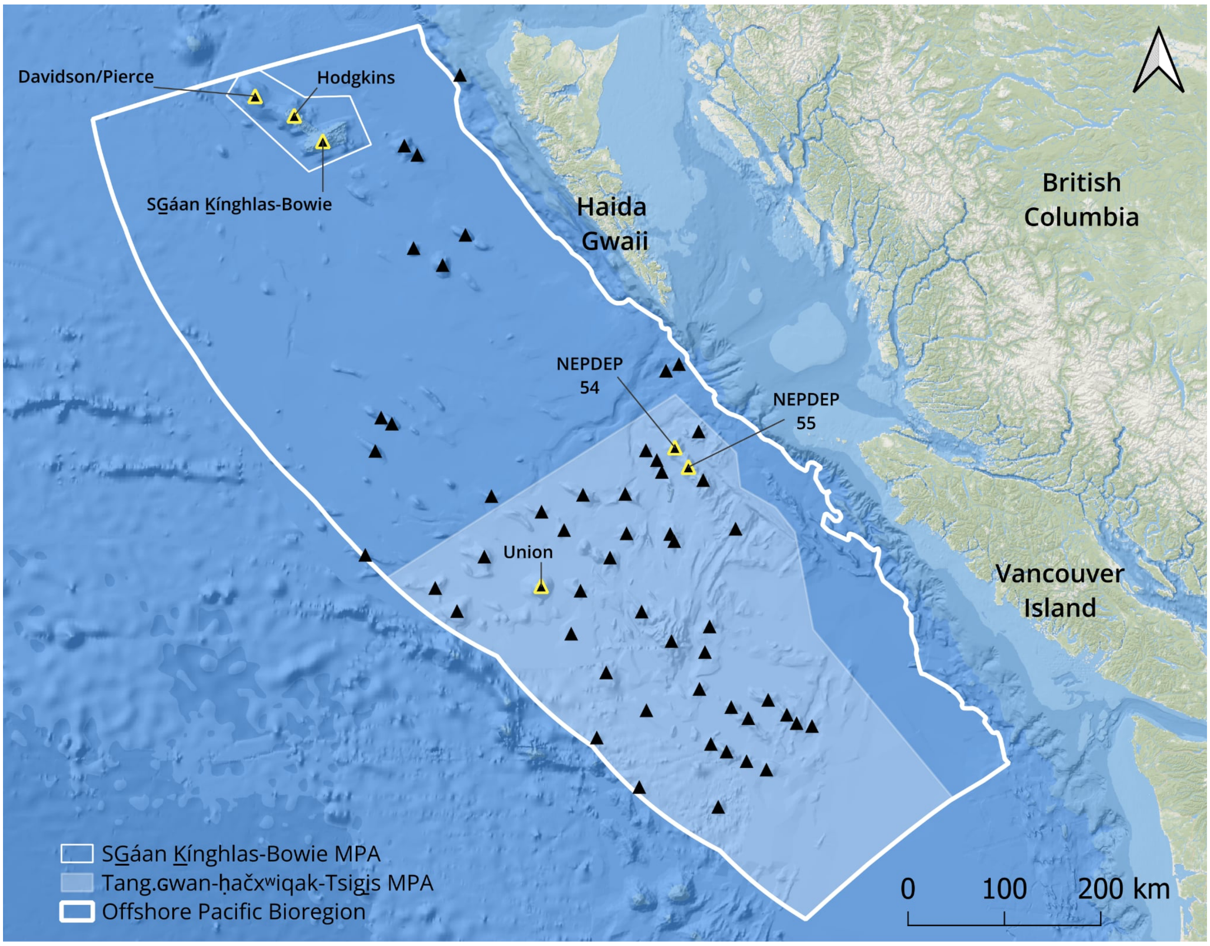

Figure 2.1. Map of the Offshore Pacific Bioregion showing identified seamounts within SG̱áan K̲ínghlas-Bowie Seamount MPA and Tang.ɢwan — ḥačxwiqak — Tsig̱is MPA. Seamounts are represented as black triangles, with yellow triangles indicating the specific seamounts included in this study. Two of the seamounts are listed on the map as NEPDEP 54 and NEPDEP 55, which are placeholder names; in this thesis, they are referred to as Dellwood and Dellwood South (historical names no longer in formal use). The Offshore Pacific Bioregion is outlined with a thick white boundary, SG̱áan K̲ínghlas-Bowie Seamount MPA is outlined with a thinner white line, and Tang.ɢwan — ḥačxwiqak — Tsig̱is MPA is shaded in white. Map created by Lindsay Clark and used with permission.

To quantify intra-seamount variability, Dellwood and Union were selected due to their more comprehensive spatial sampling. For Dellwood, three transects were analyzed from the East (B028), North (B029), and Southwest (B030) flanks. For Union, three transects were used from the Southeast (B024), East (B025), and West-Northwest (B026) flanks. These transects offered adequate depth overlap and spatial representation across multiple sides of the same seamount. However, it is important to note that the surveyed depth ranges varied slightly among these transects. For example, B025 extended to approximately 1500 m, whereas B024 and B026 reached depths exceeding 1700 m. This variation in depth coverage may influence comparative analyses, particularly in deeper zones where data for B025 are limited.

2.2.1 Combined Methods for Objectives 1 & 2

Data Processing:

Cold-water coral and sponge (CWCS) data were grouped by functional group and summarized into 10-meter depth bins. Key metrics, including mean depth, occupied bins, and binary occupancy indicators (presence/absence), were calculated to standardize datasets for analysis. These preprocessing steps, implemented using the dplyr and plyr R packages, ensured consistency across seamounts and transects.

Analytical Approach:

1. **Generalized Additive Mixed Models (GAMMs)**
   For both objectives, GAMMs were employed to investigate whether the probability of CWCS occupancy varies with depth, while accounting for nested variability among functional groups. The response variable, binary occupancy (Occ), was modelled as a function of depth, represented by a smooth term s(Mean Depth). Random effects were included for functional groups, with trends allowed to vary by seamount (Objective 1) or transect (Objective 2). The model formula was:

   $$\text{Occ} \sim s(\text{Mean Depth, by} = \text{Grouping Factor}) + (1 \mid \text{Functional Group})$$

   where "Grouping Factor" referred to seamount for Objective 1 and transect for Objective 2. Models were fitted using Generalized Additive Mixed Models with the binomial family and a logit link function, appropriate for the binary occupancy response. The models were implemented using the gamm function in the mgcv R package and fitted using restricted maximum likelihood (REML) to capture non-linear depth–occupancy relationships while accounting for group-level variation. Model complexity was evaluated using the effective degrees of freedom (EDF) associated with each smooth term. Higher EDF values indicate more complex, variable responses to depth, while lower EDF values suggest smoother, more gradual occupancy trends.

2. **Generalized Additive Models (GAMs) for Site-Specific Trends:**
   Due to convergence challenges with site-specific GAMMs, GAMs were employed for detailed predictions and visualization of depth-occupancy relationships. These models provided streamlined predictions, enabling comparisons across individual seamounts (Objective 1) and transects (Objective 2).

Peak Analysis and Visualization:

Predicted occupancy curves from the GAMs were analyzed to identify peak patterns in depth-related occupancy across seamounts and transects. A peak was defined as a distinct maximum in the predicted probability of occupancy along the depth gradient. For each functional group, three metrics were calculated to characterize these peaks: (1) the peak occupancy, representing the highest predicted probability of occurrence; (2) the peak depth, or the depth at which this maximum occurred; and (3) the peak width, calculated as the full-width at half-maximum (FWHM). FWHM refers to the range of depths over which the predicted occupancy remained above 50% of the maximum predicted value (Weik, 2000). In cases where peaks were too narrow or steep to allow for reliable FWHM estimation, peak width was recorded as NA.

Dominant Taxa Identification:

Following peak detection, contributions at the lowest taxonomic unit (e.g., species, genus, or other taxa) were assessed using occupancy data aggregated into 10-meter depth bins. For each identified peak, taxa contributing to total occupancy within a ±50 m depth range of the peak centre were identified. The dominant taxa were defined as the one or two contributors with the highest summed occupancy within this range. If no single taxon stood out as a clear contributor—due to similar occupancy values across multiple taxa—no dominant taxon was assigned. This approach ensured that only meaningful contributors were reported and acknowledged that, in some cases, group-level peaks may reflect the combined influence of several taxa rather than a single dominant driver.

Plots and Key Visual Outputs:

Depth-occupancy relationships were visualized using plots displaying predicted probabilities on the y-axis and depth on the x-axis. Confidence intervals (±1 SE) were included as shaded ribbons to indicate model uncertainty. Additionally, a severely hypoxic zone (800–1200 m) was highlighted using vertical dashed lines to contextualize ecologically relevant depth bands. Model summary tables were generated to report key statistical outputs, including effective degrees of freedom (edf), F-values, and p-values for depth-occupancy relationships. Peak analysis results were compiled into tables summarizing peak occupancy probabilities, peak depths, and peak widths for each functional group, facilitating direct comparisons across seamounts and transects.

2.2.2 Objective 3: Indicator Taxa

The third objective aimed to identify potential indicator taxa (species or lowest taxonomic units) to support the monitoring and management of seamount ecosystems. Unlike the broader functional group-level analyses in Objectives 1 and 2, this analysis focused on taxa-level contributions to observed occupancy patterns. Taxa-specific distribution trends were analyzed using data derived from previously constructed GAM models, with a particular focus on their contributions to peaks in predicted occupancy across seamounts.

Data Preparation and Metrics:

Observations were grouped by taxa, seamount, and transect and aggregated into 10 m depth bins to standardize the dataset. A binary occupancy indicator (1 for presence, 0 for absence) ensured consistency across datasets. The resulting data from Dellwood, Union, and the eastern transects of other seamounts (e.g., Hodgkins, SK̲-B, Dellwood South) were combined to form a unified dataset for analysis. This processing was facilitated by the dplyr and tidyr R packages, enabling efficient data manipulation.

For each taxon, several key metrics were calculated. Total occupancy was determined by summing the number of 10 m depth bins where the taxon was present, providing insight into its spatial and vertical extent. Minimum and maximum depths were used to calculate depth ranges, which were then classified as either Depth Specialists (depth range <100 m) or Broad Depth Range species (≥100 m). To further explore depth-related patterns, species distributions were categorized into three depth bands: Surface to 800 m, OMZ Severe Hypoxia (800–1200 m), and Oxygen Recovery (>1200 m). Taxa present across multiple bands were classified based on their band combinations, including Severe Hypoxia Specialists and All Depths Generalists.

Geographic Coverage and Indicator Classification:

The geographic distribution of each taxon was assessed by calculating the number of seamounts occupied, with seamount names and transect locations detailed (e.g., "Dellwood-East, Union-West-Northwest"). Taxa were then classified into one of four categories: Ubiquitous (present on >3 seamounts), Moderately Distributed (present on 2–3 seamounts), Local (restricted to a single seamount), or Depth-Specific (depth range <100 m). When a taxon fit both geographic spread and depth range criteria, it was classified as Depth-Specific to emphasize its ecological specialization. For example, a taxon found on multiple seamounts but restricted to a narrow depth range (<100 m) would be classified as Depth-Specific, highlighting its strong depth association despite its broader geographic distribution.

Indicator Potential, a management-oriented metric, was assigned based on two key factors: Total Occupancy and Ease of Identification. Taxa with high Total Occupancy (observed in more than 50 depth bins) and easy identification were classified as High Potential, as they are both widespread and practical for monitoring. Taxa with moderate occupancy (observed in 20–50 depth bins) or those requiring greater expertise to identify were categorized as Moderate or Low Potential, reflecting reduced feasibility for routine monitoring. Broad or ambiguous classifications, such as "Antipatharia," were excluded to focus on taxa with clear ecological roles and practical relevance for monitoring and management efforts.

Key Outputs:

Two key outputs were generated to support the characterization of taxa contributing to seamount ecosystem dynamics: an Ecological Details Table and a Management Indicators Table.

The Ecological Details Table summarizes taxa-level metrics, including minimum and maximum depths, depth ranges, and depth category classifications, such as Depth Specialist or Broad Depth Range. It also records the number of peaks identified for each taxon and evaluates their relevance to specific depth bands, including ecologically significant zones such as the oxygen minimum zone (OMZ) and areas of severe hypoxia. Additionally, this table provides geographic coverage information, detailing seamount locations where each taxon was observed and the transect directions in which they were recorded.

The Management Indicators Table categorizes taxa based on their distribution and potential use as monitoring indicators. Taxa are classified into indicator types, including Ubiquitous, Moderately Distributed, Local, or Depth-Specific, and assigned an indicator potential rating of High, Moderate, or Low. The table also incorporates practical considerations for monitoring, such as ease of identification, categorized as Easy, Moderate, or Hard, and evaluates depth band relevance to inform conservation priorities. These classifications provide a structured approach for integrating taxa into monitoring programs and refining management strategies.

This methodological approach ensured that taxa contributing meaningfully to seamount ecosystem dynamics were identified and characterized, supporting both long-term conservation goals and adaptive management strategies.

2.3 Results

2.3.1 Objective 1: Inter-seamount Variability of CWCS functional groups

Significant inter-seamount variability in depth-occupancy relationships was observed (Table 2.2). Each seamount exhibited distinct depth-dependent occupancy patterns, as reflected by variations in model complexity (Figure 2.2). The effective degrees of freedom (edf), which indicate how flexible the depth-occupancy relationship is, ranged from 3.87 for SK̲-B, where the relationship is relatively smooth, to 8.65 for Union, where occupancy fluctuates more sharply with depth. Higher edf values indicate greater complexity in the modelled trend, meaning occupancy changes more dynamically across depth, whereas lower edf values suggest smoother, more gradual trends (Figure 2.2).

All depth terms were significant ($p < 0.001$), with the most complex depth-occupancy relationship observed at Union (edf = 8.65, F-value = 35.85), where occupancy varied non-linearly with depth. In contrast, SK̲-B exhibited the simplest relationship (edf = 3.87, F-value = 11.90), while Hodgkins showed moderate complexity (edf = 5.04, F-value = 4.29). Dellwood South followed a smoother trend (edf = 4.48, F-value = 14.68), whereas Dellwood Seamount displayed a highly non-linear pattern (edf = 7.09, F-value = 6.99).

Table 2.2. Summary of GAMM Results for Depth-Occupancy Relationships Across Seamounts. Results of the Generalized Additive Mixed Model (GAMM) analyzing depth-occupancy relationships for CWCS functional groups across Dellwood, Dellwood South, Hodgkins, SK̲-B, and Union seamounts. The table includes the family (Binomial), link function (logit), model formula, adjusted R^2, and sample size (n). Parametric coefficients detail the intercept estimate, standard error, t-value, and p-value for occupancy probability, while smooth terms summarize the effective degrees of freedom (edf), reference degrees of freedom (Ref.df), F-values, and p-values for depth-occupancy relationships specific to each seamount. Significant relationships are denoted by $^{**}p < 0.01$ and $^{***}p < 0.001$.

Family	Link Function	Formula	Adjusted R^2	n
Binomial	logit	Occ ~ s(Mean Depth, by = Seamount)	0.108	4248

Parametric Coefficients

	Estimate	Std. Error	t/ F Value	edf	Ref.df	*p*-value
(Intercept)	-1.2817	0.4282	-2.993	-	-	0.00278 **
Smooth Terms						
Mean Depth: Dellwood			6.994	7.094	7.094	< 2e-16 ***
Mean Depth: Dellwood South			14.675	4.479	4.479	< 2e-16 ***
Mean Depth: Hodgkins			4.285	5.040	5.040	0.000523 ***
Mean Depth: SK̲-B			11.900	3.865	3.865	< 2e-16 ***
Mean Depth: Union			35.845	8.649	8.649	< 2e-16 ***

These patterns are further illustrated in Figure 2.2, where differences in trend complexity across seamounts can be observed visually. Seamounts with lower edf values exhibit smooth, broad occupancy trends, whereas those with higher edf values show more pronounced fluctuations in occupancy across depth. The statistical outputs in Table 2.2 provide further context for these visual patterns, confirming significant variability in depth-occupancy relationships among seamounts.

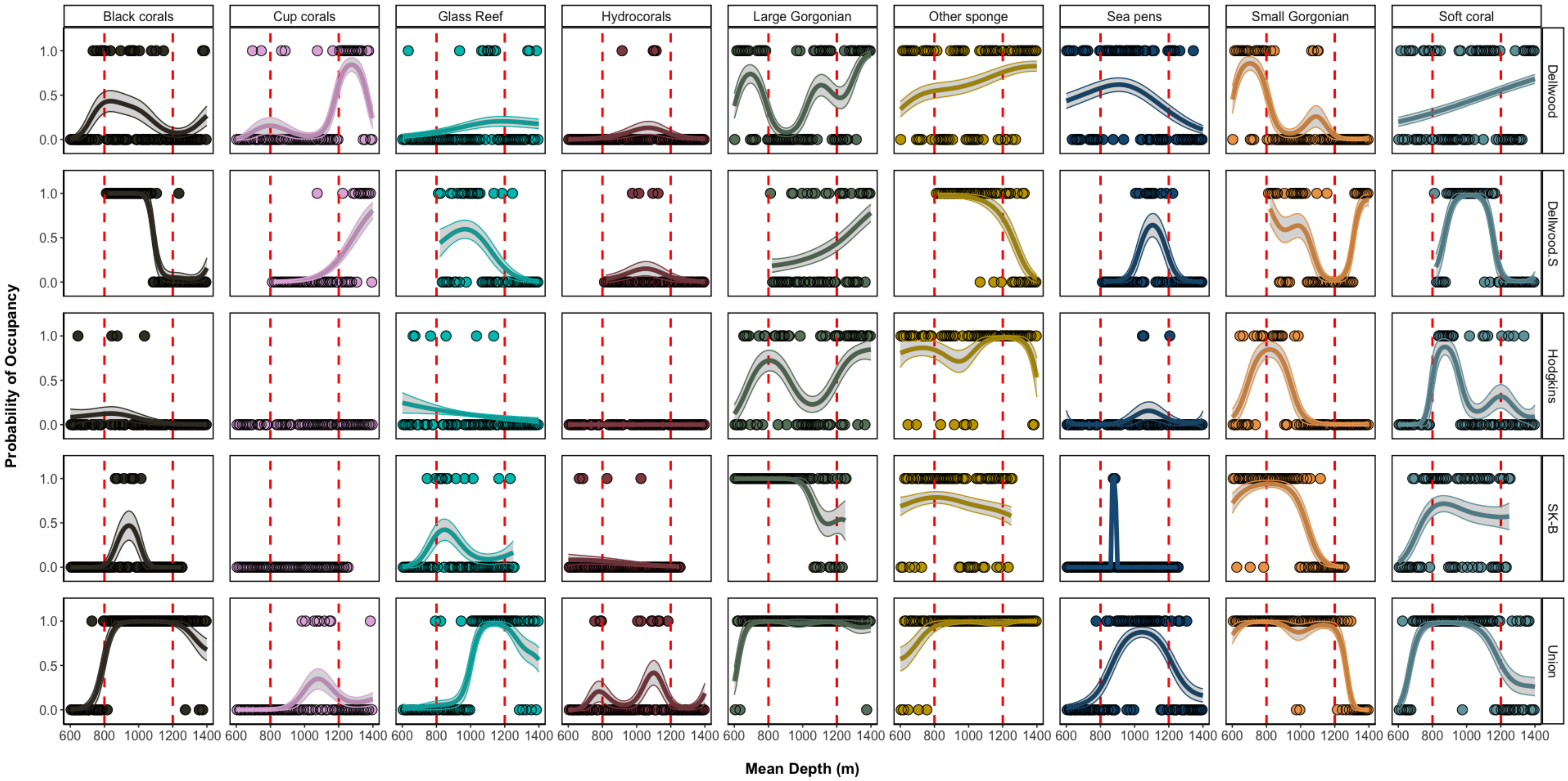

Figure 2.2. Predicted occupancy probability of CWCS functional groups across five seamounts, shown as a panel plot with mean depth on the x-axis (600–1400 m) and occupancy probability on the y-axis (0 = zero probability, 1 = predicted occupancy). Each row represents one of the five seamounts (eastern transects only), while each column represents a different functional group, with color-coded lines for each group. Smooth lines represent the predicted occupancy trends based on

the GAMM model, with shaded ribbons indicating the standard error (SE) of the predictions. Red dashed vertical lines at 800 m and 1200 m mark the depth range of the severely hypoxic water within the local oxygen minimum zone (OMZ), providing context for occupancy patterns relative to low-oxygen conditions. Dots on each plot indicate raw occupancy data points, allowing for comparison between observed and predicted occupancy trends across seamounts and functional groups.

Distinct depth ranges were identified where functional groups are most likely to occur (Figure 2.2, Table 2.3). Some groups, such as Large Gorgonians and Small Gorgonians, exhibit multiple peaks (Figure 2.2), with occupancy increasing at distinct depth intervals. Other groups show single peaks, with occupancy concentrated at specific depths (Table 2.3). Several peaks occur within the severely hypoxic oxygen minimum zone (OMZ) (800–1200 m), where functional groups are present (Figure 2.2).

Union and Dellwood South consistently exhibit high peak occupancy probabilities across multiple functional groups, with values often nearing or reaching 1.00 (Table 2.3). Taxa such as Black Coral (*Chrysopathes* spp., *Lillipathes* sp.), Glass Reef Sponges (*Farrea* spp., *Aphrocallistidae* spp.), Soft Corals (*Anthomastus* spp., Mushroom coral), and Other Sponges (*Tretodictyum* n. sp., *Pinulasma* n. sp., Demosponge white encrusting) show the highest predicted occupancies on these seamounts (Figure 2.2). In contrast, SK-B displays high occupancy for a limited number of groups, including Large and Small Gorgonians (*Parastenella* spp., *Keratoisis* sp., *Swiftia* spp.) and Sea Pens (*Halipteris* sp., *Umbellula lindahli*), but overall supports fewer functional groups compared to Union and Dellwood South (Table 2.3). Dellwood exhibits lower predicted occupancies, even relative to its geographically proximate neighbour, Dellwood South.

Table 2.3. Summary of peak occupancy values for CWCS functional groups across eastern transects of five seamounts, based on predicted occupancy trends generated using the GAM component of the GAMM analysis. For each functional group and seamount combination, the table lists the number of observed occupancy peaks (Peak No.), the peak occupancy probability (Peak Occ.), the depth at which peak occupancy occurs (Peak Depth, m), the width of the peak (Peak Width, m), and the dominant taxa contributing to the peak. Peak widths were calculated using the full-width at half maximum (FWHM) method; in some cases, this calculation returned an NA for peak width despite a defined peak depth. Peaks within the severely hypoxic depth bands of the local oxygen minimum zone (OMZ, 800–1200 m) are included, indicating potential functional group tolerance to low-oxygen conditions.

Functional Group	Seamount	Peak No.	Peak Occ.	Peak Depth	Peak Width	Dominant Taxa
Black Coral	Dellwood	1	0.44	854	376	*Chrysopathes* spp.
	Dellwood S.	1	1.00	917	361	*Chrysopathes* spp.
	SK-B	1	0.46	932	172	*Lillipathes* sp.
	Union	1	0.99	1073	705	*Lillipathes* sp.
Cup Corals	Dellwood	1	0.16	791	235	Scleractinia
		2	0.88	1277	204	Cup coral (red tentacles)
	Union	1	0.41	1073	172	*Lillipathes* sp.
Glass Reef	Dellwood	1	0.20	1183	*NA*	*Farrea* spp.
	Dellwood S.	1	0.60	964	455	*Farrea* spp.

Functional Group	Seamount	Peak No.	Peak Occ.	Peak Depth	Peak Width	Dominant Taxa
	SK̲-B	1	0.42	854	235	*Farrea* spp.
	Union	1	0.97	1136	439	*Farrea* spp.
Hydrocoral	Dellwood	1	0.13	1073	282	*Stylaster* spp.
	Dellwood S.	1	0.15	1058	282	*Stylaster* spp.
	SK̲-B	1	0.08	634	*NA*	*Stylaster* spp.
	Union	1	0.21	776	157	*Swiftia* spp.
		2	0.42	1105	172	*Stylaster* spp.
Large Gorgonian	Dellwood	1	0.74	697	220	*Isidella tentaculum*, *Parastenella* spp.
		2	0.61	1105	659	*Paragorgia pacifica*
	Hodgkins	1	0.72	807	314	*Parastenella* spp.
	SK̲-B	1	1.00	776	768	*Parastenella* spp.
		2	0.54	1230	1003	*Keratoisis* sp. (bush) & Unbranched Isididae
	Union	1	0.99	807	909	*Parastenella* spp.
		2	0.99	1136	909	*Parastenella* spp.
Other Sponge	Dellwood	1	0.83	1387	*NA*	Demosponge (white encrusting)
	Dellwood S.	1	0.98	885	815	*Tretodictyum* n.sp. (striated)
	Hodgkins	1	0.87	729	1003	*Pinulasma* n. sp.
		2	0.98	1215	988	Demosponge (white encrusting)
	SK̲-B	1	0.79	807	*NA*	Rossellidae (boot sponge)
	Union	1	0.99	995	*NA*	*Pinulasma* n. sp.
		2	1.00	1387	*NA*	Demosponge (white encrusting)
Sea Pens	Dellwood	1	0.62	9001	800	*Umbellula lindahli*
	Dellwood S.	1	0.64	1105	188	Halipteris sp. (whip)
	Hodgkins	1	0.16	1089	220	*Anthoptilum* cf *lithophilum* & Pennatulacea
	SK̲-B	1	1.00	885	47	*Halipteris* sp. (whip)
	Union	1	0.87	1042	408	*Anthoptilum grandiflorum*
Small Gorgonian	Dellwood	1	0.86	697	235	*Paragorgia* sp. (pale)
		2	0.26	1089	172	*Paragorgia* sp. (pale)
		3	0.05	1528	188	*Paragorgia* sp. (pale)
	Dellwood S.	1	0.98	697	470	*Swiftia* spp. & Unknown Paragorgiid
		2	0.64	979	517	*Swiftia* spp.
		3	0.92	1387	188	*Callogorgia* sp.

