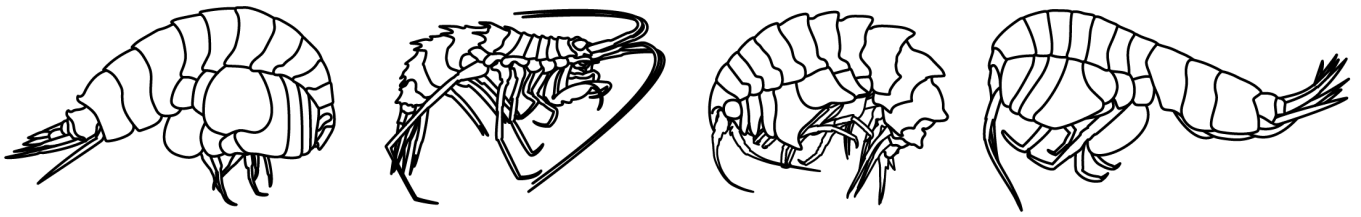


Pan-Atlantic Patterns of Mega- and Macrofaunal Biodiversity with a Focus on Benthic Amphipoda (Crustacea)



DISSERTATION

With the aim of achieving a doctoral degree (Dr. rer. Nat.)

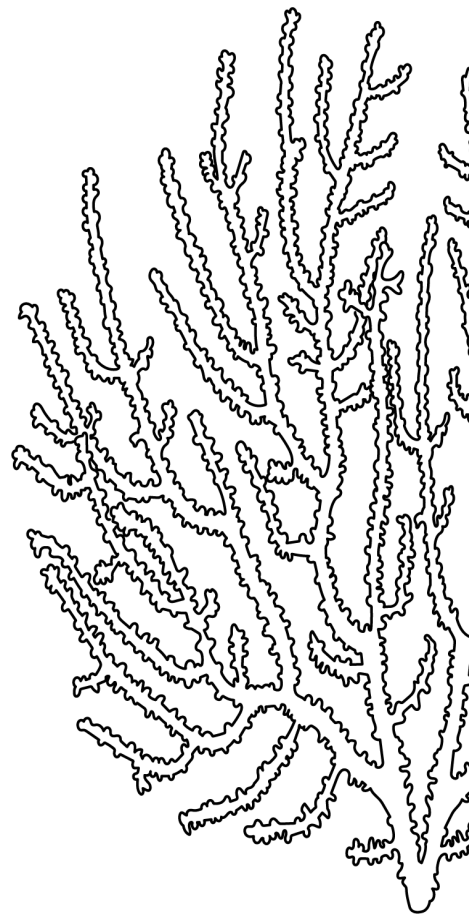
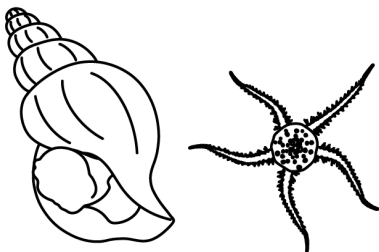
Universität Hamburg

Faculty of Mathematics, Informatics and Natural Sciences

Department of Biology

Submitted by Karlotta Kürzel

2026



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Pan-Atlantic Comparison of Deep-Sea Macro- and Megabenthos

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Conceptualization, K.K., K.L. and S.B.; methodology, all; K.K., K.L., A.B. and S.B.; formal analysis, K.K. and K.L.; investigation, all; data curation, S.B., A.B. and H.J.G.; writing—original draft preparation, K.K. and K.L.; writing—review and editing, all; visualization, K.K. and K.L.; supervision, A.-N.L. and S.B.; project administration, S.B.; funding acquisition, S.B., K.L. and J.T.; K.L., A.B., N.B., P.E., H.J.G., S.K., J.S., A.-N.L., I.F. and S.B. were responsible for the gear on board during the expeditions considered in this paper. All authors have read and agreed to the published version of the manuscript.

Species distribution modelling of benthic amphipod crustaceans in the deep North Atlantic under climate change

Karlotta Kürzel*, Craig P. Hammock, Vanessa Pitusi, Saskia Brix & Anne-Nina Lörz. *Scientific Reports* 15 (1):39581 (2025). <https://doi.org/10.1038/s41598-025-26442-x>

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Cold-water coral associated *Epimeria* (Epimeriidae, Amphipoda) from the North Atlantic and Southwest Pacific, with descriptions of two new species

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Marine Biodiversity 56:16 (2026). <https://doi.org/10.1007/s12526-025-01607-z>

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Link to publication (if published):

<https://www.mdpi.com/1424-2818/15/7/814>

Detailed description of own contribution to this manuscript

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Karlotta Kürzel*, Craig P. Hammock, Vanessa Pitusi, Saskia Brix & Anne-Nina Lörz. Species distribution modelling of benthic amphipod crustaceans in the deep North Atlantic under climate change. Scientific Reports 15, 39581 (2025).

Link to publication (if published):

<https://www.nature.com/articles/s41598-025-26442-x>

Detailed description of own contribution to this manuscript

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Karlotta Kürzel*, Anne-Nina Lörz. Cold-water coral associated Epimeria (Epimeriidae, Amphipoda) from the North Atlantic and Southwest Pacific, with descriptions of two new species. Marine Biodiversity 56,16 (2026).

Link to publication (if published):

<https://doi.org/10.1007/s12526-025-01607-z>

Detailed description of own contribution to this manuscript

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Summary

The deep sea (>200 m) is the largest and least accessible biome on Earth and plays a crucial role in global climate regulation through environmental processes. The Atlantic Ocean, one of the most important ocean basins, largely comprises deep-sea environments and is characterised by complex hydrological conditions as well as extreme environmental factors such as permanent darkness and high hydrostatic pressure. The deep sea supports high biodiversity, with mega- and macro-benthic fauna forming an integral part of ecosystem functioning. Amphipods are a prominent component of benthic communities, contributing to energy transfer within marine food webs and linking benthic and pelagic systems. However, the spatial distribution, biodiversity and abundance of deep-sea benthic fauna and particularly amphipods and their relationships with environmental variables remain poorly understood, limiting our ability to assess current biodiversity patterns and predict responses to climate change. This thesis addresses these knowledge gaps through three peer-reviewed studies.

1. Kürzel et al. (2023; Chapter 2) addresses the limited understanding of large-scale geographic and bathymetric patterns in deep-sea benthic fauna across the Atlantic. Using multivariate analyses of epibenthic sledge data at phylum and multitaxon levels, this study identifies environmental drivers of benthic community structure and abundance patterns. The results reveal a general decline in abundance with depth across most of the Atlantic, contrasted by more heterogeneous depth-related patterns in the Southern Ocean. While environmental conditions differ markedly south of the Antarctic Polar Front, benthic community composition remains broadly similar at higher taxonomic levels, suggesting limited influence of the Antarctic Circumpolar Current. By linking observed patterns to environmental variables, this study helps close a critical knowledge gap in understanding deep-sea benthic distributions at ocean-basin scales under changing environmental conditions.
2. Kürzel et al. (2025; Chapter 3) addresses the limited understanding of large-scale distributions of ecologically important deep-sea amphipods by developing species distribution models for 55 North Atlantic species under present-day and two future climate scenarios across multiple shared socioeconomic pathways. The results reveal strong species-specific responses, with some species expanding suitable habitat while others experience substantial habitat loss. Predicted distribution shifts, including poleward and coastal movements towards Greenland, are likely driven by temperature change and increased nutrient availability associated with glacial

meltwater. By providing the first large-scale, multi-scenario projections for deep-sea amphipods, this study establishes a critical baseline for assessing future biodiversity change and informing conservation and ecosystem management.

3. Kürzel and Lörz (2026; Chapter 4) advances understanding of deep-sea amphipod biodiversity and species–habitat associations through the integrative taxonomic description of Amphipoda associated with cold-water corals in the North East Atlantic and South West Pacific. Supported by in situ ROV observations, DNA barcoding, and updated taxonomic keys, this work increases the number of described *Epimeria* species to 93 and documents further undescribed diversity. These contributions substantially improve baseline knowledge of deep-sea amphipod diversity in associations of cold-water corals.

Together, these studies advance understanding of deep-sea benthic ecosystems by addressing key knowledge gaps in spatial patterns, biodiversity, species distributions, and their relationships with environmental variables. Collectively, they provide essential baseline knowledge for predicting and managing deep-sea ecosystem responses to environmental change.

Zusammenfassung

Die Tiefsee (>200 m) stellt das größte und zugleich am wenigsten zugängliche Biom der Erde dar und spielt durch zahlreiche Umweltprozesse eine zentrale Rolle in der globalen Klimaregulierung. Der Atlantische Ozean, eines der wichtigsten Ozeanbecken, gehört zu großen Teilen zur Tiefsee und ist durch komplexe hydrologische Bedingungen sowie extreme Umweltbedingungen wie permanente Dunkelheit und hohen hydrostatischen Druck geprägt. Die Tiefsee weist eine hohe Biodiversität auf, wobei die Mega- und Makrobenthosfauna einen integralen Bestandteil der Ökosystemfunktionen bildet.

Amphipoden stellen einen bedeutenden Bestandteil benthischer Gemeinschaften dar, da sie maßgeblich zum Energietransfer in marinen Nahrungsnetzen beitragen und benthische mit pelagischen Systemen verknüpfen. Trotz ihrer ökologischen Relevanz sind die räumliche Verbreitung, Abundanzmuster und Biodiversität der benthischen Tiefseefauna, insbesondere der Amphipoden, sowie deren Beziehungen zu Umweltfaktoren bislang unzureichend verstanden. Dies erschwert die Analyse und Bewertung gegenwärtiger Biodiversitäts- und Verbreitungsmuster sowie die Vorhersage ihrer Veränderungen im Zuge des Klimawandels. Die vorliegende Dissertation adressiert diese Wissenslücken anhand von drei peer-reviewten Studien.

1. Kürzel et al. (2023; Kapitel 2) untersuchen großmaßstäbliche und bathymetrische Muster der benthischen Tiefseefauna im Atlantik, die bislang nur unzureichend erforscht sind. Anhand multivariater Analysen von Epibenthoschleichen-Daten auf Phylum- und Multitaxon-Ebene werden Umweltfaktoren identifiziert, die Abundanz und Gemeinschaftsstruktur prägen. Die Ergebnisse zeigen einen allgemeinen Rückgang der Abundanz mit zunehmender Tiefe über weite Teile des Atlantiks, während im Südlichen Ozean stärker heterogene, tiefenabhängige Muster auftreten. Trotz der unterschiedlichen Umweltbedingungen südlich der Antarktischen Polarfront bleibt die Zusammensetzung der benthischen Gemeinschaften auf höheren taxonomischen Ebenen weitgehend gleich, was auf einen nur begrenzten Einfluss des Antarktischen Zirkumpolarstroms hinweist. Durch die Verknüpfung der beobachteten Muster mit benthischen und oberflächennahen Umweltvariablen liefert diese Studie einen wichtigen Beitrag zur Schließung einer zentralen Wissenslücke im Verständnis großmaßstäblicher Verbreitung benthischer Tiefseeorganismen unter sich wandelnden Umweltbedingungen.
2. Kürzel et al. (2025; Kapitel 3) untersuchen großmaßstäbliche Verbreitungsmuster ökologisch bedeutsamer Tiefsee-Amphipoden, indem sie Artverbreitungsmodelle für

55 Arten des Nordatlantiks unter gegenwärtigen Umweltbedingungen sowie unter zwei zukünftigen Klimaszenarien über mehrere gemeinsame sozioökonomische Entwicklungspfade entwickeln. Die Ergebnisse zeigen artspezifische Reaktionen, wobei einige Arten ihre geeigneten Lebensräume ausweiten, während andere einen erheblichen Verlust an Habitatsgröße erfahren. Prognostizierte Verbreitungsverschiebungen, einschließlich polwärtiger und küstennäherer Habitatverschiebungen in Richtung Grönland, werden voraussichtlich durch Temperaturänderungen sowie eine erhöhte Nährstoffverfügbarkeit infolge von Gletscherschmelzwasser gesteuert. Mit den wahrscheinlich ersten großräumigen, szenarienübergreifenden Projektionen für Tiefsee-Amphipoden liefert diese Studie eine wichtige Grundlage zur Bewertung zukünftiger Biodiversitätsveränderungen und zur Unterstützung von Schutz- und Managementmaßnahmen.

3. Kürzel & Lörz (2026; Kapitel 4) erweitern das Verständnis der Biodiversität von Tiefsee-Amphipoden und ihrer Assoziationen mit Kaltwasserkorallen durch eine integrative taxonomische Beschreibung von Arten, die im Nordostatlantik und Südwestpazifik mit diesen Korallen assoziiert sind. Gestützt auf In-situ-ROV-Beobachtungen, DNA-Barcoding und aktualisierte taxonomische Bestimmungsschlüssel erhöht diese Arbeit die Zahl der beschriebenen *Epimeria* Arten auf 93 und dokumentiert darüber hinaus weitere unidentifizierte Arten. Diese Beiträge verbessern das Grundlagenwissen zur Diversität von Tiefsee-Amphipoden in Verbindung mit Kaltwasserkorallen erheblich.

Zusammenfassend tragen diese Studien wesentlich dazu bei, das Verständnis benthischer Tiefseeökosysteme zu vertiefen, indem sie zentrale Wissenslücken zur Verbreitung, Biodiversität, Artenverteilung und deren Zusammenhang mit Umweltvariablen schließen. Sie schaffen eine fundierte Grundlage, die eine präzisere Vorhersage der Reaktionen des Tiefseeökosystems auf zukünftige Umweltveränderungen ermöglicht.

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Chapter 1 Introduction

1.1. The deep Sea

The majority of the ocean lies at depths greater than 200 m and is therefore, in much of the research literature (e.g. Quintanar-Retama et al., 2023; Saeedi et al., 2020; Sweetman et al., 2017), classified as the deep sea (Gage and Tyler, 1991). This simplistic binary classification makes the deep sea easy to define, but does so at the cost of oversimplifying its environmental and biological heterogeneity (Jamieson et al., 2025). Covering approximately 66% of the Earth's surface (Broad, 2025), it represents the largest and least accessible biome on the planet. This biome plays a critical role in global environmental processes, including carbon storage and nutrient cycling, which are essential for regulating Earth's climate (Armstrong et al., 2012; Thurber et al., 2014). The deep sea is characterised by extreme environmental conditions, such as low to absent light, high hydrostatic pressure, and limited food availability, all of which vary with depth (Gage and Tyler, 1991; Rex and Etter, 2010). Despite these conditions, the deep sea supports a remarkable diversity of fauna that are adapted to this environment (Paulus, 2021).

The deep sea is commonly divided into depth zones, each with varying environmental conditions. The bathyal zone extends from the edge of the continental shelf to approximately 3,000 m and includes features such as continental slopes, canyons, seamounts, and ridges (Ramirez-Llodra et al., 2010; Rex and Etter, 2010). Despite the low temperatures and high pressures, bathyal regions often exhibit a peak in marine diversity, which is likely driven by environmental variables such as food availability, pressure, temperature, and adaptive radiation (Brown and Thatje, 2014; Rex and Etter, 2010). Below this depth range lies the abyssal zone (3,000–6,000 m), which encompasses more than half of the deep-sea floor. This zone is dominated by fine sediments (Gage and Tyler, 1991; Smith et al., 2008), although hard substrates also occur, for example in the form of manganese nodules (Smith et al., 2008; Veillette et al., 2007) or rock patches (Riehl et al., 2020). The abyss has pronounced resource limitation, particularly with respect to food availability, with little to no local organic matter production (Monaco and Prouzet, 2015; Smith and Demopoulos, 2003). The hadal zone represents the deepest marine environment, occurring at depths greater than approximately 6,000 m and primarily associated with deep-sea trenches (Jamieson, 2015; Watling et al., 2013). It is highly isolated and topographically complex, with extreme environmental conditions. These conditions support specialised, trench-adapted fauna (Jamieson et al., 2010).

1.2. The Atlantic

As a major ocean basin on the planet and a region of complex hydrological conditions (Allcock et al., 2025), the Atlantic Ocean forms the primary focus area of this thesis. The Atlantic Ocean spans from the Arctic to the Antarctic. It is bordered in the west by the continental margins of North and South America, and in the east by the continental margins of Europe and Africa. The basin has an average depth of about 3,646 m (Koszalka and Stramma, 2019), and the North and South Atlantic are conventionally separated by the equator.

The Atlantic water column is commonly divided into upper and deeper layers. The upper ocean is predominantly influenced by wind-driven circulation and is characterised by relatively warm waters and the presence of a pronounced thermocline (Venancio et al., 2018). Sea surface temperatures generally decrease from the tropics toward the poles, ranging from values above $\sim 25^{\circ}\text{C}$ at low latitudes to near or below 0°C in polar regions (Koszalka and Stramma, 2019).

1.2.1. Atlantic Meridional Overturning Circulation

Especially in the deeper parts of the Atlantic, environmental conditions are strongly shaped by the Atlantic Meridional Overturning Circulation (AMOC), a key component of the global climate system (Alford, 2003; Kuhlbrodt et al., 2007). The AMOC plays an important role in the transport of heat (Rahmstorf et al., 2015), salt (Johns et al., 2011), and carbon (Brown et al., 2021; Kuhlbrodt et al., 2007). Large-scale ocean circulation, including the AMOC, is driven to a significant extent by density gradients that arise from differences in temperature and salinity. These create buoyancy contrasts and lead to the movement of water masses (Brix, 2001).

Deep and bottom water formation is fundamental to the AMOC system, as these regions represent areas where particularly strong buoyancy loss occurs relative to surrounding waters. Within the Atlantic, this process is concentrated primarily at two major sites (Brix, 2001). In the North Atlantic, Labrador Sea Water (LSW), Iceland–Scotland Overflow Water (ISOW), and Denmark Strait Overflow Water (DSOW) together form the North Atlantic Deep Water (NADW) (Liu and Tanhua, 2021). This water mass develops when warm water transported from the South Atlantic cools as it releases heat to the atmosphere, becomes increasingly saline through evaporation and sea-ice processes, and sinks due to increased density into greater depth (Toggweiler and Key, 2001). NADW is typically found between

depths of approximately 2000 and 4000 m (Liu and Tanhua, 2021), with characteristic temperatures of 2.0–3.5 °C and salinities of 34.9–35.0 PSU (Toggweiler and Key, 2001).

The second major site of deep-water formation is around Antarctica, particularly in the Weddell and Ross Sea (Shanmugam, 2021), where Antarctic Bottom Water (AABW) is produced from Circumpolar Deep Water (CDW) and Weddell Sea Bottom Water (WSBW) (van Heuven et al., 2011). Here, cold and salty shelf waters generated by intense winds and sea-ice formation sink into deeper layers (Gordon, 2001). AABW is the densest water mass in the global ocean (Purkey et al., 2018) and occupies depths of below 4000 m (Orsi et al., 1999; Shanmugam, 2021). As it spreads northward, it gradually becomes less dense, contributing to the lower branch of the AMOC. Compared with NADW, AABW is overall colder (−0.8 °C–2.0 °C), less saline (34.6–34.7 PSU), and denser, while also containing higher nutrient concentrations and lower levels of dissolved oxygen (de Carvalho Ferreira and Kerr, 2017; Purkey et al., 2018; Shanmugam, 2021).

1.2.2. Geomorphological features and the Mid-Atlantic Ridge

Both North Atlantic Deep Water and Antarctic Bottom Water spread into the major ocean basins and flow equatorward, eventually returning to the upper ocean through upwelling processes (Brix, 2001). Their pathways through the Atlantic are not unrestricted but are shaped by the complex seafloor topography. One of the most prominent of these features in the North Atlantic is the Greenland–Iceland–Scotland Ridge (GIS ridge). This submerged ridge extends from Greenland to Scotland, with the subsection between Greenland and the Faroe Islands referred to as the Greenland–Iceland–Faroe (GIF) ridge. The GIS ridge forms a boundary between North Atlantic waters and the Nordic Seas and the Arctic Ocean (Hansen and Østerhus, 2000; Rheinlænder et al., 2020). Through a combination of surface inflows, overflows, and deep pathways, water is exchanged across the ridge (Hansen and Østerhus, 2000). This exchange creates a major transition zone between Arctic and Atlantic water masses and contributes substantially to the global ocean circulation. For this reason, the region is often referred to as the “North Atlantic gateway” (Jöst et al., 2019).

Lengthwise, the Atlantic Ocean is divided by the Mid-Atlantic Ridge which is the longest continuous submarine mountain range on Earth. The ridge is formed by the divergence of the Eurasian and American tectonic plates (Bergstad and Falkenhaus, 2002) and extends for roughly 16,000 km (NOAA Ocean Exploration, 2022), stretching from the Gakkel Ridge in the Arctic Ocean to the Bouvet Triple Junction in the South Atlantic (Molodtsova et al., 2017).

Despite its great length, the ridge is relatively narrow, with a typical width of only 5–30 km (Macdonald, 2001), and has an average crest depth of approximately 2,500 m (NOAA Ocean Exploration, 2014). South of Iceland, the northern segment of the Mid-Atlantic Ridge is known as the Reykjanes Ridge which separates the Irminger Basin from the Iceland Basin. The ridge extends southward until it reaches the Charlie Gibbs Fracture Zone (Petit et al., 2019).

Spreading at rates of only 2–5 cm per year, the Mid-Atlantic Ridge develops gradually as molten rock from deep within the Earth rises to fill the opening gap. This slow but continuous process creates complex seafloor topography and a highly heterogeneous habitat, including rift valleys, underwater mountain ranges, seamounts and fracture zones (Bergstad and Falkenhaus, 2002) and hydrothermal vents (e.g. Langmuir et al., 1997; Taylor et al., 2021).

Although the ridge forms a partial barrier between deep waters of the western and eastern Atlantic, fracture zones and other depressions along the ridge provide pathways that allow the exchange of deep water masses and the probable migration of fauna between the two basins (Demidov et al., 2007; Mercier et al., 1994; Vecchione et al., 2010).

1.3. Benthic invertebrates and their role in the marine ecosystem

A diverse range of invertebrates inhabit the bottom of the ocean, including the in- and epibenthic fauna. They vary considerably in size, morphology, lifestyle, feeding strategies, and ecosystem function. Benthic organisms are commonly classified into size-based categories, which are operationally defined by the mesh size of sieves through which they pass or are retained. The meiobenthos generally comprises organisms ranging from 32/64 μm to 0.5/1 mm in size, the macrobenthos includes organisms between 250 μm and 1 cm, and the megabenthos consists of organisms larger than 1 cm (Stratmann et al., 2020). Benthic fauna can further be classified according to their position relative to the seafloor, specifically based on whether organisms inhabit the sediment or occur on its surface. Organisms living within the sediment are referred to as infauna, whereas those residing on or attached to the sediment surface are termed epifauna (Stratmann et al., 2020) and organisms occurring just above the seafloor in the near-bottom water layer are classified as suprafaua (Brunel et al., 1978).

Benthic fauna plays a key role in numerous marine ecosystem processes, particularly as integral components of nutrient cycling (Gogina and Piontek, 2025; Hanz et al., 2022; Ritter and Bourne, 2024). By feeding on particulate organic matter that sinks from the upper ocean

to the seafloor, and subsequently being consumed by higher trophic levels, benthic organisms facilitate the incorporation and redistribution of nutrients. These nutrients are released back into the water column, where they become available to other organisms within the food web. In this way, benthic fauna contributes to both energy transfer and nutrient cycling throughout marine ecosystems, forming a critical link between the benthic environment and the pelagic water column (Ritter and Bourne, 2024).

Benthic fauna further contribute to marine ecosystem functioning through bioturbation, a process in which sediments are physically mixed as a result of burrowing, feeding, and ventilation activities (Kristensen et al., 2012). Taxa commonly involved in bioturbation include crustaceans (Ritter and Bourne, 2024), polychaetes (Martins et al., 2025), and echinoderms (Belaústegui et al., 2017). Bioturbation increases the microheterogeneity of the substrate (Burd et al., 2008) and has been shown to alter both the physical and chemical properties of sediments. These changes include enhanced water and oxygen penetration (Limia and Raffaelli, 1997) as well as increased nutrient release (Grant, 1983; Howard and Dörjes, 1972), which can subsequently influence the structure and diversity of benthic faunal communities (Widdicombe et al., 2003).

Benthic fauna is highly diverse, with representatives from all major groups of marine phyla. Despite this, no phyla are unique to the deep-sea (Ramirez-Llodra et al., 2010). Invertebrate phyla that are among the most abundant include Arthropoda, Annelida, and Mollusca (e.g. Brandt et al., 2018; Grassle and Maciolek, 1992; Kaiser et al., 2023), with Grassle and Maciolek (1992) identifying that these three taxa accounting for 80% of total abundance retained through sieving with a 250–500 µm mesh. Arthropods, characterised by the presence of an exoskeleton (Ghafor, 2020), are well represented in deep-sea communities, with several crustacean orders commonly recorded in biodiversity studies, including Copepoda, Isopoda, and Amphipoda (e.g. Almeida et al., 2017; Brandt et al., 2019).

1.3.1. Amphipods

Amphipods are members of the phylum Arthropoda and represent a diverse (Figure 1) and ecologically important group of benthic invertebrates that play a vital role in marine ecosystems worldwide (Ritter and Bourne, 2024). To date, more than 10,700 amphipod species have been described (WoRMS Editorial Board, 2025), with the vast majority inhabiting marine environments. Amphipods exhibit a wide size range, from approximately 500 µm to 340 mm in length (Li et al., 2019).

Morphologically, amphipods are generally characterised by a bilaterally symmetrical, segmented body that is distinctly longer than it is wide. The body is divided into three main regions: the cephalon (head), pereon (thorax), and pleon (abdomen). Amphipods are relatively mobile organisms, possessing both walking and swimming appendages (Ritter and Bourne, 2024).

Amphipods predominantly reproduce sexually (Johnson et al., 2001), and sexual dimorphism is common within the order (Nahavandi et al., 2011). As members of the superorder Peracarida, amphipods exhibit a brooding reproductive strategy. Fertilised eggs are retained within a specialised brood pouch, the marsupium, until fully developed juveniles emerge. Consequently, amphipods lack a free-swimming larval stage (Dick et al., 1998), a life-history trait that limits their dispersal potential compared to many other marine invertebrates (Väinölä et al., 2008).

Despite the ecological significance of amphipods, many aspects of their ecology remain understudied (Arfianti et al., 2018; Ritter and Bourne, 2024). Amphipods contribute substantially to ecosystem functioning and energy transfer within marine food webs (Lörz, 2010; Nyssen et al., 2002; Ritter and Bourne, 2024) and serve as important links between benthic and pelagic systems (Ritter and Bourne, 2024). This role is largely attributable to their importance as a food resource for a wide range of organisms. For example, amphipods are prey for numerous fish species (e.g. Black et al., 2013; Dalpadado et al., 2016; Duffy et al., 2010) as well as for other crustaceans, including shrimp (e.g. Fry et al., 2003).

Beyond their role as prey, amphipods contribute substantially to ecosystem functioning through diverse feeding behaviours, making them key agents of benthic nutrient cycling (Dauby et al., 2001; Wang et al., 2019). Many species act as scavengers and detritivores, consuming sinking organic matter and accelerating decomposition and nutrient recycling, which is a function that is critical in deep-sea benthic environments (Blankenship and Levin, 2007; Castro et al., 2005). Some deep-sea amphipods exhibit notable physiological adaptations, such as increased oxygen uptake in response to chemical cues from decaying organic material (Smith and Baldwin, 1982), enabling quick movement towards carcasses and contributing to the transfer of nutrients from the seafloor to the water column (Havermans and Smetacek, 2018). Although comprehensive studies remain limited, amphipods display a wide range of feeding strategies, with many species likely combining multiple approaches opportunistically (Ritter and Bourne, 2024). These strategies include suspension feeding on particulate organic matter such as plankton and faecal pellets, exemplified by *Ampelisca richardsoni* Karaman, 1975, which captures particles using its antennae while generating feeding currents with its pleopods; deposit feeding on organic

material accumulated on the seafloor (e.g. *Epimeria (Hoplepimeria) georgiana* Schellenberg, 1931; Dauby et al., 2001); active predation on smaller zooplankton and crustaceans (Alexander et al., 2012), for example in *Epimeria (Drakepimeria) macrodonta* Walker, 1906; and potential micropredatory browsing on sessile organisms such as sponges without causing host mortality (Dauby et al., 2001).

The current and future distribution of benthic amphipod species, particularly in the Atlantic Ocean, remains poorly studied despite their ecological importance. Knowledge of amphipod distributions is often derived from occurrence records reported in taxonomic or ecological studies, in which species are documented from specific sampling locations but their overall distributions are not modelled (e.g. Beermann et al., 2018; Souza-Filho et al., 2024). Other studies have primarily examined patterns at higher taxonomic levels, such as family-level abundance or biodiversity, rather than focusing on species-level distributions (e.g. Frutos and Jażdżewska, 2019), or have been limited to analyses of only a small number of species (e.g. Jażdżewska et al., 2021; Maroni et al., 2025). Additionally, existing studies have typically focused on limited geographic regions, such as the waters around Iceland (e.g. Lörz et al., 2021). For example, Lörz et al. (2021) identified four distinct amphipod assemblage clusters around Iceland using a cluster-based approach, demonstrating that amphipod distribution patterns in this region are driven primarily by depth, salinity, and temperature. Additionally, Lörz et al. (2022) showed that species-level responses of amphipods to environmental variables were largely independent of taxonomic family and instead reflected species-specific ecological preferences. However, it appears that no study has modelled species-level distributions of benthic amphipods under different climate change scenarios across large spatial scales.



Figure 1 Amphipod diversity photographed by K. Kürzel during the IceAGE3 (Icelandic marine Animals: Genetics and Ecology) expedition in the North Atlantic 2020.

1.3.2. The family Epimeriidae Boeck, 1871 and genus *Epimeria* Costa in Hope, 1851

The amphipod family Epimeriidae Boeck, 1871 comprises two accepted genera, of which *Epimeria* Costa in Hope, 1851 is the most speciose (d'Udekem d'Acoz and Verheye, 2017; WoRMS Editorial Board, 2025). The genus *Epimeria* Costa in Hope, 1851 currently comprises 93 described species distributed worldwide (WoRMS Editorial Board, 2025). Species of this genus have a robust, somewhat swollen body, with segments that often bear lateral projections. The head is characterised by a pointed rostrum and a tongue-shaped lobe located just behind the antenna. Their coxal plates are distinctive: the first three pairs are narrow and pointed, whereas the 4th and 5th are larger and often strongly projected (Sars, 1893). The antennae are of moderate size and often nearly equal length with multi-segmented flagella. The gnathopods are relatively small and weakly developed, while the pereopods are slender and the last pair is shorter with a broader base. The uropods have lance-shaped rami with fine spines, and the telson is broadly rectangular with a slightly indented tip (Sars, 1893). Species-level diagnostic characters may include a combination of

rostrum shape, presence or absence of eyes, development of dorsal and dorsolateral carinae, and the shape of the coxa of pereopod 5, among other features (e.g. Beermann et al., 2018; d'Udekem d'Acoz and Verheye, 2017; Wang et al., 2020).

The genus *Epimeria* (Figure 2) is globally distributed in marine environments, with its highest species richness occurring in the Southern Ocean (d'Udekem d'Acoz and Verheye, 2017; OBIS, 2025). The genus is also well represented in the Atlantic Ocean, where 15 species have been recorded. Species of *Epimeria* have been documented from pelagic waters to the deep sea, including abyssal and hadal depths (OBIS, 2025). The genus is particularly well represented in deep-sea environments (Horton et al., 2025; OBIS, 2025) and often encountered at depths between 150 and 2,500 m (d'Udekem d'Acoz and Verheye, 2017). Most *Epimeria* species are benthic (Dauby et al., 2001), although they are capable of short periods of swimming (Moore, 1981). Feeding strategies within the genus appear to be diverse and species-specific, with *Epimeria* species assumed to function as micro-predators, scavengers, browsers, or opportunistic feeders (Dauby et al., 2001). The genus is predominantly carnivorous, feeding on organisms such as other crustaceans, bryozoans, and hydrozoans, although dietary preferences vary among species (Dauby et al., 2001).

Some species have been suggested to occur in association with habitat-forming taxa such as cold-water corals (Beermann et al., 2018), although evidence for such associations remains limited. Notably, specimens of *Epimeria* previously unknown to science have been discovered during more recent deep-sea expeditions to coral reef habitats, highlighting both the genus' taxonomic diversity and its potential associations with other benthic taxa. These characteristics make *Epimeria* a particularly suitable and compelling study organism.

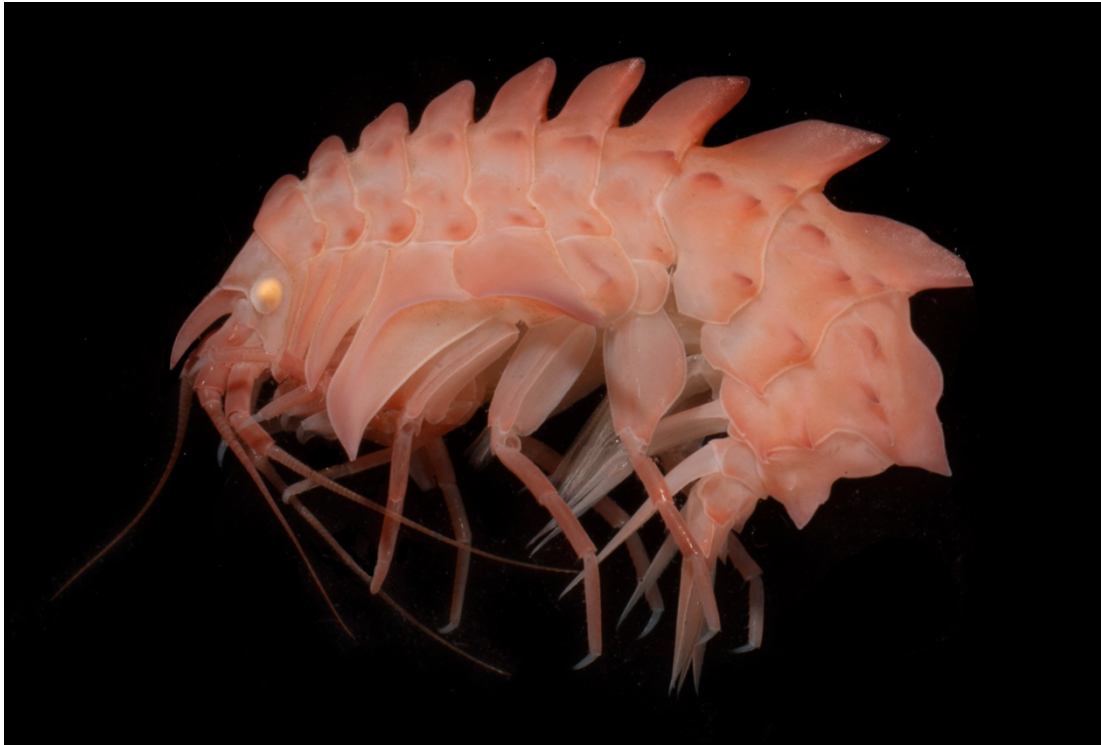


Figure 2 *Epimeria loricata* G. O. Sars, 1879, example of an amphipod belonging to the genus *Epimeria*, photographed by K. Kürzel

1.4. Researching the deep sea

1.4.1. Integrative taxonomy

Once samples are collected in the field, identification of the organisms is required, making species descriptions a critical foundation for subsequent scientific investigations (Kürzel et al., 2022). The identification of species and the description of new taxa are typically carried out by taxonomists, whose expertise is built over many years of accumulated knowledge. Their work provides the framework that enables other scientists to use biological samples reliably, by determining which organisms and species they contain.

However, taxonomy as a discipline is increasingly underfunded (e.g. Andreone et al., 2022; Dupérré, 2020; Nelson et al., 2015). This underinvestment is partly linked to the perception that taxonomy is of limited value, despite its substantial importance for many other areas of research (Löbl et al., 2023; Orr et al., 2020). In addition, modern research evaluation systems often emphasize publication quantity and journal impact, leading to the rejection of taxonomic studies by high-impact journals on the grounds that they are solely descriptive (Casadevall and Fang, 2008; Grimaldi and Engel, 2007; Löbl et al., 2023). Scientific relevance is also increasingly judged by the application of novel or technologically innovative

approaches (Löbl et al., 2023). As a result, the number of trained taxonomists is declining, owing to limited and often temporary employment opportunities, and, in part, an aging workforce (Coleman, 2015). This decline contributes to the so-called “taxonomic impediment”, referring to a growing shortfall in taxonomic expertise that results in large proportions of collected specimens remaining unidentified and therefore unavailable for further analyses (Coleman, 2015).

Today, the need for integrative taxonomy is increasing (Vinarski, 2020), providing an approach that combines traditional morphological taxonomy with modern methods such as genomics (Dayrat, 2005). Within this framework, morphological species descriptions can be supplemented with DNA sequence data, as well as ecological and/or behavioural information (Dayrat, 2005; Stec, 2023). The incorporation of these tools helps address new scientific questions and facilitates the analysis of phylogenetic relationships, the detection of cryptic species, and the resolution of taxonomic uncertainties. Furthermore, the integrative approach allows researchers to clarify and improve species identification through the revision and redescription of taxa using these multiple methods (Sigwart, 2018; Vinarski, 2020).

1.4.2. Modelling

Whilst specialised equipment such as epibenthic sledges (EBS) and remotely operated vehicles (ROV) enable sampling of the deep-sea, and integrative taxonomy enables identification of these species, limitations including geographical remoteness, research vessel availability, time, effort, funding (Paulus, 2021) and expertise often limit the quantity of sampling that is possible, and the number of species identified. Limitations in the amount of sampling conducted and species identified thereafter can mean that data is not necessarily collected with the optimal geographical coverage or resolution, or in the case of time-series studies with the optimal temporal resolution. These limitations often also apply to the collection of in situ environmental data, where this may be collected infrequently, not at the same time as physical sampling, or in some cases, not at all. Long-term sampling is further constrained by the practical challenge that only locations that have been sampled previously can be revisited when a study spans multiple years. Modelling thus provides an alternative, where limited identified specimens collected by sampling expeditions can be extrapolated across time or geographical space.

For example, species distribution models (SDMs) allow researchers to model past, present, and future species distributions with far fewer samples and at considerably lower cost. SDMs use occurrence records, for example observations collected using an ROV, combined with environmental variables to establish a statistical relationship (Elith and Leathwick, 2009; Klaassen et al., 2025). This relationship can be built using a variety of modelling algorithms, and the choice of method often depends on the type, availability, and quality of the data.

An example of a common species distribution modelling algorithm includes Maximum Entropy Modelling (MaxEnt), a regression-based SDM approach, has been widely applied across ecological fields (Yackulic et al., 2013). Robinson et al. (2017), for example, identified MaxEnt as the most commonly used algorithm for detecting invasive species. Its popularity is due in part to its ease of use because there is a dedicated software package available that requires no coding (e.g. Phillips et al., 2017). Implementations also exist in R, such as the maxent package, and in Python, such as elapid (Anderson, 2023). MaxEnt consistently outperforms many other modelling approaches in comparative studies (e.g. Aguirre-Gutiérrez et al., 2013; Elith et al., 2006; Wisz et al., 2008).

1.5. Challenges

Benthic fauna, and amphipods in particular, play a crucial role in marine ecosystems across depth zones by majorly contributing to food webs and to carbon and nutrient cycling. Despite their ecological importance, our understanding of benthic fauna, especially amphipods in the deep sea remains limited due to logistical constraints, taxonomic challenges, and uneven sampling effort. This knowledge gap restricts our ability to assess present-day biodiversity patterns and to predict how benthic ecosystems may respond to ongoing environmental change. This thesis aims to improve understanding of amphipods and other benthic fauna in the deep sea by addressing the following research questions:

- What are the spatial distribution and abundance patterns of mega- and macro-benthic fauna, and how are these related to environmental variables?
- What is the present-day distribution of amphipods, and how might this distribution change under medium- and long-term future scenarios?
- Does an integrative taxonomic study of coral-associated *Epimeria* provide new insights into the diversity and taxonomy of the genus *Epimeria*, and do newly sampled *Epimeria* associated with cold-water corals differ sufficiently from described species to be recognised as new species?

1.6. Thesis description

This thesis consists of three peer-reviewed publications that together address large-scale patterns, environmental drivers, and future distributions of benthic fauna, with a particular focus on amphipods in the North Atlantic, while also contributing to taxonomic advances through the description of new species.

Chapter 2 includes the publication “Pan-Atlantic Comparison of Deep-Sea Macro- and Megabenthos” originally published in *Diversity*, in which multivariate analyses are conducted on the abundance of benthic fauna across the Atlantic Ocean at both phylum and multitaxon levels. This chapter investigates large-scale spatial and bathymetric distribution patterns of benthic communities and examines how environmental factors influence these patterns. The results provide essential baseline knowledge on the broad-scale distribution of deep-sea macro- and megabenthos in the Atlantic, which is crucial for future monitoring, management, and conservation efforts.

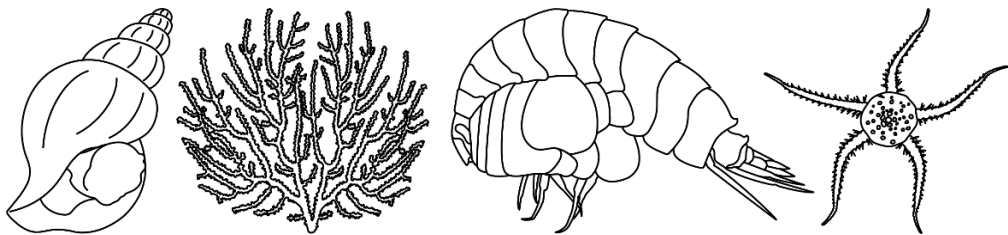
Chapter 3 comprises the publication “Species distribution modelling of benthic amphipod crustaceans in the deep North Atlantic under climate change” originally published in *Scientific Reports*. In this study, species distribution models were developed for 55 deep-sea amphipod species in the North Atlantic under present-day conditions, as well as under medium-term (2050–2060) and long-term (2090–2100) future climate scenarios. Best-case, intermediate, and worst-case Shared Socioeconomic Pathway (SSP) scenarios were applied to assess current habitat suitability and to project potential distributional shifts driven by climate change. This chapter establishes a baseline for evaluating future changes in deep-sea amphipod distributions in the North Atlantic.

Chapter 4 includes the publication “Cold-water coral-associated *Epimeria* (Epimeriidae, Amphipoda) from the North Atlantic and Southwest Pacific, with descriptions of two new species” originally published in *Marine Biodiversity*. This study describes two new *Epimeria* species associated with cold-water corals, one from Iceland and one from New Zealand using an integrative taxonomic approach. The work provides live photographs, mitochondrial cytochrome c oxidase subunit I (COI) DNA barcodes, and updated taxonomic keys for Atlantic and Pacific *Epimeria* species. In addition, photographic evidence of three unknown *Epimeria* species from New Zealand is presented.

Finally, Chapter 5 synthesises the findings from all three studies within the broader scientific context. This chapter discusses the implications of the newly gained knowledge for deep-sea

benthic fauna, with particular emphasis on amphipods, and outlines priorities for future research.

Chapter 2 Pan-Atlantic Comparison of Deep-Sea Macro- and Megabenthos





Article

Pan-Atlantic Comparison of Deep-Sea Macro- and Megabenthos

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Abstract: Deep-sea benthic fauna is vital for a well-functioning marine ecosystem but is increasingly under threat from a changing environment. To monitor and conserve this fauna, an understanding of their large-scale spatial and bathymetric distribution and their environmental drivers is necessary. In this study, we conduct a multivariate analysis on abundance benthic fauna data collected at the phylum and multitaxon levels using an epibenthic sledge (EBS) across the Atlantic, and identify the environmental factors that affect such data. Our findings show a decrease in abundance with depth in most of the Atlantic but find relatively heterogeneous abundances with depth within the Southern Ocean. Principal component analyses indicate differences in environmental conditions south of the Antarctic Polar Front (~52° S), outlining contrasts in the quantities of macronutrients and physical factors. Despite this, community composition seemed markedly similar throughout the Atlantic with the Antarctic Circumpolar Current seemingly not affecting benthic community composition for higher taxonomic levels. Those differences that did occur were largely caused by benthic chlorophyll, benthic iron, and surface silicate through a Bio-ENV. Overall, we argue that further large-scale spatial and bathymetric distribution studies are important amid environmental changes that are driving shifts in benthic community abundance and composition.

Keywords: species distribution patterns; Atlantic Ocean; Southern Ocean; benthic macrofauna; deep sea; EBS; depth gradient; environmental variables



Citation: Kürzel, K.; Brix, S.; Brandt, A.; Brenke, N.; Enderlein, P.; Griffiths, H.J.; Kaiser, S.; Svavarsson, J.; Lörz, A.-N.; Frutos, I.; et al. Pan-Atlantic Comparison of Deep-Sea Macro- and Megabenthos. *Diversity* **2023**, *15*, 814. <https://doi.org/10.3390/d15070814>

Academic Editor: Marcos Rubal

Received: 24 April 2023

Revised: 12 June 2023

Accepted: 13 June 2023

Published: 28 June 2023



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1. Introduction

Benthic marine life performs an important role in the overall function of marine ecosystems e.g., [1–3]. Benthic fauna may contribute towards the transformation and transport of organic matter, the transport of oxygen, nutrient cycling, and secondary production [4–7]. Benthic fauna can also be important in the provision of habitats e.g., [8–10] or in altering local physiochemical conditions [11], topography [12], or sediment availability through the bioturbation of sediments [11]. As different taxa perform different roles in

the maintenance and regulation of ecological processes, a diverse benthic fauna is widely considered to positively impact upon ecosystem stability and function [13,14].

Benthic fauna is vulnerable to changes in the physical and chemical properties of the water column. These changes can be caused directly or indirectly by human activities. For example, direct impacts include fisheries [15–17] and future mining for seabed minerals, which scour the seafloor and disturb important habitats, as e.g., reviewed by [18]. Indirect impacts can include those caused by anthropogenically induced climate change, which may lead to increasing sea temperatures, ocean acidification, and changes in ocean currents, amongst other changes [19]. Additionally, natural disturbances such as volcanoes, hydrothermal vents, or turbidite events can also alter benthic habitats and their communities [20–22]. These long-lasting modifications can threaten habitats necessary to species survival and lead to shifts in the distribution of species e.g., [23–25]. Changes in environmental conditions may therefore result in an irreversible loss of biodiversity.

As the largest biome on Earth, an understanding of the deep sea (>200 m) now is critical for evaluating shifts in their biodiversity patterns caused by environmental changes in the near future. However, this understanding is inhibited by the comparatively limited data, owing to the cost and time of sampling. More recently, sampling activity in the Atlantic has increased in an effort to identify benthic biodiversity and elucidate deep-sea ecosystems e.g., [26–41]. The Atlantic Ocean is considered a particularly interesting study area, as deep-sea geological features including the Mid-Atlantic Ridge and Greenland-Iceland-Faroe Ridge are believed to form barriers to benthic species migration e.g., [29,42,43]. Additionally, ocean currents including the Antarctic Circumpolar Current are suggested to influence species distribution in Antarctic waters e.g., [44], whilst the Atlantic Meridional Overturning Circulation (AMOC) dictates the regional environmental characteristics, such as salinity and temperature, throughout large parts of the Atlantic Ocean [45].

Recent investigations have focused on the relationship between deep-sea biodiversity patterns and environmental characteristics, such as depth, temperature, salinity, and nutrient availability, amongst others e.g., [28,31,46–50]. This includes studies that have attempted to unravel benthic biodiversity patterns within regions of the Atlantic e.g., [28,47]. For example, Kaiser et al. [28] found that benthic macrofauna density in the South Atlantic abyss is probably linked to food availability. In the Atlantic sector of the Southern Ocean, Di Franco et al. [47] identified depth as the main driver in shaping peracarid assemblages, while Stransky et al. [51,52] identified sediment characteristics off Greenland as important, as did Frutos et al. [53] in the southern Bay of Biscay. However, statistical analyses of benthic biodiversity patterns and abiotic variables encompassing the wider Atlantic Ocean have hitherto been limited.

Understanding the benthic spatial and bathymetric distributions and how these biodiversity patterns are influenced by abiotic variables is the basis for future monitoring and conservation efforts. In this study, we analyze Pan-Atlantic benthic data from a range (119–8338 m) of depths. This was compiled from published [28,54–60] and unpublished data from samples collected using an epibenthic sledge (EBS). The objectives of this study were to: (1) examine large-scale spatial and depth-related patterns of the Atlantic macro- and megabenthos, (2) assess abundance of the benthic fauna at the phylum and multitaxon levels (class or order level), and (3) identify environmental variables influencing these patterns.

2. Materials and Methods

Comparable deep-sea benthos data were collected using an EBS with an epi- and a suprabenthic net in the Atlantic Ocean since 2006 during the international research expeditions ANDEEP-SYSTCO II (Antarctic benthic deep-sea biodiversity, colonization history, and recent community patterns–system coupling), BIOPEARL I (biodiversity dynamics: phylogeography, evolution, and radiation of life), DIVA 1–3 (latitudinal gradients of deep-sea biodiversity in the Atlantic), IceAGE 1–3 (Icelandic marine animals: genetic and ecology) and RR (Icelandic marine animals: genetic and ecology Reykjanes Ridge), IceDIVA (Icelandic marine animals meet diversity along latitudinal gradients in the deep sea of the Atlantic Ocean), IceDIVA 2 JR275 and Vema-TRANSIT (bathymetry of the Vema fracture zone and Puerto Rico trench and abyssal Atlantic biodiversity study) (Table 1, Figure 1). While EBS data at high taxon level were published for ANDEEP-SYSTCO II, DIVA1-3 and Vema-TRANSIT [26,28,56], unpublished data for BIOPEARL I, IceAGE1-3 and RR, IceDIVA, IceDIVA 2, and JR275 was acquired from the German Centre of Marine Biodiversity (DZMB) Senckenberg and British Antarctic Survey [61]. Each of these expeditions used a standardized sampling protocol.

Table 1. Technical information of expeditions (South Atl = South Atlantic, SO = Southern Ocean, North Atl = North Atlantic, VFZ = Vema fracture zone, PRT = Puerto Rico trench).

Project	Cruise Number	Date	Vessel	Sample Area	Reference
ANDEEP-SYSTCO II	ANT-XXVIII/3	7 January 2012–11 March 2012	<i>Polarstern</i>	South Atl	[26]
BIOPEARL I	JR 144	26 February 2006–17 April 2006	<i>RRS James Clark Ross</i>	SO	[62]
DIVA 1	M48/1	6 July 2000–02 August 2000	<i>RV Meteor</i>	South Atl	[32]
DIVA 2	M63/2	26 February 2005–31 March 2005	<i>RV Meteor</i>	South Atl	[41]
DIVA 3	M79/1	10 June 2009–26 August 2009	<i>RV Meteor</i>	South Atl	[33]
IceAGE	M85/3	27 August 2011–28 September 2011	<i>RV Meteor</i>	North Atl	[34]
IceAGE 2	POS456	20 July 2013–4 August 2013	<i>RV Poseidon</i>	North Atl	[40]
IceAGE RR	MSM75	29 June 2018–8 September 2018	<i>RV Ms Merian</i>	North Atl	[37]
IceAGE 3	SO276 (MerMet17-06)	22 June 2020–26 July 2020	<i>RV Sonne</i>	North Atl	[35]
IceDIVA	SO280	8 January 2021–7 February 2021	<i>RV Sonne</i>	North Atl	[63]
IceDIVA 2	SO286	5 November 2021–8 December 2021	<i>RV Sonne</i>	North Atl	[38]
JR275	JR275	7 February 2012–2 March 2012	<i>RRS James Clark Ross</i>	SO, South Atl	[39]
Vema-TRANSIT	SO237	14 December 2014–26 January 2015	<i>RV Sonne</i>	VFZ, PRT	[64]

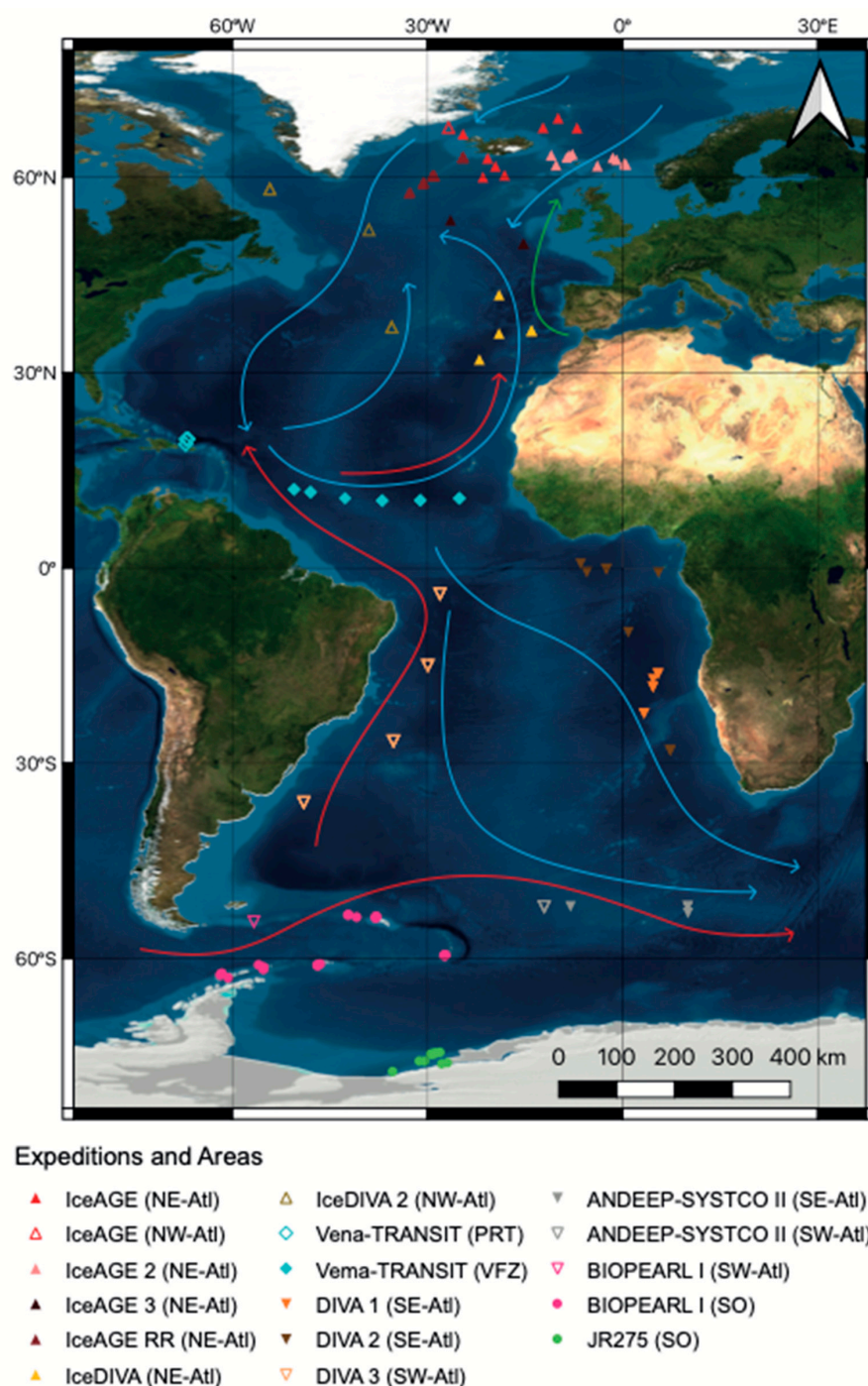


Figure 1. Map of the Atlantic Ocean showing EBS deployment locations from 13 expeditions with each symbol marking a sampling event. Red arrows indicate the major Antarctic bottom water deep-sea currents and blue arrows indicate Arctic bottom water deep-sea currents. Green arrow indicates bottom currents of common water (current scheme modified after Stow et al. [65]). (SO = Southern Ocean, SE Atl = southeast Atlantic, SW Atl = southwest Atlantic, VFZ = Vema fracture zone, PRT = Puerto Rico trench, NE-Atl = northeast Atlantic, NW = northwest Atlantic).

For the analysis, we defined seven regions to group EBS deployment locations. Four of these regions were prescribed based on their position relative to the Equator and the mid-Atlantic Ridge (MAR): northeast, northwest, southeast, and southwest Atlantic. Additional regions include the Vema fracture zone as a gap in the MAR, the Puerto Rico trench as a deep-sea trench, and the Southern Ocean south of the MAR. The sampling depth ranged from 119 m to 8338 m and included non-deep-sea stations if available for comparison reasons. As the sampling depth spanned over 8000 m, we grouped depth into depth zones: (1) shelf defined as 0 to 200 m for all areas, except the Southern Ocean, where it was defined as 0 m to 500 m due to continental depression caused by the weight of the ice sheet [66]; (2) upper slope as 200/500 m to 1000 m [66–68]; (3) lower slope as 1000 m to 3000 m [68]; (4) abyssal as 3000 m to 6000 m [68]; and (5) hadal as larger than 6000 m [69]. For different parts of the analysis, we used the regional and depth groups independent from one another while combining these groupings for others.

2.1. Sampling and Sample Processing

In total, data for 143 EBS deployments—referred to as stations from here on—from 13 expeditions were available for analyses based on identification on 50 taxon levels, including phyla, subphyla, classes, and orders [61]. During all expeditions, an EBS with an epi- and a suprabenthic net following the sizes and height defined by Brandt et al. [70] and Brenke [71] were used, enabling comparability of samples. This type of EBS was a suitable device for sampling small benthic fauna on and above the seabed, including macrofauna and small-sized megafauna. Macrofauna were defined as invertebrate organisms of a size range from 300 µm to 2 cm in size, while invertebrates larger than 2 cm in size are referred to as megafauna [72]. Each of the nets had an opening of 100 × 33 cm and net mesh size of 500 µm. The cod ends were equipped with net-buckets containing 300-µm mesh windows. On standard deployments, cable lengths that were 1.5 times longer than the water depth were laid out, with the EBS then trawled with 1 kn for 10 min on the seabed. Trawling times and cable length were shortened where required by the seafloor topography and were implemented in the haul distance calculation. Once on the deck, the content of the samplers was fixed in 96% undenaturated and pre-cooled (at −20 °C) ethanol or 4% buffered formalin. If required because of extensive collected sediment, the sampler content was sieved through 300-µm test sieves to remove mud and silt. The haul distances were calculated based on equation (4) in Brenke [61,71]. For comparison between stations, abundance data were standardized to a 1000 m² trawled seabed area.

After at least 48 h of fixation, samples from the epi- and suprabenthic net were sorted under stereomicroscopes into the lowest possible higher taxon level (phylum to order) and counted to determine abundance. Abundance counts per taxon from the epi- and suprabenthic nets were pooled following Brenke [55]. Annelida and Arthropoda were only counted if the head was present; Ophiuroidea only if the disc was present; brachiopod, molluscan, and ostracod shells were checked for soft tissues; only intact, small-sized sponges were counted, not broken sponge tissues, which occurred in samples from the southern Weddell Sea.

In this study, we included data for 41 higher taxa of the initially separated 50 taxa ranging from phyla to orders. Any classes and orders are from herein referred to together as “Multitaxa”. We excluded Foraminifera and Bryozoa due to difficulties in distinguishing whole individuals from broken pieces, as well as the subphylum vertebrata as it was outside the scope of this study. Brachiopoda, Chaetognatha, Echiura, Hemichordata, Nematoda, Nemertea, Phoronida, Platyhelminthes, Porifera, and Priapulida were not identified beyond the phylum level and subclass level for the Echiura. Other Annelida were separated into Polychaeta, Sipuncula, Oligochaeta, and Hirudinea. The phylum Arthropoda was split into the subphylum Chelicerata and Crustacea, with the former comprising Pycnogonida and Acarina and the latter comprising crustacean order levels. Chordata only consisted of Tunicates. Echinodermata and Mollusca were separated into classes. For the DIVA 1 and 2 data sets, Cnidaria and Echinodermata were not further discriminated into classes.

For the DIVA 1, IceAGE 1-3, and RR, and IceDIVA and IceDIVA 2 data sets, Aplacophora were not separated into Caudofoveata and Solenogastres. So, if corresponding data on class assignment were available, these were reported separately, but for all univariate and multivariate analyses, classes within Aplacophora, Cnidaria, and Echinodermata were grouped within their phyla.

2.2. Environmental Data

The environmental parameters for this study were provided by Bio-ORACLE <http://www.bio-oracle.org/> (accessed on 6 January 2023); Bio-ORACLE identifies average (mean) values for different physical and chemical variables over a 14-year time period from 2000–2014 through a combination of satellite and in situ measurements at a spatial resolution of 5 arcmin.g., [47,73–77]. For this study, Bio-ORACLE data for the surface measurements for salinity (PSS), silicate (mol/m^3), iron (mmol/m^3 ; mol/m^3), phosphate (mmol/m^3 ; mol/m^3), nitrate (mmol/m^3 ; mol/m^3), chlorophyll-a (mg/m^3 ; mg/cm^3), primary production ($\text{g}/\text{m}^3/\text{day}$), and calcite (mol/m^3) were included [73]. Furthermore, benthic data (maximum depth) for salinity (PSS), silicate (mol/m^3), iron (mmol/m^3 ; mol/m^3), phosphate (mmol/m^3 ; mol/m^3), nitrate (mmol/m^3 ; mol/m^3), chlorophyll-a (mg/m^3 ; mg/cm^3), primary production ($\text{g}/\text{m}^3/\text{day}$), temperature ($^{\circ}\text{C}$), and current velocity (m/s) were included from Bio-ORACLE as well [73].

2.3. Statistical Analyses

The univariate and multivariate analyses were conducted for two higher taxonomic levels, one including phyla and two arthropod subphyla only, and the other including the 41 higher taxa mentioned above. The motivation for using the two arthropod subphyla was the high abundance of the crustacea in the benthic deep sea e.g., [59,78]. To assess the patterns in taxon richness, specimen abundances, biodiversity, and community structure of the macro- and megabenthic fauna, the data were processed using Microsoft Excel 16.69.1 [79], and univariate as well as multivariate analyses were performed with PRIMER v6.0 [80]. Raw data (taxon identification and abundance) were first organized into a double entry taxon–station matrix with standardized data expressed as taxon individuals per 1000 m^2 . These faunal densities were reported to the nearest integer. The taxon density station matrix was further converted by grouping stations from the same depth range and regions. This enabled density and relative abundance results to be analyzed at an individual and regional scale.

Before conducting any further statistical analyses with PRIMER v6.0 [80], the macro- and megabenthic community data at the phylum and multitaxon levels were fourth-root transformed. This was performed to mitigate the impact of any outliers which are likely present in such a diverse and large dataset with a large range of abundance values. This fourth-root transformed dataset was used in all of the following statistical tests. To identify and visualize the level of similarities between density data at the phylum and multitaxon levels, non-metric multidimensional scaling (nMDS) was performed with combined depth region groups. The Bray–Curtis dissimilarity coefficient was applied to non-transformed and fourth-root transformed density data of the phylum and multitaxon level data to obtain similarity matrices using PRIMER v6.0 [73]. Hierarchical clustering with group-averaged linking and non-metric multidimensional scaling (nMDS) was then performed using these matrices. This was followed by one-way ANOSIM tests to investigate the differences in community composition between groups of stations. For the ANOSIM tests, stations were grouped independently into depth and region zones. A similarity percentages routine (SIMPER) was run on the region and depth zone groups [80] to understand intra-group similarities and inter-group dissimilarities. The cut-off for contributing species was applied (50%) to the SIMPER analysis using combined depth region groups. In order to characterize the environmental variables for the stations, a principal components analysis (PCA) containing all 21 abiotic environmental variables was performed. The environmental data were normalized prior to conducting the PCA. Lastly, a BIO-ENV (BEST) analysis was carried

out to determine the abiotic environmental variables driving the community patterns at the station level. For this, environmental data were normalized and categorized using Euclidean similarities. For the BIO-ENV (BEST), a Spearman rank correlation was used.

3. Results

For this study, a total of 495,893 specimens were included from 143 EBS stations and assigned into seven regions [61]. The regions were divided into depth zones, resulting in two shelf, three upper slope, three lower slope, five abyssal, and one hadal regional depth zone groupings. The sampled macrofauna used in this study included 16 phyla and 41 higher taxa of which 6 phyla and 17 higher taxa were dominant while the others were infrequent (Figure 2).

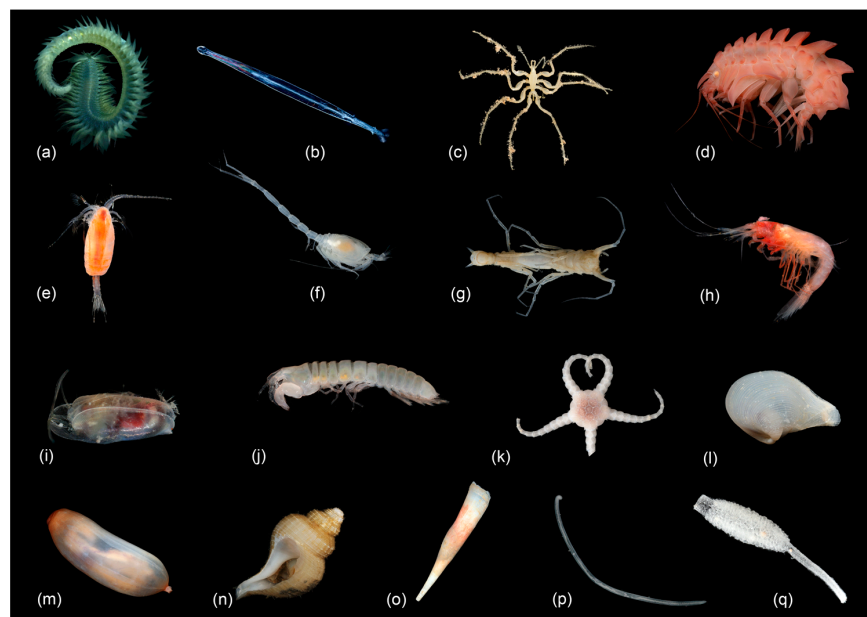


Figure 2. Representatives of the 17 dominant taxa in this study: (a) Polychaeta, (b) Chaetognatha, (c) Pycnogonida, (d) Amphipoda, (e) Calanoid Copepoda, (f) Cumacea, (g) Isopoda, (h) Mysida, (i) Ostracoda, (j) Tanaidacea, (k) Ophiuroidea, (l) Bivalvia, (m) Holothuroidea, (n) Gastropoda, (o) Scaphopoda, (p) Nematoda, (q) and Porifera. (a,c–q) photographed by Nicole Gatzemeier (Senckenberg am Meer, DZMB) and Karlotta Kürzel; (b) photographed by Solvin Zankl).

