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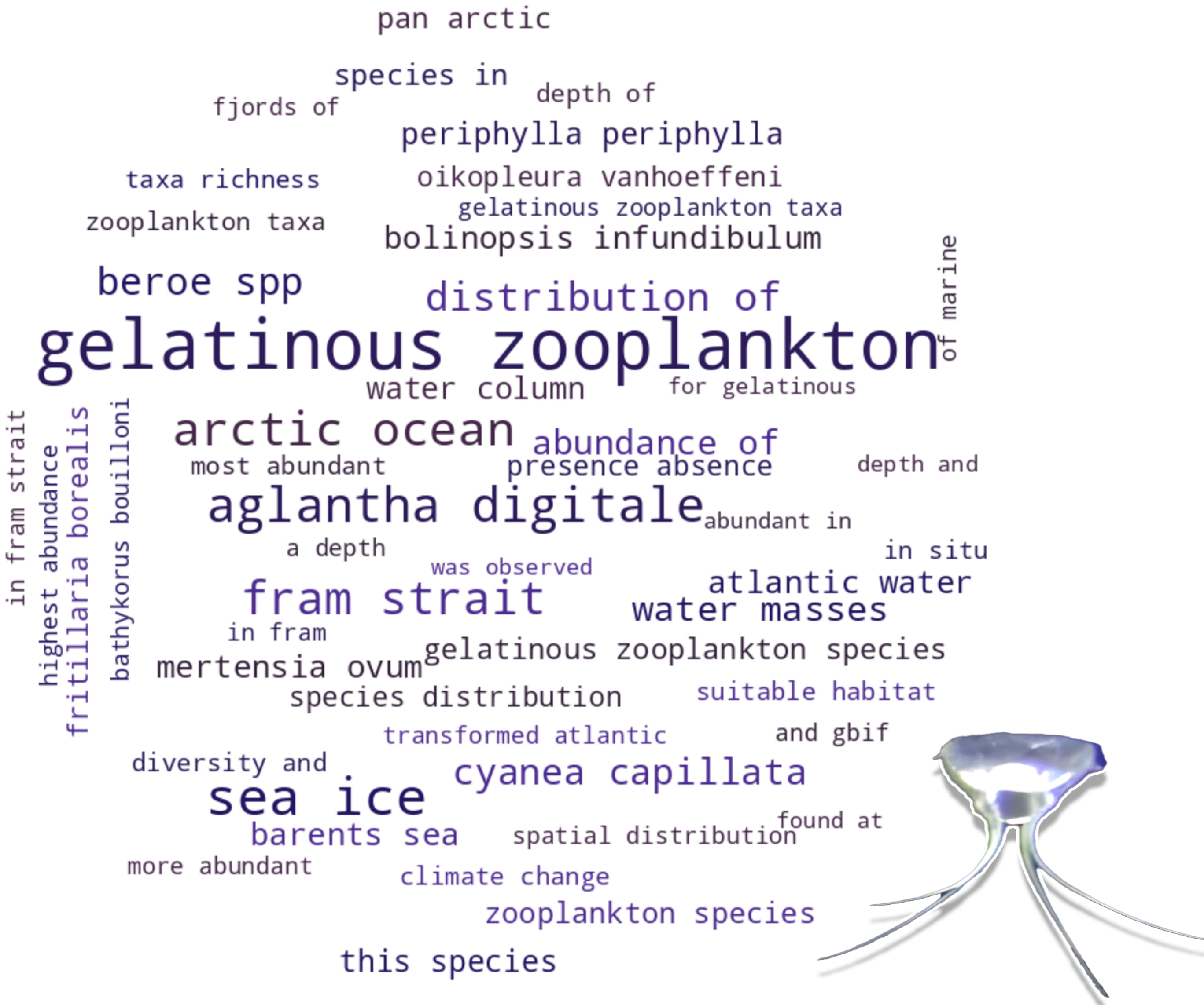

Optical observations and distribution modeling of gelatinous zooplankton in the Arctic Ocean

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Summary

One of the most understudied components of the rapidly changing Arctic ecosystems is the gelatinous zooplankton, comprising cnidarian medusae (Hydrozoa and Scyphozoa), ctenophores, pelagic tunicates, and sometimes also including chaetognaths. Although these organisms play important roles in marine ecosystems, occupying multiple trophic levels, they have been historically neglected due to the difficulties associated with sampling them and the paradigm of them representing a "dead end" in food webs. However, representatives of the different groups were recently shown to serve as a food component for commercially important fish species, act as versatile predators, and contribute significantly to the biological carbon pump. The hypothesis of an ocean "jellification", i.e., a worldwide increase in gelatinous zooplankton biomass, proposed more than a decade ago, is still debated today. For the Arctic Ocean, the questions whether gelatinous zooplankton will increase in abundance, and whether biogeographic shifts in their distributions will take place, have remained largely unanswered. In order to understand the likelihood of such distributional shifts, reliable data are needed on species diversity and abundances and to identify the key physical and biological factors that determine the distribution of gelatinous zooplankton in the Arctic at the local, meso- and pan-Arctic scale. To do so, I leveraged an extensive dataset of historical biological data and analyzed newly collected optical data from recent expeditions to study the diversity, distribution, and abundance of gelatinous zooplankton in several types of ecosystems of the Arctic Ocean. I employed species distribution modeling techniques on both large-scale datasets and regional optical datasets, to evaluate changes in species distributions in space and time, under various climate change scenarios.

For addressing these questions on the Pan-Arctic scale, I compiled extensive datasets for gelatinous zooplankton taxa from four public databases: the Ocean Biodiversity Information System (OBIS), the Global Biodiversity Information Facility (GBIF), the Jellyfish Database Initiative (JeDI), and PANGAEA, spanning six decades and comprising over 24,000 observations. Rigorous data cleaning and taxonomic examination narrowed the focus to eight dominant gelatinous zooplankton taxa with solid identification bases, including two Hydrozoa (*Aglantha digitale* and *Sminthea arctica*), two Appendicularia (*Oikopleura vanhoeffeni* and *Fritillaria borealis*), two Scyphozoa (*Cyanea capillata* and *Periphylla periphylla*), and two Ctenophora (*Mertensia ovum*, *Beroe* spp.). Three-dimensional species distribution models were applied to these datasets, revealing a pan-Arctic trend of polar shifts in the distribution of gelatinous zooplankton. The projections indicated for most studied species an expansion of suitable habitat, with the largest one for the scyphozoan *Cyanea capillata* (180% increase of its niche from 1950-2014 to 2050-2099). The largest niche contraction was found for the hydrozoan *Sminthea arctica* (15% decrease).

I further focused in-depth on different ecosystems that are at the core of the ongoing Atlantification, the open waters of the Fram Strait, the shelf system of the southern Barents Sea, and the western fjords of the Svalbard archipelago. In situ observations of gelatinous zooplankton were collected by conducting depth transects with the Pelagic In situ Observation System (PELAGIOS, for which I annotated over 3200 gelatinous zooplankton observations).

For the Fram Strait, I assessed the diversity of the water column from 20 to 2,400m, revealing seasonal migration patterns of gelatinous zooplankton communities, providing major additions to our understanding of the regional bathypelagic diversity. A significant population of *Sminthea arctica* was observed in the bathypelagic layers of Fram Strait, indicating its important, but so far neglected role, and I recorded the southernmost observation for the hydrozoan species *Bathykorus bouilloni*. Based on the optical datasets of Fram Strait, I carried out a community distribution modeling approach that was used to model gelatinous zooplankton species abundance and community richness. It was projected that environmental changes in Fram Strait will result in less diverse but more abundant gelatinous zooplankton communities. In terms of species-specific responses, the abundance of the hydrozoan *Aglantha digitale* is projected to increase by 2% in the water column by 2050, the hydrozoan *Sminthea arctica* is projected to experience a decline in abundance of up to 60%.

The analysis of optical surveys also allowed me to document large aggregations of ctenophore species. In the southwestern part of the Barents Sea, I recorded one of the largest aggregations of adults of *Bolinopsis infundibulum*. This aggregation was most likely a seasonal phenomenon, supported by a large phytoplankton bloom, and may have extended over several tens of kilometers. Similarly, in a western fjord of Svalbard, Van Mijenfjorden, I found the largest number of individuals ever recorded for the species *Beroe* sp. and could be linked with oxygen-rich waters. These findings indicate the interplay of physical and biological factors for influencing small-scale distribution patterns of gelatinous zooplankton.

A general trend in gelatinous zooplankton community structure was found shared between the results of the in- situ observational studies in Fram Strait and in the Svalbard fjords: Atlantic and transformed Atlantic waters were more abundant in gelatinous zooplankton, whereas the highest taxonomic richness was found in the intermediate and Arctic water masses. These findings hint towards a potential jellification with progressing Atlantification in some Arctic regions. With an overall trend toward niche expansions for most of the arcto-boreal and cosmopolitan species modeled, I anticipate major shifts in the distribution of gelatinous zooplankton in the Arctic regions. These changes are likely to have profound impacts on ecosystem dynamics, affecting fish stocks, biogeochemical cycles and the efficiency of the biological carbon pump.

Zusammenfassung

Eine der am wenigsten untersuchten Komponenten der sich rasch verändernden arktischen Ökosysteme ist das gelatinöse Zooplankton, das Nesseltiermedusen (Hydrozoa und Scyphozoa), Ctenophoren, pelagische Manteltiere und manchmal auch Chaetognathen umfasst. Obwohl diese Organismen eine wichtige Rolle in den marinen Ökosystemen spielen und mehrere trophische Ebenen besetzen, wurden sie in der Vergangenheit vernachlässigt, da es schwierig war, sie zu beproben, und sie als "Sackgasse" in den Nahrungsnetzen galten. Kürzlich wurde jedoch nachgewiesen, dass Vertreter der verschiedenen Gruppen eine Nahrungskomponente für kommerziell wichtige Fischarten darstellen, als vielseitige Räuber fungieren und erheblich zur biologischen Kohlenstoffpumpe beitragen. Die vor mehr als einem Jahrzehnt aufgestellte Hypothese einer "Gelierung" der Ozeane, d. h. einer weltweiten Zunahme der gelatinösen Zooplankton-Biomasse, wird auch heute noch diskutiert. Für den Arktischen Ozean ist die Frage, ob die Menge an gelatinösem Zooplankton zunehmen wird und ob es zu biogeografischen Verschiebungen in ihrer Verbreitung kommen wird, weitgehend unbeantwortet geblieben. Um die Wahrscheinlichkeit solcher Verbreitungsverschiebungen zu verstehen, ist es notwendig, zuverlässige Daten über die Artenvielfalt und -häufigkeit zu erhalten und die wichtigsten physikalischen und biologischen Faktoren zu identifizieren, die die Verteilung von gelatinösem Zooplankton in der Arktis auf lokaler, meso- und pan-arktischer Ebene bestimmen. Zu diesem Zweck nutzte ich einen umfangreichen Datensatz historischer biologischer Daten und analysierte neu gesammelte optische Daten von jüngsten Expeditionen, um die Vielfalt, Verteilung und Häufigkeit von gelatinösem Zooplankton in verschiedenen Arten von Ökosystemen des Arktischen Ozeans zu untersuchen. Ich habe Techniken zur Modellierung der Artenverteilung sowohl auf großmaßstäbliche Datensätze als auch auf regionale optische Datensätze angewandt, um Veränderungen der Artenverteilung in Raum und Zeit unter verschiedenen Szenarien des Klimawandels zu bewerten.

Um diese Fragen auf panarktischer Ebene zu beantworten, habe ich umfangreiche Datensätze für gelatinöse Zooplankton-Taxa aus vier öffentlichen Datenbanken zusammengestellt: dem Ocean Biodiversity Information System (OBIS), der Global Biodiversity Information Facility (GBIF), der Jellyfish Database Initiative (JeDI) und PANGAEA, die sich über sechs Jahrzehnte erstrecken und über 24.000 Beobachtungen umfassen. Durch eine gründliche Datenbereinigung und taxonomische Prüfung konnte der Fokus auf acht dominante gelatinöse Zooplankton-Taxa mit soliden Identifikationsgrundlagen eingegrenzt werden, darunter zwei Hydrozoa (*Aglantha digitale* und *Sminthea arctica*), zwei Appendicularia (*Oikopleura vanhoeffeni* und *Fritillaria borealis*), zwei Scyphozoa (*Cyanea capillata* und *Periphylla periphylla*) und zwei Ctenophora (*Mertensia ovum* und *Beroe* spp.). Auf diese Datensätze wurden dreidimensionale Artenverteilungsmodelle angewandt, die einen pan-arktischen Trend zu

polaren Verschiebungen in der Verteilung des gelatinösen Zooplanktons erkennen ließen. Die Projektionen zeigten für die meisten untersuchten Arten eine Ausweitung des geeigneten Lebensraums, wobei die größte Ausweitung für das Scyphozoon *Cyanea capillata* zu verzeichnen war (180 % Zunahme seiner Nische von 1950-2014 bis 2050-2099). Die größte Nischenverkleinerung wurde für den Hydrozoen *Sminthea arctica* festgestellt (Rückgang um 15 %).

Darüber hinaus habe ich mich eingehend mit verschiedenen Ökosystemen befasst, die im Mittelpunkt der laufenden Atlantifizierung stehen: die offenen Gewässer der Framstraße, das Schelfsystem der südlichen Barentssee und die westlichen Fjorde des Svalbard-Archipels. In-situ-Beobachtungen von gelatinösem Zooplankton wurden mit dem Pelagic In-situ Observation System (PELAGIOS, für das ich mehr als 3200 Beobachtungen von gelatinösem Zooplankton notiert habe) durch Tiefenfahrten gesammelt.

In der Framstraße habe ich die Vielfalt der Wassersäule von 20 bis 2400 m untersucht und dabei saisonale Migrationsmuster von gelatinösen Zooplanktongemeinschaften aufgedeckt, die unser Verständnis der regionalen bathypelagischen Vielfalt wesentlich erweitern. Eine bedeutende Population von Sminthea arctica wurde in den bathypelagischen Schichten der Framstraße beobachtet, was auf ihre wichtige, aber bisher vernachlässigte Rolle hinweist, und ich habe die südlichste Beobachtung der Hydrozoenart Bathykorus bouilloni gemacht. Auf der Grundlage der optischen Datensätze der Framstraße führte ich einen Ansatz zur Modellierung der Verteilung von Gemeinschaften durch, der zur Modellierung der Häufigkeit von gelatinösen Zooplanktonarten und des Reichtums von Gemeinschaften verwendet wurde. Es wurde prognostiziert, dass Umweltveränderungen in der Framstraße zu weniger vielfältigen, aber reichhaltigeren gelatinösen Zooplanktongemeinschaften führen werden. Für den Hydrozoen *Aglantha digitale* wird bis zum Jahr 2050 eine Zunahme von 2 % in der Wassersäule prognostiziert, für den Hydrozoen *Sminthea arctica* wird ein Rückgang von bis zu 60 % erwartet.

Die Analyse der optischen Erhebungen ermöglichte es mir auch, große Ansammlungen von Ctenophorenarten zu dokumentieren. Im südwestlichen Teil der Barentssee habe ich eine der größten Ansammlungen erwachsener Tiere von *Bolinopsis infundibulum* beobachtet. Diese Ansammlung war höchstwahrscheinlich ein saisonales Phänomen, das durch eine große Phytoplanktonblüte begünstigt wurde und sich über mehrere Dutzend Kilometer erstreckt haben könnte. In ähnlicher Weise fand ich in einem westlichen Fjord von Svalbard, dem Van Mijenfjorden, die größte Anzahl von Individuen, die jemals für die Art *Beroe* sp. aufgezeichnet wurde, was mit sauerstoffreichem Wasser in Verbindung gebracht werden könnte. Diese Ergebnisse deuten auf das Zusammenspiel physikalischer und biologischer Faktoren hin, die die kleinräumigen Verteilungsmuster von gelatinösem Zooplankton beeinflussen.

Es wurde ein allgemeiner Trend in der Struktur des gelatinösen Zooplanktons festgestellt, der sich mit den Ergebnissen der In-situ-Beobachtungsstudien in der Framstraße und in den Svalbard-Fjorden deckt: In atlantischen und transformierten atlantischen Gewässern gab es mehr gelatinöses Zooplankton, während der höchste taxonomische Reichtum in den mittleren und arktischen Wassermassen gefunden wurde. Diese Ergebnisse deuten auf eine mögliche

Gelatinierung mit fortschreitender Atlantisierung in einigen arktischen Regionen hin. Mit einem allgemeinen Trend zur Nischenerweiterung für die meisten der modellierten arktisch-borealen und kosmopolitischen Arten erwarte ich größere Verschiebungen in der Verteilung des gelatinösen Zooplanktons in den arktischen Regionen. Diese Veränderungen werden wahrscheinlich tiefgreifende Auswirkungen auf die Ökosystemdynamik haben und sich auf Fischbestände, biogeochemische Kreisläufe und die Effizienz der biologischen Kohlenstoffpumpe auswirken.

List of Abbreviations, Tables and Figures

Abbreviations

AIC - Akaike Information Criterion
ANNs - Artificial Neural Networks
AQUA (MODIS) - Aqua Moderate Resolution Imaging Spectroradiometer
ARJEL – Arctic Jellies
AUC - Area Under the Curve
AW - Atlantic Water
AWI - Alfred-Wegener-Institute
BIIGLE - Marine Image Annotation Tool
CBI - Continuous Boyce Index
CDOM - Colored Dissolved Organic Matter
cloglog - Complementary Log-Log
CMIP6 - Coupled Model Intercomparison Project Phase 6
CTD - Conductivity-Temperature-Depth
DOC - Dissolved Organic Carbon
EUMETSAT - European Organisation for the Exploitation of Meteorological Satellites
FESOM - Finite Element Sea Ice-Ocean Model
GAM - Generalized Additive Model
GBIF - Global Biodiversity Information Facility
GLM - Generalized Linear Model
GZ - Gelatinous Zooplankton
HAUSGARTEN LTER - HAUSGARTEN Long-Term Ecological Research
HE605 - R/V Heincke Expedition 605
H - Hinge
HMSC - Hierarchical modeling of Species Communities
IPCC - Intergovernmental Panel on Climate Change
IW - Intermediate Water
JeDI - Jellyfish Database Initiative
JSDMs - Joint Species Distribution Models
L - Linear
Ma - Million years ago
Maxent - Maximum Entropy Model
MCMC - Markov Chain Monte Carlo

MPEG - Moving Picture Experts Group
MPI-ESM1.2 - Max Planck Institute Earth System Model 1.2
MTS - MPEG Transport Stream
NPP - Net Primary Production
OBIS - Ocean Biogeographic Information System
OCI - Ocean Color Index
OFOS - Ocean Floor Observation System
OR10p - Omission Rate (10th percentile)
PANGAEA - Data Publisher for Earth & Environmental Science
PELAGIOS - Pelagic In situ Observation System
POC - Particulate Organic Carbon
P - Product
PS121 - Expedition R/V POLARSTERN 121
PS126 - Expedition R/V POLARSTERN 126
PSU - Practical Salinity Units
Q - Quadratic
R/V - Research Vessel
RM - Regularization Multiplier
ROV - Remotely Operated Vehicle
SBE37-SMP-ODO - Seawater Multi-Parameter - Optical Dissolved Oxygen sensor
SDMs - Species Distribution Models
SD - Standard Deviation
SSP - Shared Socio-Economic Pathway
SW - Surface Water
TAW - Transformed Atlantic Water
T - Threshold
VARS - Video Annotation and Reference System
VIF - Variance Inflation Factor
WAIC - Widely Applicable Information Criterion
WoRMS - World Register of Marine Species
WSC - West Spitsbergen Current

Tables

Figures

Chapter 1. Introduction

1.1 Gelatinous zooplankton: what's behind the name

Gelatinous zooplankton, also known as "gelata" are a diverse group of marine organisms that encompasses species from various phyla, most commonly including Ctenophora, Cnidaria (subphylum Medusozoa which includes the classes Hydrozoa, Scyphozoa, Cubozoa, and Staurozoa), and the subphylum Tunicata (Thaliacea and Appendicularia classes). In some studies, Chaetognatha are considered (semi-) gelatinous zooplankton (Larson, 1986). The more common term 'jellyfish' is used to refer to the pelagic organisms belonging to the phylum Cnidaria and Ctenophora, and has its roots in the scientific literature of the 18th century. At the same time, the name of the phylum Cnidaria has more ancient origins and first appears in Aristotle's History of Animals, where he referred to these animals as 'cnidē' (meaning "to irritate"). Based on a semantic analysis of the word 'jellyfish' from Google Books Ngram, there has been an almost three-fold increase in the relative occurrence of this word in the literature from 1980 to 2019 (Figure 1.1). Such a 'semantic rise' may reflect not only a growing scientific focus on these species but also a public interest that may reflect the increasing influence of these species on human economic activity (see subchapter 1.6; Richardson et al., 2009).

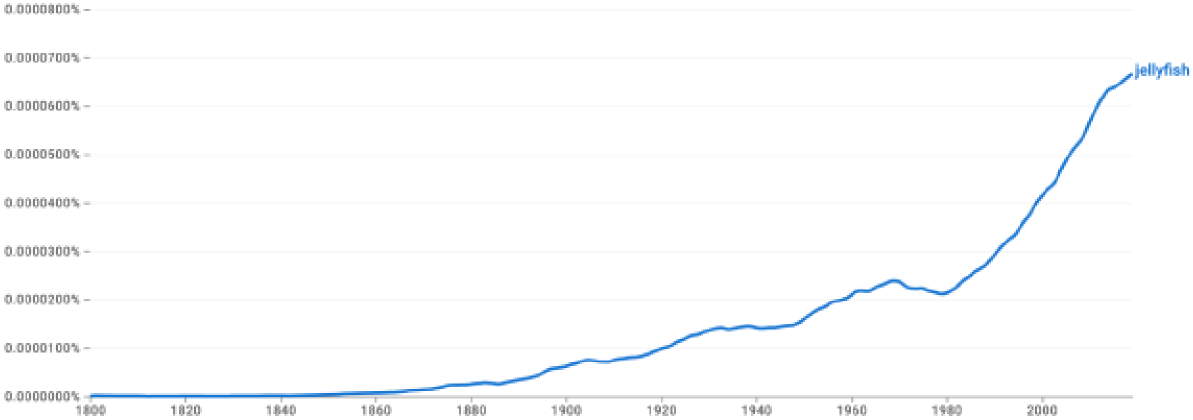

Figure 1.1 Frequency of occurrence of the word "jellyfish" in English-language literature from 1800 to 2019 according to Google Books Ngram Viewer (books.google.com/ngrams).

As gelatinous zooplankton encompass numerous pelagic taxa, they have a wide range of morphological characteristics, size scales, and ecological roles. They occupy extensive niches in food chains, ranging from grazers that can profit from particulate organic carbon (POC; e.g., class Appendicularia; Gorsky & Fenaux, et al., 1998) to versatile predators (e.g., order Narcomedusae; Choy et al., 2017) that feed on both gelatinous and non-gelatinous animal groups. However, the most common features that unite these taxa into a single subgroup are their inherent fragility, high concentration of body water content, and transparency (Larson, 1986, Haddock, 2004). Some of the key traits of these organisms include energy-efficient buoyancy, larger size with lower carbon investment, rapid growth, and body plasticity (Júnior et al., 2022). Among the groups of gelatinous zooplankton, there is a wide variety of interspecific relationships, ranging from direct predation to mutualistic relationships (Raskoff et al, 2005, Choy et al., 2017). Bioluminescence is widespread and is used for predation as well as predator avoidance (Haddock et al., 2010). Moreover, they are also an important part of the diet of marine organisms at higher trophic levels (see also subchapter 1.5; Hays et al., 2018).

The class **Hydrozoa** belonging to the phylum Cnidaria is considered to be the largest taxonomic group of all gelatinous zooplankton (Figure 1.2; Table 1.1). These organisms have a very wide morphological diversity and size range, including organisms as small as 4-5 mm (e.g. *Bougainvillia platygaster*; Bouillon 1995) to one of the largest living organisms on Earth, exceeding 40m (*Praya dubia;* Mills et al., 2007). A large fraction of the Hydrozoa are meroplanktonic, with most organisms having a polyp stage and a planktonic medusae stage (Collins, 2002). Their life cycle usually involves a sexual reproduction resulting in the development of fertilized eggs into small free-swimming larvae called planulae, which then attach to the bottom and become sessile polyps, which reproduce asexually by budding (Collins, 2002). Hydrozoan life cycles are highly variable, with many taxa having either medusa or polyp stages suppressed (Bouillon et al., 2006). For example, species of the order Trachymedusae do not have a polyp stage and the jellyfish develop directly from the planula (Kramp, 1961). A representative of this order is *Aglantha digitale*, one of the most widespread hydrozoans in the world (Table 1, Figure 1.2).

In contrast to hydrozoans, members of the class **Scyphozoa** of the phylum Cnidaria (also called "true jellyfish") almost always have a meroplanktonic life cycle, with a benthic polyp stage, called scyphostome, and a medusa stage (Arai, 1997; Figure 1.2; Table 1.1). In the medusa stage, these species are characterized by their rather large size and tend to form massive aggregations (Fernández-Alías et al., 2021). Adults can reach several meters in size and their tentacles tens of meters (e.g. *Cyanea capillata*; Figure 1.2). Unlike hydrozoans, most scyphozoans reproduce by developing a scyphistoma followed by strobilation, a process in which the polyp splits into several disk-shaped segments, each of which develops into an adult medusa (Arai, 1997).

The other two cnidarian classes, **Cubozoa**, and **Staurozoa**, have often been grouped with the true jellyfish (scyphozoans) in the past (Kingsford and Mooney, 2014; Figure 1.2; Table 1.1). The cubozoans, or box jellyfish, are the most distinctive of all cnidarians, being venomous, relatively fast swimmers, known for their active, fish-like behavior and advanced sensory system, including a complex eye (Nilsson et al., 2005). Finally, the staurozoan cnidarians differ from other representatives in that the free-swimming form is practically absent, they develop attached medusae (Kingsford and Mooney, 2014).

The phylum **Ctenophora**, also known as comb jellies, for their unique comb-like rows of cilia used for propulsion (Martindale et al., 1986; Figure 1.2; Table 1.1). This phylum previously grouped with other cnidarian classes in the phylum Coelenterata, however, older (Hyman, 1940) and more recent phylogenetic studies have contested this grouping. Recent studies are in support of the hypothesis that ctenophores are a sister group to all other animals (Schultz et al. 2023). Ctenophora species have a wide morphological spectrum, from small spherical species of a few mm (e.g. *Pleurobrachia*) in length to ribbon-like forms that can reach several meters (e.g. *Venus* *girdle*). A distinctive feature of this phylum is the presence of irradiance, and bioluminescence in almost all species (Haddock et al., 2010). The latter is used to misdirect predators, e.g., with an active release of glowing particles that cause scintillating visual effects (Widder et al., 1992).

Tunicata, belonging to the phylum Chordata, were previously known as Urochordata. They are a group of marine invertebrates that include Ascidiacea (sea squirts), Thaliacea (salps and doliolids), and Appendicularia (larvacean; Figure 1.2; Table 1.1). Of these, Thaliacea and Appendicularia belong to the gelatinous zooplankton. The main characteristic of these organisms is the presence of a "tunic" composed of proteins and complex carbohydrates (Daugavet et al., 2022). Appendicularia range in size from a few millimeters to several centimeters long (e.g. *Bathochordaeus stygius;* Sherlock et al., 2017). They are distinctive for their ability to live and feed in a mucopolysaccharide complex, referred to as a "house" (Deibel, 1986). Other members of this subphylum (class Thaliacea) are notable for containing both solitarians and colonials, while the holoplankters are all colonial (Govindarajan et al., 2011). Salp and doliolid bodies are barrel-shaped, transparent formations that can grow to tens of meters in colonies (van Soest, 1981).

Table 1.1: Main characteristics of the major groups of gelatinous zooplankton. Species richness information is taken from OBIS and GBIF databases and taxonomic data from WoRMS.

Phylum	Cnidaria				Chordata (Tunicata)		Chaetognatha	Ctenophora
Class	Hydrozoa	Scyphozoa	Cubozoa	Staurozoa	Thaliacea	Appendicularia		
Abundant species	*Aglantha digitale, Solmundella bitentaculata, Physalia physalis*	*Stomolophus meleagris, Aurelia aurita, Rhizostoma pulmo, Cyanea capillata*	*Carybdea marsupialis, Chironex fleckeri*	*Haliclystus auricula, Calvadosia campanulata*	*Thalia democratica, Salpa thompsoni, Pyrosoma atlanticum*	*Oikopleura dioica, Fritillaria borealis, Oikopleura labradoriensis, Oikopleura vanhoeffeni*	*Eukrohnia hamata, Flaccisagitta enflata, Parasagitta elegans*	*Pleurobrachia pileus, Mnemiopsis leidyi, Pleurobrachia rhodopis, Beroe cucumis*
Feeding mode	Pelagic: Predominantly carnivorous - zooplankton, small crustaceans, fish larvae. Polyps: plankton, symbiotic algae, small aquatic organisms.	Carnivorous: zooplankton, small fish	Carnivorous: small fish, invertebrates	Carnivorous: zooplankton	Filter feeders: phytoplankton	Filter feeders: phytoplankton	Carnivorous: zooplankton, small crustaceans and fish	Carnivorous: zooplankton, other gelatinous zooplankton
Life cycle	Meroplanktonic and holoplanktonic; reproduction both sexual and asexual	Mostly meroplanktonic; reproduction both sexual and asexual	Mostly meroplanktonic	Polyp stage dominates; reproduction both sexual and asexual	Solitary and colonial forms, with both asexual and sexual reproduction stages	Pelagic, sexual reproduction	Pelagic, reproduction hermaphroditic, internal fertilization	Pelagic, mostly sexual reproduction (hermaphrodites), direct development
Number of taxa discovered	3832	242	49	49	78	68	**132**	**205**

The last phylum, **Chaetognatha**, also known as arrow worms (Figure 1.2; Table 1.1), are often referred to as semi-gelatinous zooplankton (Larson, 1986) for having a rather variable water concentration ranging from 83% to 94.7% (Ikeda and Kirkwood, 1989). Their bodies are transparent, arrow-shaped, and range in size from a few millimeters up to 120 millimeters.

Chaetognaths derive their name from the Greek word "χαίτη," meaning "flowing hair," due to their similar-looking set of sharp teeth.

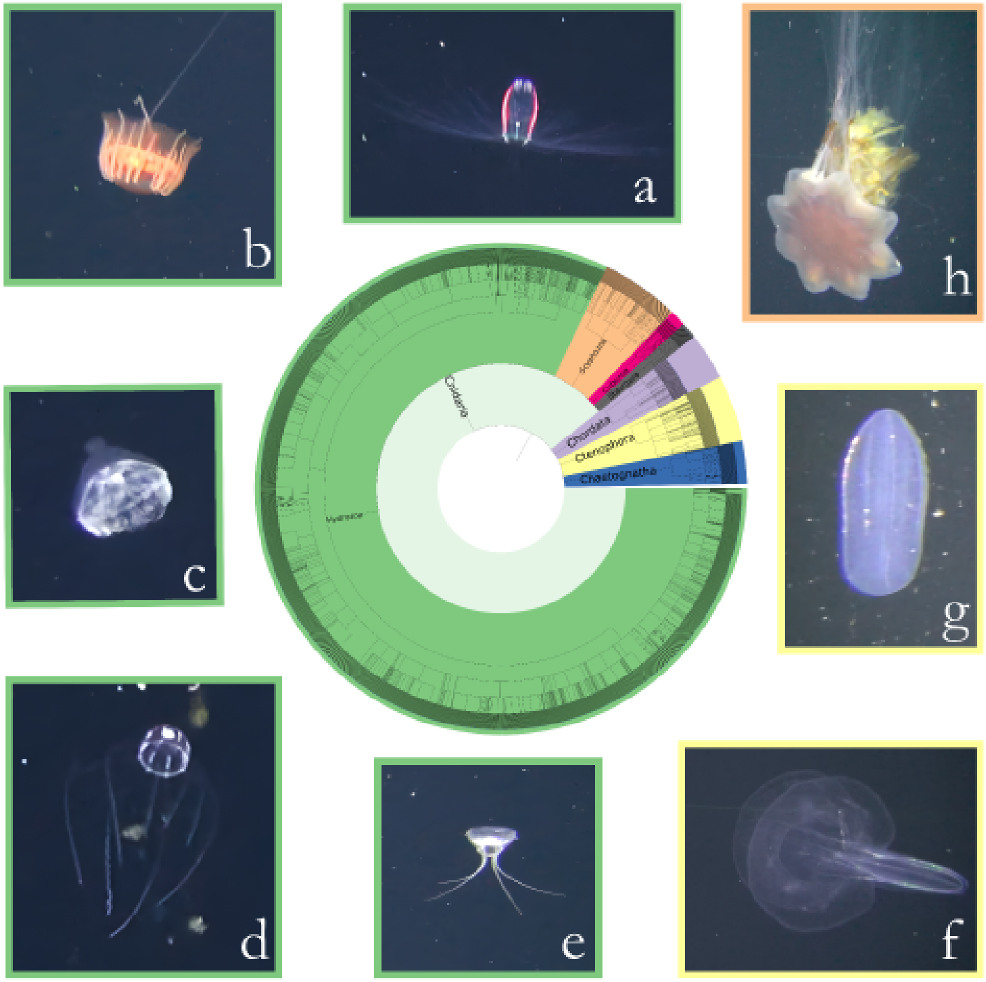

Figure 1.2. Taxonomic hierarchy displaying the classification of the taxa derived from the World Register of Marine Species (WoRMS) with representative examples of gelatinous zooplankton (green - Hydrozoa; orange - Scyphozoa; red - Cubozoa; black - Staurozoa; purple - Chordata (Tunicata); yellow - Ctenophora; blue - Chaetognatha). The following species are illustrated: Hydrozoa: (a) Aglantha digitale, (b) Atolla tenella, (c) Botrynema brucei, (d) Sminthea arctica, (e) Bathykorus bouilloni, Ctenophora: (f) Bolinopsis infundibulum, (g) Beroe sp., Scyphozoa: (h) Cyanea capillata. Images were obtained on expeditions PS121, PS126, and HE605 from the PELAGIOS video camera system.

1.2 Evolutionary history

Gelatinous zooplankton are among the oldest living marine species, with an evolutionary history dating back more than 600 Ma (Figure 1.3). Their evolutionary origins fall largely between the Ediacaran and Ordovician periods. Ctenophores are considered to be the earliest diverging group of the animal kingdom and thus the most distant of their relatives (Schultz et al., 2023). Their ancestors were found in the fossils dated back to the lower-middle Cambrian, 545-515 million years ago (Ma) (Morris et al., 1996) and Ediacaran period >600 Ma (Tang et al., 2011), which makes them one of the first Eumetazoa lineages to appear. The modern diversity however most likely originated approximately 350 Ma +/- 80 Ma (Whelan et al., 2017). The Cnidarian phylum (classes Hydrozoa, Scyphozoa, Cubozoa, and Staurozoa) originated in the Neoproterozoic Era, during the Cryogenic Period (Van Iten et al., 2014). The earliest originated taxa among gelatinous cnidarians are the Scyphozoa that are dated back to 635–577 Ma, while the oldest known hydrozoans and cubozoans might have occurred since 505 Ma (Van Iten et al., 2014). The oldest found fossils of the Chaetognatha phylum date back to the Lower Cambrian period, with the earliest identifiable taxa found approximately 520 Ma (Chen & Huang, 2002). Fossil remains of the subphylum Tunicata date back to the Late Neoproterozoic, about 543 - 555 Ma (Chen et al., 2003; Fedonkin et al., 2010), while their gelatinous forms that still exist today, separated from other taxa around 450 Ma (Appendicularia) and 240 Ma (Thaliacea; Delsuc et al., 2018). Having survived five mass extinctions, gelatinous zooplankton’s ability to adapt to extreme environmental changes may speak to their inherent resilience. At the scale of the impending sixth extinction, these organisms may not only survive but also potentially benefit from reduced competition, further strengthening their role in future marine ecosystems.

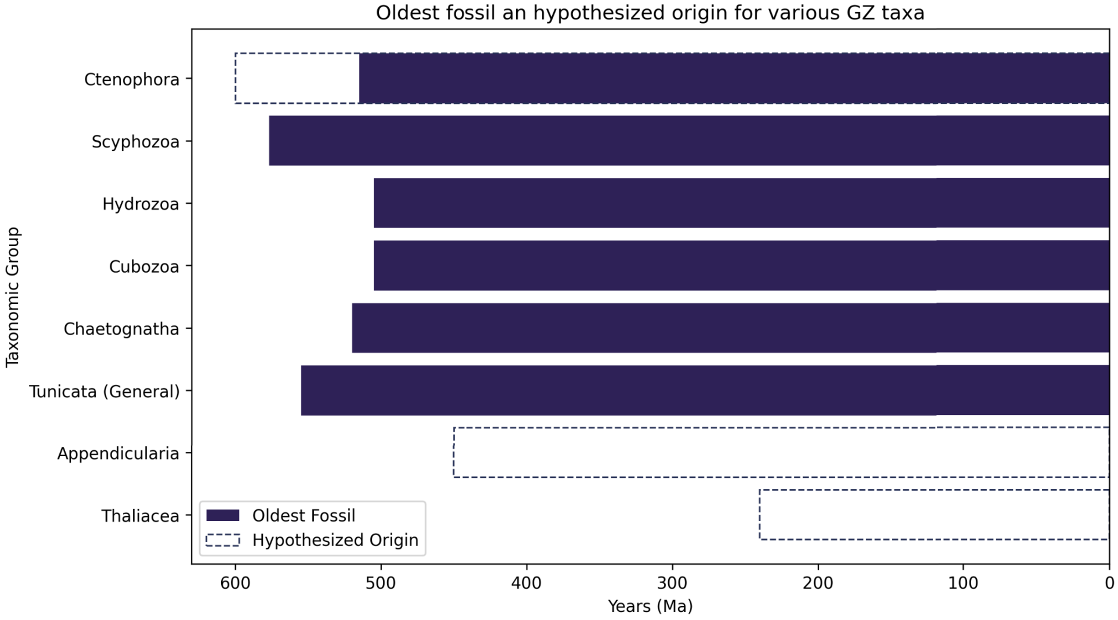

Figure 1.3. Estimated origin of different taxa of gelatinous zooplankton. Figure created based on data from Morris et al., 1996; Tang et al., 2011; Whelan et al., 2017; Van Iten et al., 2014; Chen & Huang, 2002; Chen et al., 2003; Fedonkin et al., 2010; and Delsuc et al., 2018.

1.3 Historical perspective and current state of knowledge

The research on gelatinous zooplankton taxa experienced its first "golden age" in the late 19th century when scientists began to unravel the complex phylogenetic and ecological relationships between cnidarians and ctenophores (Haddock, 2004). Analysis of data from the World Register of Marine Species (WoRMS, 2023; marinespecies.org) shows that the highest number of gelatinous species ever described was from 1900 to 1905, with 260 species (Figure 1.4). However, since 1915 there has been a significant decline in the rate of discovery of these taxa (Figure 1.4), which might be explained by a shift in focus towards studying more "industrial" zooplankton species such as copepods (Haddock, 2004). This trend generally continued until the 1980s (Figure 1.4). Moreover, throughout the 20th century, these species were considered to be a dead end of the pelagic food webs (Verity and Smetacek, 1996). However, in recent years there has been a qualitative reassessment of their trophic role and their impact on biogeochemical cycles (Hays et al., 2018). Modern surveys using optical methods have shown that their abundances are greatly underestimated, largely due to the difficulty of capturing these organisms with nets (Hosia et al., 2017; Hoving et al., 2019). In addition, molecular and in-situ observations have clarified the role of these species in food webs and have shown that they occupy important trophic positions (reviewed in Hays et al., 2018, see also subchapter 1.5). Moreover, molecular studies have helped to unravel their systematics, leading to numerous taxonomic revisions (Lindsay et al., 2015; Shiganova and Abyzova, 2022). Since the 1980s, there has been a gradual increase in the discovery of new species (Figure 1.4), which was particularly notable for the phylum Chaetognatha (41% of species discovered after the 1980s; Figure 1.4), as well as for the class Cubozoa (57% of species discovered after the 1980s; Figure 1.4). At the time of writing, there are approximately 452 species with "inquirendum" status in the WoRMS database (highest for Hydrozoa - 418 and Tunicata - 29 species). With advances in genetic research and increased efforts in deep-sea and polar exploration, we can expect many more species to be discovered in the coming decade.

1.4 Diversity and Abundance of gelatinous zooplankton

The taxonomically richest group of gelatinous zooplankton is the subphylum Medusozoa (Cnidaria), which includes the classes Hydrozoa, Scyphozoa, Cubozoa, and Staurozoa. According to the data retrieved from the World Register of Marine Species (WoRMS, 2023; marinespecies.org), there are currently 3,832 extant hydrozoan species, 242 scyphozoan species, 49 species in the classes Cubozoa and Staurozoa, 205 ctenophore species, 146 pelagic tunicate species (Appendicularia and Thaliacea classes) and 132 Chaetognatha species (Figure 1.5).

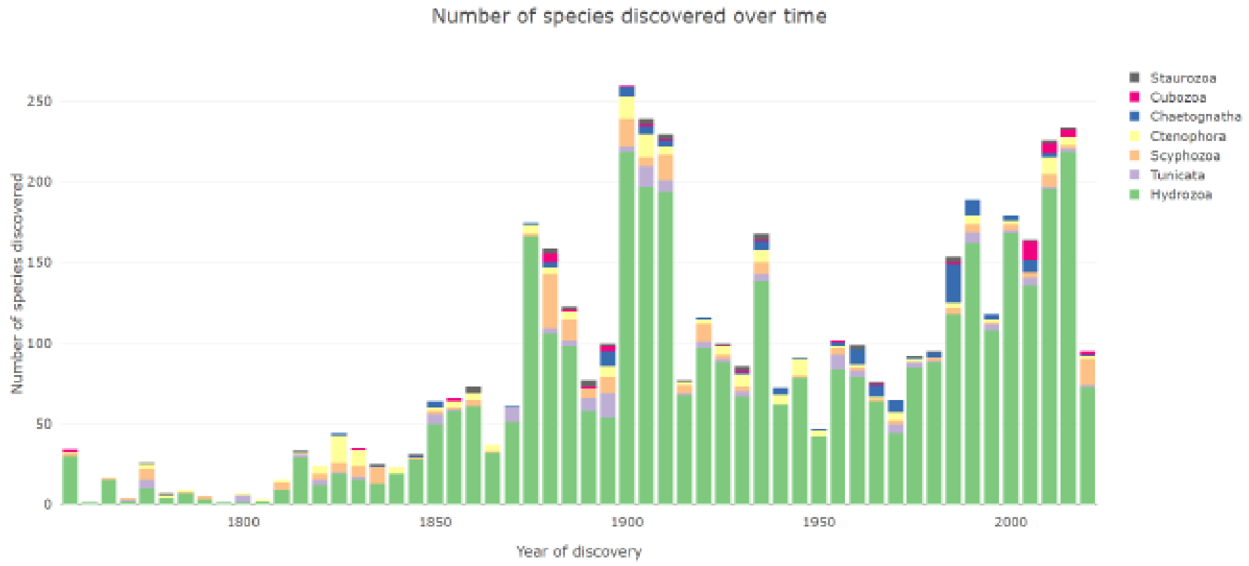

Figure 1.4. Historical overview of the description of Ctenophora, Scyphozoa, Hydrozoa, and Cubozoa. The data were obtained from the World Register of Marine Species (WoRMS) database.

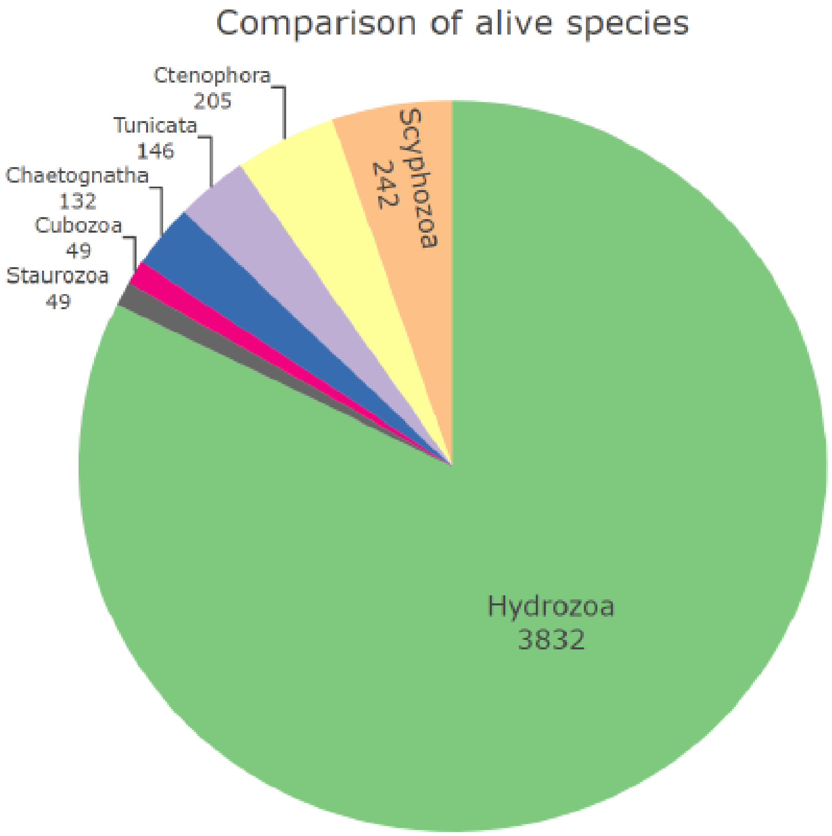

Figure 1.5. Current numbers of extant gelatinous zooplankton species from the World Register of Marine Species (WoRMS) database.

1.5 Gelatinous zooplankton's role in the food web revisited

As mentioned earlier, the role of gelatinous zooplankton in food webs and the carbon cycle has been underestimated in the past (Verity and Smetacek, 1996). Traditional diet studies using morphology have underestimated their role in the food webs, due to the fact that these species are rapidly digested in predators' stomachs and hence overlooked (Hays et al., 2018). With the application of molecular tools for diet studies, it has been shown that these organisms play a far greater role than previously thought (Diaz Briz et al., 2017; Hays et al., 2018; Urban et al., 2021, Brodeur et al., 2021). These organisms have also been shown to be an important source of food for a large number of fish (Gahan et al., 2023), commercial shrimp (Urban et al., 2021), sea turtles (Heaslip et al., 2012), birds, and even penguins (Thiebot et al., 2017).

The trophic interactions of these organisms are quite complex, with many gelatinous zooplankton groups feeding on each other (Choy et al., 2017). Of all gelatinous zooplankton, the Appendicularia are placed at the lowest trophic chain. These animals live in self-secreted, mucus 'houses' that are used for feeding and protection (Alldredge, 1976). They have a complex three-stage filtration feeding system (Gorsky and Fenaux, 1998), which allows them to feed on both DOC and POC in the water column, and to ingest particles from 0.2 µm to 2 mm in diameter (Flood, et al., 1992; Lombard et al., 2009; Sherlock et al., 2016). In this way, these species can obtain energy from the microbial level, as well as consume diatoms, and directly transfer it to metazoans directly (Gorsky and Fenaux, 1998), including to fish (Flood, et al., 1992). In addition, under certain environmental conditions, appendicularians can outcompete copepod secondary producers (Choe and Deibel, 2010). At the same time, they constitute an important portion of the diet of many gelatinous animals of higher trophic levels, including one of the largest scyphozoans, *Cyanea capillata* (Purcell et al., 2005), and one of the most dominant Chaetognatha species, *Eukrohnia hamata* (Oresland, 1990). Thaliacea, as well as Appendicularia, feed by propelling water through their mucous mesh (Madin and Deibel, 1998).

The other gelatinous phylum, Ctenophora, is mainly composed of carnivorous feeders. Ctenophores are known to feed primarily on crustaceans, but also prey on other gelatinous zooplankton (Haddock, 2007; Choy et al., 2017). Furthermore, some species are reported to cannibalize their own larvae (Javidpour et al., 2020). Their feeding mode can be divided into three categories: (1) tentacle feeding; (2) lobe feeding; (3) and engulfment feeding (Haddock, 2007). The first type of feeding involves a "sit and wait" strategy, for which the ctenophore unfolds its tentacles to form a sticky net and waits for prey to be caught in it (Tamm et al., 1985). For lobe feeding, ctenophores generate feeding currents with their auricles, or use their lobes to capture prey directly (Haddock, 2007). For the latter type of feeding, ctenophores use a direct mode of feeding in which they either ingest or take bites from their prey (Haddock, 2007). This type of feeding is mainly practiced by ctenophores (e.g. *Beroe* spp.) that prey on other relatively large gelatinous zooplankton (Swanberg et al., 1974).

Cnidaria, the most diverse phylum of gelatinous zooplankton, also exhibits the widest range of feeding modes. Their prey ranges in size from small copepods to much larger organisms such as small fish and other gelatinous zooplankton (Choy et al., 2017). Among species of

Cnidaria, it is possible to note the existence of specialists, like species in the Order Siphonophora, whose diet is mainly dominated by crustaceans, as well as the generalist species, like those of the Order Narcomedusae, which may have the most diverse diet among all gelatinous taxa (Choy et al., 2017, Larson et al., 2009).

The last phylum, Chaetognatha, is predominantly carnivorous, feeding primarily on copepods and appendicularians (Oresland, 1990). They are known to be strongly controlled by prey abundance (Feigenbaum & Maris, 1984).

1.6 Role in biological carbon pump

Gelatinous zooplankton have recently been shown to contribute significantly to the global carbon cycle (Lebrato et al., 2013; Luo et al., 2020). Multiple species of gelatinous zooplankton are known to form large aggregations, and when not utilized as prey, individual jellyfish, due to their rapid sinking rates, can export organic carbon to the seafloor more efficiently than phytoplankton and small zooplankton (Lebrato et al., 2019). The process by which a large biomass of gelatinous zooplankton abruptly sinks to the seafloor is often referred to as a "jellyfalls" (Lebrato et al., 2012). The rate of sinking varies among gelatinous zooplankton groups, with the highest rates occurring in Ctenophora (1500 m d^{-1}) and Scyphozoa (1100 m d^{-1}; Lebrato et al., 2013). At high latitudes, where remineralization is generally low, such jellyfish falls are particularly intense (Lebrato et al., 2013). The absence of gelatinous zooplankton as a component of the earlier biochemical models was shown to lead to an underestimation of 8-35% of the total global carbon input to the seafloor (Luo et al., 2020).

The processes leading to this large input of gelatinous zooplankton into the global carbon cycle vary among groups. One of the most prominent exporters is the class Scyphozoa (Hamner & Dawson, 2009). Most species of this class have the ability to form large aggregations called "blooms", which are associated with metagenic life cycles (Hamner & Dawson, 2009). Due to the large biomass in such aggregations, re-mineralization in the pelagic layers is impossible, which is the reason for their rapid sinking to the bottom after depletion of their food sources (Hamner & Dawson, 2009). Other notable components of the global carbon cycle are the Appendicularia, which, as mentioned in section 1.5, build mucus "houses", which when they become clogged with organic matter, are renewed. Old houses are rapidly transported to the seafloor, and this process can happen at rates of 40 sinking houses/day (Alldredge, 2005; Jaspers et al., 2023). Additionally, much of the gelatinous zooplankton tends to aggregate at physical oceanographic boundaries such as fronts, eddies, and convergence zones (e.g., Raskoff et al., 2005). This behavior can lead to localized increases in biomass, and if these aggregations are subject to mortality or food depletion, they may also contribute to rapid sinking in a similar way as described above.

1.7 Impact on human ecumene and the hypothesized Ocean Jellification

Gelatinous zooplankton can have both negative and positive impacts on human economic activities (Purcell et al., 2007; Duarte et al., 2022). Negative impacts include clogging of fishing nets, aquaculture fish mortality, predation on commercial fisheries stock with subsequent replacement of these species, and direct damage to tourism and infrastructure (Purcell et al., 2007; Graham et al., 2014). On the positive side, these organisms form the basis of the diet of many commercially exploited fish species, can also be used as a food source for humans (Duarte et al., 2022) and provide bioactive compounds for the medical industry (Ranasinghe et al. 2022).

The negative impacts of gelatinous zooplankton are largely correlated with human activities in the ocean (Purcell et al., 2007; Richardson et al., 2009). For example, overfishing reduces direct competition with fish for some gelatinous predators (Richardson et al., 2009). This in turn can lead to a complete collapse of the region's fisheries and a transition to jellyfish-dominated ecosystems (Roux et al., 2013). For example, overfishing in the Benguela Upwelling System in recent decades may have led to increased abundance of jellyfish (*Chrysaora hysoscella* and *Aequorea aequorea*) and decreased abundance of sardine and anchovy (Flynn et al., 2012). Restoring these fish populations to previous levels was expected to be extremely difficult (Flynn et al., 2012).

In recent decades, there have been numerous reports of increasing numbers of gelatinous zooplankton worldwide (Brodeur et al., 2002; Link et al., 2006; Lynam et al., 2006). Despite numerous claims of an “Ocean jellification", different authors have questioned this, noting that long-term studies of gelatinous zooplankton are lacking and that the ongoing increase may be the result of natural cyclical fluctuations (Condon et al. 2012; Pitt et al. 2018), as well as anthropogenic activities such as overfishing and eutrophication (Purcell et al., 2007). Nevertheless, based on the latest report of the Intergovernmental Panel on Climate Change (IPCC), there is high confidence that the abundance of gelatinous zooplankton in the shelf zones is increasing and driven primarily by ocean warming and human activities (Cooley et al., 2022). Despite doubts about the overall growth of gelatinous zooplankton biomass in the global ocean, it is clear that the economic damage caused by some groups of organisms is considerable and that the extent of this damage increased over the last few decades (Bosch-Belmar et al., 2020). Thus, the development of integrated marine management strategies must take into account the potential population dynamics of gelatinous zooplankton and their climate-change driven increases and shifts, with the ultimate goal of achieving more stable and sustainable use of marine ecosystems (Aubert et al., 2018).

1.8 The rapidly changing Arctic Ocean and its associated ecosystem shifts

Climate change, a distinctive trait of the Anthropocene era, is altering all spheres of the globe. At the current rate of greenhouse gas emissions, the Intergovernmental Panel on Climate Change (IPCC) projects global temperatures to rise by 1.5 to 2°C above pre-industrial levels by the end of the 21st century (Gulev et al., 2021). The most pronounced effects of such warming on marine ecosystems are loss of sea ice volume, acidification due to increased CO_2 uptake, and increased zones of hypoxia (Cooley et al., 2022).

One of the most rapidly changing ecosystems on Earth is the Arctic Ocean. In recent decades, due to climate change, the region has experienced significant changes in oceanographic conditions, including warming ocean temperatures (by four times the global average, Rantanen et al. 2022), increased stratification, altered currents, and circulation patterns, as well as a rapid sea-ice retreat (Polyakov et al., 2020; Gulev et al., 2021). According to the Intergovernmental Panel on Climate Change (IPCC) Sixth Assessment Report, Arctic Ocean surface waters have already warmed by ca. 1.5 °C in the last century and are projected to warm by an additional 1.5-5 °C by the end of this century under different emission scenarios (Gulev et al., 2021). As the Arctic Ocean continues to warm, sea-ice-free summers are projected to happen in the Arctic Ocean at 3-5°C warming (Gulev et al., 2021).

The Arctic Ocean is connected to other ocean systems through major gateways. On the Atlantic side, warm water masses enter the Arctic through the Barents Sea and Fram Strait via major currents such as the West Spitsbergen Current. On the Pacific side, the Alaska Coastal Current brings significant amounts of warm water through the Bering Strait. The inflow of warm water through these gates has increased in recent decades (Østerhus et al., 2019). Such increase in warm water inflow has had significant effects on the marine ecology of the Arctic, commonly referred to as "Atlantification" and "Pacification" (Ingvaldsen et al., 2021).

With this inflow of the warm water masses, since the 1950s, there has been a steady shift of marine taxa towards the poles, with different species migrating at distinct rates (Constable et al., 2022), making it critical to study such distribution shifts. On average, marine species are migrating toward northern regions with a speed of 43.7-74.7 km per decade (Constable et al., 2022). These shifts vary among taxonomic groups, with phytoplankton and zooplankton assumed to migrate at the fastest rates (>400 km and >100 km per decade, respectively; Figure 1.6; Field et al., 2014). Such shifts lead to the establishment of new communities and biotic interactions (Constable et al., 2022; Pecuchet et al., 2020), can potentially lead to severe declines in regional populations, resulting in widespread species extinctions (Cooley et al., 2022), and are projected to result in the restructuring of entire Arctic food webs (Buchholz et al., 2010; Frainer et al., 2017; Geoffroy et al., 2018; Schröter et al., 2019, Huntington et al. 2020). While the intensity of these changes will only increase over the next century, their exact nature remains unclear and requires further study (Constable et al., 2022).

Most of the studies on the boundary shifts of zooplankton communities in the Arctic Ocean have generally focused on hard-bodied organisms such as copepods (Villarino et al., 2015; Freer et al., 2021), while gelatinous organisms have been poorly covered. Thus, they remain one of the most uncertain nodes in the rapidly changing Arctic ecosystems. With subsequent Atlantification in Fram Strait, a significant restructuring of gelatinous communities towards more abundant but less diverse ones has been hypothesized (Mańko et al., 2020). Some boreal species have been observed for the first time in the high Arctic regions, for example, the scyphozoan *Periphylla periphylla*, which has in recent years established perennial populations in Svalbard fjords (Geoffroy et al., 2018). There is evidence that this species can be a successful competitor to commercial fish in the Norwegian fjords, where its economic impact has been very significant (Gjelsvik Tiller et al., 2014). In the Pacific Arctic, an increase in the biomass of gelatinous zooplankton has been observed over recent decades with the increased inflow of warm water through the Bering Strait (Brodeur et al., 2002).

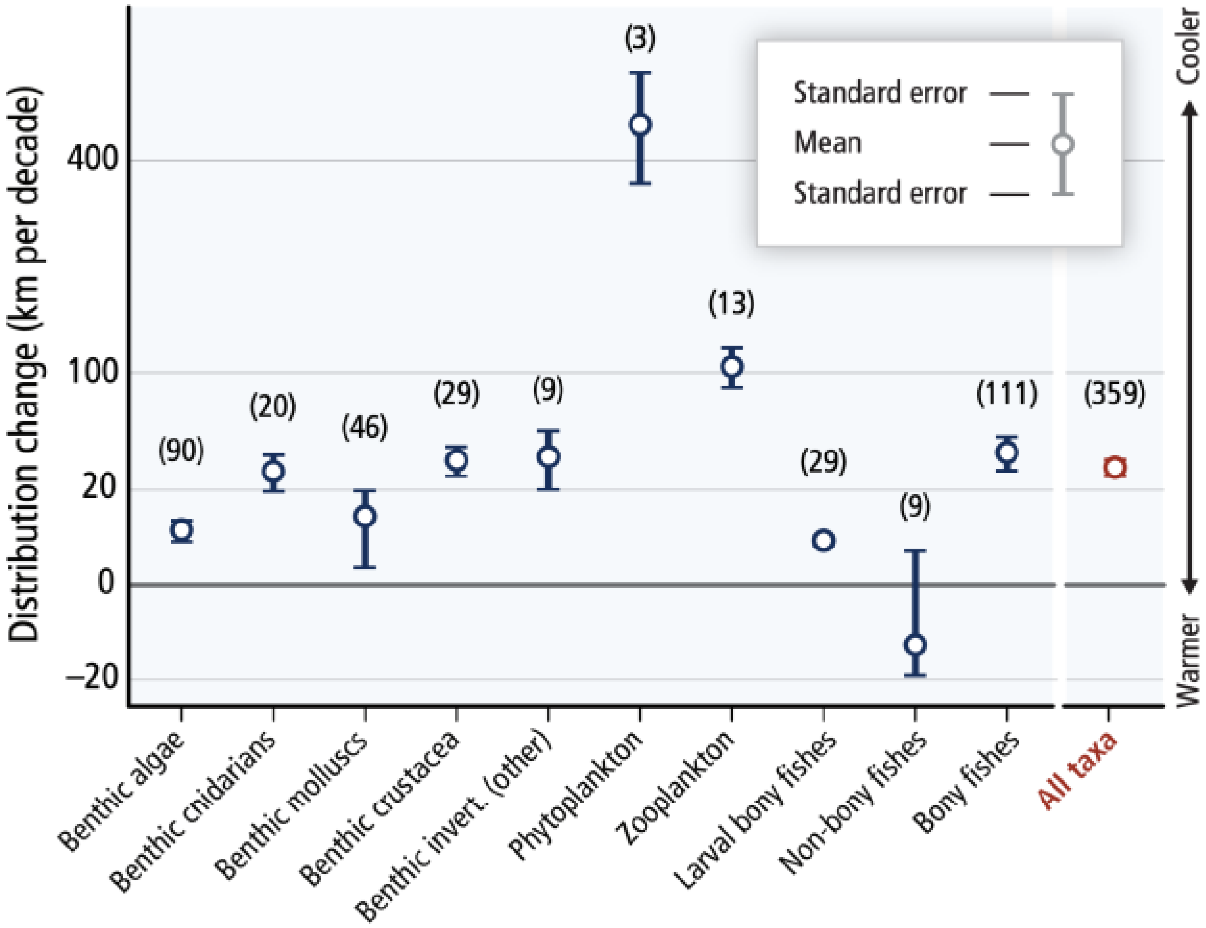

Figure 1.6. Average rates of change in distribution (km per decade) for marine taxonomic groups based on observations over 1900–2010. Positive distribution changes are consistent with warming (moving into previously cooler waters, generally poleward). The number of responses analysed is given for each category (reproduced from IPCC, 2014).

In order to detect ongoing or future shifts in the distribution of gelatinous zooplankton (GZ) in Arctic waters, it is necessary to establish a comprehensive understanding of their existing biodiversity. One of the first studies focusing on Arctic diversity, which comprehensively considered different groups of gelatinous zooplankton, was achieved by Sirenko in 2001, who described the biodiversity and distribution of free-living invertebrates in the Arctic, which included 156 species of Hydrozoa, 13 species of Chaetognatha, 7 species of Scyphozoa, 6 species of Ctenophora and 5 species of Appendicularia. Efforts to describe the vertical structure and estimate biomass on mesoscales were made by Kosobokova and Hopcroft (2011), who showed that the biomass of Chaetognatha is significant along the water column and can be up to 20% of the total biomass, while cnidarians also have a large biomass in the near bottom layers (up to 15%). Studies by Ronowicz et al. (2015) showed that the number of hydrozoans in the Arctic comprises 268 species (112 more than Sirenko's estimate of more than a decade earlier). They also showed that only 19% of these species are Arctic endemics, with the majority of these being benthic species (hydroids).

With the advent of optical methods, it became possible to obtain more accurate quantitative estimates of gelatinous zooplankton (Raskoff et al., 2005; 2010, Youngbluth et al., 2008). Raskoff et al., (2010), using ROV, in the Canada Basin, have shown that some species of siphonophores have a tendency to aggregate above the ridges. Purcell et al. (2018) revealed that some species of gelatinous zooplankton are well adapted to overwintering in Arctic seas. For example, Scyphozoa species were shown to be able to drag their tentacles along the sea floor bottom and feed on epibenthic macrofauna, while *Mertensia ovum* used the same strategy but dragged them along the undersurface of the sea ice. Hence, several species may be well adapted to survive in the Arctic environments. Despite the amount of work done so far, long-term studies are missing to describe GZ dynamics across the Arctic Ocean. One of this kind, a twelve-year study conducted by Manko et al. (2022) in Fram Strait, showed how gelatinous zooplankton communities are shifting towards more Atlantic types, while also reflecting adaptations to these shifts, including changes in reproductive strategies. In this thesis, the diversity and abundance of gelatinous zooplankton in the Arctic are re-examined using biogeographic databases (**Chapter 2**), and supplemented with new in-situ optical surveys (**Chapters 3, 4**).

1.9 Species distribution modeling

In order to predict potential shifts in the gelatinous zooplankton communities of the Arctic Ocean, it is important to have an understanding of their current diversity and distributional ranges and the factors driving their distribution. One of the best statistical tools for processing large-scale biological data are species distribution models (or “SDMs”), which are used to infer spatial and temporal ecological information. Species distribution models are commonly referred to as a group of numerical techniques that combine observations on species presence or abundance with environmental variables (Elith et al., 2009). These models are used to address a wide range of ecological and evolutionary questions and to predict species distributions across landscapes (Elith et al., 2009). Broadly, all species distribution models can be divided into two categories: mechanistic and correlative models (Elith et al., 2009). Mechanistic models, also known as process-based models, are a set of models that relate functional trait data to environmental conditions (Kearney et al., 2009). Such models require extensive knowledge of species-specific physiological responses (e.g., growth, reproduction, mortality). In contrast, correlative models link observed values of species presence/absence (or abundance) with underlying environmental variables (Elith et al., 2009). Such models are also called "black box" or "gray box" approaches, which means that these models attempt to reproduce patterns based on data, without attempting to explain or interpret internal biological or mechanistic processes (Prasad et al., 2023).

