Gelatinous zooplankton as indicator of progressing Atlantification of the European Arctic

Galaretowaty zooplankton jako wskaźnik postępującej atlantyfikacji Arktyki Europejskiej

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Gdynia, 2022

The difficult is what takes a little time; the impossible is what takes a little longer.

Fridtjof Nansen

This work has been conducted at the Division of Marine Plankton Research under the supervision of **Associate Professor Agata Weydmann-Zwolicka**.

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Abstract

The warming of the Arctic Ocean has accelerated in recent decades, with the European Arctic (EA), warming at globally unparalleled pace. The warming is fueled by the increasing sea water temperature, salinity, and volume of the advected Atlantic water, reaching the Arctic through the largest polar-boreal gateway, the Fram Strait, in a process referred to as the Atlantification. The inflow does not only alter the physical environment, but it also delivers boreal biota northward, hence affecting polar ecosystems functioning and biodiversity, yet the exact effects of the process remain largely unknown. In order to better understand the consequences of the progressing Atlantification on the pelagic ecosystems of the EA, the study was designed that focused on a poorly studied, but ecologically pivotal group – gelatinous zooplankton (GZ). These marine predators have largely escaped scientific attention, and are often absent from planktonic time series, due to their fragility and convoluted taxonomy, yet the existing evidence advocates that they may constitute promising indicators of water mass distribution due to their rapid life cycles, low commercial value, and hydrologically driven distribution. Here, a globally unique, 12-years-long zooplankton monitoring time series from the EA, was analyzed to obtain species-level, life cycle- and morphometrically-resolved GZ database, coupled with the hydrological data. These information were later used to answer the following questions: **1)** does the GZ distribution reflect water mass distribution in the EA? **2)** can the GZ species freely cross the passive fronts separating adjacent water masses? **3)** can the Atlantification progression be inferred from the population structure of the key boreal GZ expatriate? and **4)** what is the possible direction of the Atlantification-mediated EA's pelagic ecosystem evolution? To answer these questions a plethora of advanced statistical methods was applied to the time series data, including ordination techniques and model-building. This allowed to elucidate the intricate pattern of water mass- and oceanographic features (*e.g.*, fronts)-specific GZ indicatory species, abundance signatures and population structure. Described patterns were found to persist both in the temporal and spatial scales, and limited cross-frontal GZ community exchange was described. Additionally, population of the Atlantic water indicatory GZ – *Aglantha digitale* – was shown to advect northward with the flow of the West Spitsbergen Current, and the potential secondary reproductive event was inferred from the environmentally-driven changes in small-to-large jellyfish numbers ratio. Overall, the results showcased that the abundance, diversity and population structure of GZ are good indicators of the progressing Atlantification. Given that the more abundant and less speciose community of GZ was typically found in the Atlantic water, the progressing Atlantification is predicted to lead to a more gelatinous future of the pelagic ecosystems of the EA.

Streszczenie po polsku (Abstract in Polish)

Ocieplanie Oceanu Arktycznego przyspieszyło na przestrzeni ostatnich dekad, szczególnie w europejskim sektorze Arktyki. W obszarze Arktyki Europejskiej (AE) proces ten zachodzi w najszybszym tempie w skali całego globu i jest napędzany przez wzrastającą temperaturę, zasolenie oraz objętość atlantyckiej masy wodnej, napływającej do Arktyki przez największe polarno-borealne połączenie, Cieśninę Fram, w procesie nazywanym Atlantyfikacją. Napływ wód atlantyckich nie tylko przekształca środowisko abiotyczne, ale transportuje również borealne gatunki dalej na północ, wpływając w ten sposób na bioróżnorodność i funkcjonowanie arktycznych ekosystemów, przy czym dokładne efekty tego procesu są nadal słabo rozpoznane. W celu lepszego zrozumienia wpływu postępującej Atlantyfikacji na pelagiczne ekosystemy AE, zaplanowano badania skupiające się na niedostatecznie poznanej, ale ekologicznie kluczowej grupie zwierząt – galaretowatym zooplanktonie (GZ). Te morskie drapieżniki były rzadko uwzględniane w badaniach oceanograficznych, przez co praktycznie nie występują w planktonowych seriach czasowych, co zwykle uzasadnia się delikatnością ich budowy i skomplikowaną taksonomią. Nieliczne istniejące prace naukowe, wskazują, że organizmy te, dzięki swoim krótkim cyklom życia, niskiej wartości komercyjnej, a także rozmieszczeniu zależnemu od warunków środowiskowych, mogą stanowić obiecujące wskaźniki dystrybucji mas wodnych. W związku z tym, w prezentowanej pracy przenalizowano unikalną w skali globalnej, 12-letnią serię czasową monitoringu zooplanktonu z AE, połączonego z pomiarami hydrologicznymi, celem uzyskania bazy danych o rozmieszczeniu GZ, w rozdzielczości uwzględniającej poszczególne gatunki, stadia cyklu życiowego oraz dane morfometryczne. Tak uzyskane dane wykorzystano następnie celem odpowiedzenia na pytania: **1)** czy rozmieszczenie GZ odzwierciedla układ mas wodnych w AE? **2)** czy gatunki GZ mogą bez ograniczeń przekraczać pasywne fronty oddzielające sąsiadujące masy wodne? **3)** czy postępowanie Atlantyfikacji w AE można wykryć przy użyciu struktury populacji kluczowego, borealnego gatunku GZ? oraz **4)** w jakim potencjalnym kierunku zmierza, napędzana Atlantyfikacją, ewolucja ekosystemów pelagicznych AE? Do analizy danych wykorzystano liczne zaawansowane metody statystyczne, w tym techniki ordynacyjne oraz modele statystyczne. Takie kompleksowe podejście pozwoliło na objaśnienie skomplikowanych wzorców powiązań gatunków wskaźnikowych, sygnatur liczebności oraz struktury populacji, typowych dla poszczególnych mas wodnych, oraz innych elementów cyrkulacji oceanicznej (np. frontów). Stwierdzono, że opisane wzorce utrzymują się zarówno w czasie, jak i przestrzeni, oraz że wymiana zespołów GZ przez fronty jest znikoma. Dodatkowo

wykazano, że populacja gatunku wskaźnikowego dla atlantyckiej masy wodnej – *Aglantha digitale* – dostarczana jest na północ wraz z biegiem Prądu Zachodniospitsbergeńskiego, a analizując środowiskowo-zależne zmiany stosunków liczebności osobników młodocianych i dorosłych wykryto również potencjalny drugi cykl rozrodczy tego gatunku. Reasumując, uzyskane wyniki wskazują, że liczebność, różnorodność oraz struktura populacji GZ stanowią dobre wskaźniki postępującej Atlantyfikacji. Biorąc pod uwagę, że liczniejszy, ale mniej różnorodny zespół GZ charakteryzował wody atlantyckie, to przewiduje się, że postępująca Atlantyfikacja może oznaczać bardziej „galaretowatą" przyszłość dla pelagicznych ekosystemów AE.

Chapter 1. General introduction

The temperature of the Arctic increases more than twice as fast as compared to the global mean (Overland *et al.*, 2019), and although this pertains to the atmospheric warming, the sea temperature is not far behind (Belkin, 2009). The Arctic Ocean warming has already led to a dramatic loss of the sea ice extent and thickness (Kwok & Rothrock, 2009; Smedsrud *et al.*, 2022) which consequently further accelerates the ocean warming (Wang *et al.*, 2020). Concomitantly, the input of fresh water, primarily from the riverine runoff and melting ice cover, increased (McPhee *et al.*, 2009), affecting water column stratification and circulation pattern (Nummelin *et al.*, 2016).

Within the Arctic Ocean, the region encompassing three Nordic Seas (Barents, Greenland and Norwegian Seas), referred to as the European Arctic, has experienced even more pronounced warming (IPCC, 2014; Walczowski & Piechura, 2007), and is often considered a hotspot region of the climate change (Ingvaldsen *et al.*, 2021). The underlying mechanism explaining this unparalleled regional warming accounts for the Atlantic water inflow (Polyakov *et al.*, 2017), wind forcing (Timmermans & Marshall, 2020), and the subsequent, amplifying feedback loop fueled by the declining sea ice cover (Ingvaldsen *et al.*, 2021; Wang *et al.*, 2020).

Atlantic water reaches the Arctic Ocean through two gateways: the Barents Sea and the Fram Strait. The former is often disregarded from the heat transport analyses, as the Atlantic water loses most of its heat content to the atmosphere while traversing the Barents Sea (Smedsrud *et al.*, 2013). On the contrary, the Atlantic water transport across the Fram Strait in the European Arctic is unanimously considered the main heat source for the Arctic Ocean (*e.g.*, Helland-Hansen & Nansen, 1909). Recent years have seen the increasing heat content (Beszczynska-Möller *et al.*, 2012), salinity (Walczowski *et al.*, 2017), and strength of Atlantic water inflow through the Fram Strait (Beszczynska-Möller *et al.*, 2012), which propagates further north, and hence underlies present-day, accelerating warming of the Arctic Ocean (Polyakov *et al.*, 2017, 2020). Progressing inflow of the Atlantic water, which aside from higher temperature and salinity, brings along the boreal expatriates, shifts the typically polar ecosystems into Atlantic-like state, in a process referred to as the Atlantification (for a review see Ingvaldsen *et al.*, 2021).

The northward delivery of the Atlantic water through the Fram Strait occurs with the flow of the two-branched West Spitsbergen Current, which originates further south, in the Nordic Seas (Piechura & Walczowski, 1995). Its western branch, constituting the Norwegian Atlantic Current extension, flows along the Mohn and Knipovich Ridges, and then recirculates as the Return Atlantic Current partially fueling the Greenland Sea Gyre (Walczowski & Piechura, 2007). The eastern branch of the West Spitsbergen Current, flows mostly along the west slope of the Svalbard Shelf, and it carries majority of Atlantic water heat and volume (Walczowski, 2013). The flow of the West Spitsbergen Current is flanked by the two passive (*i.e.,* density-compensated), oceanic fronts, the Arctic Front on the west (van Aken *et al.*, 1995), and the Polar Front on the east (Strzelewicz *et al.*, 2022), which separate the Atlantic water from the adjacent Arctic water, hence modulating the transport of the Atlantic-origin water.

From the oceanographic standpoint, the northward propagation of the warm anomalies originating in the North Atlantic, leads to the weakening of the Eurasian Basin halocline (Polyakov *et al.*, 2010), and the shoaling of Atlantic water (Polyakov *et al.*, 2017). This inevitably allows for a deep convection to bring midwater amassed heat to the underside of the sea ice cover (Polyakov *et al.*, 2017), hence accelerating its melting (Wang *et al.*, 2020). As a result, the net southward ice export from the Arctic Ocean through the Fram Strait also decreases, causing the increase in salinity of the Greenland and the Norwegian Seas, which affects cyclonic gyre circulation and further enhances northward volume transport of Atlantic water (Wang *et al.*, 2020). In spite of the significant increase of the scientific effort put towards mechanical understanding of the Atlantification in recent years (Csapó *et al.*, 2021), the rapidity and complexity of the Arctic Ocean evolution calls for an urgent intensification of focused research, as suggested by Ingvaldsen *et al.* (2021).

The Atlantification of the Arctic comes with a magnitude of ecosystem-level consequences (Csapó *et al.*, 2021; Ingvaldsen *et al.*, 2021). Diminishing water column stratification, and increase in the extent of the open, ice-free water, may affect nutrient concentration (Polyakov *et al.*, 2020). This in turn, leads to the locally enhanced primary production (Arrigo & van Dijken, 2015) and additional phytoplankton blooms (Ardyna *et al.*, 2014), which both constitute one of the primary ecological symptoms of the Atlantification (Csapó *et al.*, 2021). These changes necessarily propagate up the trophic food web, leading to a cascading bottom-up effects (Ingvaldsen *et al.*, 2021). Interestingly, ecological responses at the higher trophic levels highlight clearcut distinction between polar taxa and their boreal counterparts, with the former usually exhibiting diminishing biomass (Aarflot *et al.*, 2018) or contracting distribution ranges (Węsławski *et al.*, 2010). This is concomitant with the northward biogeographic expansion (Beaugrand, 2009; Weydmann *et al.*, 2014), as well as phenological (Kraft *et al.*, 2013; Weydmann *et al.*, 2018), physiological (Møller & Nielsen, 2019; Węsławski *et al.*, 2020), or even gene expression level (Smolina *et al.*, 2015; Trudnowska *et al.*, 2020) adaptations of the Atlantic-origin expatriates. Shifting community structure of the lower level consumers, implies that their predators, in order to survive, have to adapt their diets, foraging strategies and distribution, what has already been documented for the Arctic birds (Stempniewicz *et al.*, 2021), fish (Haug *et al.*, 2018) or even marine mammals (Meyer-Gutbrod & Green, 2018). Unfortunately, the majority of Atlantification-related studies, employed only the widely studied system of *Calanus* copepod species group, leaving the responses of remaining taxa either poorly or completely not understood (see *e.g.*, Ingvaldsen *et al.*, 2021).

The pelagic representatives of two phyla: Cnidaria and Ctenophora, collectively referred to as gelatinous zooplankton (Haddock, 2004), or simply jellyfish are among these understudied taxa. This non-phylogenetic group, unifies animals sharing similarities in body morphology (transparent, and to a large extent made up of water) and trophic ecology (predators). Their diets range from unicellular protists to large vertebrates, and are themselves a prey of choice for a range of predators, including commercially important fish (Hays *et al.*, 2018); they also play pivotal roles in the carbon pump and biogeochemical cycles (Tinta *et al.*, 2021; Wright *et al.*, 2021). In recent years, gelatinous zooplankton has attracted more and more scientific attention (Sanz-Martín *et al.*, 2016), mostly due to their bloom-forming capability and its potential links to climate change and human activity (Mills, 2001; Purcell, 2005; Purcell *et al.*, 2007). Although there is no consensus, as to whether these jellyfish blooms are increasing globally in frequency and size (Duarte *et al.*, 2013), or are a periodically occurring phenomena (Condon *et al.*, 2013), the growing body of evidence shows the localized, regional-scale increase in abundance of gelatinous zooplankton (Attrill *et al.*, 2007; Brodeur *et al.*, 2002). Whether such potentially Atlantification-driven increases of jellyfish abundance have already appeared in the European Arctic, has yet to be tested.

Aside from their ecological significance, gelatinous zooplankton are also particularly well suited for the role of hydrological indicators (Hays *et al.*, 2005; Richardson *et al.*, 2009). Admittedly, majority of gelatinous zooplankton are not harvested commercially (Brotz *et al.*, 2017), rendering their population size unaffected by humans. Secondly, as members of plankton, their distribution is driven primarily by hydrological features of the ocean (McManus & Woodson, 2012). Finally, gelatinous zooplankton possess virtually unparalleled reproductive capabilities (paedogenesis in ctenophores – Jaspers *et al.* (2012); bloom formation in cnidarians - Mills (2001)) allowing them to quickly economize on favorable environmental conditions with a rapid population increase. Although the idea of employing various jellyfish as indicators has been around since the Challenger Expedition, when Agassiz (1883) attempted to follow the Gulf Stream flow with the observations of neustonic Porpitidae (Cnidaria), the concept has not been extensively developed (Mańko *et al.*, 2015). In turn, the majority of the current gelatinous zooplankton research focuses merely on documenting species distribution, with just few exceptions (*e.g.*, Gili *et al.*, 1991; Pagès, 1992).

A plausible explanation underlying the paucity of gelatinous zooplankton data in general (but see Sigurðsson *et al.*, 2021, and references therein), their absence from time series (Long *et al.*, 2021), and of their usage as indicators, arises most probably from the historical assumption of them constituting trophic dead ends of the pelagic food webs (Lüskow *et al.*, 2021) or the methodological issues, as gelatinous zooplankton have delicate body structure which damages easily when sampled harshly (Raskoff *et al.*, 2010). Some of them also poorly preserve, rendering subsequent identification troublesome. Finally, their complex systematics and elusive morphological features, require significant expertise to succeed with the taxonomic identification (Majaneva & Majaneva, 2013; Ronowicz *et al.*, 2015). Additional hurdle comes with the general constraints of working in polar regions, including challenging sampling, sea ice-limited accessibility, and high costs of research expeditions. As a result, data on gelatinous zooplankton in polar regions appear scarcer than elsewhere in the world (Pagès, 1997). These animals are virtually absent from the European Arctic zooplankton time series, and only handful records exists over the past century (Mańko *et al.*, 2015; Ronowicz *et al.*, 2015; Sigurðsson *et al.*, 2021; Zelickman, 1972).

Building on the urgent need to better understand the ongoing Atlantification of the Arctic, especially in the polar climate change hotspot, the European Arctic, and to provide a better understanding of the gelatinous zooplankton community, this work was designed in an attempt to answer the question: *whether gelatinous zooplankton diversity, distribution and population structure can be used as indicators of the progressing Atlantification?* The historical paucity of the gelatinous zooplankton data in the European Arctic, required that the presented work starts with the identification of species inhabiting the area – **Papers 1 and 2**. Then, the potential relationships between the extent of water masses and the distribution of gelatinous taxa had to be identified – **Papers 1 and 2**. Linking gelatinous zooplankton with water masses, was followed by the investigation of whether such water mass-defined communities, abundance signatures, and indicatory taxa persist in time – **Paper 2** – and whether they can shift their affinity as a result of the Atlantification-dependent hydrological evolution of the local ecosystems, exemplified by the relocation of oceanic fronts – **Paper 2**. Finally, because the West Spitsbergen Current constitutes the main conveyor of Atlantic water to the Arctic Ocean, and hence underlies its Atlantification, and given that *Aglantha digitale* was found to be indicatory of Atlantic water (**Paper 2**), its distribution, abundance, and population structure were thoroughly examined across the route of the West Spitsbergen Current – **Paper 3**.

Chapter 2. Thesis objectives

The hypotheses postulated in this thesis were:

I. Gelatinous zooplankton distribution and diversity reflect the water mass distribution both in the epipelagic and mesopelagic waters of the European Arctic.

II. Oceanic fronts that separate distinct water masses, constitute semi-impermeable barriers for species exchange, hence they maintain gelatinous zooplankton communities specific for distinct water masses.

III. Species phenology and population structure of gelatinous zooplankton may be used as indicatory of the state of the Atlantification, through the earlier onset of species reproduction and clear northward advection of younger developmental stages of the key boreal expatriate – *Aglantha digitale*.

IV. Progressing Atlantification will lead to a more abundant and less diverse community of the gelatinous zooplankton in the affected regions of the European Arctic.

To enable the validation of above listed hypotheses, the following specific research questions were postulated:

Q1. Which gelatinous zooplankton species inhabit the European Arctic and how are they distributed? – **Papers 1 and 2**

Q2. How is gelatinous zooplankton distribution coupled with water masses and other oceanographic features present in the European Arctic? – **Papers 1 and 2**

Q3. Is the specificity of gelatinous zooplankton relation to water masses dependent on interannual changes in their hydrological characteristics? – **Paper 2**

Q4. Do the oceanic fronts maintain the separateness of gelatinous zooplankton communities of the adjacent water masses? – **Paper 2**

Q5. Does the population structure of the most abundant gelatinous zooplankton taxa vary in spatial scale? **– Papers 2 and 3**

Q6. Does the population structure of *Aglantha digitale* vary on a year-to-year basis, and if so, is there a clear link between such variation and the environment? – **Paper 3**

Q7. Do the environmental factors associated with Atlantification (*e.g.*, increasing temperature and salinity) affect gelatinous zooplankton distribution? – **Papers 1-3**

Q8. Is the progressing Atlantification detectable at the level of the distribution of gelatinous zooplankton abundance, diversity and population structure? – **Papers 1-3**

Chapter 3. List of papers comprising the thesis

Paper 1. **Mańko M. K.**, Głuchowska M., Weydmann-Zwolicka A. 2020. Footprints of Atlantification in the vertical distribution and diversity of gelatinous zooplankton in the Fram Strait (Arctic Ocean). *Progress in Oceanography*, 189, 102414. Doi: 10.1016/j.pocean.2020.102414.

Own contribution 85%

IF: **4.060**, 5-years IF: **4.161**, Polish Ministry of Education and Science points: **140**

Paper 2. **Mańko M. K.,** Merchel M., Kwaśniewski S., Weydmann-Zwolicka A. 2022. Oceanic fronts shape biodiversity of gelatinous zooplankton in the European Arctic. *Frontiers in Marine Science*, 9, 941025. Doi: 10.3389/fmars.2022.941025.

Own contribution 70%

IF: **4.912**, 5-years IF: **4.520**, Polish Ministry of Education and Science points: **100**

Paper 3. **Mańko M. K.,** Merchel M., Kwaśniewski S., Weydmann-Zwolicka A. 2022. Atlantification alters the reproduction of jellyfish *Aglantha digitale* in the European Arctic. *Limnology and Oceanography*. Doi: 10.1002/lno.12170.

Own contribution 70%

IF: **4.745**, 5-years IF: **4.349**, Polish Ministry of Education and Science points: **140**

Total IF: **13.717**, Total 5-years IF: **13.030**

Total Polish Ministry of Education and Science points: **380**

Chapter 4. Materials and methods

Chapter 4. 1. Data collection and handling

Gelatinous zooplankton was sampled on board of S/Y *Oceania* as a part of the Arctic Research Expedition (AREX) campaigns of the Institute of Oceanology of the Polish Academy of Sciences every summer from 2003 to 2014 (Figure 1). Sampling occurred from June to July, so that each site was visited within the two week-time window. Zooplankton was collected with either the WP-2 net fitted with 180 µm filtering gauze and with 57 cm diameter inlet (**Papers 2 and 3**) or with MultiPlankton Sampler (Hydro-Bios, Germany) with 180 µm filtering gauze and a 0.25 m^2 opening (**Paper 1**). Sampling spanned epipelagic waters (0-200 m; **Papers 2 and 3**) with occasional deeper collections in 2012 (stratified sampling 0-25-50-200-600-1000 m; **Paper 1**). Collected zooplankton samples were then fixed in 4% solution of a borax-buffered formaldehyde in seawater, and stored until laboratory analyses.

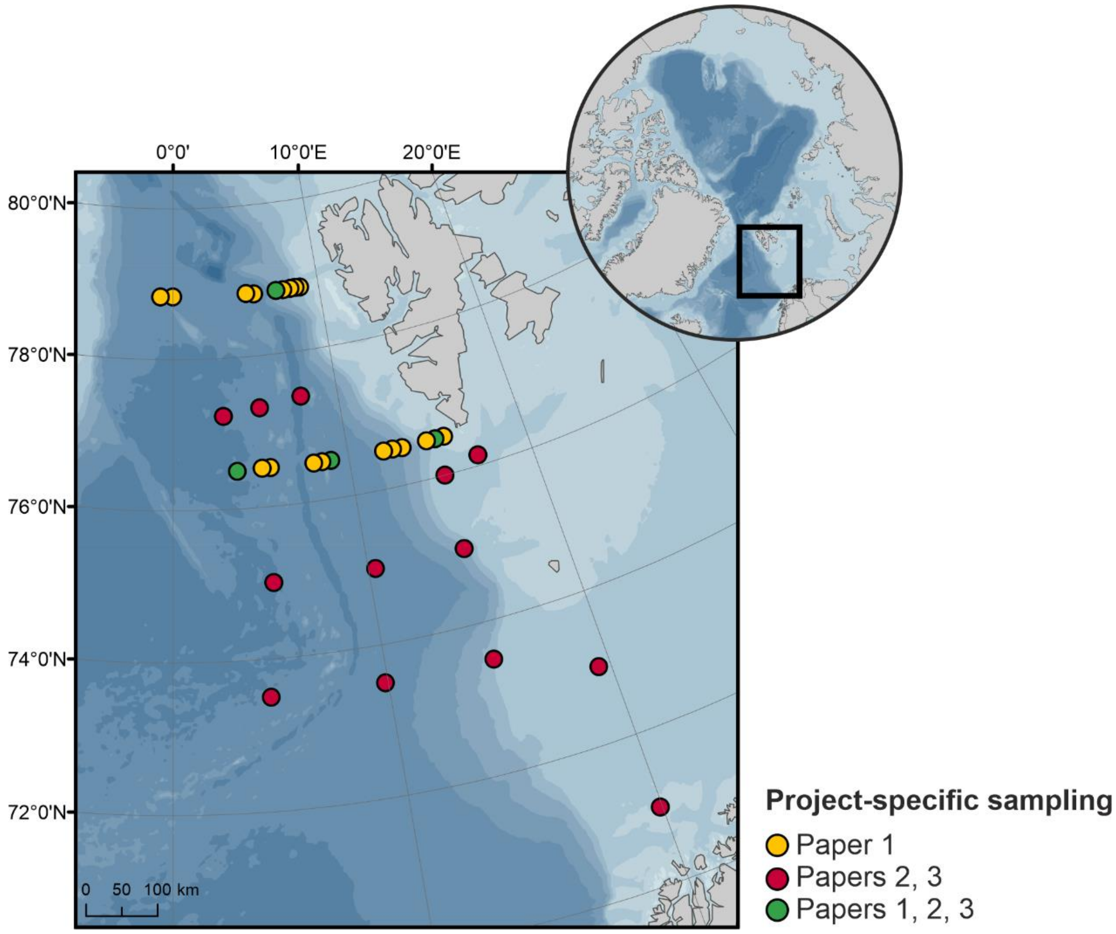

Figure 1. Location of sampling sites specific to the papers comprising presented thesis (Paper 1 – yellow, Papers 2, 3 – red, Papers 1, 2, 3 – green). Bathymetry data were derived from the International Bathymetric Chart of the Arctic Ocean (Jakobsson *et al.*, 2012). Investigated area is bordered by the black rectangle in the Arctic Ocean inset map.

When in the laboratory, each zooplankton sample was processed in full (97 samples – **Paper 1**; 386 samples – **Papers 2 and 3** – which were originally taken from three separate vertical strata, however, due to the extreme variability of these strata extent, data from a single site were pooled together to represent a single zooplankton sample spanning 0-200 m). All specimens of gelatinous zooplankton found in the samples were counted and identified to the lowest taxonomic level with the help of the most recent species inventories and taxonomic keys (see Ronowicz *et al.*, 2015 for a review). Their higher level taxonomic ranks were also noted, as was the life cycle stage (eudoxid and polygastric colony) in the case of siphonophores. The abundance estimation of colonial siphonophores was based on the number of nectophores found.

Next, each specimen was subjected to morphometric analyses, that varied depending on species morphology: bell height (distance form velum to the tip of a bell) was measured in prolate hydromedusae (*i.e.*, bullet-shaped), bell diameter in oblate hydromedusae (*e.g.*, *Obelia* sp. Péron & Lesueur, 1810), height of anterior nectophore and eudoxid bract in calycophoran siphonophores, width of nectophore in physonect siphonophores and total body length in ctenophores. In total, 14 439 specimens were identified and measured.

Hydrological measurements (temperature [°C] and salinity) were taken concomitantly to collecting zooplankton using an SBE 911plus CTD probe (Sea-Bird Electronics, Inc., Bellevue, WA, USA), comprising of duplicate SBE 3plus premium temperature sensors and SBE 4C conductivity sensors and a Digiquartz® pressure sensor.

Data preprocessing and preliminary analyses were run in R (v. 4.0.4) using ggplot2 (Wickham, 2009), tidyverse (Wickham *et al.*, 2019) and vegan (Oksanen *et al.*, 2020) packages, and in the case of hydrological data in MATLAB (2016; **Paper 3**) or Ocean Data View 4 (**Paper 2**). Ordination-based methods were implemented in Canoco v.5 (**Paper 1**; Smilauer & Leps, 2014) or in PRIMER 7 with PERMANOVA+ add-on (**Papers 2 and 3**; Anderson *et al.*, 2008), while statistical tests and models were built and validated in R using following packages: DHARMA (Hartig, 2022), glmmTMB (Brooks *et al.*, 2017), indicspecies (de Cáceres & Legendre, 2009), and vegan (Oksanen *et al.*, 2020). Maps were drawn in ArcMap 10.7.1, with the exception of Figure 3 in **Paper 2**, which was generated through interpolation of hydrological data with Data Interpolating Variational Analysis (DIVA) and plotted in the Ocean Data View 4.

Chapter 4. 2. Hydrological classifications

The analysis of gelatinous zooplankton data required information on the extent of water masses (**Papers 1 and 2**), the location of oceanic fronts (**Paper 2**) and currents (**Paper 3**), that were inferred from the recorded temperature and salinity profiles. The CTD-collected data were first averaged over strata corresponding to the zooplankton sampling layers. The specific T-S signatures, adopted from Cottier *et al.* (2005) with altered S threshold of Atlantic water (S >34.92 **Paper 1**, and S > 34.86 **Paper 2**; Strzelewicz *et al.*, 2022; Walczowski *et al.*, 2012), were then used to map the water mass extent. Hydrological definition of the West Spitsbergen Current branches T-S signatures followed that of Carstensen *et al.* (2019). The position of the Arctic Front was inferred following Walczowski *et al.* (2017) recommendation *i.e.*, it was assumed to follow the 3 °C isotherm at 100 m ± 5 m near the Knipovich Ridge. The location of the Polar Front was inferred with two methods, depending of the investigated area: in the Storfjorden Trough its position was assessed based on the extent of Atlantic water (Strzelewicz *et al.*, 2022), while along the West Spitsbergen Shelf its position was taken either directly from Strzelewicz *et al.* (2022) for years 2007-2014 or approximated from T-S distribution maps for years 2003-2006.

Chapter 4. 3. Brief description of the analytical approach

Despite the slight differences in methodological approaches to data analysis utilized in **Papers 1-3**, certain methods were common among all of them. Gelatinous zooplankton abundance was expressed as individuals per cubic meter ([ind. m^{-3}], **Papers 2 and 3**) or thousand cubic meters ([ind. 1000 m^{-3}], **Paper 1**), and was square-root transformed prior to subsequent analyses, to reduce the weight of dominant taxa or life cycle stages. Then, the Bray-Curtis dissimilarity matrix was calculated. When performing multiple comparison, the Holm-Bonferroni correction was applied to control the family-wise error rate. In all papers (**1-3**), exact values of test statistics and the p-values were given, while full results of analyses were reported as supplementary materials. Threshold of significance was set at $p \leq 0.05$, and all Monte Carlo permutations were run with 999 replications.

Aside from the taxonomically-resolved gelatinous zooplankton abundance, other variables included in the analysis pertained to hydrology (temperature [°C], salinity, maximal depth of site [m], mean sampling depth [m]), location (site identifier, latitude, longitude), and date (year of sampling, sampling date [Julian Day; 1-365/6]). Additional hydrological or geographical classifications used in analyses were: water mass (**Paper 1**), frontal zone (**Paper 2**), latitudinal groupings (**Paper 3**; assigned arbitrarily <73.500 N, 73.500 N – 75.000 N, >75.000 N), the branch of West Spitsbergen Current (**Paper 3**). Published data on whole zooplankton abundance [ind. m^{-3}] and biomass [mg m^{-3}] (Gluchowska *et al.*, 2017) were also incorporated as environmental variables into the analyses presented in the **Paper 1**.

The workflow begun with testing normality of raw data distribution with Shapiro-Wilk test, based on which either parametric or nonparametric methods were applied. Differences in gelatinous zooplankton abundance and community structure between hydrological groupings (**Paper 1** – water masses, **Paper 2** – fronts; **Paper 3** – West Spitsbergen Current branches and latitudinal groups) were evaluated with a series of one- and multi-way permutational analyses of variance (PERMANOVAs) that were always preceded by verification of the assumption of group dispersion homogeneity. Additionally, Kruskal-Wallis tests followed by Dunn's post-hoc tests were applied to infer the differences in gelatinous zooplankton abundance between the frontal zones (**Paper 2).** Then, the ordination techniques, either a constrained correspondence analysis (CCA; **Paper 1**) or distance based linear model (DistLM), followed by a distance based redundancy analysis (dbRDA; **Papers 2 and 3**), were used to disentangle the influence of environmental factors on gelatinous zooplankton abundance (**Papers 1 and 3**), community structure (**Papers 1 and 2**), and population structure (**Paper 3**). Noteworthy, potential collinearity of the explanatory variables was tested with the variance inflation factor prior to performing ordination analyses (**Paper 1**; Oksanen *et al.*, 2020). The concept of utilizing gelatinous zooplankton as indicators of water masses (**Paper 1**) and front-delimited regions (**Paper 2**) was explored with indicatory species routine of de Cáceres & Legendre (2009) implemented in R. Additional, paper-specific analyses included: analysis of similarity (ANOSIM) for comparing gelatinous zooplankton communities between water masses (**Paper 1**), Wilcoxon signed-rank test for comparing the impacts of shifting front position on gelatinous zooplankton (**Paper 2**), negative binomial generalized linear mixed model to test if the progression of Atlantification could accelerate reproduction of *Aglantha digitale* (**Paper 3**), and clustering of environmentally-defined groups of sites characterized by a distinct population structure (**Paper 3**). The latter involved simultaneous application of three methods: linkage tree analysis (LINKTREE; Anderson *et al.*, 2008) with similarity profiles tests (SIMPROF) followed by dominant population structure identification with similarity percentage analysis (SIMPER).

Chapter 5. Results summary

Chapter 5. 1. Hydrological settings

Both water temperature and salinity in the studied area of the European Arctic exemplified significant horizontal, vertical, and temporal variation (**Papers 1-3**). Water temperature, in general, decreased with an increasing depth and the distance from the continental slope, as well as in the northward direction (**Papers 1 and 2**). The temperature was highest in the vicinity of the West Spitsbergen Current **(Paper 2**), and the lowest within the Greenland Sea Gyre (**Paper 2**). On a temporal scale, temperature exemplified extensive variability (**Papers 2 and 3**), with 2-4 year long periods of anomalously high heat content, like the one recorded from 2004 to 2007 (**Papers 2 and 3**). Much like temperature, water salinity also varied with depth, and distance from the shore as well as on a temporal scale. Interestingly, temporal variation in salinity produced a stronger signal of the interannual increase, than did temperature (**Paper 3**), but in general, variation of the two variables had a comparable dynamics (**Papers 2 and 3**), concomitantly indicating the periods of an anomalous Atlantic influence over the studied area of the European Arctic (**Papers 2 and 3**).

Distribution of water salinity and temperature allowed for an unambiguous detection of water masses (**Papers 1 and 2**), even those transient (*e.g.*, Polar Surface water, **Paper 1**), oceanic fronts (**Paper 2**), and patterns of the West Spitsbergen Current circulation (**Paper 3**). Majority of the analyzed zooplankton samples were collected within the main flow of Atlantic water, the core of the West Spitsbergen Current. Additionally, modified Atlantic water was also detected in the form of Transformed Atlantic water and Intermediate water (**Paper 1**). The core was found over the slope of the West Spitsbergen Shelf, extending down to 600-500 m, depending on the latitude (**Paper** 1). The colder and less saline water were identified as the Arctic water (**Paper 1**), detected either below the flow of Atlantic water (**Paper 1**) or on the external (*i.e.*, facing outside of the West Spitsbergen Current) sides of the Arctic Front and the Polar Front (**Paper 2**). On the surface, two types of water masses, sharing T-S signatures but of different origin were present, and these were Shelf Surface water, originating from the glacial melt, and Polar Surface water, arising from the cooling and freshening of Atlantic water (**Paper 1**).

The dynamics of Atlantic heat and volume inflow were also perceivable through detection of the position of two oceanic fronts (**Paper 2**). When more Atlantic water was reaching the Fram Strait, the fronts flanking the West Spitsbergen Current were pushed on the sides (the Polar Front to the west; the Arctic Front to the east), leading to an increased presence of Atlantic water on the West Spitsbergen Shelf (**Papers 1 and 2**), and in the Storfjorden Trough (**Paper 2**). In other cases, the colder, Arctic-type water was found on the shelf, brought there with the flow of the Spitsbergen Polar Current (**Papers 1 and 2**). The circulation pattern was also informative, as to the intensity and heat content of the Atlantic water inflow – with clear temperature and salinity signals occurring simultaneously within the two branches of the West Spitsbergen Current (**Paper 3**).

Chapter 5. 2. Patterns of gelatinous zooplankton diversity and abundance in the European Arctic

Q1. *Which gelatinous zooplankton species inhabit the European Arctic and how are they distributed? –* ***Papers 1 and 2***

Gelatinous zooplankton were found in most of the samples analyzed (72% – **Paper 1**; 100% – **Papers 2**), albeit in a generally low abundance (on average from 0.176 to 0.305 ind. m^{-3}). Their numbers were almost three times higher within the waters of the West Spitsbergen Current, than outside of this current flow (**Paper 2**), and this trend held true across all the years studied (Kruskal-Wallis, $\chi 2$ = 17.808, p = 0.086; **Paper 2**), although a statistically significant variation of the abundance within the current's main flow was observed ($\chi 2$ = 23.044, p = 0.018; **Paper 2**). Horizontal differences in the gelatinous zooplankton abundance were also detected on the latitudinal gradient, with 15% more abundant community further south (**Paper 1**), and with an increasing distance form the shore, with shelf community almost twice the size of the one inhabiting open waters (**Paper 1**). Along the vertical gradient, the abundance of gelatinous zooplankton tended to be higher at the surface and reached its minimum with increasing water depth (**Paper 1**). This pattern, however, was found solely along the shelf, whereas the gelatinous zooplankton of the open ocean zones was distributed reciprocally (more abundant at larger depths; **Paper 1**). In the vicinity of the slope, the highest abundance of the gelatinous zooplankton was found within the 200-600 m depth stratum, corresponding to the location of the West Spitsbergen Current's core (**Paper 1**).

Overall, 26 distinct gelatinous zooplankton taxa were identified (17 – **Paper 1**; 15 – **Paper 2**). The species uniquely found in the **Paper 1** were either collected in the deepest samples (*i.e.*, below 600 m), and these were *Homoeonema platygonon* Maas, 1893; *Panatachogon haeckeli* Maas, 1893; *Marrus orthocanna* (Kramp, 1942); *Muggiaea bargmannae* Totton, 1954; or comprised a shallow-water, shelf community (*e.g.*, *Bougainvillia superciliaris* (L. Agassiz, 1849); *Catablema vesicarium* (A. Agassiz, 1862); *Halitholus cirratus* Hartlaub, 1913; *Physophora hydrostatica* (Forsskål, 1775)). Species identified solely in the research presented in **Paper 2** included representatives of two orders completely absent from the results shown in the **Paper 1**: Narcomedusae Haeckel, 1879 (*Aeginopsis laurentii* Brandt, 1838) and Leptothecata Haeckel, 1866 (*Obelia* sp.; *Mitrocomella polydiademata* (Romanes, 1876); *Halopsis ocellata* Agassiz, 1865 and *Melicertum octocostatum* (M. Sars, 1835)). Open water gelatinous zooplankton community was more diverse, as compared to that inhabiting shelf waters (**Paper 1**).

Chapter 5. 3. Gelatinous zooplankton distribution mirrors ocean hydrology

Q2. *How is gelatinous zooplankton distribution coupled with water masses and other oceanographic features present in the European Arctic? –* ***Papers 1 and 2***

Q3. *Is the specificity of gelatinous zooplankton relation to water masses dependent on interannual changes in their hydrological characteristics? –* ***Paper 2***

Each water mass (see Supplementary material 2 of the **Paper 1**) and front delimited zone (PERMANOVA, pseudo-F = 11.139, p = 0.003; **Paper 2**) differed significantly in the gelatinous zooplankton diversity, abundance, and in the demography of the most abundant species – *Aglantha digitale* (O. F. Müller, 1776; **Papers 1-3**). Distinct gelatinous zooplankton communities were a signature of a different water mass (ANOSIM, R = 0.230, p = 0.001; **Paper 1**). Although the classification of the most-speciose community varied with the sampling approach (Arctic water when accounting for mesopelagic depths – **Paper 1**, or Atlantic water when looking solely into epipelagic waters – **Paper 2**), most analyses retrieved the Atlantic water gelatinous zooplankton community as the most abundant, with the domination of a single species (*A. digitale*; **Papers 1 and 2**). Importantly, much like the size of gelatinous zooplankton communities, their taxonomic composition within the front-defined zones remained constant across all the years sampled, irrespectively of interannual variability of water temperature and salinity (**Paper 2**).

Water mass and hydrographic zone specific assemblages of gelatinous zooplankton were identified through the indicatory species routine (**Papers 1 and 2**). *Aglantha digitale* was found in all front-related zones (**Paper 2**), similarly as were *Dimophyes arctica* (Chun, 1897) and *Beroe* spp. Muller, 1776 (**Papers 1 and 2**), of which the former constituted the second most abundant species (**Papers 1 and 2**). The third most abundant species, *Mertensia ovum* (Fabricius, 1780) was found exclusively in the vicinity of the West Spitsbergen Shelf (**Papers 1 and 2**). The zone east of the Polar Front was mainly characterized by a presence of *M. ovum* (IndVal.g = 0.66, p = 0.001) with admixture of *A. laurentii* (IndVal.g = 0.35, p = 0.065) and *D. arctica* eudoxids (IndVal.g = 0.37, p = 0.081; **Paper 2**). When analyzing the community of the Shallow Shelf water present in that zone (**Paper 1**), additional indicatory species were identified, and these were: *C. vesicarium* (IndVal.g = 0.58, p<0.05; **Paper 1**), *B. superciliaris* (IndVal.g = 0.58, p<0.05; **Paper 1**), and *H. cirratus* (IndVal.g = 0.43, p<0.010; **Paper 1**). Gelatinous zooplankton in the vicinity of the Greenland Sea Gyre, west of the Arctic Front, was best identified with *Beroe* spp. (IndVal.g = 0.49, p = 0.044; **Paper 2**), while *A. digitale* was found indicatory of the waters delimited by both fronts, the zone corresponding to the main flow of Atlantic water with the West Spitsbergen Current (IndVal.g = 0.83, p = 0.001; **Paper 2**).

The water masses found off the West Spitsbergen Shelf also contained indicatory species (**Paper 1**). Indicators of Arctic water included non-Aglantha Trachymedusae, like *H. platygonon* (IndVal.g = 0.51, p<0.001; **Paper 1**) and *P. haeckeli* (IndVal.g = 0.40, p<0.05; **Paper 1**), as well as siphonophores: *Crystallophyes amygdalina* Moser, 1925 (IndVal.g = 0.23, p<0.001; **Paper 1**), *M. bargmannae* (IndVal.g = 0.73, p<0.001; **Paper 1**), and *Rudjakovia plicata* Margulis 1982 (IndVal.g = 0.46, p<0.05; **Paper 1**). *Aglantha digitale* was selected among indicatory species of Transformed Atlantic water (IndVal.g = 0.65, p<0.001; **Paper 1**) as was, among others, *D. arctica* (IndVal.g = 0.69, p<0.001; **Paper 1**).

Chapter 5. 4. Oceanic fronts maintain distinct gelatinous zooplankton communities

Q4**. Do the oceanic fronts maintain the separateness of gelatinous zooplankton communities of the adjacent water masses? – **Paper 2

The zones delimited by the oceanic fronts (see **Paper 2** for explanation) harbored distinct gelatinous zooplankton communities, with waters east of the Polar Front typically full of *M. ovum*, those west of the Arctic Front teeming with *Beroe* spp., and those in between the two fronts containing large quantities of *A. digitale* (**Paper 2**). Interestingly, when relocation of the front was detected between years, an extensive restructuring of the gelatinous zooplankton occurred at a given site – for example, if the site previously found on the eastern side of the Polar Front, due to front relocation in the following years was found on its western side, the previously *M. ovum* – dominated community switched to the numerical dominance of *A. digitale* (PERMANOVA, pseudo-F = 2.303, p = 0.043; **Paper 2**). This adds to the evidence, that the passive fronts of the European Arctic maintain distinct planktonic communities through a limited cross-frontal species exchange (**Paper 2**).

Chapter 5. 5. *Aglantha digitale* population responds to the Atlantification

Q5.** Does the population structure of the most abundant gelatinous zooplankton taxa vary in spatial scale? – **Papers 2 and 3

Q6.** Does the population structure of Aglantha digitale vary on a year-to-year basis, and if so, is there a clear link between such variation and the environment? – **Paper 3

The abundance of *A. digitale* varied significantly between the studied years (PERMANOVA, pseudo-F = 1.984, p = 0.042, df = 11; **Paper 3**). Although appearing to generally decrease in size (**Papers 2 and 3**), the population of *A. digitale* went through the phases of increased abundance, simultaneous to the anomalously Atlantic-influenced periods recorded (**Paper 3**). Additionally, the population size of *A. digitale* showed latitudinal structuring (PERMANOVA, pseudo-F = 3.400, p = 0.017, df = 2; **Paper 3**), with more abundant community further south.