Standardized absolute abundance (Ind./1000 m²) varied between stations, ranging from 6 to 49,105 individuals, with stations located in the northeastern Atlantic upper slope, Southern Ocean shelf, and upper slope showing the highest macrofaunal abundance. Stations in the southwestern Atlantic shelf, southwestern Atlantic, and hadal Puerto Rico trench had the lowest abundance. On average, between 163 and 12,987 individuals were sampled per 1000 m² per region (Figures 3 and 4) [61]. In most regions, abundance declined with depth. However, this was less apparent for the Southern Ocean, where upper slope stations (238–34,483 Ind./1000 m²) showed a generally higher abundance than shelf stations (49–42,459 Ind./1000 m², Figure 4).

Samples were dominated by the phylum Arthropoda, with 14.4–72.8% in relative abundance. This was followed by Annelida with 7.7–32.9%, Mollusca with 4.6–24.1%, and Echinodermata with 0.4–20.2%. The least dominant phyla were Porifera (0–32.7%), Nematoda (0.1–11.3%), and others (0–2.1%) (Figure 5a). When compared at the multitaxa level, the most abundant multitaxa were the order Isopoda, with 5.4–55.8%, followed by the classes Polychaeta with 11.4–29.8%, Ophiuroidea with 0–28.6%, and Gastropoda with

0.2–22.9%. Among the least abundant taxa were the phylum Chaetognatha (0–1.7%) and the classes Scaphopoda (0–1.8%) and Pycnogonida (0–2%) (Figure 5b).

Notably, stations in the hadal Puerto Rico trench showed a strong difference in relative abundance composition. This was mainly driven by high percentages of Isopoda and Holothuroidea appearing simultaneously with low percentages of Cumacea. In addition, fauna of the southwestern Atlantic shelf strongly differed, which was mainly caused by high percentages of Ophiuroidea and Gastropoda in combination with low percentages of isopods. Remarkably, Copepoda and Cumacea were not present in this area at all (Figure 5b).

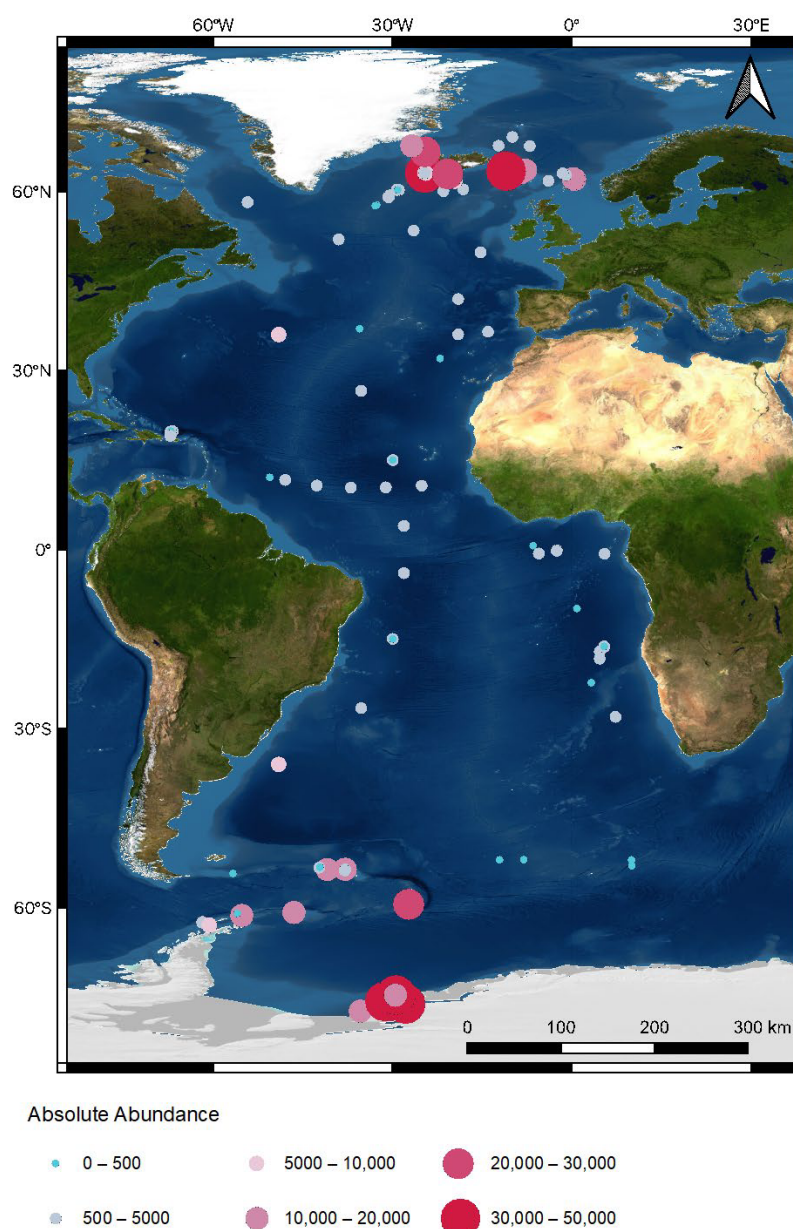


Figure 3. Density (Ind./1000 m²) of macro- and megabenthic communities per station across the Atlantic Ocean.

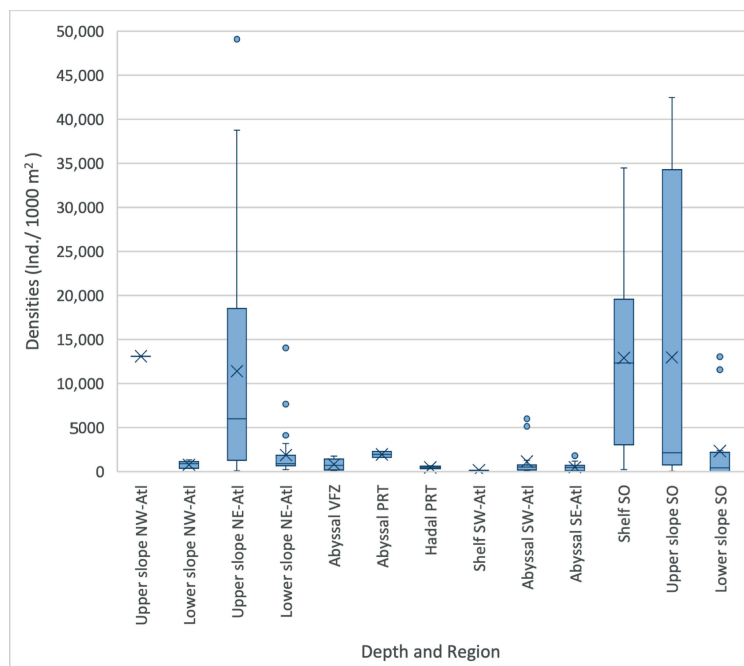
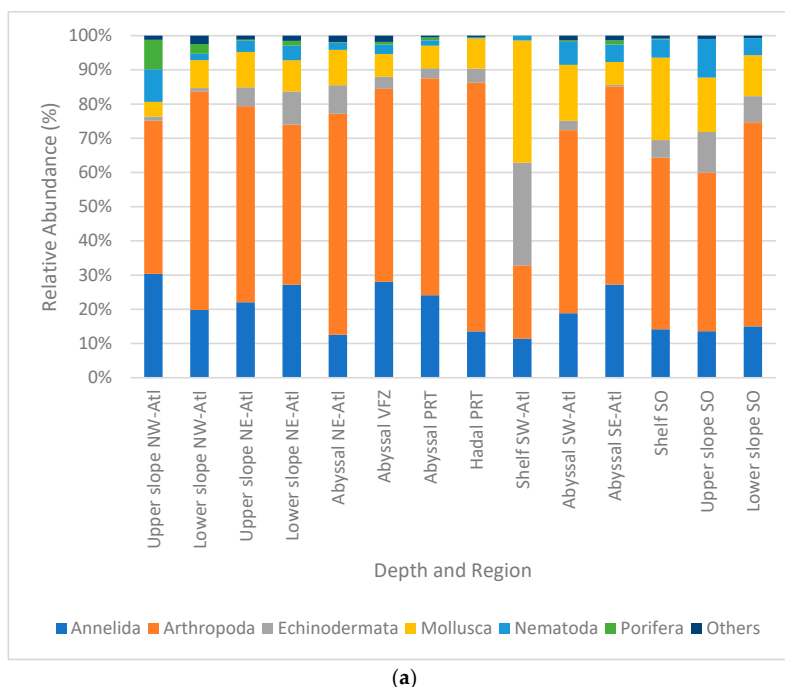


Figure 4. Densities (Ind./1000 m²) per region and depth zone of macro- and megabenthic communities across the Atlantic Ocean. (SO = Southern Ocean, SE Atl = southeast Atlantic, SW Atl = southwest Atlantic, VFZ = Vema fracture zone, PRT = Puerto Rico trench, NE-Atl = north-east Atlantic, NW = northwest Atlantic; dots represent outliers, and crosses represent the mean).



(a)

Figure 5. Cont.

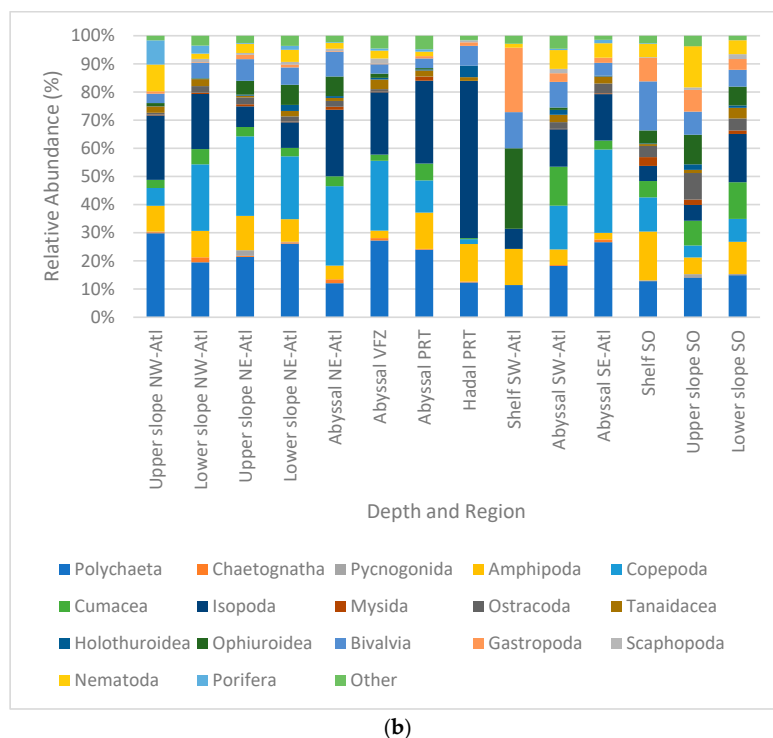


Figure 5. Relative densities (%) per region and depth zone of macro- and megabenthic communities across the Atlantic Ocean, (a) at phylum level; (b) at multitaxon level. (SO = Southern Ocean, SE Atl = southeast Atlantic, SW Atl = southwest Atlantic, VFZ = Vema fracture zone, PRT = Puerto Rico trench, NE-Atl = northeast Atlantic, NW = northwest Atlantic).

Macro- and Mega Fauna Composition

Non-metric multidimensional scaling (nMDS) provided similar results for the phyla and taxa analyses, with no clear groups of depth and region categories being formed (Figure 6).

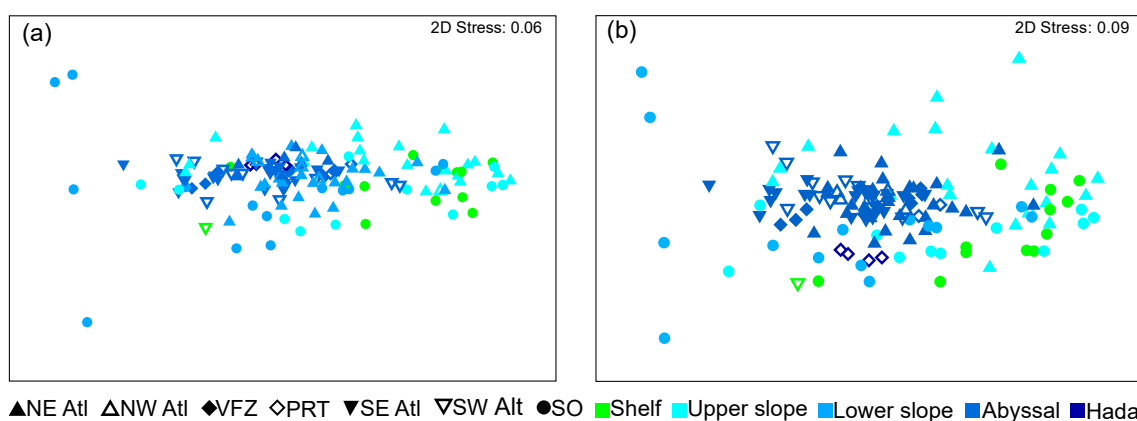


Figure 6. nMDS plots based on Bray–Curtis dissimilarity resemblance (4th-root transformed) of regions and depth zones of trans-Atlantic benthic communities. (a) at phylum; (b) multitaxon level. (SO = Southern Ocean, SE Atl = southeast Atlantic, SW Atl = southwest Atlantic, VFZ = Vema fracture zone, PRT = Puerto Rico trench, NE Atl = northeast Atlantic, NW = northwest Atlantic).

Results from the nMDS largely matched findings from the analysis of similarities (ANOSIM) and showed generally little differences between groups at both taxonomic levels. Differences that were observed in the ANOSIM (Tables 2 and 3) were largely present between groups of different depths. In general, any differences between groups were less pronounced at the phyla level than at the multitaxon level. The greatest difference between groups was seen between the abyssal and shelf/upper slope stations (R value: 0.476–0.715). In addition, the hadal stations differed to the shelf, upper slope, and abyssal stations (R value: 0.35–0.545). However, it must be noted that the hadal stations were only present from one region (the Puerto Rico trench) in the analysis. Lastly, the lower slope stations were relatively similar to the shelf, upper slope, and abyssal stations (R value: 0.13–0.256).

Table 2. One-way ANOSIM for depth at the phylum level. Statistically significant (p value = 0.05) values printed in bold. ANOSIMs performed with 4th-root transformation: Significance level of sample statistic: 0.1%; number of permutations: 999 (Random sample from a large number) and number of permuted statistics greater than or equal to Global R: 0. (SO = Southern Ocean, SE Atl = southeast Atlantic, SW Atl = southwest Atlantic, VFZ = Vema fracture Zone, PRT = Puerto Rico trench, NE Atl = northeast Atlantic, NW = northwest Atlantic).

Depth (Phylum)		Global R: 0.264
Groups	RStatistic	Significance Level (%)
Abyssal, Hadal	0.035	37.8
Abyssal, Shelf	0.591	0.1
Abyssal, Lower Slope	0.143	0.1
Abyssal, Upper Slope	0.476	0.1
Hadal, Shelf	0.35	0.9
Hadal, Lower Slope	0.077	27.2
Hadal, Upper Slope	0.186	10.4
Shelf, Lower Slope	0.209	0.7
Shelf, Upper Slope	−0.062	81.8
Bathyal, Slope	0.146	0.1

Table 3. One-way ANOSIM for depth at the multitaxa level. Statistically significant (p value = 0.05) values printed in bold. ANOSIMs performed with 4th-root transformation: Significance level of sample statistic: 0.1%; number of permutations: 999 (Random sample from a large number) and number of permuted statistics greater than or equal to Global R: 0. (SO = Southern Ocean, SE Atl = southeast Atlantic, SW Atl = southwest Atlantic, VFZ = Vema fracture Zone, PRT = Puerto Rico trench, NE Atl = northeast Atlantic, NW = northwest Atlantic).

Depth (Multitaxa)		Global R: 0.321
Groups	R Statistic	Significance Level (%)
Abyssal, Hadal	0.545	0.2
Abyssal, Shelf	0.715	0.1
Abyssal, Lower Slope	0.196	0.1
Abyssal, Upper Slope	0.501	0.1
Hadal, Shelf	0.528	0.3
Hadal, Lower Slope	0.308	5.5
Hadal, Upper Slope	0.356	1.4
Shelf, Lower Slope	0.256	0.8
Shelf, Upper Slope	−0.026	58.5
Bathyal, Slope	0.13	0.2

The ANOSIM was conducted to analyze similarities between different regions (the global R value at the phyla level was 0.264 and at the multitaxon level 0.32; Tables 4 and 5) and revealed large overlaps between most regions at both taxonomic levels. At the multi-taxa level, the Southern Ocean showed high similarity with the eastern Atlantic (southeast Atlantic R value: 0.206; northeast Atlantic R value: 0.208). Stations in the eastern Atlantic, southern Atlantic, and northern Atlantic showed some similarities (R value: 0.267). However, comparing the southern Atlantic with the northern Atlantic revealed high similarities between the southwest Atlantic and the northeast Atlantic (R value: 0.187) as well as some overlap between the northwest Atlantic and the southeast Atlantic (R value: 0.221).

Table 4. One-way ANOSIM for regions at the phylum level. Statistically significant (p value = 0.05) values printed in bold. ANOSIMs performed with 4th-root transformation: Significance level of sample statistic: 0.1%; number of permutations: 999 (Random sample from a large number) and number of permuted statistics greater than or equal to Global R: 0. (SO = Southern Ocean, SE Atl = southeast Atlantic, SW Atl = southwest Atlantic, VFZ = Vema fracture Zone, PRT = Puerto Rico trench, NE Atl = northeast Atlantic, NW = northwest Atlantic).

Regions (Phylum)		Global R: 0.111
Groups	R Statistic	Significance Level (%)
VFZ, PRT	0.244	3.8
VFZ, SW-Atl	0.054	18.1
VFZ, SO	0.066	22.7
VFZ, SE-Atl	0.169	2.5
VFZ, NE-Atl	−0.059	70.7
VFZ, NW-Atl	0.059	24.6
PRT, SW-Atl	−0.094	77.3
PRT, SO	0.013	39.2
PRT, SE-Atl	0.061	26.2
PRT, NE-Atl	0.02	42.3
PRT, NW-Atl	0.163	9.5
SW-Atl, SO	0.062	15.5
SW-Atl, SE-Atl	0.06	8.4
SW-Atl, NE-Atl	0.106	8.3
SW-Atl, NW-Atl	0.106	20
SO, SE-Atl	0.2	0.3
SO, NE-Atl	0.157	0.1
SO, NW-Atl	0.039	33.8
SE-Atl, NE-Atl	0.248	0.1
SE-Atl, NW-Atl	0.186	9.8
NE-Atl, NW-Atl	−0.054	63.3

The greatest differences were observed in the Puerto Rico trench. This region was most different from the Vema fracture zone and the southeast Atlantic (R value 0.548–0.568). Additionally, it also showed some differences to the northeast Atlantic, northwest Atlantic, and southwest Atlantic (R value: 0.301–0.378). Lastly, the Vema fracture zone showed some differences to the southeast Atlantic (R value: 0.345) and the northwest Atlantic (R value: 0.374).

At the phylum level only were a small number of samples statistically significant. However, these depict a similar pattern to the one observed at the multitaxon level. As such the Southern Ocean showed significant overlap with the eastern Atlantic. Notably, the overlap between Southern Ocean and northeast Atlantic was greater at the phylum level than at the multitaxon level. The southeast Atlantic and northeast Atlantic showed great overlap. The greatest difference observed at the phyla level was between the Puerto Rico trench and the Vema fracture zone (R value: 0.244), reflecting similar observations made at the multitaxon level. Lastly, the Vema fracture zone showed significant overlap with the southeast Atlantic (R value: 0.169). Notably, these two regions showed greater difference at the multitaxon level.

Table 5. One-way ANOSIM for regions at the multitaxa level. Statistically significant (p value = 0.05) values printed in bold. ANOSIMs performed with 4th-root transformation: Significance level of sample statistic: 0.1%; number of permutations: 999 (Random sample from a large number) and number of permuted statistics greater than or equal to Global R: 0. (SO = Southern Ocean, SE Atl = southeast Atlantic, SW Atl = southwest Atlantic, VFZ = Vema fracture Zone, PRT = Puerto Rico trench, NE Atl = northeast Atlantic, NW = northwest Atlantic).

Regions (Multitaxa)		Global R: 0.169
Groups	R Statistic	Significance Level (%)
VFZ, PRT	0.548	0.3
VFZ, SW-Atl	0.066	14.1
VFZ, SO	0.034	33.3
VFZ, SE-Atl	0.345	0.1
VFZ, NE-Atl	0.039	32.7
VFZ, NW-Atl	0.374	0.9
PRT, SW-Atl	0.301	2.1
PRT, SO	0.058	27.7
PRT, SE-Atl	0.568	0.1
PRT, NE-Atl	0.314	2.2
PRT, NW-Atl	0.378	3
SW-Atl, SO	0.062	16.6
SW-Atl, SE-Atl	0.221	0.2
SW-Atl, NE-Atl	0.187	1.3
SW-Atl, NW-Atl	0.221	6.8
SO, SE-Atl	0.206	0.2
SO, NE-Atl	0.208	0.1
SO, NW-Atl	−0.017	52.1
SE-Atl, NE-Atl	0.267	0.1
SE-Atl, NW-Atl	0.27	3.6
NE-Atl, NW-Atl	−0.13	84.5

A similarity percentage analysis (SIMPER) revealed that dissimilarities between regions and depth are largely caused by varying numbers in Crustacea, Annelida, Echinodermata, Nematoda, and Mollusca [61]. The SIMPER analysis identified the lowest dissimilarities between the abyssal northeastern Atlantic and lower slope northwestern Atlantic (20.82% at the phyla level, 25.27% at the multitaxon level). The highest dissimilarities were observed between the southwest Atlantic shelf and upper slope northwest Atlantic

(64.78% at the phyla level, 71.96% at the multitaxon level). These differences were primarily due to deviations in the number of Crustacea, Gastropoda, Annelida, and Nematoda. At the multitaxon level, crustaceans (e.g., isopods and copepods) were the primary cause for dissimilarities within the crustaceans. Furthermore, Gastropoda was very abundant on the shelf of the southwest Atlantic [61].

The Principal Component Analysis (PCA) of the 21 environmental variables explained 82.2% of the observed variance. The PCA showed two separate clusters that had a negative correlation of surface/benthic chlorophyll with depth. In both clusters, stations were largely structured by depth. One cluster consisted of all Southern Ocean stations as well as six southern South Atlantic stations, all of which were close to the Southern Ocean. Within this first cluster, upper slope and shelf stations were primarily associated with surface nutrients such as silicate, nitrate, and phosphate. Other shelf and upper slope stations overlapped with lower slope stations which were associated with higher levels of benthic primary productivity, benthic silicate, and benthic phosphate. Abyssal stations were largely characterized by benthic nitrate in the cluster (Figure 7, Table 6).

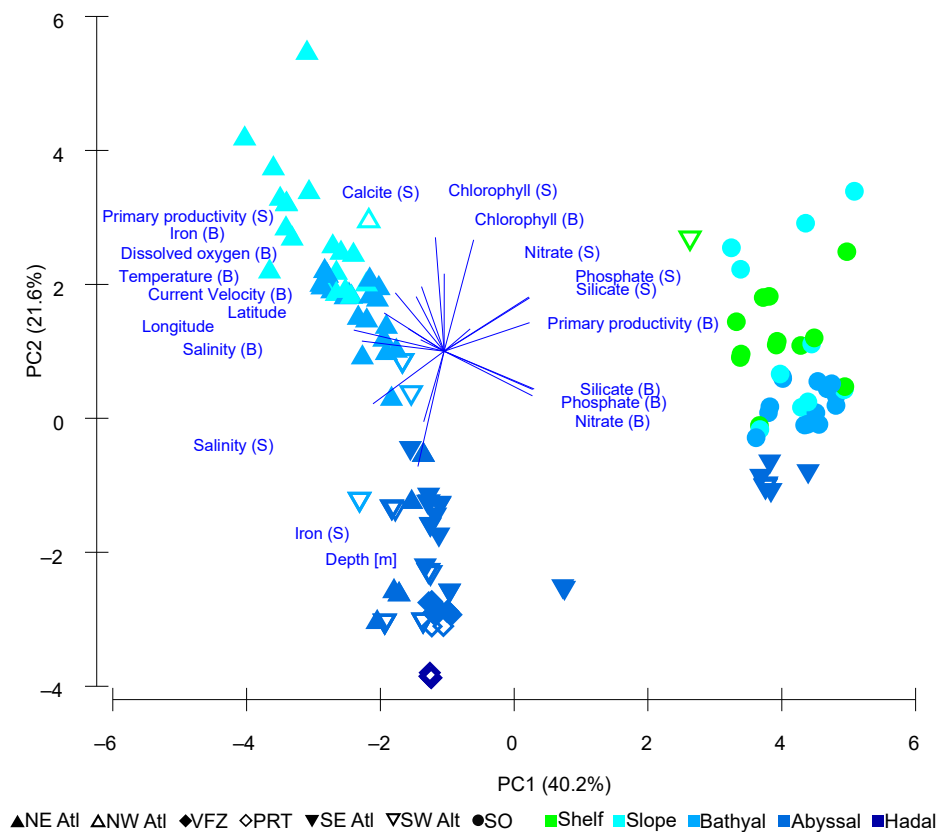


Figure 7. Principal Component Analysis (PCA) plot of 21 environmental variables, with PC1 contributing 40.2% and PC2 contributing 21.6%. Sampling sites are labelled by depth zone and region. S = Surface, B = Benthic. (SO = Southern Ocean, SE Atl = southeast Atlantic, SW Atl = southwest Atlantic, VFZ = Vema fracture zone, PRT = Puerto Rico trench, NE Atl = northeast Atlantic, NW = northwest Atlantic).

The second cluster consisted only of Atlantic stations. Similar to the first cluster, these were also structured by depth, although less overlap was present. Notably, different areas of the Atlantic such as the southwest Atlantic were not clearly separated from other Atlantic stations. Here, some upper slope stations were associated with surface calcite

and surface primary productivity. Other upper slope stations as well as some lower slope stations were strongly characterized by physical values such as benthic temperature, benthic dissolved oxygen, and benthic current velocity. Some lower slope stations were predominantly associated with large values of surface/benthic salinity as well as latitude and longitude. The deeper stations (abyssal and hadal) were generally characterized by surface iron (Figure 7, Table 6).

Table 6. Results of PCA showing the loadings of 21 environmental variables on the first two principal components and the percentage of the total variance explained by these components.

Variables	PC1	PC2
Depth (m)	−0.094	−0.414
Latitude (Decimal)	−0.325	0.076
Longitude (Decimal)	−0.084	0.041
Temperature, benthic (°C)	−0.215	0.137
Chlorophyll, surface (mg/m ³)	0.106	0.400
Chlorophyll, benthic (mg/cm ³)	0.000	0.278
Dissolved oxygen, benthic (mol/m ³)	−0.100	0.196
Iron, surface (mmol/m ³)	−0.074	−0.253
Iron, benthic (mol/m ³)	−0.176	0.210
Nitrate, surface (mmol/m ³)	0.305	0.195
Nitrate, benthic (mol/m ³)	0.317	−0.160
Phosphate, surface (mmol/m ³)	0.307	0.191
Phosphate, benthic (mol/m ³)	0.324	−0.136
Salinity, surface (PSS)	−0.256	−0.189
Salinity, benthic (PSS)	−0.195	0.037
Primary productivity, surface (g/m ³ /day)	−0.081	0.232
Primary productivity, benthic (g/m ³ /day)	0.094	0.080
Silicate, benthic (mol/m ³)	0.319	−0.137
Silicate, surface (mol/m ³)	0.307	0.102
Calcite, surface (mol/m ³)	−0.031	0.409
Current velocity, benthic (m/s)	−0.129	0.081

Bio-ENV (BEST) analysis revealed the environmental variables that were influential for community composition. At the phylum level, these variables included depth, surface and benthic chlorophyll, benthic dissolved oxygen, benthic iron, surface nitrate, surface phosphate, and surface silicate. The BIO-ENV explained between 39.9–40.3% of variance depending on the combination of environmental variables. The best subset of these included the variables benthic chlorophyll, benthic iron, and surface silicate, which explained 40.0% of the observed variance [61].

4. Discussion

The Atlantic Ocean has been the subject for previous studies on the understanding of benthic marine biodiversity patterns and their relationships to environmental factors e.g., [78,81–85]. Hypotheses including the latitudinal gradients e.g., [86–88], source vs. sink [89], and depth gradients [90] have been defined based on species distribution records and ecological studies from the Atlantic Ocean, and these hypotheses have subsequently been adopted in explaining global patterns of benthic faunal distributions. However, these studies often focused on a single taxon, such as peracarid crustaceans, Gastropoda, Bivalvia, or Polychaeta e.g., [46,85,89,91–93]; multiple taxa e.g., [94,95]; or smaller geographic-scale [28,42,56,96]. So far, only a few studies have compared benthic communities across latitudinal gradients e.g., [84].

In this study, we analyzed large-scale spatial and depth-related patterns of the Atlantic benthic macro- and megabenthos at the phylum and multitaxon levels, collected comparably using an EBS, and linked them with distributional data from environmental variables to determine their influence. At both taxonomic levels, generally high similarity of community

composition between different regions was observed. Lower similarity was observed between the shelf/upper slope stations and the abyssal/hadal stations. Additionally, our PCA revealed two clusters; one consisted of Southern Ocean and was close by south Atlantic stations, and the other corresponded with stations around the rest of the Atlantic. The two clusters were predominately influenced by different levels of environmental variables, with benthic chlorophyll, benthic iron, and surface silicate showing a particular strong influence of benthic communities within the Bio-ENV analysis.

4.1. Patterns in Absolute Abundance

Our results are in line with previous observations that benthic communities on continental shelves and upper slopes exhibit higher abundance than communities in deeper waters e.g., [97–99]. Declining abundance with depth is one of the commonly observed patterns [100–103] and has been previously shown to occur throughout the Atlantic and Southern Ocean e.g., [47,53,92]. This relationship is largely interpreted due to changes in food availability on the seafloor [67]. Consumption and disaggregation with depth results in a smaller fraction of food reaching the seafloor to deeper environments [104–106], thus affecting the amount of fauna that can live in deeper parts of the deep sea. This in turn also contributes towards a greater homogeneity in abyssal [89] and hadal zones, where overall resource availability within these environments is limited.

Despite observations of an overall macrofaunal density decline with depth, our results reveal areas that contradict this pattern due to localized heterogeneity in environmental variables. This is most apparent in the Southern Ocean, whereby a high range in absolute densities in shelf (~238 Ind./1000 m² to ~34,500 Ind./1000 m²) and upper slope environments (~49.4 Ind./1000 m² to ~42,500 Ind./1000 m²) was observed, and where maximum abundances at the upper slope stations were greater than those at the shelf stations. This reflects the findings of other authors that show that upper slope depths harbor a wealth of species and abundance [107,108]. In explaining this, Thatje et al. [109] outlines that the advance of grounded ice shelves during the Pleistocene period physically disturbed shallow benthic environments, producing environments that were unfavorable for the survival of fauna.

Macrofaunal densities obtained at our stations across the Atlantic (Figure 3) also appear to indicate a latitudinal gradient, with stations at higher latitudes providing greater absolute abundances than those within the tropics. Whilst our dataset does contain a larger quantity of stations in higher latitudes more generally, with more of these in shallower depths (shelf/upper slope) than those sampled closer to the equator, we find that macrofaunal abundances do not decline with latitude across comparable intermediate depths (e.g., lower slope Southern Ocean vs. northeast and northwest Atlantic). Our findings contrast with some previous studies of benthic abundance in high latitudes [110], highlighting an overall spatial pattern of macrofaunal density that is relatively unclear. For example, whilst Bluhm et al. [110] identified negative correlations between abundance and latitude, later expeditions identified a poleward decrease in abundance, but attributed these to enhanced productivity around the Barents and Spitsbergen shelves [111]. In the Southern Hemisphere, others have noted no apparent latitudinal gradient associated with faunal abundance e.g., [112]. Our study ultimately exemplifies that latitudinal patterns of overall benthic abundance require further consideration amid the current interest in the bimodal distribution of species richness within the Atlantic e.g., [84,113,114].

4.2. Patterns in Community Composition

Overall, our multivariate analysis showed that macrofaunal community composition between regions and depth were generally similar at the phylum level. This high level of similarity was confirmed in nMDS analysis and was still visible even after data transformation. Most stations were dominated by the phyla Arthropoda, Annelida, Molluscs, Echinodermata, and Nematoda. This is relatively typical for the Atlantic and corresponds well with a number of previous studies e.g., [28,56,115]. These five phyla are the same

groups identified in studies within the Vema fracture zone [56] and in the South Atlantic [28], reflecting the broad similarity in dominant phyla across the Atlantic. In an earlier expedition within the southwest Atlantic, Blake et al. [115] found that Annelida, Arthropoda, Mollusca, and Echinodermata were the four most dominant phyla.

Our analysis of relative abundance at a multitaxon level also indicated broad similarities in community composition across the Atlantic, with additional differences primarily found in shallow depths (shelf and upper slope) of the Southern Ocean. SIMPER results comparing the Southern Ocean shelf and upper slope found that these depth zones were indeed more similar to one another than different. These results reflect the idea that Antarctic benthic marine fauna exhibits a greater amount of eurybathic species than elsewhere in the Atlantic; an observation that has been made in numerous species-level studies [116]. Despite some differences in the Southern Ocean and southwestern Atlantic compared to the rest of the Atlantic, no clear latitudinal gradient at a multitaxon level is apparent.

Through our analysis of abundances at a multitaxon level, the most abundant taxa were Polychaeta, Isopoda, Copepoda, Amphipoda, and Bivalvia. This agrees with the findings of other expeditions e.g., [26,56,117,118]. In general agreement with our results, Crustacea e.g., [56,58,78,119–121], Polychaeta e.g., [99,122,123], and Mollusca e.g., [56,78] have all been reported to be among the dominant taxa. In our study, Polychaeta were the most abundant taxa overall, contributing more than 10% of the overall community composition across all regions and depth zones and over 30% in some regions (Northwest Atlantic). Within most of the Atlantic, Polychaeta tend to decrease with depth in comparison with other depth zones of the same region. This is partially in line with Quintanar-Retama et al. [78] who found a similar pattern, where relative abundance decreased with depth until 2300 m but became less clear beyond that. In the Southern Ocean, the bathymetric pattern in this study was less pronounced. Here, the differences in the Polychaeta relative contribution to community composition did not change much. Previous studies have highlighted the eurybathy of Southern Ocean polychaete species [93] and have postulated that this was made possible during the glacial maxima, where migration into deeper water was a necessary adaptation for survival [116].

Of the peracarid orders, Isopoda were most abundant. Isopods contributed about 56% of the relative abundance within the hadal region (Puerto Rico trench) and were among the most abundant taxa within most of the abyssal stations. Within most of our regions, the relative abundance of isopods increased in depth, in agreement with previous studies e.g., [124]. These have shown isopods to be highly adaptable and resilient to a wide range of environmental conditions [125–127]. It is well-known for many deep-sea regions that Isopoda generally become more prevalent relative to benthic Amphipoda, while on shelves Amphipoda are more abundant than Isopoda e.g., [55,128]. A potential explanation for this is the suspected in situ evolution of deep-sea isopod taxa, which contrasts with many deep-sea amphipods which have invaded from shallower waters and adapted [129]. Stransky et al. [52] analyzed 10 epibenthic samples taken at depths between 106 and 251 m on the Greenland shelf, with 58% of the almost 60,000 specimens being Amphipoda and 25% being Isopoda. The exception to this pattern occurs in the northwest Atlantic, where Isopoda dominance decreases with depth on account of a greater Copepoda dominance within this region.

Copepoda were present in all of our regions, except for the southwest Atlantic shelf region, which comprised a single station. They were the most abundant taxa in the lower slope northwest Atlantic, upper slope northeast Atlantic, abyssal northeast Atlantic, and abyssal southeast Atlantic, whilst they only provided smaller contributions to all of the Southern Ocean depth regions and the Hadal Puerto Rico trench. Our results show an apparent contrast in abundance on opposite sides of the Antarctic Polar Front. Previous Pan-Atlantic sampling efforts have identified the lowest absolute copepod abundances close to the Polar Front [130], thus suggesting that this provides an environmental barrier inhibiting the latitudinal traversal of some copepod species.

Amphipods provide a conflicting pattern of bathymetric and spatial distribution, given their presence in all regions. Generally, benthic amphipods decrease in relative abundance with depth, with a lower contribution to overall community composition at abyssal depths. This bathymetric pattern follows that of earlier studies which have described a decrease in abundance with depth in the Atlantic [97]. The exception to this pattern occurs in the Puerto Rico trench, where amphipods provide a relatively high contribution to abyssal and hadal community composition. This is expected, as Amphipods are known to be able to withstand a greater range of hydrostatic pressures [131] and are known to provide an important scavenging role at greater depths [132–136].

Ophiuroidea and Gastropoda were present in small amounts throughout the study area with the exception of the Southwest Atlantic shelf, where both taxa dominated the community with 22% abundance each. Ophiuroidea and Gastropoda are found throughout the Atlantic and Southern Ocean e.g., [58,137–141] but have rarely been found to dominate comparable macrofaunal community compositions e.g., [28,78]. Our results may support the hypothesis that benthic fauna assemblages are distributed patchily e.g., [142,143], with Ophiuroidea and Gastropoda only dominant within a single region and depth group that consists of only one station. Furthermore, this single station cannot be seen as representative for the entire depth region. The patchy distribution is also important to consider when interpreting the results as these were standardized, which may lead to an over- or underestimation for some stations.

Whilst our study discerns some differences in community composition at the phylum and multitaxon levels, it is noted that an expansion of our study to a species level would likely increase the resolution of inter-regional compositional patterns, leading to pronounced differences between regions and depth zones. At the species level, large-scale richness gradients in the Atlantic Ocean have been observed [144] as well as latitudinal and longitudinal gradients of bivalve taxonomic diversity [145]. The assumption made is that each distinct phylum and multitaxon are relatively uniform in preferred environmental conditions, whereas they often comprise a diverse species. For example, it is well known that many benthic fauna species are endemic to the Southern Ocean e.g., [26,121,146], such as certain members of the amphipod family Caprellidae [119,121].

4.3. Environmental Drivers in Community Composition

The PCA elucidates contrasts in abundance across the Atlantic and indicates different environmental drivers within these regions. The biplot depicting the result of the PCA (Figure 7) indicates two separate clusters of stations, with Southern Ocean stations grouped with a limited number of southern Atlantic stations situated below 52° S latitude, and other Atlantic stations grouped together. This split therefore appears to be marked by the Antarctic Polar Front, which has previously been discussed to form a biogeographical boundary that has delineated benthic faunal diversity and richness [147–149]. The role of the Antarctic Circumpolar Current in exhibiting a strong influence on environmental variables [150] and in preventing the latitudinal traversal of species is well-known, but given the high similarity of community composition between regions in this study, it does not influence this at higher taxonomic levels.

The split between these clusters coincides with the eigenvectors for nutrients (surface and benthic measurement for silicate, phosphate, and nitrate) for the Southern Ocean and southern Atlantic, and surface salinity as well as latitude for the rest of the Atlantic. In the Southern Ocean, nitrate, silicate, and iron are especially thought to be the primary environmental factors influencing macrofaunal densities, with differences in abundance driven by food availability [26,28]. This corresponds well with previous studies that have described the Southern Ocean as a “high nutrient, low chlorophyll” (HNLC) environment [151,152], with high levels of nitrate, silicate, and phosphate. In comparison, the Southern Ocean is iron-poor, with a relatively uneven distribution across the region [153]. The combination of these factors contributes to a complex pattern of phytoplankton productivity in the Southern Ocean, a primary food source for benthic macro- and megabenthos [154,155].

Whilst high levels in macronutrients would ordinarily present favorable conditions for phytoplankton growth, limitations in the amount of available iron inhibits nutrient assimilation and photosynthesis [156,157]. These limitations at the base of the Southern Ocean food web consequently influence the fauna that feed on them, and therefore have implications on their abundance and densities.

Interestingly, the PCA shows that depth as an environmental variable exhibits a stronger influence over the bathymetric distribution of stations within the Atlantic cluster, as opposed to those within the Southern Ocean and Southern Atlantic. Whilst this could theoretically be explained by different thermoclines, whereby temperatures across depth are more similar in the Southern Ocean compared to elsewhere around the Atlantic [158], temperature was not found to be among the most influential environmental variables shaping benthic communities within the Bio-ENV analysis. Instead, this structure coincides with the eigenvector for iron within the PCA and is shown to be influential for benthic communities in the Bio-ENV analysis. Iron is vital for most phytoplankton as it is needed to form chlorophyll and can therefore be seen as a growth-limiting nutrient [159] which influences food availability for benthic fauna. Thus, iron can be attributed to the overall heterogeneity of depth structure in the Southern Ocean. Localized elevations in iron content within the Southern Atlantic and Southern Ocean can occur around islands, attracting phytoplankton blooms to enhance primary productivity [160]. Other localized enhancements in the content of iron can occur from the localized dissolution of aeolian dust [161,162] and those derived from the melt-out of sediment particles that have been transported by icebergs [163]. In our results, differences in iron content around the Southern Ocean may also serve to explain the large range of abundance values when comparing supra-Antarctic stations with the rest of the Atlantic, thus affecting localized food availability and ultimately contributing to the overall heterogeneity of the Southern Ocean benthic environment [164].

Whilst some authors have postulated the role of seafloor ridges in precluding the traversal of species e.g., [64,165], our results show no evidence toward this as a factor at either the phylum or multitaxon level. For example, whilst height differences of up to 3000 m provided by the Mid-Atlantic Ridge have previously been described as forming a topographic barrier affecting the distribution of benthic fauna [29,166–170], our SIMPER results between the West and East Atlantic indicate that the differences between these regions are limited. Our findings correspond with a number of previous sampling studies that could not identify clear compositional differences between both sides of the mid-Atlantic ridge [171–174]. Our results instead support the idea that fracture zones and submarine ridges may aid the longitudinal traversal of benthic fauna. For example, previous studies have noted how fracture zones in the South Atlantic e.g., [175] may enable the occurrence of harpacticoid infaunal copepods in different basins [176]. In particular, the Vema fracture zone has been outlined as a passage for benthic fauna across the Mid-Atlantic Ridge [50,177–181]. Our findings may instead support the idea that the Fracture zones in general act as a passage that aids the longitudinal traversal of benthic fauna.

Amid ongoing changes in global climate, it should be noted that the environmental factors observed as driving regional macrofaunal communities are subject to future impacts. For example, ocean acidification could impact the survivability of calcifying organisms such as molluscs that need carbonate for their shell by reducing the amount of available carbonate in the ocean [182]. Furthermore, ocean warming could decrease export and transfer efficiency of particular organic carbon to benthic communities by altering phytoplankton composition to slow-sinking picoplankton [183–185]. Additionally, the freshening of polar regions through sea-ice melting could lead to increasing longer ice-free periods which could enhance phytoplankton growth and therefore food availability [186]. These changes altering food availability and habitat conditions are likely to cause shifts in community composition, abundance, and distribution for benthic fauna e.g., [187,188]. To elucidate and understand the distribution of benthic fauna in the near-future, studies investigating at lower taxonomic levels and analyzing functional traits are needed to ascertain the functional traits of each species and how they adapt to global environmental change.

5. Conclusions

We find stations in the Atlantic and the Southern Ocean to be characterized by different environmental variables, with the latter largely showing increased levels of nutrients. In the Atlantic, abundance decline was generally observed with increasing depth. South of the Polar Front, this bathymetric pattern was less apparent. This can be explained by the heterogeneity of iron supply which could influence food availability, or by the increased eurybathy observed in some Antarctic benthic fauna. Despite differences in environmental variables and absolute abundance patterns, benthic community composition was markedly similar throughout the Atlantic, with no clear geographical pattern being apparent. Therefore, the biogeographical boundary effect of the Antarctic Polar Front appeared not to be visible at the higher taxon level. Differences in community composition that did occur were likely due to the influence of benthic iron, benthic chlorophyll, and surface silicate.

These analyses, and the data from which they are composed, represent an important step toward understanding patterns of benthic macrofauna over a large spatial scale. As deep-sea environments change amid ongoing climatic shifts on the surface, knowledge of today's macrofaunal abundances and compositions are integral toward an understanding of future changes and adaptations of benthic fauna caused by external forcings. Further studies assessing the biodiversity of deep-sea fauna on lower taxonomic scales and across different geographical resolutions are needed in order to ascertain the monitoring and conservation needs for these diverse ecosystems.

Author Contributions: Conceptualization, K.K., K.L. and S.B.; methodology, all; K.K., K.L., A.B. and S.B.; formal analysis, K.K. and K.L.; investigation, all; data curation, S.B., A.B. and H.J.G.; writing—original draft preparation, K.K. and K.L.; writing—review and editing, all; visualization, K.K. and K.L.; supervision, A.-N.L. and S.B.; project administration, S.B.; funding acquisition, S.B., K.L. and J.T.; K.L., A.B., N.B., P.E., H.J.G., S.K., J.S., A.-N.L., I.F. and S.B. were responsible for the gear on board during the expeditions considered in this paper. All authors have read and agreed to the published version of the manuscript.

Funding: This study was directly funded by the German Science Foundation (DFG) through the IceAGE RR grant (MerMet17-5 (MSM75)), and by the DFG and Federal Ministry of Education and Research (BMBF) through the IceDivA grant (GPF 20-3_087 (SO280)) given to PIs Saskia Brix, James Taylor, and Katrin Linse. Karlotta Kürzel was also supported through grant GPF 20-3_087 as part of the IceDIVA project 2021–2022. Funding for previous expeditions that provided data were: IceAGE 1 and 2 (funded by the DFG under grant number BR3843-3-1 and 4-1 (M85/3 and POS456)), and IceAGE 3 (funded by DFG and BMBF under grant number MerMet17-6). Additionally, Angelika Brandt was granted funding (SO 237, Förderziffer 03G0237A) by the Bauer Foundation for the VEMA-Transit project. Inmaculada Frutos was supported through the junior research group “Vema TRANSIT. Puerto Rico Trench, Vema Fracture Zone and Abyssal Atlantic Biodiversity Study” as part of the project „Biodiversitätsnachhaltige Ressourcennutzung“ (Aktenzeichen T237/25054/). Katrin Linse, Peter Enderlein, and Huw J. Griffiths were part of the British Antarctic Survey Polar Science for Planet Earth Programme funded by The Natural Environment Research Council (NERC) [NC-Science] which includes the funding for the RSS James Clark Ross expeditions BIOPEARL I and JR275. Anne-Nina Lörz was funded by the German Science Foundation Project IceAGE Amphipoda, LO2543/1-1.

Institutional Review Board Statement: Not Applicable.

Data Availability Statement: All datasets analyzed and generated in this study and their results are publicly archived in the UK Polar Data Centre at <https://www.bas.ac.uk/data/uk-pdc/> (accessed on 26 June 2023) and available under <https://doi.org/10.5285/58080f33-884c-4e13-a419-c00cf1bab6a6> (accessed on 26 June 2023).

Acknowledgments: We like to thank the masters, nautical officers, and all crew members of the research vessels *Maria S. Merian* (MSM75), *METEOR* (M48/1; M63/2; M79/1; M85/3), *Polarstern* (ANTXXVIII-3), *Poseidon* (POS456), *RRS James Clark Ross* (JR144; JR275), and *Sonne* (SO237; SO276; SO280; SO286) as well as the science parties of these expeditions for their logistical and hands-on-deck support collecting the samples. We would like to thank the expedition leaders for DIVA1-3, the late Michael Tuerkey and Pedro Martinez Arbizu, and for VEMA and IceAGE RR, Colin Devey. Many student helpers were involved in the sample sorting of BIOPEARL I, IceAGE1-3, RR, IceDIVA, IceDIVA 2, and JR275 at the laboratories of the British Antarctic Survey, DZMB, Hamburg, University of Iceland (Nature Center Sandgerdi) and of the University of Hamburg. Special thanks to Karen Jeskulke and Antje Fischer (DZMB, Hamburg) for technical assistance in sorting, curating, and the accessibility of samples and data and to Nicole Gatzemeier for her help in the photo plate preparation. We would like to thank Craig Hammock for proofreading and Solvin Zankl for providing a picture of a Chaetognatha taken during the IceAGE3 project (Figure 2).

Conflicts of Interest: The authors declare no conflict of interest.

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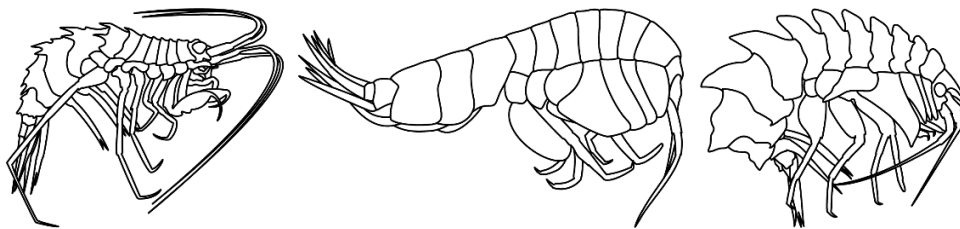
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Chapter 3 Species distribution modelling of benthic amphipod crustaceans in the deep North Atlantic under climate change



scientific reports



OPEN Species distribution modelling of benthic amphipod crustaceans in the deep North Atlantic under climate change

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Climate-driven changes in environmental factors influence vulnerable North Atlantic deep-sea (> 200 m depth) benthic ecosystems, leading to species range shifts, habitat loss, or extinctions. Amphipod Crustaceans play a crucial role in deep-sea ecosystems, contributing to food web stability and nutrient cycling. However, their large-scale distributions on species level remain poorly understood. In this study, we created species distribution models (SDMs) of 55 North Atlantic deep-sea amphipods in the present day, medium-term (2050–2060) and long-term (2090–2100) future, utilising best, likely, and worst shared socioeconomic pathways (SSPs) scenarios. The results show species-specific responses to climate change. Over half of the amphipod species expand their habitat in some scenarios, while others face habitat loss. Contrasting habitat likeliness is represented by species of the same genera. Additionally, some species experience habitat shifts, particularly northward and towards the Greenlandic coast. Glacial meltwater influx and increased nutrient availability could enhance habitat suitability in certain regions. Poleward shifts are theorised to be temperature-driven. These changes influence biodiversity, food web dynamics, and ecosystem stability. This study provides a baseline for assessing future changes in North Atlantic amphipod distributions. The findings emphasise the need for conservation strategies and taxonomy in predicting ecosystem responses to climate change.

Keywords Amphipoda, Species distribution modelling, North Atlantic, Deep sea, Crustacea, Climate change

Commonly found throughout the benthic realm^{1–5}, amphipods provide critical functions that underpin marine food webs, in addition to performing functions integral to deep-sea ecosystems. Amphipods are essential to deep-sea nutrient cycling as they help facilitate the transfer of organic matter between benthic and pelagic food webs⁶. They feed on sinking particulate organic matter, of which the nutrients are subsequently reintroduced into the water column and higher trophic levels when amphipods are consumed by predators^{7,8}. This way, amphipods facilitate the transfer of energy and nutrients across trophic levels, contributing substantially to the functioning and stability of deep-sea ecosystems^{9,9}. Many deep-sea amphipod species are also bioturbators and thus key ecosystem engineers, where tube-building and burrow construction create small-scale habitat heterogeneity and enhance nutrient availability⁶. Despite their ecological importance, many deep-sea amphipod species are suited to specific environmental niches, making them vulnerable to changing conditions¹⁰.

However, deep-sea environments, defined as any marine water mass deeper than 200 m¹¹ are vulnerable to a changing climate or anthropogenic pressures¹². As a sink for carbon and excess heat, the increasing quantities of greenhouse gases in the atmosphere, including carbon-dioxide (CO₂) and methane (CH₄) impact the marine environment directly, and indirectly. This causes multiple changes, rapid changes in temperature¹³, decreasing oxygen levels¹⁴, ocean acidification¹⁵, and alterations in ocean circulation¹⁶. The North Atlantic provides a particularly vulnerable deep-sea environment, given its integral role in ocean circulation. The Atlantic

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Meridional Overturning Circulation (AMOC), where deep, colder water is transported southwards and shallow, warmer water moves northwards¹⁷, influences temperature and salinity among other climate patterns globally¹⁸. Disruption or slowdown of the AMOC risks widespread consequences in deep-sea environmental conditions, with substantial impacts on marine ecosystems¹⁹.

Environmental pressures caused by climate change and anthropogenic pressures can have wide ranging effects that impact upon species distribution, community structures^{20–22} and ecosystem function at varying spatial scales^{23,24}. Consequences may include altered geographical and bathymetric distribution ranges^{25,26}, health declines²⁷, and even species extinctions²⁸. Since species are interconnected through the food web, the health of one species has the potential to influence the entire ecosystem. The effects could cascade across trophic, whereby the removal of one species with an integral ecosystem function causes a decline in others that relied upon it for nutrients³⁹. Amphipods may be particularly prone to the effects of climate change, as they belong to the group Peracarida, which do not have larvae. This crustacean suborder has a brooding lifestyle, limiting their dispersal and thus may affecting their response to changing environmental conditions as seen in other marine taxa^{29,30}. This response at the lower trophic levels can thus indirectly affect the overall species composition, species abundance, and community structure³¹.

To understand how marine fauna are adjusting to the changing climate, towards informing conservation and mitigation efforts, a present-day knowledge of their distribution and diversity is fundamental. However, comparatively little is known about the deep-sea biome, given the inaccessibility of the region and high economic costs of exploratory studies^{12,32,33}. For example, it is estimated that 91% of all marine species are currently undescribed³⁴. Given the infrequency and paucity of deep-sea sampling efforts, modelling is commonly used to fill this deep-sea knowledge gap. A common approach is to produce species distribution models (SDMs), in which statistical and machine learning techniques are used to predict species distributions based on occurrence data and environmental variables³⁵. In the North Atlantic, this approach has been used to model the distribution of a limited number of benthic taxa and species. For example, Burgos et al.³⁶ used SDMs to predict the distribution of vulnerable marine ecosystem indicator taxa such as corals, sponges, and sea pens, while Reiss et al.³⁷ applied this approach to model 14 different benthic species from multiple taxa, including brittle stars, polychaetes, and bivalves. Other studies have clustered amphipod distributions around Iceland by their environmental preference, to assess their regional-scale diversity³⁸. Despite these efforts, modelling of deep-sea species is piecemeal, and there is scope for further efforts given the scattered and disparate nature of current distribution knowledge for species in the deep-sea. To the authors knowledge, this study is the first to analyse large scale distribution under different climate change scenarios of amphipod on a species level.

Despite their critical role and ecosystem function, little is known about the current distribution of various amphipod species in the deep sea, and how this might change in the future. Therefore, the aim of the study is to identify the current and future distribution of benthic amphipod species in the deep North Atlantic using species distribution modelling (SDM) and open-source occurrence data. Models will be generated for present, medium- (2050–2060) and long-term predictions (2090–2100) based on three climate change scenarios (Shared Socioeconomic Pathway (SSP) 1–1.9, SSP 2–4.5, and SSP 5–8.5). As such, this study will help address the knowledge gap of deep-sea amphipod distributions, provide a baseline for evaluating future changes, support targeted conservation efforts and deepen the understanding of the cascading effects of environmental change on benthic food webs and ecosystem functions in the deep North Atlantic.

Materials & methods

Dataset

For this study, amphipod occurrence data were sourced from the Ocean Biogeographic Information System (OBIS) using the mapper tool provided on the website³⁹. The obtained dataset was filtered in Python to only include records between the latitudes 56°N and 80°N and longitudes between 45°E and 45°W. This region has been previously predicted by Burgos et al. 2020 as one of vulnerable marine ecosystems and high biodiversity. To focus on the deep sea, only records of depths of more than 200 m were included, and purely pelagic amphipod species were excluded to ensure the best suitability for modelling with environmental layers. This was further addressed by cross-referencing the sampled depth of the records with bathymetry data from the General Bathymetric Chart of the Oceans (GEBCO) for the seafloor⁴⁰. If the difference between the two depths exceeded 5%, the record was assumed to be non-benthic and it was excluded. Additionally, given that previous studies have demonstrated a decline in model robustness and evaluation metrics, such as AUC (Area Under the Curve), with insufficient sample sizes (e.g.^{41–43}), species with less than 200 occurrence records were excluded from the dataset. Furthermore, any records collected outside of the years 2000–2020 was excluded as only this period aligned with the temporal range of the Bio-ORACLE environmental data layers. The final occurrence data set contained 55,941 records from multiple sampling expeditions and studies (Fig. 1)^{44–58}.

Environmental data were sourced from Bio-ORACLE^{59,60} which provides raster layers widely used in species distribution modelling. Benthic data were extracted for average depths. Current environmental data covered the periods 2000–2010 and 2010–2020, while future projections utilized the periods 2050–2060 and 2090–2100, enabling both medium- and long-term analysis. Future environmental data from Bio-ORACLE included modelled variables based on SSPs, representing greenhouse gas emission scenarios under different policy decisions. This study used three scenarios: SSP 1–1.9 (low emissions, sustainable future), SSP 2–4.5 (moderate emissions, likely scenario), and SSP 5–8.5 (high emissions, worst case)⁶¹.

Variance Inflation Factor (VIF) analysis was performed to address multicollinearity by excluding highly correlated variables. These variables included depth, selected benthic variables (dissolved oxygen, nitrate, phosphate, salinity, temperature), and selected surface variables (iron, phosphate, primary productivity, salinity). The final environmental dataset for current and future scenarios retained benthic and surface silicate (mmol/m³) and current velocity (m/s), as well as surface chlorophyll (mmol/m³), dissolved oxygen (mmol/m³), and nitrate

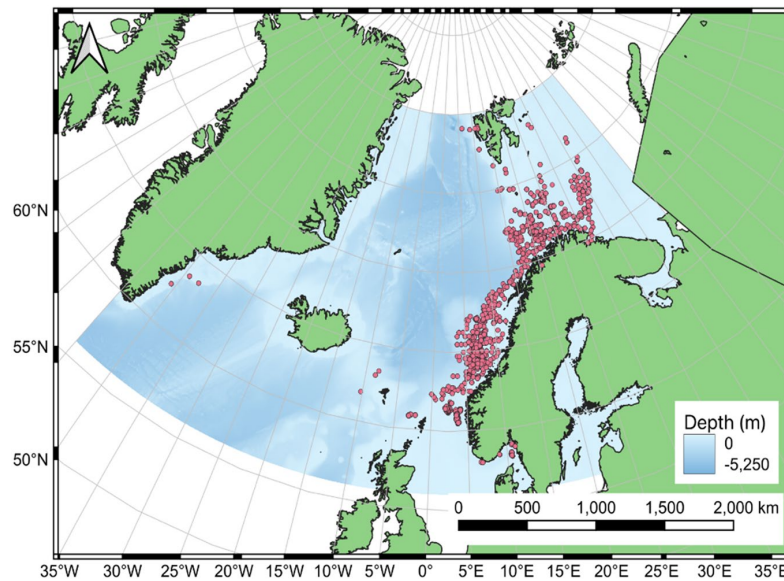


Fig. 1. Map of species occurrence points after performing all cleaning and filtration steps⁴⁰ (Mapping: Created with QGIS, version 3.40.5-Bratislava, <https://www.qgis.org>).

(mmol/m³). Additionally, benthic primary productivity (mmol/m³) and iron (mmol/m³) were included. These variables were selected based on their known or potential influence on peracarid and amphipod distribution. Although the specific environmental drivers of amphipod distribution remain poorly understood, previous studies have employed similar predictors to identify factors shaping species distribution and abundance^{4,38,62}. Other studies conducting niche breadth analyses have also highlighted their relevance in defining amphipod niche width¹⁰. Additionally, as the deep-sea is closely connected to surface processes through the vertical flux of organic matter^{63,64}, surface variables were included to account for their potential influence on benthic amphipods.

Resolving sampling bias

As samples are often collected in more accessible areas where the logistical costs of sampling expeditions are lower, marine datasets are often inherently biased which requires consideration for the production of accurate and robust SDMs. In this study, a target-group sampling approach was deployed, following the works of Phillips et al.⁶⁵ and Fourcade et al.⁶⁶. This approach uses environmental background points that are sampled with the same bias as the presence-only dataset, to be used as a model environmental input. To do this, an estimate of overall sampling effort is calculated using a Kernel Density Estimate (KDE) of presence point distribution using QGIS. A kernel bandwidth of 100 km, a grid cell size of 800 m and a quartic kernel function was used to balance spatial resolution with computing power. This KDE was then normalised in Python, such that cells that had zero values, because they persisted in regions which were not previously sampled, were given a negligible value such that there was still a small chance of these being selected by background point sampling. The probability map, produced using the KDE approach, was consequently sampled to produce background points. In this study, 50,000 background points were produced, balancing the risk of model overfitting and processing power whilst ensuring the number is large enough to represent the environmental range in the study area accurately⁶⁷.

Following this, individual datasets were produced for each species, with each record representing a geographical point where presence for that species had been determined by sampling. Background points were merged onto these individual datasets and labelled within each of them. The environmental data was sampled using these datasets, such that each record contained a column for each environmental variable at the time of collection.

Species distribution modelling

The species distribution modelling was conducted using the Maximum Entropy algorithm (MaxEnt). This approach is suitable for presence-only data as it combines samples with background/pseudo-absence points and has shown above-average performance, thus representing a standardised approach in marine species distribution modelling^{68,69}. In this study, the elapid Python package⁷⁰ was used.

Three-fold cross-validation was applied to all models, and the average Area Under the Curve (AUC) score across folds were used for model evaluation. Various combinations of feature classes and regularisation multipliers were tested. The hinge feature class, which yielded the highest mean, minimum, and maximum AUC scores, was selected for further modelling. Additionally, a regularisation multiplier of two was chosen for downstream modelling with the MaxEnt algorithm. This selection was informed by previous research indicating

that regularisation multipliers two to four times higher than the default (1.0) can mitigate overfitting while maintaining strong predictive performance in habitat suitability and species distribution modelling⁷¹.

Models were first created for each species under present-day conditions, using the individual presence points alongside background points derived utilising the target-group sampling approach. Afterwards, future SDMs for each species for the medium-term and long-term under all three SSPs were created utilising the predicted environmental data from the Bio-ORACLE layers. These models used the same setup as the optimised present-day models. The SDMs were visualised using Python rasterio v1.3.10, matplotlib v3.9.2, and QGIS 3.40.5-Batavia. Zonal statistics depicting suitable habitat area size were calculated using rasterio numpy v1.26.4, while descriptive statistics were visualised using seaborn v0.13.2. The nomenclature used in this study follows the World Register of Marine Species⁷².

Results

In total, present and future models for 55 amphipod species (Table 1) were created with an average AUC score of 0.85 (Table S1).

For the current scenario, *Paraphoxus oculatus* had the largest suitable habitat area with 1,845,852 km² (for probability threshold 0.70) while *Autonone magacheir* has the smallest suitable area with 10,471 km² (Fig. 2). On average, the suitable habitat area was 408,296 km² (Fig. 3). In comparison, for the medium-term 2050–2060 timeframe under SSP 1–1.9, the average suitable habitat area decreased to 350,432 km², with lower quartile at 63,527 km² and upper quartile at 464,116 km² (min: 10,475 km², max: 2,157,231 km²). For the same period under the SSP 2–4.5 scenario, the average habitat area increased to 420,912 km², with lower quartile at 79,770 km² and upper quartile at 656,716 km² (min: 9440 km², max: 1,853,475 km²). In contrast, under the SSP 5–8.5 scenario for 2050–2060, the average habitat area decreased to 365,381 km², with lower quartile at 60,141 km² and upper quartile at 432,233 km² (min: 14,876 km², max: 2,033,417 km²; Fig. 3).

For the long-term 2090–2100 timeframe, comparing SSP 1–1.9 to the short-term scenario, the average suitable habitat area decreased to 320,006 km², with lower quartile at 70,537 km² and upper quartile at 427,583 km² (min: 12,631 km², max: 1,945,080 km²). Comparing SSP 2–4.5 from 2090–2100 to the 2050–2060 period, the average habitat area decreased to 397,261 km², with lower quartile at 70,353 km² and upper quartile at 553,617 km² (min: 868 km², max: 1,731,375 km²). Finally, for the SSP 5–8.5 scenario, the average area increased to 385,685 km² in 2090–2100, with lower quartile at 76,937 km² and upper quartile at 537,744 km² (min: 2668 km², max: 2,311,682 km²; Fig. 3).

Out of the 55 species examined, 14 species (with a probability threshold of 0.7) were projected to lose suitable habitat across all future scenarios. However, this number doubled to 30 species when considering five out of six scenarios, highlighting a broader trend of habitat loss across a range of future conditions.

Detailed modelling for each species is shown in the Supplementary Information (Figs. S1–S55). The broader trends are visualised in Figs. 4 and 5, where the number of species in each area and the change between SDMs for different SSP scenarios and the present day are depicted. These summarise a broad range of geographic trends that were observed.

The northeastern coast of Greenland shows an increase in habitat suitability for a number of amphipods, across all SSP scenarios and timeframes. This trend is particularly pronounced under the extreme scenario SSP5–8.5 for the period 2090–2100 (Figs. 4 and 5). Examples of species exhibiting increased habitat suitability in this region in at least some scenarios include *Idunella aequicornis* and *Aceroides (Aceroides) latipes* (S20 and S36, Supplement).

The southwestern part of the study area exhibits a complex response to future climate change scenarios, with increases in species numbers observed along the western side of the Reykjanes Ridge but notable decreases in some coastal regions. A high number of species (15–20) are projected to lose habitat suitability in the coastal waters of southeastern Greenland under both the SSP2–4.5 and SSP5–8.5 scenarios. Similarly, areas adjacent to the western coast of Iceland show pronounced reductions in species numbers, particularly under these higher-emission scenarios (Figs. 4 and 5). *Laetmatophilus tuberculatus* (S8, Supplement) is an example of this declining trend, exhibiting a loss of suitable habitat across both regions.

However, slight increases in species numbers are projected in parts of the Irminger Sea, with the most pronounced changes occurring under SSP5–8.5 (Figs. 4 and 5). *Tmetonyx cicada* (S13, Supplement) is an example of this pattern. While for habitat suitability along the Reykjanes Ridge is projected to decline especially in 2090–2100 under SSP5–8.5, this species shows increasing suitability within the Irminger Sea, particularly along the southern coast of Greenland (Figs. 4 and 5).

In the southeastern part of the study area, several regions exhibit a decrease in species richness. Along the eastern side of the Reykjanes Ridge, a notable decline of approximately 10–15 species is projected across all SSP scenarios and time periods (Figs. 4 and 5). This pattern is exemplified by *Ampelisca gibba* (S1, Supplement) and *Harpinia crenulata* (S7, Supplement), whose suitable habitat within the Reykjanes Ridge region diminishes substantially and, in some scenarios, disappears entirely.

Similarly, along the Iceland–Faroe Ridge, a decrease of approximately 15–20 species is projected across all scenarios and time periods (Figs. 4 and 5). Species exhibiting this pattern include *Tmetonyx cicada* (S13, Supplement) and *Tryphosites longipes* (S14, Supplement), both of which consistently show a decline in habitat suitability under all SSPs and timeframes. For *Tmetonyx cicada*, only a small area near the centre of the ridge remains suitable, whereas the habitat suitability of *Tryphosites longipes* disappears entirely from this region under both the SSP2–4.5 and SSP5–8.5 scenarios.