Correlative species distribution models can be grouped according to their algorithmic principles. The most common group of models are the linear regression type models, including generalized linear models (GLM) and generalized additive models (GAM; Norberg et al., 2019; Table 2). They use combinations of linear predictor components and link functions to determine the relationship between these predictors, which allows them to capture non-linear relationships (van Oijen et al., 2020). Another commonly used method are tree-based models, which are based on the recursive partitioning of data into groups based on their attributes, allowing them to handle categorical and continuous data (Zhang et al., 2011). The extension of regression tree methods is called gradient boosting (Natekin & Knoll, 2013). This method represents an ensemble of weakly predictive models, usually based on the construction of a set of regression trees (Natekin & Knoll, 2013). Bayesian hierarchical models use Bayesian theory to model ecological patterns using data from multiple levels of observational units, such as traits, phylogeny, random effects, and spatial structure (Allenby et al., 2005). Another class of models, "Maximum Entropy Models", work with the principle of entropy maximization, i.e., they try to identify the closest to a uniform probability distribution. This method allows accommodating features of different complexity, from simple linear to combinations of more complex ones (e.g. quadratic, hinge, product). Artificial Neural Networks (ANNs) are sets of algorithms that attempt to mimic the way the brain works (Yang 2008). They are based on neural layers, each containing a number of neurons. These layers are interconnected, and each layer can be responsible for recognizing certain patterns. In the case of SDMs, this could be the organism's responses to certain environmental conditions, the presence of predators, etc.

In marine ecosystems, species distribution models have been widely used to model suitable habitat for commercially important marine organisms (Robinson et al., 2011), to map the distribution of invasive species (Lyons et al., 2020), and to assess the effects of environmental change on marine biodiversity (Hodapp et al., 2023). However, despite the widespread use of these models, the projected space is often modeled on a two-dimensional spatial scale, ignoring depth as a predictor. However, Bentlage et al. (2013) showed that accounting for this parameter is crucial when modeling organisms in the mid-water column, which is particularly the case for gelatinous zooplankton. Such three-dimensional studies have previously been conducted for gelatinous zooplankton (e.g., Bentlage et al. 2013; Verhaegen et al. 2023), but none for the Arctic Ocean. Furthermore, according to an analysis by Robinson et al. (2017), only 3% of modeling studies have been dedicated to the Arctic Ocean for other taxa.

1.10 Optical observations

As mentioned above, gelatinous zooplankton have been underestimated in abundances and considered a dead link in food chains for many years. One reason for this is that they disintegrate during sampling by conventional methods such as plankton nets, making it difficult to obtain reliable data on their diversity and abundances. New optical technologies for ocean exploration have made significant contributions to the understanding of the functions of gelatinous zooplankton in food webs, allowed for a more accurate quantification of their abundance, and led to the discovery of many new species. Indeed, Choy et al. (2017) used optical methods to study feeding events, showing that the importance of gelatinous zooplankton in food webs is significant. They demonstrated that gelatinous zooplankton constitute a large proportion of the prey of predators at higher trophic levels, and are themselves versatile predators, with the class of hydrozoans Narcomedusae considered to be the most versatile predators. Using a towed video camera system, Hoving et al., 2019 showed that the abundance of some Ctenophora (e.g., *Beroe* spp.) may be underestimated by a factor of 3-5. Raskoff et al. in 2010 discovered a new deep-sea Narcomedusae species, *Bathykorus bouilloni*, with the help of a Remotely-Operated-Vehicle (ROV).

1.11 Objectives

Given the significant climatic changes in the Arctic Ocean, it is particularly important to understand how changes in the physical environment will lead to reorganizations in marine ecosystems. One of the least studied groups in Arctic marine ecosystems is the gelatinous zooplankton. This group of organisms remains understudied in the Arctic for major reasons related to (1) the historical concept of their position as “trophic dead-end”, and the consequent frequent exclusion from pelagic studies; (2) challenges in quantitative and qualitative assessment of these species due to the difficulties associated with sampling them using conventional methods; (3) the fact that these organisms often occur in large numbers in the meso- and bathypelagic layers of the ocean, which are the least studied layers in the Arctic Ocean.

Within the scope of this thesis, a comprehensive investigation was undertaken to address these knowledge gaps. The study focused on the diversity and distribution of gelatinous zooplankton across various pelagic systems in the European Arctic, encompassing inshore fjord and shelf systems (**Chapter 4**) as well as the deeper, open-water system of the Fram Strait (**Chapter 3**). The former were evaluated along a poleward gradient, varying in their exposure to warmer Atlantic water masses and the corresponding influences of ongoing Atlantification. The latter, serving as the Atlantic-Arctic gateway, represents one of the most hydrographically dynamic and rapidly changing environments in the region and serves as the core area impacted by Atlantification. Leveraging video data obtained through the advanced Pelagic In Situ Observation System (PELAGIOS), the study delved into the diversity, distribution, and abundance of gelatinous zooplankton across multiple spatial scales. Employing species distribution modeling techniques on both historical and optical datasets, spatio-temporal projections were conducted to project species distributions under various climate change scenarios, thereby identifying key drivers affecting gelatinous zooplankton populations at pan-Arctic, regional, and local (submesoscale) spatial scales (**Chapters 2, 3**).

The main research questions (RQs) of this work are listed below, with their respective objectives (Obj):

RQ1: What is the state of historical data on gelatinous zooplankton in the Arctic Ocean?

Obj. 1.1) Compile and analyze historical Arctic GZ data sets from a variety of public databases (**Chapter 2**).

Obj. 1.2) Evaluate the taxonomic composition, spatial and temporal coverage, quality and reliability of available data (**Chapters 2, 5**).

RQ2: How do optical surveys contribute to the assessment of diversity, abundance, and community composition of gelatinous zooplankton in the Arctic region?

Obj. 2.1) Assess the diversity and abundance of gelatinous zooplankton communities with a pelagic video system in the hotspots of Atlantification in the Arctic region the Arctic gateways, i.e., the Fram Strait and the Barents Sea shelf system, as well as the fjords of Svalbard (**Chapters 3 and 4**).

Obj. 2.2) Document and quantify small-scale aggregations of gelatinous zooplankton with optical surveys (**Chapter 4**).

RQ3: What are the primary physical and biological drivers influencing the distribution of gelatinous zooplankton species at different spatial scales?

Obj. 3.1) Conduct statistical modeling (**Chapters 2, 3**) and descriptive **(Chapter 4)** investigations of the physical and biological drivers that influence the distribution of gelatinous zooplankton at the level of local aggregations, the mesoscale in Fram Strait, and at the broader pan-Arctic scale (**Chapters 2, 3, 4**).

RQ4: Is the Arctic Ocean, particularly the rapidly changing Atlantic gateway to the Arctic, prone to undergo a jellification, with an increase in abundances of gelatinous zooplankton?

Obj. 4.1) Model spatial and temporal shifts in gelatinous zooplankton communities with species distribution modeling based on newly collected optical data in Fram Strait (**Chapter 3**).

RQ5. Which species are likely to see expanding or contracting ecological niches across the pan Arctic until the end of the 21st century ?

Obj. 5.1) Project changes for the dominant gelatinous zooplankton species until the end of the 21st century using species distribution modeling based on data from the pan-Arctic scale (**Chapter 2**).

1.12 List of the manuscripts and contributions of authors

Manuscript #1 - Chapter 2

Pan-Arctic distribution modeling reveals climate-change driven poleward shifts of major gelatinous zooplankton species

Authors: Dmitrii Pantiukhin, Gerlien Verhaegen, Charlotte Havermans

Author Contributions

This study was conceptualized by CH and DP. DP performed all analyses, with methodological input of GV and CH. DP was responsible for writing, with extensive input from all authors resulting in the final version.

Manuscript **under review** in Limnology & Oceanography

Manuscript #2 - Chapter 3

Optical observations and spatio-temporal projections of gelatinous zooplankton in the Fram Strait, a gateway to a changing Arctic Ocean

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Author contributions

This study was conceptualized by CH and DP. DP, CH, HJH and GV carried out the field work for optical data collection. DP, GV, and PN performed visual identification of the PELAGIOS dives. DP performed all analyses, with methodological input of CK, KJ, GV and CH. DP was responsible for writing, after which extensive input from all authors resulted in the final version. All authors approved the submitted version.

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Manuscript #3 - Chapter 4

In-situ observations of gelatinous zooplankton aggregations in inshore and offshore waters along a poleward gradient

Author Contributions

This study was conceived by CH and DP. CH carried out the fieldwork. DP carried out all the optical annotations, with input of AH and JJSA. DP performed all analyses, with methodological input of CH. DP was responsible for writing, with extensive input of CH, and further corrections from all other authors resulting in the final version.

Manuscript **under review** in Polar Biology

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Chapter 2. Pan-Arctic distribution modeling reveals climate-change driven poleward shifts of major gelatinous zooplankton species

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Author Contributions

This study was conceptualized by CH and DP. DP performed all analyses, with methodological input of GV and CH. DP was responsible for writing, with extensive input from all authors resulting in the final version.

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2.1 Abstract

Climate change and other anthropogenic activities can cause an increase in abundance of gelatinous zooplankton, which impacts the ecosystem, fish stocks and biogeochemical cycles. However, this ocean 'jellification' hypothesis has not yet been verified for the Arctic Ocean, despite it being the most rapidly changing ocean on Earth. Gelatinous zooplankton are a key component of Arctic pelagic food webs. Yet, they remain critically understudied and commonly excluded from large-scale modeling studies, challenging projections of the future state of the Arctic ecosystems. Our study is based on an extensive biogeographic dataset which has been aggregated from four open-source databases. It includes data on eight of the most reported gelatinous zooplankton taxa of the pan-Arctic region, spanning all their phylogenetic groups (Tunicata, Ctenophora, Hydrozoa, and Scyphozoa) and trophic levels. By modelling three-dimensional species distributions coupled to climate change scenarios, we identified species with expanding or contracting habitat ranges. Our projections indicated a general tendency for gelatinous zooplankton distributions to shift toward the poles, with varying degrees of suitable habitat expansion (largest for the scyphozoan *Cyanea capillata*) or contraction (largest for the hydrozoan *Sminthea arctica*). Sea ice and water depth significantly influenced the distribution of gelatinous zooplankton, but the interplay of temperature, salinity, and surface carbon concentration played an important role in areas where these species are most likely to occur. We discuss how changes in gelatinous zooplankton distribution can potentially cause a shift in the Arctic food web, increase competition with fish stocks, and alter carbon transport to the seafloor.

Keywords: Arctic Ocean, environmental change, cnidarians, ctenophores, appendicularians, gelatinous zooplankton, species distribution modeling, spatio-temporal projections

2.2 Introduction

Jellyfish (cnidarian medusae and ctenophores) and other gelatinous zooplankton (e.g., siphonophores, pelagic tunicates) are generally predicted to benefit from climate change, based on increased numbers or biomass of temperate jellyfish within various regions across the globe (Brotz et al. 2012). Other anthropogenic impacts, such as eutrophication and overfishing, also favor gelatinous zooplankton (Richardson et al. 2009). The combined impact of all these factors is likely to induce “regime shifts" from highly productive, fish-dominated to jellyfish-dominated, less productive pelagic food webs (Richardson et al. 2009). This paradigm of an ocean “jellification” is supported by a growing number of records of negative impacts of jellyfish aggregations on human enterprises, including fisheries (e.g., net clogging, gear damage, reduced catch), tourism (stinging jellyfish) and clogging of water-intakes of power production systems (Condon et al. 2013). Gelatinous zooplankton taxa span different trophic levels, from grazers on microplankton (pelagic tunicates) to predators on zoo- and ichthyoplankton (Júnior et al. 2022). By competing with adult fish for zooplankton prey, and by preying on fish larvae and eggs, jellyfish may outcompete fish in stressful environments or prevent fish stock recovery after overfishing (e.g., Irish Sea, Lynam et al. 2011). Conversely, studies have highlighted the role of increasing gelatinous zooplankton blooms for enhancing vertical carbon export, which is well documented for salps (Steinberg et al. 2023) and appendicularians (Jaspers et al. 2023), but also large jellyfish can enhance downward carbon flux (Lebrato et al. 2013). Moreover, whereas gelatinous zooplankton have long been considered a dead end of the food chain, an increasing number of studies revealed that these organisms are an important food source for many fish, crustaceans, and other organisms (reviewed in Hays et al. (2018)). While there is increasing evidence of a rise in jellyfish abundance in some marine ecosystems, it is not yet clear whether this is a global trend or short-term fluctuations in their abundance (Condon et al. 2013).

Over recent decades, the Arctic Ocean has experienced more significant changes than any other ocean, including warming of ocean temperatures by four times the global average (Rantanen et al. 2022), increased stratification, altered currents and circulation patterns, as well as a rapid sea ice retreat (Gulev et al. 2021). These alterations also cause poleward range shifts of different organisms, from phytoplankton to higher trophic levels, resulting in the restructuring of entire Arctic food webs (Frainer et al. 2017). Most of the studies on range shifts of boreal taxa into the Arctic Ocean have focused on hard-bodied crustacean zooplankton (Freer et al. 2021) and fish (Frainer et al. 2017). Studies on the distribution and abundance of gelatinous zooplankton in the Arctic Ocean have mostly been limited to local assessments (Raskoff et al. 2010; Mańko et al. 2022; Pantiukhin et al. 2023). To date, a comprehensive assessment of gelatinous zooplankton communities on the pan-Arctic scale has not been carried out.

One of the most suitable approaches to better understand the ecology of marine organisms and project their spatio-temporal distribution is species distribution modeling, also synonymized as ecological niche modelling (Robinson et al. 2017). Until recently, the majority of marine species distribution modeling case studies were applied in two dimensions (i.e., longitude-latitude), neglecting the third dimension of water depth, and relying on environmental parameters derived from the sea surface layers (Duffy and Chown 2017). The distribution of gelatinous zooplankton communities is, however, highly dependent on water depth (Mańko et al. 2020; Pantiukhin et al. 2023). Moreover, two-dimensional species distribution models average environmental variables over depth layers, resulting in biased results (Duffy and Chown 2017), particularly when studying midwater taxa. Recently, more marine species distribution modeling studies are carried out in three dimensions (i.e., longitude-latitude-depth), including case-studies of widespread epipelagic or midwater (e.g., Bentlage et al. 2013; Verhaegen et al. 2023) jellyfish outside the Arctic Ocean. Despite the wide application of such studies worldwide, only 3% of species distribution modeling studies were devoted to the Arctic Ocean and none of these focused on the distribution of gelatinous zooplankton (Robinson et al. 2017).

In this study, we applied species distribution modeling in three dimensions of gelatinous zooplankton species on the pan-Arctic scale in order to reveal drivers of distributions and shifts in their suitable habitat under future climate change scenarios. To capture these three-dimensional patterns, we used a methodology proposed by Bentlage et al. (2013). This involves unwrapping the three-dimensional environment into a two-dimensional strip of rasters, with each adjacent raster corresponding to consecutive depth layers (Bentlage et al. 2013; Duffy and Chown 2017). We hypothesized that global change is altering pan-Arctic gelatinous zooplankton communities and their suitable habitats, and that boreal-Atlantic species, which are advected into the Arctic Ocean, will become more abundant with warming and sea ice retreat. We chose two representative species of each of the different taxonomic groups: hydrozoans, scyphozoans, ctenophores, and appendicularians. This combination of taxa comprised micrograzers (appendicularians) to major predators interacting with fish (scyphozoans). Each of the selected taxa are known to be very abundant in temperate or Arctic ecosystems and play a major role as prey and predators as well as for vertical carbon export. Based on this, we aimed to: (1) identify the environmental factors determining the community structure and distribution of gelatinous zooplankton within the pan-Arctic (2) describe the geographical and vertical distribution of these communities; (3) project future changes in gelatinous zooplankton communities in the Arctic Ocean using climate change scenarios.

2.3 Materials and Methods

2.3.1 Study area

We chose the pan-Arctic scale (>60ºN) as the study area (Figure 2.1). This was done to include gelatinous zooplankton species that could be considered as boreal species commonly occurring in the Arctic Ocean, or species that may expand their distribution poleward from the boreal realm. It also allowed us to examine the mixing zones of the Arctic Ocean with temperate Pacific and Atlantic waters. The oceanographic features of the Arctic Ocean are largely determined by the presence of sea ice, pronounced water stratification, freshening of coastal areas by continental river runoff, and the influence of warm water inflow from the Atlantic and Pacific oceans.

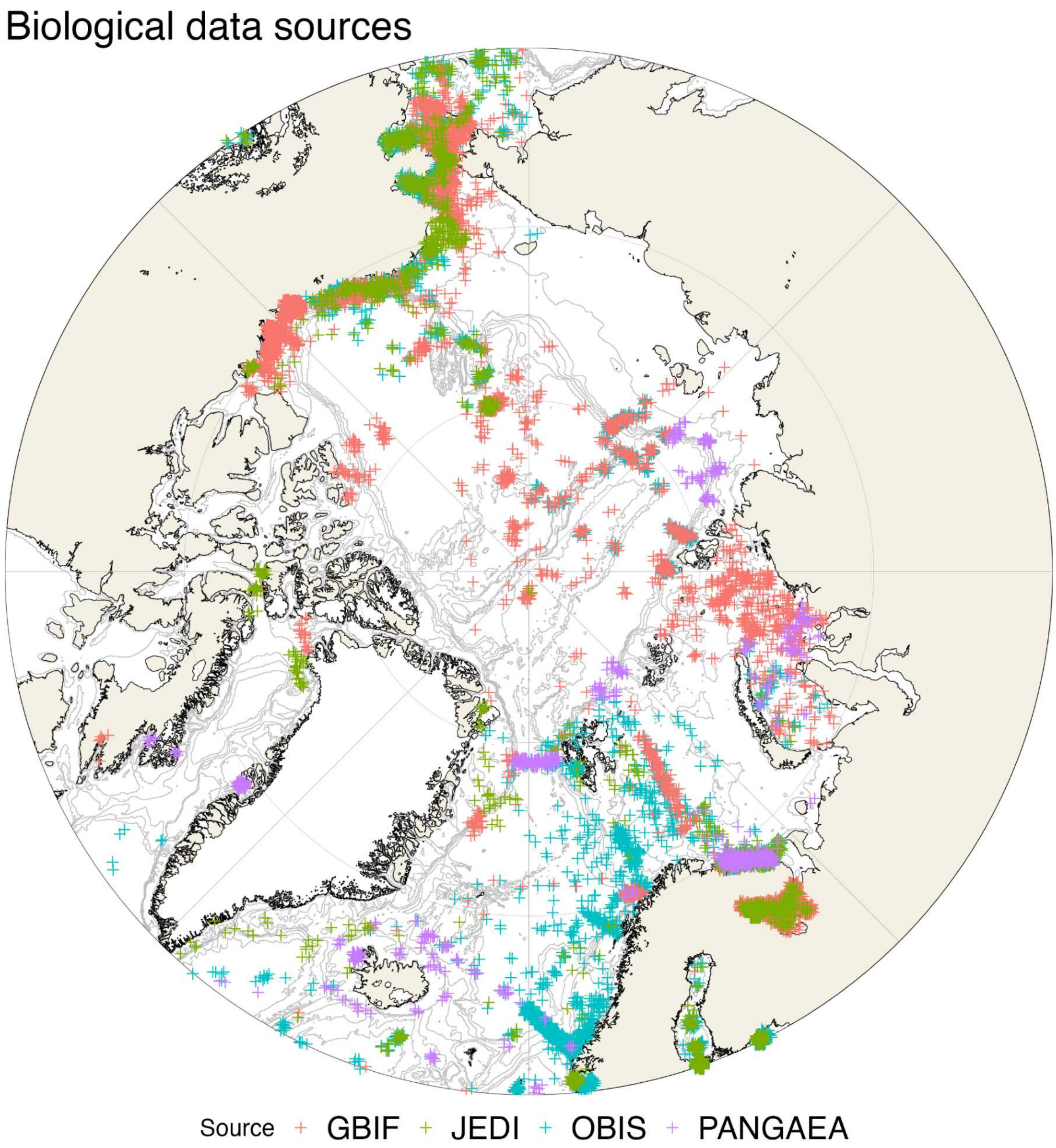

Figure 2.1. Pan-Arctic distribution of gelatinous zooplankton. Spatial distribution of gelatinous zooplankton based on data collected between 1950 and 2014. Data sources include JeDI (Jellyfish Database Initiative), OBIS (Ocean Biogeographic Information System), GBIF (Global Biodiversity Information Facility), and PANGAEA (Data Publisher for Earth & Environmental Science).

2.3.2 Biogeographic data

We obtained biogeographic data from four databases: Ocean Biodiversity Information System (OBIS), Global Biodiversity Information Facility (GBIF), Jellyfish Database Initiative (JeDI), and PANGAEA (Figures 2.1, 2.2). OBIS and GBIF are global repositories of biogeographic data (https://obis.org/, https://www.gbif.org/), JeDI is a database focused exclusively on gelatinous zooplankton (Lucas et al., 2014), and PANGAEA (https://www.pangaea.de) is a data publishing platform-aggregator for earth and environmental sciences (Table 2.S1). We retrieved data from OBIS, GBIF, and JeDI by sending direct queries to the databases, and compiled dataset from individual publications from PANGAEA (Table 2.S1). Furthermore, we selected data for the period 1950 to 2014 to match the temporal distribution of the environmental data (Figure 2.S1). Vertical resolution ranged from 0 to 3000 m, as the selected taxa were predominantly found in these depth ranges (Figure 2.S2). Due to differing quality control mechanisms in the studied databases (Moudrý and Devillers 2020), we rounded spatial longitude and latitude values to one decimal place and depth values to integers. We filtered biogeographic data to remove unreliable coordinates, incorrect depth values, and repeated values. In addition, we 'thinned' data to avoid spatial autocorrelation, (i.e., points that occurred multiple times on the same spatial cell of the predictive grid (50 x 50 km) were combined into a single occurrence). We included a total of eight gelatinous zooplankton taxa in the analysis. These included two species of the class Hydrozoa (*Aglantha digitale* and *Sminthea arctica*; Figure 2.S3), two species of the class Appendicularia (*Oikopleura vanhoeffeni* and *Fritillaria borealis*; Figure 2.S3), two species of the class Scyphozoa (*Cyanea capillata* and *Periphylla periphylla*; Figure 2.S3) and two species of the phylum Ctenophora (*Mertensia ovum*, *Beroe* spp.; Figure 2.S3). We selected these representatives of the different gelatinous zooplankton groups because they span different trophic levels from microplankton grazers to zoo- and ichthyoplankton predators, ii) showed the highest records in most databases (Figure 2.3), iii) are easily identifiable, reducing identification errors. The *Beroe* species were grouped together as *Beroe* spp. due to ongoing taxonomic revisions and controversies in species identification (Shiganova and Abyzova 2022).

2.3.3 Environmental data

We obtained environmental data from the Max Planck Institute Earth System Model (MPI-ESM1.2, Gutjahr et al. 2019; Figure 2.S4), which provided data on historical (Jungclaus et al. 2019) and future projections (Schupfner et al. 2019) of various environmental variables including temperature (°C), salinity (PSU), sea ice area coverage (%), dissolved oxygen concentration (mol m^{-3}), phytoplankton carbon concentration at the ocean surface (mol m^{-3}), and seawater phytoplankton carbon concentration (mol m^{-3}). We used data from the historical runs (1950-2014) to train the models, while data from two ssp370 emission scenarios were used to generate future projections (O'Neill et al. 2014). The scenarios ssp370 represent Shared Socioeconomic Pathways (SSPs) that describe plausible future trajectories of global societal development, with ssp370 assuming medium-high emission trajectory. We used a methodology similar to Bentlage et al. (2013), allowing us to create a predictive raster that was used to model the distribution of marine species in three-dimensional space. We divided the data into eight depth intervals, based on the most pronounced changes identified for the temperature-salinity gradients, and unfolded them into a long predictive raster (Figure 2.S4). Mean depth values were taken at 26.5 m, 103.5 m, 246.25 m, 461.25 m, 865 m, 1460 m, 2087 m, and 2797.50 m (Figure

2.S4). This aggregation was also done in order to minimize the bias associated with averaging the depth values in the databases (obtained from the maximum and minimum sampling depths). Furthermore, we checked predictive rasters for multicollinearity. Because of its strong correlation with temperature, we removed oxygen to minimize multicollinearity, thus achieving variance inflation factor values (VIF) < 5.

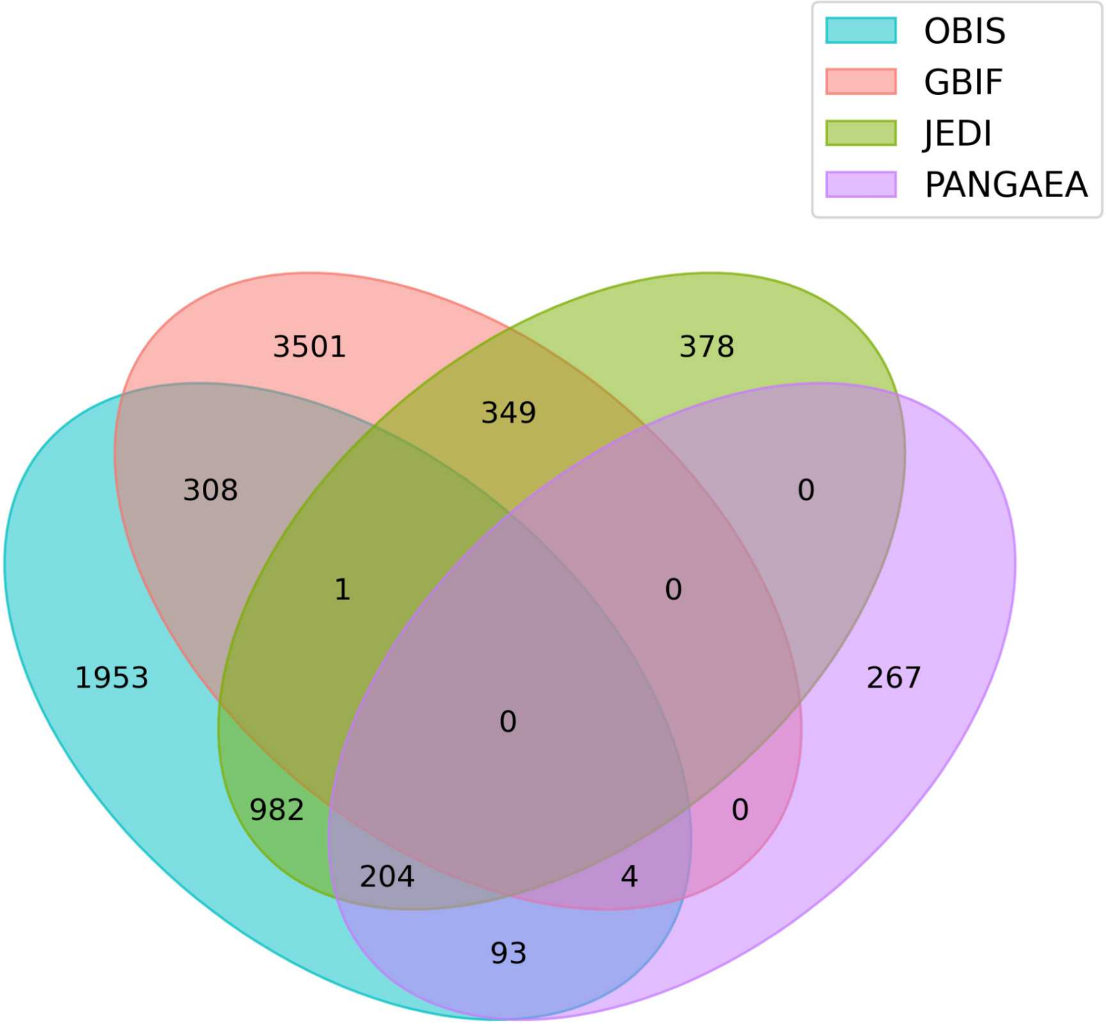

Figure 2.2. Venn diagram of unique records of gelatinous zooplankton in the pan-Arctic region. The diagram illustrates the overlap of records in four biogeographic databases: JeDI (Jellyfish Database Initiative), OBIS (Ocean Biogeographic Information System), GBIF (Global Biodiversity Information Facility), and PANGAEA (Data Publisher for Earth & Environmental Science).

Figure 2.3. Species proportions of gelatinous zooplankton. The pie chart shows the relative proportion of occurrence for eight species of gelatinous zooplankton included in the study.

2.3.4 Maxent model

We used a maximum entropy model (Maxent) to analyze the spatial distribution of the eight selected gelatinous zooplankton taxa. Maxent is a maximum likelihood estimation model that predicts the distribution of species based on the suitability of their habitats (Phillips et al. 2017). We choose the Maxent model because of its high predictive power for presence-only data (Valavi et al. 2022). We used the R package *ENMeval* v.2.0.4 for fine-tuning and model selection (Muscarella et al. 2014; Kass et al. 2021). We adjusted various parameters during the model parameterization process, such as: (1) the regularization multiplier (RM: 1, 1.5, 2, 2.5, 3, 3.5, and 4), which controls the complexity of the responses in the model; (2) a different combination of the feature classes, including linear (L), quadratic (Q), product (P), threshold (T), and hinge (H); and (3) the number of background points (10,000, 20,000, and 30,000). Background points were selected to adequately capture distribution of the environmental parameters (Figure 2.S5). We evaluated the performance of the models by partitioning the occurrence locations into validation and training bins (4-fold cross-validation). We used spatial cross validation using a pre-built function in the *ENMeval* package - 'checkerboard2' (Radosavljevic and Anderson 2014). This method is preferable over random partitioning because it reduces spatial autocorrelation (Roberts et al. 2017). We selected the optimal models based on the following cross-validation evaluation metrics (Figure 2.4): (1) average test omission rate (10th percentile; OR10p; Kass et al. 2023), (2) continuous Boyce Index (CBI; Di Cola et al. 2017), (3) Area Under the receiver operating Characteristic curve (AUC; de Hond et al. 2022) and (4) Akaike Information Criterion (AIC; Cavanaugh and Neath 2019). We preferred metrics that assessed how well the model predicted "presence" points (OR10p, CBI), and after "presence-absence" (AUC). This is because our data did not contain true absences, but instead relied on randomly selected background points. Models with AUC and CBI values below 0.7 and 0.5, respectively, were not considered for further study because of their poor fit (de Hond et al. 2022). We also preferred models with low AIC values to reduce the risk of overfitting. This was also important in the context of our study because we made projections over time (Merow et al. 2014).

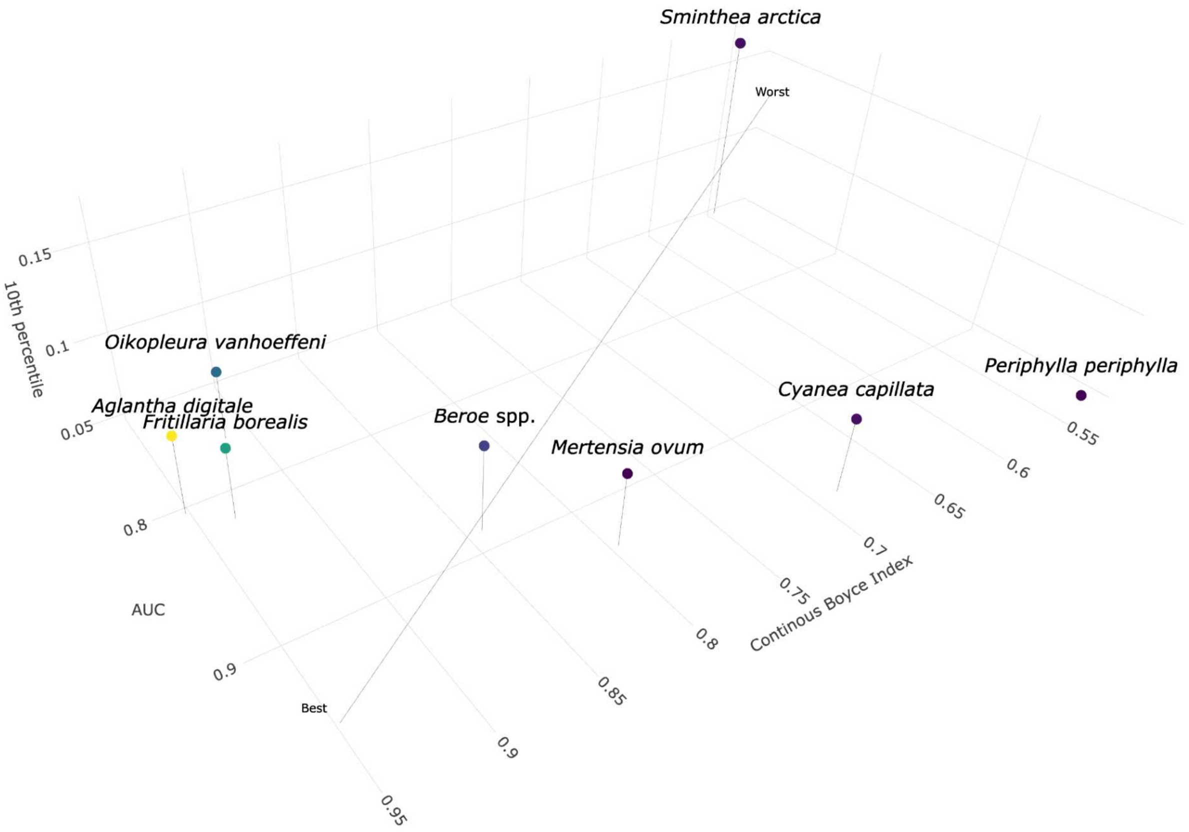

Figure 2.4. Maxent model performance scatterplot. Three-dimensional scatter plot of the relationship between the Continuous Boyce Index, AUC, and the 10th percentile evaluation metrics for the best Maxent models. Each point's color-coded based on its AICc value, with lighter shades indicating higher complexity and darker shades indicating lower complexity.

We used the Maxent permutation importance metric to determine the importance of environmental parameters (Figure 2.5). We used complementary log-log (cloglog) predictions to construct probability maps for historical time periods (1950 - 2014), as well as future scenarios (2050 - 2100). We used cloglog over the logistic transformation for its stronger theoretical justification (Phillips et al. 2017). Projected grids were interpolated onto an Arctic Polar

Stereographic projection (EPSG:3995). For visualization purposes, all depth layers were also averaged across latitudes for the western and eastern hemispheres (Figure 2.6). We also produced environmental limiting factor maps that showed the least favorable variables on the spatial scale (Elith et al. 2010; Baumgartner et al., 2023; Figure 2.7).

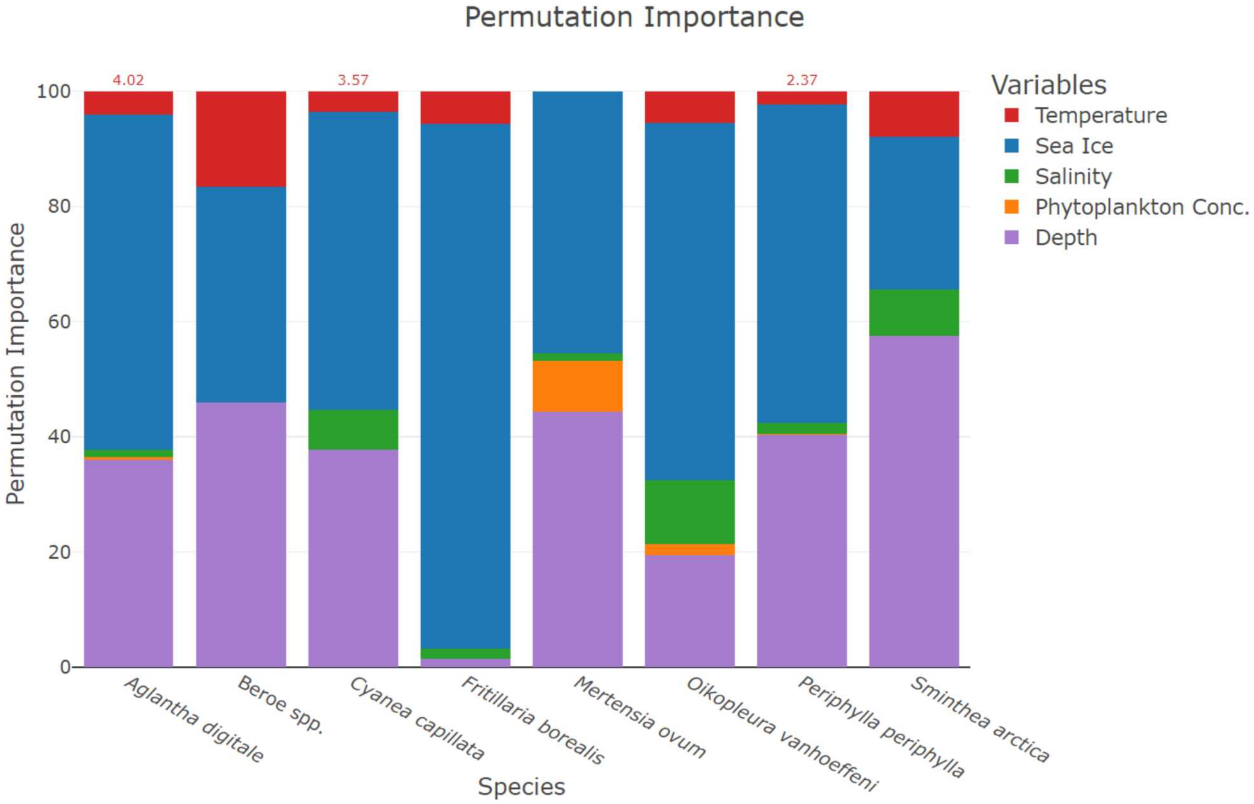

Figure 2.5. Permutational importance of the environmental variables for the studied gelatinous zooplankton taxa, based on the best Maxent models.

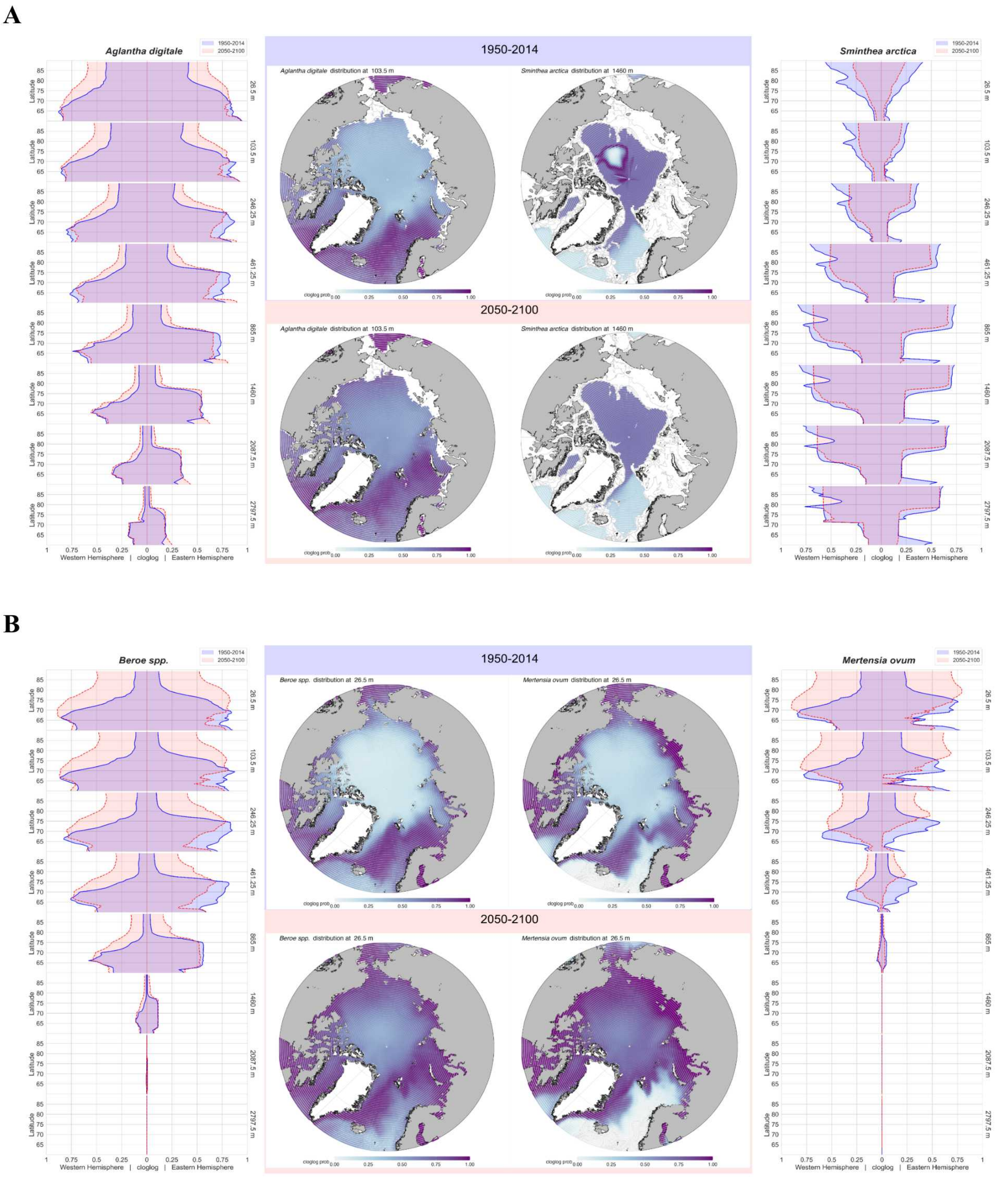

Figure 2.6. Projected spatial distribution of gelatinous zooplankton species. Maps illustrating spatial distribution for eight marine gelatinous zooplankton species for the period 1950-2014 and 2050-2099.

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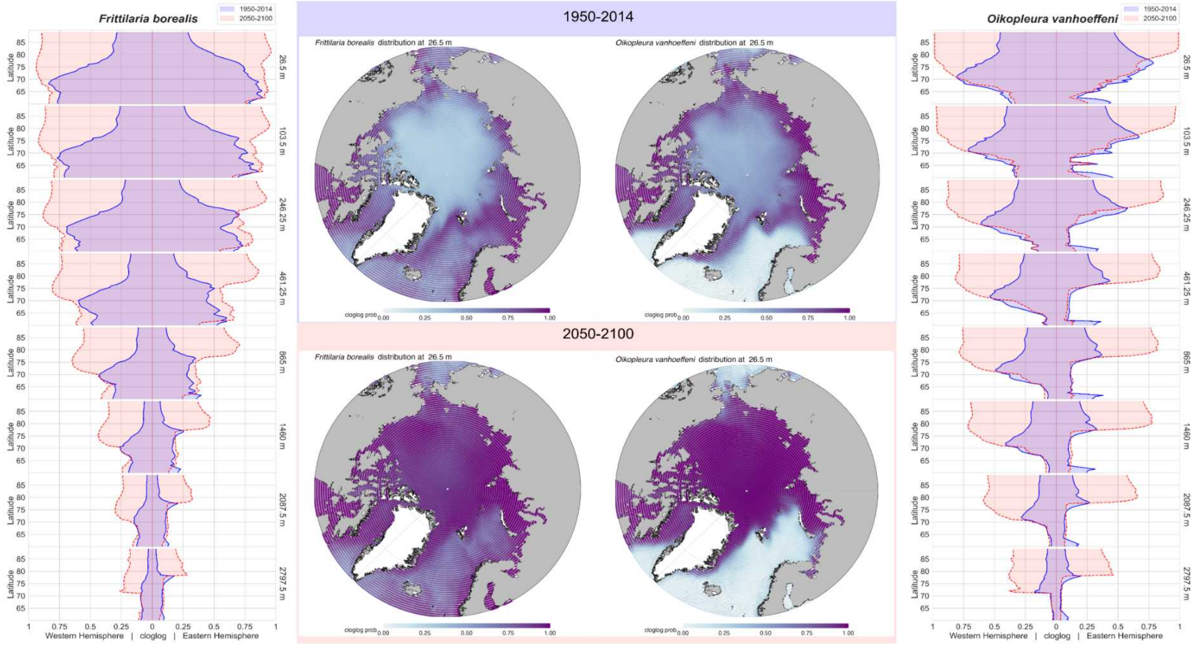

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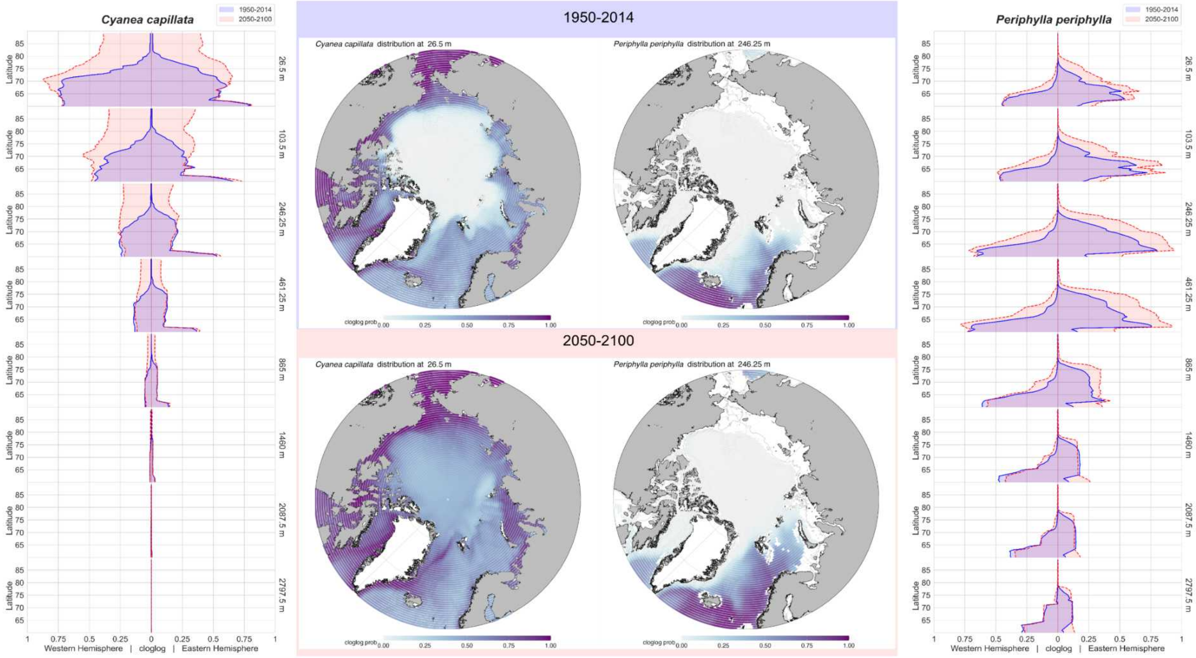


Continued Figure 2.6. Projected spatial distribution of gelatinous zooplankton species. Maps illustrating spatial distribution for eight marine gelatinous zooplankton species for the period 1950-2014 and 2050-2099.

2.4 Results

2.4.1 Biogeographic data collection

For the eight selected gelatinous zooplankton taxa, we collected 24,160 occurrence points with available metadata on longitude, latitude, and depth values from four databases: GBIF, OBIS, JeDI, and PANGAEA (Figures 2.1, 2.2). Each database contributed a different set of unique records (Figure 2.2). We found no records which were shared by all four databases and each of them contributed to the coverage of unique regions in the pan-Arctic (Figure 2.1). In GBIF we observed the largest number of unique records (3,501), and 308 duplicated records with OBIS, 349 with JeDI, and 0 with PANGAEA. From the OBIS database we retrieved 1,953 unique records, and a number of duplicated records of 308, 982, and 93 shared with GBIF, JeDI, and PANGAEA, respectively. In JeDI, we found 378 unique records, as well as 982 duplicated records shared with OBIS, 349 with GBIF, and 0 with PANGAEA. Finally, from PANGAEA we gathered 267 unique records, with duplicate records only found with OBIS (93 records). Data present in more than two databases were found among OBIS, JeDI, and PANGAEA (208 occurrences). We observed five temporal peaks of gelatinous zooplankton counts per year over the whole study period: a first 1953-1955 peak, with the highest count of 568 in 1955, 1967 (330 counts), 1976 (568 counts), 1987 (492 counts), and 1995 (484 counts) (Figure 2.S1). Since the 2000s, the gelatinous zooplankton presence data have been more consistently sampled without large fluctuations. Whereas some taxa, such as *Aglantha digitale* and *Fritillaria borealis*, showed a rather stable sampling effort throughout our study period, records of other taxa were characterized by more sporadic sampling patterns, such as *Sminthea arctica*, *Oikopleura vanhoeffeni*, as well as both ctenophore and scyphozoan species.

We grouped the gelatinous zooplankton species in our study into three distinct categories based on their major depth distributions (Figure 2.S2): epipelagic (0-200 m), epi-mesopelagic (0-1,000 m), and meso-bathypelagic (200-3,000 m). Epipelagic species included *Cyanea capillata* with a mean depth and standard deviation (SD) of 34.08 ± 88.56 m, *Mertensia ovum* - 86.55 ± 255.61 m, and *Beroe* spp. - 96,54 ± 210.99 m. Epi-mesopelagic species included *Periphylla periphylla* (335.92 ± 330.82 m), *Fritillaria borealis* (209.60 m ± 426.09 m), *Oikopleura vanhoeffeni* (341.58 ± 566.06 m), and *Aglantha digitale* (178.93 m ± 365.86 m). Our only meso-bathypelagic species was *Sminthea arctica* (850.20 ± 755.58 m).

After the pre-processing steps, we included the following number of occurrence points into the SDMs: *Aglantha digitale* (1,060 points), *Fritillaria borealis* (623), *Oikopleura vanhoeffeni* (381), *Beroe* spp. (245), *Cyanea capillata* (80), *Sminthea arctica* (46), *Periphylla periphylla* (41), and *Mertensia ovum* (30).

2.4.2 Evaluation of the model performance

In total, we ran 49 models (with four replicates each) for each of the eight selected gelatinous zooplankton taxa. We selected the best performing models with the following feature classes, regularization multipliers, and number of background points (Figures 2.4, 2.S6, Table 2.S2). The best model fit according to the OR10p metric was observed for *Periphylla periphylla* (0.052), and *Mertensia ovum* (0.094), while *Sminthea arctica* showed the worst fit (0.164; Figure 2.4; Table 2.S3). In terms of CBI values, *Aglantha digitale* (0.954), *Fritillaria borealis* (0.936), and *Oikopleura vanhoeffeni* (0.915) had the best model fit. In contrast, *Periphylla periphylla* (0.531) and *Sminthea arctica* (0.552) showed the worst CBI results (Figure 2.4). Regarding AUC values, the best models were fitted for *Periphylla periphylla* (0.975), *Cyanea capillata* (0.959). Conversely, *Sminthea arctica* had the worst fit with an AUC (0.728; Figure 2.4). Correlation analysis between the metrics showed the lowest negative correlation between OR10p and AUC values (-0.71) and the highest positive correlation between CBI and AICc (0.74; Figure S7).

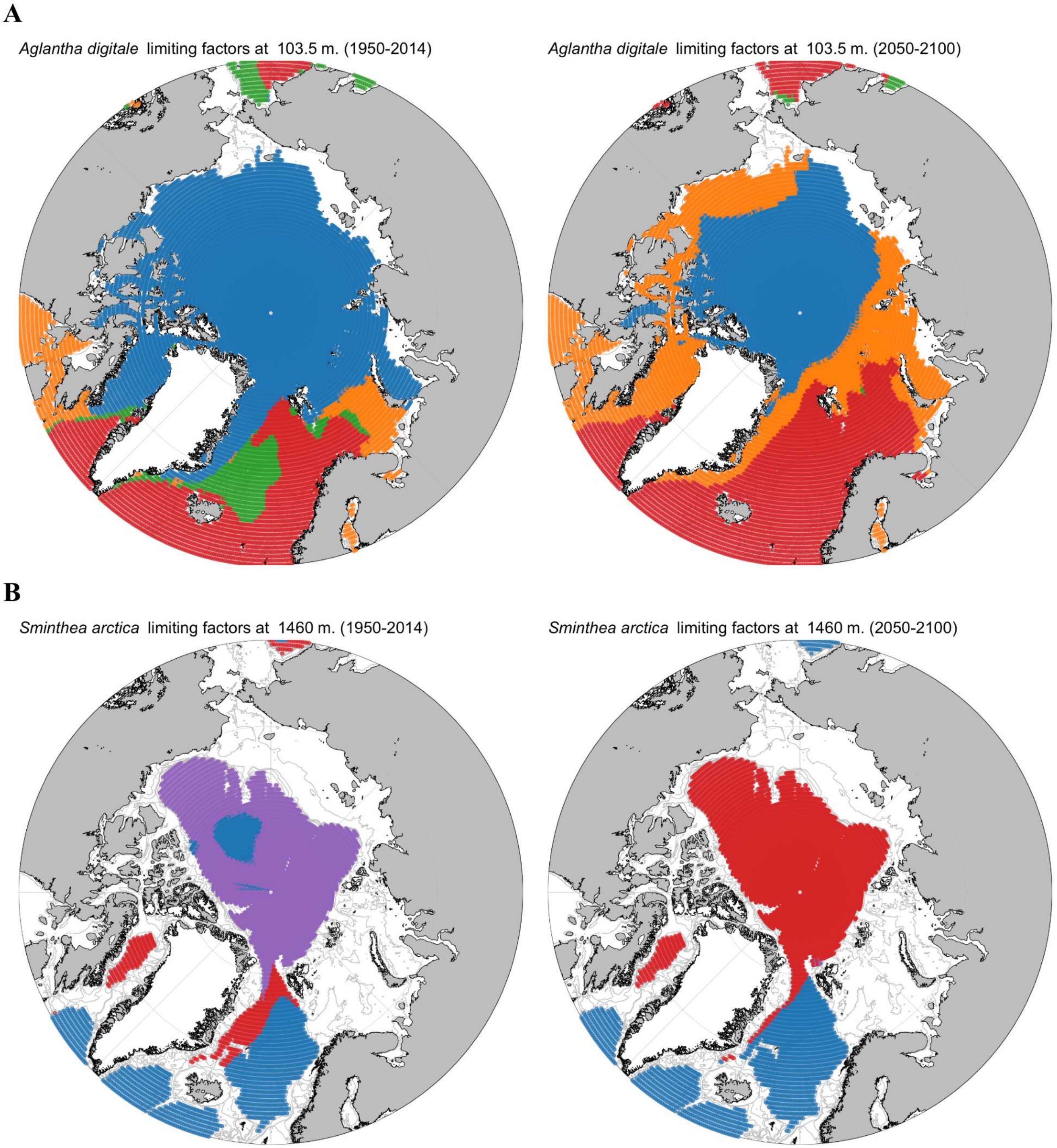
2.4.3 Environmental drivers

Sea ice and depth values showed the highest mean permutational importance (53.5%, and 35.4%, respectively; Figure 2.5), while salinity, temperature, and sea ice concentrations had lower mean permutational importance values (4.03%, 5.70%, and 1.39%, respectively; Figure 2.5). However, the relative importance of environment drivers varied along the depth column. For instance, when considering the historical distribution projections of *Aglantha digitale*, below 1,460 m it was exclusively limited by depth (Figures 2.7, 2.S8, 2.S9), while in the upper layers, sea ice concentrations were the most important factor (Figures 2.7, 2.S9). Temperature predominantly limited the distribution of *Aglantha digitale* in the North Atlantic and Norwegian Sea, while phytoplankton concentrations were the main factor in sea ice marginal zones. Salinity made the smallest contribution in the upper layers and partially limited the presence of *Aglantha digitale* in the Greenland Sea. For future projections, the importance of sea ice decreased significantly, while the importance of zones with temperature and phytoplankton concentrations increased. The strongest changes were observed in the zones of sea ice retreat (in the Beaufort Sea as well as around the Eurasian shelf). The distribution of the other species of the class Hydrozoa, *Sminthea arctica*, was mostly limited by depth for historical and future projections (Figures 2.7, 2.S8, 2.S9). However, on the historical projections at a depth of 865 m, which is characterized by its greatest occurrence, *Sminthea arctica* was almost exclusively limited by temperature values. In future scenarios, the temperature importance zone extends to depths of 1,460 m. In the Fram Strait, the absence of sea ice in both current and future projections was the greatest limiting factor.

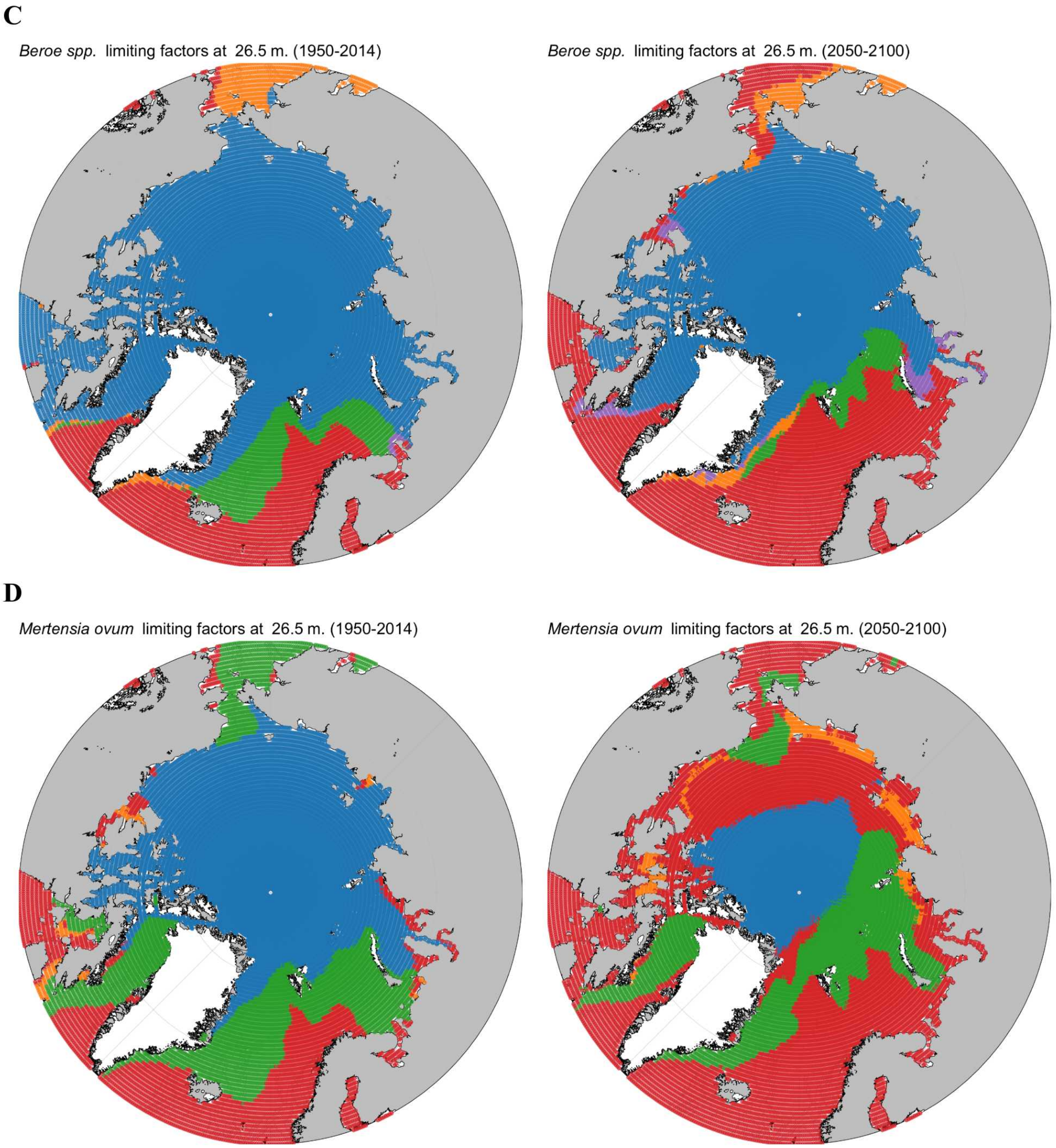
The occurrence of the scyphozoan species *Cyanea capillata* was limited by high concentrations of sea ice in the central regions (Figures 2.7, 2.S8, 2.S9). This was especially noticeable in the depth layers with the highest probability of occurrence (i.e., 26 and 103 m). In the sea ice-free zones, as well as at the marginal sea ice zones, temperature and salinity had the greatest limiting effect on the species' distribution. Temperature had the highest influence in the coastal areas from the Kara to the Beaufort seas, while in the Fram Strait and some parts of the North Atlantic, salinity played a more significant role. As for phytoplankton concentrations, they had a limiting role on *Cyanea capillata* occurrence in the coastal areas of the Barents Sea, as well as in some parts of the Norwegian and Bering Seas. By the end of the century, following the decrease of sea ice concentrations in the central regions, the importance of phytoplankton concentration as a limiting factor for *Cyanea capillata* also decreases, while the limiting values of temperature increase. Also, at the boundaries of marginal sea ice zones, the influence of phytoplankton concentrations as a limiting factor is more pronounced. The other scyphozoan species, *Periphylla periphylla*, was mostly limited by the presence of sea ice, which had a dominant effect at all depths (Figures 2.7, 2.S8, 2.S9). At the boundaries of the North Atlantic, where the probability of occurrence of the species is highest, phytoplankton concentrations had the greatest limiting effect, compared to salinity (to a depth of 246 m) and temperature (246 to 2,797 m) in the Norwegian Sea. By 2050-2100, due to the retreat and thinning of sea ice, its influence decreases, similar to *Cyanea capillata*. Following the retreat of sea ice, the salinity and temperature limiting zones shift proportionally, with the former in the southern regions and the latter in the northern boundaries, which is especially noticeable within the boundaries of the Barents Sea.

The ctenophore species *Mertensia ovum* was predominantly limited by depth below 246 m on the historical projections (Figures 2.7, 2.S8, 2.S9). However, in the epipelagic layers, sea ice concentrations had the strongest limiting impact, particularly in the central parts of the Arctic, the Kara Sea, and the Beaufort Sea. In the North Atlantic and Norwegian Sea, temperature had the greatest importance as a limiting value, while salinity in the Greenland, Barents and Bering seas. In projections from 2050 to 2100, the limiting influence of sea ice decreases drastically. In the sea ice free areas, as well as in the marginal sea ice zones, salinity and temperature values will become the main limiting factors. The other ctenophore taxon, *Beroe* spp., has similar limiting factors driving the historical projections (Figures 2.7, 2.S8, 2.S9). However, the factor depth determines the distribution of these species only from 1,460 m. Compared to *Mertensia ovum*, *Beroe* spp distributions are characterized by a more pronounced influence of phytoplankton concentrations in the Bering Sea. In 2050-2100, *Beroe*’s distribution in the central parts of the ocean remains limited by sea ice cover, while in the open ocean areas, temperature values have the greatest influence.

The historically projected distributions of the appendicularian species *Fritillaria borealis* were mostly limited by sea ice concentrations in the upper 1,460 m, below this, the depth limited the presence of this species (Figures 2.7, 2.S8, 2.S9). In the layers where the probability of occurrence was highest, we observed a significant limiting importance of carbon concentrations, particularly in the North Atlantic, Greenland Sea, and Bering Strait. In the Barents Sea, salinity and temperature played the main limiting role. By 2050-2100, the influence of sea ice and phytoplankton concentrations as limiting factors are decreasing. Within the boundaries of these zones, temperature starts to play a major role, especially at depths of 26 and 100 m. At greater depths, salinity limits the distribution of this species. The historically projected distributions of the other appendicularian species, *Oikopleura vanhoeffeni*, has been mainly limited by the concentrations of sea ice (Figures 2.7, 2.S8, 2.S9). However, in coastal areas, a high influence of phytoplankton concentration and temperature was observed. Salinity also had a limiting influence, but more locally, in the northern parts of the Greenland, Barents and Kara seas. In future projections, the influence of the presence of sea ice is declining, except for the North Atlantic and the Barents Sea, where the absence of sea ice limits the presence of the species. In deeper layers (246 - 1,460 m), salinity concentrations gain a stronger limiting influence.



Continued Figure 2.7. Environmental limiting factors for gelatinous zooplankton species. Maps illustrating environmental limiting factors for eight marine gelatinous zooplankton species for the period 1950-2014 and 2050-2099 (for the most probable depth layers). Blue - sea ice; red - temperature; green - salinity, purple - depth, orange - phytoplankton.