Functional Group	Seamount	Peak No.	Peak Occ.	Peak Depth	Peak Width	Dominant Taxa
	Hodgkins	1	0.85	823	282	*Paragorgia* sp. (pale)
	SK̲-B	1	0.94	823	517	*Paragorgia* sp. (pale) & Unknown Paragorgiid
	Union	1	0.99	776	*NA*	*Swiftia* spp.
		2	0.96	1136	*NA*	*Swiftia* spp.
Soft Coral	Dellwood S.	1	0.98	1011	314	Mushroom coral cf. *Anthomastus* sp.
	Hodgkins	1	0.88	870	188	Mushroom coral (stalked)
		2	0.32	1199	235	Mushroom coral cf. *Anthomastus* sp. & Mushroom coral (stalked)
	SK̲-B	1	0.72	870	*NA*	Mushroom coral cf. *Anthomastus* sp.
	Union	1	0.98	885	549	Mushroom corals

Peak occupancies occur across a broad range of depths (Figure 2.2, Table 2.3), with many concentrated between 800 and 1200 m, overlapping with the severely hypoxic region of the OMZ. For instance, Black Coral on Union reaches a peak occupancy near 1070 m, driven by *Lillipathes* sp., while *Chrysopathes* spp. contributes to peaks around 850–900 m on Dellwood (Table 2.3). Large Gorgonians peak at 807 m on Hodgkins and 1136 m on Union. Sea Pens and Soft Corals consistently reach their highest occupancies within this depth range across multiple seamounts (Figure 2.2). Shallower depths (<800 m) generally show lower peak occupancy values, while deeper peaks, such as Other Sponges on Union at 1387 m, extend into zones with higher oxygen levels (Table 2.3).

Certain functional groups exhibit multiple peaks on the same seamount side (Figure 2.2, Table 2.3). For example, Large Gorgonians on SK̲-B show peaks at 776 m and 1230 m, driven by *Parastenella* spp. and *Keratoisis* sp., while on Union, peaks occur at 807 m and 1136 m, primarily contributed by *Parastenella* spp.. Similarly, Small Gorgonians exhibit up to three peaks on Dellwood and Dellwood South, spanning depths from 700 m to 1390 m, with dominant taxa such as *Swiftia* spp., *Callogorgia* sp., and *Paragorgia* sp. (pale).

Peak widths, representing the range of depths with high occupancy predictions, vary across seamounts and functional groups (Table 2.3). Large Gorgonians and Other Sponges on Union and SK̲-B exhibit wider peak widths, often exceeding 500 m. These variations reflect differences in the depth ranges occupied by functional groups (Figure 2.2).

Functional Groups

Seamounts exhibit both shared depth-occupancy trends and distinct differences in functional group distributions (Figure 2.3). Black Corals (Figure 2.3, A) show peak occupancy within the severely hypoxic zone of the oxygen minimum zone (OMZ; 800–1200 m) across all seamounts. Union and Dellwood South display high peak occupancies (0.99 and 1.0, respectively), while lower peaks occur on Dellwood (0.44) and SK-B (0.46). Peak depths range from 854 m on Dellwood to 1073 m on Union, remaining within the OMZ. Union exhibits the widest peak (705 m), while Dellwood and SK-B show narrower peaks (376 m and 172 m, respectively), indicating variability in the depth range of high occupancy.

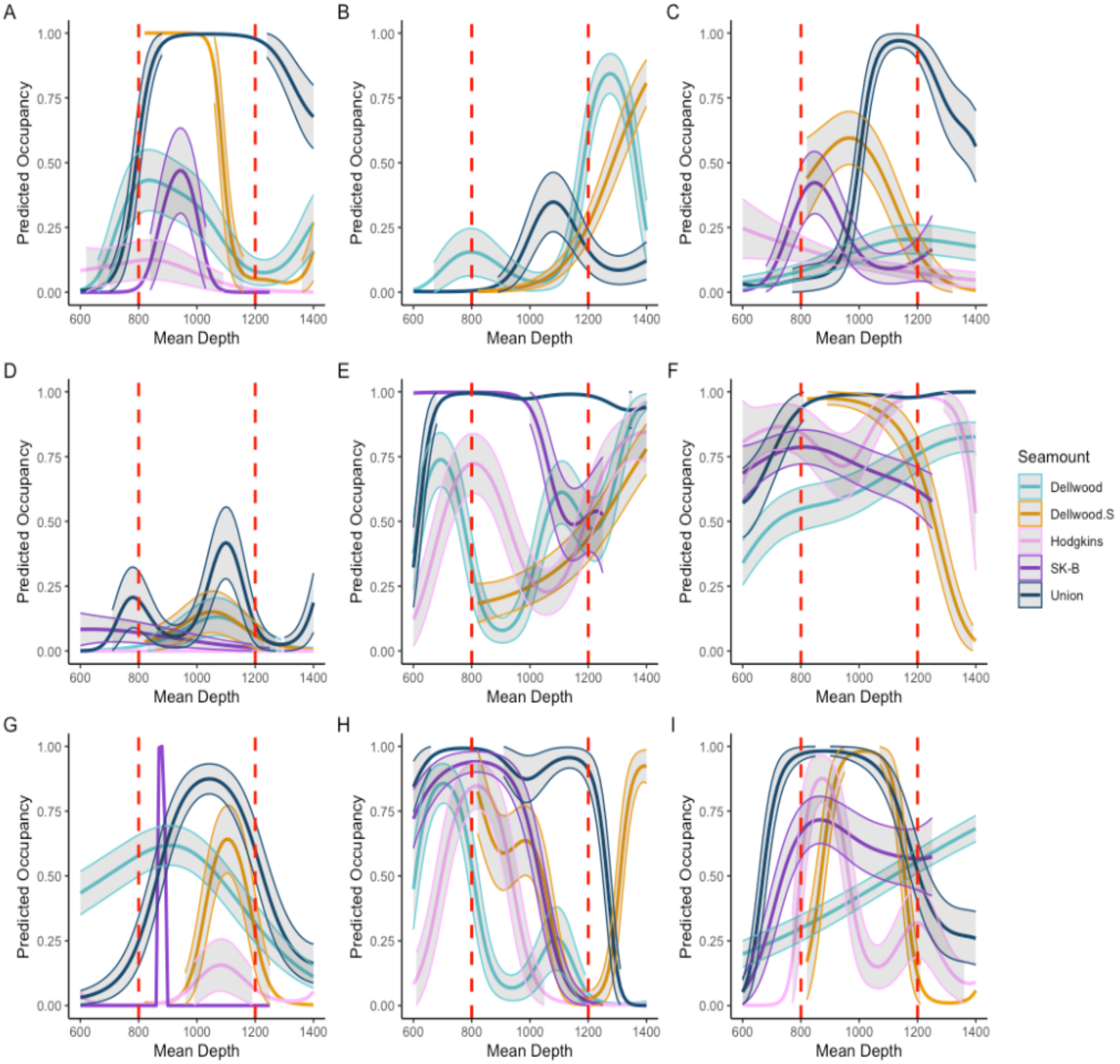

Figure 2.3. Predicted occupancy trends for cold-water coral and sponge (CWCS) functional groups across seamounts. Each plot displays predicted occupancy probabilities (y-axis) along depth gradients (x-axis) for a specific functional group, with lines color-coded by seamount to illustrate spatial differences. Dashed red lines at 800 m and 1200 m indicate the severely hypoxic zone of the oxygen minimum zone (OMZ), and key peaks are annotated to highlight seamount-specific depth-occupancy relationships. Panels represent different functional groups: **(A)** Black Corals, **(B)** Cup Corals, **(C)** Glass Reef Sponges, **(D)** Hydrocorals, **(E)** Large Gorgonians, **(F)** Other Sponges, **(G)** Sea Pens, **(H)** Small Gorgonians, and **(I)** Soft Corals, each exhibiting distinct depth-related trends, with some showing single peaks indicative of narrow habitat preferences, while others display multiple peaks suggesting broader depth adaptability.

Cup Corals (Figure 2.3, B) exhibit distinct occupancy patterns across seamounts. Dellwood has two peaks at 791 m and 1277 m, while Union shows a single peak at 1073 m. Dellwood's higher peak occupancy of 0.88 at 1277 m contrasts with Union's peak of 0.41. Dellwood's peaks span both inside and outside the OMZ, whereas Union's is entirely within it. Peak widths are relatively narrow (Union: 172 m; Dellwood: 235 m and 204 m). Dellwood South shows a gradual increase in occupancy around 1100 m, suggesting deeper habitat use.

Glass Reef Sponges (Figure 2.3, C) display variable depth-occupancy trends. Union has the highest peak occupancy (0.97 at 1136 m), followed by Dellwood South (0.60 at 964 m) and SK̲-B (0.42 at 854 m), while Dellwood has the lowest peak (0.20 at 1183 m). Peak depths are concentrated within or near the OMZ. Union and Dellwood South have broader peak widths (455 m and 439 m, respectively), while Dellwood and SK̲-B show narrower peaks, suggesting more localized depth preferences.

Hydrocorals (Figure 2.3, D) have low peak occupancy probabilities across all seamounts, with Union showing the highest peak at 0.42. Union has two peaks (776 m and 1105 m), while Dellwood, Dellwood South, and SK̲-B each show a single peak. SK̲-B has the shallowest peak (634 m), whereas Dellwood and Dellwood South have peaks just above 1050 m. Dellwood South exhibits broader peaks, suggesting a more stable depth range, while narrower peaks on Union and Dellwood indicate more localized occupancy. Hydrocorals are absent from Hodgkins' eastern transect, and SK̲-B's occupancy predictions decline steadily with depth.

Large Gorgonians (Figure 2.3, E) exhibit high peak occupancies on SK̲-B and Union, both approaching 1.0. SK̲-B and Union each display two distinct peaks: one within the OMZ (775–807 m) and another at deeper depths (1136 m on Union; 1230 m on SK̲-B). Peak depths range from 697 m on Dellwood to 1230 m on SK̲-B. SK̲-B and Union show broad peak widths (768 m and 909 m, respectively), suggesting stable conditions, whereas Dellwood and Hodgkins display narrower peaks. Predicted occupancy patterns vary considerably across seamounts, with no consistent trend.

Other Sponges (Figure 2.3, F) have high predicted occupancy across most depth bands, particularly on Dellwood South and Union (0.98 and 1.0, respectively). Hodgkins displays two peaks, while Dellwood South, Dellwood, SK̲-B, and Union show a single peak or broad, less-defined peaks. Peak depths range from 729 m on Hodgkins to 1387 m on Union, indicating adaptability across depths. Hodgkins (1003 m) and Dellwood South (815 m) have broad peak widths, suggesting extensive suitable habitat, whereas Union's peak at 1387 m is narrower. Occupancy declines beyond 1000 m on Dellwood South and around 1300 m on Hodgkins.

Sea Pens (Figure 2.3, G) exhibit variable predicted occupancy patterns. SK̲-B reaches the highest peak occupancy (1.0), while Union and Dellwood follow with peaks of 0.87 and 0.62. Peak depths range from 885 m on SK̲-B to 1105 m on Dellwood South, mostly aligning with the OMZ. SK̲-B has a sharply localized peak (47 m width), indicating a restricted depth range, while Dellwood (800 m) and Union (408 m) exhibit broader peaks, suggesting more gradual occupancy changes.

Small Gorgonians (Figure 2.3, H) show complex occupancy patterns, with peak occupancies highest on Union (0.99 at 776 m) and Dellwood South (0.98 at 697 m). SK̲-B and Dellwood follow with peaks of 0.94 and 0.86. Peak depths range widely, from 697 m on Dellwood to 1387 m on Dellwood South. Broad peak widths on Dellwood South (470 m) and SK̲-B (517 m) contrast with narrower peaks on Dellwood, indicating more localized depth preferences. Predicted occupancy declines beyond 1200 m on Union, while Dellwood South shows increasing occupancy at deeper depths.

Soft Corals (Figure 2.3, I) reach high peak occupancies on Dellwood South (0.98 at 1011 m), Union (0.98 at 885 m), and Hodgkins (0.88 at 870 m). SK̲-B has a lower peak (0.72 at 870 m). Hodgkins is the only seamount with two peaks (870 m and 1199 m). Most peak depths align with the OMZ, such as Union's peak at 885 m, while Hodgkins' secondary peak extends deeper. Peak widths vary, with Union (549 m) and Dellwood South (314 m) showing broader widths, whereas Hodgkins and SK̲-B have narrower peaks.

2.3.2 Objective 2: Intra-seamount Variability of CWCS functional groups

2.3.2.1 Case Study #1: Dellwood Seamount

There is variation in the occupancy trends between the eastern (B028), northern (B029), and southwestern (B030) transects of Dellwood Seamount. Distinct patterns in functional group distributions with depth were evident, emphasizing the influence of transect-specific environmental and ecological factors (Table 2.4).

Table 2.4. Summary of GAMM output for depth-occupancy relationships across Dellwood Seamount transects. The table includes the effective degrees of freedom (EDF), reference degrees of freedom (Ref.df), F-values, and p-values for each transect-specific smooth term (s(Mean Depth, by Transect)), along with the model's adjusted R² and overall significance of depth as a predictor of CWCS functional group occupancy.

Family	**Link Function**	**Formula**				**Adjusted R²**	**n**
Binomial	logit	Occ ~ s(Mean Depth, by =Transect)				0.11	3987
Parametric Coefficients							
	Estimate	**Std. Error**	**t/ F Value**	**edf**	**Ref.df**	***p*-value**	
(Intercept)	-1.0753	0.3251	-3.307	-	-	0.00095 ***	
Smooth Terms							
Mean Depth: B028			6.116	6.499	6.499	9.95e-07***	
Mean Depth: B029			29.318	6.590	6.590	< 2e-16 ***	
Mean Depth: B030			23.776	8.555	8.555	< 2e-16 ***	

Depth-occupancy relationships varied among transects, as indicated by differences in effective degrees of freedom (edf) (Figure 2.4, Table 2.4). B028 exhibited the simplest depth-occupancy trend, with an edf of 6.50, while B030 showed the most complex trend, with an edf of 8.56. B029 displayed an edf of 6.59. All depth terms were statistically significant ($p < 0.001$; Table 2.4), confirming that depth is a strong predictor of CWCS occupancy across all transects.

Predicted occupancy on B028 remained relatively low beyond 1200 m, while B029 displayed a broader range of high occupancy probabilities across depths. B030 showed multiple peaks in predicted occupancy, suggesting variation in depth preferences. Each transect exhibited distinct occupancy trends, with differences in peak depths and occupancy probabilities across the surveyed depth range (Figure 2.4).

Figure 2.4 illustrates these depth-occupancy relationships, and Table 2.4 provides a summary of GAMM output for Dellwood Seamount transects.

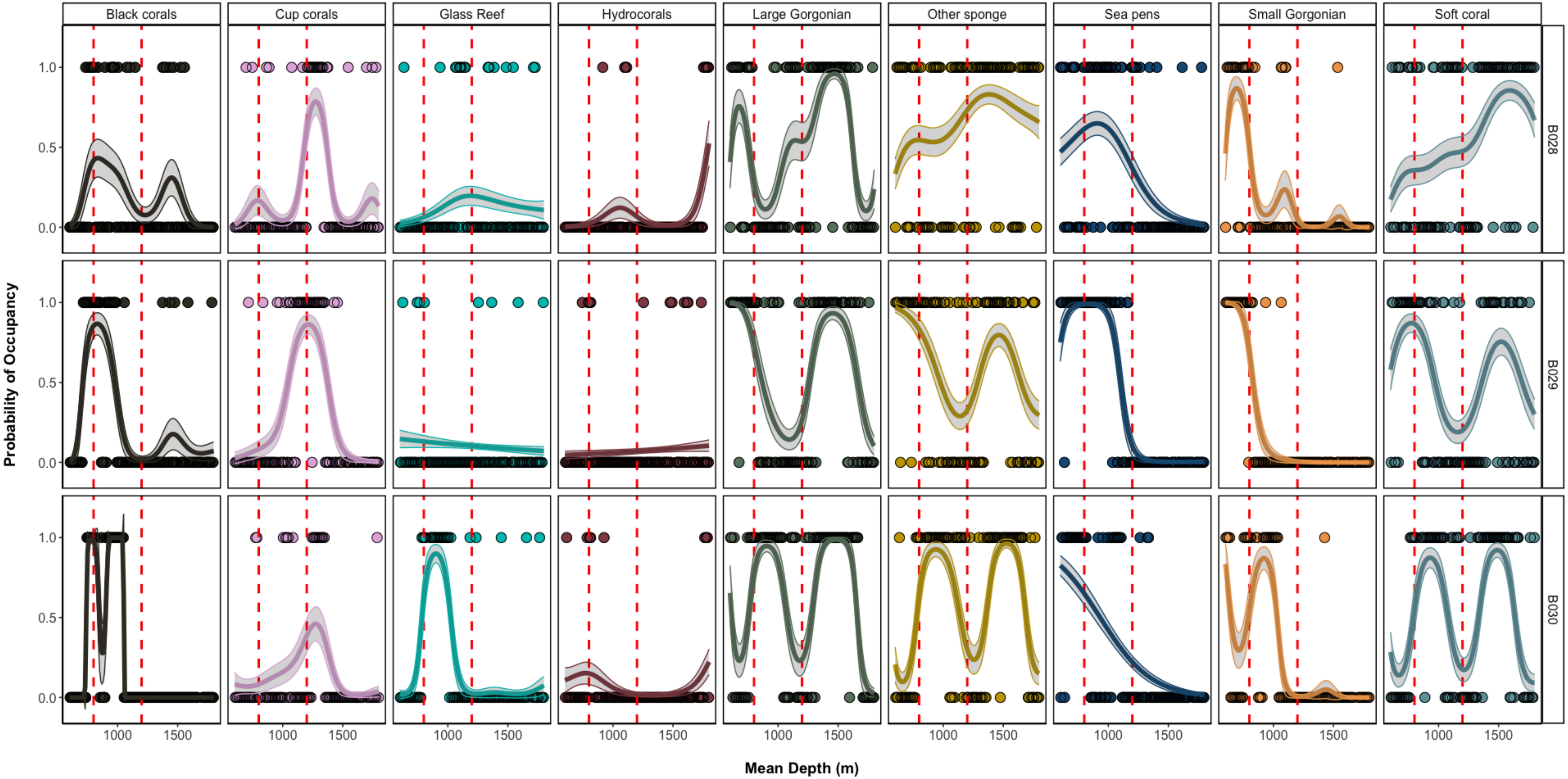

Figure 2.4. Panel plot showing predicted occupancy probability of CWCS functional groups across three Dellwood transects (B028, B029, B030). The x-axis represents mean depth (600–1800 m), and the y-axis represents occupancy probability (0–1). Smooth lines represent predicted occupancy trends, with shaded

ribbons indicating standard error (SE). Dashed red vertical lines at 800 m and 1200 m denote the severely hypoxic depth range of the local oxygen minimum zone (OMZ). Each panel corresponds to a functional group, illustrating how their predicted occupancy varies across transects relative to depth and hypoxia.

Predicted peak occupancy values for CWCS functional groups across the eastern (B028), northern (B029), and southwestern (B030) transects of Dellwood Seamount reveal notable variation in depth preferences and functional group distributions (Figure 2.4, Table 2.5). Some groups, such as Large Gorgonians, exhibit consistently high peak occupancy values across all transects, while others, like Black Corals, show more variability. Black Corals reach a peak occupancy of 1.00 on B030 at 997 m, compared to a lower peak of 0.44 on B028 at 880 m.

Several functional groups display distinct depth preferences, with many peaks occurring within or near the severely hypoxic portion of the OMZ (800–1200 m; Figure 2.4). Sea Pens on B028 reach a peak occupancy of 0.87 at 914 m, while Soft Coral on B029 peaks at 777 m. Other groups extend beyond the OMZ, such as Soft Coral on B030 at 1598 m and Other Sponges on B028 at 1376 m, indicating their occurrence in deeper habitats.

Some functional groups exhibit multiple peaks across transects, reflecting varied depth distributions. Small Gorgonians show peaks on B028 at 692 m 1085 m and 1547 m, similarly, Cup Corals on B028 peak at 794 m, 1273 m and 1735 m. These multiple peaks indicate variation in predicted occupancy across Dellwood Seamount (Figure 2.4).

Table 2.5. Peak Occupancy Values for CWCS Functional Groups on Dellwood Transects. Summary of peak occupancy values for CWCS functional groups across Dellwood transects (B028, B029, B030), based on predicted occupancy trends from the GAM component of GAMM models. For each functional group and transect, the table lists the number of observed occupancy peaks (Peak No.), the peak occupancy probability (Peak Occ.), the depth at which peak occupancy occurs (Peak Depth, m), the width of the peak (Peak Width, m), and the dominant taxa associated with each peak. Peak widths were calculated using the full-width at half-maximum (FWHM) method. *NA* in the "Dominant Taxa" column indicates that no single species or genus contributed clearly to the peak (e.g., due to multiple co-dominant taxa or a lack of consistent contribution). *NA* in "Peak Width" reflects peaks that were not wide enough to meet the threshold required to calculate a full FWHM value.

Functional Group	Seamount Side	Transect	Peak No.	Peak Occ.	Peak Depth	Peak Width	Dominant Taxa
Black Corals	E	B028	1	0.44	880	342	*Chrysopathes* spp.
			2	0.24	1444	342	*Bathypathes* sp.
	N	B029	1	0.89	829	2774	*Chrysopathes* spp.
			2	0.17	1478	240	*Bathypathes* sp. & *Chrysopathes* spp.
	SW	B030	1	0.99	780	111	*NA*
			2	1.00	997	153	*NA*
Cup Corals	E	B028	1	0.17	794	240	*NA*
			2	0.79	1273	325	Cup coral (red tentacles)

Functional Group	Seamount Side	Transect	Peak No.	Peak Occ.	Peak Depth	Peak Width	Dominant Taxa
			3	0.18	1735	188	Scleractinia
	N	B029	1	0.86	1222	376	Cup coral (red tentacles)
	SW	B030	1	0.46	1273	325	Cup coral (red tentacles)
Glass Reef	E	B028	1	0.20	1188	1026	*Farrea* spp.
	SW	B030	1	0.90	897	2567	*Farrea* spp.
			2	0.03	1393	*NA*	*NA*
Hydrocorals	E	B028	1	0.12	1051	325	*Stylaster* spp.
	SW	B030	1	0.15	777	*NA*	*Stylaster* spp.
Large Gorgonian	E	B028	1	0.76	675	205	*Isidella tentaculum*
			2	0.54	1136	667	*Paragorgia pacifica*
			3	0.96	1461	564	*Keratoisis* sp. (bush)
	N	B029	1	0.93	1461	445	*Keratoisis* sp. (bush)
	SW	B030	1	0.95	914	342	*Parastenella* spp.
			2	0.99	1478	393	*Keratoisis* sp. (bush)
Other Sponge	E	B028	1	0.55	794	*NA*	Rossellidae (boot sponge)
			2	0.83	1376	*NA*	Demosponge (white encrusting)
	N	B029	1	0.80	1461	462	Demosponge (white encrusting)
	SW	B030	1	0.93	931	393	Hexactinellida
			2	0.96	1530	359	Demosponge (white encrusting)
Sea Pens	E	B028	1	0.65	914	*NA*	*Umbellula lindahli*
	N	B029	1	0.99	829	581	*Halipteris* sp. (whip)
Small Gorgonian	E	B028	1	0.87	692	222	*Paragorgia* sp. (pale)
			2	0.24	1085	171	*Paragorgia* sp. (pale)
			3	0.07	1547	137	*Paragorgia* sp. (pale)
	SW	B030	1	0.87	914	291	*Paragorgia* sp. (pale)
			2	0.05	1444	188	*Paragorgia* sp. (pale)
Soft Coral	E	B028	1	0.86	1598	906	Mushroom corals
	N	B029	1	0.87	777	445	Mushroom corals
			2	0.75	1530	462	Mushroom corals
	SW	B030	1	0.87	931	325	Mushroom corals

Functional Group	Seamount Side	Transect	Peak No.	Peak Occ.	Peak Depth	Peak Width	Dominant Taxa
			2	0.92	1495	325	Mushroom corals

Peak widths vary considerably, providing insight into the depth range of high occupancy. Wider peaks, such as Glass Reef Sponges on B028 (1026 m) and Soft Coral on B028 (906 m), suggest broader high-occupancy depth zones. In contrast, narrower peaks, such as Sea Pens on B029 (581 m), indicate more localized occupancy patterns (Table 2.5).

For some predicted peaks, including Black Corals on B030 at 780 m and 997 m and Cup Corals on B030 at 794 m, no corresponding species contributions were found in the observational data. These cases are reported as *NA* in Table 2.5. Such discrepancies may be due to gaps in depth coverage during surveys or the patchy distribution of certain taxa, leading to low detection probabilities despite predicted occupancy.

Functional Groups

Black Coral exhibits similar depth-occupancy patterns on the Eastern (B028) and Northern (B029) transects of Dellwood Seamount, with primary peaks occurring within the severely hypoxic zone of the OMZ (800–1200 m). Peak depths for these transects are close, with B029 peaking at 830 m and B028 slightly deeper at 835 m. Peak widths are also similar (B029: 290 m, B028: 365 m), suggesting comparable habitat conditions on these sides of the seamount. However, predicted occupancy is higher on B029 (0.87) compared to B028 (0.43).

The Southwestern transect (B030) shows a different pattern, with two peaks at 780 m and 997 m. The shallower peak at 780 m lies outside the severely hypoxic zone and has a predicted occupancy of 0.99, while the deeper peak at 997 m within the OMZ reaches 1.0 occupancy. These peaks are narrower (B030: 110 m and 150 m) compared to the broader peaks on B028 and B029. See Figure 2.5, A for Black Coral occupancy trends across Dellwood transects.