The area between northern Iceland and the southwest of Svalbard shows a marked decrease in habitat suitability for numerous species across all scenarios and time periods. This decline is particularly pronounced, with reductions exceeding 15 species in all scenarios except SSP1–1.9 for the period 2050–2060 (Figs. 4 and 5). Examples of species exhibiting this pattern include *Unciola leucopis* (S39, Supplement) and *Hippomedon*

Species	Authority	Family	Sample size
<i>Aceroides (Aceroides) latipes</i>	(G.O. Sars, 1883)	Oedicerotidae	386
<i>Ampelisca aequicornis</i>	Bruzeliuss, 1859	Ampeliscidae	646
<i>Ampelisca eschrichtii</i>	Krøyer, 1842	Ampeliscidae	317
<i>Ampelisca gibba</i>	G.O. Sars, 1883	Ampeliscidae	472
<i>Ampelisca macrocephala</i>	Liljeborg, 1853	Ampeliscidae	696
<i>Ampelisca odontoplax</i>	G. O. Sars, 1879	Ampeliscidae	619
<i>Ampelisca pusilla</i>	G.O. Sars, 1891	Ampeliscidae	1085
<i>Amphilocheus manudens</i>	Spence Bate & Westwood, 1862	Amphilocheidae	853
<i>Arrhis phyllonix</i>	(M. Sars, 1858)	Oedicerotidae	800
<i>Autonoe longipes</i>	(Liljeborg, 1852)	Aoridae	658
<i>Autonoe megacheir</i>	G. O. Sars, 1879	Aoridae	1045
<i>Bathymedon longimanus</i>	(Boeck, 1871)	Oedicerotidae	749
<i>Bathymedon saussurei</i>	(Boeck, 1871)	Oedicerotidae	370
<i>Bruzelia typica</i>	Boeck, 1871	Synopiidae	303
<i>Byblis crassicornis</i>	Metzger, 1875	Ampeliscidae	1568
<i>Byblis gaimardii</i>	(Krøyer, 1846)	Ampeliscidae	371
<i>Eriopisa elongata</i>	(Bruzeliuss, 1859)	Eriopisidae	7427
<i>Halice abyssii</i>	Boeck, 1871	Pardaliscidae	570
<i>Haploops setosa</i>	Boeck, 1871	Ampeliscidae	3202
<i>Haploops tubicola</i>	Liljeborg, 1856	Ampeliscidae	1571
<i>Harpinia abyssii</i>	G.O. Sars, 1879	Phoxocephalidae	743
<i>Harpinia antennaria</i>	Meinert, 1890	Phoxocephalidae	2769
<i>Harpinia crenulata</i>	(Boeck, 1871)	Phoxocephalidae	1115
<i>Harpinia laevis</i>	G.O. Sars, 1891	Phoxocephalidae	274
<i>Harpinia mucronata</i>	G. O. Sars, 1879	Phoxocephalidae	2087
<i>Harpinia pectinata</i>	G.O. Sars, 1891	Phoxocephalidae	5612
<i>Harpinia plumosa</i>	(Krøyer, 1842)	Phoxocephalidae	427
<i>Harpinia propinqua</i>	G.O.Sars, 1891	Phoxocephalidae	235
<i>Hippomedon denticulatus</i>	(Spence Bate, 1857)	Tryphosidae	795
<i>Hippomedon propinquus</i>	G.O. Sars, 1890	Tryphosidae	499
<i>Idunella aequicornis</i>	(G.O. Sars, 1877)	Liljeborgiidae	633
<i>Ischyrocerus megacheir</i>	(Boeck, 1871)	Ischyroceridae	270
<i>Laetmatophilus tuberculatus</i>	Bruzeliuss, 1859	Podoceridae	717
<i>Leptophoxus falcatus</i>	(G.O. Sars, 1883)	Phoxocephalidae	1092
<i>Liljeborgia fissicornis</i>	(M. Sars, 1858)	Liljeborgiidae	922
<i>Liljeborgia pallida</i>	(Spence Bate, 1857)	Liljeborgiidae	441
<i>Lysianassa plumosa</i>	Boeck, 1871	Lysianassidae	413
<i>Medicorophium affine</i>	(Bruzeliuss, 1859)	Corophiidae	211
<i>Melphidippa borealis</i>	Boeck, 1871	Melphidippidae	266
<i>Neohela monstrosa</i>	(Boeck, 1861)	Unciolidae	832
<i>Nicippe tumida</i>	Bruzeliuss, 1859	Pardaliscidae	1811
<i>Nototropis nordlandicus</i>	(Boeck, 1871)	Atylidae	796
<i>Oediceropsis brevicornis</i>	Liljeborg, 1865	Oedicerotidae	495
<i>Paraphoxus oculatus</i>	(G. O. Sars, 1879)	Phoxocephalidae	394
<i>Syrrhoe crenulata</i>	Goës, 1866	Synopiidae	758
<i>Themisto abyssorum</i>	(Boeck, 1871)	Hyperiididae	216
<i>Tmetonyx cicada</i>	(Fabricius, 1780)	Uristidae	2521
<i>Tmetonyx similis</i>	(G.O. Sars, 1891)	Uristidae	233
<i>Tryphosella horingi</i>	(Boeck, 1871)	Tryphosidae	206
<i>Tryphosites longipes</i>	(Spence Bate & Westwood, 1861)	Tryphosidae	684
<i>Unciola leucopis</i>	(Krøyer, 1845)	Unciolidae	422
<i>Unciola planipes</i>	Norman, 1867	Unciolidae	657
<i>Urothoe elegans</i>	Spence Bate, 1857	Urothoidae	1745
<i>Westwoodilla caecula</i>	(Spence Bate, 1857)	Oedicerotidae	516
<i>Xenodice frauenfeldti</i>	Boeck, 1871	Podoceridae	426

Table 1. List of all 55 amphipod species included for modelling, sorted alphabetically.

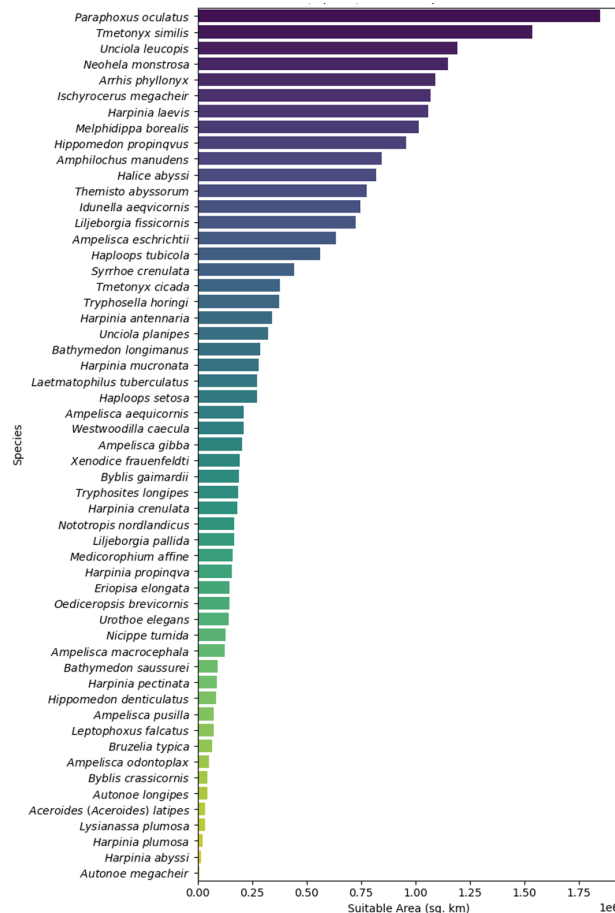


Fig. 2. Sutable Area Size per species under current environmental conditions (2000–2020).

propinquus (S30, Supplement), both of which consistently show a decline in habitat suitability across all scenarios. Notably, both species lose all suitable habitat in this region under SSP2–4.5 by 2090–2100.

Discussion

Species response to climate change

Predicted models of species distribution under future scenarios show a complex and varied response of amphipods to climate forcing, echoing the findings of other studies modelling the distribution of benthic species. For example, Moraitis et al.⁷³ investigated the distribution of benthic indicator species under climate change scenarios and found reduction in habitat area for three of these species, while the remaining species showed a habitat expansion. Similarly, Xu et al.⁷⁴ investigated five benthic species and determined that two of them would experience an increase in suitable habitat under future climate conditions. However, these studies and our findings contrast with the hypotheses outlined by Sandulli et al.⁷⁵ and Weinert et al.⁷⁶, which suggest that benthic species will generally undergo declines under future climate scenarios.

In our study, relatively few amphipod species project a decline in suitable habitat area under all climate scenarios, and just over half showed a decline under most scenarios. Examples of species that show a decline, such as *Ampelisca gibba* or *Nicippe tumida*, indicate the role of bathymetric features in providing biogeographical barriers that inhibit migration within the North Atlantic. These ridges separate distinct ocean basins with unique physicochemical conditions, providing temperature and salinity gradients, and serve as areas with particularly strong interactions in water masses that lead to oceanographic conditions that can shape marine organism distribution. In the North Atlantic, these include the Reykjanes Ridge and the Greenland-Iceland-Faroe (GIF) Ridge, the latter of which is known particularly for unique environmental conditions hosting specialised benthic fauna^{77–82}.

In contrast, many species are shown to increase their suitable habitat area across at least some future climate scenarios, echoing the findings in other benthic fauna such as Gastropoda (e.g.⁸³), other Crustacea (e.g.⁸⁴) and corals (e.g.⁸⁵). One common pattern of habitat expansion is a latitudinal shift toward the continental margins of Greenland, where climate impacts on marine biogeochemistry and nutrient cycling are apparent⁸⁶. Temperature

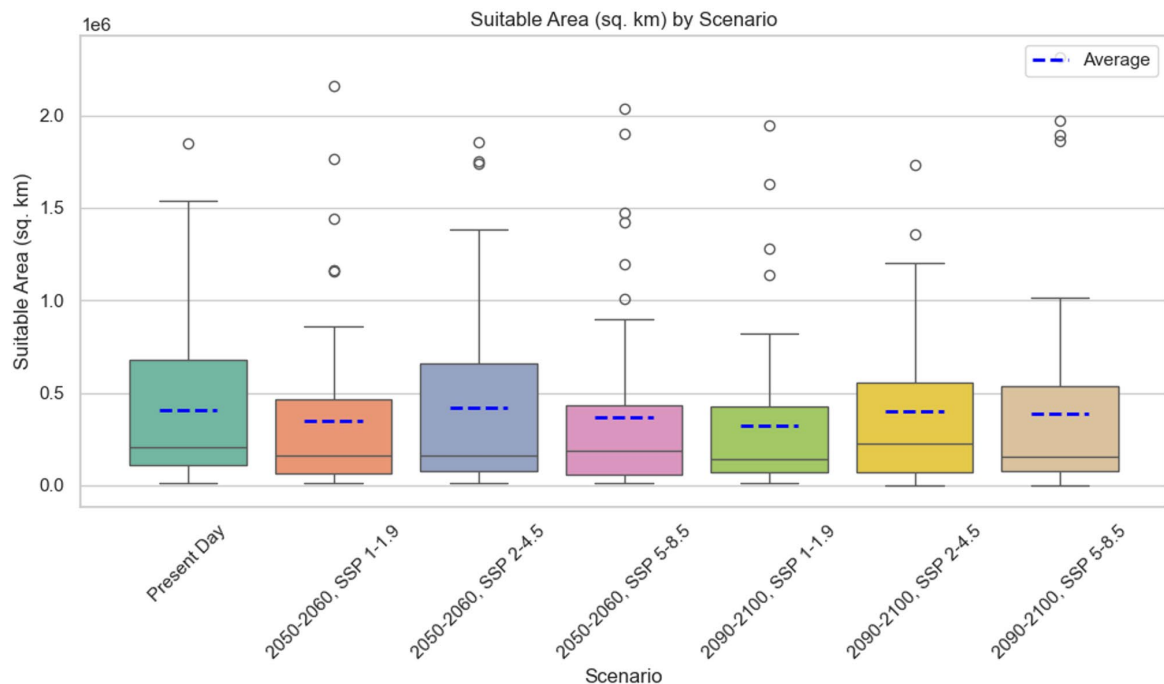


Fig. 3. Suitable habitat area for all species for the present day, SSPs and future scenarios for all species for the present day, SSPs, and future scenarios.

increases result in increased glacial melt, leading to more glacial meltwater entering the ocean through run-off. This freshwater is rich in nutrients such as nitrogen⁸⁷, phosphate⁸⁸, and iron^{86,89}, and thus impacts upon local nutrient availability, increases primary productivity, and enhances habitat suitability. The movement and increase in suitable habitat area for many amphipod species likely reflects the predicted increase in nutrient availability and primary productivity proximal to the Greenlandic coast.

While a number of species show an increase or decrease in total suitable habitat area across the study region, the pattern often reflects a migration of suitable habitat in response to changing environmental conditions. One common pattern of a migration in suitable habitat area is a northward shift towards the pole in many species (e.g., *Westwoodilla caecula*). As hypothesised with other benthic species (e.g.⁹⁰), poleward shifts are primarily driven by temperature changes, as species have thermal tolerances that physiologically restrict their distribution⁹¹. As temperatures of waters closer towards the poles are cooler, species migrate to the waters which fit their temperature preference (e.g.⁹⁰). Temperature, alongside other climate forced oceanographic processes, will also lead to Atlantification, whereby Arctic and subpolar waters become more similar to the Atlantic waters in environmental characteristics such as salinity⁹². The wider impact of this includes the loss of stratification in the deep-sea North Atlantic, whereby the colder and less saline Arctic Ocean that mixes across depth with the warmer and saltier Atlantic Ocean become more alike. Critically, this impacts upon the food web, with changes in nutrient availability and primary productivity across the region⁹³, that the SDMs reflect.

The heterogeneity of species-level responses to climate scenarios outlines the importance of analysing distributional patterns at the species level, in amphipods and in other benthic species. The variation in SDMs of the same family is consistent with Lörz et al.¹⁰, who reported that the environmental niche of many examined amphipod species was not directly transferable to other species within the same family. While acknowledging that some families were underrepresented in terms of species numbers in this study, it remains essential to not only increase sampling efforts but also ensure accurate taxonomic identification at a species level. Many museums and natural history collections hold thousands of amphipod specimens that currently cannot be included in ecological or modelling analyses due to identification being limited to the order level. Applying an integrative taxonomic approach will deepen our understanding of species distributions and potential implications on the entire ecosystem, particularly in the context of ongoing environmental changes.

Ecological and conservation implications

Changes in amphipod distribution could have cascading effects on other organisms within the deep-sea, disrupting nutrient cycling and energy flows throughout the water column. A decline in amphipods in certain regions could contribute to the destabilization of the food web. Conversely, a significant influx of amphipod species into new areas may lead to population increases in their predators, which could subsequently increase competition pressure on other species. This could alter community structures and contribute to localized biodiversity loss by favouring certain species that thrive on the new abundance of prey⁹⁴. As different taxa

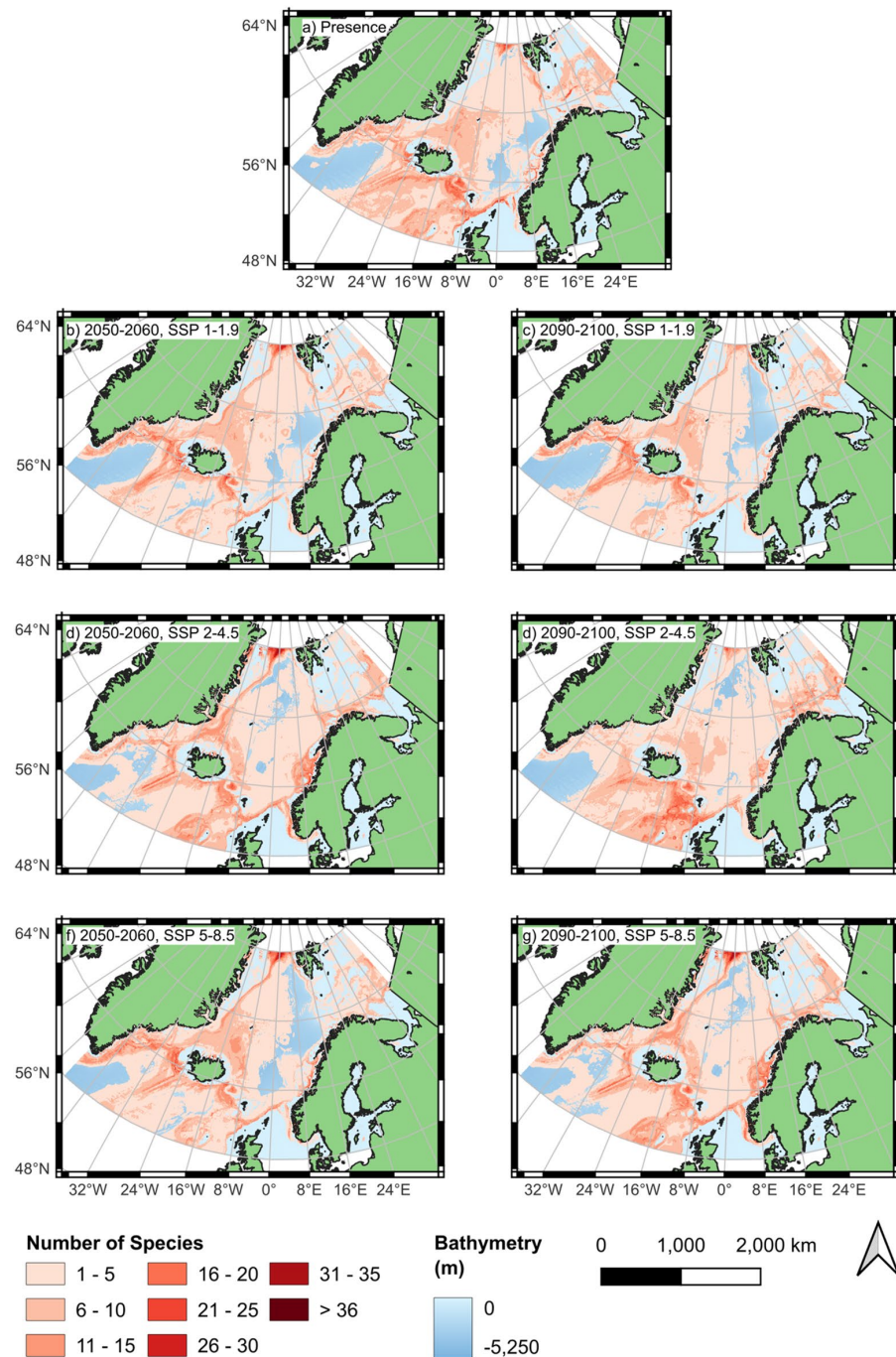


Fig. 4. Number of species modelled present in each area based on all 55 individual species distribution models (SDMs). (Mapping: Created with QGIS, version 3.40.5-Bratislava, <https://www.qgis.org>).

contribute to ecosystem stability and function, a reduction in amphipod populations may therefore diminish critical processes of organic matter transport, oxygenation, nutrient cycling, and secondary production, with cascading effects across trophic levels.

The impact on the deep-sea ecosystem emphasises the need for conservation and management efforts in regions where habitat suitability is projected to decline. The GIF ridge is an area with particular cause for concern, given the unique environmental conditions and faunal diversity in the region⁷⁹. Changes in sediment

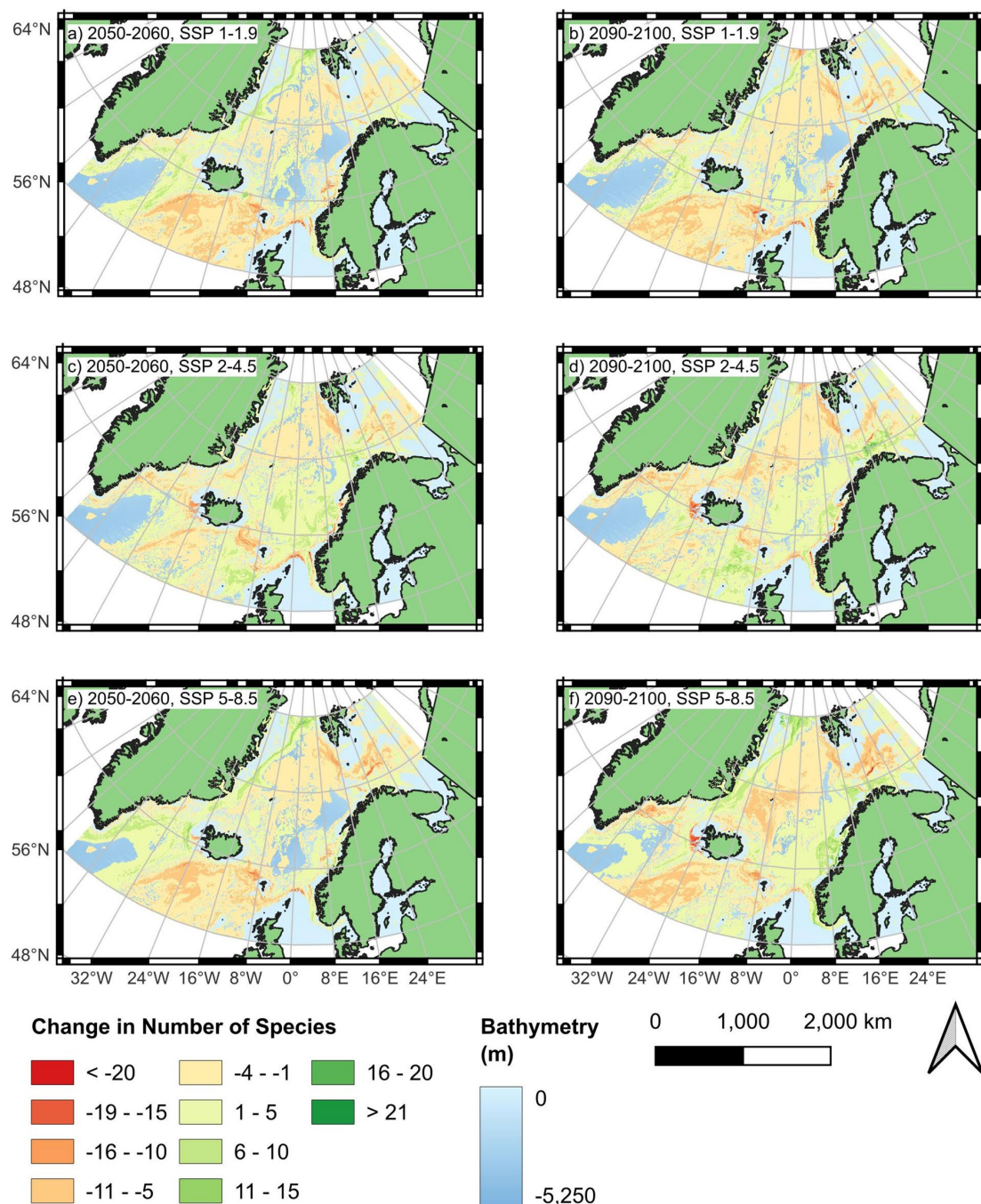


Fig. 5. Number of species modeled present in each area based on all 55 individual species distribution models (SDMs). (Mapping: Created with QGIS, version 3.40.5-Bratislava, <https://www.qgis.org>).

composition and water chemistry south of the GIF Ridge have already been linked to biodiversity shifts in other benthic communities^{95,96}, whilst SDMs in this study show the habitat as becoming unsuitable for species such as *Ampelisca gibba*. The loss of biodiversity in the GIF Ridge could lead to the restructuring of a unique marine community, potentially altering nutrient cycling, energy flow, and trophic interactions. In terms of economic impacts, the damage to feeding grounds for fish could impact regional fish stocks. Whilst fishing is restricted in

some areas of the GIF Ridge hosting vulnerable marine ecosystems, including the Lonsjúp trough⁹⁷ and the Steinhóll vent field⁹⁸, it is uncertain what impact this has to fishing operations in the wider region.

Owing to the migration and expansion of suitable habitat area, management and conservation efforts may have to consider some amphipod species as invasive, with consequent effects on regional community structures. Examples of species that might become invasive is *Oediceropsis brevicornis*, with its substantial growth in suitable habitat area and its substantial migration across a broad range of scenarios. These invasive species of amphipods could lead to a loss of biodiversity, as they may outcompete native species and alter ecosystem dynamics^{99,100}. This may result in the decline of other species of amphipods in this study, or in other benthic fauna with similar ecosystem roles. Invasive species management frameworks therefore need to consider the SDMs presented in this study, especially given the important roles that amphipods play in ecosystem function.

Study evaluation and future considerations

As with all modelling studies, this research relies on a number of assumptions and limitations that should be acknowledged when interpreting the results. One key consideration is the use of projected environmental layers from Bio-ORACLE, which, while widely used in the literature (e.g.^{74,83}), introduces some uncertainty due to its spatial resolution of 0.05 degrees and decadal temporal aggregation. This resolution is appropriate for examining broader regional patterns but may limit the detection of fine-scale habitat variations and short-term environmental changes, such as marine heatwaves¹⁰¹. Nevertheless, in the absence of high-resolution in situ data across the study area, these modelled layers represent the most comprehensive option available and have been validated against quality-controlled data where possible^{59,102}.

This study also presumes that the present sampling data is sufficient for a precise prediction of amphipod environmental preference, and in predicting future distributions, that this environmental preference is steady-state and unable to adapt. Whilst this study uses the best information presently available to our knowledge, future research should consider how further in situ observations can refine present-day species distributions further, and evaluate the models presented in this study for their validity. Combining these in situ observations with laboratory investigations could also help enable deeper insights into the adaptive capabilities of amphipods, leading to a greater understanding of their environmental preference.

In using open-source data in a region where information was previously limited, this study has produced new SDMs that provide a valuable baseline for understanding potential shifts in response to climate change. The SDMs show a complex and varied response of amphipods to climate forcings, with some species indicating an expansion of suitable habitat area under warming scenarios, whilst others are projected to decline in distribution. Many species show a migration of suitable habitat area toward more favourable thermohaline and biogeochemical conditions, with common patterns including a latitudinal shift towards the continental margins of Greenland or a temperature driven northward shift. The critical ecosystem roles of amphipods therefore require consideration of modelling in management and conservation efforts, with particular focus on areas where biodiversity may be irreversibly lost (e.g. GIF ridge), or where amphipods form invasive species that change ecosystem dynamics. This study highlights how species distribution modelling within the deep-sea forms an important tool for forming a baseline of present-day knowledge, and projecting future environmentally forced changes.

Data availability

All the data utilised in this study is open-access and can be found here <https://zenodo.org/records/15396200>. Amphipod occurrences are available through the database OBIS (<https://obis.org/>), the environmental dataset can be accessed via Bio-ORACLE (<https://bio-oracle.org/>) and the bathymetry data can be downloaded from GEBCO (<https://www.gebco.net/data-products/gridded-bathymetry-data>).

Received: 18 June 2025; Accepted: 28 October 2025

Published online: 12 November 2025

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Acknowledgements

We would like to thank Dr. Jayashree Rajesh Prasad for her advice and support. The team of the DZMB is thanked for all support and enjoyable discussions during the coffee breaks.

Author contributions

Conceptualisation KK, CPH, VP; data curation and cleaning, KK; methodology, KK and CPH; formal analysis, KK and CPH; writing—original draft preparation, KK; writing—review and editing, KK, CPH, VP, SB, ANL; visualisation, KK; supervision, ANL and SB. All authors have read and agreed to the published version of the manuscript.

Funding

Open Access funding enabled and organized by Projekt DEAL. We acknowledge financial support for the Open Access Publication Fund of the Universität Hamburg, Germany. SB received support via the Leibniz foundation and the ALONGate project (A Long-term Observatory of the North Atlantic Gateway to the Arctic Ocean) via grant number PS150/2023 in the program for women professors.

Declarations

Competing interests

The authors declare no competing interests.

Ethical approval

No approval of research ethics committees was required to fulfil the goals of this study.

Additional information

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1038/s41598-025-26442-x>.

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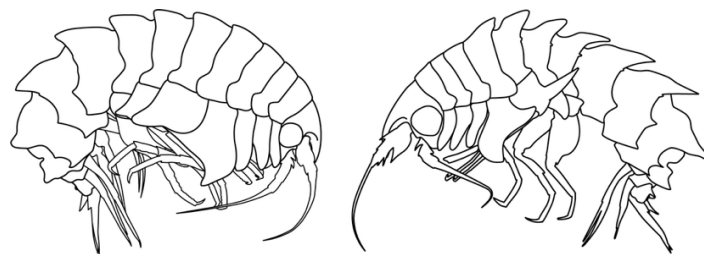
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Chapter 4 Cold-water coral-associated *Epimeria* (Epimeriidae, Amphipoda) from the North Atlantic and Southwest Pacific, with descriptions of two new species





Cold-water coral associated *Epimeria* (Epimeriidae, Amphipoda) from the North Atlantic and Southwest Pacific, with descriptions of two new species

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Received: 26 July 2025 / Revised: 10 November 2025 / Accepted: 15 November 2025
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Abstract

Cold-water corals are hotspots of biodiversity in the deep sea, and amphipod crustaceans are dominant members of these associations. Amphipoda are ecologically diverse and play a crucial role in the marine realm. Within the family Epimeriidae Boeck, 1871, the genus *Epimeria* Costa in Hope, 1851 is globally distributed and notably species-rich. Although some *Epimeria* species have been assumed to associate with deep-sea corals, these relationships remain poorly documented as of now. In this study, we describe two new *Epimeria* species associated with cold-water corals: *Epimeria craigi* sp. nov. from Iceland and *Epimeria freiwalddi* sp. nov. from New Zealand via integrative taxonomy. Both species new to science were filmed and collected using a remotely operated vehicle (ROV), providing live observations of the amphipods and their coral hosts. We provide live photographs, DNA barcodes based on the mitochondrial cytochrome c oxidase subunit I gene (COI), and updated taxonomic keys to the Atlantic and Pacific species of *Epimeria*. With these two newly described species, the total number of known *Epimeria* species increases to 93 worldwide. Additionally, we present photographic evidence for *E. aff. sophie* and two uncollected *Epimeria* species from New Zealand.

Keywords Amphipods · Integrative taxonomy · Synecology · Deep sea · Cold-water corals

Introduction

Cold-water corals play a vital role in deep-sea ecosystems around the world (e.g. Freiwald et al. 2012; Roberts et al. 2009, 2006) and can be considered biodiversity hotspots (e.g. Ashford et al. 2019). These coral habitats are characterised by their slow growth and slow recovery rates (Clark et al. 2015; FAO 2009; Freiwald et al. 2004), which could make them particularly vulnerable to climate change impacts such as ocean acidification (e.g. Hennige et al. 2020) as well as human disturbance such as fishing activities (Ashford

et al. 2019; Freiwald et al. 2004; Ramirez-Llodra et al. 2011). By creating complex three-dimensional structures, cold-water corals increase habitat heterogeneity (Buhl-Mortensen et al. 2010) and provide important ecological functions, including shelter (Buhl-Mortensen et al. 2020; Davies et al. 2017), feeding grounds, and nursery areas for a variety of invertebrate taxa (Buhl-Mortensen et al. 2010; Davies et al. 2017). Among the fauna frequently associated with these habitats are amphipod crustaceans (e.g. Buhl-Mortensen and Mortensen 2004; Zettler et al. 2018).

Amphipods are ecologically diverse crustaceans that play important roles in their respective biotopes (Dauby et al. 2001). Many amphipod species form close associations with other marine invertebrates, such as sponges (Amsler et al. 2009; Krapp-Schickel and Vader 2015; Ortiz et al. 2000), corals (Myers 1985; Navarro-Mayoral et al. 2024; Schwenner and Lörz 2021; Thomas 1999), bryozoans (Lörz et al. 2014), crinoids (Lowry and Bar 2008), and molluscs (Krapp-Schickel and Vader 2015; Vader and Tandberg 2013). For example, Buhl-Mortensen and Mortensen (2004) found amphipods to be the most abundant and species-rich crustaceans living on gorgonian corals in the Northeast Channel in

Communicated by S. Kaiser

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the Atlantic Ocean. In this paper, we focus on the association of certain species of the family Epimeriidae Boeck, 1871 to cold-water corals. The family Epimeriidae comprises 7 genera, with *Epimeria* Costa in Hope, 1851 being by far the largest, currently containing 91 described species (Horton et al. 2025).

The genus *Epimeria* is globally distributed in the marine realm (World Amphipoda Database 2025) and well represented in the deep sea (Horton et al. 2025; Kürzel et al. 2023; OBIS 2025), with species of this genus being recorded at wide range of depths including abyssal and hadal zones (OBIS 2025). As of now, 17 species have been described from the Pacific Ocean and 5 species from the North-East Atlantic Ocean. While some *Epimeria* species have been assumed to be associated with larger taxa such as deep-sea coral, their association with corals remains poorly documented (Beermann et al. 2018).

In this study, we describe two new cold-coral associated *Epimeria* species, collected using a Remotely Operated Vehicle (ROV) from two regions: near Iceland in the North Atlantic at a depth of 660 m, and near New Zealand in the Pacific at a depth of 287 m. Additionally, we provide identification keys to the species of this dominant genus of both oceans. We further document, through photographic and locality data, the occurrence of three additional, potentially undescribed *Epimeria* species from New Zealand, two of which were also observed in association with cold-water corals.

Material and methods

Sample collection

Atlantic specimens were collected using the robotic arm of the ROV KIEL 6000 during the IceAge 3 (Icelandic marine Animals: Genetics and Ecology; Brix et al. 2020) expedition with RV Sonne, conducted from June 22 to July 26 2020. Specimens were found at two stations around Iceland (106 and 97) at depths of 660 m and 300 m (Fig. 1, Table 1).

Pacific samples were taken during the 2025 Coral NewZ expedition with RV Sonne (expedition SO309, Freiwald and Beuck 2025) conducted from January 16 to February 15, 2025. The sampling gear was the ROV MARUM Squid, which is equipped with cameras, a manipulator arm named GÖFFEL and the epibenthic sled (EBS, Brenke 2005). The herein presented amphipod material was sampled during several ROV dives: dive 49 off Stewart Island at a depth of 227 m; Dive 61 in Dusky Sound at 287-m depth; Dives 75 and 89 close to the Ghaul Seamount at depths of 1006 m and 939 m, respectively, and via EBS station 86 on the chatham rise at Morgue Seamount at 1194-m depth (Table 1, Fig. 2).

For both expeditions, samples were taken directly from individual corals, ascertaining that only taxa directly associated with the coral were sampled and stored in a biobox. Immediately after collection, samples were sorted on board the research vessel following the protocol of Riehl et al. (2014), maintaining an uninterrupted cooling chain. Specimens were photographed on board using a Canon EOS 5D

Fig. 1 Map with sampling locations of a new *Epimeria* species in the North Atlantic during the RV Sonne expedition IceAge 3 (GEBCO Compilation Group 2024). Map created using QGIS

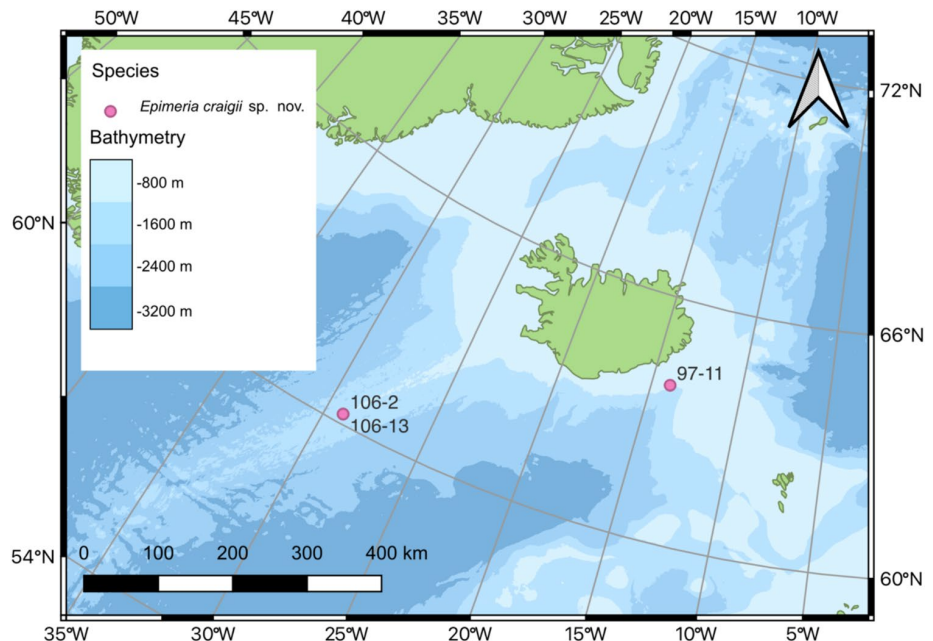
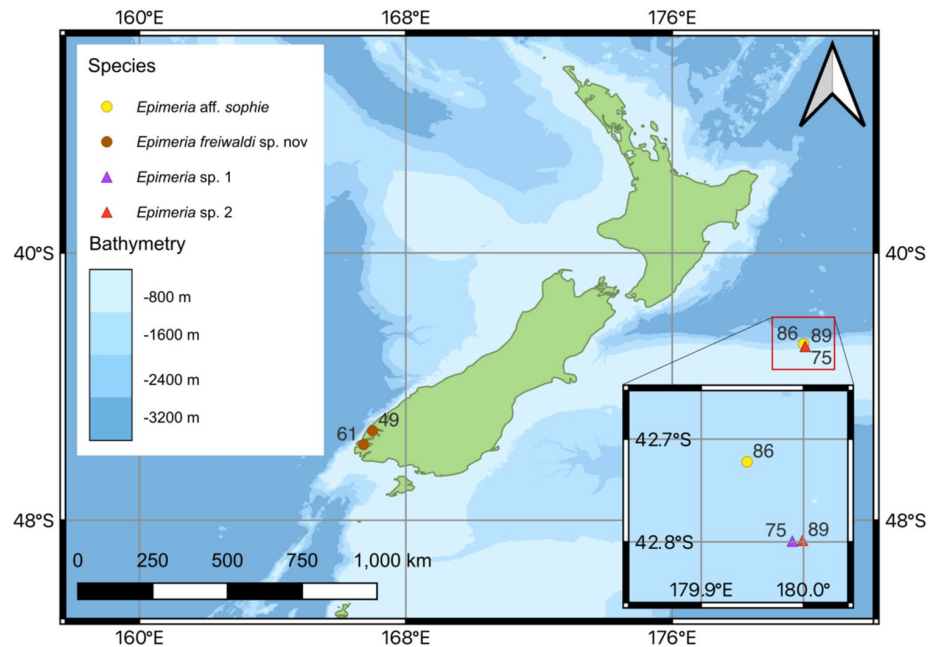


Table 1 Overview of each *Epimeria* specimen included in this study, along with their respective IDs, cruise detail, station number, sampling gear, date, depth (m), sampling location (latitude and longitude), associated fauna and sex (f=female, m=male)

Species	Cruise	ID	Station	Gear	Date	Depth (m)	Sampling location	Associated fauna	Sex
<i>Epimeria craigi</i> sp. nov.	IceAGE 3 (SO276)	SMF 61054	106–2	ROV	13.07.2022	665	60° 13.956' N 029° 08.946' W	<i>Paramuricea</i> K��lliker, 1865	f
<i>Epimeria craigi</i> sp. nov.	IceAGE 3 (SO276)	SMF 61055	106–2	ROV	13.07.2022	665	60° 13.956' N 029° 08.946' W	<i>Paramuricea</i> K��lliker, 1865	f
<i>Epimeria craigi</i> sp. nov.	IceAGE 3 (SO276)	SMF 61056	97–11	ROV	09.07.2020	295	63° 52.404' N 014° 00.155' W	<i>Paramuricea</i> K��lliker, 1865	f
<i>Epimeria craigi</i> sp. nov.	IceAGE 3 (SO276)	DZMB-HH 1241	97–11	ROV	09.07.2020	295	63° 52.404' N 014° 00.155' W	<i>Paramuricea</i> K��lliker, 1865	f
<i>Epimeria craigi</i> sp. nov.	IceAGE 3 (SO276)	SMF 61058	106–13	ROV	13.07.2022	668	60° 13.896' N 029° 08.742' W		f
<i>Epimeria freiwalddi</i> sp. nov.	CoralNewZ (SO309)	NIWA 175264	49–6	ROV	27.01.2025	227	45° 19.186' S 166° 59.871' E	Alcyoniidae Lamouroux, 1812	f
<i>Epimeria freiwalddi</i> sp. nov.	CoralNewZ (SO309)	*	61–1	ROV	29.01.2025	287	45° 44.103' S 166° 43.701' E	Candidae d'Orbigny, 1851	–
<i>Epimeria</i> aff. <i>sophie</i>	CoralNewZ (SO309)	DZMB-2-HH 23703	86–1	EBS	08.02.2025	1194	42° 43.327' S 179° 56.691' W	–	f
<i>Epimeria</i> sp. 1	CoralNewZ (SO309)	*	75–1	ROV	06.02.2025	1006	42° 47.955' S 179° 59.339' E	Acanthogorgiidae Gray, 1859	–
<i>Epimeria</i> sp. 2	CoralNewZ (SO309)	*	89–1	ROV	08.02.2025	939	42° 47.910' S 179° 59.939' E	<i>Solenosmilia variabilis</i> Duncan, 1873	–

*Specimens were only photographed but not physically sampled

Fig. 2 Map with sampling locations of Epimeriidae in the Pacific during the RV Sonne expedition CoralNewZ. Circles indicate locations where physical samples were collected; Triangles indicate locations with photographic evidence only (GEBCO Compilation Group 2024). Map created using QGIS



Mark IV equipped with an MP-E 65 mm f/2.8 1–5× macro lens, and preserved in 98% ethanol.

Morphological analyses

The Atlantic specimens were examined and dissected at the Institute for Marine Ecosystems and Fishery Science, University of Hamburg, Germany. All appendages were transferred into glycerine and a Leica DM1000 microscope with a Lucida camera attachment was used to illustrate the new species.

The Pacific specimens were examined at the Earth Sciences New Zealand (ESNZ, formally known as the National Institute of Water and Atmospheric Research (NIWA), New Zealand), Wellington, New Zealand. Dissections were performed under a Leica MZ 125 stereomicroscope, and the appendages were mounted in using glycerine. The habitus was illustrated using a Leica MZ 125 stereoscope, and appendage drawings were made with a Zeiss Axioskop 2 plus microscope.

For all specimens, body length was measured from tip of rostrum to end of telson tracing along the specimen's

mid-trunk length. Digital drawings were created using Adobe Illustrator 29.5.1 following Coleman (2003, 2009). The Atlantic type material is deposited at the Senckenberg Natural History Museum in Frankfurt, Germany, while additional non-type material is stored at the Deutsches Zentrum für Marine Biodiversitätsforschung (DZMB). The Pacific-type material is deposited at ESNZ in Wellington, New Zealand.

Genetical analyses

For all five specimens of *Epimeria craigi* sp. nov., DNA was extracted using one leg, usually the first left pleopod. DNA extraction for selected specimens was performed using the NucleoSpin® Tissue Genomic DNA Kit (Macherey–Nagel, Düren, Germany), following the manufacturer's protocol. For the single specimen of *Epimeria freiwalderi* sp. nov., DNA extraction was carried out directly during the cruise (SO309) on board RV Sonne using the Qiagen DNeasy Blood & Tissue Kit and stored at –20 °C.

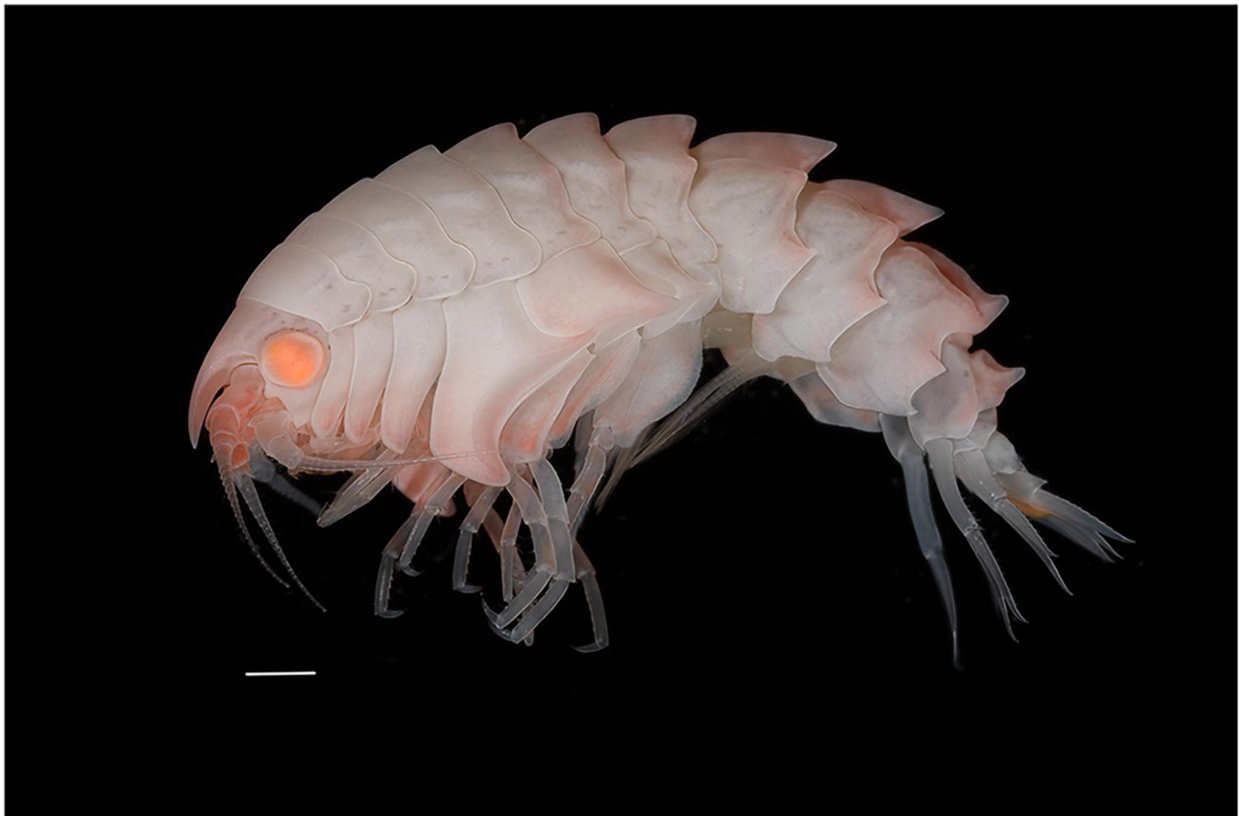


Fig. 3 Photograph of *Epimeria craigi* sp. nov. paratype, adult female, 14 mm, SMF 61055; taken on board the RV Sonne during cruise SO276 by Karlotta Kürzel shortly after the specimen was sampled close to the Reykjanes Ridge, Iceland, at 665-m depth (scale 1 mm)

For both species, further molecular analyses were conducted at the DZMB in Hamburg using the same procedures. For PCR, the mitochondrial cytochrome c oxidase subunit I (COI; Ca. 670 bp fragment) gene was amplified. The primers LCO1490/HCO2198 (Folmer et al. 1994) and AccuStart PCR Master Mix (Avantor) were used. The PCR thermal cycling consisted of 38 cycles, beginning with an initial denaturation step of 5 min at 94 °C, followed by 94 °C for 45 s, 45 °C for 50 s, and 72 °C for 1 min. This was followed by a final elongation step at 72 °C for 5 min, and the reaction was then held at 4 °C.

PCR products were visualised on 1% agarose/TAE gels. Reactions were cleaned using the ExoSAP-IT PCR Product Cleanup Reagent (Thermo Fisher, Waltham, Massachusetts, USA) and then bidirectionally sequenced by Macrogen Europe. Sequences were edited using Geneious 10.1.2 and deposited in BOLD.

To assess whether the potentially new species are genetically differentiated from other *Epimeria* species, phylogenetic and species delimitation methods were employed. *Epimeria* sequences were obtained from NCBI and BOLD, focusing on specimens collected in the Atlantic and Pacific Oceans. For better clarity and to account for possible

biogeographic differences, the Atlantic and Pacific datasets were analysed separately. Alignments were generated using the alignment tool in Geneious Prime, and subsequently inspected for indels and stop codons. *Rhachotropis saskia* (GenBank accession number MH272111.1) was used as the outgroup for both the Atlantic and Pacific analyses.

Initial clustering of COI sequences into putative species was performed using ASAP (Assemble Species by Automatic Partitioning; Puillandre et al. 2021) via the iTaxoTools web platform (Vences et al. 2021), employing uncorrected p-distances under default settings. Pairwise uncorrected p-distances for COI were calculated in MEGA-X (Kumar et al. 2018). Maximum likelihood phylogenetic trees were constructed in IQ-TREE using automatic model selection and 1000 bootstrap replicates. The resulting trees were visualised and formatted in FigTree version 1.4.4.

Results

Systematics

Order Amphipoda Latreille, 1816

Suborder Gammaridea Latreille, 1802

Family Epimeriidae Boeck, 1871

Genus *Epimeria* Costa in Hope, 1851

Epimeria craigi sp. nov.

(Figs. 3, 4, 5, 6, 7, and 8)

Material examined

Holotype: SMF 61054, 14 mm, adult female, Iceland (60° 13.956' N, 029° 08.946' W), 665 m, ROV KIEL 6000, SO276, station 106–2, 13 July 2020.

Paratypes: SMF 61055, 14 mm, adult female, location identical to holotype.

Further material

Two females (SMF 61056, DZMB-HH 1241), Iceland (63° 52.404' N, 014° 00.155' W), 295 m, ROV KIEL 6000, SO276 97–11, 09 July 2020, one female (SMF 61058), Iceland (60° 13.896' N, 029° 08.742' W), 668 m, ROV KIEL 6000, SO276 106–13, 13 July 2020.

Etymology

Epimeria craigi sp. nov. is dedicated to Dr. Craig Hammock, partner of the first author. The name *craigi* is the Latin genitive derived from his name.

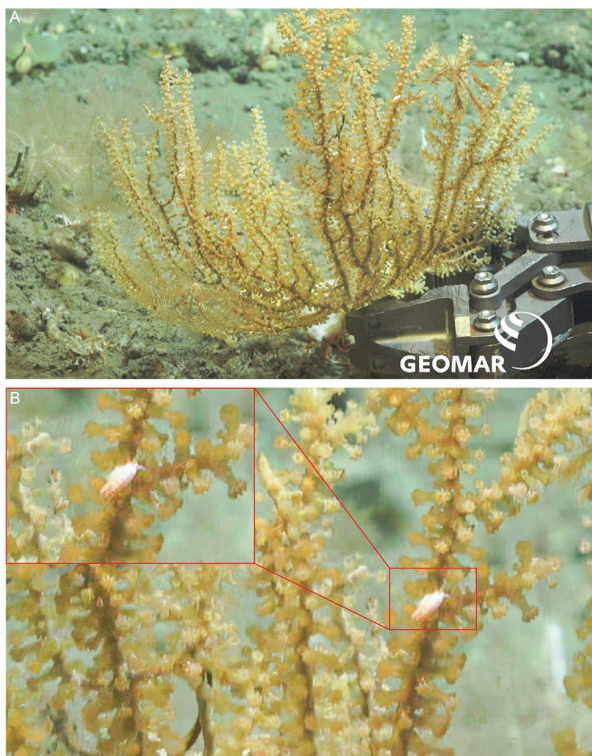
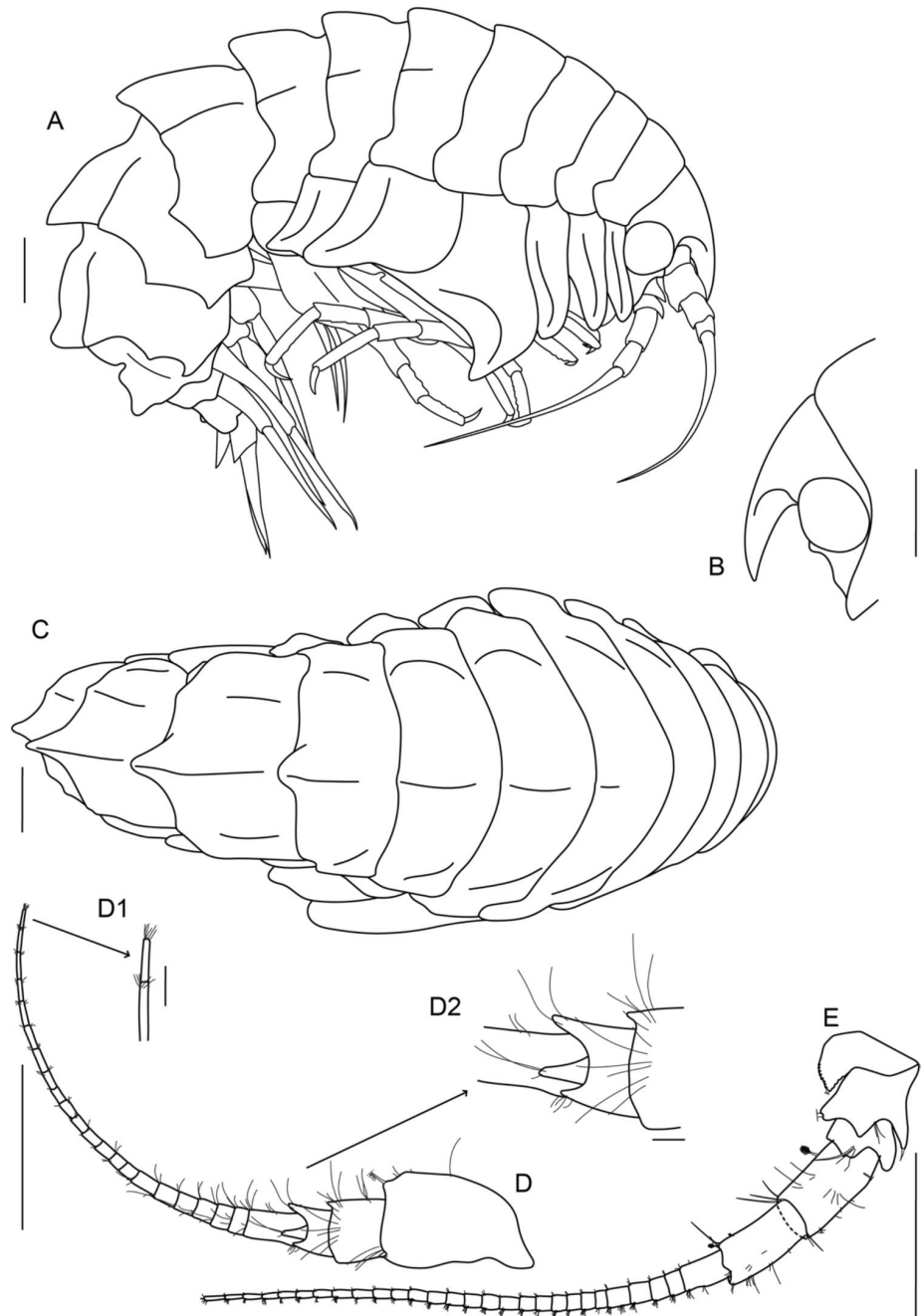


Fig. 4 *Epimeria craigi* sp. nov. observed in association with cold-water coral of the genus *Paramuricea* Kölliker, 1865 in the Lónsþjúp area, Iceland, at 295-m depth, at station 97 of expedition SO276 with RV Sonne. **A** In situ overview of the cold-water coral habitat photographed by ROV Kiel 6000; **B** Close-up of *Epimeria craigi* sp. nov. photographed by ROV Kiel 6000 (copyright both: GEOMAR)

Fig. 5 *Epimeria craigi* sp. nov., SMF 61054, holotype, adult female, 14 mm, Iceland, 665-m depth; (A) lateral habitus; (B) head in lateral view; (C) dorsal habitus; (D) antenna 1, (D1) tip of flagellum, (D2) magnification of peduncular articles; (E) antenna 2; scale bars (A)–(D) represent 1 mm; scale bars (D1) and (D2) represent 0.1 mm

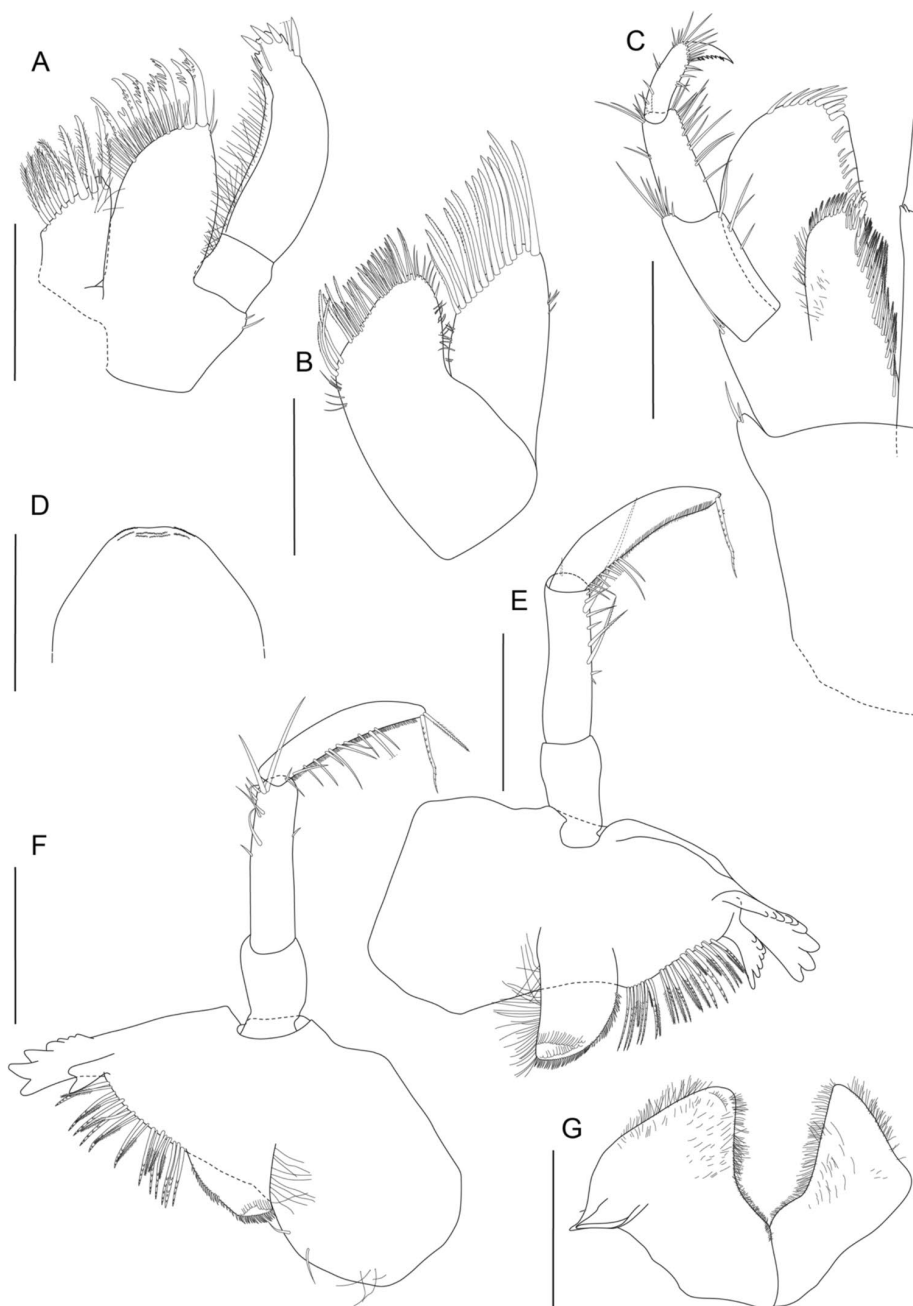


Diagnosis

Rostrum clearly curved, extending to about halfway along the length of the second peduncular article of antenna 1; eyes large, rounded, and bulging; flagellum of antenna 1 with 22 articles; body dorsally smooth on pereonites 1–3; pereonites 4 with dorsal hump; pereonites 5–7 dorsally carinate, increasing in size; pereonite 5–7 with dorsolateral protrusions; pleonites 1–3 strongly with carina dorsally and

each with a blunt dorsolateral ridge; dorsal carina of pleonite 3 clearly pointing upwards; epimeron 1 produced into a rounded posterodistal tooth; epimeron 2 bearing subacute posterodistal tooth and epimeron 3 bearing a distinctly acute tooth, posteriorly directed tooth; urosomite 1 with mamilli-form, upwards pointing carina; coxa 4 wing-shaped, projecting ventrally with concave posteroapical margin and rounded tip; coxa 5 moderately extended posteroventrally (about as long as broad); telson with deep v-shaped notch.

Fig. 6 *Epimeria craigi* sp. nov., SMF 61054, holotype, adult female, 14 mm, Iceland, 665-m depth; **A** maxilla 1; **B** maxilla 2; **C** maxiliped; **D** upper lip; **E** left mandible 1; **F** right mandible; **G** lower lip; all scale bars represent 0.5 mm



Description

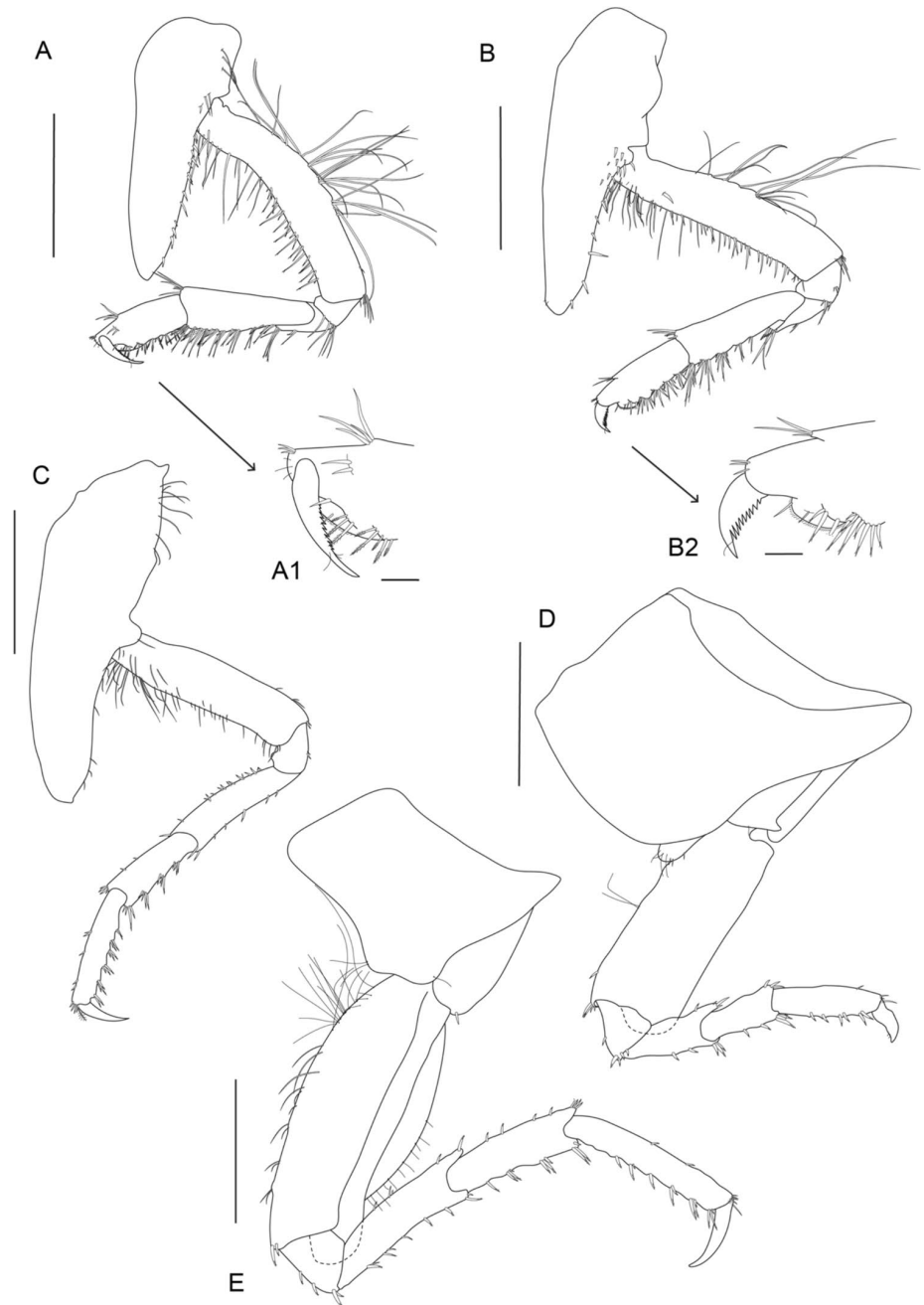
Based on holotype, adult female, 14 mm.

Colouration (Based on specimen SMF 61055, Fig. 3) eyes a vivid orange, with body primarily light rose. Edges of the pereonites, particularly pereonite 5 onwards, pleonites and epimera, as well as the first articles of the antennae and rostrum, display a deeper, more intense rose colour. Coxae similarly exhibit this deep rose coloration. Pereopods

excluding coxa, pleonites, and urosome lighter, ranging from pale rose to near white.