An important finding comes with the analysis of the gelatinous zooplankton communities of Atlantic water and Transformed Atlantic water that shared the same indicatory species – *A. digitale* (**Paper 1**). Upon closer examination, it was found that *A. digitale* population structure differed between these water masses, with juveniles typical for Atlantic water, while older stages were indicatory of Transformed Atlantic water (**Paper 1**). Notably, a similar life cycle stage dependent association with water masses was found for *D. arctica*, in which case the polygastric colonies were predominantly indicatory of Transformed Atlantic water (IndVal.g = 0.69, p<0.001; **Paper 1**), while eudoxids indicated mostly Arctic water (IndVal.g = 0.67, p<0.01; **Paper 1**). Populations of *A. digitale* associated with the two branches of the West Spitsbergen Current also differed in their composition (PERMANOVA, pseudo-F = 9.805, p = 0.003, df = 1; **Paper 3**). The eastern branch community was on average 105 times larger than that from the western branch, except for the 2011, when 2.4 times more *A. digitale* were found in the western branch.

The generalized linear mixed model (**Paper 3**) allowed to quantify differing responses of juveniles and mature *A. digitale* to an increasingly Atlantic-like environment. Smaller jellyfish were found to almost double their abundance in a scenario where temperature increased by one standard deviation from the average for 2003-2014, whereas for mature jellyfish the increase was just 1.2-fold (**Paper 3**). Model also captured finer geographical patterning of *A. digitale* with simultaneous decrease in the numbers of small and large jellyfish along latitudinal gradient (**Paper 3**), and an extreme decrease in the numbers of small jellyfish with an increasing water depth (**Papers 2 and 3**). The modelled population structure latitudinal gradient resonated well with the data, which showed that when more smaller specimens were found in the south, then more larger jellyfish were found in the north (**Paper 3**), thus pointing at the interconnection of the southern and northern populations.

Chapter 5. 6. Atlantification promotes a more gelatinous future for pelagic ecosystems in the European Arctic

Q7. *Do the environmental factors associated with Atlantification (e.g., increasing temperature and salinity) affect gelatinous zooplankton distribution? –* ***Papers 1-3***

Q8. *Is the progressing Atlantification detectable at the level of the distribution of gelatinous zooplankton abundance, diversity and population structure? –* ***Papers 1-3***

Gelatinous zooplankton species composition and their population structure were driven by the complex interplay of biotic and abiotic factors (**Papers 1-3**). The constructed ordination models indicated a strong relationship between the Atlantic water conditions (high temperature and salinity) and the overall gelatinous zooplankton community composition, as well as the abundance and population structure of *A. digitale* (**Papers 1-3**). Depending on the analytical approach, a different proportion of variation in species composition (19.0% with dbRDA; **Paper 2** or 26.5% with CCA; **Paper 1**) and population structure (21.0% with dbRDA; **Paper 3**) was explained. Irrespectively of small differences, all approaches attributed the highest explanatory power to the gradients of water temperature and water depth, and their interplay in shaping the composition of gelatinous zooplankton (**Papers 1 and 2**). However, when looking just at the drivers of *A. digitale* population structure, the influence of salinity became comparable to that of temperature (**Paper 3**).

More abundant gelatinous zooplankton community was generally found with the flow of the West Spitsbergen Current (**Papers 1-3**), with the exception of Shallow Shelf water sampled in 2012 (**Paper 1**), where sampling occurred probably during *M. ovum* bloom. Otherwise, Atlantic water was found to consistently harbor denser gelatinous zooplankton population (**Paper 2**). Irrespectively of the area studied, *A. digitale* was the most common species encountered, accounting from 41.94% (**Paper 1**) to 72.33% (**Papers 2 and 3**) of all jellyfish found. However, in the main flow of the West Spitsbergen Current, this species comprised about 96% of all gelatinous zooplankton records (**Paper 2**). Although few other species were recorded in the frontal zone C (in-between the two fronts; **Paper 2**), majority of these records come from the shallower regions, affected by the Norwegian Coastal Current. Therefore, the core of the Atlantic inflow could undoubtedly be characterized as maintaining the most abundant and least diverse gelatinous zooplankton community (**Papers 1-3**).

Chapter 6. Conclusions

The presented thesis constitutes globally unique resource of the gelatinous zooplankton distribution and diversity data, spanning extensive temporal and spatial scales (**Papers 1-3**). The magnitude of analytical approaches utilized to analyze the data, allowed to validate all of the postulated hypotheses. This led to an overall conclusion, that the gelatinous zooplankton are good indicators of the progressing Atlantification, and that the continuation of the process may translate into a more abundant, but less diverse, single species dominated community of the gelatinous zooplankton in the European Arctic.

Distribution of gelatinous zooplankton, both in the upper 200 m of the water column, as well as in the mesopelagic (200-1000 m) depths, was found to reflect particularly well the intricate pattern of water mass extent (**Papers 1 and 2**), and the presence of other oceanographic features (**Papers 2 and 3**). Moreover, the mere abundance signature of the gelatinous zooplankton, was found to be distinct between the water masses (**Paper 1**), front-delimited zones (**Paper 2**) and branches of the West Spitsbergen Current (**Paper 3**). In general, the more Atlantic in its T-S profile the environment was, the more abundant gelatinous zooplankton community it harbored.

Notably, despite detecting minor variability, the patterns of gelatinous zooplankton distribution and diversity described above, persisted in time (**Papers 1-3**), hence corroborating specificity of their associations. Detection of relocation of the Arctic and Polar Fronts (**Paper 2**), created a unique opportunity to examine the exchange of gelatinous zooplankton communities across such passive fronts. Thorough restructuring of the gelatinous zooplankton community, following the front relocation, proved that species exchange across the oceanic fronts is limited, leading to an additional conclusion that water mass specific communities are maintained by the fronts in the European Arctic (**Paper 2**).

Demography-level resolution of gelatinous zooplankton data allowed for elucidating life cycle stages indicatory of a particular oceanographic features in the European Arctic (**Papers 1-3**), with a characteristic demographic signature occurring concomitantly with the periods of anomalous Atlantic influence. Signs of interconnection between northern and southern populations were detected, highlighting the potential advection of *A. digitale* to the Arctic Ocean from subarctic/boreal regions (**Paper 3**). The data also provided preliminary evidence for the occurrence of a second reproductive cycle of *A. digitale* in the European Arctic, as a result of Atlantification (**Paper 3**), forecasting a thorough restructuring of the pelagic ecosystems.

Chapter 7. References

Aarflot, J. M., Skjoldal, H. R., Dalpadado, P., & Skern-Mauritzen, M. (2018). Contribution of Calanus species to the mesozooplankton biomass in the Barents Sea. *ICES Journal of Marine Science*, *75*, 2342–2354. https://doi.org/10.1093/icesjms/fsx221

Agassiz, A. (1883). Exploration of the surface fauna of the Gulf-Stream under the auspices of the Coast Survey. Part I. The Porpitidae and Velellidae. Memoirs of the Museum of Comparative Zoology, 8, 1-16

Anderson, M. J., Gorley, R. N., & Clarke, K. R. (2008). *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods*. Primer-E Ltd., Plymouth, UK

Ardyna, M., Babin, M., Gosselin, M., Devred, E., Rainville, L., & Tremblay, J. É. (2014). Recent Arctic Ocean sea ice loss triggers novel fall phytoplankton blooms. *Geophysical Research Letters*, *41*, 6207–6212. https://doi.org/10.1002/2014GL061047

Arrigo, K. R., & van Dijken, G. L. (2015). Continued increases in Arctic Ocean primary production. *Progress in Oceanography, 136,* 60–70. https://doi.org/10.1016/j.pocean.2015.05.002

Attrill, M. J., Wright, J., & Edwards, M. (2007). Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea. *Limnology and Oceanography*, *52*(1), 480–485. https://doi.org/10.4319/lo.2007.52.1.0480

Beaugrand, G. (2009). Decadal changes in climate and ecosystems in the North Atlantic Ocean and adjacent seas. *Deep-Sea Research Part II: Topical Studies in Oceanography*, *56*(8–10), 656–673. https://doi.org/10.1016/j.dsr2.2008.12.022

Belkin, I. M. (2009). Rapid warming of Large Marine Ecosystems. *Progress in Oceanography, 81*, 207–213. https://doi.org/10.1016/j.pocean.2009.04.011

Beszczynska-Möller, A., Fahrbach, E., Shauer, U., & Hansen, E. (2012). Variability in Atlantic water temperature and transport at the entrance to the Arctic Ocean, 1997–2010. *ICES Journal of Marine Science, 69,* 852–863. https://doi.org/10.1093/icesjms/fss056

Brodeur, R. D., Sugisaki, H., & Hunt, G. L. (2002). Increases in jellyfish biomass in the Bering Sea: Implications for the ecosystem. *Marine Ecology Progress Series*, *233*, 89–103. https://doi.org/10.3354/meps233089

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal, 9*, 378–400. https://doi.org/10.32614/rj-2017-066

Brotz, L., Schiariti, A., López-Martínez, J., Álvarez-Tello, J., Peggy Hsieh, Y. H., Jones, R. P., Quiñones, J., Dong, Z., Morandini, A. C., Preciado, M., Laaz, E., & Mianzan, H. (2017). Jellyfish fisheries in the Americas: origin, state of the art, and perspectives on new fishing grounds. *Reviews in Fish Biology and Fisheries*, *27,* 1–29. https://doi.org/10.1007/s11160-016-9445-y

Carstensen, J., Olszewska, A., & Kwasniewski, S. (2019). Summer mesozooplankton biomass distribution in the West Spitsbergen Current (2001-2014). *Frontiers in Marine Science*, *6*, 202. https://doi.org/10.3389/fmars.2019.00202

Condon, R. H., Duarte, C. M., Pitt, K. A., Robinson, K. L., Lucas, C. H., Sutherland, K. R., Mianzan, H. W., Bogeberg, M., Purcell, J. E., Decker, M. B., Uye, S. I., Madin, L. P., Brodeur, R. D., Haddock, S. H. D., Malej, A., Parry, G. D., Eriksen, E., Quinõnes, J., Acha, M., … Graham, W. M. (2013). Recurrent jellyfish blooms are a consequence of global oscillations. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(3), 1000–1005. https://doi.org/10.1073/pnas.1210920110

Cottier, F., Tverberg, V., Inall, M., Svendsen, H., Nilsen, F., & Griffiths, C. (2005). Water mass modification in an Arctic fjord through cross-shelf exchange : The seasonal hydrography of Kongsfjorden, Svalbard. *Journal of Geophysical Research*, *110,* C12005. https://doi.org/10.1029/2004JC002757

Csapó, H. K., Grabowski, M., & Węsławski, J. M. (2021). Coming home - Boreal ecosystem claims Atlantic sector of the Arctic. *Science of the Total Environment*, *771,* 144817. https://doi.org/10.1016/j.scitotenv.2020.144817

de Cáceres, M., & Legendre, P. (2009). Associations between species and groups of sites: Indices and statistical inference. *Ecology, 90,* 3566–3574. https://doi.org/10.1890/08-1823.1

Duarte, C. M., Pitt, K. A., Lucas, C. H., Purcell, J. E., Uye, S. I., Robinson, K., Brotz, L., Decker, M. B., Sutherland, K. R., Malej, A., Madin, L., Mianzan, H., Gili, J. M., Fuentes, V., Atienza, D., Pages, F., Breitburg, D., Malek, J., Graham, W. M., & Condon, R. H. (2013). Is global ocean sprawl a cause of jellyfish blooms? *Frontiers in Ecology and the Environment*, *11*(2), 91–97. https://doi.org/10.1890/110246

Gili, J. M., Pagès, F., & Fusté, X. (1991). Mesoscale coupling between spatial distribution of planktonic cnidarians and hydrographic features along the Galician Coast (Northwestern Iberian Peninsula). *Scientia Marina*, *55*, 419–426

Gluchowska, M., Trudnowska, E., Goszczko, I., Kubiszyn, A. M., Blachowiak-Samolyk, K., Walczowski, W., & Kwasniewski, S. (2017). Variations in the structural and functional diversity of zooplankton over vertical and horizontal environmental gradients en route to the Arctic Ocean through the Fram Strait. *PLoS ONE, 12,* e0171715. https://doi.org/10.1371/journal.pone.0171715

Haddock, S. H. D. (2004). A golden age of gelata: past and future research on planktonic ctenophores and cnidarians. *Hydrobiologia*, *530/531*, 549–556. https://doi.org/10.1007/s10750-004-2653-9

Hartig, F. (2022). DHARMa: Residual diagnostics for hierarchical (multi-level mixed) regression models. R package version 0.4.5. Available from http://florianhartig.github.io/DHARMa

Haug T., Bogstad B., Chierici M., Gjøsæter H., Hallfredsson E. H., Høines Å. S., Hoel A. H., Ingvaldsen R. B., Jørgensen L. L., Knutsen T., Loeng H., Naustvoll L. J., Røttingen I., Sunnanå K. (2017). Future harvest of living resources in the Arctic Ocean north of the Nordic and Barents Seas: a review of possibilities and constraints. *Fisheries Research*, 188, 38–57. doi:10.1016/j.fishres.2016.12.002

Hays, G. C., Doyle, T. K., & Houghton, J. D. R. (2018). A paradigm shift in the trophic importance of jellyfish? *Trends in Ecology & Evolution, 33,* 874–884. https://doi.org/10.1016/j.tree.2018.09.001

Hays, G. C., Richardson, A. J., & Robinson, C. (2005). Climate change and marine plankton. *Trends in Ecology and Evolution*, *20*, 337–344. https://doi.org/10.1016/j.tree.2005.03.004

Helland-Hansen, B., & Nansen, F. (1909). *The Norwegian Sea: Its physical oceanography based upon the Norwegian researches 1900–1904*. Det Mallingske bogtrykkeri.

Ingvaldsen, R. B., Assmann, K. M., Primicerio, R., Fossheim, M., Polyakov, I. V, & Dolgov, A. V. (2021). Physical manifestations and ecological implications of Arctic Atlantification. *Nature Reviews Earth & Environment*, *2*, 874–889. https://doi.org/10.1038/s43017-021-00228-x

IPCC 2014. Climate change 2014: Synthesis report. In: Pachauri R.K., Meyer L.A., Core Writing Team (Eds.) *Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change*. Geneva, Switzerland: IPCC

Jakobsson, M., Mayer, L., Coakley, B., Dowdeswell, J. A., Forbes, S., Fridman, B., Hodnesdal, H., Noormets, R., Pedersen, R., Rebesco, M., Schenke, H. W., Zarayskaya, Y., Accettella, D., Armstrong, A., Anderson, R. M., Bienhoff, P., Camerlenghi, A., Church, I., Edwards, M., … Weatherall, P. (2012). The International Bathymetric Chart of the Arctic Ocean (IBCAO) Version 3.0. *Geophysical Research Letters*, *39*, L12609. https://doi.org/10.1029/2012GL052219

Jaspers, C., Haraldsson, M., Bolte, S., Reusch, T. B. H., Thygesen, U. H., & Kiørboe, T. (2012). Ctenophore population recruits entirely through larval reproduction in the central Baltic Sea. *Biology Letters*, *8*(5), 809–812. https://doi.org/10.1098/rsbl.2012.0163

Kraft, A., Nöthig, E. M., Bauerfeind, E., Wildish, D. J., Pohle, G. W., Bathmann, U. V., Beszczynska-Möller, A., & Klages, M. (2013). First evidence of reproductive success in a southern invader indicates possible community shifts among Arctic zooplankton. *Marine Ecology Progress Series*, *493*, 291–296. https://doi.org/10.3354/meps10507

Kwok, R., & Rothrock, D. A. (2009). Decline in Arctic sea ice thickness from submarine and ICESat records: 1958-2008. *Geophysical Research Letters*, *36*, L15501. https://doi.org/10.1029/2009GL039035

Long, A. P., Haberlin, D., Lyashevska, O., Brophy, D., O'Hea, B., O'Donnell, C., Scarrott, R. G., Lawton, C., & Doyle. (2021). Interannual variability of gelatinous mesozooplankton in a temperate shelf sea: greater abundance coincides with cooler sea surface temperatures. *ICES Journal of Marine Science*, *78*, 1372–1385. https://doi.org/10.1093/icesjms/fsab030

Lüskow, F., Galbraith, M. D., Hunt, B. P. V, Perry, R. I., & Pakhomov, E. A. (2021). Gelatinous and soft-bodied zooplankton in the Northeast Pacific Ocean: organic, elemental, and energy contents. *Marine Ecology Progress Series*, *665*, 19–35. https://doi.org/10.3354/meps13663

Majaneva, S., & Majaneva, M. (2013). Cydippid ctenophores in the coastal waters of Svalbard: Is it only Mertensia ovum? *Polar Biology*, *36*, 1681–1686. https://doi.org/10.1007/s00300-013-1377-6

Mańko, M. K., Panasiuk-Chodnicka, A., & Żmijewska, M. I. (2015). Pelagic coelenterates in the Atlantic sector of the Arctic Ocean − species diversity and distribution as water mass indicators. *Oceanological and Hydrobiological Studies*, *44*, 466–479. https://doi.org/10.1515/ohs-2015-0044

MATLAB. 2016. *Version 9.1 (R2016b)*. The MathWorks Inc.

McManus, M. A., & Woodson, C. B. (2012). Plankton distribution and ocean dispersal. *Journal of Experimental Biology*, *215*, 1008–1016. https://doi.org/10.1242/jeb.059014

McPhee, M. G., Proshutinsky, A., Morison, J. H., Steele, M., & Alkire, M. B. (2009). Rapid change in freshwater content of the Arctic Ocean. *Geophysical Research Letters*, *36*, L10602. https://doi.org/10.1029/2009GL037525

Meyer-Gutbrod, E. L., Greene, C. H. (2018). Uncertain recovery of the North Atlantic right whale in a changing ocean. *Global Change Biology,* 24, 455–464. https://doi.org/10.1111/gcb.13929

Mills, C. E. (2001). Jellyfish blooms: Are populations increasing globally in response to changing ocean conditions? *Hydrobiologia*, *451*, 55–68. https://doi.org/10.1023/A:1011888006302

Møller, E. F., & Nielsen, T. G. (2019). Borealization of Arctic zooplankton — smaller and less fat zooplankton species in Disko Bay, Western Greenland. *Limnology and Oceanography*, 65, 1175-1888. https://doi.org/10.1002/lno.11380

Nummelin, A., Ilicak, M., Li, C., & Smedsrud, L. H. (2016). Consequences of future increased Arctic runoff on Arctic Ocean stratification, circulation, and sea ice cover. *Journal of Geophysical Research: Oceans*, *121*, 617–637. https://doi.org/10.1002/2015JC011156

Oksanen, J., and others. (2020). vegan: Community Ecology Package. R package version 2.5-7

Overland, J. E., Hanna, E., Hannsen-Bauer, I., Kim, S.-J., Walsh, J. E., Wang, M., & Bhatt, U. S. (2019). The Arctic surface air temperature. In *State of the Climate in 2018*. Bulletin of the American Meteorological Society, 100, S142-S144

Pagès, F. (1992). Mesoscale coupling between planktonic cnidarian distribution and water masses during a temporal transition between active upwelling and abatement in the northern Benguela system. *South African Journal of Marine Science*, *12*(1), 41–52. https://doi.org/10.2989/02577619209504689

Pagès, F. (1997). The gelatinous zooplankton in the pelagic system of the Southern Ocean: a review. *Annales de l'Institute Oceanographique*, *73*(2), 139–158

Piechura, J., & Walczowski, W. (1995). The Arctic Front: structure and dynamics. *Oceanologia*, *37*, 47–73

Polyakov, I. V., Alkire, M. B., Bluhm, B. A., Brown, K. A., Carmack, E. C., Chierici, M., Danielson, S. L., Ellingsen, I., Ershova, E. A., Gårdfeldt, K., Ingvaldsen, R. B., Pnyushkov, A. V., Slagstad, D., & Wassmann, P. (2020). Borealization of the Arctic Ocean in response to anomalous advection from sub-Arctic seas. *Frontiers in Marine Science*, *7*, 491. https://doi.org/10.3389/fmars.2020.00491

Polyakov, I. v., Pnyushkov, A. v., Alkire, M. B., Ashik, I. M., Baumann, T. M., Carmack, E. C., Goszczko, I., Guthrie, J., Ivanov, V. v., Kanzow, T., Krishfield, R., Kwok, R., Sundfjord, A., Morison, J., Rember, R., & Yulin, A. (2017). Greater role for Atlantic inflows on sea-ice loss in the Eurasian Basin of the Arctic Ocean. *Science*, *356*, 285–291. https://doi.org/10.1126/science.aai8204

Polyakov, I. v., Timokhov, L. A., Alexeev, V. A., Bacon, S., Dmitrenko, I. A., Fortier, L., Frolov, I. E., Gascard, J. C., Hansen, E., Ivanov, V. v., Laxon, S., Mauritzen, C., Perovich, D., Shimada, K., Simmons, H. L., Sokolov, V. T., Steele, M., & Toole, J. (2010). Arctic ocean warming contributes to reduced polar ice cap. *Journal of Physical Oceanography*, *40*, 2743–2756. https://doi.org/10.1175/2010JPO4339.1

Purcell, J. E. (2005). Climate effects on formation of jellyfish and ctenophore blooms: A review. *Journal of the Marine Biological Association of the United Kingdom*, *85*, 461–476. https://doi.org/10.1017/S0025315405011409

Purcell, J. E., Uye, S. I., & Lo, W. T. (2007). Anthropogenic causes of jellyfish blooms and their direct consequences for humans: A review. *Marine Ecology Progress Series*, *350*, 153–174. https://doi.org/10.3354/meps07093

Raskoff, K. A., Hopcroft, R. R., Kosobokova, K. N., Purcell, J. E., & Youngbluth, M. (2010). Jellies under ice: ROV observations from the Arctic 2005 Hidden Ocean expedition. *Deep-Sea Research Part II: Topical Studies in Oceanography*, *57*, 111–126. https://doi.org/10.1016/j.dsr2.2009.08.010

Richardson, A. J., Bakun, A., Hays, G. C., & Gibbons, M. J. (2009). The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends in Ecology and Evolution*, *24*(6), 312–322. https://doi.org/10.1016/j.tree.2009.01.010

Ronowicz, M., Kukliński, P., & Mapstone, G. M. (2015). Trends in the diversity, distribution and life history strategy of Arctic Hydrozoa (Cnidaria). *PLoS ONE*, *10*, e0120204. https://doi.org/10.1371/journal.pone.0120204

Sanz-Martín, M., Pitt, K. A., Condon, R. H., Lucas, C. H., Novaes de Santana, C., & Duarte, C. M. (2016). Flawed citation practices facilitate the unsubstantiated perception of a global trend toward increased jellyfish blooms. *Global Ecology and Biogeography*, *25*(9), 1039–1049. https://doi.org/10.1111/geb.12474

Sigurðsson, G. M., Lüskow, F., Gislason, A., & Svavarsson, J. (2021). Summer phenology of the sub-surface gelatinous zooplankton assemblage in two North-Western Icelandic fjords. *Polar Biology*, *44*, 2139–2149. https://doi.org/10.1007/s00300-021-02947-9

Smedsrud, L. H., Esau, I., Ingvaldsen, R. B., Eldevik, T., Haugan, P. M., Li, C., Lien, V. S., Olsen, A., Omar, A. M., Risebrobakken, B., Sandø, A. B., Semenov, V. A., & Sorokina, S. A. (2013). The role of the Barents Sea in the Arctic climate system. *Reviews of Geophysics*, *51*(3), 415–449. https://doi.org/10.1002/rog.20017

Smedsrud, L. H., Muilwijk, M., Brakstad, A., Madonna, E., Lauvset, S. K., Spensberger, C., Born, A., Eldevik, T., Drange, H., Jeansson, E., Li, C., Olsen, A., Skagseth, Ø., Slater, D. A., Straneo, F., Våge, K., & Årthun, M. (2022). Nordic Seas Heat Loss, Atlantic Inflow, and Arctic Sea Ice Cover Over the Last Century. *Reviews of Geophysics*, *60*, e2020RG000725. https://doi.org/10.1029/2020RG000725

Smilauer, P., & Leps, J. (2014). *Multivariate analysis of ecological data using Canoco 5*. Cambridge University Press, Cambridge, UK. https://doi.org/10.1017/CBO9781139627061

Smolina, I., Kollias, S., Møller, E. F., Lindeque, P., Sundaram, A. Y. M., Fernandes, J. M. O., & Hoarau, G. (2015). Contrasting transcriptome response to thermal stress in two key zooplankton species, Calanus finmarchicus and C. glacialis. *Marine Ecology Progress Series*, *534*, 79–93. https://doi.org/10.3354/meps11398

Stempniewicz, L., Weydmann-zwolicka, A., Strzelewicz, A., Marta, G., Kidawa, D., Walczowski, W., Marcin, J., & Zwolicki, A. (2021). Advection of Atlantic water masses influences seabird community foraging in a high-Arctic fjord. *Progress in Oceanography*, *193*, 102549. https://doi.org/10.1016/j.pocean.2021.102549

Strzelewicz, A., Przyborska, A., & Walczowski, W. (2022). Increased presence of Atlantic Water on the shelf south-west of Spitsbergen with implications for the Arctic fjord

Hornsund. *Progress in Oceanography*, *200*, 102714. https://doi.org/10.1016/j.pocean.2021.102714

Timmermans, M. L., & Marshall, J. (2020). Understanding Arctic Ocean Circulation: A Review of Ocean Dynamics in a Changing Climate. *Journal of Geophysical Research: Oceans*, *125*, e2018JC014378. https://doi.org/10.1029/2018JC014378

Tinta, T., Klun, K., & Herndl, G. J. (2021). The importance of jellyfish–microbe interactions for biogeochemical cycles in the ocean. *Limnology and Oceanography*, *66*(5), 2011–2032. https://doi.org/10.1002/lno.11741

Trudnowska, E., Balazy, K., Stoń-Egiert, J., Smolina, I., Brown, T., & Gluchowska, M. (2020). In a comfort zone and beyond — Ecological plasticity of key marine mediators. *Ecology and Evolution*, *10*, 14067–14081. https://doi.org/10.1002/ece3.6997

van Aken, H. M., Budéus, G., & Hähnel, M. (1995). The anatomy of the Arctic Frontal Zone in the Greenland Sea. *Journal of Geophysical Research*, *100*, 15999–16014.

Walczowski, W. (2013). Frontal structures in the West Spitsbergen current margins. *Ocean Science*, *9*, 957–975. https://doi.org/10.5194/os-9-957-2013

Walczowski, W., Beszczynska-Möller, A., Wieczorek, P., Merchel, M., & Grynczel, A. (2017). Oceanographic observations in the Nordic Sea and Fram Strait in 2016 under the IOPAN long-term monitoring program AREX. *Oceanologia*, *59*, 187–194. https://doi.org/10.1016/j.oceano.2016.12.003

Walczowski, W., & Piechura, J. (2007). Pathways of the Greenland Sea warming. *Geophysical Research Letters*, *34*, L10608. https://doi.org/10.1029/2007GL029974

Walczowski, W., Piechura, J., Goszczko, I., & Wieczorek, P. (2012). Changes in Atlantic water properties: an important factor in the European Arctic marine climate. *ICES Journal of Marine Science*, *69*, 864–869. https://doi.org/10.1093/icesjms/fss068 Changes

Wang, Q., Wekerle, C., Wang, X., Danilov, S., Koldunov, N., Sein, D., Sidorenko, D., von Appen, W. J., & Jung, T. (2020). Intensification of the Atlantic Water Supply to the Arctic Ocean Through Fram Strait Induced by Arctic Sea Ice Decline. *Geophysical Research Letters*, *47*, e2019GL086682. https://doi.org/10.1029/2019GL086682

Węsławski, J. M., Legeżyńska, J., & Włodarska-kowalczuk, M. (2020). Will shrinking body size and increasing species diversity of crustaceans follow the warming of the Arctic littoral ? *Ecology and Evolution*, *10*, 10305–10313. https://doi.org/10.1002/ece3.6780

Węsławski, J. M., Wiktor, J., & Kotwicki, L. (2010). Increase in biodiversity in the arctic rocky littoral, Sorkappland, Svalbard, after 20 years of climate warming. *Marine Biodiversity*, *40*, 123–130. https://doi.org/10.1007/s12526-010-0038-z

Weydmann, A., Carstensen, J., Goszczko, I., Dmoch, K., Olszewska, A., & Kwasniewski, S. (2014). Shift towards the dominance of boreal species in the Arctic: Inter-annual and spatial zooplankton variability in the West Spitsbergen Current. *Marine Ecology Progress Series*, *501*(2011), 41–52. https://doi.org/10.3354/meps10694

Weydmann, A., Walczowski, W., Carstensen, J., & Kwaśniewski, S. (2018). Warming of Subarctic waters accelerates development of a key marine zooplankton *Calanus finmarchicus*. *Global Change Biology*, *24*, 172–183. https://doi.org/10.1111/gcb.13864

Wickham, H. (2009). *Elegant Graphics for Data Analysis: ggplot2*. Springer New York, USA

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms, J., Robinson, D., Seidel, D., Spinu, V., … Yutani, H. (2019). Welcome to the Tidyverse. *Journal of Open Source Software*, *4*, 1686. https://doi.org/10.21105/joss.01686

Wright, R. M., Quéré, C. le, Buitenhuis, E., Pitois, S., & Gibbons, M. J. (2021). Role of jellyfish in the plankton ecosystem revealed using a global ocean biogeochemical model. *Biogeosciences*, *18*, 1291–1320. https://doi.org/10.5194/bg-18-1291-2021

Zelickman, E. A. (1972). Distribution and ecology of the pelagic hydromedusae, siphonophores and ctenophores of the Barents Sea, based on perennial plankton collections. *Marine Biology*, *17*, 256–264. https://doi.org/10.1007/BF00366301

Chapter 8. Footprints of Atlantification in the vertical distribution and diversity of gelatinous zooplankton in the Fram Strait (Arctic Ocean)

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Published in Progress in Oceanography 189: 102414.
Doi: 10.1016/j.pocean.2020.102414
IF: 4.060, 5-years IF: 4.161, ME&S: 140 points

Paper received the distinction at the 2020 Scientific Competition for the Early Career Scientists organized by the Gdańsk Branch of the Polish Academy of Sciences.

Progress in Oceanography 189 (2020) 102414

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

Footprints of Atlantification in the vertical distribution and diversity of gelatinous zooplankton in the Fram Strait (Arctic Ocean)

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ARTICLE INFO

Keywords:
Jellyfish
Ctenophores
Atlantification
Climate change
Arctic

ABSTRACT

Gelatinous zooplankton (GZ), here understood as pelagic cnidarians and ctenophores, are an important component of marine ecosystems. Their diversity and distribution reflect local hydrological settings especially well, thus allowing the development of biotic indices for studying climate-mediated changes in the world's oceans. The effects of global warming are most pronounced in the Arctic Ocean and have been further accelerated by the strengthening inflow of relatively warm Atlantic waters (AtW) *via* the Fram Strait, referred to as Atlantification. Here, we use the GZ distribution to describe the current state of Atlantic water inflow into the Arctic Ocean and to discuss the future of this fragile ecosystem. For this purpose, we characterized the abundance, diversity, and demography of the GZ identified from vertically stratified samples (down to 1000 m) collected in the Fram Strait along two latitudinally parallel transects of varying influence of AtW. Overall, we identified 17 taxa, with *Aglantha digitale*, *Dimophyes arctica* and *Mertensia ovum* being the most abundant. We then contrasted our jellyfish and ctenophore data with both biotic and environmental ecosystem characteristics and analysed the associations between the GZ community and water mass distribution. We showed that the more abundant GZ community was found along the southern transect; that the sampling depth and bathymetric zone played the most important roles in structuring the GZ diversity; that water mass distribution affected GZ demography; and that AtW was dominated by *A. digitale*, that constituted 66% of the total GZ abundance. Our results, although temporarily limited, suggest that the Atlantification will promote the expansion of boreal species into the Arctic, and could lead to a less diverse, but more abundant GZ community in the future. In addition, we compare in detail the GZ community found in different water masses, at different depths, and in different bathymetric zones, and supported with literature data, discuss the future of the European Arctic under the scenario of increasing inflow of Atlantic water.

1. Introduction

Pelagic cnidarians and ctenophores, here referred to as gelatinous zooplankton (GZ), are integral components of marine food webs (Hays et al., 2018) and are equally important for the functioning of shallow and deep pelagic food webs (e.g., Choy et al., 2017). GZ themselves are versatile predators that feed on prey ranging from protists to fish (Purcell, 1997; Colin et al., 2005); despite their low energy density, they also constitute a food source of choice for a diverse array of predators (Hays et al., 2018). Jellyfish and ctenophores are also able to rapidly increase their population size in response to favourable environmental conditions and have been hypothesized to do so in response to anthropogenic stressors (Richardson et al., 2009; Duarte et al., 2013), periodically forming large population outbreaks, which are collectively referred to as jellyfish blooms (Mills, 2001). The notion of a globally increasing frequency of jellyfish blooms has been explored on numerous occasions (Condon et al., 2012), but it remains unsupported by robust global data. Instead, this phenomenon has been attributed to natural oscillations (Brodeur et al., 2008; Condon et al., 2013) or locally variable reporting efforts (Brotz et al., 2012) within certain oceanic regions, such as the polar seas (e.g., Pagès, 1997), which suffer from undersampling and a lack of long-term data sets.

Data on the distribution of GZ taxa oftentimes comes from the fishery bycatch reporting (e.g., Decker et al. 2018), but this applies solely to larger scyphozoan jellyfish. Difficulties in the sampling of smaller and often more fragile taxa, like some hydromedusae, siphonophores and most notably ctenophores, which tend to disintegrate in plankton net samples when handled harshly (e.g., Raskoff et al., 2010),

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https://doi.org/10.1016/j.pocean.2020.102414
Received 27 August 2019; Received in revised form 28 June 2020; Accepted 31 July 2020

and their convoluted taxonomy impede their correct identification and enumeration (Ronowicz et al., 2015). As a result, the actual diversity and distribution of the GZ tends to be poorly resolved even in more accessible regions (Majaneva and Majaneva, 2013) but more so in the deep ocean (Lindsay et al., 2004; Hosia et al., 2008).

As the distribution of planktonic communities reflects the local environmental settings particularly well (see Hays et al., 2005 for a review), it is tempting to advocate their usage for monitoring climate-mediated changes occurring in the world's oceans. This holds especially true for the most vulnerable areas of the globe, the polar regions. According to recent estimates, the water temperature has increased most rapidly in the Arctic Ocean and in sub-Arctic seas (IPCC, 2014), with the European Arctic warming at the most rapid pace (Walczowski and Piechura, 2007). This is most likely due to the strengthening and warming of the Atlantic waters inflow to the Arctic, the so-called "Atlantification" (Beszczynska-Möller et al., 2012; Polyakov et al., 2017). Atlantification has already had an impact on the biodiversity and functioning of the pelagic zone in the European Arctic (Wassmann et al. 2011), affecting species phenology (Gluchowska et al., 2017a; Weydmann et al., 2018) and food-web structure (Eriksen et al., 2017), and prompting the northward expansion of distribution ranges (Kraft et al., 2013; Weydmann et al., 2014). The lack of a solid diversity baseline, however, hampers any interpretation of the potential climate-mediated changes in the distribution and reproductive patterns of the GZ in the European Arctic. GZ were the focal group for only a handful of studies in this region (see Ronowicz et al. 2015 for a review) but were sometimes included in whole zooplankton assays (e.g., Błachowiak-Samołyk et al., 2007; Gluchowska et al., 2017b). Since these studies were biased towards the well-known and most abundant hard-bodied taxa (Gluchowska et al., 2017b) or relied largely on techniques that provided data of a low taxonomic resolution (such as the laser optical plankton counter; Basedow et al., 2018), little can be gleaned from them with regard to the biodiversity of GZ.

Due to the less challenging sampling, fewer methodological constraints and obviously lower costs, studies of the GZ distribution are usually undertaken in the horizontal plane and rarely extend below the euphotic zone (e.g., Mańko et al. 2015). In the Arctic Ocean, the vertical distribution of GZ down to the mesopelagic zone has been characterized on only a few occasions (e.g., Raskoff et al., 2005; 2010), but these were either spatially limited to the Canadian Basin or were not directly focused on the GZ (e.g., Kosobokova and Hopcroft, 2010; Kosobokova et al., 2011; Smoot and Hopcroft, 2017).

Global-scale analyses of the vertical distribution of the GZ have found that planktonic ctenophores and cnidarians are distributed not only according to the water mass characteristics but also according to the bottom topography (Raskoff et al., 2005; Hosia and Båmstedt, 2008; Raskoff et al., 2010; Mańko et al., 2015). GZ tend to aggregate in horizontal layers of varying thickness (Graham et al., 2001; Raskoff et al., 2005; Hosia and Båmstedt, 2008), which are often near discontinuities in the water column (Graham et al., 2001; Purcell et al., 2010; Trudnowska et al., 2016). This behaviour potentially enhances secondary production and trophic interactions (Purcell et al., 2014) or may be a simple response to physical cues (Graham et al., 2001; Frost et al., 2010). Additionally, GZ may occupy relatively narrow depth ranges, which often do not overlap between species (e.g., Lindsay and Hunt, 2005; Youngbluth et al., 2008). Raskoff et al. (2005, 2010), by studying the GZ in the Canadian Arctic, also demonstrated that their vertical distribution may reflect the higher-level taxonomy, with siphonophores and ctenophores being more numerously represented in shallow waters and medusae dominating in deep waters. Notably, the vertical distribution of jellyfish and ctenophores may vary seasonally (Hosia and Båmstedt, 2008; Bandara et al., 2016 and references herein) and may change due to diel vertical migrations (e.g., Pagès and Gili, 1991). However, in some cases, biotic interactions could be equally significant in structuring the distribution of GZ (see, Arai, 1992). There is evidence that some gelatinous predators follow their prey through the water column (Majaneva et al., 2013; Bandara et al., 2016), that different life cycle stages (e.g., eudoxids and polygastric colonies, in the case of siphonophores) can be vertically separated (Takahashi and Ikeda, 2006; Hosia and Båmstedt, 2008), or that their life cycles may limit dispersal with, for example, meroplanktonic taxa being represented more abundantly in neritic assemblages (Rodriguez et al., 2017).

This study constitutes the first attempt to thoroughly characterize the vertical distribution of gelatinous zooplankton down to the mesopelagic zone in the Fram Strait (the European Arctic) and to disentangle its environmental and biotic drivers, thus providing a diversity baseline for further studies on the zooplankton distribution. Sampling along the two latitudinally parallel transects of varying hydrographic conditions and across the different bathymetric zones (shelf, slope, offshore, and exterior) was designed to investigate the influence of Atlantic water on the GZ community of the European Arctic.

2. Materials and methods

2.1. Sampling and data collection

The samples were collected in early summer of 2012 (13–21 of July) along the two parallel latitudinal transects, which were the southern transect N (76°30′N) and the northern transect EB (79°N) (Fig. 1), west of Svalbard Archipelago on-board the RV *Oceania* (Institute of Oceanology, Polish Academy of Sciences). Each transect encompassed the following four zones, which were distinguished based on bathymetry, from east to west: shelf (N – 3 stations, EB – 1 station), slope (N – 3 stations, EB – 4 stations), offshore (N – 3 stations, EB – 2 stations), exterior (N – 3 stations, EB – 2 stations), totalling 21 stations (Fig. 1). The three westernmost zones (exterior, offshore, and slope) were, in some of the subsequent analyses, grouped under the term open ocean to facilitate their comparison to the shelf.

Stratified vertical zooplankton samples were collected with a Multi Plankton Sampler (Hydro-Bios, Germany) with 0.180 mm mesh size gauze and a 0.25 m^2 square opening. Five fixed-depth strata, 0–25 m, 25–50 m, 50–200 m, 200–600 m, and 600–1000 m, were sampled at each station, with the exception of the shelf stations and those where the bottom was shallower (Table 1). The samples were fixed with 4% formaldehyde in a seawater solution buffered with borax immediately after collection and were stored until taxonomic analysis. The water temperature (°C) and salinity were simultaneously measured at each station using an SBE 911plus CTD probe (Sea-Bird Electronics, Inc., Bellevue, WA, USA) made up of duplicate SBE 3plus premium temperature sensors and SBE 4C conductivity sensors and a Digiquartz® pressure sensor.

The water masses detected at each of the sampling sites were classified using temperature and salinity data averaged per depth stratum of zooplankton sampling. The characteristic T-S signatures of each water mass were adapted from Cottier et al. (2005), with Walczowski et al.'s (2012) modification of the S threshold for Atlantic water ($S > 34.92$) (Table 1).

2.2. Sample processing

Gelatinous zooplankton from the total zooplankton samples were identified to the lowest possible taxonomic level, enumerated and measured down to 0.01 mm under a NIKON SMZ800 stereomicroscope equipped with a calibrated ocular micrometer. The species abundance was then expressed as the number of individuals per 1000 m^3. This unit was chosen due to the frequent low abundance of GZ (see, e.g., Hosia et al. 2017). The species identification followed the key references on gelatinous zooplankton taxonomy, including those of Russel (1953), Kramp (1961), Totton (1965), Bouillon et al. (2006), and the species records (Ronowicz et al., 2015; Schuchert, 2019). For each species, the higher taxonomic ranks (i.e., order for medusae, suborder for

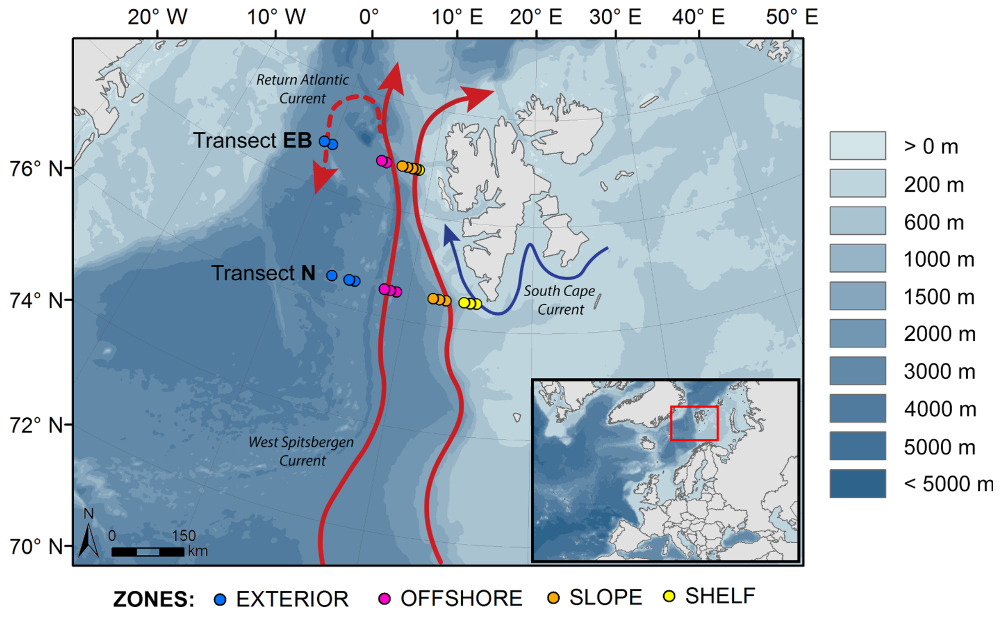


Fig. 1. Location of the zooplankton sampling in the western part of the Svalbard Archipelago, with the main ocean currents (after Beszczynska-Möller et al., 2011). Bathymetry data from the International Bathymetric Chart of the Arctic Ocean (Jakobsson et al., 2012).

siphonophores and phylum for ctenophores) were also noted for the sake of comparison of the general abundance patterns.