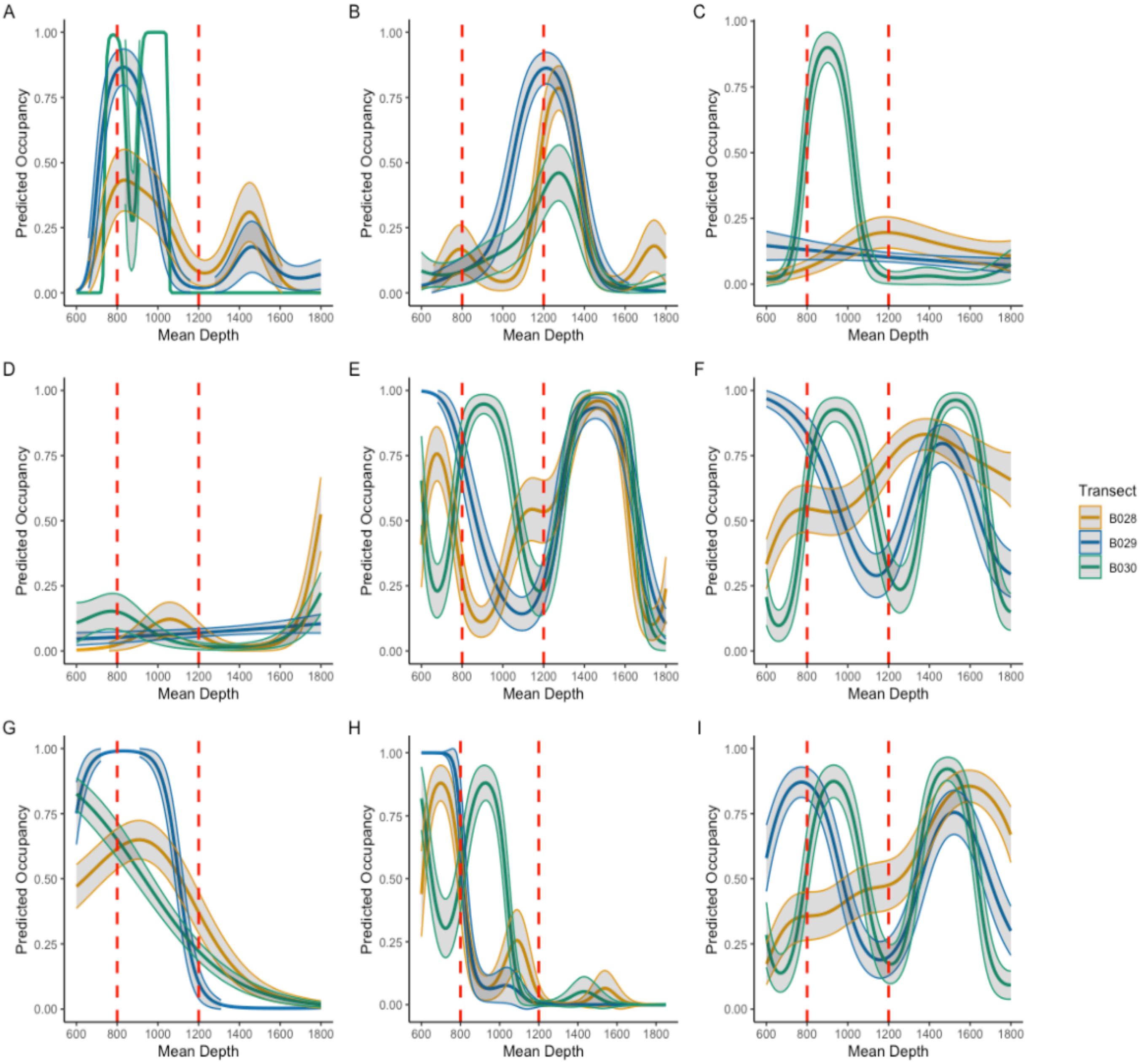

Figure 2.5. Predicted occupancy trends for CWCS functional groups across transects of Dellwood Seamount. Each panel represents a different functional group, displaying predicted occupancy probabilities (y-axis) along depth gradients (x-axis) across the eastern (B028), northern (B029), and southwestern (B030) transects. Lines are color-coded by transect: orange (B028), blue (B029), and green (B030). Dashed red lines at 800 m and 1200 m indicate the severely hypoxic zone of the oxygen minimum zone (OMZ). (A) Black Corals, (B) Cup Corals, (C) Glass Reef Sponges, (D) Hydrocorals, (E) Large Gorgonians, (F) Other Sponges, (G) Sea Pens, (H) Small Gorgonians, and (I) Soft Corals. Peak occupancy values and depth preferences vary across transects, highlighting intra-seamount variability in CWCS distributions. See Table 2.5 for summary statistics of peak occupancy values, depths, and peak widths.

Cup Corals show consistent depth preferences, with primary peaks occurring between 1200–1300 m. The Northern (B029) transect has the highest peak occupancy (0.86) at 1220 m, with a broad peak width of 375 m. The Southwestern (B030) and Eastern (B028) transects share a deeper peak at 1270 m, with lower predicted occupancies of 0.46 (B030) and 0.79 (B028), and similar peak widths (~325 m).

The Eastern transect (B028) also has additional peaks at 795 m (0.17 occupancy) and 1735 m (0.18 occupancy), though these have narrower peak widths (240 m at 795 m and 190 m at 1735 m). See Figure 2.5, B for Cup Coral occupancy trends across Dellwood transects.

Glass Reef Sponges display notable depth-occupancy variability across transects. The Southwestern transect (B030) has the highest peak occupancy (0.97) at 897 m, aligning with the lower end of the severely hypoxic region of the OMZ. The Eastern transect (B028) has a deeper peak at 1190 m, but with a much broader peak width (1025 m). See Figure 2.5, C for Glass Reef Sponge occupancy trends across Dellwood transects.

Hydrocorals show differences in depth preferences between transects. The Eastern (B028) transect has a deeper peak at 1050 m, while the Southwestern (B030) transect peaks at 777 m, just outside the severely hypoxic OMZ. These patterns suggest variation in depth suitability across transects. See Figure 2.5, D for Hydrocoral occupancy trends across Dellwood transects.

Large Gorgonians exhibit consistent deep-water peaks across all transects, with peak occupancies of 0.96 (B028), 0.99 (B030), and 0.93 (B029) around 1460–1480 m. However, shallow depth trends vary by transect. The Eastern transect (B028) has a shallow peak at 675 m (0.76 occupancy), while the Southwestern transect (B030) shows a trough at a similar depth but a peak at 914 m (0.95 occupancy). These differences in shallow occupancy suggest contrasting habitat conditions at comparable depths. See Figure 2.5, E for Large Gorgonian occupancy trends across Dellwood transects.

Other Sponges display variation in depth-occupancy patterns across transects. The Southwestern transect (B030) has two peaks: 931 m (0.93 occupancy) and 1530 m (0.96 occupancy), while the Eastern transect (B028) peaks at 795 m (0.55 occupancy) and 1375 m (0.83 occupancy). The Northern transect (B029) has a single peak at 1460 m (0.80 occupancy) with a broad width of 460 m. These patterns indicate mid-depth and deep habitat use on B030, while B028 shows a wider depth range with more localized habitat influences. See Figure 2.5, F for Other Sponge occupancy trends across Dellwood transects.

Sea Pens display notable variability among transects, with the Northern (B029) transect reaching the highest occupancy (0.99) at 830 m, and a broad peak width of 580 m, suggesting extensive habitat suitability. The Eastern (B028) transect has a lower peak occupancy (0.65) at 914 m, though its peak width is undefined due to sampling limits. The Southwestern (B030) transect shows a consistent decline in occupancy with no discernible peaks. See Figure 2.5, G for Sea Pen occupancy trends across Dellwood transects.

Small Gorgonians exhibit variable depth-occupancy patterns across transects. The Eastern (B028) transect has a primary peak at 692 m (0.87 occupancy) with a narrow peak width of 220 m, whereas the Southwestern (B030) transect has a similar occupancy (0.87) at a deeper peak of 914 m with a slightly broader width of 290 m. Additional smaller peaks occur at 1085 m and 1545 m on B028, while B030 has a weak secondary peak at 1444 m (0.05 occupancy). See Figure 2.5, H for Small Gorgonian occupancy trends across Dellwood transects.

Soft Corals display dual peak patterns across Dellwood transects. The Northern (B029) and Southwestern (B030) transects have shallower peaks at 777 m and 931 m, respectively, near the upper OMZ boundary. All transects also exhibit deeper peaks, with B028 peaking at 1600 m, B029 at 1530 m, and B030 at 1495 m. Peak widths are broadest on B028 (906 m) and B029 (462 m), suggesting more stable deep-water conditions, while B030 has narrower peaks (325 m), indicating more localized habitat suitability. See Figure 2.5, I for Soft Coral occupancy trends across Dellwood transects.

2.3.2.2 Case Study #2: Union Seamount

The GAMM analysis indicates significant depth-occupancy relationships across the Eastern (B024), Northern (B025), and Southwestern (B026) transects of Union Seamount (Table 2.6). The smooth term for depth was highly significant ($p < 0.001$), demonstrating that depth strongly influences CWCS occupancy patterns.

The effective degrees of freedom (EDF) values range from 6.20 (Northern transect, B025) to 8.50 (Eastern transect, B024), highlighting differences in the complexity of depth-occupancy relationships across Union Seamount. An adjusted R^2 value of 0.11 suggests that depth explains part of the variability in CWCS distributions, but additional environmental factors may also contribute. Depth-occupancy relationships also differ among transects. The Northern (B025) and Southwestern (B026) transects display gradual occupancy trends, reflected in lower EDF values, whereas the Eastern transect (B024) exhibits a more complex trend (EDF = 8.50), suggesting greater variability in depth preferences (see Methods for interpretation of EDF values).

Table 2.6. Summary of GAMM output for depth-occupancy relationships across Union Seamount transects. The table includes the effective degrees of freedom (EDF), reference degrees of freedom (Ref.df), F-values, and p-values for each transect-specific smooth term (s(Mean Depth, by Transect)), along with the model's adjusted R^2 and overall significance of depth as a predictor of CWCS functional group occupancy.

Family	**Link Function**	**Formula**	**Adjusted R^2**	**n**
Binomial	logit	Occ ~ s(Mean Depth, by =Transect)	0.11	3726

Parametric Coefficients

	Estimate	**Std. Error**	**t/ F Value**	**edf**	**Ref.df**	***p*-value**
(Intercept)	-0.6183	0.2990	-2.068	-	-	0.0387 *
Smooth Terms						
Mean Depth: B024			11.24	8.504	8.504	< 2e-16 ***
Mean Depth: B025			34.80	6.202	6.202	< 2e-16 ***
Mean Depth: B036			13.11	6.586	6.586	< 2e-16 ***

Predicted occupancy trends illustrate both consistent patterns and transect-specific differences (Figure 2.6). Distinct depth preferences are observed across functional groups, with many peaks occurring within or near the hypoxic zone (800–1200 m), while others extend into deeper zones, reflecting variable habitat suitability across transects.

Several functional groups reach high occupancy within the hypoxic zone, particularly Black Corals (*Lillipathes* sp., *Bathypathes* sp.) and Sea Pens (*Anthoptilum grandiflorum*), suggesting potential tolerance to low-oxygen conditions. In contrast, Large Gorgonians (*Parastenella* spp., Unbranched Isididae) and Hydrocorals (*Stylaster* spp.) exhibit broader depth distributions, with peaks extending into deeper zones.

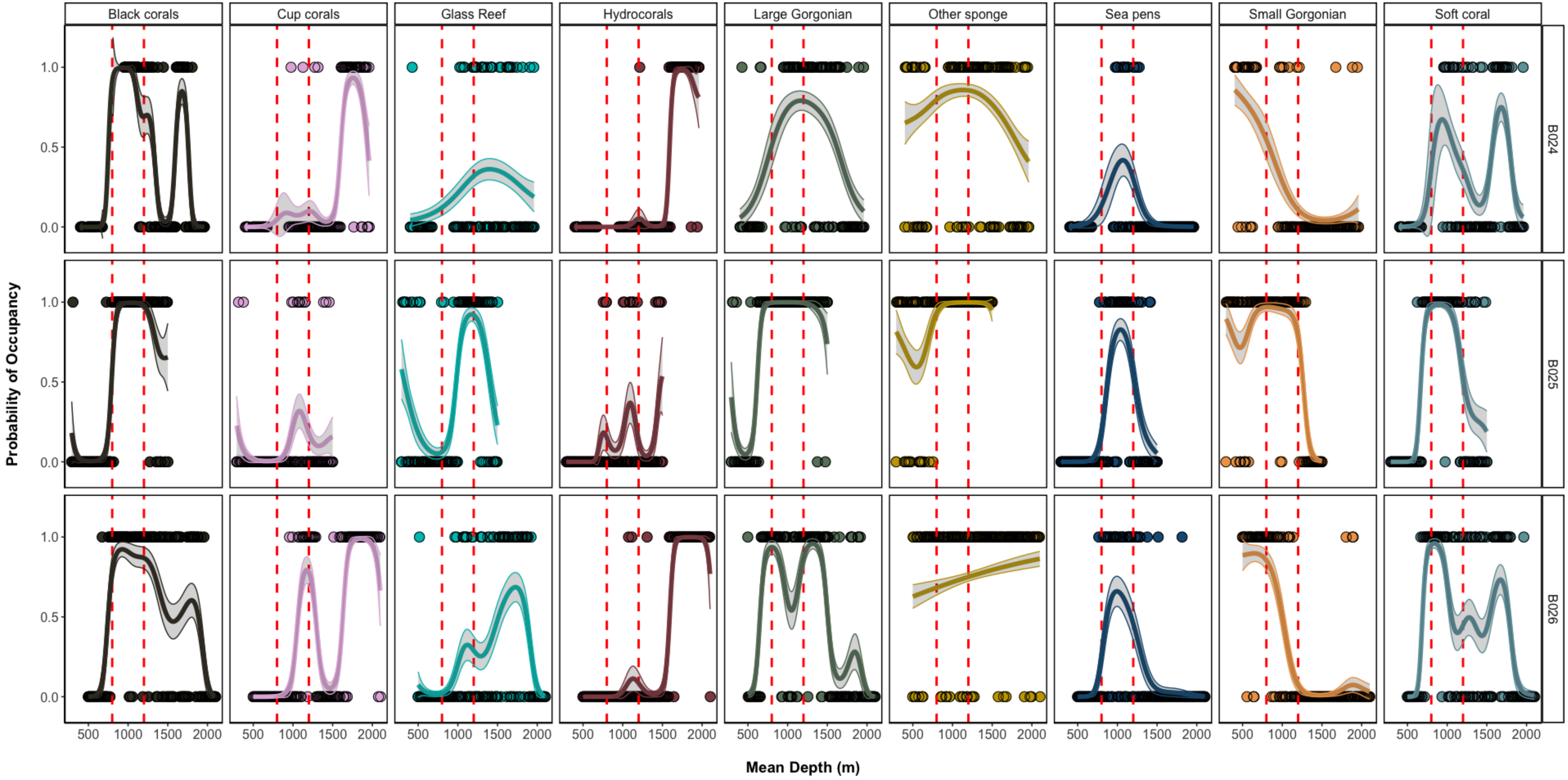

Figure 2.6. Predicted occupancy probability of CWCS functional groups across Union Seamount transects. The plot shows predicted occupancy probabilities (y-axis) along mean depth gradients (x-axis) for the Eastern (B024), Northern (B025), and Southwestern (B026) transects. Lines are color-coded by transect, with shaded

ribbons representing the standard error (SE) of the predictions. Dashed red vertical lines at 800 m and 1200 m mark the severely hypoxic zone of the local oxygen minimum zone (OMZ), contextualizing functional group distributions relative to low-oxygen conditions.

Peak occupancy values vary across the Southeastern (B024), Eastern (B025), and Western-Northwestern (B026) transects of Union Seamount (Table 2.7). Higher occupancy values at mid-depths and deeper zones are observed on the Southeastern transect (B024), particularly for *Bathypathes* sp. (Black Corals) and Scleractinia (Cup Corals) The Eastern transect (B025) displays consistent peaks within the hypoxic zone, particularly for *Farrea* spp. (Glass Reef Sponges) and Mushroom Corals. The Western-Northwestern transect (B026) exhibits broader depth ranges, with occasional deeper peaks, such as Unbranched Isididae and *Paragorgia* sp. within the Large and Small Gorgonians, reflecting diverse habitat conditions on this side of the seamount.

Peak width varies across transects, indicating differences in habitat suitability. Large Gorgonians and Soft Corals (Mushroom Corals) exhibit broad peak widths, suggesting a wider range of favorable conditions. In contrast, Hydrocorals (*Stylaster* spp.) display narrower peaks, indicating more localized depth preferences (Table 2.7).

Table 2.7. Peak Occupancy Values for CWCS Functional Groups on Union Transects. Summary of peak occupancy values for CWCS functional groups across Union transects (B024, B025, B026), based on predicted occupancy trends from GAM models. For each functional group and transect, the table lists the number of observed occupancy peaks (Peak No.), the peak occupancy probability (Peak Occ.), the depth at which peak occupancy occurs (Peak Depth, m), the width of the peak (Peak Width, m), and the dominant taxa associated with each peak. Peak widths were calculated using the full-width at half-maximum (FWHM) method. Peaks within the severely hypoxic depth bands of the local oxygen minimum zone (OMZ, 800–1200 m) are included, indicating potential functional group tolerance to low-oxygen conditions.

Functional Group	Seamount Side	Transect	Peak No.	Peak Occ.	Peak Depth	Peak Width	Dominant Taxa
Black Corals	SE	B024	1	1.00	894	605	*NA*
	SE		2	0.82	1682	202	*Bathypathes* sp.
	E	B025	1	1.00	1041	751	*Lillipathes* sp.
	W_NW	B026	1	0.93	949	806	*Bathypathes* sp.
	W_NW		2	0.63	1792	*NA*	*Bathypathes* sp.
Cup Corals	SE	B024	1	0.09	912	586	*NA*
	SE		2	0.10	1206	550	*NA*
	SE		3	0.93	1755	366	Scleractinia
	E	B025	1	0.32	1077	257	Cup coral (red tentacles)
	W_NW	B026	1	0.79	1169	275	Cup coral (red tentacles)
	W_NW		2	0.99	1865	*NA*	Scleractinia
Glass Reef	SE	B024	1	0.36	1407	1063	*Farrea* spp.
	E	B025	1	0.92	1169	458	*Farrea* spp.
	W_NW	B026	1	0.32	1114	1008	*Farrea* spp.
	W_NW		2	0.69	1718	513	*Farrea* spp.

Functional Group	Seamount Side	Transect	Peak No.	Peak Occ.	Peak Depth	Peak Width	Dominant Taxa
Hydrocoral	SE	B024	1	0.05	1206	183	*Stylaster* spp.
	SE		2	0.99	1737	*NA*	*Stylaster* spp.
	E	B025	1	0.18	766	165	*Stylaster* spp.
	E		2	0.37	1096	184	*Stylaster* spp.
	E		3	0.54	1517	184	*Stylaster* spp.
	W_NW	B026	1	0.11	1132	238	*Stylaster* spp.
	W_NW		2	1.00	1847	*NA*	*Stylaster* spp.
Large Gorgonian	SE	B024	1	0.79	1169	971	Unbranched Isididae
	E	B025	1	1.00	967	953	*Parastenella* spp.
	W_NW	B026	1	0.94	803	879	*Parastenella* spp.
	W_NW		2	0.96	1315	879	Unbranched *Isididae*
	W_NW		3	0.28	1847	238	*Parastenella* spp. & Unbranched Isididae
Other Sponge	SE	B024	1	0.86	1132	*NA*	Hexactinellida
	E	B025	1	1.00	1187	*NA*	Hexactinellida
Sea Pens	SE	B024	1	0.42	1077	403	*Anthoptilum grandiflorum*
	E	B025	1	0.83	1041	421	*Anthoptilum grandiflorum*
	W_NW	B026	1	0.66	986	476	*Anthoptilum grandiflorum*
Small Gorgonian	E	B025	1	0.97	821	*NA*	*Swiftia* spp.
	W_NW	B026	1	0.90	638	*NA*	*Paragorgia* sp. (pale)
	W_NW		2	0.07	1883	366	*Paragorgia* sp. (pale)
Soft Corals	SE	B024	1	0.67	931	440	Mushroom corals
	SE		2	0.75	1682	293	Mushroom corals
	E	B025	1	0.99	894	568	Mushroom corals
	W_NW	B026	1	0.96	839	403	Mushroom corals
	W_NW		2	0.50	1279	1191	Mushroom corals
	W_NW		3	0.73	1664	1136	Mushroom corals

Functional Groups

Black Corals exhibit high predicted occupancy across all transects, particularly in shallower depths within the OMZ. The Southeastern transect (B024) reaches peak occupancy of 1.00 at 894 m, with a broad peak width of 605 m. The Eastern transect (B025) has a peak at 1041 m (occupancy 1.00) with the widest peak width (751 m). The Western-Northwestern transect (B026) shows two peaks: one at 949 m (occupancy 0.93) and a secondary peak at 1792 m (occupancy 0.63). See Figure 2.7, A for Black Coral occupancy trends across Union transects.

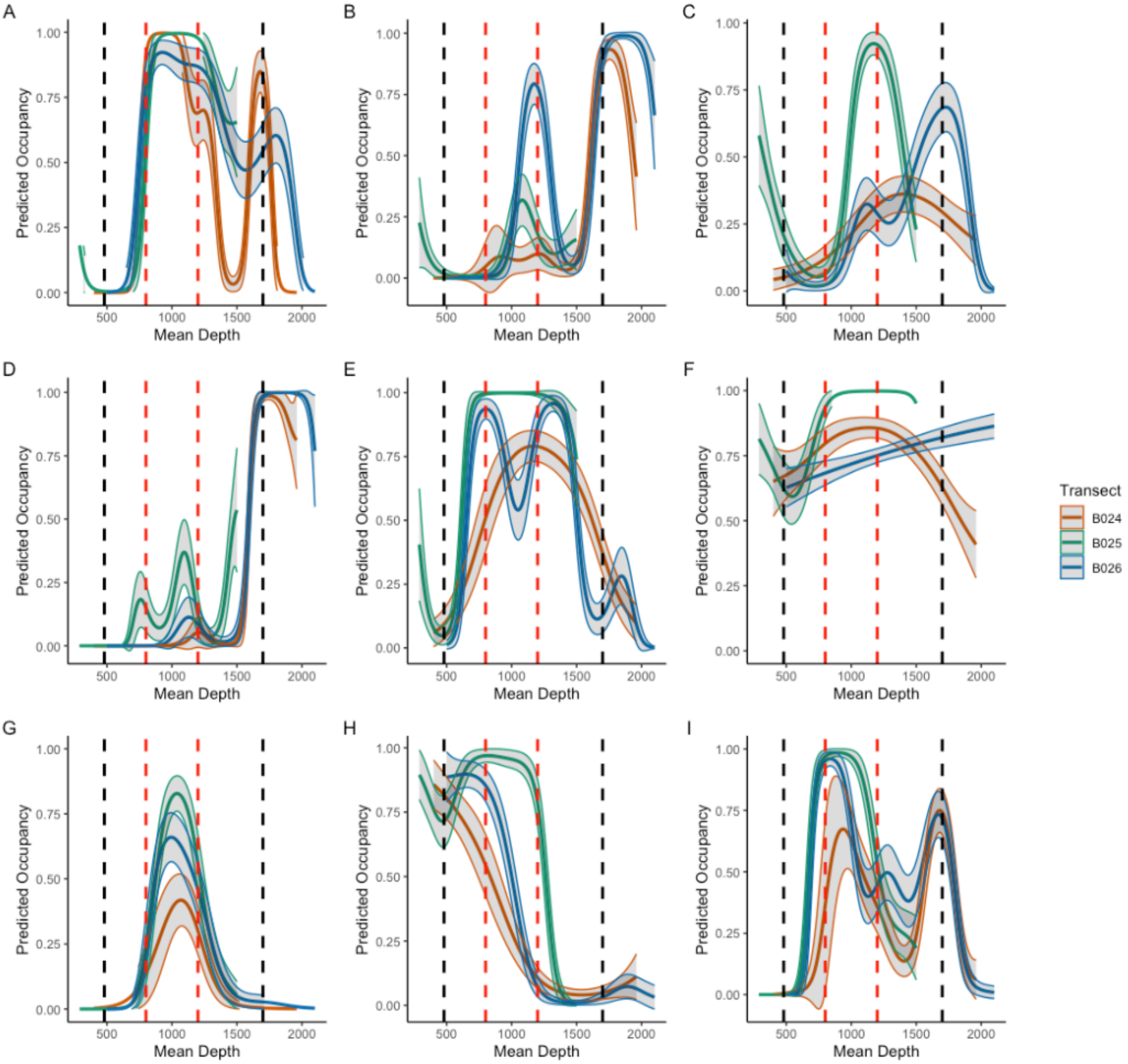

Figure 2.7. Predicted occupancy trends for CWCS functional groups across transects of Union Seamount. Each panel represents a different functional group, displaying predicted occupancy probabilities (y-axis) along depth gradients (x-axis) across the southeastern (B024), eastern (B025), and western-northwestern (B026) transects. Lines are color-coded by transect: green (B024), orange (B025), and blue (B026). Dashed red lines at 800 m and 1200 m indicate the severely hypoxic zone of the oxygen minimum zone (OMZ), while black dashed lines at 480 m and 1700 m mark the broader depth limits of the OMZ. (A) Black Corals, (B) Cup Corals, (C) Glass Reef Sponges, (D) Hydrocorals, (E) Large Gorgonians, (F) Other Sponges, (G) Sea Pens, (H) Small Gorgonians, and (I) Soft Corals. Peak occupancy values and depth preferences vary across transects, highlighting intra-seamount variability in CWCS distributions. See Table 2.6 for summary statistics of peak occupancy values, depths, and peak widths.

Cup Corals show depth variability across transects. The Southeastern transect (B024) has three peaks: 912 m (occupancy 0.09), 1206 m (occupancy 0.10), and 1755 m (occupancy 0.93). The Eastern transect (B025) has a single peak at 1077 m (occupancy 0.32). The Western-Northwestern transect (B026) features two peaks: 1169 m (occupancy 0.79) and 1865 m (occupancy 0.99), indicating habitat suitability both within and beyond the OMZ. See Figure 2.7, B for Cup Coral occupancy trends across Union transects.

Glass Reef Sponges display distinct depth-occupancy patterns. The Southeastern transect (B024) has a moderate peak at 1407 m (occupancy 0.36, width 1063 m). The Eastern transect (B025) peaks at 1169 m (occupancy 0.92, width 458 m). The Western-Northwestern transect (B026) has two peaks: 1114 m (occupancy 0.32, width 1008 m) and 1718 m (occupancy 0.69, width 513 m), reflecting adaptability to varying depth zones. See Figure 2.7, C for Glass Reef Sponge occupancy trends across Union transects.

Hydrocorals show depth variability across transects. The Southeastern transect (B024) has a small peak at 1206 m (occupancy 0.05) and a higher peak at 1737 m (occupancy 0.99). The Eastern transect (B025) has peaks at 766 m (occupancy 0.18) and 1517 m (occupancy 0.54), both with narrow widths (~165–184 m). The Western-Northwestern transect (B026) peaks at 1132 m (occupancy 0.54, width 238 m) and 1847 m (occupancy 1.00), highlighting depth adaptability. See Figure 2.7, D for Hydrocoral occupancy trends across Union transects.