Body (Fig. 5) dorsally smooth on pereonites 1–3; pereonite 4–7 with dorsal carina increasing in size; pereonites 4 with dorsal hump; pereonites 5–7 dorsally carinate; pereonite 5–7 with dorsolateral protrusions; pleonites 1–3 strongly with carina dorsally and each with a blunt dorsolateral ridge; dorsal carina of pleonite 3 clearly pointing upwards; epimeral plates biangular, epimeron 1 produced into a rounded posterodistal

Fig. 7 *Epimeria craigi* sp. nov., SMF 61054, holotype, adult female, 14 mm, Iceland, 665-m depth; (A) gnathopod 1; (A1) palm of gnathopod 1 (B) gnathopod 2; (B1) palm of gnathopod 2 (C) pereopod 3; (D) pereopod 5; (E) pereopod 6; scale bars (A), (B), (C), (D) and (E) represent 1 mm; scale bars (A1) and (B1) represent 0.1 mm



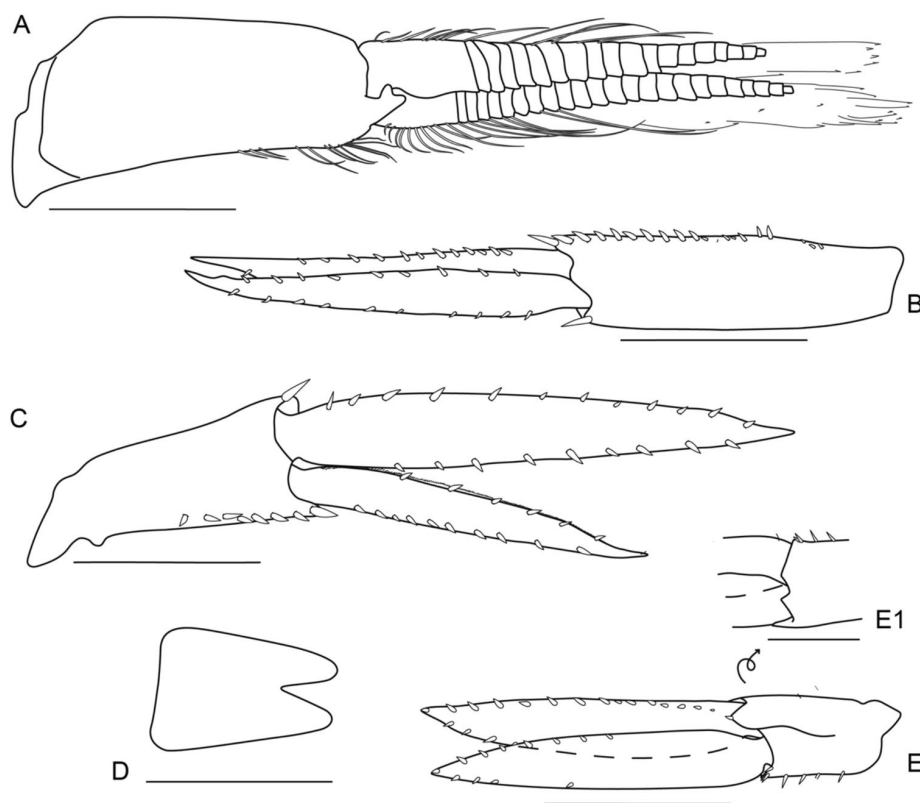
tooth; epimeron 2 bearing subacute posterodistal tooth and epimeron 3 bearing a distinctly acute tooth, posteriorly directed tooth; urosomite 1 with mamilliform, upwards pointing carina, notched at the mid-dorsal line; urosomite 2 shortest; urosomite 3 with a distinctly upwards-pointed projection.

Head (Fig. 5) rostrum clearly curved, shorter than the head, extending to about halfway along the length of the second peduncular article of antenna 1; eyes large, rounded, and bulging.

Antenna 1 (Fig. 5) with peduncle length ratios approximately 1.0:0.3:0.1, with the first peduncular article about twice as long (ratio 1.9) as the combined lengths of the second and third articles; accessory flagellum reduced, comprising a single tapering article approximately half the length (ratio 0.4) of the first primary flagellar article; primary flagellum with 22 articles.

Antenna 2 (Fig. 5) slightly longer than antenna 1; flagellum composed of 27 articles.

Fig. 8 *Epimeria craigi* sp. nov., SMF 61054, holotype, adult female, 14 mm, Iceland, 665-m depth; (A) pleopod 1; (B) uropod 1; (C) uropod 2; (D) telson; (E) uropod 3; (E1) margin of peduncle; scale bars (A)–(E) represent 1 mm; scale bar (E1) represents 0.5 mm



Upper lip (Fig. 6) ventrally rounded, with a slightly dentate margin.

Lower lip (Fig. 6) with broad, distally tapering lobes, densely covered in fine, hair-like setae along the inner and outer margins.

Left mandible (Fig. 6) with a nine-dentate incisor and a seven-dentate lacinia mobilis; molar process protruding; mandibular palp with 3 articles, article 2 with setae of varying lengths along the distal half of the inner margin; article 3 bearing a fine comb of hair-like setae on the inner margin, with additional setae of variable length along the proximal third of the article in the left mandible, and along the proximal two-thirds in the right mandible; right mandible with two long setae distally, one plumose and the other dentate, while the left mandible lacks the plumose seta.

Maxilla 1 (Fig. 6) inner plate subtriangular, with nine stout, plumose setae along the distal margin, distally, two small setae and multiple fine, hair-like setae present; outer plate obliquely convex, with eight stout, serrated setae distally, along with a single, small, stout, forked setae; palp with two articles, article 2 approximately four times longer than article 1, exceeding the length of the outer plate, slightly curved on both margins, and distally serrated with

five spines and several setae; lateral comb of hair-like setae possibly present.

Maxilla 2 (Fig. 6) inner lobe with numerous setae along the distal margin; outer lobe with numerous slender, serrated setae distally.

Maxilliped (Fig. 6) inner plate approximately as long as the first palp article, bearing a row of long, plumose setae, blunt spines, and simple setae along the medial, anterior face; outer plate extending to about $\frac{3}{4}$ the length of palp article 2, rounded distally, with stout setae and spines medi-odistally; palp composed of four articles, with the medial margin densely setose, article 4 distinctly curved, bearing several teeth along the inner curvature.

Gnathopod 1 (Fig. 7) coxa slender, tapering distally to a pointed, rounded apical tip, with a row of small setae along the posterior margin; basis slightly curved on both margins, approximately as long as the coxa, with numerous fine setae along both margins and a tuft of slender setae anterodistally; ischium slightly wider than long, with a row of setae along the posterior margin; merus slightly longer than the ischium, with a short anterior margin, setae along the posterior margin, and a tuft of setae distally; carpus slightly widened distally, with tufts of long setae along the anterior margin

and a group of mixed-length setae distally; propodus with groups of plumose setae along the posterior margin, palm convex and finely serrated, dactylus slender, slightly curved, with a finely serrated posterior margin.

Gnathopod 2 (Fig. 7) coxa tapering distally to a rounded apical tip, slightly less pointed but longer than that of gnathopod 1, posterior margin setose; basis with a straight anterior margin and slightly convex posterior margin, both densely setose; ischium, merus, carpus, and propodus similar in structure to those of gnathopod 1.

Pereopod 3 (Fig. 7) coxa slightly longer and broader than coxa 2, tapering distally with a rounded apical tip similar to coxa 2; basis slightly sinuous, with long, slender setae along the distal half of the anterior margin and sparse setae along the posterior margin; ischium longer than wide; merus approximately 1.2 times the length of the carpus, slightly concave anteriorly, with short setae along the anterior margin and sparse, short setae along the posterior margin, and a tuft of setae posterodistally; carpus with tufts of stout setae along the posterior margin and sparse setae along the anterior margin; propodus approximately 1.2 times the length of the carpus, with tufts of setae along the posterior margin, sparse setae along the anterior margin, and a tuft of setae, including one plumose seta, anterodistally; dactylus approximately 0.4 times the length of the propodus, curved.

Pereopod 5 (Fig. 7) coxa robust and winglike, with an evenly concave anterior margin, convex posterior margin that forms a rounded right angle, anteroventral margin sinuous, moderately extended posteroventrally (about as long as broad), apical tip of the process broadly rounded; basis rectangular, slightly expanding distally, with a posteriorly produced margin forming a lobe posterodistally, anterior margin sparsely setose, with tufts of setae along the distal margin, while the posterior margin is largely bare; ischium longer than wide, setose; merus approximately 1.3 times the length of the carpus, slightly sinuous and distally expanding, with sparse setae along the anterior margin and a row of short setae distally; carpus with sparse setation along both margins and tufts of setae anterodistally and posterodistally; propodus about 1.3 times the length of the carpus, with stout setae along the anterior margin and a sparsely setose posterior margin; dactylus curved, about 0.3 times the length of the propodus.

Pereopod 6 (Fig. 7) coxa wing-shaped, with two lobes on the anteroventral margin, posterior margin slightly convex, apical tip of the process rounded; basis curved anteriorly, with tufts of setae along the distal half of the anterior margin, posterior margin with a posterodistal lobe, bearing a row of short, slender setae along the distal half of the posteromedial margin; ischium longer than wide, with short, stout setae along the anterior margin; merus approximately the same length as the carpus, slightly curved on both margins and expanding slightly distally, with short, stout setae present along both margins; carpus slightly expanding

distally, with tufts of stout setae along the anterior margin and setae along the posterior margin, with an additional tuft of setae posterodistally; propodus about 1.3 times the length of the carpus, with pairs of stout, short setae along the anterior margin; dactylus about 0.3 times the length of the propodus, curved.

Pleopod 1 (Fig. 8) peduncle approximately 2.5 times longer than wide, with a setose outer margin and two pronounced coupling hooks; inner ramus slightly longer than the outer, both rami articulated, with each article bearing a single long, plumose seta on both margins.

Uropod 1 (Fig. 8) peduncle subrectangular, with small spines along the outer margin, increasing in size from proximal to distal; rami nearly subequal, approximately 1.2 times the length of the peduncle, with small spines along both margins.

Uropod 2 (Fig. 8) peduncle noticeably expanding distally, with spines along the outer margin that increase in size from proximal to distal; outer ramus distinctly shorter than the inner ramus; inner ramus approximately 1.4 times the length of the outer ramus and 1.4 times the length of the peduncle, both rami with small spines along both margins.

Uropod 3 (Fig. 8) peduncle short, with small spines along the inner margin and short spines distally, approximately 0.3 times the length of the inner ramus; rami nearly subequal, with spination similar to the rami of uropods 1 and 2.

Telson (Fig. 8) approximately 1.6 times as long as wide, with a strong, deep notch reaching about one-third the total length of the telson; apices rounded.

Remarks

Epimeria craigi sp. nov. was found in association with a non-reef-building octocoral of the genus *Paramuricea* K  l-
liker, 1865, at depths of 295–668 m south of Iceland. *Epimeria craigi* sp. nov. closely resembles *Epimeria* (*Epimeria*) *tuberculata* G.O. Sars, 1893, *Epimeria* (*Epimeria*) *parasitica* (M. Sars, 1858) and *Epimeria* (*Epimeria*) *cornigera* (Fabricius, 1779), as it shares with all of these species the carination of pereonite 7 as well as pleonites 1–3. However, it is distinctly different from *E. tuberculata* in having a clearly curved rostrum that extends well beyond the distal margin of the first peduncular article, the pereonite 4 bearing a dorsal process, pereonites 5 and 6 bearing dorsolateral protrusions, and pleonite 3 having an upwards pointing carina as well as the telson having a deep v-shaped notch. It can be distinguished from *E. (Epimeria) parasitica* and *E. cornigera* by its coloration as the body is light rose to whitish with rosy accents, and the urosomite 1 possesses a mamilliform, upwards-pointing carina. The main morphological differences between these species are summarised in Table 2 and an updated identification keys for *Epimeria* species of the Atlantic can be found in Table 3.

Table 2 Morphological differences between *Epimeria craigi* sp. nov., *E. (Epimeria) tuberculata*, *E. (Epimeria) parasitica* and *E. cornigera*. Additional distribution and bathymetry data sourced from OBIS (2025)

Characters	State	<i>E. craigi</i> sp. nov	<i>E. (Epimeria) tuberculata</i> G.O. Sars, 1893	<i>E. (Epimeria) parasitica</i> (M. Sars, 1858)	<i>E. (Epimeria) cornigera</i> (Fabricius, 1779)
Colouring		Light rose to whitish with rosy accents	Light rose to whitish with rosy accents	Dark read	Body white with red accents
Rostrum	Rostrum shape	Curved	(nearly) straight	Curved	Curved
	Reaching at least halfway along 2nd article of antenna 1	Yes	No	No	No
Eyes	Shape	Rounded	Rounded	Triangular	Rounded
	Eye width: head width	0.8	0.6	0.6	0.7
Antenna 1	Number of flagellum articles	22 articles	24 articles	20 articles	36 articles
Pereonites	Pereonite 4 dorsal process	Projection	Smooth	Projection	Smooth
	Pereonite 5 dorsal process	Carina	Weak projection	Distinct carina	Smooth
	Pereonite 6 dorsal process	Carina	Carina	Carina	Smooth
	Dorsolateral protrusions	Pereonite 5–7	Pereonite 7	Pereonite 6 and 7	Pereonite 7
Coxa	Coxa 4 apical tip of process	Rounded	Rounded	Subacute	Subacute
	Coxa 5 posterior spine extends	Beyond posterior margin of 6	To posterior margin of 6	Beyond posterior margin of 6	Beyond posterior margin of 6
	Coxa 5 apical tip of process	Rounded	Rounded	Subacute	Subacute
Pleonite	Pleonite 3 carina	Clearly pointing upwards	Pointing posteriorly	Pointing posteriorly	Pointing posteriorly
Epimeron	3rd epimeral plate	Triangular	Triangular	Angular	Triangular
	Posterior margin of 3rd epimeral plate	With pointed process	With pointed process	Straight	With pointed process
Urosom	Urosomite 1	With mamilliform, upwards pointing carina	With mamilliform, upwards pointing carina	With apically rounded, posteriorly pointing carina	With apically rounded, posteriorly pointing carina
Telson	Ratio width to length	1.6	1.1	1.2	1.5
	Shape of apices	Rounded	Broadly rounded	Pointed	Pointed
	Shape of notch	V-shaped	U-shaped	U-shaped	U-shaped
Distribution	Latitude	63° 52.404' N–60° 13.896' N	39°54.00'N–74°59.484'N	39°0.402'N–49.235'N	33°14.028'S–39°39.380'N
	Longitude	014° 00.155' W–029° 08.946'W	70°19.980'W–16°55.443'E	1°24.000'E–33°47.470'E	11°20.909'W–13°39.380'E
Depth		295–668 m	130–800 m	90–700 m	0–700 m

Epimeria freiwaldi sp. nov.

(Figs. 9, 10, 11, 12, 13, 14, and 15)

Type material

Holotype: NIWA 175264, 12 mm, adult female, New Zealand, Pendulo Reach (45° 19.186' S, 166° 59.871' E), 227 m, ROV MARUM Squid, SO309 49–6, 27 Jan 2025.

Etymology

Epimeria freiwaldi sp. nov. is dedicated to Prof. Dr. André Freiwald, expedition leader of CoralNewZ; his passion and commitment to shine a light on cold-water coral biodiversity in all its facets led to the discovery of this new species. The name *freiwaldi* is the Latin genitive derived from his name.

Table 3 Updated key to the *Epimeria* species of the Atlantic based on Beermann et al. (2018) and Souza-Filho et al. (2024)

1a. Rostrum flexed.....	2
1b. Rostrum straight.....	8
2a. Body smooth.....	3
2b. Body with carinae and additional teeth.....	5
3a. Pleonite 2 without carina or very small and rounded carina	<i>E. obtusa</i> Watling, 1981
3b. Pleonite 2 present and subacute	4
4a. Tip of pereopod 5 coxa process subacute and pleonite 1 carina absent.....	<i>E. bathyalis</i> Wakabara & Serejo, 1999
4b. Tip pereopod 5 coxa process broadly rounded and pleonite 1 carina present and pointed	<i>E. rotunda</i> Wakabara & Serejo, 1999
5a. Pereonite 7 with blunt to subacute dorsolateral process and triangular third epimeral plate with pointed process on posterior margin	6
5b. Pereonite 7 with acute dorsolateral process and biangular third epimeral plate with straight posterior margin	<i>E. (Epimeria) parasitica</i> (M. Sars, 1858)
6a. Only Pereonite 6 and/or 7 carinate	7
6b. Pereonite 4 with dorsal hump, 5–7 dorsally carinate	<i>E. craigi</i> sp. nov.
7a. Coxa 5 anteroventral margin strongly concave and urosomite 3 not produced or only with blunt hump.....	<i>E. (Epimeria) cornigera</i> (Fabricius, 1779)
7b. Coxa 5 anteroventral margin nearly straight or only slightly concave and urosomite 3 with pointed projection	<i>E. (Epimeria) franki</i> Beermann & Raupach, 2018
8a. Pereon with strongly developed dorsal carinae and dorsolateral teeth.....	<i>E. (Epimeria) loricate</i> G.O. Sars, 1879
8b. Pereon smooth, lacking strongly developed dorsal carinae and additional teeth, a small carina may be present on pereonite.....	9
9a. Pereonite 7 carina small and rounded.....	10
9b. Pereonite 7 carina absent.....	11
10a. Pereonites 1–7 with ventrolateral rounded bulge and pleonites 1–3 with carinae small and rounded.....	<i>E. (Epimeria) tuberculata</i> G.O. Sars, 1893
10b. Pereonites 1–7 ventrolaterally smooth and pleonites 1–3 with carinae well developed.....	<i>Epimeria potiguarensis</i> Souza-Filho, Guedes-Silva and Andrade 2024
11a. Pleonites 1–2 carinae absent and pleonite 3 with carina small and rounded	<i>E. semiarmata</i> K.H. Barnard, 1916
11b. Pleonites 1–3 with well-developed carinae.....	12
12a. Pleonites 1–3 with dorsolateral protrusion.....	<i>E. longispinosa</i> K.H. Barnard, 1916
12b. Pleonites 1–3 without dorsolateral protrusion.....	13
13a. Projection of coxa 5 not reaching distal margin of pereonite 7; carina of urosomite subacute; epimeral plates 1–3 with postero-mid-lateral margin slightly pointed	<i>E. concordia</i> Griffiths, 1977
13b. Projection of coxa 5 extending to the distal margin of pleonite 2; carina of urosomite 2 robust and rounded; epimeral plates 1–2 with postero-mid-lateral margin slightly rounded	<i>E. ultraspinosa</i> Wakabara and Serejo, 1999

Diagnosis

Rostrum curved; eyes large, rounded, and bulging; body dorsally smooth on pereonites 1–3; pereonites 4–7 dorsally carinate and with subacute dorsolateral spines; pleonites 1–3 strongly with carina dorsally and each with two dorsolateral spines; epimeral plates 1–3 biangular, with epimeron 2 bearing subacute posterodistal tooth and epimeron 3 bearing a distinctly acute tooth; epimeron 1–3 biangular, each produced into posterodistal tooth with epimeron 2 having a more acute posterodistal tooth; epimeron 3 with a distinctly acute; urosomite 1 with a pointed carina, notched mid-dorsally; coxa 4 with anterior margin sinuous and strongly curved ventrally, posteriorly forming into a pointed tip; coxa 5 strongly extended posteriorly, with concave ventral margin and a convex dorsal margin, tip of the process pointed;

flagellum of first antenna with 27 articles, flagellum of second antenna with 34 articles.

Description

Based on holotype, adult female, 12 mm.

Colouration (Fig. 9) eyes a vivid dark orange to red, with body partially in oranges and partially in reds. Antennas, telson and uropods of a more uniform red colour with some lighter accents. Pereopods excluding coxa, nearly white with some red splotches.

Body (Fig. 12) dorsally smooth on pereonites 1–3; pereonite 4–7 with strong lateral carinae and dorsolateral spines; pleonites 1–3 each with lateral carinae, two mid dorsolateral spines; epimeron 1–3 biangular, each produced into tooth, epimeron 1 with a rounded posterodistal tooth; epimeron 2

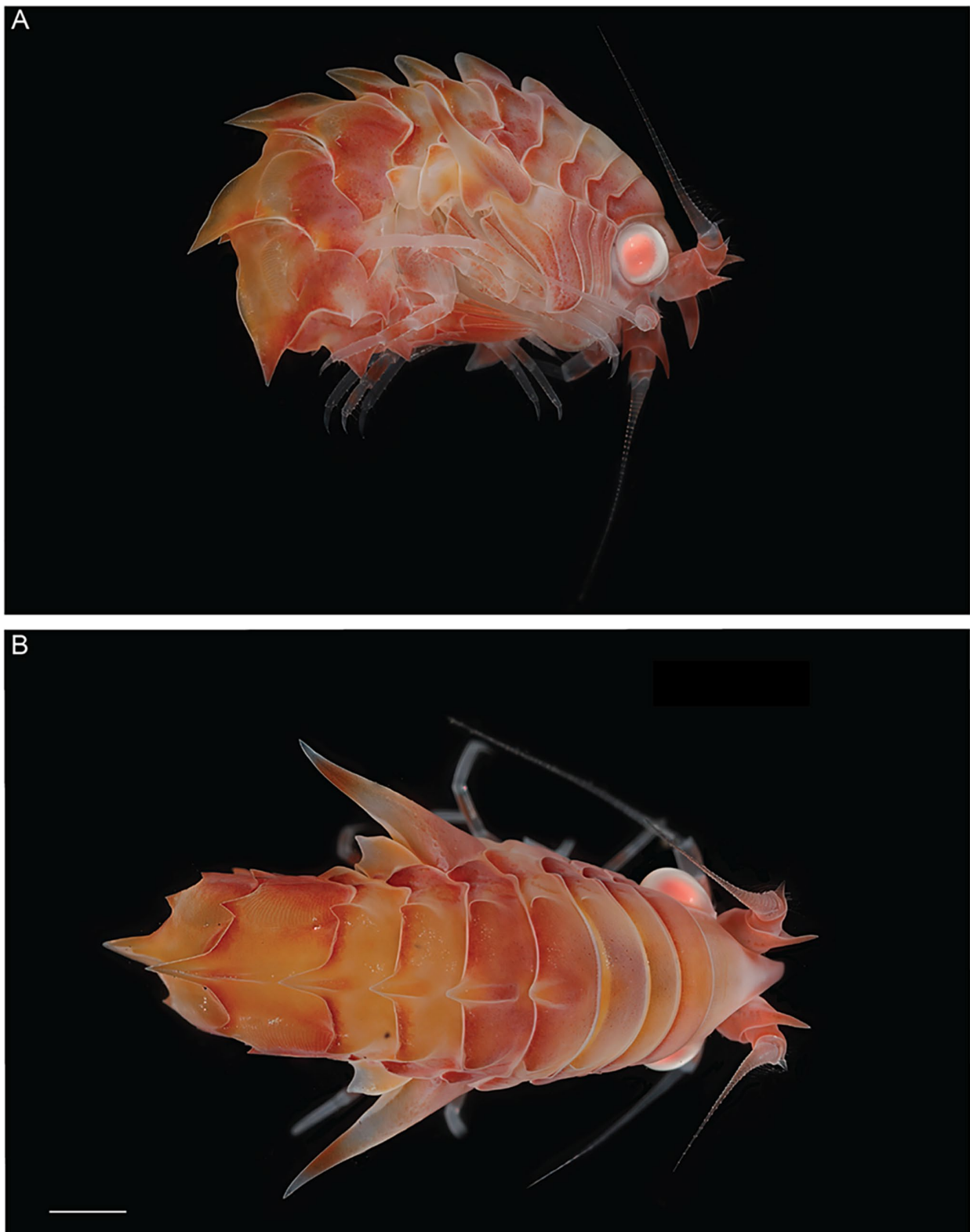
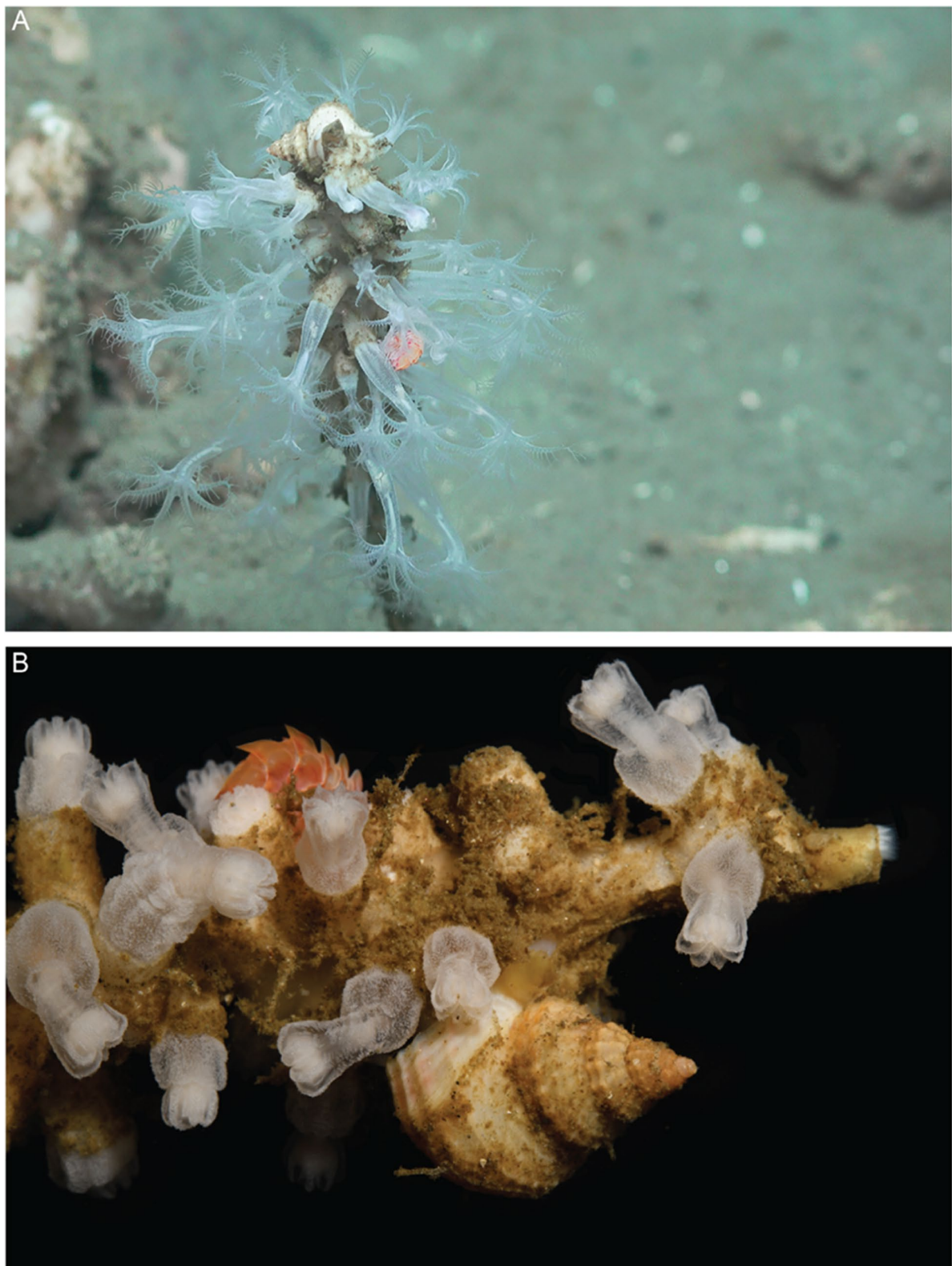


Fig. 9 Photograph of *Epimeria freiwaldi* sp. nov., holotype, adult female, 12 mm NIWA 175264, taken on board the RV Sonne during cruise SO309; **A** laterally by Severin Korfage and **B** dorsally by Peter

‘Chazz’ Marriott shortly after the specimen was sampled, close to the Pendulo Reach, Fiordland, New Zealand, at 227-m depth (scale 1 mm)



◀**Fig. 10** *Epimeria freiwalddi* sp. nov. NIWA 175264 holotype observed in association with cold-water coral of the family Alcyoniidae Lamouroux, 1812 at Pendulo Reach, Fiordland, New Zealand, at 227-m depth, at station 49–6 of expedition SO309 with RV Sonne; **A** In situ overview of the cold-water coral habitat photograph by ROV MARUM Squid (copyright: MARUM University of Bremen); **B** Close up made on board shortly after sampling by Peter ‘Chazz’ Marriott shortly after sampling

with a slightly more acute posterodistal tooth; epimeron 3 with a distinctly acute, posteriorly directed tooth, angles on the posterior margins of the epimera are subacute, particularly pronounced in epimeron 2; urosomite 1 with a pointed carina, notched at the mid-dorsal line; urosomite 2 shortest.

Head (Fig. 12) rostrum curved, about same length as the head; eyes large, rounded, and bulging.

Antenna 1 (Fig. 12) with peduncle article length ratios approximately 1.0: 0.4: 0.2, with the first peduncular article about twice as long (ratio 1.8) as the combined lengths of the second and third articles; accessory flagellum reduced, comprising a single tapering article approximately half the length (ratio 0.6) of the first primary flagellar article; primary flagellum with 27.

Antenna 2 (Fig. 12) slightly longer than antenna 1; flagellum composed of 34 articles.

Upper lip (Fig. 13) subtrapezoid, with a slightly concave margin distally.

Lower lip (Fig. 13) with broad, distally tapering lobes, covered in fine, hair-like setae along the inner and outer margins. Group of thicker setae at the tip of the lobes.

Left mandible (Fig. 13) with a 10-dentate incisor and a five-dentate lacinia mobilis; molar process protruding; mandibular palp with 3 articles, article 2 with setae of varying lengths along the distal half of the outer margin; article 3



Fig. 11 *Epimeria freiwalddi* sp. nov. observed in association with a Bryozoa of the family Candidae d'Orbigny, 1851 in the Dusky Sound, Fiordland, New Zealand, at 287-m depth, at station 61–1 of expedition SO309 with RV Sonne photographed by ROV MARUM Squid (not physically sampled; copyright: MARUM University of Bremen)

bearing setae of variable length along the full margin of the article.

Maxilla 1 (Fig. 13) inner plate subtriangular, with nine stout, plumose setae along the distal margin, multiple fine, hair-like setae present; outer plate slightly tapering distally, with 11 stout, serrated setae distally; palp with two articles, article 2 approximately four times longer than article 1, exceeding the length of the outer plate, margin slightly curved, and distally serrated with four spines and one slender seta; laterally multiple hair-like setae.

Maxilla 2 (Fig. 13) inner lobe with numerous setae along the margins; outer lobe with numerous slender, serrated setae distally.

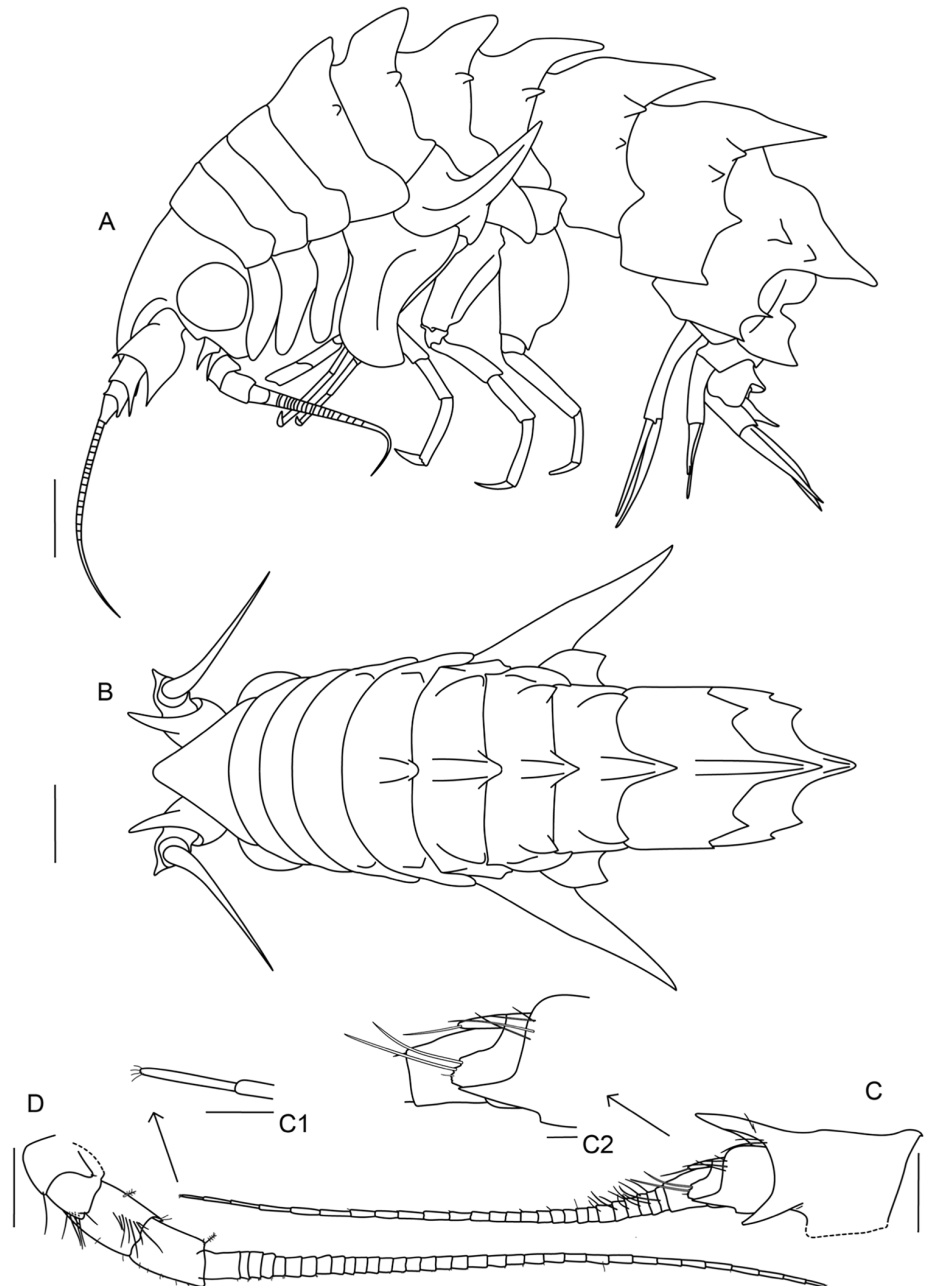
Maxilliped (Fig. 13) inner plate approximately as long as the first palp article, bearing a row of simple, slender setae and thicker flame-shaped spines mediodistally; outer plate extending to about $\frac{3}{4}$ the length of palp article 2, rounded distally, with simple setae and stout spines mediodistally; palp composed of four articles, with the both margin setose, article 4 curved, bearing several teeth along the inner curvature.

Gnathopod 1 (Fig. 14) coxa slender, tapering distally to a rounded apical tip, with a row of small setae along the posterior margin; basis curved on both margins, slightly longer than coxa, with numerous fine setae along both margins; ischium about as wide as long, with a tuft of setae posterodistally; merus nearly double the length of ischium, with a tuft of setae posterodistally; carpus slightly widened distally, with tufts of long setae along the posterior margin and a tuft of setae anterio- and posterodistally; propodus with groups of setae along the posterior margin, palm convex and finely serrated, with multiple simple setae and two forked setae, tuft of setae anteriodistally; dactylus slender, slightly curved, with a finely serrated posterior margin.

Gnathopod 2 (Fig. 14) coxa tapering distally to a rounded apical tip, slightly broader and longer than the coxa of gnathopod 1, anterior margin setose; basis with a straight anterior margin and slightly convex posterior margin, both setose; ischium without any setae, merus, carpus similar to gnathopod 1 but with plumose setae on the posterior margins; propodus also similar in structure to that of gnathopod 1 but palm with three forked setae; dactylus similar to that of gnathopod 1.

Pereopod 3 (Fig. 14) coxa slightly longer and broader than coxa 2, tapering distally with a broadly rounded apical tip; basis slightly convex on the posterior margin, with long, slender setae, anterior margin with setae of varying sizes; ischium about as long as wide; merus approximately 1.2 times the length of the carpus, anterior margin, with short setae along the anterior and posterior; carpus with tufts of stout setae along the posterior margin and sparse setae along the anterior margin, tuft of setae anteriodistally; propodus approximately 1.2 times the length of the carpus, with tufts

Fig. 12 *Epimeria freiwalddi* sp. nov., NIWA 175264, holotype, adult female, 12 mm, New Zealand, 227-m depth; (A) lateral habitus; (B) dorsal habitus; (C) antenna 1 (C1) tip of flagellum (C2) magnification of peduncular articles (D) antenna 2; scale bars (A) and (B) represent 1 mm, scale bars (C) and (D) represent 0.5 mm, scale bars (C1) and (C2) represent 0.1 mm



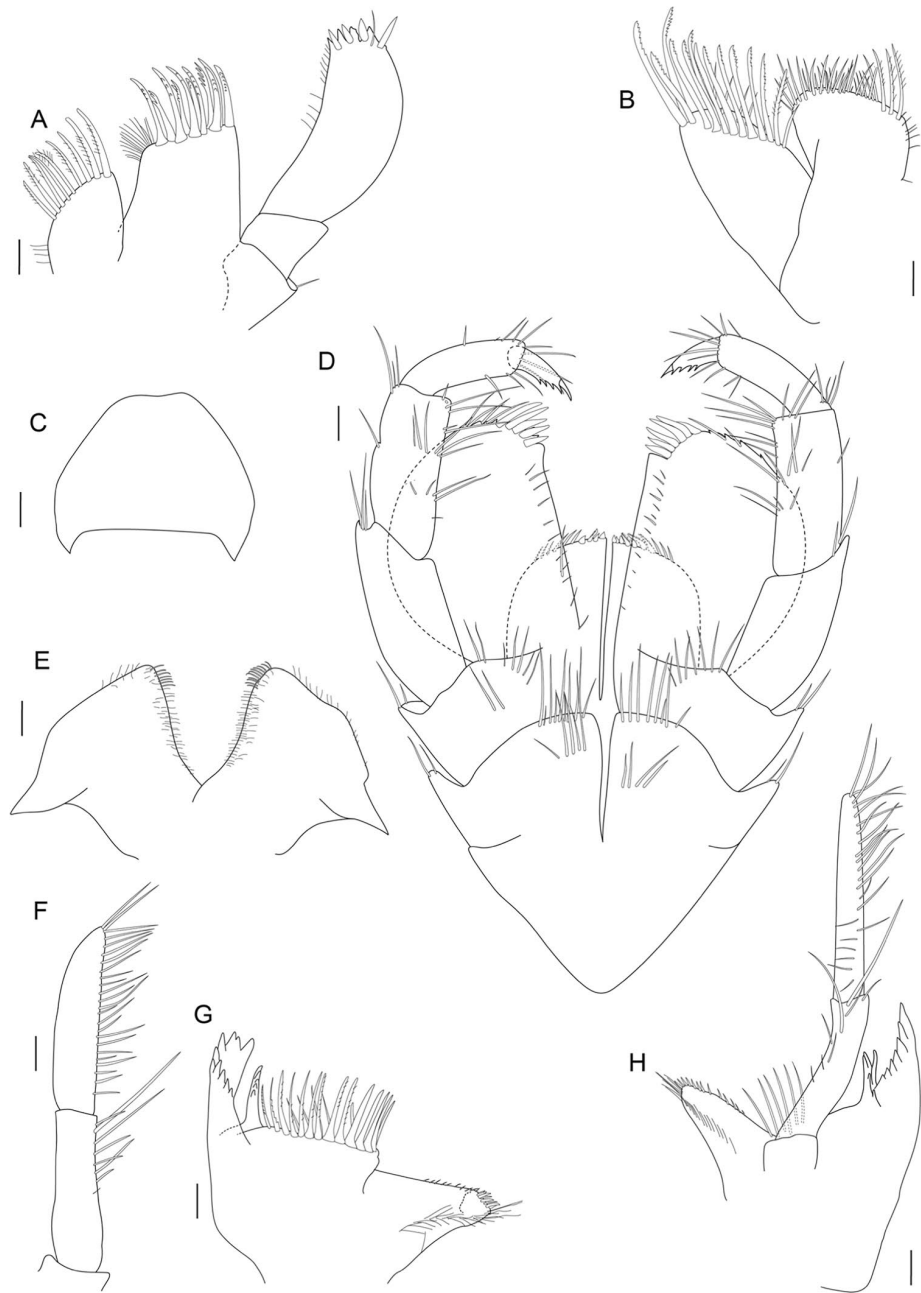
of setae along the posterior margin; dactylus approximately 0.5 times the length of the propodus, curved.

Pereopod 4 (Fig. 14) coxa robust, projecting ventrally, anterior margin sinuous and strongly curved, posteriorly forming into a pointed tip; basis linear, posterior margin convex and some slender setae, anterior margin straight and with slender setae, distally with tufts of plumose setae; ischium slightly longer than wide, with a slender seta on posterior margin and tuft of plumose setae posterodistally;

merus about 1.1 the size of carpus, sublinear with few short setae along both margins; carpus with tufts of stout setae along the posterior margin and anterodistally with one seta; propodus about 1.3 the size of carpus, with groups of short setae posteromarginally; dactylus about half the length of propodus, curved.

Pereopod 5 (Fig. 15) coxa robust, strongly extended posteriorly with a concave ventral margin and a convex dorsal margin, tip of the process pointed; basis rectangular, with a

Fig. 13 *Epimeria freiwaldi* sp. nov., NIWA 175264, holotype, adult female, 12 mm, New Zealand, 227-m depth; **A** maxilla 1; **B** maxilla 2; **C** upper lip; **D** maxilliped; **E** lower lip; **F** left mandibular palp; **G** left mandibular palpus; **H** right mandible; all scale bars represent 0.1 mm

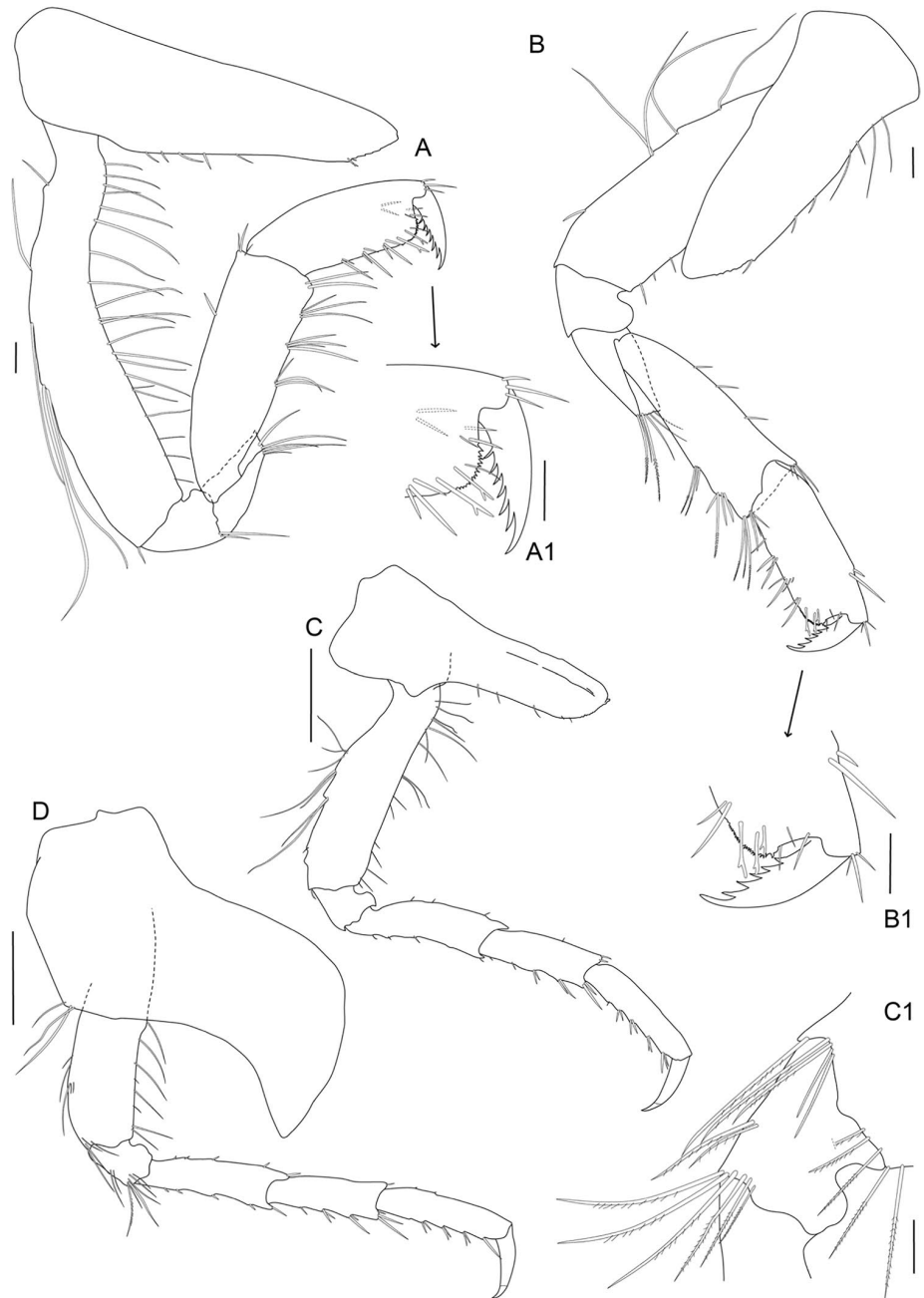


posteriorly produced margin forming a lobe posterodistally, posterior margin with numerous simple and plumose setae, anterior margin sparsely setose; ischium wider than long; merus approximately same length as the carpus, slightly sinuous and distally expanding, with small setae along both margins; carpus with pairs of setae along the anterior and tuft of setae anterodistally, posterior margin with setation and tuft of setae posterodistally; propodus about 1.6 times

the length of the carpus, with pairs of stout setae along the anterior margin and sparse setation on the posterior margin; dactylus curved, about half the length of the propodus.

Pereopod 6 (Fig. 15) coxa suboval, wider than long; basis curved posteriorly and with simple and plumose setae along, anterior margin sublinear with simple setae; ischium about as long as wide, with short, stout seta anterodistally; merus approximately 0.8 length as the carpus, slightly curved on

Fig. 14 *Epimeria freiwalddi* sp. nov., NIWA 175264, holotype, adult female, 12 mm, New Zealand, 227-m depth; (A) gnathopod 1; (A1) palm of gnathopod 1; (B) gnathopod 2; (B1) palm of gnathopod 2; (C) pereopod 3; (C1) pereopod 4 detail; (D) pereopod 4; scale bars (A), (A1), (B), (B1), (C1) represent 0.1 mm; scale bars (C), (D) represent 0.5 mm

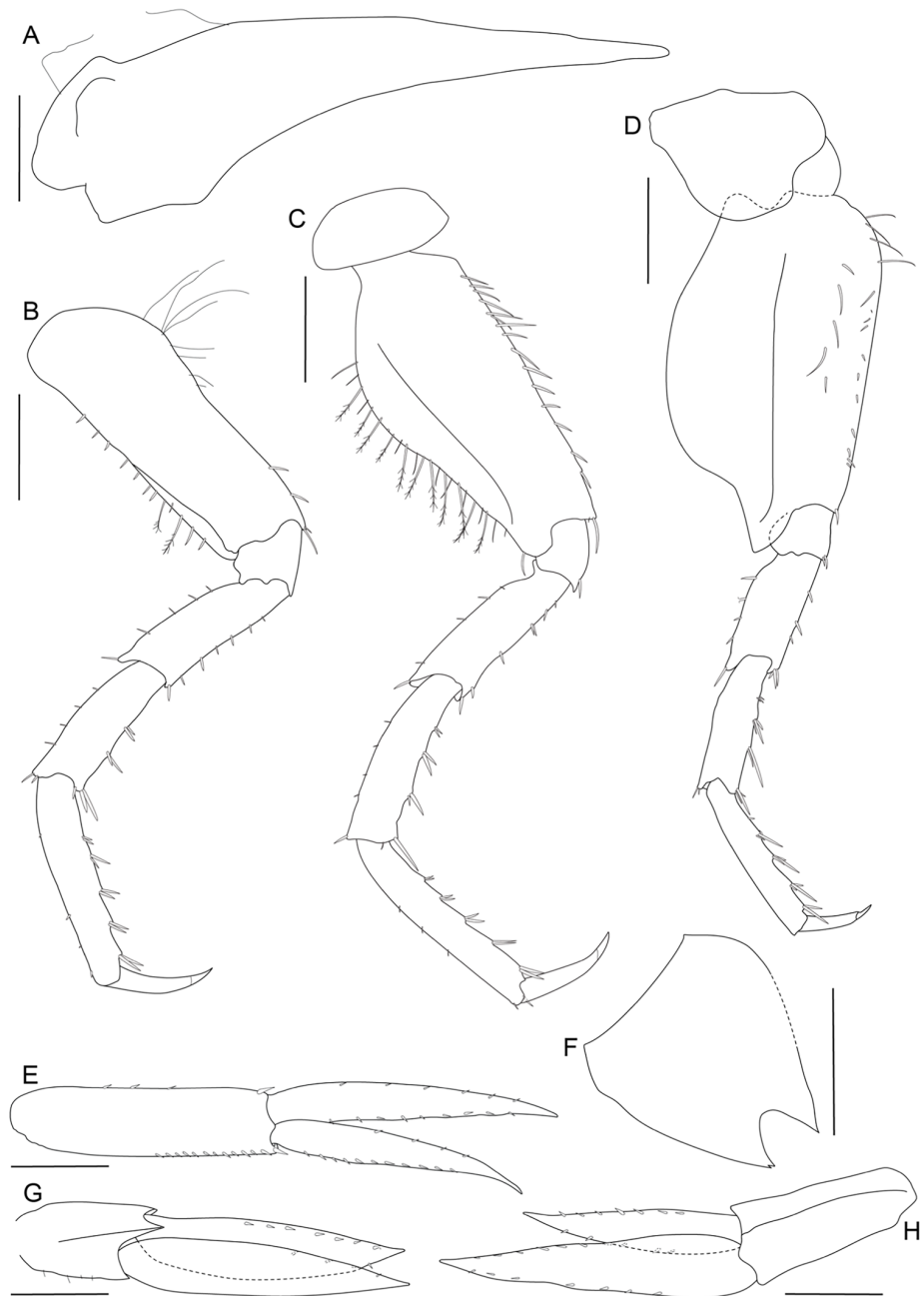


both margins, with short, stout setae present along both margins; carpus posterior margin slightly convex, with small setae; anterior margin with pairs of stout setae; propodus about 1.2 times the length of the carpus, with pairs of stout setae along the anterior margin; dactylus about 0.5 times the length of the propodus, curved.

Pereopod 7 (Fig. 15) coxa suboval, wider than long; basis strongly convex posteriorly with a pointed process, anterior margin slightly convex with multiple simple

setae; ischium wider than long, with short, stout seta anterodistally; merus approximately 0.8 length as the carpus, slightly convex posterior margin, both margins with short, stout setae; carpus margins slightly sinuous, anterior margin with groups of three stout setae and small setae posterodistally; propodus about 1.3 times the length of the carpus, with groups of three stout setae along the anterior margin; dactylus about 0.4 times the length of the propodus, curved.

Fig. 15 *Epimeria freiwaldi* sp. nov., NIWA 175264, holotype, adult female, 12 mm, New Zealand, 227-m depth; **A** coxa pereopod 5; **B** pereopod 5; **C** pereopod 6; **D** pereopod 7; **E** uropod 1; **F** telson; **G** uropod 2; **H** uropod 3; all scale bars represent 0.5 mm



Uropod 1 (Fig. 15) peduncle subrectangular, with sparse small spines along the inner margin, setation in the distal half of the outer margin increasing in size from proximal to distal; outer ramus shorter than the inner ramus; inner ramus approximately 1.1 times the length of the outer ramus and same length as the peduncle, both rami with small spines along both margins.

Uropod 2 (Fig. 15) peduncle noticeably expanding distally; outer ramus distinctly shorter than the inner ramus;

inner ramus approximately 1.5 times the length of the outer ramus and 0.8 times the length of the peduncle, both rami with small spines along both margins.

Uropod 3 (Fig. 15) peduncle short, approximately 0.5 times the length of the inner ramus; rami nearly subequal, with spination similar to the rami of uropods 1 and 2.

Telson (Fig. 15) about as wide as long, with a strong, deep notch reaching about a quarter of the total length of the telson; apices pointed.

Table 4 Morphological differences between *Epimeria freiwalddi* sp. nov., *Epimeria victoria* and *Epimeria panamensis*. Additional distribution and bathymetry data sourced from OBIS (2025) and Varela (2020)

Character	State	<i>E. freiwalddi</i> sp. nov	<i>E. victoria</i> Hurley, 1957	<i>E. panamensis</i> Varela, 2020
Rostrum	Shape	Curved	Curved	(Nearly) straight
Eyes		Present	Present	Absent
Antenna 1	Reaches about ¾ of the body length	No	Yes	No
Upper lip	Shape	Subtrapezoid	Suboval	Subtriangular
Pereonites	Dorsal carina of pereonite 4	Big and rounded	Small and (sub-) acute	Big and rounded
	Dorsal carina of pereonite 5	Rounded	Subacute	Rounded
	Dorsal carina of pereonite 6	Rounded	Acute	Subacute
	Dorsal carina of pereonite 7	Subacute	Acute	Subacute
	Dorsolateral protrusions	Pereonite 4–7	Pereonite 5–7	None
Telson	Shape of apices	Acute	Subacute	Rounded
	Shape of notch	U-shaped	V-shaped	V-shaped
	Triangular process in midline	No	Yes	No
Distribution	Latitude	45° 19.186' S –45°44.103' S	45°53.930'S–34°32.202'S	6°51.00'N
	Longitude	166° 43.701' E – 166° 59.871' E	171°2.640'E–174°48.000'E	79°28.00'W
Depth		227–287	129–500 m	3193–3200 m

Remarks

Epimeria freiwalddi sp. nov. was observed in association with a non-reef-building coral of the family Alcyoniidae Lamouroux, 1812 and a Bryozoa of the family Candidae d'Orbigny 1851, at depths of 227–287 m to the southwest of New Zealand. *Epimeria freiwalddi* sp. nov. is morphologically closest to *Epimeria victoria* Hurley, 1957 and *Epimeria panamensis* Varela 2020, as it shares with them the carination of pereonites 4–7 and pleonites 1–3, as well as a strongly produced and pointed coxa 5. The characters to separate the three species are summarised in Table 4 and an updated identification keys for *Epimeria* species of the Pacific can be found in Table 5.

Molecular species delimitation

A total of 107 sequences were analysed for the COI alignment of Atlantic *Epimeria* species, each with a length of 658 bp. Five sequences belonged to *Epimeria craigi*, while the remaining 102 were sourced from NCBI GenBank and BOLD Systems. For the COI alignment of Pacific *Epimeria* species, six sequences were analysed in total, also with a length of 658 bp. One sequence represented *Epimeria freiwalddi*, one *Epimeria* aff. *sophie* and the remaining four were obtained from NCBI GenBank and BOLD w.

The best ASAP analysis of the Atlantic *Epimeria* dataset suggested delimiting four putative species, based on a distance threshold of 5.1% for ASAP 1.5 (Fig. 16). This also

resulted in the delimitation of *Epimeria craigi* sp. nov. as a distinct lineage. Due to the limited number of sequences available for the Pacific *Epimeria*, ASAP was not performed, as the method is only informative with larger datasets and only a phylogenetic tree was provided (Fig. 17).

For the Atlantic species, uncorrected p-distances ranged from 11 to 24% between species, and 0 to 3% within species (*Epimeria craigi* sp. nov. was assigned to BIN BOLD:ACV1528, *Epimeria freiwalddi* sp. nov. to BIN BOLD:AGY5535, and *Epimeria* aff. *sophie* to BIN BOLD:AAG2806.

Table 6). Within *Epimeria craigi* sp. nov., intra-specific distances were 0%, and this species exhibited a minimum genetic distance of 10% to all other analysed species (*Epimeria craigi* sp. nov. was assigned to BIN BOLD:ACV1528, *Epimeria freiwalddi* sp. nov. to BIN BOLD:AGY5535, and *Epimeria* aff. *sophie* to BIN BOLD:AAG2806.

Table 6). For the Pacific *Epimeria* species, inter-specific genetic distances ranged from 15 to 25% (Table 7). Due to the limited number of sequences available, intra-specific distances could only be calculated for *Epimeria horsti*, where they were 0%. *Epimeria freiwalddi* sp. nov. exhibited a minimum genetic distance of 15% to all other analysed species (Table 7).

Epimeria craigi sp. nov. was assigned to BIN BOLD:ACV1528, *Epimeria freiwalddi* sp. nov. to BIN BOLD:AGY5535, and *Epimeria* aff. *sophie* to BIN BOLD:AAG2806.

Table 5 Updated key to the *Epimeria* species of the Pacific based on Wang et al. (2020)

1a. Pereon segments lacking strong dorsal carinae	2
1b. Pereon segments bearing strong dorsal carinae	13
2a. Eyes present	3
2b. Eyes absent.....	9
3a. Urosomite 1 bearing dorsally pointed tooth; rostrum extending beyond first peduncle article of antenna 1	4
3b. Urosomite 1 lacking dorsally pointed tooth; rostrum not extending beyond first peduncle article of antenna 1.....	7
4a. Coxa 5 projection not reaching to epimeral plate 1	<i>E. cora</i> J.L. Barnard, 1971
4b. Coxa 5 projection reaching to epimeral plate 1.....	5
5a. Head ventral lobe not produced.....	6
5b. Head ventral lobe produced.....	<i>E. pacifica</i> Gurjanova, 1955
6a. Eyes oval; carina of pleonite 3 rounded; coxa of pereopod 5 reaching approximately halfway along pleonite 1	<i>E. ortizi</i> Varela & García-Gómez, 2015
6b. Eyes kidney-shaped; carina of pleonite 3 acute; coxa of pereopod 5 extending beyond the distal margin of pleonite 1	<i>E. karamani</i> Winfield & Hendrickx, 2020
7a. Coxa 5 with protrusion reaching posterior margin of epimeral plate 2; telson not cleft	<i>E. norfanzi</i> Lörz, 2011
8a. Telson with deep and broad V-shaped excavation	<i>E. pelagica</i> Birstein and M. Vinogradov, 1958
8b. Telson with deep and narrow Y-shaped excavation	<i>E. abyssalis</i> Shimomura & Tomikawa, 2016
9a. Coxa 5 produced	10
9b. Coxa 5 not produced.....	<i>E. yaquinae</i> McCain, 1971
10a. Pleonites 1–3 with dorsal carinae; coxae 1–3 ventrally rounded.....	11
10b. Pleonites 1–2 smooth; coxae 1–3 ventrally pointed	<i>E. subcarinata</i> Nagata, 1963
11a. Rostrum not extending beyond first peduncle article of antenna 1	<i>E. glauca</i> J.L. Barnard, 1961
11b. Rostrum extending beyond second peduncle article of antenna 1	12
12a. Pereon 16 without dorsal carinae	<i>E. morronei</i> Winfield, Ortiz & Hendrickx, 2012
12b. Pereon 4–7 with dorsal carina.....	<i>E. panamensis</i> Varela, 2020
13a. Coxa 5 strongly produced	14
13b. Coxa 5 not or weakly produced	18
14a. Dorsal carina starting on pereon 4 or 5	15
14b. Dorsal carinae starting on pereon 6 or 7; posterolateral corners of epimeral plates 1 and 2 rounded or weakly produced	16
15a. pereonite 4 smooth, pereonite 5–7 with acute dorsolateral spines; first antenna with at least 40 articles, second antenna with at least 45 articles	<i>E. victoria</i> Hurley, 1957
15b. pereonite 4–7 with subacute dorsolateral spines; first antenna with 27 articles, second antenna with 34 articles	<i>E. freiwaldi</i> sp. nov.
16a. Pereonites 6 and 7 dorsolaterally smooth; coxa 1 ventrally rounded.....	17
16b. Pereonites 6 and 7 dorsolaterally bearing projections; coxa 1 ventrally subquadrate	<i>E. emma</i> Lörz and Coleman, 2014
17a. Rostrum not extending to distal margin of first peduncular article of antenna 1.....	<i>E. liui</i> Wang, Zhu, Sha & Ren, 2020
17b. Rostrum beyond distal margin of first peduncular article of antenna 1	<i>E. horsti</i> Lörz, 2008
18a. Double dorsal carinae present on pleonites 1–3.....	19
18b. Single dorsal carinae present on pleonites 1–3	<i>E. bruuni</i> J.L. Barnard, 1961
19a. Pleonites dorsolaterally smooth	<i>E. sophie</i> Lörz & Coleman, 2014
19b. Pleonites dorsolaterally bearing several projections	<i>E. (Metepimeria)</i> Lörz, 2012

Additional *Epimeria* species encountered during the expedition CoralNewZ

Three additional potential new *Epimeria* species were observed around New Zealand during cruise SO309. While no fully detailed species descriptions are given in this paper, these observations provide further evidence that *Epimeria* species are associated with cold-water corals.

The first observed species, *Epimeria* aff. *sophie* (Fig. 18), might represent a new species distinct from *Epimeria sophie* Lörz & Coleman, 2014. This evaluation is based on its markedly different eye shape, which appears relatively larger in proportion to the head and exhibits an irregular margin rather than a smooth outline. Additionally, the rostrum extends beyond the distal margin of the second peduncular article of antenna 1, and the carinae of pereonite 7 and

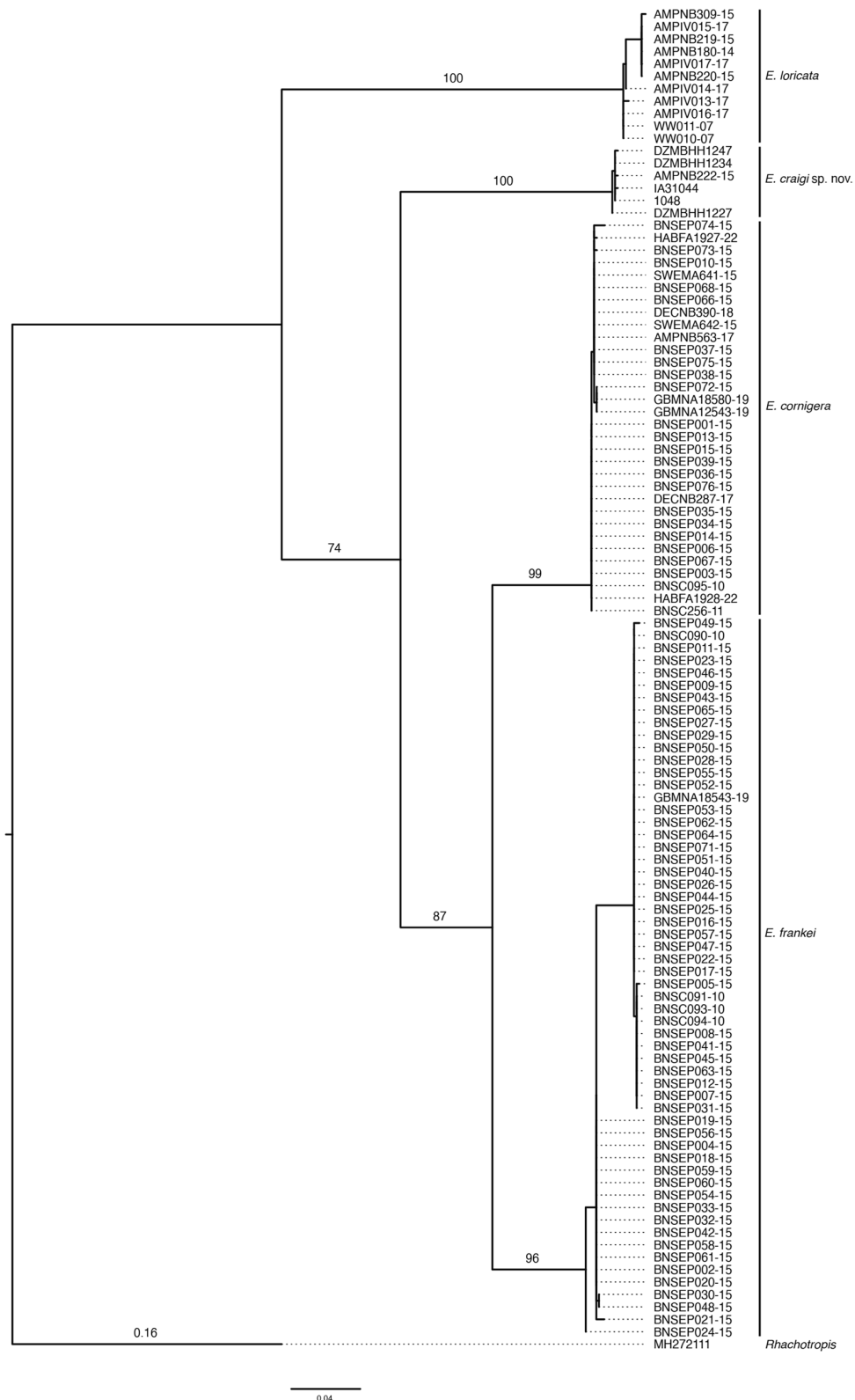


Fig. 16 Maximum likelihood phylogenetic tree of the analysed COI sequences of Atlantic *Epimeria* species. Bootstrap values $\geq 70\%$ are shown on branches. Vertical lines indicate proposed putative species by ASAP 1.5

Fig. 17 Maximum likelihood phylogenetic tree of the analysed COI sequences of Pacific *Epimeria* species. Bootstrap values $\geq 70\%$ are shown on branches

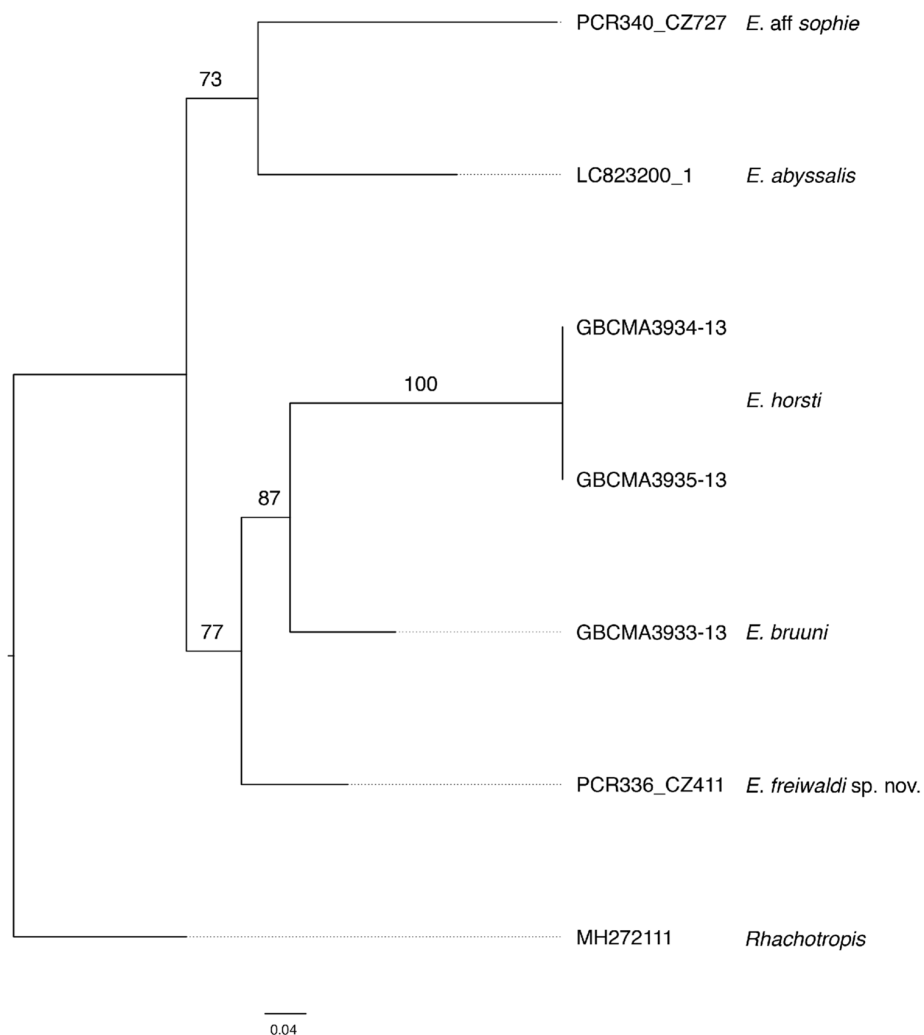


Table 6 COI intra- and interspecific p-distances in percentages of *Epimeria* species of the Atlantic

	<i>E. cornigera</i>	<i>E. craigi</i> sp. nov	<i>E. frankei</i>	<i>E. loricata</i>
<i>E. cornigera</i>	0–1%	–	–	–
<i>E. craigi</i> sp. nov	0–15%	0–0%	–	–
<i>E. frankei</i>	11–24%	10–16%	0–3%	–
<i>E. loricata</i>	20–24%	20–24%	20–24%	0–2%

Table 7 COI intra- and interspecific p-distances in percentages of *Epimeria* species of the Pacific

	<i>E. abyssalis</i>	<i>E. aff. sophie</i>	<i>E. bruuni</i>	<i>E. freiwalddi</i> sp. nov	<i>E. horsti</i>
<i>E. abyssalis</i>	–	–	–	–	–
<i>E. aff. sophie</i>	23%	–	–	–	–
<i>E. bruuni</i>	20%	25%	–	–	–
<i>E. freiwalddi</i> sp. nov	21%	24%	15%	–	–
<i>E. horsti</i>	20–24%	26–30%	19–20%	20–22%	0%



Fig. 18 Photograph of *Epimeria* aff. *sophie*, adult female, DZMB-2-HH 23703; taken on board the RV Sonne during cruise SO309 by Severin Korfhage shortly after the specimen was sampled on the Chatham Rise, New Zealand, at 665-m depth (scale 1 mm)

pleonite 1 appear less pronounced in this species. However, since this single specimen was found on the Chatham Rise in 1194-m depth, and the type material of *Epimeria sophie* is also from the Chatham Rise, we chose the conservative approach not describing this specimen as a new species until further material is available. Morphological variables can only be analysed with more material available.