For the calycophoran siphonophores, the life cycle stage/colony fragment (eudoxid bracts and gonophore, anterior nectophore, and posterior nectophore) was also determined. The abundance of polygastric colonies equalled the number of anterior nectophores found. The abundance of eudoxids was determined as the number of eudoxid bracts found, since each eudoxid has only one eudoxid bract but could potentially have more than one gonophore (Carré and Carré, 1991). Since only in the case of *Dimophyes arctica* were both polygastric colonies and eudoxids found, whenever the relative abundance of this species was estimated, the sum of both the eudoxids and polygastric colonies of *D. arctica* was used. In the case of physonect siphonophores, the nectophores were counted and measured. The species abundance was expressed as the number of pneumatophores found; each colony has only one pneumatophore but can possess numerous nectophores; thus, this approach offers the most reliable estimate of the actual number of colonies (e.g., Hosia and Båmstedt, 2008). When only nectophores were found, as was the case for *Rudjakovia plicata*, the number of colonies was calculated based on an *a priori* assumption that the maximum nectophore count for a single colony of this species was 12. This assumption arose from a zoological examination of specimens collected by remotely operated vehicles, of which the longest colony bore 12 nectophores (unpublished data).

The specimen measurements included bell height for the prolate hydromedusae (i.e., bullet shaped bell like that of *Aglantha digitale*) and pandeids, nectophore width for physonect siphonophores, nectophore/bract/gonophore height for calycophoran siphonophores and total body length in the case of ctenophores (e.g., Costello et al., 2008). Specimens of *A. digitale* were classified into three size classes based on bell height (BH) using the previously published size ranges for each class: juveniles 4–5 mm BH; intermediate > 5–11 mm; and mature > 11 mm (Takahashi and Ikeda, 2006). Although Takahashi and Ikeda's (2006) data came from the subarctic Pacific, similar size ranges and diets of *A. digitale* in the north-eastern Atlantic (Pagès et al., 1996) and in the European Arctic (e.g., Zelickman, 1972) allow for a rough approximation of the similarity between the maturation sizes of this species in these regions. As gelatinous animals tend to shrink after fixation, the acquired measurements only approximate the actual sizes of the specimens and thus cannot serve as the basis for biomass calculation (Purcell, 1988; De Lafontaine and Leggett, 1989).

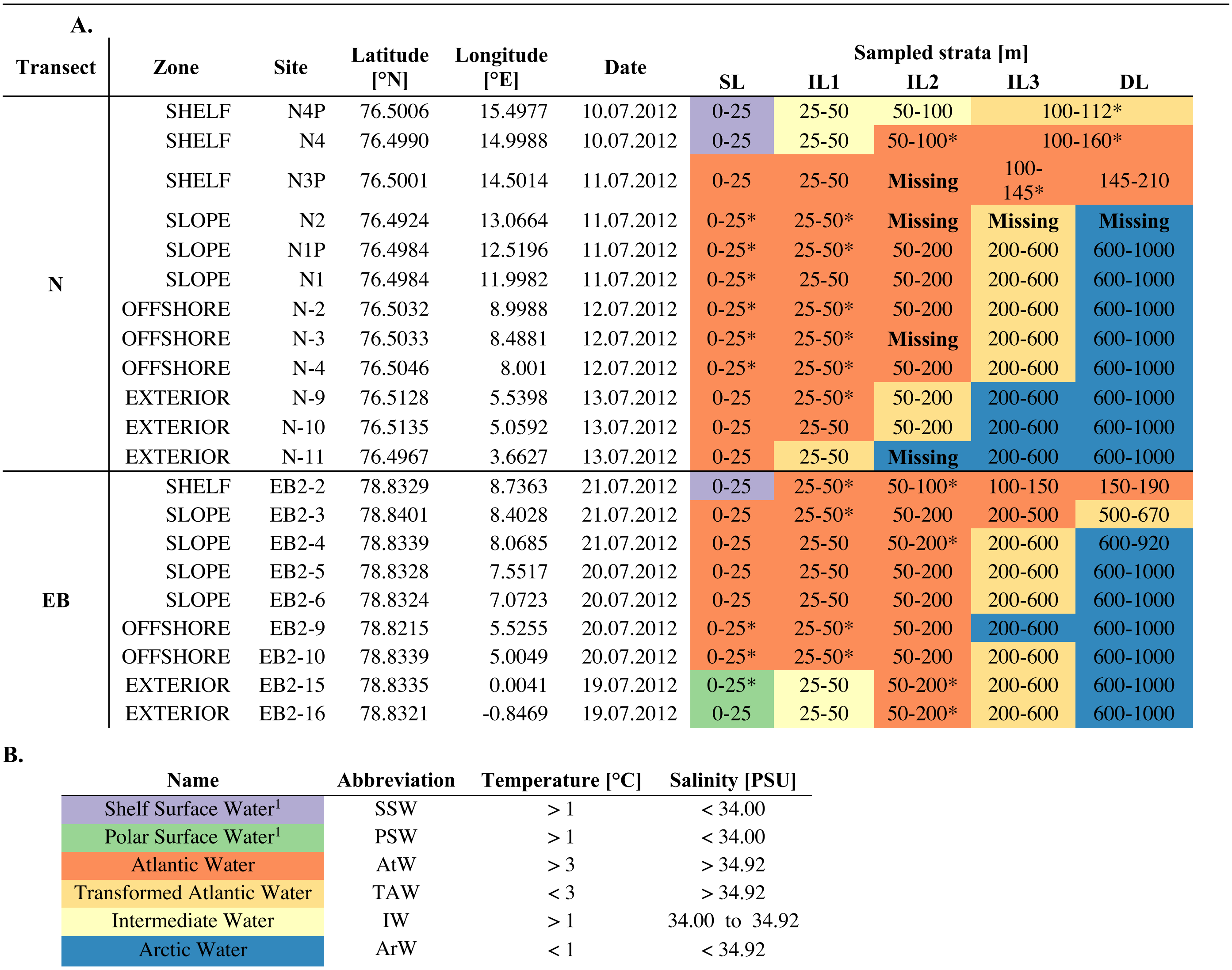
The non-gelatinous zooplankton were identified to the lowest possible taxonomic level using the subsampling method (Harris et al. 2000), and these data have already been reported elsewhere (Gluchowska et al., 2017b). The species abundance was then used to calculate the zooplankton biomass using individual dry mass or weight-length regressions, as reported in Gluchowska et al. (2017b). Both the abundance [ind. m^{-3}] and biomass of the zooplankton [mg m^{-3}] were used as the environmental background for the subsequent analyses.

2.3. Data handling and analysis

The abundance data of the gelatinous zooplankton and of the other zooplankton were square root transformed prior to the analyses. To avoid the overrepresentation and production of meaningless similarity matrices, the samples with no GZ detected were omitted from the analyses. Data pre-processing and exploratory analyses were conducted in R (v. 3.3.2., R Core Team, 2016) using the *tidyverse* package (Wickham, 2019).

The differences between the GZ data and the explanatory variables were tested with a series of uni- and multivariate permutational analyses of variance (PERMANOVAs) run with 999 permutations in R using the *adonis* function in the *vegan* package (Oksanen et al., 2007). To control for the familywise error rate resulting from multiple comparisons, the p values were adjusted with the Holm-Bonferroni method. The GZ data used included the GZ standing stocks ("abundance of GZ") and GZ community composition ("community of GZ") and the diversity indices (richness, equal to the species number; "inv. Simpson" – inverse Simpson diversity index) and life cycle stage composition of the two most abundant taxa, *A. digitale* and *D. arctica.* The explanatory variables were grouped into hydrographic (salinity and temperature [°C], which were both averaged for each sampled depth stratum), geographic (transect [N, EB], zone [shelf, slope, offshore, or exterior]) biotic (total abundance of zooplankton – "tot. abundance", total biomass of zooplankton – "tot. biomass"), while the water mass types were tested individually. The collinearity of the explanatory variables was examined with the variance inflation factor (VIF; *vegan* package in R; Oksanen et al., 2007). Although none of the continuous variables examined have been shown to be collinear (VIF values < 5; Stine, 1995), it must be noted that the categorical variables were excluded from the

Table 1
A. Sampling details with the detected water mass type encoded for each sampled depth stratum. Samples with no gelatinous zooplankton are marked with an asterisk.
B. T-S characteristics of the water masses detected in the present study.



A.

Transect	Zone	Site	Latitude [°N]	Longitude [°E]	Date	Sampled strata [m]				
						SL	IL1	IL2	IL3	DL
N	SHELF	N4P	76.5006	15.4977	10.07.2012	0-25	25-50	50-100	100-112*	
	SHELF	N4	76.4990	14.9988	10.07.2012	0-25	25-50	50-100*	100-160*	
	SHELF	N3P	76.5001	14.5014	11.07.2012	0-25	25-50	**Missing**	100-145*	145-210
	SLOPE	N2	76.4924	13.0664	11.07.2012	0-25*	25-50*	**Missing**	**Missing**	**Missing**
	SLOPE	N1P	76.4984	12.5196	11.07.2012	0-25*	25-50*	50-200	200-600	600-1000
	SLOPE	N1	76.4984	11.9982	11.07.2012	0-25*	25-50	50-200	200-600	600-1000
	OFFSHORE	N-2	76.5032	8.9988	12.07.2012	0-25*	25-50*	50-200	200-600	600-1000
	OFFSHORE	N-3	76.5033	8.4881	12.07.2012	0-25*	25-50*	**Missing**	200-600	600-1000
	OFFSHORE	N-4	76.5046	8.001	12.07.2012	0-25*	25-50*	50-200	200-600	600-1000
	EXTERIOR	N-9	76.5128	5.5398	13.07.2012	0-25	25-50*	50-200	200-600	600-1000
	EXTERIOR	N-10	76.5135	5.0592	13.07.2012	0-25	25-50	50-200	200-600	600-1000
	EXTERIOR	N-11	76.4967	3.6627	13.07.2012	0-25	25-50	**Missing**	200-600	600-1000
EB	SHELF	EB2-2	78.8329	8.7363	21.07.2012	0-25	25-50*	50-100*	100-150	150-190
	SLOPE	EB2-3	78.8401	8.4028	21.07.2012	0-25	25-50*	50-200	200-500	500-670
	SLOPE	EB2-4	78.8339	8.0685	21.07.2012	0-25	25-50	50-200*	200-600	600-920
	SLOPE	EB2-5	78.8328	7.5517	20.07.2012	0-25	25-50	50-200	200-600	600-1000
	SLOPE	EB2-6	78.8324	7.0723	20.07.2012	0-25	25-50	50-200	200-600	600-1000
	OFFSHORE	EB2-9	78.8215	5.5255	20.07.2012	0-25*	25-50*	50-200	200-600	600-1000
	OFFSHORE	EB2-10	78.8339	5.0049	20.07.2012	0-25*	25-50*	50-200	200-600	600-1000
	EXTERIOR	EB2-15	78.8335	0.0041	19.07.2012	0-25*	25-50	50-200*	200-600	600-1000
	EXTERIOR	EB2-16	78.8321	-0.8469	19.07.2012	0-25	25-50	50-200*	200-600	600-1000

B.

Name	Abbreviation	Temperature [°C]	Salinity [PSU]
Shelf Surface Water[1]	SSW	> 1	< 34.00
Polar Surface Water[1]	PSW	> 1	< 34.00
Atlantic Water	AtW	> 3	> 34.92
Transformed Atlantic Water	TAW	< 3	> 34.92
Intermediate Water	IW	> 1	34.00 to 34.92
Arctic Water	ArW	< 1	< 34.92

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[1] Although both the SSW and the PSW have the same T-S characteristics they can be distinguished by their different origin. While the SSW originates from the glacial melt (Cottier et al., 2005, Svendsen et al., 2002), the PSW forms in the open ocean during cooling and freshening of the Atlantic water (e.g., Beszczynska-Möller et al., 2011).

test as they tended to create or inflate the issue of multicollinearity (for theoretical considerations, see Wissmann et al., 2007).

The influence of the environmental (hydrographic and geographic) and biotic factors on the gelatinous zooplankton was explored with ordination analyses performed in Canoco v.5 (Lepš and Šmilauer, 2003). The detrended correspondence analysis (DCA) was first run to test the length of the main gradient. The results of the DCA (gradient length of 6.1 SD) prompted the choice of the unimodal constrained canonical correspondence analysis (CCA) (Lepš and Šmilauer, 2003) as the most appropriate procedure. The CCA was run with unrestricted permutations (N = 1000) and the following explanatory variables: temperature, salinity, zooplankton abundance, zooplankton biomass, zone, transect and depth (as factors: DL – deep layer; IL3, IL2, IL1 – intermediate layers; and SL – shallow layer; for corresponding depths, see Table 1A). The CCA was supplemented with variation partitioning, where the species composition was explained by the three groups of variables: geographic (zone, depth, and transect), hydrographic (temperature and salinity) and biotic (zooplankton abundance and zooplankton biomass). Members of each group were filtered by a stepwise selection that tested the simple effects. The Holm-Bonferroni method was also used to correct the results of all significance tests performed in Canoco v.5.

Analysis of similarity (ANOSIM) was performed in R (*vegan* package, Oksanen et al., 2007) to test the differences between GZ community (Bray-Curtis dissimilarity matrix) among different water masses. Then the strength of association between each species and each water mass type was evaluated with *strassoc()* function using IndVal.g statistic (De Cáceres and Legendre, 2009; De Cáceres et al., 2010), followed by computing the permutation p-value of the association with *signassoc()* function, both implemented in the R package *indicspecies* (De Cáceres and Legendre, 2009).

3. Results

3.1. Hydrography

The environmental conditions of the investigated area were thoroughly described by Gluchowska et al. (2017b) and later analysed from

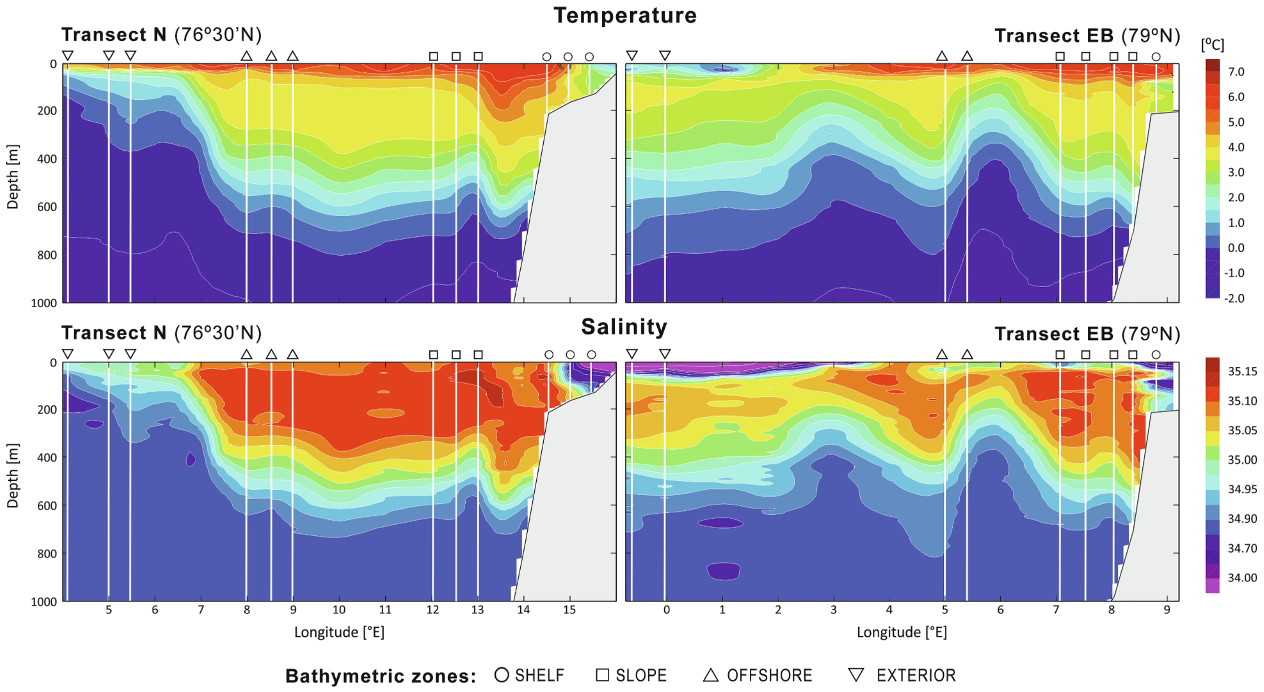

Fig. 2. Water salinity and temperature along the two transects (northern EB, southern N) down to 1000 m, with the marked bathymetric zones sampled. Source: Gluchowska M et al. (2017b) Variations in the structural and functional diversity of zooplankton over vertical and horizontal environmental gradients en route to the Arctic Ocean through the Fram Strait. PLoS ONE 12(2): e0171715. doi:https://doi.org//10.1371/journal.pone.0171715 - modified.

a broader, multiyear perspective by Merchel and Walczowski (2018). Based on our data, the water temperature decreased with increasing distance from the slope towards the exterior, either throughout the water column (transect N) or only in the 0–50 m stratum (transect EB) (Fig. 2).

The temperature of the deepest water (below 600 m) on average ranged from −0.27 °C (northern transect) to 0.11 °C (southern transect). When considering both transects and all depths, the water temperature ranged from −0.51 °C to 6.37 °C. The salinity was lower at the stations along transect EB compared with the stations along transect N, with the highest variation in salinity in the surface waters and the highest values within the layer spanning from 50 to 200 m. The water with the lowest salinity (33.61) was found in the surface layer of the exterior zone along transect EB, whereas the highest salinity (35.16) was detected in the waters from 25 to 50 m in depth above the slope along the southern transect (Fig. 2). The shelf stations in both transects were characterized by strongly differing conditions: those located along transect N remained under the influence of the cold Sørkapp (South Cape) Current, whereas more Atlantic conditions prevailed in the shallow sites above the shelf in transect EB (Fig. 2). Formation of the surface shelf water (SSW) was detected in the upper 25 m of the water column in the shelf stations, with the exception of station N3P were only Atlantic water (AtW) was found (Table 1B). The core of the West Spitsbergen Current (WSC) was located over the slope, extending as deep as 500 m in transect EB and 600 m in transect N. The sampling sites in the offshore zone were under the influence of the WSC offshore branch (characterized by weaker northward velocities) in transect N, and in EB, they were situated within a rotating structure that presumably arose as a consequence of the local topography. Vertical distribution of the water masses detected at the slope and offshore sampling sites was the same at both transects i.e., AtW occupied upper 200 m, Arctic water (ArW) was found below 600 m, and the transformed Atlantic water was squeezed between the two (Table 1B). The only exception was one of the offshore sites along transect EB (EB2-9) where, due to the presence of the rotating structure, ArW was brought to the 200–600 m depth stratum. Similar shallowing of ArW was documented for the sites of the exterior zone in transect N, where AtW was found only down to 50 m (25 m at N-11). Westernmost stations in transect EB (exterior zone) were under the influence of the Return Atlantic Current, which flows southward and was found between thin layer (25–50 m) of the intermediate water (IW) at the top, and the transformed Atlantic water (TAW) at the bottom (Fig. 2, Table 1). The IW formed as a result of mixing between the AtW and polar surface water (PSW) present in the top 25 m of the water column.

3.2. General horizontal distribution patterns of gelatinous zooplankton

Gelatinous zooplankton were present in 70 out of the 97 examined samples (see Table 1). In total 1928 individual specimens were identified and measured. The average abundance of all gelatinous zooplankton per station was significantly higher along southern transect N (305 ind.·1000 m^{-3}) than along transect EB (265 ind.·1000 m^{-3}) (Table 2, Supp. mat. 1). The difference in the average abundance was more pronounced for the shelf stations (N: 568 ind.·1000 m^{-3}; EB: 432 ind.·1000 m^{-3}), while the abundances averaged for all zones of the open ocean (i.e., slope, offshore, and exterior) were more consistent (N: 217 ind.·1000 m^{-3}; EB: 210 ind.·1000 m^{-3}) (Supp. mat. 1), but the differences between the zones were still statistically significant (Table 2).

In total, 17 taxa of gelatinous zooplankton were identified, and the species richness for the open ocean zones was higher (12 taxa) than that for the shelf stations (8 taxa; Fig. 3). *A. digitale* constituted 41.94% of all GZ observed, while *D. arctica* and *Mertensia ovum* were the second and third most abundant species, contributing 25.43% and 19.07%, respectively, of all species found (Fig. 3). The lowest total abundance was found for two siphonophores, *Marrus orthocanna* and *Crystallophyes amygdalina*, each represented by a single colony, what accounts for 0.04% of all GZ found.

Although *A. digitale* dominated in both transects, the numerical contributions of this species to the total abundance of GZ in each transect were different: 5451 ind.·1000 m^{-3} (southern transect N) and 3689 ind.·1000 m^{-3} (northern transect EB; Supp. mat. 3). The second most abundant species, *D. arctica,* reached relatively similar abundances in both transects (2684 ind.·1000 m^{-3} in N; 2858 ind.·1000 m^{-3}

Table 2
The results of the 2- and 3-way PERMANOVA test are reported as the pseudo-F value and the significance levels are marked as follows: ** $p < 0.001$ and * $p < 0.05$ (for full results see Supp. Mat. 2).

	Df	Abundance of GZ	Community of GZ	Species richness	Inverse Simpson	*A. digitale* stage	*D. arctica* stage
Temperature	1	5.28 **	2.92 *	31.13 **	19.71 **	6.78 **	1.17
Salinity	1	1.98	0.52	1.43	0.01	3.66 **	1.41
Temperature × Salinity	1	3.59 **	0.94	2.01	2.11	3.22 *	4.13 **
Residuals	65						
Total	68						
Zooplankton abundance	1	1.03	0.25	6.67 *	2.18	3.63 **	0.52
Zooplankton biomass	1	3.80 **	3.54 *	0.08	3.06 *	2.00 *	1.07
Zoop. abund. × Zoop. biom.	1	5.31 **	0.02	3.59	2.27	1.34	1.11
Residuals	65						
Total	68						
Zone	3	9.01 **	27.79 **	14.62 **	2.99 **	1.76 *	0.80
Depth	4	58.22 **	9.64 **	47.87 **	10.93 **	8.79 **	1.85 *
Transect	1	21.09 **	6.74 *	2.70 *	0.19	0.66	0.59
Zone × Depth	9	3.08 **	8.93 **	5.62 **	2.27 *	1.24	1.52
Zone × Transect	3	3.42 **	10.91 **	10.89 **	2.31	2.43 **	2.61 *
Depth × Transect	4	3.28 **	1.85	2.59 *	2.30	2.13 *	1.05
Zone × Depth × Transect	3	5.23 **	7.00 **	9.72 **	1.43	0.92	0.50
Residuals	30						
Total	57						
Water mass type	4	5.46 **	8.78 **	18.13 **	12.75 **	3.94 **	1.68
Residuals	64						
Total	68						

in EB), while the large contribution of *M. ovum* to the average relative abundance resulted solely from its presence at the shelf stations (3153 ind.·1000 m^{-3} in N; 1003 ind.·1000 m^{-3} in EB; Supp. mat. 3). There were also species that were present in one transect but absent from the other. The taxa that were unique to transect N were *Catablema vesicarium*, *Halitholus cirratus*, *Bougainvillia superciliaris*, and *Physophora hydrostatica*, while for transect EB, these were *C. amygdalina* and *M. orthocanna* (Fig. 3). The species present only along the southern transect were found solely in the waters above the shelf.

Three taxa were present in all zones along both transects: *A. digitale, D. arctica* and *Beroe* spp. (absent only from the exterior stations on transect EB); however, *D. arctica* was found at shelf stations only in a single sample collected from the waters above the bottom of transect N. Five taxa (*Homoeonema platygonon,* Trachymedusae indet., *Muggiaea bargmannae*, Diphyid eudoxid indet. and *Rudjakovia plicata*) could be characterized as having open ocean distributions since they were found at the slope, offshore and exterior stations and were absent from the shelf waters. Distribution of three taxa was restricted to a single zone: *C. amygdalina* and unidentified ctenophores were found only at the offshore, while *M. orthocanna* at the exterior stations.

3.3. Vertical distribution of gelatinous zooplankton

3.3.1. Abundance and diversity

The vertical distribution of the gelatinous zooplankton abundance and diversity varied significantly both within the zones and between zones (Table 2). Above the shelf, the highest abundance of GZ was observed in the surface layer (0–25 m; transect N: 1911 ind.·1000 m^{-3};

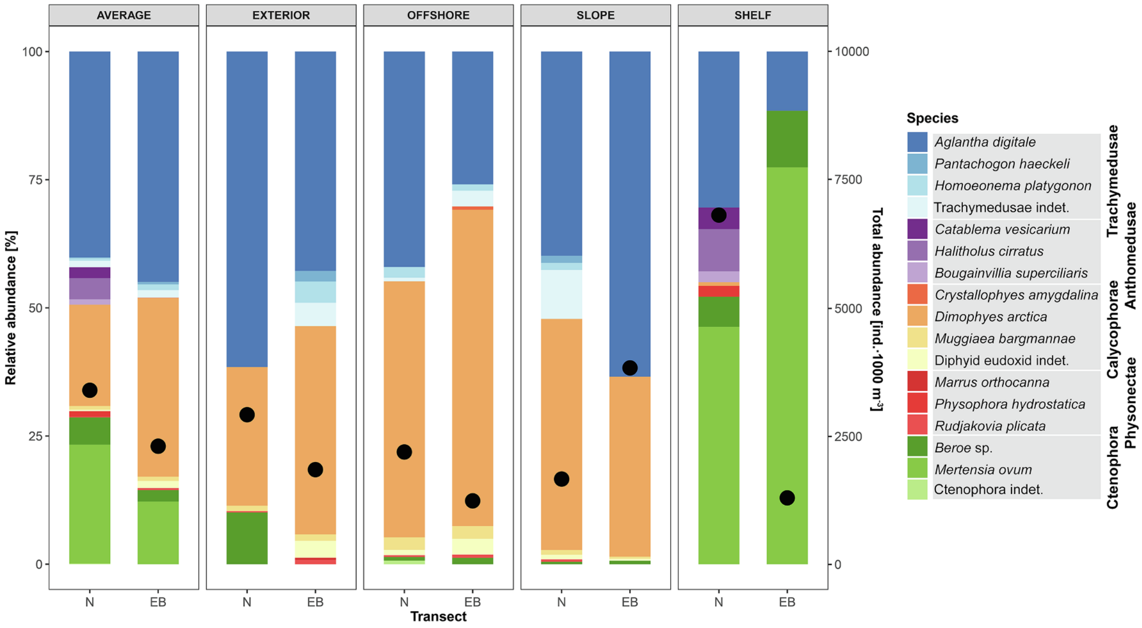

Fig. 3. Depth-averaged relative abundances [%] of all taxa and higher taxonomic ranks, which were averaged over each transect and are shown separately for each bathymetric zone. Black dots represent the total abundance of gelatinous zooplankton [ind.·1000 m^{-3}], which is equal to the sum of the abundance of all species observed at particular transect and bathymetric zone.

transect EB: 1147 ind.·1000 m^{-3}; Supp. mat. 1). Then, the average abundance of gelatinous zooplankton decreased with depth until reaching its minimum in the water just above the bottom (Supp. mat. 1). A similar pattern was observed in the upper 200 m stratum in the exterior zone, but the average abundance of GZ below that depth suddenly increased, reaching an average of 309 ind.·1000 m^{-3} (transect N) and 364 ind.·1000 m^{-3} (transect EB) at depths of 200–600 m before gradually decreasing (Supp. mat. 1). In the water above the slope, the highest average abundance of GZ was found in the water that was 200–600 m deep along transect N, while in the case of transect EB, both the 200–600 m and 25–50 m water strata harboured GZ populations of similar abundance. No representatives of GZ were found in the upper 50 m of the water column in the offshore zone along either transect, while the highest average abundance in this zone was documented in the 200–600 m stratum (Supp. mat. 1). The abundance of GZ in the open ocean zones was the highest at depths of 200–600 m and decreased with depth; however, the average abundances in the deepest samples were still higher than in either of the upper layers (i.e., 0–25 m; 25–50 m; 50–200 m; Supp. mat. 1). This led to an overall higher average abundance of gelatinous zooplankton in the waters from 200 to 1000 m deep (transect N: 314 ind.·1000 m^{-3}; transect EB: 288 ind.·1000 m^{-3}; Supp. mat. 1) than from 0 to 200 m (transect N: 113 ind.·1000 m^{-3}; transect EB: 118 ind.·1000 m^{-3}; Supp. mat. 1).

The open ocean and shelf zones harboured inverse diversity patterns, with more species-rich communities being present in the deeper open ocean layers and in the shallow water above the shelf (Fig. 4). The species classified as Anthomedusae were restricted to the shelf stations. Similarly, the ctenophores were present at high relative abundance in the shelf stations; however, this group was also found in small numbers in the shallow exterior waters and in the water layer from 200 to 600 m in all open ocean stations (Fig. 4). Trachymedusae had the highest relative abundance in the water layer from 25 to 50 m in all zones (shelf included) and in the water layer from 50 to 200 m in only the open ocean zones (Fig. 4). Then, the proportion of Trachymedusae decreased in favour of Calycophorae. Calycophoran siphonophores were also present in the surface (0–25 m) layer in the exterior and slope zones and in minute quantities in the deep shelf waters. Most of the physonect siphonophores identified were present in the deep water (> 200 m) in the open ocean zones, with the exception of *P. hydrostatica* that was found in the surface water over the shelf.

Zonal partitioning of the vertical distribution, which was observed for higher taxonomic ranks, could also be discerned at the species level (Fig. 4). *A. digitale* was present throughout the water column in all bathymetric zones, while *D. arctica* predominated in the deeper layers of the open ocean and had a very limited vertical distribution above the shelf, being found there on only one occasion. Although both species were collected at most depths in the open ocean, there were depths with a clear numerical dominance of either species, with *D. arctica* prevailing in the deeper water (starting at depths of 200–600 m along transect EB and only in the deepest waters of transect N; Fig. 4). Differences in the vertical distributions of the same species between zones were identified for a few species; notably, *M. bargmannae* and *R. plicata* had a broader range of distribution in the offshore zone than in the exterior and slope zone. Most of the Trachymedusae were found only in the samples collected from depths exceeding 600 m. In contrast, *Beroe* spp. were present throughout the shelf water column and had a limited depth range in the slope and offshore zone (200–600 m) but penetrated shallower waters in the exterior zone (up to the surface).

Of the taxa found in only a single bathymetric zone, *C. vesicarium*, *H. cirratus*, *B. superciliaris* and *P. hydrostatica* had vertical distributions that were restricted to the surface layers (0–25 m; 25–50 m; all being found in shelf zone; Fig. 4). The species unique to the open ocean zone were usually characteristic of the deeper water (*M. orthocanna*: 600–1000 m, exterior zone; *C. amygdalina*: 600–1000 m, offshore zone; Fig. 4).

3.3.2. Demography

Further examination of the vertical distribution of the two most abundant species, *A. digitale* and *D. arctica,* revealed that the different life cycle stages occupied different depths and zones and were present with significantly different frequencies in both transects (Table 2, Fig. 5).

In the case of *A. digitale,* the large, mature specimens were restricted to deep open ocean water (overall > 200 m, but few were found in 25–50 m stratum in the exterior zone along EB, and > 50 m in the slope zone along the same transect), and some were found in the water 50–100 m deep at the shelf stations along transect N (Fig. 5, Table 2). The juveniles were mostly restricted to the upper 50 m of the water column; however, a small number of individuals of this life cycle stage were also identified in deeper waters. *A. digitale* was also present at the shelf stations, with only intermediate specimens identified from the

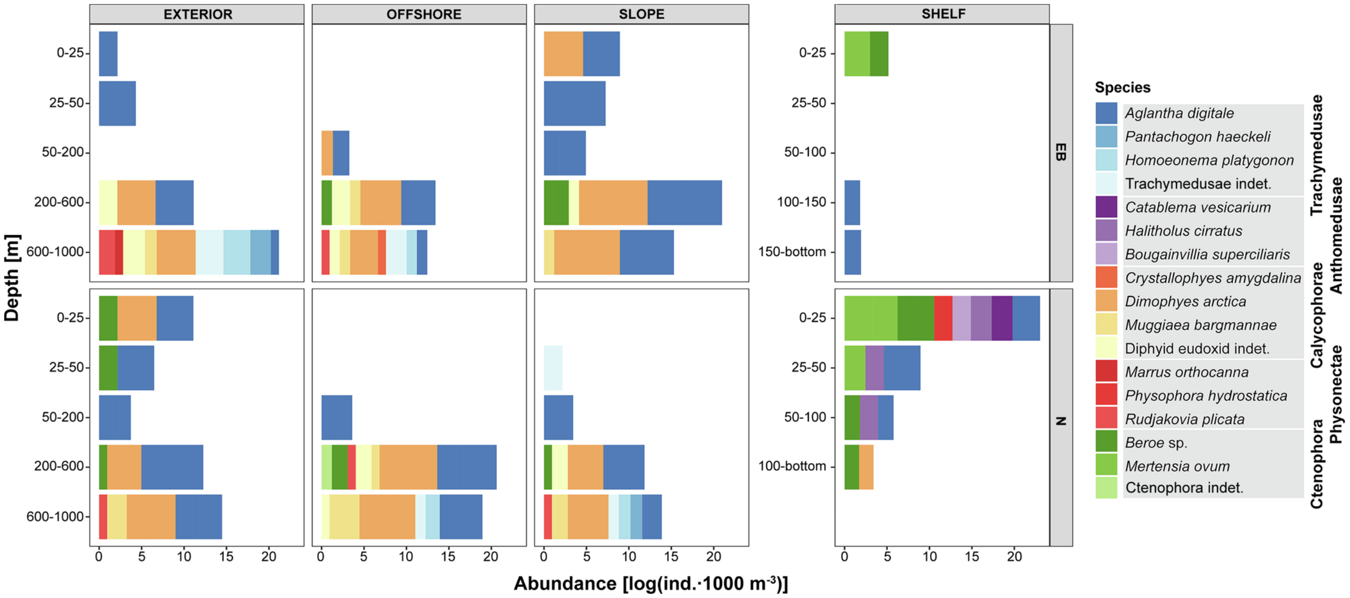

Fig. 4. Log transformed abundance [log(ind.·1000 m^{-3})] of all taxa identified and the higher taxonomic ranks, along the depth gradient, separated by bathymetric zones and transects (upper row – EB, lower row – N).

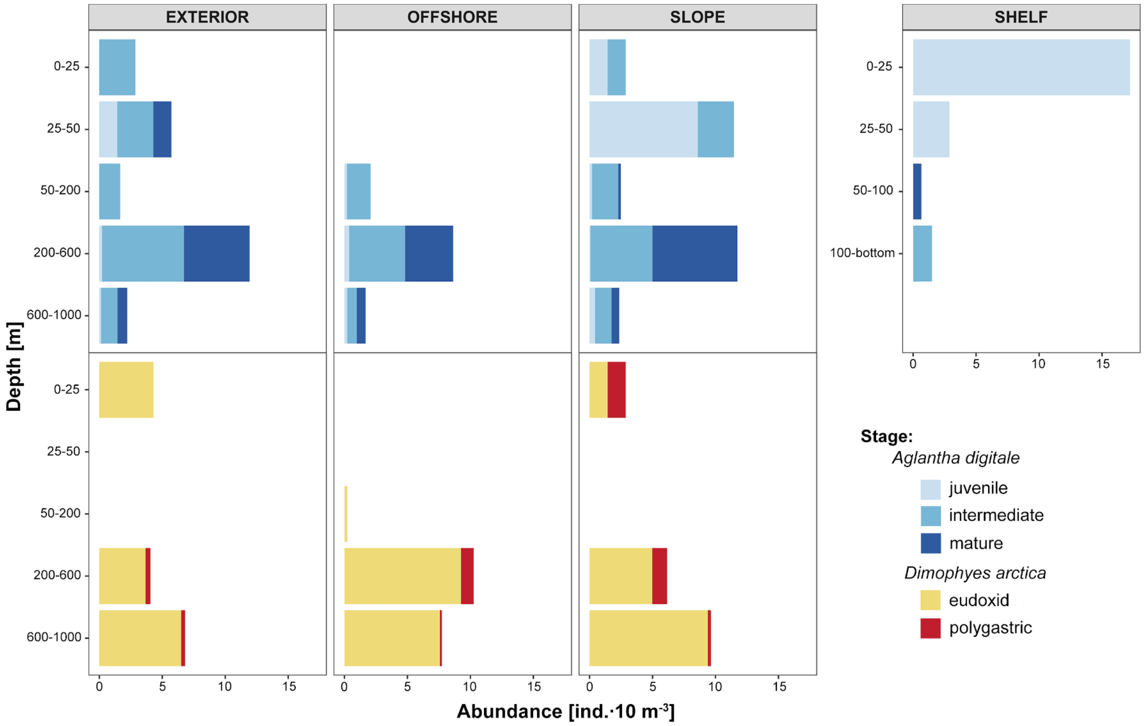

Fig. 5. Abundance [ind. ·10 m^{-3}] of the different life cycle stages of *Aglantha digitale* (upper row) and *Dimophyes arctica* (lower row) in all zones along, summed for both transects.

northern transect samples, while both mature and juvenile jellyfish were observed in the samples from southern transect N (Fig. 5). The general size distribution trend was that the deeper the sample was collected, the larger the specimens were that were found (Fig. 5, Table 2), except for in the water layer from 200 to 600 m, where the largest specimens were observed.

Most *D. arctica* observations came from deep water ($>$ 200 m); however, small quantities of eudoxids were also identified from samples collected from the 50–200 m stratum in the offshore zone and from the 0–25 m stratum above the slope along transect EB and from the 0–25 m stratum in the exterior zone along transect N; very few were collected from the deep waters above the shelf along transect N (omitted in Fig. 5). The polygastric colonies of *D. arctica* occurred mostly in water of $>$ 200 m deep, although in the surface samples (0–25 m) from the slope stations along transect EB, these colonies were equally as abundant as the eudoxids; however, the overall number of *D. arctica* in these samples was exceptionally low. All life cycle stages of this calycophoran appeared to be absent from the 25–50 m depth layer and in some zones also from 50 to 200 m (in all zones along transect N; Fig. 5). The enumeration of the two morphological components of eudoxids (bracts and gonophores), which were often found separately in the sample, revealed that in the case of *D. arctica,* the ratio of bracts:gonophores was 45:55 (Fig. 5). In case of Diphyid eudoxid indet., the proportion was 1:1, while the eudoxid stage of *M. bargmannae* remains undescribed and that of *C. amygdalina* was not found in the present study.

3.4. Drivers of gelatinous zooplankton vertical distribution

Based on the CCA model ($p = 0.001$), which was supported with variation partitioning (Fig. 6; Table 3), all tested explanatory variables explained 26.5% of the variation in gelatinous zooplankton abundance, with the geographic factors (zones, depths) accounting for most of the explanatory strength of the variables (Table 3). The factorial variable transect was excluded from the analysis, as its addition decreased the adjusted explained variation, and its effects were insignificant ($p = 0.84$). Relatively high explanatory power was attributable to the interplay between the groups of factors: 20.3% to the geographic and hydrographic (temperature, salinity) interactions, 14.2% to the hydrographic and biotic (zooplankton abundance and biomass) interactions and to the combined effect of all factors (22.7%; Table 3). Interestingly, when analysed separately, the hydrographic factors explained only 1.1% of the variation (Fig. 6).

The CCA model supported the previous analyses (Table 2), indicating the existence of strong and statistically significant relationships between specific species and the analysed environmental variables. *P. hydrostatica* was associated with higher temperatures, which was similar to the association of the abundance of the juveniles of *A. digitale.* The distribution of the *Beroe* ctenophores was unexpectedly strongly correlated with the total abundance of zooplankton (Fig. 6), whereas the distribution of other species, such as the remaining Trachymedusae, was mostly explained by the increasing depth, potentially implying their avoidance of warmer surface waters (Fig. 6).

3.5. Water mass type related community of gelatinous zooplankton

Out of six water masses detected in the present study (Table 1) only five were incorporated in the subsequent analyses, as PSW was found only at two sites, at one of which there was no GZ, while at the other only few (143 ind.·1000 m^{-3}) juvenile *A. digitale* were present. Each of the analysed water masses, harboured a significantly different GZ community (ANOSIM, $R = 0.23$, $p = 0.001$). A series of PERMANOVAs have revealed that the GZ diversity, the abundance of all GZ, but also demography of *A. digitale* differed significantly between the water masses (Table 2). The most species rich GZ community was associated with the Arctic waters, followed by slightly less diverse community found in the intermediate water and the polar surface water (Table 4). In contrast, the GZ community found in the Atlantic waters comprised almost solely of *A. digitale*, that overall constituted c. 66% of all GZ

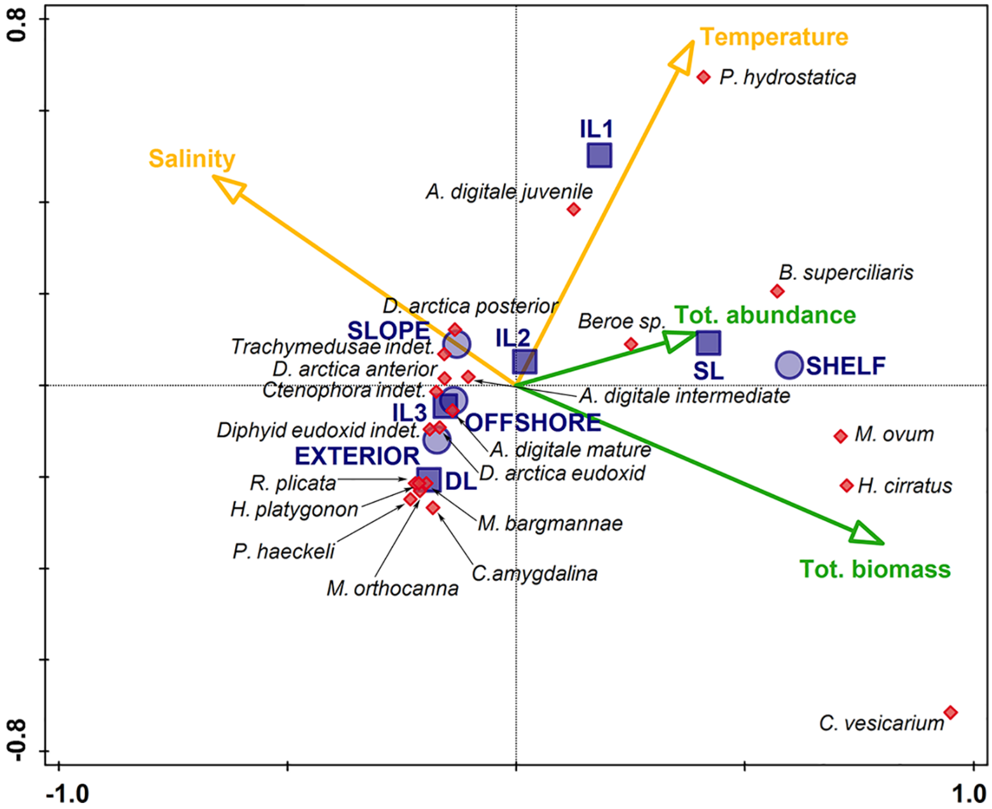

Fig. 6. The results of the canonical correspondence analysis (CCA). Ordination diagram showing the relationships between the abundances of the gelatinous taxa and significant environmental and biotic drivers.

Table 3
Partitioning of variation ($p = 0.001$) explained by three groups of factors in the CCA (Fig. 5).

	Fraction	Members	Variation (adjusted)	% of explained	% of all	*df*	Mean square
Geographic	a	Zone, Depth	0.408	35.3	9.3	8	0.0953
Hydrographic	b	Temperature, Salinity	0.013	1.1	0.3	2	0.0528
Biotic	c	Zooplankton abundance, zooplankton biomass	0.057	4.9	1.3	2	0.0716
Combined	d	a × b	0.235	20.3	5.4	–	–
	e	b × c	0.165	14.2	3.8	–	–
	f	a × c	0.017	1.5	0.4	–	–
	g	a × b × c	0.262	22.7	6.0	–	–
		Total explained	1.158	100.0	26.5	12	0.1437

found in this water mass.

Most GZ taxa studied showed affinity to more than one water mass (Table 5). Few species were found to share relatively high association index with more than 2, or even 3 water masses, yet even in such cases, either of the water masses always prevailed (Table 5). For example, all three life cycle stages of *A. digitale* were found to associate with waters of Atlantic origins, but each life cycle stage of this species favoured the particular water mass. Both the juvenile and mature *A. digitale* seemed to prefer AtW, whereas the intermediate specimens of this species dominated in TAW (Table 5). Non-*Aglantha* Trachymedusae were all found solely in ArW, as were the two siphonophores, *C. amygdalina* and *M. orthocanna*. Polygastric colonies of *D. arctica* appeared to prefer TAW, while the strongest association of this species eudoxids was found with the Arctic water.