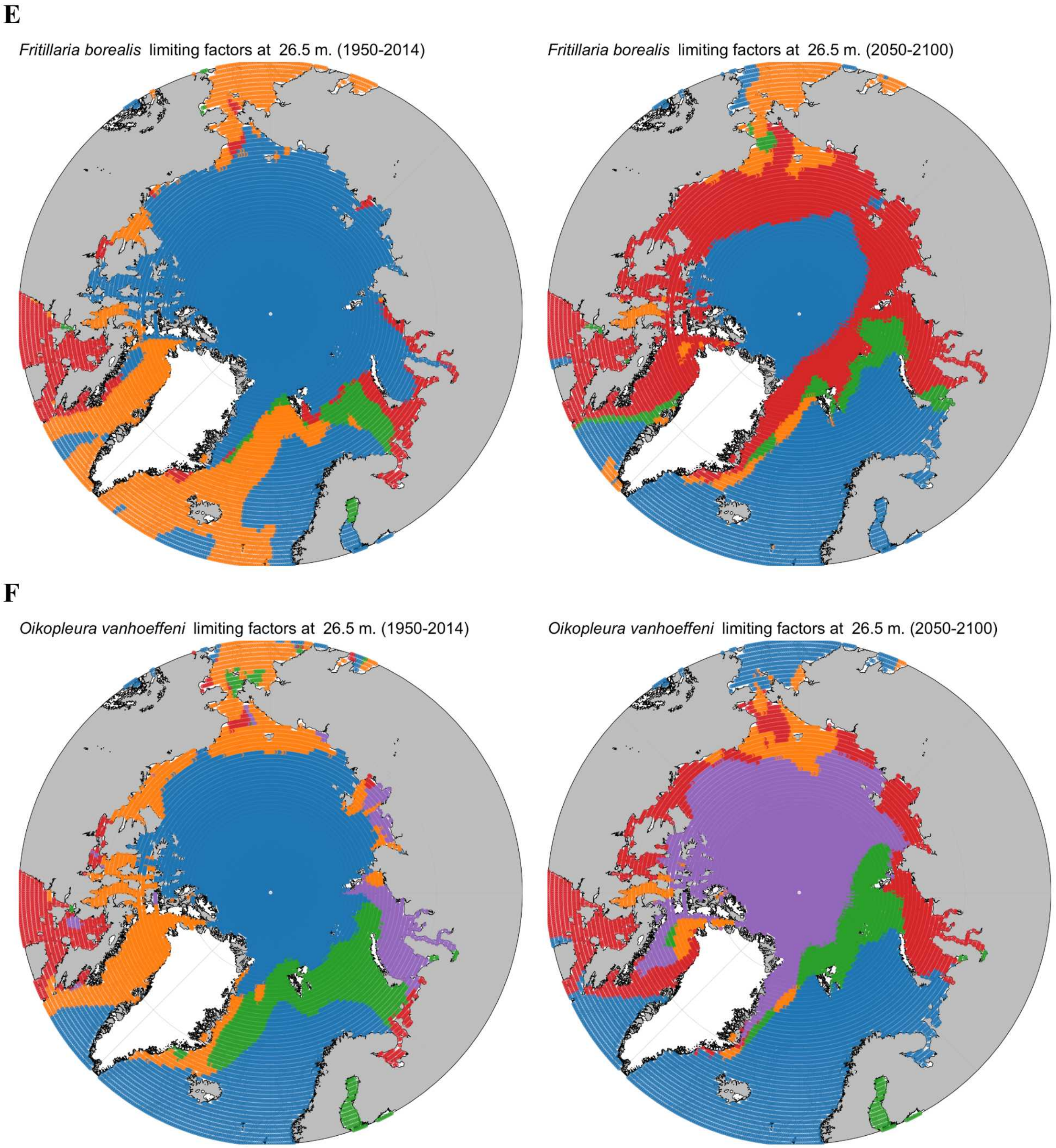
Beroe spp. limiting factors at 26.5 m. (1950-2014)

Beroe spp. limiting factors at 26.5 m. (2050-2100)

Mertensia ovum limiting factors at 26.5 m. (1950-2014)

Mertensia ovum limiting factors at 26.5 m. (2050-2100)

Continued Figure 2.7. Environmental limiting factors for gelatinous zooplankton species. Maps illustrating environmental limiting factors for eight marine gelatinous zooplankton species for the period 1950-2014 and 2050-2099 (for the most probable depth layers). Blue - sea ice; red - temperature; green - salinity, purple - depth, orange - phytoplankton.



E

Fritillaria borealis limiting factors at 26.5 m. (1950-2014)

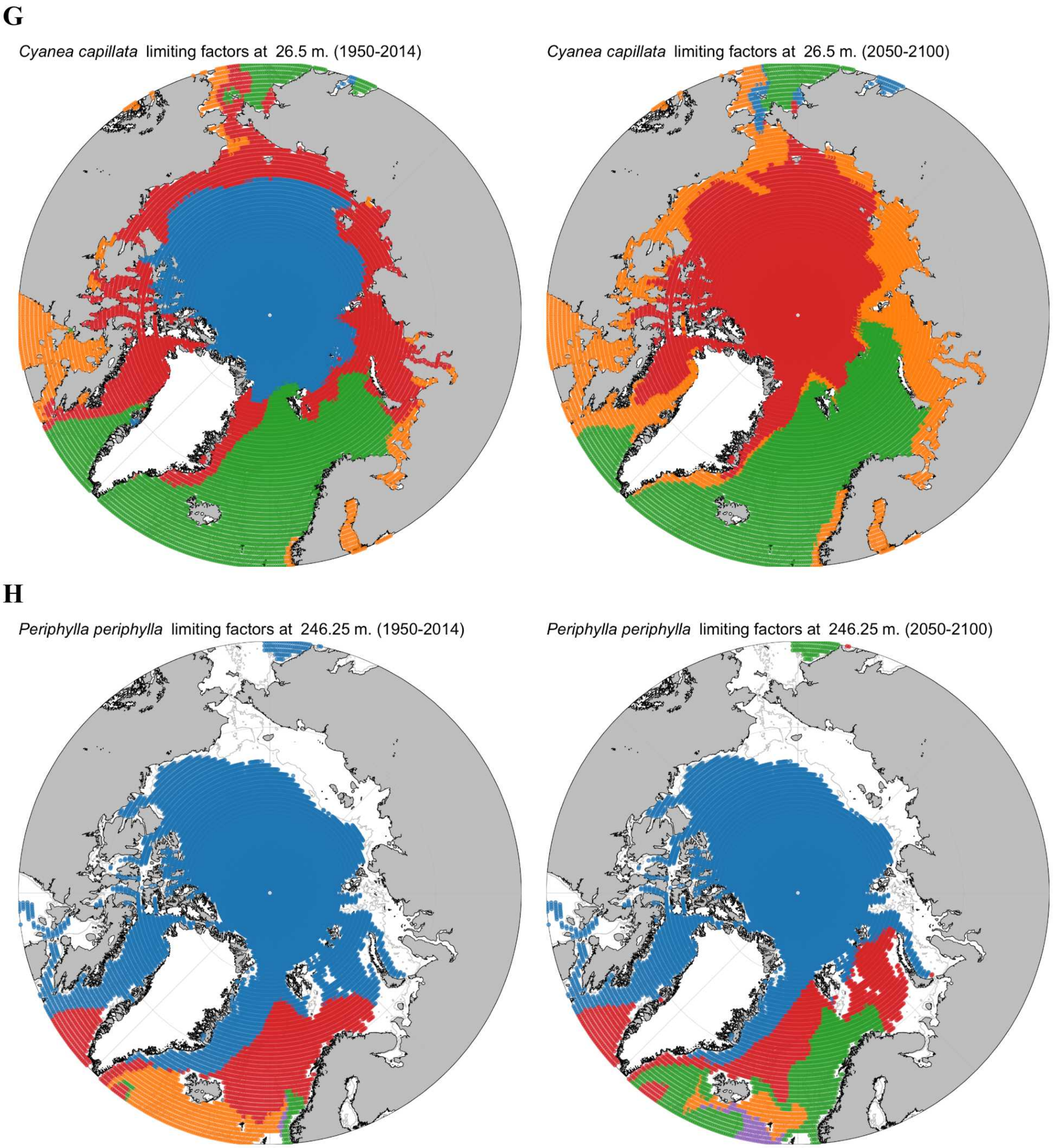
Fritillaria borealis limiting factors at 26.5 m. (2050-2100)

F

Oikopleura vanhoeffeni limiting factors at 26.5 m. (1950-2014)

Oikopleura vanhoeffeni limiting factors at 26.5 m. (2050-2100)

Continued Figure 2.7. Environmental limiting factors for gelatinous zooplankton species. Maps illustrating environmental limiting factors for eight marine gelatinous zooplankton species for the period 1950-2014 and 2050-2099 (for the most probable depth layers). Blue - sea ice; red - temperature; green - salinity, purple - depth, orange - phytoplankton.



Continued Figure 2.7. Environmental limiting factors for gelatinous zooplankton species. Maps illustrating environmental limiting factors for eight marine gelatinous zooplankton species for the period 1950-2014 and 2050-2099 (for the most probable depth layers). Blue - sea ice; red - temperature; green - salinity, purple - depth, orange - phytoplankton.

2.4.4 Spatial distribution mapping and vertical profiling

Based on the spatial rasters from the MPI-ESM1.2 model, we constructed predictive maps for both observed (1950-2014) and future time periods (2050-2100; Figure 2.6). We found that both hydrozoan species had a clear segregation of their preferred depth zone at 860 m (Figures 2.6, 2.S8) with *Aglantha digitale* mainly distributed above this depth and *Sminthea arctica* below it. A similar spatial segregation was also observed in the horizontal dimension, with the highest probability of occurrence of *Aglantha digitale* in the region south of 70 N, whereas *Sminthea arctica* was mostly recorded in the regions north of 70 N. By the end of the century, the distribution of *Sminthea arctica* contracted towards the pole, with the main retreat observed in the Fram Strait and a total loss of preferred suitable habitat of ~ -15%. In contrast, *Aglantha digitale* will be characterized by higher occurrences in the central Arctic Ocean by the end of the century with high presence values throughout the study region by 2050-2100, resulting in an overall increase in suitable habitat of ~ 29%.

The two ctenophore taxa *Beroe* spp. and *Mertensia ovum* were aggregated in the upper layers of the water column (Figure 2.6). *Beroe* spp. were represented mainly at depths up to 461 m, while *Mertensia ovum* was predominantly found in the epipelagic layers of 26 and 100 m. In historical projections, both species had the greatest presence in the marginal sea ice zones. *Beroe* spp. had the highest probability of occurrence in the Greenland, Barents, Bering, and Norwegian seas. *Mertensia ovum* was also observed in large numbers in these seas, except for the Norwegian Sea. By 2050-2100, the projected distribution of *Beroe* spp. contracted poleward, which is especially noticeable in the Norwegian and Greenland seas. However, closer to the pole (>75ºN) there was an increase in species occurrence at most sites, and the total suitable habitat increased by ~110% across the region. *Mertensia ovum* occurrence probability decreased in the Norwegian, Greenland, and Barents seas, but this decrease was more pronounced compared to *Beroe* spp. *Mertensia ovum* became more common near the pole, with the total values of suitable habitat increasing by ~ 84%.

The appendicularian species *Fritillaria borealis* and *Oikopleura vanhoeffeni* were observed to have a broad vertical distribution, extending down to depths of 865 m in the historical projection (Figure 2.6). Beyond this depth, the probability of occurrence decreased significantly. On the historical projections, *Fritillaria borealis* occurred predominantly in the Greenland Sea, Fram Strait, Barents Sea, Kara Sea, and Baffin Bay, with the highest occurrence values between 60 and 70ºN. *Oikopleura vanhoeffeni* had a more northern distribution, with the highest occurrence values between 70 and 75ºN. This species was found in the Kara and Laptev Seas, as well as in Baffin Bay. However, both species show a poleward distribution shift. *Fritillaria borealis* is projected to extend its presence throughout the entire Arctic Ocean, while *Oikopleura vanhoeffeni* narrows its suitable habitats toward the pole, disappearing from the Bering and Barents Seas and increasing its presence in the central parts of the Arctic Ocean. The total increase in suitable habitats is 130% and 102% for *Fritillaria borealis* and *Oikopleura vanhoeffeni*, respectively.

The scyphozoan species *Cyanea capillata* and *Periphylla periphylla* showed highest occurrences at the margins of the Arctic Ocean (Figure 2.6). In the historical projections, *Cyanea capillata* had its highest presence in the Bering Sea, Baffin Bay, and in some parts of the Norwegian and Barents seas. *Periphylla periphylla* was found in the North Atlantic and also in the southern parts of the Norwegian and Barents seas. The spatial maps show a shift of *Cyanea capillata* towards the Barents and Kara Seas, also this species becomes more common in Baffin Bay and the Beaufort Sea, with a total increase in suitable habitat of ~ 180%. *Periphylla periphylla* also shifts northward and occupies areas in the Svalbard fjords, in parts of the Barents Sea, and becomes more prevalent in the northern parts of the Bering Sea. The total increase in its suitable habitat is ~ 62%.

2.5 Discussion

2.5.1 Biogeographic data

Biogeographic data showed unevenness in overall records and spatial distribution (Figures 2.1, 2.2). Moreover, each of the four databases contributed a considerable number of unique values. The overlap between the values of the largest OBIS and GBIF databases was remarkably small ~5% (Figure 2.2). This could be explained by different data entry and quality control mechanisms, as well as poor exchange between data aggregators (Moudrý and Devillers 2020). Moudrý and Devillers (2020) found a rather similar low overlap between OBIS and GBIF in their study, which further supports the importance of thinning biogeographic data in both horizontal and vertical dimensions. None of the databases in our study had complete coverage of all studied regions (Figure 2.1) but when combined, spatial coverage improved. With the exception of some parts of the Arctic Ocean, such as Baffin Bay and the East Siberian Sea, the rest of the area was fairly well covered by survey stations. Data from JeDI and PANGAEA had a smaller overall proportion compared to GBIF and OBIS (Figure 2.2), but they contributed significantly to the spatial coverage of the region, at poorly studied sites (Figure 2.1). Ignoring spatial coverage and relying solely on a single database could lead to the underrepresentation of species in certain environments. Therefore, the use of a multi-database approach to collect biogeographic data for species distribution modeling increases accuracy particularly when modeling large-scale spatial distributions, as shown by our findings.

Temporal inconsistencies in historical data are a major challenge to understanding Arctic species spatial distributions (Piepenburg et al. 2011). These inconsistencies can be caused by a variety of factors. For example, inconsistent sampling effort due to difficult regional accessibility caused by variability in sea ice conditions. Peaks of records could also be related to the publication of research data following major research programs. For instance, a large amount of data from the 1960s to 1970s (Figure 2.S1) can be linked to the efforts of the International Biological Program (Aronova et al. 2010). The increase in data after the 1990s can be attributed to technological advances, such as the implementation of powerful new icebreaking research vessels, and increased attention to the region due to the accelerated climate change processes.

Furthermore, this increase might also be the result of greater accessibility to post-Soviet areas of the Eurasian shelf seas to international research (Piepenburg 2005). Data from the 2000s and 2010s are more consistent, which may reflect more consistent and systematic sampling efforts established during this period (Aronova et al. 2010).

To minimize sampling bias, we selected species for which we had a sufficiently good identification base and which were the most abundant in the study area. Most of the species inhabited the epi- or epi-mesopelagic zones of the study, with the exception of *Sminthea arctica*, which was found in significant numbers in the bathypelagic zone. While the number of samples available for *Sminthea arctica* in open databases was rather low (Figure 2.S2), this Trachymedusa represents a well-known dominant species in colder and deeper areas of the Arctic Ocean (Raskoff et al. 2010; Pantiukhin et al. 2023). In some areas studied, their abundances recorded were comparable to those of *Aglantha digitale* (Raskoff et al. 2010; Pantiukhin et al. 2023), often referred to as one of the most abundant hydromedusae of the Northern Hemisphere (Kosobokova and Hirche 2000). Our findings highlight the need for further surveys of underexplored deep-water species in the central Arctic.

2.5.2 Spatial Distribution: Limiting Drivers and Trends

In our analysis, water depth and sea ice concentrations had the greatest influence on the distribution of gelatinous zooplankton species (Figures 2.5; 2.S9). The importance of water depth reflects the fact that most of the species appear bound to certain depths (occurring mainly in epi- or epi-mesopelagic layers). As an exception, *Periphylla periphylla* had an eurybathic distribution; for this species, depth had the least importance (Figures 2.5, 2.7, 2.S9). In contrast to water depth, sea ice coverage had the largest impact in the epi- and mesopelagic layers (Figures 2.7, 2.S9). This is to be expected since sea ice is considered one of the main factors determining the structure of marine ecosystems in the Arctic (Post et al. 2013). The effect of sea ice cover on the distribution of gelatinous zooplankton species can have both direct and indirect limiting effects (Arrigo 2014). For example, sea ice coverage can affect light penetration, stratification, and nutrient and organic matter supply (Arrigo 2014), which in turn also affects the availability of major prey sources for gelatinous zooplankton such as copepods (Stige et al. 2019).

Following sea ice retreat, we observe a northward expansion of distribution for most species, representing an increase in suitable habitat, with the exception of *Sminthea arctica* (habitat reduction of -15%) (Figure 2.6). The observed increase in suitable habitat for most species can be explained by the fact that most species in our study, mirroring the documented biogeographic patterns of gelatinous zooplankton communities in the Arctic Ocean, represented boreal or arcto-boreal species (Ronowicz et al. 2015), and their presence in the historical projections is maximal in sea ice-free zones or marginal sea ice zones (Figures 2.6, 2.S4). Despite the rather low contribution of temperature, salinity, and phytoplankton concentration to the overall explanatory power of gelatinous zooplankton distribution (Figure 2.5), these parameters had a strong limiting influence at depth and in zones where species were most likely to be found (Figures 2.7, 2.S9). This was especially noticeable in areas of the North Atlantic without sea ice cover, where for most of the species, the aforementioned parameters had the greatest importance (Figures 2.7, 2.S9).

2.5.2.1 Scyphozoa

With regard to taxonomic groups, the two scyphozoan species were projected to expand their suitable habitat to the greatest extent by 2050-2100 (Figure 2.6). The combined effect of retreating sea ice and pronounced increases in temperature gradients could explain this pattern (Figure 2.S4), as these factors alternated in their limiting importance on the spatial maps (Figures 2.7, 2.S9). Temperature plays an important limiting role in scyphozoan survival and reproduction (Widmer et al. 2016) and significantly influences their biochemical responses (Thuesen and Childress 1994). Moreover, temperature is the main environmental factor controlling blooms in scyphozoans (Fernández-Alías et al. 2021).

On the spatial maps, *Cyanea capillata* will become more widely distributed over most of the Arctic Ocean shelf areas by 2050-2100. According to Widmer et al. (2016), *Cyanea capillata* can reproduce at temperatures as low as 4°C, which will be characteristic for most parts of the Eurasian shelf, where we also see the greatest increase in their modeled numbers. Despite the increased freshwater inflow from rivers in some parts of the Eurasian shelf, such desalination is unlikely to greatly limit the distribution of *Cyanea capillata*, because this species can develop and reproduce in estuaries at low PSU values (Holst and Jarms 2010; Figure 2.6, S4).

The distribution of *Periphylla periphylla* also increases quite significantly, which is especially notable for the northern parts of the Atlantic sector of the Arctic Ocean. Interestingly, despite the lack of data on *Periphylla periphylla* in the Pacific sector of the Arctic Ocean, its distribution is increasing in these areas as well. As the species is occurring in the Pacific Ocean below 60°N (Bentlage et al. 2013), the model's predictions regarding their potential suitable habitats may indicate its strong extrapolation power. *Periphylla periphylla* is known to maintain stable populations in fjords (Fosså 1992) despite limited prey availability (Youngbluth and Båmstedt 2001). This is corroborated by our spatial limitation maps, where carbon concentrations were of minimal importance.

The recent appearance of this species in Spitsbergen fjords (Geoffroy et al. 2018) could evolve in a potential establishment of year-round populations with increasing warming. This is supported by our modeling results, with most of the fjords in this sector showing relatively high presence values of this species by 2050-2100. The northward expansion of *Periphylla periphylla*'s suitable habitat is mostly restricted by the presence of sea ice and temperature (Figures 2.7, 2.S8). The known tolerance range of *Periphylla periphylla* ranges from 4 to 19.8°C (Arai 1997; Bozman et al. 2017; Geoffroy et al. 2018), but this species has also been found in 0°C waters in the Antarctic (Larson 1986). A temperature threshold lower than 4°C would be necessary for their successful overwintering in the high Arctic (Geoffroy et al. 2018). This is well reflected in our predictive curves (Figure 2.S7), with the probability of occurrence of *Periphylla periphylla* limited by 0°C and more strongly increased occurrence at > 4°C (Figure

2.S8). On our predictive maps, we also observe the strongest increase in the presence of these species in regions where temperature values will exceed 4°C (Figures 2.6, 2.S4). In addition to a persistent presence in Svalbard, the species is also likely to establish year-round populations in the fjords of Novaya Zemlya and Franz-Josef-Land (Figure 2.6).

2.5.2.2 Hydrozoa

The hydrozoan species (*Aglantha digitale* and *Sminthea arctica*), both belonging to the family Rhopalonematidae, showed a reverse three-dimensional segregation of suitable habitats, as well as inverse responses to changes in environmental conditions (Figure 2.6). Such habitat segregation and responses for these species were already highlighted for the Fram Strait (Pantiukhin et al. 2023). Despite a marked increase in the probability of occurrence of *Aglantha digitale* in the northern regions, its suitable habitat slightly narrowed in the southern epi- and mesopelagic layers (Figure 2.6). This may be due to the fact that this species is likely to reach its upper-temperature limit in the southern parts of the region by 2050-2100 (Figures 2.7, 2.S9), which could be caused by a marked increase in metabolic costs witnessed at temperatures > 10-15 °C (Larson 1987). This is also noticeable on the limiting maps, with the limiting importance of temperature increasing in the southern parts of the region by 2050-2100 (Figure 2.S9). A poleward range shift was already noted within the Fram Strait, where the highest abundance of *Aglantha digitale* was found on the Atlantic and Arctic current fronts (Mańko et al. 2022; Pantiukhin et al. 2023). The maximum values of the presence of *Aglantha digitale* are following the northward shift of these fronts (Tesi et al. 2021). The distribution of *Sminthea arctica*, in turn, exhibits a narrowing of suitable habitat that is particularly noticeable in the Fram Strait (Figure 2.6). By 2050-2100, this species will become exclusively concentrated in the central Arctic basin. As with *Aglantha digitale*, we also observe an increase in the limiting impact of temperature by 2050-2100 along the vertical profile.

2.5.2.3 Appendicularia

We found that the distribution of the appendicularian species was greatest in the marginal sea ice zones. *Oikopleura vanhoeffeni* had a normal distribution with a peak at 50% of the sea ice coverage, while *Fritillaria borealis* preferred more open areas and had the highest probability of presence at 35% of sea ice coverage. Studies by Arashkevich et al. (2002) and Deibel et al. (2017) confirm this trend, with *Oikopleura vanhoeffeni* commonly found in regions near the sea ice edge, while *Fritillaria borealis* was more abundant in subpolar habitats. Despite their differences in habitat preferences (Figure 2.S8) we did not observe substantial habitat segregation where these species co-occurred (Figure 2.6). Such patterns were confirmed by Deibel et al. (2017), who concluded that *Fritillaria borealis* and *Oikopleura vanhoeffeni* can successfully coexist in similar habitats due to their utilization of specific food sources.

Appendicularians and other gelatinous filter feeders are projected to become more abundant in the polar regions at the expense of omnivorous copepods decline (Heneghan et al. 2023). We observed similar shifts in distributional patterns by 2050-2100, with both species increasing their presence in the region. Moreover, these two species are becoming more noticeably limited by water depth by 2050-2100, which may indicate that their suitable habitat, in terms of the other environmental conditions, is expanding (Figure 2.S4). Despite this absolute increase, we observe a slight decrease in suitable habitat of *Oikopleura vanhoeffeni* in the southern zones. This is largely due to the fact that this species was poorly represented in sea ice free zones.

2.5.2.4 Ctenophora

For the ctenophore taxa, we observe a moderate increase in suitable habitats in the central parts of the Arctic region (Figure 2.6). For *Mertensia ovum*, a slight decrease in suitable habitat in the southern regions was observed (Figure 2.6), and a pronounced increase in the limiting value of temperature in the marginal sea ice zones by 2050-2100 (Figures 2.7, 2.S9). This could be explained by the fact that at temperatures above 7°C, the metabolism of this species increases dramatically (Percy 1988). A similar pattern was also evident on the predictive curves (Figure 2.S8), where the occurrence of *Mertensia ovum* reaches near-zero probability at temperatures of 7-8 °C. Similarly, *Beroe* spp. slightly retreat from the southern parts of the region and are also more limited by increasing temperatures (Figure 2.6, S9), which could presumably be explained by increased metabolic costs at warmer temperatures, however, supporting data from literature are lacking.

2.5.3 Potential impact of expanding GZ communities

Gelatinous zooplankton, in particular cnidarian medusae and ctenophores, can compete with fish, by preying on the same zooplankton prey or by preying on ichthyoplankton. They can outcompete fish as they are considered more resilient to fluctuations and long-term changes in the ocean because of their ability to thrive in disturbed marine environments (Richardson et al. 2009). Over the past decades, there have been more than 130 reports of adverse impacts of gelatinous zooplankton on marine fisheries and aquaculture, with frequency and severity increasing in recent years (Bosch-Belmar et al. 2020). Our study demonstrates a poleward expansion of suitable habitats for the large, predatory scyphozoan *Cyanea capillata*, which could have a negative impact on local fish populations such as those of one of the most important Arctic fish species, polar cod (*Boreogadus saida*). At high abundances of *Cyanea capillata*, *B. saida* tends to be replaced from its typical habitat (Crawford 2016). Based on our projections by 2050-2100, the northward expansion of *Cyanea capillata* could significantly affect spawning habitat of *B. saida* (Dahlke et al. 2018), especially in regions around Novaya Zemlya and Spitsbergen, where suitable habitats for *Cyanea capillata* are expected to increase significantly (Figure 2.6). Moreover, for the other scyphozoan species, *Periphylla periphylla*, suitable temperature conditions around Spitsbergen by 2050-2100 are likely to induce blooming events (Fernández-Alías et al. 2021). Here, this predatory jellyfish may also impact *B. saida* at its spawning sites, in a similarly dramatic way as it affected Atlantic cod populations in the fjords of Norway (Tiller et al. 2015). At the same time, several boreal fish species, many of which being commercially exploited, are known to migrate northward, followed by their fisheries (Mueter et al. 2021), where these species may encounter an increasing competition with gelatinous zooplankton species (Fosså 1992; Tiller et al. 2014). For example, the diet of *Cyanea capillata* shows a high overlap with that of some commercially exploited fish species, such as the pink salmon (*Oncorhynchus gorbuscha*) (Purcell and Sturdevant 2001). Furthermore, increasing populations of predatory ctenophores in central regions, such as *Mertensia ovum*, may also pose a potential competitive threat to fish populations in the Arctic. With a diet mainly composed of large herbivorous copepods such as *Calanus* spp., *Mertensia ovum* directly competes with fish for the same food resources (Majaneva et al. 2013).

A study by Heneghan et al. (2023) showed that the expansion of filter feeders in the Arctic will lead to a decrease in omnivorous copepods and an increase in carnivorous zooplankton. This, in turn, will lead to an elongation of food chains and, as a consequence, less effective carbon transfer from primary producers to fish (Heneghan et al. 2023). *Oikopleura vaenhoffeni* is known to outcompete copepod secondary producers under certain environmental conditions (Choe and Deibel 2011). Given that the environmental conditions nearer to the pole will become increasingly favorable for the distribution of *O. vaenhoffeni* (Figure 2.6), it can be assumed that this will make a noticeable contribution to the transformation of the Arctic food web and have profound impact on local fish populations.

Conversely, gelatinivore species might benefit from the expansion of their prey into the Arctic Ocean. An increasing number of studies report the hitherto neglected importance of gelatinous zooplankton as prey for various organisms (Hays et al. 2018). As an example, the projected expansion of the Atlantic mackerel, *Scomber scombrus*, into the Arctic realm (Berge et al. 2015), may benefit from the increasing population size of *Aglantha digitale* (Figure 2.6). This is because *Aglantha digitale* constitutes an important food source for *S. scombrus*, which actively preys on this hydrozoan, even in the presence of copepod prey (Runge et al. 1987).

Gelatinous zooplankton are able to form extensive blooms and can contribute significantly to deep-sea carbon transport (Lebrato et al. 2013). A study by Luo et al. (2020) showed that this transport can be as high as 35% of total particulate organic carbon transport on a global scale. In the Pacific sector of the Arctic, the carbon pump has been shown to increase significantly with increasing temperature and retreating sea ice (O'Daly et al. 2020). We can expect that, as the areas suitable for bloom formation increase (Figure 2.6), we will also witness an increase in the efficiency of carbon transfer to the seafloor. As an example, a study in Hudson Bay observed a significant bloom of *Aglantha digitale* in response to increasing temperatures (Lalande and Fortier 2011). This bloom contributed considerably to particulate organic carbon export, while there was a significant decrease in copepods in the sediment traps (Lalande and Fortier 2011). Moreover, two other massively bloom-forming species, *Cyanea capillata,* and *Periphylla periphylla*, will also experience an increase in habitats suitable for bloom formation (Figure 2.6, Fernández-Alías et al. 2021), potentially further amplifying carbon export. The aforementioned increase in appendicularians presence will also increase the efficiency of the biological carbon pump (Jaspers et al. 2023). We thus emphasize the need to better understand the ecological impact of gelatinous zooplankton blooms in the Arctic Ocean and the role of gelatinous zooplankton as prey for higher trophic levels and in biogeochemical cycles.

Gelatinous zooplankton span different trophic levels and are characterized by a wide array of ecological habits, hence, poleward expansions of suitable habitats of the different gelatinous zooplankton taxa studied will result in a myriad of potential impacts on the energy flow, trophodynamics, and biogeochemistry in Arctic Ocean ecosystems. At first, we need to better understand their population dynamics, by obtaining accurate estimates of their abundance using modern technologies including pelagic video surveys (e.g., Pantiukhin et al. 2023), and environmental DNA methods (Havermans et al. 2022). To fully understand the potential impact of the expansion of gelatinous zooplankton taxa on Arctic ecosystems, it is necessary to gain a more detailed understanding of their role in the food web, using techniques such as molecular diet analysis (Havermans et al. 2022). In order to assess their interactions with arctic and boreal fish stocks, comprehensive long-term and cost-effective monitoring programs involving the fishing industry are needed (Aubert et al. 2018). Given the expected expansion of gelatinous zooplankton, fisheries need to incorporate these dynamics into their management plans, preventing major impacts on fish stocks, and potentially leading to stock collapses as witnessed elsewhere in the world (Richardson et al. 2009).

2.6 Conclusion

To analyze the potential impact of climate change on the distribution of Arctic gelatinous zooplankton, we performed pan-Arctic species distribution modeling in three dimensions of the eight most reported gelatinous zooplankton taxa in the Arctic Ocean (*Aglantha digitale*, *Sminthea arctica*, *Periphylla periphylla*, *Cyanea capillata*, *Oikopleura vanhoeffeni*, *Fritillaria borealis*, *Mertensia ovum*, and *Beroe* spp.). The synthesis of biogeographic data has demonstrated the need for a multi-database approach that significantly improves the spatial coverage of sampling surveys. We used a customized three-dimension version of the Maximum Entropy Model (Maxent) for the oceanic domain. Our habitat projections under the SSP370 emission scenario suggest a dominant trend towards poleward shifts of gelatinous zooplankton taxa. In particular, the scyphozoan *Cyanea capillata* is likely to shift poleward and expand into most coastal areas of the Arctic Ocean. In contrast, some species, in particular the hydrozoan *Sminthea arctica*, may experience a contraction of their range towards the deep basins of the Arctic Ocean. These shifts may lead to a potential displacement of local fish populations and affect the carbon cycle and trophic dynamics. The results of this study can be used to guide further observations in areas most vulnerable to change and should also help develop more effective marine resource management strategies in the Arctic.

2.7 Acknowledgments

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2.8 Data and materials availability

All details on the data retrieval process are available in the main text or in the supplementary materials. Biogeographic data were retrieved from four databases: Ocean Biodiversity Information System (OBIS), Global Biodiversity Information Facility (GBIF), Jellyfish Database Initiative (JeDI), and PANGAEA, with data extracted directly from OBIS, GBIF, and JeDI, and through individual publications from PANGAEA (Table 2.S1). Environmental data were derived from 'CMIP6.ScenarioMIP.DKRZ.MPI-ESM1-2-HR' (doi:10.22033/ESGF/CMIP6.2450) and 'CMIP6.CMIP.MPI-M.MPI-ESM1-2-HR.historical' (doi:10.22033/ESGF/CMIP6.6594). The results of the major simulations are available at https://doi.org/10.5061/dryad.f7m0cfz2j.

2.9 References for Chapter 2

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2.10 Supplementary materials

Text 2.S1. Pipeline of data processing

We extracted data on GZ occurrences from the biological repositories OBIS, GBIF and PANGAEA using the packages (robis, rgbif and pangaear), data from the JEDI database were taken from (bco-dmo.org). Environmental data were obtained from the Earth System Grid Federation (ESGF) data repository hosted by the German Climate Computing Centre (DKRZ; esgf-data.dkrz.de). The data were extracted from the MPI-ESM1-2-HR climate model runs with a nominal spatial resolution of 50 km and a monthly temporal resolution. We used the variant label r1i1p1f1 for all six extracted environmental variables. To pre-process the environmental data, we used the 'xarray' package in Python and 'raster' library in R. The MaxEnt models were fitted using the ENMeval package, with the maxent.jar model from the dismo package (both R packages). The continuous boyce index was calculated using the ecospat package in R. Maps and figures were generated using the ggOceanMaps (R), matplotlib and plotly (Python) packages. For quality control of the biological metadata, we used marine boundary shapes provided by the Marine Institute of Flanders (2018) and bathymetric data from Tozer et al. (2019). We used the package github.com/johnbaums/rmaxent to create maps of spatial limiting factors.

Text 2.S2. Models complexity and multi-metric evaluation

We found that for each species, the best model was represented by a unique set of feature classes, regularisation multipliers, and number of background points (Figures 2.4, 2.S6) When the AICc method was used exclusively for the selection of the optimal model (Warren & Seifert 2011), the optimal models were almost always those with the maximum number of feature classes (LQHPT) and the lowest regularisation multipliers (Figure 2.S6). However, these models had rather low predictive values based on the omission rate and CBI metrics, indicating their poor prediction of 'presences', which may further say about their overfitting. In the final selection, we preferred the metrics for assessing 'presences' due to the nature of our data (omission rate and CBI values), we also considered acceptable values for the AUC (>0.7) and AICc metrics. This approach resulted in the selection of a less parameterised model with larger values of regularisation multipliers compared to the models selected by AICc (Figures 2.4, 2.S6). These models showed smoother spatial prediction lines, which is consistent with the high uncertainty and dynamism of the oceanic domain. The selection of models with a simpler set of feature classes and a higher level of regularisation parameters is also recommended for large-scale studies and temporal interpolation (Merow et al., 2014), which was the case for our study.

The comparison of the best models selected for each species showed that the values of the evaluation metrics varied, depending on the distribution of the species in the study region (Figures 2.4, 2.S6). For example, Schyphozoa species such as *Periphylla periphylla* and *Cyanea capillata* showed relatively high AUC values, while their CBI values were among the lowest. This can be explained by the fact that the models for these species quite well capture the boundaries of their presence and absence (by AUC) at the border of the boreal and arctic realms.

However, the predictive power was greatly reduced when attempting to predict only presence values (by CBI values). Another group of species, *Beroe* spp. and *Mertensia ovum*, had similar evaluation results despite a large difference in the total number of predicted presence points (245 for *Beroe* spp. and 30 for *Mertensia ovum*). These species had the most balanced modelling fit based on all three of the main metrics (omission rate, CBI, and AUC). We obtained similar values for the appendicularian species *Fritillaria borealis* and *Oikopleura vanhoeffeni*. Similar as for the ctenophore species, they also showed balanced values for all three metrics, but their AUC values were lower than those recovered for the ctenophore taxa, while their CBI values were higher. In contrast to the ctenophore taxa, the appendicalarian species were characterized by a greater number of points of presence values and also covered most of the region. In contrast to the three previous groups, the two hydrozoan species, *Aglantha digitale* and *Sminthea arctica*, had a greater difference in predictive metrics. *Aglantha digitale* had the highest values for the CBI and an excellent fit for the other metrics, while *Sminthea arctica* had the worst model fit observed for all metrics. The reason for this could be the striking difference in the number of presence points (1060 for *Aglantha digitale* vs. 46 for *Sminthea arctica*). In addition, *Sminthea arctica* inhabited the deepest parts of the region where environmental variables did not vary much (Figure 2.S9), which may indicate that additional factors influence the distribution of *Sminthea arctica*.

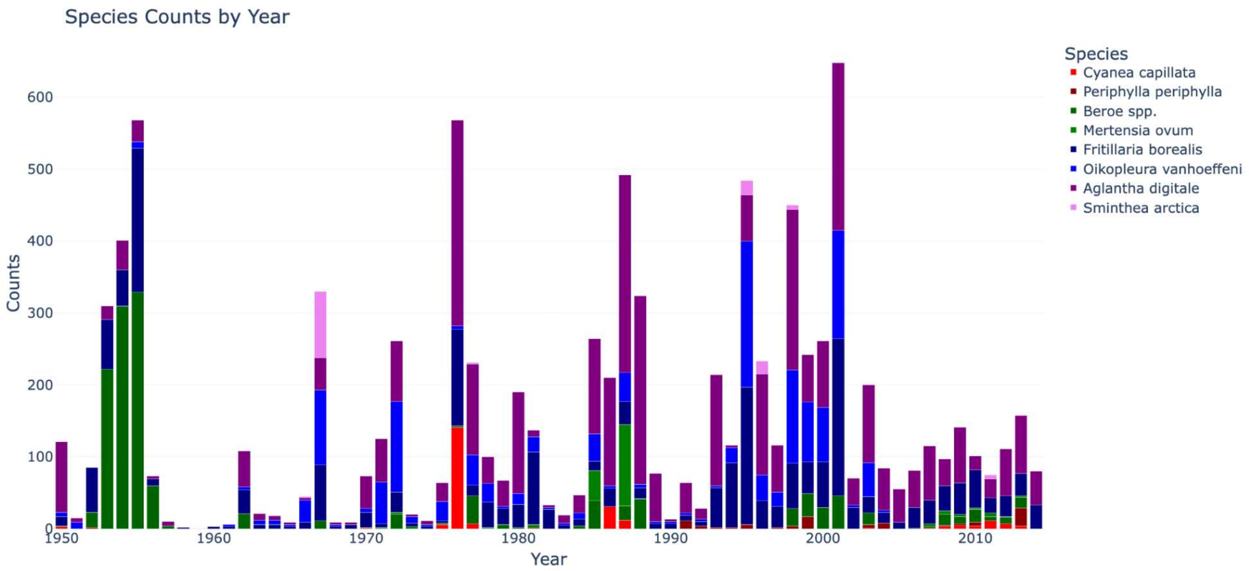


Figure 2.S1. Species counts by year in the Pan-Arctic region, based on data collected between 1950 and 2014. The bar plot shows the number of observations for eight commonly observed species over time.

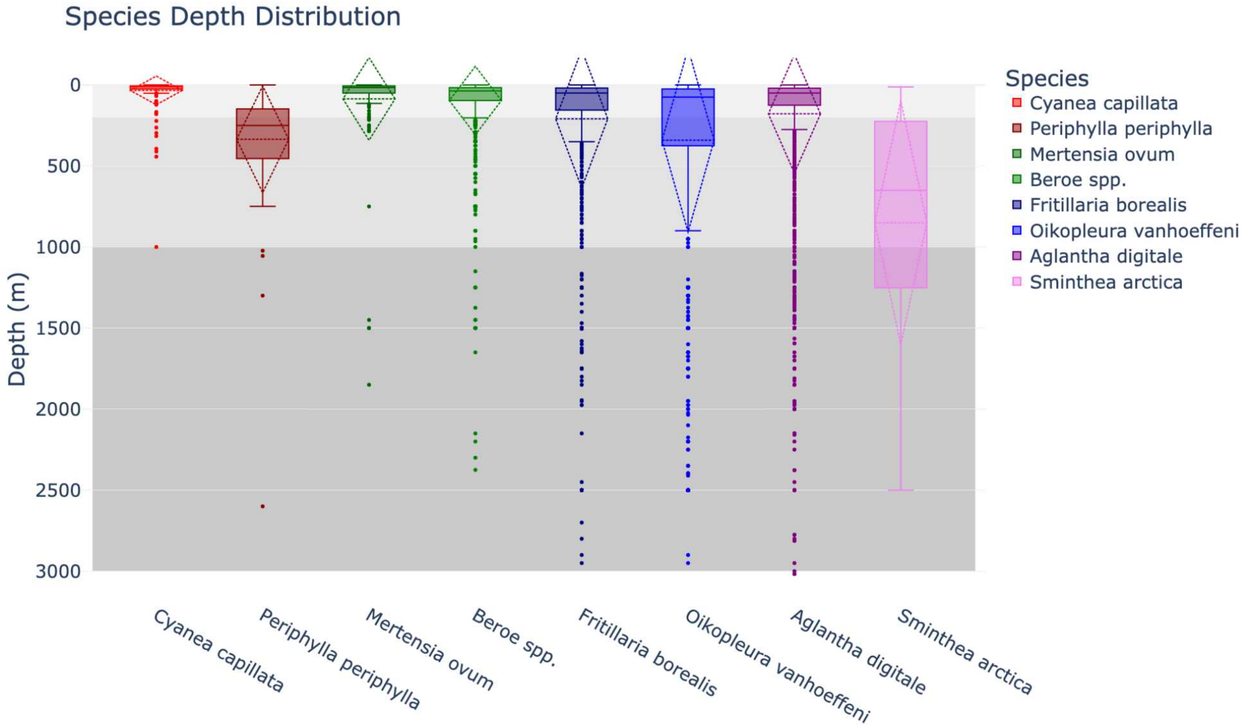


Figure 2.S2. Depth distribution of gelatinous zooplankton (GZ) in the Pan-Arctic region, based on data collected between 1950 and 2014. The box plot shows the distribution of GZ depths for eight commonly observed species. The boxes represent the interquartile range (IQR) of the depth distribution, the horizontal line inside the box represents the median depth, and the whiskers represent the range of depths within 1.5 times the IQR. The mean depth and the standard deviation is represented by a rhombus for each species. Outliers are shown as individual points. The background color indicates the depth zones of the ocean (epipelagic: 0-200m, mesopelagic: 200-1000m, bathypelagic: 1000-3000m).

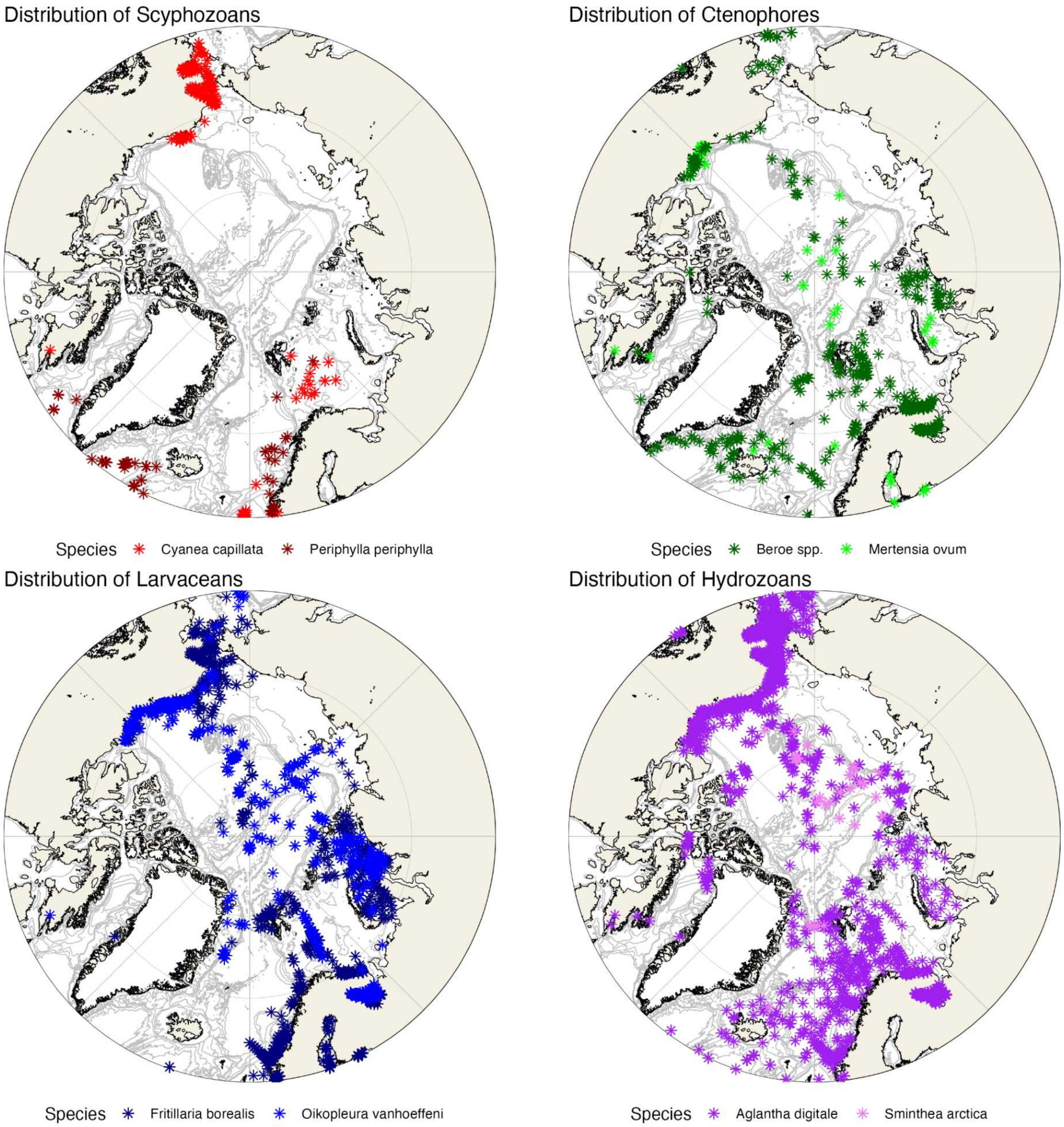


Figure 2.S3. Distribution of gelatinous zooplankton by taxonomic group. Each panel displays the distribution of two species within a class/phylum, with each species represented by a different color.

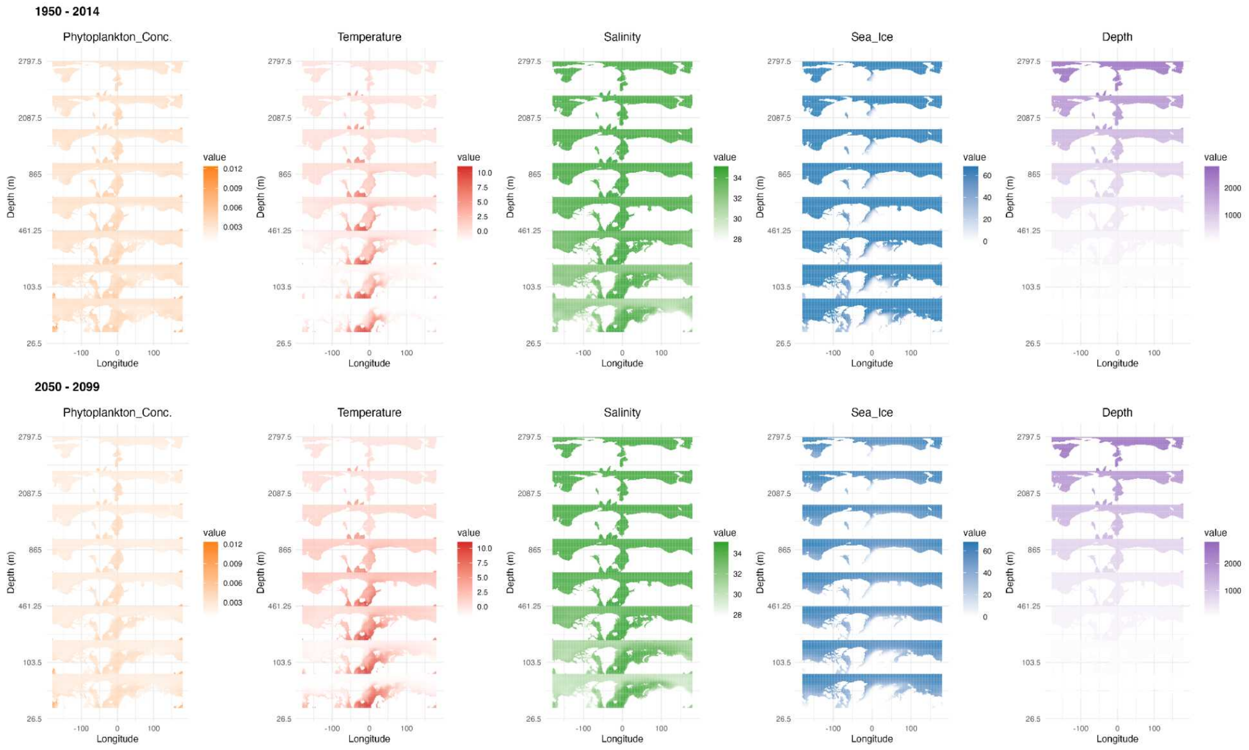


Figure 2.S4. Environmental data layers from MPI-ESM1.2 (Max Planck Institute Earth System Model 1.2).

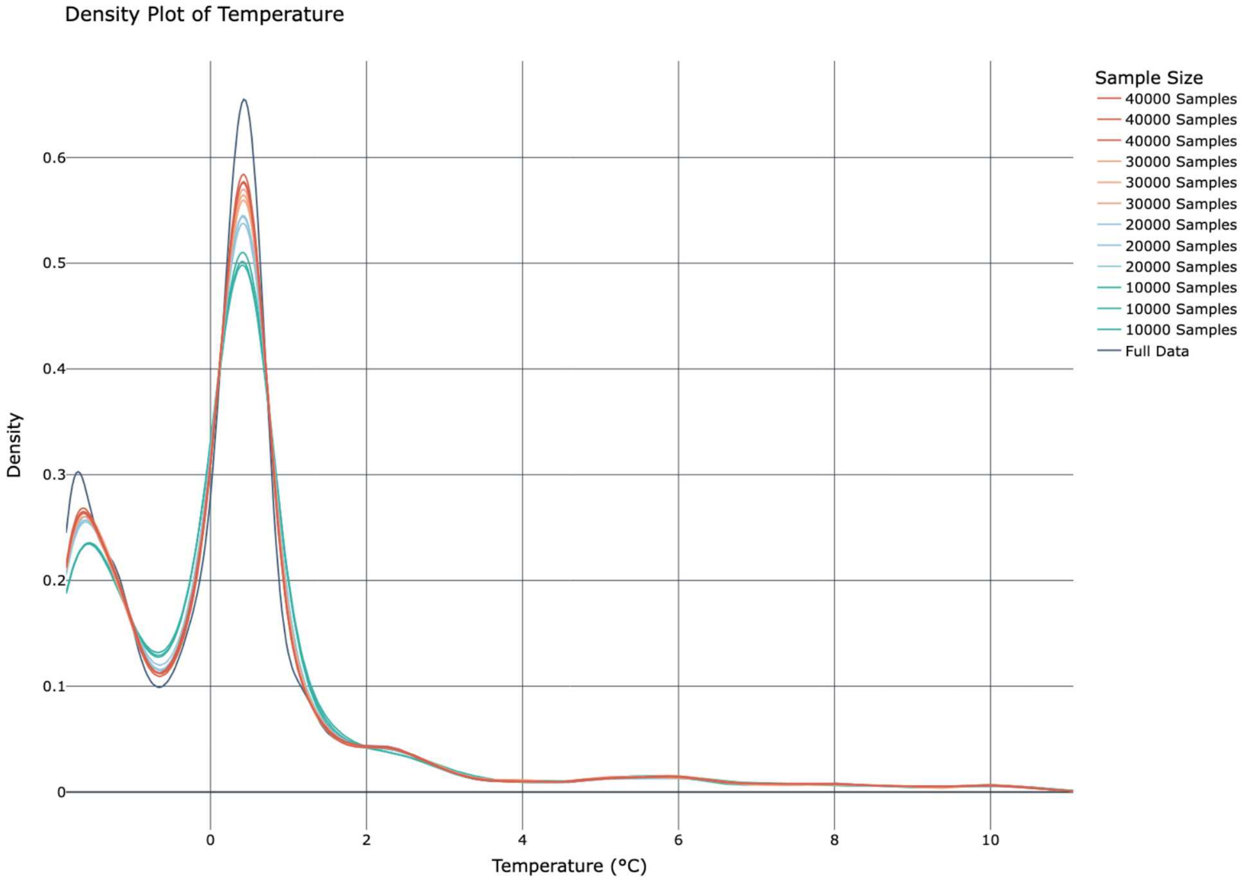


Figure 2.S5. Density distribution of temperature measurements from all cells in different depth layers of the MIP model. The plot shows the distribution of temperature for the full dataset and randomly subsampled datasets of 10k, 20k, 30k, and 40k cells with distinguishable colors.

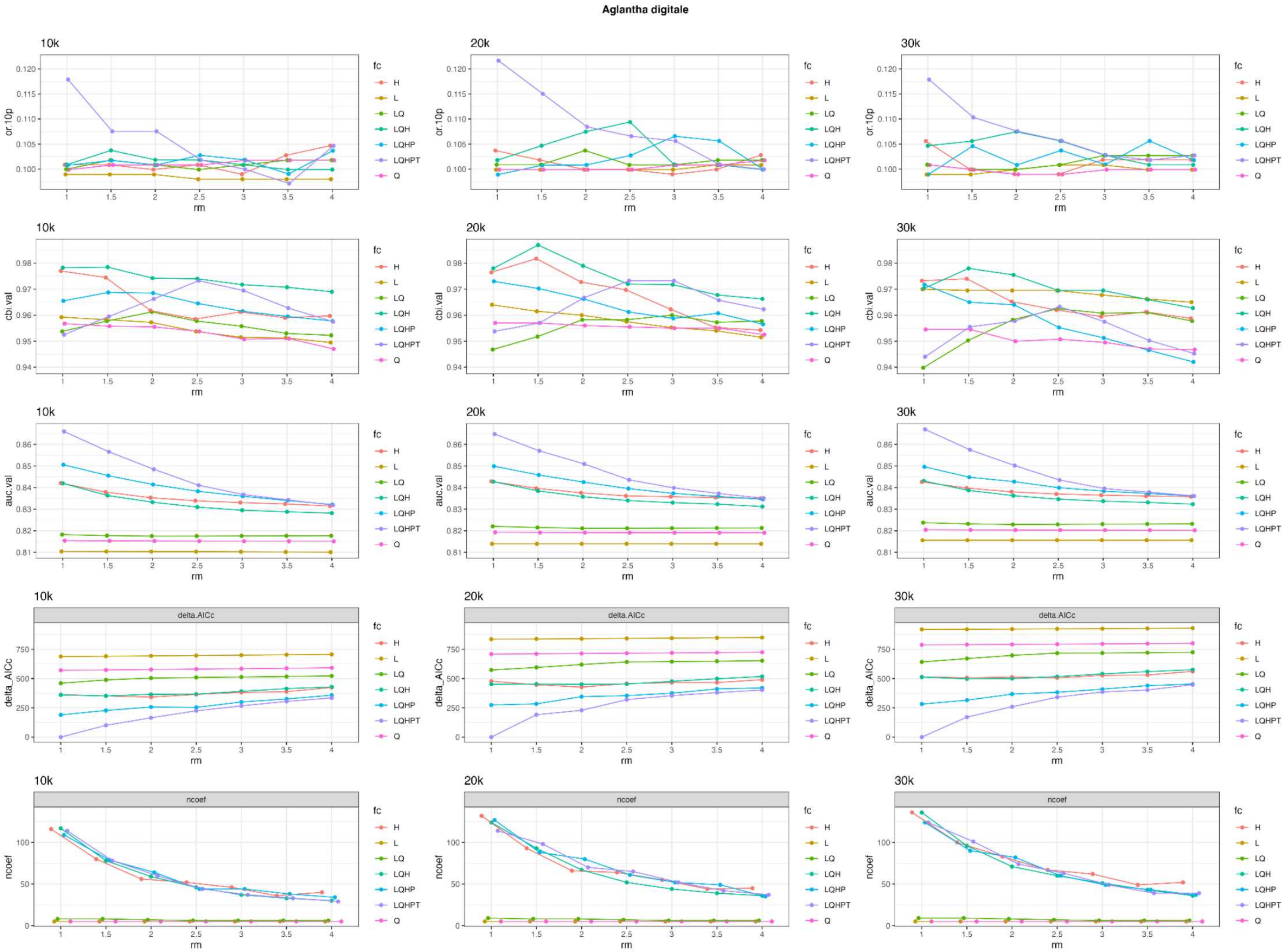
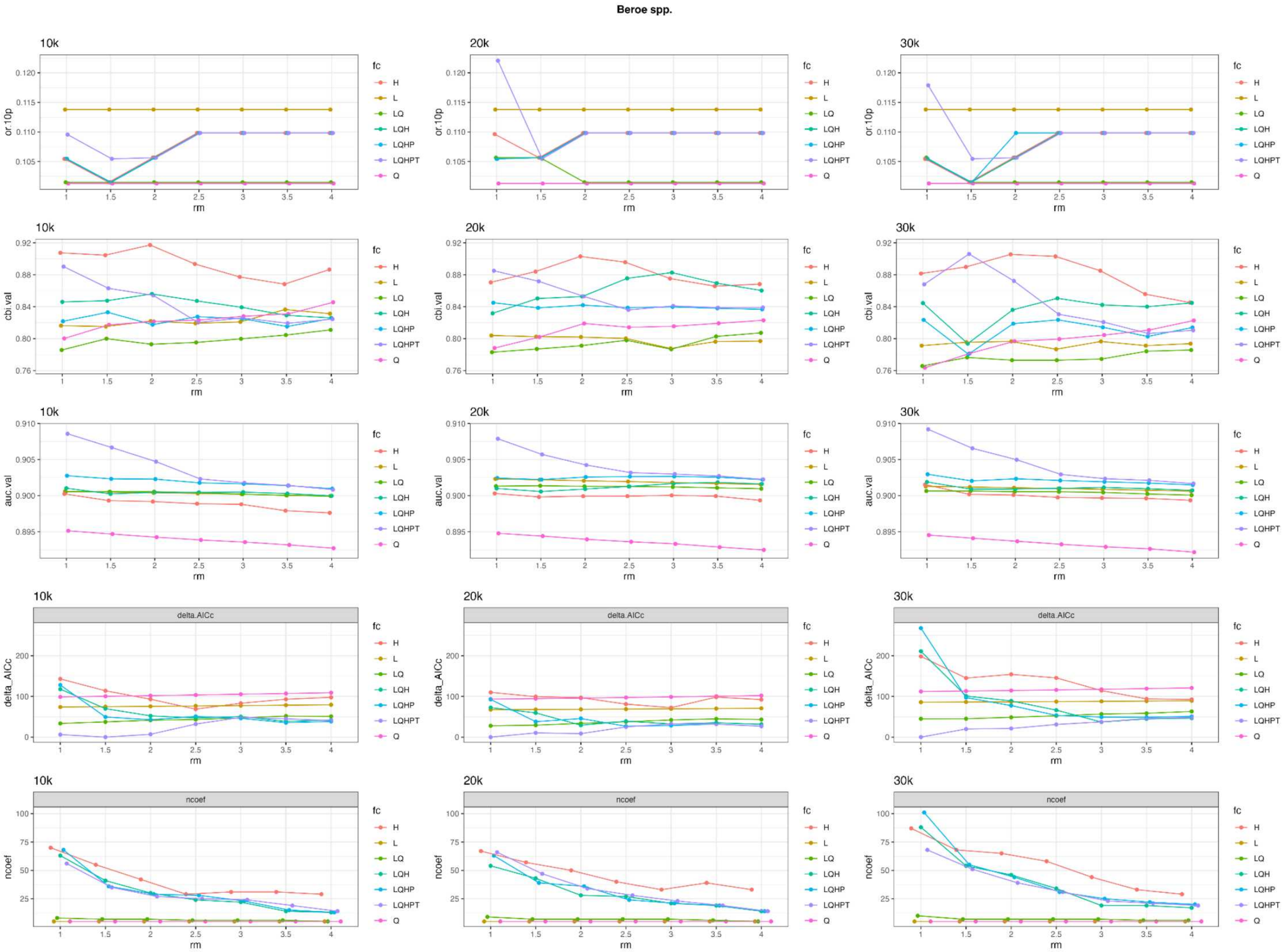
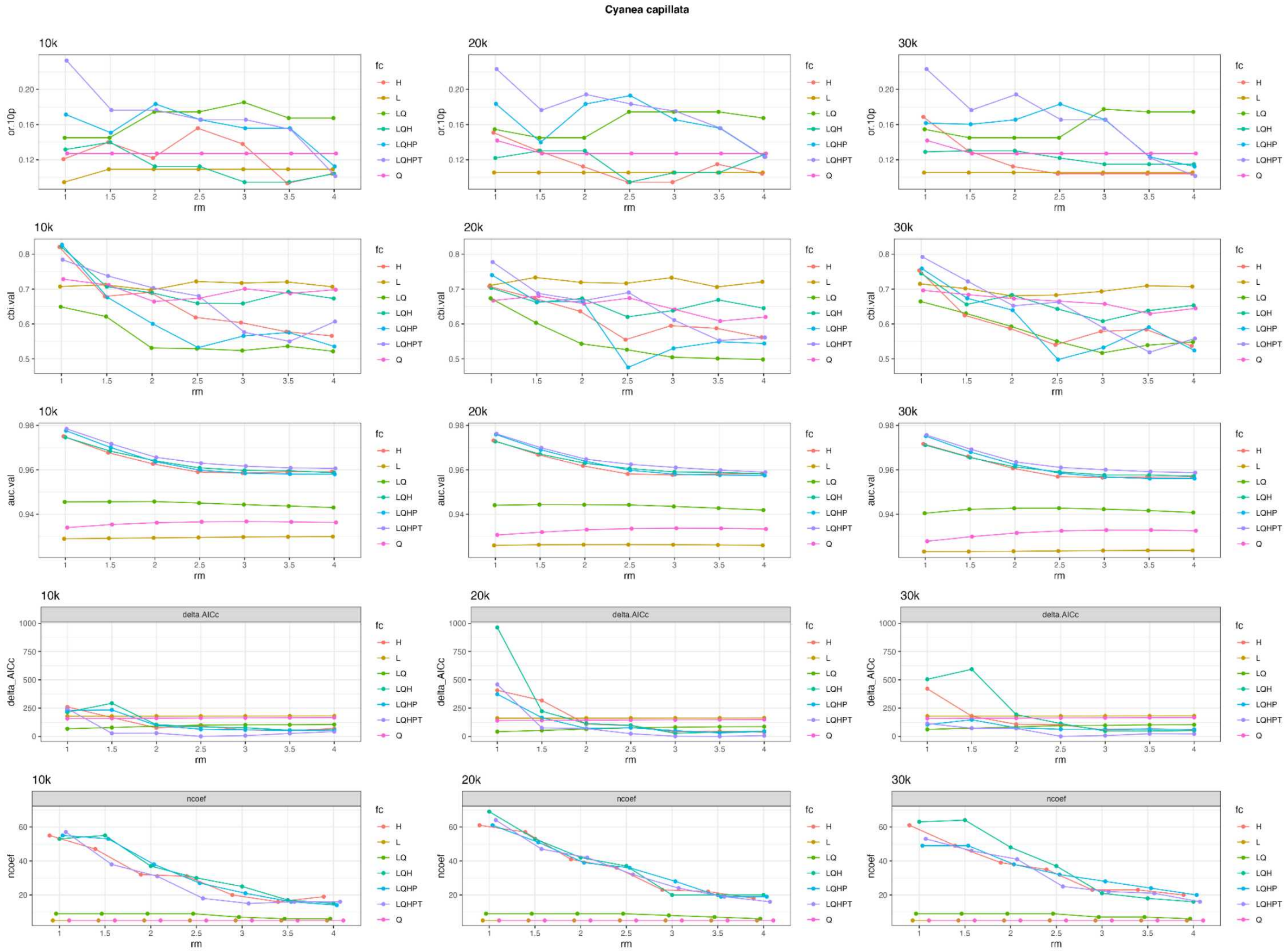


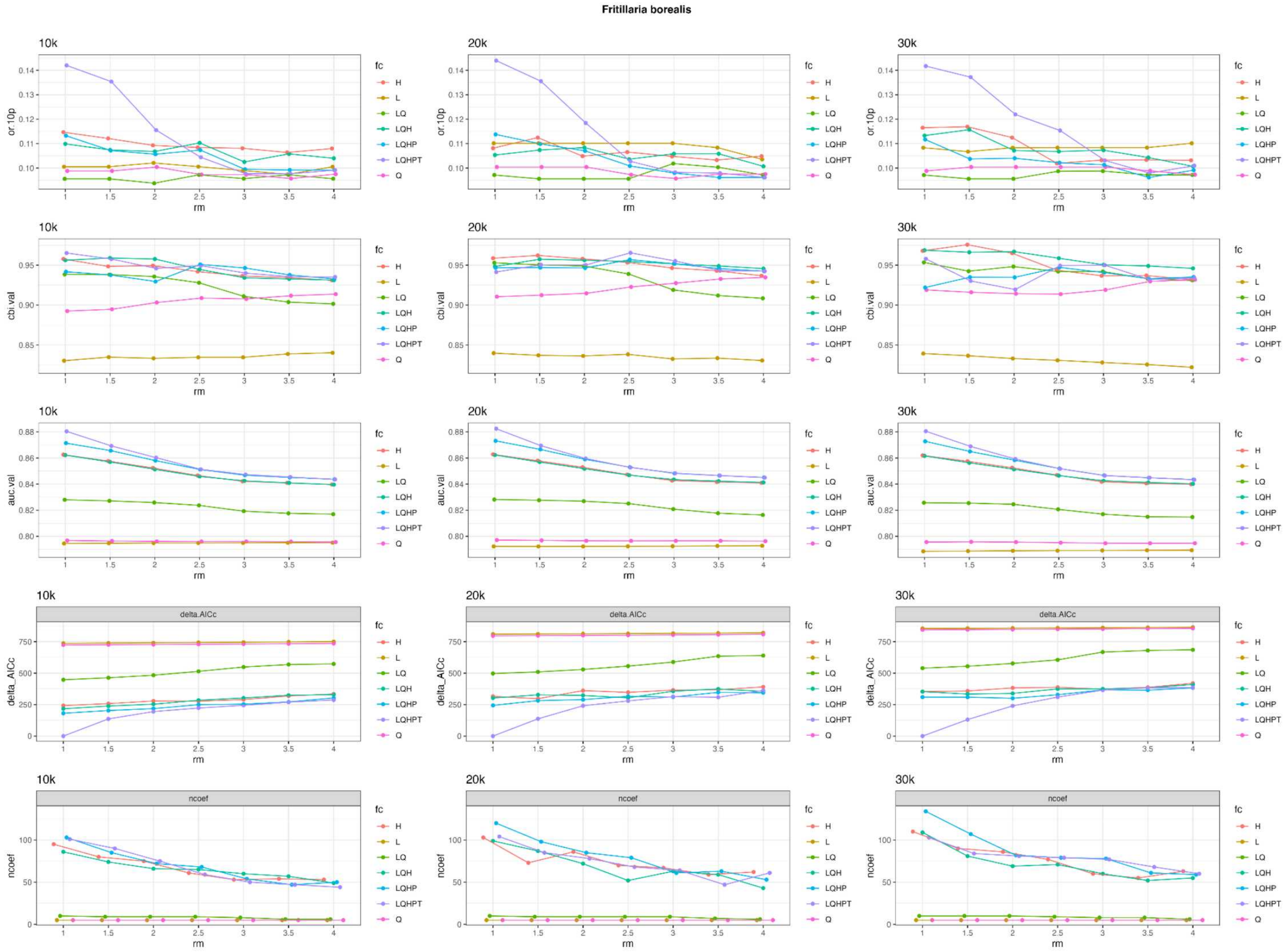
Figure 2.S6. Evaluation metricies for the MaxEnt models. The metrics include: estimates of the 10th percentile, continuous Boyce index (CBI), area under the receiver operating characteristic curve (AUC), Akaike information delta criterion (AICc) and number of coefficients (ncoef) for three sets of the background points (10000, 20000, 30000).