For two further *Epimeria* species on cold-water corals only photographic evidence is given in this paper. Due to the physical conditions at the sampling sites (e.g. strong currents), both species could not be collected. *Epimeria* sp. 1 (Fig. 19) and *Epimeria* sp. 2 (Fig. 20) could not be assigned to species known to science. Both species exhibit markedly different colouration compared to other *Epimeria* species that can be found around New Zealand. *Epimeria* sp. 1 has prominent yellow eyes and a dark pink head, while the body is a soft purple/white tone. *Epimeria* sp. 2 has a pale rose to white body, with the coxa of pereopod 4 displaying a deep pink stripe along the ventral and distal margins. The head and mouthparts are also of a dark pink.

Both species were observed in association with corals in the New Zealand, close to the *Ghoul Seamount*. *Epimeria* sp. 1

was found with a non-reef-building gorgonian coral of the family Acanthogorgiidae Gray, 1859, at a depth of 921 m, whereas *Epimeria* sp. 2 was observed on the reef-building coral *Solenosmilia variabilis* Duncan, 1873, at a depth of 925 m.

Discussion

Cold-water coral ecosystems are recognised as biodiversity hotspots including for crustaceans such as amphipods (Lörz and Tandberg 2025; Roberts et al. 2006; Schwentner and Lörz 2021). Our study found reef-building as well as non-reef-building corals to be associated with a variety of *Epimeria* species. Especially reef-building corals like *Solenosmilia variabilis* have been previously reported to host diverse associated fauna, including ophiuroids (O'Hara et al. 2008) and polychaetes (Miranda and Brasil 2014). Similarly, non-reef-building corals such as those in the families Acanthogorgiidae and Alcyoniidae, as well as the genus *Paramuricea*, have also been shown to support various invertebrate taxa, including amphipods (e.g. Fuller et al. 2008; Miller et al. 2012; Schwentner and Lörz 2021). For instance,

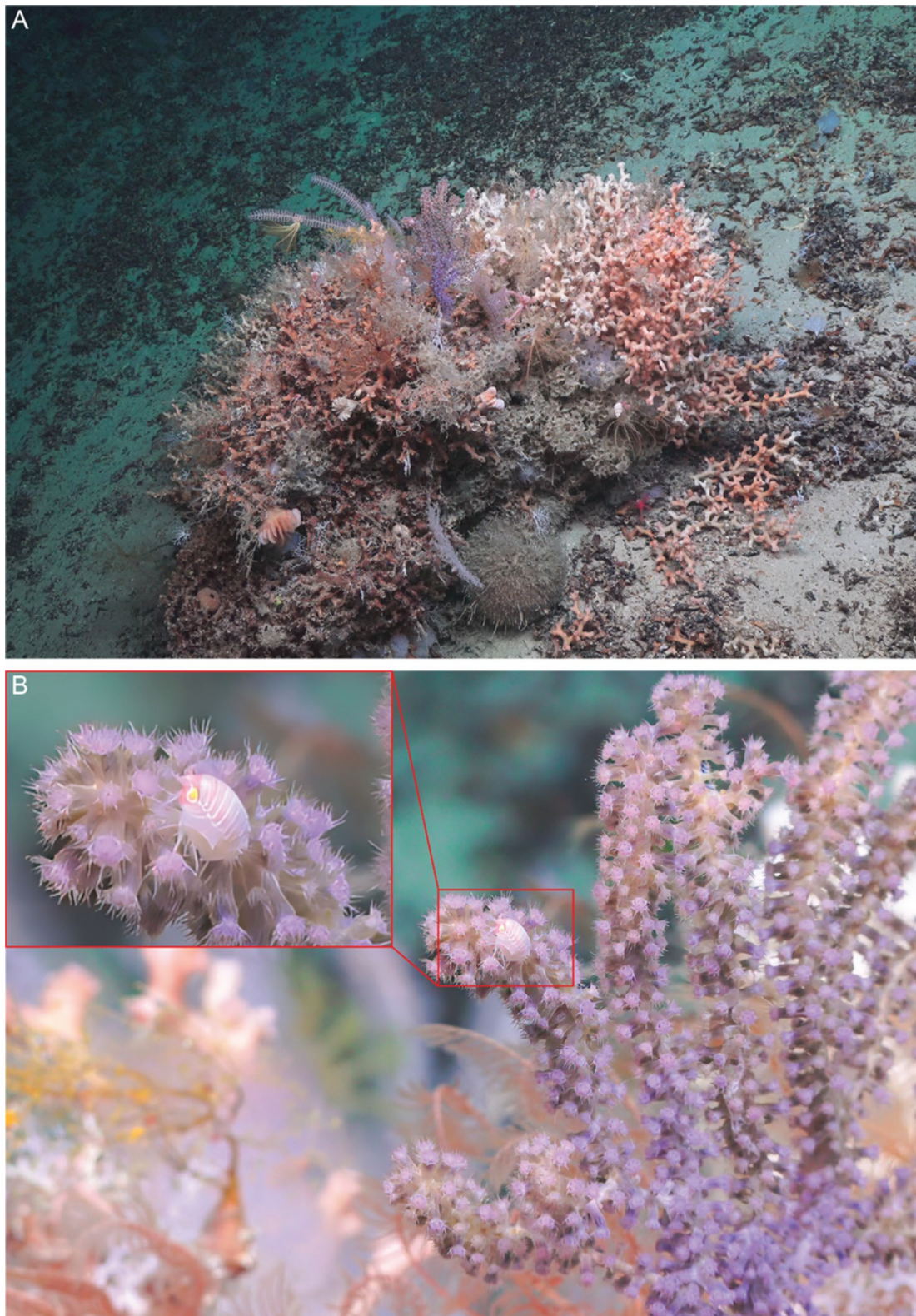


Fig. 19 *Epimeria* sp. 1 observed in association with a purple coral of the family Acanthogorgiidae Gray, 1859 in the Ghaul seamount area, New Zealand, at 921-m depth, at station 75 of expedition SO309 with RV Sonne. **A** Overview of the cold-water coral habitat; **B** Close-up of *Epimeria* sp. 1 photographed by ROV MARUM Squid (copyright: MARUM University of Bremen)

Schwentner and Lörz (2021) documented an association between the amphipod *Stenopleustes* aff. *nodifera* and the gorgonian coral *Acanthogorgia* cf. *armata*, while Lörz and Tandberg (2025) documented an association of *Neopleustes schwentneri* Lörz & Tandberg, 2025 and *Stenopleustes jeskulkeae* Lörz & Tandberg, 2025 to *Paragorgia arborea* (Linnaeus, 1758) and *Paramuricea* Kölliker, 1865.

While research on associations between the genus *Epimeria* and cold-water corals has so far been limited, our study provides new evidence supporting such relationships for multiple *Epimeria* species. This association is likely to offer benefits to the *Epimeria* species, including providing shelter and access to prey. Many species of the genus are suspected to be (micro-)predators (Dauby et al. 2001), and as corals increase habitat heterogeneity they may also attract prey species, thereby serving as favourable hunting grounds for *Epimeria*.

With the addition of the two newly described *Epimeria* species in this study, the number of known *Epimeria* species increases to 93, 14 of which can be found in the Atlantic and 20 of which can be found in the Pacific. The COI barcoding results support the delimitation of these species. The genetic patterns follow patterns observed previously for amphipod barcoding, with interspecific distances typically exceeding 7% and intraspecific variation generally remaining below 4% (Beermann et al. 2018; Jażdżewska et al. 2018; Morhun et al. 2022; Tempestini et al. 2017). In our case, interspecific distances were at least 10%, while intraspecific distances were approximately 3% or lower, which is therefore well within the previously observed range.

One sequence currently assigned to *Epimeria tuberculata* in BOLD clustered with *Epimeria craigi* sp. nov. and exhibited nearly 0% genetic divergence, sharing the same BIN (BOLD:ACV1528). Inspection of the reference image further supports this interpretation. The specimen exhibits a distinctly curved rostrum extending beyond half the length of article 2 of antenna 1, a feature characteristic of *Epimeria craigi* sp. nov. Based on this, we therefore conclude that this BOLD specimen has been misidentified and should be regarded as *Epimeria craigi* sp. nov. Species descriptions such as this one remain fundamentally important for almost any kind of biological research, as the accurate species determination forms the basis for almost any of those studies (Kürzel et al. 2022).

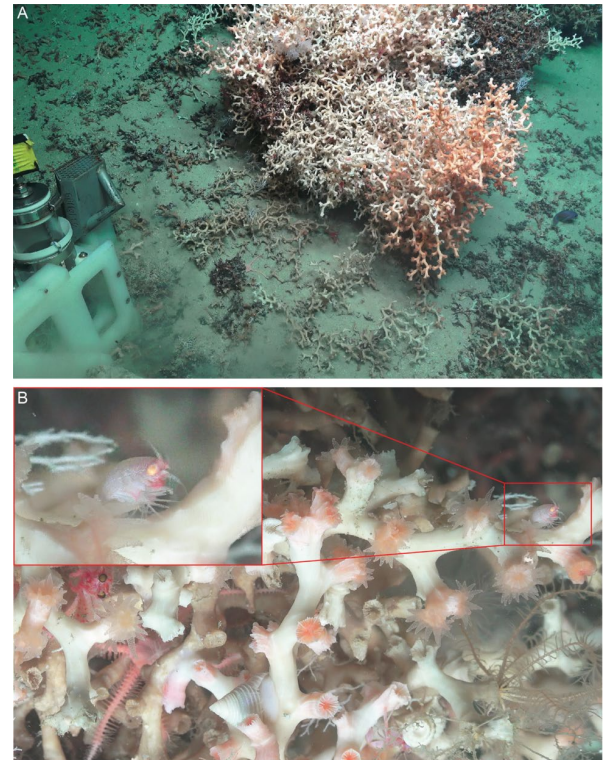


Fig. 20 *Epimeria* sp. 2 observed in association with the coral *Solenosmilia variabilis* Duncan, 1873 on the Chatham Rise, New Zealand, at 925-m depth, at station 89 of expedition SO309. **A** Overview of coral habitat; **B** close up of *Epimeria* sp. 2 photographed by ROV MARUM Squid (copyright: MARUM University of Bremen)

Overall, our study highlights the important role of cold-water corals in supporting amphipod biodiversity, specifically emphasising the association of *Epimeria* species with both reef-building and non-reef-building corals. This is especially important given the vulnerability of cold-water corals to anthropogenic disturbances and climate change, and considering their inherent fragility (Freiwald 2003; Sanna and Freiwald 2024). As such, future studies on coral ecology and biodiversity should take amphipod associations into account. Considering this synecology is essential for informing conservation strategies and promoting the long-term health of deep-sea ecosystems.

Acknowledgements We would like to thank Prof. Dr. Saskia Brix, the expedition leader of the IceAGE3 cruise (SO276), as well as the crew of the RV Sonne for their logistical support and hands-on assistance in collecting the samples. Furthermore, we are grateful to the GEOMAR ROV team for taking some of the photographs used in this paper and for sampling the specimens. Our thanks also go to Nicole Gatzemeier (DZMB Hamburg) for her support with the genetic work and database assistance.

We thank the captain, crew, and the scientific personnel of the RV Sonne 309 for a successful collecting expedition, led by Prof. Dr. André Freiwald, of which Anne-Nina Lörz had the pleasure of taking part. The efforts, patience, and expertise of the ROV MARUM Squid team are especially acknowledged. We also thank Dr. Martin Schwenner for his assistance with the genetic analyses in this study. Karen Jeskulke (DZMB, Hamburg) is thanked for her help in the molecular lab and sorting 1000s of amphipod samples. Severin Korfhage (Senckenberg Wilhelmshaven) and Peter 'Chazz' Marriott (ESNZ) are thanked for their onboard photography. We are grateful to Dr. Kareen Schnabel (ESNZ) for control of the sample processing and Jaret Bilewicz (ESNZ) for the coral identifications. Dr. Dennis Gordon (ESNZ) kindly identified the Bryozoa on the MARUM photographs. Diana MacPherson and Sadie Mills (both ESNZ) are thanked for hosting the senior author in the labs of the ESNZ Invertebrate Collection and curating the amphipod samples. We would also like to thank Severin Korfhage and Prof. Dr. André Freiwald for identifying the corals from both expeditions, and Dr. Craig Hammock for proofreading the English. We are most grateful to three anonymous reviewers whose detailed comments significantly improved the quality of this paper.

Funding Open Access funding enabled and organized by Projekt DEAL. We are grateful to the German Ministry of Education and Science (BMBF) for funding the CoralNewZ project, incl. the funding of ship time on RV Sonne and the funding of ROV MARUM Squid operations through grants 03G0309A and 03G0309B.

We acknowledge financial support from the Open Access Publication Fund of Universität Hamburg.

Declarations

Ethical approval No approval of research ethics committees was required to fulfil the goals of this study.

Conflict of interest The authors declare no competing interests.

Data availability The genetic sequences of both new *Epimeria* species described in this paper are available in BOLD under the following accession numbers: *Epimeria craigi* AMPIV321-25, AMPIV322-25, AMPIV323-25, AMPIV324-25, AMPIV325-25; *Epimeria freiwaldi* CZAMP003-25. Additionally, the sequence for *Epimeria* aff. *sophie* can be found under accession number CZAMP004-25.

Author contribution Conceptualisation: KK and A-NL; analyses—original drawings: KK and A-NL; digital inkings: KK; visualisations: KK; writing—original draft preparation: KK; review and editing: KK and A-NL; supervision: A-NL.

All authors have read and agreed to the published version of the manuscript.

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Chapter 5 Discussion

5.1. Restatement of objectives

This thesis aims to advance understanding of deep-sea benthic ecosystems by addressing critical knowledge gaps related to the distribution, abundance, community composition, and environmental drivers of benthic fauna, with a particular focus on amphipods. Benthic organisms play a central role in marine ecosystem functioning through their contributions to food-web dynamics and to nutrient cycling across depth gradients. Despite their ecological importance, deep-sea benthic communities remain poorly understood, which limits our ability to accurately characterise present-day biodiversity patterns and assess how these ecosystems may respond to ongoing and future environmental change.

To address these challenges and advance understanding of benthic deep-sea fauna, this thesis applies multivariate spatial analyses, species distribution modelling, and integrative taxonomic approaches. Specifically, it aims to characterise spatial patterns in the distribution and abundance of mega- and macro-benthic communities and evaluate the environmental conditions shaping these patterns. Additionally, it investigates the present-day distribution of amphipods and assesses potential shifts in their suitable habitat under medium- and long-term future scenarios. Finally, this thesis investigates species diversity within the widely distributed amphipod genus *Epimeria* through integrative taxonomy. It evaluates newly collected specimens associated with cold-water corals and describes species new to science. By combining ecological analyses with detailed taxonomic research, this work provides a robust framework for improving baseline knowledge of deep-sea benthic biodiversity and for supporting future research, monitoring, and conservation efforts in data-limited marine environments.

This section, contains a synthesis and discussion of the broader findings of this thesis, outline methodological reflections, and indicate the wider implications of this research and further avenues for future exploration.

5.2. Environmental drivers in the deep sea

Marine environmental conditions have been shown to influence benthic fauna diversity, abundance, richness, community composition, and spatial distribution (e.g. Lörz et al., 2021; Saeedi et al., 2022). Different species can exhibit distinct preferences for environmental conditions and vary in the range of conditions they can tolerate without adverse effects,

defining their environmental niche breadth. It is hypothesised that species with a broader niche breadth have wider distributions and can tolerate a greater variety of habitat types, whereas species with narrower niche breadths are restricted to specific conditions and locations (Brown, 1984; Lörz et al., 2022). Tolerance to environmental conditions underpins large-scale patterns of overall abundance, richness, and diversity, as well as species-level geographical distributions.

Depth is widely used to analyse and predict distribution patterns of benthic fauna (e.g. Brix et al., 2018b; Taranto et al., 2023; van der Grient and Rogers, 2021). Yet depth more likely represents an integrative proxy for a suite of environmental variables that change with increasing depth, for example pressure (Elith, 2017). Across many benthic taxa, depth has emerged as a predictor variable of species distributions, as shown for amphipods (e.g. Brix et al., 2018a), corals (e.g. Taranto et al., 2023), and polychaetes (van der Grient and Rogers, 2021). In this thesis, depth was also considered a potential driver of the community composition of benthic macro- and megafauna at the phylum level (Kürzel et al., 2023; Chapter 2). Species richness and abundance appear to generally decline with depth, a pattern that has been attributed largely to the reduction in particulate organic carbon flux to the seafloor and the increasing distance from productive coastal and surface waters (Rex et al., 2005). For example, richness in Tanaidacea has been shown to decrease with depth in sub-Arctic regions (Kamila et al., 2025). A similar pattern was observed in this thesis (Kürzel et al., 2023; Chapter 2), where the abundance of benthic macro- and megafauna generally declined with depth across most regions. However, this chapter also revealed contrasting patterns in certain areas, such as the Southern Ocean, where abundance was highest at upper slope stations. Depth itself is unlikely to be the direct causal factor underlying these patterns, as it is often strongly correlated with other environmental variables. This intercorrelation can justify excluding depth from certain analyses, as in Kürzel et al. (2025; Chapter 3), to reduce redundancy and improve model interpretability.

Temperature is also frequently proposed to shape distribution patterns and has been a central focus of marine research until today (e.g. Danovaro et al., 2004; Tittensor et al., 2010). It has been suggested that the relationship between temperature and diversity is unimodal, with a peak at approximately 5–10 °C (Yasuhara and Danovaro, 2016). This view arises from the fact that some studies report increasing diversity with increasing temperature, whereas others document the opposite pattern (Yasuhara and Danovaro, 2016). Studies reporting negative relationships appeared to originate more often from warmer regions, while those showing positive relationships are more frequently from colder environments, thereby likely supporting the idea of a temperature–diversity peak (Yasuhara

and Danovaro, 2016). Deep-sea organisms may also be particularly sensitive to even small thermal shifts, and more generally to subtle environmental change, because deep-sea conditions are comparatively stable. For example, Danovaro et al. (2004) found that even a small decrease in temperature resulted in a notable decline in nematode abundance. Nevertheless, the precise role of temperature in structuring benthic communities remains uncertain, and temperature did not emerge as a major factor shaping community composition at phylum or multitaxon level in the North Atlantic (Kürzel et al., 2023; Chapter 2).

Food availability is also considered an important driver of deep-sea communities (Kaiser et al., 2023; Kröncke et al., 2013; Kröncke and Türkay, 2003; McClain, 2004), and emerged as a key factor structuring community composition at the phylum and multitaxon level in this thesis (Kürzel et al., 2023; Chapter 2). In the deeper ocean, food supply largely depends on the downward flux of organic matter produced in surface (Carney, 2005; Maier et al., 2023; McClain, 2004). Consequently, variables such as chlorophyll concentration, phytoplankton biomass, primary production, and particulate organic carbon are commonly used as proxies for food availability in deep-sea studies (e.g. Di Franco et al., 2021; Levin et al., 2001; Lins et al., 2014). Lower fluxes of organic material are likely to sustain less faunal biomass and abundance, and therefore regions with limited food supply such as deeper waters or areas far from continental margins are likely to support sparser benthic communities. For instance, Kaiser et al. (2023) suggested that differences in macrofaunal densities among ocean basins were likely driven by variation in food availability, although community composition itself appeared comparatively unaffected. Similarly, Degen et al. (2015) concluded that particulate organic carbon flux was a major factor structuring benthic communities in the Arctic Ocean.

In this thesis, silicate and iron were shown to have a strong influence on the composition of benthic macro- and megafaunal communities (Kürzel et al., 2023; Chapter 2). Nutrients such as silicate, iron, nitrate and phosphate may influence benthic communities directly, as organisms require them for essential metabolic and structural processes (e.g. Saeedi et al., 2022), and indirectly, because they can regulate food production in surface waters (e.g. Street and Paytan, 2005). A likely example of a direct effect was reported by Saeedi et al. (2022), who found that silicate likely played an important role in shaping sponge communities, as it was suggested many sponges use amorphous silica to construct their skeletons. Indirect effects can arise through nutrient limitation of phytoplankton, which contributes substantially to the particulate organic matter that sinks to the deep sea. Iron, for instance, is required for chlorophyll synthesis and photosynthesis. When iron is scarce,

phytoplankton growth can be reduced, ultimately decreasing the amount of organic material reaching the seafloor (Street and Paytan, 2005).

Beyond nutrients and food supply, oxygen availability is a key environmental factor shaping deep-sea benthic communities, as low-oxygen conditions are generally associated with reduced species diversity (Grassle et al., 1990) and have been shown to likely influence community composition at the phylum level in this thesis (Kürzel et al., 2023; Chapter 2). Oxygen minimum zones (OMZs), typically defined as regions where dissolved oxygen concentrations fall below approximately 20 μM (Paulmier and Ruiz-Pino, 2009), often support reduced abundances across most benthic taxa. Nevertheless, some species persist under these conditions through specific physiological or morphological adaptations, such as smaller body size or enlarged respiratory structures that enhance oxygen uptake efficiency (Gooday et al., 2009). Patterns of species richness also appear to respond strongly to oxygen availability. Levin and Gage (1998) reported lower macrofaunal richness within OMZs compared with adjacent, better-oxygenated habitats. Their results further suggested taxon-specific sensitivities, with polychaetes showing comparatively high tolerance, whereas crustaceans and molluscs were more strongly affected and were, in some cases, nearly absent under severe hypoxia.

5.3. Biogeographical patterns and areas of interest

Differences in environmental variables likely influence the distribution of benthic fauna, resulting in biogeographical patterns across the Atlantic. In the multivariate analysis of benthic abundance data in Kürzel et al. (2023; Chapter 2), greater abundances were found in higher latitudes, contrasting with other studies that suggested negative correlations between latitude and abundance (Bodil et al., 2011), or no latitudinal gradient at all (Griffiths et al., 2008). Although benthic density generally decreased with increasing depth across most regions, this pattern differed in the Southern Ocean, where the highest abundances were observed on the upper slope rather than at the shallowest shelf station. As only one comparable shelf station was available in the other study regions, this pattern represents a potentially important observation that warrants further investigation in future studies. At a multi-taxon level, broad similarities in community composition were generally identified across the Atlantic, with some differences in shallow depths of the Southern Ocean, attributable to increased eurybathy in Antarctic benthic marine fauna (Brey et al., 1996). While only limited differences in community composition at higher taxonomic levels were identified in this study, stronger spatial and depth-related patterns would be expected at finer

taxonomic resolution, such as the species level. Consequently, this study provides a robust foundation for future research exploring biogeographical patterns using higher taxonomic resolution.

Kürzel et al. (2025; Chapter 3) expands and focuses the multivariate analysis Kürzel et al. (2023; Chapter 2), investigating the distribution of amphipods at a species-level within the North Atlantic using species distribution modelling. A baseline model of amphipod distribution at species-level was produced, to enable an assessment and prediction of change. These models found that, with the exception of the deepest regions, most areas of the North Atlantic were suitable for at least one species of amphipod, and most areas south of the Arctic Circle hosted six or more species. However, whilst the samples which composed the models largely came from the Norwegian continental shelf, models outlined the GIF Ridge to be suitable for the greatest number of species; and additionally, the extension of the ridge to Scotland. The distribution results were also varying for species of the same family in line with Lörz et al. (2022) et al who observed a similar pattern of niche breath analyses of amphipods.

The findings of Kürzel et al. (2025; Chapter 3) provide further evidence towards the regional importance of the GIF Ridge for benthic fauna. Previous studies on benthic fauna have already identified the GIF Ridge as important (e.g. Brix and Svavarsson, 2010; Lörz et al., 2021), given its role as a hydrographical and geomorphological breakpoint that separates colder and fresher Nordic Seas from the warmer, more saline North Atlantic (Hansen and Østerhus, 2000; Jöst et al., 2019). This creates unique environmental conditions which host distinctive, and specialised benthic fauna (Brix and Svavarsson, 2010; Jöst et al., 2019; Pampoulie et al., 2024; Weissappel, 2000). For example, previous studies of amphipods around Iceland have identified clear faunal differences between deep-north, deep-south, and ridge-associated communities (Lörz et al., 2021). The high habitat suitability of the GIF ridge, as well as the adjacent continental shelves, indicate favourable environmental conditions within the transition between water masses, whilst the differences in species habitat suitability north and south of the GIF ridge region indicated its potential role as a biogeographical barrier. This is corroborated by earlier research on Crustacea, where sampling by the GIF ridge outlined differing diversity patterns north and south of the ridge, with statistical analysis outlining salinity as the most important variable in explaining this (Weissappel and Svavarsson, 1998). The species distribution modelling presented in Kürzel et al. (2025; Chapter 3) corroborates this, providing further support towards the species richness of the region and the biogeographical role the ridge plays.

The SDMs in Kürzel et al. (2025; Chapter 3) also highlight that the Reykjanes Ridge indicates greater numbers of species compared to the surrounding area, thus outlining this as an area of particular interest for amphipods and benthic faunal biodiversity more widely. The complex topography of the Reykjanes Ridge guides submarine currents, creating hydrographical fronts that impact environmental conditions and produce distinctive environmental niches (Bober et al., 2018; Schmidt et al., 2024). Additionally, the presence of hydrothermal vents on the Reykjanes Ridge produces a unique, energy-rich ecosystem, although initial studies have outlined that the region does not contain chemosynthetic endemic taxa characteristic of vent systems more generally, but rather opportunistic species capable of utilising the environment (Taylor et al., 2021). The species distribution models presented as part of Kürzel et al. (2025; Chapter 3) support the uniqueness of this ecosystem and how it therefore supports faunal diversity, with models indicating that the Reykjanes Ridge provides the strongest probability of habitat support for some species.

5.4. Habitat associations and cold-water coral ecosystems

In addition to the identification of baseline biogeographical patterns, this thesis also identifies habitat associations of amphipods. Cold-water corals have long been recognised as biodiversity hotspots (e.g. Ashford et al., 2019). While associations between cold-water corals and various crustacean taxa have been well documented (e.g. Lörz and Tandberg, 2025; Roberts et al., 2006; Schwentner and Lörz, 2021), the widely distributed amphipod genus *Epimeria* had so far only been assumed to be associated with these habitats. Kürzel and Lörz (2026; Chapter 4) provides direct visual evidence of *Epimeria* occurring in association with cold-water corals at two geographically distant locations: in the Atlantic Ocean around Iceland and in the Pacific Ocean around New Zealand. This represents a significant contribution to our understanding of the ecology and lifestyle of *Epimeria* in the deep sea, where direct observations are rare due to the inaccessibility of the habitat.

Although many modern deep-sea expeditions are equipped with cameras and video systems, smaller organisms such as *Epimeria* are still frequently overlooked, as their detection requires additional time and targeted zooming on specific structures such as corals. It is therefore particularly noteworthy that Kürzel and Lörz (2026; Chapter 4) documents this association across multiple *Epimeria* species, several individual specimens, and two highly distinct geographical regions. This suggests that the observed association is not incidental but represents a common ecological relationship.

Future research should aim to investigate whether *Epimeria* use cold-water corals primarily as habitat and refuge from predators, or whether corals also function as hunting grounds. Species of *Epimeria* have previously been suggested to include micropredatory taxa (Dauby et al., 2001). By increasing habitat heterogeneity, cold-water corals may support presence of prey species, thereby indirectly facilitating foraging opportunities for *Epimeria*. Targeted video observations would be valuable to test this hypothesis. The photographic evidence presented in Kürzel and Lörz (2026; Chapter 4) strengthens the rationale for investing additional resources, such as increased ROV time and funding, to further investigate these ecological interactions.

5.5. Climate change

Climate change is expected to impact deep-sea ecosystems by altering environmental conditions, likely driving distributional shifts in fauna (Rakka et al., 2025), affect metabolic processes and potentially leading to extinctions (Duarte, 1991; Sweetman et al., 2017). Rising atmospheric CO₂ concentrations lead to global warming, with the oceans absorbing much of this excess heat, resulting in increases in ocean temperature (Levitus et al., 2000). Warming is not confined to surface waters; projections indicate that heat will increasingly penetrate to the deep seafloor, with benthic systems in parts of the Atlantic expected to experience temperature increases of approximately 1–4°C over the coming decades (Sweetman et al., 2017). In addition, climate-driven oceanographic changes are promoting “Atlantification”, whereby Arctic and subpolar waters become more similar to Atlantic waters in environmental conditions such as salinity (Ingvaldsen et al., 2021). These changes consequently likely produce a wide range of complex effects that will vary across geographical space, bathymetry, and time, affecting environmental conditions including oxygen, nutrients, and food availability, amongst other attributes. This is likely to affect benthic fauna abundance, composition and distribution (Kürzel et al., 2023 (Chapter 2), Kürzel et al., 2025 (0)).

One example of an effect that climate change is expected to have is on particulate organic carbon (POC) flux, which is largely derived from surface primary production (Smith et al., 2009). In most regions, both the quantity and quality of material reaching the deep sea are likely to decline (Sweetman et al., 2017). Reductions in surface primary productivity of up to approximately 40% have been estimated (Jones et al., 2014). The reduced quantity and nutritional value of POC reaching the seafloor reduces deep-sea food availability and contributes to decreased biodiversity and smaller body sizes among benthic organisms

(Ehrnsten et al., 2020). However, in some high-latitude regions, the quantity of POC reaching the seafloor may increase. Increased glacial melt may deliver nutrient-rich freshwater containing iron, nitrate, and phosphate, enhancing surface productivity (Hopwood et al., 2020; Pan et al., 2025).

Increasing stratification in a warming ocean further impacts food availability in the benthic deep sea, limiting vertical mixing and restricting the resupply of nutrients to surface waters (Sweetman et al., 2017). This impacts surface productivity, with phytoplankton community structure likely shifting from larger, fast-sinking diatoms to smaller cells that sink more slowly and are more readily consumed in the upper water column (e.g. Feng et al., 2021; Fu et al., 2016; Lee et al., 2025). Less organic matter reaching the seafloor thus impacts the food availability for benthic fauna, and a reduction in nutritional quality (Ehrnsten et al., 2020; Sweetman et al., 2017). Consistent with these mechanisms, results from the present study indicate that food availability plays a key role in shaping benthic community composition at both the phylum and multitaxon levels, and is likely to be an important driver of amphipod distribution patterns (Kürzel et al., 2023 (Chapter 2), Kürzel et al., 2025 (0)).

In warmer waters, decreases in vertical mixing and lower oxygen solubility are expected to reduce oceanic oxygen levels more generally (Keeling et al., 2010; Long et al., 2016). Evidence for this trend is already apparent in the North Atlantic (Stendardo et al., 2015), and projections indicate that bottom-water oxygen concentrations may decline by approximately 0.03–0.05 mL L⁻¹ by 2100 (Sweetman et al., 2017). Declining oxygen availability is likely to have significant consequences for benthic fauna. Oxygen availability has been shown to influence benthic community composition, and to affect amphipod distribution as demonstrated in this thesis (Kürzel et al., 2023 (Chapter 2), Kürzel et al., 2025 (0)). More broadly, hypoxic conditions are associated with reduced biodiversity, as many benthic species are highly sensitive to low oxygen concentrations. This is consistent with the wider research literature. For example, octocoral abundance has been shown to decrease in areas with reduced oxygen (Buhl-Mortensen et al., 2010; Etnoyer and Morgan, 2005; Roberts et al., 2009). A decline in coral cover also reduces the availability of hard substrate, which provides critical habitat and structural complexity, thereby further diminishing overall benthic biodiversity. However, this trend is not globally or temporally ubiquitous. In the short-term within the Atlantic, climate change is projected to weaken the Atlantic Meridional Overturning Circulation (AMOC), which may lead to temporarily lower oxygen levels at the deep seafloor (Schmittner et al., 2007). However, over longer timescales, enhanced convection of Antarctic Bottom Water may increase oxygenation again (Yamamoto et al., 2015).

The increasing uptake of atmospheric CO₂ under climate change by the oceans leads to ocean acidification, as the formation of additional carbonic acid lowers seawater pH (Levitus et al., 2000; Mora et al., 2013; Roemmich et al., 2015). Although research is ongoing and many uncertainties remain, ocean acidification is anticipated to have widespread biological consequences across marine taxa. For example, declines in pH may hinder the calcification processes that many organisms rely upon to build and maintain external shells or exoskeletons (e.g. Gattuso et al., 1998; Gazeau et al., 2007; Ross et al., 2016; Waldbusser et al., 2011), affecting many cnidarians, echinoderms, and molluscs, among other organisms. In bivalves, Waldbusser et al. (2011) reported reduced calcification rates with ocean acidification, potentially resulting in weaker shells and greater vulnerability to predation (Sweetman et al., 2017). Additionally, many species appear to have a limited physiological capacity to buffer against increasing acidity (e.g. Dupont et al., 2010; Fabry et al., 2008; Melzner et al., 2009).

5.6. Future shifts

The establishment of present-day distributions and environmental preferences of benthic fauna, particularly amphipods, provides a baseline for understanding their ecology. Combined with knowledge of how environmental variables may change under climate change, this allows us to model and predict future biogeographical shifts and changes. Kürzel et al. (2025; Chapter 3) reveals heterogeneous responses to environmental change under different possible emission scenarios. In contrast to some studies that project more uniform long-term declines in benthic fauna with climate change (e.g. Sandulli et al., 2021; Weinert et al., 2021), many species of amphipod are suggested to increase in habitat area under many climate scenarios, echoing findings found in other taxa (González et al., 2024; Liu et al., 2022; Principe et al., 2021).

Some of the future change patterns identified across species reflect those found or hypothesised elsewhere within other species in the research literature. For example, a latitudinal shift towards the poles has long been theorised and predicted for many species (e.g. Hastings et al., 2020; Jones and Cheung, 2014; Simões et al., 2021), as increases in ocean temperatures globally with climate change lead to species migration towards regions that meet their thermal niche. However, other patterns are less well understood, including the shift of amphipod species towards the continental margins of Greenland. The move towards these margins, and potentially more shallower waters, can be hypothesised to be related to the ongoing thinning and melting of the Greenland Ice Sheet (GrIS; Rignot et al.,

2008; Rignot et al., 2011). Glacial meltwaters are not saline, and are rich in nutrients including nitrogen (Wadham et al., 2016), phosphate (Hawkings et al., 2016), and iron (Bhatia et al., 2013; Hendry et al., 2019). The incursion of these meltwaters into the marine realm could thus impact localised food and nutrient availability, and could thus increase habitat suitability. These patterns of migration and expansion in habitat area may warrant some amphipod species to be considered as invasive, with consequences on ecosystem dynamics, including the loss of diversity within the amphipod taxa, or in other benthic fauna.

5.7. Direct anthropogenic impacts

Deep sea mining has been suggested to impact benthic fauna communities (Glover and Smith, 2003; Stewart et al., 2025), with multiple regions of the Atlantic have been designated as deep-sea mining exploration zones (Magali and Sandrine, 2019). Deep-sea mining involves the extraction of mineral resources, such as copper, from the deep ocean using large-scale machinery that can disturb the seafloor and resuspend sediment, with the potential to significantly impact benthic fauna (Folkersen et al., 2019; Paulus, 2021). One major impact results from the tracks left by mining vehicles, which can crush organisms, particularly affecting sessile taxa such as sponges (Vonnahme et al., 2020). In addition, mining activities generate sediment plumes composed of resuspended sediments and metals that can spread beyond the mined area and smother benthic communities (Cordes et al., 2016). Observed ecological effects include a reduction in benthic species richness of up to 32% in mined areas (Stewart et al., 2025), along with notable declines in diversity and abundance (Vonnahme et al., 2020; Yao et al., 2025). Although recent advances in mining technology may reduce disturbance, for example by limiting sediment resuspension compared to earlier expectations (Gazis et al., 2025; Ingels et al., 2026), careful evaluation is still required to accurately assess the severity of this threat to deep-sea ecosystems.

Another direct threat to deep-sea fauna arises from deep-sea fishing, which can cause substantial physical destruction through trawling and results in killing of non-target taxa. Impacts can occur through direct contact with fishing equipment and through sediment clouds generated by trawling that can suffocate benthic organisms (Clark et al., 2016). These disturbances are likely to lead to reduced abundance, biodiversity, and spatial distribution of benthic invertebrates (Clark et al., 2016). As fish stocks in shallower waters have become increasingly exploited, fishing activities have progressively expanded into deeper environments (Koslow et al., 2000), a trend that is likely to continue in the future. Whilst not directly assessed within this thesis, the impact of deep-sea mining and fisheries

on amphipods requires consideration in future studies, for its potentially destructive and uncertain impact on benthic faunal interactions with their habitat.

5.8. Integrative taxonomy

While recent years have seen an increasing emphasis on high-throughput and molecular approaches, Kürzel and Lörz (2026; Chapter 4) highlights the continued importance of a robust taxonomic framework that integrates traditional taxonomy, including morphological identification keys, alongside genetic analyses. Taxonomic keys remain a valuable tool for species identification, although their effectiveness strongly depends on their design. To maximise their utility, it is essential to carefully select diagnostic characters that are both reliable and practical, and to consider the taxa and contexts in which the keys are intended to be used.

For *Epimeria* species from the Atlantic and Pacific Oceans, the identification keys developed in Kürzel and Lörz (2026; Chapter 4) rely on robust morphological characters that are less to be damaged, such as the presence of lateral spines and the shape of the rostrum. These characters can largely be assessed without dissecting specimens, which greatly enhances the applicability of the keys. In contrast, species from other genera may be more difficult to distinguish morphologically, as diagnostic differences can be subtle (e.g. variation in setae), easily broken, or require dissection, or a combination of these factors. In such cases, genetic analyses may represent a more reliable approach for species identification, underscoring the importance of the molecular component within integrative taxonomy.

Additionally, taxonomic keys developed at a regional scale are often more accessible and efficient, as they include fewer species and reduce the likelihood of misidentification. However, regional keys are based on the assumption that faunal assemblages are geographically restricted. This assumption is typically supported by differences in environmental conditions or the presence of topographic barriers, such as the Mid-Atlantic Ridge, which may limit faunal exchange (e.g. Brix and Svavarsson, 2010; Riehl et al., 2018). Nevertheless, the degree to which such features function as strict barriers has been questioned, as fracture zones may instead facilitate dispersal (e.g. Brandt et al., 2018; Vecchione et al., 2010). This raises the possibility that some species may appear regionally restricted due to limited and uneven sampling in the deep sea. In the case of *Epimeria*, however, there is strong evidence for high levels of endemism in Antarctica, where the genus reaches its highest documented richness (d'Udekem d'Acoz and Verheye, 2017).

Until it is demonstrated that these species occur more broadly, the use of regional identification keys remains a pragmatic and efficient approach that balances taxonomic accuracy with practical constraints.

Whilst this study emphasises the importance of taxonomy, through the publication of taxonomic keys, as valuable towards species identification, there is much further work to be done considering the potentially high number of undescribed species, even in regions that are relatively well sampled and surveyed. Arfianti et al. (2018) outlines that there are over 9,000 species, over 1,600 genera, and over 220 families of amphipods. Yet at the time of their analysis, 20% of these had only been discovered within the last decade, and that modelling indicates that a third of amphipod species are likely to remain to be discovered. The discovery of two new *Epimeria* species in Kürzel and Lörz (2026; Chapter 4) contributes directly towards closing this discovery gap. The finding of new species in cold-water coral assemblages from two geographically distant regions reinforces the view that amphipods are among the least well-catalogued macrofaunal groups (Arfianti et al., 2018). Focusing on specific habitat types, such as coral reefs as per Kürzel and Lörz (2026; Chapter 4), may be particularly effective for the discovery of additional species.

Even among the described amphipod species, true diversity may be obscured by an over-reliance on genetic methods, misidentification and by the absence of integrative taxonomic approaches. The study of Hupalo et al. (2023) on *Echinogammarus sicilianus* Karaman and Tibaldi, 1973 provides one example where DNA barcoding using a COI marker alone results in overestimations of diversity. They identified that using double digest restriction site-associated DNA sequencing and information of mate choice supported far fewer lineages than the COI data suggested. Conversely, similar COI or the sparsity of reference library data could incorrectly combine distinct species, leading to the under-detection of true diversity. For example, the marine amphipod *Caprella penantis* Leach, 1814 had been treated previously as a single species. However, a more integrative approach combining genetics and taxonomy outlined that this encompassed multiple distinct species, leading to the illusion of a single, widespread species as opposed to the true number of species (Cabezas et al., 2022). Kürzel and Lörz (2026; Chapter 4) illustrates the importance of integrative taxonomy alongside well-practiced genetic techniques for identification of new species. By coupling morphological analyses with COI barcoding, new species are described and comprehensive species-level information is generated. This enables species to be identified both morphologically and genetically and facilitates their inclusion in a diverse range of future studies.

The identification of true species diversity through accurate description is critical, considering how inaccuracies are propagated through the research literature which may presume that species are described correctly. The availability of data on amphipods and other benthic species, through open-source platforms such as Ocean Biogeographic Information System (OBIS) and other derivatives, makes the accuracy of species description especially important, considering how these data are used by other researchers, including those who are not trained or well versed in the complications of species identification.

The combination of available open-access data with the development of increases in computation power has expanded the possibilities of modelling studies. Whilst the use of open-source data from OBIS, Bio-ORACLE and other related sources are not novel per se, the use of species distribution modelling is comparatively limited in deep-sea studies. This thesis addresses this gap by demonstrating how the processing and modelling of open-source datasets can generate new insights into amphipods and other benthic taxa. Kürzel et al. (2023; Chapter 2) shows how open-source environmental data can be combined with occurrence records to examine how faunal patterns are shaped by environmental conditions. Kürzel et al. (2025; Chapter 3) demonstrates how open-source data occurrence, together with modelled environmental data, can be used to forecast and predict change in species distribution. Lastly, Kürzel and Lörz (2026; Chapter 4) demonstrates how primary taxonomic work, including new species descriptions, extension of keys, and critical analyses of previous descriptions, feed back into these open data sources, leading to the gradual closure of data gaps and enhance the value of species-level records for the broad plethora of modelling approaches.

These chapters demonstrate that taxonomy acts as a central enabler of deep-sea research, as opposed to a separate, isolated and solely descriptive discipline. Modern approaches, including DNA barcoding and genetic analyses, provide powerful tools for investigating benthic biodiversity. However, they must be interpreted within the framework of robust taxonomic studies, to ensure that genetic results are correctly interpreted. The combination of genetic research with taxonomy fundamentally underpins species-level modelling and ecological analyses. This, in turn, enables the assessment of amphipod distributional and diversity responses to future environmental change.

5.9. Modelling

The accurate identification of species enables species distribution modelling, allowing researchers to predict and estimate benthic fauna distributions more widely. Kürzel et al. (2025; Chapter 3) applies one of the most widely used species distribution modelling algorithms, MaxEnt, which is known to produce robust results. This algorithm has demonstrated strong performance across a range of applications, including studies with comparable methodological frameworks, such as the modelling of vulnerable marine ecosystems in the North Atlantic. Given the wide range of available algorithms, each with distinct strengths and limitations, future studies could benefit from comparing the results of Kürzel et al. (2025; Chapter 3) with those generated by alternative modelling approaches to assess potential differences in predictions. Similarly, the use of the Area Under the Curve (AUC) as an evaluation metric is a common and well-established practice in species distribution modelling (e.g. Liu et al., 2022; Phillips et al., 2006; Zhang et al., 2019). However, additional evaluation metrics, such as the Boyce index, are also frequently applied (e.g. Lazagabaster et al., 2024; Liu et al., 2025) and could be incorporated to provide a broader basis for model comparison and to further assess model performance.

Modelling inherently involves a number of assumptions and limitations, many of which are directly linked to the data used. The environmental variables applied Kürzel et al. (2025; Chapter 3) are derived from modelled datasets provided by BIO-ORACLE, which have a spatial resolution of 0.5°. While this resolution may be insufficient to capture fine-scale environmental heterogeneity, these datasets are widely used in ecological and biogeographical research (e.g. Liu et al., 2022; Xu et al., 2022; Zhang et al., 2019). In situ environmental measurements would undoubtedly provide higher accuracy; however, such data are often unavailable, particularly for deep-sea habitats, as parameters such as nutrient concentrations are rarely recorded during specimen collection. Additionally, environmental data with higher temporal resolution would allow seasonal variability to be assessed. Although deep-sea environments were previously assumed to be relatively environmentally stable, evidence suggests that seasonal dynamics can influence deep-sea conditions (Hartman et al., 2021). Despite these limitations, the use of modelled environmental data currently represents the most practical and comprehensive option, as direct measurements are either extremely sparse or incomplete. Consequently, these datasets enable baseline ecological assessments in habitats where sampling is logistically challenging, and where studies of this kind would otherwise be difficult or impossible to conduct.

This thesis demonstrates the fundamental role of species distribution data as the foundation for a wide range of downstream ecological and biogeographical research. Species that have

not yet been formally described cannot be included in distribution modelling, nor can they be considered in conservation planning or management strategies. This limitation is closely linked to the extensive backlog of unanalysed samples from past deep-sea expeditions, which likely contain both undescribed species and valuable, underutilised information on species occurrence and habitat conditions. Analysing these samples requires targeted funding, particularly to support taxonomic expertise. Such efforts would enable the description of new species, the addition of verified occurrence records, and improved characterisation of the environmental conditions under which species occur. Incorporating these data would ultimately lead to more robust species distribution models and a stronger taxonomic framework.

Closely related to this issue is the importance of publicly accessible biodiversity data. While there has been a growing push towards open-access publication of both research outputs and associated datasets, a substantial proportion of biodiversity data likely remains difficult to locate or inaccessible. This may be due to data being retained privately by researchers or dispersed across individual publications without centralised archiving. Open-access databases such as the OBIS provide a powerful platform for data synthesis; however, their effectiveness depends on the extent to which researchers contribute data and adhere to standardised reporting practices. As demonstrated in Kürzel et al. (2025; Chapter 3), openly accessible data from such repositories can be used effectively to generate new insights without the immediate need for additional sampling in some cases. Nevertheless, the data-cleaning process required for model development revealed significant data limitations, including records with incorrect coordinates or missing important metadata such as depth. These issues highlight the need not only for open data sharing, but also for improved data quality control and standardisation to maximise the utility of existing biodiversity datasets.

5.10. Concluding remarks

Given the multiple and increasing threats to deep-sea ecosystems, establishing robust baseline knowledge of benthic fauna is essential for effective management and conservation. Accurate species descriptions and reliable taxonomic identification form a critical foundation, as they determine which species are present, how they are distributed, and how communities are structured. Together, baseline studies provide the reference framework needed to assess future change, evaluate anthropogenic impacts, and design appropriate mitigation measures. In this context, species distribution models offer a valuable

tool for synthesising available data and identifying areas of potential ecological importance (e.g. the GIF Ridge), particularly in regions where direct sampling remains limited.

Chapter 6 References

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Chapter 7 Acknowledgements

I would like to sincerely thank my supervisors, Dr. Anne-Nina Lörz and Prof. Dr. Saskia Brix. Both introduced me to deep-sea biology, and my participation in the IceAGE 3 cruise, facilitated by Saskia, was a defining moment in shaping my scientific interests.

Anne-Nina, thank you for introducing me to the wonderful world of amphipods, for showing me all the beautiful live specimens to photograph during the IceAGE 3 cruise, and for sharing your knowledge of their taxonomy and biology. This undoubtedly had a profound influence on the direction and subject of my PhD. I am especially grateful for your constant support, including your encouragement of my sometimes rather unconventional way of conducting my PhD.

I would also like to thank Dr. Katrin Linse for sharing her knowledge on deep-sea benthos and for her support in analysing samples. My sincere thanks go to Dr. Martin Schwentner for his guidance and expertise in all matters related to genetic work, and to Dr. James Taylor for his statistical advice.

I am very grateful to the wonderful team at DZMB for their continuous kindness and support, from locating specimens to retrieving sampling information. A special thank you to Nicole Gatzemeier for giving me confidence in laboratory work and for always keeping track of things, especially when I occasionally did not.

I would like to thank my family for making this endeavour possible and for their unwavering support throughout this journey. To my friends, thank you for always having an open ear, even when my research topics often have sounded somewhat unfamiliar. I also thank Andrew Kiio and the Sheldrick Wildlife Trust, who, while working in a very different field, have always been a source of motivation through their passion for wildlife and conservation.

Finally, I am deeply grateful to my partner Craig. Thank you not only for your expertise and work as a co-author, but also for always standing by my side and taking on every challenge as if it were your own.

Chapter 8 Appendix

8.1. Supplementary information: Species distribution modelling of benthic amphipod crustaceans in the deep North Atlantic under climate change

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Figure S2: Maps show the habitat suitability of *Harpinia laevis* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S3: Maps show the habitat suitability of *Amphilocheus manudens* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S4: Maps show the habitat suitability of *Eriopisa elongata* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S5: Maps show the habitat suitability of *Melphidippa borealis* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S6: Maps show the habitat suitability of *Westwoodilla caecula* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S7: Maps show the habitat suitability of *Harpinia crenulata* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S8: Maps show the habitat suitability of *Laetmatophilus tuberculatus* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S9: Maps show the habitat suitability of *Harpinia plumosa* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S10: Maps show the habitat suitability of *Autonoe longipes* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S11: Maps show the habitat suitability of *Byblis crassicornis* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

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Figure S13: Maps show the habitat suitability of *Tmetonyx cicada* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f)

2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

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Figure S15: Maps show the habitat suitability of *Harpinia pectinata* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S16: Maps show the habitat suitability of *Leptophoxus falcatus*

for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S17: Maps show the habitat suitability of *Nototropis nordlandicus* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S18: Maps show the habitat suitability of *Neohela monstrosa* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S19: Maps show the habitat suitability of *Ampelisca eschrichtii* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S20: Maps show the habitat suitability of *Idunella aeqvicornis* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S21: Maps show the habitat suitability of *Harpinia abyssi* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S22: Maps show the habitat suitability of *Urothoe elegans* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S23: Maps show the habitat suitability of *Tryphosella horingi* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S24: Maps show the habitat suitability of *Arrhis phyllonyx* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S25: Maps show the habitat suitability of *Harpinia propinqua* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S26: Maps show the habitat suitability of *Unciola planipes* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S27: Maps show the habitat suitability of *Bathymedon longimanus* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP

scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S298: Maps show the habitat suitability of *Ampelisca macrocephala* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S29: Maps show the habitat suitability of *Themisto abyssorum* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S30: Maps show the habitat suitability of *Hippomedon propinquus* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S31: Maps show the habitat suitability of *Liljeborgia fissicornis* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S32: Maps show the habitat suitability of *Syrrhoe crenulata* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S33: Maps show the habitat suitability of *Hippomedon denticulatus* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S34: Maps show the habitat suitability of *Ampelisca aequicornis* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S35: Maps show the habitat suitability of *Tmetonyx similis* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S36: Maps show the habitat suitability of *Aceroides (Aceroides) latipes* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S37: Maps show the habitat suitability of *Harpinia mucronata* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S38: Maps show the habitat suitability of *Haploops tubicola* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S39: Maps show the habitat suitability of *Unciola leucopis* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S40: Maps show the habitat suitability of *Haploops setosa* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S41: Maps show the habitat suitability of *Bruzelia typica* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f)

2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S42: Maps show the habitat suitability of *Xenodice frauenfeldti* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S43: Maps show the habitat suitability of *Ischyrocerus megacheir* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S44: Maps show the habitat suitability of *Nicippe tumida* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S45: Maps show the habitat suitability of *Liljeborgia pallida* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S46: Maps show the habitat suitability of *Bathymedon saussurei* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S47: Maps show the habitat suitability of *Autonoe megacheir* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S48: Maps show the habitat suitability of *Halice abyssi* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S49: Maps show the habitat suitability of *Ampelisca odontoplax* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S50: Maps show the habitat suitability of *Medicorophium affine* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S51: Maps show the habitat suitability of *Ampelisca pusilla* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S52: Maps show the habitat suitability of *Oediceropsis brevicornis* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S53: Maps show the habitat suitability of *Paraphoxus oculatus* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S54: Maps show the habitat suitability of *Lysianassa plumosa* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Figure S55: Maps show the habitat suitability of *Byblis gaimardii* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f)

2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

Table S1. Table of Average AUC Scores per Species

Species	Avg AUC
<i>Ampelisca gibba</i>	0.93
<i>Harpinia laevis</i>	0.88
<i>Amphilochus manudens</i>	0.76
<i>Eriopisa elongata</i>	0.85
<i>Melphidippa borealis</i>	0.79
<i>Westwoodilla caecula</i>	0.86
<i>Harpinia crenulata</i>	0.81
<i>Laetmatophilus tuberculatus</i>	0.82
<i>Harpinia plumosa</i>	0.96
<i>Autonoe longipes</i>	0.88
<i>Byblis crassicornis</i>	0.88
<i>Harpinia antennaria</i>	0.85
<i>Tmetonyx cicada</i>	0.79
<i>Tryphosites longipes</i>	0.9
<i>Harpinia pectinata</i>	0.87
<i>Leptophoxus falcatus</i>	0.83

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<i>Nototropis nordlandicus</i>	0.81
<i>Neohela monstrosa</i>	0.8
<i>Ampelisca eschrichtii</i>	0.87
<i>Idunella aeqvicornis</i>	0.89
<i>Harpinia abyssi</i>	0.99
<i>Urothoe elegans</i>	0.9
<i>Tryphosella horingi</i>	0.74
<i>Arrhis phyllonyx</i>	0.88
<i>Harpinia propinqva</i>	0.92
<i>Unciola planipes</i>	0.86
<i>Bathymedon longimanus</i>	0.82
<i>Ampelisca macrocephala</i>	0.88
<i>Themisto abyssorum</i>	0.84
<i>Hippomedon propinqvus</i>	0.78
<i>Liljeborgia fissicornis</i>	0.72
<i>Syrrhoe crenulata</i>	0.82
<i>Hippomedon denticulatus</i>	0.86
<i>Ampelisca aequicornis</i>	0.82
<i>Tmetonyx similis</i>	0.74
<i>Aceroides (Aceroides) latipes</i>	0.97
<i>Harpinia mucronata</i>	0.89

<i>Haploops tubicola</i>	0.88
<i>Unciola leucopis</i>	0.89
<i>Haploops setosa</i>	0.78
<i>Bruzelia typica</i>	0.88
<i>Xenodice frauenfeldti</i>	0.86
<i>Ischyrocerus megacheir</i>	0.78
<i>Nicippe tumida</i>	0.84
<i>Liljeborgia pallida</i>	0.87
<i>Bathymedon saussurei</i>	0.77
<i>Autonoe megacheir</i>	0.9
<i>Halice abyssi</i>	0.76
<i>Ampelisca odontoplax</i>	0.87
<i>Medicorophium affine</i>	0.91
<i>Ampelisca pusilla</i>	0.91
<i>Oediceropsis brevicornis</i>	0.88
<i>Paraphoxus oculatus</i>	0.82
<i>Lysianassa plumosa</i>	0.92
<i>Byblis gaimardii</i>	0.89

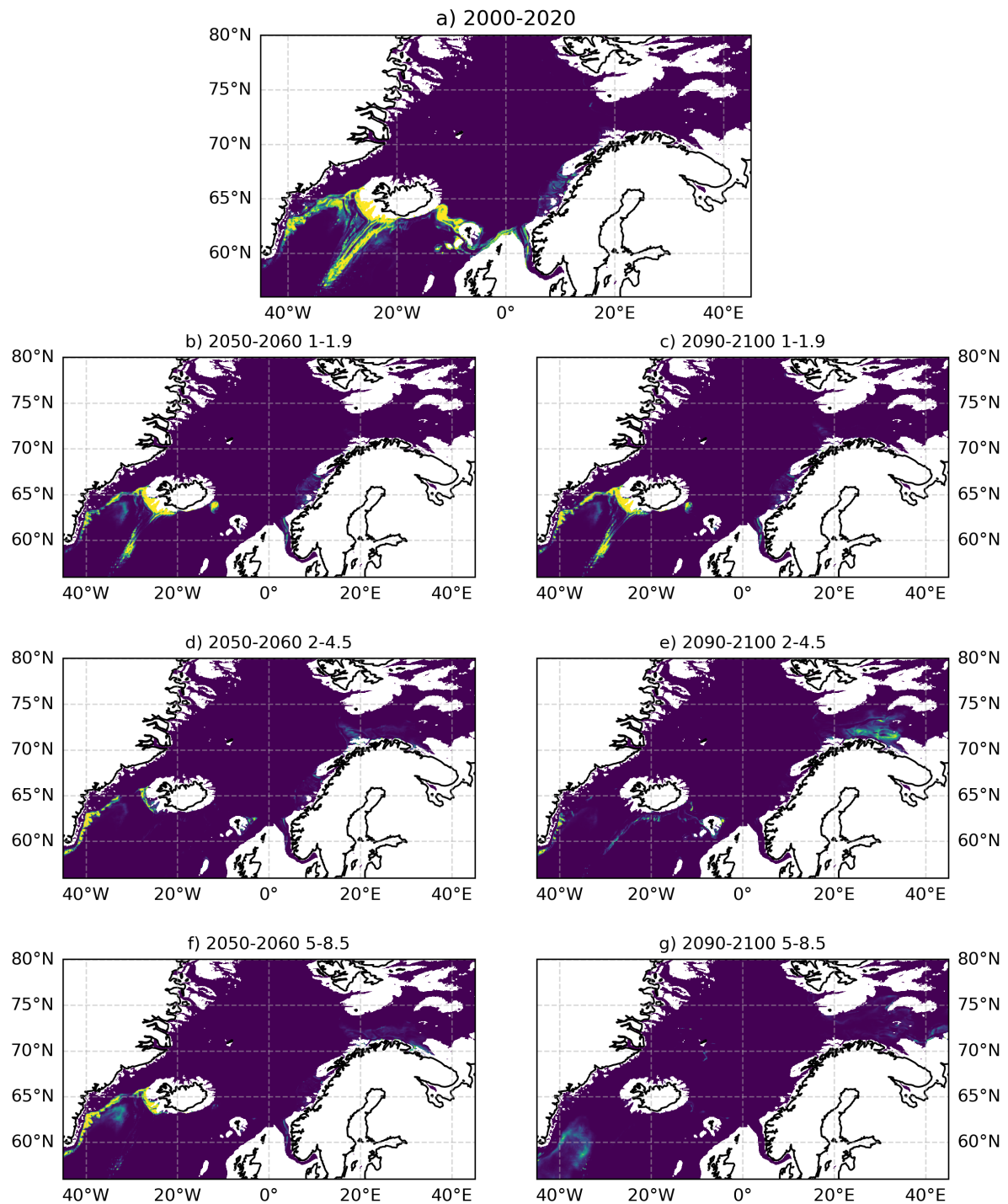
Ampelisca gibba

Figure S1: Maps show the habitat suitability of *Ampelisca gibba* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

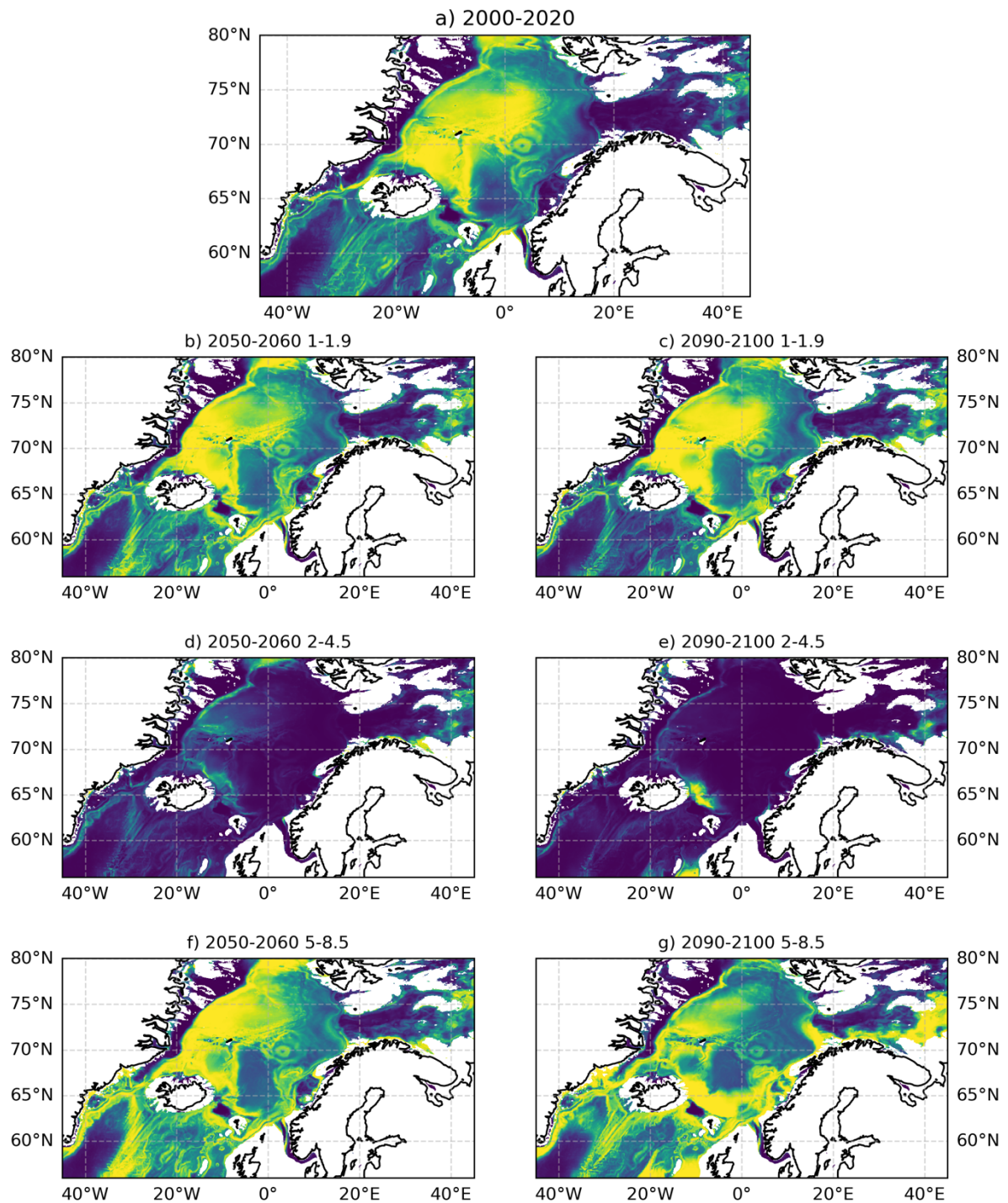
Harpinia laevis

Figure S2: Maps show the habitat suitability of *Harpinia laevis* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

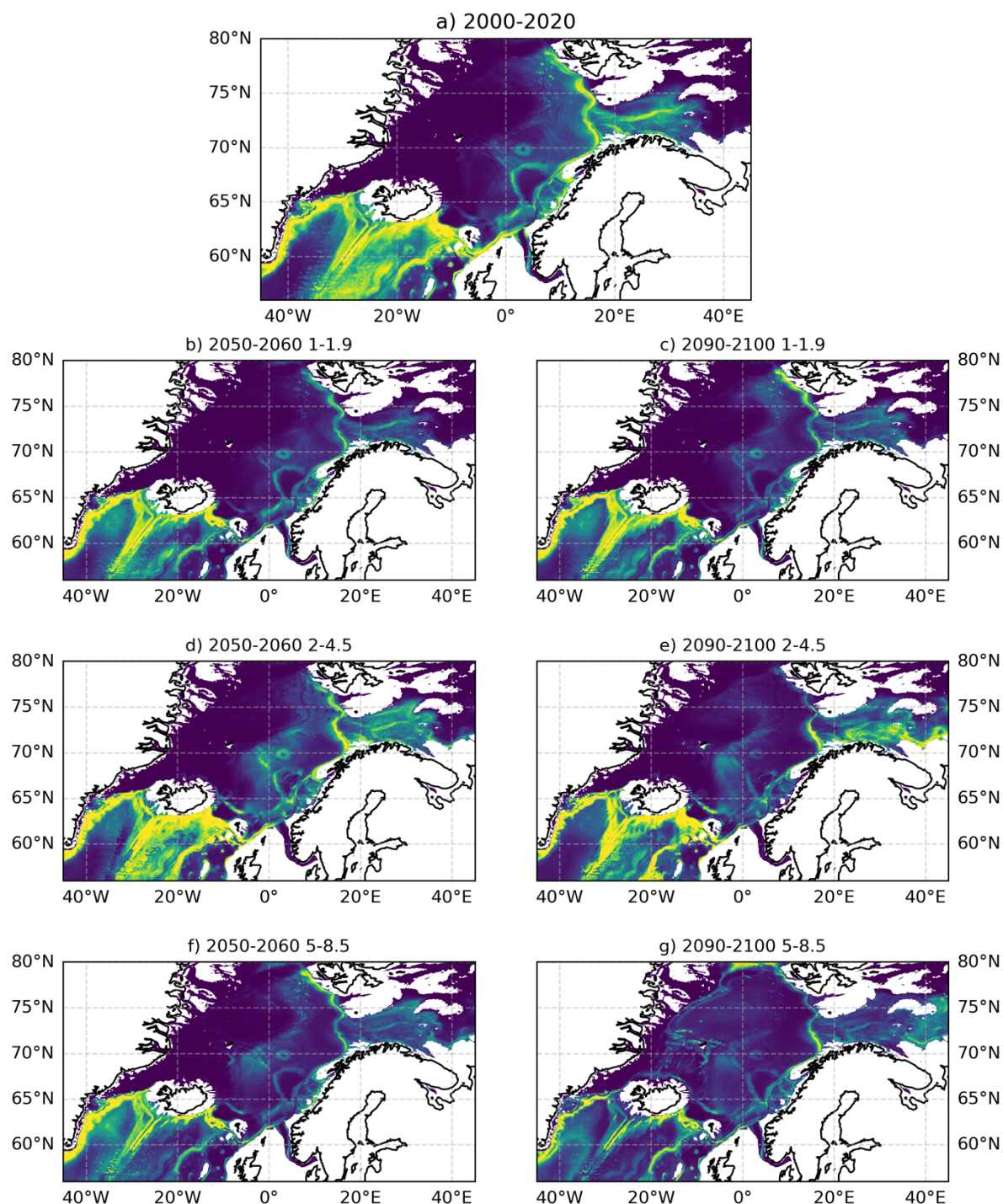
Amphilochus manudens

Figure S3: Maps show the habitat suitability of *Amphilochus manudens* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