Partitioning of distribution of distinct life cycle stages between different water masses was clear for *A. digitale,* but not for *D. arctica* (Fig. 7, Table 2). However, in the case of the latter, it can be deduced that the higher abundance of this species was associated with ArW (Fig. 7), presumably because of the eudoxids' proclivity to that particular water mass (Table 5). Whereas for *A. digitale*, juveniles, although present in all water masses (Fig. 7), clearly preferred warmer AtW (Table 5, Fig. 7), while the intermediate stage, though also occurring in the colder ArW and AtW, associated mostly with TAW.

Table 4
Summary statistics of GZ and *Aglantha digitale* abundance [ind.·1000 m^{-3}], and diversity of GZ community [number of species] within each water mass.

	Abundance of GZ [ind.·1000 m^{-3}]		**Abundance of *A. digitale* [ind.·1000 m^{-3}]**			**Number of species**		
	Mean	**SD**	**Mean**	**SD**	**% of all GZ**	**Max**	**Mean**	**SD**
SSW	1672.18	743.23	-	-	0.00	4	3.00	0.82
AtW	250.55	387.44	85.88	260.77	66.01	3	0.65	0.76
TAW	452.47	174.83	162.99	73.06	38.42	3	2.81	1.33
IW	224.55	112.66	99.14	57.98	44.15	5	1.60	0.80
ArW	401.88	188.13	75.13	98.23	18.69	8	3.89	1.74

Table 5

Value of association index (IndVal.g) between GZ species and water mass types. Association index of value 0 not shown, as they correspond to no specimens of particular species detected in the tested water mass. Grey shading indicates the association with the highest significance. Significance levels: * $p < 0.05$; ** $p < 0.005$.

	SSW	AtW	TAW	IW	ArW
Aglantha digitale					
juvenile		0.43*	0.09	0.22	0.25
intermediate		0.35	0.65**	0.15	0.43
mature		0.05**	0.62**	0.31	0.42
Trachymedusae indet.		0.09			0.49*
Homoeonema platygonon					0.51**
Pantachogon haeckeli					0.40*
Catablema vesicarium	0.58*				
Halitholus cirratus	0.43			0.43	
Bougainvillia superciliaris	0.58*				
Crystallophyes amygdalina					0.23
Dimophyes arctica					
eudoxid		0.15*	0.58**		0.67**
polygastric		0.09	0.69**		0.27
Muggiaea bargmannae			0.07		0.73**
Diphyid eudoxid indet.			0.58**		0.31
Marrus orthocanna					0.23
Physophora hydrostatica		0.20			
Rudjakovia plicata			0.12		0.46*
Beroe spp.	0.85**	0.08*	0.24	0.14	0.02**
Mertensia ovum	0.96**			0.13	
Ctenophora indet.			0.26		

4. Discussion

Here, we provide the first description of the vertical structuring of the GZ community down to the mesopelagic zone in the Fram Strait and characterize the statistically supported ordering of its biotic and environmental drivers. Our results indicated a prevailing role of water mass distribution in shaping of the local planktonic community, affecting the GZ diversity and the vertical structuring of their demography, suggesting susceptibility of the Arctic GZ to the Atlantification.

4.1. Northward decrease in GZ abundance

When considered all together, stations along the southern transect N harboured a more abundant community of the GZ (Fig. 3). Stronger influence of AtW along the transect N than along the transect EB (Fig. 2), could thus justify the claims of numerically richer boreal planktonic communities there (e.g., Hop et al., 2019). This notion was further supported by the statistically significant dependence of the GZ abundance on the water temperature and salinity and their interplay (Table 2, Fig. 6), but also on the water mass distribution (Table 2).

Majority of the differences in the GZ abundance along the two transect was attributed to the shelf stations, whereas the GZ communities of the open ocean zones were relatively similar in size, though still more abundant community was detected along transect N. Surface waters in the shelf zone were classified as SSW (Table 1A), that in the case of transect N probably originated in the Barents Sea and got there *via* the Sørkapp Current, which flows northward along the southern shore of Svalbard (Swerpel, 1985), while in the transect EB comprised a mixture of the glacial meltwater and the AtW. Presence of this particular water mass explains why these waters were teeming with the typically Arctic ctenophore, *M. ovum*, (Fig. 3; Majaneva and Majaneva, 2013), while the different origin of the SSW could account for the differences in the abundance of other GZ taxa found there. Discovery of a thin layer of a relatively warm surface water above the shelf may also explain why *A. digitale* (mostly juveniles) was also particularly abundant there, as this species is often associated with higher temperatures (e.g., Haberlin et al., 2019). Disproportion in abundance of these two species between the two transects, and the occurrence of additional taxa along the transect N, are thus very likely explained by the varying influence of the Sørkapp Current, and the proximity to the core of the West Spitsbergen Current (Fig. 2).

Outside of the shelf waters, that are known to host abundant planktonic assemblage (e.g., Sabatès et al., 1989, Graham et al., 2001; Coyle et al. 2008), GZ reached highest abundance in the transformed Atlantic water that originated in between of AtW and ArW (Table 1A, Cottier et al. 2005). Surprisingly, the AtW did not harbour the most abundant GZ community, but in turn had the highest contribution of a single species, *A. digitale*, to the abundance of all gelatinous taxa (c. 66%, Table 1A). Presence of a more abundant assemblage of GZ in ArW, when taking into account the patchiness of zooplankton (Trudnowska et al., 2016), could potentially be related to the unequal sampling efforts in AtW compared to ArW (52 and 19 samples, respectively).

The third most abundant species (after *A. digitale* and *M. ovum*) the siphonophore *D. arctica*, had a relatively similar abundance along both transects, although it was absent from the shelf samples along the northern transect and was less abundant along the slope of transect N.

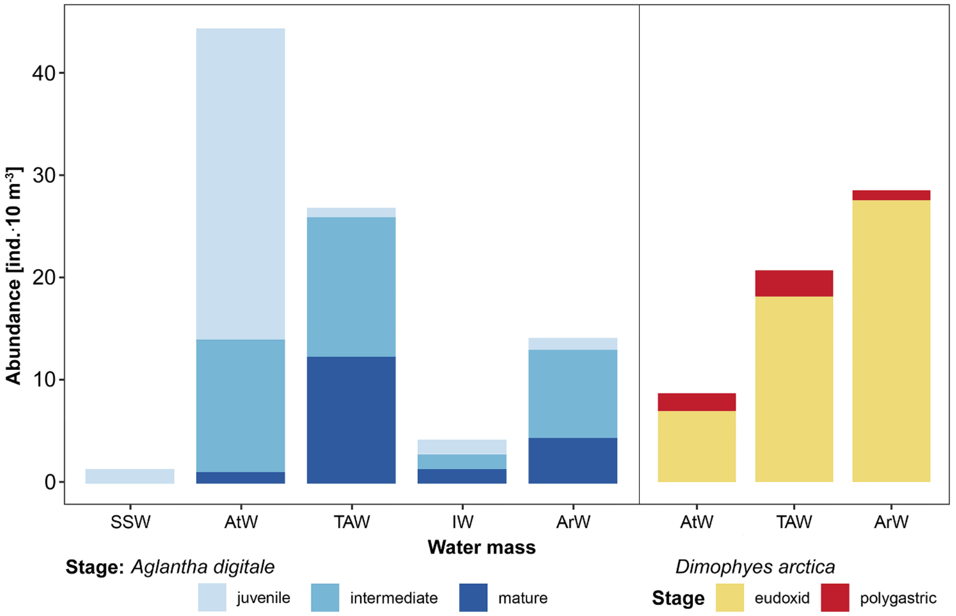

Fig. 7. Abundance [ind. · 10 m^{-3}] of different life cycle stages of *Aglantha digitale* and *Dimophyes arctica* in water masses detected in the present study.

Due to its presumed bipolar biogeography (Stepanjants et al., 2006; but see Pugh and Gasca, 2009), the spatial distribution of our records of *D. arctica* matched the preference of this species towards colder waters (Figs. 4 and 6; Table 5). Unsurprisingly, the lower abundance of this siphonophore above the slope along the southern transect could be attributed to the presence of the warm core of the West Spitsbergen Current (Carstensen et al., 2019; Gluchowska et al., 2017b; Walczowski and Piechura, 2007). At first glance, the GZ community above the slope of EB seemed to have virtually double the abundance of GZ in comparison with that in the corresponding region of southern transect N. This, however, resulted purely from unequal sampling efforts (see Table 1A), and when the average abundance per sample was taken into account, the abundance of GZ was far more even, and the resulting contributions of the different species (*A. digitale* was more abundant along transect N, and *D. arctica* dominated along northern transect EB) fit our literature-based expectations (e.g., Licandro et al., 2015; Mańko et al., 2015).

Our data revealed that the abundance of GZ decreased with increasing depth above the shelf, while in the open ocean, the vertical pattern of abundance was more intricate (Supp. mat. 1). In general, GZ were most abundant at the subsurface from 25 to 50 m, followed by the surface from 0 to 25 m; the abundance decreased from 50 to 200 m but reached a maximum at 200–600 m and then slightly decreased in the deepest layer. Similar to our case, Raskoff et al. (2010) studied GZ community in the Canada Basin and Chukchi Plateau and found that the lowest biomass was associated with shallow slopes and ridges. It has often been noted that the warmer Atlantic waters are bringing more diverse and abundant zooplankton communities to the Arctic Ocean (Hop et al., 2019) that can reach even the deep central regions of the Arctic (Kosobokova and Hirche, 2000). Although the abundance of zooplankton tends to generally decrease with increasing depth (e.g., in the NE Atlantic; Angel and Baker, 1982; however, not necessarily for the GZ, see e.g., Youngbluth et al., 2008), the pattern of the vertical distribution of zooplankton abundance in the Arctic can diverge from this assumption as a result of Atlantic inflow (Kosobokova and Hirche, 2009). The core of the WSC, which extends down to 500 m along transect EB and to 600 m along transect N, is usually characterized by the highest abundance of zooplankton, which remains fairly constant along the continental margin, though the contributions of different taxa change (Kosobokova and Hirche, 2009; Weydmann et al., 2014). As the vertical distribution of zooplankton may fluctuate seasonally, the advected biomass is also expected to vary within a year (Basedow et al., 2018). Additionally, the complex hydrological situation along the continental slope of Svalbard forces any prognoses on the advection of zooplankton to distinguish among the different branches of the core of the WSC, which may each bring distinct planktonic communities (Carstensen et al., 2019).

4.2. Patterns of GZ diversity

The pattern of GZ biodiversity established here exemplifies strong spatial and vertical structuring (Table 2, Figs. 4 and 5), with a more speciose community associated with colder, Arctic water and a rich assemblages associated with the shallow shelf waters, and the deepest waters in the open ocean zone (Fig. 4). We showed that geographic factors (zone and sampling depth) played the largest role in shaping the GZ diversity overall (Fig. 4), but also, that their diversity depended on the distribution of the water masses (Table 2). When considering GZ community separately for each of the water masses detected, ArW appeared to harbour the most diverse community (Table 4). This may however, be explained by the vertical extent of ArW (the deepest of the water masses found; Table 1A) that allowed to capture the typically mesopelagic species (like non-*Aglantha* Trachymedusae), absent from the shallower depth strata. Stations remaining under the influence of AtW were characterized by the lowest diversity of GZ, and the highest contribution of *A. digitale* to the GZ abundance (66.01% for AtW, 38.42% for TAW). Such a monospecific GZ community may be indicatory of the blooming potential of this species (see e.g., Pertsova et al., 2006) thus the strengthening of AtW inflow to the Arctic, may potentially render *A. digitale* more important for the polar pelagic ecosystems (e.g., Hop et al., 2006).

The richer shelf community reflected the presence of meroplanktonic cnidarians, i.e., species possessing benthic polyps in their life cycle, such as Anthomedusae (Figs. 3 and 4), which in the case of our study were absent from the open ocean. There are however, anthomedusan taxa that can be found in deeper waters, further away from the shore where they overcome the lack of an abiotic substrate needed for polyps to develop with an alternative strategy in which polyps colonize living midwater organisms (see Lindsay et al., 2008 and reference therein). Interestingly, no representatives of Anthomedusae were found along the northern transect, presumably as a consequence of the differing environmental conditions that might have delayed the release of medusae by the polyps (Boero et al., 2016), or because of an unequal sampling effort between the two shelf zones. The absence of *B. superciliaris* at the shelf stations of both transects may reflect more Atlantic-like water conditions, as this species is typically considered to be associated with cold water (Schuchert, 2007) or even to be indicative of Arctic waters (Mańko et al., 2015). A plausible explanation of this unequal representation of this Arctic species could also be based on the vulnerability of the medusae stage of *B. superciliaris* to higher temperature, or to the fact that medusae release in this species occurs only in waters 5–7 °C warm, as shown in the experimental work by Werner (1961).

In the open ocean zone, a more diverse GZ community was found in the deepest depth stratum (Fig. 4). The vertical distribution of the calycophoran siphonophores and Trachymedusae were inversely proportional, with the former being more abundant in the waters deeper than 200 m, while the later, although also present in the deep waters, dominated in the shallow waters. The non-*Aglantha* Trachymedusae, except for the Trachymedusae indet., were found exclusively in the 600–1000 m depth stratum (Fig. 4). Comparing our vertical distribution data with similar work from other regions of the Arctic Ocean is hampered by the differences in the encountered diversity of the GZ community, as ranges of vertical distribution are species-specific. Studies in the Canadian Arctic and central Arctic Ocean have found that medusae often dominate the deep ocean diversity of GZ (e.g., Kosobokova and Hopcroft, 2010; Raskoff et al., 2010), or prevail just below the non-mixed layer (25 m; Raskoff et al., 2005). These studies have also documented that a bimodal numerical dominance of siphonophores occurs as a result of varying abundances of physonects and calycophorans, with the former peaking in shallower waters and the latter closer to the bottom (Raskoff et al., 2005, 2010). Our data did not support such a trend, as we identified only a small number of physonects, which in our case dominated the deepest sampling layer of the open ocean, and some were present in the surface waters above the shelf. Raskoff et al. (2010) commented that deep-sea ridges might be responsible for aggregating siphonophores, but no such topographic features were identifiable in our study area. Ctenophores are expected to constitute most of the epipelagic community of the Arctic gelatinous zooplankton (Raskoff et al., 2005; Purcell et al., 2010). With increasing depth, the contribution of the gelatinous zooplankton to the overall zooplankton abundance is also predicted to increase (Kosobokova and Hopcroft, 2010), which was demonstrated even for the Fram Strait (Gluchowska et al., 2017b). Our data agree with the expectations provided above of the high abundance of the epipelagic ctenophores (Fig. 4); however, contrary to the referenced studies from the Canadian Arctic (Raskoff et al., 2005; Purcell et al., 2010), the epipelagic zone of the open ocean region of the Eurasian Basin seems to be dominated by calycophoran siphonophores. This observation has to be treated cautiously, as the sampling and fixing methods employed in our study may have led to the sever underestimation of the ctenophore abundance.

The number of GZ taxa documented in this study is consistent with that provided by similar research endeavours for corresponding regions and depths of the European Arctic (e.g., Zelickman, 1972; Licandro et al., 2015; Mańko et al., 2015). Minor differences in the GZ diversity could have resulted either from pronounced seasonality of some GZ taxa (Hosia and Båmstedt, 2007) or from the location/depth of sample collection. For example, when more shelf area was covered (e.g., in the eastern Barents Sea as reported in Mańko et al., 2015), more meroplanktonic and boreal taxa were found that were not detected here, such as *Plotocnide borealis* or *Euphysa flammea*. Likewise, when the deeper basins of the central Arctic Ocean were sampled, the diversity of GZ comprised, to a large extent, Trachymedusae and Narcomedusae (Raskoff et al., 2010; Kosobokova et al., 2011). Our results corroborated the dominance of the Arctic-boreal taxa in the Fram Strait (Ronowicz et al., 2015) and agreed with the prevalence of Trachymedusae in the open ocean stations (Fig. 4, Raskoff et al., 2005), however, we did not encounter any Narcomedusae. These hydromedusae are an integral yet understudied (Lindsay et al., 2017) component of the deep-sea ecosystems around the world (Robison, 2004; Raskoff et al., 2010); thus, their absence in this study may be surprising, especially since some species in this order have been previously found in the vicinity of Svalbard (Ronowicz et al., 2015; Mańko et al., 2015) or further south from this archipelago (Licandro et al., 2015).

The distribution of siphonophore species identified here conformed to their assumed typical distribution. *P. hydrostatica*, although generally considered a typical warm-water species, has previously been recorded in the Nordic Seas (Zelickman, 1972; Mańko et al., 2015) as a result of the encroachment of Atlantic waters into the Arctic. The use of *P. hydrostatica* as an indicator of Atlantic waters has already been advocated by Naumov (1951), who connected the high abundance of this species along the shores of eastern Murmansk with the unprecedented progression of warm waters into the Barents Sea (Zelickman, 1972). We recorded this species only in the outermost station in shelf waters along southern transect N, that remain under constant influence of Atlantic waters. Two deep-sea species, *M. orthocanna* and *R. plicata,* have distribution ranges that are restricted to the Arctic and sub-Arctic waters, with *M. orthocanna* often referred to as a high-Arctic species (Andersen, 1981). The latter species is far more elusive due to its minute, inconspicuous nectophores, which shrink greatly upon fixation (Margulis, 1982). Therefore, supported by our results, it is justified to assume that *R. plicata* is far more abundant in Arctic waters than previously believed and that the scarcity of records is attributable to its incomplete description. We also identified two more calycophoran species, *M. bargmannae* and *C. amygdalina,* that were typical of deep, Arctic water (below 600 m, Fig. 4). Records of *M. bargmannae* are scarce, as this species is easily confused with *D. arctica* (e.g., Morita et al., 2017), but the work of Pugh et al. (1997) indicated that the vertical distribution of these two species does not entirely overlap, as their peaks in abundance occur at different depths. The presence of *C. amygdalina* over a relatively narrow depth range within the Arctic waters aligns with the suggestion of Pugh et al. (1997). These authors suggested that this species predominated in shallower waters in Antarctica, but in the northern Atlantic Ocean, it dominates from 600 to 900 m, which matched our observations (Fig. 4). During laboratory work, we also encountered a peculiar eudoxid (herein "Diphyid eudoxid indet.") that, based on the distinguishable morphological characters, could be assigned to the calycophoran family Diphyidae Quoy and Gaimard, 1827, but further identification was impossible. These specimens appeared to have their bracts and gonophores fused together, as is the case in the fuseudoxid stage of *C. amygdalina*, but the overall shape resembled that of the eudoxid stage of *D. arctica,* which in turn has separate gonophores and bracts. Since the eudoxid stage of *M. bargmannae* has not been formally described (though see Stepanjants, 1967), it is highly probable that our problematic eudoxids belong to this species. Final confirmation will, however, require molecular work.

Taxonomic uncertainty also arose around the *Beroe* spp. records. Global ctenophore diversity is not well resolved (Podar et al., 2001) but is even less resolved in the Arctic (Majaneva and Majaneva, 2013). Due to the often overlapping distributions (Oliveira and Miggotto, 214)), inability to preserve fragile ctenophore tissue (Podar et al., 2001) and elusive morphological traits (Tamm and Tamm, 1993), classic morphology-based taxonomy is often inadequate to discriminate between closely related species using fixed specimens. Hence, we restricted our identification of *Beroe* spp. to the genus level. Discontinuity in the vertical records of *Beroe* spp. (Fig. 4) and in their spatial distribution across the hydrographic gradient may suggest that in our case, the community of Beroidae comprised two or more closely related species, which were most likely *B. cucumis* and *B. abyssicola*. Both species are found in the northern Atlantic and the Arctic Ocean and are known to share similar habitats (Raskoff et al., 2010; Knutsen et al., 2018). Vertical partitioning of the water column by congeners is well documented for planktonic communities (Laakman et al., 2009; Kosobokova and Hopcroft, 2010), which further corroborates our assumption of the presence of more than one *Beroe* species in the Fram Strait. Likewise, our identification of the remaining ctenophores as *M. ovum*, although highly probable, must acknowledge the potential for confusion of this species with other cydippid ctenophores that are also present in the coastal waters of Svalbard (Majaneva and Majaneva, 2013).

Potential discrepancies in the number of species found in different regions of the Arctic Ocean, aside from the species distribution ranges, may very likely be attributed to methodological differences. Although below certain depths, planktonic communities are considered convergent to some extent (Robison, 2004; Vecchione et al., 2015), there may still be differences in the local diversity even among closely spaced sampling sites (see, e.g., Licandro et al., 2015 and this study), but these can be captured by applying diverse sampling methodologies (Hosia et al., 2017). Employing remotely operated vehicles (Raskoff et al., 2005; Youngbluth et al., 2008; Raskoff et al., 2010) allows for the detection of sparsely distributed large taxa, but in contrast with net-based studies, such an approach tends to overlook inconspicuous, minute species or elusive life cycle stages (Williams and Conway, 1981, Raskoff et al., 2005). Therefore, species missing from our report are possibly present in the Fram Strait; thus, to eliminate sampling bias from future endeavours, simultaneous deployment of various sampling tools should be prioritized. Furthermore, molecular techniques should be also considered when working with gelatinous zooplankton, as they can allow for circumventing the problem of fixation-related tissue disintegration, frequently occurring while working with more fragile taxa, like ctenophores (e.g., Hosia and Båmstedt, 2007).

4.3. Demographically structured vertical distribution

The distribution of the two most abundant species, *A. digitale* and *D. arctica,* was better resolved and easier to explain within the context of the local hydrological settings when their life cycle stages were taken into account (Fig. 5). Our dataset indicated strong vertical, bathymetric and water mass dependent structuring of both *A. digitale* and *D. arctica* abundance (Table 2., Figs. 5 and 7). Although distinguishing life cycle stages was straightforward in the case of *D. arctica*, dividing the population of *A. digitale* into stages of development was arbitrary and was based on previously published bell heights that may indicate sexual maturity (Takahashi and Ikeda, 2006). These should be interpreted carefully, as the correlation between bell height and gonad production exhibits some geographical variation (Russell, 1938, Williams and Conway, 1981, Pertsova et al., 2006). Ideally, the presence of gonads should be indicated, and their size should be measured to determine the sexual maturity of the specimen. However, this was impossible due to the long formalin storage of the specimens investigated here, which caused the gonads to deteriorate.

The vertical distribution of the boreal jellyfish, *A. digitale* (Kosobokova et al., 2011), was tightly coupled with local hydrography and bathymetry (Table 2, Figs. 5 and 6). We corroborated that the mature, or at least the largest specimens, persisted in the deepest water layers, whereas the juveniles dominated the surface waters, with the sole exception of the exterior stations along the northern transect, where mature specimens were found at depths $>$ 50 m (Fig. 5). This could be attributed to the presence of Return Atlantic Current, that might have carried along some individuals of *A. digitale* from neighbouring region. Williams and Conway (1981), in studying the population of this species in the NE Atlantic Ocean, showed a similar pattern of vertical distribution, with smaller specimens (up to 3 mm in bell height) dominating in the top 100 m, while larger jellyfish (bell height $>$ 6 mm) were as deep as 500 m (though no sampling was conducted below 500 m). The most likely explanation of this seemingly general pattern was drawn from the dietary preferences of this species; *A. digitale* juveniles feed upon the protists or copepod nauplii that dominate the surface waters, while adults tend to predate on the larger copepods that are mostly found in deeper regions (Pagès et al., 1996, Colin et al., 2003). Interestingly, our data revealed the absence of *A. digitale* above the shelf along the northern transect, but this might have resulted from unequal sampling effort. However, Carstensen et al. (2019) also documented a northward decrease in *A. digitale* biomass. These authors argued that this trend could be explained either by the deeper distribution of *A. digitale* (as they sampled only the upper 200 m of the water column) or by dietary competition with *Eukrohnia hamata*. Pertsova et al. (2006) suggested that the onset of reproduction of this species begins when the surface temperature reaches 9–11 °C, at least in the White Sea. Even if reproduction of *A. digitale* in the Fram Strait is triggered at lower temperatures, the environmental conditions along the transect EB might still be too harsh for this species to spawn. Temperature has already been demonstrated as the main factor influencing body length (Nicholas and Frid, 1999) and the number of generations of this medusae, which can have as many as 5–6 generations per year in the English Channel (Russel, 1953) but only two in the colder Toyama Bay (Ikeda and Imamura, 1996). Although our data did not allow for determination of a number of generation per year of *A. digitale* in the Fram Strait, given the observed plasticity of this species' phenology, one might expect that the progressive intrusion of Atlantic waters might alter the current dogma pertaining to reproduction of this species, leading to the development of more than one generation, as was the case for one of the local copepod species (Weydmann et al., 2018). Additionally, *A. digitale* has been found in the stomach content of numerous fish (e.g., *Onchorhynchus keta*, Tsuruta, 1963), while experimental work by Runge et al. (1987) demonstrated that mackerel (*Scomber scombrus*) feeds preferentially on this hydromedusa. With both the predicted and already observable northern expansions of commercially important fish (Haug et al., 2017), an increase in *A. digitale* abundance may allow for the development of a sustainable population of these fish in polar waters.

The pattern of the vertical distribution of *D. arctica* was not as straightforward in interpretation as was that of *A. digitale*. Our data demonstrated the numerical dominance of eudoxids in the local population of this species. *D. arctica* can at times reach high abundances in various ecosystems (e.g., Weddell Sea; Pugh et al., 1997) and can be evenly distributed in the water column (e.g., near Fuerteventura; Pugh, 1974). The few studies that analysed in depth the population structure of this species showed that eudoxids usually outnumber polygastric stages throughout the year, with a peak of eudoxid production late in the spring and in the summer (Korsfjord, Norway; Hosia and Båmstedt, 2008; but see Pagès and Kurbjeweit, 1994), and that eudoxids are usually more abundant in deeper depth strata (Mapstone 2009). Pugh et al. (1997) revealed the existence of a similar distribution pattern of *D. arctica* in the Weddell Sea, with the polygastric colonies dominating from 250 to 400 m and a more widespread distribution of eudoxids (down to 800 m). Additionally, the results of Pagès and Kurbjeweit (1994) and Pagès and Schnack-Schiel (1996), who studied GZ distribution in the Weddell Sea, showed a lack of eudoxids from the surface to 50 m. These authors argued that *D. arctica* avoided colder surface waters and concentrated near the thermocline in the vicinity of Antarctic Slope Front. All these observation, agree with our data (Figs. 4 and 5), as we identified a bulk of *D. arctica* distribution in the deepest strata sampled; we showed that eudoxids outnumbered polygastric stages; and that only a small population of *D. arctica* was present in the surface layer in the exterior zone of the southern transect N and in the slope of transect EB. The ratio of eudoxid bracts to gonophores found in this study, indicate that the eudoxids of this species are most likely able to produce more than one gonophore (Carré and Carré, 1991, Pugh et al., 1997). This has major ecological implications, as it translates to the high reproductive potential of *D. arctica* (Carré and Carré, 1991).

4.4. Atlantic inflow and GZ community of the Fram Strait

The results of our analyses, revealed that the abundance, diversity and demography of GZ community in the Fram Strait are strongly dependent on the distribution of the water masses (Tables 2, 4, and 5).

The abrupt changes in the diversity of GZ between adjacent water masses have been shown in literature on numerous occasions (e.g., Graham et al., 2001; Hosia et al., 2008; Haberlin et al., 2019). They were usually attributed to various physical barriers (Graham et al. 2001), like shelf-breaks (Pagès and Schnack-Schiel, 1996; Guerrero et al., 2018) or fronts, a strong thermohaline gradients arising at the interface of distinct water bodies (Haberlin et al., 2019; Pagès et al., 2001).

Recent findings show the strengthening and warming of the inflow of Atlantic water to the Arctic (Beszczynska-Möller et al., 2012; Polyakov et al., 2017), occurring even at the greater depths (Merchel and Walczowski, 2018). We demonstrated that the Atlantic water community of GZ was dominated by a boreal species, *A. digitale* (Table 4), whose demography was also tightly coupled with the distribution of warmer Atlantic water (Table 5, Fig. 7). This could indicate, that the Atlantification of the Arctic water would manifest in the dominance of this species further north, a trend that was already documented for some copepods occurring in the West Spitsbergen Current (Weydmann et al., 2014, 2018). For another highly abundant GZ species, *D. arctica,* warming of the Arctic water could translate to greater numbers of eudoxids produced, as this process seems to accelerate with increasing temperature (Carré and Carré, 1991), but also with the increasing food availability (Purcell, 1982; Dallot et al., 1988). Although this species was found to thrive in a broad range of temperatures (approximately 1.1–13.3 °C; Totton 1965), it was shown not to reproduce if the temperature exceeds 10 °C (Stepanjants, 1967). Therefore, it is also equally probable, that the Atlantification of the Arctic could limit the distribution range of this species only to the ArW.

An interesting point in the discussion on the potential influence of the increasing Atlantification of the Arctic is the future of the shelf waters. When the Sørkapp Current (SC) flows northward along the western coast of Spitsbergen, it gains the heat from the adjacent West Spitsbergen Current (WSC), which enhances melting of the drifting sea ice in the SC (Saloranta and Haugan, 2004; Tverberg et al., 2014) and accelerates the formation of the SSW. We showed, that the SSW harboured the most abundant GZ community (Table 4), comprising species of Arctic origin (Table 5), numerically dominated by *M. ovum*. Increase in the SSW extent may thus lead to the development of an even more abundant assemblage of species adapted to thrive in these slightly less saline waters, like the mentioned ctenophore. It must be noted however, that the AtW is known to propagate onto the shelf and further into some of the Svalbard's fjords (e.g., Cottier et al., 2005). As recently shown by Nilsen et al. (2016), winter cyclones in the Fram Strait, through accelerating and widening of the West Spitsbergen Current, may force more AtW to spread along the shelf and within the fjords. Given the increasing density of winter cyclones in the region (Wickström et al., 2019), the striking differences in abundance of the shelf and open ocean GZ community might blur to some extent, with the shelf assemblage of GZ acquiring more of the Atlantic character.

Although our interpretation of the influence of the Atlantification on the GZ community is well supported by the published data (e.g., Wassmann et al., 2011; Weydmann et al., 2014), presented here is only a snapshot of a diversity of GZ and its environmental and biotic drivers. The direct observations of the shifts in the GZ community diversity and distribution will require long-term dataset, that is currently still missing. Some caution in the interpretation of our results must also remain due to the potential timing bias. Although our sampling campaign was undertaken within a relatively narrow time window (two weeks), this still might have been long enough to capture phenological differences among the GZ at the two transects, leading to differences in their abundances (Søreide et al., 2010). We thus emphasize that although our data on the GZ spatial and vertical abundance conform to the expected summer distribution of zooplankton, and reveal a strong dependence on the Atlantic waters, further reasoning on the potential effects of the progression of Atlantification on the GZ community requires a long-term dataset.

5. Conclusions

This study constitutes the first diversity baseline for the vertical distribution of the gelatinous zooplankton in the Fram Strait (Arctic Ocean), which is the main pathway for Atlantic waters into the Arctic. The distributions of GZ abundance, diversity and demography were shaped by an intricate network of factors, of which sampling depth and bathymetric zone were the most important. These GZ community descriptors were also found to reflect particularly well the distribution pattern of water masses. Our data, although temporarily limited, allow for the prognosis that with the observable warming and strengthening of the Atlantic water inflow to the Arctic, referred to as Atlantification (Polyakov et al., 2017), the local GZ community of the Fram Strait will undergo significant remodelling. We showed that the GZ community found along the southern transect was more abundant and that the GZ associated with Atlantic waters was dominated by *A. digitale,* abundance of which constituted c. 66% of the abundance of all GZ. We also demonstrated that the GZ abundance peaked at the intermediate depths (200–600 m), that corresponded with the extent of the West Spitsbergen Current. Its northward flow was strongest above the continental slope, thus rendering this particular community prone to reaching farthest north. Furthermore, we also describe the GZ community found in other water masses, and supported with a literature data, we offer a plausible prognosis of their future, that further supports the notion of the significant impact of Atlantification on the GZ community.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We wish to express our sincere gratitude to all those who have participated in the demanding plankton sampling in the Fram Strait on board of R/V *Oceania* (Institute of Oceanology PAS). Special thanks are due to Emilia Trudnowska for the time and the jointed work during the cruise and in the lab. MKM thanks Sławomir Kwaśniewski and Jacob Carstensen for a helpful discussion on the water masses. Finally, we thank the anonymous reviewers for their helpful suggestions that allowed us to improve the manuscript.

This study was supported by the Polish Ministry of Science and Higher Education project KongHau_ZOOM (No. W37/Svalbard/2012). Work of MKM was financed by the Polish Ministry of Science and Higher Education Diamond Grant DI2014 020344 and the University of Gdańsk program Research Projects for PhD students and early career scientists no. 538-6250-B104-18. The work of AWZ was supported by a grant no. 2017/27/B/NZ8/01056 from the National Science Centre, Poland, while MG participation was funded by a grant no. 2017/25/B/NZ8/01100 from the National Science Centre (Tax4Fun) and she was also supported by the Ministry of Science and Higher Education Outstanding Young Scientist Scholarship.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2020.102414.

References

Andersen, O.G.N., 1981. Redescription of *Marrus orthocanna* (Kramp, 1942) (Cnidaria, Siphonophora). Steenstrupia 7, 293–307.

Angel, M.V., Baker, A.C., 1982. Vertical distribution of the standing crop of plankton and micronekton at three stations in the Northeast Atlantic. Biol. Oceanogr. 2, 1–30. https://doi.org/10.1080/01965581.1982.10749451.

Arai, M.N., 1992. Active and passive factors affecting aggregations of hydromedusae: a review. Scientia Marina 56, 99–108.

Bandara, K., Varpe, Ø., Søreide, J.E., Wallenschus, J., Berge, J., Eiane, K., 2016. Seasonal vertical strategies in a high-Arctic coastal zooplankton community. Mar. Ecol. Prog. Ser. 555, 49–54. https://doi.org/10.3354/meps11831.

Basedow, S.L., Sundfjord, A., von Appen, W.-J., Halvorsen, E., Kwaśniewski, S., Reigstad, M., 2018. Seasonal variation in transport of zooplankton into the Arctic Basin through the Atlantic Gateway. Fram Strait. Front. Mar. Sci. 5, 194. https://doi.org/10.3389/fmars.2018.00194.

Beszczynska-Möller, A., Woodgate, R.A., Lee, C., Melling, H., Karcher, M., 2011. A synthesis of exchanges through the main oceanic gateways to the Arctic Ocean. Oceanography 24, 82–99. https://doi.org/10.5670/oceanog.2011.59.

Beszczynska-Möller, A., Fahrbach, E., Schauer, U., Hansen, E., 2012. Variability in Atlantic water temperature and transport at the entrance to the Arctic Ocean. 1997–2010. ICES J. Mar. Sci. 69, 852–863. https://doi.org/10.1093/icesjms/fss056.

Błachowiak-Samołyk, K., Kwaśniewski, S., Dmoch, K., Hop, H., Falk-Petersen, S., 2007. Trophic structure of zooplankton in the Fram Strait in spring and autumn 2003. Deep-Sea Res. II 54, 2716–2728. https://doi.org/10.1016/j.dsr2.2007.08.004.

Boero, F., Brotz, L., Gibbons, M.J., Piraino, S., Zampardi, S., 2016. Impacts and effects of ocean warming on jellyfish. In: Laffoley, D., Baxter, J.M. (Eds.), Explaining Ocean Warming: Causes, Scale, Effects and Consequences. UICN, Gland, Switzerland, pp. 213–237.

Bouillon, J., Gravili, C., Pagès, F., Gili, J. M., and Boero, F. 2006. An introduction to Hydrozoa. Mémoires du Muséum national d'Histoire naturelle no. 194, Publications Scientifiques du Muséum, Paris.

Brodeur, R.D., Decker, M.B., Ciannelli, L., Purcell, J.E., Bond, N.A., Stabeno, P.J., Acuna, E., Hunt Jr., G.L., 2008. Rise and fall of jellyfish in the eastern Bering Sea in relation to climate regime shifts. Prog. Oceanogr. 77, 103–111. https://doi.org/10.1016/j.pocean.2008.03.017.

Brotz, L., Cheung, W.W.L., Kleisner, K., Pakhomov, E., Pauly, D., 2012. Increasing jellyfish populations: trends in large marine ecosystems. Hydrobiologia 690, 3–20. https://doi.org/10.1007/s10750-012-1039-7.

Carré, C., Carré, D., 1991. A complete life cycle of the calycophoran siphonophore *Muggiaea kochi* (Will) in the laboratory, under different temperature conditions: ecological implications. Philos. Trans. Roy. Soc. Lond. B 334, 27–32. https://doi.org/10.1098/rstb.1991.0095.

Carstensen, J., Olszewska, A., Kwaśniewski, S., 2019. Summer mesozooplankton biomass distribution in the West Spitsbergen Current (2001–2014). Front. Mar. Sci. 6, 202. https://doi.org/10.3389/fmars.2019.00202.

Choy, C.A., Haddock, S.H.D., Robison, B.H., 2017. Deep pelagic food web structure as revealed by in situ feeding observations. Proc. Roy. Soc. B: Biol. Sci. 284, 20172116. https://doi.org/10.1098/rspb.2017.2116.

Colin, S.P., Costello, J.H., Klos, E., 2003. In situ swimming and feeding behavior of eight co-occurring hydromedusae. Mar. Ecol. Prog. Ser. 253, 305–309. https://doi.org/10.3354/meps253305.

Colin, S.P., Costello, J.H., Graham, W.M., Higgins III, J., 2005. Omnivory by the small cosmopolitan hydromedusa *Aglaura hemistoma*. Limnol. Oceanogr. 50, 1264–1268. https://doi.org/10.4319/lo.2005.50.4.1264.

Condon, R.H., Graham, W.M., Duarte, C.M., Pitt, K.A., Lucas, C.H., Haddock, S.H.D., Sutherland, K.R., Robinson, K.L., Dawson, M.N., Decker, M.B., Mills, C.M., Purcell, J.E., Malej, A., Mianzan, H., Uye, S., Gelcich, S., Madin, L.P., 2012. Questioning the rise of gelatinous zooplankton in the world's oceans. Bioscience 62, 160–169. https://doi.org/10.1525/bio.2012.62.2.9.

Condon, R.H., Duarte, C.M., Pitt, K.A., Robinson, K.L., Lucas, C.H., Sutherland, K.R., Mianzan, H.W., Bogeber, M., Purcell, J.E., Decker, M.B., Uye, S., Madin, L.P., Brodeur, R.D., Haddock, S.H.D., Malej, A., Parry, G.D., Eriksen, E., Quiñones, J., Acha, M., Harvey, M., Arthur, J.M., Graham, W.M., 2013. Recurrent jellyfish blooms are a consequence of global oscillations. Proceeding of National Academy of Sciences of the United States of America1 10, 1000–1005. https://doi.org/10.1073/pnas.1210920110.

Costello, J.H., Colin, S.P., Dabiri, J.O., 2008. Medusan morphospace: phylogenetic constraints, biomechanical solutions, and ecological consequences. Invertebr. Biol. 127, 265–290. https://doi.org/10.1111/j.1744-7410.2008.00126.x.

Cottier, F., Tverberg, V., Inall, M., Svendsen, H., Nilsen, F., Griffiths, C., 2005. Water mass modification in an Arctic fjord through cross-shelf exchange: The seasonal hydrography of Kongsfjorden, Svalbard. Journal of Geophysical Research 110, C12005. https://doi.org./10.1029/2004JC002757.

Coyle, K.O., Pinchuk, A.I., Eisner, L.B., Napp, J.M., 2008. Zooplankton species composition, abundance and biomass on the eastern Bering Sea shelf during summer: The potential role of water-column stability and nutrients in structuring the zooplankton community. Deep-Sea Res. II 55, 1775–1791. https://doi.org/10.1016/j.dsr2.2008.04.029.

Dallot, S., Goy, J., Carré, C., 1988. Peuplements de carnivores planctoniques gelatineux et structures productives en Mediterranee occidentale. Oceanol. Acta 9, 193–209 (in French).

Decker, M.B., Robinson, K.L., Dorji, S., Cieciel, K.D., Barceló, D., Ruzicka, J.J., Brodeur, R.D., 2018. Jellyfish and forage fish spatial overlap on the eastern Bering Sea shelf during periods of high and low jellyfish biomass. Mar. Ecol. Prog. Ser. 59, 57–69. https://doi.org/10.3354/meps12273.

De Cáceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. Ecology 90, 3566–3574. https://doi.org/10.1890/08-1823.1.

De Cáceres, M., Legendre, P., Moretti, M., 2010. Improving indicator species analysis by combining groups of sites. Oikos 119, 1674–1684. https://doi.org/10.1111/j.1600-0706.2010.18334.x.

De Lafontaine, Y., Leggett, W.C., 1989. Changes in size and weight of hydromedusae during formalin preservation. Bull. Mar. Sci. 44, 1129–1137.

Duarte, C.M., Pitt, A.M., Lucas, C.H., Purcell, J.E., Uye, S., Robinson, K., Brotz, L., Decker, M.B., Sutherland, K.R., Malej, A., Madin, L., Mianzan, H., Gili, J.M., Fuentes, V., Atienza, D., Pagès, F., Breiburg, D., Malej, J., Graham, W.M., Condon, R.H., 2013. Is global ocean sprawl a cause of jellyfish blooms? Front. Ecol. Environ. 11, 91–97. https://doi.org/10.1890/110246.

Eriksen, E., Skjoldal, H.R., Gjøsæter, H., Primicerio, R., 2017. Spatial and temporal changes in the Barents Sea pelagic compartment during the recent warming. Prog. Oceanogr. 151, 206–226. https://doi.org/10.1016/j.pocean.2016.12.009.

Frost, J.R., Jacoby, C.A., Youngbluth, M.J., 2010. Behavior of *Nemopsis bachei* L. Agassiz, 1849 medusae in the presence of physical gradients and biological thin layers. Hydrobiologia 645, 97–111. https://doi.org/10.1007/978-90-481-9541-1_8.

Gluchowska, M., Dalpadado, P., Beszczyńska-Möller, A., Olszewska, A., Ingvaldsen, R.B., Kwaśniewski, S., 2017a. Interannual zooplankton variability in the main pathways of the Atlantic water flow into the Arctic Ocean (Fram Strait and Barents Sea branches). ICES J. Mar. Sci. 74, 1921–1936. https://doi.org/10.1093/icesjms/fsx033.

Gluchowska, M., Trudnowska, E., Goszczko, I., Kubiszyn, A.M., Błachowiak-Samołyk, K., Walczowski, W., Kwaśniewski, S., 2017b. Variations in the structural and functional diversity of zooplankton over vertical and horizontal environmental gradients en route to the Arctic Ocean through the Fram Strait. PLoS ONE 12, e0171715. https://doi.org/10.1371/journal.pone.0171715.

Graham, W.M., Pagès, F., Hamner, W.M., 2001. A physical context for gelatinous zooplankton aggregations: a review. Hydrobiologia 451, 199–212. https://doi.org/10.1023/A:1011876004427.

Guerrero, E., Gili, J.M., Maynou, F., Sabatès, A., 2018. Diversity and mesoscale spatial changes in the planktonic cnidarian community under extreme warm summer conditions. J. Plankton Res. 40, 178–196. https://doi.org/10.1093/plankt/fby001.

Haberlin, D., Raine, R., McAllen, R., Doyle, T.K., 2019. Distinct gelatinous zooplankton communities across a dynamic shelf sea. Limnol. Oceanogr. 64, 1802–1818. https://doi.org/10.1002/lno.11152.

Harris, R., Wiebe, P., Lenz, J., Skjoldal, H.-R., Huntley, M., 2000. ICES zooplankton methodology manual. Academic Press.

Haug, T., Bogstad, B., Chierici, M., Gjøsæter, H., Hallfredsson, E.H., Høines, Å.S., Hoel, A.H., Ingvaldsen, R.B., Jørgensen, L.L., Knutsen, T., Loeng, H., Naustvoll, L.J., Røttingen, I., Sunnanå, K., 2017. Future harvest of living resources in the Arctic Ocean north of the Nordic and Barents Seas: a review of possibilities and constraints. Fish. Res. 188, 38–57. https://doi.org/10.1016/j.fishres.2016.12.002.