Large Gorgonians exhibit broad distributions across transects. The Southeastern (B024) and Eastern (B025) transects have peaks within the OMZ: B024 peaks at 1169 m (occupancy 0.79, width 971 m), while B025 peaks at 967 m (occupancy 1.00, width 953 m). The Western-Northwestern transect (B026) has three peaks: 803 m (occupancy 0.94), 1315 m (occupancy 0.96), and a smaller peak at 1847 m (occupancy 0.28, width 238 m), indicating depth variability. See Figure 2.7, E for Large Gorgonian occupancy trends across Union transects.

Other Sponges maintain consistently high occupancy across transects. The Southeastern (B024) and Eastern (B025) transects have broad peaks at mid-depths: B024 peaks at 1132 m (occupancy 0.86), while B025 reaches maximum occupancy (1.00) at 1187 m. The Western-Northwestern transect (B026) lacks distinct peaks, with occupancy increasing steadily from ~500 m, suggesting broad depth suitability. See Figure 2.7, F for Other Sponge occupancy trends across Union transects.

Sea Pens exhibit similar depth-occupancy trends across Union, with peaks clustering between 985–1077 m. The Southeastern transect (B024) peaks at 1077 m (occupancy 0.42, width 403 m), while the Eastern transect (B025) reaches a higher peak at 1041 m (occupancy 0.83, width 421 m). The Western-Northwestern transect (B026) peaks at 986 m (occupancy 0.66) and has the widest peak width (476 m), suggesting similar depth preferences across transects. See Figure 2.7, G for Sea Pen occupancy trends across Union transects.

Small Gorgonian Corals exhibit variability across transects. The Eastern transect (B025) has a single peak at 821 m (occupancy 0.97). The Western-Northwestern transect (B026) has two peaks: 638 m (occupancy 0.90) and 1883 m (occupancy 0.07). The Southeastern transect (B024) does not display a distinct peak but has a slight occupancy increase at ~1883 m without forming a defined peak. See Figure 2.7, H for Small Gorgonian occupancy trends across Union transects.

Soft Corals display dual peaks across transects. An initial peak occurs at mid-depths (~800–930 m), followed by a decline through the OMZ. The Southeastern (B024) and Western-Northwestern (B026) transects show occupancy increases beyond 1500 m, whereas the Eastern transect (B025) lacks deeper data.

On the Southeastern transect (B024), peaks occur at 931 m (occupancy 0.67) and 1682 m (occupancy 0.75). The Eastern transect (B025) has a broad peak at 894 m with the highest overall occupancy (0.99, width 568 m). The Western-Northwestern transect (B026) has three peaks: 839 m (occupancy 0.96), 1279 m (occupancy 0.50), and 1664 m (occupancy 0.73). See Figure 2.7, I for Soft Coral occupancy trends across Union transects.

2.3.3 Objective 3: Indicator Species

The analysis of indicator species across all seamounts, including Dellwood, Union, and eastern transects, identified distinct patterns in species distributions and depth preferences. Species were categorized into four groups based on their spatial distribution and depth-related trends: Ubiquitous, Moderately distributed, Depth-specific, and Local indicators.

Table 2.8 outlines species' distribution patterns, depth-related trends, and relevance to adaptive management strategies for each species. Additionally, a detailed ecological table providing supplementary context and rationale for these categorizations is included in Appendix A. Together, these resources aim to enhance long-term monitoring efforts and inform decision-making processes in deep-sea marine protected areas.

Table 2.8. Management Indicators Table. Summary of potential indicator species for seamount ecosystem monitoring and management, derived from inter- and intra-seamount predictive occupancy models across Dellwood, Union, and eastern seamount transects (Hodgkins, Dellwood, Dellwood South, Union, and SK-B). Metrics include Taxa Name, Seamounts Covered, Total Occupancy (sum of 10 m depth bins with presence), Ease of Identification (categorized as Easy, Moderate, or Hard), Indicator Type (e.g., Ubiquitous, Moderately Distributed, Local, Depth-Specific), Indicator Potential (assessed based on Total Occupancy thresholds and Ease of Identification), and Depth Band Relevance (Surface to 800 m, OMZ Severe Hypoxia, Oxygen Recovery). These metrics highlight the ecological and management relevance of species, supporting targeted conservation efforts and adaptive monitoring strategies.

Taxa Name	Functional Group	Seamounts Covered	Total Occupancy	Ease of ID	Indicator Type	Indicator Potential	Depth Band Relevance
Acanthogorgia sp. (yellow, CA32)	Small gorgonian	1	3	Medium	Depth-Specific	Low	Severe Hypoxia Specialist
Anthoptilum cf *lithophilum* (CA41)	Sea pen	1	1	Easy	Depth-Specific	Low	Severe Hypoxia Specialist
Anthoptilum grandiflorum (CA01)	Sea pen	3	92	Medium	Moderately Distributed	Low	Severe Hypoxia Specialist
Aphrocallistidae spp.	Glass reef	2	12	Medium	Moderately Distributed	Low	Hypoxia and Deep
Asbestopluma sp. (bush, PD14)	Other sponge	1	33	Easy	Depth-Specific	High	Severe Hypoxia Specialist
Auletta sp. (PD11)	Other sponge	1	1	Medium	Depth-Specific	Low	Surface Influenced
Bathydorus sp. (PH07)	Other sponge	2	112	Medium	Moderately Distributed	Low	Hypoxia and Deep
Bathypathes sp. (CA06)	Black coral	2	750	Medium	Moderately Distributed	Low	All Depths Generalist
Callogorgia sp. (CA29)	Small gorgonian	1	27	Medium	Depth-Specific	Moderate	Deeper Waters
Chonelasma oreia (PH08)	Other sponge	5	126	Easy	Ubiquitous	High	All Depths Generalist
Chrysopathes spp. (CA21)	Black coral	3	504	Medium	Moderately Distributed	Low	All Depths Generalist
Cup coral (red tentacles, CA14)	Cup coral	2	358	Medium	Moderately Distributed	Low	Hypoxia and Deep

Taxa Name	Functional Group	Seamounts Covered	Total Occupancy	Ease of ID	Indicator Type	Indicator Potential	Depth Band Relevance
Demosponge (ball PD01)	Other sponge	3	16	Hard	Moderately Distributed	Low	Hypoxia and Deep
Demosponge (nipple, PD07)	Other sponge	1	1	Medium	Depth-Specific	Low	Deeper Waters
Demosponge (pale yellow, PD04)	Other sponge	3	136	Medium	Moderately Distributed	Low	Hypoxia and Deep
Demosponge (white encrusting, PD06)	Other sponge	3	576	Medium	Moderately Distributed	Low	Hypoxia and Deep
Farrea sp. (branching, PH03)	Glass reef	2	60	Easy	Moderately Distributed	Low	Hypoxia and Deep
Farrea spp.	Glass reef	4	510	Easy	Ubiquitous	High	Hypoxia and Deep
Gersemia sp. (CA20)	Soft coral	4	83	Medium	Ubiquitous	Moderate	Severe Hypoxia Specialist
Halipteris sp. (whip, CA02)	Sea pen	3	106	Medium	Moderately Distributed	Low	Severe Hypoxia Specialist
Hexactinella sp. (Undulated, PH01)	Other sponge	2	14	Hard	Moderately Distributed	Low	Hypoxia and Deep
Hexactinellida (Bright yellow, PH12)	Other sponge	1	1	Easy	Depth-Specific	Low	Severe Hypoxia Specialist
Homoieurete sp. (PH10)	Other sponge	3	22	Hard	Moderately Distributed	Low	Surface and Hypoxia
Isidella tentaculum (CA07)	Large gorgonian	3	144	Easy	Moderately Distributed	Low	Surface and Hypoxia
Keratoisis sp. (bush, CA05)	Large gorgonian	4	702	Medium	Ubiquitous	Moderate	All Depths Generalist
Lillipathes sp. (CA04)	Black coral	4	1068	Medium	Ubiquitous	Moderate	All Depths Generalist
Mushroom coral cf *Anthomastus* sp. (CA31)	Soft coral	3	52	Easy	Moderately Distributed	Low	Severe Hypoxia Specialist

Taxa Name	Functional Group	Seamounts Covered	Total Occupancy	Ease of ID	Indicator Type	Indicator Potential	Depth Band Relevance
Mushroom coral (stalked, CA30)	Soft coral	3	47	Easy	Moderately Distributed	Low	Severe Hypoxia Specialist
Mycale sp. (vase, PD09)	Other sponge	1	4	Medium	Local	Low	Hypoxia and Deep
Paragorgia pacifica (CA18)	Large gorgonian	4	210	Medium	Ubiquitous	Moderate	All Depths Generalist
Paragorgia sp. (pale, CA15)	Large gorgonian	5	1095	Medium	Ubiquitous	Moderate	All Depths Generalist
Parastenella spp. (CA10)	Large gorgonian	4	1749	Easy	Ubiquitous	High	All Depths Generalist
Pinulasma sp. (PH04)	Other sponge	5	645	Easy	Ubiquitous	High	All Depths Generalist
Rossellidae, boot sponges (PH06)	Other sponge	5	570	Easy	Ubiquitous	High	All Depths Generalist
Schaudinnia sp.	Other sponge	3	10	Medium	Moderately Distributed	Low	Surface and Hypoxia
Stichopathes sp. (CA38)	Black coral	1	1	Easy	Depth-Specific	Low	Severe Hypoxia Specialist
Stolonifera (encrusting, CA43)	Soft coral	1	3	Medium	Depth-Specific	Low	Severe Hypoxia Specialist
Stylaster spp. (CH01)	Hydrocoral	4	1032	Medium	Ubiquitous	Moderate	All Depths Generalist
Swiftia spp.	Small gorgonian	5	906	Easy	Ubiquitous	High	All Depths Generalist
Swiftia pacifica (CA12)	Small gorgonian	1	1	Medium	Depth-Specific	Low	Severe Hypoxia Specialist
Tretodictyum sp. (striated, PH05)	Other sponge	4	160	Medium	Ubiquitous	Moderate	Surface and Hypoxia
Umbellula lindahli (CA03)	Sea pen	1	37	Easy	Depth-Specific	High	Severe Hypoxia Specialist

Taxa Name	Functional Group	Seamounts Covered	Total Occupancy	Ease of ID	Indicator Type	Indicator Potential	Depth Band Relevance
Unbranched Isididae (CA33)	Large gorgonian	3	1245	Medium	Moderately Distributed	Low	All Depths Generalist
Unknown Paragorgiid	Small gorgonian	2	17	Medium	Moderately Distributed	Low	Severe Hypoxia Specialist

The identified indicator species exhibit distinct distribution patterns and depth associations, highlighting their potential for monitoring and managing seamount ecosystems. Ubiquitous indicators, such as *Parastenella* spp., *Farrea* spp., and Rossellidae (boot sponge), were consistently recorded across all surveyed seamounts and occupied a broad depth range. For example, *Parastenella* spp. (Figure 2.8) was found from 691 m to over 2000 m, demonstrating its adaptability and potential as a baseline indicator for tracking broad-scale ecological trends across seamounts. In contrast, local or depth-specific indicators, such as *Bathypathes sp.* found predominantly at deeper hypoxic zones, could serve as sentinels for detecting environmental change within specific habitat bands. High total occupancy and ease of identification further support the use of these species in long-term monitoring efforts.

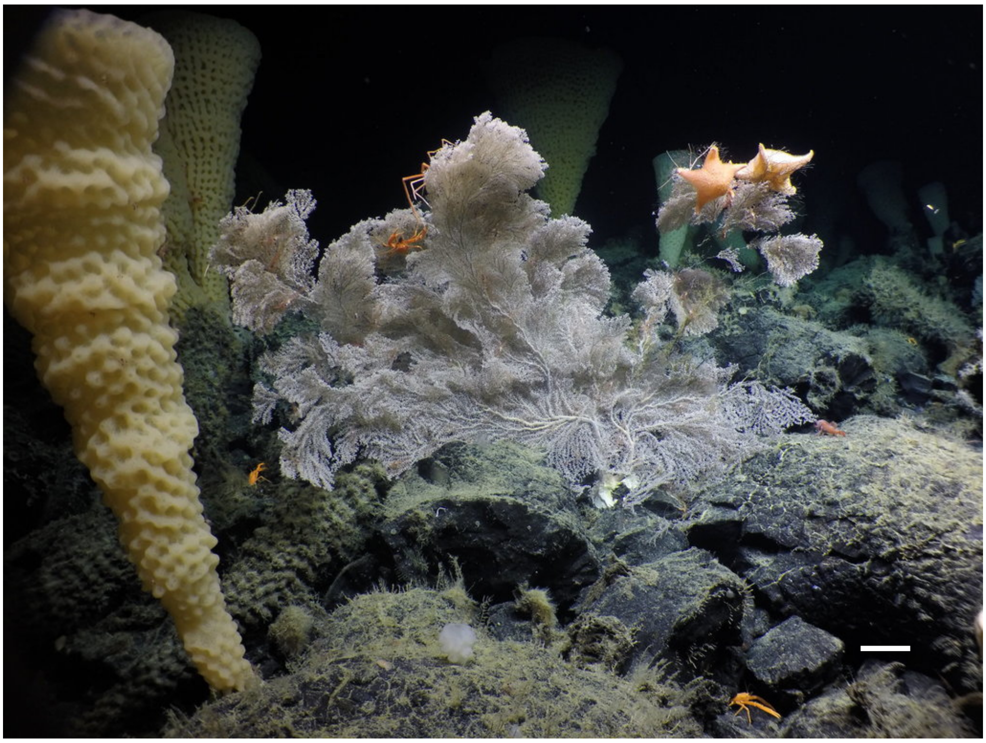

Figure 2.8. *In situ* photograph of *Parastenella* spp., a Large Gorgonian Coral, and *Pinulasma* sp., a hexactinellid sponge visible in the foreground on the left. *Parastenella* spp., exhibits a broad depth range and presence across multiple seamounts, making it a valuable ubiquitous indicator for monitoring ecological trends and changes in seamount ecosystems. White scale bar represents 30 cm. Image courtesy of Fisheries and Oceans Canada, Haida Nation, Ocean Networks Canada and Oceana Canada, taken using the Ocean Exploration Trust's ROV, *Hercules.*

Depth-specific indicators, including *Asbestopluma* sp. (bush) and *Umbellula lindahli*, exhibited restricted distributions, primarily within the severely hypoxic zone of the oxygen minimum zone (OMZ) (800–1200 m). *Asbestopluma* sp. (bush) (Figure 2.9), a carnivorous sponge, was exclusively recorded on SK̲-B-East within this depth band, emphasizing its strong association with hypoxic conditions. These species provide valuable insights into habitat preferences and potential responses to oxygen depletion.

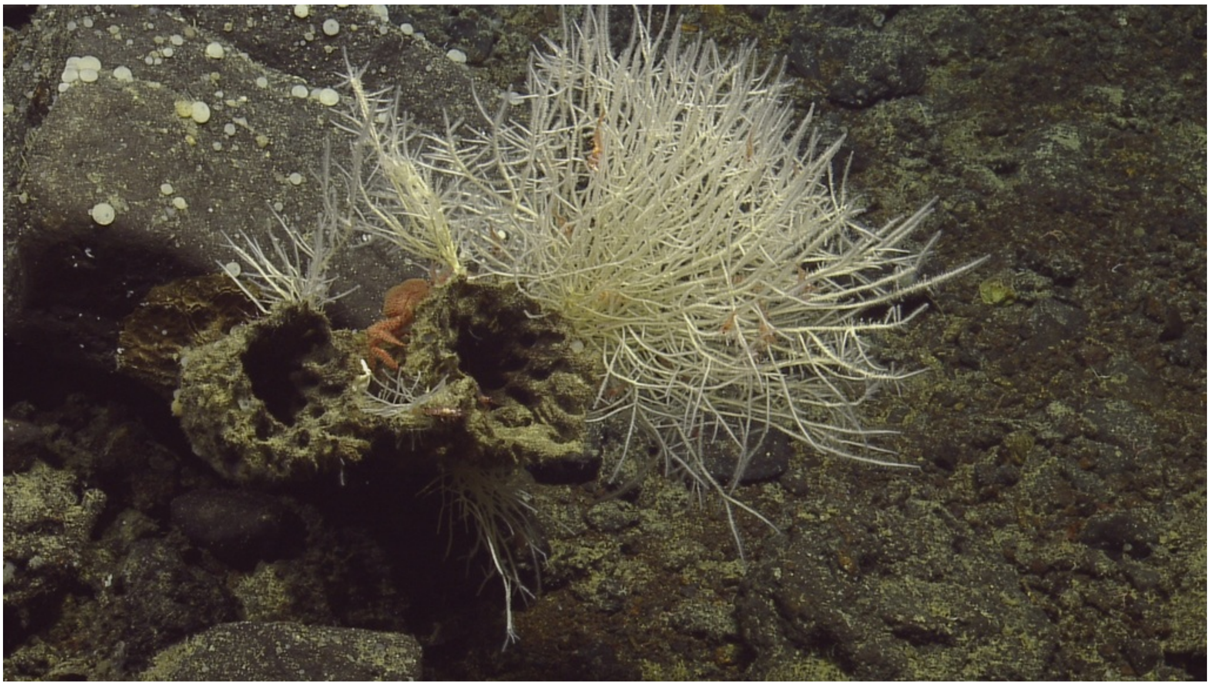

Figure 2.9. Photograph of *Asbestopluma sp.* (bush), a species of Other Sponge, illustrating its unique morphology and strong association with the severely hypoxic zone of the oxygen minimum zone (800–1200 m). This species' restricted range makes it a critical Depth-Specific indicator for assessing ecological conditions in hypoxic environments. Image courtesy of Fisheries and Oceans Canada, Haida Nation, Ocean Networks Canada and Oceana Canada, taken using the Ocean Exploration Trust's ROV, *Hercules.*

Moderately distributed indicators, such as sea pens *Anthoptilum grandiflorum* and *Halipteris* sp. (whip), were observed across multiple seamounts but with more limited occupancy than Ubiquitous indicators. Their distributions suggest potential for identifying environmental gradients and supporting management strategies at intermediate spatial scales.

A single Local indicator, *Mycale* sp. (vase), was restricted to Union-East and exhibited a narrow depth range. Its presence underscores the importance of localized monitoring for detecting unique ecological communities and site-specific habitat characteristics.

Depth band associations further refine the ecological relevance of these species. Severe Hypoxia Specialists, such as *Umbellula lindahli* and *Asbestopluma* sp. (bush), were predominantly confined to the severely hypoxic OMZ, indicating their potential as indicators of hypoxic stress. Multi-Band Generalists, including *Farrea* spp. and *Swiftia* spp., were present across multiple depth bands, from the OMZ to deeper oxygen recovery zones (>1200 m), reflecting broad environmental adaptability.

Surface and Deep-Water Specialists, such as *Callogorgia* sp. and Demosponge (white encrusting), were restricted to either surface-influenced waters or deep recovery zones, highlighting their relevance for detecting vertical habitat shifts.

Total occupancy varied across species, influencing their utility as indicators. *Farrea* spp. and *Swiftia* spp. had the highest total occupancy, recorded in 510 and 906 depth bins, respectively (Figure 2.10). Their widespread distribution supports their role as robust, broad-scale indicators. In contrast, species with lower total occupancy, such as *Auletta* sp., exhibited more restricted distributions, making them particularly relevant for site-specific monitoring and localized conservation efforts.

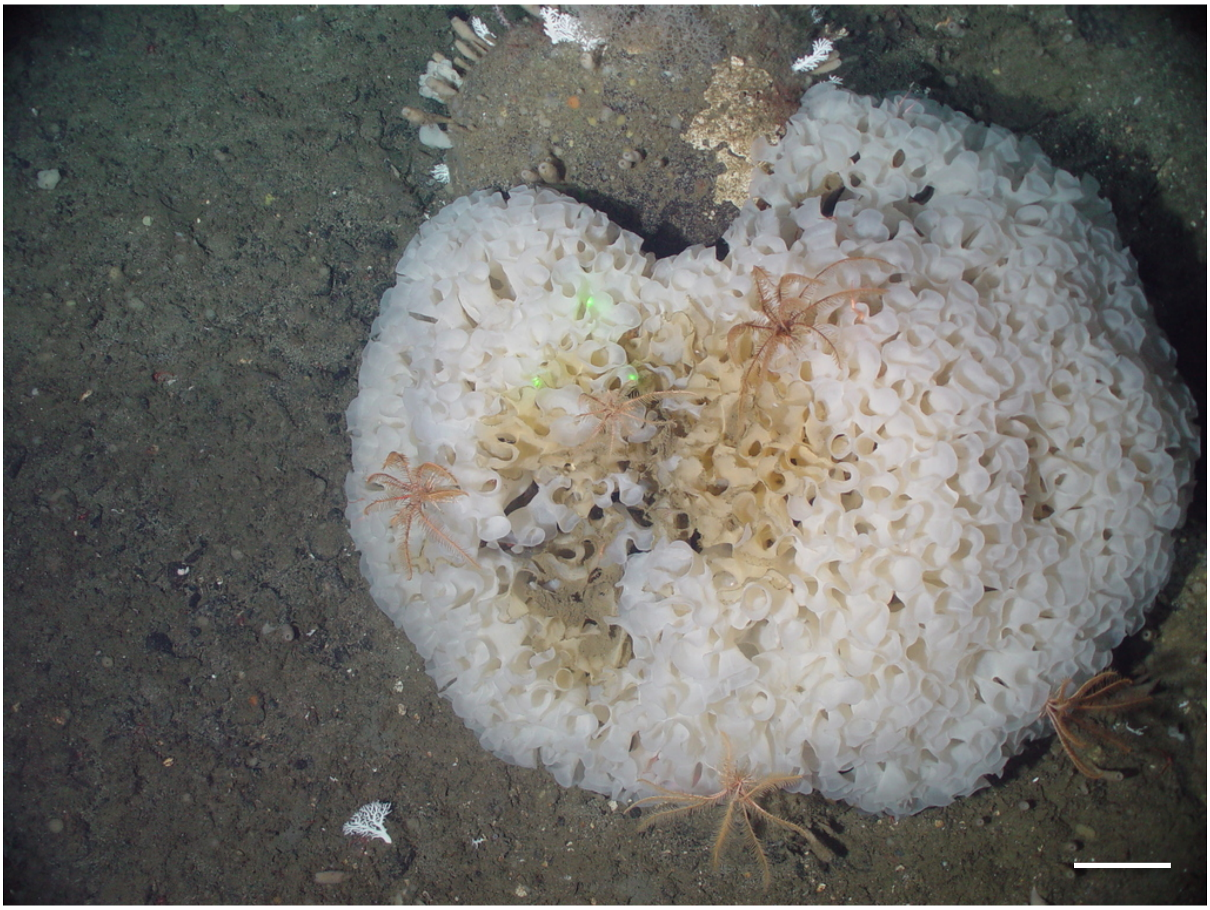

Figure 2.10. *Farrea* spp*.,* glass reef sponge functional group. Characterized by its distinctive skeletal structure, serves as a robust indicator for deep-sea ecosystem monitoring due to its broad adaptability and consistent occupancy patterns. White scale bar represents 10 cm. Image courtesy of Fisheries and Oceans Canada, Haida Nation, Ocean Networks Canada and Oceana Canada, taken using the Ocean Exploration Trust's ROV, *Hercules.*

2.4 Discussion

Long-term ecological monitoring is essential for detecting ecosystem shifts and ensuring effective conservation planning (Havstad & Herrick, 2003; Vaughan et al., 2001). However, monitoring vast, remote MPAs presents logistical challenges, requiring efficient strategies that balance conservation objectives with resource constraints. In deep-sea ecosystems, where complex environmental gradients shape species distributions (McClain et al., 2010; Preez et al., 2016; Thresher et al., 2014), identifying scalable approaches to monitoring is particularly important. One key consideration for MPA managers is the degree to which seamount communities vary across different geological features (Clark et al., 2012). Understanding whether functional groups exhibit consistent depth-occupancy patterns or if distributions are primarily site-specific has direct implications for the design of monitoring protocols. This study identified common trends and distinct differences in depth distributions by analyzing inter- and intra-seamount variability in CWCS occupancy patterns. Notably, peaks of predicted occupancy within the severely hypoxic region of the OMZ (800–1200 m) were consistently observed across seamounts, reinforcing its ecological importance as a priority for targeted monitoring. Additionally, multiple potential indicator species were identified, though their suitability depends on specific monitoring objectives. Some taxa provide broad-scale insights, while others are better suited for detecting localized environmental changes, emphasizing the need for a flexible monitoring framework.

CWCS occupancy patterns exhibited differing degrees of variation across functional groups, emphasizing the need for monitoring strategies that capture both broad-scale trends and fine-scale ecological differences. Some functional groups, such as Black Corals and Large Gorgonians, exhibited relatively stable depth-occupancy trends across multiple seamounts and transects, suggesting their reliability as broad-scale indicators. In contrast, Soft Corals and Glass Reef Sponges displayed significant variation in peak depths and occupancy trends, likely driven by localized factors such as substrate composition, oxygen levels, and current regimes (Goode et al., 2021, 2021; McClain et al., 2009; Preez et al., 2016; Thresher et al., 2014). Across seamounts, shifts in species dominance at similar depths were observed, highlighting that while broad functional group patterns can provide general monitoring guidance, species-specific differences must be considered. Additionally, within individual seamounts, occupancy patterns varied between transects, with different species, at times, driving peak occupancies on opposing flanks. This suggests that fine-scale environmental heterogeneity plays a key role in structuring benthic communities, aligning with previous studies on horizontal seamount community structure (Kennedy et al., 2025; Mejía-Mercado & Baco, 2023). The observed variability underscores the need for caution when extrapolating occupancy patterns across seamounts, emphasizing that monitoring efforts should be designed to capture ecological variability effectively (Vos et al., 2000). Functional group-based monitoring provides a practical approach for large-scale conservation, reducing the need for extensive species-level identification, though site-specific assessments remain necessary in highly heterogeneous environments (Caughlan & Oakley, 2001).