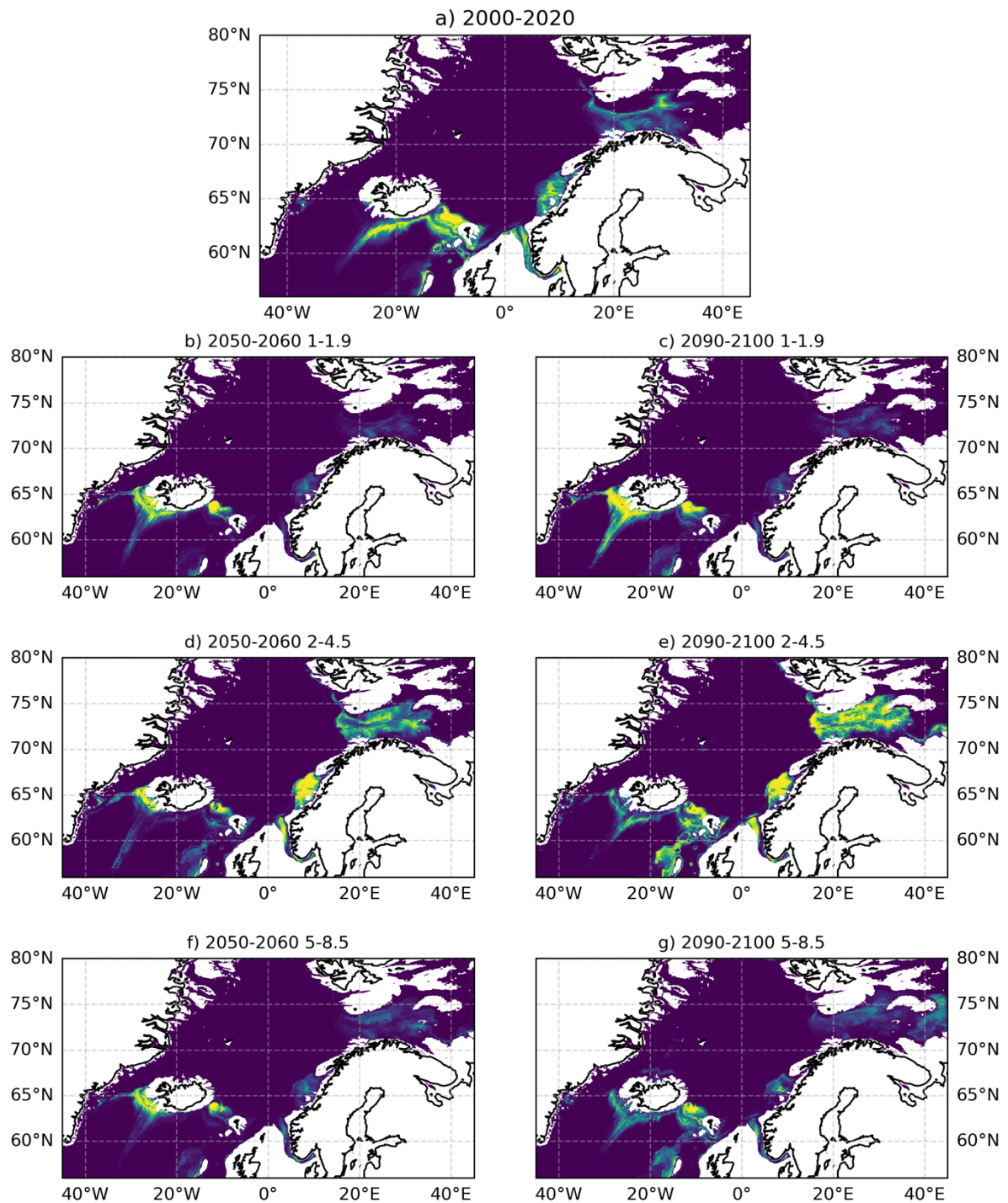
Eriopisa elongata

Figure S4: Maps show the habitat suitability of *Eriopisa elongata* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

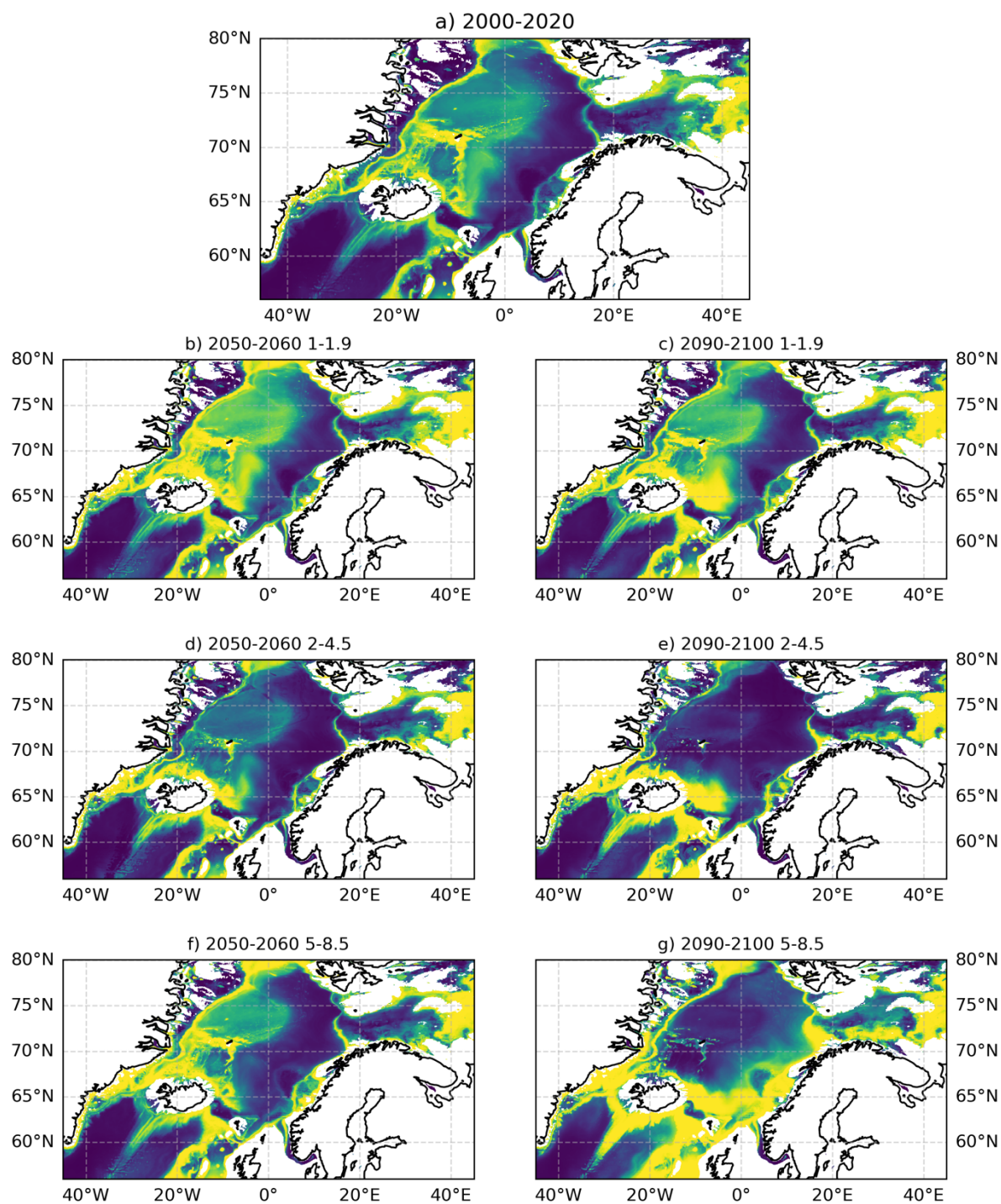
Melphidippa borealis

Figure S5: Maps show the habitat suitability of *Melphidippa borealis* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

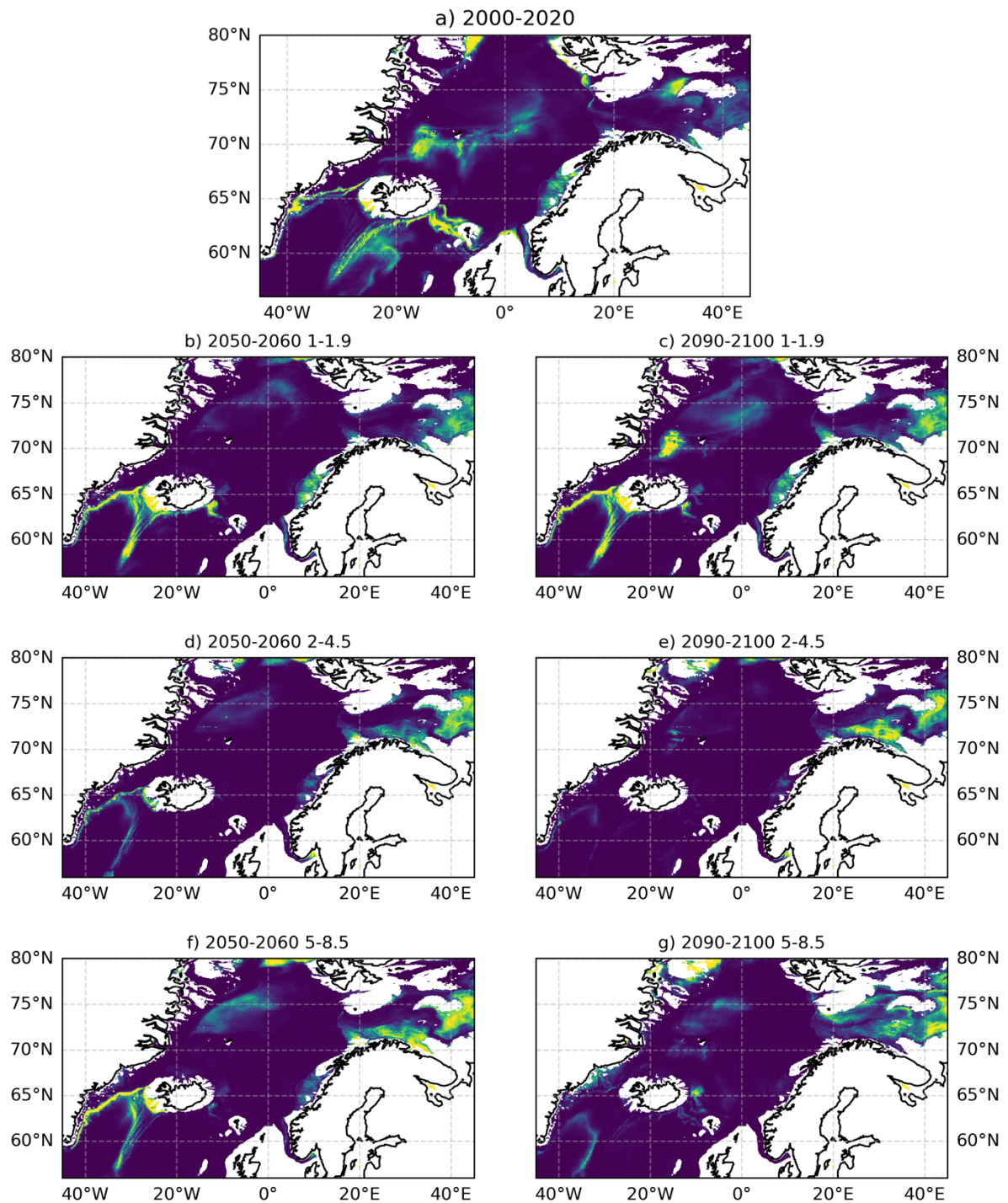
Westwoodilla caecula

Figure S6: Maps show the habitat suitability of *Westwoodilla caecula* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

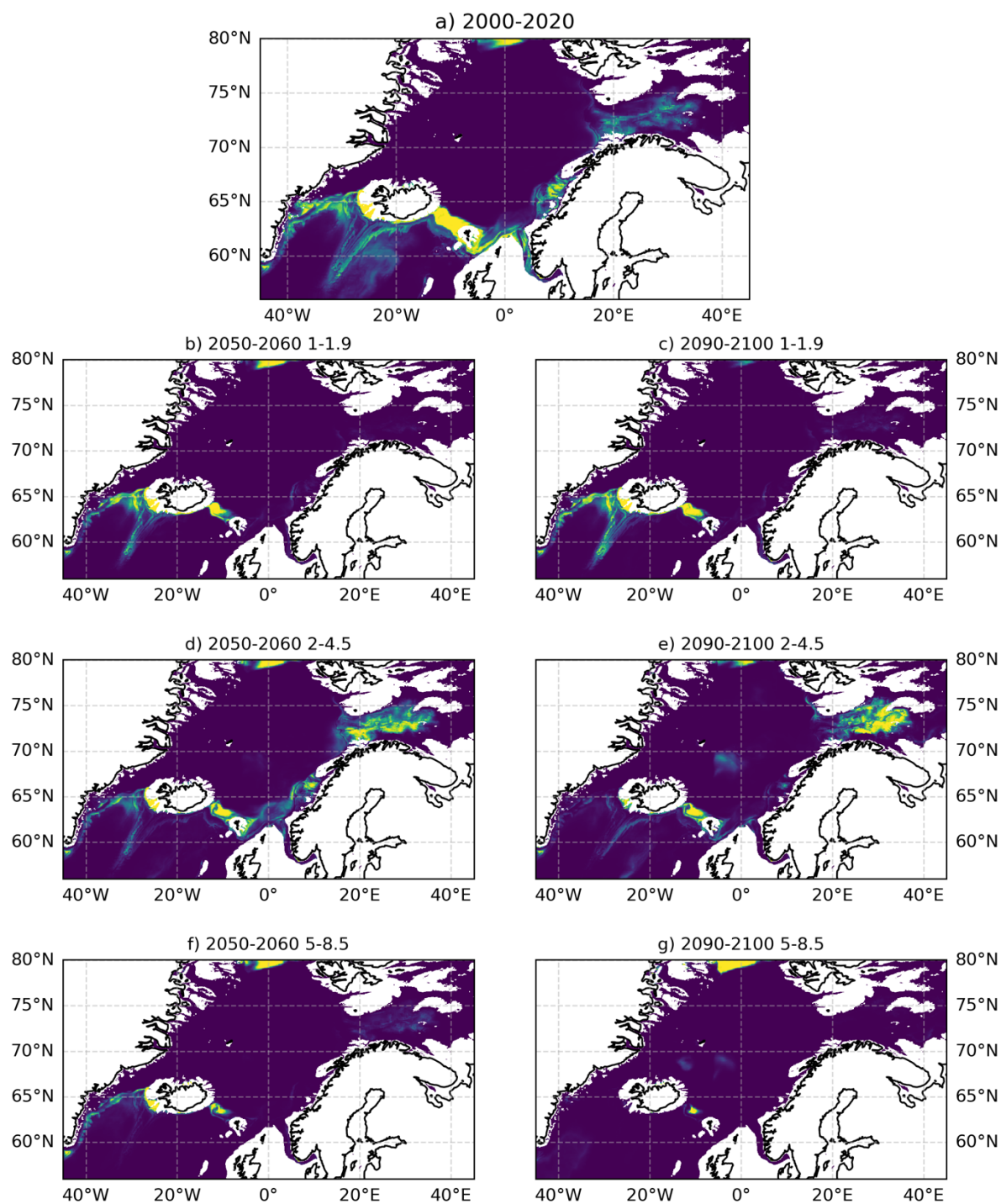
Harpinia crenulata

Figure S7: Maps show the habitat suitability of *Harpinia crenulata* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

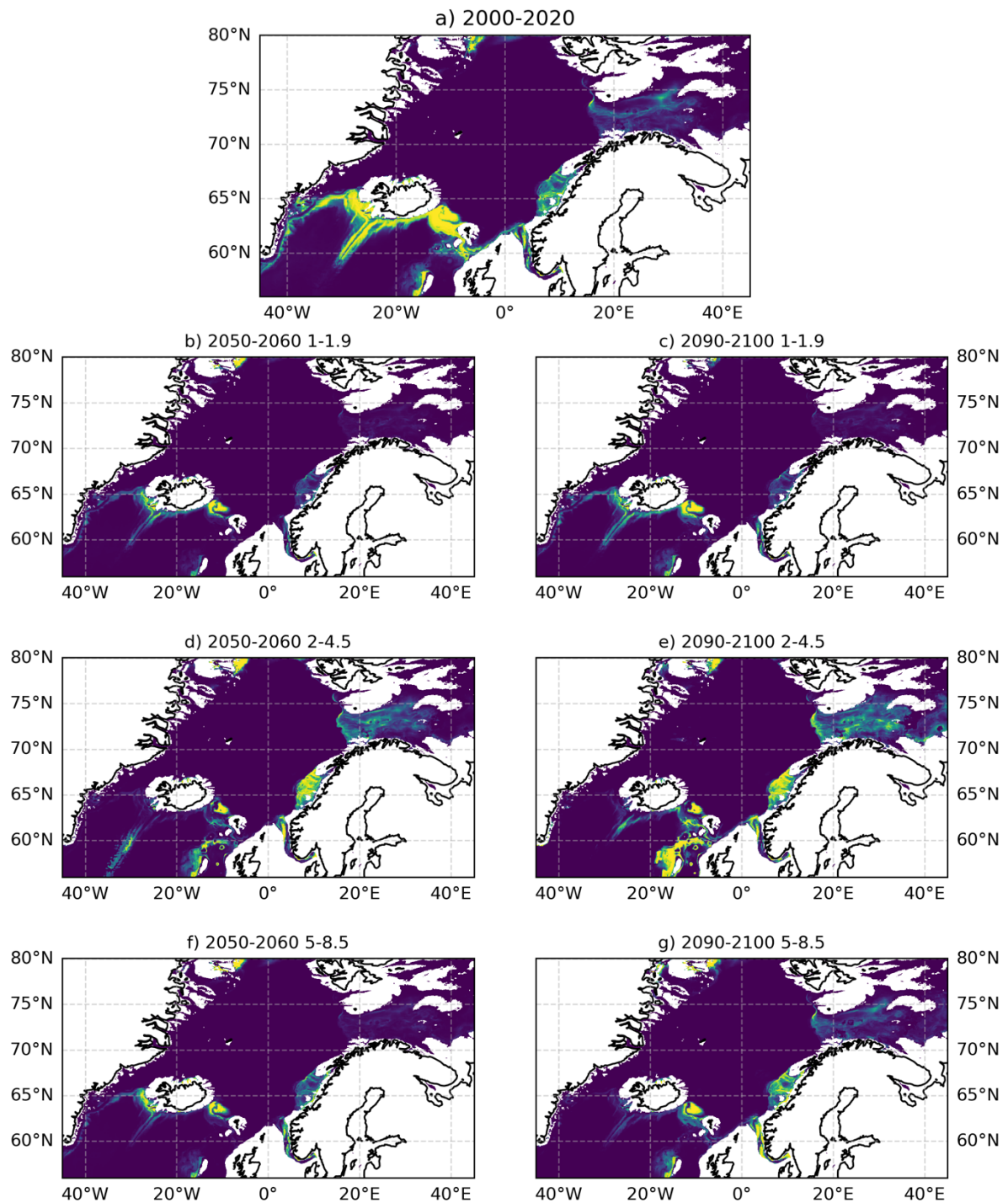
Laetmatophilus tuberculatus

Figure S8: Maps show the habitat suitability of *Laetmatophilus tuberculatus* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

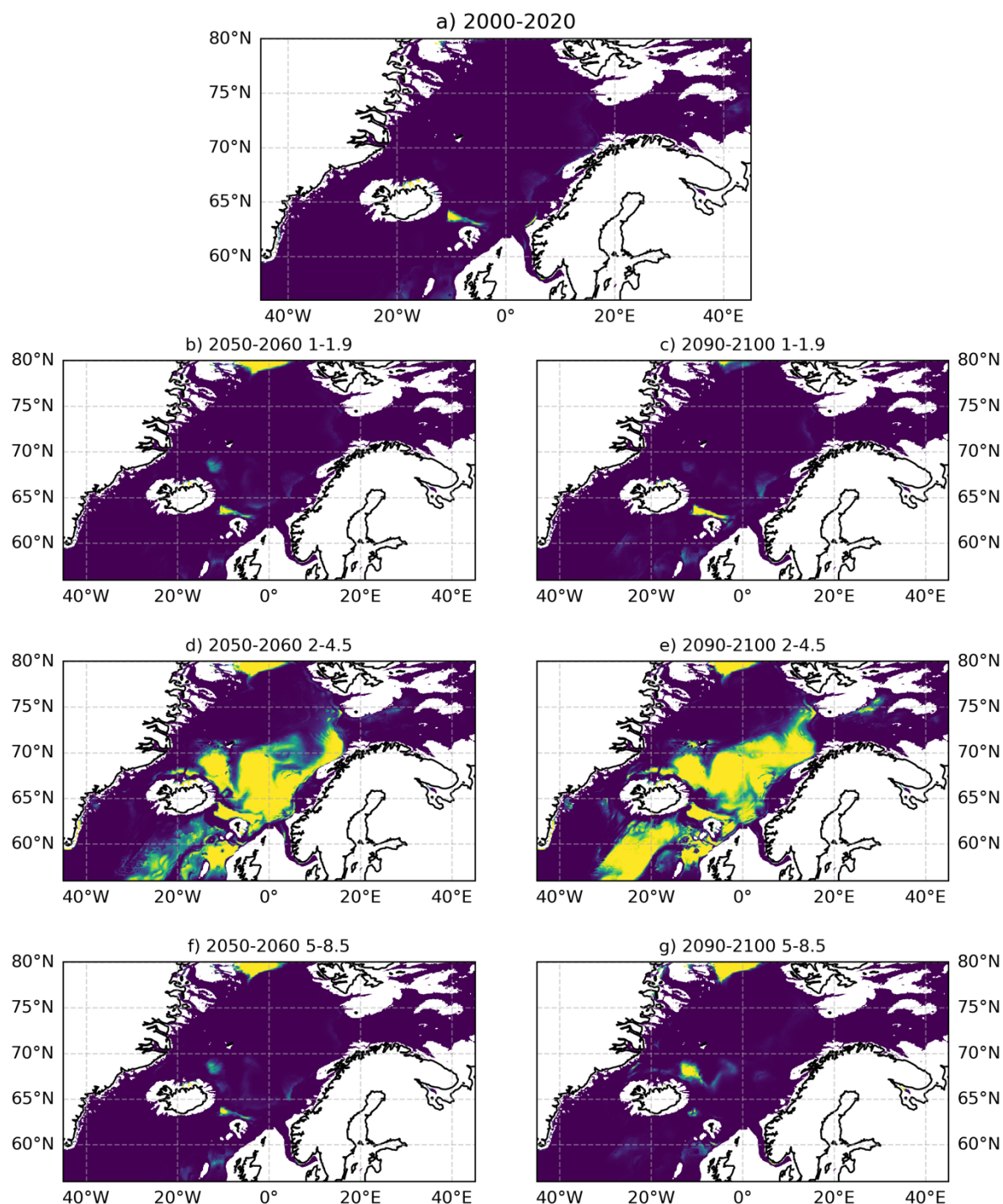
Harpinia plumosa

Figure S9: Maps show the habitat suitability of *Harpinia plumosa* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

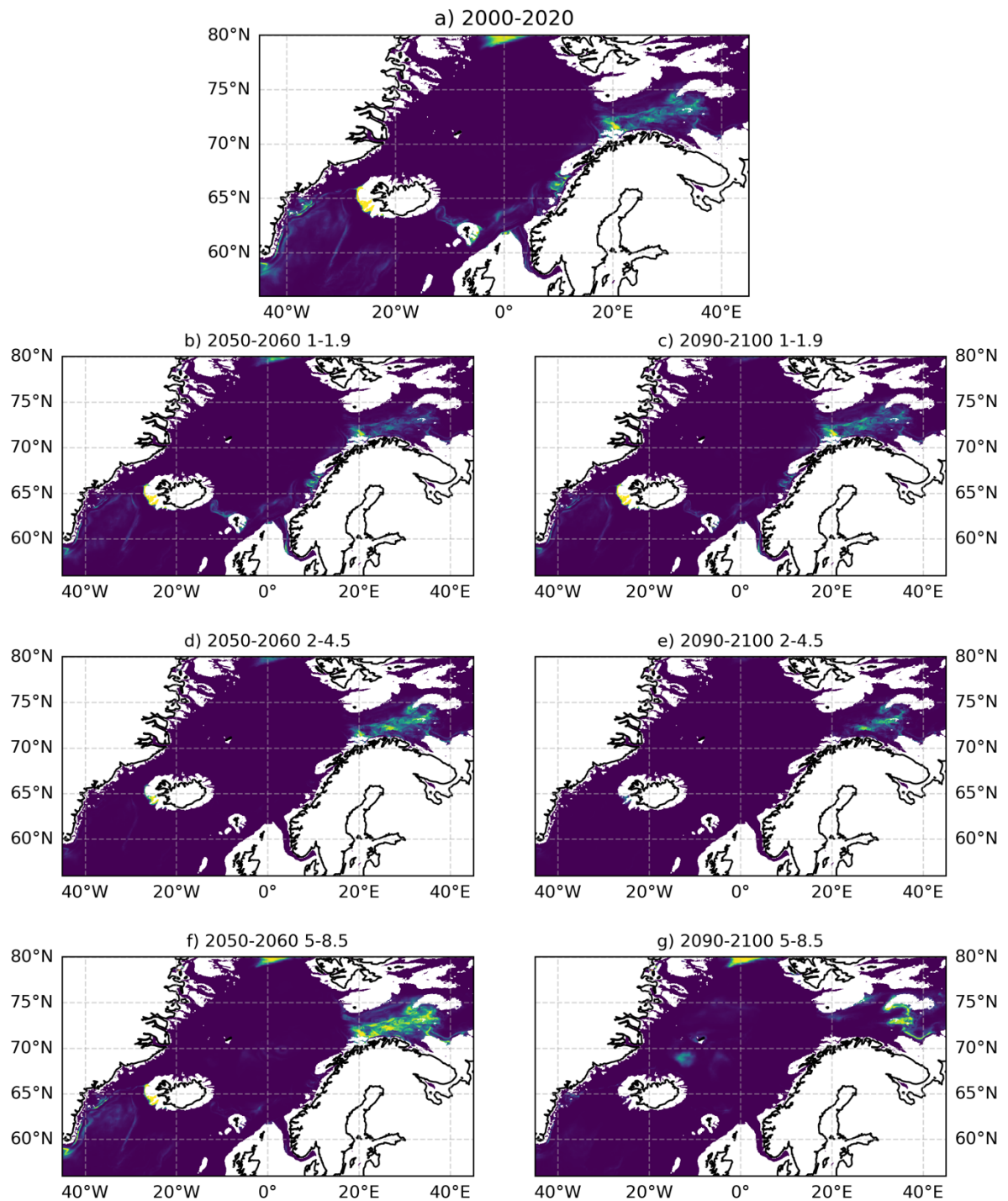
Autonoe longipes

Figure S10: Maps show the habitat suitability of *Autonoe longipes* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

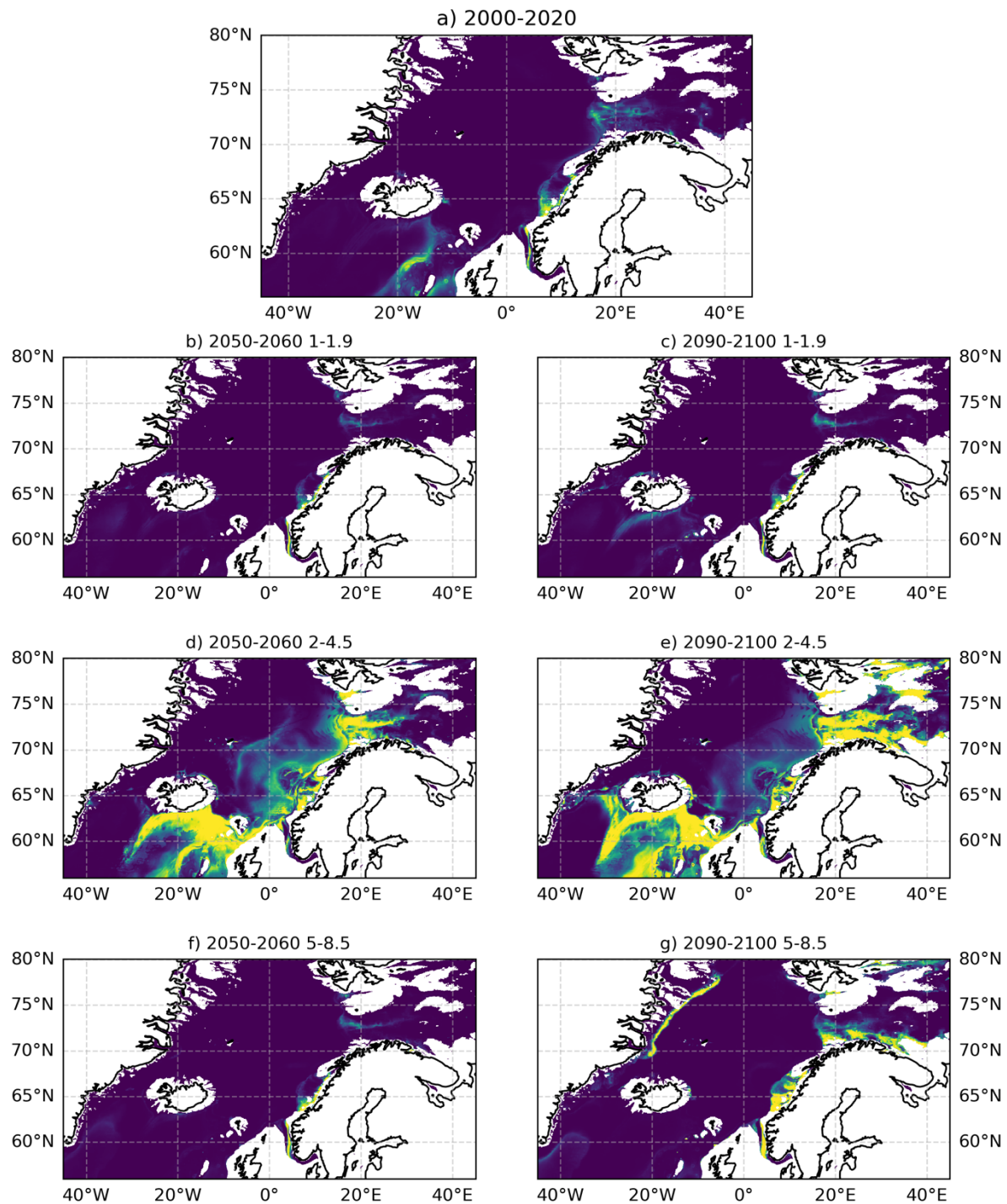
Byblis crassicornis

Figure S11: Maps show the habitat suitability of *Byblis crassicornis* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

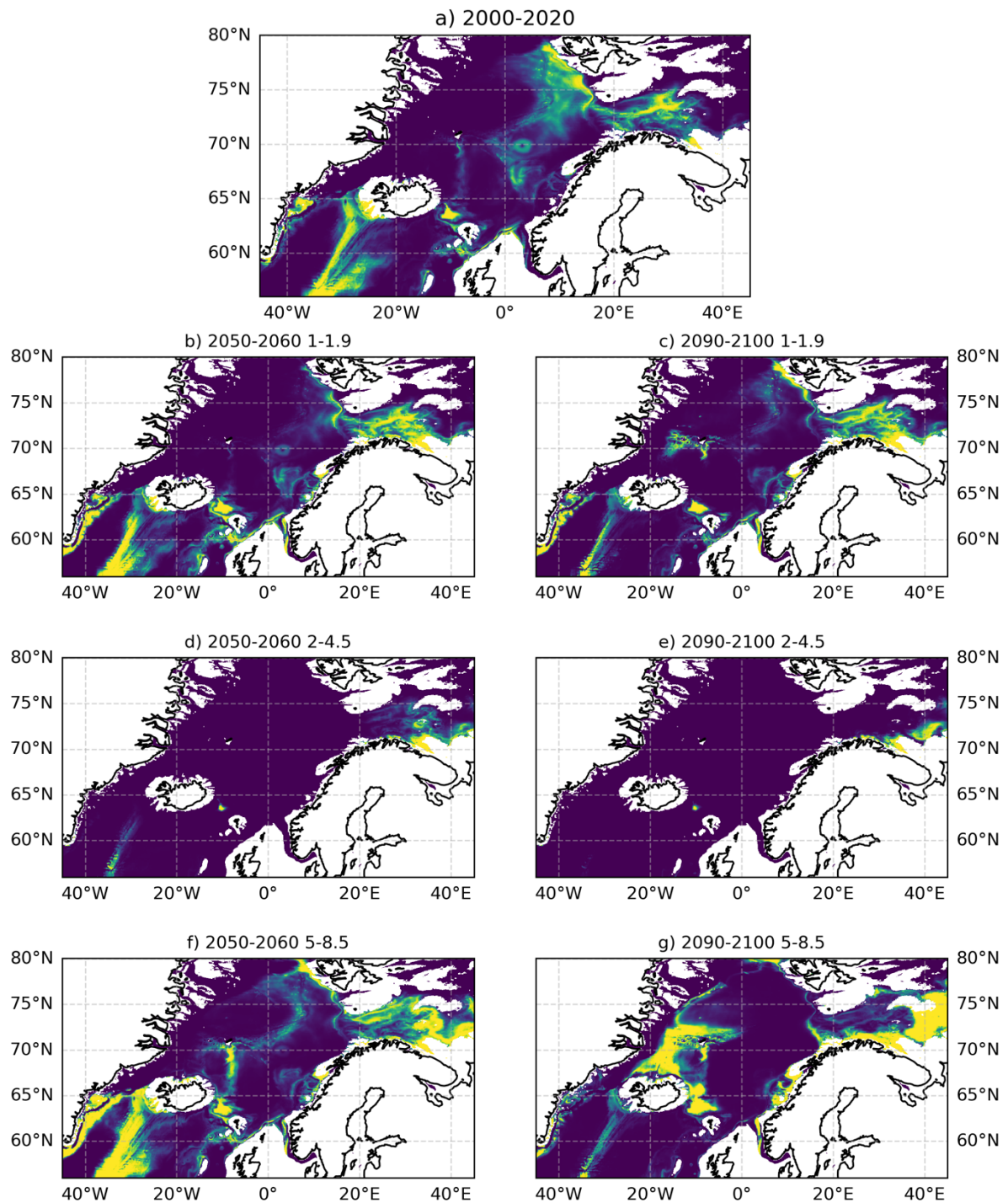
Harpinia antennaria

Figure S12: Maps show the habitat suitability of *Harpinia antennaria* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

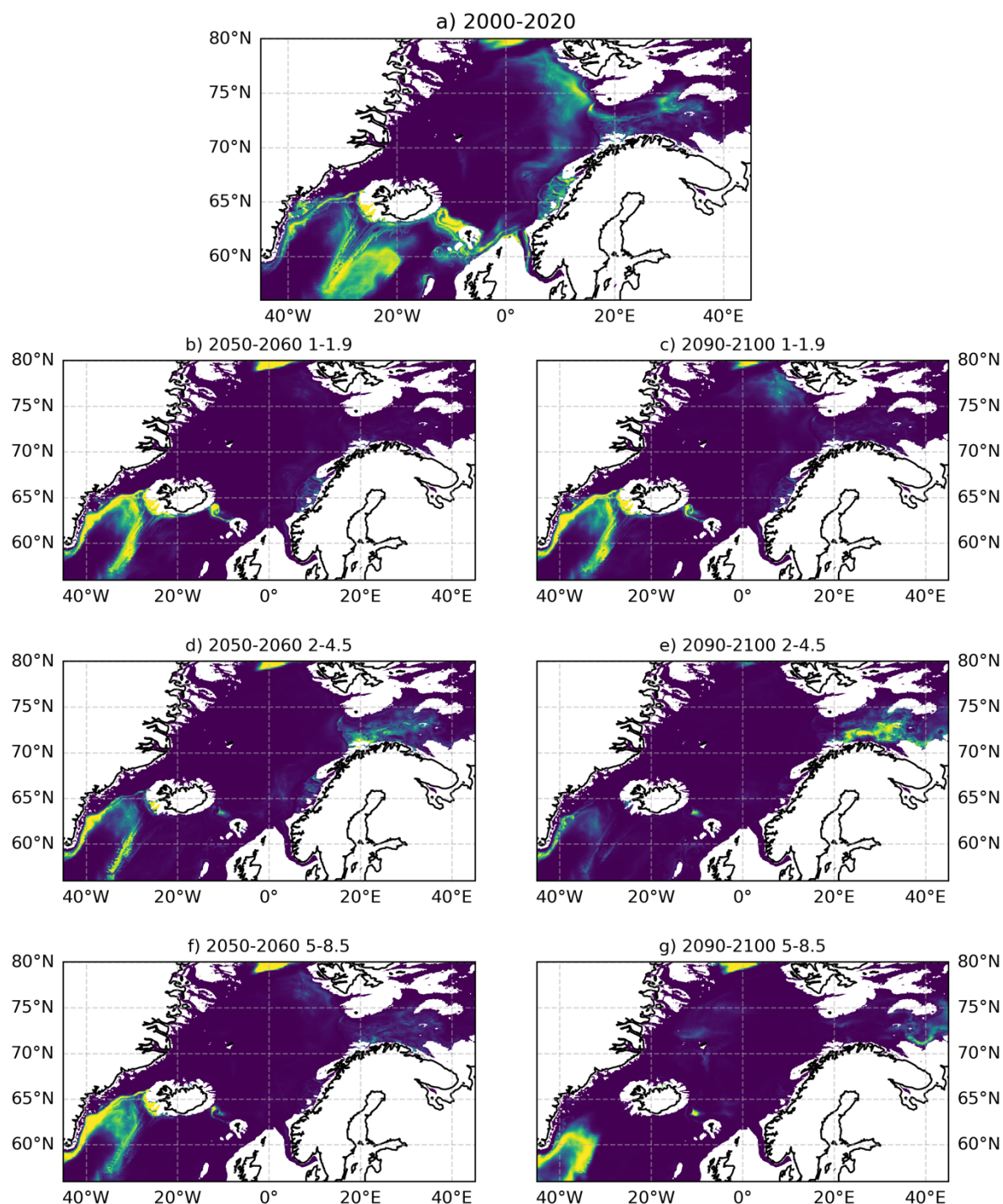
Tmetonyx cicada

Figure S13: Maps show the habitat suitability of *Tmetonyx cicada* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

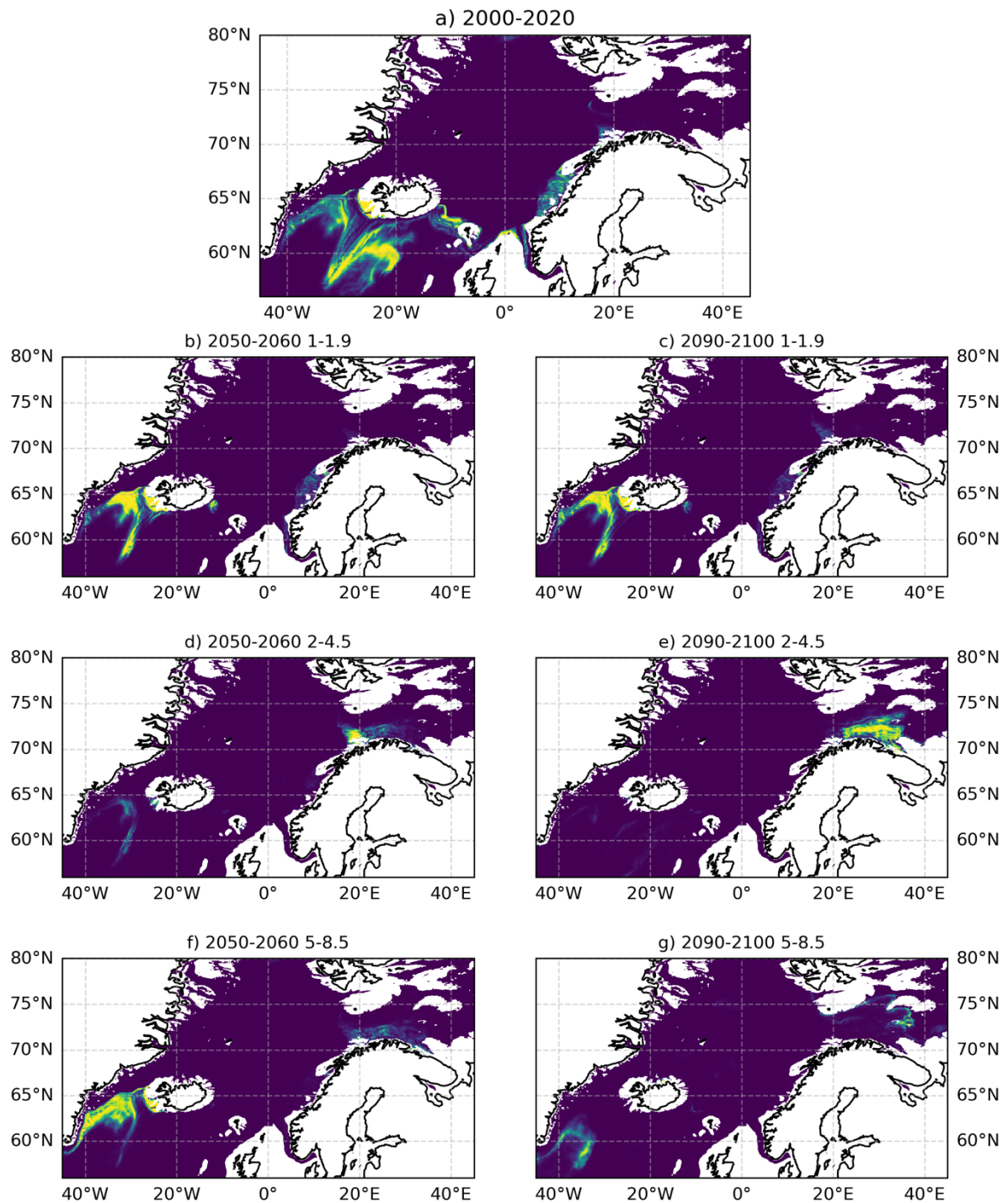
Tryphosites longipes

Figure S14: Maps show the habitat suitability of *Tryphosites longipes* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

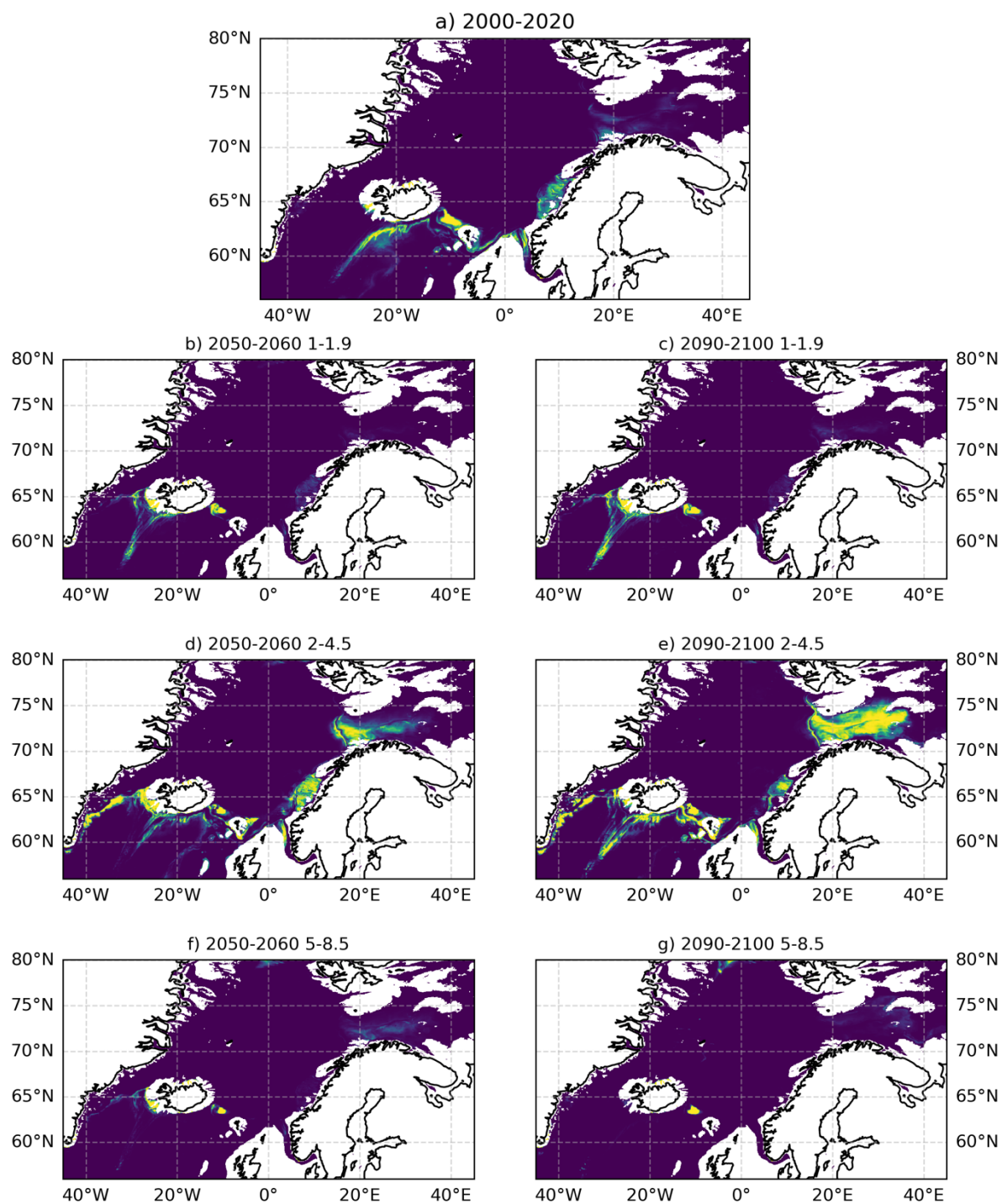
Harpinia pectinata

Figure S15: Maps show the habitat suitability of *Harpinia pectinata* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

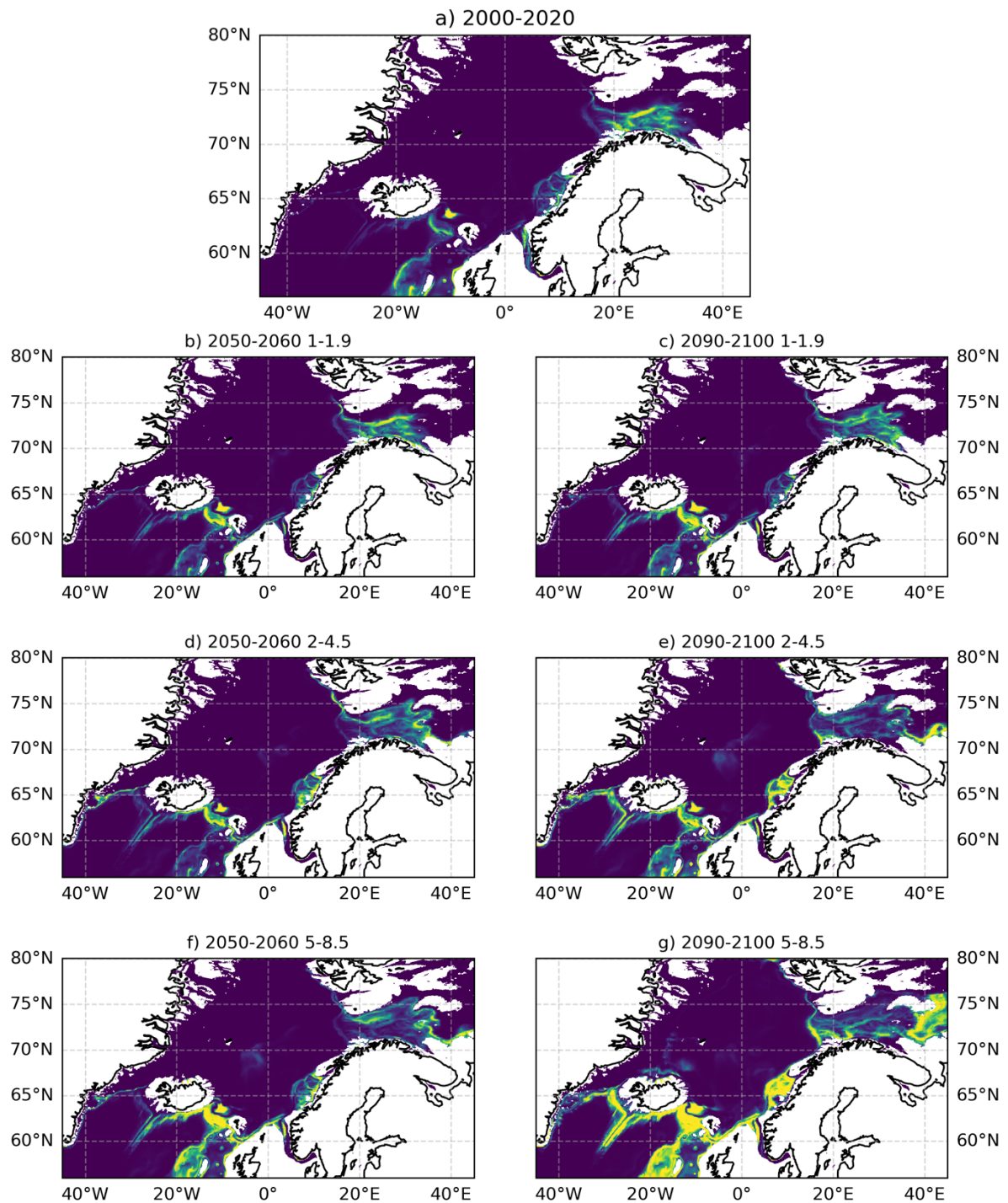
Leptophoxus falcatus

Figure S16: Maps show the habitat suitability of *Leptophoxus falcatus* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

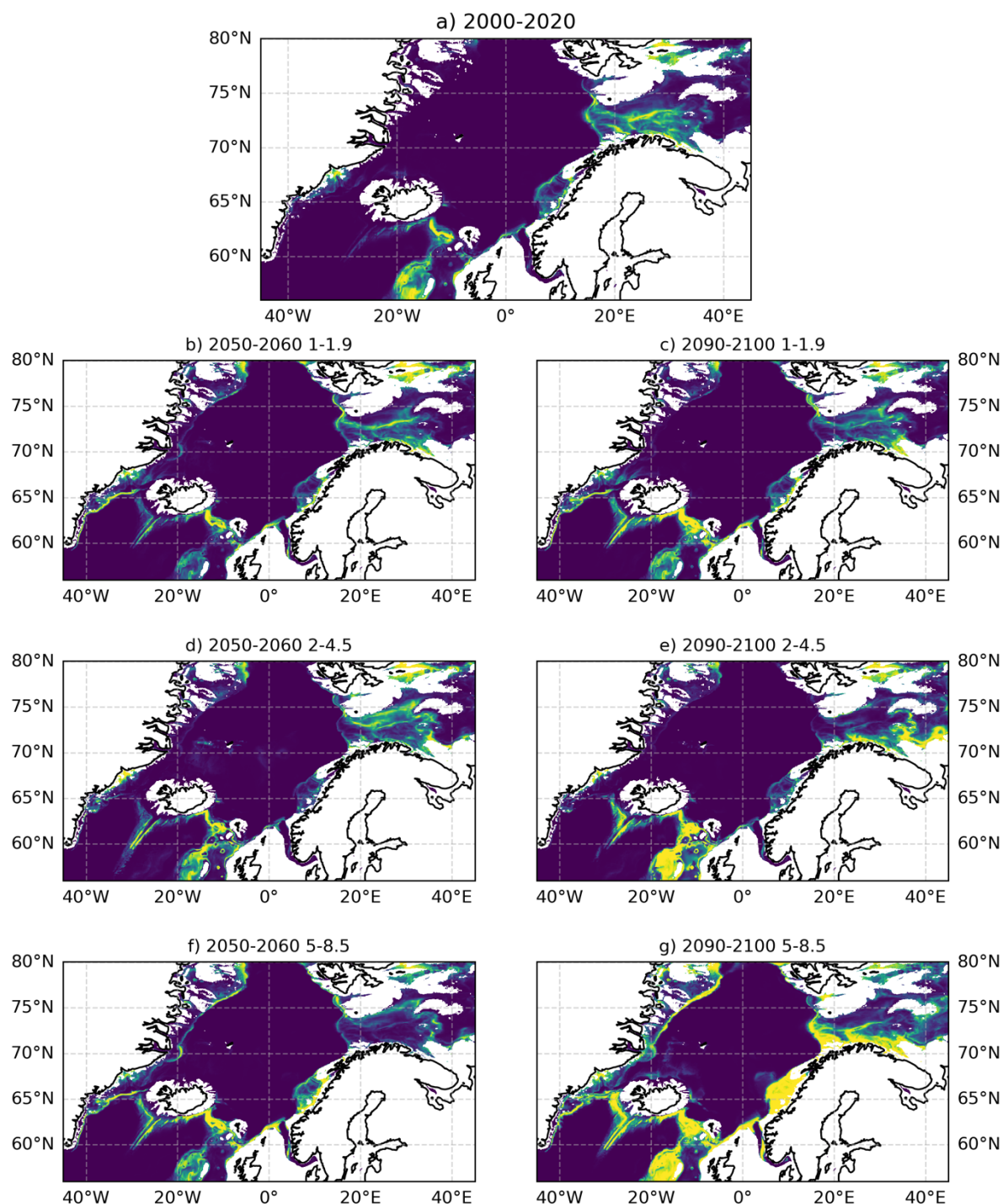
Nototropis nordlandicus

Figure S17: Maps show the habitat suitability of *Nototropis nordlandicus* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

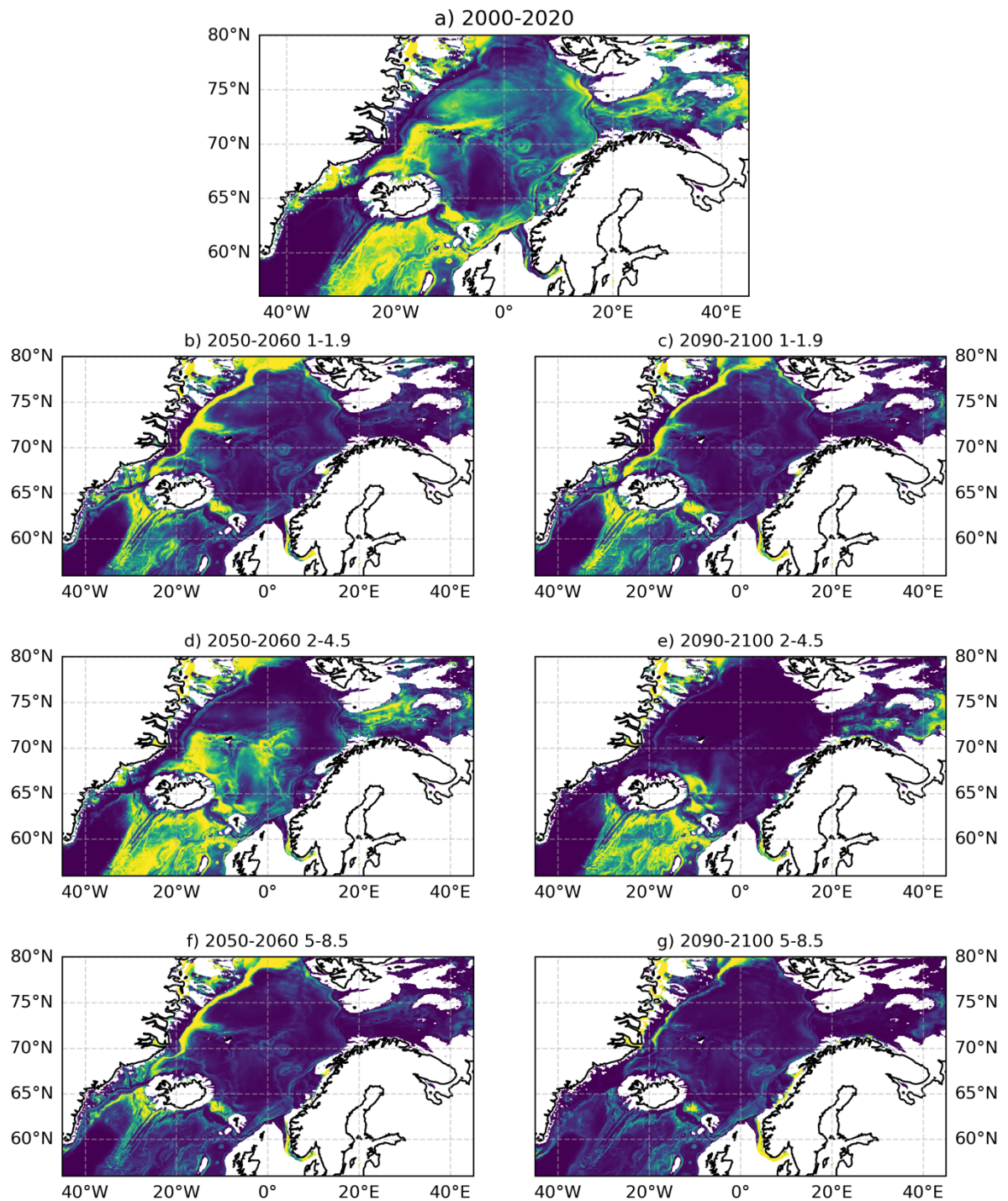
Neohela monstrosa

Figure S18: Maps show the habitat suitability of *Neohela monstrosa* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

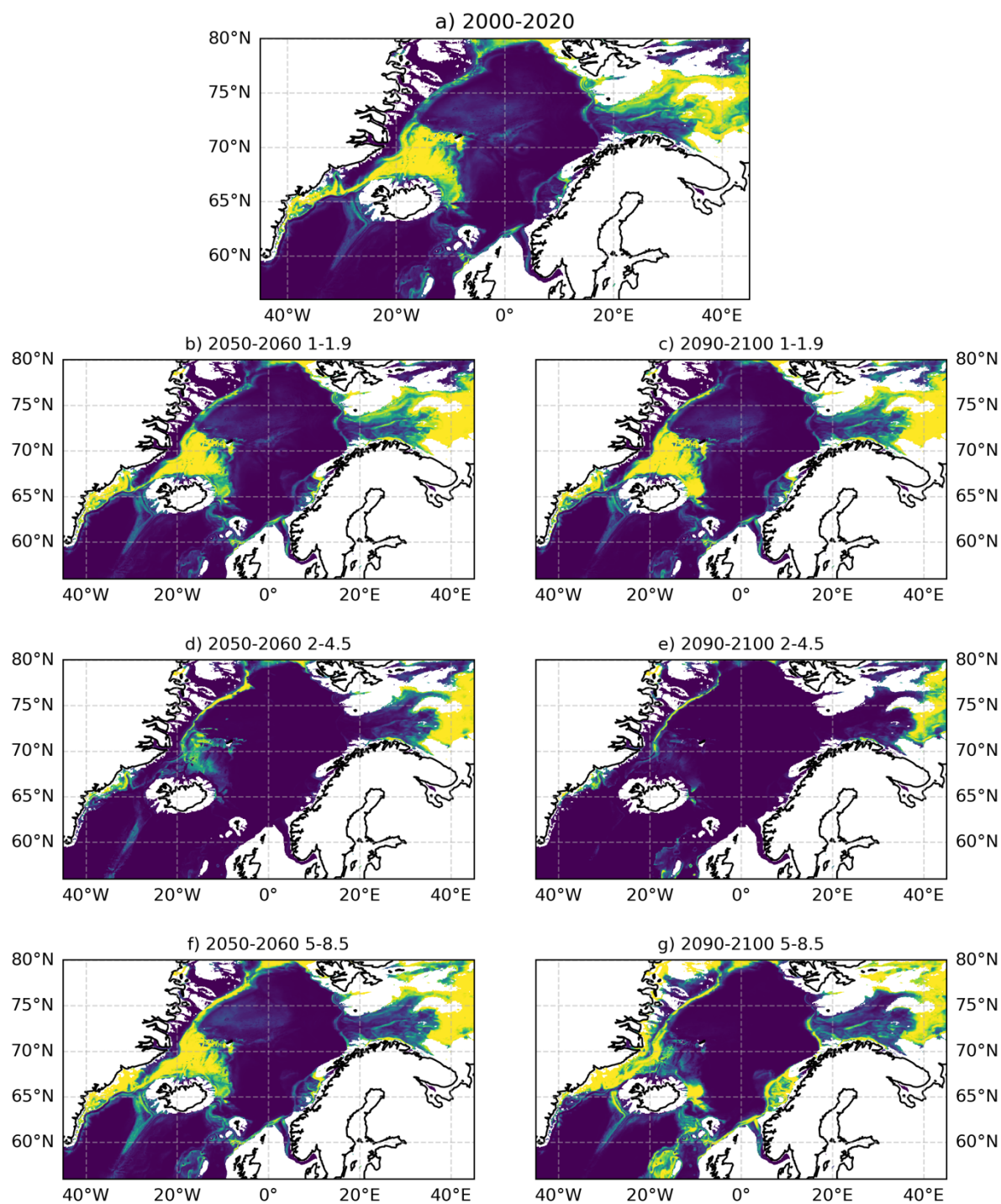
Ampelisca eschrichtii

Figure S19: Maps show the habitat suitability of *Ampelisca eschrichtii* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

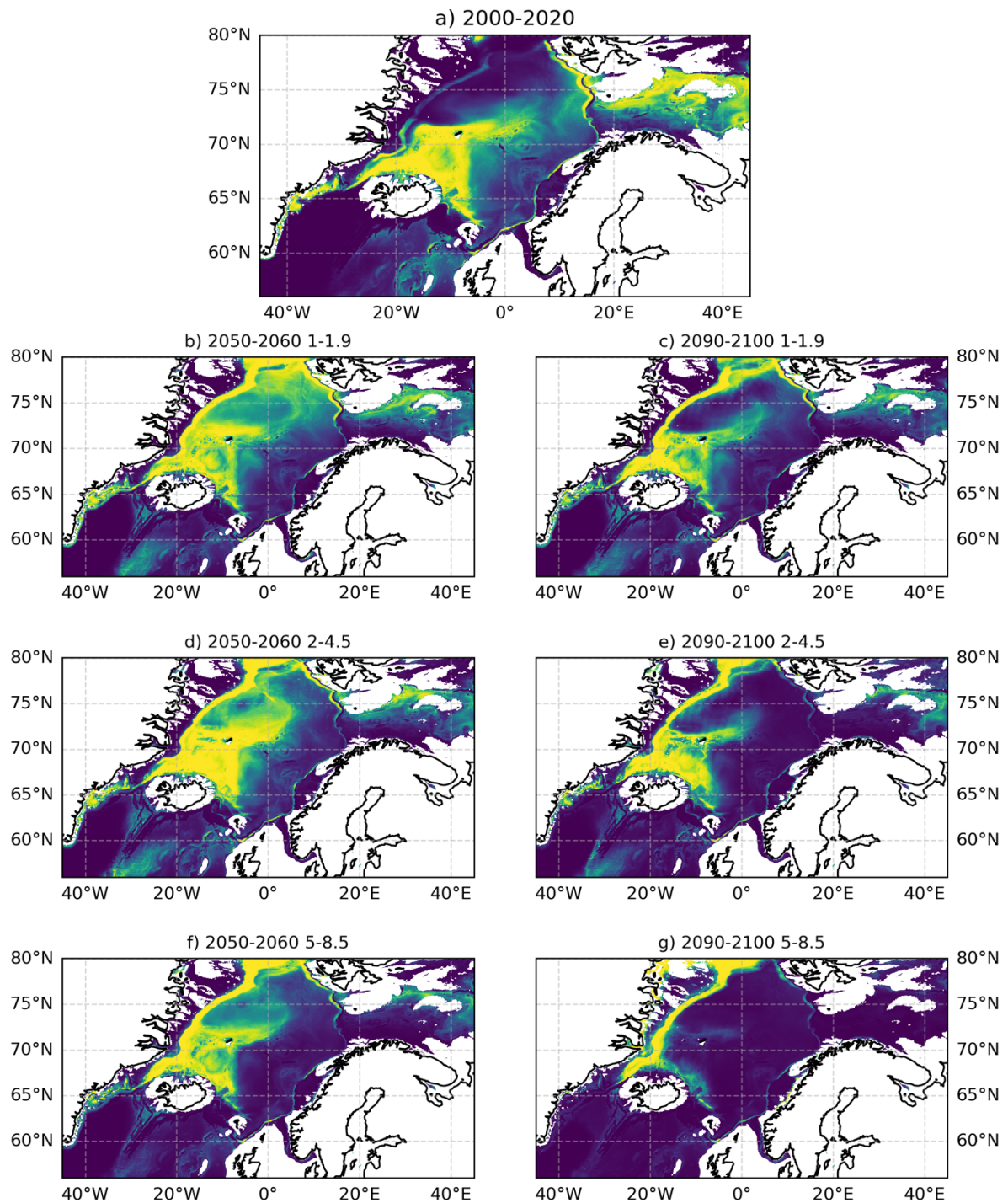
Idunella aeqvicornis

Figure S20: Maps show the habitat suitability of *Idunella aeqvicornis* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