Hays, G.C., Richardson, A.J., Robinson, C., 2005. Climate change and marine plankton. Trends Ecol. Evol. 20, 337–344. https://doi.org/10.1016/j.tree.2005.03.004.

Hays, G.C., Doyle, T.K., Houghton, J.D.R., 2018. A paradigm shift in the trophic importance of jellyfish. Trends Ecol. Evol. 33, 874–884. https://doi.org/10.1016/j.tree.2018.09.001.

Hop, H., Falk-Petersen, S., Svendsen, H., Kwasniewski, S., Pavlov, V., Pavlova, O., Søreide, J.E., 2006. Physical and biological characteristics of the pelagic system across Fram Strait to Kongsfjorden. Prog. Oceanogr. 71, 182–231. https://doi.org/10.1016/j.pocean.2006.09.007.

Hop, H., Assmy, P., Wold, A., Sundfjord, A., Daase, M., Duarte, P., Kwaśniewski, S., Gluchowska, M., Wiktor, J.M., Tatarek, A., Wiktor, jr., Kristiansen, S., Fransson, A., Chierici, M., Vihtakari, M., 2019. Pelagic ecosystem characteristics across the Atlantic Water Boundary Current from Rijpfjorden, Svalbard, to the Arctic Ocean during summer (2010-2014). Frontiers in Marine Science 6, 181. https://doi.org/10.3389/fmars.2019.00181.

Hosia, A., Falkenhaug, T., Baxter, E.J., Pagès, F., 2017. Abundance, distribution and diversity of gelatinous predators along the northern Mid-Atlantic Ridge: A comparison of different sampling methodologies. PLoS ONE 12, e0187491. https://doi.org/10.1371/journal.pone.0187491.

Hosia, A., Båmstedt, U., 2007. Seasonal changes in the gelatinous zooplankton community and hydromedusa abundances in Korsfjord and Fanafjord, western Norway. Mar. Ecol. Prog. Ser. 351, 113–127.

Hosia, A., Båmstedt, U., 2008. Seasonal abundance and vertical distribution of siphonophores in western Norwegian fjords. J. Plankton Res. 30, 951–962. https://doi.org/10.1093/plankt/fbn045.

Hosia, A., Stemmann, L., Youngbluth, M., 2008. Distribution of net-collected planktonic cnidarians along the northern Mid-Atlantic Ridge and their associations with the main water masses. Deep-Sea Research Part II 55, 106–118. https://doi.org/10.1016/j.dsr2.2007.09.007.

Ikeda, T., Imamura, A., 1996. Abundance, vertical distribution and life cycle of a hydromedusa *Aglantha digitale* in Toyama Bay, southern Japan Sea. Bull. Plankton Soc. Japan 43, 31–43.

IPCC, 2014. Climate change 2014: Synthesis report. In: Pachauri R.K., Meyer L.A., Core Writing Team (Eds.), Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change. Geneva, Switzerland: IPCC.

Jakobsson, M., Mayer, L. A., Coakley, B., Dowdeswell, J.A., Forbes, S., Fridman, B., Hodnesdal, H., Noormets, R., Pedersen, R., Rebesco, M., Schenke, H.-W., Zarayskaya Y., Accettella, D., Armstrong, A., Anderson, R.M., Bienhoff, P., Camerlenghi, A., Church, I., Edwards, M., Gardner, J.V., Hall, J.K., Hell, B., Hestvik, O.B., Kristoffersen, Y., Marcussen, C., Mohammad, R., Mosher, C.D., Nghiem, S.V., Pedrosa, M.T., Travaglini, P.G., Weatherall, P., 2012. The International Bathymetric Chart of the Arctic Ocean (IBCAO) Version 3.0. Geophysical Research Letters, L12609, https://doi.org/10.1029/2012GL052219.

Knutsen, T., Hosia, A., Falkenhaug, T., Skern-Mauritzen, R., Wiebe, P.H., Larsen, R.B., Aglen, A., Berg, E., 2018. Coincident mass occurrence of gelatinous zooplankton in Northern Norway. Front. Mar. Sci. 5, 158. https://doi.org/10.3389/fmars.2018.00158.

Kosobokova, K., Hopcroft, R.R., Hirche, H.-J., 2011. Patterns of zooplankton diversity through the depths of the Arctic's central basin. Mar. Biodivers. 41, 29–50. https://doi.org/10.1007/s12526-010-0057-9.

Kosobokova, K., Hopcroft, R.R., 2010. Diversity and vertical distribution of Mesozooplankton in the Arctic's Canada Basin. Deep-Sea Research Part II 57, 96–110. https://doi.org/10.1016/j.dsr2.2009.08.009.

Kosobokova, K.N., Hirche, H.J., 2009. Biomass of zooplankton in the eastern Arctic Ocean—a baseline study. Prog. Oceanogr. 82, 265–280. https://doi.org/10.1016/j.pocean.2009.07.006.

Kosobokova, K.N., Hirche, H.J., 2000. Zooplankton distribution across the Lomonosov Ridge, Arctic Ocean: species inventory, biomass and vertical structure. Deep-Sea Research Part I 47, 2029–2060. https://doi.org/10.1016/S0967-0637(00)00015-7.

Kraft, A., Nöthing, E.-M., Bauerfeind, E., Wildish, D.J., Pohle, G.W., Bathmann, U.V., Beszczyńska-Möller, A., Klages, M., 2013. First evidence of reproductive success in a southern invader indicates possible community shifts among Arctic zooplankton. Mar. Ecol. Prog. Ser. 493, 291–296. https://doi.org/10.3354/meps10507.

Kramp, 1961. Synopsis of the medusae of the world. Journal of Marine Biological Association of UK 7–382. https://doi.org/10.1017/S0025315400007347.

Laakman, S., Kochzius, M., Auel, H., 2009. Ecological niches of Arctic deep-sea copepods: Vertical partitioning, dietary preferences and different trophic levels minimize inter-specific competition. Deep-Sea Research Part I 56, 741–756. https://doi.org/10.1016/j.dsr.2008.12.017.

Lepš, J., Šmilauer, P., 2003. Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge.

Licandro, P., Blackett, M., Fischer, A., Hosia, A., Kennedy, J., Kirby, R.R., Raab, K., Stern, R., Tranter, P., 2015. Biogeography of jellyfish in the North Atlantic, by traditional and genomic methods. Earth Syst. Sci. Data 7, 173–191. https://doi.org/10.5194/essd-7-173-2015.

Lindsay, D.J., Grossmann, M.M., Bentlage, B., Collins, A.G., Minemizu, R., Hopcroft, R.R., Miyake, H., Hidaka-Umetsu, M., Nishikawa, J., 2017. The perils of online biogeographic databases: a case study with the 'monospecific' genus *Aegina* (Cnidaria, Hydrozoa, Narcomedusae). Mar. Biol. Res. 13, 494–512. https://doi.org/10.1080/17451000.2016.1268261.

Lindsay, D.J., Pagès, F., Corbera, J., Miyake, H., Hunt, J.C., Ichikawa, T., Segawa, K., Yoshida, H., 2008. The anthomedusan fauna of the Japan Trench: Preliminary results from in situ surveys with manned and unmanned vehicles. J. Mar. Biol. Assoc. United Kingdom 88, 1519–1539. https://doi.org/10.1017/S0025315408002051.

Lindsay, D.J., Hunt, J.C., 2005. Biodiversity in midwater cnidarians and ctenophores: submersible-based results from deep-water bays in the Japan Sea and north-western Pacific. J. Marine Biol. Assoc. United Kingdom 85, 503–517. https://doi.org/10.1017/S0025315405011434.

Lindsay, D.J., Furushima, Y., Miyake, H., Kitamura, M., Hunt, J.C., 2004. The scyphomedusan fauna of the Japan Trench: preliminary results from a remotely-operated vehicle. Hydrobiologia 530 (531), 537–547. https://doi.org/10.1007/s10750-004-2645-9.

Majaneva, S., Majaneva, M., 2013. Cyddipid ctenophores in the coastal waters of Svalbard: is it only *Mertensia ovum*. Polar Biol. 36, 1681–1686. https://doi.org/10.1007/s00300-013-1377-6.

Majaneva, S., Berge, J., Renaud, P.E., Vader, A., Stübner, E., Rao, A.M., Sparre, Ø., Lehtiniemi, M., 2013. Aggregations of predators and prey affect predation impact of the Arctic ctenophore *Mertensia ovum*. Mar. Ecol. Prog. Ser. 476, 87–100. https://doi.org/10.3354/meps10143.

Mańko, M.K., Panasiuk-Chodnicka, A.A., Żmijewska, M.I., 2015. Pelagic coelenterates in the Atlantic sector of the Arctic Ocean – species diversity and distribution as water mass indicators. Oceanol. Hydrobiol. Stud. 44, 466–479. https://doi.org/10.1515/ohs-2015-0044.

Mapstone, G.M., 2009. Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters. NRC Research Press, Ottawa, Ontario, Canada.

Margulis, R.Y., 1982. A new siphonophore *Rudjacovia plicata* gen. n., sp. n., (Coelenterate, Hydrozoa) from the Polar Basin and some notes on other siphonophores. Zoologicheskii Zhurnal 61, 440–444.

Merchel, M., Walczowski, W., 2018. Changes in the properties of deep and intermediate water masses in the Nordic Seas from 1997 to 2016. Ocean Sci. Discuss. https://doi.org/10.5194/os-2018-93.

Mills, C., 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? Hydrobiologia 451, 55–68. https://doi.org/10.1023/A:1011888006302.

Morita, H., Toyokawa, M., Hidaka, K., Nishimoto, A., Sugisaki, H., Kikuchi, T., 2017. Spatio-temporal structure of the jellyfish community in the transition zone of cold and wamr currents in the northwest Pacific. Plankton Benthos Res. 12, 266–284. https://doi.org/10.3800/pbr.12.266.

Naumov, D.V., 1951. Mass appearance of thermophilic siphonophores in plankton of the Barents Sea. Priroda, Moskwa 11, 1–62 (in Russian).

Nicholas, K.R., Frid, C.L.J., 1999. Occurrence of Hydromedusae in the Plankton Off Northumberland (Western Central North Sea) and the Role of Planktonic Predator. J. Mar. Biol. Assoc. United Kingdom 79, 979–992. https://doi.org/10.1017/S0025315499001216.

Nilsen, F., Skogseth, R., Vaardal-Lunde, J., Inall, M., 2016. A simple shelf circulation model—intrusion of Atlantic Water on the West Spitsbergen Shelf. J. Phys. Oceanogr. 46, 1209–1230.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Henry, M., Stevens, H., 2007, The vegan package. Community ecology package 10, 631–637.

Oliveira, O.M.P., Miggotto, A.E., 2014. First occurrence of Beroe forskalii (Ctenophora) in South American Atlantic coastal waters, with notes on the use of macrociliary patterns for beroid identification. Zootaxa 3779, 440–476. https://doi.org/ 10.11646/zootaxa.3779.4.5.

Pagès, F., González, H.E., Ramon, M., Sobarzo, M., Gili, J.-M., 2001. Gelatinous zooplankton assemblages associated with water masses in the Humboldt Current System, and potential predatory impact by *Bassia bassensis* (Siphonophora: Calycophorae). Mar. Ecol. Prog. Ser. 210, 13–24.

Pagès, F., Kurbjeweit, F., 1994. Vertical distribution and abundance of mesoplanktonic medusae and siphonophores from the Weddell Sea, Antarctica. Polar Biol. 14, 243–251. https://doi.org/10.1007/BF00239172.

Pagès, F., Schnack-Schiel, S.B., 1996. Distribution patterns of the mesozooplankton, principally siphonophores and medusae, in the vicinity of the Antarctic Slope Front (eastern Weddell Sea). J. Mar. Syst. 9, 231–248.

Pagès, F., 1997. The gelatinous zooplankton in the pelagic system of the Southern Ocean: a review. Annales de l'Institut Océanographique Paris 73, 139–158.

Pagès, F., Gili, J.-M., 1991. Vertical distribution of epipelagic siphonophores at the confluence between Benguela waters and the Angola Current over 48 hours. Hydrobiologia 216 (217), 355–362. https://doi.org/10.1007/BF00026486.

Pagès, F., González, H.E., González, S.R., 1996. Diet of the gelatinous zooplankton in Hardangerfjord (Norway) and potential predatory impact by *Aglantha digitale* (Trachymedusae). Mar. Ecol. Prog. Ser. 139, 69–77.

Pertsova, N.M., Kosobokova, K.N., Prudkovsky, A.A., 2006. Population size structure, spatial distribution, and life cycle of the hydromedusa *Aglantha digitale* (O.F. Müller, 1766) in the White Sea. Okeanologiya 46, 249–258. https://doi.org/10.1134/S0001437006020093.

Podar, M., Haddock, S.H.D., Sogin, M.L., Harbison, G.R., 2001. A molecular phylogenetic framework for the phylum Ctenophora using 18S rRNA genes. Mol. Phylogenet. Evol. 21, 218–230. https://doi.org/10.1006/mpev.2001.1036.

Polyakov, I.B., Pnyushkov, A.V., Alkire, M.B., Ashik, I.M., Baumann, T.M., Carmack, E.C., Goszczko, I., Guthrie, J., Ivanov, V.V., Kanzow, T., Krishfield, R., Kwok, R., Sundfjord, A., Morison, J., Rember, R., Yulin, A., 2017. Greater role for Atlantic inflows on sea-ice loss in the Eurasian Basin of the Arctic Ocean. Science 356, 285–291. https://doi.org/10.1126/science.aai8204.

Pugh, P.R., 1974. The vertical distribution of the siphonophores collected during the SOND Cruise 1965. J. Mar. Biol. Assoc. United Kingdom 45, 25–90.

Pugh, P.R., Pagès, F., Boorman, B., 1997. Vertical distribution and abundance of pelagic cnidarians in the Eastern Weddell Sea, Antarctica. J. Mar. Biol. Assoc. United Kingdom 77, 341–360. https://doi.org/10.1017/S002531540007171X.

Pugh, P.R., Gasca, R., 2009. Siphonophorae (Cnidaria) of the Gulf of Mexico. In: Felder, D. L., Camp, D.K. (eds.), Gulf of Mexico–Origins, Waters, and Biota. Biodiversity. Texas AandM Press, College Station, Texas pp. 395–402.

Purcell, J.E., 1982. Feeding and growth of the siphonophore *Muggiaea atlantica* (Cunningham 1893). J. Exp. Mar. Biol. Ecol. 62, 39–54. https://doi.org/10.1016/0022-0981(82)90215-5.

Purcell, J.E., 1988. Quantification of *Mnemiopsis leidyi* (Ctenophora, Lobata) from formalin-preserved plankton samples. Mar. Ecol. Prog. Ser. 45, 197–200.

Purcell, J.E., 1997. Pelagic cnidarians and ctenophores as predators: Selective predation, feeding rates and effects on prey populations. Annales de l'Institut Océanographique de Paris 73, 125–137.

Purcell, J.E., Hopcroft, R.R., Kosobokova, K.N., Whitledge, T.E., 2010. Distribution, abundance and predation effects of epipelagic ctenophores and jellyfish in the western Arctic Ocean. Deep-Sea Res. Part II 57, 127–135. https://doi.org/10.1016/j.dsr2.2009.08.011.

Purcell, J.E., Decker, M.B., Breitburg, D.L., Broughton, K.J., 2014. Fine-scale vertical distributions of *Mnemiopsis leidyi* ctenophores: predation on copepods relative to stratification and hypoxia. Mar. Ecol. Prog. Ser. 500, 103–120. https://doi.org/10.3354/meps10741.

Raskoff, K.A., Purcell, J.E., Hopcroft, R.R., 2005. Gelatinous zooplankton of the Arctic Ocean: in situ observations under the ice. Polar Biol. 28, 207–217. https://doi.org/10.1007/s00300-004-0677-2.

Raskoff, K.A., Hopcroft, R.R., Purcell, J.E., Youngbluth, M.J., 2010. Jellies under ice: ROV observations from the Arctic 2005 Hidden Ocean Expedition. Deep-Sea Research Part II 57, 111–126. https://doi.org/10.1016/j.dsr2.2009.08.010.

R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2016 URL https://www.R-project.org/.

Richardson, A.J., Bakun, A., Hays, G.C., Gibbons, M.J., 2009. The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. Trends Ecol. Evol. 24, 312–322. https://doi.org/10.1016/j.tree.2009.01.010.

Robison, B.H., 2004. Deep pelagic biology. J. Exp. Mar. Biol. Ecol. 300, 253–272. https://doi.org/10.1016/j.jembe.2004.01.012.

Rodriguez, C.S., Marques, A.C., Mianzan, H.W., Tronolone, V.B., Migotto, A.E., Genzano, G.N., 2017. Environment and life cycles influence distribution patterns of hydromedusae in austral South America. Mar. Biol. Res. 13, 659–670. https://doi.org/10.1080/17451000.2017.1280170.

Ronowicz, M., Kukliński, P., Mapstone, G.M., 2015. Trends in the diversity, distribution and life history strategy of Arctic Hydrozoa (Cnidaria). PLoS ONE 10, e0120204. https://doi.org/10.1371/journal. pone.0120204.

Runge, J.A., Pepin, P., Silvert, W., 1987. Feeding behavior of the Atlantic mackerel *Scomber scombrus* on the hydromedusa *Aglantha digitale*. Mar. Biol. 94, 329–333. https://doi.org/10.1007/BF00428238.

Russell, F.S., 1938. The Plymouth offshore medusa fauna. J. Mar. Biol. Assoc. United Kingdom 22, 769–809. https://doi.org/10.1017/S0025315400012339.

Russel, F.S., 1953. The Medusae of the British Isles. Cambridge University Press, Cambridge.

Sabatès, A., Gili, J.-M., Pagès, F., 1989. Relationship between zooplankton distribution, geographic characteristics and hydrographic patterns off the Catalan coast (Western Mediterranean). Mar. Biol. 103, 153–159.

Saloranta, T.M., Haugan, P., 2004. Northward cooling and freshening of the warm core of the West Spitsbergen Current. Polar Res. 23, 79–88.

Schuchert, P., 2007. The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Filifera part 2. Rev. Suisse Zool. 114, 195–396. https://doi.org/10.5962/bhl.part.80395.

Schuchert, P., 2019. World Hydrozoa Database. Accessed through: World Register of Marine Species at: www.marinespecies.org on 2019-04-15.

Smoot, C.A., Hopcroft, R.R., 2017. Cross-shelf gradients of epipelagic zooplankton communities of the Beaufort Sea and the influence of localized hydrographic features. J. Plankton Res. 39, 65–78. https://doi.org/10.1093/plankt/fbw080.

Søreide, J.E., Leu, E., Berge, J., Graeve, M., Falk-Petersen, S., 2010. Timing in blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. Glob. Change Biol. 16, 3154–3163. https://doi.org/10.1111/j.1365-2486.2010.02175.x.

Stepanjants, S.D., 1967. Siphonophora in the seas of the USSR and the northern part of the Pacific. Leningrad: Nauka. (in Russian).

Stepanjants, S.D., Cortese, G., Kruglikova, S.B., Bjørklund, K.R., 2006. A review of bipolarity concepts: History and examples from Radiolaria and Medusozoa (Cnidaria). Mar. Biol. Res. 2, 200–241. https://doi.org/10.1080/17451000600781767.

Stine, R.A., 1995. Graphical interpretation of variance inflation factors. The American Statistician 4, 53–56.

Svendsen, H., Beszczynska-Moller, A., Hagen, J.O., Lefauconnier, B., Tverberg, V., Gerland, S., Ørbøk, J.B., Bischof, K., Papucci, C., Zajaczkowski, M., Azzolini, R., Bruland, O., Wiencke, C., Winther, J.-G., Dallmann, W., 2002. The physical environment of Kongsfjorden-Krossfjorden, an Arctic fjord system in Svalbard. Polar Res. 21, 133–166.

Swerpel, S., 1985. The Hornsund fiord: water masses. Polish Polar Res. 6, 475–496.

Takahashi, D., Ikeda, T., 2006. Abundance, vertical distribution and life cycle patterns of the hydromedusa *Aglantha digitale* in the Oyashio region, western subarctic Pacific. Plankton Benthos Res. 1, 91–96. https://doi.org/10.3800/pbr.1.91.

Tamm, S.L., Tamm, S., 1993. Diversity of macrociliary size, tooth patterns, and distribution in Beroe (Ctenophora). Zoomorphology 113, 79–89. https://doi.org/10.1007/bf00403086.

Totton, A.K., 1965. A synopsis of the Siphonophora. Trustees of the British Museum (Natural History), London.

Trudnowska, E., Gluchowska, M., Beszczyńska-Möller, A., Błachowiak-Samołyk, K., Kwaśniewski, S., 2016. Plankton patchiness in the Polar Front region of the West Spitsbergen Shelf. Mar. Ecol. Prog. Ser. 560, 1–18. https://doi.org/10.3354/meps11925.

Tsuruta, A., 1963. Distribution of plankton and its characteristics in the oceanic fishing grounds with special reference to their relation to fishery. J. Shimonoseki College of Fisheries 12, 13–214.

Tverberg, V., Nøst, O.A., Lydersen, C., Kovacs, K., 2014. Winter sea ice melting in the Atlantic Water subduction area, Svalbard Norway. J. Geophys. Res.—Oceans 119, 5945–5967.

Vecchione, M., Falkenhaug, T., Sutton, T., Cook, A., Gislason, A., Hansen, H.Ø., Heino, M., Miller, P.I., Piatkowski, U., Porteiro, F., Søiland, H., Bergstad, O.A., 2015. The effect of the North Atlantic Subpolar Front as a boundary in pelagic biogeography decreases with increasing depth and organism size. Prog. Oceanogr. 138, 105–115. https://doi.org/10.1016/j.pocean.2015.08.006.

Walczowski, W., Piechura, J., 2007. Pathways of the Greenland Sea warming. Geophys. Res. Lett. 34, L10608. https://doi.org/10.1029/2007gl029974.

Walczowski, W., Piechura, J., Goszczko, I., Wieczorek, P., 2012. Changes of the Atlantic Water properties: an important factor of the European Arctic marine climate. ICES J. Mar. Sci. 69, 864–869.

Wassmann, P., Duarte, C.M., Agusti, S., Sejr, M.K., 2011. Footprints of climate change in the Arctic marine ecosystem. Glob. Change Biol. 17, 1235–1249.

Werner, B., 1961. Morphologie und Lebensgeschichte, sowie Temperaturabhängigkeit der Verbreitung und des jahreszeitlichen Auftretens von *Bougainvillia superciliaris* (L. Agassiz) (Athecatae-Anthomedusae). Helgoländer Meeresun. 7, 206–237 (in German).

Weydmann, A., Carstensen, J., Goszczko, I., Dmoch, K., Olszewska, A., Kwaśniewski, S., 2014. Shift towards the dominance of boreal species in the Arctic: Inter-annual and spatial zooplankton variability in the West Spitsbergen Current. Mar. Ecol. Prog. Ser. 501, 41–52. https://doi.org/10.3354/meps10694.

Weydmann, A., Walczowski, W., Carstensen, J., Kwaśniewski, S., 2018. Warming of Subarctic waters accelerates development of a key marine zooplankton *Calanus finmarchicus*. Glob. Change Biol. 24, 172–183. https://doi.org/10.1111/gcb.13864.

Wickham, H., Averick, M., Bryan, J., Chang, W., D'Agostino, L., McGowan, F., Romain, F., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T.L., Miller, E., Bache, S.M., et al., 2019. Welcome to the tidyverse. Journal of Open Source Software 4, 1686. https://doi.org/10.21105/joss.01686.

Wickström, S., Jonassen, M.O., Vihma, T., Uotila, P., 2019. Trends in cyclones in the high-latitude North Atlantic during 1979–2016. Quart. J. Roy. Meteorol. Soc. https://doi.org/10.1002/qj.3707.

Williams, R., Conway, D.V.P., 1981. Vertical distribution and seasonal abundance of *Aglantha digitale* (O.F. Müller) (Coelenterata: Trachymedusae) and other planktonic coelenterates in the northeast Atlantic Ocean. J. Plankton Res. 3, 633–643. https://doi.org/10.1093/plankt/3.4.633.

Wissmann, M., Toutenburg, H., Shalabh, S., 2007. Role of categorical variables in multicollinearity in the linear regression model. J. Appl. Statist. Sci. 19, 1–34.

Youngbluth, M., Sornes, T., Hosia, A., Stemmann, L., 2008. Vertical distribution and relative abundance of gelatinous zooplankton, in situ observations near the Mid-Atlantic Ridge. Deep-Sea Res. Part II 55, 119–125. https://doi.org/10.1016/j.dsr2.2007.10.002.

Zelickman, E.A., 1972. Distribution and ecology of the pelagic hydromedusae, siphonophores and ctenophores of the Barents Sea, based on perennial plankton collections. Mar. Biol. 17, 256–264. https://doi.org/10.1007/BF00366301.

Chapter 8. 1. Supplementary files

Supp. mat. 1 Abundance of gelatinous zooplankton [ind. 1000 m^{-3}] summed for all samples and averaged per water layers sampled shown separately for each bathymetric zone and transect.

Zone	Layer	N			EB		
		Sum	Average	SD	Sum	Average	SD
SHELF	0-25	5733	1911	645	1147	1147	0
	25-50	717	239	135			
	50-100	263	88	124	66	66	0
	100-bottom	99	33	47	84	84	0
	Integrated	6812	568	238	1296	432	0
SLOPE	0-25				717	179	62
	25-50	143	48	68	1147	287	336
	50-200	104	52	10	145	36	27
	200-600	804	402	4	1136	284	58
	600-1000	612	306	15	687	172	77
	Integrated	1663	202	24	3831	192	112
OFFSHORE	50-200	125	62	0	104	52	31
	200-600	1255	418	22	788	394	80
	600-1000	811	270	151	344	172	142
	Integrated	2191	250	58	1237	206	84
EXTERIOR	0-25	860	287	234	143	72	72
	25-50	430	143	117	287	143	0
	50-200	166	83	42			
	200-600	926	309	89	727	364	19
	600-1000	536	179	63	689	344	8
	Integrated	2918	200	109	1846	231	25

Supp. mat. 2. Full results of PERMANOVA analyses.

	Abundance of gelatinous zooplankton						
	Df	**Sums of squares**	**MS**	**F.model**	**R^2**	**Pr (>F)**	**Significance**
Temperature	1	1.2014	1.2014	5.2791	0.0696	0.0020	***
Salinity	1	0.4517	0.4517	1.9847	0.0262	0.1069	>0.1
Temperature × Salinity	1	0.8178	0.8178	3.5935	0.0474	0.0050	***
Residuals	65	14.7924	0.2276		0.8569		
Total	68	17.2632			1.0000		
Zooplankton abundance	1	0.2368	0.2368	1.0308	0.0137	0.3776	>0.1
Zooplankton biomass	1	0.8723	0.8723	3.7964	0.0505	0.0060	***
Zoop. abund. × Zoop. biom.	1	1.2194	1.2194	5.3071	0.0706	0.0010	****
Residuals	65	14.9347	0.2298		0.8651		
Total	68	17.2632			1.0000		
Zone	3	0.8591	0.2864	9.0100	0.0486	0.0010	****
Depth	5	9.2523	1.8505	58.2220	0.5230	0.0010	****
Transect	1	0.6702	0.6702	21.0870	0.0379	0.0010	****
Zone × Depth	10	4.1585	0.4159	3.0840	0.2351	0.0010	****
Zone × Transect	3	0.3264	0.1088	3.4240	0.0185	0.0080	***
Depth × Transect	4	0.4174	0.1044	3.2830	0.0236	0.0050	***
Zone × Depth × Transect	5	0.8312	0.1662	5.2300	0.0470	0.0010	****
Residuals	37	1.1760	0.0318		0.0665		
Total	68	17.6911			1.0000		
Water mass type	4	3.5785	0.8946	5.4627	0.2545	0.0010	****
	64	10.4813	0.1638	0.7455			
	68	14.0598	1.0000				

Supp. mat. 2. Full results of PERMANOVA analyses. - continued

	Sum of gelatinous zooplankton abundance						
	Df	**Sums of squares**	**MS**	**F.model**	**R^2**	**Pr (>F)**	**Significance**
Temperature	1	399919	399919	2.9169	0.0420	0.0789	*
Salinity	1	71551	71551	0.5219	0.0075	0.3816	>0.1
Temperature × Salinity	1	129206	129206	0.9424	0.0136	0.3027	>0.1
Residuals	65	8911885	137106		0.9369		
Total	68	9512561			1.0000		
Zooplankton abundance	1	34077	34077	0.2465	0.0036	0.6164	>0.1
Zooplankton biomass	1	489558	489558	3.5414	0.0515	0.0470	**
Zoop. abund. × Zoop. biom.	1	3406	3406	0.0246	0.0004	0.8701	>0.1
Residuals	65	8985520	138239		0.9446		
Total	68	9512561			1.0000		
Zone	3	2333914	777971	27.7850	0.2454	0.0010	****
Depth	5	1349328	269866	9.6382	0.1419	0.0080	****
Transect	1	188794	188794	6.7427	0.0199	0.0220	**
Zone × Depth	10	2500106	250011	8.9290	0.2628	0.0010	****
Zone × Transect	3	916808	305603	10.9145	0.0964	0.0010	****
Depth × Transect	4	207145	51786	1.8495	0.0218	0.1668	>0.1
Zone × Depth × Transect	5	980475	196095	7.0035	0.1031	0.0040	***
Residuals	37	1035990	28000		0.1089		
Total	68	9512561			1.0000		
Water mass type	4	4132373	1033093	8.7826	0.3544	0.0010	****
	64	7528305	117630	0.6456			
	68	11660677	1.0000				

Supp. mat. 2. Full results of PERMANOVA analyses. - continued

	Shannon diversity index						
	Df	**Sums of squares**	**MS**	**F.model**	**R^2**	**Pr (>F)**	**Significance**
Temperature	1	4.5918	4.5918	32.7350	0.3180	0.0010	****
Salinity	1	0.0770	0.0770	0.5490	0.0053	0.4735	>0.1
Temperature × Salinity	1	0.6547	0.6547	4.6680	0.0453	0.0280	**
Residuals	65	9.1177	0.1403		0.6314		
Total	68	14.4412			1.0000		
Zooplankton abundance	1	0.8572	0.8572	4.3489	0.0594	0.0360	**
Zooplankton biomass	1	0.1130	0.1130	0.5733	0.0078	0.4765	>0.1
Zoop. abund. × Zoop. biom.	1	0.6592	0.6592	3.3445	0.0457	0.0719	*
Residuals	65	12.8118	0.1971		0.8872		
Total	68	14.4412			1.0000		
Zone	3	1.2359	0.4120	9.4048	0.0856	0.0010	****
Depth	5	6.0248	1.2050	27.5073	0.4172	0.0010	****
Transect	1	0.1114	0.1114	2.5436	0.0077	0.1249	>0.1
Zone × Depth	10	3.9348	0.3935	8.9825	0.2725	0.0010	****
Zone × Transect	3	0.1866	0.0622	1.4200	0.0129	0.2507	>0.1
Depth × Transect	4	0.7882	0.1970	4.4981	0.0546	0.0070	***
Zone × Depth × Transect	5	0.5387	0.1077	2.4594	0.0373	0.0519	*
Residuals	37	1.6208	0.0438		0.1122		
Total	68	14.4412			1.0000		
Water mass type	4	12.0860	3.0215	18.1340	0.5313	0.0010	****
	64	10.6640	0.1666		0.4687		
	68	22.7500			1.0000		

Supp. mat. 2. Full results of PERMANOVA analyses. - continued

	Inverse Simpson diversity index						
	Df	**Sums of squares**	**MS**	**F.model**	**R^2**	**Pr (>F)**	**Significance**
Temperature	1	1.2991	1.2991	27.7606	0.2795	0.0010	****
Salinity	1	0.0357	0.0357	0.7619	0.0077	0.4545	>0.1
Temperature × Salinity	1	0.2714	0.2715	5.8008	0.0584	0.0150	**
Residuals	65	3.0417	0.0468		0.6544		
Total	68	4.6478			1.0000		
Zooplankton abundance	1	0.2204	0.2204	3.3945	0.0474	0.0609	*
Zooplankton biomass	1	0.0140	0.0140	0.2149	0.0030	0.6873	>0.1
Zoop. abund. × Zoop. biom.	1	0.1931	0.1931	2.9742	0.0416	0.0809	*
Residuals	65	4.2204	0.0649		0.9080		
Total	68	4.6478			1.0000		
Zone	3	0.3457	0.1152	7.7210	0.0744	0.0010	****
Depth	5	1.8519	0.3704	24.8154	0.3985	0.0010	****
Transect	1	0.0504	0.0504	3.3779	0.0109	0.0629	*
Zone × Depth	10	1.3216	0.1322	8.8544	0.2843	0.0010	****
Zone × Transect	3	0.0410	0.0137	0.9167	0.0088	0.4376	>0.1
Depth × Transect	4	0.2845	0.0711	4.7659	0.0612	0.0040	***
Zone × Depth × Transect	5	0.2003	0.0401	2.6846	0.0431	0.0360	**
Residuals	37	0.5522	0.0149		0.1188		
Total	68	4.6478			1.0000		
Water mass type	4	2.6028	0.6507	12.7510	0.4435	0.0010	****
	64	3.2661	0.0510		0.5565		
	68	5.8690			1.0000		

Supp. mat. 2. Full results of PERMANOVA analyses. - continued

	Life cycle stages of *Aglantha digitale*						
	Df	**Sums of squares**	**MS**	**F.model**	**R^2**	**Pr (>F)**	**Significance**
Temperature	1	1.5428	1.5428	6.7808	0.1002	0.0010	****
Salinity	1	0.8338	0.8338	3.6646	0.0542	0.0040	***
Temperature × Salinity	1	0.7316	0.7316	3.2154	0.0475	0.0110	**
Residuals	54	12.2862	0.2275		0.7981		
Total	57	15.3943			1.0000		
Zooplankton abundance	1	0.9167	0.9167	3.6308	0.0596	0.0070	***
Zooplankton biomass	1	0.5057	0.5057	2.0029	0.0329	0.0979	*
Zoop. abund. × Zoop. biom.	1	0.3376	0.3376	1.3372	0.0219	0.2587	>0.1
Residuals	54	13.6343	0.2525		0.8857		
Total	57	15.3943			1.0000		
Zone	3	0.8059	0.2686	1.7605	0.0524	0.0579	*
Depth	4	5.3662	1.3416	8.7921	0.3486	0.0010	****
Transect	1	0.1008	0.1008	0.6603	0.0065	0.6314	>0.1
Zone × Depth	9	1.7056	0.1895	1.2420	0.1108	0.2008	>0.1
Zone × Transect	3	1.1143	0.3714	2.4342	0.0724	0.0060	***
Depth × Transect	4	1.3029	0.3257	2.1348	0.0846	0.0130	**
Zone × Depth × Transect	3	0.4211	0.1404	0.9200	0.0274	0.5315	>0.1
Residuals	30	4.5776	0.1526		0.2974		
Total	57	15.3943			1.0000		
Water mass type	4	3.5294	0.8824	3.9414	0.2293	0.0010	****
	53	11.8649	0.2239	0.7707			
	57	15.3943	1.0000				

Supp. mat. 2. Full results of PERMANOVA analyses. - continued

	Life cycle stages of *Dimophyes arctica*						
	Df	**Sums of squares**	**MS**	**F.model**	**R^2**	**Pr (>F)**	**Significance**
Temperature	1	0.1689	0.1689	1.1700	0.0287	0.2907	>0.1
Salinity	1	0.2033	0.2033	1.4084	0.0346	0.2428	>0.1
Temperature × Salinity	1	0.5966	0.5966	4.1335	0.1015	0.0090	***
Residuals	34	4.9070	0.1443		0.8351		
Total	37	5.8757			1.0000		
Zooplankton abundance	1	0.0830	0.0830	0.5182	0.0141	0.5944	>0.1
Zooplankton biomass	1	0.1709	0.1709	1.0675	0.0291	0.3686	>0.1
Zoop. abund. × Zoop. biom.	1	0.1779	0.1779	1.1111	0.0303	0.3297	>0.1
Residuals	34	5.4439	0.1601		0.9265		
Total	37	5.8757			1.0000		
Zone	3	0.3244	0.1082	0.7950	0.0552	0.5584	>0.1
Depth	4	1.0090	0.2523	1.8544	0.1717	0.0879	*
Transect	1	0.0804	0.0804	0.5909	0.0137	0.6883	>0.1
Zone × Depth	3	0.6184	0.2062	1.5155	0.1053	0.1459	>0.1
Zone × Transect	2	0.7091	0.3546	2.6065	0.1207	0.0260	**
Depth × Transect	1	0.1422	0.1422	1.0453	0.0242	0.3666	>0.1
Zone × Depth × Transect	2	0.1354	0.0677	0.4976	0.0230	0.8571	>0.1
Residuals	21	2.8567	0.1360		0.4862		
Total	37	5.8757			1.0000		
Water mass type	2	0.5142	0.2571	1.6754	0.0874	0.1209	
	35	5.3715	0.1535	0.9126			
	37	5.8857	1.0000				

Supp. mat. 3. Sum of abundances [ind. 1000 m^{-3}] of each taxa identified.

	N					**EB**				
	Shelf	**Slope**	**Offshore**	**Exterior**	**MEAN**	**Shelf**	**Slope**	**Offshore**	**Exterior**	**MEAN**
Aglantha digitale	2072.3	662.5	920.5	1795.5	1362.7	149.6	2429.6	320.3	789.7	922.3
Pantachogon haeckeli	0.0	23.0	0.0	0.0	5.7	0.0	0.0	0.0	38.3	9.6
Homoeonema platygonon	0.0	23.0	45.9	0.0	17.2	0.0	0.0	15.3	76.5	23.0
Trachymedusae indet.	0.0	158.6	15.3	0.0	43.5	0.0	0.0	38.3	84.2	30.6
Catablema vesicarium	286.7	0.0	0.0	0.0	71.7	0.0	0.0	0.0	0.0	0.0
Halitholus cirratus	561.4	0.0	0.0	0.0	140.3	0.0	0.0	0.0	0.0	0.0
Bougainvillia superciliaris	143.3	0.0	0.0	0.0	35.8	0.0	0.0	0.0	0.0	0.0
Crystallophyes amygdalina	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.7	0.0	1.9
Dimophyes arctica	49.6	750.1	1094.5	789.7	671.0	0.0	1345.2	763.2	750.1	714.6
Muggiaea bargmannae	0.0	15.3	53.6	30.6	24.9	0.0	15.3	30.6	23.0	17.2
Diphyid eudoxid indet.	0.0	15.3	23.0	0.0	9.6	0.0	15.3	38.3	61.2	28.7
Marrus orthocanna	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.7	1.9
Physophora hydrostatica	143.3	0.0	0.0	0.0	35.8	0.0	0.0	0.0	0.0	0.0
Rudjakovia plicata	0.0	7.7	7.7	7.7	5.7	0.0	0.0	7.7	15.3	5.7
Beroe sp.	401.9	7.7	15.3	294.3	179.8	143.3	25.5	15.3	0.0	46.0
Mertensia ovum	3153.3	0.0	0.0	0.0	788.3	1003.3	0.0	0.0	0.0	250.8
Ctenophora indet.	0.0	0.0	15.3	0.0	3.8	0.0	0.0	0.0	0.0	0.0
sum	**6811.8**	**1663.0**	**2191.0**	**2917.8**	**3395.9**	**1296.2**	**3831.0**	**1236.5**	**1846.0**	**2052.4**

Chapter 8. 2. Author contribution statement

We hereby confirm, that the specific contributions to the publication:

Mańko M. K., Głuchowska M., Weydmann-Zwolicka A. 2020. Footprints of Atlantification in the vertical distribution and diversity of gelatinous zooplankton in the Fram Strait (Arctic Ocean). Progress in Oceanography 189: 102414. doi: 10.1016/j.pocean.2020.102414

were as follows:

Mańko Maciej Karol – 85%

conceptualization and design of the study, laboratory work, statistical analyses, figure preparation, writing of the first draft of the manuscript, revision and editing, funding acquisition, corresponding author

Głuchowska Marta – 5%

field work, commenting on the first draft

Weydmann-Zwolicka Agata – 10%

conceptualization and design of the study, supervision, revision and commenting on the first draft, funding acquisition

Maciej Mańko
……………………………………
Maciej Karol Mańko

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Chapter 9. Oceanic fronts shape biodiversity of gelatinous zooplankton in the European Arctic

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Published in Frontiers in Marine Science 9: 941025.

Doi: 10.3389/fmars.2022.941025

IF: 4.912, 5-years IF: 4.520, ME&S: 100 points frontiers | Frontiers in Marine Science

ORIGINAL RESEARCH
published: xx xx 2022
doi: 10.3389/fmars.2022.941025

Oceanic Fronts Shape Biodiversity of Gelatinous Zooplankton in the European Arctic

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Oceanic fronts constitute boundaries between hydrologically distinct water masses and comprise one of the most productive regions of the world's ocean. Fronts associated with density gradients (active fronts) profoundly structure planktonic communities in adjacent waters, but less is known about the impacts of density-compensated (passive) fronts. Two such fronts are found in the European Arctic, the Arctic Front (AF) and the Polar Front (PF), that both separate warmer and saltier, Atlantic water from the colder, but fresher Arctic water. As scrutinized research on the influence of passive fronts on zooplankton at large spatial and temporal scales had been lacking, we tackled the question of their role in maintaining distinct communities, employing globally unique, 12-year-long gelatinous zooplankton (GZ) and hydrological time series from the European Arctic. The GZ, owing to their fast reproductive cycles and passive dispersal, reflect particularly well the local environment. We therefore compared GZ communities between zones separated by the two fronts, disentangled their drivers, and analyzed community shifts occurring whenever front relocation occurred. We have identified fifteen GZ taxa, distributed among three distinct communities, specific for front-maintained zones, and selected the following taxa as indicators of each zone: W—west of the AF, within the Greenland Sea Gyre, *Beroe* spp.; C—central, in between the AF and the PF, *Aglantha digitale*; and E—east of the PF, in the West Spitsbergen Shelf *Mertensia ovum*. Taxonomic composition of these communities, and their specific abundance, persisted throughout time. We also showed that relocation of either front between the sampling years was subsequently followed by the restructuring of the GZ community. Our results indicate that passive oceanic fronts maintain distinct GZ communities, with probable limited exchange across a front, and provide a new perspective for the Arctic ecosystem evolution under progressing Atlantification.

Keywords: jellyfish, Atlantification, West Spitsbergen Current, arctic front, polar front, climate change

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Specialty section:
This article was submitted to Marine Ecosystem Ecology, a section of the journal Frontiers in Marine Science

Received: *11 May 2022*
Accepted: *06 June 2022*
Published: *00 Month 2022*

Citation:
Manko MK, Merchel M, Kwasniewski S and Weydmann-Zwolicka A (2022) Oceanic Fronts Shape Biodiversity of Gelatinous Zooplankton in the European Arctic. Front. Mar. Sci. 9:941025. doi: 10.3389/fmars.2022.941025

INTRODUCTION

Hydrographic fronts form at the junction of distinct water masses, and hence are usually defined by a sharp gradient of water properties, like temperature, salinity, and/or density. The existence of a horizontal density gradient fuels cross-frontal, vertical circulation and surface convergence of water masses (Belkin et al., 2009), leading to the upwelling of nutrients (Allen et al., 2005) and sinking of organic matter (Stukel et al., 2017), both linked to the enhanced primary and secondary production at a front (le Fèvre, 1987; Russell et al., 1999). Density-related fronts also attract representatives of the upper trophic levels, as evidenced by records of local aggregations of schooling fish (e.g., Herron et al., 1989), seabirds, and whales (reviewed in Olson et al., 1994). Moreover, the presence of a geostrophic, along-front currents associated with the density fronts, plays a leading role in large-scale transport of heat, salt, and nutrients (Belkin, 2004), and in maintaining the boundary between the adjacent water masses (Belkin et al., 2009). Not all fronts are, however, associated with the strong horizontal gradients of density, and these so-called density-compensated or passive fronts thus do not exhibit enhanced primary or secondary production (Drinkwater and Tande, 2014). The extent to which such density-compensated fronts can structure adjacent ecosystems has yet to be explored.