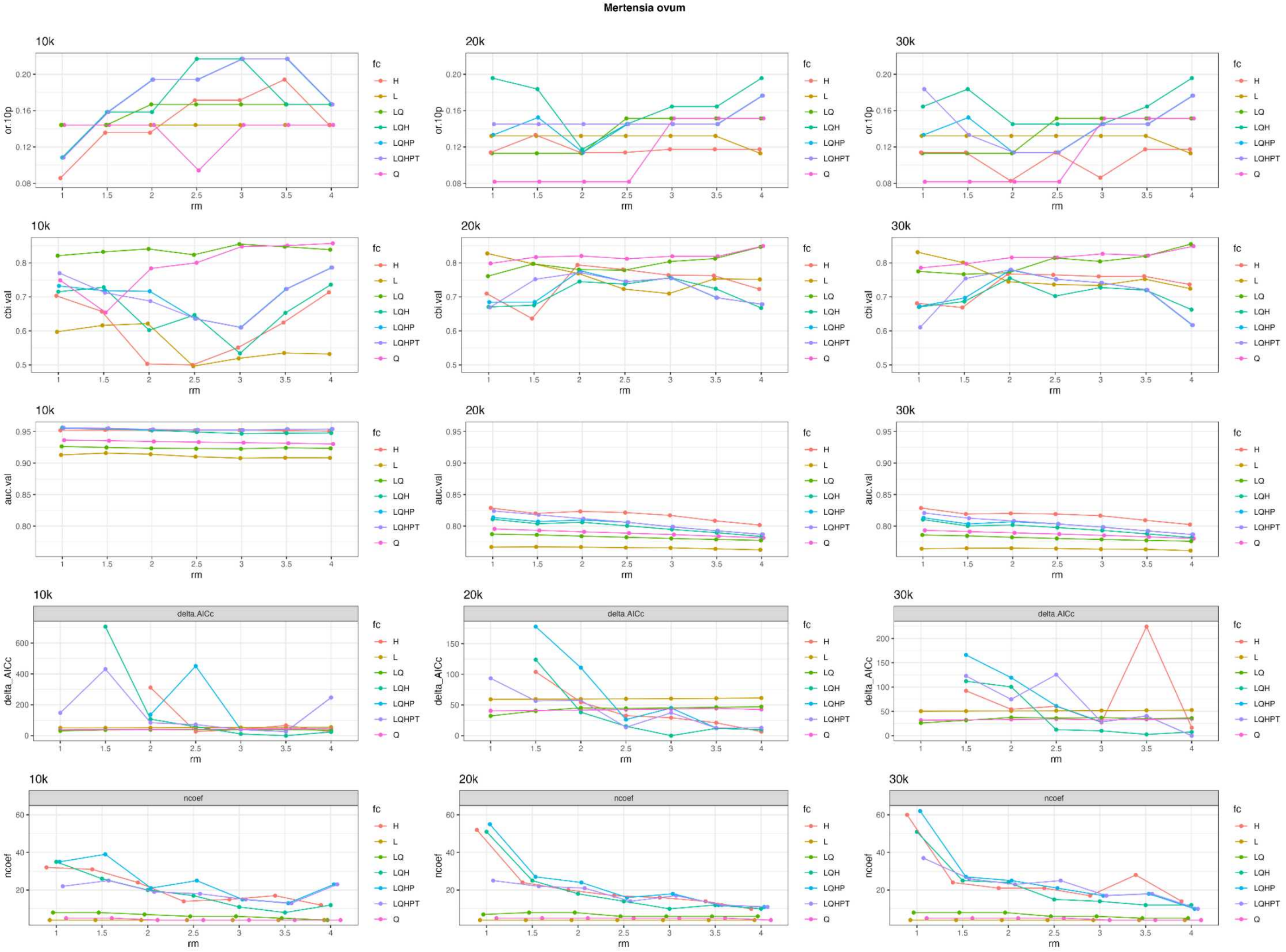
Continued Figure 2.S6. Evaluation metricies for the MaxEnt models. The metrics include: estimates of the 10th percentile, continuous Boyce index (CBI), area under the receiver operating characteristic curve (AUC), Akaike information delta criterion (AICc) and number of coefficients (ncoef) for three sets of the background points (10000, 20000, 30000).



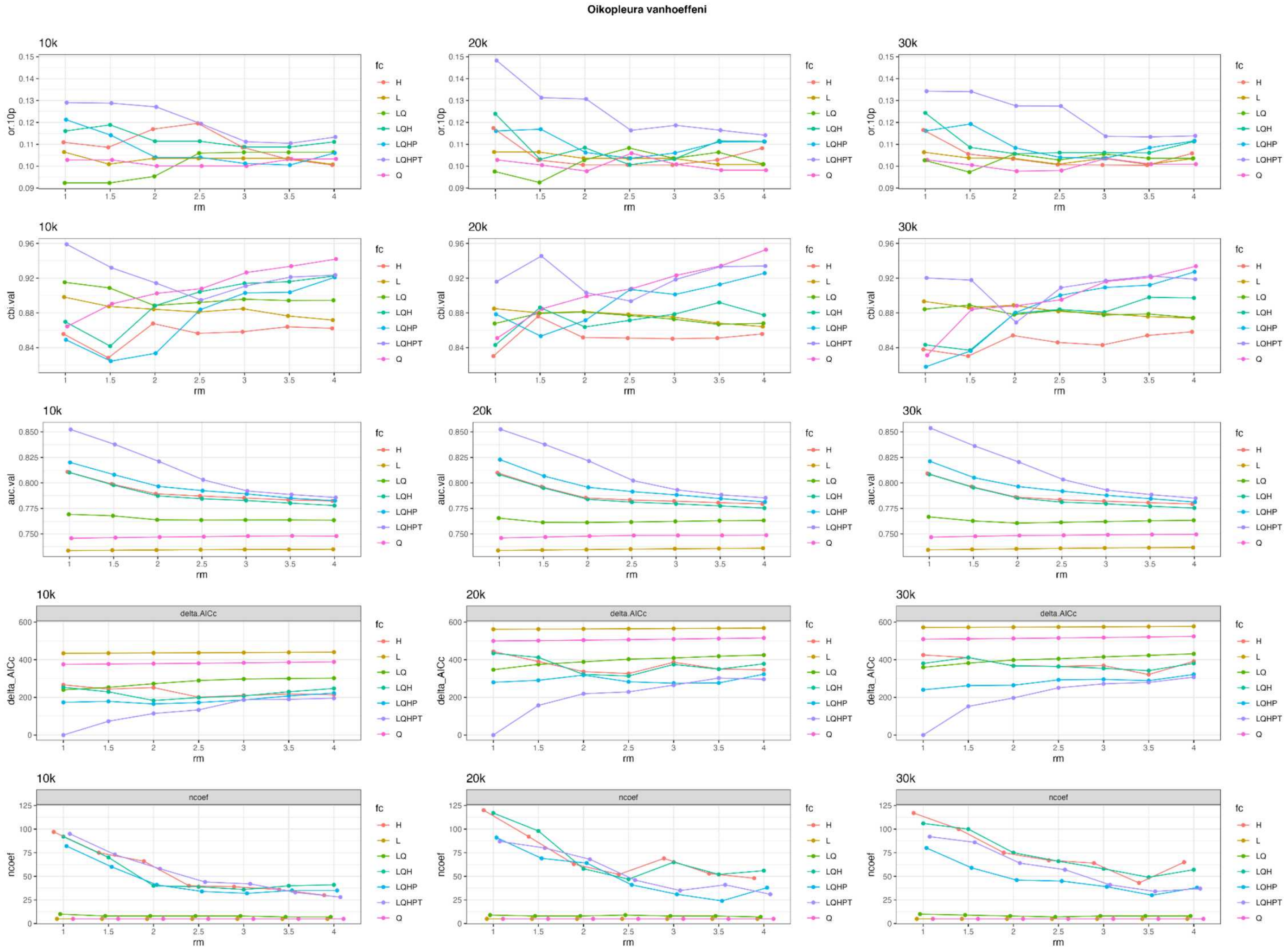
Continued Figure 2.S6. Evaluation metricies for the MaxEnt models. The metrics include: estimates of the 10th percentile, continuous Boyce index (CBI), area under the receiver operating characteristic curve (AUC), Akaike information delta criterion (AICc) and number of coefficients (ncoef) for three sets of the background points (10000, 20000, 30000).



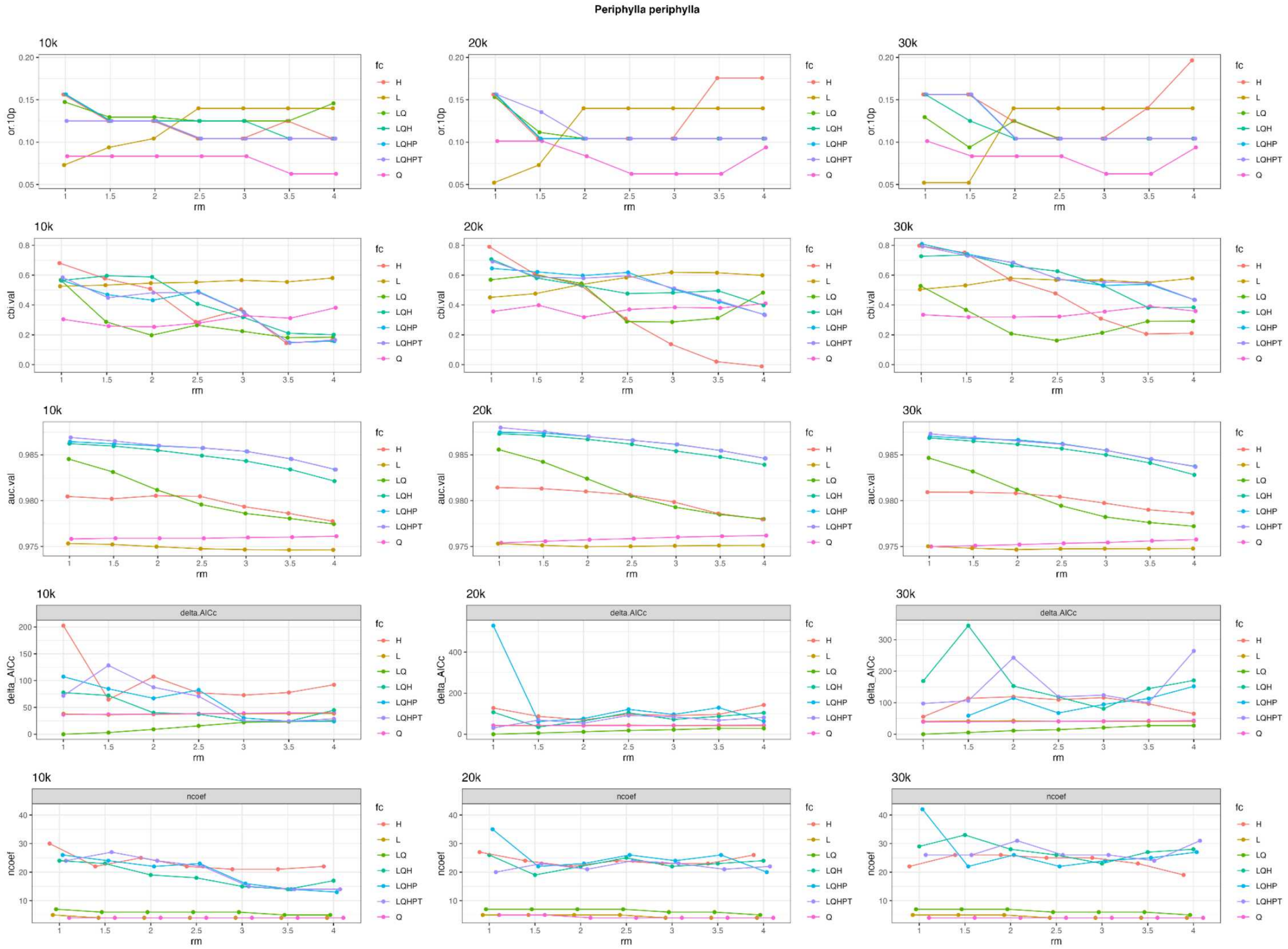
Continued Figure 2.S6. Evaluation metricies for the MaxEnt models. The metrics include: estimates of the 10th percentile, continuous Boyce index (CBI), area under the receiver operating characteristic curve (AUC), Akaike information delta criterion (AICc) and number of coefficients (ncoef) for three sets of the background points (10000, 20000, 30000).



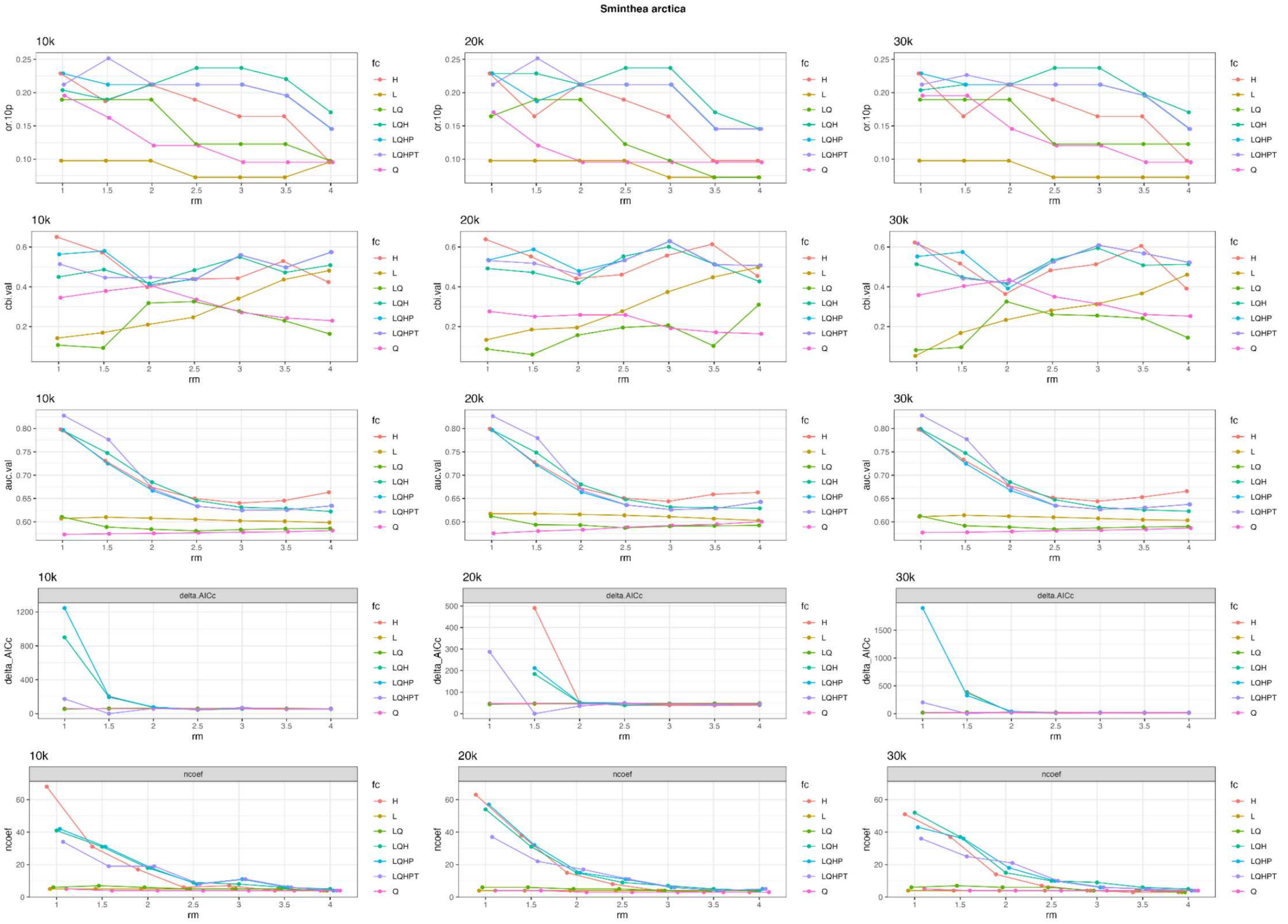
Continued Figure 2.S6. Evaluation metricies for the MaxEnt models. The metrics include: estimates of the 10th percentile, continuous Boyce index (CBI), area under the receiver operating characteristic curve (AUC), Akaike information delta criterion (AICc) and number of coefficients (ncoef) for three sets of the background points (10000, 20000, 30000).



Continued Figure 2.S6. Evaluation metricies for the MaxEnt models. The metrics include: estimates of the 10th percentile, continuous Boyce index (CBI), area under the receiver operating characteristic curve (AUC), Akaike information delta criterion (AICc) and number of coefficients (ncoef) for three sets of the background points (10000, 20000, 30000).



Continued Figure 2.S6. Evaluation metricies for the MaxEnt models. The metrics include: estimates of the 10th percentile, continuous Boyce index (CBI), area under the receiver operating characteristic curve (AUC), Akaike information delta criterion (AICc) and number of coefficients (ncoef) for three sets of the background points (10000, 20000, 30000).



Continued Figure 2.S6. Evaluation metricies for the MaxEnt models. The metrics include: estimates of the 10th percentile, continuous Boyce index (CBI), area under the receiver operating characteristic curve (AUC), Akaike information delta criterion (AICc) and number of coefficients (ncoef) for three sets of the background points (10000, 20000, 30000).

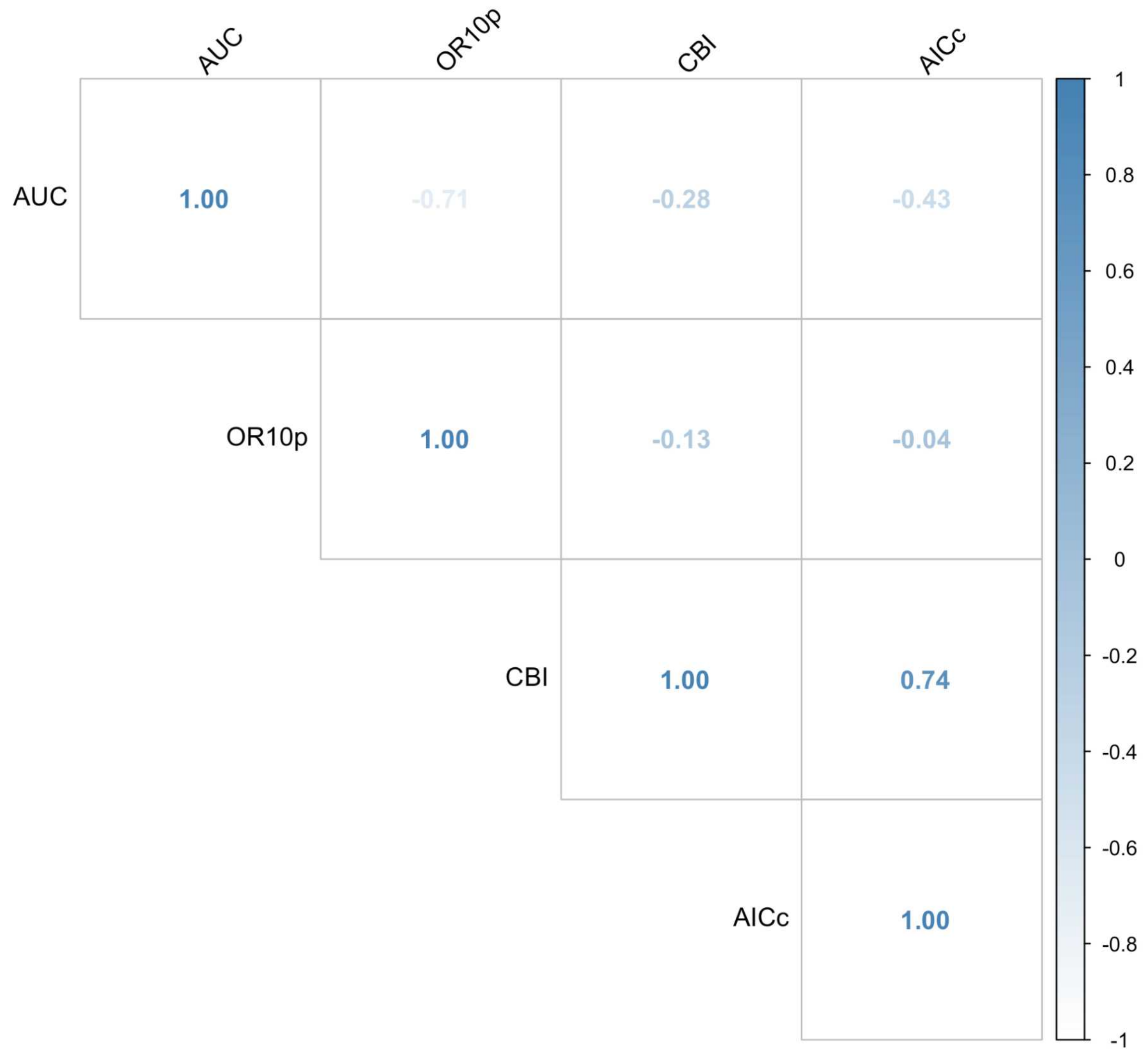


Figure 2.S7. Correlation matrix of evaluation metrics for all species: OR10p (omission rate, 10th percentile), CBI (Continuous Boyce Index), AUC (Area Under the Curve) and AICc (Akaike Information Criterion).

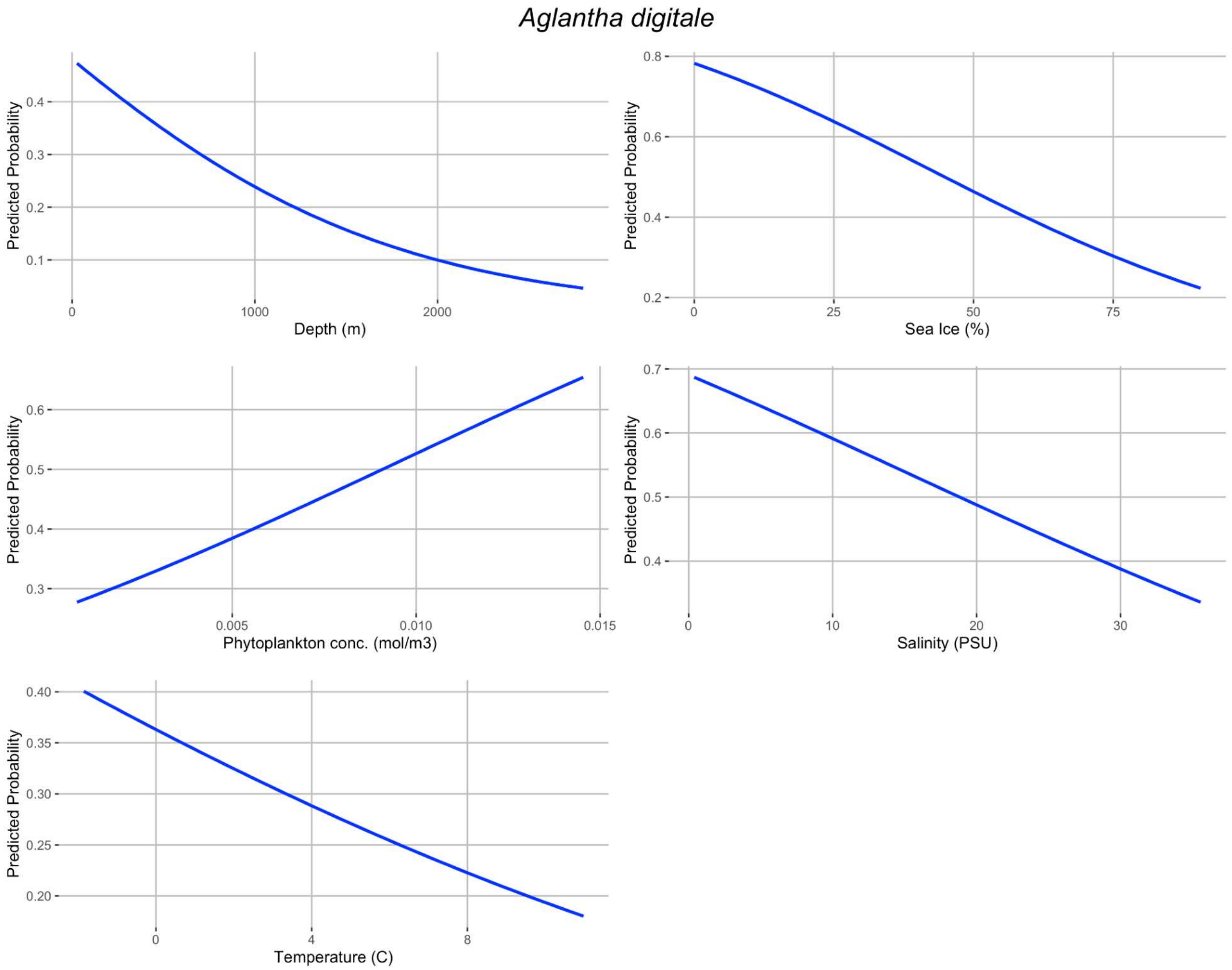
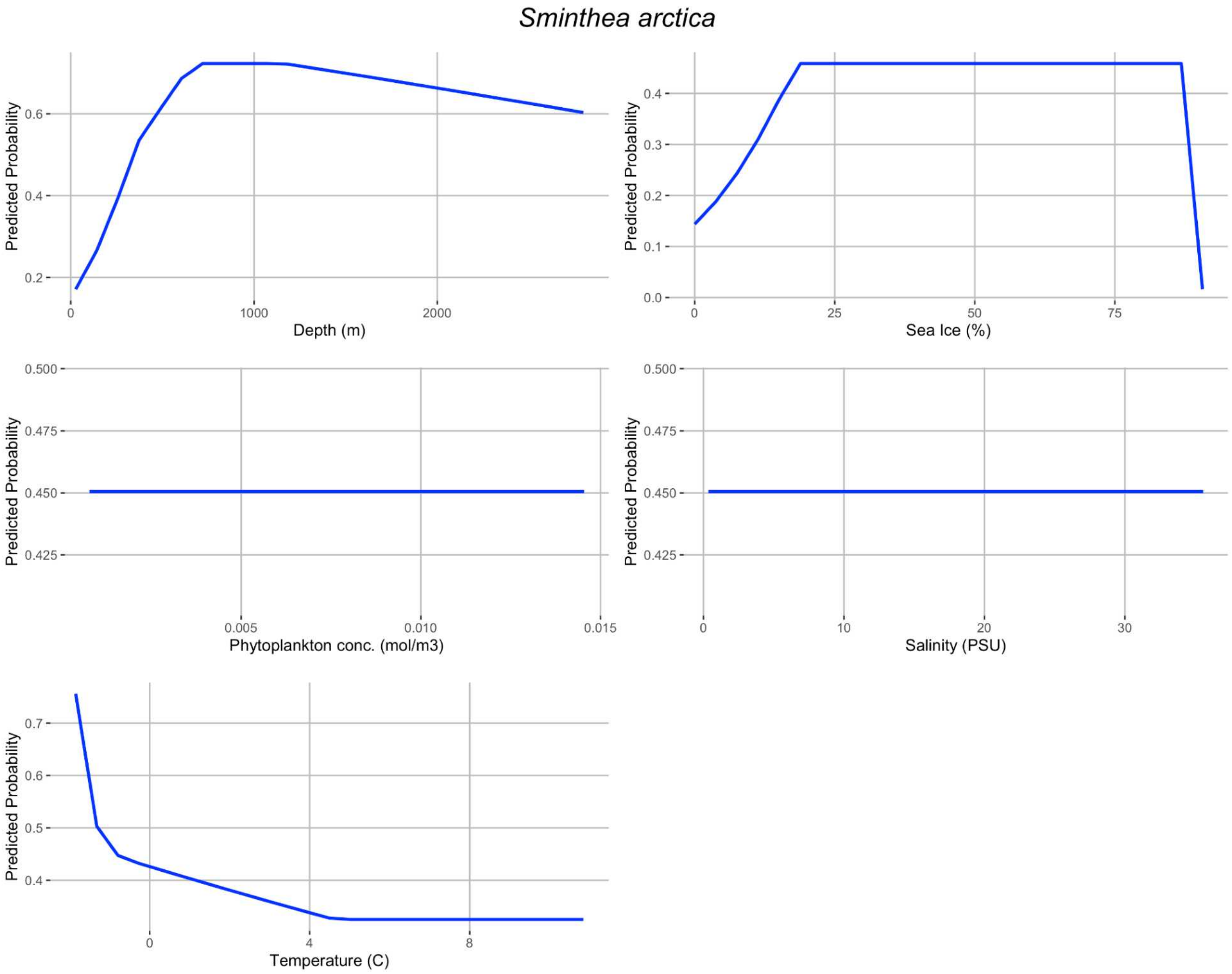
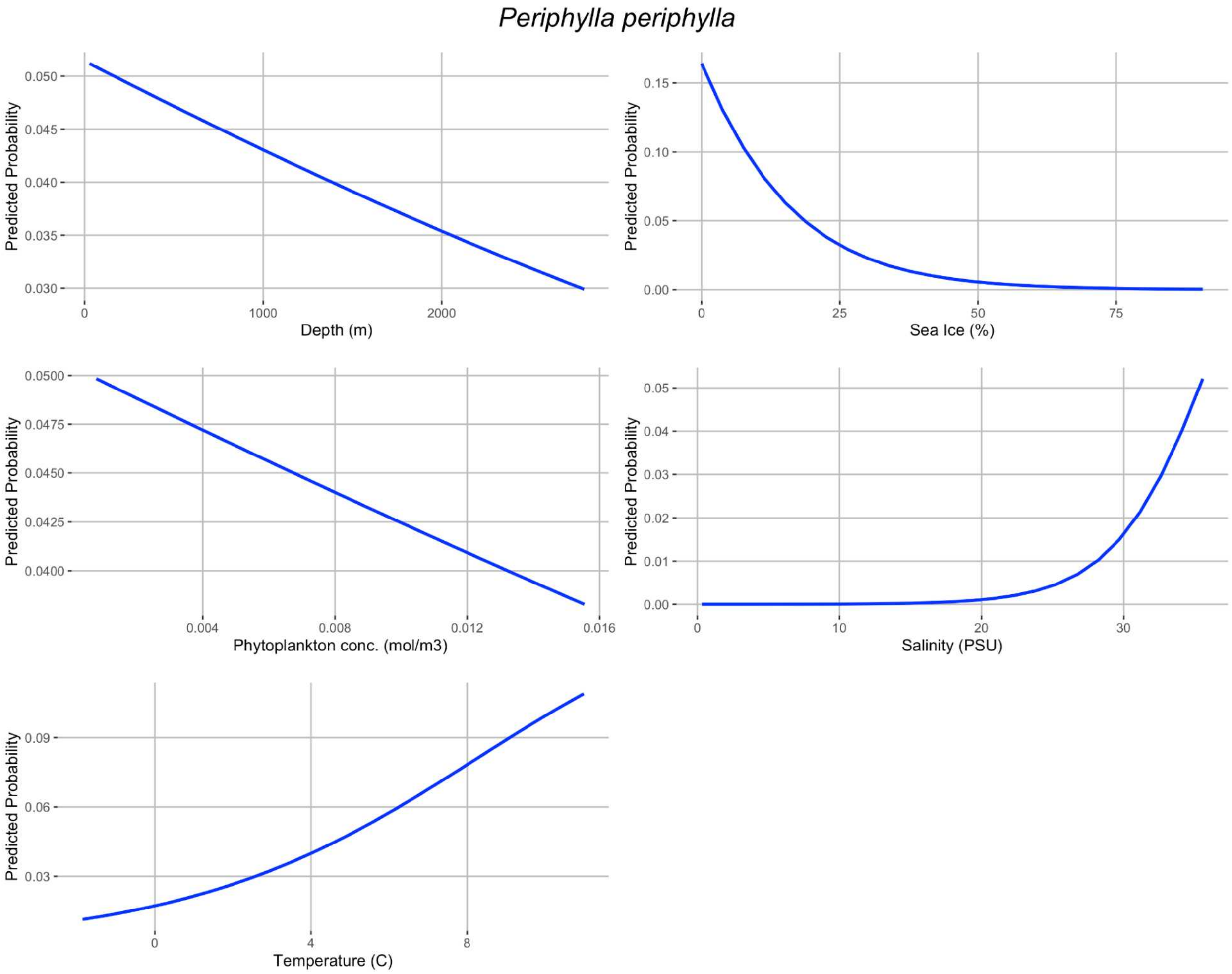


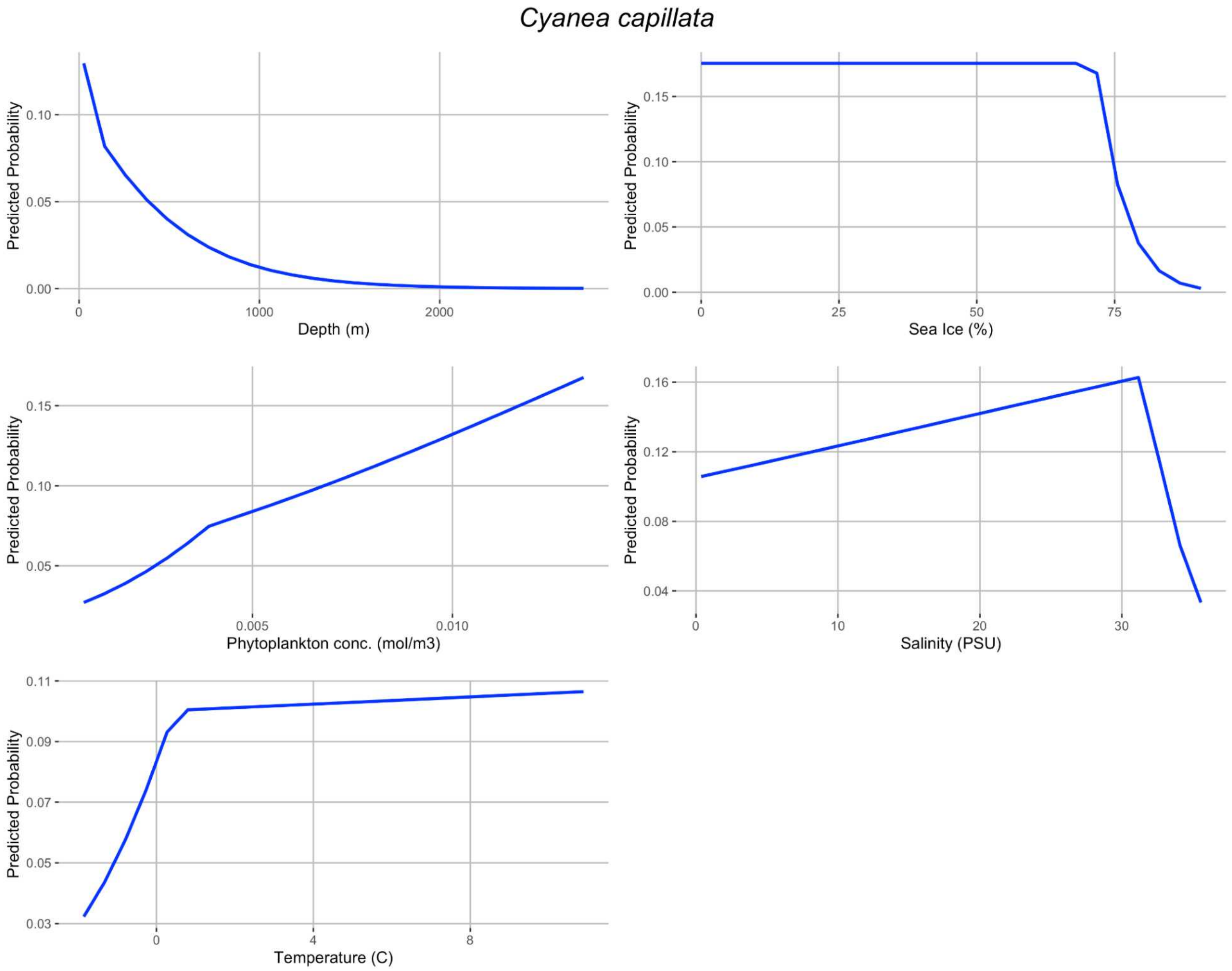
Figure 2.S8. Total response curves showing how five environmental variables affect species distributions. In total responses, the rest of the variables were kept at their median values.



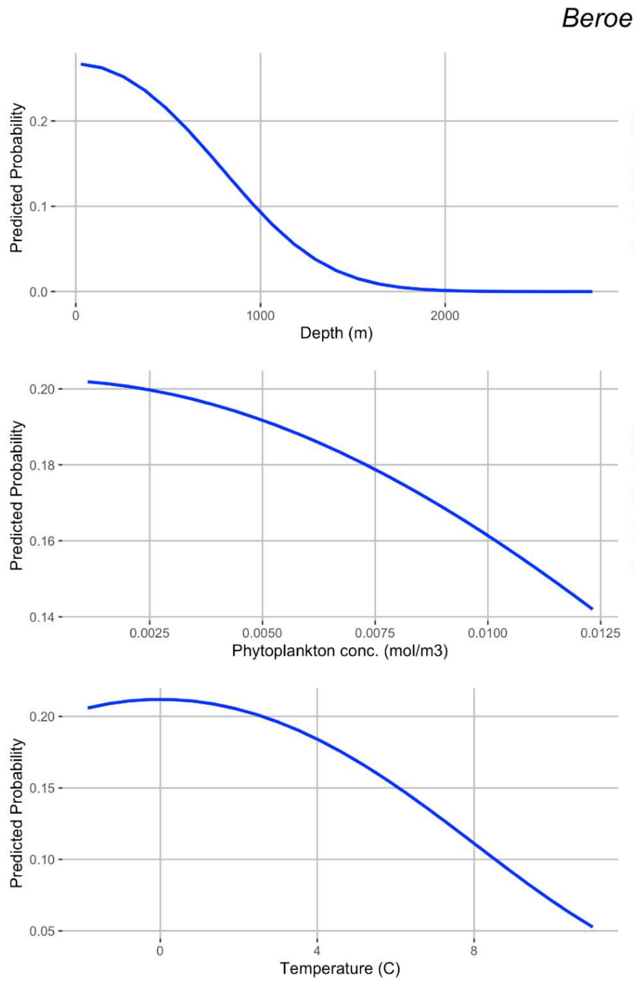
Continued Figure 2.S8. Total response curves showing how five environmental variables affect species distributions. In total responses, the rest of the variables were kept at their median values.

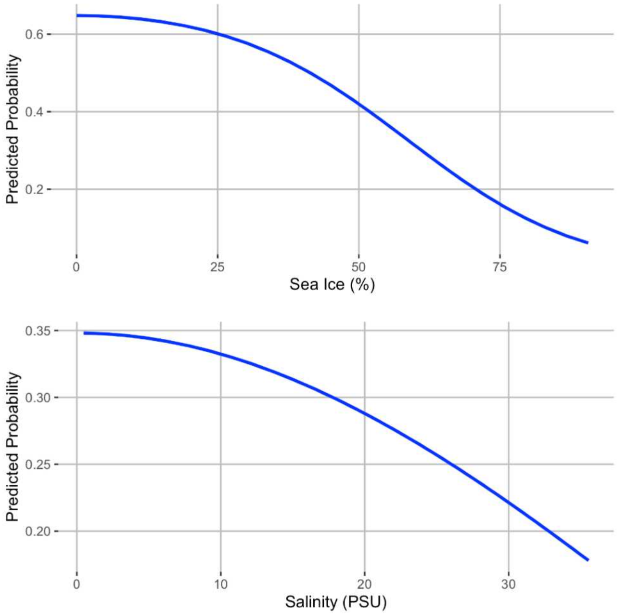


Continued Figure 2.S8. Total response curves showing how five environmental variables affect species distributions. In total responses, the rest of the variables were kept at their median values.

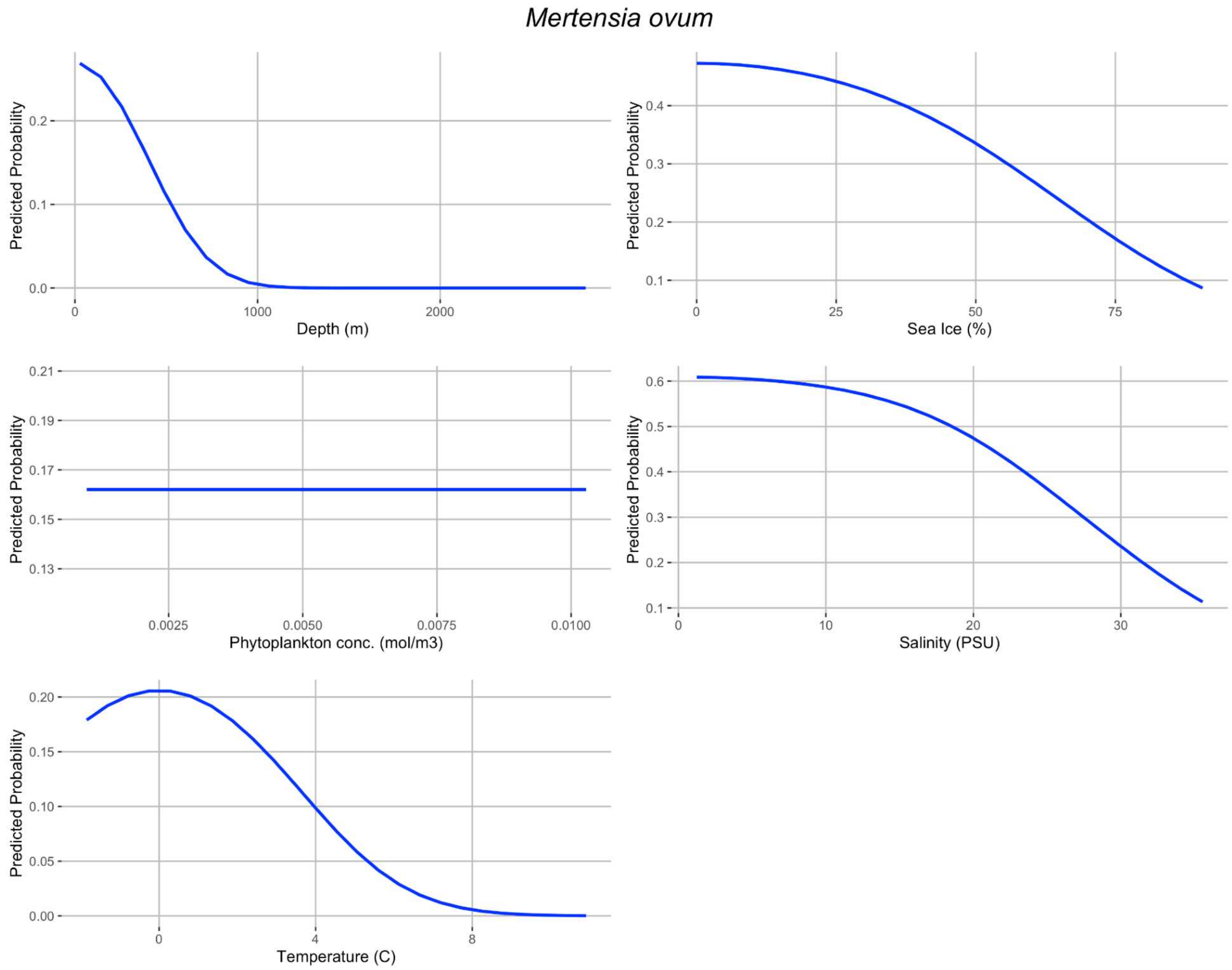


Continued Figure 2.S8. Total response curves showing how five environmental variables affect species distributions. In total responses, the rest of the variables were kept at their median values.

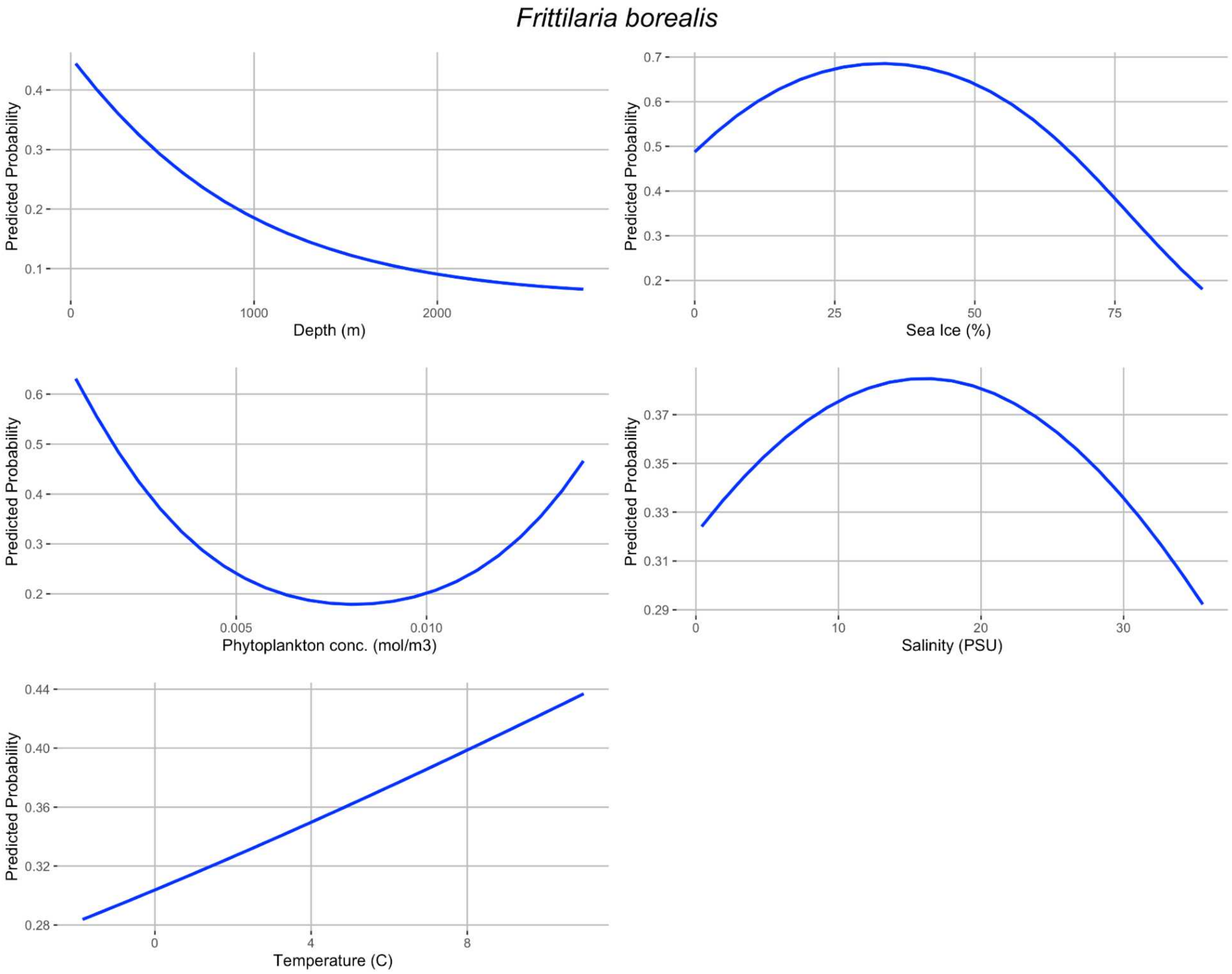




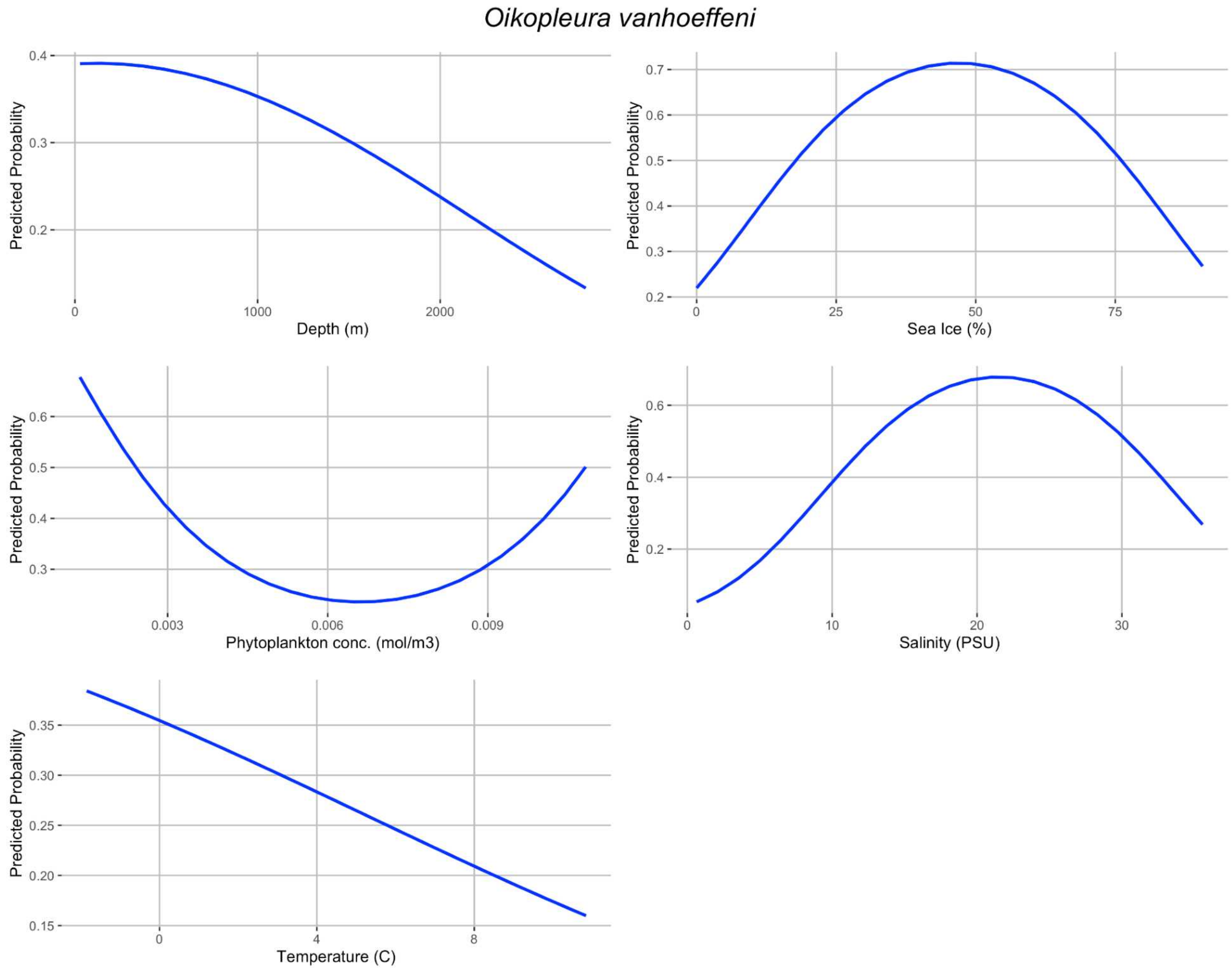
Continued Figure 2.S8. Total response curves showing how five environmental variables affect species distributions. In total responses, the rest of the variables were kept at their median values.



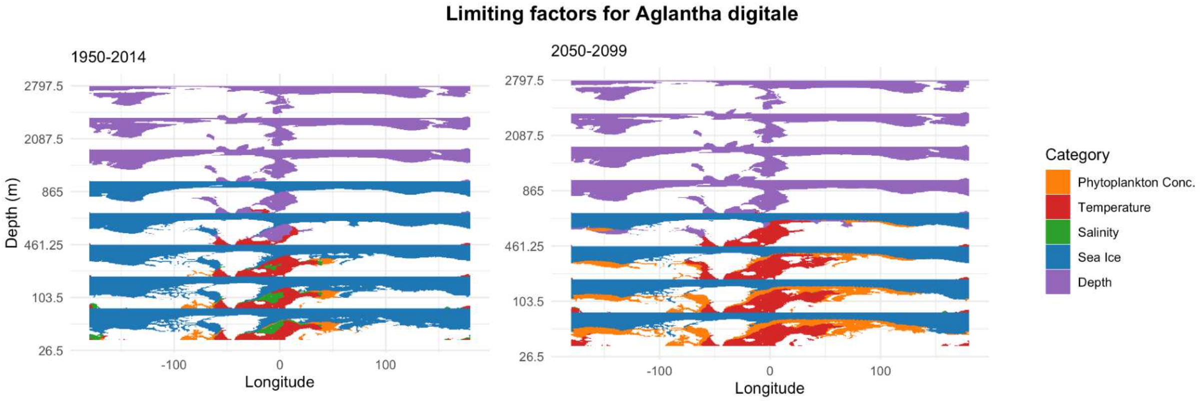
Continued Figure 2.S8. Total response curves showing how five environmental variables affect species distributions. In total responses, the rest of the variables were kept at their median values.



Continued Figure 2.S8. Total response curves showing how five environmental variables affect species distributions. In total responses, the rest of the variables were kept at their median values.



Continued Figure 2.S8. Total response curves showing how five environmental variables affect species distributions. In total responses, the rest of the variables were kept at their median values.



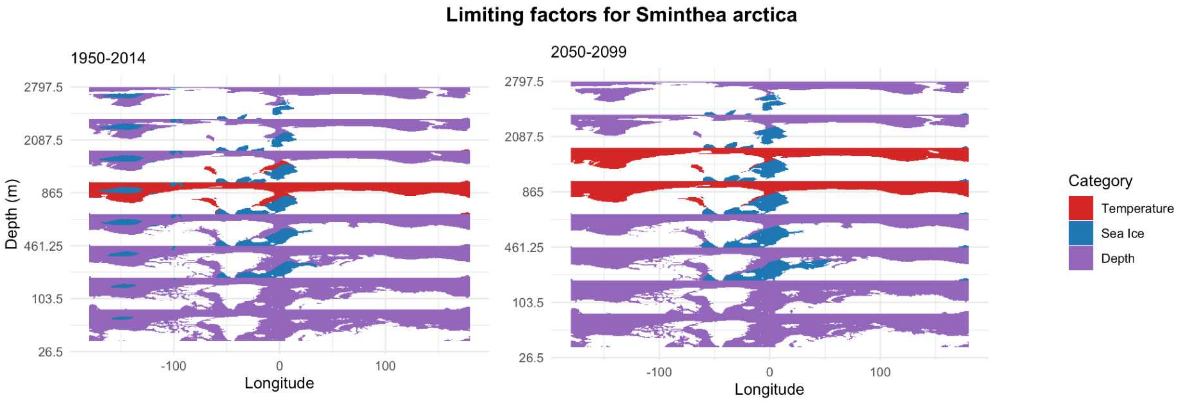
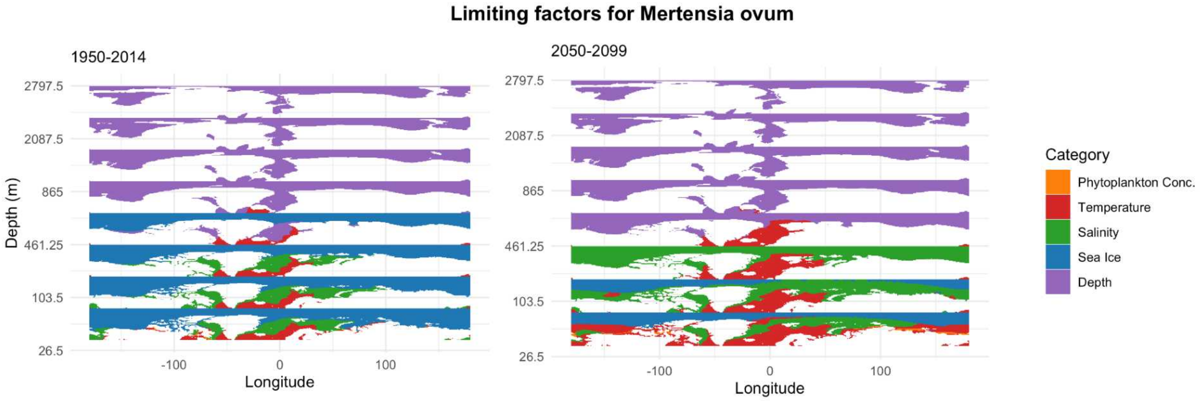
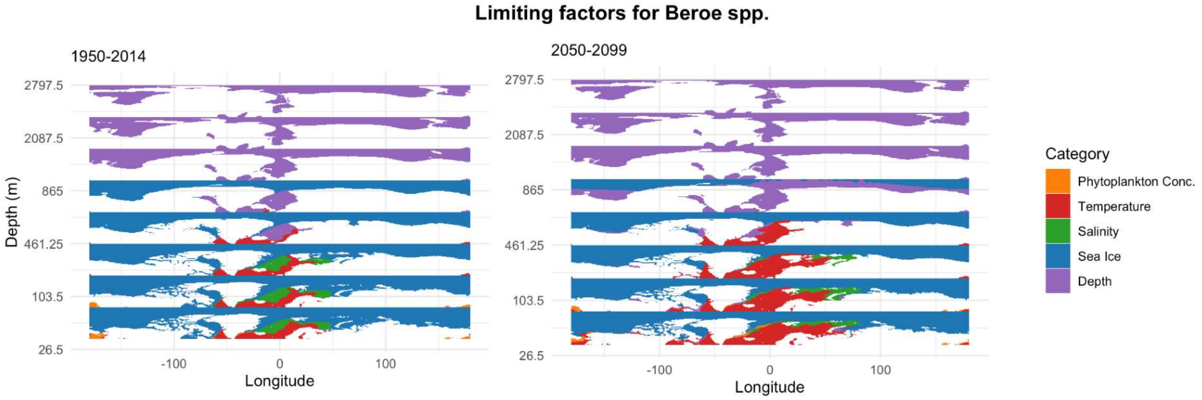
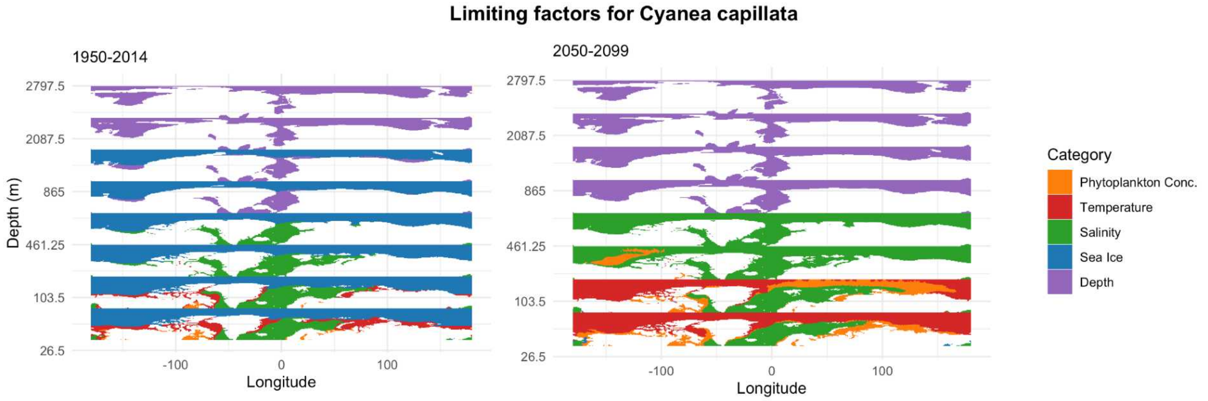


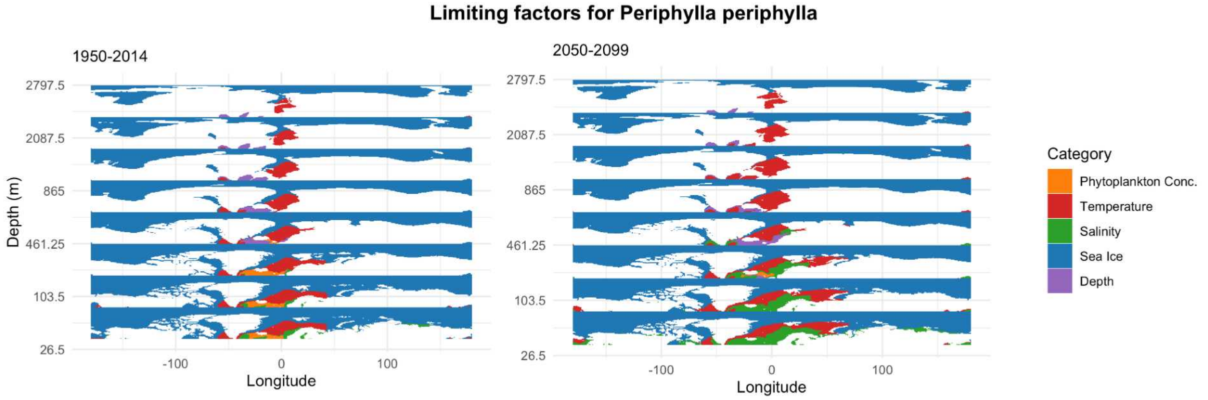
Figure 2.S9. Maps illustrating limiting factors for eight marine GZ species for the period 1950-2014 and 2050-2099. We used the function 'limiting' from the rmaxent package (https://github.com/johnbaums/rmaxent).