Despite spatial variability, the consistent clustering of CWCS peaks in the severely hypoxic region of the OMZ highlights it as an ecologically significant zone that should be a priority for long-term monitoring. Large Gorgonians and Glass Sponges exhibited particularly high predicted occupancy within this region, contributing to habitat complexity and supporting associated deep-sea biodiversity. The OMZ is a dynamic and vulnerable habitat, with deoxygenation and climate-driven habitat compression (Ross et al., 2020) threatening its long-term stability. Long-term data from the Line P monitoring program indicate that oxygen levels within the OMZ continue to decline, with the lower OMZ boundary deepening at a rate of 3.0 ± 0.7 m per year (Ross et al., 2020). Given that CWCS assemblages are highly sensitive to environmental change (Carballo & Bell, 2017; Roberts et al., 2016; Roberts & Cairns, 2014), monitoring species within the OMZ can provide early indicators of ecosystem shifts, reinforcing its role as a critical depth zone for long-term conservation efforts. The presence of habitat-forming species within extreme hypoxic zones aligns with previous research suggesting that deep-sea taxa may exhibit physiological adaptations to low-oxygen conditions (Childress & Seibel, 1998; Micaroni et al., 2022; Rogers, 2000). However, as deoxygenation accelerates, understanding how these species respond to prolonged oxygen stress will be critical for predicting future ecosystem resilience.

While the OMZ emerged as a priority monitoring target, managers may also need to monitor CWCS in other depth zones, requiring a flexible approach that incorporates multiple indicator species. No single species emerged as a universal monitoring proxy, reinforcing the need for adaptive monitoring approaches tailored to specific conservation objectives. Ubiquitous indicators (e.g., *Parastenella* spp., *Farrea* spp.) are useful for broad-scale monitoring due to their widespread presence and high occupancy across seamounts. Depth-specific indicators (e.g., *Umbellula lindahli*) are valuable for tracking hypoxia-related changes, particularly within the OMZ. Local indicators (e.g., *Mycale* sp.) highlight the importance of single-seamount monitoring for detecting unique ecological communities. The selection of ecological indicators must align with key monitoring priorities, balancing efficiency and scientific accuracy (Havstad & Herrick, 2003). Integrating functional groups and indicator species allows managers to scale monitoring programs effectively across multiple MPAs (Edgar et al., 2016). Additionally, the differential responses of closely related species highlight the limitations of functional group-based monitoring. For example, a reported 86% decline in *Pinulasma* spp. populations at a monitored site on Explorer Seamount, with localized mortality reaching 97%, illustrates how species within the same functional group can exhibit drastically different responses to environmental changes (pers. comm., Cherisse Du Preez; Lindsay Clark, 2024). Interestingly, *Farrea* spp., another glass sponge in the same functional group, appeared stable despite occupying similar depths and environmental conditions. These observations underscore the need to incorporate species-level assessments within functional group frameworks to avoid overlooking species-specific vulnerabilities, a challenge highlighted in previous research on benthic invertebrates (Frainer et al., 2017; Ryznar et al., 2021).

Further research is needed to refine monitoring frameworks by integrating vulnerability assessments and targeted OMZ investigations. Integrating vulnerability assessments (e.g., Chapter 3) will help identify species most at risk from climate-related stressors. Investigating CWCS responses to deoxygenation in the OMZ will provide critical insights into habitat suitability and resilience. Long-term monitoring should prioritize the OMZ within the MPAs included in this study due to the observed clustering of CWCS occupancy peaks across multiple seamounts, the predicted expansion of the OMZ, and the sensitivity of life to oxygen. Developing data-driven approaches to ecological monitoring will strengthen conservation planning efforts (Lindenmayer & Likens, 2010). Given the challenges of predictive modelling in deep-sea ecosystems, future work should also focus on improving habitat suitability models. The ecological heterogeneity of seamounts complicates broad-scale predictions, as even the same taxa may exhibit variable depth preferences across sites (Azevedo et al., 2024). Although machine learning algorithms and computational approaches may improve model performance, deep-sea monitoring frameworks should account for uncertainty and prioritize empirical observations to inform conservation planning (Silva et al., 2022).

This study provides a case study for applying functional group-based monitoring in offshore MPAs, demonstrating its potential while emphasizing the need for site-specific considerations. By quantifying inter- and intra-seamount variability, I provide new insights into the spatial patterns of CWCS in Northeast Pacific seamounts. The OMZ emerges as a critical monitoring priority due to its biodiversity significance and potential vulnerability to climate-driven changes. This research highlights both the strengths and limitations of functional group-based monitoring for offshore MPAs, reinforcing the need for adaptive management strategies. Effective monitoring frameworks should integrate functional group-based approaches with ecological indicators to enhance conservation decision-making (Vos et al., 2000; White et al., 2025). The results presented here contribute to the broader discourse on marine conservation strategies, emphasizing that monitoring frameworks must balance efficiency with ecological accuracy to ensure long-term protection of deep-sea ecosystems.

Chapter 3 – Assessing Climate Vulnerability of Molluscs in the Azores Marine Park Using a Trait-Based Framework

Abstract

Molluscs play critical ecological roles in marine ecosystems, yet their vulnerability to ocean warming and acidification remains poorly understood in the Azores Marine Park. Here I develop a trait-based vulnerability framework to quantify species' exposure, sensitivity, and adaptive capacity based on biological and ecological traits. I apply this framework to 163 mollusc species, integrating species traits with projected climate exposure across MPAs in the Azores. I find that bivalves in northern MPAs are particularly vulnerable, with high sensitivity, low adaptive capacity and exposure to relatively higher rates of acidification in this region. By contrast, cephalopods have greater adaptive capacity and gastropods exhibit variable vulnerability, with some vent-endemic species showing lower sensitivity. Climate exposure varies across the region, with greater warming projected in the south and higher acidification in the north. This framework provides evidence upon which to assess species' climate vulnerabilities and highlights taxa that may warrant conservation attention under future ocean conditions.

3.1 Introduction

As climate change intensifies, marine species face increasing threats from ocean warming and acidification, two significant drivers of environmental change in marine ecosystems. Ocean acidification, caused by the uptake of atmospheric carbon dioxide, reduces carbonate ion availability, weakening the structural integrity of calcifying organisms such as molluscs (Gazeau et al., 2013; Guinotte & Fabry, 2008). Concurrently, rising sea temperatures can disrupt metabolic processes (Horwitz et al., 2020; Lannig et al., 2010; Matoo et al., 2021), alter reproductive cycles (Valdizan et al., 2011), and shift species distributions (Barnes et al., 2009; Gallagher & Albano, 2023; Weinberg, 2005). Understanding species' resilience or vulnerability to these climate-driven stressors is critical for conservation and management efforts.

Trait-based approaches have emerged as a powerful tool in conservation research, providing a framework for understanding species' responses to environmental changes (Miatta et al., 2021). Traits are measurable characteristics of an organism's morphology, physiology, life history, or behaviour that influence its ecological function and resilience (Costello et al., 2015; Miatta et al., 2021; Violle et al., 2007). Functional traits fall into two categories: *effect traits*, which describe how species contribute to ecosystem processes, and *response traits*, which determine species' ability to withstand environmental change (Edwards et al., 2013; Harvey et al., 2022; Nock et al., 2016). Identifying the key traits that shape species' vulnerability is crucial for informing conservation strategies, particularly in marine protected areas (MPAs), where management decisions must account for climate-driven shifts in biodiversity. However, important gaps remain in identifying which traits are most relevant for assessing climate vulnerability, highlighting the need for a systematic evaluation of trait applicability.

A trait-based vulnerability framework provides a structured approach to assess species across three key dimensions: *exposure*, *sensitivity*, and *adaptive capacity*. Exposure represents the degree of environmental change a species is expected to experience based on its geographic and depth distribution. Sensitivity reflects the biological and ecological traits that influence a species' susceptibility to environmental stressors. Adaptive capacity describes the potential for a species to adjust or recover from climate disturbances, influenced by traits such as reproductive strategy and dispersal ability. Together, these dimensions provide a comprehensive understanding of species' climate vulnerability and inform conservation strategies.

Molluscs, one of the most ecologically diverse marine phyla, provide an ideal group for applying trait-based vulnerability assessments. They play critical roles in marine ecosystems, contributing to habitat structuring, nutrient cycling, and food web stability (e.g., Newell, 2004; Prins et al., 1995; Vaughn & Hoellein, 2018). Bivalves, such as mussels and oysters, can act as ecosystem engineers by creating structured habitats that support diverse marine communities (Gutiérrez et al., 2003; Seed & Suchanek, 1992). Cephalopods, as active predators, influence trophic dynamics by controlling prey populations (Villanueva et al., 2017). Molluscs also display a wide range of feeding strategies, from filter feeding in bivalves (Vaughan et al., 2001) to specialized diets in spongivorous and xylophagous gastropods (Belmonte et al., 2015; Romano et al., 2014). Given their ecological significance and diverse life histories, molluscs provide an excellent model for assessing species' vulnerability to climate change.

To address these gaps, this study evaluates mollusc vulnerability within the Azores Marine Park, a network of MPAs encompassing diverse deep-sea habitats, including seamounts and hydrothermal vents (Calado et al., 2011; Campanyà-Llovet et al., 2023). These environments are increasingly affected by ocean warming and acidification, making them ideal for studying species' responses to climate stressors (Campanyà-Llovet et al., 2023; Ferreira et al., 2019). We utilized the recently published FUN Azores Trait Database, which compiles information on 14 traits for 1,210 species across 10 phyla (Campanyà-Llovet et al., 2023). However, not all available traits are equally relevant for assessing vulnerability, necessitating a systematic evaluation of their applicability.

In this study, I (1) evaluate the 14 traits in the FUN Azores Trait Database for their relevance in assessing exposure, sensitivity, and adaptive capacity in molluscs, classifying them as effect or response traits; (2) conduct a comprehensive literature review to refine trait classifications and identify knowledge gaps; (3) apply a trait-based vulnerability framework to quantify exposure, sensitivity, and adaptive capacity at both the species and class levels; (4) compare trait-based vulnerability scores to IUCN Red List classifications to assess alignment with existing conservation priorities; and (5) analyze trait dispersion among mollusc classes to determine whether certain groups exhibit functional redundancy or are disproportionately vulnerable. By integrating trait-based assessments with conservation frameworks, this study enhances understanding of species' climate vulnerability and supports the development of monitoring and management strategies for mollusc populations in a changing ocean.

3.2 Methods

3.2.1 Trait Selection - FUN Azores

The FUN Azores Trait Database includes 177 mollusc species and information on 14 traits: minimum body size (cm), body form, skeleton material, feeding structure, motility, environmental position, substratum affinity, distribution, depth range, feeding mode, trophic position, sociability, developmental mechanism, and reproductive type (Campanyà-Llovet et al., 2023). To refine this list, I conducted a comprehensive literature review focusing on the effects of ocean acidification, ocean warming, and their combined impacts on molluscs. While this was not a systematic review, I used targeted searches in Google Scholar, Web of Science and the University of Victoria library database, employing keyword combinations such as *mollusc traits and climate change*, *molluscs and ocean acidification*, *molluscs and warming*, and *functional traits and environmental stressors*. As patterns emerged in the literature, searches were adjusted to ensure balanced taxonomic representation, particularly for less-studied groups such as cephalopods.

Scoring of traits was informed by the dominant trends observed in the literature. For example, skeleton material was consistently identified as a key factor influencing vulnerability to ocean acidification, with exoskeletal species showing greater susceptibility than those with endoskeletons. While some studies suggested that endoskeletal species could also experience negative effects, the overwhelming body of evidence indicated stronger impacts on exoskeletal species, leading to a higher vulnerability score (as highlighted in the review article by Gazeau et al., 2013). This approach was applied across all traits, ensuring that scores reflected the prevailing consensus in the literature while acknowledging areas of uncertainty.

In addition to the literature review, members of the FUN Azores Trait Database working group were consulted to provide expert insights into the ecological roles, trait definitions, and scoring criteria. Experts were engaged through structured discussions and feedback sessions, helping to refine trait categorization and address ambiguities in the available data. This collaborative approach ensured that scoring decisions were well-grounded in both empirical research and expert knowledge.

Based on this assessment, traits were categorized as: (1) recommended for use, (2) recommended for use with caution, or (3) recommended for use in the context of evaluating mollusc vulnerability to climate change (Appendix B). This process also helped identify data gaps for traits that would otherwise be recommended for use. The traits deemed crucial for assessing vulnerability, with sufficient data currently available, were skeleton material, feeding structure, distribution, motility, and depth range. Species lacking high-confidence data, particularly regarding their location, were excluded from further analysis, resulting in a final list of 163 species for this study (Appendix B).

In addition to traits from the database, I incorporated new traits based on the literature review: whether species were endemic to hydrothermal vents (*vent-specific*) and whether the species has an endoskeleton or an exoskeleton (*skeleton type*). *Vent specific* is important because vent ecosystems can be very toxic and corrosive environments due to having naturally lower pH (Tunnicliffe, 1991). Robust animals that have evolved to withstand these harsh chemical environments make this a distinguishing characteristic separating them from other molluscs in the Azores. *Skeleton type* was categorized as whether the species has an endoskeleton or an exoskeleton. Primary literature and expert knowledge were used to assign scores for each trait, ranking them in terms of their relative vulnerability to climate change stressors. This step ensured that the traits most relevant to assessing the impact of climate change on mollusc species were appropriately prioritized in the analysis.

Exposure was assessed using species' location (i.e., the MPA(s) where they have been observed) and depth range to score both horizontal and vertical exposure. For horizontal exposure, I used the Climate Model Intercomparison Project (CMIP6) experiment SSP585 from the NOAA Climate Change Portal (Scott et al., 2016) and primary literature (Amorim et al., 2017) to score which MPAs are predicted to experience the most significant changes in warming and acidification, resulting in a map of exposure results. For vertical exposure, the water column was divided into different depth bands, each with a distinct exposure score. This division and the accompanying score were based on findings from Brito-Morales et al. (2020) and Sweetman et al. (2017), which predicted varying levels of exposure to climate change impacts, such as temperature and acidification, across different depths. Exposure scores were assigned as follows: for both temperature and pH, the shallowest zone (0–200 m) was scored as most exposed (score = 1). For temperature, the next bands were 200–1000 m (score = 2), 1000–3500 m (score = 3), and >3500 m (score = 4). For pH, the second band was broader, covering 200–3500 m (score = 2), followed by >3500 m (score = 3).

When a species' depth range spanned multiple exposure categories, an average vertical exposure score was calculated based on the proportion of its depth range falling into each zone. Finally, each species received a combined exposure score that averaged its vertical and horizontal scores, providing an integrated measure of overall exposure to climate change across both space and depth. By applying these exposure scores to species' vertical distributions, the analysis more accurately represented the varying risks faced by species at different depth zones.

3.2.2 Vulnerability Framework

To develop a robust preliminary vulnerability framework, methodologies were from Potter et al., (2017) and Richards et al., (2022) were adapted to assess mollusc species' susceptibility to ocean acidification and warming within the Azores Marine Park. This framework evaluates species' vulnerability across three key dimensions: exposure, sensitivity, and adaptive capacity —each of which contributes to a species' overall vulnerability score. Exposure quantifies the degree of ocean warming and acidification a species is expected to experience based on its depth range (vertical exposure) and geographic distribution (horizontal exposure), with higher scores indicating greater exposure. Sensitivity measures how inherently susceptible a species is to these stressors based on biological and ecological traits. Adaptive capacity represents a species' ability to adjust or recover from environmental stressors. However, higher scores in this dimension indicate lower adaptive capacity, meaning the species is less able to respond to climate change and is therefore more vulnerable. All three dimensions were scored on a continuous scale from 0 to 1, where higher values indicate greater vulnerability (Potter et al., 2017; Richards et al., 2022). Since this chapter focuses solely on adult life stages, potential ontogenetic shifts in exposure, sensitivity, and adaptive capacity were not considered.

Trait-based Vulnerability Scoring

Each trait was evaluated at the modality level (e.g., endoskeleton vs. exoskeleton within "skeleton type"), rather than at the broader trait level. To quantify vulnerability, a stepwise scoring process was applied following methods adapted from Potter et al., (2017) and Richards et al., (2022). Scores were assigned ranging from 0 to 1, where higher values indicate greater vulnerability.

Within each trait, species were grouped into discrete modalities, and modalities were ranked according to their relative susceptibility to ocean acidification and warming. For example, within the *skeleton material* trait, species with exoskeletons received higher vulnerability scores due to their greater susceptibility to ocean acidification, while species with endoskeletons received lower scores.

This ensured that each species' total vulnerability score reflected the cumulative influence of its specific trait modalities rather than a generalized trait category.

To prevent common traits from disproportionately influencing the overall vulnerability assessment, quantile scores were calculated based on the cumulative frequency of each trait modality within the dataset. For example, for a trait with three modalities, the scoring followed these steps:

Trait category 1 (modality with the least vulnerability) = 0

Trait category 2 = $(n_1 + n_2) / n_{total}$

Trait category 3 (highest vulnerability) = $(n_1 + n_2 + n_3) / n_{total} = 1$

Where n represents the number of species per trait category and n_{total} is the total number of species assessed (Richards et al., 2022). Under this scoring system, the cumulative frequency represents the proportion of species occupying a given modality and all less vulnerable modalities combined. This approach ensures that trait modalities associated with higher vulnerability are assigned higher scores relative to their position and prevalence within the dataset.

For example, the *motility* trait was divided into three categories: *motile* (category 1 = 131 species), *discretely motile-low* (category 2 = 26 species), and *sessile/none* (category 3 = 6 species), out of a total of 163 species (n_{total}). Motile species were considered the least vulnerable and therefore assigned a score of 0. The additional motility categories were assigned scores proportionally based on the cumulative number of species within that category and less vulnerable categories. Accordingly, discretely motile-low species' score is $(131 + 26) / 163 = 0.96$ and sessile species' score is $(131 + 26 + 6) / 163 = 1$. These equations were applied independently to each trait, and the number of categories per trait varied depending on trait structure. This approach helped ensure that species' vulnerability scores reflected not only trait susceptibility, but also the relative distribution of those traits across the dataset, preventing rare but highly vulnerable modalities from being underrepresented.

Final vulnerability score

After scoring traits individually, the final vulnerability score for each species was determined by averaging the scores across all three dimensions (exposure, sensitivity, and adaptive capacity) (Figure 3.1). These initial vulnerability scores were based on ranked cumulative frequencies of trait modalities, where less vulnerable traits were assigned lower scores and more vulnerable traits were assigned higher scores. However, after averaging scores across traits, species with lower mean scores were inherently more vulnerable. To make the interpretation more intuitive—where higher scores represent greater vulnerability—a *1 – mean score* transformation was applied after aggregation (Foden et al., 2013; Richards et al., 2022).

Species with high final scores across all dimensions were considered the most vulnerable. This composite score provides a preliminary identification of species most at risk, highlighting those that may require targeted conservation efforts. To evaluate whether this trait-based framework aligns with broader conservation priorities, the final vulnerability scores, derived from the combined exposure, sensitivity, and adaptive capacity metrics, were compared to existing IUCN Red List classifications. This comparison helped assess whether species identified as highly vulnerable in this framework are already recognized as conservation concerns, or whether the results highlight species that may have been previously overlooked in the context of climate change.

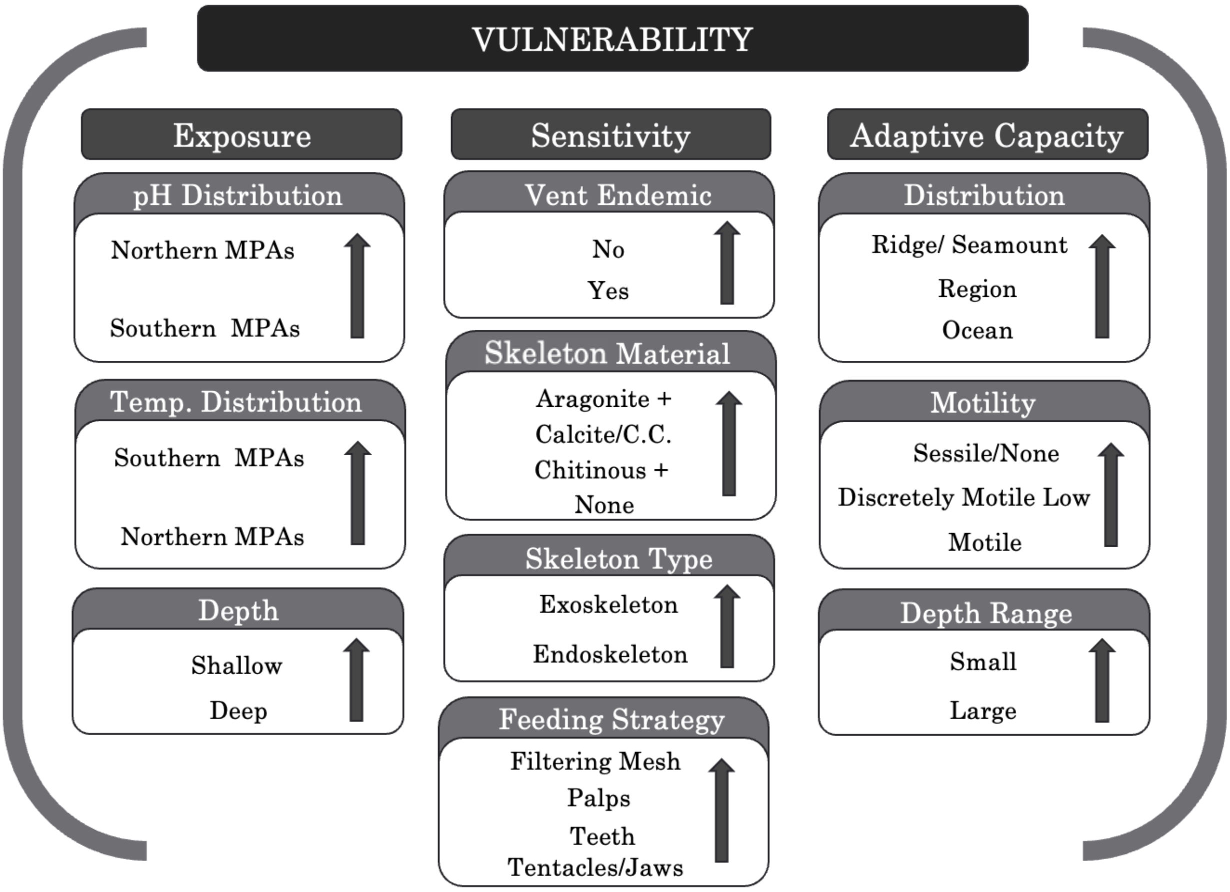

Figure 3.1: Conceptual framework to quantify mollusc vulnerability to ocean acidification and warming. The vulnerability of a species is categorized into three dimensions: exposure, sensitivity, and adaptive capacity. Each dimension includes specific traits (10 used in total) that contribute to overall vulnerability. For simplicity, certain traits have been simplified in the diagram: pH Distribution, Temperature Distribution, Depth, and Depth Range (e.g., depth range is represented as “small” and “large”, indicating how many depth bands of six a species occupies). Arrows indicate the direction of vulnerability, illustrating how changes in each dimension can influence a species’ overall vulnerability to climate change. The figure is based upon published images (Potter et al., 2022; Richards et al., 2022).

3.2.3 Data Visualization and Statistical Analysis

All statistical analyses were conducted in R, using the following packages: dplyr for data manipulation, ggplot2 for visualization, and vegan for multivariate analyses.

To examine whether individual vulnerability dimensions (exposure, sensitivity, and adaptive capacity) differed significantly among mollusc classes, a Kruskal-Wallis rank sum tests were performed– a non-parametric test suited for comparing multiple independent groups. Mollusc classes were defined as Monoplacophora (n = 3), Bivalvia (n = 27), Gastropoda (n = 116), Cephalopoda (n = 16), and Scaphopoda (n = 1). If significant differences were detected, Dunn's test with Bonferroni corrections was applied to identify which pairwise comparisons were statistically different.

To differences in overall vulnerability profiles across mollusc classes, a PERMANOVA (Permutational Multivariate Analysis of Variance) was conducted. This test evaluates whether species' multivariate vulnerability compositions (considering exposure, sensitivity, and adaptive capacity together) differ significantly among lasses, providing insight into broader patterns of functional trait composition.

Additionally, PERMDISP (Permutational Analysis of Multivariate Dispersions) was used to assess the homogeneity of dispersion among classes. This test determines whether variability in vulnerability profiles is consistent across groups, helping to clarify whether significant PERMANOVA results are driven by true differences among group centroids or by differences in within-group variability. This distinction ensures a more robust interpretation of the results.

3.3 Results

3.3.1 Comprehensive Literature Review of Traits

The literature review provided key insights into which traits should be prioritized, used with caution, or excluded when assessing the vulnerability of mollusc species to ocean acidification and warming (Appendix B). This evaluation helped refine trait selection by identifying those with strong empirical support for their role in climate vulnerability and highlighting key data gaps. Specifically, I found that traits related to skeleton composition and motility were highly relevant for understanding species' susceptibility and adaptive capacity. Traits such as feeding structure and depth range had potential utility but required careful interpretation due to variability in species responses or data limitations. Additionally, traits like body size were deemed unreliable for predicting vulnerability due to inconsistent responses to climate stressors across species. By systematically assessing the applicability of these traits, this review ensured that the selected traits provided meaningful ecological insights while minimizing uncertainty.

Body size, categorized as both a response and effect trait, was not recommended for use in this assessment due to inconsistencies in how it relates to climate change stressors. While many studies suggest a general decrease in body size with warming (e.g., Carey & Sigwart, 2014; Lavin et al., 2022; Melatunan et al., 2013; Ortega et al., 2016; Sheridan & Bickford, 2011), this response is not universal across mollusc species (Boavida-Portugal et al., 2022; Borges et al., 2023; Neige, 2021) or even within other marine taxa such as fish, crustaceans, and cephalopods (Hunt & Roy, 2006; Rosa et al., 2012). The metabolic theory of ecology predicts that smaller individuals may be more sensitive to warming due to their higher surface-area-to-volume ratio, which increases metabolic demands and accelerates oxygen limitation (Carey & Sigwart, 2014; Verberk et al., 2021). However, some species exhibit stable or even increased sizes at higher latitudes, challenging the assumption of a universal temperature-size response (Boavida-Portugal et al., 2022; Neige, 2021). Additionally, in some cases, a reduction in body size may be an adaptive response to thermal stress, enabling species to maintain physiological function under higher temperatures (Johansen et al., 2024; Leung et al., 2021). This creates a fundamental ambiguity—while a decrease in body size can indicate climate stress, it may also represent a successful short-term coping mechanism, making it difficult to interpret as an indicator of vulnerability.