Two such passive fronts are found in the European Arctic, where they bound the northward flow of the Atlantic water on both sides (Wassmann et al., 2015). In the Greenland Sea, the Arctic Front (AF), topographically steered by the Mohn and Knipovich Ridges (Swift and Aagaard, 1981; van Aken et al., 1995), separates the colder and fresher Arctic water of the Greenland Sea Gyre from the warmer and saltier Atlantic water in the western branch of the West Spitsbergen Current (Walczowski, 2013). The other passive front, the Polar Front (PF), crosses most of the Barents Sea (Oziel et al., 2016), where it marks the boundary between the inflowing Atlantic water, and that originating in the Arctic. In its western part, along the southern and western Spitsbergen shelf and near the Bear Island, the front location is largely controlled by the bottom topography (Loeng, 1991) and it borders the eastern branch of the West Spitsbergen Current and the Spitsbergen Polar Current (Strzelewicz et al., 2022). Although both the AF and the PF are topographically steered, the presence of topographic discontinuities (e.g., submarine canyons) that leads to the baroclinic and the barotropic instabilities (Teigen et al., 2010), promotes cross-front exchange and interleaving of the Atlantic and Arctic waters (Huthnance, 1995; Saloranta and Svendsen, 2001; Drinkwater and Tande, 2014). Such instabilities are associated with a higher concentration of particles and often with a larger primary production (Trudnowska et al., 2016), but whether these can propagate up the trophic chain remains unresolved.

The position of both the AF and the PF changes with the increasing inflow of the Atlantic water (e.g., Walczowski, 2013; Wassmann et al., 2015)—a manifestation of the Atlantification of the European Arctic (reviewed in Ingvaldsen et al., 2021). During warm years, when more of the warmer and saltier Atlantic water reaches the Arctic with the flow of the West Spitsbergen Current (Beszczynska-Möller et al., 2012; Walczowski et al., 2012), it pushes the AF westwards (Walczowski, 2013), while on the other side of the current, it increases the presence of the Atlantic water on the West Spitsbergen Shelf, weakening the PF in the northward direction, and shifting its southern part eastwards (Saloranta and Svendsen, 2001; Strzelewicz et al., 2022). Assuming that both fronts maintain, to some extent, the distinctiveness of adjacent ecosystems, shifts in their position, irrespective of the underlying mechanisms, should be traceable with the analysis of local biota distribution, provided the availability of the diversity baseline and a time-series dataset at the appropriate spatial scale.

Planktonic organisms, owing to their short generation times and rapid growth in response to favorable environmental conditions, have been advocated as sentinels of the climate change in marine ecosystems (Hays et al., 2005). Patterns of their distribution and diversity have already been linked with the locations of oceanic fronts (e.g., Basedow et al., 2014), though in the European Arctic, such studies have disproportionately focused on the PF (Basedow et al., 2014; Trudnowska et al., 2016; Balazy et al., 2018), seemingly omitting the AF. Overall, these works have identified the Atlantic-facing side of the fronts as more productive (Basedow et al., 2014), and harboring more abundant planktonic communities (Kwasniewski et al., 2010; Trudnowska et al., 2016). However, referenced data pertain to the well-studied planktonic groups, like hard-bodied copepods, or provide low taxonomic resolution, hampering interpolation of such results across the whole diversity of plankton.

One such group of animals, gelatinous zooplankton (GZ; here as pelagic cnidarians and ctenophores), has received surprisingly little attention in the front-position related studies (Luo et al., 2014; Haberlin et al., 2019), especially given that their passive and active mechanisms of aggregations at physical discontinuities in the ocean are well-recognized (Arai, 1992; Graham et al., 2001), as is the front-related partitioning of their diversity across adjacent water masses (Pagès and Gili, 1992; Haberlin et al., 2019). Although the majority of studies agree that the fronts act as an impermeable barrier for the GZ (e.g., Graham et al., 2001), contradictory evidence exists, which would suggest that they, in fact, allow for a continuous exchange between the adjacent GZ communities (e.g., Luo et al., 2014). These two opposing patterns could be related to the different nature of the active and passive fronts, but the paucity of data from the density-compensated fronts precludes further reasoning.

Additional support for using the GZ, as a model system to study the ecology at the passive fronts, comes with the existence of a solid baseline of their diversity in the North Atlantic (Licandro et al., 2015; Hosia et al., 2017) and the European Arctic (Mańko et al., 2015; Ronowicz et al., 2015; Mańko et al., 2020). Unfortunately, the GZ is either completely absent from the local zooplankton time series, or the taxonomic resolution of their records is insufficient (Long et al., 2021), due to their fragile body structure that often damages when sampled harshly. From a broader perspective, the recent recognition of the GZ's trophic importance (Hays et al., 2018; Lüskow et al., 2021) as well as their diverse roles in the biogeochemical cycles (Wright et al., 2021) and the biological pump (Lebrato et al., 2019) renders understanding of the factors structuring their community pivotal for monitoring marine ecosystems and forecasting their climate-mediated evolution.

The Arctic Ocean is warming up at an unprecedented pace (IPCC, 2014) that is even more rapid in its European sector (Walczowski and Piechura, 2007), owing to the strengthening advection of Atlantic water flowing with the West Spitsbergen Current. Monitoring of the spatial extent of Atlantic water inflow is thus crucial for predicting the Arctic's future. With that in mind, we designed a study that attempted to use the GZ to track the position of the AF and the PF, which flank the West Spitsbergen Current, and their role in maintaining distinctive pelagic communities across the European Arctic. For that purpose, we examined the 12-year-long (2003–2014) zooplankton time series, combined with detailed hydrographic measurements spanning Greenland, Norwegian, and Barents Seas, the so-called European Arctic. We hypothesize that (1) the GZ found on the side of the AF and PF that faces the West Spitsbergen Current will be more abundant but less diverse, and that (2) the two passive fronts would constitute a semi-impermeable barrier, with only a small proportion of the shared GZ taxa on either side of each front, thus justifying the use of GZ to monitor the shifting position of the fronts.

MATERIALS AND METHODS

Data Collection

Zooplankton was sampled at 17 sites scattered throughout the European Arctic (**Figure 1**), from 2003 to 2014, onboard the R/V *Oceania* as part of the Institute of Oceanology of the Polish Academy of Sciences annual monitoring campaign—AREX (Arctic Research Expedition). Sampling took place from June to July, so that each site was visited within a 2-week time window each year. Noteworthy, the presence of the sea ice or rough sea has sometimes precluded accessing all planned sites in a given year; thus, data only from the sites sampled more than five times over the study period were included in the analyses.

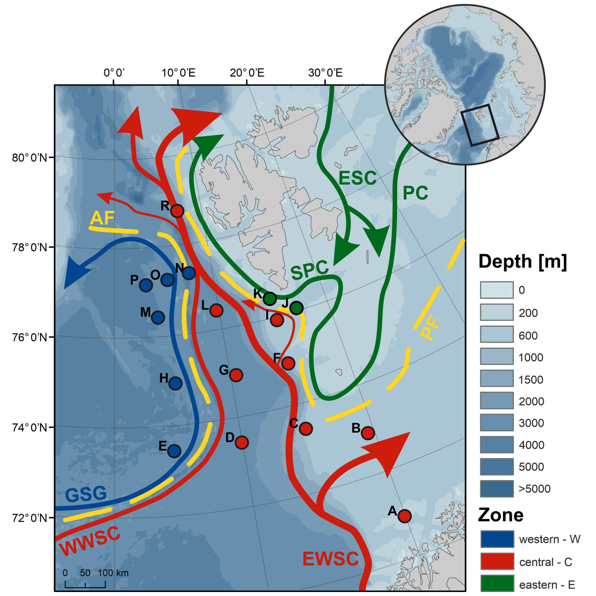

FIGURE 1 | Location of sampling sites (A to R) with a general circulation pattern (ESC, East Spitsbergen Current; EWSC and WWSC, east and west branch of the West Spitsbergen Current; GSG, Greenland Sea Gyre; PC, Persey Current and SPC, Spitsbergen Polar Current), and with the two oceanic fronts (AF, Arctic Front and PF, Polar Front) marked in yellow. Both the oceanic currents and sites are colored according to the frontal zone classification (western W, blue; central C, red and eastern E, green), which, in the case of sites, reflects their prevailing classification (>70% of years falling within a given zone). Bathymetry data were derived from the International Bathymetric Chart of the Arctic Ocean (Jakobsson et al., 2012), while ocean currents were mapped after Beszczynska-Möller et al. (2012) and Lien et al. (2017). Inset map depicts the Arctic Ocean with the investigated area bordered by the black rectangle.

When on site, the Sea-Bird Electronics CTD (SBE 911plus) probe was first lowered down to the seabed, to record the vertical profiles of temperature and salinity. Then, the zooplankton was vertically sampled from the epipelagic zone (down to 200 m, or less at shallower, shelf sites) with the standard WP-2 net fitted with 180-μm filtering gauze, and then fixed with a borax-buffered 4% solution of formaldehyde in seawater. Noteworthy, no clogging of the net or any other issue that could impact calculations of the volume of water filtered by the net was reported for either of the sampling events. In all subsequent analyses, temperature and salinity were averaged over 0–200 m to match the zooplankton data.

Gelatinous animals were identified to the lowest taxonomic level possible, based on the key taxonomic references and species lists from the region (see Ronowicz et al., 2015, and references therein), and enumerated in each sample using a NIKON SMZ800 stereomicroscope. The abundance of GZ was expressed as the number of individuals per cubic meter [ind. m^{-3}]. In the case of calycophoran siphonophores, separate numbers were given for the eudoxids and the polygastric colonies, with the latter corresponding to the numbers of anterior nectophores encountered, while the former equaled the number of eudoxid bracts. The number of physonect colonies was approximated, based on the nectophore counts, with the threshold of ten nectophores per colony (Guerrero et al., 2018) applied uniformly to all species found.

Position of the Fronts

The position of the AF was assumed to follow the 3°C isotherm at 100 m ± 5 m in the vicinity of the Knipovich Ridge (Walczowski et al., 2017). The position of the PF in Storfjorden Trough was evaluated based on the salinity averaged over 0–100 m, with the salinity of 34.86 taken as the threshold of the Atlantic water (Strzelewicz et al., 2022). The location of the PF along the West Spitsbergen Shelf was inferred from Strzelewicz et al. (2022) for years 2007–2014, and estimated from temperature and salinity distribution maps for 2003–2006. To facilitate comparison of the GZ community on either side of the fronts, a classification of sites, hereafter referred to as the frontal zone or zone for short, was introduced: sites located to the west of the AF, within the Greenland Sea Gyre—frontal zone W; sites to the east of the PF, on the West Spitsbergen Shelf—frontal zone E; and sites positioned centrally, between the two fronts—zone C (**Figure 1**). To analyze the consequences of the shifting biogeographic domains, an additional classification was used, which grouped the W and E frontal zones as the Arctic domain and referred to zone C as the Atlantic domain.

Interannual variation in the water mass distribution and position of the AF and PF was visualized based on the temperature and salinity measured at 100 m (± 5 m buffer), interpolated with the Data-Interpolating Variational Analysis (DIVA) and plotted in the Ocean Data View 4. A depth of 100 m was chosen as it corresponds to the upper part of the Atlantic water core in the European Arctic (Walczowski et al., 2012).

Data Preprocessing and Analysis

Analyzed data included GZ abundance and site-associated environmental data: temperature (averaged over 0–200 m; [°C]), salinity (averaged over 0–200 m), depth [m], latitude [DD], longitude [DD], and the frontal zone classification. The distribution of some data deviated significantly from the normal distribution (see the **Supplementary Material** for the results of Shapiro–Wilk tests); hence, non-parametric methods were used for testing differences between the frontal zones, and summaries were given as median ± interquartile range, unless otherwise stated. Exact values of test statistics and p were given in all cases, while the threshold for significance was set at $p \leq 0.05$. To control the family-wise error rate, Holm–Bonferroni correction was used whenever multiple comparisons were run. Prior to further analyses, to reduce the weight of dominant taxa, GZ abundance was square root transformed, and the Bray–Curtis dissimilarity matrix was calculated.

First, the total abundance of GZ was compared between the frontal zones, between years and within each zone on an interannual scale with a series of Kruskal–Wallis tests, each followed by the Dunn's *post-hoc* test for pairwise comparisons. Then, a permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001) was run with the adonis function from the vegan package (Oksanen et al., 2020) in R (v. 4.0.4) to test whether frontal zones differed in the GZ community composition, and, if so, then whether these differences were independent of time. Prior to running PERMANOVA, the assumption of homogeneity of group dispersion was tested with the permutest.betadisper function from the same package. Each Monte Carlo permutation was run in 999 replications. Full results of PERMANOVA are available in the **Supplementary Material**, while only pseudo-F and p-values are reported here.

Next, the community of the GZ in each frontal zone was analyzed, first with the comparative description of the percentage contribution of each species to the GZ community. Then, the median percentage contribution of the most abundant, Atlantic water-related species, *Aglantha digitale* (O. F. Müller, 1776), to the total abundance of GZ was compared between each frontal zone. Last, the data on the GZ community were scanned in the search of the taxa indicatory of the frontal zones, through the IndVal method using the strassoc function from the indicspecies package (de Cáceres and Legendre, 2009). Permutation p-values of the associations between species and frontal zones were then calculated with the signassoc function implemented in the same package (de Cáceres and Legendre, 2009).

In order to evaluate which environmental variables were the most influential in shaping the GZ community structure across the frontal zones, distance-based linear models (DistLM) were built, aided by a visual representation with the distance-based redundancy analysis (dbRDA), all run in PRIMER 7 with PERMANOVA+ add-on (Anderson et al., 2008). First, marginal effects were assessed separately for each explanatory variable (temperature, salinity, depth, longitude, and latitude). Because the GZ community remained under the joint influence of all variables, they were incorporated into the target model through the forward selection based on the adjusted R^2 criterion (Legendre and Anderson, 1999).

Finally, to test whether position shifts of the AF and the PF were followed by changes in the GZ community, a series of tests were run. First, a subset of sites was chosen, which, throughout the study period, shifted from the Arctic domain (zone E or W) to the Atlantic domain, at least once. These were sites E, H, J, K, M, and N. Then, the GZ abundance and the median proportion of *A. digitale* were compared between the Arctic and the Atlantic community at a given site with the Wilcoxon signed-rank test. Additionally, another PERMANOVA with the test of multivariate homogeneity of group dispersion (permutest.betadisper) was run, to test whether shifting frontal association was followed by the change in the taxonomic composition of the GZ community.

RESULTS

Oceanographic Data

The three front-related zones differed significantly in terms of hydrological conditions (**Figure 2**). The central zone C, located between the AF and the PF, was characterized by the highest median temperature (5.13°C ± 1.45°C) and salinity (35.11 ± 0.06) compared to the W and E zones (**Figures 2A, B**). The lowest median salinity was typical of zone E, which was located east of the PF (34.87 ± 0.07), while the lowest median temperature was recorded in zone W, west from the AF (1.40°C ± 1.54°C; **Figures 2A, B**). Uniformly shallow depths characterized the sites located within the eastern zone E, on the West Spitsbergen Shelf (166.5 m ± 126.0 m), while those scattered across zone C exemplified the largest variation in depth, with a median of 1,110.0 m ± 1,954.0 m. The deepest sampling sites were found in the western zone W, within the Greenland Sea Gyre (2,815.0 m ± 343.0 m). Overall, no significant differences in salinity or temperature were found between the zones belonging to the Arctic domain (zones W and E), but they did differ in terms of the average depth (**Figure 2**).

Considerable temporal variations of both the temperature and the salinity were detected during the studied period (**Figure 3**). Interannual differences in temperature and salinity were observed during the two anomalously Atlantic-influenced periods (2004–2006 and 2011-2014), when the warm water masses (>6°C) occupied the largest part of the investigated area and reached the furthest north. Noteworthy, comparatively elevated temperatures were also detected in 2009. The presence of the colder, less saline waters over the West Spitsbergen Shelf also varied in time, with their largest extent onto the shelf during years 2003 and 2010 (**Figure 3**). Notable interannual differences were also observed regarding the Atlantic water penetration of the Storfjorden Trough, with years 2005, 2008, and 2010 characterized by the weakest presence of the warmer water in the trough. The varying position of the isotherm 3°C, indicatory of the AF, showcased maximal eastward displacement of the front in years 2003, 2008, and 2011. The spatial distributions of salinity and

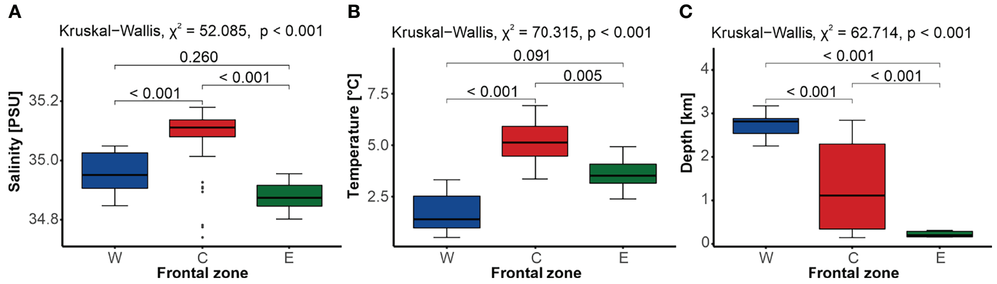

FIGURE 2 | Comparison of water salinity **(A)**, temperature **(B)**, and depth **(C)** between sites located in the three frontal zones (western W, blue; central C, red; and eastern E, green), with the results of the Kruskal–Wallis test and the p-value of the Dunn's *post-hoc* pairwise comparisons. Gray dots represent outliers.

temperature corresponded well with each other, corroborating that in the anomalously warm years, more saline waters reached further north, as exemplified by the extremely high salinity in the southern region, exceeding even 35.3 (years: 2006, 2009, 2010, and 2013; **Figure 3**). Salinity distribution was also a good indicator of the extent of fresher, Arctic waters on the shelf, and these results agreed with the distribution of temperature. Additionally, the presence of the warm, but relatively fresh waters associated with the Norwegian Coastal Current could be inferred from **Figure 3**, as well as from **Figure 2A**, as evidenced by the presence of outliers.

Gelatinous Zooplankton Abundance

GZ were present in all of the 120 examined samples. Their abundance was relatively low, with a median of 0.176 ind. m^{-3} ± 1.133 ind. m^{-3} and varied significantly between the frontal zones (Kruskal–Wallis, χ^2 = 37.846, p < 0.001), though upon further examination, significant difference was identified only between the frontal zones W and C (**Figure 4A**). Consistently small numbers of GZ were typical of the zone W, with a median abundance of 0.059 ind. m^{-3} ± 0.056 ind. m^{-3} (**Figure 4A**). A slightly higher abundance of gelatinous animals was found in zone E (0.235 ind. m^{-3} ± 0.558 ind. m^{-3}), while the most abundant community characterized the area between the fronts, in zone C (0.392 ind. m^{-3} ± 2.458 ind. m^{-3}). Although based on the visual examination, the abundance of GZ seemed to vary interannually (**Figure 4B**), statistical analysis failed to uncover significant differences between years (Kruskal–Wallis, χ^2 = 17.808, p = 0.086). However, when the frontal zones were analyzed separately, significant variation was found in the temporal variation of the GZ abundance within zone C (Kruskal–Wallis, χ^2 = 23.044, p = 0.018; **Supplementary Material**).

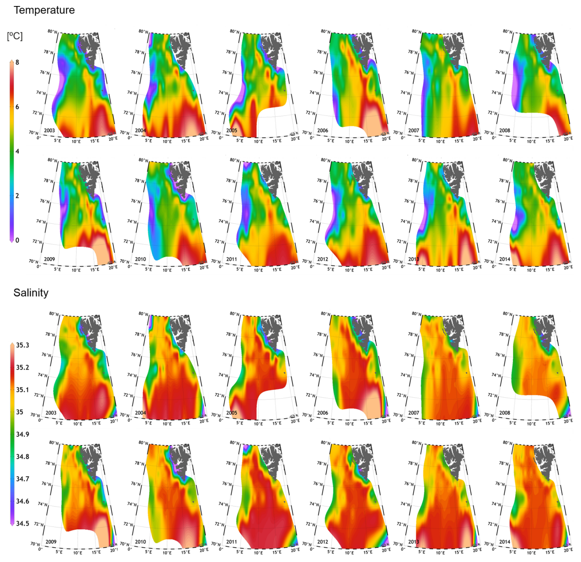

FIGURE 3 | Interannual (2003–2014) variation in temperature (two upper rows) and salinity (two lower rows) at 100 m ± 5 m, within the European Arctic.

Gelatinous Zooplankton Diversity

Overall, fifteen taxa of the GZ were recorded throughout the study period (**Figure 5C**). The majority of these taxa were observed within the central zone C; however, these were mostly sporadic observations, with the most abundant species, *A. digitale*, comprising about 96% of all records. This species was found in all zones, with an average contribution to GZ abundance of ~67% in the frontal zone W, and ~56% in zone E (**Figure 5A**). The other taxa present in all zones were a siphonophore *Dimophyes arctica* (Chun, 1897) and a ctenophore *Beroe* spp. Interestingly, life-cycle stages (eudoxids and polygastric colonies) of *D. arctica* varied in their distribution between the zones, with no eudoxids found in the frontal zone W, and their numerical dominance (~5× times more abundant) over polygastric colonies in zones C and E. All the other siphonophore species identified in this study were restricted to the central zone C, while the other ctenophore species, *Mertensia ovum* (Fabricius, 1780), appeared both in frontal zones C and E. There were also some unidentified cydippid larvae, which occurred solely between the investigated oceanic fronts, in zone C. The only Narcomedusae species identified, *Aeginopsis laurentii* Brandt, 1838, was found exclusively in the frontal zone E, while no Anthomedusae were present there. Four species of Leptomedusae were identified, which, except for *Melicertum octocostatum* (M. Sars, 1835), were distributed only in the frontal zone C.

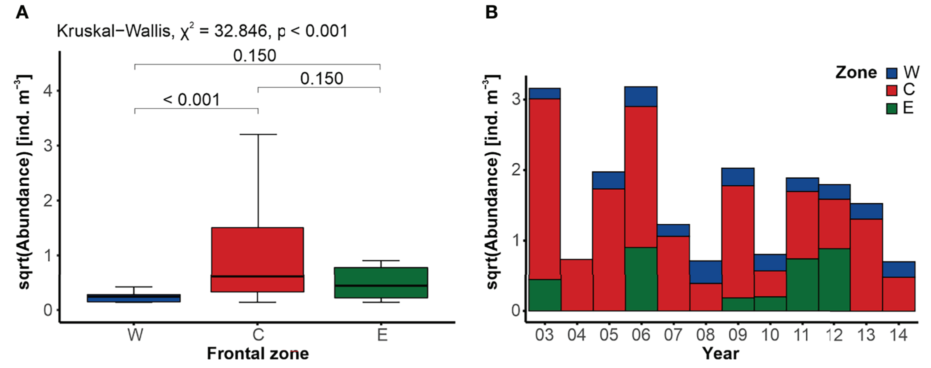

FIGURE 4 | Differences in the abundance of gelatinous zooplankton. **(A)** Comparison of the average abundance between the three frontal zones (western W, blue; central C, red; and eastern E, green), with the results of statistical tests (Kruskal–Wallis followed by Dunn's *post hoc*). **(B)** Interannual trend in the abundance within the frontal zones.

The emerging picture of species/life-cycle stage affinity to a particular frontal zone was corroborated with the analysis of association. *M. ovum* (IndVal.g = 0.661, *p* = 0.001) was found to be indicatory of the eastern frontal zone E, alongside *A. laurentii* (IndVal.g = 0.354, *p* = 0.065) and eudoxids of *D. arctica* (IndVal.g = 0.369, *p* = 0.081). *Beroe* spp. exemplified strong affinity to zone W, located west of the AF (IndVal.g = 0.487, *p* = 0.044), while *A. digitale* was strongly associated with the central frontal zone C (IndVal.g = 0.833, *p* = 0.001).

Species composition of the GZ varied significantly between frontal zones (PERMANOVA, pseudo-*F* = 11.139, *p* = 0.003), and on the interannual scale (PERMANOVA, pseudo-*F* = 1.843, *p* = 0.003). Surprisingly, significant variation in the GZ community was found also on an interannual scale, within each zone (two-way PERMANOVA, pseudo-*F* = 2.429, *p* = 0.003). The analysis of multivariate homogeneity of group dispersion (pseudo-*F* = 1.515, *p* = 0.076) indicated, however, that the significance of the two-way PERMANOVA might have resulted from the variation in data dispersion within the two-factorial (Year × Frontal zone) groups.

Drivers of Gelatinous Zooplankton Community

A modelling approach revealed that species composition of GZ was tightly coupled with temperature and depth gradients and

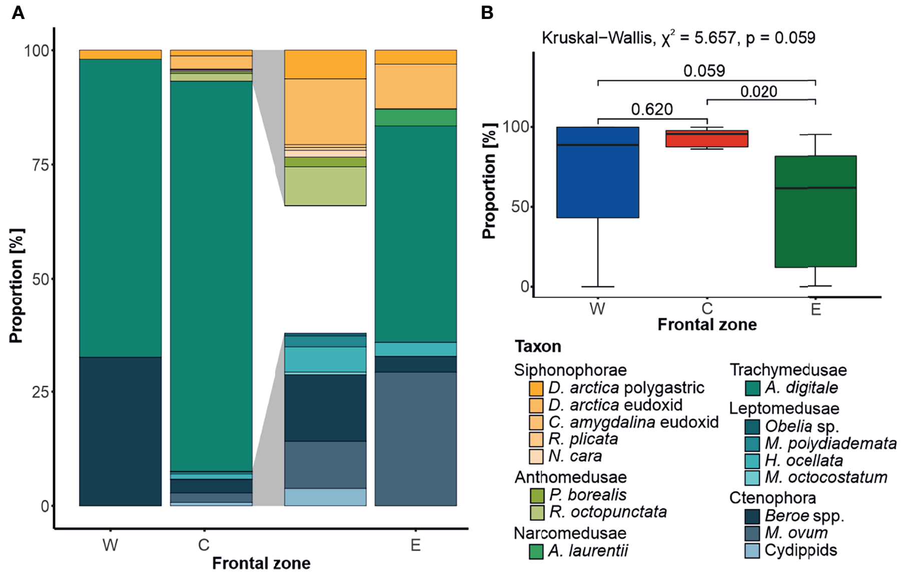

FIGURE 5 | Front-related diversity of gelatinous zooplankton. **(A)** Species contribution to the gelatinous zooplankton diversity in the investigated frontal zones (W, western; C, central; and E, eastern), calculated based on the square root transformed data, with the 5× magnification of the portions of the middle bar highlighted in gray. **(B)** Comparison of Aglantha digitale median contribution [%] to the abundance of gelatinous zooplankton community in frontal zones, with the results of statistical tests (Kruskal–Wallis followed by Dunn's *post hoc*).

reflected the frontal zonation resulting from the presence of the AF and PF (**Figure 6**). Marginal tests within the DistLM framework revealed statistically significant influence on the community structure of the following variables: latitude (pseudo-$F = 6.750$, $p = 0.001$), longitude (pseudo-$F = 16.831$, $p = 0.001$), depth (pseudo-$F = 13.661$, $p = 0.001$), temperature (pseudo-$F = 24.630$, $p = 0.001$), and salinity (pseudo-$F = 5.481$, $p = 0.002$). However, when simultaneously incorporated to the model in the sequential test approach, only gradients of temperature (adjusted $R^2 = 0.166$, $p = 0.001$) and depth (adjusted $R^2 = 0.176$, $p = 0.038$) were found to significantly shape the community structure, with the explanatory power of 19% (**Figure 6**). Noteworthy, the addition of the remaining explanatory variables increased the explanatory power of the model to 21.1%, but this increment was not statistically significant.

Impact of Shifting Fronts on GZ

Changes in the positions of oceanic fronts were accompanied by thorough restructuring of the local GZ community. Whenever a site went from being within the Arctic domain (zone W or E) to the Atlantic domain (zone C) or *vice versa*, a significant shift in the taxonomic composition was detected (PERMANOVA, pseudo-$F = 2.303$, $p = 0.043$). Moreover, when the front relocated, the site previously found in the Arctic domain ended up within the Atlantic domain (zone C), then the more abundant community was typically found at that site (**Figure 7A**). Interestingly, the shift in the domain was concomitant with the increase of the proportion of *A. digitale* in the abundance of the GZ community (**Figure 7B**).

DISCUSSION

Taking advantage of the unique, 12-year-long, polar planktonic time series, we showed that the two passive fronts of the European Arctic, the AF and the PF, maintained a certain degree of distinctiveness of the GZ communities between the adjacent water masses. We have documented that changes in the front position, mediated by the varying strength of the Atlantic water advection, were followed by a shift in the GZ community composition and abundance, thus further supporting the notion of oceanic fronts acting as impermeable barriers for GZ exchange. In a broader context, such shifts were found to reflect the clear-cut differences between the GZ in the Atlantic and Arctic domains, adding to the growing body of literature on the possible ecological impacts of the Atlantification (reviewed in Csapó et al., 2021).

The generally low abundance of GZ (0.176 ind. m^{-3} ± 1.133 ind. m^{-3}; **Figure 4**) detected in this study, with the higher GZ numbers documented in the warmer, Atlantic water side of the AF and PF, is consistent with other records from the European Arctic (Mańko et al., 2020) and elsewhere in the world (e.g., Haberlin et al., 2019). When the front separates the dynamic shelf water from a warmer offshore water, more abundant GZ is usually found on the offshore-facing side of the front (Pagès et al., 1992). A plausible explanation is that the more stable, stratified oceanic waters provide a favorable condition for GZ to thrive (Pagès et al., 1992; Haberlin et al., 2019). However, epipelagic waters in the European Arctic, contrary to the remaining parts of the Arctic Ocean, are weakly stratified due to the increasing Atlantic water inflow (Polyakov et al., 2017; Polyakov et al., 2020), hence probably another mechanism underlies the GZ abundance pattern. Interestingly, an opposing GZ abundance distribution was described for the Mediterranean Sea, where the offshore water was numerically impoverished in GZ (Guerrero et al., 2016). Shelf waters are usually inhabited by the neritic taxa that exemplify a biphasic (polyp-medusae) life cycle, known to strongly relate to seasonality and local productivity (Gili et al., 1991), which could explain the atypical pattern of abundance found there. This points to the diversity of species as an important perspective for analyzing mesoscale patterns of GZ abundance distribution.

The two passive fronts of the investigated area have maintained distinct communities of the GZ (**Figures 5**, **6**), in that a portion of taxa were unique for a particular frontal zone, but the few, most abundant ones, were common everywhere. Previous studies from the region arrived at a similar conclusion, like Descôteaux et al. (2021) who found that only one-third of

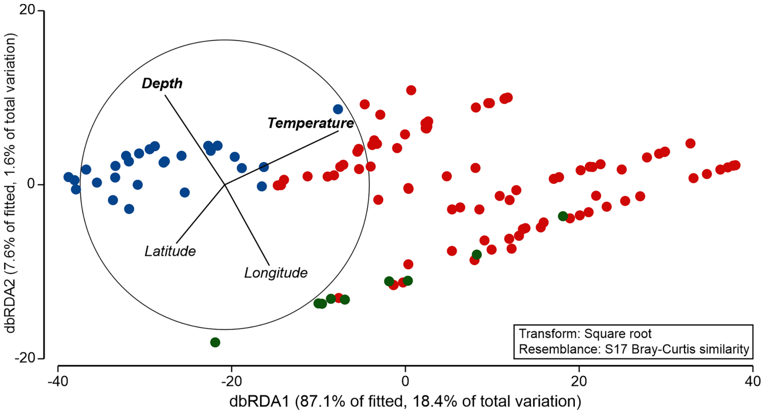

FIGURE 6 | Similarity of the gelatinous zooplankton community in the frontal zones (W—blue, C—red, and E—green) along environmental gradients resolved by distance-based redundancy analysis (dbRDA). Variables in bold were statistically significant according to the DistLM model.

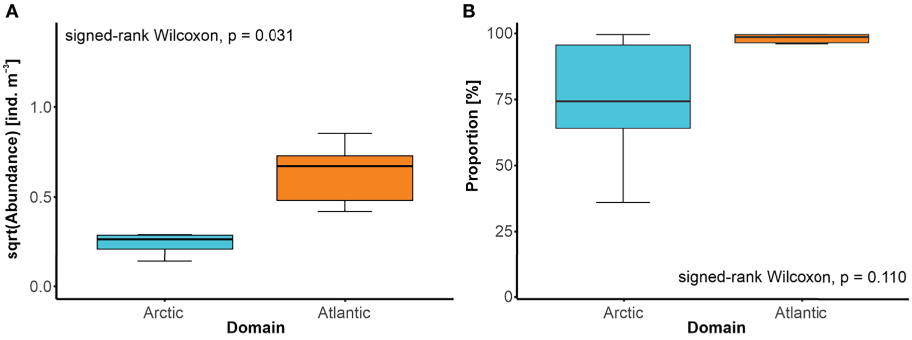

FIGURE 7 | Modifications of the GZ community related to the shift in the front position. **(A)** Abundance of the GZ and **(B)** median proportion of *Aglantha digitale* [%] in the GZ abundance, on sites before and after the change in their affinity from the Arctic domain to the Atlantic domain, and *vice versa*, with the results of the Wilcoxon signed-rank test.

meroplankton were shared among both sides of the PF. In any other place in the world's ocean, the presence of the same taxa on both sides of the front would lead to the conclusion of the GZ community exchange across the passive fronts. However, in the European Arctic, an alternative explanation exists that accounts for an intricate pattern of the Atlantic water circulation. North of 76°N, a considerable portion of Atlantic water from the western branch of the West Spitsbergen Current recirculates towards the west and south as a Return Atlantic Current, which eventually combines with Polar water of the East Greenland Current, to form Arctic water flowing within the Greenland Sea Gyre (Walczowski, 2014; Raj et al., 2019). Similarly, the branch of the West Spitsbergen Current that wraps around the northern coast of Svalbard branches off and enters the Barents Sea, where it feeds the East Spitsbergen Current (Lind and Ingvaldsen, 2012) that reaches the Arctic-facing side of the PF. The presence of Atlantic-origin water in the eastern (E) and western (W) zones could thus plausibly justify the appearance of a typically boreal or boreo-Arctic species, like *A. digitale*, within the Arctic domain, simultaneously supporting barrier effects of the fronts (**Figure 5**). Alternatively, the presence of transient, shallow eddies, known to occur along the AF (van Aken et al., 1995), could provide some support for the notion of partial GZ community exchange between zones W and C.

The remaining part of the similarity in the GZ community composition between the frontal zones can be attributed to a puzzling taxonomy of the Arctic ctenophores. Their significant abundance detected here (**Figure 5**) is in line with a common assumption of their numerical dominance in the epipelagic GZ community of the Arctic (Raskoff et al., 2005; Purcell et al., 2010). In spite of that, the diversity of the Arctic ctenophores remains poorly resolved (e.g., Majaneva & Majaneva, 2013), mostly due to the inability to preserve their delicate bodies in the regular plankton samples. Therefore, our genus level records of *Beroe* spp. likely corresponded to more than one species, probably to the epipelagic *B. cucumis* and a deeper water species *B. abyssicola* (Raskoff et al., 2010; Licandro et al., 2015), hence justifying the presence of *Beroe* records in both zones W and E.

The overall number of species detected here is in line with previous works from the region (Zelickman, 1972; Mańko et al., 2015; Mańko et al., 2020). The fact that the central zone C harbored the most diverse GZ community could potentially be attributed to the large spatial extent of this zone, which encompassed not only purely oceanic ecosystems, but also a shallow shelf region under the influence of the Norwegian Coastal Current (**Figures 1**, **3**). Therefore, the detection of meroplanktonic species (with benthic polyp phase) there is unsurprising, as they are known to numerically prevail in the shallower, coastal areas (Gili et al., 1991; Mańko et al., 2020). Additionally, some authors argued that, in general, GZ communities are more diverse with the increasing oceanic influence (see Haberlin et al., 2019 and references therein), but this assumption does not align with the paucity of GZ taxa found in the frontal zone W (**Figure 5**).

The most abundant species, *A. digitale*, was found in all zones, but constituted the largest proportion of the GZ in zone C. This species has previously been attributed to waters of Atlantic origin (Mańko et al., 2020), and was found to be a key driver of dissimilarity between neritic and oceanic GZ communities in the Celtic Sea (Haberlin et al., 2019). Likewise, we also found this species to be indicatory of zone C (IndVal.g = 0.833, p = 0.001). As for the remaining zones, the strongly associated species belong to Ctenophora, with *Beroe* spp. typical for the western zone W (IndVal.g = 0.487, p = 0.044) and *M. ovum* for the eastern zone E (IndVal.g = 0.661, p = 0.001). Interestingly, a similar set of indicatory species were found in previous studies of the local GZ community (Mańko et al., 2015; Mańko et al., 2020), hence strengthening the notion that spatial distribution of these three taxa should suffice to approximate the location of the polar fronts.

The community of GZ across the whole investigated area was structured mainly by depth and temperature (**Figure 6**). Proximity to the seabed is a key factor shaping the relative contribution of meroplanktonic to holoplanktonic cnidarian species, as the former are more common in shallower regions. Temperature, in turn, was advocated as a major driver of the GZ diversity (Guerrero et al., 2018), and probably also their abundance (Purcell, 2005). Having found the same set of GZ community drivers, Luo et al. (2014) suggested that these drivers may have a controlling role in shaping the GZ community, with only a regulating effect of the front position. However, it must be noted that the work of Luo et al. (2014) pertained to a transient, salinity-related, mesoscale front; hence, their finding cannot be adequately extrapolated to the permanent, but spatially variable fronts of the European Arctic.

Temporal trends of the Atlantic water advection depicted in **Figure 3** confirm that waters of the European Arctic are becoming noticeably warmer and more saline. The increase in Atlantic water inflow, in terms of both the heat content and the volume transported northwards (Ingvaldsen et al., 2021), is inevitably followed by shifts in the position of the AF and PF that flank the Atlantic water (**Figure 3**). Their position may also vary with the tidal currents (the PF; Saloranta & Svendsen, 2001), and large-scale atmospheric forcing, like the North Atlantic Oscillation (the AF; Schlichtholz & Goszczko, 2006; Walczowski, 2013), though conflicting results of the lack of the atmospheric forcing impact on the AF position also exist (Raj et al., 2019).

The results of our analysis on the consequences of shifting position of the fronts for the GZ community (**Figure 7**) provided additional support for the barrier effect at the front. When a particular site switched its position relative to the front, a restructuring of the GZ community followed, which reflected the distinct abundance and diversity patterns associated with a given domain (**Figure 7**). In agreement with literature data (Drinkwater and Tande, 2014; Wassmann et al., 2015; Mańko et al., 2020), we also showed that the Atlantic zooplankton community is far more abundant than that in the Arctic domain. An important observation is also that the extremely substantial proportion of *A. digitale* in the GZ community is a typical feature of the Atlantic-facing side of either front (**Figures 7B**, **5B**). The expansion of the Atlantic domain (Csapó et al., 2021), which could even reach the Arctic fjords (Weydmann-Zwolicka et al., 2021), through increasing the abundance of *A. digitale*, and that of the other small-bodied zooplankton in the Arctic (Balazy et al., 2018), may thus accelerate the restructuring of the local ecosystems (Ingvaldsen et al., 2021). Atlantification-related shifts in the plankton composition have already been linked to the diet alterations of the planktivorous seabirds (Vihtakari et al., 2018) and their foraging strategies (Jakubas et al., 2017; Stempniewicz et al., 2021). These shifts may also explain why the distribution ranges of more and more boreal fish species expand northwards (Haug et al., 2018) or why the North Atlantic population of the right whale struggles to recover (Meyer-Gutbrod and Green, 2018).

Although our main conclusion on the role of passive fronts in maintaining distinct GZ communities appears to be supported by the presented results and their discussion, certain limitations of this study must be acknowledged. First, the relatively coarse spatial and vertical resolution of zooplankton sampling (**Figure 1**; Luo et al., 2014) might have concealed some of the more intricate, fine patterns of the GZ distribution. For example, their patchiness (Trudnowska et al., 2016) at the mesoscale oceanographic features like the AF-associated eddies (diameter 40-60 km; van Aken et al., 1995). Moreover, since both the AF and the PF undergo seasonal variation, confined to their surface layer (van Aken et al., 1995; Raj et al., 2019), we might have failed to capture the more dynamic situation of the GZ there. However, since the seasonal variation (at least in the case of the PF; Strzelewicz et al., 2022) often leads to the formation of a strong density gradient in the upper 50 m of the water column (Strzelewicz et al., 2022), then this should only reinforce the barrier effect of the front. Despite these two limitations, our sampling framework was detailed enough to capture the large-scale pattern of the front-related structuring of the GZ diversity.

CONCLUSIONS

The two passive fronts of the European Arctic, the AF and the PF, maintained distinct GZ communities, which differed not only in their abundance, but also in their taxonomic composition. The community associated with the warmer and saltier Atlantic water was characterized by the overall higher abundance and diversity, but with a clear numerical dominance of a single species, *A. digitale*. In contrast, the colder Arctic water harbored less abundant and less diverse communities, which were readily identifiable by the largest proportion of ctenophores, with *Beroe* spp. for the Greenland Sea Gyre, west of the AF, and *M. ovum* for the West Spitsbergen Shelf, east of the PF. This adds to the growing body of literature that advocates the usage of GZ as hydrological indicators, but more importantly points to the potential direction of the Arctic ecosystems evolution, in the progressing Atlantification scenario.

Interannual shifts in the position of the fronts were coupled with the dynamics of Atlantic water inflow, which is flanked on both sides by the fronts. GZ was found to tightly follow the front relocations, in that if a particular site shifted its position relative to the front, from the Atlantic-facing side to the Arctic-facing side or *vice versa*, then a GZ community specific for a given domain appeared. Taking the intricate pattern of water circulation in the European Arctic into account, e.g., recirculating/return currents, the two passive fronts, the AF and the PF, appeared to provide a semi-impermeable barrier for the GZ community, with only a minor cross-frontal exchange.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

MKM and AW-Z contributed to the conception and design of the study. MKM conducted laboratory work, statistical analyses, data visualization and wrote the first draft of the manuscripts. AW-Z supervised the project and participated in the statistical analysis. MM analyzed hydrological data. SK coordinated field work and curated sample collection. MKM, MM, and AWZ acquired funding for this research. All authors contributed to the review and editing of the first draft, and have read, and approved the submitted version.

FUNDING

This work was supported by the following grants: MKM received funding from the Polish Ministry of Science and Higher Education through a Diamond Grant program (no. DI2014 020344); AW-Z was supported by the grant HIDEA—Hidden diversity of plankton in the European Arctic no. 2017/27/B/NZ8/01056 from the National Science Centre, Poland; MM's work was financed by the National Science Centre, Poland through the DWINS Project (2016/21/N/ST10/02920).

ACKNOWLEDGMENTS

We want to thank all the crew members of the R/V *Oceania* and those who participated in the AREX expeditions for their demanding work in often challenging conditions that allowed for this study to come into existence.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.941025/full#supplementary-material

REFERENCES

Allen, J. T., Brown, L., Sanders, R., Moore, C. M., Mustard, A., Fielding, S., et al. (2005). Diatom Carbon Export Enhanced by Silicate Upwelling in the Northeast Atlantic. *Nature* 437, 728–732. doi: 10.1038/nature03948

Anderson, M. J. (2001). Permutation Tests for Univariate or Multivariate Analysis of Variance and Regression. *Can. J. Fish. Aquat. Sci.* 58, 626–639. doi: 10.1139/cjfas-58-3-626

Anderson, M. J., Gorley, R. N. and Clarke, K. R. (2008). *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods.*

Arai, M. N. (1992). Active and Passive Factors Affecting Aggregations of Hydromedusae: A Review. *Sci. Mar.* 56, 99–108.