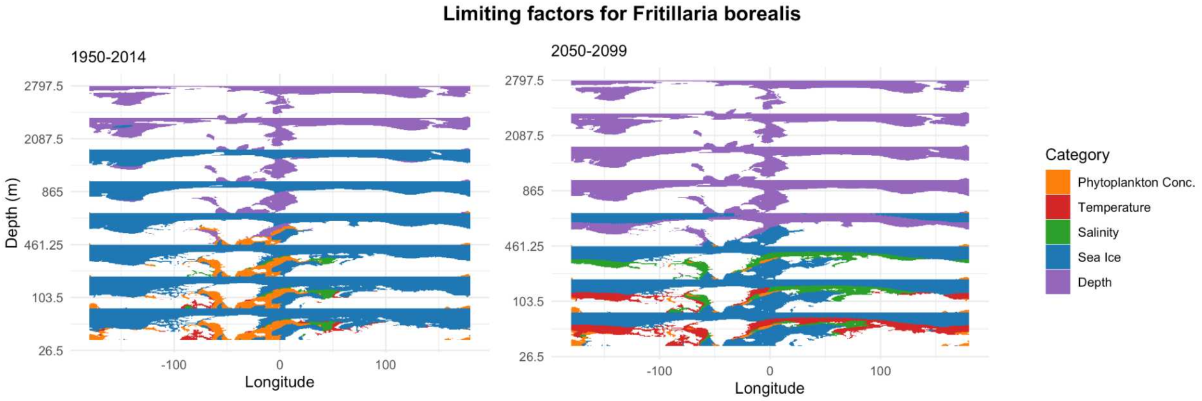


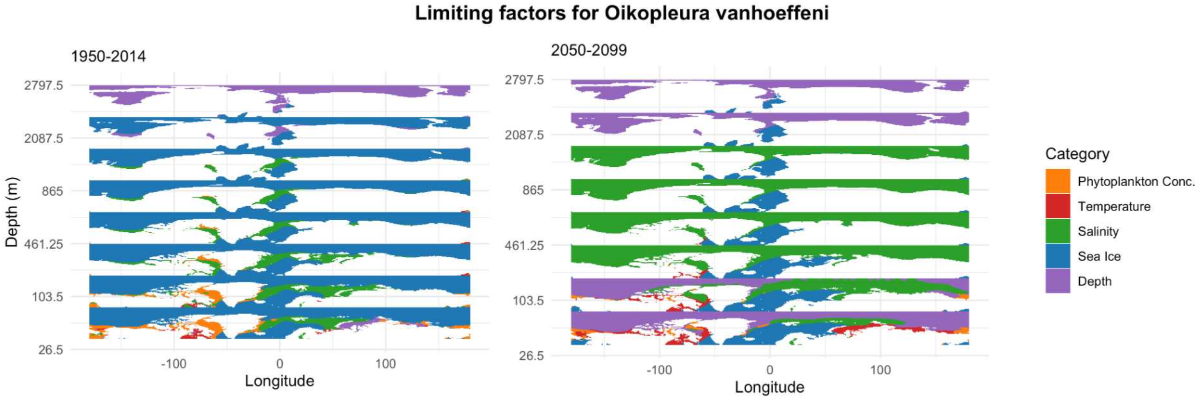
Continued Figure 2.S9. Maps illustrating limiting factors for eight marine GZ species for the period 1950-2014 and 2050-2099. We used the function 'limiting' from the rmaxent package (https://github.com/johnbaums/rmaxent).





Continued Figure 2.S9. Maps illustrating limiting factors for eight marine GZ species for the period 1950-2014 and 2050-2099. We used the function 'limiting' from the rmaxent package (https://github.com/johnbaums/rmaxent).





Continued Figure 2.S9. Maps illustrating limiting factors for eight marine GZ species for the period 1950-2014 and 2050-2099. We used the function 'limiting' from the rmaxent package (https://github.com/johnbaums/rmaxent).

Table 2.S1. Presence data of gelatinous zooplankton (GZ) extracted from the PANGAEA publications.

Publication	doi	Aglantha digitale	Beroe spp.	Cyanea capillata	Fritillaria borealis	Mertensia ovum	Oikopleura vanhoeffeni	Periphylla periphylla	Sminthea arctica
Licandro, Priscilla; Blackett, Michael (2014): Abundance of Cnidaria and Ctenophora taxa in the North Atlantic sampled during the M87/1 cruise in April 2012. Sir Alister Hardy Foundation for Ocean Science, PANGAEA, https://doi.org/10.1594/PANGAEA.826211	10.1594/PANGAEA.826211	Yes	-	-	-	-	-	-	-
Fetzer, Ingo (2005): Abundance of zooplankton during cruise BP97 (southern Kara Sea). PANGAEA, https://doi.org/10.1594/PANGAEA.269139	10.1594/PANGAEA.269139	Yes	-	-	Yes	-	Yes	-	-
Licandro, Priscilla; Aino, Hosia (2014): Abundance of Cnidaria and Ctenophora taxa in the North Atlantic sampled during the G. O. Sars Cruise in May 2013. Sir Alister Hardy Foundation for Ocean Science, PANGAEA, https://doi.org/10.1594/PANGAEA.829702	10.1594/PANGAEA.829702	Yes	Yes	-	-	Yes	-	Yes	Yes
Leonova, G A; Bobrov, Vyacheslav A; Shevchenko, Vladimir P; Prudkovsky, Andrey (2006): Dominant zooplankton species and microelements in plankton obtained from White Sea surface waters. PANGAEA, https://doi.org/10.1594/PANGAEA.793122, Supplement to: Leonova, GA et al. (2006): Comparative analysis of the microelemental composition of seston and bottom sediments in the White Sea. Doklady Earth Sciences, 406(1), 136-140, https://doi.org/10.1134/S1028334X06010338	10.1594/PANGAEA.793120	Yes	-	-	-	-	-	-	-
Lebedeva, Lyudmila P; Marasaeva, E F; Anokhina, L L (2001): Mesozooplankton of the northern Barents Sea in October 1998. PANGAEA, https://doi.org/10.1594/PANGAEA.761577, Supplement to: Lebedeva, LP et al. (2001): Mesozooplankton of high-latitude regions of the Barents Sea during the autumn-winter period. Translated from Okeanologiya, 2001, 41(5), 736-744, Oceanology, 41(5), 703-711	10.1594/PANGAEA.761575	Yes	-	-	-	-	-	-	-
Lebedeva, Lyudmila P; Marasaeva, E F; Anokhina, L L (2001): Mesozooplankton of the northern Barents Sea in October 1998. PANGAEA, https://doi.org/10.1594/PANGAEA.761577, Supplement to: Lebedeva, LP et al. (2001): Mesozooplankton of high-latitude regions of the Barents Sea during the autumn-winter period. Translated from Okeanologiya, 2001, 41(5), 736-744, Oceanology, 41(5), 703-711	10.1594/PANGAEA.761576	Yes	-	-	-	-	-	-	-
Vinogradov, Georgy M; Druzhkov, Nikolay V; Marasaeva, E F; Larionov, Viktor V (2001): Abundance and biomass of sub-ice mesozooplankton in the Pechora and Kara Seas in January-April 2000. PANGAEA, https://doi.org/10.1594/PANGAEA.763230, Supplement to: Vinogradov, GM et al. (2001): The under-ice mesozooplankton of the Pechora and Kara Seas in the winter-spring period, 2000. Translated from Okeanologiya, 2001, 41(5), 728-735, 41(5), 696-702	10.1594/PANGAEA.763228	Yes	-	-	-	-	Yes	-	-
Vinogradov, Georgy M; Druzhkov, Nikolay V; Marasaeva, E F; Larionov, Viktor V (2001): Abundance and biomass of sub-ice mesozooplankton in the Pechora and Kara Seas in January-April 2000. PANGAEA, https://doi.org/10.1594/PANGAEA.763230, Supplement to: Vinogradov, GM et al. (2001): The under-ice mesozooplankton of the Pechora and Kara Seas in the winter-spring period, 2000. Translated from Okeanologiya, 2001, 41(5), 728-735, 41(5), 696-702	10.1594/PANGAEA.763229	-	-	-	Yes	-	Yes	-	-
Leonova, G A; Bobrov, Vyacheslav A; Bogush, A A; Bychinskii, V A (2013): (Table 2) Relative mass contents of zooplankton species in samples from 7 stations in the White Sea, September 2002. PANGAEA, https://doi.org/10.1594/PANGAEA.816546, In: Leonova, GA et al. (2013): Zooplankton and seston in the White Sea and its chemical composition. PANGAEA, https://doi.org/10.1594/PANGAEA.816630	10.1594/PANGAEA.816546	Yes	-	-	-	-	-	-	-

Publication	doi	Aglantha digitale	Beroe spp.	Cyanea capillata	Fritillaria borealis	Mertensia ovum	Oikopleura vanhoeffeni	Periphylla periphylla	Sminthea arctica
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during DIANA cruise 90DI5370. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827039, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827039	Yes	Yes	-	Yes	-	-	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during Georgiy Sedov cruise 90SE3080. Arctic and Antarctic Research Institute, St. Petersburg, PANGAEA, https://doi.org/10.1594/PANGAEA.827070, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827070	Yes	Yes	-	Yes	-	-	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during Persey II cruise 90PS62A0. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827095, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827095	Yes	Yes	-	Yes	-	-	-	-
Licandro, Priscilla; Raab, Kristina; Hosia, Aino (2014): Biogeography of jellyfish in the North Atlantic. PANGAEA, https://doi.org/10.1594/PANGAEA.835732, Supplement to: Licandro, Priscilla; Blackett, Michael; Fischer, Astrid; Hosia, Aino; Kennedy, Janelle; Kirby, Richard R; Raab, Kristina; Stern, Robert J; Tranter, Paul (2015): Biogeography of jellyfish in the North Atlantic, by traditional and genomic methods. Earth System Science Data, 7(2), 173-191, https://doi.org/10.5194/essd-7-173-2015	10.1594/PANGAEA.830250	Yes	Yes	-	-	Yes	-	-	-
Licandro, Priscilla; Raab, Kristina; Hosia, Aino (2014): Biogeography of jellyfish in the North Atlantic. PANGAEA, https://doi.org/10.1594/PANGAEA.835732, Supplement to: Licandro, Priscilla; Blackett, Michael; Fischer, Astrid; Hosia, Aino; Kennedy, Janelle; Kirby, Richard R; Raab, Kristina; Stern, Robert J; Tranter, Paul (2015): Biogeography of jellyfish in the North Atlantic, by traditional and genomic methods. Earth System Science Data, 7(2), 173-191, https://doi.org/10.5194/essd-7-173-2015	10.1594/PANGAEA.830244	Yes	Yes	-	-	Yes	-	Yes	Yes

Publication	doi	Aglantha digitale	Beroe spp.	Cyanea capillata	Fritillaria borealis	Mertensia ovum	Oikopleura vanhoeffeni	Periphylla periphylla	Sminthea arctica
Licandro, Priscilla; Raab, Kristina; Hosia, Aino (2014): Biogeography of jellyfish in the North Atlantic. PANGAEA, https://doi.org/10.1594/PANGAEA.835732, Supplement to: Licandro, Priscilla; Blackett, Michael; Fischer, Astrid; Hosia, Aino; Kennedy, Janelle; Kirby, Richard R; Raab, Kristina; Stern, Robert J; Tranter, Paul (2015): Biogeography of jellyfish in the North Atlantic, by traditional and genomic methods. Earth System Science Data, 7(2), 173-191, https://doi.org/10.5194/essd-7-173-2015	10.1594/PANGAEA.830242	Yes	Yes	-	-	Yes	-	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Present of zooplankton during Georgiy Sedov cruise 90SE2980. Institute for Scientific Exploration of the North, PANGAEA, https://doi.org/10.1594/PANGAEA.827132, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827132	Yes	-	-	Yes	-	-	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during Professor Deryugin cruise 90PD5610. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827093, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827093	Yes	Yes	-	Yes	-	-	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during PROTRACTOR cruise 90P15430. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827088, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827088	Yes	Yes	-	Yes	-	-	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during DIANA cruise 90DI54C0. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827083, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827083	Yes	Yes	-	-	-	-	-	-

Publication	doi	Aglantha digitale	Beroe spp.	Cyanea capillata	Fritillaria borealis	Mertensia ovum	Oikopleura vanhoeffeni	Periphylla periphylla	Sminthea arctica
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during DIANA cruise 90DI5720. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827053, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827053	Yes	Yes	-	-	-	-	-	-
Cornils, Astrid; Thomisch, Karolin; Hase, Joanna; Hildebrandt, Nicole; Auel, Holger; Niehoff, Barbara (2022): Abundance, biovolume, biomass and length measurements of mesozooplankton from the POLARSTERN cruise PS78 (ARK-XXVI/1). PANGAEA, https://doi.org/10.1594/PANGAEA.944235	10.1594/PANGAEA.943571	Yes	-	-	-	-	-	-	Yes
Cornils, Astrid; Thomisch, Karolin; Hase, Joanna; Hildebrandt, Nicole; Auel, Holger; Niehoff, Barbara (2022): Abundance, biovolume, biomass and length measurements of mesozooplankton from the POLARSTERN cruise PS78 (ARK-XXVI/1). PANGAEA, https://doi.org/10.1594/PANGAEA.944235	10.1594/PANGAEA.944290	Yes	-	-	-	-	-	-	Yes
Cornils, Astrid; Thomisch, Karolin; Hase, Joanna; Hildebrandt, Nicole; Auel, Holger; Niehoff, Barbara (2022): Abundance, biovolume, biomass and length measurements of mesozooplankton from the POLARSTERN cruise PS78 (ARK-XXVI/1). PANGAEA, https://doi.org/10.1594/PANGAEA.944235	10.1594/PANGAEA.944285	Yes	-	-	-	-	-	-	-
Cornils, Astrid; Thomisch, Karolin; Hase, Joanna; Hildebrandt, Nicole; Auel, Holger; Niehoff, Barbara (2022): Abundance, biovolume, biomass and length measurements of mesozooplankton from the POLARSTERN cruise PS78 (ARK-XXVI/1). PANGAEA, https://doi.org/10.1594/PANGAEA.944235	10.1594/PANGAEA.944249	Yes	-	-	-	-	-	-	-
Cornils, Astrid; Thomisch, Karolin; Hase, Joanna; Hildebrandt, Nicole; Auel, Holger; Niehoff, Barbara (2022): Abundance, biovolume, biomass and length measurements of mesozooplankton from the POLARSTERN cruise PS78 (ARK-XXVI/1). PANGAEA, https://doi.org/10.1594/PANGAEA.944235	10.1594/PANGAEA.943570	Yes	-	-	-	-	-	-	Yes
Cornils, Astrid; Thomisch, Karolin; Hase, Joanna; Hildebrandt, Nicole; Auel, Holger; Niehoff, Barbara (2022): Abundance, biovolume, biomass and length measurements of mesozooplankton from the POLARSTERN cruise PS78 (ARK-XXVI/1). PANGAEA, https://doi.org/10.1594/PANGAEA.944235	10.1594/PANGAEA.944294	Yes	-	-	-	-	-	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton abundance during Dalniye Zelentsy cruise 90BY8180. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827027, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827027	Yes	-	-	-	Yes	Yes	-	-

Publication	doi	Aglantha digitale	Beroe spp.	Cyanea capillata	Fritillaria borealis	Mertensia ovum	Oikopleura vanhoeffeni	Periphylla periphylla	Sminthea arctica
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during POLYARNIK cruise 90PO5490. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827094, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827094	Yes	Yes	-	-	-	-	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Present of zooplankton during Mikhail Lomonosov cruise 90ML3190. Arctic and Antarctic Research Institute, St. Petersburg, PANGAEA, https://doi.org/10.1594/PANGAEA.827130, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827130	Yes	Yes	-	Yes	Yes	Yes	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during DIANA cruise 90DI5390. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827080, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827080	Yes	Yes	-	Yes	-	-	-	-
Kosobokova, Ksenia N; Hirche, Hans-Jürgen (2014): Zooplankton abundance and physical oceanography during POLARSTERN cruise ARK-IX/4 to the Laptev Sea and Arctic Ocean in 1993. PANGAEA, https://doi.org/10.1594/PANGAEA.839762	10.1594/PANGAEA.839758	Yes	-	-	-	-	-	-	Yes
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Biological Atlas of the Arctic Seas 2000: Physical oceanography, hydrochemistry, meteorology, and plankton of the Barents and Kara Seas. PANGAEA, https://doi.org/10.1594/PANGAEA.828112, Supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827034	-	-	-	Yes	-	-	-	-

Publication	doi	Aglantha digitale	Beroe spp.	Cyanea capillata	Fritillaria borealis	Mertensia ovum	Oikopleura vanhoeffeni	Periphylla periphylla	Sminthea arctica
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Biological Atlas of the Arctic Seas 2000: Physical oceanography, hydrochemistry, meteorology, and plankton of the Barents and Kara Seas. PANGAEA, https://doi.org/10.1594/PANGAEA.828112, Supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827035	-	Yes	-	Yes	-	-	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Biological Atlas of the Arctic Seas 2000: Physical oceanography, hydrochemistry, meteorology, and plankton of the Barents and Kara Seas. PANGAEA, https://doi.org/10.1594/PANGAEA.828112, Supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827081	-	Yes	-	-	-	-	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Biological Atlas of the Arctic Seas 2000: Physical oceanography, hydrochemistry, meteorology, and plankton of the Barents and Kara Seas. PANGAEA, https://doi.org/10.1594/PANGAEA.828112, Supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827051	-	Yes	-	Yes	-	-	-	-
Swalethorp, Rasmus; Kjellerup, Sanne; Nielsen, Torkel Gissel (2013): Mesozooplankton size data from Disko Bay, West Greenland, 2008. PANGAEA, https://doi.org/10.1594/PANGAEA.815151	10.1594/PANGAEA.815151	Yes	-	-	Yes	-	-	-	-
Sigurdsson, Gudjon M; Lüskow, Florian; Gislason, Astthor; Svavarsson, Jörundur (2022): Sub-surface gelatinous zooplankton assemblages and their seasonality in two Northwestern Icelandic fjords. PANGAEA, https://doi.org/10.1594/PANGAEA.942811	10.1594/PANGAEA.942811	Yes	Yes	Yes	-	-	-	-	-
Wei, Chih-Lin; Cusson, Mathieu; Archambault, Philippe; Belley, Renald; Brown, Tanya; Burd, Brenda J; Edinger, Evan; Kenchington, Ellen L; Gilkinson, Kent; Lawton, Peter; Link, Heike; Ramey-Balci, Patricia A; Scrosati, Ricardo A; Snelgrove, Paul V R (2020): TOBB: Canada's three oceans of benthic biodiversity database - species presence. PANGAEA, https://doi.org/10.1594/PANGAEA.915037, In: Wei, C-L et al. (2020): TOBB: Canada's three oceans of benthic biodiversity database. PANGAEA, https://doi.org/10.1594/PANGAEA.915041	10.1594/PANGAEA.915037	Yes	-	-	-	-	-	-	-

Publication	doi	Aglantha digitale	Beroe spp.	Cyanea capillata	Fritillaria borealis	Mertensia ovum	Oikopleura vanhoeffeni	Periphylla periphylla	Sminthea arctica
Fetzer, Ingo (2005): Abundance of zooplankton during cruise BP99 (southern Kara Sea). PANGAEA, https://doi.org/10.1594/PANGAEA.269142	10.1594/PANGAEA.269142	-	Yes	-	Yes	-	Yes	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during DIANA cruise 90DI5580. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827050, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827050	Yes	Yes	-	Yes	-	Yes	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Present of zooplankton during cruise 90XX1570. Hydrographic Service of the Navy, Leningrad, PANGAEA, https://doi.org/10.1594/PANGAEA.827144, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827144	-	Yes	-	Yes	-	-	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Present of zooplankton during cruise 90XX1380. Hydrographic Service of the Navy, Leningrad, PANGAEA, https://doi.org/10.1594/PANGAEA.827142, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827142	-	-	-	Yes	-	-	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Present of plankton during NERPA cruise 90NE3680. Arctic and Antarctic Research Institute, St. Petersburg, PANGAEA, https://doi.org/10.1594/PANGAEA.828082, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.828082	-	Yes	-	Yes	-	-	-	-

Publication	doi	Aglantha digitale	Beroe spp.	Cyanea capillata	Fritillaria borealis	Mertensia ovum	Oikopleura vanhoeffeni	Periphylla periphylla	Sminthea arctica
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Present of plankton during TAYMYR cruise 904D3280. Hydrographic Service of the Navy, Leningrad, PANGAEA, https://doi.org/10.1594/PANGAEA.828083, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.828083	-	Yes	-	Yes	-	-	-	-
OMEX Project Members; Wassmann, Paul (2013): Zooplankton abundance measured on water bottle samples during Jan Mayen cruise JM3. PANGAEA, https://doi.org/10.1594/PANGAEA.806456	10.1594/PANGAEA.806456	-	-	-	Yes	-	-	-	-
OMEX Project Members; Wassmann, Paul (2013): Zooplankton abundance measured on water bottle samples during Jan Mayen cruise JM1. PANGAEA, https://doi.org/10.1594/PANGAEA.806454	10.1594/PANGAEA.806454	-	-	-	Yes	-	-	-	-
OMEX Project Members; Wassmann, Paul (2013): Zooplankton abundance measured on water bottle samples during Jan Mayen cruise JM7. PANGAEA, https://doi.org/10.1594/PANGAEA.806460	10.1594/PANGAEA.806460	-	-	-	Yes	-	-	-	-
OMEX Project Members; Wassmann, Paul (2013): Zooplankton abundance measured on water bottle samples during Jan Mayen cruise JM5. PANGAEA, https://doi.org/10.1594/PANGAEA.806458	10.1594/PANGAEA.806458	-	-	-	Yes	-	-	-	-
OMEX Project Members; Wassmann, Paul (2013): Zooplankton abundance measured on water bottle samples during Jan Mayen cruise JM2. PANGAEA, https://doi.org/10.1594/PANGAEA.806455	10.1594/PANGAEA.806455	-	-	-	Yes	-	-	-	-
OMEX Project Members; Wassmann, Paul (2013): Zooplankton abundance measured on water bottle samples during Jan Mayen cruise JM8. PANGAEA, https://doi.org/10.1594/PANGAEA.806461	10.1594/PANGAEA.806461	-	-	-	Yes	-	-	-	-
OMEX Project Members; Wassmann, Paul (2013): Zooplankton abundance measured on water bottle samples during Jan Mayen cruise JM6. PANGAEA, https://doi.org/10.1594/PANGAEA.806459	10.1594/PANGAEA.806459	-	-	-	Yes	-	-	-	-
OMEX Project Members; Wassmann, Paul (2013): Zooplankton abundance measured on water bottle samples during Jan Mayen cruise JM4. PANGAEA, https://doi.org/10.1594/PANGAEA.806457	10.1594/PANGAEA.806457	-	-	-	Yes	-	-	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Present of zooplankton during cruise 90XX1490. Hydrographic Service of the Navy, Leningrad, PANGAEA, https://doi.org/10.1594/PANGAEA.827143, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827143	-	-	-	Yes	-	-	-	-

Publication	doi	Aglantha digitale	Beroe spp.	Cyanea capillata	Fritillaria borealis	Mertensia ovum	Oikopleura vanhoeffeni	Periphylla periphylla	Sminthea arctica
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during DIANA cruise 90DI5570. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827085, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827085	-	Yes	-	Yes	-	-	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during Professor Deryugin cruise 90PD54A0. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827091, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827091	-	Yes	-	Yes	-	-	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during Professor Deryugin cruise 90PD5552. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827066, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827066	-	Yes	-	Yes	-	-	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during DIANA cruise 90DI5330. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827078, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827078	-	Yes	-	Yes	-	-	-	-

Publication	doi	Aglantha digitale	Beroe spp.	Cyanea capillata	Fritillaria borealis	Mertensia ovum	Oikopleura vanhoeffeni	Periphylla periphylla	Sminthea arctica
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during DIANA cruise 90DI5340. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827079, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827079	-	Yes	-	Yes	-	-	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during DIANA cruise 90DI5670. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827086, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827086	-	Yes	-	-	-	-	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during DIANA cruise 90DI5350. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827038, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827038	Yes	-	-	-	-	-	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during DIANA cruise 90DI5520. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827084, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827084	-	Yes	-	Yes	-	-	-	-

Publication	doi	Aglantha digitale	Beroe spp.	Cyanea capillata	Fritillaria borealis	Mertensia ovum	Oikopleura vanhoeffeni	Periphylla periphylla	Sminthea arctica
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during Professor Deryugin cruise 90PD5460. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827090, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827090	Yes	Yes	-	-	-	-	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during Professor Deryugin cruise 90PD5540. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827092, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827092	-	Yes	-	-	-	-	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during Professor Deryugin cruise 90PD54B0. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827063, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827063	-	Yes	-	-	-	-	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during DIANA cruise 90DI5571. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827049, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827049	-	Yes	-	-	-	-	-	-
Hoving, Henk-Jan Ties; Neitzel, Philipp; Hosia, Aino; Piatkowski, Uwe (2021): Deep-sea fauna observed by pelagic video transects during HEINCKE cruise HE518, Norwegian Sea. PANGAEA, https://doi.org/10.1594/PANGAEA.927705	10.1594/PANGAEA.927705	Yes	Yes	-	-	-	-	-	-

Publication	doi	Aglantha digitale	Beroe spp.	Cyanea capillata	Fritillaria borealis	Mertensia ovum	Oikopleura vanhoeffeni	Periphylla periphylla	Sminthea arctica
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during Nicolai Knipovich cruise 90KN5620. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827087, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827087	-	Yes	-	-	-	-	-	-
David, Carmen L; Lange, Benjamin Allen; Rabe, Benjamin; Flores, Hauke (2015): Under-ice fauna from the Eurasian central Arctic Ocean during August-September 2012. PANGAEA, https://doi.org/10.1594/PANGAEA.858586, In supplement to: David, CL et al. (2015): Community structure of under-ice fauna in the Eurasian central Arctic Ocean in relation to environmental properties of sea-ice habitats. Marine Ecology Progress Series, 522, 15-32, https://doi.org/10.3354/meps11156	10.1594/PANGAEA.858586	-	Yes	-	-	Yes	Yes	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during Professor Deryugin cruise 90PD52B0. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827089, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827089	-	Yes	-	-	-	-	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during DIANA cruise 90DI5410. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827082, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827082	-	Yes	-	-	-	-	-	-
Matishov, Gennady G; Makarevich, Pavel R; Timofeev, Sergey F; Kuznetsov, Leonid L; Druzhkov, Nikolay V; Larionov, Viktor V; Golubev, Valery A; Zuyev, Aleksey N; Denisov, V I; Adrov, Nikolai M; Iliyn, G; Kuznetsov, A; Denisenko, Stanislav G; Savinov, Vladimir M; Shavikyn, A; Smolyar, I; Levitus, Sydney; O'Brien, Todd; Baranova, O (2000): Zooplankton in counts per sample during Nicolai Knipovich cruise 90KN5450. Murmansk Marine Biological Institute, PANGAEA, https://doi.org/10.1594/PANGAEA.827057, In supplement to: Matishov, GG et al. (2000): Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas (in english). International Ocean Atlas Series, Murmansk Marine Biological Institute, Russia; Ocean Climate Laboratory, NODC/NOAA, USA, 2, 348 pp, hdl:10013/epic.42580.d025	10.1594/PANGAEA.827057	-	Yes	-	-	-	-	-	-

Publication	doi	Aglantha digitale	Beroe spp.	Cyanea capillata	Fritillaria borealis	Mertensia ovum	Oikopleura vanhoeffeni	Periphylla periphylla	Sminthea arctica
Wei, Chih-Lin; Cusson, Mathieu; Archambault, Philippe; Belley, Renald; Brown, Tanya; Burd, Brenda J; Edinger, Evan; Kenchington, Ellen L; Gilkinson, Kent; Lawton, Peter; Link, Heike; Ramey-Balci, Patricia A; Scrosati, Ricardo A; Snelgrove, Paul V R (2020): TOBB: Canada's three oceans of benthic biodiversity database - species counts. PANGAEA, https://doi.org/10.1594/PANGAEA.915040, In: Wei, C-L et al. (2020): TOBB: Canada's three oceans of benthic biodiversity database. PANGAEA, https://doi.org/10.1594/PANGAEA.915041	10.1594/PANGAEA.915040	-	-	Yes	-	-	-	-	-

Table 2.S2. Feature classes (fc), regularization multipliers (rm), and background points (bp) for the best performing models of the eight GZ taxa.

Species	**fc**	**rm**	**bp**
Aglantha digitale	L	2.5	10k
Beroe spp.	Q	4	10k
Cyanea capillata	LQH	3.5	10k
Fritillaria borealis	LQ	2	10k
Mertensia ovum	Q	2.5	10k
Oikopleura vanhoeffeni	LQ	1	10k
Periphylla periphylla	L	1.5	30k
Sminthea arctica	H	1.5	20k

Table 2.S3. Variance Inflation Factors (VIFs) and correlation coefficients for a set of environmental variables, including Phytoplankton concentrations at surface, Depth, Temperature, Salinity, Oxygen, Sea Ice, and Depth.

Variables	**All Variables VIF**	**Without Oxygen VIF**
Phyc_depth	2.523838	1.619665
Temp	6.128646	2.537825
Salinity	1.84107	1.817529
Oxygen	5.278548	N/A
Ice	3.156431	3.228373
Phyc_surface	1.985738	1.749896
Depth	1.30501	1.371256
	Min Correlation	**Max Correlation**
All Variables	Depth ~ Phyc_surface (-0.02575719)	Oxygen ~ Temperature (-0.7679276)
Without Oxygen	Depth ~ Phyc_surface (-0.00125356)	Sea Ice ~ Temperature (-0.68772)

Chapter 3. Optical observations and spatio-temporal projections of gelatinous zooplankton in the Fram Strait, a gateway to a changing Arctic Ocean

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[4]GEOMAR Helmholtz Centre for Ocean Research Kiel (Germany)
†These authors share senior authorship

Author contributions

This study was conceptualized by CH and DP. DP, CH, HJH and GV carried out the field work for optical data collection. DP, GV, and PN performed visual identification of the PELAGIOS dives. DP performed all analyses, with methodological input of CK, KJ, GV and CH. DP was responsible for writing, after which extensive input from all authors resulted in the final version. All authors approved the submitted version.

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3.1 Abstract

Global warming causes profound environmental shifts in the Arctic Ocean, altering the composition and structure of communities. In the Fram Strait, a transitional zone between the North-Atlantic and Arctic Ocean, climate change effects are particularly pronounced and accelerated due to an increased inflow of warm Atlantic water. Gelatinous zooplankton are known as key predators, consuming a great variety of prey and playing an important role in marine ecosystems. Insufficient knowledge of how gelatinous zooplankton are affected by environmental change has resulted in a notable gap in the understanding of the future state of Arctic ecosystems. We analysed the diversity and abundance of gelatinous zooplankton down to 2600 m depth and established the first regional baseline dataset using optical observations obtained by the towed underwater camera system PELAGIOS (Pelagic In situ Observation System). Our data estimate the abundance of 20 taxa of gelatinous zooplankton. The most abundant taxa belong to the family of Rhopalonematidae, mainly consisting of *Aglantha digitale* and *Sminthea arctica*, and the suborder Physonectae. Using the observational data, we employed a joint species distribution modelling approach to better understand their distributional patterns. Variance partitioning over the explanatory variables showed that depth and temperature explained a substantial amount of variation for most of the taxa, suggesting that these parameters drive diversity and distribution. Spatial distribution modelling revealed that the highest abundance and diversity of jellyfish are expected in the marginal sea-ice zones. By coupling the model with climate scenarios of environmental changes, we were able to project potential changes in the spatial distribution and composition of gelatinous communities from 2020 to 2050 (during the summer season). The near-future projections confirmed that with further temperature increases, gelatinous zooplankton communities in the Fram Strait would become less diverse but more abundant. Among taxa of the Rhopalonematidae family, the abundance of *Aglantha digitale* in the entire water column would increase by 2%, while a loss of up to 60% is to be expected for *Sminthea arctica* by 2050. The combination of *in situ* observations and species distribution modelling shows promise as a tool for predicting gelatinous zooplankton community shifts in a changing ocean.

Keywords: Gelatinous zooplankton, optical *in situ* observations, distribution modelling, spatio-temporal projections, environmental changes, Fram Strait, Arctic Ocean

3.2 Introduction

Arctic regions are experiencing temperature increases approximately four times greater than the rest of the world (Rantanen *et al.,* 2022). Due to this warming, over the past decade the average annual Arctic sea-ice extent has reached its lowest level since 1850 (Fox-Kemper *et al.,* 2021). An increase in sea-ice free areas, as well as a prolongation of open water days, extend the growing season of open ocean type phytoplankton communities (Arrigo, *et al.*, 2008). This extension is also obvious from long-term satellite observation data which show an increase in net primary production (NPP) in the Arctic Ocean by ca. 20-25% per decade from 1998 to 2015 (Arrigo and van Dijken, 2015; Kahru *et al.*, 2016). At the same time, the proportion of primary production from sea-ice algae blooms that rapidly falls to the seafloor will decrease (Constable et al., 2022). Open ocean ecosystems may support new pelagic communities of secondary and tertiary consumers (zooplankton and foraging fish) and upper trophic level mammals (Moore and Stabeno, 2015).

Ocean warming and subsequent sea-ice retreat have already caused a northward migration of subarctic and temperate species (Buchholz *et al.*, 2010; Frainer *et al.*, 2017; Geoffroy *et al.*, 2018; Neukermans *et al.*, 2018; Schröter *et al.*, 2019), increased abundance and reproductive success of subarctic species (Kraft *et al.*, 2013), and a decline in abundance and retraction of some Arctic species linked to sea-ice (Wassmann *et al.*, 2011; Ingvaldsen *et al.*, 2021). Zooplankton taxa are propagating toward the poles at a relatively fast average rate of 100 km per decade (Field et al., 2014), making them important indicators for monitoring ecosystem changes due to climate shifts in the Arctic Ocean. This northward shift of subarctic zooplankton species leads to the emergence of new feeding interactions, which in turn increases connectivity and decreases the modularity of the Arctic marine ecosystems (Pecuchet *et al.*, 2020).

Most studies on changes in zooplankton distribution and abundance in the Arctic have focused on hard-bodied forms of zooplankton taxa such as crustaceans (Basedow *et al.*, 2018; Hop *et al.*, 2021). Gelatinous zooplankton (GZ), is a polyphyletic group consisting of zooplankton that often have transparent and fragile bodies. The focus of our study is on cnidarians and ctenophores as representatives of gelatinous zooplankton (GZ). While other organisms, such as larvaceans, chaetognaths and molluscs, are sometimes classified as GZ, they will not be considered in this study. Due to their high water content these pelagic organisms were long considered dead-ends in marine food webs (Verity and Smetacek, 1996). Recent studies, however, show GZ to be pivotal and abundant components of oceanic food webs (Hays *et al.*, 2018). GZ are considered to be versatile predators, and consume a great variety of prey (Choy et al., 2017). Despite a typically low nutritional value, GZ are an important food source for various predators including fish, birds, turtles, and various invertebrates (Decker *et al.*, 2014; Hoving and Haddock, 2017; Urban *et al.*, 2022; Yaragina *et al.*, 2022). Under favorable environmental conditions, GZ can become overwhelmingly abundant and form episodic ‘blooms’ (Boero *et al.*, 2008). Over the last few decades, the magnitude of such blooms has been increasing in various parts of the world (Brodeur *et al.*, 2008; Riisgård *et al.*, 2012), and these blooms are believed to be driven by overfishing, eutrophication and changing oceanographic conditions (Purcell, 2012).

However, the general hypotheses of global increases in GZ populations have been questioned and are hard to prove (Condon *et al.*, 2012, 2013), as jellyfish blooms are subject to global fluctuations (Condon *et al.*, 2013). The future state of GZ in changing Arctic ecosystems remains particularly uncertain in this context due to a lack of reliable long-term datasets (Mańko *et al.*, 2020).

Our knowledge of the abundance and composition of GZ in polar seas is scarce (Raskoff *et al.*, 2005). One reason for this data gap is the extreme fragility of GZ. Collecting GZ with nets destroys many species or degrades them into fragments, which are subsequently unidentifiable and often excluded from analysis (Raskoff *et al.*, 2003). Various net sampling methodologies have been shown to be biased toward certain groups of GZ (Hosia *et al.*, 2017). Comparative studies of net-based and optical samplers revealed that nets may dramatically underestimate abundances and diversity of GZ (Remsen et al., 2004; Raskoff *et al.*, 2010; Hosia *et al.*, 2017; Hoving *et al.*, 2019). For example, the abundance estimates of Beroidae comb jellies was three to five times higher when using optical methods compared to multinets (Hoving *et al.*, 2019). Net-based systems also under-sample many GZ species, such as Aeginidae spp., *Sminthea arctica*, *Botrynema* spp., *Atolla* spp., lobate ctenophores and siphonophores (Raskoff *et al.*, 2010). Some of the larger GZ taxa are known only from *in situ* observations and have never been captured in a good state with nets, e.g., *Thalassocalyce inconstans* (Swift *et al.*, 2009), *Kiyohimea usagi* (Hoving *et al.,* 2018).

Insufficient knowledge about GZ has led to a notable gap in understanding the structure of the pelagic Arctic ecosystem, particularly in the deep-sea (meso- and bathypelagic) habitats (Raskoff *et al.*, 2005). Only a few studies focused on the changes in the biomass and diversity of GZ in the Arctic Ocean and its marginal seas. Brodeur *et al.*, (1999) observed the increase of the biomass of large medusae from 1979 to 1997 in the Bering Sea. Since the Bering Sea is the Pacific-Arctic gateway, it is likely that the export of GZ from the North Pacific to the Arctic also increased. In the Barents Sea, continued warming may be favorable for cnidarian abundances (Eriksen *et al.*, 2012). A northward shift to a high Arctic fjord (> 78°N) and an abundance increase in the northern Barents Sea since 2014 has been documented for the deep-water scyphozoan *Periphylla periphylla* (Geoffroy *et al.,* 2018).

In the Fram Strait, the main gateway to the Arctic Ocean, the transfer of heat from the North Atlantic has intensified over the course of decades, a phenomenon referred to as "Atlantification" (Beszczynska-Moller *et al.*, 2012; Polyakov *et al.*, 2012; Ingvaldsen *et al.*, 2021) making this region essential for monitoring ongoing changes in ecosystems. Further Atlantification in the Fram Strait is likely to facilitate the expansion of boreal species into the Arctic and may lead to a less diverse but more abundant GZ community in the future (Mańko *et al.*, 2020). To increase large-scale knowledge of GZ species assemblages in the Fram Strait, we obtained baseline data on vertical distribution and diversity of deep-water Arctic GZ with the Pelagic In situ Observation System (Hoving et al., 2019). The data were collected during the cruises to the HAUSGARTEN Long-Term Ecological Research (LTER) site (Soltwedel et al. 2005) in 2019 and 2021. Quantitative estimations of abundance, diversity and vertical distribution of GZ taxa was obtained using a horizontal video transect methodology (Hoving et al., 2020a). In order to understand current and future patterns of vertical species distributions, we fitted Bayesian Joint Species Distribution Models (JSDMs; Ovaskainen and Abrego, 2020) on the obtained abundance data. These trained models were coupled with climate change scenarios, which allowed us to forecast spatial niche range shifts of dominant species of gelatinous zooplankton. Our modelling effort is limited to a rather small section across Fram Strait, with the aim to project the redistribution related to the spatial shift of two distinguishable currents (West Spitsbergen Current and East Greenland Current) of the Fram Strait.

We hypothesized that global warming is affecting the composition of gelatinous zooplankton communities and changing their abundance and habitable niches in the Fram Strait region. To test this hypothesis, we used the JSDM-based assessment with a focus on the mesopelagic and bathypelagic GZ communities in the Fram Strait, with the specific objectives to (1) assess the significance of specific environmental drivers on structuring GZ communities; (2) delineate spatial distribution and vertical zonation of GZ communities; (3) use climate-change scenarios to project future distributions of GZ communities in the Fram Strait.

3.3 Methods and materials

3.3.1 Expeditions and deployments

During the expeditions PS121 (Hoving *et al.*, 2020b) and PS126 (Havermans *et al.*, 2021) of the R/V Polarstern (Alfred-Wegener-Institute, 2017) to the Fram Strait in August/September 2019 and June 2021 (Figure 3.1), we deployed the Pelagic In situ Observation System (PELAGIOS; Hoving *et al.*, 2019) at the HAUSGARTEN Long-Term Ecological Research (LTER) stations in Fram Strait. The PELAGIOS is a towed video camera system that collects high definition (HD) videos at 50 frames per second using the 1Cam Alpha camera as well as Conductivity-Temperature-Depth-Optical data. PELAGIOS was towed horizontally through the water column at approximately 1 knot speed over ground. Horizontal transects were conducted at specific depths down to 2600 m based on prior knowledge of the water masses and ecosystem domains in the study area, with the aim of covering a representative range of habitats for gelatinous zooplankton. (Figure 3.S1, Table 3.S1). Seven deployments were performed at four different stations (4 during PS121, and 3 during PS126), resulting in a total of 13.5 hours of pelagic video (Figure 3.1, Sn; Table 3.S1.). PELAGIOS data from the ascent and descent phases of the transects were not used in the analysis due to limitations in their conversion to species abundance values resulting from the direct horizontal projection design of the PELAGIOS system. A total of 50 unique horizontal transects (sampling points) were identified across the seven stations studied, based on their distinct (longitude, latitude, depth) values (Figure 3.1, Figure 3.S1, Table 3.S1). Species abundance values at these transects were converted from the number of specimens per minute to the number of specimens per cubic meter given that PELAGIOS records an average volume of 0.116 m3 s-1 at a tow speed of 1 knot (= 0.51 ms-1) (Hoving et al., 2019).

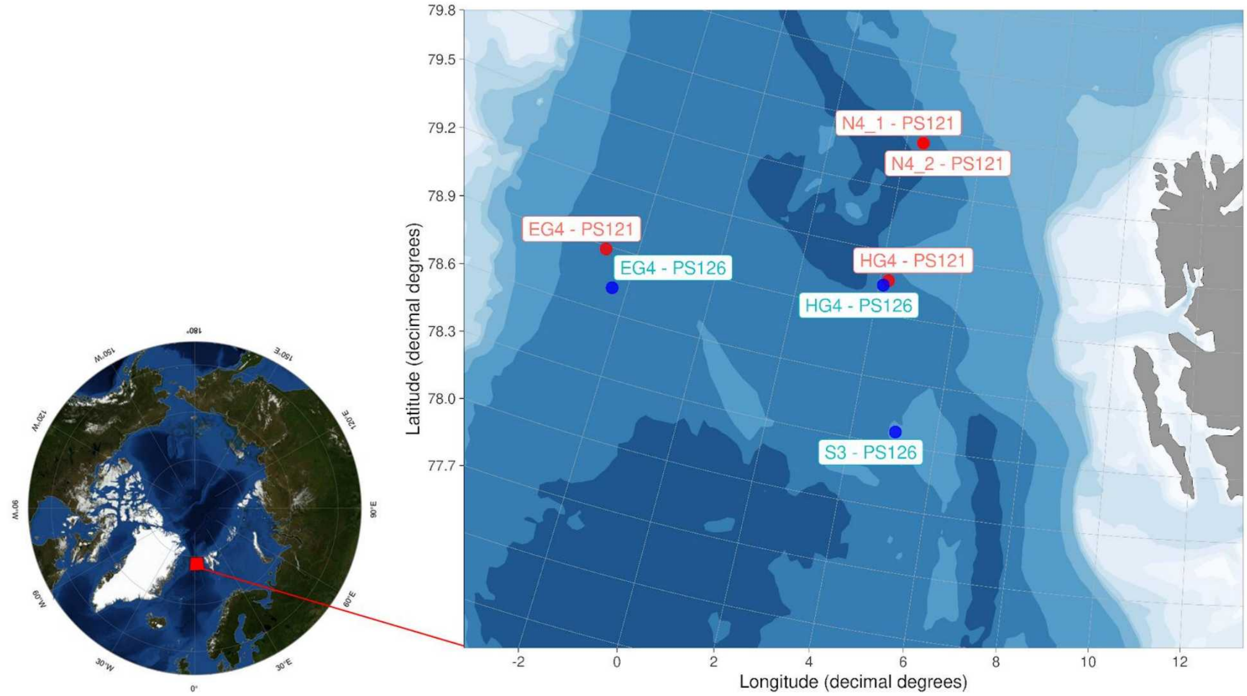

Figure 3.1. Study area and dive stations of the towed camera PELAGIOS during two expeditions to the HAUSGARTEN LTER in Fram Strait, PS121 (2019, stations in red on the map) and PS126 (2021, stations in green). The map of the Pan-Arctic region uses 'Blue Marble' data from the NASA Earth Observatory (Stöckli et al., 2006). The visualization for the Fram Strait was created using the PlotSvalbard R package (Vihtakari, 2020).

3.3.2 Biological data

The video transects were analyzed using the Video Annotation and Reference System "VARS" (Schlining and Stout, 2006). The VARS annotation program enables the capture of frames from the video with corresponding time codes. It also includes a knowledge base for inputting taxonomic names and hierarchy, and a database search function for easy retrieval of information. We identified the species *Botrynema brucei* and *Botrynema ellinorae* based on the presence/absence (respectively) of a sharp knob at the top of the bell. Individuals that could not be distinguished were grouped as *Botrynema* spp. Other species of Trachymedusae that could not be identified to a lower taxonomic level were assigned to Trachymedusae spp. For the family Aeginidae (Narcomedusae), species identification was based on the number of tentacles, with *Solmundella bitentaculata* having two tentacles and *Bathykorus bouilloni* four. Specimens belonging to the order Siphonophorae were divided into two suborders: Calycophorae and Physonectae. The phylum Ctenophora included the genus *Beroe spp.* and the order Lobata. Rarely occurring GZ taxa (*Euplokamis spp.*, *Aulacoctena* spp., *Bathyctena* spp., *Dryodora glandiformis*, *Ptychogena hyperborea*) were not incorporated into the modelling section. In addition, unidentified Ctenophora spp. and Trachymedusa spp. were also excluded from further analysis due to lack of ecological significance. During the deployments, identification of species in the epipelagic layer was challenged by high amounts of particulate organic matter and intense light, limiting the quality of video transects. This was particularly true for ctenophores for which diversity in the epipelagic could not be estimated. Each annotated event is presented on the Data Publisher for Earth & Environmental Science (PANGAEA) as a 4-second video clip, with associated metadata (Pantiukhin et al., 2023a; 2023b). The video clips for each event, with a spread of +/-2 seconds around the actual occurrence, were cropped from the original video using the FFmpeg tool (FFmpeg Developers, 2006).

3.3.3 Environmental parameters

The conductivity-temperature-depth (CTD) data for the PS121 expedition were obtained from the ship's CTD/rosette system which consists of a Sea-Bird Electronics - Seawater Multi-Parameter - Optical Dissolved Oxygen (SBE37-SMP-ODO) sensor (temperature, salinity, oxygen) and Wetlabs Ecotriplet system (Chlorophyll and colored dissolved organic matter (CDOM) fluorescence plus scattering). For the PS126 expedition, a CTD system was mounted directly on PELAGIOS (temperature, salinity sensors), whereas the oxygen and fluorescence were extracted from the ship's CTD. The correlation of PELAGIOS CTD data (salinity, temperature) with shipboard CTD data was > 0.95 at depth transects on PS126, thus we used them in combination. For each depth transect of the PELAGIOS, data from the closest ship's CTD station was used.

Environmental factors used in the models were selected based on their potential importance to the GZ distribution. Temperature, salinity, oxygen and depth are known to affect the distribution of the GZ in the marine environment (Tittensor *et al.*, 2010; Lucas *et al.*, 2014). Moreover, sea-ice is considered as an important driver of Arctic ecosystems, and it has been hypothesized that its reduction will increase the abundance of GZ (Wassmann et al., 2011). The values of temperature (°C), salinity (practical salinity units, or PSU), oxygen saturation (μmol kg^{-1}) were taken from CTD's (see above) for initial training of the model. Values of sea-ice coverage (%), which were used in the analysis, were obtained from the European Organisation for the Exploitation of Meteorological Satellites (EUMETSAT), Ocean and Sea Ice Satellite Application Facility (EUMETSAT, Ocean, 2017). For the initial training of the model, we used sea-ice concentrations measured 2 weeks prior to the deployment of PELAGIOS at the sampling point. The spatial values were averaged around each sampling point (within a 0.5-degree radius).

To perform spatio-temporal projections of the current and future state of the Fram Strait region, we projected the results of the Joint species distribution model (JSDM) onto environmental grids obtained from the Coupled Model Intercomparison Project Phase 6 (CMIP6). We used the results of the Finite Element Sea Ice-Ocean Model (FESOM; Semmler et al., 2018) as a source of oceanographic data sea in this study for spatial modelling (sea-ice concentrations (%), salinity (PSU), and temperature (°C). FESOM is an ocean-ice model that employs an unstructured grid with a horizontal resolution of 25 km. We projected the JSDM results onto the environmental grids obtained from the FESOM simulations using the shared socio-economic pathway (SSP) scenario SSP245, which represents a medium level emissions scenario (Meinshausen et al., 2020). For the present study, we chose 2020, 2030, 2040, and 2050 (from June to September) as time frames. To avoid spatial bias and ensure consistency with the PELAGIOS camera dives, we considered a vertical resolution of 10 layers (230 m, 410 m, 580 m, 790 m, 1040 m, 1330 m, 1700 m, 1920 m, 2150 m, 2400 m). A polygon with a spatial extent of 77° to 82° lat N and 6° long W to 8° long E served as the study region on which the projections were made. These specific latitudinal and longitudinal coordinates were chosen to cover the deep-sea part of the studied region, while excluding the shelf zones of the Fram Strait where the community structure of GZ is different and was not the target of our study.

3.3.4 Study design and joint distribution modelling

The Joint Distribution Model framework 'Hierarchical Modelling of Species Communities' (HMSC; Ovaskainen and Abrego, 2020) was used. This model allows us to link data on species occurrence and environmental covariates with processes of community formation. Environmental filtering is simulated at the species level by analyzing how the occurrences of species vary with environmental variables. Species co-occurrences are expressed as residual species-to-species association matrices, which may be evaluated at various spatial and temporal scales (Tikhonov *et al.*, 2020). The latest version of the HMSC 3.0 model is implemented in the “HMSC” package (Tikhonov *et al.*, 2020) in R (R Core Team, 2022).

As the biotic response variable, we included counts of the 13 different taxa at 50 sampling locations (Figures 3.2, 3.3; Figure 3.S1; Table S2). We fitted two different models: first a Poisson model (for count data) to analyze abundance analyses, and second a presence-absence model (presence-absence matrices for this model generated from the count data) to estimate the taxa richness on the predictive gradients. To choose the explanatory variables for the models, we tested temperature (°C), salinity (PSU), oxygen saturation (μmol kg-1), depth (m) (CTD measurements), and concentrations of sea-ice (%) (MODIS sensors) for correlation. The oxygen saturation showed a negative correlation with depth (Pearson’s r = -0.89, Figure 3.S3), and a positive correlation with temperature (Pearson’s r = 0.86, Figure 3.S3). To avoid the risk of over-parameterization, we evaluated the goodness-of-fit of two models with and without oxygen saturation. The models were evaluated according to the Widely Applicable Information Criterion (WAIC; Watanabe 2013). The models with the lowest WAIC values maximize their predictive power and reduce complexity. In this study, the model excluding oxygen showed WAIC values of 69.03, while including oxygen 72.94. Thus, due to the lower predictive power of the model with oxygen, as well as the difficulty in estimating the influence of oxygen, as it is highly correlated with temperature and depth, the choice was made in favor of a model without oxygen.

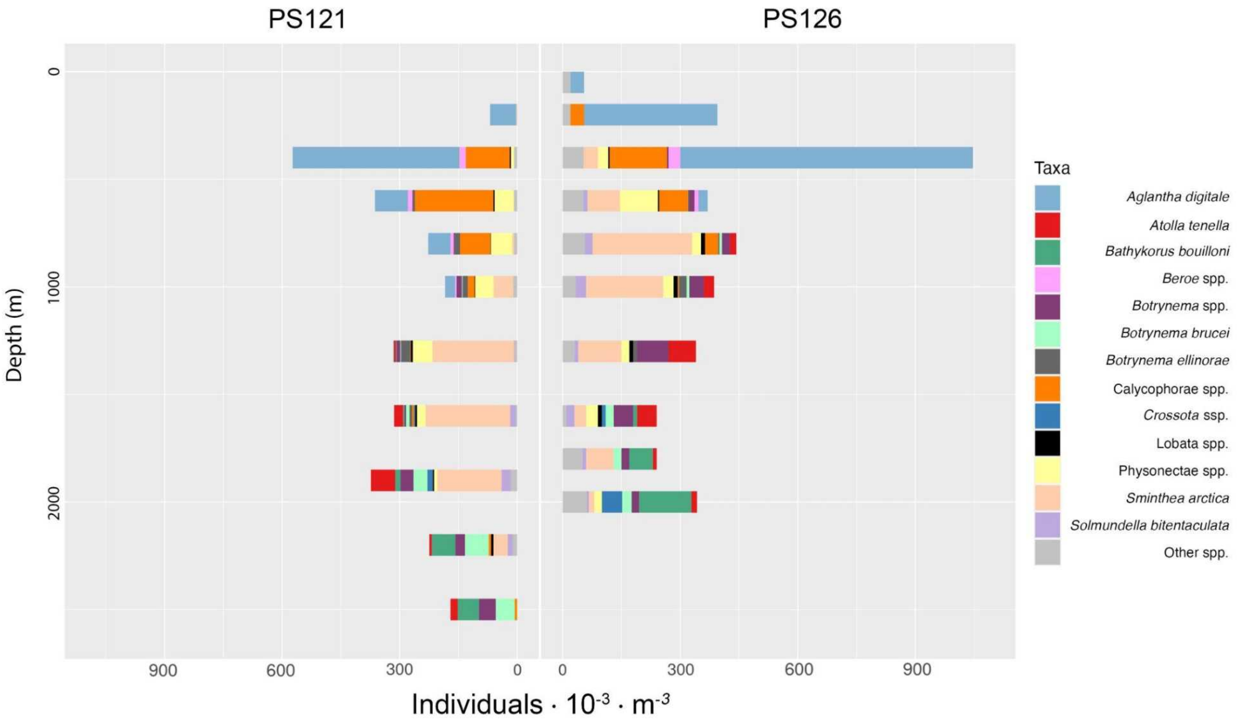

Figure 3.2. Vertical distribution of gelatinous zooplankton groups encountered with PELAGIOS. The figure displays 13 most dominant taxa that were used for modeling, while the remaining taxa annotated were collapsed into the "Other spp." category.

The HMSC model was trained using default prior distributions (Ovaskainen and Abrego, 2020). In order to sample the posterior distribution, we used four Markov Chain Monte Carlo (MCMC) chains and ran each for 375000 iterations. The first 125000 iterations were removed as burn-in and the chains thinned by 1000 to yield 250 posterior samples per chain. In total, we had 1000 posterior samples. To examine MCMC convergence, we looked at the potential scale reduction factors (Gelman and Rubin, 1992) of the model parameters.

We estimated the explanatory and predictive power of the presence-absence model using species-specific area under the receiver operating characteristic curve (AUC-ROC; Pearce & Ferrier 2000) values and Tjur R2 values (Tjur, 2009), while the explanatory and predictive power of the Poisson model were estimated using pseudo-R2 (Ovaskainen and Abrego, 2020). To calculate the explanatory power (i.e., how well the model predicts the data used for fitting), we used the model trained on all the available data (without partitioning). To estimate the predictive power, we performed a 4-fold cross-validation, partitioning the data into four equal subsets and using three subsets to fit the model and one subset to test its predictive accuracy. We partitioned the explained variation among the predictive variables to quantify the drivers of community structure. To examine how species communities respond to environmental conditions, we estimated species responses to the explanatory variables, counting what proportion of species showed a positive or negative response with at least 95% posterior probability.

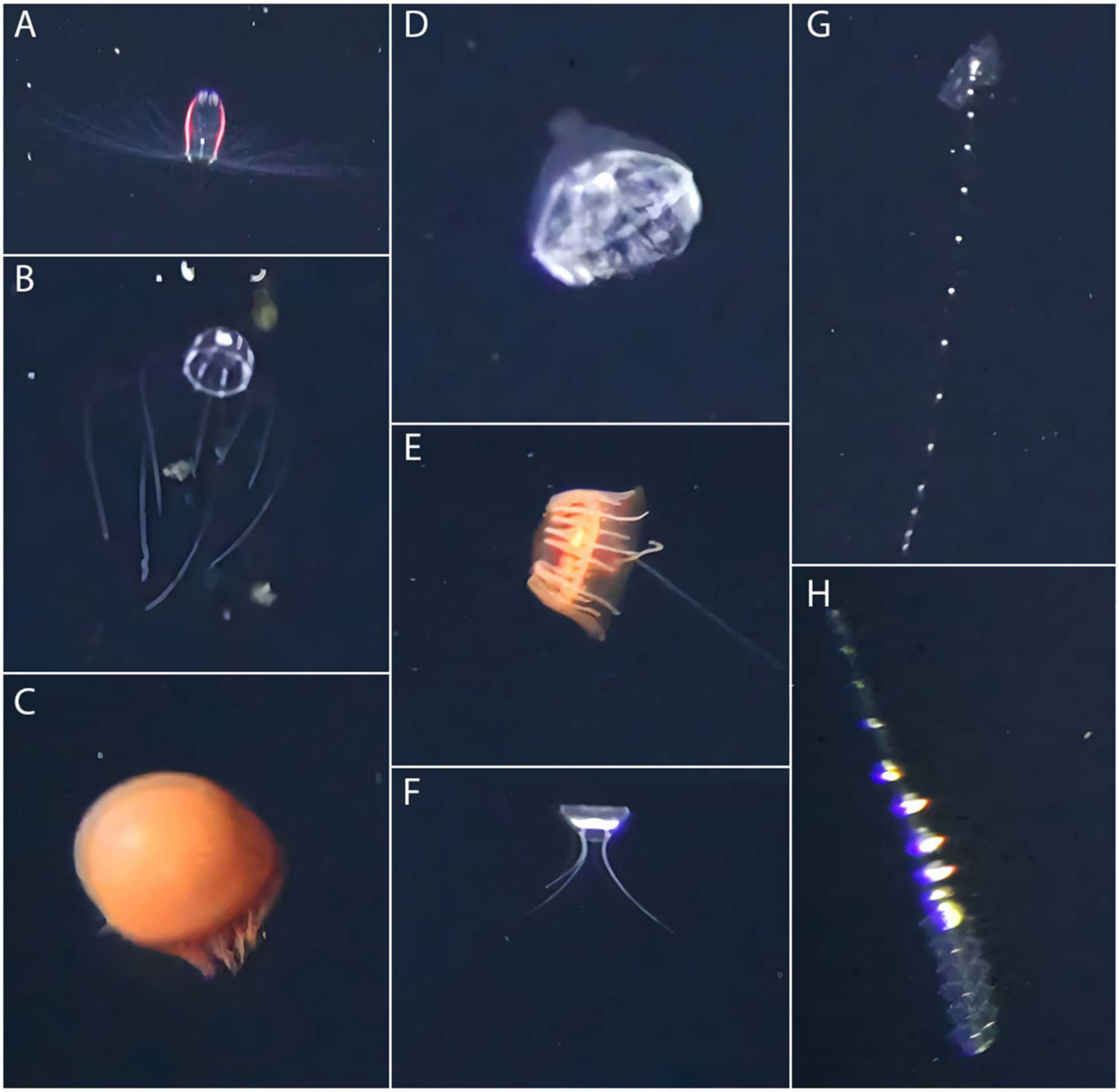

Figure 3.3. Examples of organisms encountered during pelagic video transects with PELAGIOS: (A) Aglantha digitale, (B) Sminthea arctica, (C) Crossota sp., (D) Botrynema brucei, (E) Atolla tenella, (F) Bathykorus bouilloni, (G) Calycophorae spp., (H) Physonectae spp.

3.4 Results

3.4.1 Regional oceanography

The PELAGIOS stations were located in the deep part of the Fram Strait, with depths ranging from 2338 m (S3; Figure 3.1) to 2667 m (N4; Figure 3.1). The temperature and salinity in the Fram Strait are affected by two main current systems: the warmer West Spitsbergen Current, which is part of the Atlantic water in the region, and the colder East Greenland Current, which brings Arctic water masses into the region. The branch of West Spitsbergen Current recirculates south-westwards as the Return Atlantic Current. To determine the water masses present at each site, we used temperature and salinity data and adapted the characteristic temperature-salinity signatures of each water mass from Beszczynska-Moller et al., 2011, Walczowski et al., 2012 and Mańko et al., 2020 (see Figure 3.S2). The strongest presence of Atlantic water was observed at station N4 (August/September 2019), where transformed Atlantic water extended to a depth of 700 m and intermediate water to a depth of 800 m (Figure 3.S2). This station was also characterized by a high level of mixing between different water masses, as well as the presence of all five distinguished water masses (Figure 3.S2). The largest extent of Arctic water was observed at station S3 (June 2021), where the transition from transformed Atlantic to Arctic water occurred at a depth of 500 m (Figure 3.S2). At stations where an interannual comparison was possible (HG4 and EG4), we found distinguishable interseasonal patterns (Figure 3.S2). In August/September (PS121) at the station EG4, we observed the presence of both Atlantic water and transformed Atlantic water; the latter extended in the water column down to depths of 650 m (Figure 3.S2). In June (PS126, station EG4), we observed only transformed Atlantic water, which spread to a depth of 550 m (Figure 3.S2). Similar changes in water masses were found at station HG4, but here the lower boundary of the transformed Atlantic water varied only slightly, at depths of 600 m (Figure 3.S2). However, in the epipelagic layer in August/September (PS121), the presence of Atlantic water was observed, while in June (PS126) the upper 0-50 m layer was occupied by Arctic water. Sea-ice conditions strengthened in the northwest direction, with maximum sea-ice concentrations found at station EG4 in August/September (PS121) - 62.72%.

3.4.2 General patterns of gelatinous zooplankton on stations

We recorded a total of 20 distinguishable taxa, among the 13 most dominant on horizontal transects were: *Aglantha digitale* - 706 obs.; *Sminthea arctica* - 522 obs.; Calycophorae spp. - 375 obs.; Physonectae spp. - 215 obs.; *Botrynema* spp. - 91 obs.; *Atolla tenella* - 66 obs.; *Bathykorus bouilloni* - 64 obs.; *Botrynema brucei* - 52 obs.; *Botrynema ellinorae* - 49 obs.; *Beroe* spp. - 41 obs.; *Solmundella bitentaculata* - 39 obs.; Lobata spp. - 23 obs.; *Crossota* spp. - 22 obs (Figures 3.2, 3.3; Table 3.S2). The most diverse stations in terms of taxa richness were EG4 and HG4 (17 and 16 taxa present), while the lowest was S3 (11 taxa). The highest abundance was found at station HG4 (PS126; Figure 3.1) with an average of 549 individuals per 1000 m^3, and the lowest abundance was observed at station S3 (PS121; Figure 3.1) with an average of 183 individuals per 1000 m^3. The majority of recorded taxa (12) belonged to the class Hydrozoa (*Aglantha digitale* ~29% and *Sminthea arctica* ~22% of all observations), while the class Scyphozoa was represented only by one species - *Atolla tenella*. The highest abundance values during the PS121 expedition were recorded at depths of 400-600 m, as well as at 1900 m. In terms of taxon diversity, the highest biodiversity was found at depths of 1300 (13 taxa; Figure 3.2). During the PS126 expedition, the greatest abundance was found at depths of 400 and 2000 m, while taxonomic diversity was highest at a depth of 600 m (13 taxa; Figure 3.2).

3.4.3 Hierarchical Modelling of Species Communities

The convergence of MCMC chains, measured by the potential scale reduction factors (β-parameter; which measure species responses to environmental covariates; Ovaskainen *et al.,* 2017), were on average 1.02 (maximum 1.12) for the Poisson model and 1.001 (maximum 1.004) for the presence-absence model (Figure 3.S4). The 4-fold cross-validation for the presence-absence model showed a mean Tjur R2 (AUC) of 0.29 (0.79). The Poisson model showed the mean pseudo-R2 being 0.43 for explanatory power and 0.29 for predictive power (Figure 3.S5).