In contrast, body size responses to ocean acidification are less predictable and species-dependent. Calcifying molluscs may experience reduced growth rates due to increased energetic costs associated with shell maintenance under acidified conditions, potentially leading to smaller adult body sizes (Gazeau et al., 2013; Melatunan et al., 2013; Melzner et al., 2011). However, other species exhibit no significant size changes under acidification or even increased growth rates under moderate pCO_2 conditions, highlighting a lack of clear directional trends (Gazeau et al., 2013; Melzner et al., 2011). Additionally, some molluscs exhibit compensatory mechanisms such as increased feeding rates to offset acidification-induced metabolic costs (Clements & Darrow, 2018).

Further complicating the interpretation, marine molluscs do not consistently conform to Bergmann's Rule, which predicts larger body sizes at higher latitudes due to cooler temperatures (Chattopadhyay & Chattopadhyay, 2020). Instead, their size variability throughout the Cenozoic era suggests that evolutionary, ecological, and environmental drivers interact in complex ways to shape body size patterns over time (Chattopadhyay & Chattopadhyay, 2020). Similar complexities have been observed in other taxa, such as deep-sea ostracodes, where body size shifts are linked more to long-term climate fluctuations than to a straightforward temperature-size rule (Hunt & Roy, 2006). Given the inconsistencies in the nature of body size responses to warming and acidification and in whether reductions in body size represent increased vulnerability or adaptive potential, body size is not a reliable trait for assessing mollusc susceptibility to climate change.

Skeletal material, a response trait, was recommended for use with caution due to uncertainties surrounding the role of calcite composition in determining species vulnerability. Specifically, the magnesium content in calcite significantly influences dissolution rates and susceptibility to acidification (Andersson et al., 2008; Chan et al., 2012; Ries, 2010). In this assessment, species with aragonite-based skeletons (*aragonite* + in Figure 3.1, as some species contained both aragonite and other skeleton materials) were classified as most vulnerable due to aragonite's higher solubility compared to calcite (Chan et al., 2012; Ries, 2010). Some species were identifies as containing calcium carbonate without further specification of its form. For this reason, calcite and calcium carbonate were grouped into the same vulnerability category, as species identified as containing calcium carbonate without further specification were assumed to exhibit similar vulnerability unless specifically indicated as aragonite. Skeleton type, also a response trait, was recommended for use without caution because the literature provides strong and consistent evidence that exoskeleton-bearing species are more susceptible to environmental stressors than those with endoskeletons. Exoskeletons are directly exposed to corrosive waters, making them more vulnerable to acidification-induced degradation (Dorey et al., 2013; Gardner et al., 2017; Gaylord et al., 2011; Lischka et al., 2011; Michaelidis et al., 2005).

Feeding structure, an effect trait, was suggested for use with caution. While it provides some insight into species' feeding ecology, it is less informative than feeding mode or trophic position. Feeding structures, in some instances, depend on specific food sources and can have distinct mineral compositions that may be affected by climate change (Krings et al., 2022; Shaw et al., 2010). The feeding structure categories assessed were filtering mesh, palps, radula, and tentacles.

The vulnerability of different feeding structures was ranked as follows: filtering mesh was deemed the most vulnerable due to ocean acidification's negative effects on suspension feeders (e.g., Clements & Darrow, 2018; Gray et al., 2017; Vargas et al., 2015), particularly given projected declines in particulate organic carbon (POC) in the Atlantic (Sweetman et al., 2017). Palps were ranked next due to their reliance on organic matter in sediment, making them susceptible to fluctuations in POC. This feeding strategy, although less studied, is considered less vulnerable than filter feeding (Van Colen et al., 2020). The radula was ranked third; while some studies have demonstrated damage to the radula under exposure to CO_2-acidified seawater (Marchant et al., 2010), others have found minimal or no effect (Sigwart & Carey, 2014). Tentacles were ranked as least vulnerable. Species using tentacles for feeding often exhibit high feeding plasticity, allowing them to adapt to varying prey availability under changing environmental conditions (Villanueva et al., 2017). Rather than depending on a narrow food source, tentacle feeders can adjust their diet in response to shifts in prey communities, potentially buffering them against the impacts of climate-induced changes in food supply. The size of feeding appendages was not recommended for assessment due to significant data gaps.

Motility, an effect trait, was recommended for use, as it plays a critical role in a species' adaptive capacity (Matoo & Neiman, 2021). Species were classified into three motility categories—sessile/none, discretely motile-low, and motile—which were ranked according to their relative vulnerability, with sessile species considered the most vulnerable due to their limited ability to relocate in response to environmental stressors. In contrast, environmental position, defined as whether a species is epibenthic, infaunal, pelagic, or benthopelagic, was found to be more useful in distinguishing broad taxonomic groups (e.g., cephalopods vs. other molluscs) rather than providing meaningful insights into climate vulnerability. As such, it was not prioritized in this assessment. Distribution, a trait functioning as both a response and effect trait, was recommended for use, while depth range was suggested for use with caution due to preliminary data limitations. Specifically, depth range data were primarily sourced from the Ocean Biogeographic Information System (OBIS), which may not accurately reflect species' actual depth distributions within Azores MPAs.

Feeding mode and trophic position, both effect traits, were identified as ecologically valuable for understanding mollusc vulnerability, but substantial data gaps limited their use in this assessment. Although these traits provide important insights into species' functional roles—distinguishing, for example, between predators, deposit feeders, and other trophic categories—the extent of missing data led to their exclusion from the final vulnerability scoring. Similarly, trophic position is essential for understanding food web dynamics and the ecological significance of species (Spooner et al., 2012, but incomplete coverage across species prevented its application here. Another trait with significant data gaps was larval development, which, if available, would offer important insights into dispersal capacity. This is particularly relevant for molluscs with limited adult motility but extended larval stages that may facilitate range shifts in response to climate change (Bashevkin et al., 2020).

The vent-specific trait, categorized as both a response and effect trait, was recommended for use with caution due to the limited research on how vent species will respond to climate change pressures. These organisms have evolved to thrive in extreme environments characterized by high acidity, low oxygen, large temperature gradients, and complete darkness (Tunnicliffe, 1991). Their ability to withstand the natural disturbances typical of vent ecosystems suggests they are generally resilient (Van Dover, 2014). Given this inherent resilience, vent species were ranked as having lower overall vulnerability, despite the lack of comprehensive studies on how they may fare as these environments undergo further changes due to climate change.

3.3.2 Exposure

The exposure of mollusc species to ocean acidification and warming, as predicted from ocean models, varies geographically across the Azores Marine Park. Southern MPAs, such as MPA 04 and MPA 12, are projected to experience greater warming, while northern MPAs, including MPA 05 and MPA 14, are expected to become more acidic (Figure 3.2).

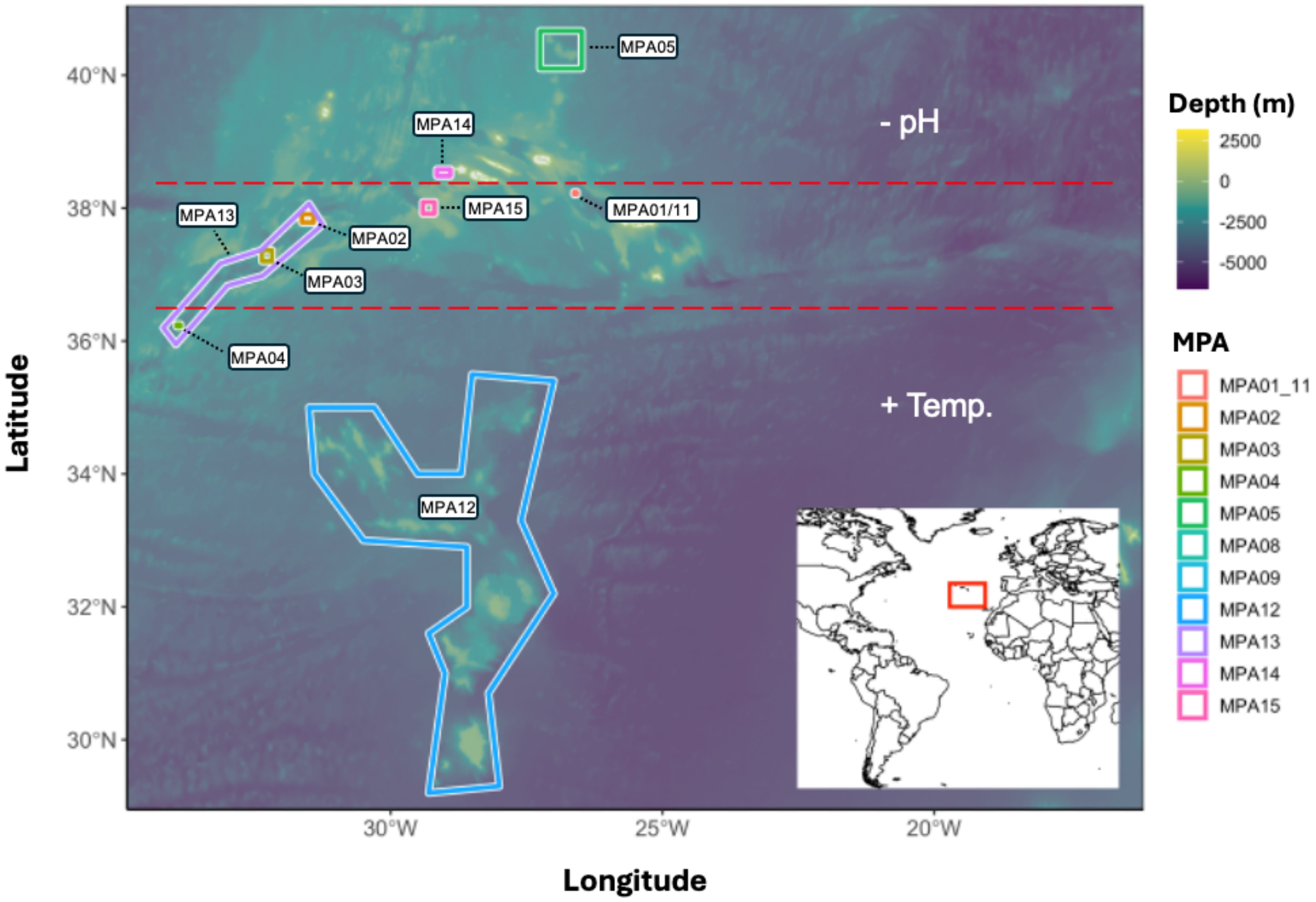

Figure 3.2. Map of the Azores Marine Park showing the predicted exposure of MPAs to ocean acidification and warming. Red dashed lines indicate the latitudinal shift in exposure, with northern MPAs (e.g., MPA 05, MPA 14) expected to experience increased acidification (*-pH*), while southern MPAs (e.g., MPA 04, MPA 12) are projected to undergo greater warming (+*Temp.*). The inset map highlights the study region within the North Atlantic.

3.3.3 Mollusc Vulnerabilities

3.3.3.1 Overview of Vulnerability Assessment

Exposure

Exposure values, reflecting the extent to which species are subjected to warming and acidification, ranged from 0.25 to 0.75, with all species facing some level of exposure to these climate-related stressors (see Figure 3.3). The median exposure value was 0.41. Twenty-six species had the highest exposure scores, with 19 being gastropods and 7 bivalves. These species were found in MPA 01/11 and predominantly at shallower depths, indicating higher vulnerability to climate stressors. Interestingly, gastropods were also among those with the lowest exposure scores, inhabiting deeper waters in MPAs 03/04/13, where exposure to warming and acidification is comparatively less severe.

Sensitivity

Sensitivity values among the mollusc species ranged from 0.03 to 1, with a median value of 0.57, as the data were not normally distributed (See Figure 3.3). Bivalves exhibited the highest sensitivity to both warming and acidification, with 22 species demonstrating the most sensitive traits across all categories. Key traits contributing to their high sensitivity included exoskeletons predominantly composed of aragonite, filter-feeding mechanisms, and occurrence in non-hydrothermal vent environments. In contrast, vent-endemic gastropods displayed the lowest sensitivity values, closely followed by cephalopods. Cephalopods had traits that were less sensitive, such as endoskeletons made of more resilient materials like chitin and tentacle-based feeding mechanisms.

Sensitivity scores exhibited a wider range than Adaptive Capacity and Exposure, with a higher number of outliers (see Figure 3.3). The distribution of sensitivity values was more variable across species, whereas Adaptive Capacity and Exposure scores showed narrower ranges and fewer extreme values.

Adaptive Capacity

Adaptive capacity scores ranged from 0 to 0.76, where higher scores indicate greater vulnerability due to lower ability to adjust to environmental change. The median adaptive capacity score across species was 0.42.

Bivalves exhibited the highest adaptive capacity scores, making them the most vulnerable in this dimension (See Figure 3.3). The two species with the highest scores, *Pseudochama gryphina* and *Pinna rudis*, were sessile, had regional distributions, and were confined to narrow depth ranges, traits that limit their ability to respond to environmental changes.

Conversely, species with lower adaptive capacity scores (indicating lower vulnerability and greater adaptability) included *Antalis agilis*, a scaphopod, and *Abraliopsis morisii*, a cephalopod. These species had oceanic distributions, large depth ranges, and high motility, traits that enhance their ability to adjust to changing conditions.

Vulnerability Score

Averaging exposure, sensitivity, and adaptive capacity scores provides a comprehensive assessment of overall vulnerability. Each species' final vulnerability score represents the mean of its trait-based scores across all three dimensions, reflecting its overall susceptibility to ocean acidification and warming. Final vulnerability scores for individual species are presented in Table B.2, and a visual summary of vulnerability scores across mollusc classes is shown in Figure 3.3. These scores are used to identify species most at risk and to aid in prioritizing conservation efforts.

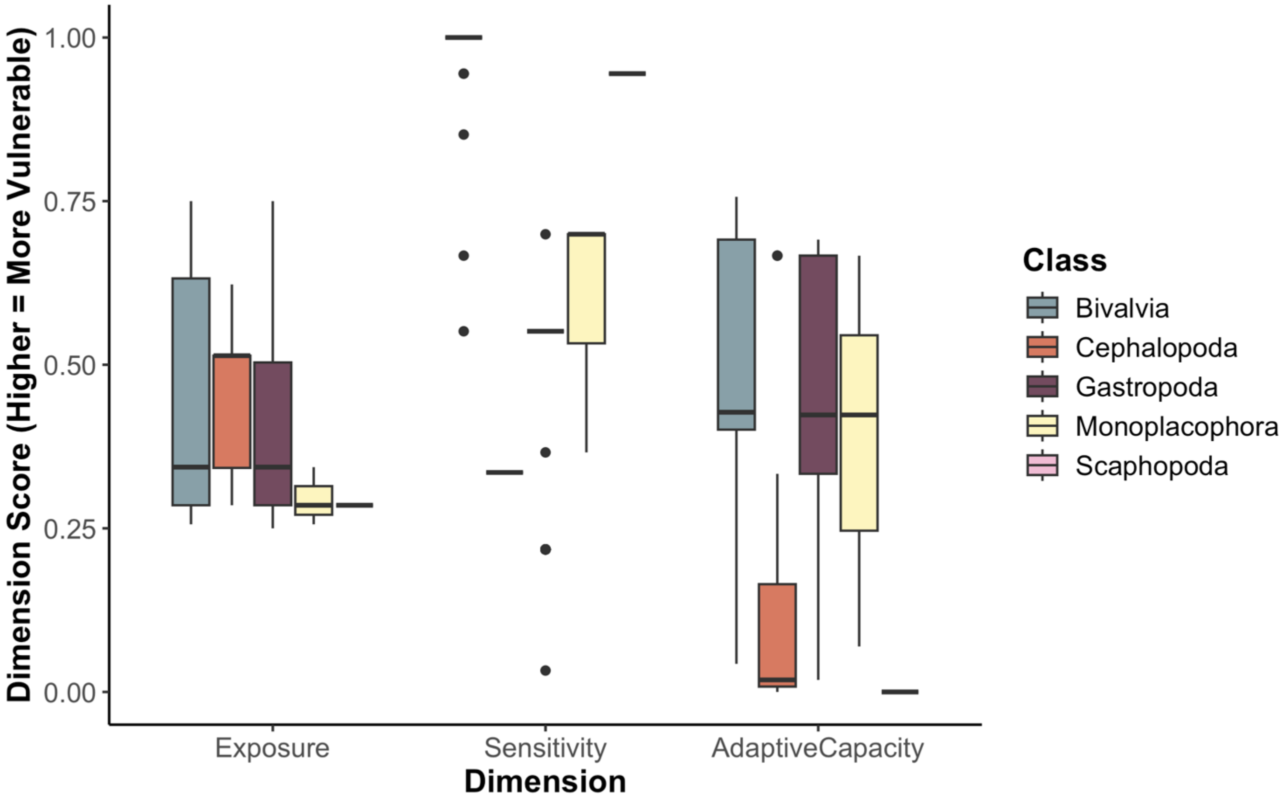

Figure 3.3: Boxplot of vulnerability dimension scores for mollusc species in the Azores Marine Park, split by Exposure, Sensitivity, and Adaptive Capacity dimensions. Scores range from 0 to 1. Following transformation, higher scores across all dimensions represent greater vulnerability to ocean acidification and warming. Different colours represent different mollusc classes. Notably, bivalves show the highest sensitivity and exposure scores, while cephalopods and scaphopods demonstrate lower vulnerability in adaptive capacity due to their greater ability to adjust to environmental changes. Sensitivity scores exhibit a wider range with more outliers, particularly among bivalves, reflecting the influence of skeleton composition and feeding strategy on climate vulnerability.

Overall Vulnerability

The five species with the highest overall vulnerability were all bivalves, exhibiting a combination of high exposure, high sensitivity, and low adaptive capacity. All five species were found in MPA 01/11. They shared the highest possible sensitivity scores, being non-vent species with aragonite-dominated exoskeletons and filter-feeding mechanisms and experienced the greatest exposure to warming and acidification stressors.

While these top five species shared similar exposure and sensitivity scores, differences in their adaptive capacities set them apart. The most vulnerable species, *Pseudochama gryphina*, had a regional distribution, a narrow depth range, and was sessile, making it the least adaptive. Other bivalves in the top five had oceanic distributions, with minor differences in their motility and depth ranges.

Conversely, the five least vulnerable species comprised a mix of gastropods and cephalopods. The species with the least vulnerable traits was *Phymorhynchus ovatus*, closely followed by *Phymorhynchus moskalevi*. These vent-endemic snails, found in the southwest Azores vent MPAs (MPAs 03, 04, and 13), were primarily differentiated by their exposure and adaptive capacity. *Phymorhynchus ovatus* exhibited lower exposure and higher adaptive capacity, with a larger oceanic distribution and a broader depth range, while *P. moskalevi* had a regional distribution with slightly narrower environmental tolerance. The remaining species in the least vulnerable category were cephalopods inhabiting MPA 12, characterized by large oceanic distributions, lower exposure, and greater motility. The traits driving lower vulnerability in these species included inhabiting deeper waters (lower exposure), possessing skeleton materials less prone to acidification (lower sensitivity), and exhibiting greater motility (higher adaptive capacity).

3.3.3.2 IUCN Vulnerability Assessment

Out of the 163 species included in this study, 28 were included in the IUCN Red List (Table 3.1). Among these, 15 species are endemic to hydrothermal vent ecosystems. Notably, eight of these vent species were classified as Least Concern (LC), including the monoplacophoran *Veleropilina segonzaci* (LC), the bivalve *Bathymodiolus azoricus* (LC), and the gastropods *Lirapex costellatus* (LC), *Dendronotus comteti* (LC), *Protolira valvatoides* (LC), *Xylodiscula analoga* (LC), *Lurifax vitreus* (LC), and *Divia briandi* (LC). These eight species had final vulnerability scores ranging from 0.29 to 0.46. While not the lowest scores observed in the dataset (which ranged from 0.19 to 0.84), these values place them toward the lower end of the vulnerability spectrum, aligning with their IUCN classifications as Least Concern.

Conversely, two vent species—*Phymorhynchus moskalevi* (Endangered, EN) and *Phymorhynchus ovatus* (Near Threatened, NT)—received higher IUCN threat classifications despite having low vulnerability scores in this study. Their final vulnerability scores were 0.20 and 0.19, respectively, placing them among the least vulnerable species assessed. This mismatch between trait-based vulnerability scores and IUCN threat classifications suggests that additional stressors not captured by this framework may influence the conservation status of these species.

Table 3.1. List of mollusc species included in the IUCN Red List, with corresponding vulnerability framework scores and conservation status. Columns show species name, class, sensitivity, adaptive capacity, exposure, overall vulnerability score, and IUCN listing categories: Vulnerable (VU), Least Concern (LC), Near Threatened (NT), and Endangered (EN). Species are listed here in order of overall vulnerability score (larger to smaller).

Species	Class	Exposure	Sensitivity	Adaptive Capacity	Vulnerability Score	IUCN
Haliotis tuberculata	Gastropoda	0.75	0.70	0.07	0.51	VU
Veleropilina segonzaci	Monoplacophora	0.34	0.37	0.67	0.46	LC
Bathymodiolus azoricus	Bivalvia	0.29	0.67	0.40	0.45	LC
Ranella olearium	Gastropoda	0.62	0.55	0.16	0.44	NT
Loligo forbesii	Cephalopoda	0.33	0.34	0.67	0.44	LC
Lirapex costellatus	Gastropoda	0.26	0.22	0.67	0.38	NT
Histioteuthis corona	Cephalopoda	0.34	0.34	0.33	0.34	LC
Octopus vulgaris	Cephalopoda	0.62	0.34	0.04	0.33	LC
Bathothauma lyromma	Cephalopoda	0.51	0.34	0.11	0.32	LC
Dendronotus comteti	Gastropoda	0.26	0.03	0.67	0.32	LC
Protolira valvatoides	Gastropoda	0.29	0.22	0.40	0.30	LC
Xylodiscula analoga	Gastropoda	0.29	0.22	0.40	0.30	LC
Lurifax vitreus	Gastropoda	0.26	0.22	0.42	0.30	LC
Divia briandi	Gastropoda	0.29	0.22	0.38	0.29	NT
Peltospira smaragdina	Gastropoda	0.29	0.22	0.38	0.29	NT
Laeviphitus desbruyeresi	Gastropoda	0.26	0.22	0.40	0.29	LC
Paralepetopsis ferrugivora	Gastropoda	0.26	0.22	0.40	0.29	NT
Pseudorimula midatlantica	Gastropoda	0.26	0.22	0.40	0.29	NT
Cranchia scabra	Cephalopoda	0.51	0.34	0.02	0.29	LC
Histioteuthis meleagroteuthis	Cephalopoda	0.51	0.34	0.02	0.29	LC
Taonius pavo	Cephalopoda	0.51	0.34	0.02	0.29	LC
Pterygioteuthis giardi	Cephalopoda	0.51	0.34	0.01	0.29	LC
Pyroteuthis margaritifera	Cephalopoda	0.51	0.34	0.01	0.29	LC
Stigmatoteuthis dofleini	Cephalopoda	0.51	0.34	0.01	0.29	LC
Japetella diaphana	Cephalopoda	0.34	0.34	0.02	0.23	LC
Lepetodrilus atlanticus	Gastropoda	0.29	0.22	0.13	0.21	LC
Phymorhynchus moskalevi	Gastropoda	0.25	0.22	0.13	0.20	EN
Phymorhynchus ovatus	Gastropoda	0.34	0.22	0.02	0.19	NT

3.3.3.3 Multivariate Analysis

Kruskal-Wallis Test

A significant difference was found in sensitivity scores across classes (Kruskal-Wallis chi-squared of 109.85 and a p-value < 2.2e-16: Table 3.2). Post hoc pairwise comparisons using Dunn's test with

Bonferroni adjustments indicated significant differences between several classes, as shown in table 3.2)

Table 3.2. Results of the Kruskal-Wallis test comparing sensitivity scores across mollusc classes. The test showed a significant difference in sensitivity scores (chi-squared = 109.85, $p < 2.2e-16$). Post hoc pairwise comparisons using Dunn's test with Bonferroni adjustments revealed significant differences between several classes.

Comparison	Mean Difference	p-value
Cephalopoda vs. Bivalvia	9.66	< 0.0001*
Gastropoda vs. Bivalvia	8.41	< 0.0001*
Gastropoda vs. Cephalopoda	-4.69	< 0.0001*
Monoplacophora vs. Bivalvia	1.89	0.3119
Monoplacophora vs. Cephalopoda	-3.04	0.0117*
Monoplacophora vs. Gastropoda	-1.14	1.0000
Scaphopoda vs. Bivalvia	0.19	1.0000
Scaphopoda vs. Cephalopoda	-2.77	0.0277*
Scaphopoda vs. Gastropoda	-1.60	0.5464
Scaphopoda vs. Monoplacophora	-0.82	1.0000

*Significant at $\alpha = 0.05$

Results for the Kruskal-Wallis test for adaptive capacity also yielded significant differences among classes, with a chi-squared value of 29.43 and a p-value of 6.386e-06 (Table 3.3). Dunn's post hoc tests revealed significant differences in adaptive capacity between some species classes, as summarized in Table 3.3.

Table 3.3. Results of the Kruskal-Wallis test comparing adaptive capacity scores across mollusc classes. The test revealed significant differences in adaptive capacity (chi-squared = 29.43, p = 6.386e-06). Post hoc pairwise comparisons using Dunn's test highlighted significant differences between some species classes.

Comparison	Mean Difference	p-value
Cephalopoda vs. Bivalvia	4.99	< 0.0001*
Gastropoda vs. Bivalvia	1.73	0.4225

Comparison	Mean Difference	p-value
Gastropoda vs. Cephalopoda	-4.52	< 0.0001*
Monoplacophora vs. Bivalvia	0.80	1.0000
Monoplacophora vs. Cephalopoda	-1.73	0.4222
Monoplacophora vs. Gastropoda	0.21	1.0000
Scaphopoda vs. Bivalvia	2.13	0.1653
Scaphopoda vs. Cephalopoda	0.56	1.0000
Scaphopoda vs. Gastropoda	1.79	0.3640
Scaphopoda vs. Monoplacophora	1.46	0.7272

*Significant at $\alpha = 0.05$

In contrast, the Kruskal-Wallis test for exposure scores did not show significant differences among the classes, with a chi-squared value of 4.91 and a p-value of 0.2968, indicating that exposure levels are similar across species classes.

Permutational Multivariate Analysis of Variance (PERMANOVA)

A PERMANOVA was conducted to assess how functional trait composition differs between mollusc classes, utilizing Bray-Curtis similarities. The analysis revealed a significant effect of class on trait composition, with a p-value of 0.001 (Table 3.4).