Balazy, K., Trudnowska, E., Wichorowski, M. and Błachowiak-Samołyk, K. (2018). Large Versus Small Zooplankton in Relation to Temperature in the Arctic Shelf Region. *Polar. Res.* 37, 1427409. doi: 10.1080/17518369.2018.1427409

Basedow, S. L., Zhou, M. and Tande, K. S. (2014). Secondary Production at the Polar Front, Barents Sea , August 2007. *J. Mar. Syst.* 130, 147–159. doi: 10.1016/j.jmarsys.2013.07.015

Belkin, I. M. (2004). Propagation of the "Great Salinity Anomaly" of the 1990s Around the Northern North Atlantic. *Geophys. Res. Lett.* 31, L08306. doi: 10.1029/2003GL019334

Belkin, I. M., Cornillon, P. C. and Sherman, K. (2009). Fronts in Large Marine Ecosystems. *Prog. Oceanogr.* 81, 223–236. doi: 10.1016/j.pocean.2009.04.015

Beszczynska-Möller, A., Fahrbach, E., Shauer, U. and Hansen, E. (2012). Variability in Atlantic Water Temperature and Transport at the Entrance to the Arctic Ocean 1997–2010. *ICES. J. Mar. Sci.* 69, 852–863. doi: 10.1093/icesjms/fss056

Csapó, H. K., Grabowski, M. and Węsławski, J. M. (2021). Coming Home - Boreal Ecosystem Claims Atlantic Sector of the Arctic. *Sci. Total. Environ.* 771, 144817. doi: 10.1016/j.scitotenv.2020.144817

de Cáceres, M. and Legendre, P. (2009). Associations Between Species and Groups of Sites: Indices and Statistical Inference. *Ecology* 90, 3566–3574. doi: 10.1890/08-1823.1

Descôteaux, R., Ershova, E., Wangensteen, O. S., Præbel, K., Renaud, P. E., Cottier, F., et al. (2021). Meroplankton Diversity, Seasonality and Life-History Traits Across the Barents Sea Polar Front Revealed by High-Throughput DNA Barcoding. *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.677732

Drinkwater, K. F. and Tande, K. (2014). Biophysical Studies of the Polar Front in the Barents Sea and the Arctic Front in the Norwegian Sea: Results From the NESSAR Project. *J. Mar. Syst.* 130, 131–133. doi: 10.1016/j.jmarsys.2013.11.011

Gili, J. M., Pagès, F. and Fusté, X. (1991). Mesoscale Coupling Between Spatial Distribution of Planktonic Cnidarians and Hydrographic Features Along the Galician Coast (Northwestern Iberian Peninsula). *Sci. Mar.* 55, 419–426.

Graham, W. M., Pagès, F. and Hamner, W. M. (2001). A Physical Context for Gelatinous Zooplankton Aggregations: A Review. *Hydrobiologia* 451, 199–212. doi: 10.1023/A:1011876004427

Guerrero, E., Gili, J.-M., Grinyó, J. and Sabatés, A. (2018). Long-Term Changes in the Planktonic Cnidarian Community in a Mesoscale Area of the NW Mediterranean. *PLos One* 13, e0196431. doi: 10.1371/journal.pone.0196431

Guerrero, E., Marrodán, A., Sabatés, A., Orejas, C. and Gili, J. M. (2016). High Spatial Heterogeneity of Two Planktonic Cnidarian Species Related to the Variability of a Shelf-Slope Front at Short Time Scales. *Sci. Mar.* 80, 487–497. doi: 10.3989/scimar.04452.03A

Haberlin, D., Raine, R., McAllen, R. and Doyle, T. K. (2019). Distinct Gelatinous Zooplankton Communities Across a Dynamic Shelf Sea. *Limnol. Ocean.* 64, 1802–1818. doi: 10.1002/lno.11152

Haug, T., Bogstad, B., Chierici, M., Gjøsæter, H., Hallfredsson, E. H., Høines, Å.S., et al. (2017). Future Harvest of Living Resources in the Arctic Ocean North of the Nordic and Barents Seas: A Review of Possibilities and Constraints. *Fish. Res.* 188, 38–57. doi: 10.1016/j.fishres.2016.12.002

Hays, G. C., Doyle, T. K. and Houghton, J. D. R. (2018). A Paradigm Shift in the Trophic Importance of Jellyfish? *Trends Ecol. Evol.* 33, 874–884. doi: 10.1016/j.tree.2018.09.001

Hays, G. C., Richardson, A. J. and Robinson, C. (2005). Climate Change and Marine Plankton. *Trends Ecol. Evol.* 20, 337–344. doi: 10.1016/j.tree.2005.03.004

Herron, R. C., Leming, T. D. and Li, J. (1989). Satellite-Detected Fronts and Butterfish Aggregations in the Northeastern Gulf of Mexico. *Cont. Shelf. Res.* 9, 569–588. doi: 10.1016/0278-4343(89)90022-8

Hosia, A., Falkenhaug, T., Baxter, E. J. and Pagès, F. (2017). Abundance, Distribution and Diversity of Gelatinous Predators Along the Northern Mid-Atlantic Ridge: A Comparison of Different Sampling Methodologies. *PLos One* 12, 1–18. doi: 10.1371/journal.pone.0187491

Huthnance, J. M. (1995). Circulation, Exchange and Water Masses at the Ocean Margin: The Role of Physical Processes at the Shelf Edge. *Prog. Oceanogr.* 35, 353–431. doi: 10.1016/0079-6611(95)80003-C

Ingvaldsen, R. B., Assmann, K. M., Primicerio, R., Fossheim, M., Polyakov, I. V. and Dolgov, A. V. (2021). Physical Manifestations and Ecological Implications of Arctic Atlantification. *Nat. Rev. Earth Environ.* 2, 874–889. doi: 10.1038/s43017-021-00228-x

IPCCCore Writing Team (2014). "Climate Change 2014: Synthesis Report," in *Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Eds. Pachauri, R. K. and Meyer, L. A. (Geneva, Switzerland: IPCC).

Jakobsson, M., Mayer, L., Coakley, B., Dowdeswell, J. A., Forbes, S., Fridman, B., et al. (2012). The International Bathymetric Chart of the Arctic Ocean (IBCAO) Version 3.0. *Geophys. Res. Lett.* 39, L12609. doi: 10.1029/2012GL052219

Jakubas, D., Wojczulanis-Jakubas, K., Iliszko, L. M., Strøm, H. and Stempniewicz, L. (2017). Habitat Foraging Niche of a High Arctic Zooplanktivorous Seabird in a Changing Environment. *Sci. Rep.* 7, 16203. doi: 10.1038/s41598-017-16589-7

Kwasniewski, S., Gluchowska, M., Jakubas, D., Wojczulanis-Jakubas, K., Walkusz, W., Karnovsky, N., et al. (2010). The Impact of Different Hydrographic Conditions and Zooplankton Communities on Provisioning Little Auks Along the West Coast of Spitsbergen. *Prog. Oceanogr.* 87, 72–82. doi: 10.1016/j.pocean.2010.06.004

Lebrato, M., Pahlow, M., Frost, J. R., Küter, M., Mendes, P. D. J., Molinero, J. C., et al. (2019). Sinking of Gelatinous Zooplankton Biomass Increases Deep Carbon Transfer Efficiency Globally. *Global Biogeochem. Cycles.* 33, 1764–1783. doi: 10.1029/2019GB006265 le Fèvre, J. (1987). Aspects of the Biology of Frontal Systems. *Adv. Mar. Biol.* 23, 163–299. doi: 10.1016/S0065-2881(08)60109-1

Legendre, P. and Anderson, M. J. (1999). Distance-Based Redundancy Analysis: Testing Multispecies Responses in Multifactorial Ecological Experiments. *Ecol. Monogr.* 69, 1–24. doi: 10.1890/0012-9615(1999)069[0001:DBRATM]2.0.CO;2

Licandro, P., Blackett, M., Fischer, A., Hosia, A., Kennedy, J., Kirby, R. R., et al. (2015). Biogeography of Jellyfish in the North Atlantic, by Traditional and Genomic Methods. *Earth Syst. Sci. Data* 7, 173–191. doi: 10.5194/essd-7-173-2015

Lien, V. S., Schlichtholz, P., Skagseth, Ø. and Vikebø, F. B. (2017). Wind-Driven Atlantic Water Flow as a Direct Mode for Reduced Barents Sea Ice Cover. *J. Clim.* 30, 803–812. doi: 10.1175/JCLI-D-16-0025.1

Lind, S. and Ingvaldsen, R. B. (2012). Variability and Impacts of Atlantic Water Entering the Barents Sea From the North. *Deep. Res. Part I. Oceanogr. Res. Pap.* 62, 70–88. doi: 10.1016/j.dsr.2011.12.007

Loeng, H. (1991). Features of the Physical Oceanographic Conditions of the Barents Sea. *Polar. Res.* 10, 5–18. doi: 10.3402/polar.v10i1.6723

Long, A. P., Haberlin, D., Lyashevska, O., Brophy, D., O'Hea, B., O'Donnell, C., et al. (2021). Interannual Variability of Gelatinous Mesozooplankton in a Temperate Shelf Sea: Greater Abundance Coincides With Cooler Sea Surface Temperatures. *ICES. J. Mar. Sci.* 78, 1372–1385. doi: 10.1093/icesjms/fsab030

Luo, J. Y., Grassian, B., Tang, D., Irisson, J. O., Greer, A. T., Guigand, C. M., et al. (2014). Environmental Drivers of the Fine-Scale Distribution of a Gelatinous Zooplankton Community Across a Mesoscale Front. *Mar. Ecol. Prog. Ser.* 510, 129–149. doi: 10.3354/meps10908

Lüskow, F., Galbraith, M. D., Hunt, B., Perry, R. I. and Pakhomov, E. A. (2021). Gelatinous and Soft-Bodied Zooplankton in the Northeast Pacific Ocean: Organic, Elemental, and Energy Contents. *Mar. Ecol. Prog. Ser.* 665, 19–35. doi: 10.3354/meps13663

Majaneva, S. and Majaneva, M. (2013). Cydippid Ctenophores in the Coastal Waters of Svalbard: Is it Only Mertensia Ovum? *Polar. Biol.* 36, 1681–1686. doi: 10.1007/s00300-013-1377-6

Mańko, M. K., Głuchowska, M. and Weydmann-Zwolicka, A. (2020). Footprints of Atlantification in the Vertical Distribution and Diversity of Gelatinous Zooplankton in the Fram Strait (Arctic Ocean). *Prog. Oceanogr.* 189, 102414. doi: 10.1016/j.pocean.2020.102414

Mańko, M. K., Panasiuk-Chodnicka, A. and Żmijewska, M. I. (2015). Pelagic Coelenterates in the Atlantic Sector of the Arctic Ocean – Species Diversity and Distribution as Water Mass Indicators. *Oceanol. Hydrobiol. Stud.* 44, 466–479. doi: 10.1515/ohs-2015-0044

Meyer-Gutbrod, E. L. and Greene, C. H. (2018). Uncertain Recovery of the North Atlantic Right Whale in a Changing Ocean. *Glob. Change Biol.* 24, 455–464. doi: 10.1111/gcb.13929

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Henry, M. and Stevens, H. (2007). "The Vegan Package," in *Community Ecology Package*, vol. 10. , 631–637.

Olson, D., Hitchcock, G., Mariano, A., Ashjian, C., Peng, G., Nero, R., et al. (1994). Life on the Edge: Marine Life and Fronts. *Oceanography* 7, 52–60. doi: 10.5670/oceanog.1994.03

Pagès, F. and Gili, J. M. (1992). Influence of Agulhas Waters on the Population Structure of Planktonic Cnidarians in the Southern Benguela Region. *Sci. Mar.* 56, 109–123.

Pagès, F., Gili, J.-M. and Bouillon, J. (1992). Medusae (Hydrozoa, Scyphozoa, Cubozoa) of the Benguela Current (Southeastern Atlantic). *Sci. Mar.* 56, 1–64.

Polyakov, I. V., Alkire, M. B., Bluhm, B. A., Brown, K. A., Carmack, E. C., Chierici, M., et al. (2020). Borealization of the Arctic Ocean in Response to Anomalous Advection From Sub-Arctic Seas. *Front. Mar. Sci.* 7. doi: 10.3389/fmars.2020.00491

Polyakov, I. V., Pnyushkov, A. V., Alkire, M. B., Ashik, I. M., Baumann, T. M., Carmack, E. C., et al. (2017). Greater Role for Atlantic Inflows on Sea-Ice Loss in the Eurasian Basin of the Arctic Ocean. *Science* 356, 285–291. doi: 10.1126/science.aai8204

Purcell, J. E. (2005). Climate Effects on Formation of Jellyfish and Ctenophore Blooms: A Review. *J. Mar. Biol. Assoc. United. Kingdom.* 85, 461–476. doi: 10.1017/S0025315405011409

Purcell, J. E., Hopcroft, R. R., Kosobokova, K. N. and Whitledge, T. E. (2010). Distribution, Abundance, and Predation Effects of Epipelagic Ctenophores and Jellyfish in the Western Arctic Ocean. *Deep. Res. Part II. Top. Stud. Oceanogr.* 57, 127–135. doi: 10.1016/j.dsr2.2009.08.011

Raj, R. P., Chatterjee, S., Bertino, L., Turiel, A. and Portabella, M. (2019). The Arctic Front and its Variability in the Norwegian Sea. *Ocean. Sci.* 15, 1729–1744. doi: 10.5194/os-15-1729-2019

Raskoff, K. A., Hopcroft, R. R., Kosobokova, K. N., Purcell, J. E. and Youngbluth, M. (2010). Jellies Under Ice: ROV Observations From the Arctic 2005 Hidden Ocean Expedition. *Deep. Res. Part II. Top. Stud. Oceanogr.* 57, 111–126. doi: 10.1016/j.dsr2.2009.08.010

Raskoff, K. A., Purcell, J. E. and Hopcroft, R. R. (2005). Gelatinous Zooplankton of the Arctic Ocean: In Situ Observations Under the Ice. *Polar. Biol.* 28, 207–217. doi: 10.1007/s00300-004-0677-2

Ronowicz, M., Kukliński, P. and Mapstone, G. M. (2015). Trends in the Diversity, Distribution and Life History Strategy of Arctic Hydrozoa (Cnidaria). *PLos One* 10, 1–19. doi: 10.1371/journal.pone.0120204

Russell, R. W., Harrison, N. M. and Hunt, J. G.L. (1999). Foraging at a Front: Hydrography, Zooplankton, and Avian Planktivory in the Northern Bering Sea. *Mar. Ecol. Prog. Ser.* 182, 77–93. doi: 10.3354/meps182077

Saloranta, T. M. and Svendsen, H. (2001). Across the Arctic Front West of Spitsbergen: High- Resolution CTD Sections From 1998 – 2000. *Polar. Res.* 20, 177–184. doi: 10.3402/polar.v20i2.6515

Schlichtholz, P. and Goszczko, I. (2006). Interannual Variability of the Atlantic Water Layer in the West Spitsbergen Current at 76.5N in Summer 1991-2003. *Deep. Res. Part I. Oceanogr. Res. Pap.* 53, 608–626. doi: 10.1016/j.dsr.2006.01.001

Stempniewicz, L., Weydmann-Zwolicka, A., Strzelewicz, A., Goc, M., Głuchowska, M., Kidawa, D., et al. (2021). Advection of Atlantic Water Masses Influences Seabird Community Foraging in a High-Arctic Fjord. *Prog. Oceanogr.* 193, 102549. doi: 10.1016/j.pocean.2021.102549

Strzelewicz, A., Przyborska, A. and Walczowski, W. (2022). Increased Presence of Atlantic Water on the Shelf South-West of Spitsbergen With Implications for the Arctic Fjord Hornsund. *Prog. Oceanogr.* 200, 102714. doi: 10.1016/j.pocean.2021.102714

Stukel, M. R., Aluwihare, L. I., Barbeau, K. A., Chekalyuk, A. M., Goericke, R., Miller, A. J., et al. (2017). Mesoscale Ocean Fronts Enhance Carbon Export Due to Gravitational Sinking and Subduction. *Proc. Natl. Acad. Sci.* 114, 1252–1257. doi: 10.1073/pnas.1609435114

Swift, J. H. and Aagaard, K. (1981). Seasonal Transitions and Water Mass Formation in the Iceland and Greenland Seas. *Deep. Res.* 28A, 1107–1129. doi: 10.1016/0198-0149(81)90050-9

Teigen, S. H., Nilsen, F. and Gjevik, B. (2010). Barotropic Instability in the West Spitsbergen Current. *J. Geophys. Res. Oceans.* 115, C07016. doi: 10.1029/2009JC005996

Trudnowska, E., Gluchowska, M., Beszczynska-Möller, A., Blachowiak-Samolyk, K. and Kwasniewski, S. (2016). Plankton Patchiness in the Polar Front Region of the West Spitsbergen Shelf. *Mar. Ecol. Prog. Ser.* 560, 1–18. doi: 10.3354/meps11925

van Aken, H. M., Budéus, G. and Hähnel, M. (1995). The Anatomy of the Arctic Frontal Zone in the Greenland Sea. *J. Geophys. Res.* 100, 15999–16014. doi: 10.1029/95JC01176

Vihtakari, M., Welcker, J., Moe, B., Chastel, O., Tartu, S., Hop, H., et al. (2018). Black-Legged Kittiwakes as Messengers of Atlantification in the Arctic. *Sci. Rep.* 8, 1178. doi: 10.1038/s41598-017-19118-8

Walczowski, W. (2013). Frontal Structures in the West Spitsbergen Current Margins. *Ocean. Sci.* 9, 957–975. doi: 10.5194/os-9-957-2013

Walczowski, W. (2014). *Atlantic Water in the Nordic Seas. Properties, Variability, Climatic Importance* (Berlin Heidelberg: Springer). doi: 10.1007/978-3-319-01279-7

Walczowski, W., Beszczynska-Möller, A., Wieczorek, P., Merchel, M. and Grynczel, A. (2017). Oceanographic Observations in the Nordic Sea and Fram Strait in 2016 Under the IOPAN Long-Term Monitoring Program AREX. *Oceanologia* 59, 187–194. doi: 10.1016/j.oceano.2016.12.003

Walczowski, W. and Piechura, J. (2007). Pathways of the Greenland Sea Warming. *Geophys. Res. Lett.* 34, L10608. doi: 10.1029/2007GL029974

Walczowski, W., Piechura, J., Goszczko, I. and Wieczorek, P. (2012). Changes in Atlantic Water Properties: An Important Factor in the European Arctic Marine Climate. *ICES. J. Mar. Sci.* 69, 864–869. doi: 10.1093/icesjms/fss068Changes

Wassmann, P., Kosobokova, K. N., Slagstad, D., Drinkwater, K. F., Hopcroft, R. R., Moore, S. E., et al. (2015). The Contiguous Domains of Arctic Ocean Advection: Trails of Life and Death. *Prog. Oceanogr.* 139, 42–65. doi: 10.1016/j.pocean.2015.06.011

Weydmann-Zwolicka, A., Prątnicka, P., Łącka, M., Majaneva, S., Cottier, F. and Berge, J. (2021). Zooplankton and Sediment Fluxes in Two Contrasting Fjords Reveal Atlantification of the Arctic. *Sci. Total. Environ.* 773. doi: 10.1016/j.scitotenv.2021.145599

Wright, R. M., le Quéré, C., Buitenhuis, E., Pitois, S. and Gibbons, M. J. (2021). Role of Jellyfish in the Plankton Ecosystem Revealed Using a Global Ocean Biogeochemical Model. *Biogeosciences* 18, 1291–1320. doi: 10.5194/bg-18-1291-2021

Zelickman, E. A. (1972). Distribution and Ecology of the Pelagic Hydromedusae, Siphonophores and Ctenophores of the Barents Sea, Based on Perennial Plankton Collections. *Mar. Biol.* 17, 256–264. doi: 10.1007/BF00366301

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Chapter 9. 1. Supplementary files

Tab. S1. Verification of data distribution normality with the Shapiro-Wilk test.

		Frontal zone		
		W	**C**	**E**
Salinity	W statistic	0.929	0.722	0.961
	p	0.066	0.000	0.820
Temperature	W statistic	0.913	0.965	0.970
	p	0.027	0.021	0.901
Depth	W statistic	0.942	0.837	0.712
	p	0.134	0.000	0.003
Abundance of GZ	W statistic	0.811	0.543	0.821
	p	0.000	0.000	0.048

Tab. S2. Results of **A.** PERMANOVA for differences in GZ community composition between fronts, years, and years within fronts (interaction term), and **B.** permutation test for homogeneity of multivariate dispersions within respective groups.

A.

	Df	**SS**	**MS**	**F.model**	**R^2**	**Pr (>F)**	**adjusted p**
Front	2	3.385	1.693	11.139	0.131	0.001	0.003
Year	11	3.080	0.280	1.843	0.119	0.003	0.003
Year x Front	15	5.535	0.369	2.428	0.214	0.001	0.003
Residuals	91	13.828	0.152		0.535		
Total	119	25.829			1.000		

Tab. S2. Results of **A.** PERMANOVA for differences in GZ community composition between fronts, years, and years within fronts (interaction term), and **B.** permutation test for homogeneity of multivariate dispersions within respective groups. - continued

B.

		Df	SS	MS	F.model	Pr (>F)
Year						
		11	0.388	0.035	0.709	0.713
	Residuals	108	5.374	0.050		
Front						
	Groups	2	0.104	0.052	1.324	0.278
	Residuals	117	4.605	0.039		
Year x Front						
	Groups	28	1.631	0.058	1.515	0.076
	Residuals	91	3.498	0.038		

Tab. S3. Comparison of GZ abundance within frontal zones (W, C, E) on the interannual scale (interaction term: Front x Year) with the Kruskal-Wallis test.

	Frontal zone		
	W	**C**	**E**
df	10	11	5
χ^2	7.906	23.004	6.583
p	0.638	0.018	0.254

Tab. S4. Results of **A.** PERMANOVA for differences in GZ community composition between the Arctic and Atlantic domains, and **B.** permutation test for homogeneity of multivariate dispersions within domains..

A.

	Df	**SS**	**MS**	**F.model**	**R^2**	**Pr (>F)**
Domain	1	0.511	0.511	2.303	0.056	0.043
Residuals	39	8.650	0.222		0.944	
Total	40	9.161			1	

B.

	Df	**SS**	**MS**	**F.model**	**Pr (>F)**
Domain	1	0.039	0.039	0.726	0.398
Residuals	39	2.081	0.053		

Chapter 9. 2. Author contribution statement

We hereby confirm, that the specific contributions to the publication:

Mańko M. K., Merchel M., Kwaśniewski S., Weydmann-Zwolicka A. 2022. Oceanic fronts shape biodiversity of gelatinous zooplankton in the European Arctic. Frontiers in Marine Science

were as follows:

Mańko Maciej Karol – 70%

conceptualization and design of the study, laboratory work, statistical analyses, preparation of figures 1, 2, 4, 5, 7 and coordination of other figure design (Fig. 3, and 6), writing of the first draft of the manuscript, revision and editing, funding acquisition, corresponding author

Merchel Małgorzata – 5%

analysis of hydrological data, figure preparation (Fig. 3), revision and commenting on the first draft, funding acquisition

Kwaśniewski Sławomir – 5%

field work coordination, curation of sample collection, revision and commenting on the first draft

Weydmann-Zwolicka Agata – 20%

conceptualization and design of the study, supervision, participation in the statistical analysis and figure preparation (Fig. 3, and 6), revision and commenting on the first draft, funding acquisition

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Chapter 10. Atlantification alters the reproduction of jellyfish *Aglantha digitale* in the European Arctic

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Published in Limnology and Oceanography.
Doi: 10.1002/lno.12170
IF: 4.745, 5-years IF: 4.349, ME&S: 140 points

LIMNOLOGY
and
OCEANOGRAPHY

Limnol. Oceanogr. 9999, 2022, 1–14

doi: 10.1002/lno.12170

Atlantification alters the reproduction of jellyfish *Aglantha digitale* in the European Arctic

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Abstract

Increasing heat content, salinity, and velocity of the Atlantic water masses passing northward through the Fram Strait accelerate the transition of the European Arctic toward more Atlantic state, a process referred to as Atlantification. A pronounced environmental shift leads to a poleward expansion of boreal species ranges and alters seasonal rhythms of local taxa, potentially affecting the whole food web structure. Here, we monitored a pelagic cnidarian, *Aglantha digitale*, commonly associated with boreal waters, throughout 12 consecutive summers (2003–2014) and along 2 branches of the West Spitsbergen Current, the main conveyor of Atlantic water to the Arctic. We documented a steady decrease in *A. digitale* abundance in the epipelagic waters of the European Arctic and a disproportionately larger northward advection of this jellyfish with the eastern branch of the West Spitsbergen Current compared to the western branch. Supported with modeling techniques, we found that year after year, *A. digitale* reproduced earlier in the southern region, thus leading to an earlier descent of the larger, more mature specimens, toward deeper waters, where they avoided our epipelagic sampling. Moreover, the prevalence of smaller jellyfish during years with record-level water temperature and salinity (2005–2007) in the southern region of the Fram Strait indicated that a 2nd reproductive cycle may have occurred. We also showed that the northern population of *A. digitale*, or at least part of it, originates in the south and is advected northward with the West Spitsbergen Current. In addition, our work highlights the need to include jellyfish in zooplankton monitoring.

The European Arctic suffers from the most pronounced warming of the surface air temperatures globally (IPCC 2014), and thus faces dramatic environmental shifts. Alterations in the physical and chemical conditions of the Arctic Ocean are mediated by an increasing sea water temperature (Beszczynska-Möller et al. 2012) and salinity (Walczowski et al. 2017) of the Atlantic water advected there through the Fram Strait (Polyakov et al. 2020), which is the only large gateway connecting the Atlantic and Arctic domains (Beszczynska-Möller et al. 2012). Extensive heat transport of Atlantic water, accompanied by the modifications of local marine ecosystems, leads to a more boreal state in the Arctic Ocean, manifested by an increasing number of subarctic taxa (reviewed in Polyakov et al. 2020 and in Csapó et al. 2021), which has been referred to as the Atlantification of the Arctic (Polyakov et al. 2020). The large, northward advective supply of allochthonous organisms along latitudinal gradients (Basedow et al. 2018) occurs mostly along continental slopes (Bluhm et al. 2020) and has accelerated in recent years (Oziel et al. 2020). Such inflow homogenizes pelagic ecosystems, providing further support for the existence of a contiguous Atlantic Arctic Domain (Wassmann et al. 2015).

The short life cycle and poikilothermic nature render pelagic fauna particularly vulnerable to environmental change (Hays et al. 2005; Richardson 2008). Increased proportions of boreal species in the Arctic plankton (Weydmann et al. 2014), their northward range extension with simultaneous retreat of the polar taxa (Berge et al. 2005; Grabowski et al. 2019), and successful reproductive events further north (Kraft et al. 2013; Weydmann et al. 2018) were all documented within the sub-Arctic community of the primary consumers. Adverse effects of even such seemingly subtle changes, could lead to a cascading

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Additional Supporting Information may be found in the online version of this article.

Author Contribution Statement: MKM and AWZ conceived the study. MKM conducted laboratory and statistical analyses and wrote the first draft of manuscript. AWZ supervised the project and participated in data analysis. MM led the analysis of hydrological data. SK coordinated field expeditions and curated sample collection. MKM, MM, AWZ acquired funding for this work. All authors commented on and edited the manuscript and approved its final version.

bottom-up restructuring of the polar food web, affecting even higher trophic levels (Kwaśniewski et al. 2012; Stempniewicz et al. 2021).

The recent advent of jellyfish research stems not only from recognizing their role in monitoring water mass distribution and climate change (Hays et al. 2005; Mańko et al. 2015) but also from their increasingly apparent role in pelagic food webs (Choy et al. 2017). *Aglantha digitale* (O. F. Müller, 1776) is a versatile predator with an ontogenetically dependent diet (Pagès et al. 1996). The smallest specimens are known to prey upon protists, rendering population outbreaks potentially algal-bloom dependent (Williams and Conway 1981). Larger *A. digitale* feed preferentially on various life cycle stages of copepods but also on other zooplankters (Pagès et al. 1996), thus explaining their susceptibility to shifts in planktonic community structure. In addition, *A. digitale* was found to constitute a prey of choice for some of the common temperate fish species (Atlantic mackerel, Runge et al. 1987; Chum salmon, Tsuruta 1963); hence, its abundance may also shape the distribution pattern of species in the higher trophic levels.

A. digitale is often perceived as one of the most abundant hydrozoans in the Northern Hemisphere, classified interchangeably as either circumpolar or boreal (Kramp 1959; Kosobokova and Hirche 2000). Clearly, *A. digitale* has a widespread distribution in the Arctic Ocean (Pacific Arctic—Ershova et al. 2015; central Arctic Ocean—Kosobokova et al. 2011, Kara Sea—Dvoretsky and Dvoretsky 2017, and East Siberian Sea—Ershova and Kosobokova 2019), with an abundance typically higher both in waters of Atlantic origin (Mańko et al. 2020) and further south. The lower depth boundary of the Atlantic layer limits the vertical distribution of *A. digitale* in the central Arctic Ocean (Kosobokova and Hirche 2000) but not so much in the Fram Strait (Mańko et al. 2020). The timing of the *A. digitale* life cycle varies by location, most likely due to the differences in water temperature (*see* Pertsova et al. 2006; Takahashi and Ikeda 2006). Populations inhabiting the Arctic and sub-Arctic are believed to reproduce once a year but may differ in the temporal onset of reproduction and most likely in size at maturity (Williams and Conway 1981; Pertsova et al. 2006; Takahashi and Ikeda 2006). Populations with more generations per year, smaller size at maturity and earlier start of reproduction were found within warmer, temperate basins (Russell 1938) and neritic embayments (summarized in Shiota et al. 2012). Whether such a temperate and reproducing more often, population of *A. digitale* has already reached the European Arctic, remains unknown.

Any conclusions on *A. digitale* phenology are hampered by the overwhelming lack of jellyfish data in planktonic time series (discussed in Long et al. 2021), attributable mostly to the historical assumption of the low trophic importance of gelatinous animals (Lüskow et al. 2021) that led to the identification of only more abundant, hard-bodied taxa from samples. Unfortunately, even when *A. digitale* was included in polar zooplankton time series, its population structure was unassessed (Weydmann et al. 2014; Carstensen et al. 2019), or routine sampling was too shallow (Mańko et al. 2020), which hampered having a thorough understanding of the fate of *A. digitale* in the European Arctic.

The increasingly boreal state of a warming European Arctic may offer favorable conditions for *A. digitale* population development, thus further reshaping local ecosystems, although the lack of long time series, with an appropriate taxonomic and population-level resolution of gelatinous zooplankton data, hinders any conclusions on their fate in the Arctic. We therefore took advantage of the extant zooplankton time series samples from the European Arctic (Weydmann et al. 2014), covering the upper 200 m of the water column, and counted and measured all *A. digitale* specimens found in the samples. As a result, we compiled a unique 12-yr-long, demographically resolved abundance time series of *A. digitale* that we used to test our hypotheses: (1) that continued Atlantification may promote earlier onset of *A. digitale* reproduction in the European Arctic and (2) that the *A. digitale* population north of Svalbard is advected there from a source population further south.

Materials and methods

Arctic-Atlantic gateway

Atlantic water flows into the Nordic Seas with the North Atlantic Current through the Greenland-Scotland Ridge; then, it continues as the Norwegian Atlantic Current (Orvik and Niiler 2002) and as a two-branched West Spitsbergen Current (Piechura and Walczowski 1995). The eastern branch of the West Spitsbergen Current, a continuation of the along-shelf Norwegian Atlantic Slope Current (Skagseth et al. 2004), transports Atlantic water along the Barents Sea/Svalbard Shelf Break into the Arctic Ocean, while the western branch of the West Spitsbergen Current, the extension of the Norwegian Atlantic Current, transports Atlantic water over the Mohn and Knipovich Ridges, where it recirculates westward and southward (Piechura and Walczowski 1995; Orvik and Niiler 2002). The Fram Strait's complicated topographic structure between 77°N and 77°30′N forces both branches to converge and then to diverge once again (Walczowski et al. 2012).

The two West Spitsbergen Current branches and related hydrological fronts form dynamic boundaries in the region occupied by Atlantic water. There is a large-scale oceanic front in the west (Arctic Front) and a shallow-water, local-scale front in the east (Polar Front). Both fronts separate Atlantic water from the surrounding, much colder, and fresher water masses. The eastern branch is an intense, narrow flow with the core over the 800 m isobath. In this stream, the Atlantic water temperature and salinity reach their maximum values. The western branch flows northward as a wide stream, less concentrated than the eastern branch (Walczowski 2013). Consequently, the phenology and taxonomic composition of zooplankton differ among branches (Weydmann et al. 2014).

The properties of the West Spitsbergen Current undergo considerable seasonal, interannual, and longer-term variability in patterns consistent from the northern North Atlantic to the Fram Strait (Schlichtholz and Goszczko 2006; Beszczynska-Möller et al. 2012). This concerns both branches of the West Spitsbergen Current. The Atlantic water in the western branch of the West Spitsbergen Current is colder and less saline than that in the eastern branch of the West Spitsbergen Current. According to Walczowski (2013), at a latitude of 76°30′N, at 200 m, the mean differences for summers in 1996–2010 equaled 1.75°C for temperature and 0.062 for salinity. The changes in these properties appear in both branches simultaneously, with positive trends and maximum values in 2005 and 2006. Temperature increased by 0.81°C and 1°C per 10 yr, and salinity increased by 0.073 and 0.082 per 10 yr in the eastern and western West Spitsbergen Current branches, respectively. Temperature and salinity differences are caused by various origins and pathways of Atlantic water. The western branch is fed by Atlantic water inflows between Iceland and the Faroes, which is less saline and ~2°C colder than the Atlantic water flows between the Faroes and Shetland Islands that feed the eastern branch (Holliday et al. 2008; Walczowski 2013).

Sample collection

Sampling was undertaken at the end of June and beginning of July every year from 2003 until 2014 as a part of the Arctic Research Expedition (AREX) research program—the annual monitoring of the European Arctic conducted by the Institute of Oceanology of the Polish Academy of Sciences on board their flag ship R/V *Oceania*. Each year, the same sampling sites, falling along the eastern and western branches of the West Spitsbergen Current (Fig. 1), were visited within a 2-week time window. However, the challenging environment of the Arctic (e.g., rough sea and presence of sea ice) has prohibited systematic access to the investigated area; thus, not all planned sampling sites were visited every year. Therefore, only data from those sites that were visited at least five times during the study period were retained for analysis.

At each site, zooplankton sampling followed the standard protocol of the Institute of Oceanology of the Polish Academy of Sciences (Weydmann et al. 2014). First, the Sea-Bird Electronics CTD (SBE 911plus) system with temperature and conductivity sensors was deployed down to the seabed to map the extent of water masses of different origins. Then, to obtain zooplankton samples, the WP-2 net fitted with 180-μm filtering gauze was towed vertically across three strata spanning from the bottom to the surface or from the upper 200 m at the sites deeper than 200 m. The extent of strata matched local hydrography (i.e., surface waters layer, intermediate layer, and deep layer), but due to the large spatial and depth variability over the study area, data were integrated to a 0–200 m stratum (or 0 m—maximal depth sampled, at the shallower sites or when the deepest sample was unavailable). Upon collection, samples were fixed with a borax-buffered 4% solution of formaldehyde in seawater and stored until taxonomic analysis.

Data collection and handling

In each sample, all specimens of *A. digitale* were enumerated, and their bell height was measured down to the nearest 0.01 mm under a NIKON SMZ800 stereomicroscope with a calibrated ocular micrometer. Their abundance was expressed as individuals per cubic meter (ind. m^{-3}). The size distribution of *A. digitale* in any given sample was expressed as the species abundance in 1 mm size classes (referred to as A1, …, A12). Due to postfixation tissue shrinkage of jellyfish, the morphometric measurements taken had an approximate nature and did not allow for biomass calculation (De Lafontaine and Leggett 1989). In addition, lengthy storage of specimens in formaldehyde resulted in damage or even loss of gonads, thus precluding direct assessment of specimen maturity.

Environmental data linked with each sample contained the following variables: year of sampling (Year; 2003–2014), site identifier (ID; A to M), branch of the West Spitsbergen Current (Branch; eastern or western), latitudinal classification (Group; Low—sites A, B, and C; Mid—sites D, E, and F; and High—sites G, H, I, J, K, L, and M), depth of the sea at the site (Depth; [m]), mean depth of sampled stratum (Mean depth; [m]), mean temperature averaged over 0–200 m (Temperature; [°C]), mean salinity averaged over 0–200 m (Salinity; [PSU]), sampling latitude (Latitude; [DD]), sampling date (Julian Day; 1–365/6). Branch classification was based on hydrological analysis of temperature and salinity profiles according to the thresholds published in Carstensen et al. (2019), whereas latitudinal grouping (Group) corresponded to the latitudinal proximity of sites and represented the northward cooling and decrease in salinity of the West Spitsbergen Current (Walczowski et al. 2012). The arbitrarily assigned latitudinal thresholds for this grouping were: Low ~ 73.500 N, Mid ~ 75.000 N, and High > 75.000 N.

Data analysis

All maps were drawn with ArcMap 10.7.1, while hydrological analyses were performed in MATLAB (2016). Standard procedures provided by the manufacturer of the SeaBird system (software modules SeaSave and SBEDataProc) were used for collection, processing, and quality control of the hydrographic data. The mean values of temperature and salinity were calculated using CTD profiles taken at each zooplankton sampling site included in this study and the two adjacent sites (for more information on hydrographic measurements taken as part of the AREX program, *see* Walczowski et al. 2017). Data preprocessing and exploratory analyses were run in R (v. 4.0.4) using the *ggplot2* (Wickham 2016), *tidyverse* (Wickham Wickham et al. 2019) and *vegan* (Oksanen et al. 2020) packages. The significance level of all statistical

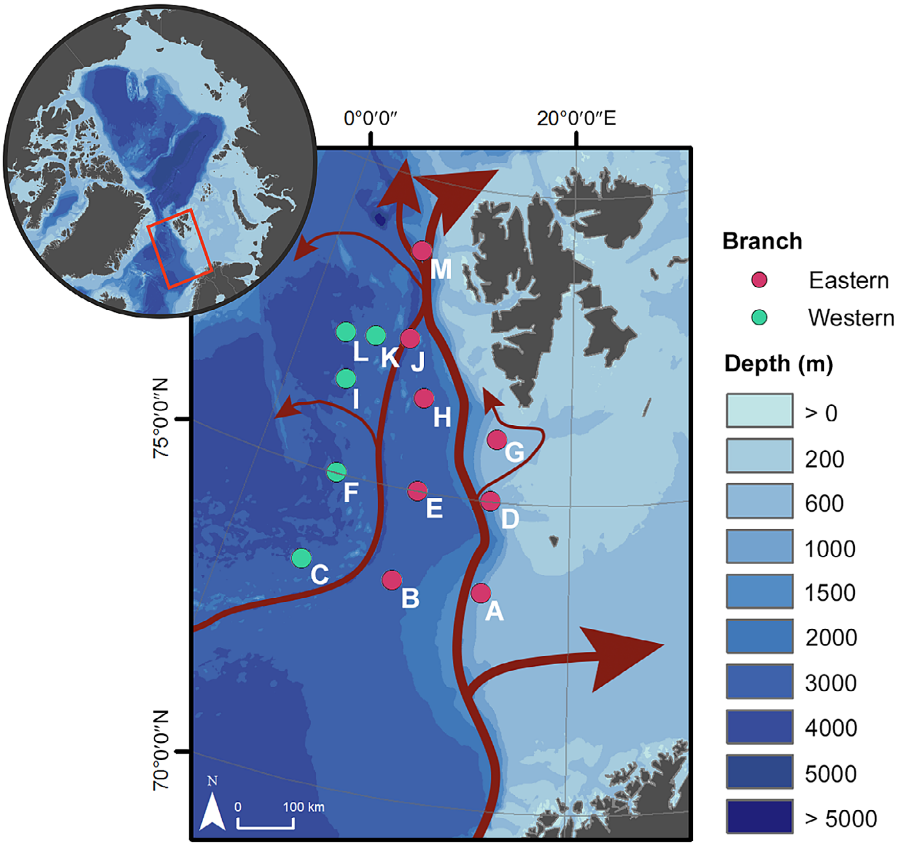

Fig. 1. The area influenced by the two branches of the West Spitsbergen Current, with sampling sites labeled and colored according to their hydrographic (= branch) classification. Bathymetry data were derived from the International Bathymetric Chart of the Arctic Ocean (Jakobsson et al. 2012), while the schematic Atlantic inflow was from Beszczynska-Möller et al. (2012). Smaller map shows the Arctic Ocean while the red rectangle delimits the investigated area.

tests was set at $p \leq 0.05$, and 999 replications were run in each Monte Carlo permutation.

First, the interannual differences in *A. digitale* abundance among West Spitsbergen Current branches and along the northward gradient (factor: Group) were tested separately for the total abundance and species population structure with a series of one-, two- and three-way permutational ANOVA (PERMANOVA) on square root transformed data (either total abundance or Bray–Curtis similarity matrix) with the *adonis* function from the *vegan* package (Oksanen et al. 2020). Only pseudo-*F* and *p*-values are reported in the following text, while full results are available in Supporting Information File S1. Prior to PERMANOVA runs, a series of permutation-based tests of multivariate homogeneity of group dispersion were performed for each of the factors included in the model with *permutest* in *vegan*. This approach allowed us to ensure that the PERMANOVA outcomes resulted from differences in group centroids and not data dispersion within the groups.

Then, the interannual variability and the effects of salinity, temperature, depth, sampling latitude, and sampling date were explored with distance-based linear models (DistLM), which additionally allowed for intercomparison of variation in *A. digitale* population structure explained by these variables. The marginal effects were evaluated separately for each variable, and then the final model was built through the forward selection of variables based on the adjusted R^2 criterion and statistical significance. Then, the whole dataset was analyzed with distance-based redundancy analysis (dbRDA; Legendre and Anderson 1999), which provided a more realistic description of the influence of not only the individual variables but also their interplay on the *A. digitale* population structure. Afterward, the population structure of *A. digitale* was compared among all samples through linkage tree analysis (LINKTREE, Anderson et al. 2008) with a series of similarity profile tests (SIMPROF), which is a discriminant clustering method that allows for constraining population structure by inequalities in significant explanatory variables chosen based on previous analyses. Consequently, the predominant population structure, typical for each significant LINKTREE group, was identified by similarity percentage analysis (SIMPER). This led to a thorough characterization of population structure (SIMPER) of sample groups clustered by a particular environmental setting (LINKTREE + SIMPROF). DistLM, dbRDA and LINKTREE were run in PRIMER 7 with PERMANOVA+ add-on (Anderson et al. 2008).

Finally, to test the main hypothesis of the accelerated reproduction of *A. digitale* in response to the progression of Atlantification, a generalized linear mixed model was built in R using the *glmmTMB* package (Brooks et al. 2017). To warrant ecologically sound reasoning of size-dependent environmental drivers of jellyfish abundance, counts of *A. digitale* were grouped into two representative size classes: small, probably immature specimens (bell height < 5 mm); and large ones (bell height > 5 mm) that could have already been mature, and were probably feeding on a larger, more mobile prey (Costello and Colin 1994; Mańko et al. 2020, and literature therein). A single response variable (counts of jellyfish) was then regressed against a series of predictors. To estimate different responses of small and large specimens, the size class was encoded as a dummy variable and introduced interaction terms with each predictor to our model (size class × predictor; Hilbe 2011).

A series of negative binomial models (Warton 2005) were built that differed in the number of fixed effects and then their performance was compared through the likelihood ratio test (Supporting Information File S1). Each model tested was offset by the log sample volume to deal with the differing sampling effort, included a site-based random effect to account for multiple measures at any given site and the year-based random effect. Time-series analysis should also account for a possible autocorrelation between observations separated by a time interval. However, since the stationarity of presented time series was determined through a visual inspection of the autocorrelation function (ACF) plots (Hyndman and Athanasopoulos 2018), no additional covariance structure had to be encoded within the model. Subsequent model diagnostics were run with the *DHARMA* package (Hartig 2022), the results of which are included in Supporting Information File S1.

The best model found (Supporting Information File S1) described the size class-specific trends in *A. digitale* abundance as a function of water temperature (standardized continuous variable), depth (standardized continuous variable), and geographic location (Latitude; standardized continuous variable). As the link function of the negative binomial model is a log, the estimated coefficients were exponentiated to facilitate their ecological interpretation.