Variance partitioning over the explanatory variables showed that temperature and depth explained a substantial amount of variation in both Poisson and presence-absence models, in contrast to the minor explanatory power of sea-ice and salinity (Figures 3.4a,b). Among the taxa, temperature had the highest explanatory value for *Sminthea arctica* (0.58 - Poisson; 0.45 - presence-absence), *Aglantha digitale* (0.38 - Poisson; 0.22 - presence-absence), suborder Physonectae (0.31 - Poisson; 0.32 - presence-absence), and *Botrynema* spp. (0.32 - Poisson; 0.36 - presence-absence). Depth zonation showed the highest values for *B. brucei* (0.41 - Poisson; 0.35 - presence-absence), *Bathykorus bouilloni* (0.28 - Poisson; 0.35 - presence-absence), *Atolla tenella* (0.25 - Poisson; 0.23 - presence-absence). For the suborder Calycophora, salinity had the major contribution to the explanation of variations was e. In the Poisson model, its contribution was 0.17 and in the presence-absence model - 0.08. Sea-ice did not contribute significantly to the explanatory power of the models (<0.1 for all taxa).

No significant response to salinity was found in any of the taxa, however all exhibited responses to temperature (Figure 3.S6a, b). Six taxa in the presence-absence model (*Atolla tenella*, *B. brucei*, *Botrynema* spp., *Crossota* sp., *Sminthea arctica*, *Solmundella bitentaculata*) responded negatively to the second-order term of temperature while only *Sminthea arctica* showed a clear negative response in the Poisson model. In other cases, taxa responded positively to the first-order term polynomials of temperature and negatively to the second-order term polynomials. This means that their abundance/probability of occurrence peaked at some intermediate temperature value. The responses of taxa to depth in the Poisson model were mostly characterized by peaks at some intermediate value. The exception was *Beroe* spp., which had a negative response. In the presence-absence models *Atolla tenella*, *Bathykorus bouilloni*, *B. brucei*, and *Crossota* sp. showed a clear positive response to the increase of depth. The responses of *Atolla tenella*, *Sminthea arctica*, *Solmundella bitentaculata* in both models showed a positive association with sea-ice, *B. brucei* showed the same association only in the presence-absence model. *Bathykorus bouilloni* showed a negative response to the presence of sea-ice in both the presence-absence and Poisson models.

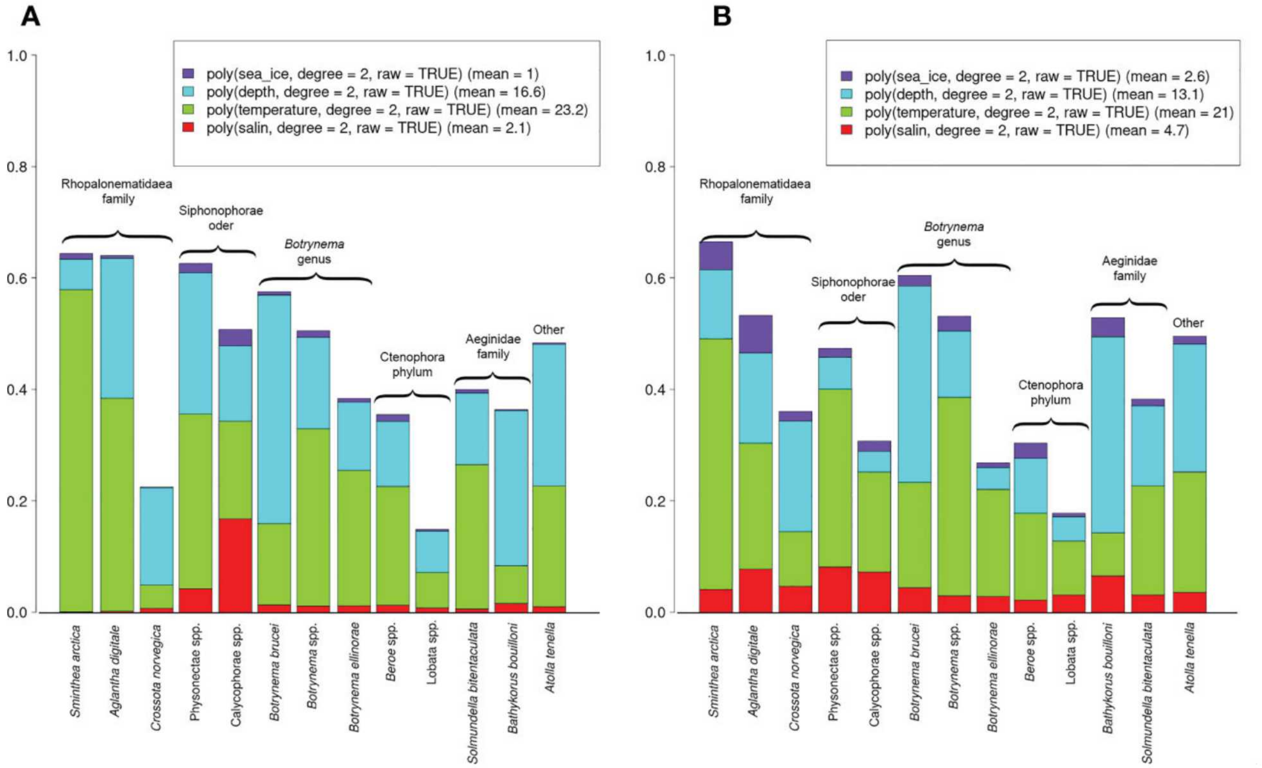

Figure 3.4. Variance partitioning among the explanatory variables. The values for the Poisson (A) and presence-absence (B) models are estimated by Tjur R2 and R2 respectively. The mean values of variance for all species are presented in the legends.

3.4.4 Prediction gradients

Predictive gradients were constructed for total taxa richness based on the presence-absence model, while the Poisson model was used to construct predictive gradients of abundance for each studied taxon.

3.4.5 Taxon abundance and richness

Predictions over environmental gradients (Figure 3.5) showed that the abundance of different taxa peaked at the lower end of the mesopelagic zone (700-800 m), while taxa richness peaked in the upper bathypelagic zone (1100-1200 m). Higher taxa diversity was found in colder waters with a peak of taxa richness at 0.3-0.4°C. In contrast, total abundance peaked at mean temperatures of 1.2-1.3 °C. At higher salinities, an increase in both total taxa abundance and richness was observed. The same patterns of positive response were found for sea-ice concentrations.

3.4.6 Individual taxa

The studied taxa were divided into six distinct taxonomic groups (Figures 3.6, 3.S6) based on their vertical distribution ranges and responses to the environmental parameters (the family

Rhopalonematidae, the order Siphonophorae, the genus *Botrynema*, the phylum Ctenophora, the family Aeginidae and the species *Atolla tenella*).

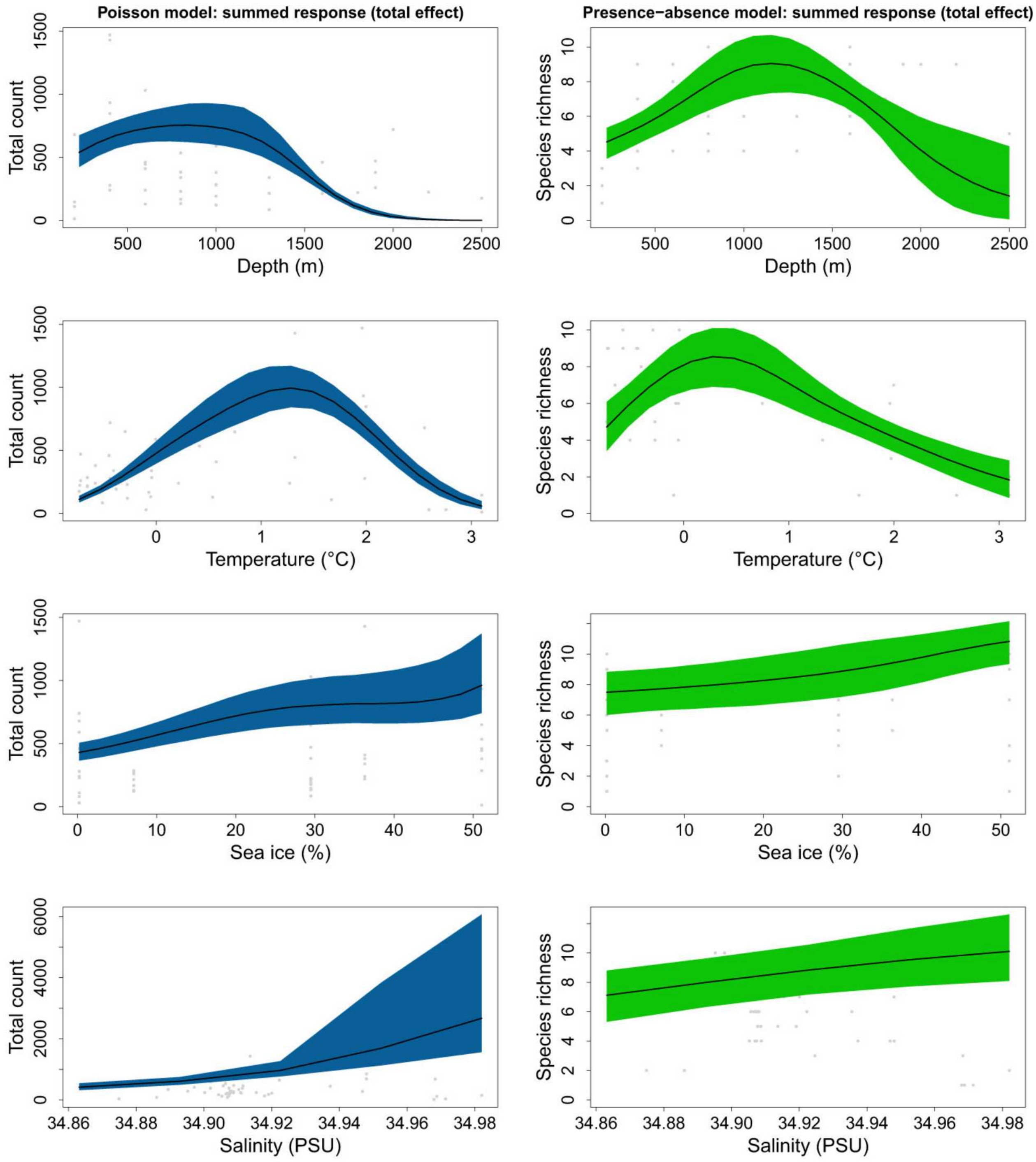

Figure 3.5. Predicted gradients of total count (Poisson model; left) and taxa richness (presence-absence model; right) for all taxa.

3.4.6.1 Rhopalonematidae family

The Rhopalonematidae family, here composed of *Aglantha digitale*, *Sminthea arctica*, and *Crossota sp.*, represented the most dominant group in the study area, accounting for 49% of the observations (Figure 3.2). We observed a clear separation in the preferred environmental conditions for *Aglantha digitale* and *Sminthea arctica*, which were found at approximately 800 m depth and 0.8 °C (Figure 3.6a). *Aglantha digitale* is normally distributed with a peak at 1.8 °C and a depth of 250-300 m (Figure 3.6a). In contrast, *Sminthea arctica* was most abundant at 0 °C and 1250-1300 m depth. *Crossota* sp. showed its highest abundance values at a depth of 1300 m and a temperature of 0.2 °C. Analysis of sea-ice conditions revealed that *Aglantha digitale* preferred more open ocean areas, while *Sminthea arctica* and *Crossota* sp. were more abundant in sea-ice-covered waters (Figure 3.6a).

3.4.6.2 Siphonophorae order

The order Siphonophorae, including Calycophorae and Physonectae spp., was the second most dominant group in our study, representing 29% of the total observations (Figure 3.2). Within this order, we also observed a separation of preferred niche conditions (Figure 3.6b). The abundances of Calycophorae and Physonectae spp. were normally distributed around 750-800 m and 950-1000 m respectively (Figure 3.6b). In terms of temperature, Calycophorae spp. showed its peak abundance at 1.1°C, while Physonectae spp. reached its peak at 0.5°C (Figure 3.6b). The predictive gradient across the sea-ice gradient showed that both sub-orders were more abundant at average sea-ice cover of 25-30%, mainly in marginal sea-ice zones (Figure 3.6b). Regarding salinity, representatives of the suborder Calycophorae and Physonectae spp. responded positively to an increase in salinity (Figure 3.6b), with the former showing a stronger response and reaching an abundance of 300 individuals per 1000 m3 at 34.96 PSU, and the latter reaching 70 individuals per 1000 m3 at the same values.

3.4.6.3 Botrynema genus

The *Botrynema* genus represented 7% of the observations and included *B. brucei, Botrynema ellinorae*, and unidentified *Botrynema* spp. (Figure 3.2). Both *B. brucei* and *Botrynema ellinorae* had a similar depth distribution with a peak at 1250-1300 m, whereas unidentified *Botrynema* spp. were observed at shallower depths with a maximum distribution at 950-1000 m (Figure 3.S7a). The temperature distribution followed a similar pattern, with *B. brucei* and *Botrynema ellinorae* having peaks of abundance at 0.1-0.15 °C, while the undetermined *Botrynema* spp. showed maximum abundance at slightly warmer temperatures of 0.4-0.5 °C. All taxa exhibited a moderately positive response to sea ice (Figure 3.S7a).

3.4.6.4 Ctenophora phylum

The Ctenophora phylum included Lobata spp. and *Beroe* spp., which accounted for 5% of all observations (Figure 3.2). These taxa showed distinct unimodal patterns along temperature and depth gradients (Figure 3.S7b). *Beroe* spp. had a peak of abundance at 550-600 m and 1.4 °C, whereas Lobata spp. peaked at 1150 m and 0.5 °C (Figure 3.S7b). Within the study area, *Beroe* spp. preferred sea-ice free conditions, with the highest abundances observed at 13% sea-ice coverage. In contrast, Lobata spp. showed higher abundance in denser sea-ice conditions, with a peak at 40% sea-ice coverage (Figure 3.S7b).

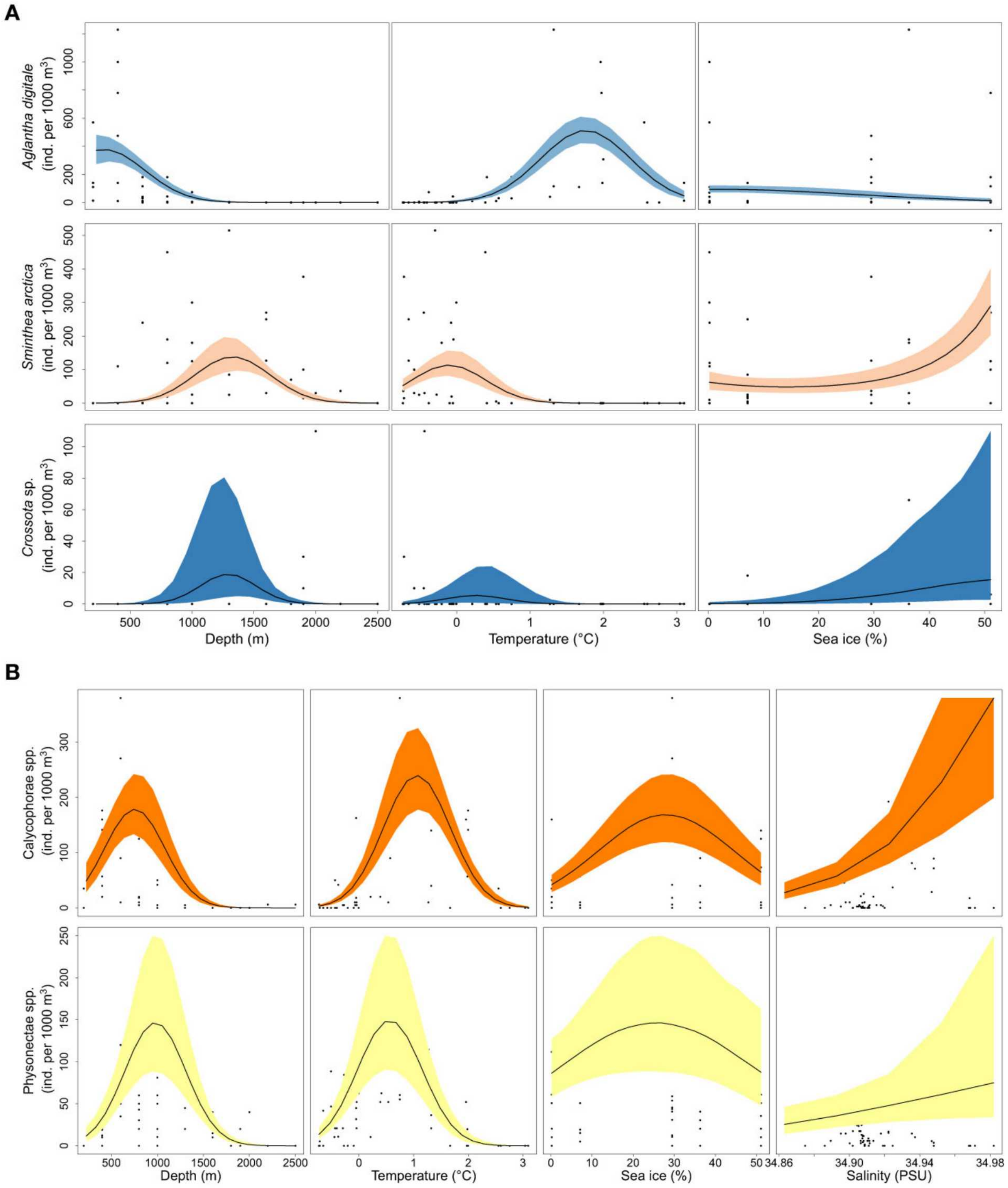

Figure 3.6. Predicted gradients of total count (Poisson model) of the (A) Rhopalonematidae family and (B) the Siphonophorae order.

3.4.6.5 Aeginidae family

The family Aeginidae, comprising *Bathykorus bouilloni* and *Solmundella bitentaculata*, represented 4.5% of all recorded taxa (Figure 3.2). Both species showed similar distribution patterns with respect to depth and temperature, with *Bathykorus bouilloni* being most abundant at 1350 m and 0.15°C, and *Solmundella bitentaculata* at 1300 m and 0.1°C. Both species showed a positive association with dense sea ice (Figure 3.S6c).

3.4.6.6 Atolla tenella

The only scyphozoan species observed in our study was *Atolla tenella*. This species was found at depths between 800 and 2500 m, with a maximum abundance at 1400 m. It was found at the lowest temperatures observed in the region, with a peak abundance at -0.2°C, and in areas of high sea ice cover (>50% sea ice cover; Figure 2.S6d).

3.4.7 Spatial patterns and projections

3.4.7.1 Taxon richness

Based on the results of the presence-absence model, we were able to estimate the richness of taxa in the study area for the years 2020, 2030, 2040, and 2050 (from June to September). The maximum values of taxa richness for all modelled time intervals were observed at a depth of 1700 m (9-11 taxa), and the lowest in the pelagic layer of 230 m (4-6 taxa; Figure 3.7, Figure 3.S9). Throughout the entire period of simulation, we found a gradual decrease in taxa richness with a maximum richness loss at the year 2050 (-14.06% compared to 2020, for all vertical layers; Figure 3.7). We observed the greatest loss of taxa richness in the pelagic layer at a depth of 230 m (-31.25%; Figure 3.7, Figure 3.S9). The loss of taxa richness gradually decreased with depth, in the bathypelagic layer the decline was on average ~10% (Figure 3.7, Figure 3.S9).

For the upper 230-410 m layers (in the year 2020), we observe the lowest taxa richness in the northeastern part of the region, where the West Spitsbergen Current dominates (Figure 3.S9). The highest taxa richness in these layers is observed in the convergence zones of the West Spitsbergen and East Greenland Currents (Figure 3.S9). By 2050, there is a decrease in taxa richness in these layers in the western region (Figure 3.S9). Comparing this to oceanographic conditions, we may see an increase in temperature in the western region due to an amplification of Return Atlantic Current. At depths of 580 and 790 (in the year 2020), the greatest taxa richness is observed in the northern part of the region, as well as in the convergence zones of currents. By the year 2050, the northern region will have lost most of its taxa richness on these depths, but it will still persist at the edges of the currents (Figure 3.S9). At depths from 1040 to 2400 m in 2020, the greatest taxa richness is observed in the northwestern part of the region. By 2050, taxonomic diversity at these depths will be reduced throughout the entire region (on average, 8-9 taxa per site), with a slight preponderance (6-7 taxa per site) in the southeastern part (Figure 3.S9).

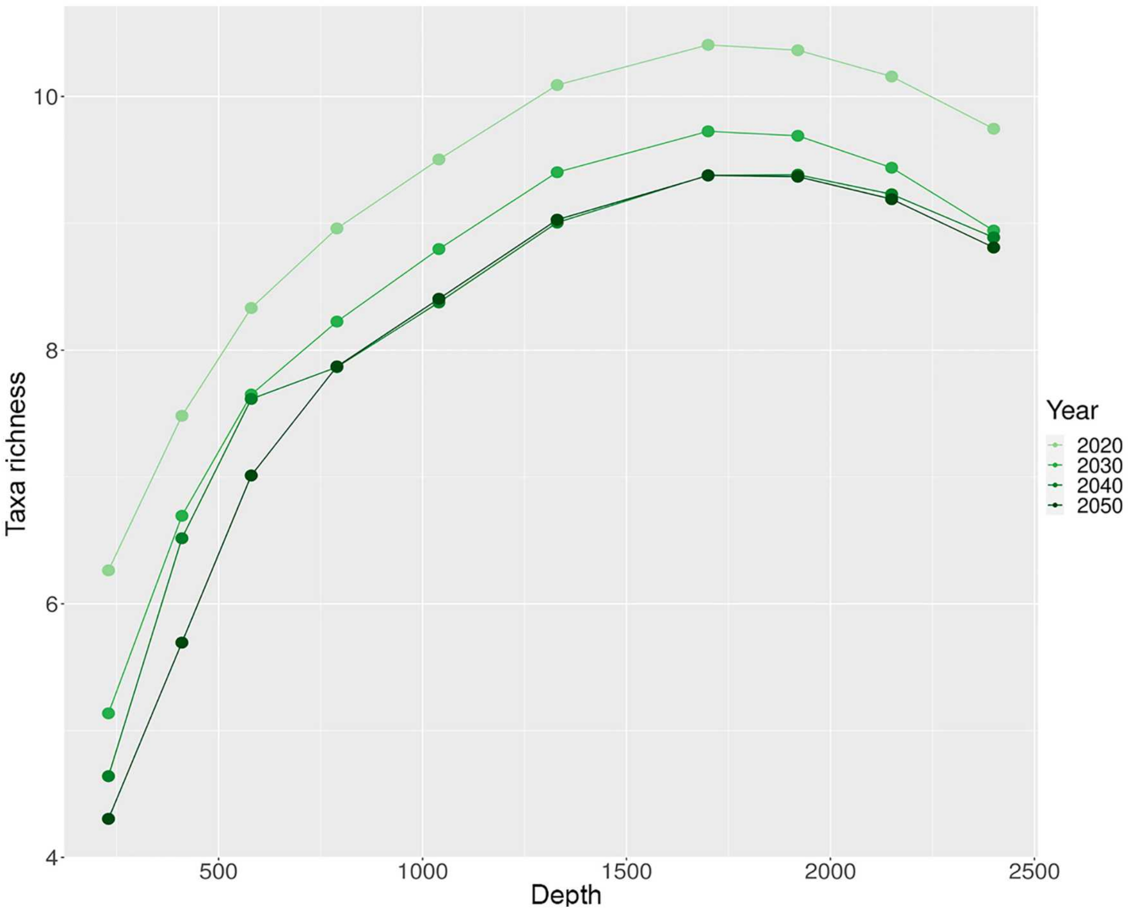

Figure 3.7. Current and future values (summer season) of species richness at different depth layers. Species richness values were calculated as the mean for each depth layer.

3.4.7.2 Individual taxa

Based on the results of the 4-fold cross-validation of the Poisson model, we selected four taxa for spatial projections with the highest predictive power (pseudo-R2 > 0.4; Figure 3.S5). These included two species of the family Rhopalonematidae (*Aglantha digitale* and *Sminthea arctica*) and the suborder of Siphonophorae (Physonectae spp.). These taxa were projected onto the most favorable depth layers, based on the information derived from prediction gradients (Figures 3.6a, b).

3.4.7.2.1 Rhopalonematidae family

The vertical niches of *Aglantha digitale* in Fram Strait will narrow over the period from 2020 to 2050, but overall the abundance in the entire water column will increase by 2% (Figure 3.8, Figure 3.S8a). By 2050, *Aglantha digitale* will lose up to a quarter of its abundance in the upper 290 m and also decrease at 790 m, but its abundance will increase in the middle layers of 410 and 580 m by 24% and 18% correspondingly (Figure 3.8, Figure 3.S8a). The spatial distribution patterns of *Aglantha digitale* are described by the Arctic and Atlantic water masses convergence zones, with the maximum number of individuals found in these areas (Figure 3.8). With warming in the northwestern part of the region and the retreat of the sea-ice by 2050, the area of high abundance of *Aglantha digitale* will disappear at the depth of 290 m (Figure 3.8). A similar high abundance area at this depth along the entire western section from 6 to 8 west longitude will move to a deeper depth of 410 m, where an increase in the abundance of *Aglantha digitale* will be observed (Figure 3.8).

Another member of the family Rhopalonematidae, *Sminthea arctica*, will experience a greater reduction in preferred niche conditions compared to *Aglantha digitale* (Figure 3.S8). *Sminthea arctica* will lose up to 60% of its abundance at all depths by 2050 (Figure 3.9, Figure 3.S8b). The highest projected abundance of *Sminthea arctica* for 2020 was found in the northwestern section of the region where it reaches fairly high numbers of >1000 individuals per 1000 m^3 (Figure 3.9). However, with the retreating of the sea-ice and warming in this part of the Fram Strait, we will observe the loss of the northwestern high abundance area and a shift of the main center of abundance to the southeastern part of the region with much lower numbers of ~300 individuals per 1000 m^3 (Figure 3.9).

3.4.7.2.2 Siphonophorae order

Physonectae spp. will experience a reduction in abundance by 17.62% across all vertical strata by 2050 (Figure 3.S10, Figure 3.S11). The highest abundance of Physonectae spp. is found present in layers of 580 and 790 m in the northeastern part of the region in 2020 (Figure 3.S11). Until 2050, spatial patterns in these depth layers will not undergo strong transformations (Figure 3.S11). In the layers of 1040 and 1330 m, the highest abundances of Physonectae spp. are observed in the southeastern part of the region, which will also not be submitted to strong changes on the temporal scale (Figure 3.S11). However, by 2050, an increase of the Physonectae spp. abundances will be observed in the northwestern part of the region (Figure 3.S11).

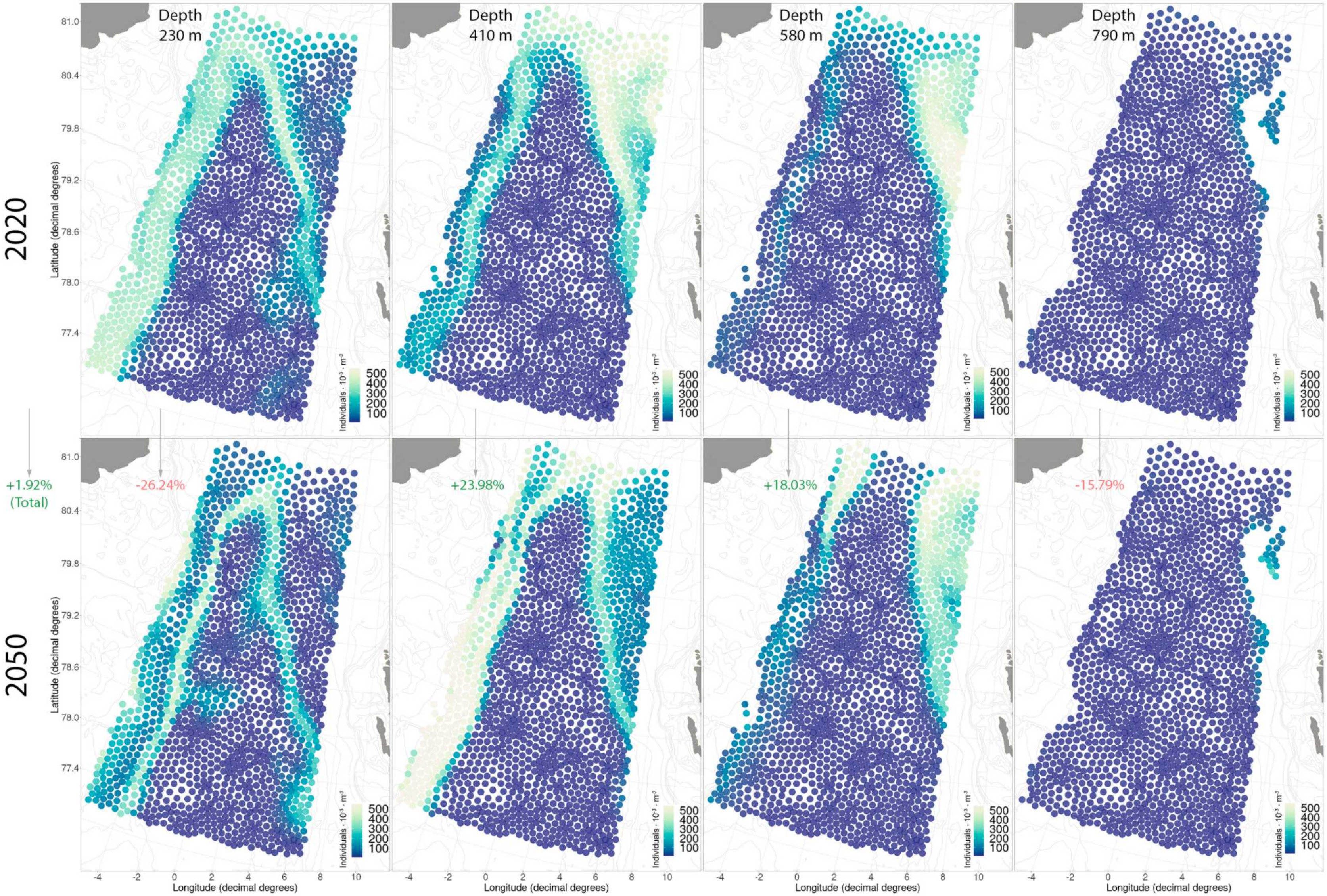

Figure 3.8. Current and future distributions of Aglantha digitale in the studied region. The red/green values in parentheses give a comparative measure of the retreat/increase in abundance of the selected taxa (summer season of 2050 compared to 2020).

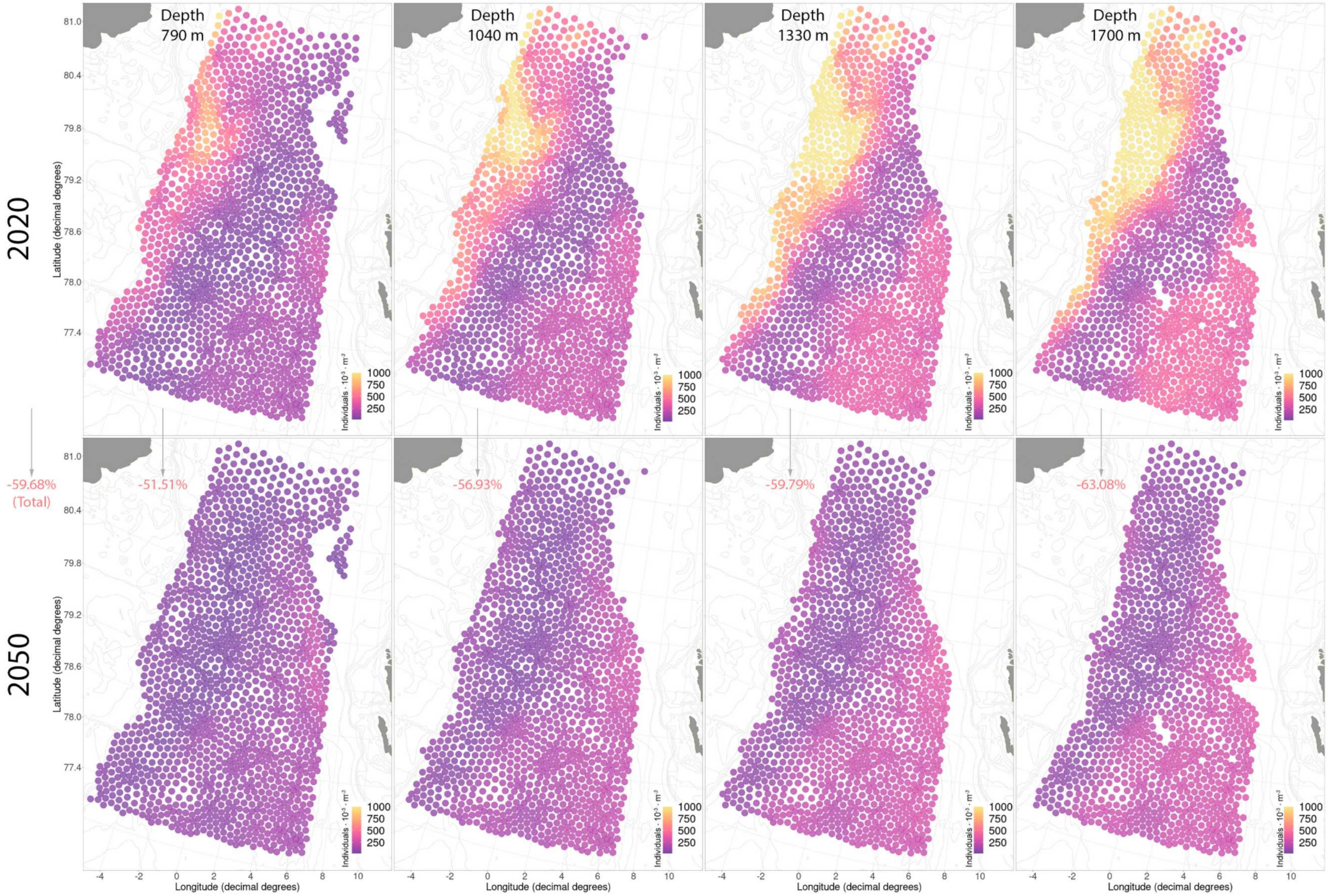

Figure 3.9. Current and future distributions of Sminthea arctica in the studied region. The red/green values in parentheses give a comparative measure of the retreat/increase in abundance of the selected taxa (summer season of 2050 compared to 2020).

3.5 Discussion

3.5.1 Gelatinous zooplankton data and modelling

Gelatinous zooplankton in the Fram Strait has previously been studied via multiple-open-and-closing nets in epipelagic and mesopelagic layers (Mańko *et al.*, 2020). Our study is the first survey in mesopelagic and bathypelagic layers of the Fram Strait using a video-transect approach, which in combination with joint distribution modelling allowed us to reconstruct a three-dimensional structure of mesopelagic and bathypelagic GZ diversity and abundance. Monitoring via video-transects with ROVs (e.g., Robison *et al.*, 2010) is a well-established method in the deep sea and has advantages over traditional multiple-open-and-closing nets in that it provides a precise spatial position of the detected object as well as the corresponding environmental data (Robison 2004; Hoving *et al.*, 2019). Some GZ taxa can only be observed or more reliably identified with *in situ* surveys as they are damaged or fragmented in nets due to their fragility (Raskoff *et al.*, 2003; Hosia *et al.*, 2017; Hoving *et al.*, 2020a). Despite their many advantages, deep-sea video transects also have their limitations. For some taxonomic groups, the video resolution did not allow identification to the species level (e.g., for the suborders Calycophorae and Physonectae). To enhance the reliability/resolution of the taxonomic data, future surveys in the area could combine the use of ROV and PELAGIOS for close-range observations and subsequent sampling.

Generally, studies identifying preferred niche conditions for some GZ species in the Fram Strait are presented only as part of global species biodiversity distribution projects (e.g., Palomares *et al.* 2021), with maps based only on presence data obtained from public datasets (e.g., OBIS, GBIF). Due to the lack of traceability and quality control of the data on GZ in these databases, the subsequent modelling is accompanied by a strong bias, and, as a consequence, these results should be treated with care (Lindsay *et al.*, 2017). Such models produce output in a probabilistic form and are mainly done on a two-dimensional scale. Neglecting depth in the modelling process can lead to incorrect and potentially misleading results (Duffy and Chown, 2017). Due to the accurate spatial *in situ* data on the GZ community obtained with PELAGIOS, we were able to apply a joint species distribution modelling approach (HMSC). Based on this, we were able to project the model results of the three taxa with the highest predictive power (*Aglantha digitale, Sminthea arctica,* Physonectae spp.) onto three-dimensional oceanographic grids from the FESOM model. Despite good predictive power for some taxa, the predictive curves for the deep-sea taxa *Atolla tenella* and *Bathykorus bouilloni* showed a rather weak fit with the raw data. By adding data from upcoming expeditions, the predictive response of less abundant taxa should increase and will allow us to conduct spatio-temporal projections also for these species.

3.5.2 Current state of the knowledge on gelatinous zooplankton in the Fram Strait

The taxonomic composition of the GZ communities in our study area are consistent with previous studies of mesopelagic and deep-water GZ communities in the Arctic Ocean (Raskoff *et al.*, 2005; Raskoff *et al.*, 2010) and in particular in the Fram Strait (Mańko *et al.*, 2020). However, a discrepancy with the previously mentioned studies can be found for the epipelagic layer. Light disturbance and large amounts of particulate organic matter decreased the quality of the video transects in the epipelagic zone. Hence, ctenophore diversity could not be estimated for the epipelagic layer, where this group is known to be abundant (Raskoff *et al.*, 2010). It is likely that the epipelagic ctenophores, recorded and annotated under Ctenophora spp., mainly represented the species *Mertensia ovum*. The latter is known to be the most common ctenophore species in the epipelagic layer of the Arctic Ocean (Raskoff, Purcell and Hopcroft, 2005; Raskoff *et al.*, 2010), particularly in the Fram Strait (Mańko *et al.,* 2020). Due to their similar morphological traits, these ctenophores may consist of different, hitherto undescribed, closely related cryptic species (Majaneva and Majaneva, 2013). Since studies focusing on Arctic GZ connectivity and assessing species status with molecular tools are limited, it is likely that several of the species considered in this study could be complexes of overlooked, or cryptic, species. As an example, recent findings combining molecular and morphological tools have revealed several new species in the genus *Atolla* in the Pacific (Matsumoto *et al.*, 2022).

Overall, PELAGIOS provided a greater understanding of the diversity and abundance of the mesopelagic and deep-sea GZ communities. We observed the genuine Arctic deep-sea Narcomedusae species *Bathykorus bouilloni*, which was considered to be absent in the Fram Strait (Ronowicz *et al.*, 2015; Mańko *et al.,* 2020). Surprisingly, we recorded a relatively high abundance at the northern and north-western stations. Another representative of the order Narcomedusae, *Solmundella bitentaculata*, was observed with PELAGIOS at all stations in the depth range 600-2200 m, but it is rarely sampled with nets. These depths were however well sampled in this region using multinets (Mańko *et al.,* 2020; Havermans *et al.,* 2021); such an undersampling with nets may be due to their relatively low density in the water column and active escape reaction.

Our data support the suggested prevalence of Arcto-boreal taxa in the Fram Strait (Table S2). Among all taxa, we recorded only two true Arctic species, *Bathykorus bouilloni* and *Atolla tenella.* All other species mainly represented Arcto-boreal or cosmopolitan taxa (according to the classification by Ronowicz *et al.*, 2015). Pronounced niche segregation along the temperature gradient was found among both the true Arctic and cosmopolitan species of the order Narcomedusae. Namely, *Bathykorus bouilloni*, which is a true deep-sea Arctic species, was found in the lowest temperature conditions and deeper depths. In contrast, *Solmundella bitentaculata*, which is a cosmopolitan species (although it has been suggested it may be actually composed of multiple cryptic species; (Lindsay *et al.*, 2017; Verhaegen *et al.*, 2021), was found across a wider temperature and depths ranges.

3.5.3 The effect of environmental drivers on gelatinous zooplankton

Temperature and depth were the major explanatory variables in the distribution of GZ. This coincides with the results of another community modelling study of GZ by Luo *et al.* (2014) in the Southern California Bight which revealed similar patterns, with temperature and depth having a large influence on GZ population dynamics in the epipelagic layer. We found that the majority of GZ taxa belong to the class of Hydrozoa (12 out of 20 identified taxa) and their distribution patterns were predominantly explained by the temperature gradient. The high explanatory power of temperature on hydrozoan abundance could be explained by increased respiration and growth rates associated with warmer waters (Ma and Purcell, 2005; Møller and Riisgård, 2007). Although salinity has been stated to clearly affect the distribution of GZ (Mills, 1984), it only had a minor influence on the distribution of GZ in a previous modelling study by Luo *et al.* (2014). Similarly, in our study, salinity only played a minor role among the explanatory variables. While the overall contribution of salinity to the explanatory power of the models was low, this factor influenced the distribution of the order Siphonophorae in the Poisson model. Similar patterns were observed by Luo *et al.* (2014); one possible explanation for this may come from the fact that the buoyancy of siphonophores is driven by passive osmotic accommodation in response to changes in the salinity of the medium, rather than active density regulation (Mackie *et al.*, 1988). The explanatory power of the sea-ice on the distribution and abundance of GZ was low, and only had minor importance for taxa that occurred in the upper water column such as Calycophorae spp. A possible explanation is the spatial and temporal mismatch between PELAGIOS sampling stations and data obtained from satellites, as well as the limited number of dives. In addition, sea-ice indirectly affects the abundance and distribution of GZ and alternates more direct proxies such as energy and carbon flux in the water column. The inclusion of more direct proxies, such as values of particulate organic carbon at different depths in combination with sea-ice concentrations, could potentially increase the explanatory power of the models.

3.5.4 Vertical niche segregation and current spatial patterns of gelatinous zooplankton

The total diversity of GZ tends to increase with depth (Kosobokova *et al.,* 2011; Gluchowska *et al.*, 2017; Mańko *et al.,* 2020). Our study corroborated this result: the highest taxa richness was found at 1100-1200 m depth. GZ taxa often aggregate and feed at pycnoclines and convergence zones (Youngbluth and Båmstedt, 2001; Toyokawa *et al.*, 2003; Youngbluth *et al.*, 2008). On the projected spatial grids the highest taxa richness in the mesopelagic layer was found at the convergence zone of Arctic and Atlantic water masses. Similar patterns were found by the spatio-temporal projection of both taxa richness and abundance of selected taxa.

Gelatinous zooplankton tends to occupy relatively narrow depth ranges that often do not overlap between species (Lindsay and Hunt, 2005; Hoving *et al.*, 2020a). Distinctive vertical niche segregation was found within the family of Rhopalonematidae (*Aglantha digitale*, *Sminthea arctica*) and the order of Siphonophorae (Physonectae spp., Calycophorae spp.). In addition to the vertical niche segregation of *Aglantha digitale* and *Sminthea arctica*, a clear separation was found in the horizontal dimension, in the layers where their vertical niches partially intersect (580 and 1040 m; based on the FESOM grids for the year 2020). *Aglantha digitale* is mainly occurring in the northeastern parts of the region where the warmer West

Spitsbergen Current is present, while *Sminthea arctica* is occurring in the western and southeastern parts of the region where the colder East Greenland Current is dominant. The most prominent separation is observed at the convergence zone of the warm West Spitsbergen Current and the East Greenland Current, characterized by higher sea-ice coverage, in the northeastern part of the Fram Strait.

Siphonophores are also well known for their mutually exclusive depth distribution ranges among species (Musayeva *et al.*, 1976), in particular in the Arctic Ocean (Raskoff *et al.*, 2010; Mańko *et al.,* 2020). A study in the Canada Basin of the Arctic Ocean showed a distinctive vertical niche segregation of siphonophores with Physonectae spp. found in the shallower water column, while Calycophorae spp. inhabit deeper layers by (Raskoff *et al.*, 2005). The inverse vertical distribution of these siphonophores was found in Fram Strait (Mańko *et al.,* 2020). The latter is in agreement with our data, as we found Calycophorae and Physonectae spp. peaking in abundances at 750-800 and 950-1000 m, respectively. The difference in vertical distribution with the Pacific sector most likely lies in the fact that Atlantic water in the Beaufort Sea extends deeper into the water column (Raskoff *et al.*, 2005). Moreover, different developmental stages of Calycophorae spp. tend to aggregate in different parts of the water column (Mańko *et al.*, 2020). To clarify the distribution of these suborders, additional information on the species composition and life cycle stages is needed.

3.5.5 Gelatinous zooplankton in a changing Arctic

In recent decades, an increase in the inflow of warmer Atlantic water into the Arctic through the Fram Strait has been recorded (Polyakov *et al.*, 2017), which in turn leads to ecosystem responses, including increased production and poleward expansion of boreal species (Ingvaldsen *et al.*, 2021). Based on the results of the FESOM oceanographic model from CMIP6 (Semmler *et al.*, 2018), the trend of an Atlantification of water masses in the Fram Strait will continue with increasing force in the coming decades, with changes in mean temperature being particularly pronounced in the mesopelagic layer. As a result, the region is expected to harbor more abundant, but less diverse GZ communities (Mańko *et al.,* 2020). Our study supports this hypothesis, the highest richness on the predictive gradient was found at 0.3-0.4 °C, which correlates to Arctic water. Moreover, spatial modelling results based on the FESOM model indicate that the average change in total richness in the region will be a decrease of ~ 14% by the year 2050 (during the summer season). This decline will be more pronounced in the mesopelagic zone, compared to a milder decline in the bathypelagic zone. On the other hand, based on the Poisson model, we can hypothesize that GZ may become more abundant in these waters. The most abundant communities were found in the temperature range of 1.2-1.3 °C, which corresponds to transformed Atlantic water (Beszczynska-Möller *et al.*, 2011). This type of water mass will be more abundant by the end of 2050 compared to 2020 (based on FESOM data). The recovery of spatio-temporal patterns of GZ abundance from the Poisson model appears rather difficult owing to the model's high sensitivity to values of environmental variables beyond the limits of the trained data.

Based on the study by Mańko *et al.*, (2020), *Aglantha digitale* is a likely climate change winner, benefiting from the Atlantification. In our study, we found that despite a slight overall increase in the abundance of *Aglantha digitale* by 2% by 2050, the preferred niche conditions will narrow from 240-790 m to 410-580 m. In contrast, in a long-term study (Hop *et al.*, 2019), *Aglantha digitale* abundance in the Fram Strait showed a non-linear trend, with their numbers decreasing at offshore stations while increasing at coastal stations. A possible explanation is that the highest abundance of the *Aglantha digitale* occurs under marginal sea-ice conditions. As stated earlier, we observed a higher abundance of GZ in marginal sea-ice zones. However, with subsequent warming the sea-ice will further retreat, which will reduce the duration of the sea-ice bloom and, consequently, could cause a potential decrease in productivity. Thus, predicting the future spatio-temporal abundance of *Aglantha digitale* in the offshore zones of the Fram Strait is difficult and would require further studies, including time series data and the inclusion of additional predictive factors (e.g., proxies for organic matter).

3.6 Conclusions

Our approach, combining underwater camera-born observations and Bayesian Joint Species Distribution Modelling, revealed the diversity and abundance of mid- and deep-water GZ communities in Fram Strait. The study showed that temperature and depth are the main explanatory factors influencing GZ abundance and taxon diversity. By coupling the model with climate scenarios of environmental changes, we were able to project potential changes in the spatial distribution and composition of gelatinous communities to the year 2050 (during the summer season). The future projections predicted a decrease in the total richness of GZ species in the Fram Strait of 14% by 2050. The decline of taxa richness will be more pronounced in the mesopelagic layer, while changes in the bathypelagic layer will be less pronounced. The abundance of the *Aglantha digitale* in the Fram Strait will increase by 2% by 2050, however, its preferred niche conditions will narrow throughout the water column. In contrast, the abundance of *Sminthea arctica* will decrease across the whole water column with an average decline of 60%. The results of these projections can be used to adjust expeditionary efforts to target those areas that would be considered most susceptible to change. With further automation of such surveys, for example, using autonomous underwater observation systems, as well as models for auto-recognition of taxa from the cameras, we will be able to get the most complete picture of the functioning of GZ communities in the Fram Strait.

3.7 Acknowledgements

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3.9 Supplementary materials

Table 3.S1 Metadata of PELAGIOS stations during the PS121 and PS126 expeditions.

Station		PS121 (HG4/2)	PS121 (EG4)	PS121 (N4/1)	PS121 (N4/2)	PS126 (S3)	PS126 (HG4)	PS126 (EG4)	Total
Latitude		7,906,278	7,888,378	7,973,317	7,973,308	7,860,277,778	7,906,138,889	7,871,694,444	
Longitude		4,242,583	-24,308	4,478,667	4,484,317	50,825	4,225	-25,328	
Date		24.08.19	30.08.19	04.09.19	06.09.19	31.05.21	02.06.21	13.06.21	
Sum transects duration time [hh:mm:ss]		2:46:04	2:36:00	2:39:14	1:24:41	1:10:00	1:10:00	1:41:00	13:26:59
Transect depth [m.] and ransect duration [mm]	20	x	x	x	x	10:00	10:00	x	0:20:00
	35	x	10:00	10:00	x	x	x	x	0:20:00
	50	15:14	15:00	15:00	x	10:00	10:00	x	1:05:14
	200	15:00	16:00	15:02	2:00	10:00	10:00	10:00	1:18:02
	400	15:50	15:00	14:45	16:17	10:00	10:00	10:00	1:31:52
	600	20:00	20:00	15:32	17:00	10:00	10:00	10:00	1:42:32
	800	20:15	20:00	20:54	16:27	10:00	10:00	10:00	1:47:36
	1000	19:45	20:00	19:10	x	10:00	10:00	10:00	1:28:55
	1300	20:00	20:00	20:03	x	x	x	10:00	1:10:03
	1600	20:00	10:00	15:00	x	x	x	10:00	0:55:00
	1800	x	x	x	x	x	x	10:00	0:10:00
	1900	20:00	10:00	13:48	x	x	x	x	0:43:48
	2000	x	x	x	x	x	x	21:00	0:21:00
	2200	x	x	x	16:30	x	x	x	0:16:30
	2500	x	x	x	16:27	x	x	x	0:16:27

Table 3.S2. Biological and environmental data used for modeling.

Expedition	Station	Longitude	Latitude	*Aglantha digitale* (*ind.* $10^{-3}*m^{-3}$)	*Atolla* spp. (*ind.* $10^{-3}*m^{-3}$)	*Aulacoctena* spp. (*ind.* $10^{-3}*m^{-3}$)	*Bathyctena* spp. (*ind.* $10^{-3}*m^{-3}$)	*Bathykorus bouilloni* (*ind.* $10^{-3}*m^{-3}$)	*Beroe* spp. (*ind.* $10^{-3}*m^{-3}$)	*Botrynema* spp. (*ind.* $10^{-3}*m^{-3}$)
PS121	EG4	-2.74	78.88	12.50	0.00	0.00	0.00	0.00	0.00	0.00
PS121	EG4	-2.74	78.88	780.00	0.00	0.00	0.00	0.00	6.67	0.00
PS121	EG4	-2.74	78.88	115.00	0.00	0.00	0.00	0.00	15.00	0.00
PS121	EG4	-2.74	78.88	180.00	0.00	0.00	0.00	0.00	0.00	5.00
PS121	EG4	-2.74	78.88	5.00	0.00	5.00	0.00	0.00	5.00	20.00
PS121	EG4	-2.74	78.88	0.00	15.00	0.00	0.00	5.00	0.00	15.00
PS121	EG4	-2.74	78.88	0.00	70.00	0.00	0.00	10.00	0.00	0.00
PS121	EG4	-2.74	78.88	0.00	100.00	0.00	0.00	10.00	0.00	0.00
PS121	HG4	4.24	79.06	138.98	0.00	0.00	0.00	0.00	0.00	0.00
PS121	HG4	4.24	79.06	10.00	0.00	0.00	0.00	0.00	20.00	5.00
PS121	HG4	4.24	79.06	4.94	0.00	0.00	0.00	0.00	9.88	4.94
PS121	HG4	4.24	79.06	0.00	0.00	0.00	0.00	0.00	0.00	5.06
PS121	HG4	4.24	79.06	0.00	0.00	0.00	0.00	0.00	0.00	5.00
PS121	HG4	4.24	79.06	0.00	0.00	0.00	0.00	0.00	0.00	5.00
PS121	HG4	4.24	79.06	0.00	15.00	0.00	0.00	30.00	0.00	85.00
PS121	N4_1	4.48	79.73	119.72	0.00	0.00	0.00	0.00	0.00	0.00
PS121	N4_1	4.48	79.73	474.58	0.00	0.00	0.00	0.00	0.00	0.00
PS121	N4_1	4.48	79.73	180.30	0.00	0.00	0.00	0.00	0.00	0.00
PS121	N4_1	4.48	79.73	0.00	0.00	0.00	0.00	0.00	9.57	0.00
PS121	N4_1	4.48	79.73	73.07	0.00	5.10	0.00	0.00	5.22	15.66
PS121	N4_1	4.48	79.73	4.99	0.00	0.00	0.00	0.00	0.00	9.98
PS121	N4_1	4.48	79.73	0.00	0.00	0.00	0.00	0.00	0.00	6.67
PS121	N4_1	4.48	79.73	0.00	72.46	0.00	0.00	0.00	0.00	14.49
PS121	N4_2	4.48	79.73	300.92	0.00	0.00	0.00	6.14	61.43	0.00
PS121	N4_2	4.48	79.73	29.41	0.00	0.00	0.00	0.00	11.76	0.00
PS121	N4_2	4.48	79.73	42.55	0.00	0.00	0.00	0.00	12.16	0.00
PS121	N4_2	4.48	79.73	0.00	6.06	0.00	12.12	60.61	0.00	24.24
PS121	N4_2	4.48	79.73	0.00	18.24	0.00	0.00	54.71	0.00	42.55
PS126	EG4	-2.32	78.43	1230.00	0.00	10.00	0.00	0.00	40.00	0.00
PS126	EG4	-2.32	78.43	30.00	0.00	0.00	0.00	0.00	10.00	10.00
PS126	EG4	-2.32	78.43	0.00	10.00	0.00	0.00	0.00	0.00	20.00

Expedition	Station	Longitude	Latitude	*Aglantha digitale* *(ind. $10^{-3}*m^{-3}$)*	*Atolla* spp. *(ind. $10^{-3}*m^{-3}$)*	*Aulacoctena* spp. *(ind. $10^{-3}*m^{-3}$)*	*Bathyctena* spp. *(ind. $10^{-3}*m^{-3}$)*	*Bathykorus bouilloni* *(ind. $10^{-3}*m^{-3}$)*	*Beroe* spp. *(ind. $10^{-3}*m^{-3}$)*	*Botrynema* spp. *(ind. $10^{-3}*m^{-3}$)*
PS126	EG4	-2.32	78.43	0.00	30.00	0.00	0.00	0.00	0.00	30.00
PS126	EG4	-2.32	78.43	0.00	70.00	0.00	0.00	0.00	0.00	80.00
PS126	EG4	-2.32	78.43	0.00	50.00	0.00	0.00	10.00	0.00	50.00
PS126	EG4	-2.32	78.43	0.00	10.00	0.00	0.00	60.00	0.00	20.00
PS126	EG4	-2.32	78.43	0.00	14.29	0.00	0.00	133.33	0.00	19.05
PS126	HG4	4.14	78.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PS126	HG4	4.14	78.04	70.00	0.00	0.00	0.00	0.00	0.00	0.00
PS126	HG4	4.14	78.04	570.00	0.00	0.00	0.00	0.00	0.00	0.00
PS126	HG4	4.14	78.04	1000.00	0.00	0.00	0.00	0.00	20.00	0.00
PS126	HG4	4.14	78.04	40.00	0.00	0.00	0.00	0.00	20.00	0.00
PS126	HG4	4.14	78.04	0.00	30.00	0.00	0.00	0.00	0.00	40.00
PS126	HG4	4.14	78.04	0.00	40.00	0.00	0.00	0.00	0.00	60.00
PS126	S3	5.05	78.36	0.00	0.00	0.00	0.00	0.00	10.00	0.00
PS126	S3	5.05	78.36	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PS126	S3	5.05	78.36	110.00	0.00	0.00	0.00	0.00	0.00	0.00
PS126	S3	5.05	78.36	10.00	0.00	0.00	0.00	0.00	30.00	10.00
PS126	S3	5.05	78.36	0.00	0.00	0.00	0.00	0.00	0.00	30.00
PS126	S3	5.05	78.36	0.00	10.00	0.00	0.00	0.00	0.00	0.00
PS126	S3	5.05	78.36	0.00	10.00	0.00	0.00	0.00	0.00	20.00

Expedition	Station	*Botrynema brucei* *(ind. $10^{-3}*m^{-3}$)*	*Botrynema ellinorae* *(ind. $10^{-3}*m^{-3}$)*	Calycophorae spp. *(ind. $10^{-3}*m^{-3}$)*	*Crossota* spp. *(ind. $10^{-3}*m^{-3}$)*	Ctenophore spp. *(ind. $10^{-3}*m^{-3}$)*	*Dryodora glandiformis* *(ind. $10^{-3}*m^{-3}$)*	*Euplokamis* spp. *(ind. $10^{-3}*m^{-3}$)*	Lobata spp. *(ind. $10^{-3}*m^{-3}$)*	Physonectae spp. *(ind. $10^{-3}*m^{-3}$)*
PS121	EG4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PS121	EG4	0.00	0.00	73.33	0.00	0.00	0.00	0.00	0.00	0.00
PS121	EG4	0.00	0.00	140.00	0.00	0.00	0.00	0.00	0.00	35.00
PS121	EG4	0.00	25.00	125.00	0.00	0.00	0.00	0.00	5.00	60.00
PS121	EG4	5.00	40.00	5.00	0.00	0.00	0.00	0.00	5.00	50.00
PS121	EG4	5.00	55.00	5.00	0.00	0.00	0.00	0.00	5.00	20.00
PS121	EG4	20.00	0.00	10.00	10.00	0.00	0.00	0.00	0.00	10.00
PS121	EG4	50.00	0.00	0.00	10.00	0.00	0.00	0.00	10.00	20.00
PS121	HG4	0.00	0.00	56.84	0.00	6.32	0.00	0.00	0.00	18.95

Expedition	Station	*Botrynema brucei* *(ind. $10^{-3}*m^{-3}$)*	*Botrynema ellinorae* *(ind. $10^{-3}*m^{-3}$)*	Calycophorae spp. *(ind. $10^{-3}*m^{-3}$)*	*Crossota* spp. *(ind. $10^{-3}*m^{-3}$)*	Ctenophore spp. *(ind. $10^{-3}*m^{-3}$)*	*Dryodora glandiformis* *(ind. $10^{-3}*m^{-3}$)*	*Euplokamis* spp. *(ind. $10^{-3}*m^{-3}$)*	Lobata spp. *(ind. $10^{-3}*m^{-3}$)*	Physonectae spp. *(ind. $10^{-3}*m^{-3}$)*
PS121	HG4	0.00	15.00	10.00	0.00	0.00	0.00	5.00	0.00	50.00
PS121	HG4	0.00	24.69	4.94	0.00	9.88	0.00	0.00	0.00	83.95
PS121	HG4	0.00	0.00	5.06	0.00	0.00	0.00	0.00	0.00	81.01
PS121	HG4	0.00	15.00	0.00	0.00	0.00	0.00	0.00	10.00	85.00
PS121	HG4	0.00	0.00	5.00	0.00	0.00	0.00	0.00	0.00	15.00
PS121	HG4	50.00	0.00	0.00	30.00	0.00	0.00	0.00	0.00	5.00
PS121	N4_1	0.00	0.00	0.00	0.00	0.00	0.00	6.65	0.00	0.00
PS121	N4_1	0.00	0.00	183.05	0.00	6.78	0.00	13.56	0.00	0.00
PS121	N4_1	0.00	0.00	379.83	0.00	12.88	0.00	12.88	6.44	57.95
PS121	N4_1	0.00	0.00	162.68	0.00	4.78	0.00	0.00	0.00	43.06
PS121	N4_1	0.00	0.00	41.74	0.00	0.00	0.00	0.00	0.00	10.44
PS121	N4_1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	44.89
PS121	N4_1	6.67	20.00	0.00	0.00	0.00	0.00	0.00	13.33	40.00
PS121	N4_1	7.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PS121	N4_2	0.00	0.00	135.11	0.00	0.00	0.00	6.14	12.29	12.29
PS121	N4_2	0.00	5.88	270.59	0.00	0.00	0.00	0.00	5.88	52.94
PS121	N4_2	0.00	6.08	18.24	0.00	6.08	0.00	0.00	0.00	30.40
PS121	N4_2	60.61	0.00	6.06	0.00	0.00	0.00	0.00	6.06	0.00
PS121	N4_2	48.63	0.00	6.08	0.00	0.00	0.00	0.00	0.00	0.00
PS126	EG4	0.00	0.00	80.00	0.00	50.00	0.00	0.00	0.00	20.00
PS126	EG4	0.00	10.00	180.00	0.00	30.00	0.00	10.00	0.00	120.00
PS126	EG4	0.00	0.00	20.00	0.00	0.00	0.00	0.00	0.00	20.00
PS126	EG4	10.00	50.00	0.00	0.00	0.00	0.00	0.00	20.00	0.00
PS126	EG4	0.00	10.00	0.00	0.00	0.00	0.00	0.00	10.00	20.00
PS126	EG4	20.00	0.00	0.00	10.00	0.00	0.00	0.00	10.00	30.00
PS126	EG4	20.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PS126	EG4	23.81	0.00	0.00	52.38	0.00	0.00	0.00	0.00	19.05
PS126	HG4	0.00	0.00	0.00	0.00	30.00	0.00	0.00	0.00	0.00
PS126	HG4	0.00	0.00	0.00	0.00	10.00	0.00	0.00	0.00	0.00
PS126	HG4	0.00	0.00	70.00	0.00	40.00	0.00	0.00	0.00	0.00
PS126	HG4	0.00	0.00	320.00	0.00	70.00	0.00	10.00	0.00	50.00
PS126	HG4	0.00	0.00	20.00	0.00	30.00	20.00	0.00	10.00	110.00
PS126	HG4	20.00	10.00	40.00	0.00	0.00	20.00	0.00	20.00	50.00

Expedition	Station	*Botrynema brucei* *(ind. $10^{-3}*m^{-3}$)*	*Botrynema ellinorae* *(ind. $10^{-3}*m^{-3}$)*	Calycophorae spp. *(ind. $10^{-3}*m^{-3}$)*	*Crossota* spp. *(ind. $10^{-3}*m^{-3}$)*	Ctenophore spp. *(ind. $10^{-3}*m^{-3}$)*	*Dryodora glandiformis* *(ind. $10^{-3}*m^{-3}$)*	*Euplokamis* spp. *(ind. $10^{-3}*m^{-3}$)*	Lobata spp. *(ind. $10^{-3}*m^{-3}$)*	Physonectae spp. *(ind. $10^{-3}*m^{-3}$)*
PS126	HG4	10.00	10.00	0.00	0.00	0.00	0.00	0.00	10.00	60.00
PS126	S3	0.00	0.00	0.00	0.00	20.00	0.00	0.00	0.00	0.00
PS126	S3	0.00	0.00	0.00	0.00	30.00	0.00	0.00	0.00	0.00
PS126	S3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PS126	S3	0.00	0.00	40.00	0.00	10.00	0.00	0.00	10.00	10.00
PS126	S3	0.00	0.00	20.00	0.00	0.00	0.00	0.00	0.00	60.00
PS126	S3	0.00	0.00	40.00	0.00	0.00	0.00	0.00	10.00	0.00
PS126	S3	0.00	0.00	10.00	0.00	0.00	0.00	0.00	0.00	20.00