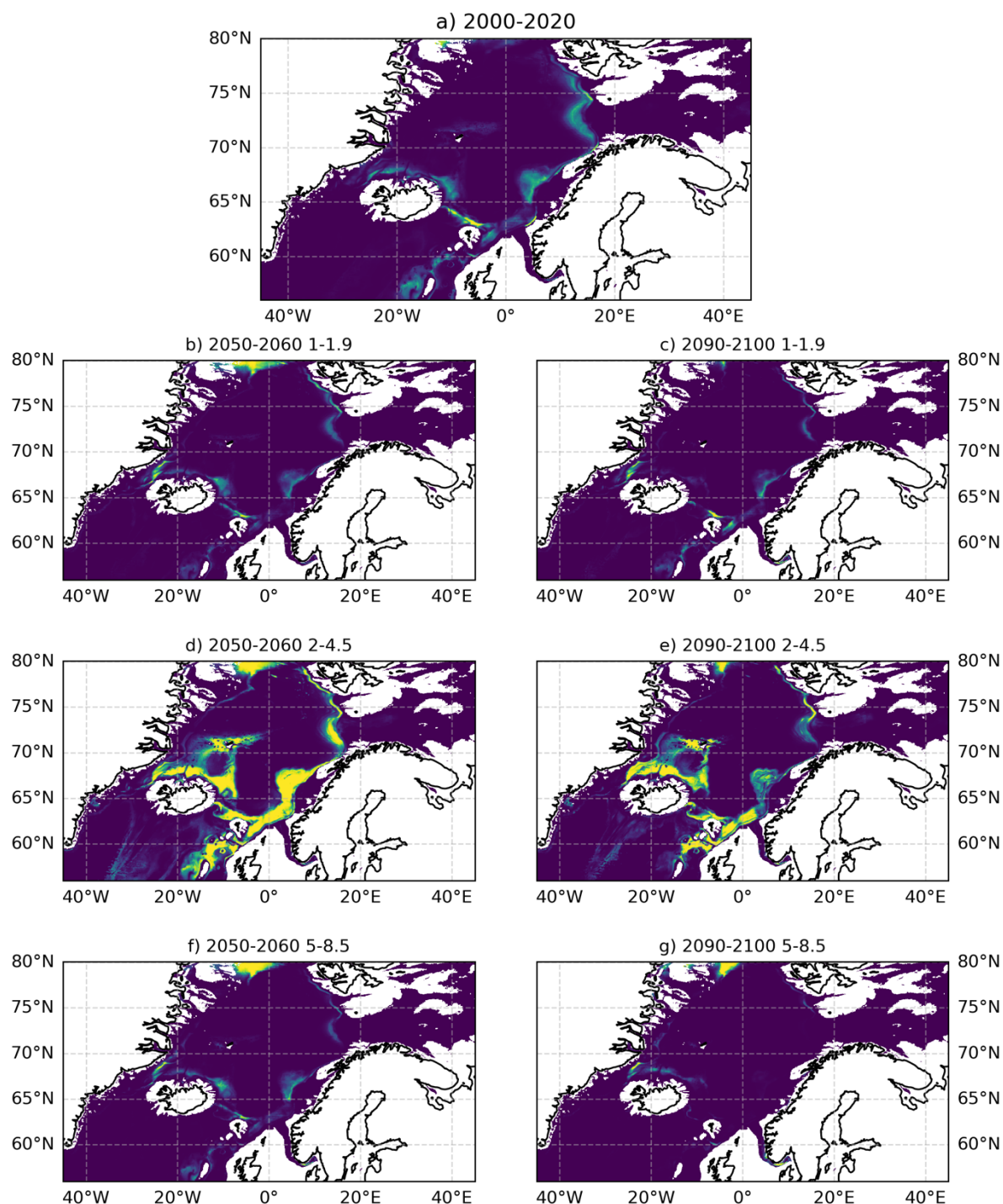
Harpinia abyssi

Figure S21: Maps show the habitat suitability of *Harpinia abyssi* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

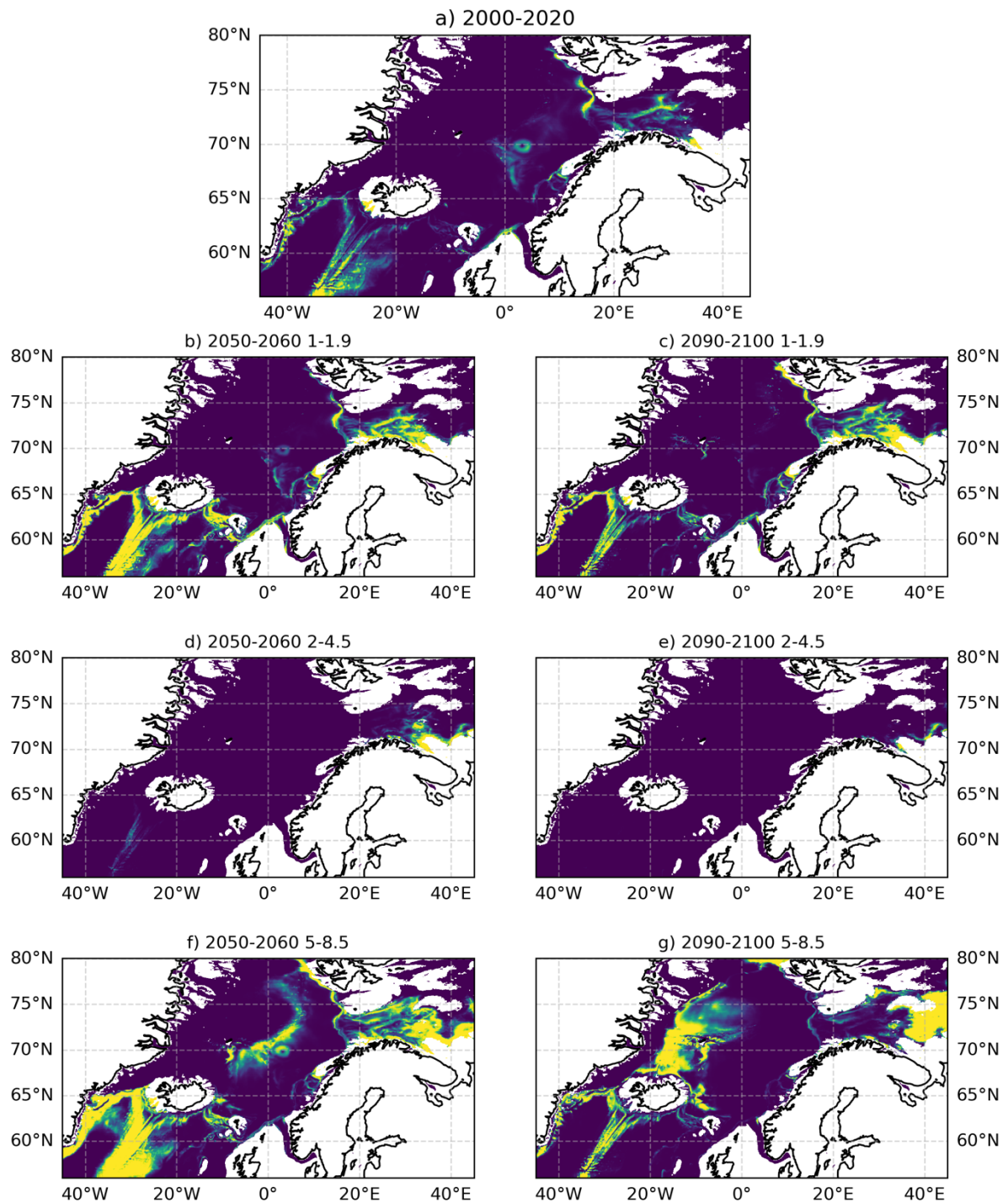
Urothoe elegans

Figure S22: Maps show the habitat suitability of *Urothoe elegans* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

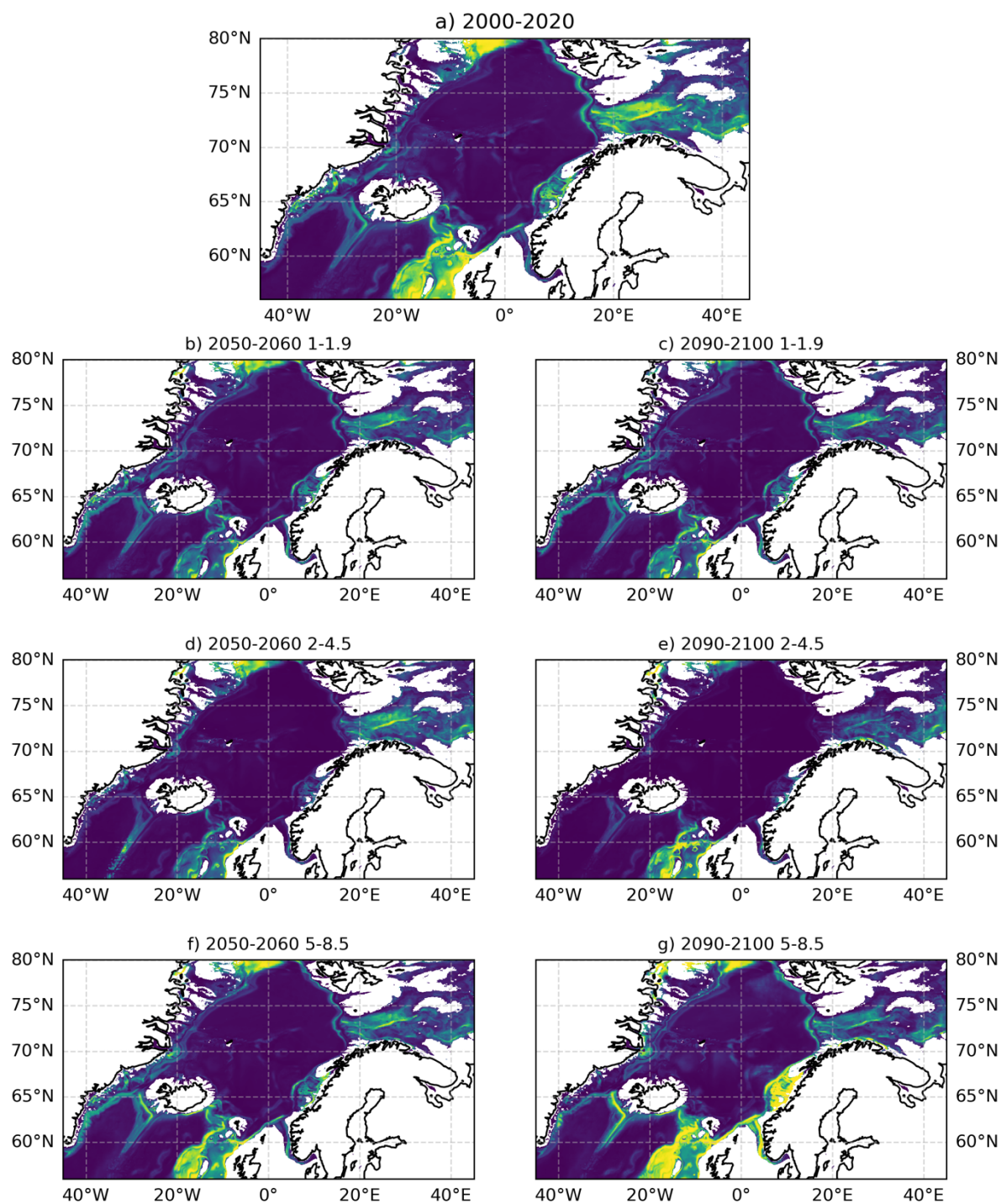
Tryphosella horingi

Figure S23: Maps show the habitat suitability of *Tryphosella horingi* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

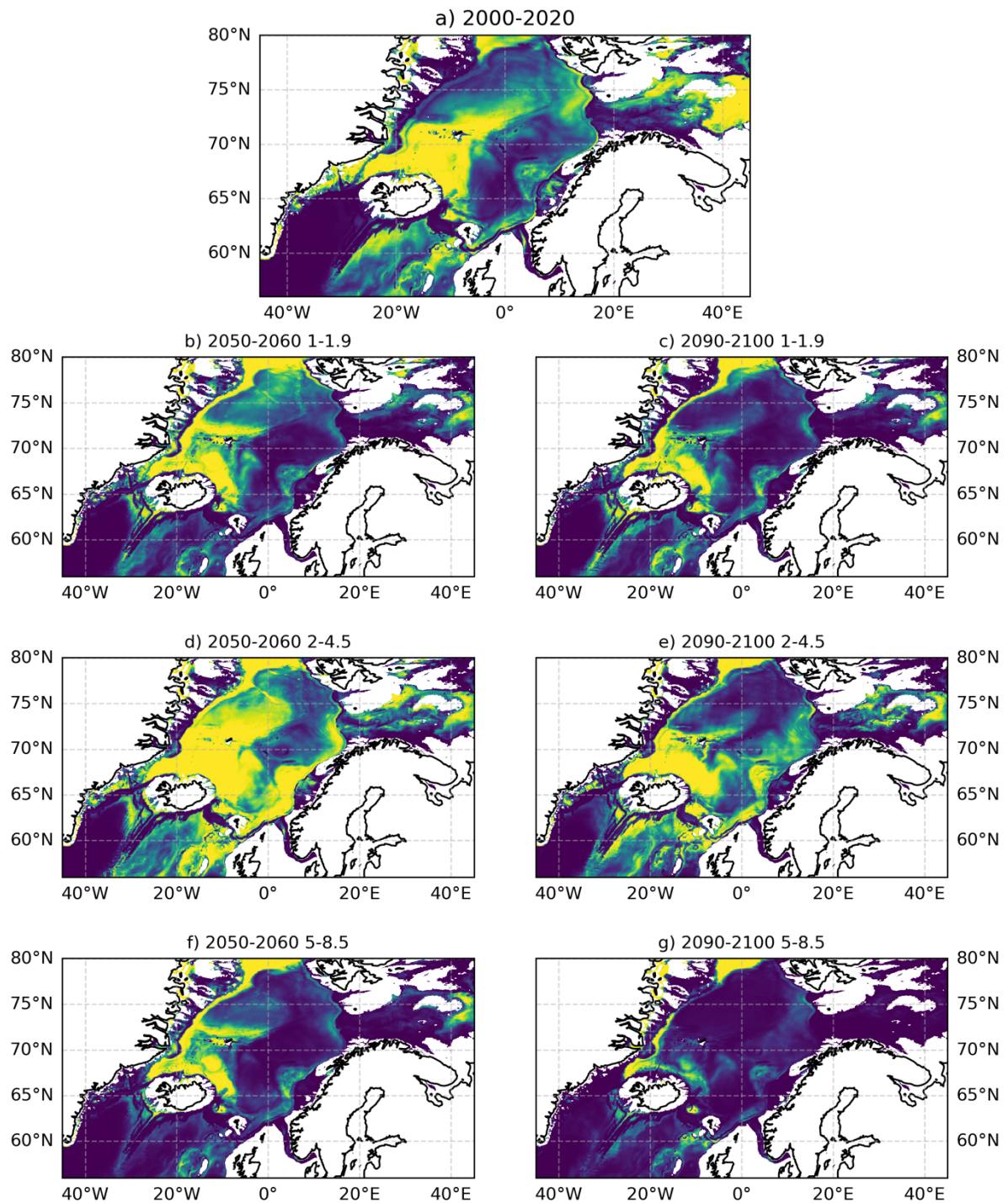
Arrhis phyllonyx

Figure S24: Maps show the habitat suitability of *Arrhis phyllonyx* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

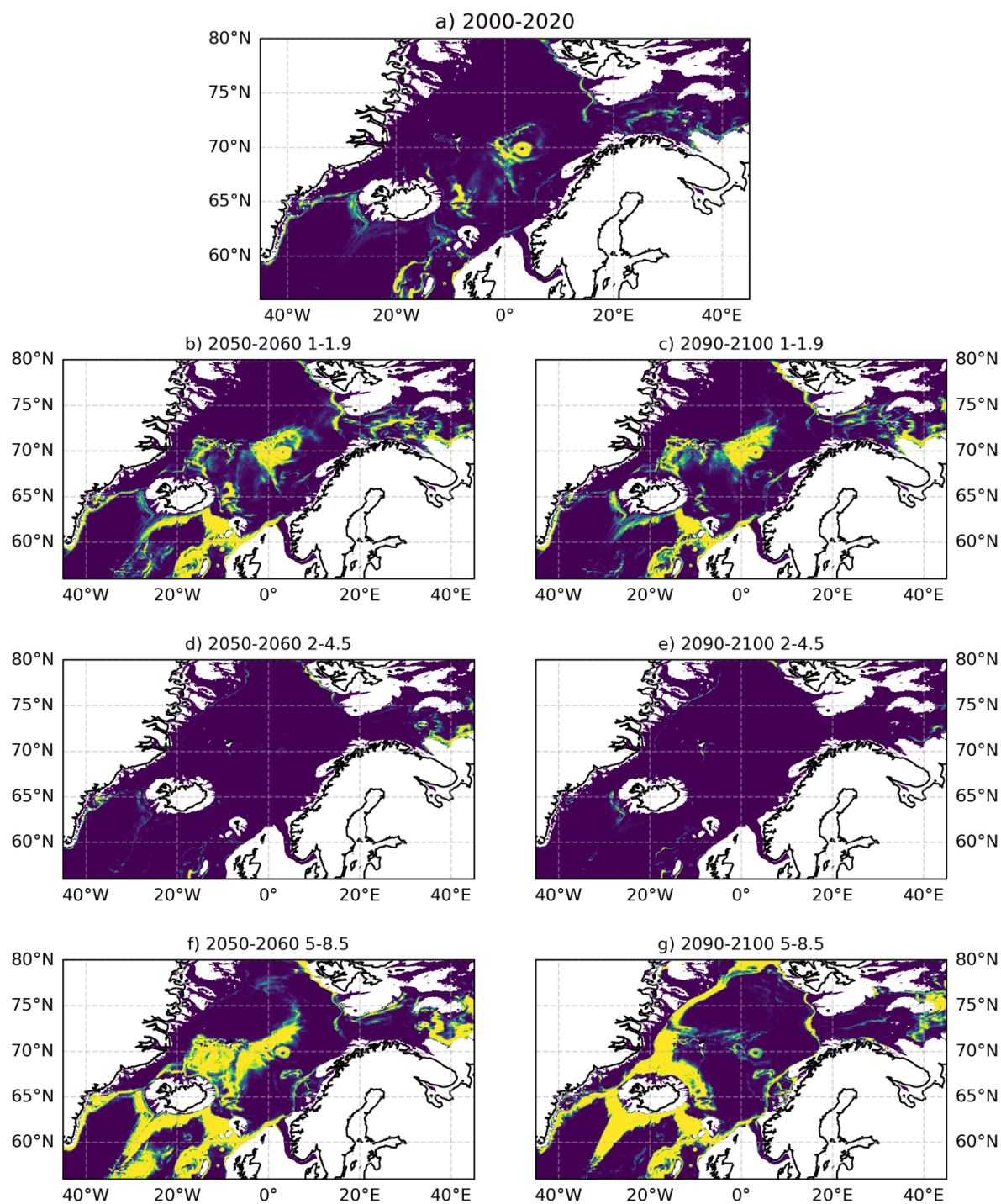
Harpinia propinqua

Figure S25: Maps show the habitat suitability of *Harpinia propinqua* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

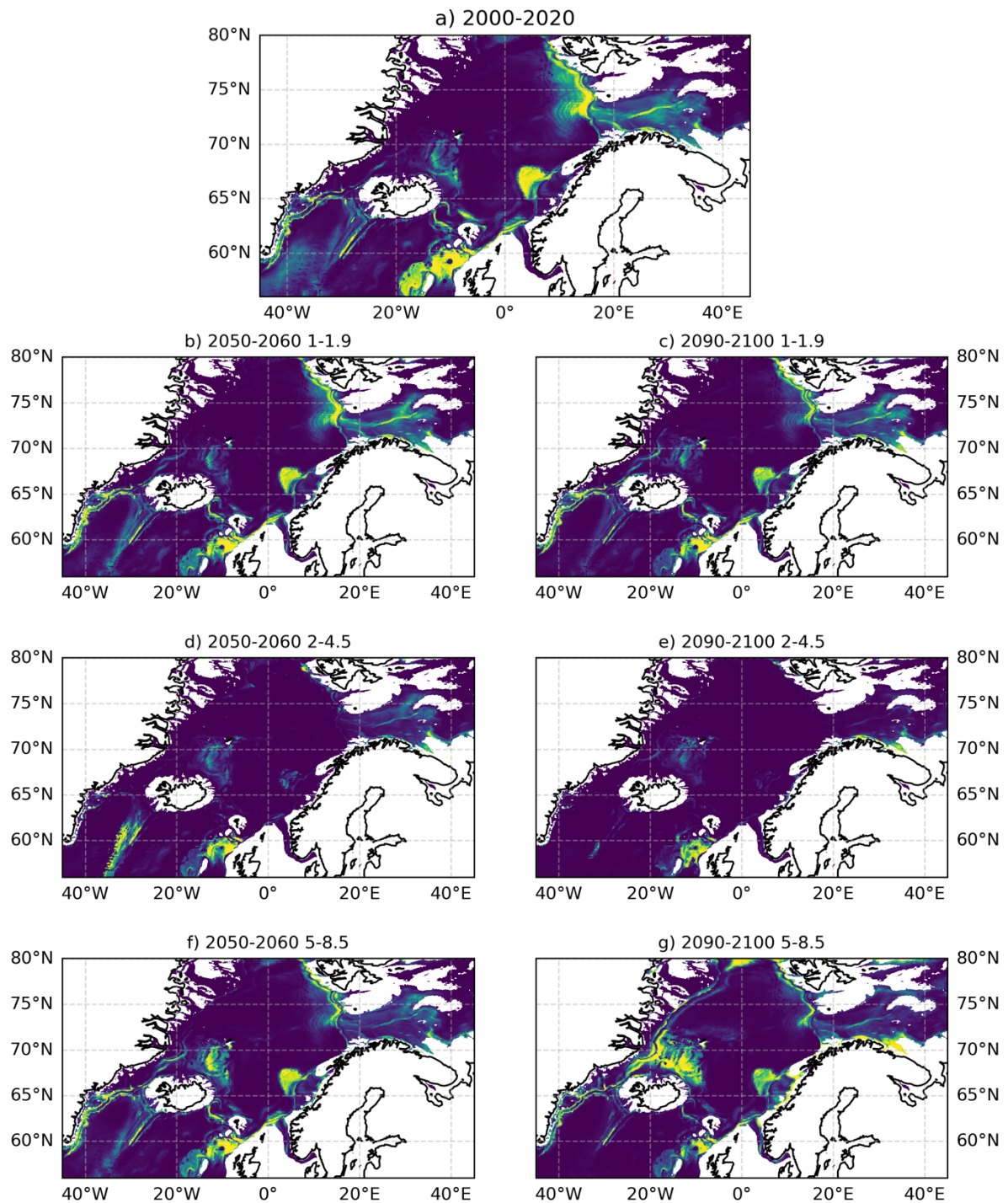
Unciola planipes

Figure S26: Maps show the habitat suitability of *Unciola planipes* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

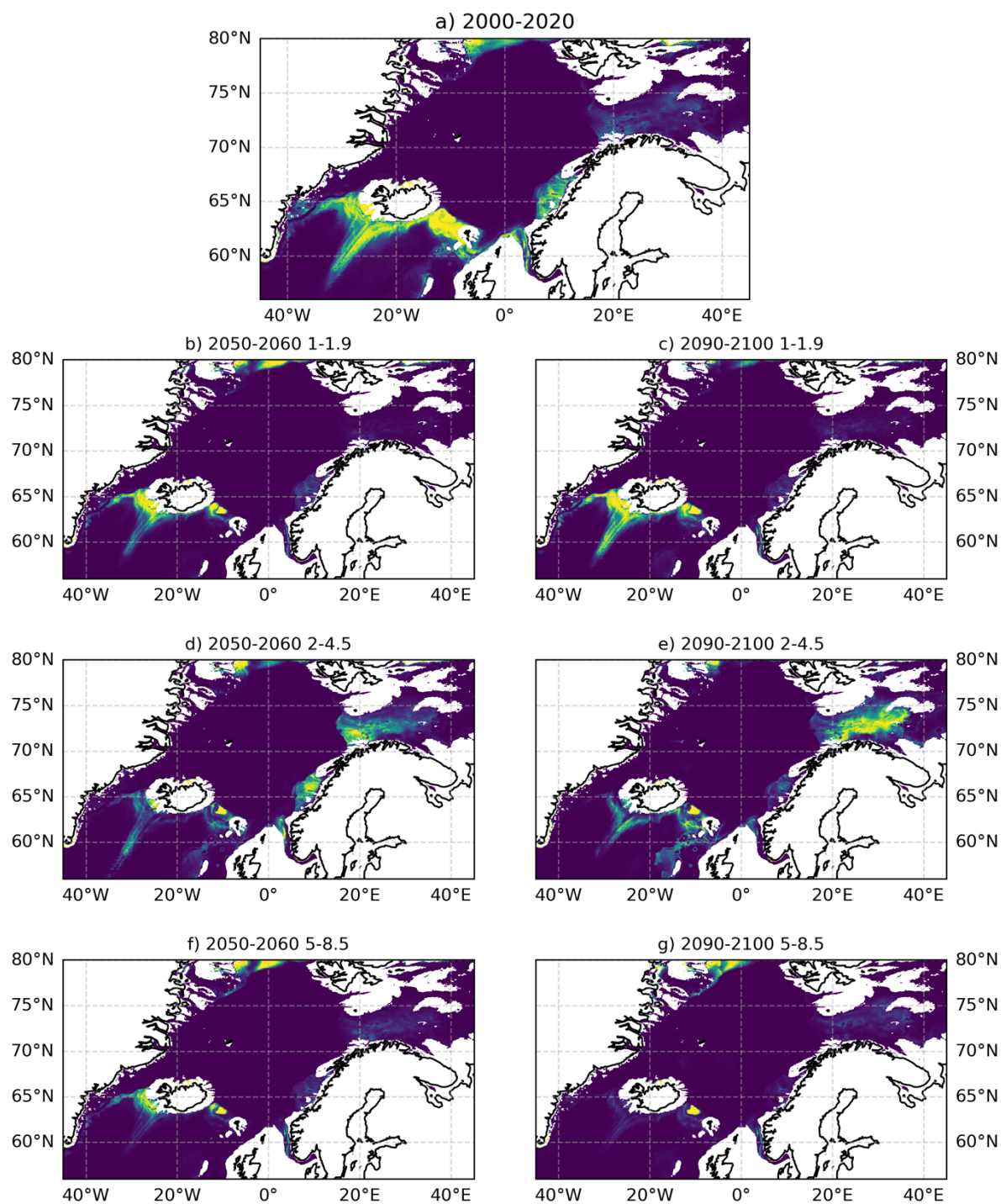
Bathymedon longimanus

Figure S27: Maps show the habitat suitability of *Bathymedon longimanus* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

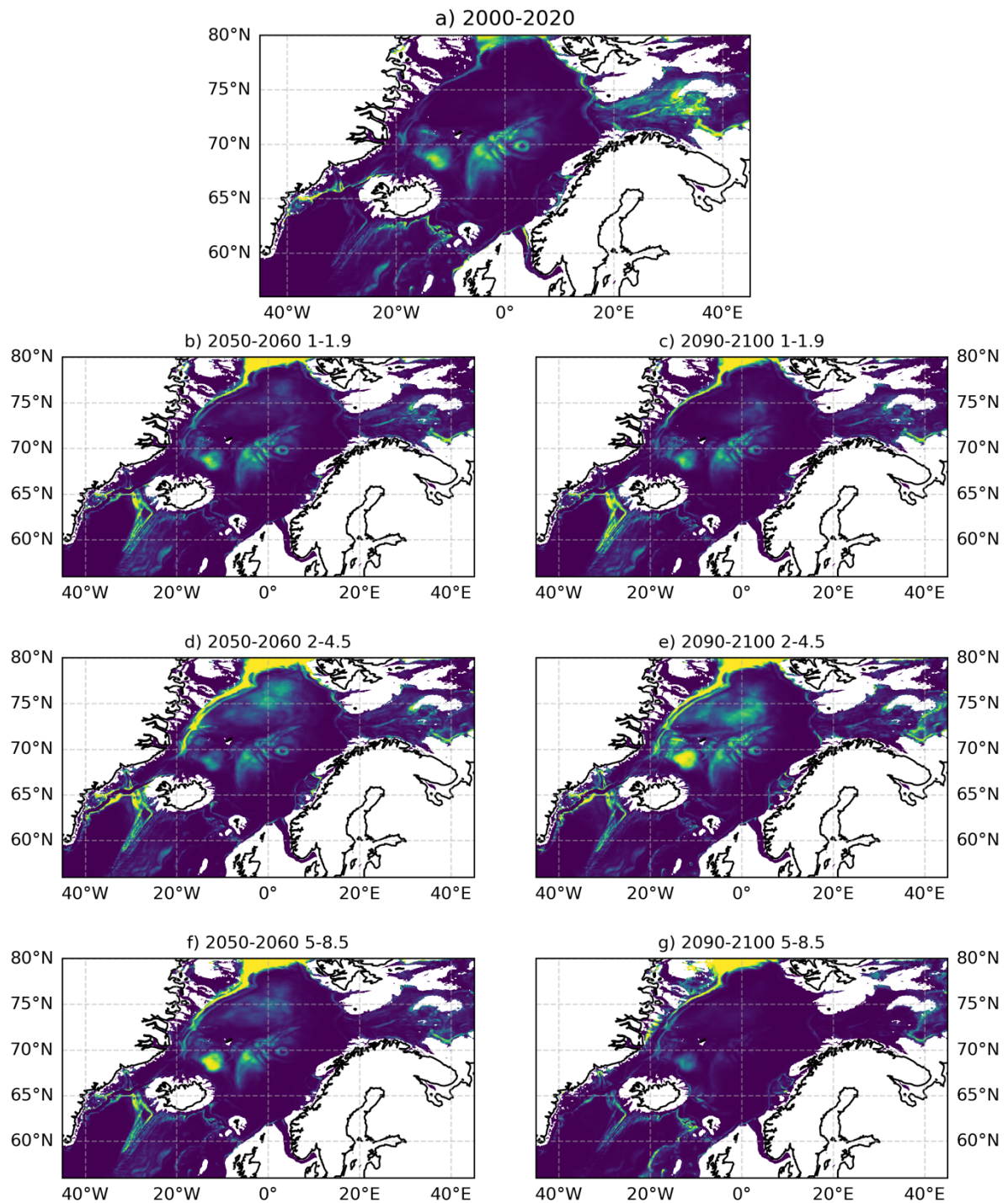
Ampelisca macrocephala

Figure S28: Maps show the habitat suitability of *Ampelisca macrocephala* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

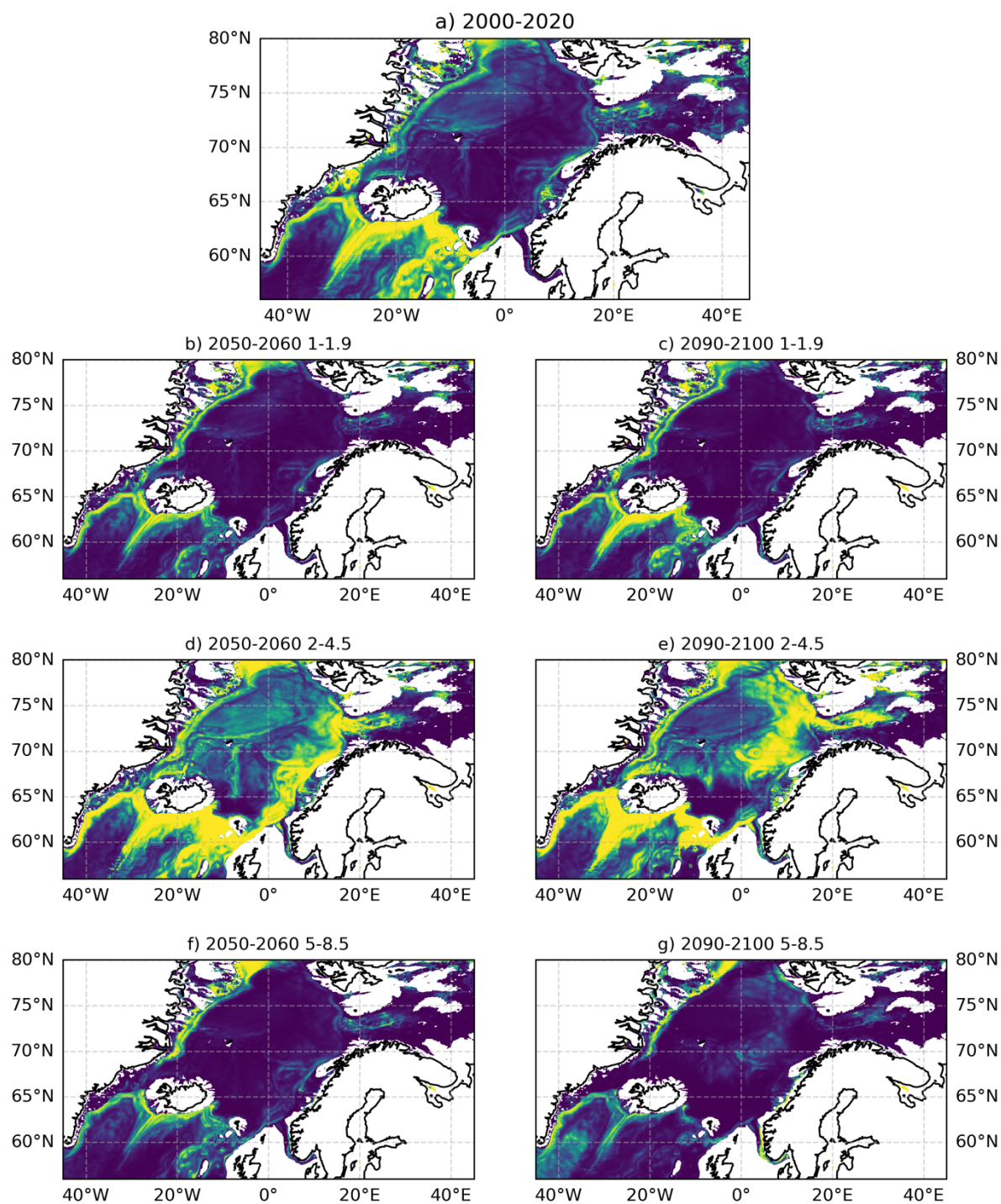
Themisto abyssorum

Figure S29: Maps show the habitat suitability of *Themisto abyssorum* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

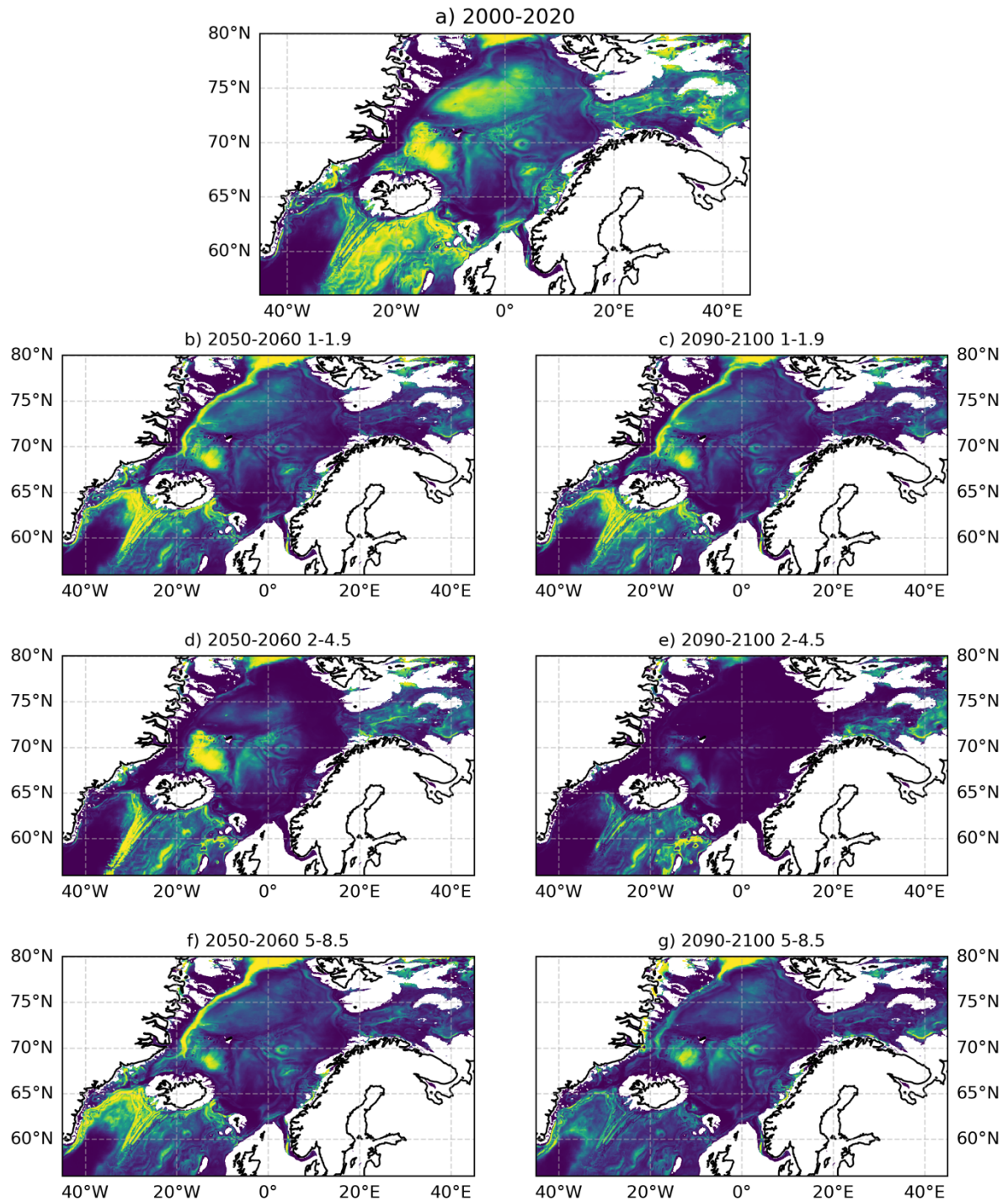
Hippomedon propinquus

Figure S30: Maps show the habitat suitability of *Hippomedon propinquus* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

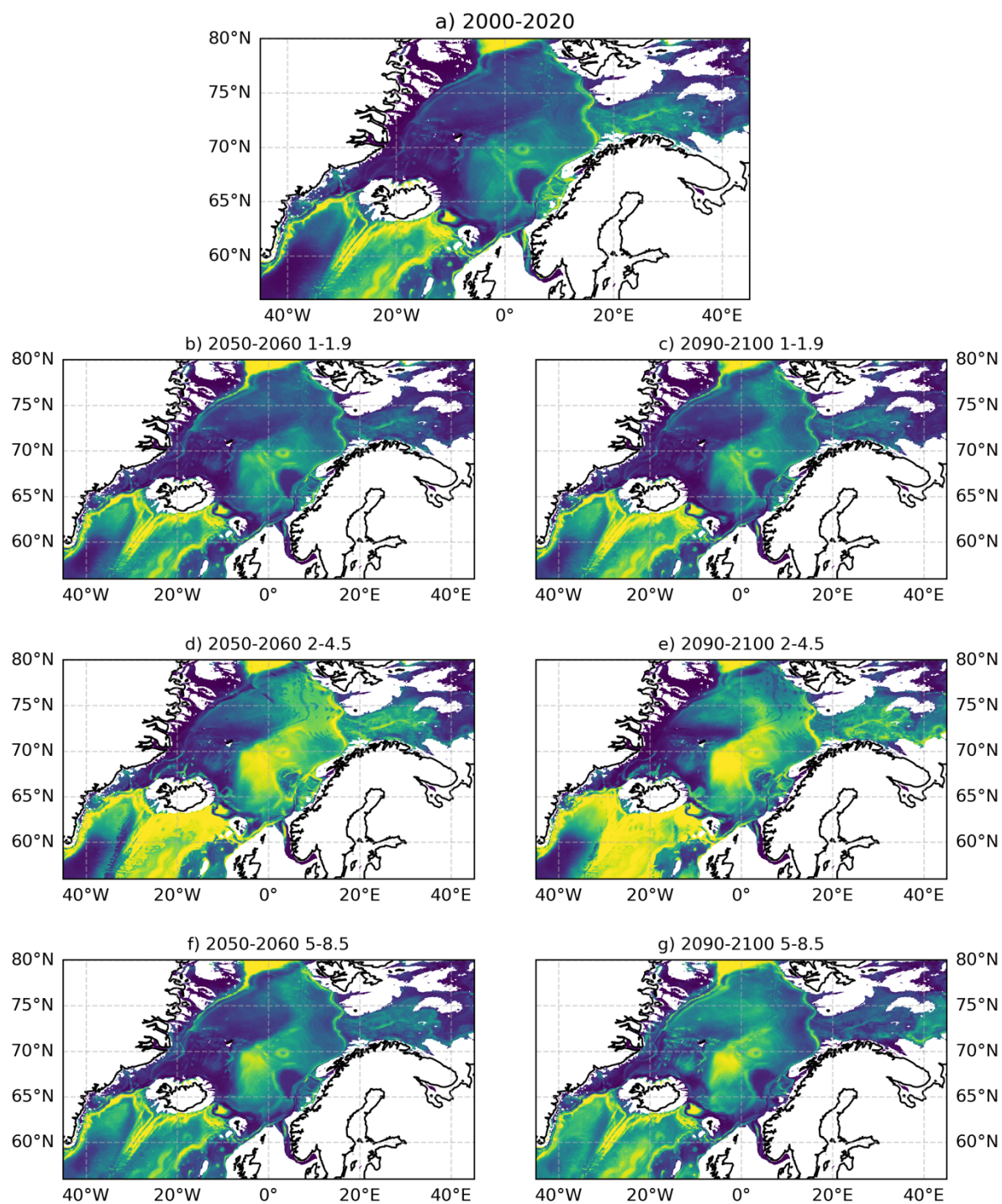
Liljeborgia fissicornis

Figure S31: Maps show the habitat suitability of *Liljeborgia fissicornis* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

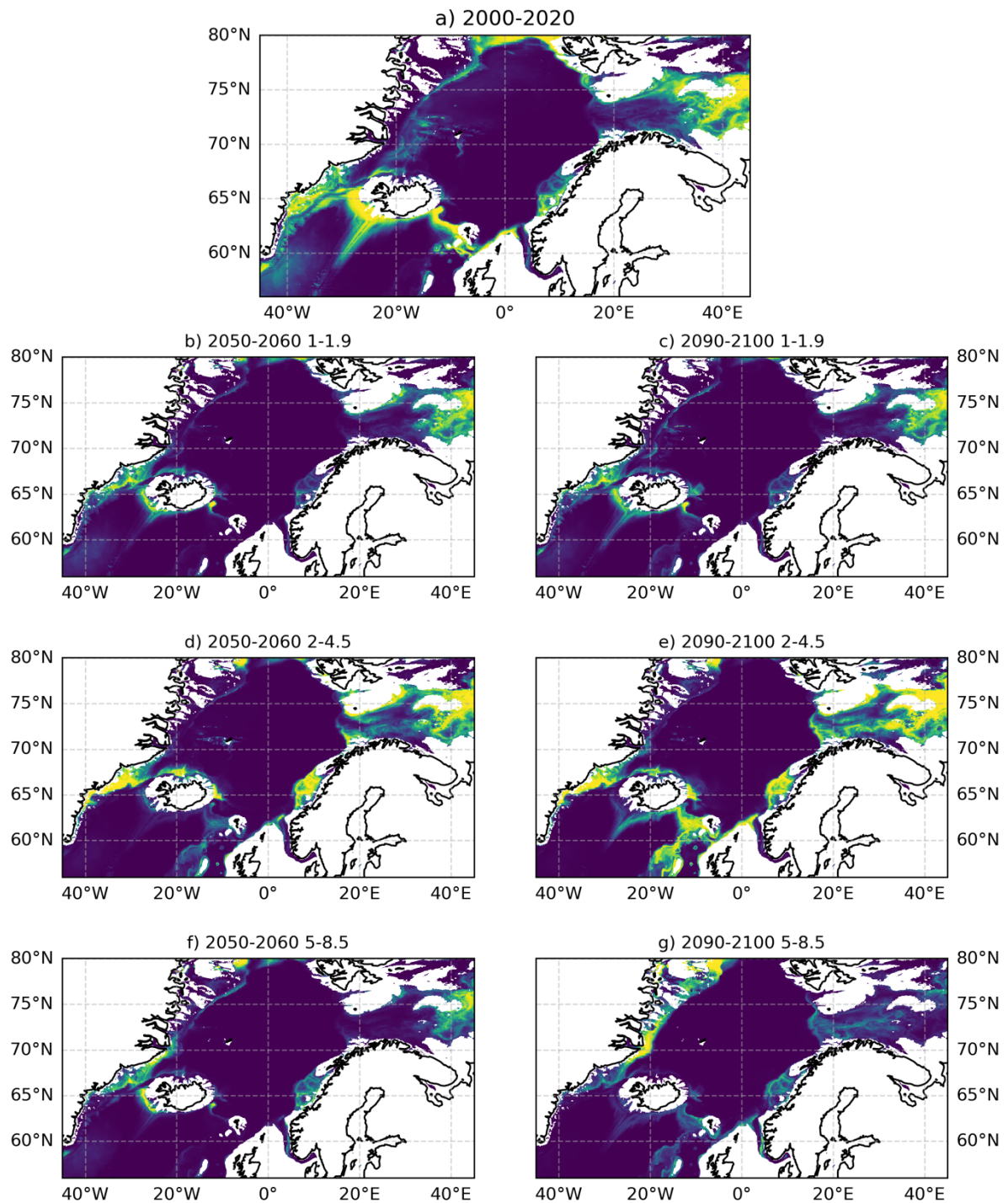
Syrrhoe crenulata

Figure S32: Maps show the habitat suitability of *Syrrhoe crenulata* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

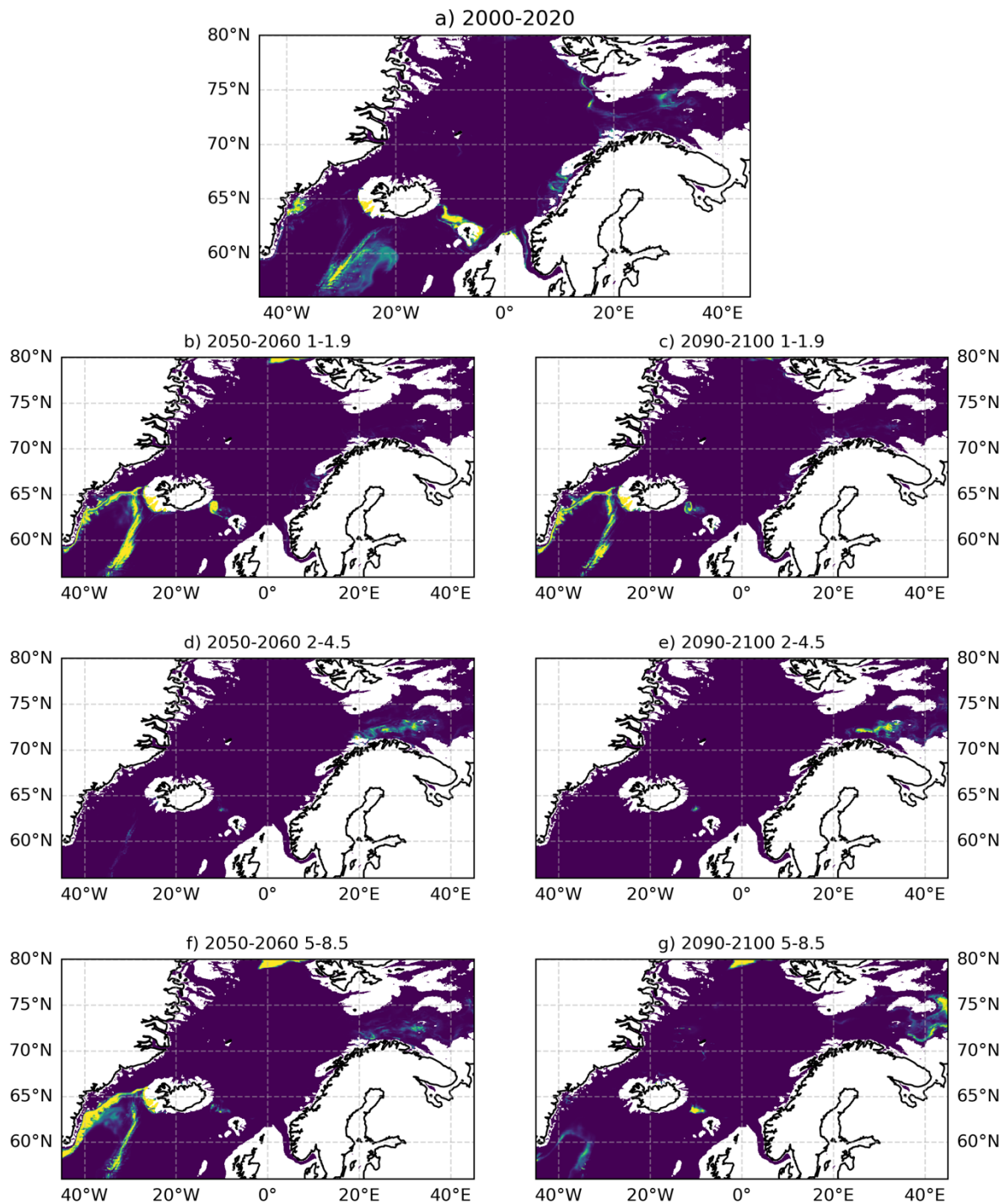
Hippomedon denticulatus

Figure S33: Maps show the habitat suitability of *Hippomedon denticulatus* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

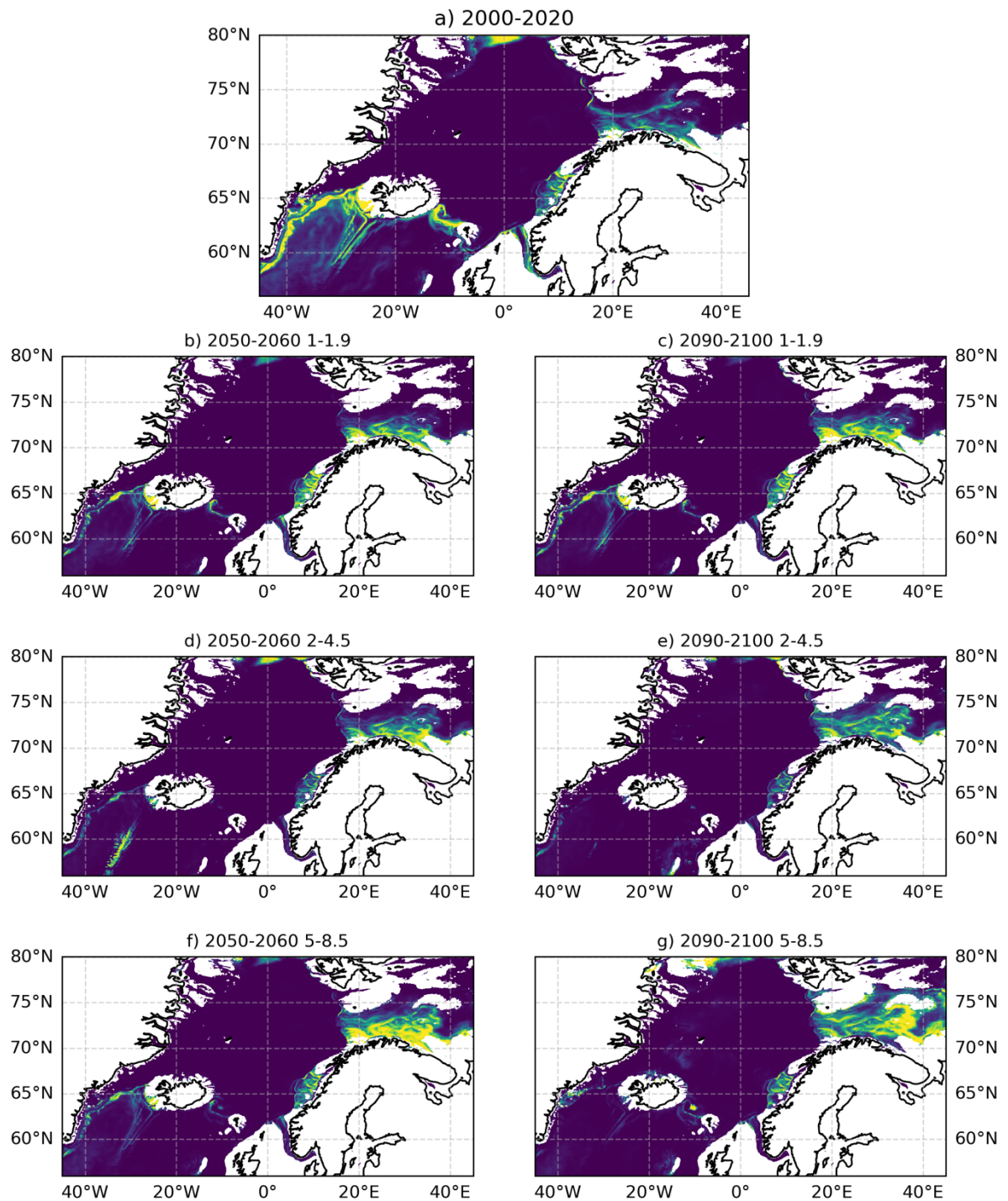
Ampelisca aequicornis

Figure S34: Maps show the habitat suitability of *Ampelisca aequicornis* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

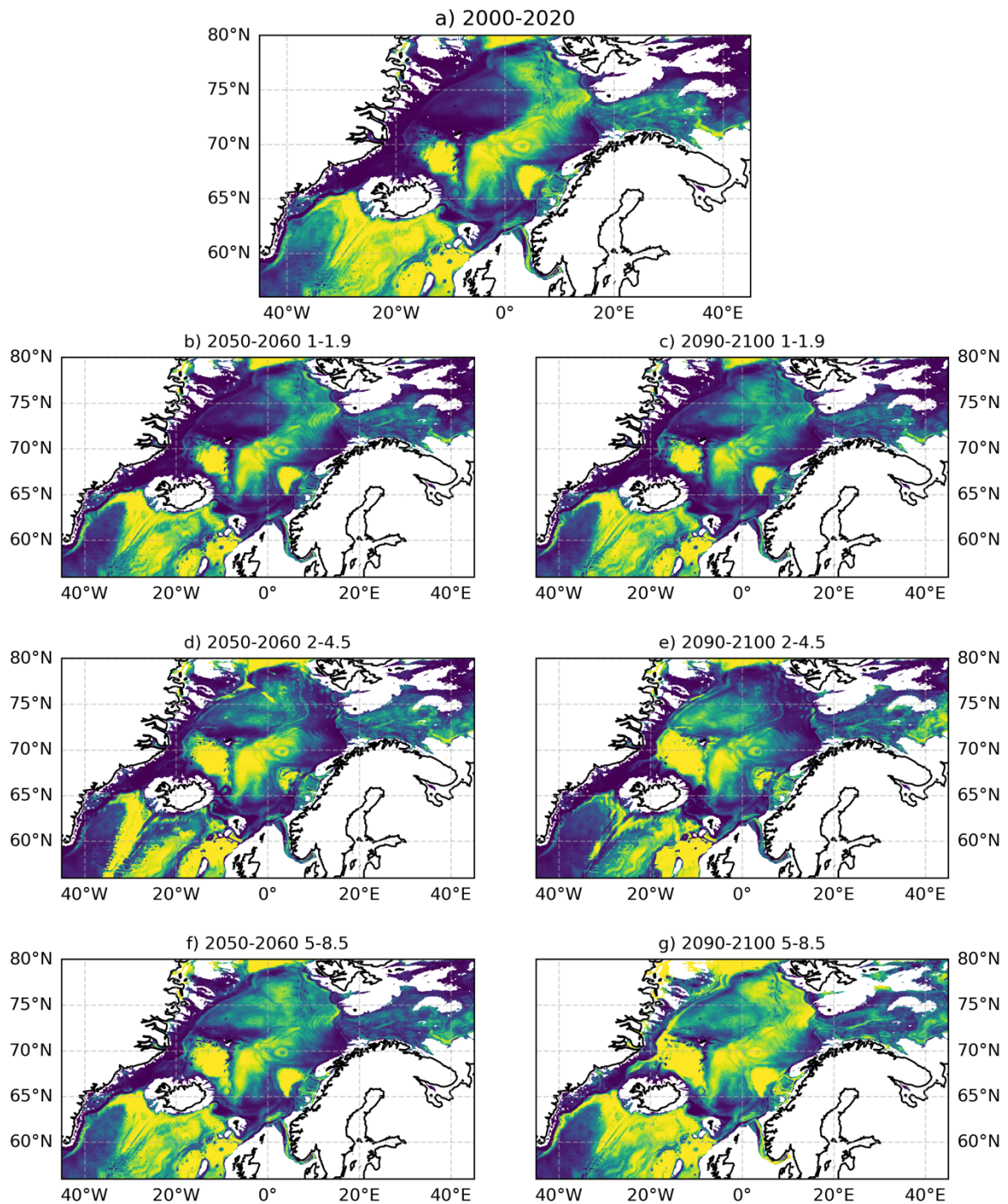
Tmetonyx similis

Figure S35: Maps show the habitat suitability of *Tmetonyx similis* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

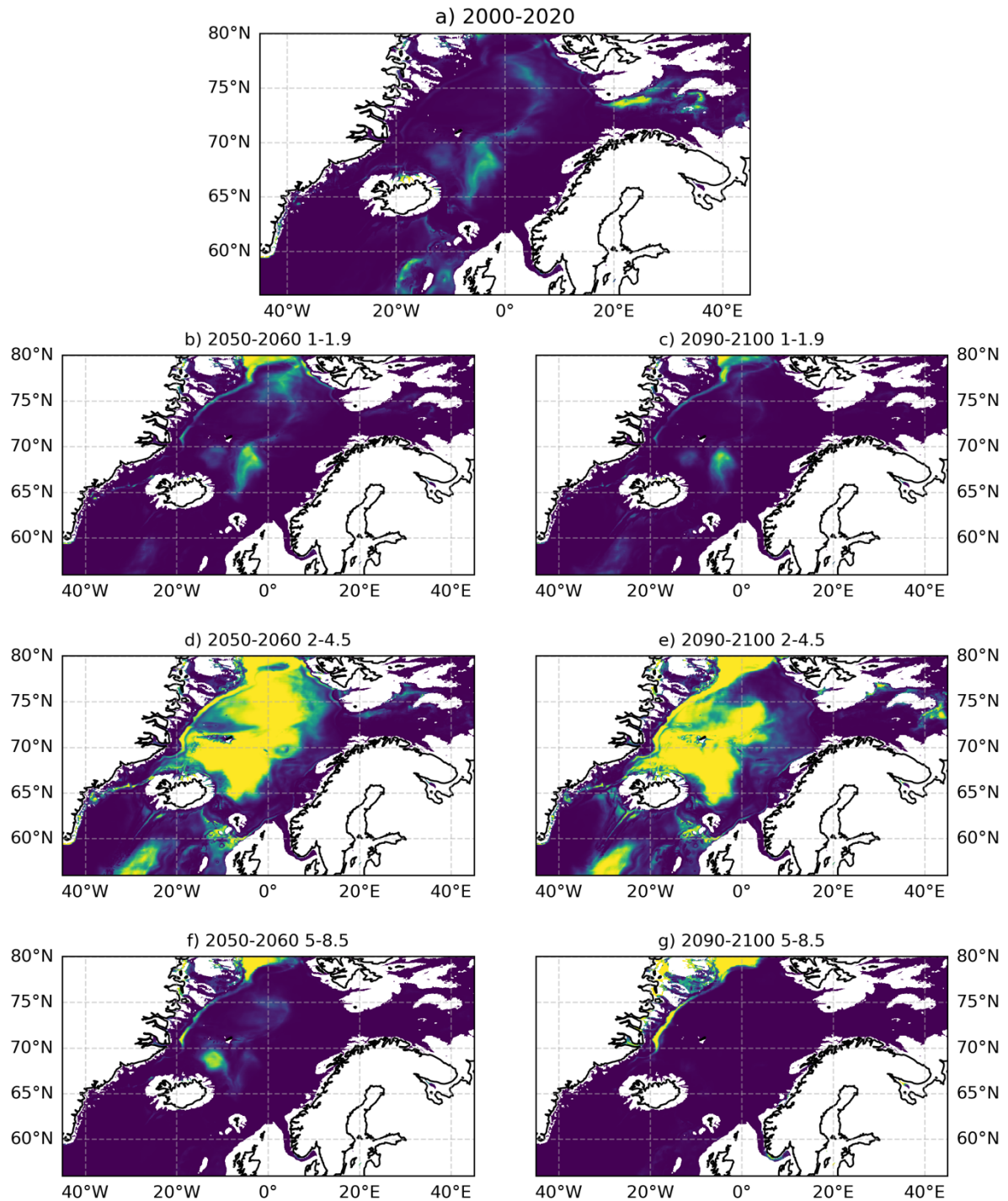
Aceroides (Aceroides) latipes

Figure S36: Maps show the habitat suitability of *Aceroides (Aceroides) latipes* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

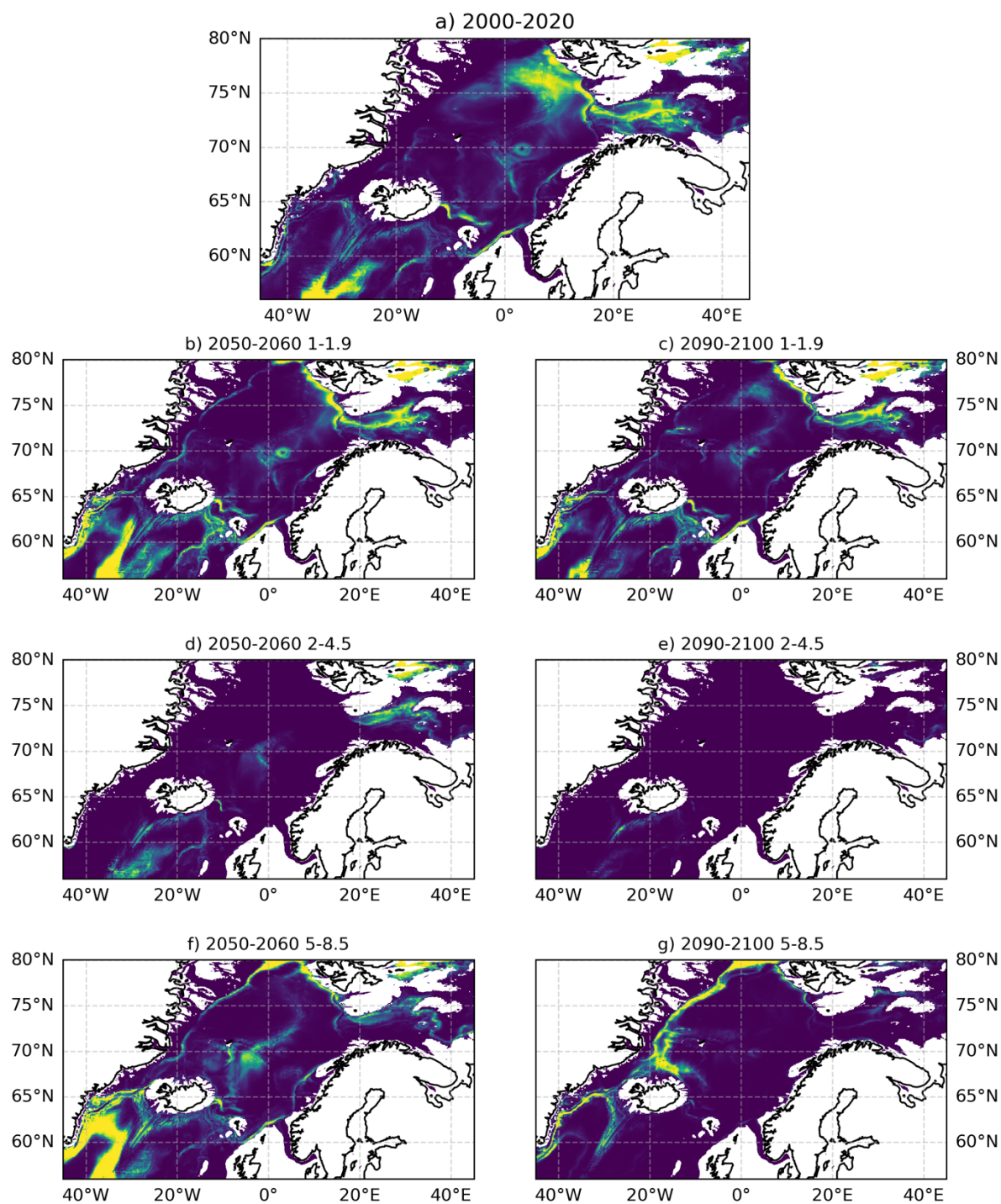
Harpinia mucronata

Figure S37: Maps show the habitat suitability of *Harpinia mucronata* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

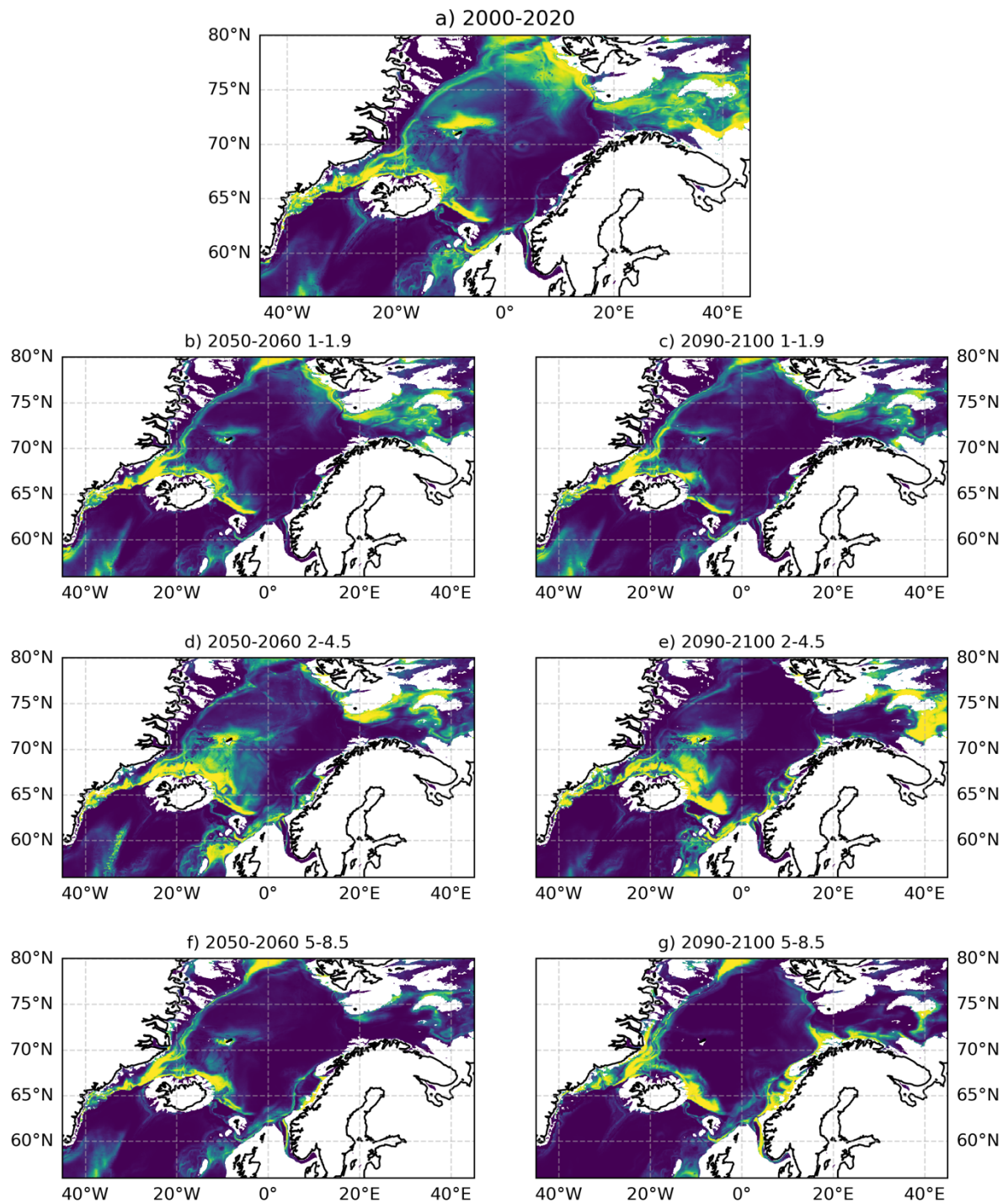
Haploops tubicola

Figure S38: Maps show the habitat suitability of *Haploops tubicola* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