Table 3.4. Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) assessing the effect of mollusc class on trait composition using Bray-Curtis similarities. The analysis showed a significant effect of class on trait composition (p = 0.001).

Source	Df	SumOfSqs	R2	F	Pr(>F)
Model	4	1.0977	0.45129	32.486	0.001
Residual	158	1.3347	0.54871		
Total	162	2.4324	1.00000		

PERMDISP Analysis

To evaluate the homogeneity of variances, a PERMDISP analysis was conducted on the Bray-Curtis distances of the classes. The analysis revealed significant differences in distances to centroid among groups (p = 0.016), indicating that the dispersion of community trait composition varied significantly across mollusc classes (Table 3.5, Figure 3.3).

Table 3.5. Results of the PERMDISP analysis assessing the homogeneity of variances in Bray-Curtis distances among mollusc classes. The analysis revealed significant differences in distances to centroid among groups (p = 0.016), indicating varying dispersion of community trait composition across classes.

Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Groups	4	12.507	3.12669	3.1371	0.01627
Residual	158	157.477	0.99669		

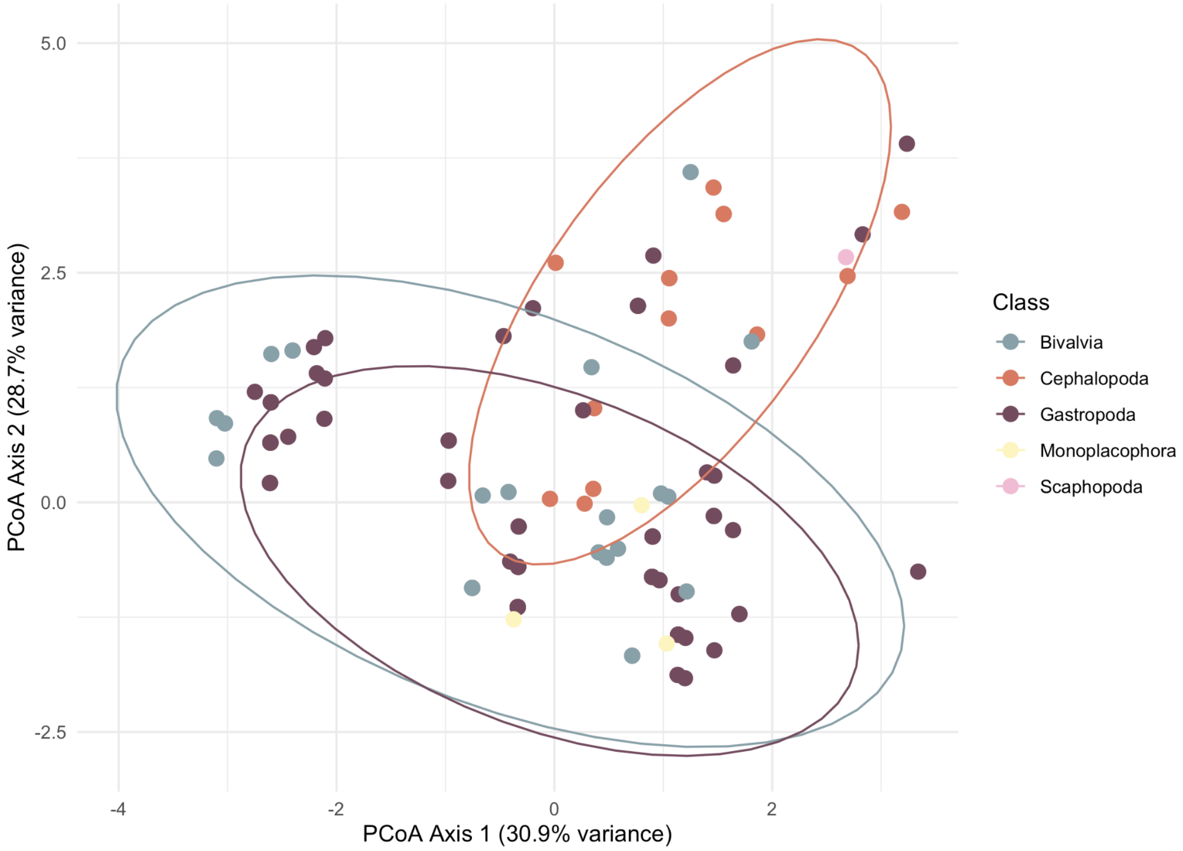

Figure 3.4. Dispersion of functional trait compositions among mollusc classes. The plot represents the spread (dispersion) of functional traits within five mollusc classes: Bivalvia, Cephalopoda, Gastropoda, Monoplacophora, and Scaphopoda, as analyzed using betadisper. Each ellipse encapsulates the variation in trait composition within a class, with larger ellipses indicating higher dispersion or functional trait diversity. Bivalvia exhibits the largest trait variation, followed by Gastropoda and Cephalopoda. The ellipse for Gastropoda is nested within that of Bivalvia, suggesting functional overlap, whereas the Cephalopoda ellipse diverges, indicating distinct trait compositions.

The Betadisper plot (Figure 3.4) shows that some mollusc classes exhibit greater functional trait redundancy than others. Bivalvia exhibits the largest trait variation, followed by Gastropoda and Cephalopoda. The nested structure of Gastropoda within Bivalvia suggests functional overlap, whereas Cephalopoda diverges, indicating distinct trait compositions.

3.4 Discussion

Climate change poses a significant threat to marine biodiversity, particularly in vulnerable ecosystems like the Azores Marine Park, where shifts in temperature and ocean acidification are accelerating (Sweetman et al., 2017). This study assessed the vulnerability of mollusc communities by integrating species traits and exposure data across different MPAs. Significant differences were found in sensitivity and adaptive capacity among mollusc classes, with bivalves emerging as particularly at risk due to their low adaptive capacity and high sensitivity to environmental stressors. By using trait-based approaches and exposure assessments, this study provides insights into how climate pressures may impact mollusc species and highlights taxa that may warrant conservation concern. Additionally, this work underscores the importance of addressing data gaps in trait information, which can enhance conservation decision-making in the face of ongoing climate pressures.

The spatial variation in exposure to climate change stressors across the Azores Marine Park has important ecological implications. Results indicate that northern MPAs, including MPA 05 and MPA 14, are projected to experience greater acidification, whereas southern MPAs, such as MPA 04 and MPA 12, are expected to undergo more intense warming. These patterns are influenced by regional currents, such as the North Atlantic Current in the north and the Azores Current in the south, as well as by the presence of unstable Mediterranean water eddies, known as meddies, which complicate exposure dynamics (Frazão et al., 2022; Sala et al., 2024; Sy, 1988). The predicted acidification in the northern MPAs is particularly concerning for calcifying organisms, as it may reduce carbonate saturation and exacerbate dissolution rates of aragonite-based skeletons, making it more difficult for bivalves and gastropods to maintain their shells. In contrast, the elevated temperatures in the southern MPAs could drive metabolic shifts, alter reproductive timing, and influence species distributions, with motile species potentially migrating to cooler habitats while sessile species may face significant physiological stress. Understanding these exposure dynamics is critical for anticipating species' responses and implementing targeted conservation efforts in different regions of the marine park.

The trait-based analysis revealed significant variability in how different mollusc classes may respond to environmental changes. Cephalopods exhibit traits that suggest greater resilience to climate stressors compared to bivalves, primarily due to their high motility, flexible diets, and lack of external calcium carbonate structures. A study by Stewart et al. (2013) highlights this adaptability, showing that certain cephalopod species, such as *Dosidicus gigas* (jumbo squid), can rapidly adjust their behaviour in response to environmental shifts. A recent meta-analysis by Borges et al. (2023) further suggests that cephalopods may even benefit from ongoing environmental changes, including ocean warming. These findings align with this perspective, indicating that cephalopods may be among the "winners" of climate change. With their rapid life cycles and reproductive strategies, they are well-positioned to expand their geographic ranges and exploit new niches as other species decline (Rosa et al., 2019). Their adaptability has broader ecosystem consequences, as cephalopods play a critical role in marine food webs, both as prey and predators, influencing the structure and stability of marine communities.

In contrast, the heightened sensitivity of bivalves, primarily due to their reliance on aragonite-based exoskeletons and filter-feeding mechanisms, underscores their vulnerability. Research by Berge et al. (2006) found that ocean acidification significantly reduced the growth rates of bivalve species, indicating their potential decline under ongoing climate change. As bivalves are essential for nutrient cycling and water filtration, their decline could lead to significant shifts in ecosystem functioning and health, potentially exacerbating the effects of climate change on marine habitats. A notable example is the decline of bivalve populations in Australia, where reduced filtration capacity has contributed to increased turbidity and nutrient levels, promoting harmful algal blooms that further degrade water quality and disrupt marine life (Gillies et al., 2018; Petersen et al., 2019). This trend raises concerns about cascading ecosystem effects in the Azores Marine Park, particularly in shallow MPAs where bivalves play an integral role in benthic-pelagic coupling and water clarity.

Trait dispersion among mollusc classes further highlights disparities in functional diversity and potential resilience. Bivalves exhibited the widest range of trait compositions, followed by gastropods and cephalopods. While initially counterintuitive, greater trait dispersion within a class suggests that species within that group have highly variable traits, which can either buffer against environmental change (if redundant species can compensate for lost functions) or indicate that individual species have unique ecological roles, making them irreplaceable. In contrast, the nested structure of Gastropoda within Bivalvia suggests some functional overlap, whereas the divergence of Cephalopoda indicates distinct ecological strategies. A loss of key bivalve species could lead to a reduction in essential ecosystem functions, such as water filtration and sediment stabilization, with limited redundancy to compensate for their decline.

While this study provides valuable insights into mollusc vulnerability within the Azores Marine Park, further refinements to the approach could enhance its applicability. One limitation of this framework is the reliance on depth data from the Ocean Biogeographic Information System (OBIS), which, while comprehensive globally, may not accurately reflect region-specific depth distributions. The unique oceanographic features of the Azores, including seamounts and complex current systems, influence species' vertical distributions in ways that may not be captured in broad-scale databases. Future research should integrate regional datasets and *in situ* observations to refine species' depth distributions and improve vulnerability assessments.

Additionally, the trait classifications used in this study, while effective for broad-scale analyses, could be refined to capture species-specific ecological traits more accurately. For example, motility was categorized broadly, yet there are fundamental differences in movement capabilities between gastropods and cephalopods. Gastropods primarily rely on a muscular foot and mucus secretion (Davies & Hawkins, 1998), whereas cephalopods employ jet propulsion via mantle contractions (Ward, 1972), allowing for rapid and agile movement. Recognizing these finer-scale trait distinctions in future trait-based frameworks will improve the accuracy of assessments and conservation planning.

Another key area for future research is the integration of additional stressors beyond ocean warming and acidification. Deep-sea mining, for instance, poses an emerging threat to vent-associated species, yet it was not included in this study's framework. Findings indicate that some vent species currently classified as Least Concern (LC) by the IUCN may be at risk due to increasing industrial activities in deep-sea habitats. Incorporating stressors such as habitat destruction, oxygen loss, and pollution into vulnerability assessments will provide a more comprehensive understanding of species' long-term viability.

The identification of species with higher adaptive capacities provides a foundation for strategic conservation approaches. Cephalopods, which exhibit high mobility and broad environmental tolerances, are likely to persist under changing conditions, whereas bivalves, with their high sensitivity and low adaptive capacity, require targeted conservation efforts. The establishment of well-managed MPAs—defined as areas with clear conservation objectives, effective enforcement, and adaptive management practices—plays a crucial role in maintaining biodiversity and promoting ecosystem resilience. Recent studies emphasize that biodiversity-rich ecosystems with greater functional redundancy are better equipped to withstand environmental change (Aurelle et al., 2022; Flensborg et al., 2023).

Incorporating species' functional traits into MPA management strategies can enhance their effectiveness. For example, management could prioritize areas supporting functionally vulnerable groups, such as sessile, calcifying species, or design zoning strategies that preserve critical ecosystem functions like water filtration and sediment stabilization. A world with marine reserves will always be better equipped to support mollusc biodiversity than one without these protections (Palacios-Abrantes et al., 2023). By integrating functional trait assessments into conservation planning, management efforts can prioritize species that are most at risk while leveraging the resilience of adaptive taxa.

Chapter 4: Conclusion

4.1 Integrated Thesis Summary

Remote, offshore MPAs play a critical role in marine conservation, yet monitoring their biodiversity remains challenging due to logistical constraints and the vast, deep-sea environments they encompass. Effective conservation requires biological assessment tools that can detect ecological changes while remaining feasible for long-term implementation. This thesis examines two complementary approaches to support deep-sea MPA monitoring and management: a functional-group monitoring approach for cold-water corals and sponges (CWCS) in the Northeast Pacific (Chapter 2) and a species-level trait-based vulnerability framework for mollusc species in the Azores Marine Park (Chapter 3).

The research in this thesis identified:

1. Functional groups capture broad CWCS occupancy patterns across Pacific seamounts, but species-level assessments reveal variability in depth-occupancy trends that functional groups alone do not always detect (Chapter 2).
2. Certain species exhibit consistent occupancy across multiple seamounts, but the selection of indicator species for long-term monitoring depends on management objectives. For example, managers may prioritize ubiquitous species for broad-scale monitoring or depth-specific species to track hypoxia-related changes within the OMZ (Chapter 2).
3. Species' vulnerability to climate change is influenced by functional traits rather than broad taxonomic groupings alone. Within molluscs, vulnerability varied based on traits such as shell composition, mobility, and depth range, with northern MPA bivalves emerging as particularly at risk due to their high sensitivity and low adaptive capacity (Chapter 3).
4. Trait-based vulnerability assessments offer a predictive tool for conservation planning, though their effectiveness is limited by data gaps, particularly for deep-sea species (Chapter 3).

4.2 Monitoring Strategies for Remote, Offshore MPAs

Given the logistical and environmental challenges of deep-sea MPAs, effective monitoring strategies must balance ecological accuracy with feasibility. Large-scale assessments require tools that provide meaningful ecological insights while being practical for long-term application. This thesis explores how functional-group monitoring and species-level vulnerability assessments can inform biodiversity patterns and conservation decision-making in offshore MPAs.

In Chapter 2, I evaluate functional-group monitoring as a tool for assessing CWCS distributions across Pacific seamounts. While functional groups captured broad occupancy patterns, species-level analyses revealed finer-scale variability, demonstrating that functional-group monitoring alone may overlook ecologically significant trends. Some species exhibited consistent occupancy patterns across multiple seamounts, making them strong candidates for indicator taxa in long-term monitoring programs. Functional groups offer a practical approach for large-scale biodiversity tracking but should be complemented by species-level assessments to capture species-specific shifts that may signal ecological change.

In Chapter 3, I applied a trait-based vulnerability framework to assess mollusc species' responses to climate change in the Azores Marine Park. This framework provided a predictive approach for conservation planning, identifying species at greatest risk before population declines are observed in traditional monitoring surveys. Bivalves in northern MPAs emerged as highly vulnerable, while cephalopods exhibited greater resilience, aligning with previous research on physiological plasticity in mobile marine species (Borges et al., 2023). Integrating species vulnerability data into biodiversity assessments ensures that conservation priorities reflect not only current biodiversity patterns but also future risks.

Together, these studies reinforce that no single monitoring approach is sufficient on its own. Functional-group monitoring is valuable for large-scale biodiversity tracking, but species-level assessments—particularly through indicator species and trait-based vulnerability models—are essential for detecting ecological changes. By integrating multiple approaches, deep-sea MPAs can develop more adaptive monitoring frameworks that account for both broad-scale patterns and fine-scale species-specific responses.

4.3 Broader Ecological & Conservation Implications

Deep-sea MPAs are increasingly vulnerable to climate change and human activities, raising concerns about whether static protection measures can effectively safeguard biodiversity in dynamic environments. There exists a need for adaptive, ecosystem-specific monitoring strategies that not only track biodiversity trends but also inform proactive conservation responses.

One of the key challenges in deep-sea conservation is that vulnerable species and biodiversity hotspots often overlap with regions experiencing intensified climate stress (Childress & Seibel, 1998; Micaroni et al., 2022; Rogers, 2000). This underscores the risks of relying solely on functional-group monitoring, as species-specific shifts may serve as early indicators of ecosystem change. MPAs designed to protect slow-growing, long-lived species such as CWCS must account for variability in species responses to environmental stressors rather than assuming uniform functional group behaviour.

A major implication of this research is the need to integrate climate vulnerability assessments into MPA management frameworks. The trait-based vulnerability framework applied in Chapter 3 offers a scalable method for identifying species most at risk, enabling managers to prioritize conservation actions before declines become evident. Incorporating such assessments into existing biodiversity monitoring programs would enhance the adaptive capacity of MPAs, ensuring that conservation strategies remain responsive to environmental change.

Additionally, these findings emphasize that MPAs should not be treated as isolated refuges but as components of broader climate resilience strategies. Some vulnerable species may require dynamic conservation measures, such as shifting protected area boundaries or establishing networked MPAs that facilitate species range shifts. As climate change continues to reshape biodiversity patterns, static MPA models may need to evolve toward more flexible, climate-informed conservation planning.

4.4 Future Research Directions

To strengthen deep-sea MPA monitoring, future research should focus on refining and expanding biological assessment tools to ensure conservation strategies remain adaptive and data driven.

A key research priority is expanding vulnerability assessments to incorporate a broader range of anthropogenic stressors. Many existing frameworks, including the trait-based approach applied to molluscs in the Azores (Chapter 3), typically focus on a subset of climate-driven threats, such as ocean warming and acidification. However, marine ecosystems face a plethora of additional pressures—such as deep-sea mining, bottom trawling, and oil and gas exploration—that were not considered in this framework. The exclusion of these stressors may contribute to discrepancies between vulnerability rankings in this study and the high-risk status of some species in the IUCN Red List. Future assessments should aim to integrate multiple human-induced pressures to provide a more comprehensive evaluation of species' long-term risks.

Another important direction is improving trait databases with site-specific ecological data. The FUN Azores Trait Database provided a valuable foundation for assessing species vulnerability (Chapter 3), but the reliance on general OBIS depth distributions rather than Azores-specific depth ranges limits the accuracy of predictions. Incorporating site-specific ecological data is particularly important for non-endemic species to ensure trait-based assessments better reflect regional environmental conditions and conservation needs. Large trait databases should aim to continuously update their information to include site-specific data when possible, though this remains a challenge given the logistical constraints of deep-sea research.

Developing a trait-based vulnerability framework for CWCS in the Northeast Pacific is another key research priority. The mollusc framework (Chapter 3) demonstrated that trait-based approaches can identify species-specific risks that broad taxonomic classifications may overlook. Applying a similar framework to CWCS in the Pacific, where species are already affected by deoxygenation and expanding oxygen minimum zones, could improve predictions of species most at risk. This would complement the functional-group monitoring approach used in Chapter 2, integrating species-level climate vulnerability into long-term monitoring strategies for Northeast Pacific MPAs.

A particularly promising research direction is developing hybrid monitoring frameworks that integrate multiple biological assessment tools. Functional-group monitoring (Chapter 2) provides an efficient way to track biodiversity trends, while trait-based vulnerability assessments (Chapter 3) offer insight into species-specific climate risks. Combining these approaches within the same monitoring framework would enhance conservation planning by linking species distribution trends with climate risk factors, improving the ability of MPA managers to make proactive, evidence-based conservation decisions.

By addressing these research priorities, future studies can further refine biological assessment tools for deep-sea MPAs, ensuring that conservation strategies remain robust, adaptive, and responsive to ongoing environmental change.

4.5 Conclusion

Applying biological assessment tools to deep-sea MPAs offered new perspectives on the effectiveness of different monitoring strategies. Functional-group monitoring offered a broad-scale approach to tracking biodiversity patterns, while species-level trait assessments allowed for a more detailed understanding of species vulnerabilities to environmental change. Together, these approaches provide complementary insights that can strengthen long-term conservation planning. Integrating these tools into MPA management frameworks offers opportunities to improve biodiversity assessments in remote, data-limited ecosystems. I hope this work contributes to the continued refinement of functional-group and trait-based monitoring approaches, helping to develop adaptive strategies that strengthen deep-sea MPA conservation in an era of rapid environmental change.

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Appendix A Supporting information for Chapter 2

Table A.1. Taxa Name and Functional Group Assignments. This table provides a summary of all taxa considered in this study, including their assigned functional group. The listed taxa include both species observed on the transects selected for analysis and those considered in the broader study scope but not present in the final transect data. All taxa, regardless of presence or absence in the transects, were categorized to ensure comprehensive representation of functional group assignments.

Taxa Name	Functional Group
Acanthogorgia sp., yellow (CA32)	Small Gorgonian
Ancorina sp.	Other sponge
Anthoptilum cf. lithophilum (CA41)	Sea pens
Anthoptilum grandiflorum, feather boa (CA01)	Sea pens
Antipatharia (black coral)	Black corals
Aphrocallistidae spp.	Glass Reef
Asbestopluma sp., bush (PD14)	Other sponge
Auletta sp. (PD11)	Other sponge
Bathypathes sp. (CA06)	Black corals
Callogorgia sp. (CA29)	Small Gorgonian
Calyptrophora sp. (CA36)	Large Gorgonian
Chonelasma oreia (PH08)	Other sponge
Chrysopathes spp. (CA21)	Black corals
Cladorhizidae (PD05)	Other sponge
Cup coral, orange tentacles (CA24)	Cup corals
Cup coral, red tentacles (CA14)	Cup corals
Demosponge, ball (PD01)	Other sponge
Demosponge, bulbous (PD02)	Other sponge
Demosponge, leather orb (PD03)	Other sponge
Demosponge, nipple (PD07)	Other sponge
Demosponge, Pale-Yellow (PD04)	Other sponge

Demosponge, white encrusting (PD06)	Other sponge
Demospongiae	Other sponge
Desmophyllum dianthus	Cup corals
Farrea omniclavata, mound (PH02)	Glass Reef
Farrea sp., branching (PH03)	Glass Reef
Farrea sp., Small Tubes (PH09)	Glass Reef
Gersemia sp. (CA20)	Soft coral
Haliclona sp., finger (PD12)	Other sponge
Halipteris sp., whip (CA02)	Sea pens
Hamigera spp. (PD15)	Other sponge
Hexactinella n. sp., Undulated (PH01)	Other sponge
Hexactinellida (glass sponge)	Other sponge
Hexactinellida, Bright Yellow (PH12)	Other sponge
Hexactinellida, stalked vase (PH11)	Other sponge
Homoieurete n. sp. (PH10)	Other sponge
Hydrozoa (Hydrocorals)	Hydrocorals
Isidella tentaculum (CA07)	Large Gorgonian
Isididae (bamboo coral)	Large Gorgonian
Keratoisis sp., branching tree (CA22)	Large Gorgonian
Keratoisis sp., bush (CA05)	Large Gorgonian
Lillipathes sp. (CA04)	Black corals
Mushroom coral, cf *Anthomastus* sp. (CA31)	Soft coral
Mushroom coral, stalked (CA30)	Soft coral
Mushroom Corals	Soft coral
Mycale sp., vase (PD09)	Other sponge
Paragorgia pacifica (CA18)	Large Gorgonian

Paragorgia sp., pale (CA15)	Small Gorgonian
Paragorgia spp. (bubble gum coral)	Large Gorgonian
Parastenella spp. (CA10)	Large Gorgonian
Penares cortius	Other sponge
Pinulasma n. sp. (PH04)	Other sponge
Poecillastra tenuilaminaris, plate sponge (PD10)	Other sponge
Porifera sp., orb (PO01)	Other sponge
Primnoa pacifica (CA16)	Large Gorgonian
Ptilosarcus sp. (CA40)	Sea pens
Rossellidae	Other sponge
Rossellidae, Boot Sponges (PH06)	Other sponge
Rossellidae, translucent (PH07)	Other sponge
Schaudinnia sp. nov.	Other sponge
Stichopathes sp. (CA38)	Black corals
Stolonifera, Encrusting (CA43)	Soft coral
Stylaster sp., pink	Hydrocorals
Stylasteridae sp., white (CH01)	Hydrocorals
Swiftia cf pacifica (CA12)	Small Gorgonian
Swiftia spp.	Small Gorgonian
Tretodictyum n. sp., striated (PH05)	Other sponge
Umbellula lindahli (CA03)	Sea pens
Unbranched *Isididae* (CA33)	Large Gorgonian
Unknown Paragorgiid (CA39)	Small Gorgonian

Table A.2. Ecological Details of Taxa. This table summarizes ecological characteristics for taxa analyzed in this study, including minimum and maximum depths of occupancy (Min. Depth, Max. Depth), depth range, and depth category (e.g., Depth Specialist or Broad Depth Range). Additional metrics include the number of observed occupancy peaks (Num. Peaks), associated depth bands (e.g., Surface to 800 m, OMZ Severe Hypoxia, Oxygen Recovery), total occupancy (Total Occ., sum of 10 m depth bins with presence), and geographic distribution across seamount locations (Seamount Locations). These metrics provide a detailed overview of the ecological roles and spatial distribution of taxa, supporting insights into their habitat preferences and functional contributions.