Expedition	Station	*Ptychogena hyperborea* *(ind. $10^{-3}*m^{-3}$)*	*Sminthea arctica* *(ind. $10^{-3}*m^{-3}$)*	*Solmundella bitentaculata* *(ind. $10^{-3}*m^{-3}$)*	Trachymedusae *(ind. $10^{-3}*m^{-3}$)*	Depth (meters)	Temperature (°C)	Salinity (PSU)	Oxygen (%)	Sea Ice (%)
PS121	EG4	0.00	0.00	0.00	0.00	200.00	3.10	34.97	92.22	62.73
PS121	EG4	0.00	0.00	0.00	0.00	400.00	1.97	34.92	89.71	62.73
PS121	EG4	0.00	0.00	0.00	0.00	600.00	1.32	34.94	88.94	62.73
PS121	EG4	0.00	0.00	0.00	10.00	800.00	0.41	34.91	86.72	62.73
PS121	EG4	0.00	125.00	0.00	20.00	1000.00	-0.04	34.90	84.66	62.73
PS121	EG4	5.00	515.00	5.00	0.00	1300.00	-0.29	34.91	84.66	62.73
PS121	EG4	0.00	270.00	40.00	10.00	1600.00	-0.45	34.91	82.22	62.73
PS121	EG4	10.00	100.00	60.00	20.00	1900.00	-0.58	34.91	81.58	62.73
PS121	HG4	0.00	0.00	0.00	0.00	400.00	1.98	34.95	91.14	9.42
PS121	HG4	0.00	5.00	0.00	0.00	600.00	0.54	34.92	88.06	9.42
PS121	HG4	0.00	19.75	0.00	0.00	800.00	-0.07	34.90	86.10	9.42
PS121	HG4	0.00	25.32	0.00	0.00	1000.00	-0.27	34.91	85.29	9.42
PS121	HG4	0.00	85.00	0.00	15.00	1300.00	-0.51	34.91	84.49	9.42
PS121	HG4	0.00	250.00	5.00	0.00	1600.00	-0.66	34.91	81.91	9.42
PS121	HG4	0.00	15.00	10.00	20.00	1900.00	-0.72	34.91	80.75	9.42
PS121	N4_1	0.00	0.00	0.00	0.00	200.00	3.10	34.98	93.46	37.77
PS121	N4_1	0.00	0.00	0.00	0.00	400.00	2.00	34.95	91.19	37.77
PS121	N4_1	0.00	0.00	0.00	0.00	600.00	0.75	34.92	88.36	37.77
PS121	N4_1	0.00	0.00	0.00	0.00	800.00	-0.05	34.91	85.87	37.77
PS121	N4_1	0.00	0.00	0.00	0.00	1000.00	-0.38	34.91	85.44	37.77
PS121	N4_1	0.00	24.94	0.00	0.00	1300.00	-0.51	34.91	84.49	37.77
PS121	N4_1	0.00	126.67	0.00	0.00	1600.00	-0.66	34.91	81.91	37.77
PS121	N4_1	0.00	376.81	0.00	0.00	1900.00	-0.72	34.91	80.75	37.77
PS121	N4_2	0.00	0.00	0.00	0.00	400.00	2.00	34.95	91.19	37.77

Expedition	Station	*Ptychogena hyperborea* (*ind.* $10^{-3}*m^{-3}$)	*Sminthea arctica* (*ind.* $10^{-3}*m^{-3}$)	*Solmundella bitentaculata* (*ind.* $10^{-3}*m^{-3}$)	Trachymedusae (*ind.* $10^{-3}*m^{-3}$)	Depth (meters)	Temperature (°C)	Salinity (PSU)	Oxygen (%)	Sea Ice (%)
PS121	N4_2	0.00	0.00	0.00	0.00	600.00	0.75	34.92	88.36	37.77
PS121	N4_2	0.00	0.00	0.00	0.00	800.00	-0.05	34.91	85.87	37.77
PS121	N4_2	0.00	36.36	12.12	0.00	2200.00	-0.73	34.91	80.36	37.77
PS121	N4_2	0.00	0.00	0.00	0.00	2500.00	-0.73	34.92	80.57	37.77
PS126	EG4	0.00	0.00	0.00	0.00	400.00	1.32	34.91	88.00	46.05
PS126	EG4	0.00	0.00	0.00	10.00	600.00	0.57	34.90	84.83	46.05
PS126	EG4	0.00	190.00	30.00	50.00	800.00	-0.04	34.89	83.26	46.05
PS126	EG4	0.00	180.00	30.00	30.00	1000.00	-0.21	34.90	82.83	46.05
PS126	EG4	0.00	110.00	10.00	30.00	1300.00	-0.41	34.91	82.46	46.05
PS126	EG4	0.00	30.00	20.00	10.00	1600.00	-0.58	34.91	81.09	46.05
PS126	EG4	20.00	70.00	10.00	30.00	1800.00	-0.65	34.92	79.88	46.05
PS126	EG4	0.00	14.29	4.76	61.90	2000.00	-0.44	34.91	79.15	46.05
PS126	HG4	0.00	0.00	0.00	0.00	20.00	-0.10	34.42	96.28	0.00
PS126	HG4	0.00	0.00	0.00	0.00	50.00	3.04	34.89	95.81	0.00
PS126	HG4	0.00	0.00	0.00	0.00	200.00	2.55	34.97	94.08	0.00
PS126	HG4	0.00	0.00	0.00	0.00	400.00	1.96	34.94	89.70	0.00
PS126	HG4	0.00	10.00	0.00	0.00	600.00	1.27	34.92	84.94	0.00
PS126	HG4	0.00	450.00	30.00	50.00	800.00	0.39	34.90	84.41	0.00
PS126	HG4	0.00	300.00	50.00	50.00	1000.00	-0.01	34.90	83.12	0.00
PS126	S3	0.00	0.00	0.00	0.00	20.00	2.76	34.87	96.28	0.00
PS126	S3	0.00	0.00	0.00	0.00	50.00	2.60	34.97	95.81	0.00
PS126	S3	0.00	0.00	0.00	0.00	200.00	1.67	34.97	94.08	0.00
PS126	S3	0.00	110.00	0.00	10.00	400.00	0.21	34.90	89.70	0.00
PS126	S3	0.00	240.00	30.00	60.00	600.00	-0.08	34.91	84.94	0.00
PS126	S3	0.00	120.00	0.00	50.00	800.00	-0.28	34.91	84.41	0.00
PS126	S3	0.00	110.00	0.00	20.00	1000.00	-0.44	34.91	83.12	0.00

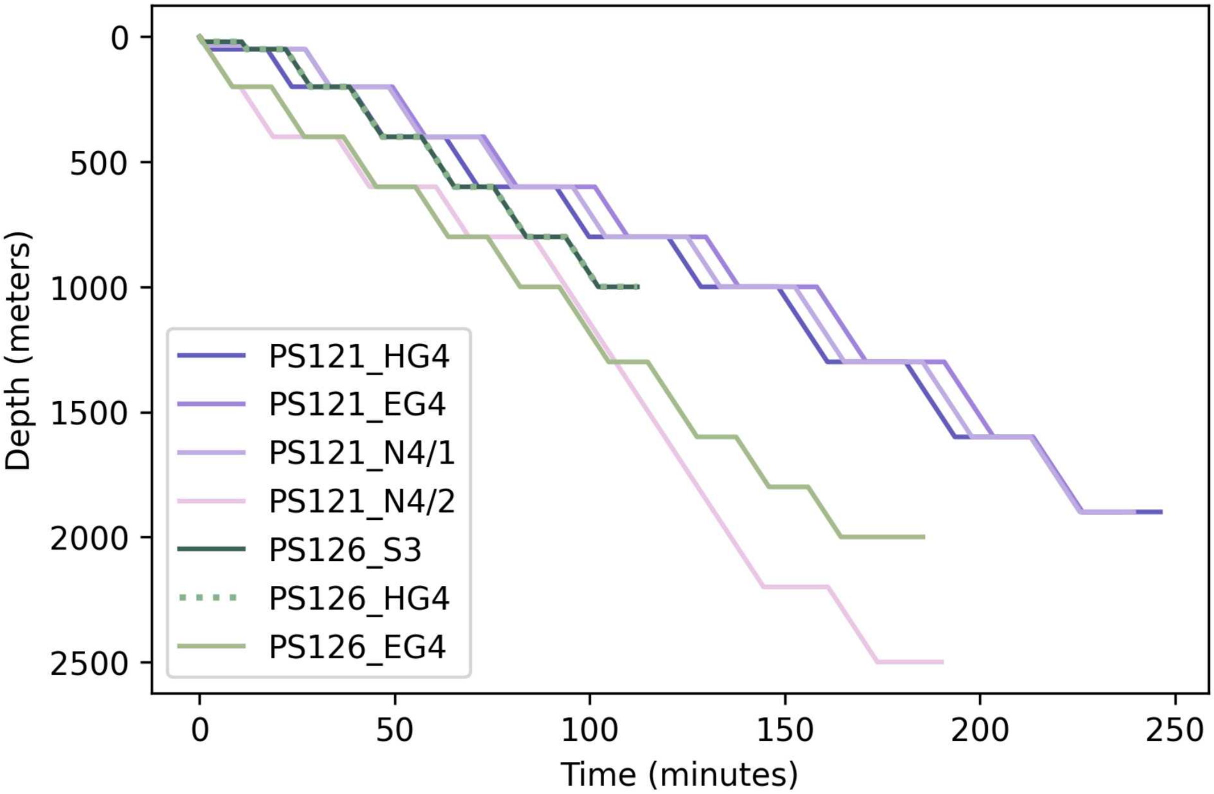
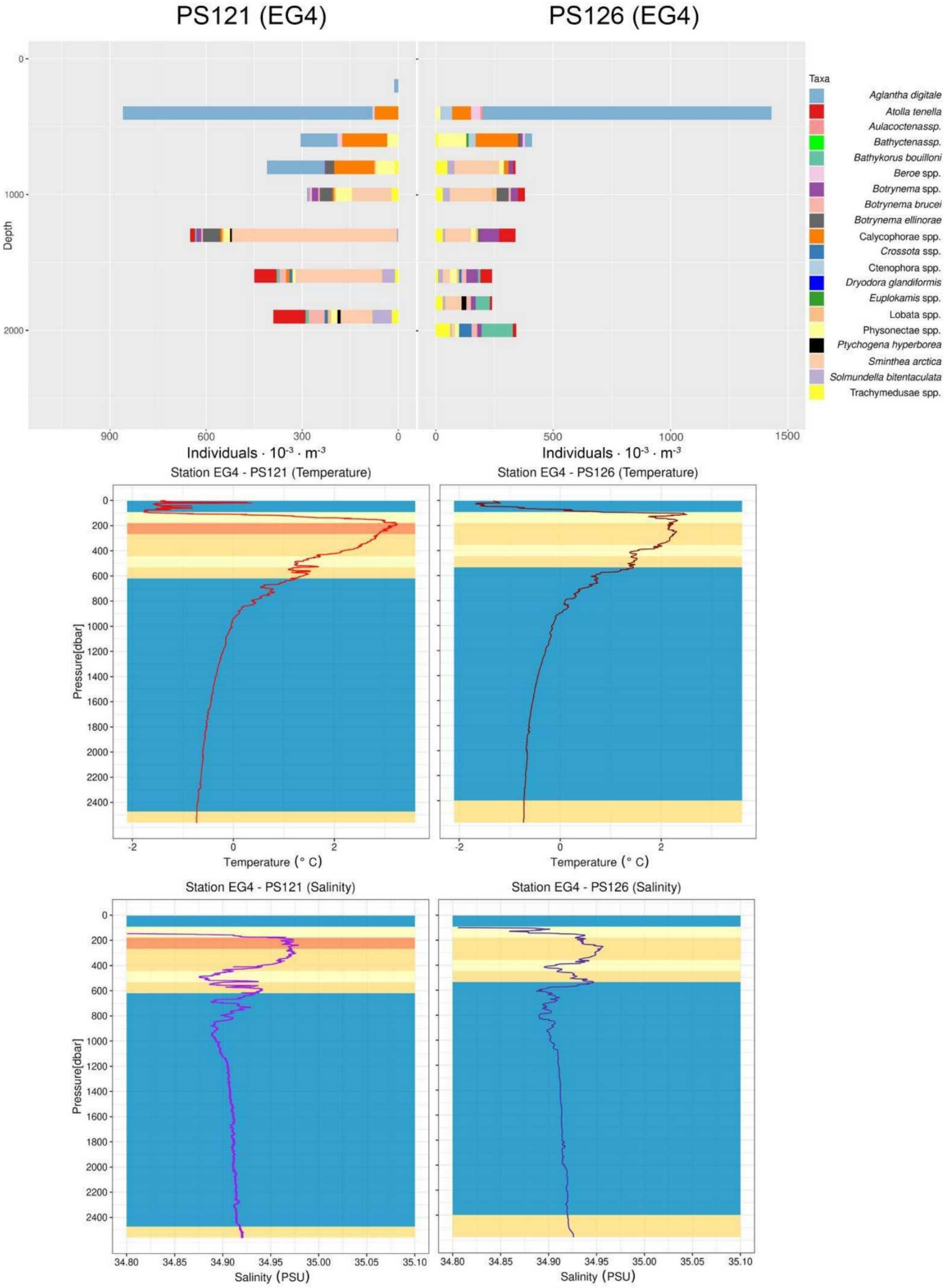
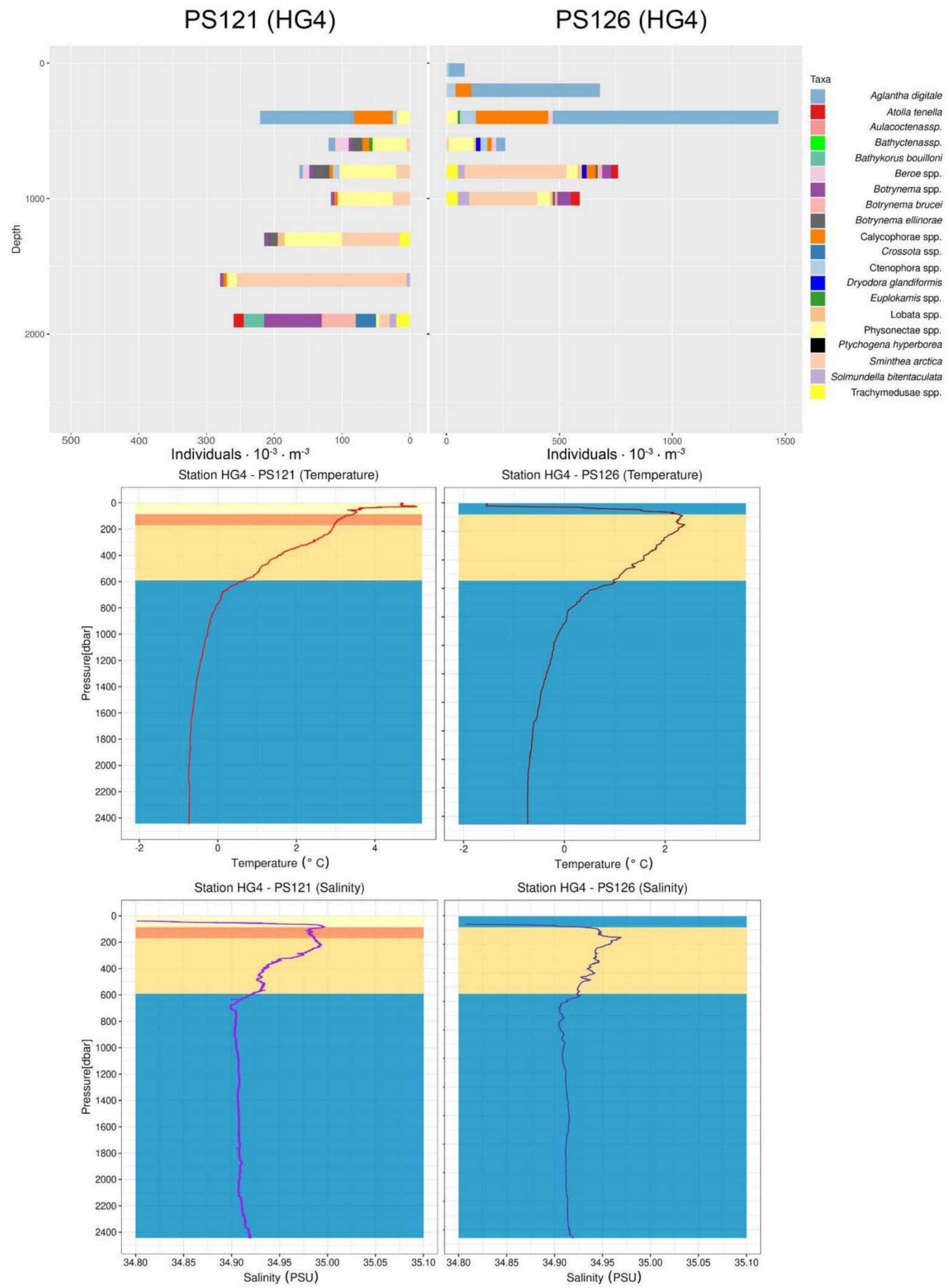


Figure 3.S1. PELAGIOS transects at stations PS121 (HG4/2), PS121 (EG4), PS121 (N4/1), PS121 (N4/2), PS126 (S3), PS126 (HG4), PS126 (EG4). Only the horizontal sections were selected for analysis.



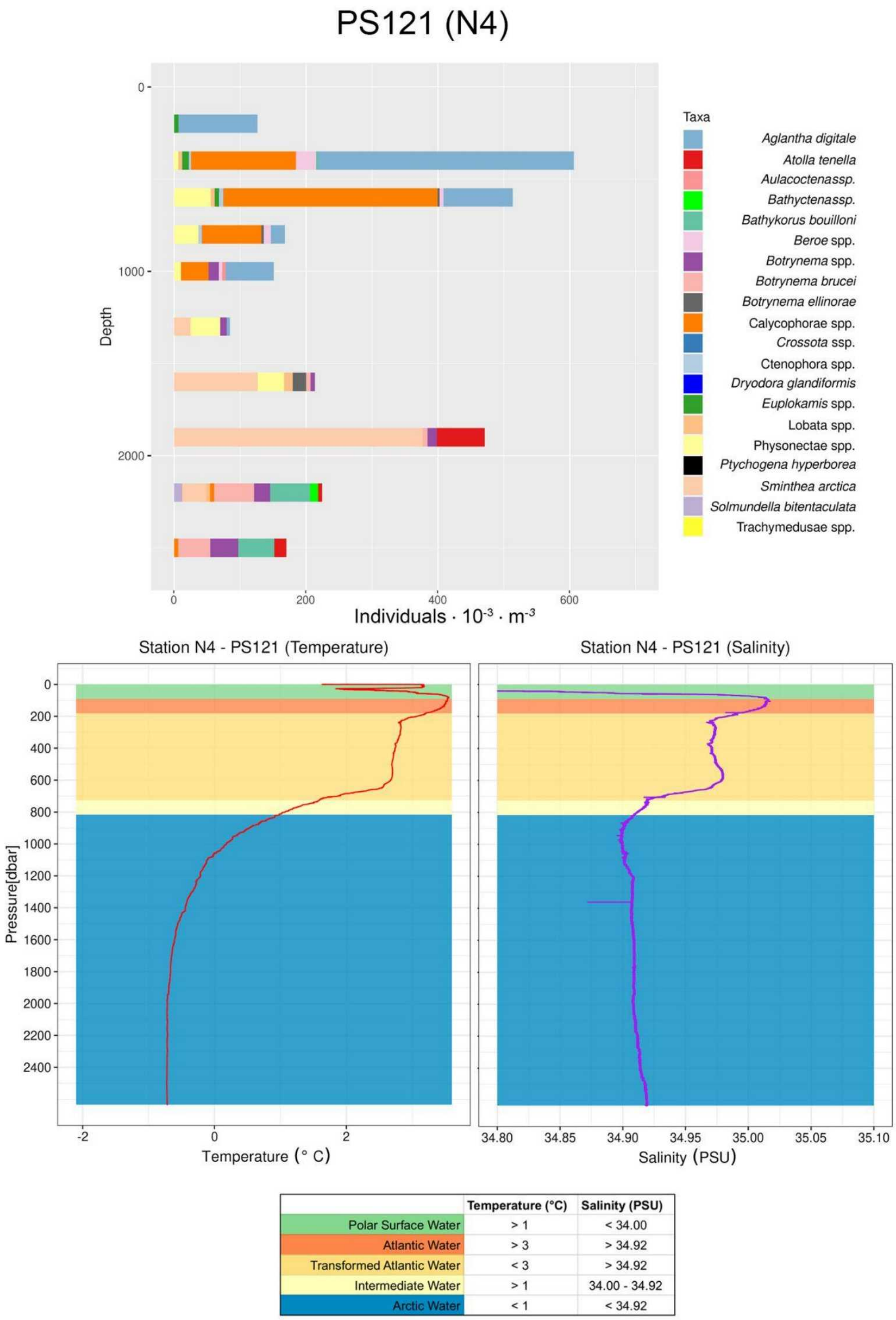
	Temperature (°C)	Salinity (PSU)
Polar Surface Water	> 1	< 34.00
Atlantic Water	> 3	> 34.92
Transformed Atlantic Water	< 3	> 34.92
Intermediate Water	> 1	34.00 - 34.92
Arctic Water	< 1	< 34.92

Figure 3.S2. Vertical distribution of faunal groups encountered with PELAGIOS and hydrographic profiles of the sampled stations. The water masses are grouped according to Beszczynska-Moller et al., 2011, Walczowski et al., 2012 and Mańko et al., 2020.



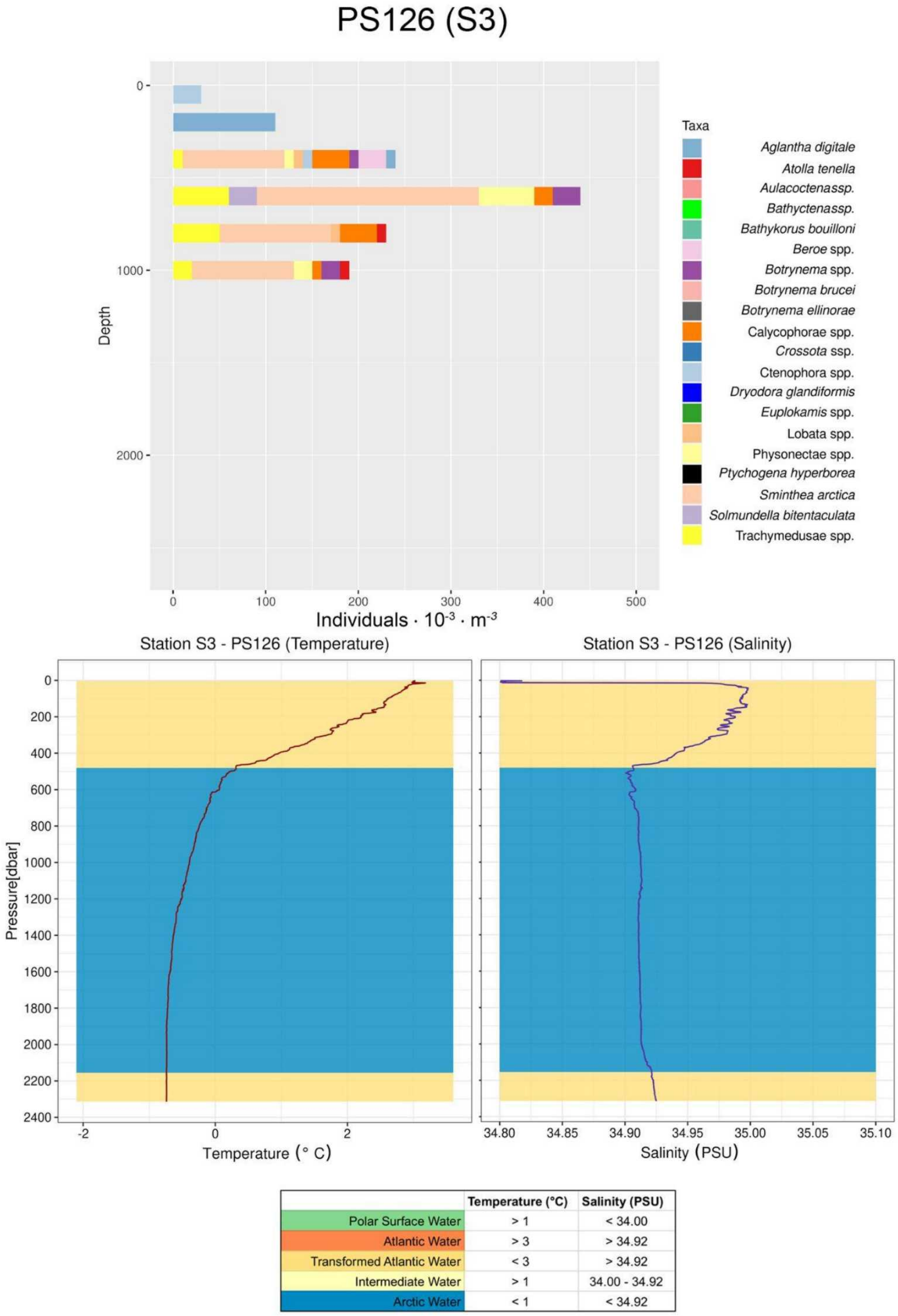
	Temperature (°C)	Salinity (PSU)
Polar Surface Water	> 1	< 34.00
Atlantic Water	> 3	> 34.92
Transformed Atlantic Water	< 3	> 34.92
Intermediate Water	> 1	34.00 - 34.92
Arctic Water	< 1	< 34.92

Continued Figure 3.S2. Vertical distribution of faunal groups encountered with PELAGIOS and hydrographic profiles of the sampled stations. The water masses are grouped according to Beszczynska-Moller et al., 2011, Walczowski et al., 2012 and Mańko et al., 2020.



	Temperature (°C)	Salinity (PSU)
Polar Surface Water	> 1	< 34.00
Atlantic Water	> 3	> 34.92
Transformed Atlantic Water	< 3	> 34.92
Intermediate Water	> 1	34.00 - 34.92
Arctic Water	< 1	< 34.92

Continued Figure 3.S2. Vertical distribution of faunal groups encountered with PELAGIOS and hydrographic profiles of the sampled stations. The water masses are grouped according to Beszczynska-Moller et al., 2011, Walczowski et al., 2012 and Mańko et al., 2020.



	Temperature (°C)	Salinity (PSU)
🟩 Polar Surface Water	> 1	< 34.00
🟧 Atlantic Water	> 3	> 34.92
🟨 Transformed Atlantic Water	< 3	> 34.92
🟨 Intermediate Water	> 1	34.00 - 34.92
🟦 Arctic Water	< 1	< 34.92

Continued Figure 3.S2. Vertical distribution of faunal groups encountered with PELAGIOS and hydrographic profiles of the sampled stations. The water masses are grouped according to Beszczynska-Moller et al., 2011, Walczowski et al., 2012 and Mańko et al., 2020.

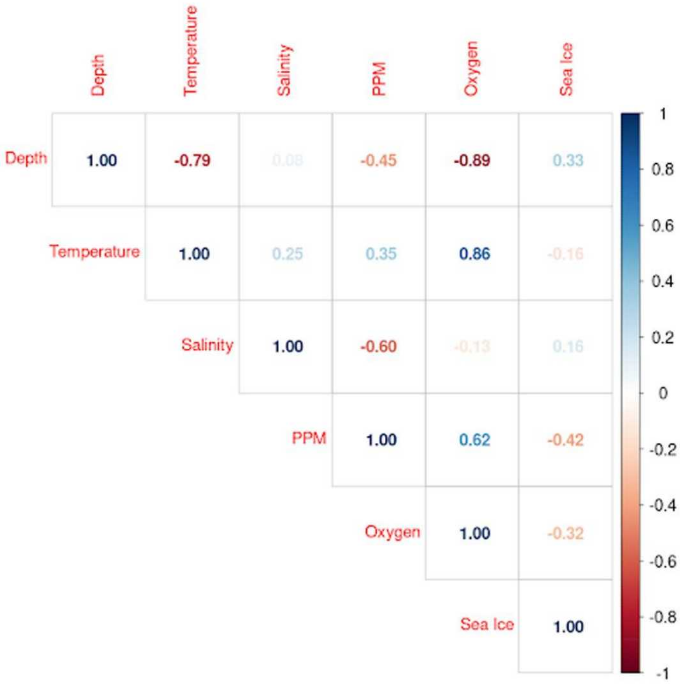


Figure 3.S3. Pearson's correlation between environmental predictors.

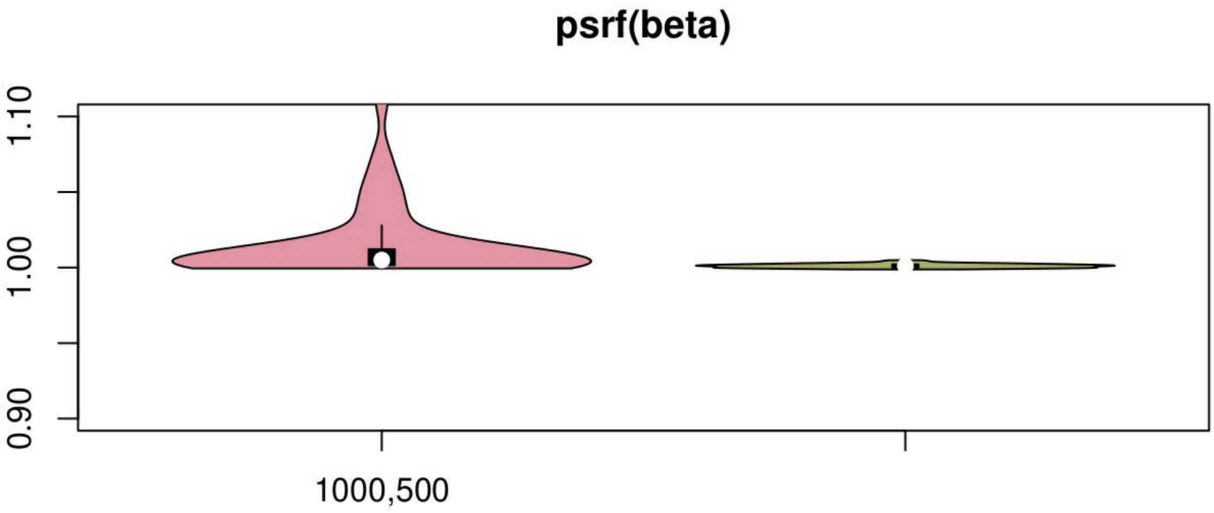


Figure 3.S4. MCMC convergence diagnostics. A violin plots represents the potential scale reduction factors (β-parameter) of MCMC for poisson (left) and probit (right) models.

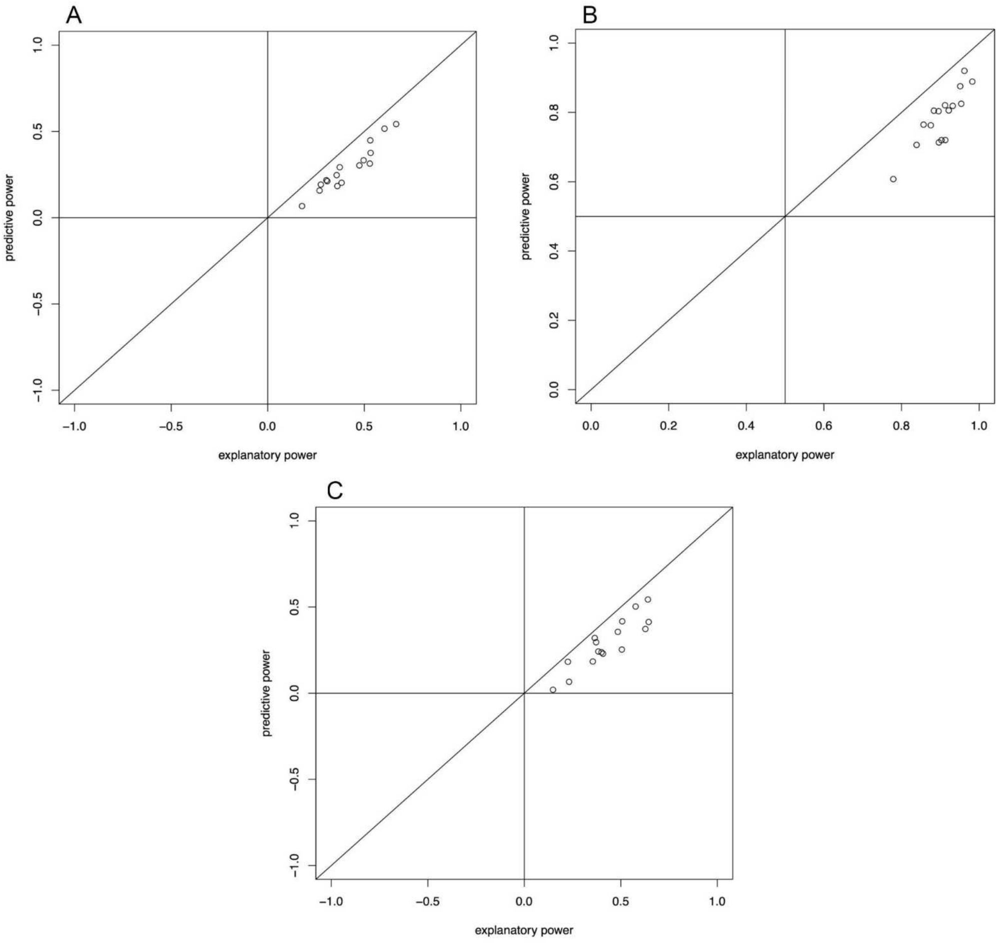


Figure 3.S5. Explanatory and predictive power of probit model evaluated by TJuR2 (a), and AUC (b). Poisson model evaluated by pseudo-R2 (c).

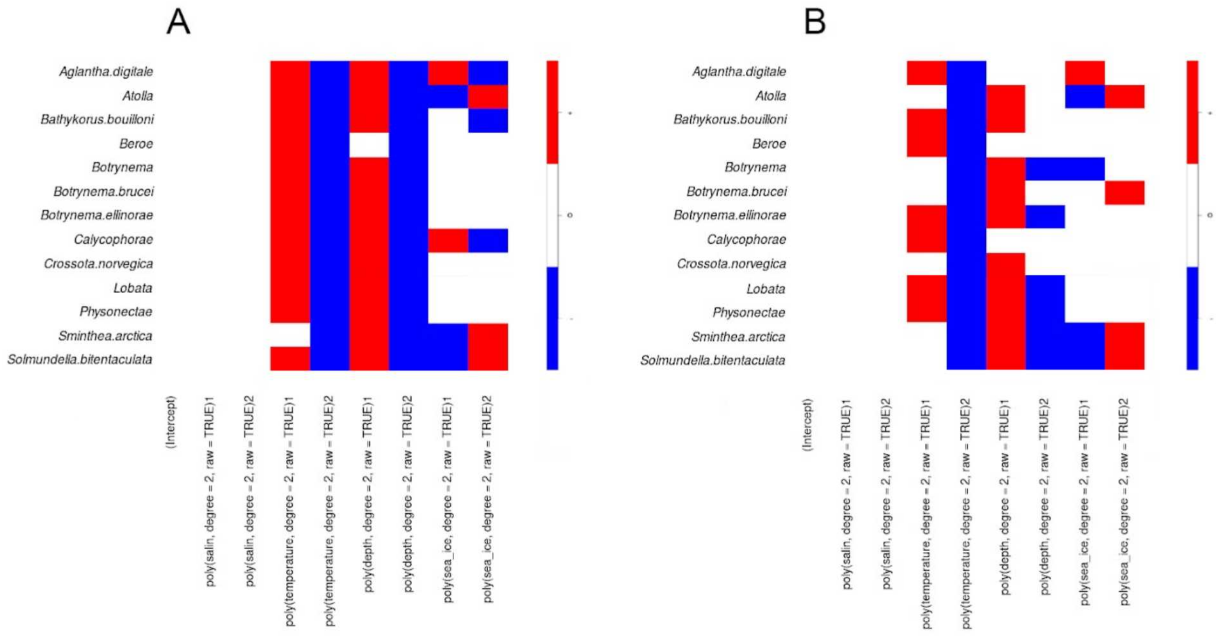


Figure 3.S6. The responses of the species to environmental covariates. Panel (a) shows the results for the Poisson model and panel (b) for the presence-absence model. In both panels, responses that are positive with at least 95% posterior probability are shown in red, responses that are negative with at least 95% posterior probability are shown in blue, and responses that did not gain strong statistical support are shown in white.

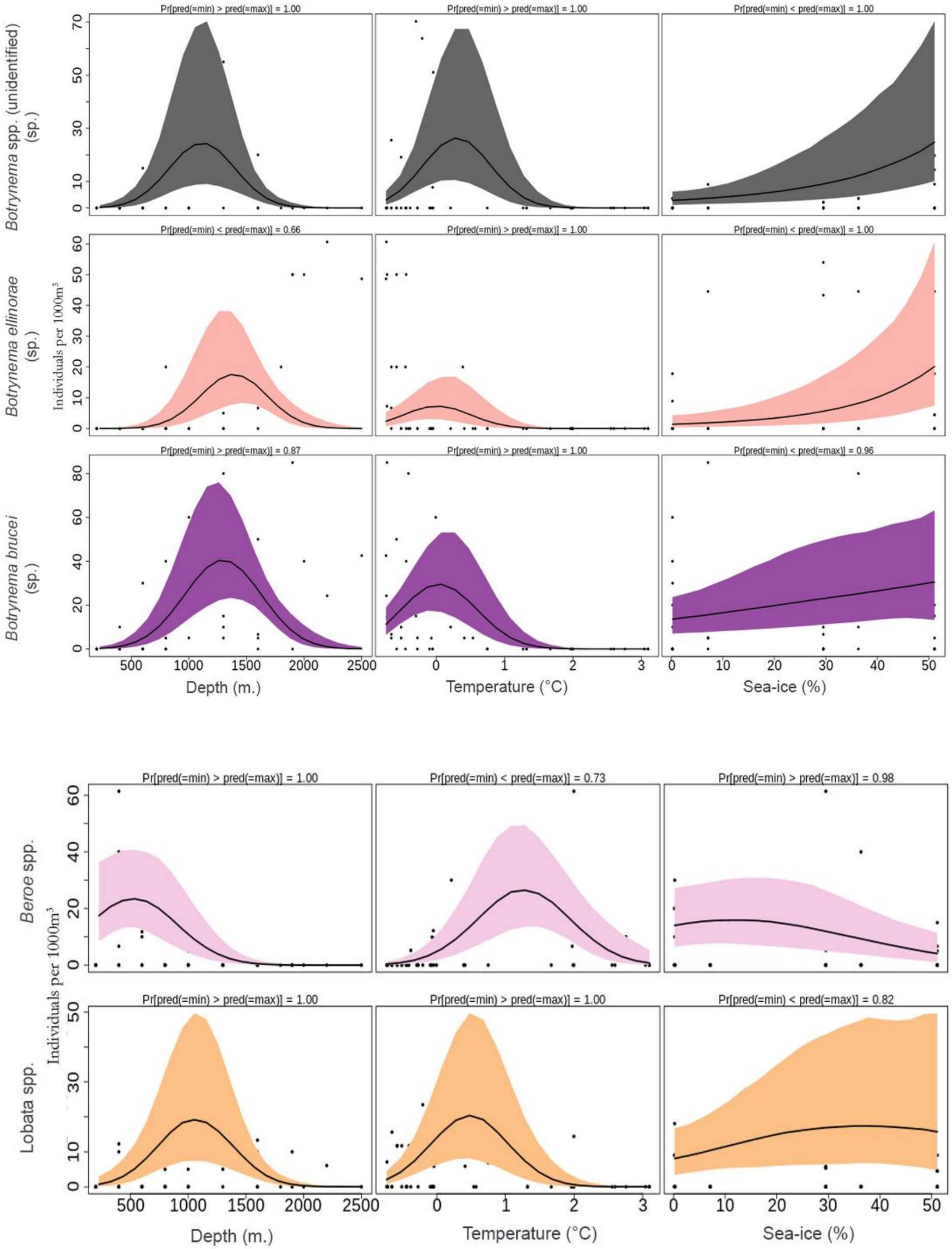
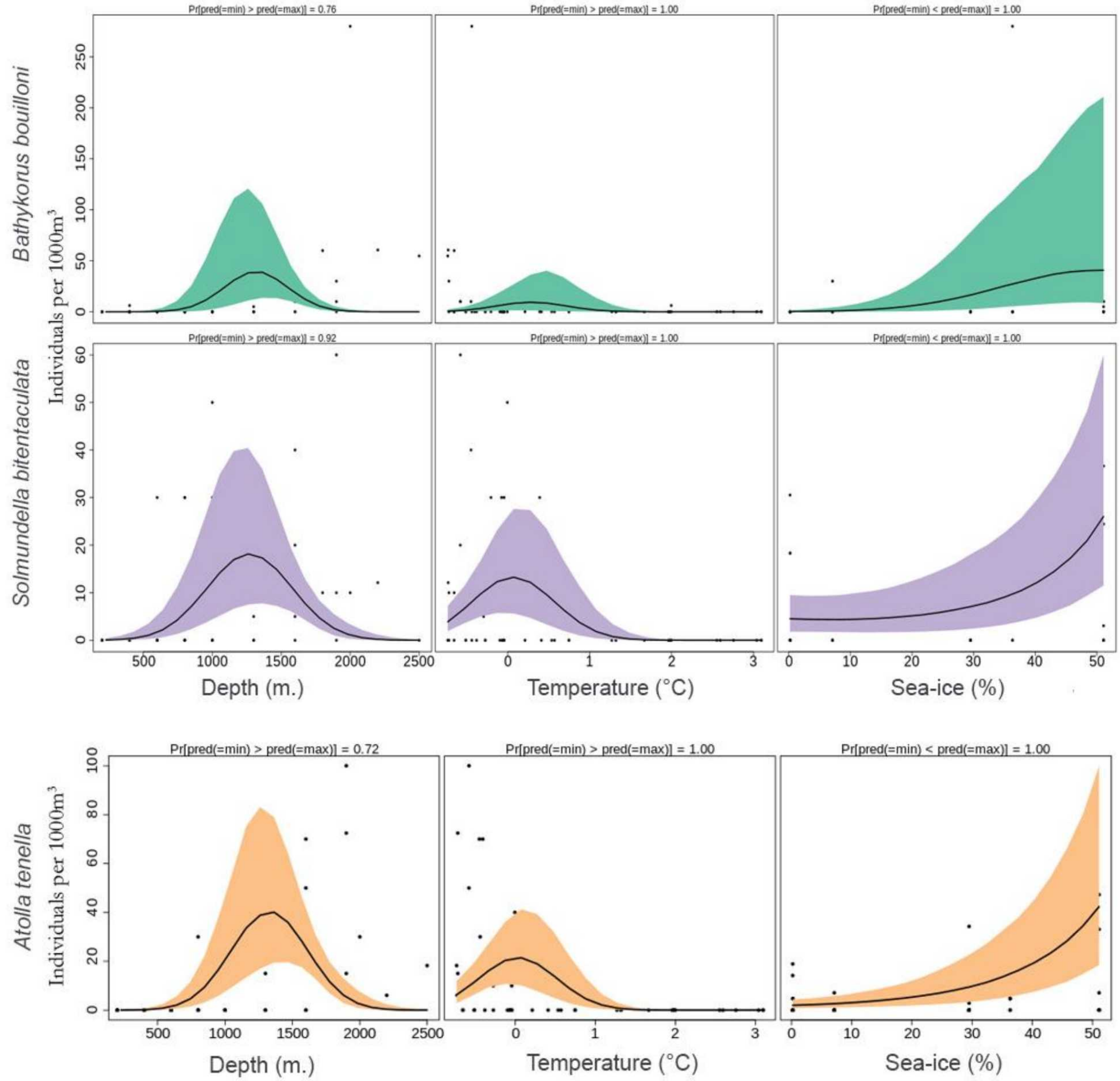


Figure 3.S7. Predicted gradients of total count for gelatinous taxa.



Continued Figure 3.S7. Predicted gradients of total count for gelatinous taxa.

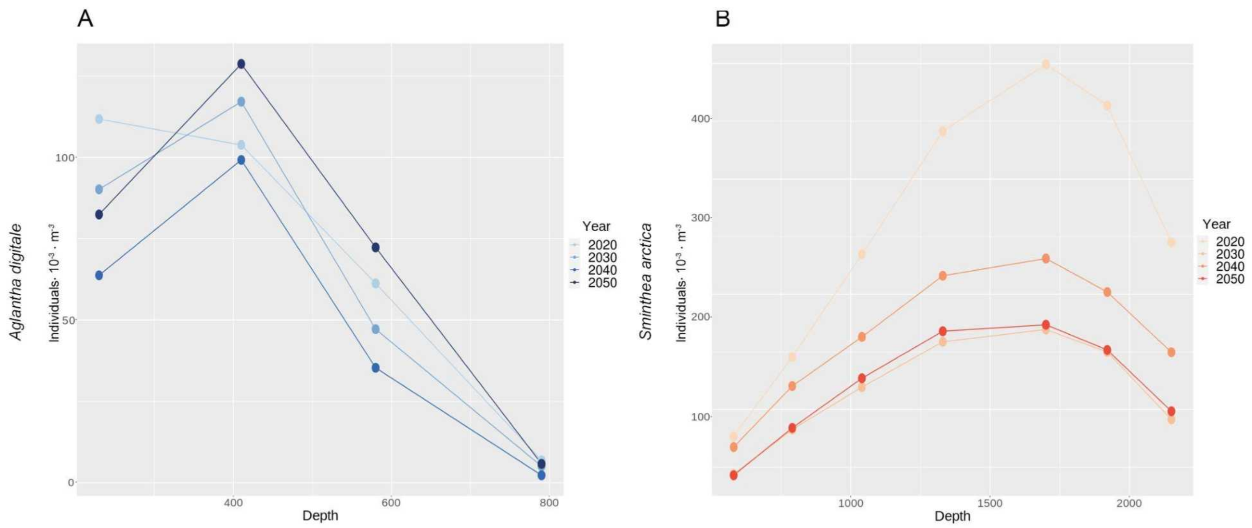


Figure 3.S8. Current and future abundance (summer season) values of Aglantha digitale (a) and Sminthea arctica (b) at different depth layers. The abundance values were calculated as the mean for each depth layer.

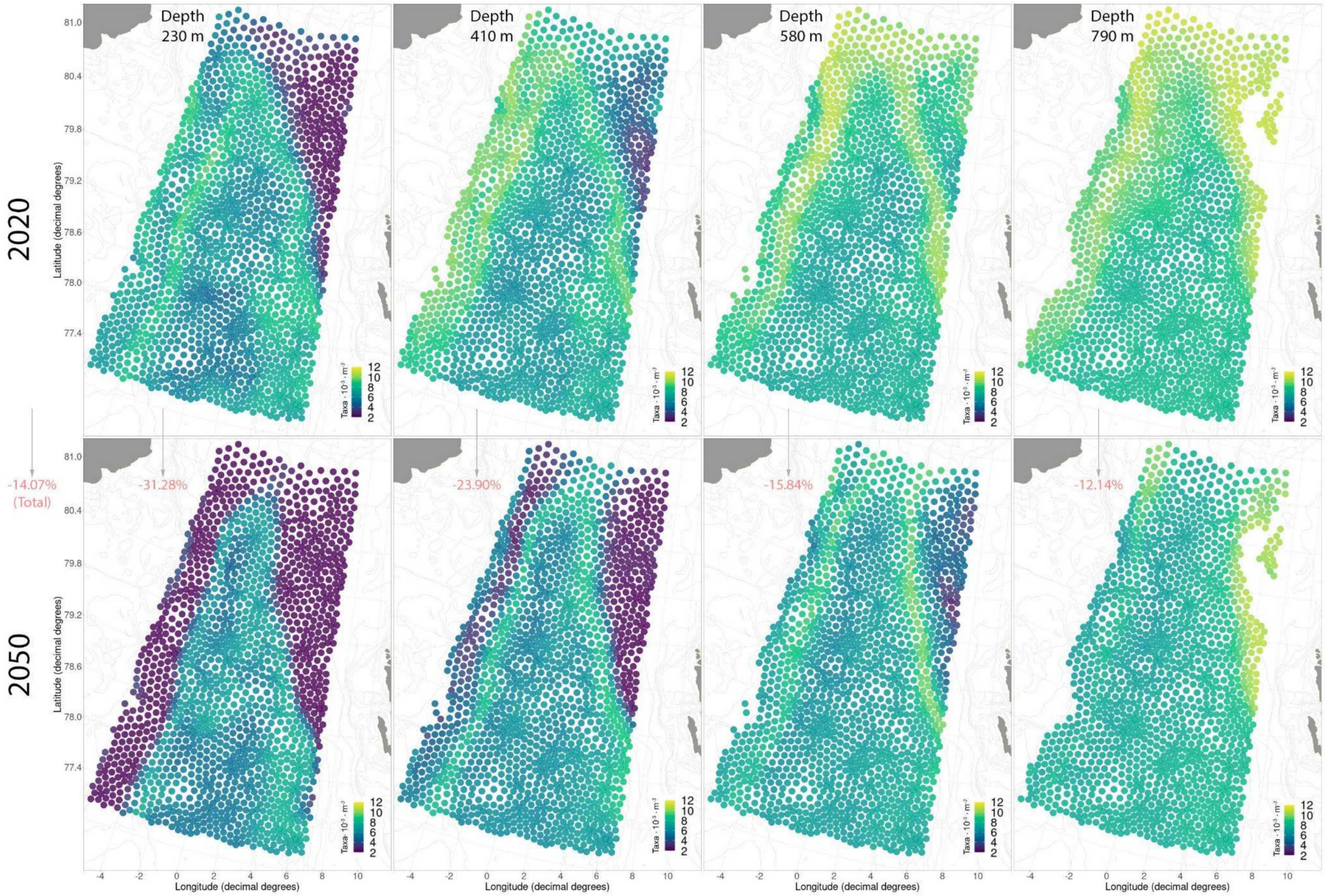
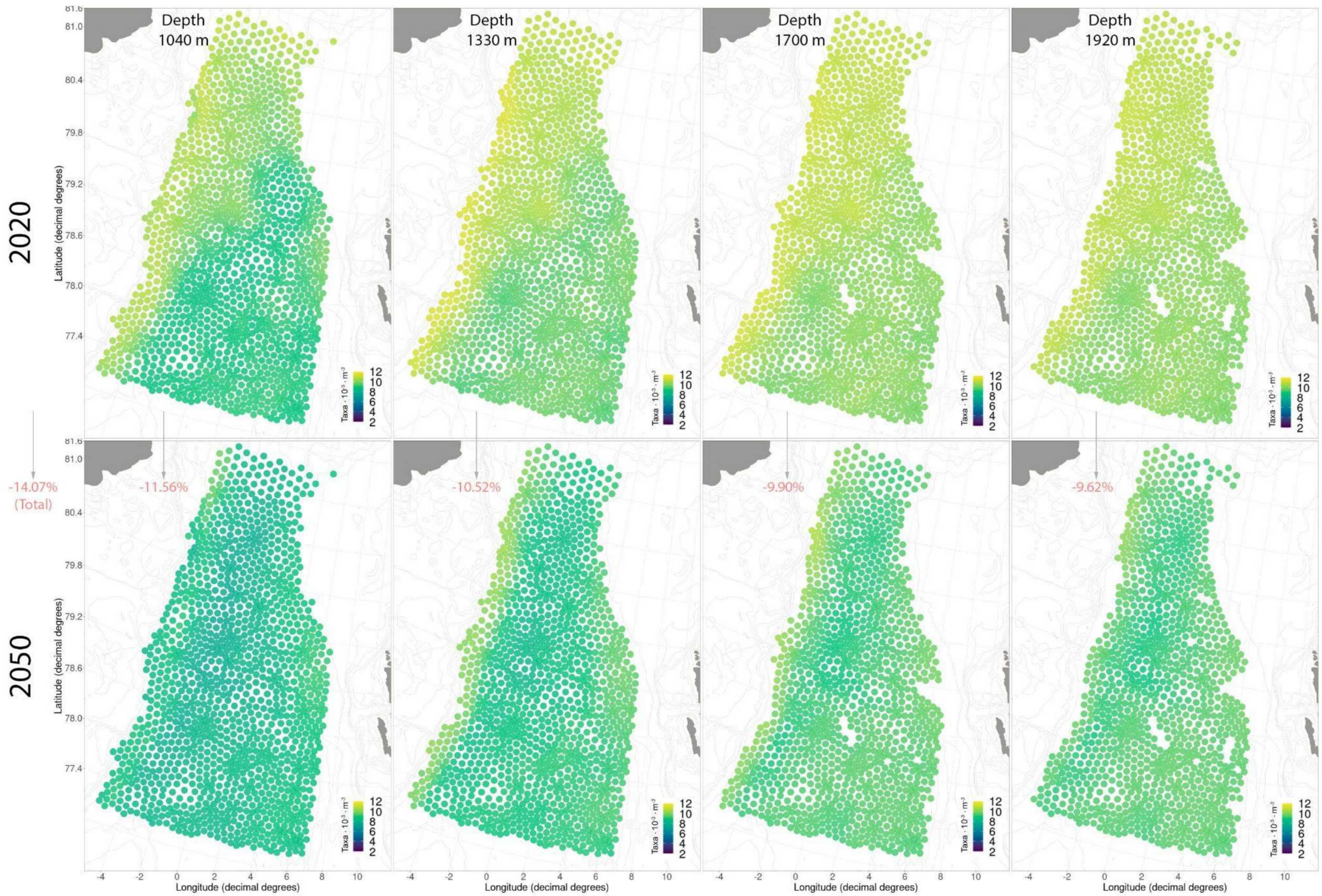
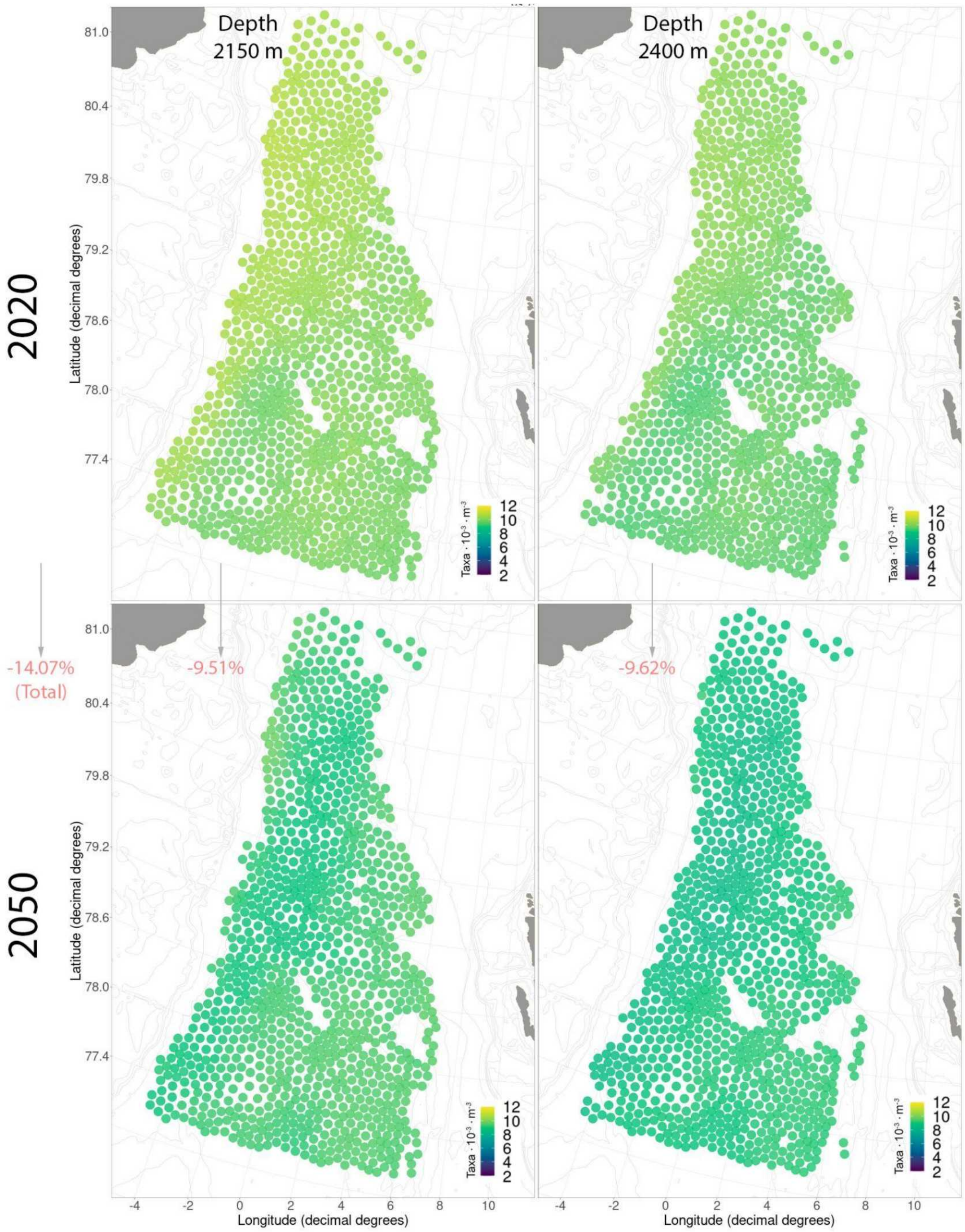


Figure 3.S9. Current and future taxa richness in the studied region. The red values in parentheses give a comparative measure of the retreat/increase in richness of the selected taxa (summer season of 2050 compared to 2020).



Continued Figure 3.S9. Current and future taxa richness in the studied region. The red values in parentheses give a comparative measure of the retreat/increase in richness of the selected taxa (summer season of 2050 compared to 2020).



Continued Figure 3.S9. Current and future taxa richness in the studied region. The red values in parentheses give a comparative measure of the retreat/increase in richness of the selected taxa (summer season of 2050 compared to 2020).

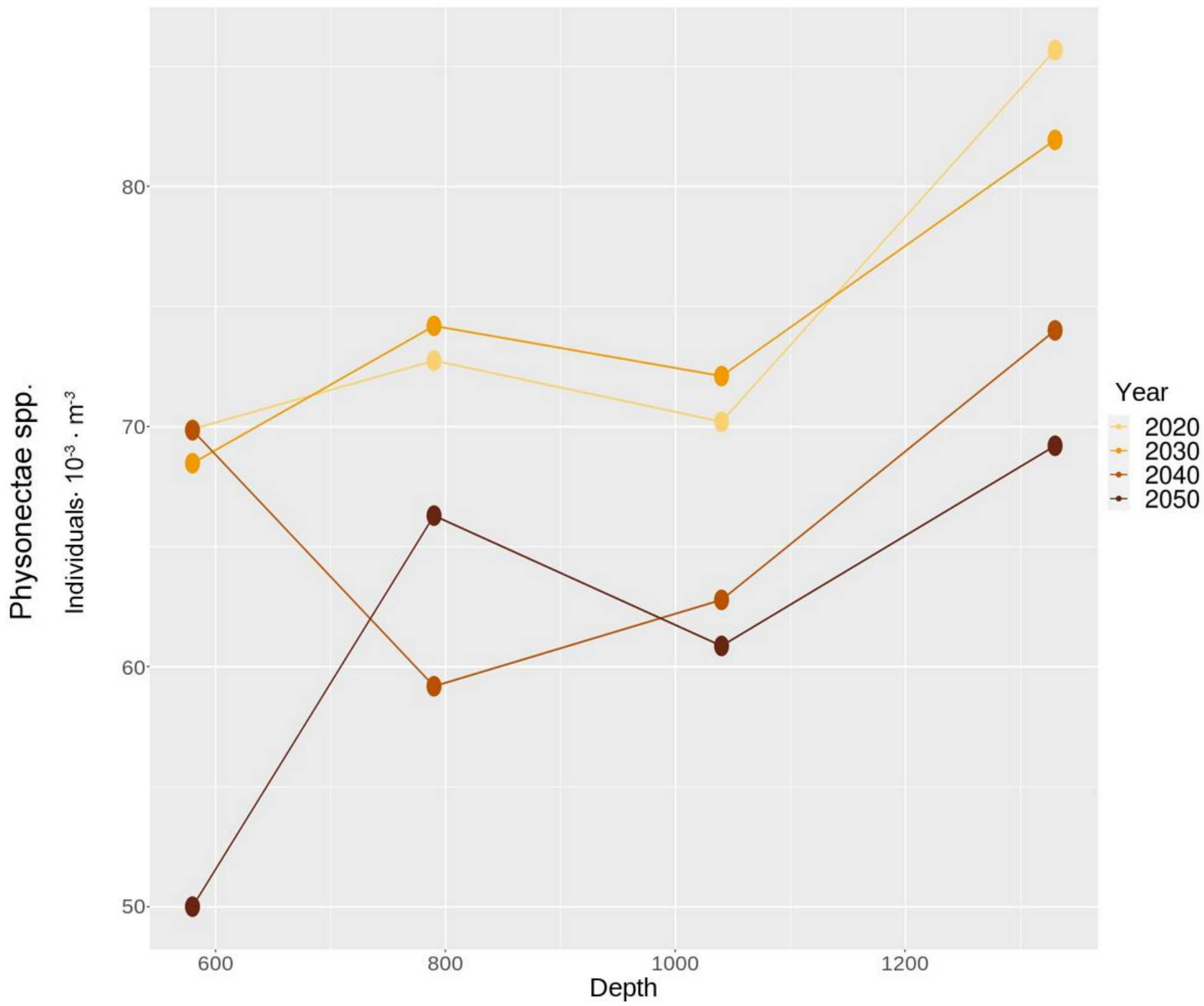


Figure 3.S10. Current and future abundance values of Physonectae at different depth layers. The abundance values were calculated as the mean for each depth layer.

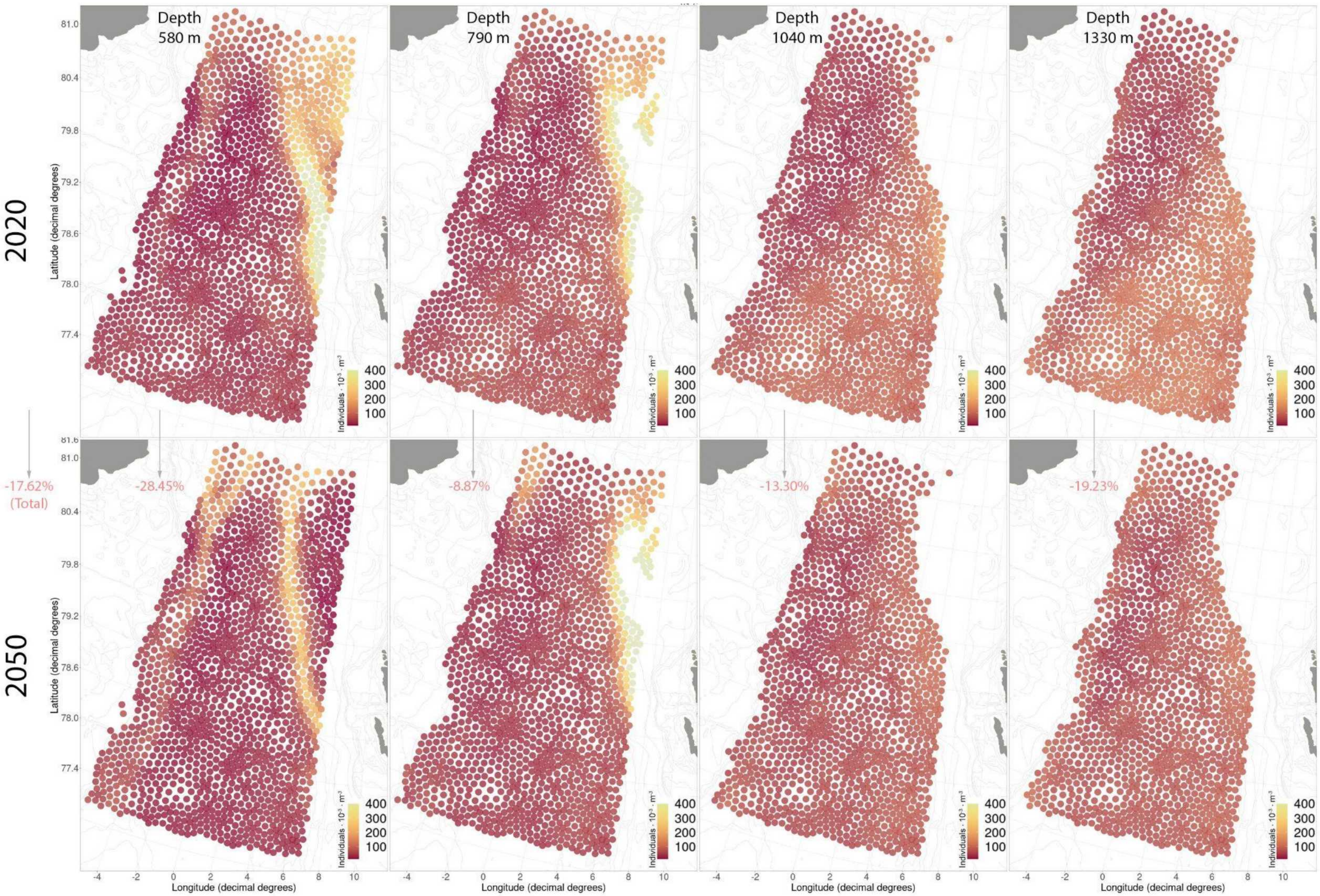


Figure 3.S11. Current and future distributions of the suborder Physonectae in the studied region. The red values in parentheses give a comparative measure of the retreat/increase in abundance of the selected taxa (summer season of 2050 compared to 2020).