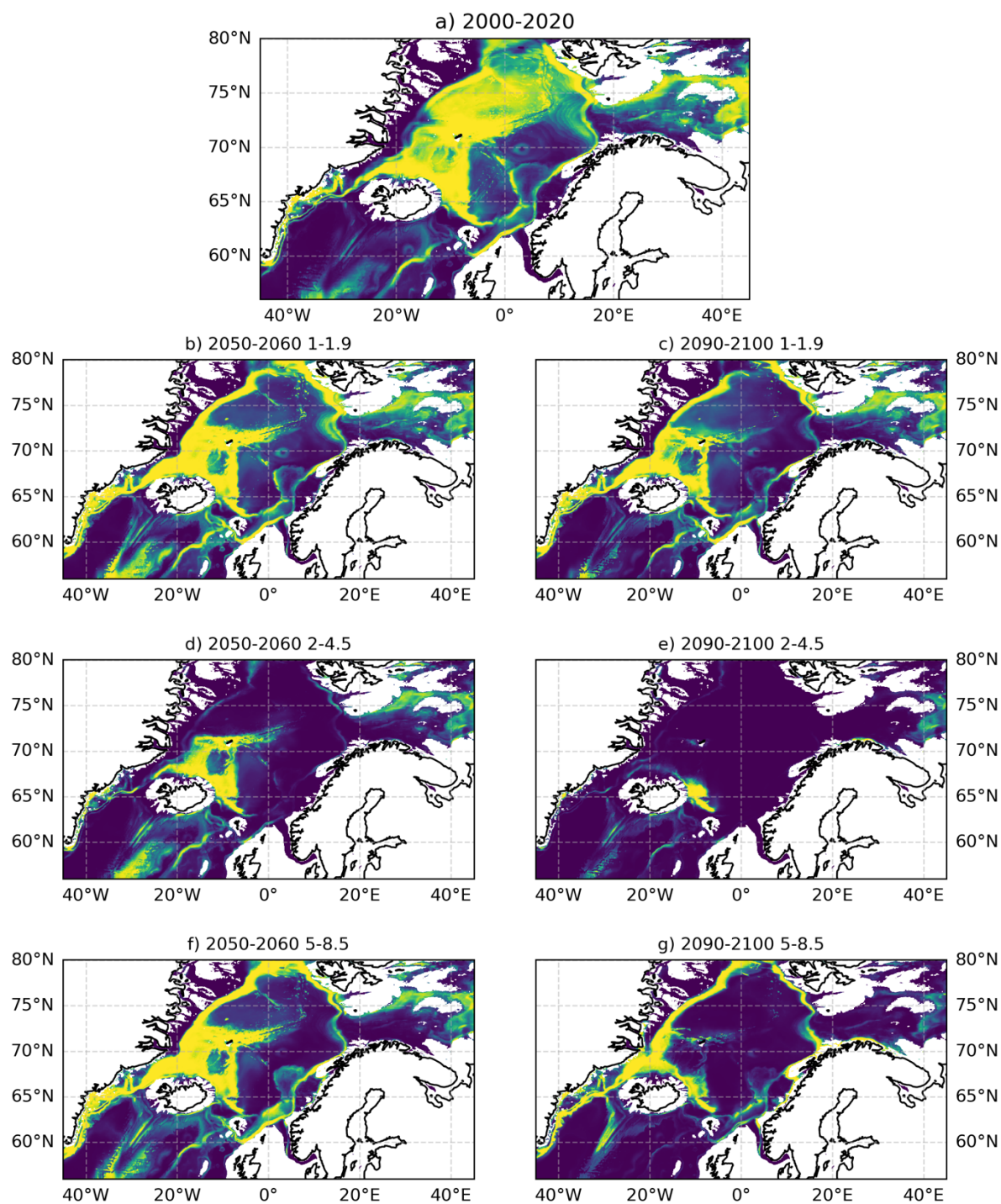
Unciola leucopis

Figure S39: Maps show the habitat suitability of *Unciola leucopis* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

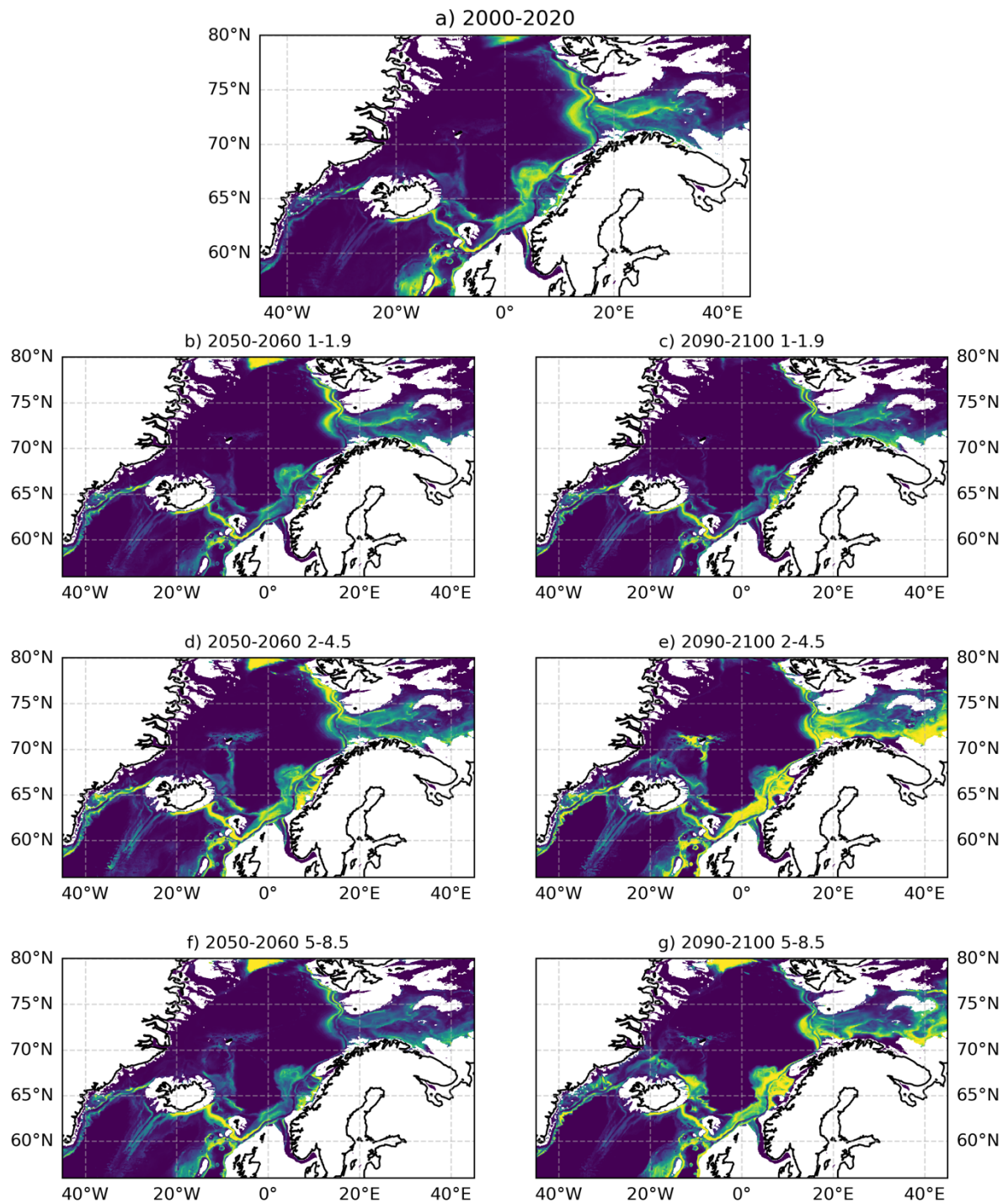
Haploops setosa

Figure S40: Maps show the habitat suitability of *Haploops setosa* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat

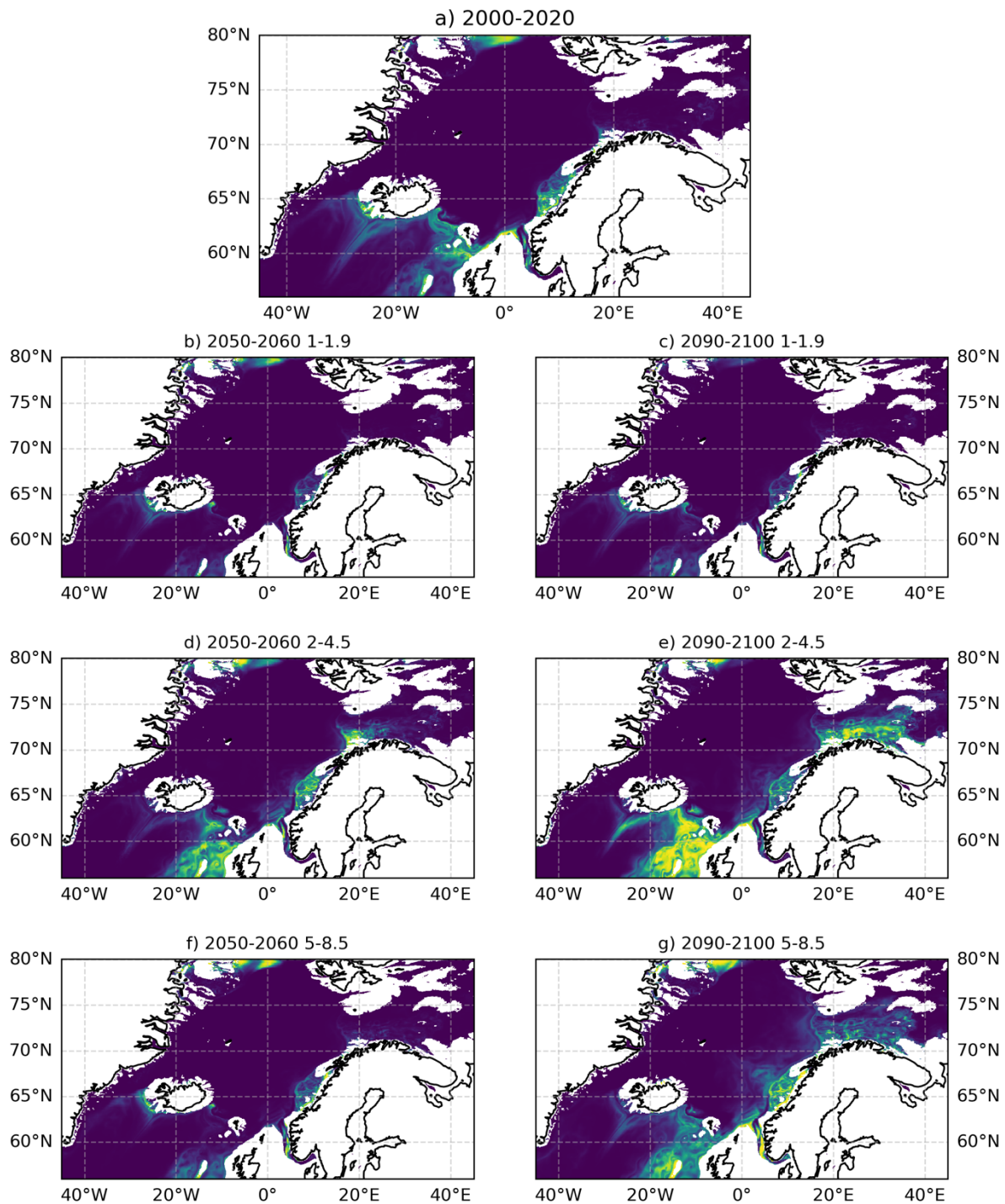
Bruzelia typica

Figure S41: Maps show the habitat suitability of *Bruzelia typica* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

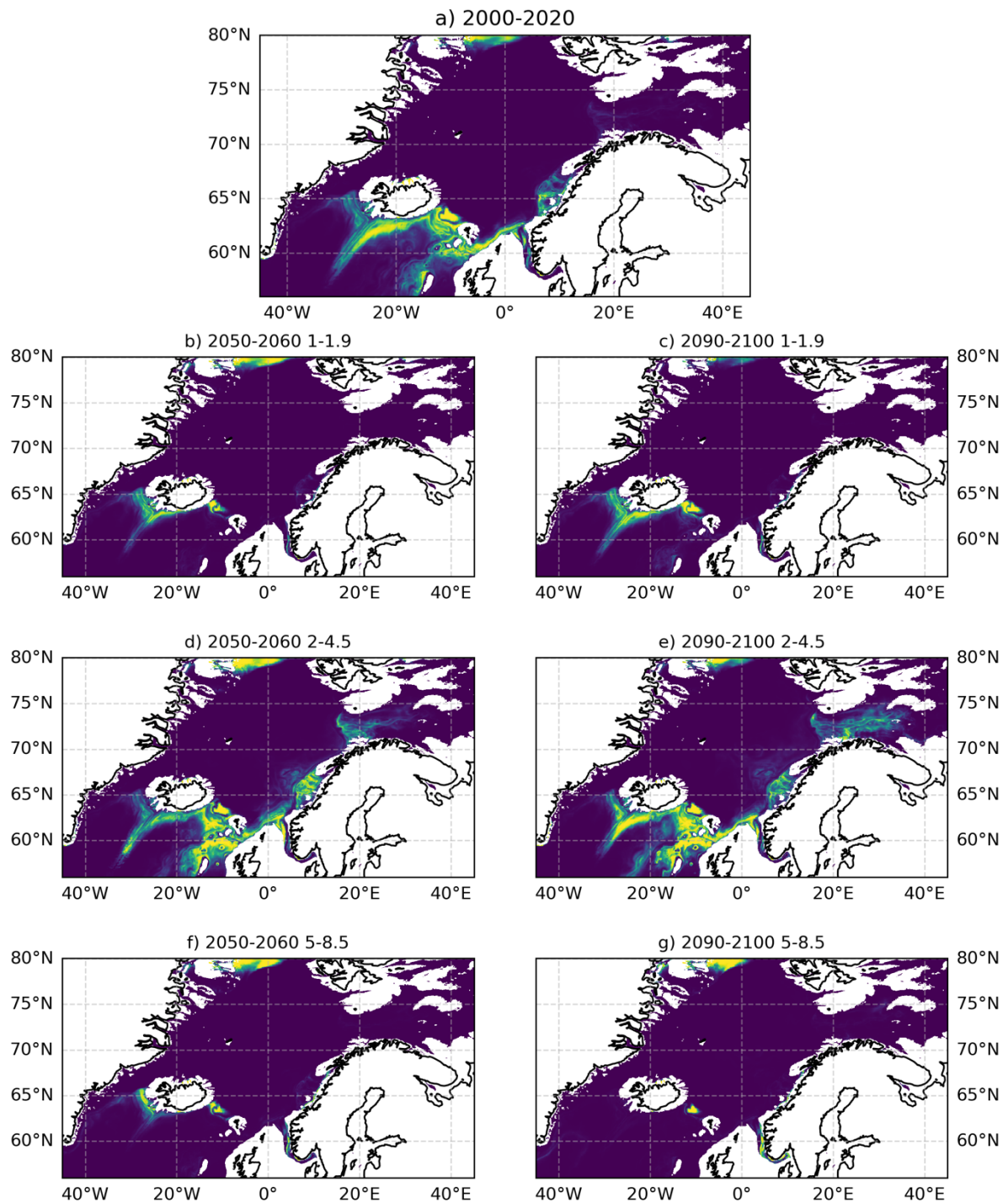
Xenodice frauenfeldti

Figure S42: Maps show the habitat suitability of *Xenodice frauenfeldti* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

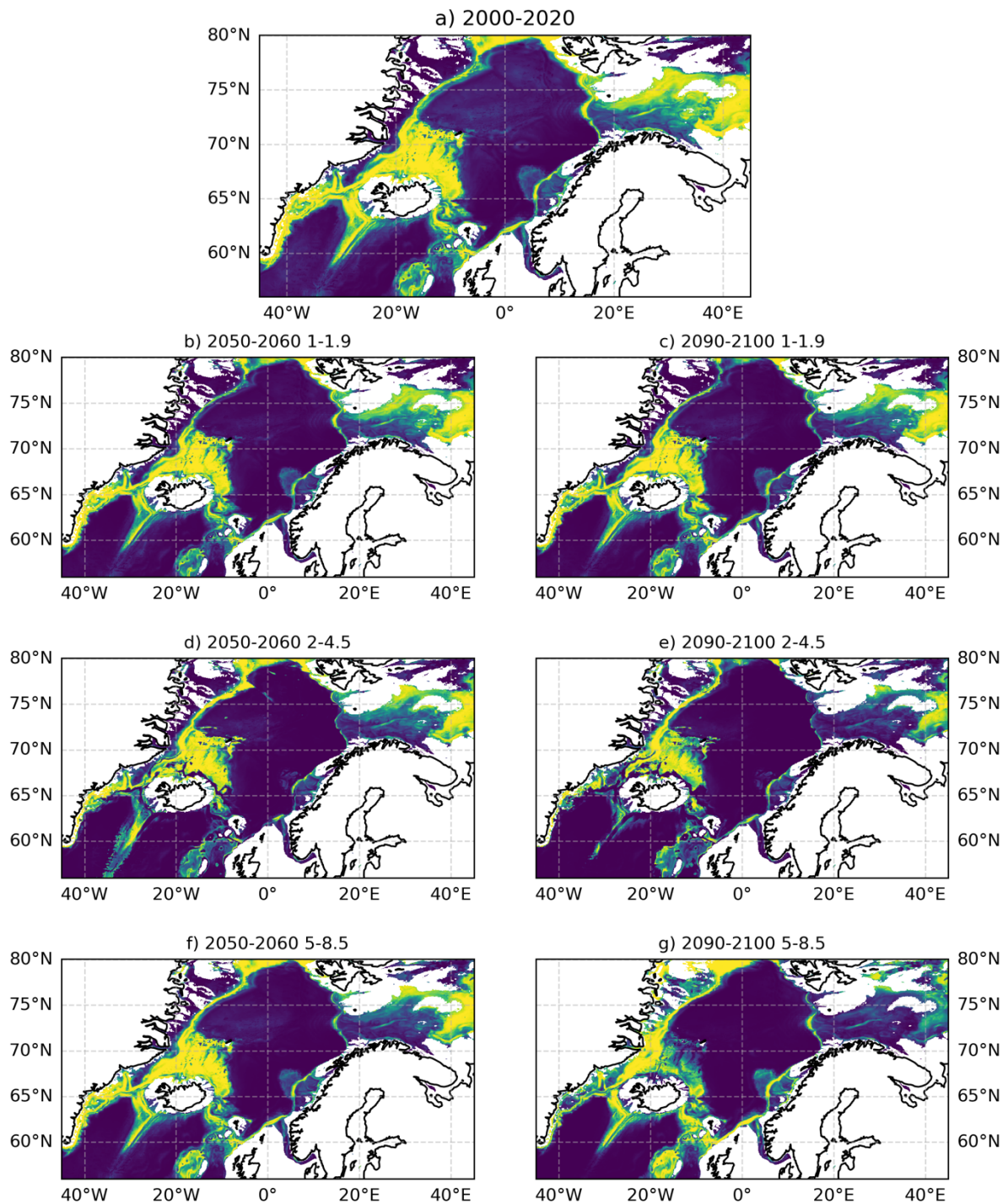
Ischyrocerus megacheir

Figure S43: Maps show the habitat suitability of *Ischyrocerus megacheir* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

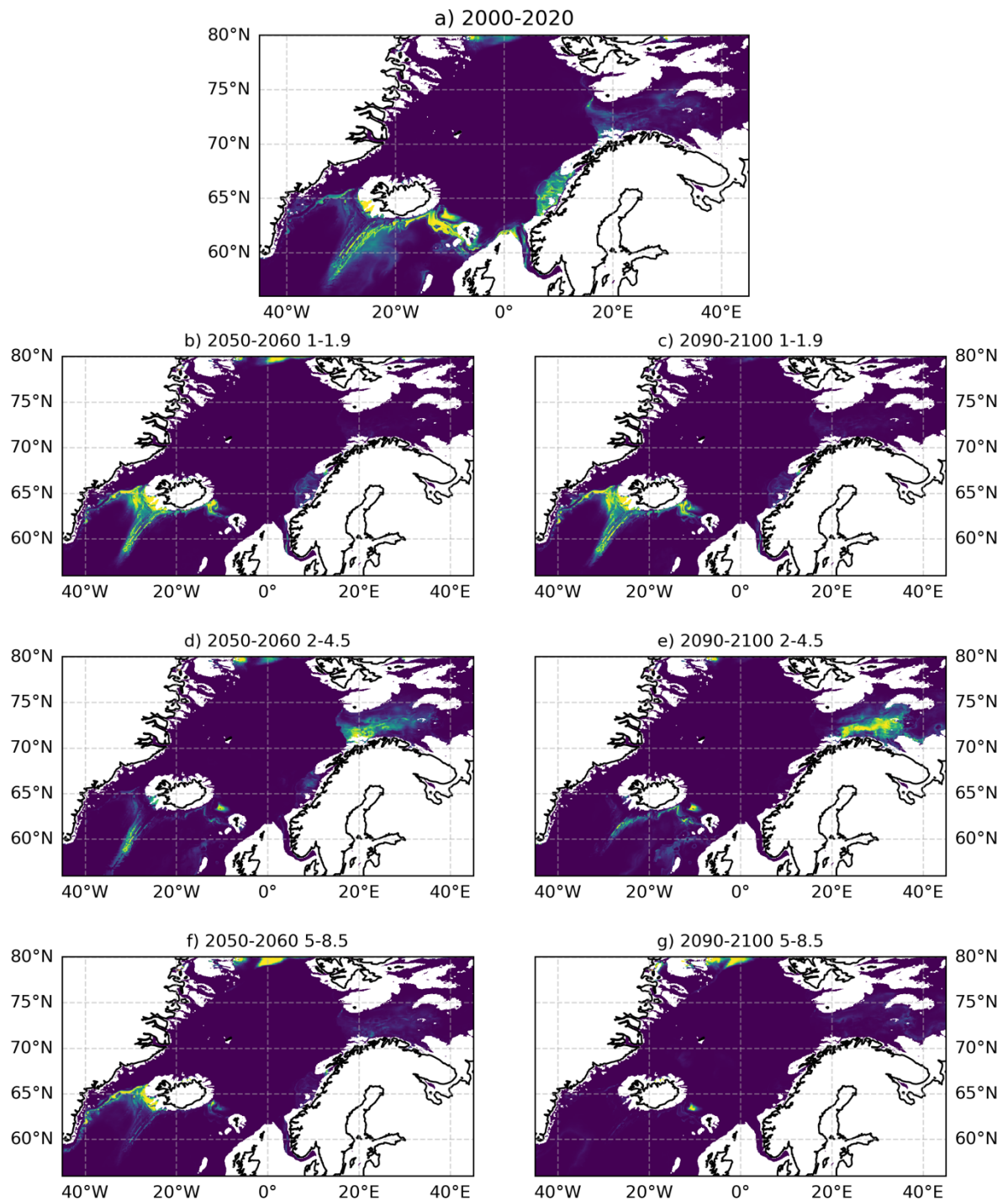
Nicippe tumida

Figure S44: Maps show the habitat suitability of *Nicippe tumida* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

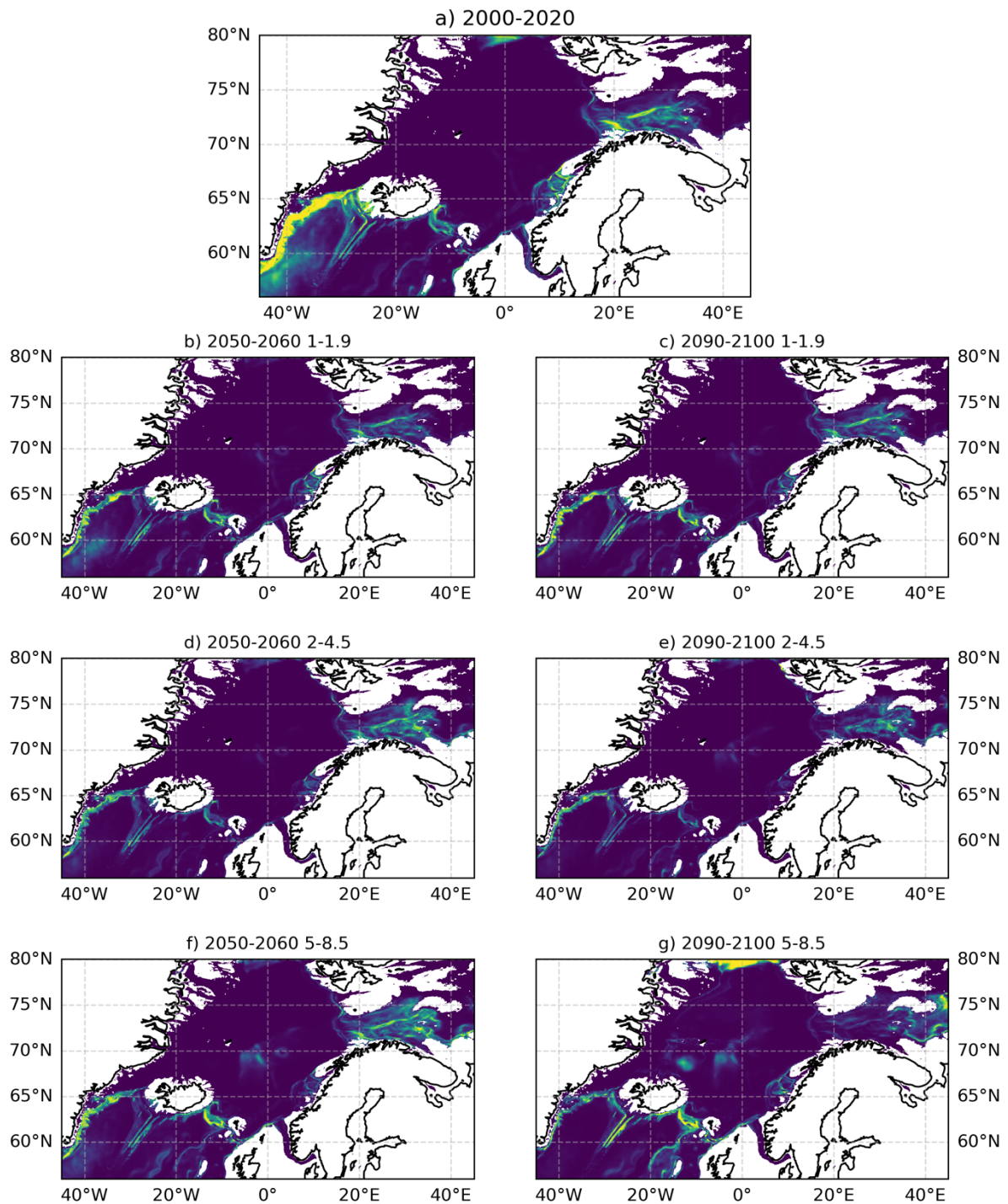
Liljeborgia pallida

Figure S45: Maps show the habitat suitability of *Liljeborgia pallida* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

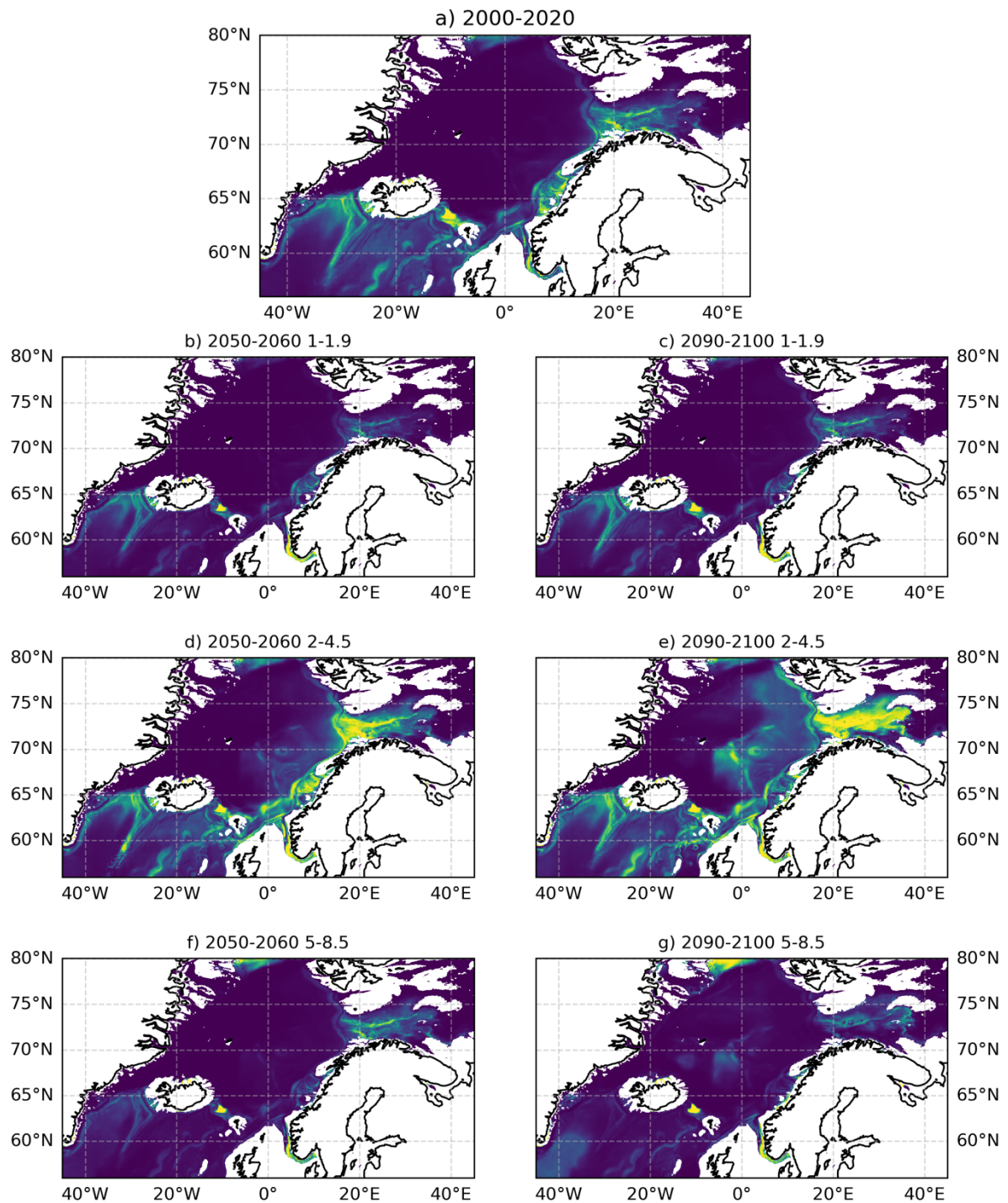
Bathymedon saussurei

Figure S46: Maps show the habitat suitability of *Bathymedon saussurei* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

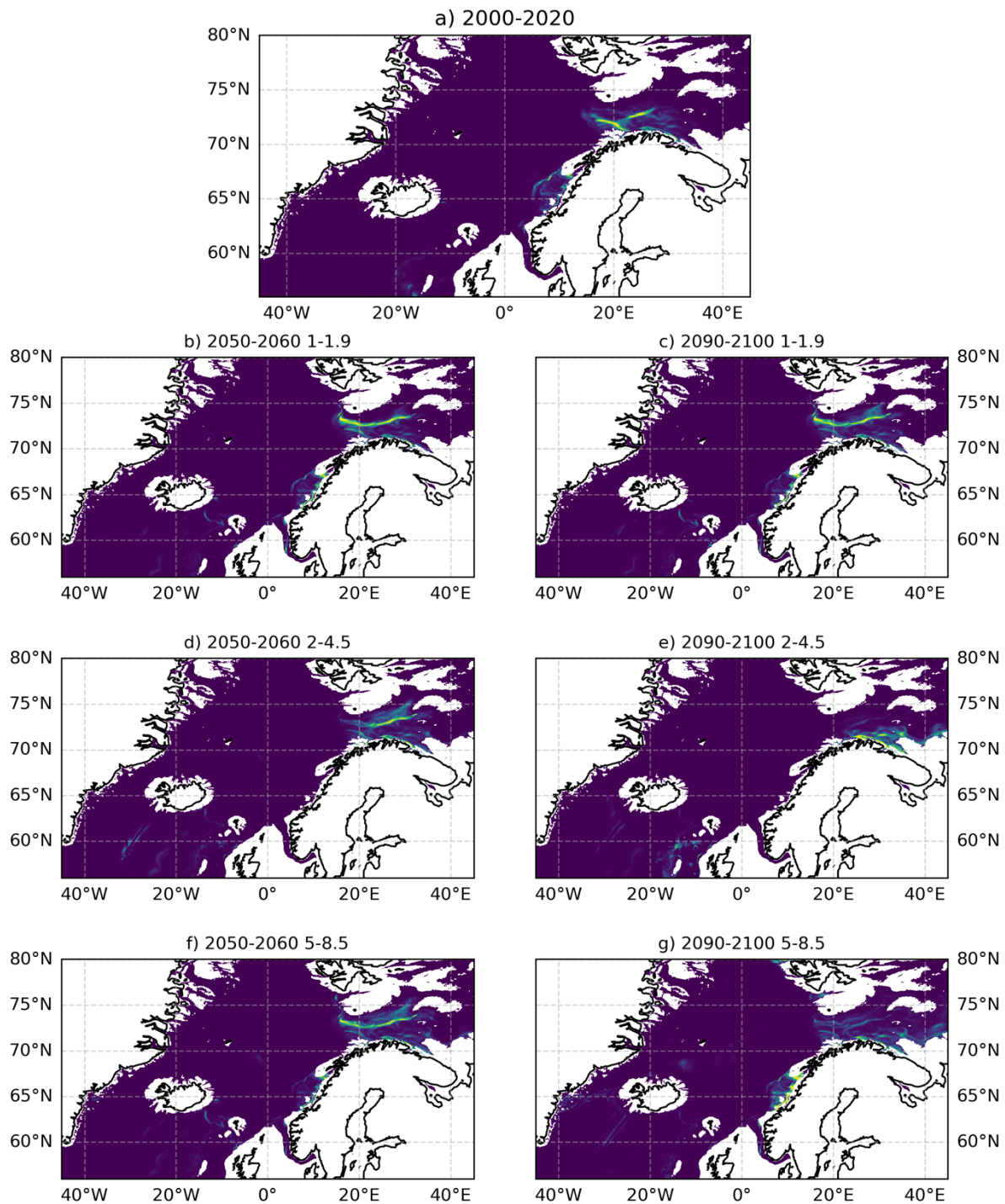
Autonoe megacheir

Figure S47: Maps show the habitat suitability of *Autonoe megacheir* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

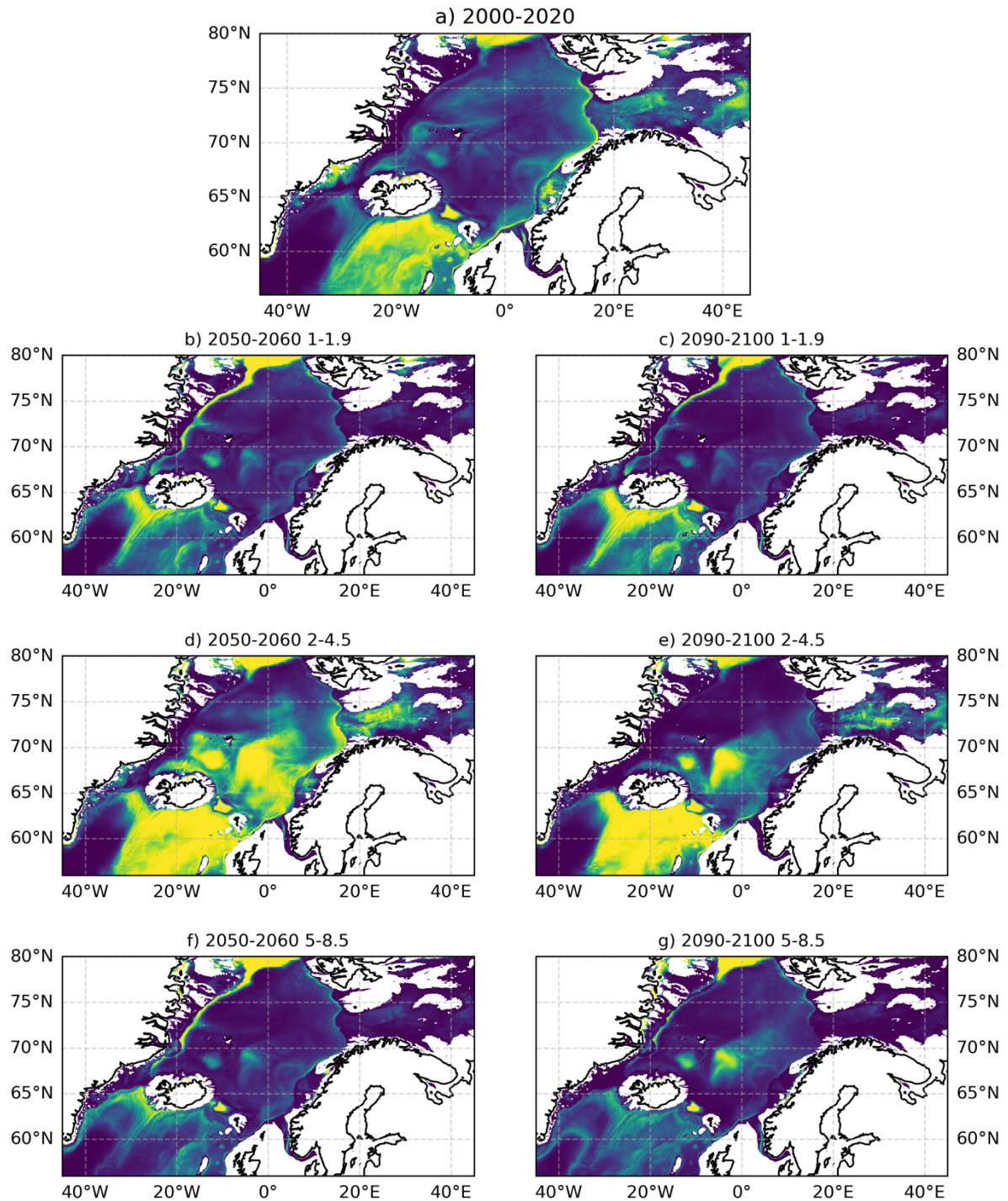
Halice abyssii

Figure S48: Maps show the habitat suitability of *Halice abyssii* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

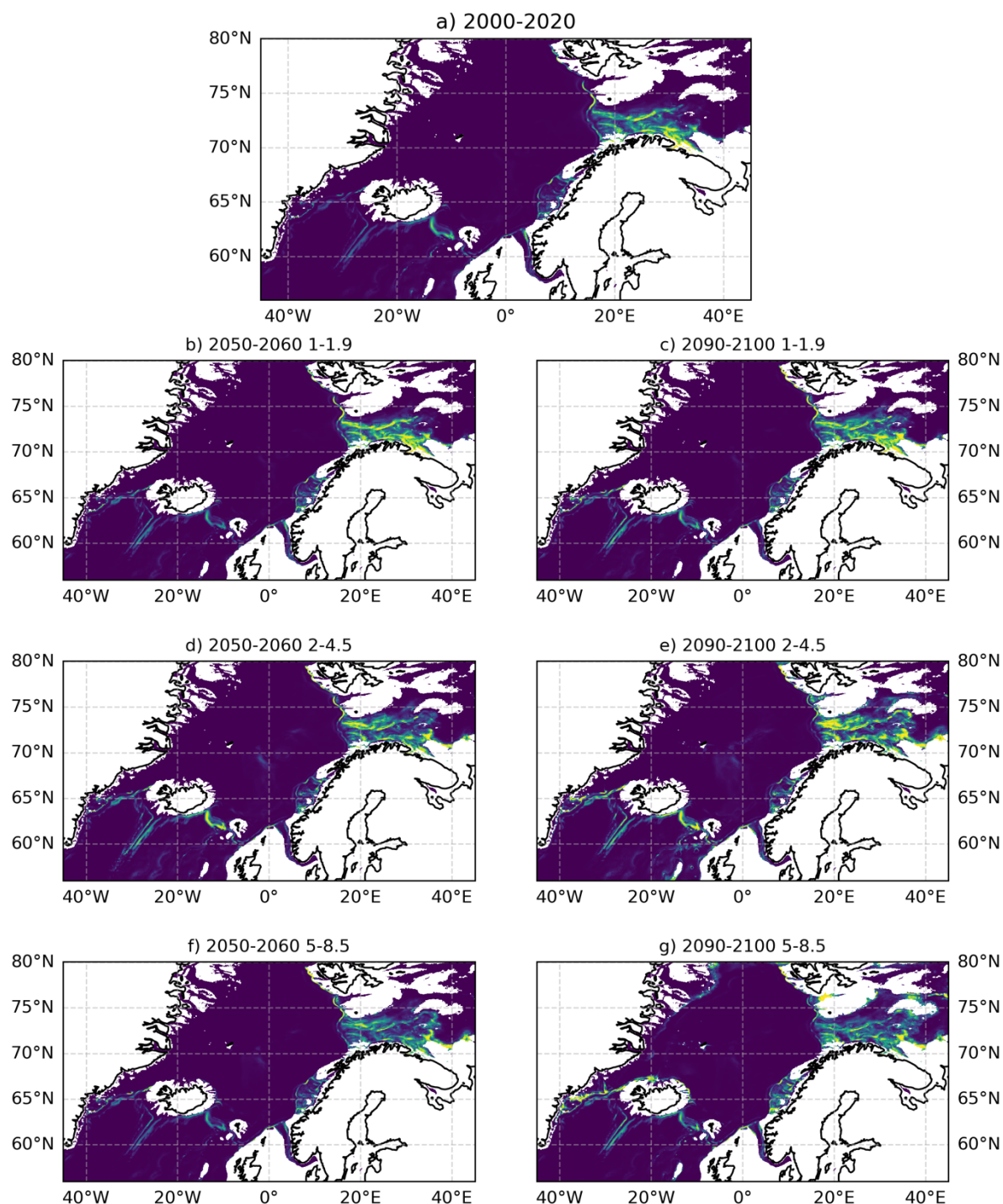
Ampelisca odontoplax

Figure S49: Maps show the habitat suitability of *Ampelisca odontoplax* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

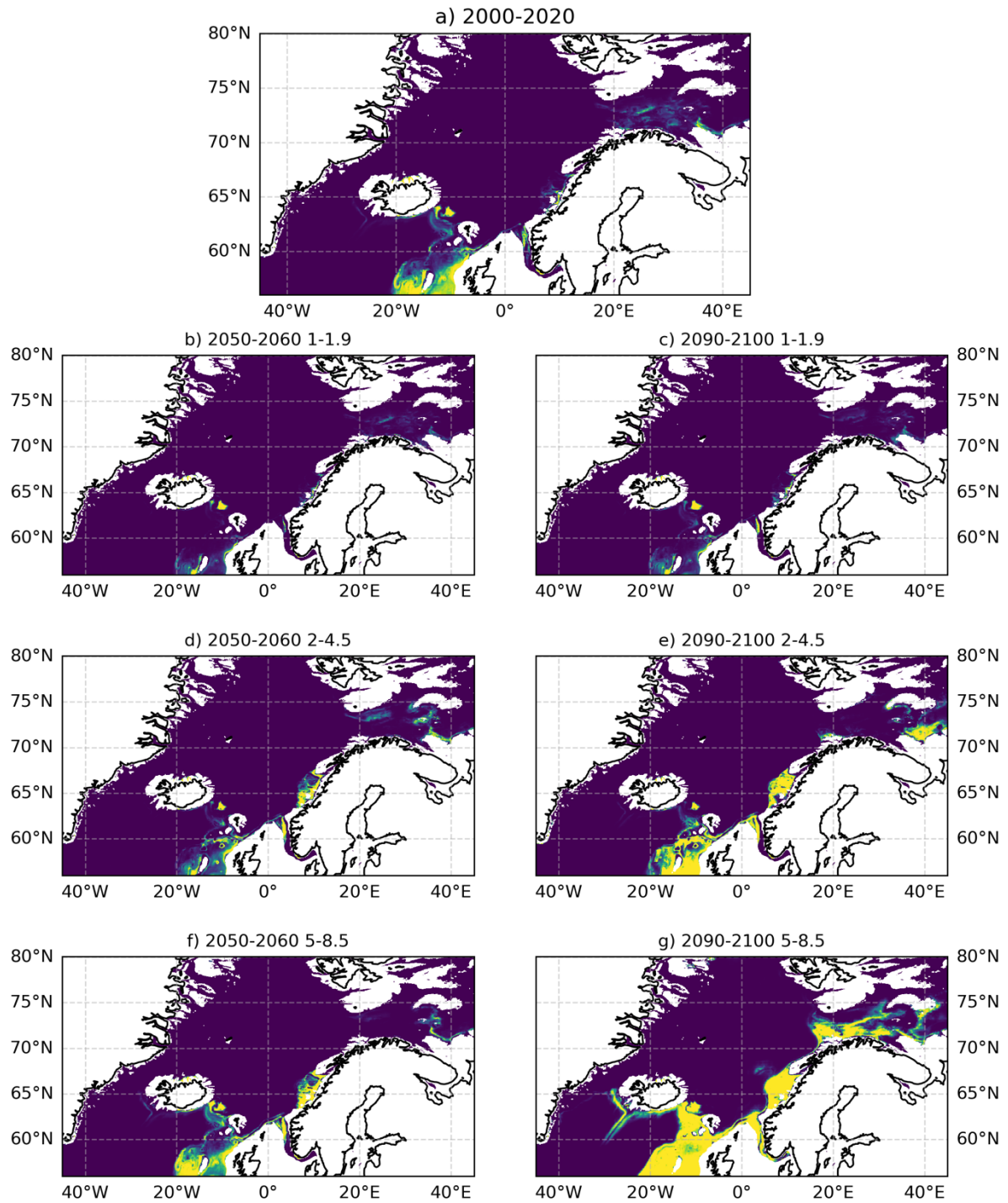
Medicorophium affine

Figure S50: Maps show the habitat suitability of *Medicorophium affine* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

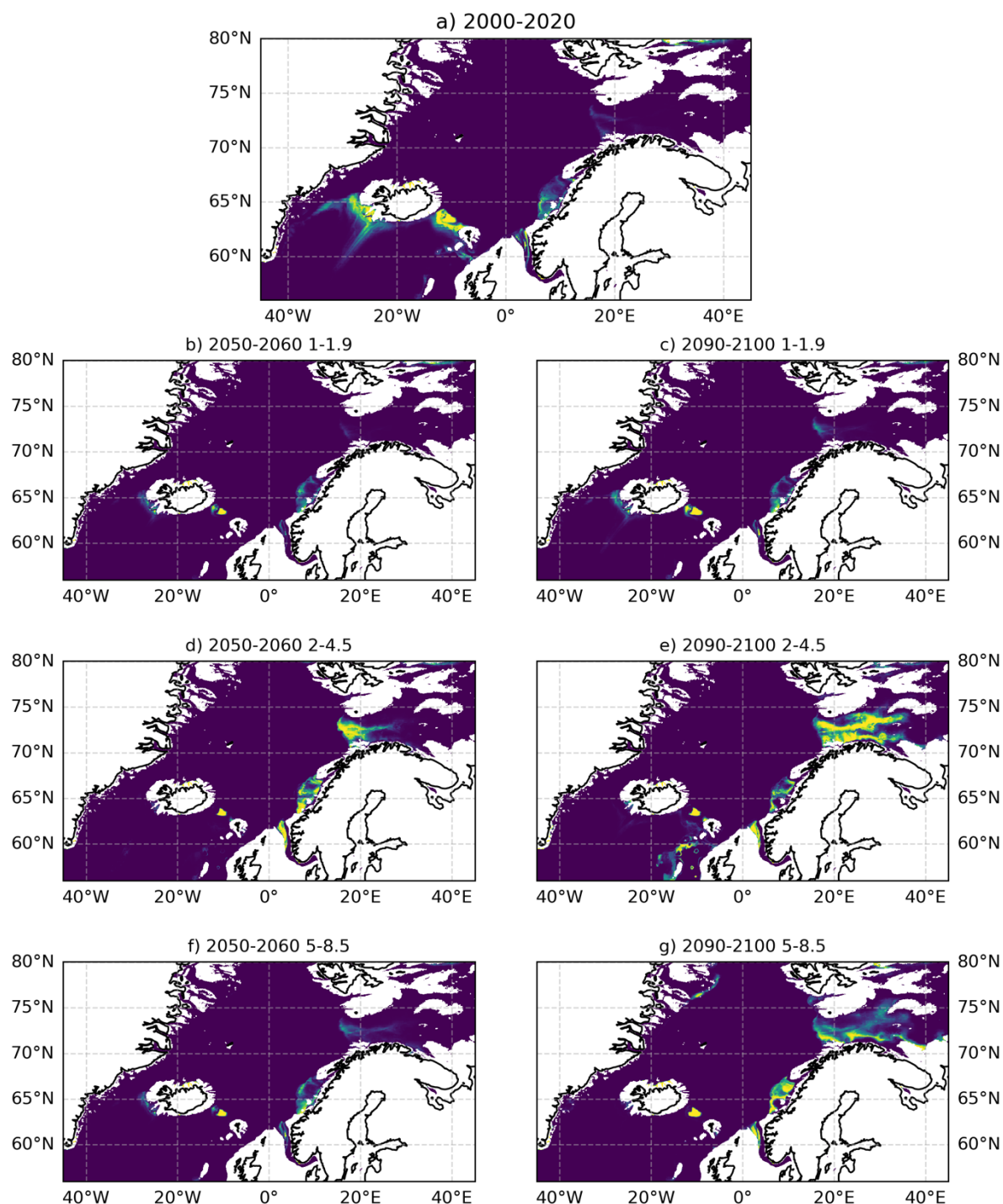
Ampelisca pusilla

Figure S51: Maps show the habitat suitability of *Ampelisca pusilla* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

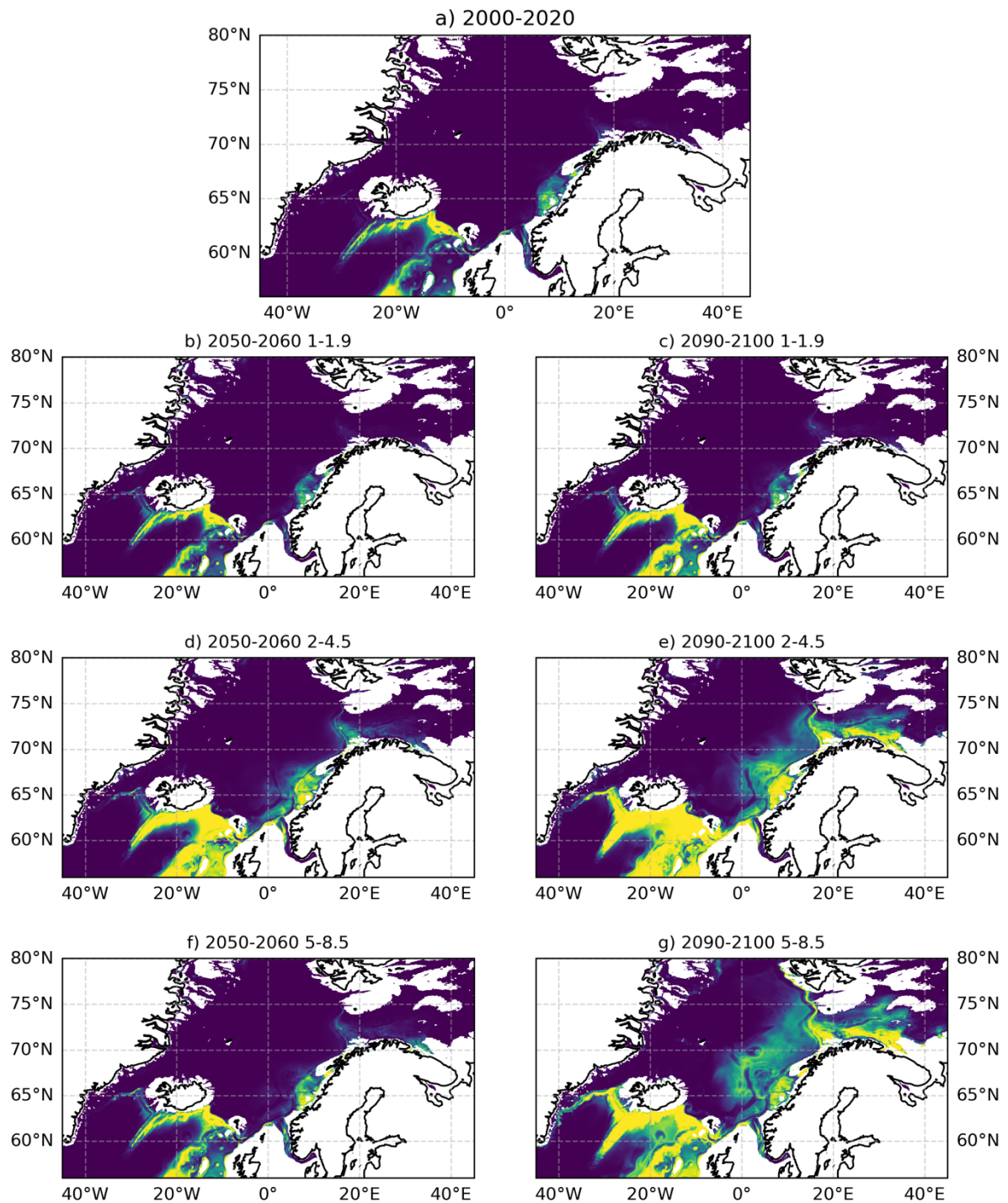
Oediceropsis brevicornis

Figure S52: Maps show the habitat suitability of *Oediceropsis brevicornis* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

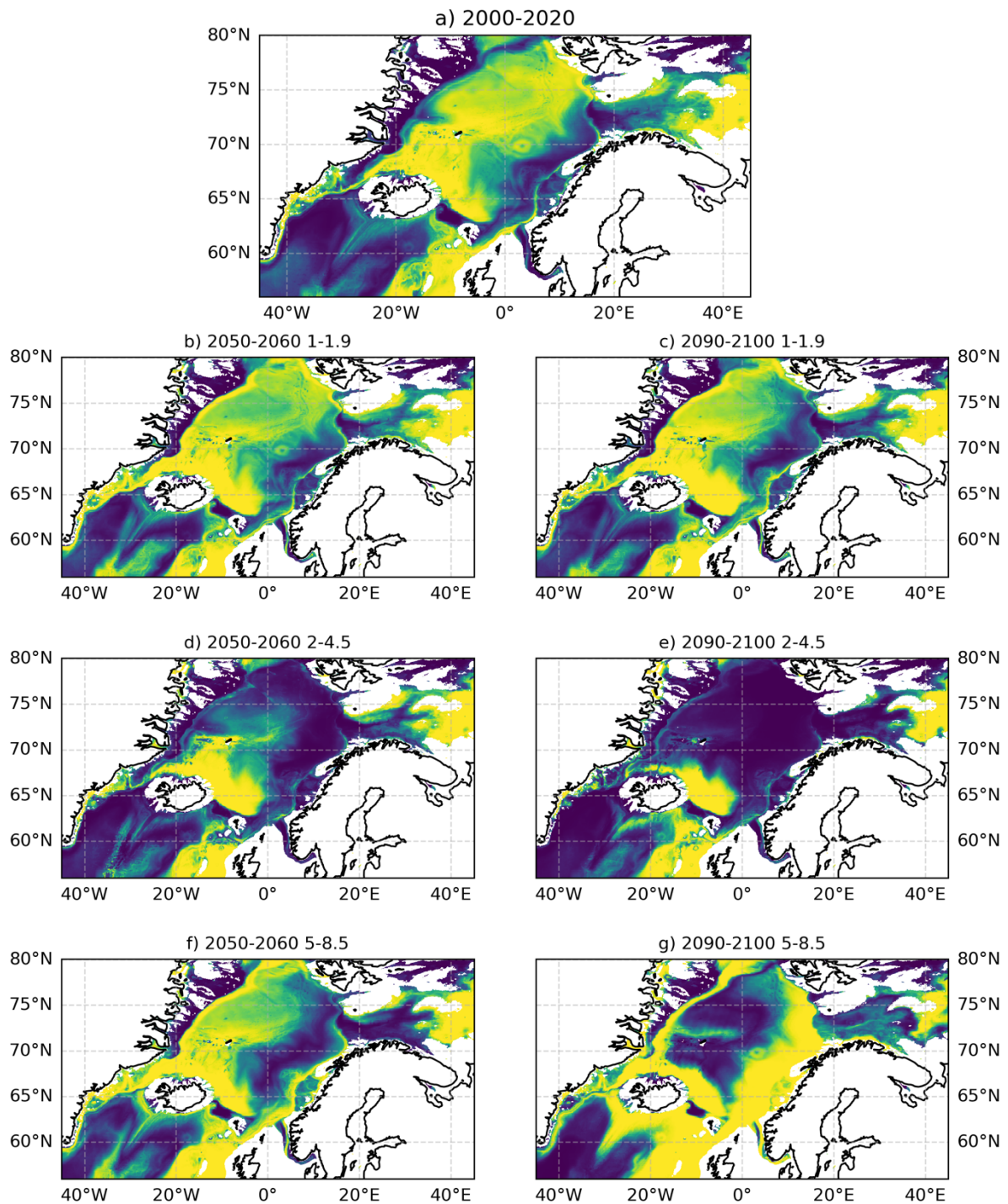
Paraphoxus oculatus

Figure S53: Maps show the habitat suitability of *Paraphoxus oculatus* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

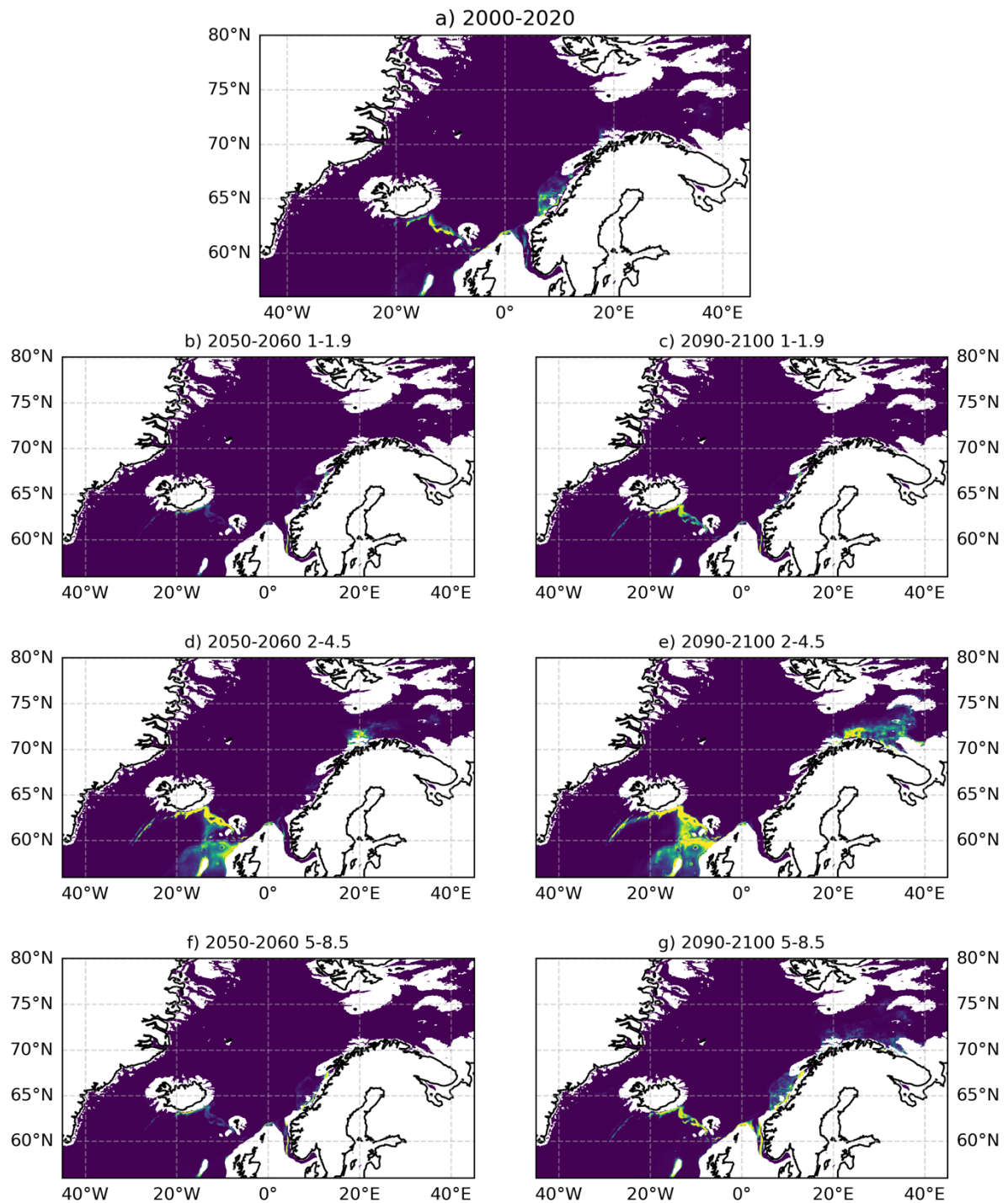
Lysianassa plumosa

Figure S54: Maps show the habitat suitability of *Lysianassa plumosa* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

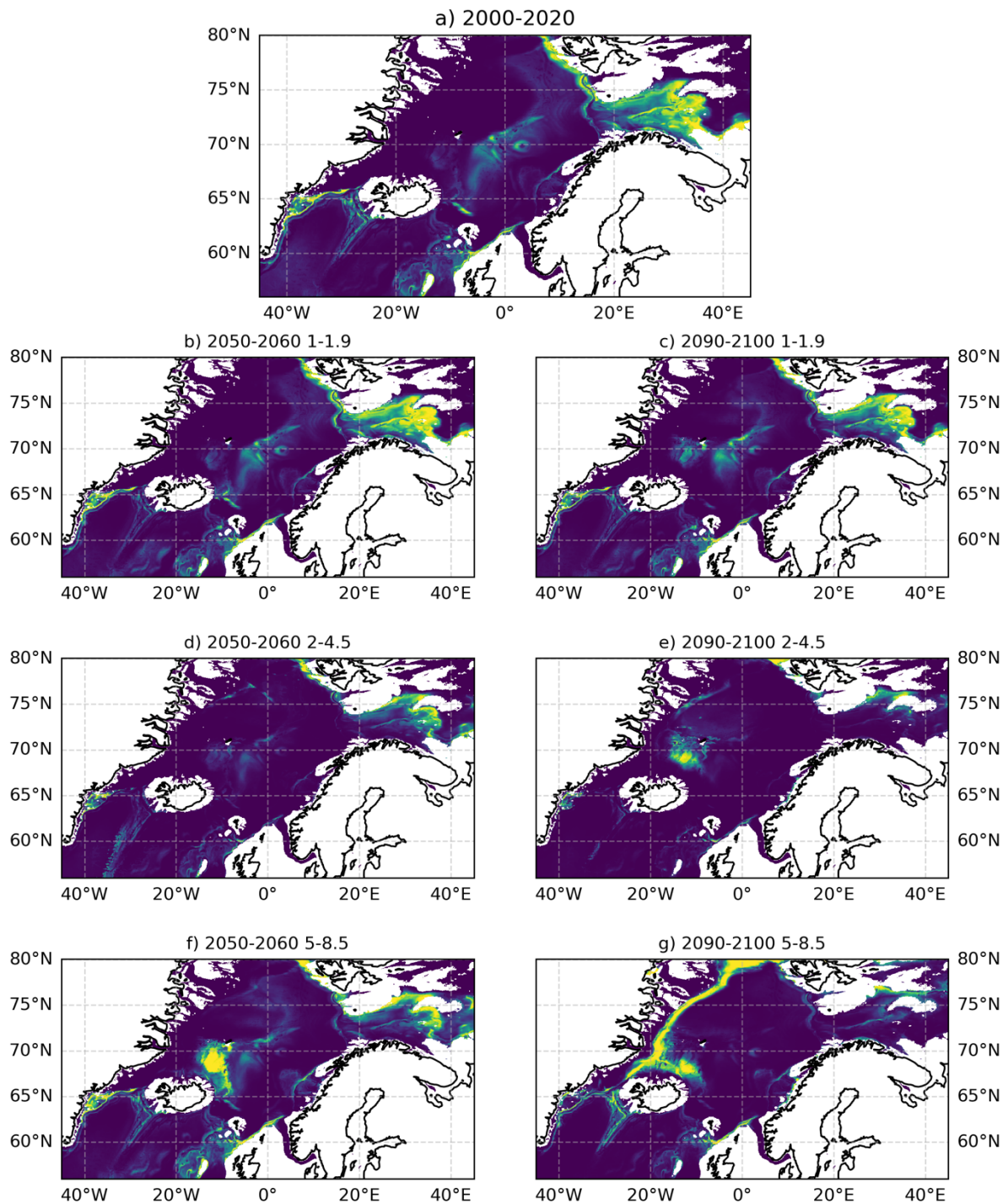
Byblis gaimardii

Figure S55: Maps show the habitat suitability of *Byblis gaimardii* for a) present day, b) 2050–2060 and 1–1.9 SSP scenario, c) 2090–2100 and 1–1.9 SSP scenario, d) 2050–2060 and 2–4.5 SSP scenario, e) 2090–2100 and 2–4.5 SSP scenario, f) 2050–2060 and 5–8.5 SSP scenario, and g) 2090–2100 and 5–8.5 SSP. Purple indicating unsuitable habitat, yellow indicating highly suitable habitat.

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