Taxa Name	Min. Depth	Max. Depth	Depth Range	Depth Category	Num. Peaks	Depth Bands	Total Occ.	Seamount Locations
Acanthogorgia sp., yellow (CA32)	979.3	979.3	0.0	Depth Specialist	1	OMZ Severe Hypoxia (800-1200m)	3	Dellwood.S-East
Anthoptilum cf. lithophilum (CA41)	1089.1	1089.1	0.0	Depth Specialist	1	OMZ Severe Hypoxia (800-1200m)	1	Hodgkins-East
Anthoptilum grandiflorum, feather boa (CA01)	824.8	1104.7	280.0	Broad Depth Range	6	OMZ Severe Hypoxia (800-1200m)	92	Dellwood.S-East, Union-East, Dellwood-North, Union-Southeast, Union-West_Northwest
Aphrocallistidae spp.	902.6	1640.2	737.5	Broad Depth Range	4	OMZ Severe Hypoxia (800-1200m), Oxygen Recovery (1200m+)	12	Union-East, Dellwood-Southwest, Union-West_Northwest
Asbestopluma sp. (bush, PD14)	806.9	806.9	0.0	Depth Specialist	1	OMZ Severe Hypoxia (800-1200m)	33	SḴ-B-East
Auletta sp. (PD11)	728.5	728.5	0.0	Depth Specialist	1	Surface to 800m	1	Hodgkins-East

Taxa Name	Min. Depth	Max. Depth	Depth Range	Depth Category	Num. Peaks	Depth Bands	Total Occ.	Seamount Locations
Bathydorus sp. (PH07)	934.0	1386.9	452.9	Broad Depth Range	5	OMZ Severe Hypoxia (800-1200m), Oxygen Recovery (1200m+)	112	Union-East, Dellwood-Southwest, Union-Southeast
Bathypathes sp. (CA06)	777.1	1791.7	1014.6	Broad Depth Range	14	OMZ Severe Hypoxia (800-1200m), Oxygen Recovery (1200m+), Surface to 800m	750	Dellwood-East, Union-East, Dellwood-North, Dellwood-Southwest, Union-Southeast, Union-West_Northwest
Callogorgia sp.(CA29)	1386.9	1386.9	0.0	Depth Specialist	1	Oxygen Recovery (1200m+)	27	Dellwood.S-East
Chonelasma oreia (PH08)	728.5	1546.0	817.5	Broad Depth Range	7	OMZ Severe Hypoxia (800-1200m), Oxygen Recovery (1200m+), Surface to 800m	126	Dellwood.S-East, Hodgkins-East, SK-B-East, Dellwood-North, Dellwood-Southwest, Union-East
Chrysopathes spp.(CA21)	777.1	1791.7	1014.6	Broad Depth Range	10	OMZ Severe Hypoxia (800-1200m), Oxygen Recovery (1200m+), Surface to 800m	504	Dellwood-East, Dellwood.S-East, Union-East, Dellwood-North, Dellwood-Southwest, Union-West_Northwest
Cup coral (red tentacles, CA14)	1073.4	1865.0	791.6	Broad Depth Range	10	OMZ Severe Hypoxia (800-1200m), Oxygen Recovery (1200m+)	358	Dellwood-East, Union-East, Dellwood-North, Dellwood-Southwest, Union-Southeast, Union-West_Northwest

Taxa Name	Min. Depth	Max. Depth	Depth Range	Depth Category	Num. Peaks	Depth Bands	Total Occ.	Seamount Locations
Demosponge (ball PD01)	934.0	2063.8	1129.8	Broad Depth Range	5	OMZ Severe Hypoxia (800-1200m), Oxygen Recovery (1200m+)	16	Hodgkins-East, Union-East, Dellwood-North, Dellwood-Southwest
Demosponge (nipple, PD07)	1467.5	1467.5	0.0	Depth Specialist	1	Oxygen Recovery (1200m+)	1	Dellwood-North
Demosponge (pale yellow, PD04)	806.9	1546.0	739.1	Broad Depth Range	7	OMZ Severe Hypoxia (800-1200m), Oxygen Recovery (1200m+)	136	Dellwood-East, SK-B-East, Union-East, Dellwood-Southwest
Demosponge (white encrusting, PD06)	1187.2	1546.0	358.8	Broad Depth Range	7	OMZ Severe Hypoxia (800-1200m), Oxygen Recovery (1200m+)	576	Dellwood-East, Hodgkins-East, Union-East, Dellwood-North, Dellwood-Southwest
Farrea sp. (branching, PH03)	902.6	1718.4	815.8	Broad Depth Range	5	OMZ Severe Hypoxia (800-1200m), Oxygen Recovery (1200m+)	60	Union-East, Dellwood-Southwest, Union-Southeast, Union-West_Northwest
Farrea spp.	853.9	1969.7	1115.8	Broad Depth Range	12	OMZ Severe Hypoxia (800-1200m), Oxygen Recovery (1200m+)	510	Dellwood-East, Dellwood.S-East, SK-B-East, Union-East, Dellwood-Southwest, Union-Southeast, Union-West_Northwest
Gersemia sp. (CA20)	839.1	1010.7	171.5	Broad Depth Range	7	OMZ Severe Hypoxia (800-1200m)	83	Dellwood.S-East, SK-B-East, Union-East, Dellwood-Southwest, Union-Southeast, Union-West_Northwest

Taxa Name	Min. Depth	Max. Depth	Depth Range	Depth Category	Num. Peaks	Depth Bands	Total Occ.	Seamount Locations
Halipteris sp. (whip, CA02)	824.8	1104.7	280.0	Broad Depth Range	4	OMZ Severe Hypoxia (800-1200m)	106	Dellwood.S-East, SK-B-East, Dellwood-East, Dellwood-North
Hexactinella sp. (Undulated, PH01)	995.0	1546.0	551.0	Broad Depth Range	6	OMZ Severe Hypoxia (800-1200m), Oxygen Recovery (1200m+)	14	Dellwood-East, Union-East, Dellwood-Southwest
Hexactinellida (Bright yellow, PH12)	806.9	806.9	0.0	Depth Specialist	1	OMZ Severe Hypoxia (800-1200m)	1	SK-B-East
Homoieurete sp. (PH10)	728.5	885.3	156.8	Broad Depth Range	3	OMZ Severe Hypoxia (800-1200m), Surface to 800m	22	Dellwood.S-East, Hodgkins-East, SK-B-East
Isidella tentaculum (CA07)	691.4	1136.1	444.6	Broad Depth Range	8	OMZ Severe Hypoxia (800-1200m), Surface to 800m	144	Dellwood-East, SK-B-East, Union-East, Dellwood-Southwest, Union-West_Northwest
Keratoisis sp. (bush, CA05)	775.5	1846.7	1071.1	Broad Depth Range	14	OMZ Severe Hypoxia (800-1200m), Oxygen Recovery (1200m+), Surface to 800m	702	Dellwood-East, Hodgkins-East, SK-B-East, Union-East, Dellwood-North, Dellwood-Southwest, Union-Southeast, Union-West_Northwest

Taxa Name	Min. Depth	Max. Depth	Depth Range	Depth Category	Num. Peaks	Depth Bands	Total Occ.	Seamount Locations
Lillipathes sp. (CA04)	777.1	1954.0	1176.9	Broad Depth Range	10	OMZ Severe Hypoxia (800-1200m), Oxygen Recovery (1200m+), Surface to 800m	1068	Dellwood.S-East, SK-B-East, Union-East, Dellwood-North, Dellwood-Southwest, Union-West_Northwest
Mushroom coral cf *Anthomastus* sp.(CA31)	869.6	1198.8	329.2	Broad Depth Range	4	OMZ Severe Hypoxia (800-1200m)	52	Dellwood.S-East, Hodgkins-East, SK-B-East
Mushroom coral (stalked, CA30)	869.6	1198.8	329.2	Broad Depth Range	4	OMZ Severe Hypoxia (800-1200m)	47	Dellwood.S-East, Hodgkins-East, SK-B-East
Mycale sp. (vase, PD09)	1187.2	1386.9	199.7	Broad Depth Range	2	OMZ Severe Hypoxia (800-1200m), Oxygen Recovery (1200m+)	4	Union-East
Paragorgia pacifica (CA18)	775.5	1452.2	676.7	Broad Depth Range	8	OMZ Severe Hypoxia (800-1200m), Oxygen Recovery (1200m+), Surface to 800m	210	Dellwood-East, Hodgkins-East, SK-B-East, Union-East, Dellwood-North, Dellwood-Southwest, Union-West_Northwest
Paragorgia sp (pale, CA15)	637.6	1883.3	1245.7	Broad Depth Range	16	OMZ Severe Hypoxia (800-1200m), Oxygen Recovery (1200m+), Surface to 800m	1095	Dellwood-East, Dellwood.S-East, Hodgkins-East, SK-B-East, Union-East, Dellwood-Southwest, Union-West_Northwest

Taxa Name	Min. Depth	Max. Depth	Depth Range	Depth Category	Num. Peaks	Depth Bands	Total Occ.	Seamount Locations
Parastenella spp. (CA10)	691.4	2016.8	1325.3	Broad Depth Range	20	OMZ Severe Hypoxia (800-1200m), Oxygen Recovery (1200m+), Surface to 800m	1749	Dellwood-East, Hodgkins-East, SK-B-East, Union-East, Dellwood-North, Dellwood-Southwest, Union-Southeast, Union-West_Northwest
Pinulasma sp. (PH04)	728.5	1386.9	658.4	Broad Depth Range	9	OMZ Severe Hypoxia (800-1200m), Oxygen Recovery (1200m+), Surface to 800m	645	Dellwood.S-East, Hodgkins-East, SK-B-East, Union-East, Dellwood-East, Dellwood-Southwest, Union-Southeast
Rossellidae, boot sponges (PH06)	728.5	1546.0	817.5	Broad Depth Range	13	OMZ Severe Hypoxia (800-1200m), Oxygen Recovery (1200m+), Surface to 800m	570	Dellwood-East, Dellwood.S-East, Hodgkins-East, SK-B-East, Union-East, Dellwood-North, Dellwood-Southwest
Schaudinnia sp.	728.5	885.3	156.8	Broad Depth Range	3	OMZ Severe Hypoxia (800-1200m), Surface to 800m	10	Dellwood.S-East, Hodgkins-East, SK-B-East
Stichopathes sp (CA38)	916.6	916.6	0.0	Depth Specialist	1	OMZ Severe Hypoxia (800-1200m)	1	Dellwood.S-East

Taxa Name	Min. Depth	Max. Depth	Depth Range	Depth Category	Num. Peaks	Depth Bands	Total Occ.	Seamount Locations
Stolonifera (encrusting, CA43)	869.6	869.6	0.0	Depth Specialist	1	OMZ Severe Hypoxia (800-1200m)	3	Hodgkins-East
Stylaster spp. (CH01)	634.4	1938.3	1303.9	Broad Depth Range	16	OMZ Severe Hypoxia (800-1200m), Oxygen Recovery (1200m+), Surface to 800m	1032	Dellwood-East, Dellwood.S-East, SK-B-East, Union-East, Dellwood-Southwest, Union-Southeast, Union-West_Northwest
Swiftia spp.	637.6	1883.3	1245.7	Broad Depth Range	12	OMZ Severe Hypoxia (800-1200m), Oxygen Recovery (1200m+), Surface to 800m	906	Dellwood-East, Dellwood.S-East, Hodgkins-East, SK-B-East, Union-East, Dellwood-North, Dellwood-Southwest, Union-West_Northwest
Swiftia pacifica (CA12)	822.6	822.6	0.0	Depth Specialist	1	OMZ Severe Hypoxia (800-1200m)	1	SK-B-East
Tretodictyum sp. (striated, PH05)	728.5	1187.2	458.7	Broad Depth Range	5	OMZ Severe Hypoxia (800-1200m), Surface to 800m	160	Dellwood.S-East, Hodgkins-East, Union-East, Dellwood-Southwest
Umbellula lindahli (CA03)	824.8	907.1	82.3	Depth Specialist	3	OMZ Severe Hypoxia (800-1200m)	37	Dellwood-East, Dellwood-North

Taxa Name	Min. Depth	Max. Depth	Depth Range	Depth Category	Num. Peaks	Depth Bands	Total Occ.	Seamount Locations
Unbranched *Isididae* (CA33)	691.4	2016.8	1325.3	Broad Depth Range	20	OMZ Severe Hypoxia (800-1200m), Oxygen Recovery (1200m+), Surface to 800m	1245	Dellwood-East, SK-B-East, Union-East, Dellwood-North, Dellwood-Southwest, Union-Southeast, Union-West_Northwest
Unknown Paragorgiid	822.6	979.3	156.8	Broad Depth Range	2	OMZ Severe Hypoxia (800-1200m)	17	Dellwood.S-East, Hodgkins-East

Appendix B Supporting information for Chapter 3

Table B.1. Recommendations for mollusc traits to assess vulnerability to ocean acidification and warming, based on a comprehensive literature review of the FUN Azores Trait Database (Campanyà-Llovet et al., 2023). Traits are categorized as: (1) recommended for use, (2) recommended for use with caution, and (3) not recommended for use in evaluating mollusc vulnerability to climate pressures.

Trait	Trait Type	Recommendation	Data Gap	Notes
Body Size	Response/effect	3	No	Not clear in literature the impacts as a response or effect. Some studies suggest an overall decrease in size with climate change, while others report increases.
Skeleton Material	Response	2	No	If the skeletal composition, especially magnesium levels in calcite, is unknown, then this trait should be used with caution.
Skeleton Type	Response	1	No	
Feeding Structure	Effect	2	No	Not as useful as the traits Feeding Mode and Trophic position, but no data gap.
Size of Feeding Structure	Effect	3	Yes	
Motility	Effect	1	No	
Environmental Position	Effect	2	No	
Distribution	Response/effect	1	No	
Depth Range	Response/effect	1	No	
Feeding Mode	Effect	2	Yes	
Trophic Position	Effect	2	Yes	
Larval Development	Response/effect	1	Yes	A very useful trait but large data gap present.
Vent Species	Response/effect	1	No	

Table B.2. Full list of all 163 mollusc species included in the vulnerability framework, detailing their class, sensitivity, adaptive capacity, exposure, and overall vulnerability scores. Species are listed here in order of overall vulnerability score (largest to smallest).

Species	Class	Exposure	Sensitivity	Adaptive Capacity	Vulnerability Score
Pseudochama gryphina	Bivalvia	0.75	1.00	0.76	0.84
Pinna rudis	Bivalvia	0.75	1.00	0.67	0.81
Gregariella semigranata	Bivalvia	0.75	1.00	0.60	0.78
Talochlamys multistriata	Bivalvia	0.75	1.00	0.60	0.78
Tetrarca tetragona	Bivalvia	0.75	1.00	0.40	0.72
Neopycnodonte zibrowii	Bivalvia	0.34	1.00	0.76	0.70
Asperarca nodulosa	Bivalvia	0.34	1.00	0.69	0.68
Cetomya neaeroides	Bivalvia	0.34	1.00	0.69	0.68
Cuspidaria meteoris	Bivalvia	0.34	1.00	0.69	0.68
Panacca montana	Bivalvia	0.34	1.00	0.69	0.68
Ervilia castanea	Bivalvia	0.75	0.94	0.34	0.68
Limaria hians	Bivalvia	0.75	0.94	0.34	0.68
Anachis avaroides	Gastropoda	0.75	0.55	0.67	0.66
Columbella adansoni	Gastropoda	0.75	0.55	0.67	0.66
Sinezona cingulata	Gastropoda	0.75	0.55	0.67	0.66
Tricolia pullus azorica	Gastropoda	0.75	0.55	0.67	0.66
Parvamussium propinquum	Bivalvia	0.26	1.00	0.69	0.65
Rhinoclama teres	Bivalvia	0.26	1.00	0.69	0.65
Talochlamys pusio	Bivalvia	0.51	1.00	0.43	0.65
Parilimya	Bivalvia	0.51	1.00	0.38	0.63
Ledella messanensis	Bivalvia	0.51	1.00	0.28	0.60
Spondylus gussonii	Bivalvia	0.29	1.00	0.49	0.59
Tritia incrassata	Gastropoda	0.75	0.55	0.43	0.58
Alvania angioyi	Gastropoda	0.75	0.55	0.42	0.57
Alvania sleursi	Gastropoda	0.75	0.55	0.42	0.57
Coralliophila meyendorffii	Gastropoda	0.75	0.55	0.42	0.57
Cyrillia linearis	Gastropoda	0.75	0.55	0.42	0.57
Isara cornea	Gastropoda	0.75	0.55	0.42	0.57
Mitromorpha crenipicta	Gastropoda	0.75	0.55	0.42	0.57
Pedicularia sicula	Gastropoda	0.50	0.55	0.67	0.57
Cardiomya cadiziana	Bivalvia	0.29	1.00	0.43	0.57
Haliris lamothei	Bivalvia	0.29	1.00	0.43	0.57
Limopsis minuta	Bivalvia	0.29	1.00	0.43	0.57
Oocorys verrillii	Gastropoda	0.75	0.55	0.40	0.57
Bathyneaera tillamookensis	Bivalvia	0.29	1.00	0.40	0.56
Halonympha depressa	Bivalvia	0.26	1.00	0.43	0.56
Bittium latreillii	Gastropoda	0.75	0.55	0.33	0.54
Ocinebrina aciculata	Gastropoda	0.75	0.55	0.33	0.54
Philippia hybrida	Gastropoda	0.75	0.55	0.33	0.54
Talisman scrobilator	Gastropoda	0.75	0.55	0.33	0.54

Species	Class	Exposure	Sensitivity	Adaptive Capacity	Vulnerability Score
Propeamussium lucidum	Bivalvia	0.29	1.00	0.34	0.54
Kaiparapelta askewi	Gastropoda	0.34	0.55	0.69	0.53
Odostomia fehrae	Gastropoda	0.62	0.55	0.40	0.53
Spinosipella acuticostata	Bivalvia	0.29	0.85	0.43	0.52
Chrysallida seamounti	Gastropoda	0.34	0.55	0.67	0.52
Eudolium bairdii	Gastropoda	0.34	0.55	0.67	0.52
Eulimella atlantis	Gastropoda	0.34	0.55	0.67	0.52
Eulimella phaula	Gastropoda	0.34	0.55	0.67	0.52
Eulimella protofunis	Gastropoda	0.34	0.55	0.67	0.52
Eulimella similebala	Gastropoda	0.34	0.55	0.67	0.52
Eulimella sudis	Gastropoda	0.34	0.55	0.67	0.52
Fusinus meteoris	Gastropoda	0.34	0.55	0.67	0.52
Odostomia buzzurroi	Gastropoda	0.34	0.55	0.67	0.52
Odostomia lesuroiti	Gastropoda	0.34	0.55	0.67	0.52
Odostomia prona	Gastropoda	0.34	0.55	0.67	0.52
Odostomia restii	Gastropoda	0.34	0.55	0.67	0.52
Odostomia testiculus	Gastropoda	0.34	0.55	0.67	0.52
Papuliscala atlantisa	Gastropoda	0.34	0.55	0.67	0.52
Papuliscala daani	Gastropoda	0.34	0.55	0.67	0.52
Papuliscala luuki	Gastropoda	0.34	0.55	0.67	0.52
Papuliscala mikra	Gastropoda	0.34	0.55	0.67	0.52
Papuliscala platoensis	Gastropoda	0.34	0.55	0.67	0.52
Papuliscala seamountae	Gastropoda	0.34	0.55	0.67	0.52
Papuliscala vixcostata	Gastropoda	0.34	0.55	0.67	0.52
Personella lewisi	Gastropoda	0.34	0.55	0.67	0.52
Personopsis grasi	Gastropoda	0.34	0.55	0.67	0.52
Pseudosetia azorica	Gastropoda	0.34	0.55	0.67	0.52
Trituba anelpistos	Gastropoda	0.34	0.55	0.67	0.52
Trituba constricta	Gastropoda	0.34	0.55	0.67	0.52
Trituba elatissima	Gastropoda	0.34	0.55	0.67	0.52
Trituba fallax	Gastropoda	0.34	0.55	0.67	0.52
Trituba hirta	Gastropoda	0.34	0.55	0.67	0.52
Trituba incredita	Gastropoda	0.34	0.55	0.67	0.52
Trituba lima	Gastropoda	0.34	0.55	0.67	0.52
Trituba recurvata	Gastropoda	0.34	0.55	0.67	0.52
Trituba superstes	Gastropoda	0.34	0.55	0.67	0.52
Turbonilla atlantica	Gastropoda	0.34	0.55	0.67	0.52
Turbonilla gofasi	Gastropoda	0.34	0.55	0.67	0.52
Turbonilla vaillanti	Gastropoda	0.34	0.55	0.67	0.52
Haliotis tuberculata	Gastropoda	0.75	0.70	0.07	0.51
Asthelys hyeresensis	Gastropoda	0.26	0.55	0.67	0.49
Odostomia umbilicatissima	Gastropoda	0.26	0.55	0.67	0.49
Lamellaria latens	Gastropoda	0.75	0.55	0.16	0.49

Species	Class	Exposure	Sensitivity	Adaptive Capacity	Vulnerability Score
Veleropilina euglypta	Monoplacophora	0.26	0.70	0.42	0.46
Veleropilina segonzaci	Monoplacophora	0.34	0.37	0.67	0.46
Omalogyra atomus	Gastropoda	0.75	0.55	0.07	0.46
Bathymodiolus azoricus	Bivalvia	0.29	0.67	0.40	0.45
Limacina retroversa	Gastropoda	0.52	0.55	0.29	0.45
Scaeurgus unicirrhus	Cephalopoda	0.34	0.34	0.67	0.45
Ranella olearium	Gastropoda	0.62	0.55	0.16	0.44
Tritonoranella ranelloides	Gastropoda	0.62	0.55	0.16	0.44
Loligo forbesii	Cephalopoda	0.33	0.34	0.67	0.44
Alvania cancellata	Gastropoda	0.34	0.55	0.42	0.44
Latirus rugosissimus	Gastropoda	0.34	0.55	0.42	0.44
Neusas marshalli	Gastropoda	0.34	0.55	0.42	0.44
Parthenina flexuosa	Gastropoda	0.34	0.55	0.42	0.44
Turbonilla eodem	Gastropoda	0.34	0.55	0.42	0.44
Turbonilla mediocris	Gastropoda	0.34	0.55	0.42	0.44
Basilissopsis athenae	Gastropoda	0.29	0.55	0.40	0.41
Calliostoma cyrtoida	Gastropoda	0.29	0.55	0.40	0.41
Carenzia marismontis	Gastropoda	0.29	0.55	0.40	0.41
Chrysallida boucheti	Gastropoda	0.29	0.55	0.40	0.41
Cirsonella ateles	Gastropoda	0.29	0.55	0.40	0.41
Eulimella neoattenuata	Gastropoda	0.29	0.55	0.40	0.41
Odostomia odostomella	Gastropoda	0.29	0.55	0.40	0.41
Papuliscala carolienae	Gastropoda	0.29	0.55	0.40	0.41
Papuliscala dictyophora	Gastropoda	0.29	0.55	0.40	0.41
Papuliscala meteorica	Gastropoda	0.29	0.55	0.40	0.41
Pisanianura grimaldii	Gastropoda	0.29	0.55	0.40	0.41
Akritogyra similis	Gastropoda	0.26	0.55	0.42	0.41
Papuliscala praelonga	Gastropoda	0.26	0.55	0.42	0.41
Seamountiella azorica	Gastropoda	0.26	0.55	0.42	0.41
Turbonilla hamonvillei	Gastropoda	0.26	0.55	0.42	0.41
Turbonilla inobservata	Gastropoda	0.26	0.55	0.42	0.41
Antalis agilis	Scaphopoda	0.29	0.94	0.00	0.41
Halgyrineum louisae	Gastropoda	0.34	0.55	0.33	0.41
Trituba additicia	Gastropoda	0.34	0.55	0.33	0.41
Stramonita haemastoma	Gastropoda	0.62	0.55	0.04	0.41
Tibersyrnola unifasciata	Gastropoda	0.51	0.55	0.13	0.40
Akibumia orientalis	Gastropoda	0.26	0.55	0.33	0.38
Lirapex costellatus	Gastropoda	0.26	0.22	0.67	0.38
Cavolinia inflexa	Gastropoda	0.29	0.55	0.27	0.37
Clio pyramidata	Gastropoda	0.29	0.55	0.27	0.37
Amphissa acutecostata	Gastropoda	0.51	0.55	0.02	0.36
Heliconoides inflatus	Gastropoda	0.51	0.55	0.02	0.36
Strobiligera brychia	Gastropoda	0.51	0.55	0.02	0.36

Species	Class	Exposure	Sensitivity	Adaptive Capacity	Vulnerability Score
Veleropilina zografi	Monoplacophora	0.29	0.70	0.07	0.35
Clione limacina	Gastropoda	0.62	0.37	0.04	0.34
Chtenopteryx sicula	Cephalopoda	0.34	0.34	0.33	0.34
Histioteuthis corona	Cephalopoda	0.34	0.34	0.33	0.34
Octopus vulgaris	Cephalopoda	0.62	0.34	0.04	0.33
Alvania stenolopha	Gastropoda	0.29	0.55	0.16	0.33
Amiantofusus amiantus	Gastropoda	0.29	0.55	0.16	0.33
Fusinus bocagei	Gastropoda	0.29	0.55	0.16	0.33
Turbonilla hoeki	Gastropoda	0.29	0.55	0.16	0.33
Turbonilla micans	Gastropoda	0.29	0.55	0.16	0.33
Batheulima fuscoapicata	Gastropoda	0.29	0.55	0.13	0.32
Bathothauma lyromma	Cephalopoda	0.51	0.34	0.11	0.32
Dendronotus comteti	Gastropoda	0.26	0.03	0.67	0.32
Protolira valvatoides	Gastropoda	0.29	0.22	0.40	0.30
Xylodiscula analoga	Gastropoda	0.29	0.22	0.40	0.30
Lurifax vitreus	Gastropoda	0.26	0.22	0.42	0.30
Divia briandi	Gastropoda	0.29	0.22	0.38	0.29
Peltospira smaragdina	Gastropoda	0.29	0.22	0.38	0.29
Protolira thorvaldssoni	Gastropoda	0.29	0.22	0.38	0.29
Vesicomya atlantica	Bivalvia	0.29	0.55	0.04	0.29
Laeviphitus desbruyeresi	Gastropoda	0.26	0.22	0.40	0.29
Mitrella nitidulina	Gastropoda	0.26	0.55	0.07	0.29
Paralepetopsis ferrugivora	Gastropoda	0.26	0.22	0.40	0.29
Pseudorimula midatlantica	Gastropoda	0.26	0.22	0.40	0.29
Cranchia scabra	Cephalopoda	0.51	0.34	0.02	0.29
Helicocranchia pfefferi	Cephalopoda	0.51	0.34	0.02	0.29
Histioteuthis meleagroteuthis	Cephalopoda	0.51	0.34	0.02	0.29
Taonius pavo	Cephalopoda	0.51	0.34	0.02	0.29
Pterygioteuthis giardi	Cephalopoda	0.51	0.34	0.01	0.29
Pyroteuthis margaritifera	Cephalopoda	0.51	0.34	0.01	0.29
Stigmatoteuthis dofleini	Cephalopoda	0.51	0.34	0.01	0.29
Japetella diaphana	Cephalopoda	0.34	0.34	0.02	0.23
Lepetodrilus atlanticus	Gastropoda	0.29	0.22	0.13	0.21
Mastigoteuthis agassizii	Cephalopoda	0.29	0.34	0.01	0.21
Abraliopsis morisii	Cephalopoda	0.29	0.34	0.00	0.21
Phymorhynchus moskalevi	Gastropoda	0.25	0.22	0.13	0.20
Phymorhynchus ovatus	Gastropoda	0.34	0.22	0.02	0.19