Chapter 4. In-situ observations of gelatinous zooplankton aggregations in inshore and offshore waters along a poleward gradient

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Author Contributions

This study was conceived by CH and DP. CH carried out the fieldwork. DP carried out all the optical annotations, with input of AH and JJSA. DP performed all analyses, with methodological input of CH. DP was responsible for writing, with extensive input of CH, and further corrections from all other authors resulting in the final version.

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4.1 Abstract

Gelatinous zooplankton (GZ), encompasses species from several phyla (Cnidaria, Ctenophora, Chordata and Chaetognatha), are a critical component of marine food webs, and have an important role in nutrient cycling, and carbon sequestration. Despite recent hypotheses that climate change may result in increases in gelatinous zooplankton, quantifying their abundances remains challenging due to their delicate body structure, complex life cycles and variable population dynamics. In addition, their tendency to form ephemeral, large-scale aggregations makes it difficult to distinguish true ecosystem changes from stochastic fluctuations in their abundance. This is particularly the case for the Arctic ecosystems, where climate change is inducing some of the most rapid abiotic and biotic shifts. Here, baseline studies are generally missing, and GZ has been, until recently, an overlooked component in pelagic surveys. Our understanding of the nature of GZ aggregations and blooms remains generally incomplete. This study assesses the diversity and in-situ vertical distributions of GZ using the towed pelagic camera system “PELAGIOS” in fjord and offshore environments along a poleward gradient from northern Norway, the Barents Sea, to the Svalbard archipelago. We found that Atlantic water masses harbored the highest GZ abundance, while intermediate waters showed the highest diversity. We documented large aggregations of the ctenophores *Beroe* spp. in Van Mijenfjorden in Svalbard, and *Bolinopsis infundibulum* in the open waters of the Barents Sea (> 2670 ind. 1000 m^{-3} at a depth of 100 meters). Other species, including hydrozoans (*Aglantha digitale*, *Melicertum octocostatum*, Pandeidae sp. and Physonectae sp.), the scyphozoan *Cyanea capillata,* ctenophores (*Mertensia ovum* and *Euplokamis* sp.) and other unidentifiable species were found in the different surveys. By linking the vertical distribution and observation on local aggregations with physical and biotic factors, we provide hypotheses on what drives their small-scale distributional patterns. The towed camera surveys allow for accurate in-situ observations and hence provide a better picture of GZ aggregations and small-scale distributions, which are only sparsely documented in the Arctic Ocean.

Keywords: Gelatinous zooplankton, optical *in situ* observations, vertical distribution, ctenophore aggregations, Arctic Ocean

Chapter 5. Discussion

5.1 Major findings

In one of the world's most rapidly changing ecosystems, the Arctic Ocean, gelatinous zooplankton communities are the least studied component, however, recent studies indicate major distribution changes within this group. This dissertation attempts to analyze distribution of gelatinous communities at different spatial scales, from local aggregations (**Chapter 4**), mesoscale studies in Fram Strait (**Chapter 3**), to examining the distribution of the dominant groups of gelatinous zooplankton on a pan-Arctic scale (**Chapter 2**). This work employs a multi-level data collection approach informed by historical data (**Chapter 2**) and newly collected high-quality optical observations (**Chapters 3 and 4**), together with advanced spatio-temporal modeling (**Chapter 3**). This thesis provides a comprehensive overview of the distribution, abundance, community structure, and spatiotemporal dynamics of gelatinous zooplankton, both in historical context and projected for the end of this century on the Pan-Arctic scale (**Chapter 2**).

RQ1: What is the state of historical data on gelatinous zooplankton in the Arctic Ocean?

- The analysis of the biogeographic databases has shown that the degree of overlap in the gelatinous zooplankton occurrence data in the Arctic regions, retrieved from different public databases, is very low. For example, a comparative analysis of the two largest databases has shown that the number of repeated values in the OBIS and GBIF databases is about 5% of the total (**Chapter 2**). This low level of overlap highlights the need for the use of multiple databases in order to build reliable models of species distributions. Such an approach significantly reduces sampling bias and also improves the spatial coverage of the data.
- Publicly available data on gelatinous zooplankton in the Arctic Ocean mainly include records for the epi- and mesopelagic zones. Data for bathypelagic species and zones are extremely limited. Considering the data obtained in this work, as well as the analysis of public databases, it can be suggested that true Arctic species tend to inhabit deeper layers of the Arctic Ocean (**Chapters 2, 3)**. Thus, the importance of further research in the deep ocean is critical.

RQ2: How do optical surveys contribute to the assessment of diversity, abundance, and community composition of gelatinous zooplankton in the Arctic region?

- Using optical data, I described several new findings on species distributions: The presence of the species *Bathykorus bouilloni* was described for the first time in the deep waters of Fram Strait, and its southernmost Atlantic distribution was recorded here. A significant population of *Sminthea arctica* was observed in the bathypelagic layers of Fram Strait, which may indicate an important, so far neglected, role of this species in the bathypelagic layers (**Chapter 3)**.

- In the southwestern part of the Barents Sea, I documented one of the largest recorded aggregations of adult individuals belonging to the species *Bolinopsis infundibulum* (2.67 ind. m^{-3}). This aggregation was most likely a seasonal phenomenon, supported by a large phytoplankton bloom, and may have extended over several tens of kilometers. In the western part of Svalbard, Van Mijenfjorden, the largest number ever of individuals belonging to the species *Beroe* sp. was also recorded (3-5 ind. m^{-3}), starting right above the seafloor to 103m depth, and was found in oxygen-rich waters below the oxycline (**Chapter 4**).
- In the Svalbard fjords and Fram Strait, differences in the gelatinous zooplankton community structure were found. The highest gelatinous zooplankton abundances were observed in the Atlantic and transformed Atlantic water masses. In contrast, the highest taxonomic richness was found in the intermediate and Arctic water masses (**Chapters 3, 4**).

RQ3: What are the primary physical and biological drivers influencing the distribution of gelatinous zooplankton species at different spatial scales?

- The environmental factors influencing the distribution of gelatinous zooplankton vary significantly between spatial scales and study regions (**Chapters 2, 3, 4**). At the pan-Arctic scale, depth and sea ice cover are the most important parameters. Depth played a significant role in the distribution of gelatinous zooplankton species, with some species having relatively narrow depth ranges (**Chapters 2, 3, 4**). At the marginal sea-ice zone, the influence of sea-ice as a driving factor decreases and other parameters such as phytoplankton concentration, salinity and temperature become more important (**Chapters 2, 3**).
- The local aggregation of the ctenophore *Beroe* sp., found in the fjords of Svalbard, was predominantly associated with a zone of high dissolved oxygen concentrations. The *Bolinopsis infundibulum* aggregation observed in the southwest part of the Barents Sea was primarily associated with a high phytoplankton concentration.

RQ4: Is the Arctic Ocean, particularly the rapidly changing Atlantic gateway to the Arctic, prone to undergo a jellification, with an increase in abundances of gelatinous zooplankton?

- In Fram Strait, the projected environmental shifts are leading to less diverse but more abundant gelatinous zooplankton communities, with specific taxa like the hydrozoan *Aglantha digitale* expected to increase in abundance by 2% in the water column by 2050, while the hydrozoan *Sminthea arctica* is projected to experience a decline in abundance of up to 60%.
- The aforementioned differences in the gelatinous zooplankton community between Atlantic-type water masses and intermediate-Arctic ones (**Chapters 3, 4**) hint towards a potential jellification with progressing Atlantification, since an increased inflow of Atlantic waters will cause an increase in gelatinous zooplankton abundances.

RQ5: Which species are likely to see expanding or contracting ecological niches across the pan Arctic until the end of the 21st century ?

- Corroborating the modeling results found for Fram Strait (**Chapter 3**), we found opposite trends for the hydrozoans *Aglantha digitale* and *Sminthea arctica*, the latter being the only true Arctic species studied in **Chapter 2**. Whereas *Aglantha*'s habitats are projected to expand by ~29% throughout the Arctic Ocean, *Sminthea arctica* was projected to decline, by ~15% on a pan-Arctic scale, with the most significant decline in Fram Strait, along the East.
- The highest niche expansion for all studied species was observed for the scyphozoan *Cyanea capillata*, of which the distribution was projected to experience a range expansion of ~180% by 2050-2099, in comparison to its distributional state from 1950-2014, expanding primarily over Arctic Ocean shelf areas, especially the Eurasian shelf (**Chapter 2**). The other scyphozoan species, *Periphylla periphylla*, was projected to increase by ~62%, shifting northward into the Svalbard fjords and parts of the Barents Sea, and expanding in the Bering Sea (**Chapter 2**).
- For the Appendicularia, I projected an increase in suitable niche by ~130% for *Fritillaria borealis*, expanding throughout the Arctic Ocean. *Oikopleura vanhoeffeni* is expected to expand its habitat niche by ~102% into the central Arctic Ocean, but to contract in the Bering and Barents Seas (**Chapter 2**).
- In terms of ctenophore taxa, *Beroe* spp. is projected to increase its habitat range by about 110%, expanding into the central Arctic Ocean but contracting in the Norwegian and Greenland Seas, whereas *Mertensia ovum* is projected to moderately expand its habitat range by ~84%, with a contraction of range in the Bering and Barents Seas (**Chapter 2**).

5.2 That's all about data

5.2.1 Biases related to sampling devices

Before outlining the diversity of gelatinous zooplankton in Arctic waters, it is necessary to reiterate the challenges associated with their fragility and, as a consequence, the biases introduced by historical sampling activities (which was the major limitation in the selection of species for Pan Arctic modeling in **Chapter 2**). As noted above, conventional sampling methods such as nets and trawls often fragment or completely destroy gelatinous zooplankton, making accurate identification difficult or impossible (Hamner et al., 1975). Furthermore, as shown by Hosia et al. (2017), different sampling devices provide very different views of community richness. For example, only 21% of taxa were captured simultaneously by macrozooplankton trawls and multinets when deployed at the same station (Figure 5.1; Hosia et al. 2017). Based on an analysis of the most commonly used sampling devices for gelatinous zooplankton from the GBIF database, only ~40% of all gelatinous zooplankton observations had associated values for the sampling device used, hence, for the majority of data, sampling devices cannot be derived.

Among the sampling devices specified, nets and macrozooplankton trawls account for more than half of all sampled individuals (Figure 5.1). One of the most commonly used plankton nets is the Bongo net that is often towed obliquely or vertically hauled from depth (sometimes from 1000 m and deeper) to the surface. Thus, depth data related to the net catches are not accurate, as they average the depth over the entire vertical transect. While, as has been shown in **Chapters 2, 3, and 4** of this thesis, the vertical dimension is critically important in understanding the distribution of gelatinous zooplankton. On the other hand, video surveys can more accurately assess the diversity and abundance of the most sensitive GZ groups (e.g. ctenophores), and have exact depth data associated with the in-situ observations (Raskoff et al., 2005; Hoving et al., 2019). Although optical imaging techniques (mostly ROV-based observations) have been predominantly used since the early 2000s, they already account for 25% of all records in the GBIF database (Figure 5.1).

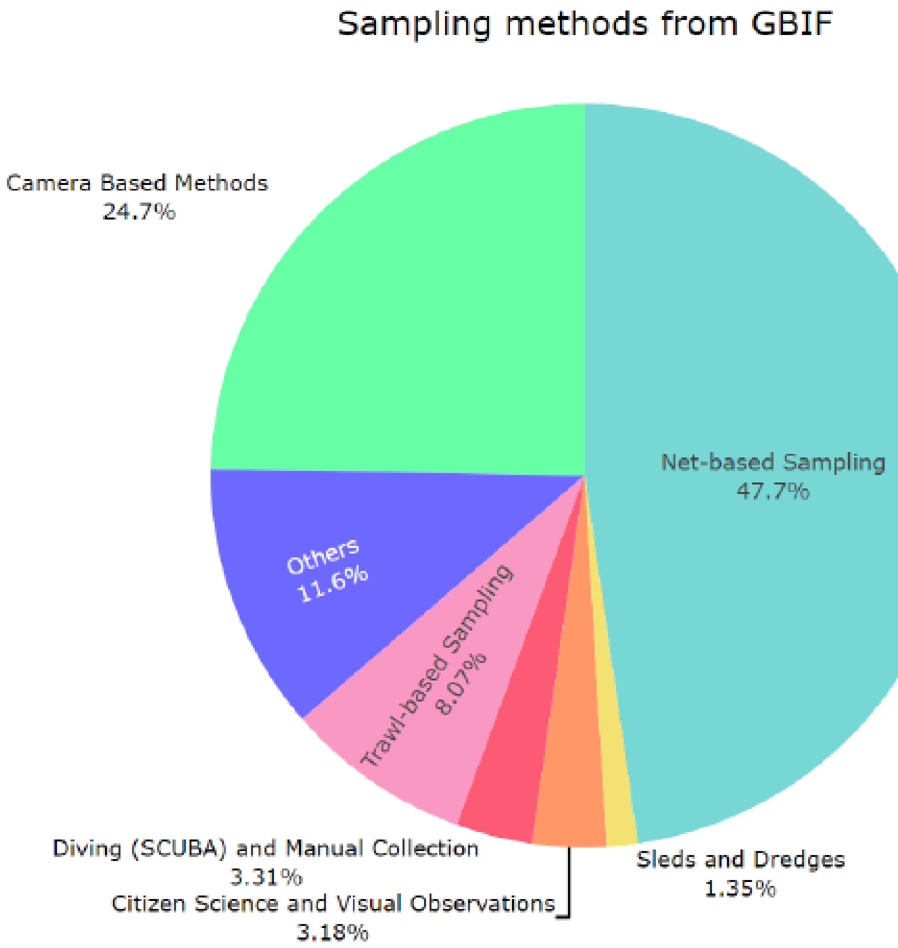

Figure 5.1. Pie chart showing the use of different methods for sampling gelatinous zooplankton. Over 400 of the most used devices have been grouped into 7 categories. Data were taken from Global Biodiversity Information Facility (gbif.org), for the taxa Ctenophora, Cnidaria (Hydrozoa, Scyphozoa, Cubozoa, and Staurozoa), Tunicata (Thaliacea and Appendicularia), and Chaetognatha.

5.2.2 Current state of the databases

Historical data were retrieved from several databases, including JeDI (Jellyfish Database Initiative), OBIS (Ocean Biogeographic Information System), GBIF (Global Biodiversity Information Facility), and PANGAEA, which had constraining factors that limited the variety of species that could be analyzed and the types of models that could be applied to them (**Chapter 2**). For example, the JeDI database had an extremely small amount of data collected for the Arctic. The data from PANGAEA were of higher quality, presented in a station-based format, and as a result it was possible to get not only presence, but also presence-absence, or sometimes, abundance data. However, as with JeDI, the amount of gelatinous zooplankton data submitted in PANGAEA was very limited. As for OBIS and GBIF, despite the large amount of records, almost all data in these databases were in presence-only format. In addition, the quality of the data from OBIS and GBIF was often poor, e.g., the data often had land-based geographic coordinates or depths that exceeded bathymetric limits. Among the most striking quality problems was the overlap of occurrences in the OBIS and GBIF databases for the taxa examined in Chapter 2, which was only 5%. These databases showed significant differences in data entry and a rather pronounced spatial bias.

Another problem was the inability to cross-check presence data, as only a few percent of the original data had supported metadata such as photos or genetic sequences. For gelatinous zooplankton this was particularly critical, as misidentification is rather common (Lindsay et al., 2017). One of the most typical errors we found in these databases was the occurrence of *Aeginopsis laurentii* (a species that occupies shallow, coastal environments) in the central deep Arctic. This species was likely misidentified and is most likely *Bathykorus bouilloni*, a species recently described by Raskoff in 2010, morphologically similar to *Aeginopsis laurentii*.

Thus, the aforementioned neglect of the GZ in pelagic studies in the past has also dramatically affected the quality of the data in public databases. For example, most zooplankton studies in the PANGAEA database only occasionally recorded gelatinous zooplankton species, while crustaceans and other groups were much better covered. This limitation made community level modeling impossible and significantly reduced the ability to select optimal species distribution models in **Chapter 2**. Considering these issues, we used only presence data in **Chapter 2**. Data were aggregated from multiple databases, which allowed us to increase the spatial coverage of the resulting dataset. In addition, we selected only those species that were least prone to misidentification problems.

5.2.3 Species diversity and presence data from open source databases

To gain a comprehensive understanding of the diversity and occurrence data for gelatinous taxa, sampling data from the OBIS and GBIF databases are presented below and compared to taxonomic diversity information from WoRMS. On the basis of this comparison, we can see that the available observations and species richness of these taxa are quite different (Figure 5.2). For example, the class Hydrozoa, with the highest number of described species (3,832), is represented by 629,493 occurrences in the OBIS and GBIF databases. At the same time, the phylum Chaetognatha, has, in contrast to Hydrozoa, only 132 species, and also rather high occurrence values in OBIS and GBIF databases with 401,328 presences. The same is true for the Scyphozoa class, which has 242 species to 195,902 occurrences. Similar patterns are observed for the subphylum Tunicata (Appendicularia and Thaliacea), which has 146 species in WoRMS, while in the OBIS and GBIF databases, we find 151,801 records for Appendicularia and 114,356 for Thaliacea. Species of the class Ctenophora (205 species) have only 37,507 occurrences. The Cubozoa and Staurozoa taxa have the least number of species as well as occurrences, both of which have 49 documented species each and 2,735 and 2,560 occurrences, respectively (Figure 5.2).

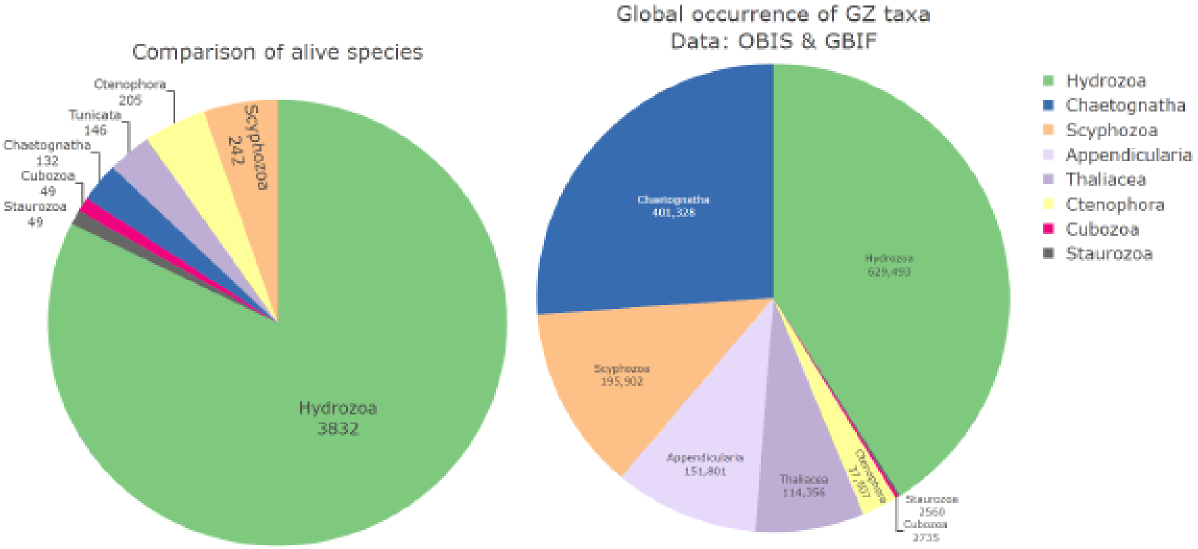

Figure 5.2. Currently extant gelatinous zooplankton species worldwide retrieved from the World Register of Marine Species (WoRMS) database (left). Gelatinous zooplankton taxa occurrences (right) are based on data retrieved from Ocean Biodiversity Information System (OBIS) and Global Biodiversity Information Facility (GBIF).

To this end, I analyzed data from the OBIS and GBIF databases, providing further insights into such differentiation (Figure 5.3). It should be noted, however, that the picture of diversity presented below may be distorted by the fact that the representation of taxa in the OBIS and GBIF databases is lower than the number of species that actually exist. For example, there are 83 species of Ctenophora in OBIS and GBIF, while the number of species based on the WoRMS taxonomic database reaches 205.

5.3 New insights into the diversity and distribution of gelatinous taxa based on optical surveys

In addition to the existing biogeographical data collected from public databases (in **Chapter 2**), this thesis also contributes to the understanding of gelatinous zooplankton biodiversity in the Arctic Seas via newly obtained in situ data (in **Chapters 3 and 4**). Using the PELAGIOS underwater video observing system, the knowledge about the gelatinous biodiversity of the fjords of Svalbard, Northern Norway, the shelf system of the Barents Sea and the deep waters of the Fram Strait has been extended.

One of the most interesting observations is the high abundance of *Sminthea arctica* in the northern parts of Fram Strait, in waters associated with the East Greenland Current system. This species was as abundant in these water regimes as *Aglantha digitale*, another member of the family Rhopalonematidae, is in Atlantic waters, which is considered to be the most abundant hydrozoan in the northern hemisphere. *Sminthea arctica* and *Aglantha digitale* in the Fram Strait showed diametrically non-overlapping distributions, both in terms of depth and geographic extent. Data for *Sminthea arctica*, obtained by Raskoff et al. (2005) using an ROV system, also found this species to be extremely abundant in the Pacific sector of the Arctic Ocean. Based on the fact that the suitable niches of this species cover most of the central Arctic Ocean (shown in **Chapter 2**), it is likely that *Sminthea arctica* is one of the dominant deep-sea species in the Arctic Ocean. In addition, it has been suggested that the species currently classified as *Sminthea arctica* may actually be a complex of closely related species (Schuchert, 2023), but research on this is lacking, with almost no sequences in the genetic databases. Thus, given the presumed ecological importance of *Sminthea arctica* and the lack of molecular data, it represents an interesting target for further research. Regarding *Aglantha digitale*, as mentioned above, this species was indeed the most abundant in our studies, being found in practically all stations from northern Norway to the northernmost points of the Fram Strait (**Chapters 2, 3**). Regarding the distribution of *Sminthea arctica* and *Aglantha digitale* in the Fram Strait, a rather remarkable seasonal variation in the distribution of these species was observed (**Chapter 3**). The mean depth of *Aglantha digitale* ranged from 300-400 m in June to 400-600 m in August/September. *Sminthea arctica*, on the other hand, moved from 800 m in June to the deeper layers of 1600 m in August/September. Such vertical shifts have been well described for *Aglantha digitale* and were explained by its ontogenetic migrations (Pertsova et al., 2006).

Another noteworthy observation was the detection of a significant number of individuals of *Bathykorus bouilloni* in the deep areas of the Fram Strait. As shown in Ronowicz et al. (2015), this species has not been previously recorded in this region, nor is it present in the current versions of the OBIS and GIBF databases. Thus, we document here the southernmost occurrence of this species in the Atlantic sector. Surprisingly, considering the fact that this species belongs to the order Narcomedusae, which are versatile predators, we found their abundances to be quite high in deeper regions, with more than 0.15 ind. 10^{-3} m at depth below 1600m, suggesting that the importance of this species in the Fram Strait food web could be significant.

With regard to the use of optical surveys for providing accurate abundance estimates, I show in **Chapter 4**, that, the PELAGIOS system was able to document large aggregations of the ctenophore species *Beroe* spp. and *Bolinopsis infundibulum*, while the nets greatly underestimated their abundances and overlooked their local aggregations. While the nets recorded an abundance of 0.1 ind. 10^{-3} m of *Bolinopsis infundibulum*, the PELAGIOS system recorded a much higher abundance, estimated at about 2.67 ind. 10^{-3} m at depth 100m, and 0.67

ind. 10^{-3}m over the entire water column (i.e. 6.7 times higher than the nets as documented in Havermans, 2023). These aggregations have been found at a specific depth, a layer ~50 meters, which to a large extent explains the strong bias in their abundance when they were sampled by nets. In addition, the species *Bolinopsis infundibulum* is particularly sensitive to net sampling and posterior handling of the samples, as mature individuals are almost completely disintegrated during the sampling and sorting process and identification can only be achieved on parts caught, or with molecular methods.

Since the PELAGIOS system generally had its limitations, small hydrozoan and ctenophores species were not always identified to species or genus levels (in **Chapters 3, 4**). This was mainly due to the fact that the data analyzed in **Chapter 4** were obtained in fjords, where the large amount of POC influenced the focus of the camera, challenging species identifications. Conversely, data collected in the deeper, less turbid waters of Fram Strait, down to 2400 m, allowed for better species identification along the water column (**Chapter 3**). In this case, a large number of species were identified to species and genus level, and outperformed nets.

Given the aforementioned pros- and cons- of sampling methods, PELAGIOS is optimal for studying mid- to deep-water organisms (> 1 cm). PELAGIOS has been shown to estimate the abundance of *Bolinopsis infundibulum* in the Barents Sea at rates seven times higher than other net-based methods (Bongo, multi- and WP3 nets; Havermans 2023). However, in environments where the amount of noise introduced by (POC) and increased light was high, identification of small organisms becomes problematic. This issue is particularly evident in the euphotic depth layer (typically the upper 50 meters). For instance, it was notably challenging to identify species of Calycophorae siphonophores during the PELAGIOS transects of the PS126 expedition, which occurred in the summer season (June) when these organisms were primarily found as juveniles, in very high abundances in the nets (Havermans et al. 2021). In contrast, identification was easier on expedition PS121, later in the season (August), when these species were more mature and the amount of POC was much lower. Additionally, one of the most significant limiting factors is the physical presence of sea-ice; PELAGIOS cannot operate in dense sea-ice conditions and is limited to usage in open waters or polynyas. Interestingly, from these polynyas the most valuable data on truly Arctic species were obtained. In this way, PELAGIOS is advised to be used in combination with depth-stratified net hauls and eDNA methods (Havermans et al., 2022), which should provide better coverage of species richness and a more complete picture of biodiversity.

5.4 Modeling of the suitable niches and ecological drivers of distribution of GZ

In **Chapters 2 and 3**, we focused on the modeling of the suitable niches for gelatinous zooplankton taxa. Since the concept of ecological niches is interpreted differently in the scientific literature (Leibold 1995), we define a niche as an n-dimensional hypervolume (of environmental and resource factors) within which species are able to persist and reproduce (Ovaskainen & Abrego, 2020). In **Chapter 2**, the realized niches for gelatinous zooplankton were considered at the pan-Arctic scale, independent of the effects of other species, while at the mesoscale study in Fram Strait (**Chapter 3**), gelatinous species were modeled in the context of communities.

At the pan-Arctic scale, Maximum entropy modeling approach (MaxEnt) has been used to model suitable habitat niches for gelatinous zooplankton throughout the pan Arctic region. To date, MaxEnt is the most widely used SDM tool in oceanographic research and has the highest predictive metrics among presence-only models (Valavi et al., 2022). Despite its widespread use, only a small fraction of studies follow strict model selection procedures (Melo-Merino et al., 2020). In **Chapter 2**, we followed strict model selection protocols and used the modeling selection R package 'ENMeval' (Kass et al., 2021). The 'ENMeval' package allowed us to select the most optimal models based on feature classes, background points, regularization parameters, as well as allowed the selection between multiple sets of the environmental parameters. Furthermore, we selected the optimal models from over 20k models based on multiple predictive parameters (AUC, AIC, 10th omission rate, and CBI). In **Chapter 3**, we selected HMSC for its highest performance among community species distribution models (Norberg et al., 2019). In Chapter 3, we employed the Hierarchical Modelling of Species Communities (HMSC) framework to link species occurrence and environmental covariates with community formation processes (Ovaskainen & Abrego 2020). In order to sample the posterior distribution, we used four Markov Chain Monte Carlo (MCMC) chains and ran each for 375000 iterations.

Chapter 2 uses high-resolution environmental data from the Max Planck Institute Earth System Model (MPI-ESM1.2; Gutjahr et al. 2019) to address pan-Arctic shifts in the coming decades, comparing changes in habitat niches from 1950-2014 to 2050-2099. In contrast, **Chapter 3** focuses on a mesoscale study in Fram Strait to estimate summer abundance of gelatinous zooplankton taxa for the coming decades (2030, 2040, 2050) using the Finite Element Sea Ice-Ocean Model (FESOM; Semmler et al., 2018) for spatio-temporal projections. We also applied two types of climate scenarios, SSP245 and SS370, with medium-low and medium-high ratios, respectively. Since most gelatinous zooplankton groups are highly depth-zoned, we also modeled the niches of the studied species in three-dimensional space (**Chapters 2, 3)**.

The model in Fram Strait was run on high-quality abundance data from Arctic expeditions conducted shortly before or during this thesis, allowing for community level modeling of gelatinous taxa. Since the PELAGIOS has a CTD mounted on its frame, the use of direct CTD measurements as predictors was expected to improve the quality of the environmental signals. Although the number of stations surveyed with PELAGIOS was rather limited, the projected redistribution of abundance is consistent with those predicted on longer-term studies (Manko et al., 2020, 2022). Adequate sampling of representative water masses allowed us to interpolate (rather than extrapolate over unknown environmental conditions for the region) distributional changes over the projected period. As a result, we obtained regional current and projected abundances for Fram Strait, which has not yet been achieved for GZ taxa. In the case of historical data, modeling at the community level is considered rather challenging, as GZ communities have rarely been sampled and targeted by previous expeditions (Table 2S1); moreover, only presence data are available, which limits the choice of methods. As noted above, MaxEnt performs extremely well based on performance metrics; through a rigorous model selection process, we established a unique model for each species (with a unique number of feature classes, background points, and regularization parameters) that allowed us to capture the essence of the data and its responses to the environment for each species. An intermodal comparison of results for two taxa present in both studies, *Aglantha digitale* and *Sminthea arctica*, revealed a high degree of agreement between trends in Fram Strait. Specifically, the decline of *Sminthea arctica* in the regions dominated by the East Greenland Current was observed in both models (**Chapters 2** and **3**), while Aglantha digitale experienced a decline from the surface layers, but showed a slight overall increase in the water column.

5.5 Environmental drivers

In **Chapters 2 and 3**, I assessed the environmental variables with the greatest influence on the distribution of gelatinous zooplankton. With both datasets and methods used, depth was identified as the key factor, explaining from 20 to 40% and 10 to 60% at the Pan-Arctic and at the Fram Strait mesoscale, respectively. One of the most remarkable observations was the segregation of depth niches among closely related species, e.g. one species of the family Rhopalonematidae, *Aglantha digitale*, occurred in the upper epi- and mesopelagic layers, while another species of this family, *Sminthea arctica*, occurred in the depths at the lower mesopelagic boundaries and was most abundant in the bathypelagic layers. This difference was typical of the results of both **Chapters 2 and 3**, where their ecological niche boundary was situated at depths of about 800-1000 meters, both at the level of the Fram Strait mesoscale and the pan-Arctic. Other closely related hydrozoan species also had non-overlapping preferred depths, but less prominent than in *Aglantha digitale* and *Sminthea arctica*. Both species were also heavily driven by the temperature gradient in both studies (Chapter 2, 3), this is in congruence with Luo et al., 2014, who found that depth and temperature explained over 52% of the variation. In the observational study in Chapter 4, depth zonation preliminarily appeared to be the most important determinant of *Bolinopsis infundibulum* aggregations, with over 95% of its abundance observed between depths of 100 and 150 meters, largely due to the potential avoidance of predators in the surface and near-bottom layers.

When considering the influence of environmental factors in general in the Fram Strait and on the pan-Arctic scale, the most striking difference is the importance of sea ice cover in the explanatory power of the models. On the mesoscale in the Fram Strait, as shown in **Chapter 3**, sea ice made a minor contribution to the explanatory power of the distribution models. In contrast, in **Chapter 2**, sea ice was found to be a significant variable in explaining taxa distributions (ranging from 25 to 90% of permutational importance). However, if we consider the two spatial scale limitations, for species analyzed in **Chapters 2 and 3**, which are the hydrozoans *Aglantha digitale* and *Sminthea arctica*, the major limiting factors affecting their distribution in the Fram Strait were interplay of depth and temperature (**Chapter 2**). The importance of the sea-ice was rather minor in this area (based on **Chapter 3**) which is in line with **Chapter 2** findings. Its importance increased in areas more densely covered by sea ice (**Chapter 2**).

In general, our modeling results and observations agree well with existing knowledge about the driving factors of gelatinous zooplankton distribution. As shown earlier, temperature and depth were the major limiting factors for hydrozoans such as *Aglantha digitale* and *Sminthea arctica*, especially in the open and sea ice marginal zones. In support of this, a study by Luo et al. (2014), with a similar set up with optical observations and SDMs, found that these two parameters (temperature and depth) accounted for over 52% of the explanatory power for hydrozoan taxa in North Pacific waters. Although salinity had limited explanatory power due to low variation, Siphonophorae taxa in Fram Strait responded notable to its variation, with salinity accounting for 17% of variation of Calycophorae species. This is consistent with Luo et al. (2014), where salinity also accounted for a small proportion of variation, with Calycophorae taxa having the highest values, contributing an average of 13%. While oxygen was not included in our modeling studies, due to its strong correlation with temperature, based on the observational studies in Svalbard fjords highlighted its significant influence on *Beroe* sp. distribution. In particular, large aggregations of Beroe sp. were found in oxygen-rich waters below the oxycline. These observations are consistent with the avoidance of oxygen minimum zones by *Beroe* spp. previously observed with PELAGIOS in the North Atlantic (Hoving et al., 2019).

This thesis also discusses the potential ecophysiological causes that influence such responses to environmental variables. In particular, *Beroe* spp. preferred more oxygenated waters, possibly due to the fact that this taxa is known to be an active hunter and its metabolic costs increase dramatically during hunting. Regarding ecophysiological explanations for ecogeographic shifts, the highest increase in abundance observed for *Cyanea capillata* across the Eurasian shelf could be explained by the fact that average temperatures around the Eurasian shelf are projected to exceed 4 degrees Celsius, under which *Cyanea capillata* is known to have a high survival rate of scyphistomae (Widmer et al., 2016). In addition, this species can tolerate relatively low salinities, which is a feature of the Eurasian shelf region due to strong riverine inflow and would be further enhanced.

5.6 Gelatinous zooplankton species in the Arctic region

In order to better interpret my results on the projection of potential shifts in the gelatinous zooplankton communities of the Arctic Ocean, it is important to also have an understanding of their diversity and distribution on a global scale in relation to the northern (Atlantic and Arctic) regions. It can be observed that Ctenophora and Appendicularia are particularly abundant in Arctic ecosystems. Specifically, 8.16% of all globally recorded occurrences of Ctenophora and 6.97% of Appendicularia are observed in the Arctic regions. From an evolutionary perspective, one possible explanation for the high abundance of Appendicularia in the Arctic region is that these species are well adapted to feeding close to ice edges (Deibel et al., 2005). They can benefit most from both the microbial protists and diatoms that are prevalent in these areas (Deibel et al., 2005), and are known to outcompete copepods in microbial food web-based systems (Touratier et al., 2003). Despite their abundance, only a few species are well documented in the Arctic (*Oikopleura vanhoeffeni, Fritillaria polaris and Fritillaria borealis*; Figure 5.4.) Of these, *Oikopleura vanhoeffeni* and *Fritillaria borealis* were the most represented in the four databases I used, and their distribution was examined in **Chapter 2**. Among them, *Oikopleura vanhoeffeni* can be considered as the northernmost species, with an average latitudinal distribution centered around 71°N (Figure 5.4). Surprisingly, other members of the Tunicata (salps and pyrosomes) are virtually absent from the Arctic Ocean, with only sporadic observations at the southern boundaries of the region (Figures 5.3, 5.4). The other most 'Arctic' taxon, Ctenophora, is also represented by a small number of species, the most northerly of which are *Pleurobrachia arctica* and *Mertensia ovum* (Figure 5.4). *Mertensia ovum* was found to be very abundant in the under-ice environment (Purcell et al., 2018, pers. obs. from video data analyses of the MOSAiC PS122 campaign). They are also known to overwinter under the sea ice, which provides physical protection and a constant supply of food (Purcell et al., 2018).

Arctic occurrence data of Hydrozoa and Scyphozoa represent 3.6% and 1.5%, respectively, of the world's total (Figure 5.3). Hydrozoa have the highest number of Arctic species compared to any other gelatinous taxon, with more than 38 species found predominantly above the Arctic circle (Figure 5.4). One of the most abundant and widely distributed species within Hydrozoa is *Aglantha digitale* (**Chapter 2**). The most northerly species of hydrozoans are *Sminthea arctica*, *Bathykorus bouilloni* and the siphonophore *Rudjakovia plicata*, both of which represent the deep water members of their group (Figure 5.4). Interestingly, despite their modest relative abundance, the scyphozoans are represented by only six species that are predominantly found above the Arctic circle, of which *Atolla tenella* is the most northerly species (Figure 5.4). Some Scyphozoa taxa (e.g., *Chrysaora melanaster*, not studied here) are well adapted to overwinter in Arctic coastal environments, descending to the bottom during winter and using their long tentacles to drag themselves along the bottom to feed on epibenthic macrofauna (Purcell et al., 2018).

The phylum Chaetoghatha, which is highly abundant in the Arctic region (4.2% from the global recorded population found in these waters; Figure 5.3), does not have purely Arctic species, but is mainly represented by cosmopolitan and arcto-boreal species (Figure 5.4). Among these, *Eukrohnia hamata* (cosmopolitan) and *Parasagitta elegans* (arcto-boreal) are two of the most common species of Chaetoghatha in the Arctic Ocean (Kosobokova et al., 2021). Chaetognatha species are important predators in the Arctic Ocean and can account for up to 10-15% of the community's zooplankton biomass (Kosobokova et al., 2010; Kosobokova et al., 2021). These two species are also known to have different niche preferences, with *Eukrohnia hamata* mainly found in deep water, and *Parasagitta elegans* in coastal areas (Kosobokova et al., 2021).

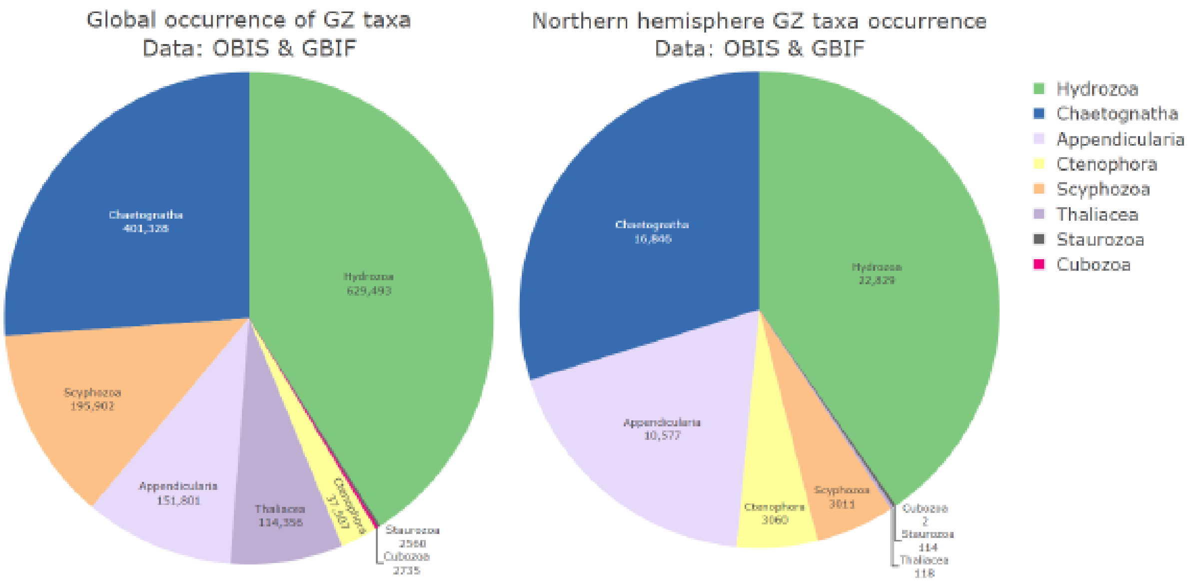

Figure 5.3. Comparative analysis of global and northern hemisphere marine gelatinous zooplankton taxa occurrences based on data retrieved from Ocean Biodiversity Information System (OBIS) and Global Biodiversity Information Facility (GBIF). Repeated values from the database were removed.

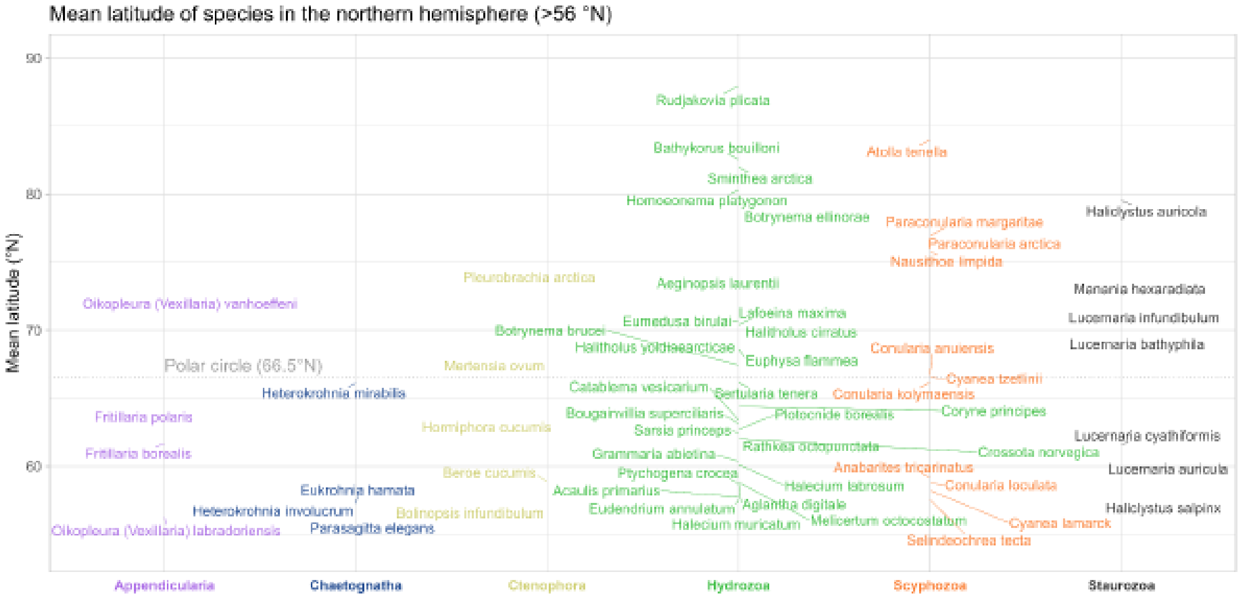

Figure 5.4: Mean latitudinal distribution of gelatinous zooplankton species in the northern hemisphere (>56°N). Mean latitudinal distributions were calculated using occurrence data from the GBIF and OBIS databases. For Hydrozoa, only the most abundant species at each latitude were shown.

Before proceeding to the results of the discussion of spatial shifts, it is appropriate to review the spatial distribution of gelatinous zooplankton groups in the Arctic Ocean. On the spatial distribution scale we can see that the most recorded species (according to OBIS and GBIF databases for 1950 to 2014; Figure 5.5), covering most of the region, are members of the Hydrozoa, Appendicularia and Chaetognatha. Hydrozoa have the largest number of species and cover the largest area of the region (Figure 5.5). Ctenophora species are mainly found near the sea ice margin and in coastal areas (Figure 5.5). Scyphozoa species are mostly recorded at the boundaries of the arcto-boreal shallow water zones, but a few species are also found in the central Arctic regions. Staurozoa and Cubozoa species are extremely rare and mostly found in the warmer waters of the Atlantic sector of the Arctic Ocean. While species of the Appendicularia cover most of the Arctic region, the Thaliacea are mainly restricted to the North Atlantic and occur in very small numbers. Coverage of the region by Chaetognatha species is also extremely high and is dominated by just a few species (Figure 5.4).

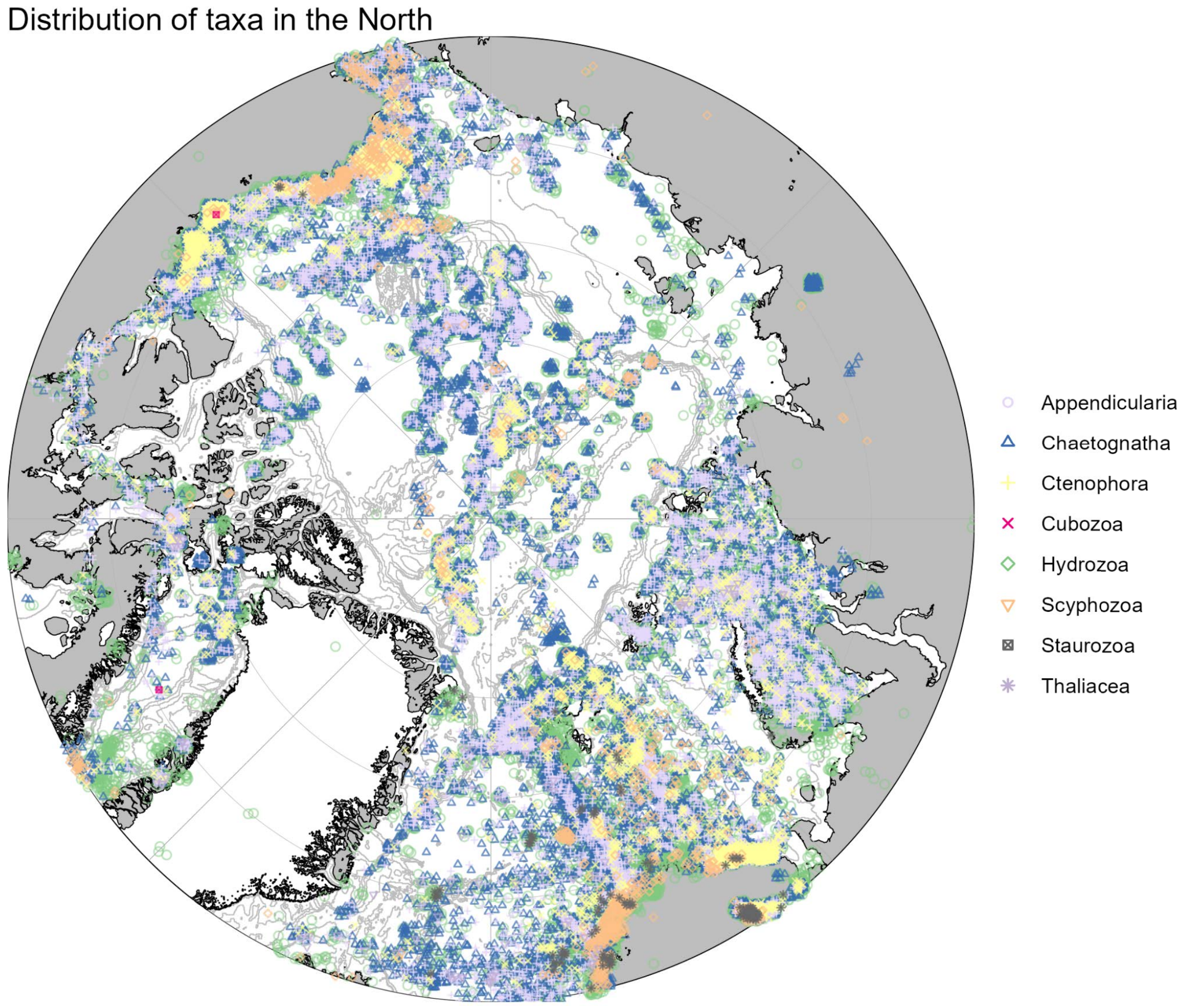

Figure 5.5: Arctic distribution of gelatinous zooplankton based on OBIS and GBIF databases.

5.7 Modeling results of ecogeographical shifts of gelatinous species distributions

This thesis considers projections of changes in abundance for four taxa of gelatinous communities in Fram Strait (**Chapter 3**), two of which are at the species level (*Sminthea arctica* and *Aglantha digitale*). At the pan-Arctic level, we projected the suitable niche for eight taxa (**Chapter 2)**, of which seven are at the species level (*Aglantha digitale*, *Sminthea arctica*, *Periphylla periphylla*, *Cyanea capillata*, *Oikopleura vanhoeffeni*, *Fritillaria borealis*, *Mertensia ovum*) and one at the genus level (*Beroe* spp.). Among these species, two are classified as cosmopolitan, being both representatives of the class Scyphozoa (*Cyanea capillata* and *Periphylla periphylla*), one as having a subtropical-arctic distribution (*Aglantha digitale*), and the rest as arcto-boreal species (*Sminthea arctica*, *Mertensia ovum*, *Oikopleura vanhoeffeni*, *Fritillaria borealis*). Of the latter two, *Oikopleura vanhoeffeni* is considered a stenothermal cryophile, while *Fritillaria borealis* is an eurythermic euryhaline species (Choe and Deibel, 2008). Among these species, the most likely climate-change winners are *Cyanea capillata* and *Fritillaria borealis*, whose niches are projected to increase by ~180% and ~130%, respectively (Table 5.1). The expansion of *Cyanea capillata* along the Eurasian shelf is particularly noteworthy. Another Scyphozoa species, *Periphylla periphylla*, increases its suitable niches by ~62%, with the largest increases in the Svalbard fjords and parts of the Barents Sea. Ctenophora species (*Mertensia ovum* and *Beroe* spp.) increase their niches in the central parts of the Arctic Ocean by ~110% and ~84%, respectively (Table 5.1), while the niches of *Mertensia ovum* narrow in the Bering and Barents Seas. *Aglantha digitale*, the most abundant gelatinous zooplankton species in the Arctic Ocean, is expected to expand its preferred niches even further across the Arctic Ocean, with an expansion of ~29%. The strongest decline is observed for *Sminthea arctica*, whose niches narrow towards the poles, with a total loss of ~ -15%, while based on predicted abundance values for Fram Strait, the decline is even stronger ~ -60% of abundance, (Table 5.1), especially noticeable in the East Greenland Current.

Before discussing in depth these main findings it is worth recalling the previously mentioned dominance of arctic boreal and boreal taxa in the historical databases. First, as shown with *Bathykorous bouilloni* and *Sminthea arctica*, many species of gelatinous zooplankton, which are indeed abundant, have only been proven to be so in recent decades using optical methods (Raskoff et al., 2005; 2010; **Chapter 3, 4**). This circumstance, as well as the problem of misidentification, limited the selection of species available for analysis in **Chapter 2**, where the pan-Arctic scale was considered. This is because most reliable data were mainly found for boreal or arcto-boreal taxa, while true Arctic species are rarely found in large numbers in these databases. As shown in Ronowicz et al. 2015 study, only 19% of all Hydrozoa found in the Arctic can be considered truly Arctic, and most of these are benthic hydroids. At the same time, we can observe from Figure 5.4 that Hydrozoa are the most abundant gelatinous group in the Arctic, with their species having the most northerly distribution. While other groups of organisms such as Appendicularia and Chaetognatha, despite their abundant distribution throughout the Arctic, have almost no truly Arctic species (Figure 5.4). This low number of truly Arctic species may be due to several factors; first, the high connectivity between Atlantic and

Arctic waters has resulted in a variety of adaptive strategies that allow different gelatinous taxa to thrive in both environments (Ronowicz et al. 2015). Second, the relatively young age of the Arctic ecosystem, primarily as a result of Pleistocene glaciations, is a factor explaining the low number of endemic species (Dunton et al., 1992). Third, sampling bias, especially in deep Arctic waters, may play a significant role in distorting our knowledge about gelatinous zooplankton biodiversity. Fourth, it is likely that true Arctic gelatinous species inhabit predominantly deep sea zones, which are likely to contain the highest biodiversity of Arctic species yet to be discovered, of which some may be endemic. Given the strong trend toward niche expansion for most of the arcto-boreal and cosmopolitan species modeled, this would imply a number of further poleward colonizations (e.g., by *Periphylla periphylla*) and cause a profound restructuring of high and central- Arctic pelagic communities.

Table 5.1 Projected changes in the distribution of gelatinous zooplankton and their potential ecological impacts.

Species	Change in Pan-Arctic habitat niches (by 2050-2099)	Changes in the Fram Strait (abundances; by 2050)	Regional changes in habitat (Pan-Arctic)
Cyanea capillata	~180%	-	Expanding over Arctic Ocean shelf areas, notably the Eurasian shelf.
Fritillaria borealis	~130%	-	Expanding throughout the entire Arctic Ocean.
Beroe spp.	~110%	-	Expanding to the central Arctic Ocean, but contracting in the Norwegian and Greenland seas.
Oikopleura vanhoeffeni	~102%	-	Expanding towards the central parts, but narrowing habitats in Bering and Barents Seas.
Mertensia ovum	~84%	-	Narrowing habitats towards the central Arctic. Loss of suitable habitat in Bering and Barents Seas.
Periphylla periphylla	~62%	-	Shifting northward to Svalbard fjords and parts of the Barents Sea. Also expanding in the Bering Sea.
Aglantha digitale	~29%	~ 2%	Expanding in the central Arctic Ocean. In the Fram Strait abundance is more concentrated in the mid water column (410-580 m). Increased advection with the eastern branch of the West Spitsbergen Current.
Sminthea arctica	~ -15%	~ -60%	Contracting towards the pole. Highest retreat observed in the Fram Strait.

The current projections conducted in **Chapters 3 and 4** are rather in line with other studies on the long-term dynamics and modeling of the gelatinous zooplankton groups in the region. A recent study by Heneghan et al. (2023) has revealed that appendicularians and chaetognaths in the Arctic Ocean are expected to increase their abundance at the expense of the reduction of the omnivorous copepods. This is supported by our results of **Chapter 2,** where we projected that the suitable niches of the *Fritillaria borealis* and *Oikopleura vanhoeffeni* will expand by 130% and 102% respectively over the entire three dimensional space in the Arctic Ocean. The expected expansion of suitable niches is also likely to happen at the expense of omnivorous copepods (Heneghan et al., 2023). Such an increase has been hypothesized to lead to longer food webs, resulting in less efficient transport of energy resources to top predators (Heneghan et al., 2023). Regarding the temporal projections of *Aglantha digitale* distribution in **Chapter 3**, we found that this species will become more concentrated in the deeper layers from 400 to 600 meters, while there will be a decrease in abundance in the first 200 meters. Manko et al., 2022, in their long-term summer study (2003-2014) have documented a rather similar decrease in the epipelagic abundance (<200 m) of *Aglantha digitale*, largely explained by its stronger northward advection, earlier spawning and faster ontogenetic descent to deeper waters.

Based on the results of the models in **Chapter 3**, we can conclude that more abundant but less diverse communities of gelatinous zooplankton may be established with warming of the Fram Strait. According to this study, the weakening of the East Greenland Current and the strengthening of the West Spitsbergen Current would restructure communities to be more abundant but less diverse. This hypothesis is supported by Manko et al. 2020 who found that the most diverse communities are found in Arctic water masses, while Atlantic waters hosted highest abundance. This observation was further confirmed in **Chapter 4**, particularly in the fjords of Svalbard and northern Norway. Here we found the highest abundance of gelatinous zooplankton in the Atlantic and transformed Atlantic water masses. Conversely, the greatest taxonomic richness was observed in the coldest water masses represented in the study, the intermediate water masses. These findings hint towards a potential jellification with progressing Atlantification, since an increased inflow of Atlantic waters will cause an increase in gelatinous zooplankton abundances, but a decline in their diversity.

Despite the rather limited comparability of **Chapters 2 and 3** due to the different spatial and temporal scales of the modeling studies, the two species present in both - *Aglantha digitale* and *Sminthea arctica* - were consistently well predicted at the Fram Strait scale. Particularly noteworthy in both studies was the rather strong contraction of *Sminthea arctica* abundances along the East Greenland Current.

The cause of some incongruences observed between the different projections obtained in **Chapters 2 and 3** may be linked to the oceanographic models used. Although the MIP and FESOM models perform well compared to historical data for the Arctic Ocean (Semmler et al., 2020; Gutjahr et al. 2019), they have some limitations in projecting certain regional features. The North Atlantic bias, common to all CMIP6 models, was a key factor influencing the results in **Chapter 2** (Semmler et al., 2020; Gutjahr et al. 2019). For example, in the North Atlantic (60-65 N for our region), the models project colder and fresher water conditions (Gutjahr et al. 2019), which may ultimately affect habitat projections for species such as *Periphylla periphylla* and *Aglantha digitale*. The model may underestimate the presence of *Periphylla periphylla* and overestimate the presence of *Aglantha digitale*. In addition, the MPI model predicts higher salinity in the coastal regions of the Laptev and East Siberian Seas (Gutjahr et al. 2019). A similar bias can be observed in the prediction maps for *Cyanea capillata*; we observe moderate presence values in these regions in the historical projections, but this species has not been found in these seas. Regarding future projections, although *Cyanea capillata* is known to have low salinity tolerance, its settlement and strobilation are limited by ecophysiological constraints imposed by salinity (Holst et al., 2010; Widmer et al., 2016). Therefore, increases in *Cyanea capillata* in these regions must be treated with caution due to the possibility of overestimation.

Although the models used in this thesis showed good predictive performance and revealed distribution patterns of dominant groups of gelatinous zooplankton, a number of shortcomings and challenges related to modeling gelatinous taxa need to be considered. First, the modeling of meroplanktonic species such as *Cyanea capillata*, which has both benthic and planktonic life stages, deserves further investigation, as it has been shown that the tolerance to environmental conditions of the stages is different. Second, in the community models applied in **Chapter 3**, I did not include traits and phylogeny. The reason for not including traits was the lack of reliable trait data for gelatinous zooplankton taxa. The absence of phylogeny was due to the fact that phylogenetic relationships were not available for some of the gelatinous species used in the modeling process in **Chapter 3**. Although test runs of the HMSC models with phylogenetic relationships (derived from WoRMS) showed an increase in predictive power, this block was ultimately excluded from the analysis. Third, modeling of certain taxa can be biased by the potential, so far overlooked, existence of cryptic species, since different lineages may also be characterized by different environmental tolerances and drivers. Including *Beroe* ctenophores at the species level in my models would have been inaccurate due to the known biases associated with species identification, despite the fact that most specimens in the databases are identified as *Beroe cucumis*. Individuals observed in the PELAGIOS transects also resembled *Beroe cucumis* descriptions, but Jucker (2022) showed that the use of the current diagnostic features are incongruent with molecular analyses. Thus, refinement of phylogenetic data and compilation of traits databases are important to improve existing species distribution models on gelatinous zooplankton.

5.8 Mass scaling optical data aggregation and mining of reliable biogeographic data

As the amount of optical data collected in the ocean is increasing significantly (Katija et al., 2022), there is an acute need to automate the process of annotating such data, as the manual process is rather time-consuming. Automatic optical processing tools are used in a variety of biological tasks, such as automatic counting cells, fish, and true jellyfish (Putzu et al., 2014; Yang et al., 2021; Ruiz-Frau et al., 2022; Zhang et al., 2023). Some of the most revolutionary detection methods are based on semantic object detection and segmentation (Kirillov et al., 2023; Liu et al., 2023). This has been made possible by the fusion of computer vision with large language models (Zhu et al., 2023). Inversely, such methods could be used to infer information from the images and answer questions from them (Zhu et al., 2023). For example, such models, when fine-tuned to the biological datasets, could be used to answer a wide range of questions, which could be particularly useful for mining trait information (e.g., for jellyfish, it could answer whether the animal is in motion or resting state, escaping, alive/dead, count number of tentacles, measure length, or detect feeding events, etc.). With such advances, it makes sense to apply video-based data, such as those obtained with PELAGIOS, to conveyor-based data mining. For example, camera systems could be deployed from fishing boats, or ideally mounted on AUV. Ultimately, this would lead to more reliable data sets and allow a wider range of ecological questions to be answered, improving science-based conservation and management strategies.

5.9 Outlook on the impact of gelatinous zooplankton range shifts

The expansion of the niches of a considerable number of gelatinous zooplankton species is expected to have several potential impacts on Arctic ecosystems. In particular, the expansion of *Cyanea capillata* into the fjords of Spitsbergen and Novaya Zemlya could negatively affect the spawning grounds of polar cod situated in these areas (Crawford 2016, Dahlke et al. 2018). In addition, *Cyanea* is known to feed extensively on ichthyoplankton, hence impacting local fish stocks, which could be a problem for local fisheries. Similarly, an increased presence of *Periphylla periphylla* in the fjords of Spitsbergen could also affect the spawning sites of polar cod. An increase in the presence of the appendicularians *Fritillaria borealis* and *Oikopleura vanhoeffeni* could lead to elongated food webs, resulting in less efficient carbon transfer from primary producers to fish. Surprisingly, such an increase in appendicularian abundance has already been recorded by the Inuit in Amundsen Bay, where they have noted an increase in *Oikopleura* spp., which caused clogging of their fishing nets, as well as concerns about possible impacts on mammal and fish populations (Pettitt-Wade et al., 2020). On the other hand, the expansion of *Aglantha digitale* in the Arctic Ocean may benefit certain fish species, such as Atlantic mackerel and other gelatinivorous fish, which are known to feed on this species (Runge et al. 1987).

Jellyfish are perceived with surprisingly contrasting views in different cultures. As noted above, the word 'cnidae' is associated in Western culture with the word 'to sting', and the word 'Medusa' is a homonym for the ancient Greek deity who was often regarded with fear. Oppositely, in Chinese culture, the word for jellyfish "shuǐmǔ" can be translated as "mother of water". In contrast to Western perception, jellyfish are more integrated into Chinese culture and economy, with some species being harvested for traditional medicine and food (You et al., 2007, Duarte et al., 2022). For example, the Scyphozoa *Rhopilema esculentum*, which is known to be used in traditional Chinese medicine to treat arthritis, high blood pressure, and asthma, has an active protein that possesses antioxidant and insecticidal activities (You et al., 2007). It can also be noted that the market demand for edible jellyfish is concentrated exclusively in China, South Korea, and Japan (Duarte et al., 2022). Although jellyfish have not traditionally been used commercially in the West, the recent increase in the presence of some species in European waters (e.g. *Periphylla periphylla*) is encouraging policymakers to look for ways to exploit these species. For example, increasing populations of *Periphylla periphylla* have been proposed for commercial harvest, particularly for collagen production (Tiller et al., 2014). Another positive indirect effect of gelatinous zooplankton may be the removal of plastic and other contaminants from the upper part of the water column. Some species of appendicularia, including the giant larvacean *Bathochordaeus stygius*, may be responsible for removing microplastics from the water column and transporting them to the deep sea (Katija et al., 2017). Due to the high turnover of appendicularia, they may be important not only as carbon pumps, but also as plastic pumps.

In the rapidly changing ecosystems of the Arctic Ocean, the potential impact of gelatinous zooplankton on ecosystems remains enigmatic, their expanding niche and potentially increasing role in ecosystems underscore the need for future research. Future investigations could take advantage of the use of autonomous platforms that are designed to drift with zooplankton aggregations or that are statically deployed in the water column to assess the temporal and spatial dynamics of gelatinous zooplankton and to collect long-term data.

5.10 References for Chapter 5

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Contribution to multi-author articles

Declaration on the contribution of the candidate to a multi-author article/manuscript which is included as a chapter in the submitted doctoral thesis

Chapter 2: Pan-Arctic distribution modeling reveals climate-change driven poleward shifts of major gelatinous zooplankton species

Contribution of the candidate in % of the total work load (up to 100% for each of the following categories):

Experimental concept and design: ca. 85%

Experimental work and/or acquisition of (experimental) data: ca. 95%

Data analysis and interpretation: ca. 95%

Preparation of Figures and Tables: ca. 100%

Drafting of the manuscript: ca. 90%

Chapter 3: Optical observations and spatio-temporal projections of gelatinous zooplankton in the Fram Strait, a gateway to a changing Arctic Ocean

Contribution of the candidate in % of the total work load (up to 100% for each of the following categories):

Experimental concept and design: ca. 85%

Experimental work and/or acquisition of (experimental) data: ca. 85%

Data analysis and interpretation: ca. 90%

Preparation of Figures and Tables: ca. 100%

Drafting of the manuscript: ca. 85%

Chapter 4: In-situ observations of gelatinous zooplankton aggregations in inshore and offshore waters along a poleward gradient

Contribution of the candidate in % of the total work load (up to 100% for each of the following categories):

Experimental concept and design: ca. 80%

Experimental work and/or acquisition of (experimental) data: ca. 85%

Data analysis and interpretation: ca. 85%

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