Results

Both temperature and salinity of the upper water column varied between years, with periodical increases and decreases every 2–4 yr (Fig. 2). The warmest period recorded lasted from 2005 to 2007 and coincided with increased salinity. Then, from 2008, another increase in temperature and salinity was observed, although less pronounced in terms of temperature than the previous warm anomaly, which was characterized by a much higher salinity, mostly along the eastern branch of the West Spitsbergen Current. Waters of the eastern branch of the West Spitsbergen Current were persistently warmer and more saline than those further to the west. Temporal changes in water temperature and salinity were comparable along the two branches, with a mean trend of ≈ 0.004 unit increase in salinity every year and a steady decrease in temperature ($\approx -0.01^{\circ}\mathrm{C\ yr^{-1}}$).

When present, *A. digitale* abundance averaged 2 ind. $\mathrm{m^{-3}}$, whereas the highest number recorded was 36 ind. $\mathrm{m^{-3}}$. Since the abundance peak in 2003, the population size of *A. digitale* steadily decreased throughout the study period (Fig. 3), with some elevated mean abundances also observed in 2006 and 2013. Overall, the abundance of *A. digitale* varied significantly between years (PERMANOVA, pseudo-$F = 1.984$, $p = 0.042$, df = 11), with a mean abundance higher prior to 2009 (2.90 ± 5.16 ind. $\mathrm{m^{-3}}$) than after that year (0.67 ± 1.27 ind. $\mathrm{m^{-3}}$). This trend was, however, more intricate, with short periods of year-to-year increases in the mean abundance, most pronounced for 2008–2009 (10.6%) and 2012–2013 (36.7%). The abundances of *A. digitale* differed between the two branches of the West Spitsbergen Current (PERMANOVA, pseudo-$F = 9.805$, $p = 0.003$, df = 1) and were on average 105 times higher within the eastern branch of the West Spitsbergen Current than within the western branch of the West Spitsbergen Current (Fig. 3), with the sole exception of 2011, when the reciprocal pattern was observed with the western branch of the West Spitsbergen Current population 2.4 times the size of that within the eastern branch of the West Spitsbergen Current. Notably, the differences between *A. digitale* population size along the two West Spitsbergen Current branches were more apparent within the 1st half of the study period (2003–2008) than within the 2nd half (2009–2014), with their population being 185 and 39 times more abundant in the eastern branch of the West Spitsbergen Current than in the western branch of the West Spitsbergen Current within these two periods, respectively. Aside from the interbranch abundance pattern, the population size of *A. digitale* was also latitudinally structured (PERMANOVA, pseudo-$F = 3.400$, $p = 0.017$, df = 2), with fewer specimens observed farther north, consistent throughout the years, except for 2006 and 2013, when the highest abundance of this jellyfish was observed in the latitudinal group Mid (Figs. 3, 4). Interestingly, the low abundance of *A. digitale* at the southernmost sites always coincided with the elevated abundance at sites situated further north (both within the Mid and High groups), and vice versa (Figs. 3, 4).

Smaller specimens, with bell heights less than 5 mm, contributed more to the overall abundance of the *A. digitale* population than did the larger, presumably more mature, jellyfish. Their numerical dominance was more pronounced in the eastern branch of the West Spitsbergen Current than in the western branch of the West Spitsbergen Current, leading to significant differences in the overall population structure

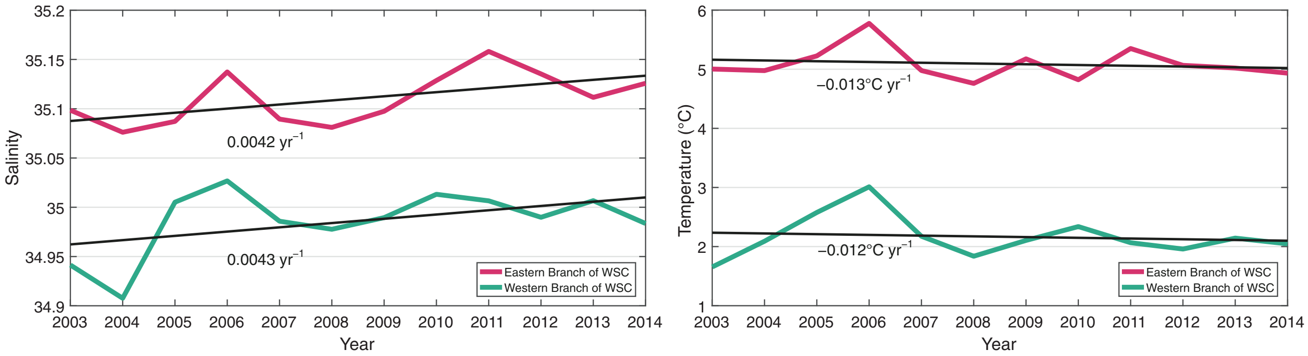

Fig. 2. Temporal (2003–2014) variation in salinity (left) and temperature (°C) (right) of the upper water column (0–200 m) along the two branches of the West Spitsbergen Current with trend lines.

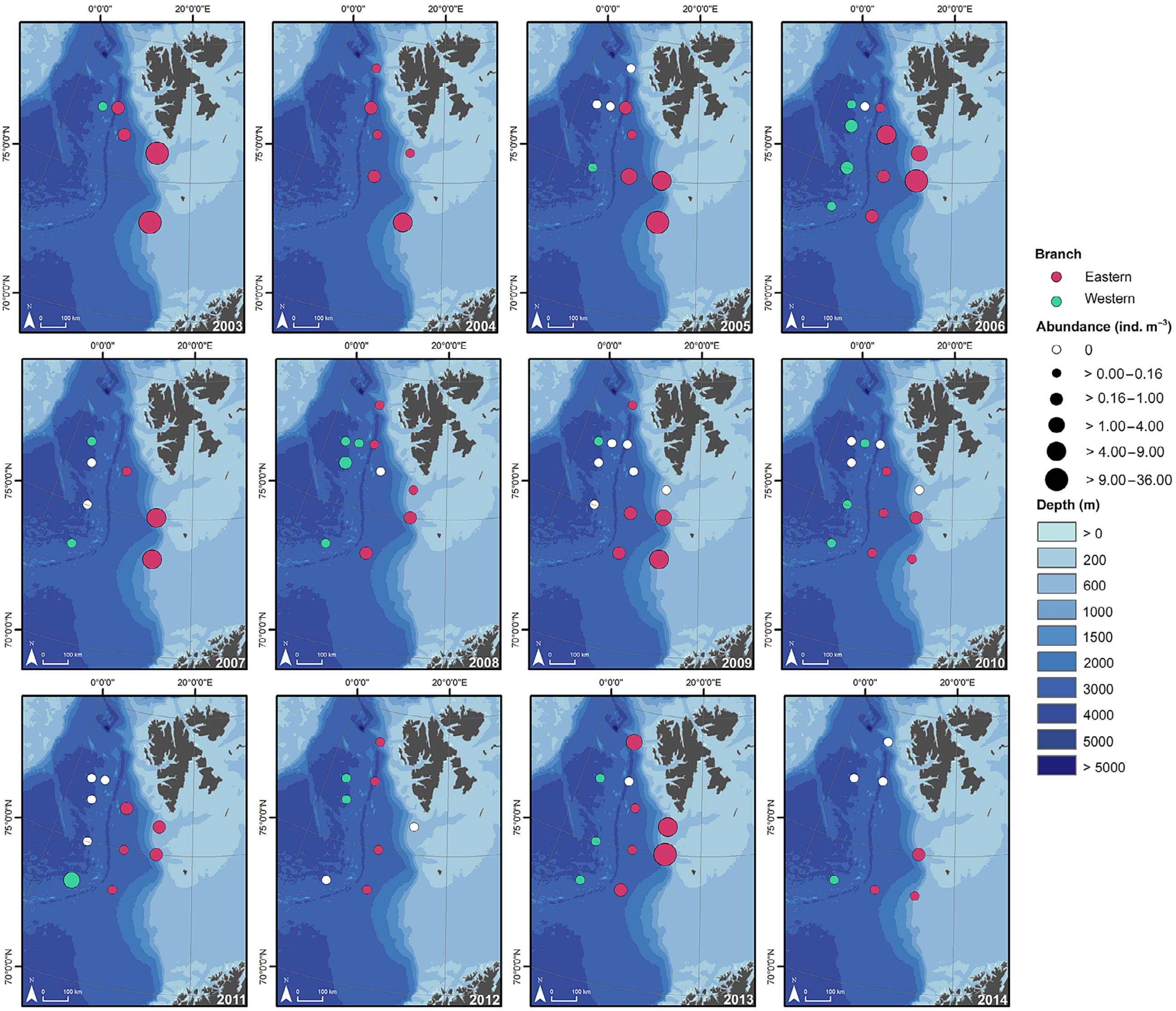

Fig. 3. Distribution of *Aglantha digitale* over the study area from 2003 to 2014. The size of the circles corresponds to the abundance (ind. m^{-3}) and the two branches of the West Spitsbergen Current are color-coded, while the white circles represent sites where no *A. digitale* were found in samples.

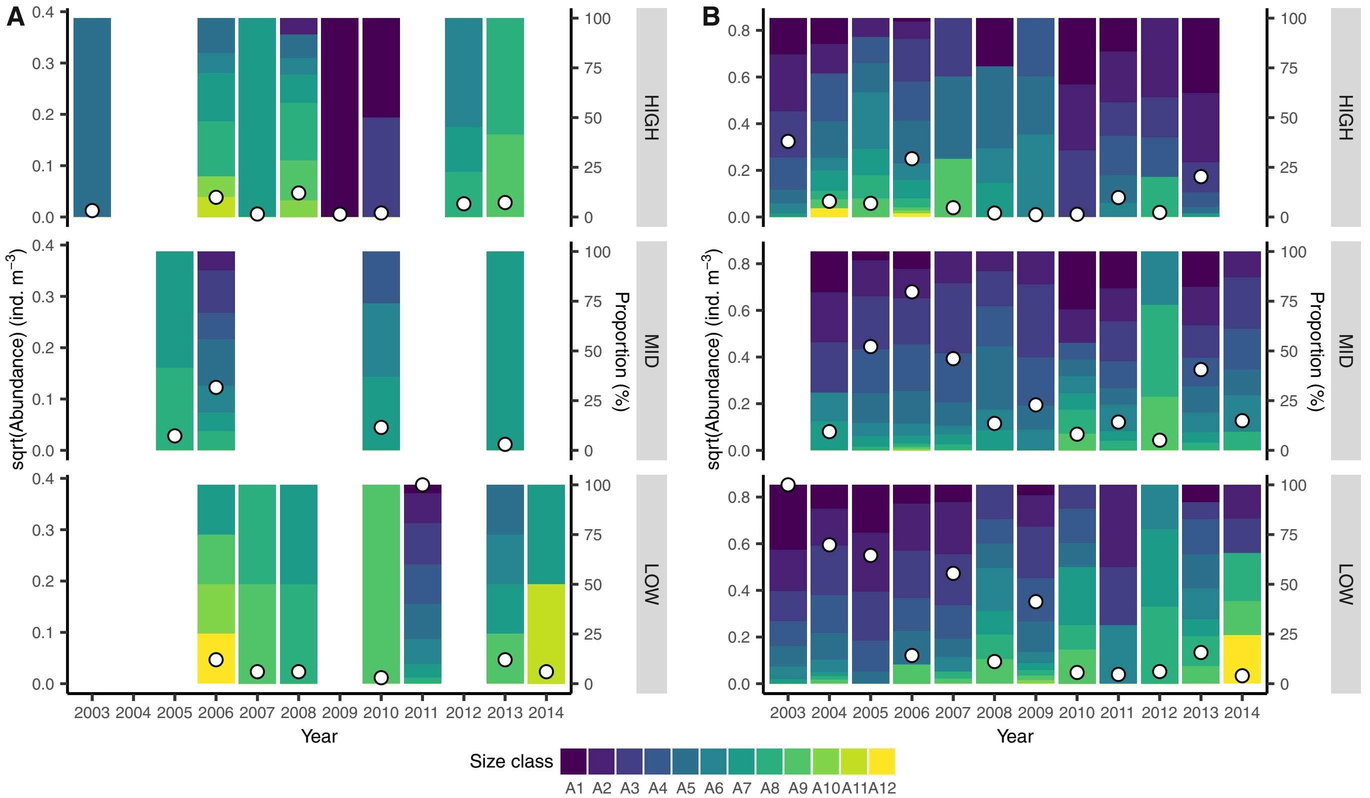

Fig. 4. Interannual changes in population structure (proportional stacked bars; %) and mean abundance (white circles; ind. m^{-3}) of *Aglantha digitale* along the two branches of the West Spitsbergen Current (**A**, western and **B**, eastern) and within three latitudinal groups (Low, Mid, and High).

between these two branches (PERMANOVA, pseudo-$F = 6.538$, $p = 0.001$, df = 1), but also between years (PERMANOVA, pseudo-$F = 1.627$, $p = 0.004$, df = 11). Notably, a clear latitudinal gradient in the *A. digitale* population was also detected (Fig. 4; PERMANOVA, pseudo-$F = 1.858$, $p = 0.046$, df = 2), yet there was no support for either its interannual (two-way PERMANOVA, pseudo-$F = 0.933$, $p = 0.639$, df = 20), or hydrological structuring (two-way PERMANOVA, pseudo-$F = 1.382$, $p = 0.175$, df = 2). Latitudinal structuring of the western branch of the West Spitsbergen Current population of *A. digitale* was difficult to assess due to low sample coverage, with sampling within all three latitudinal groups occurring only in 2006, 2009, and 2013. Based on these limited data, the southernmost *A. digitale* population appeared to be composed of slightly younger specimens compared to the north, apart from 2009 to 2010, when the size difference was more pronounced, with the northernmost population comprising mostly the smallest specimens (Fig. 4). The *A. digitale* population structure proved less elusive within the eastern branch of the West Spitsbergen Current than in the western branch of the West Spitsbergen Current. Until 2009, the majority of *A. digitale* specimens found at the southernmost sites were small, less than 5 mm in bell height, while after that year, this pattern reversed. In 2005–2007, the numerical dominance of the smallest specimens was even more pronounced within the latitudinal group Low, whereas the northernmost population of *A. digitale* was characterized by unprecedented quantities of the largest specimens. Interestingly, only a few small (< 5 mm bell height) specimens were found in the latitudinal group Low or Mid in 2010 and 2012, while not only their proportion but also abundance was much higher at the northernmost sites.

The population structure of *A. digitale* was governed by the intricate pattern of environmental gradients and their interplay (Fig. 5; Table 1). Overall, depth, salinity, latitude, and year explained 21.0% of the variation in the population structure, while the addition of the remaining variables resulted in a statistically insignificant increase (4.3%) of explanatory power in either sequential, marginal or both tests (Table 1). Although temperature explained more variation (marginal effect test: pseudo-$F = 6.106$, variation explained = 7.3%, $p < 0.001$) than did salinity (marginal effect test: pseudo-$F = 4.923$, variation explained = 5.9%, $p < 0.001$), and both were statistically significant, when simultaneously incorporated into the sequential model only the influence of salinity proved statistically significant. Out of all variables tested, the depth-related gradient exerted the strongest influence on species population, explaining 12.2% of the variation observed (Fig. 5; Table 1).

Two-dimensional ordering of the *A. digitale* population structure constrained by the matrix of environmental

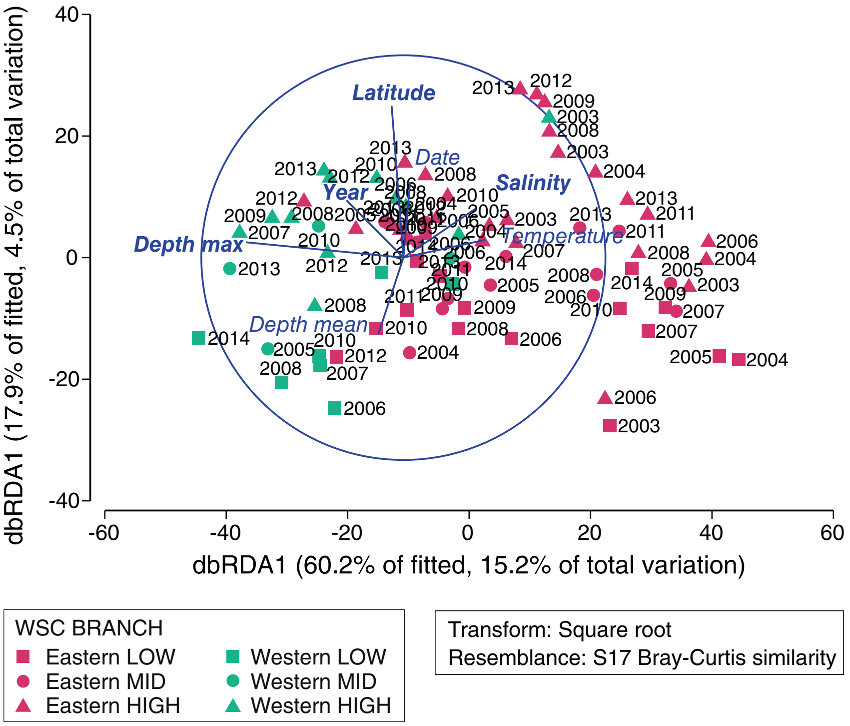

Fig. 5. Environmental gradients affecting similarity of *Aglantha digitale* population structure detected by distance-based redundancy analysis. The effects of factors in bold were statistically significant according to the DistLM model (Table 1).

gradients, revealed clear-cut grouping of samples associated with a particular West Spitsbergen Current branch, with only a few exceptions (Fig. 5; group High in the western branch sample from 2003). The similarity of the population structure among the eastern branch of the West Spitsbergen Current samples was more obviously associated with hydrological characteristics (salinity and temperature), whereas the similarity of the *A. digitale* population within the western branch of the West Spitsbergen Current samples was mostly attributable to the depth gradient. Intriguingly, although relatively impactful latitudinal and salinity-associated gradients of this jellyfish population structure were recovered from the whole dataset, they proved more explanatory for the northernmost sample groupings (Fig. 5).

LINKTREE analysis revealed sharply outlined sample groups characterized by distinctive *A. digitale* population structures (Fig. 6). The oldest population of *A. digitale* (Group VI) was associated with the deepest waters (>2570 m), predominantly from the western branch of the West Spitsbergen Current, with an addition of the High-2012 and Mid-2013 samples originating from the eastern branch of the West Spitsbergen Current. The 2$^{\text{nd}}$ split (Split B) distinguished the population with a low abundance of A1 to A4 and a high proportion of A5 and the largest *A. digitale* (Group I), from Groups II–V, which were characterized by an overall large contribution of A1 to A4 jellyfish (Fig. 6). This split was associated with a temperature threshold < 3.09°C for the Group I and > 3.16°C for the remaining groups. Group I constituted a mixture of the

Table 1. Environmental drivers of *Aglantha digitale* population structure as inferred from DistLM marginal and sequential tests. Variables in bold were statistically significant according to the sequential effect test.

	Marginal test		Sequential test				
Variable	**Pseudo-*F***	***p***	**Adj. R^2**	**SS (trace)**	**Pseudo-*F***	***p***	**Variation explained (%)**
Depth	10.824	0.001	0.111	30,169	10.824	0.001	12.2
Salinity	4.923	0.001	0.136	8825	3.258	0.003	3.6
Latitude	2.547	0.027	0.157	7881	2.985	0.004	3.2
Year	1.944	0.078	0.167	4959	1.900	0.050	2.0
Sampling depth	1.028	0.444	0.176	4583	1.774	0.106	1.9
Temperature	6.106	0.001	0.180	3523	1.371	0.212	1.4
Date	2.215	0.039	0.180	2584	1.006	0.440	1.0

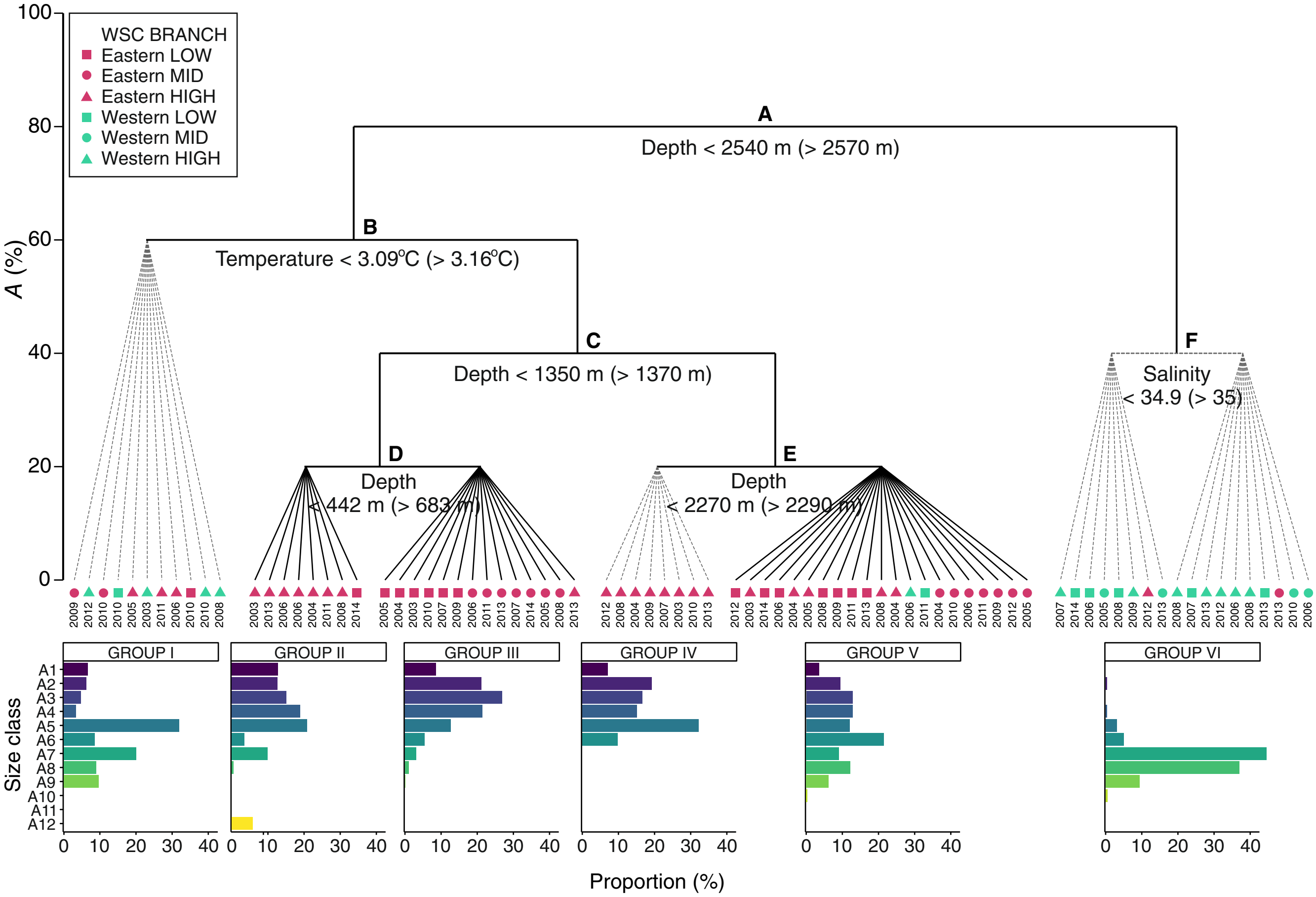

Fig. 6. Binary partitioning of samples based on similarities in *Aglantha digitale* population structure (Groups I–VI) obtained by the six (**A**–**F**) splits, with corresponding thresholds of maximum bottom depth, mean temperature, and salinity, based on LINKTREE analysis. Significant splits (according to SIMPROF tests) are shown with solid lines; thus, note that Group VI consists of all samples remaining after Split F.

eastern branch of the West Spitsbergen Current samples from 2005 to 2006 and 2009 to 2011 and those from the western branch of the West Spitsbergen Current sampled in 2003, 2008, 2010, and 2012. The environmental thresholds partitioning the remaining groups (II–V) were all depth related. The group with the highest proportion of jellyfish with bell heights >9 mm (Group II) was associated with the shallowest sites (<442 m) located farthest to the north (plus the Mid-eastern branch of the West Spitsbergen Current from 2014), whereas Group III, found to be more similar to Group II than to the remaining groups, was distinguished by slightly deeper depths (>683 m). Group V comprised similar proportions of A1–A5 and A6–A9 size classes of *A. digitale* and was characterized by depths in a range of 2290–2540 m and $T > 3.16$°C (Fig. 6).

Size-resolved environmental dependency of *A. digitale* population structure was well described with the constructed generalized linear mixed model (Supporting Information File S1). The model coefficients differed significantly between small (bell height < 5 mm) and large jellyfish (bell height >5 mm) and in general were higher for the smaller jellyfish (for full results, *see* Supporting Information File S1). A significant, jellyfish size-related difference in coefficients was observed along the temperature gradient; a one standard deviation increase in temperature, translated to an approximately 1.7-fold increase in small jellyfish abundance and only to an approximately 1.2-fold increase in large ones. On the other hand, according to the model, the deeper the sampling site was, the lower the expected numbers of jellyfish, with a 0.2-fold decrease in small jellyfish and a smaller, 0.9-fold decrease in large jellyfish per standard deviation increase in depth. The model captured a similar trend of a decreasing jellyfish abundance along the latitudinal gradient, with an approximately 50% decrease in both small and large jellyfish.

Discussion

The population of the holoplanktonic jellyfish, *A. digitale*, underwent tremendous, environmentally mediated alterations within the Atlantic-influenced sector of the European Arctic.

Year after year, the abundance of *A. digitale* decreased in the epipelagic waters (>200 m), more so in the eastern branch of the West Spitsbergen Current than in the western branch of the West Spitsbergen Current, leading to a less concentrated jellyfish population during early summer (June–July). However, the size distribution of jellyfish, here used as a proxy of their population structure, revealed that the gradual decline in abundance reflects a shift in their reproductive cycle over time rather than their overall disappearance from the region.

Previous studies from the European Arctic associated the presence of *A. digitale* with waters of Atlantic origin (*see* Weydmann et al. 2014). Intuitively, the strengthening of Atlantic water inflow to the Arctic should translate into more *A. digitale* farther north, yet both Carstensen et al. (2019) and the present study (Figs. 3, 4) found the opposite trend in this jellyfish distribution. Carstensen et al. (2019) argued that this trend stemmed either from alterations in seasonal reproductive and developmental cycles of *A. digitale* (Williams and Conway 1981), changes in their vertical distribution or some ecological drivers, such as feeding competition with *Eukrohnia hamata* (Möbius, 1875) or predation by *Cyanea capillata* (Linnaeus, 1758) and pelagic fish. In light of recent findings (Mańko et al. 2020) of *A. digitale* exhibiting an ontogenetically structured vertical distribution, with larger specimens restricted to deeper waters and juveniles accumulating near the surface (Pertsova et al. 2006), the most plausible explanation for the decrease in *A. digitale* abundance is their accelerated reproduction in the European Arctic that leads to an earlier descent of larger jellyfish and thus their evasion from epipelagic plankton sampling.

Further support for an accelerated reproduction hypothesis derives from increasing temperature and salinity of the Atlantic waters reaching the European Arctic (Turrell et al. 2003; Beszczynska-Möller et al. 2012). Slight differences between the temperature trends revealed in our study (Fig. 2) and those from other studies (Beszczynska-Möller et al. 2012) result from differing calculation methods and Atlantic water parametrization (Walczowski 2013). To better represent the direct effects of temperature and salinity on *A. digitale* (Table 1; Fig. 5), we used CTD data collected only at zooplankton sampling sites; thus, Fig. 2 recapitulates local environmental variation and not the Fram Strait trends. Nevertheless, the link between temperature and salinity and species reproduction has long been established for a variety of zooplanktonic taxa, including jellyfish (Purcell et al. 1999; Richardson 2008). Higher temperatures within species thermal optima (Beaugrand and Kirby 2018) usually translate into earlier reproduction and accelerated development (reviewed in Rossi et al. 2019). Surprisingly, the warmest years recorded 2005–2007 and 2009 (Fig. 2, except for 2011; Beszczynska-Möller et al. 2012), were all characterized by an unprecedently young population of *A. digitale* within the southernmost range of the investigated area (Fig. 4). Our modeling efforts (Table 1; Supporting Information File S1) have pointed at temperature as one of the key drivers of *A. digitale* population structure, with an increase in jellyfish numbers, that was more pronounced for smaller jellyfish, concomitant with warming of water. Considering accelerated reproduction as a typical response of mid-high latitude taxa to warming (Mackas et al. 2012) and accounting for the geographically variable number of reproductive cycles of *A. digitale* (Pertsova et al. 2006; Takahashi and Ikeda 2006), our data can be interpreted as depicting an additional reproductive event occurring during those warm anomalies at least along the eastern branch of the West Spitsbergen Current. An increasing number of reproductive cycles in response to Atlantic water warming was documented for yet another planktonic species found in the European Arctic—*Calanus finmarchicus* (Gluchowska et al. 2017; Weydmann et al. 2018; Skjoldal et al. 2021), hence adding to the plausibility of our interpretation. Additionally, in support of the 2nd reproductive cycle of *A. digitale* in the European Arctic are our statistical analyses. Figures 5 and 6 collectively depict an obvious similarity in the demographic structure of *A. digitale* populations found across the investigated areas. The relatively younger population from the southern sites during warmer years contrasts with the more mature population found in deeper and colder waters, mostly associated with the western branch of the West Spitsbergen Current (Figs. 5, 6).

The different *A. digitale* population structures of the western branch of the West Spitsbergen Current and the eastern branch of the West Spitsbergen Current (Fig. 3–6) reflect the hydrological differences between both branches (Fig. 2). The western branch of the West Spitsbergen Current transports not only colder and less saline Atlantic water than the eastern branch of the West Spitsbergen Current but also traverses much deeper regions of the Fram Strait (Walczowski 2013). Our models found depth (Table 1; Figs. 5, 6; Supporting Information File S1) to be a prevailing factor shaping the *A. digitale* population size structure, hence adding to the growing body of literature on the drivers of jellyfish distribution (reviewed in Graham et al. 2001). However, as our data lacked vertical resolution, they cannot be used to infer how increasing depth affects the population of *A. digitale*, but they point at the distinct demography of the population associated with the regions with varying depths.

Our analyses also revealed that salinity plays an important role in shaping the *A. digitale* population (Table 1). Although experimental evidence linking increasing salinity and the onset of sexual reproduction in hydrozoans is lacking, salinity alone and its interplay with temperature have been found to affect asexual reproduction and development (e.g., colony growth or strobilation) in many cnidarian representatives (Purcell et al. 1999; Willcox et al. 2007). In light of the salinification of the Eurasian Basin (Polyakov et al. 2020), a further alteration of *A. digitale* reproduction in the European Arctic can thus be expected.

An important point in the discussion is the connectivity of the *A. digitale* populations within European Arctic. Ideally, the existence of a source population that could seed the northern population through northward advection would be validated with molecular assays (Bucklin et al. 2018). Although such an unbiased approach has not yet been applied to the *A. digitale* population, multiple examples of the use of molecular markers to uncover connectivity among polar planktonic species exist (Weydmann et al. 2016; DeHart et al. 2020). The results of past phylogeographic studies of polar zooplankton indicated the lack of clear genetic structure in the Atlantic-Arctic community (DeHart et al. 2020); hence, supported with morphological analyses of the zooplankton advected with the West Spitsbergen Current (Basedow et al. 2018), it seems safe to assume that there is substantial connectivity and specimen exchange along the latitudinal gradient of the West Spitsbergen Current. The absolute dependence of the northern population on juveniles from the south appears unlikely. However, the advective supply of the southern specimens to the northern population seems to be corroborated by the gradual transition from a younger population in the south into a population dominated by larger specimens in the north during warm years and an inverse pattern during cold years (Fig. 4). The reciprocal demographic structure of the *A. digitale* population in the north and south could alternatively suggest their separateness and slightly delayed reproduction onset within the northern population. Nevertheless, considering the current understanding of the contiguity of the Atlantic Arctic Domain (Wassmann et al. 2015) and the physical characteristics of the West Spitsbergen Current flow (Walczowski 2013; Basedow et al. 2018), the advective supply scenario seems more likely.

Irrespective of the driving force of the phenological changes within the *A. digitale* population, the potential consequences of such alterations may be profound. Phenological changes usually occur at a species-specific pace, potentially resulting in predatory–prey mismatches that in turn could alter the whole food web structure (Edwards and Richardson 2004; Richardson 2008). In the already perturbed ecosystems of the European Arctic, even slightly accelerated *A. digitale* reproduction could alter the functioning of the pelagic food web. The ontogenetically variable feeding pattern of *A. digitale* (Pagès et al. 1996) could allow juveniles to economize on the already accelerating onset of the spring algae bloom (Ji et al. 2013), whereas large jellyfish could then prey upon the boreal copepod *C. finmarchicus*, which has also advanced its development in the European Arctic (Weydmann et al. 2018). Similarities in the biogeographic origins of both *A. digitale* and *C. finmarchicus* (Weydmann et al. 2014) may translate into a match in their phenological response to the Atlantification and, as such, may fuel even more pronounced alterations in their reproductive cycles. Interestingly, the accelerated development of *A. digitale* and other zooplankters in the European Arctic may offer an additional explanation for the well-documented northward range expansion of a plethora of planktivorous fish species (Haug et al. 2017), including that of gelativorous mackerel (Astthorsson et al. 2012).

Data availability statement

The datasets generated during the current study are available from the corresponding author on reasonable request.

References

Anderson, M. J., R. N. Gorley, and K. R. Clarke. 2008. PERMANOVA+ for PRIMER: Guide to software and statistical methods. PRIMER-E.

Astthorsson, O. S., H. Valdimarsson, A. Gudmundsdottir, and G. J. Oskarsson. 2012. Climate-related variations in the occurrence and distribution of mackerel (*Scomber scombrus*) in Icelandic waters. ICES J. Mar. Sci. **69**: 1289–1297. doi: 10.1093/icesjms/fss084

Basedow, S. L., A. Sundfjord, W. J. von Appen, E. Halvorsen, S. Kwaśniewski, and M. Reigstad. 2018. Seasonal variation in transport of zooplankton into the Arctic Basin through the Atlantic Gateway. Fram Strait. Front. Mar. Sci. **5**: 194. doi: 10.3389/fmars.2018.00194

Berge, J., G. Johnsen, F. Nilsen, B. Gulliksen, and D. Slagstad. 2005. Ocean temperature oscillations enable reappearance of blue mussels *Mytilus edulis* in Svalbard after a 1000 year absence. Mar. Ecol. Prog. Ser. **303**: 167–175. doi:10.3354/meps303167

Beszczynska-Möller, A., E. Fahrbach, U. Schauer, and E. Hansen. 2012. Variability in Atlantic water temperature and transport at the entrance to the Arctic Ocean, 1997—2010. ICES J. Mar. Sci. **69**: 852–863. doi: 10.1093/icesjms/fss056

Beaugrand, G., and R. R. Kirby. 2018. How do marine pelagic species respond to climate change? Theories and observations. Ann. Rev. Mar. Sci. **10**: 169–197. doi:10.1146/annurev-marine-121916-063304

Bluhm, B. A., and others. 2020. The pan-Arctic continental slope: A narrow band of strong physical gradients affecting pelagic and benthic ecosystems. Front. Mar. Sci. **7**: 544386. doi:10.3389/fmars.2020.544386

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Maechler, and B. M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. **9**: 378–400.

Bucklin, A., K. R. DiVito, I. Smolina, M. Choquet, J. M. Questel, G. Hoarau, and R. J. O'Neill. 2018. Population genomics of marine zooplankton. *In* M. Oleksiak and O. Rajora [eds.], Population genomics: Marine organisms. Population genomics. Springer. doi:10.1007/13836_2017_9

Csapó, H. K., M. Grabowski, and J. M. Węsławski. 2021. Coming home – Boreal ecosystem claims Atlantic sector of the Arctic. Sci. Total Environ. **771**: 144817. doi: 10.1016/j.scitotenv.2020.144817

Carstensen, J., A. Olszewska, and S. Kwaśniewski. 2019. Summer mesozooplankton biomass distribution in the West

Spitsbergen Current (2001–2014). Front. Mar. Sci. **6**: 202. doi:10.3389/fmars.2019.00202

Choy, C. A., S. H. D. Haddock, and B. H. Robison. 2017. Deep pelagic food web structure as revealed by in situ feeding observations. Proc. Roy. Soc. B **284**: 20172116. doi:10.1098/rspb.2017.2116

Costello, J. H., and S. P. Colin. 1994. Morphology, fluid motion and predation by the scyphomedusa *Aurelia aurita*. Mar. Biol. **121**: 327–334. doi: 10.1007/BF00346741

DeHart, H. M., L. Blanco-Bercial, M. Passacantando, J. M. Questel, and A. Bucklin. 2020. Pathways of pelagic connectivity: *Eukrohnia hamata* (Chaetognatha) in the Arctic Ocean. Front. Mar. Sci. **7**: 396. doi:10.3389/fmars.2020.00396

De Lafontaine, Y., and W. C. Leggett. 1989. Changes in size and weight of hydromedusae during formalin preservation. Bull. Mar. Sci. **44**: 1129–1137.

Dvoretsky, V. G., and A. G. Dvoretsky. 2017. Macrozooplankton of the Arctic—The Kara Sea in relation to environmental conditions. Estuar. Coast. Shelf Sci. **188**: 38–55. doi:10.1016/j.ecss.2017.02.008

Edwards, M., and A. J. Richardson. 2004. The impact of climate change on the phenology of the plankton community and trophic mismatch. Nature **430**: 881–884. doi: 10.1038/nature02808

Ershova, E. A., R. R. Hopcroft, K. N. Kosobokova, K. Matsuno, R. J. Nelson, A. Yamaguchi, and L. Eisner. 2015. Long-term changes in summer zooplankton communities of the western Chukchi Sea, 1945–2012. Oceanography **28**: 100–115. doi:10.5670/oceanog.2015.60

Ershova, E. A., and K. N. Kosobokova. 2019. Cross-shelf structure and distribution of mesozooplankton communities in the East-Siberian Sea and the adjacent Arctic Ocean. Polar Biol. **42**: 1353–1367. doi:10.1007/s00300-019-02523-2

Gluchowska, M., P. Dalpadado, A. Beszczynska-Möller, A. Olszewska, R. B. Ingvaldsen, and S. Kwaśniewski. 2017. Interannual zooplankton variability in the main pathways of the Atlantic water flow into the Arctic Ocean (Fram Strait and Barents Sea branches). ICES J. Mar. Sci. **74**: 1921–1936. doi: 10.1093/icesjms.fsx033

Grabowski, M., A. Jabłońska, A. Weydmann-Zwolicka, M. Gantsevich, P. Strelkov, M. Skazina, and J. M. Węsławski. 2019. Contrasting molecular diversity and demography patterns in two intertidal amphipod crustaceans reflect Atlantification of High Arctic. Mar. Biol. **166**: 1–14. doi:10.1007/s00227-019-3603-4

Graham, W. M., F. Pagès, and W. M. Hamner. 2001. A physical context for gelatinous zooplankton aggregations: A review. Hydrobiologia **451**: 199–212. doi: 10.1023/A:1011876004427

Hartig, F. 2022. DHARMa: Residual diagnostics for hierarchical (multi-level mixed) regression models. R package version 0.4.5. Available from http://florianhartig.github.io/DHARMa/

Haug, T., and others. 2017. Future harvest of living resources in the Arctic Ocean north of the Nordic and Barents Seas: A review of possibilities and constraints. Fish. Res. **188**: 38–57. doi:10.1016/j.fishres.2016.12.002

Hays, G. C., A. J. Richardson, and C. Robinson. 2005. Climate change and marine plankton. Trends Ecol. Evol. **20**: 337–344. doi:10.1016/j.tree.2005.03.004

Hilbe, J. M. 2011. Negative binomial regression, 2nd ed. Cambridge Univ. Press. doi:10.1017/CBO9780511973420

Holliday, N. P., and others. 2008. Reversal of the 1960s to 1990s freshening trend in the northeast North Atlantic and Nordic Seas. Geophys. Res. Lett. **35**: L03614. doi: 10.1029/2007GL032675

Hyndman, R. J., and G. Athanasopoulos. 2018. Forecasting: Principles and practice, 2nd ed. OTexts.

IPCC. 2014. Climate change 2014: Synthesis report. *In* R. K. Pachauri, L. A. Meyer, and Core Writing Team [eds.], Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC.

Jakobsson, M., and others. 2012. The International Bathymetric Chart of the Arctic Ocean (IBCAO) version 3.0. Geophys. Res. Lett. **39**: L12609. doi:10.1029/2012GL052219

Ji, R., M. Jin, and Ø. Varpe. 2013. Sea ice phenology and timing of primary production pulses in the Arctic Ocean. Glob. Change Biol. **19**: 734–741. doi: 10.1111/gcb.12074

Kosobokova, K. N., and H. J. Hirche. 2000. Zooplankton distribution across the Lomonosov Ridge, Arctic Ocean: Species inventory, biomass and vertical structure. Deep Sea Res. Part I Oceanogr. Res. Pap. **47**: 2029–2060. doi: 10.1016/S0967-0637(00)00015-7

Kosobokova, K. N., R. R. Hopcroft, and H. -J. Hirche. 2011. Patterns of zooplankton diversity through the depths of the Arctic's central basin. Mar. Biodivers. **41**: 29–50. doi:10.1007/s12526-010-0057-9

Kraft, A., E. M. Nöthing, E. Bauerfeind, D. J. Wildish, G. W. Pohle, U. V. Bathmann, A. Beszczyńska-Möller, and M. Klages. 2013. First evidence of reproductive success in a southern invader indicates possible community shifts among Arctic zooplankton. Mar. Ecol. Prog. Ser. **493**: 291–296. doi:10.3354/meps10507

Kramp, P. L. 1959. The hydromedusae of the Atlantic Ocean and adjacent waters. Dana Rep. **46**: 1–283.

Kwasniewski, S., and others. 2012. Interannual changes in zooplankton on the West Spitsbergen shelf in relation to hydrography and their consequences for the diet of planktivorous seabirds. ICES J. Mar. Sci. **69**: 890–901. doi: 10.1093/icesjms/fss076

Legendre, P., and M. J. Anderson. 1999. Distance-based redundancy analysis: Testing multispecies responses in multifactorial ecological experiments. Ecol. Monogr. **69**: 1–24. doi: 10.1890/0012-9615(1999)068[0001:DBRATM]2.0.CO;2

Long, A. P., D. Haberlin, O. Lyashevksa, D. Brophy, B. O'Hea, C. O'Donnell, R. G. Scarrott, C. Lawton, and T. K. Doyle. 2021. Interannual variability of gelatinous mesozooplankton in a temperate shelf sea: Greater abundance coincides with cooler sea surface temperatures. ICES J. Mar. Sci. **78**: 1372–1385. doi: 10.1093/icesjms/fsab030

Lüskow, F., M. D. Galbraith, B. P. V. Hunt, R. I. Perry, and E. Pakhomov. 2021. Gelatinous and soft-bodied zooplankton in the Northeast Pacific Ocean: Organic, elemental, and energy contents. Mar. Ecol. Prog. Ser. **665**: 19–35. doi: 10.3354/meps13663

Mackas, D. L., P. Pepin, and H. Verheye. 2012. Interannual variability of marine zooplankton and their environments: Within-and between-region comparisons. Prog. Oceanogr. **97-100**: 1–14. doi: 10.1016/j.pocean.2011.11.002

Mańko, M. K., A. A. Panasiuk-Chodnicka, and M. I. Żmijewska. 2015. Pelagic coelenterates in the Atlantic sector of the Arctic Ocean—Species diversity and distribution as water mass indicators. Oceanol. Hydrobiol. Stud. **44**: 466–479. doi:10.1515/ohs-2015-0044

Mańko, M. K., M. Gluchowska, and A. Weydmann-Zwolicka. 2020. Footprints of Atlantification in the vertical distribution and diversity of gelatinous zooplankton in the Fram Strait (Arctic Ocean). Prog. Oceanogr. **189**: 102414. doi: 10.1016/j.pocean.2020.102414

MATLAB. 2016. Version 9.1 (R2016b). The MathWorks Inc..

Oksanen, J., and others. 2020. vegan: Community Ecology Package. R package version 2.5-7.

Orvik, K. A., and P. Niiler. 2002. Major pathways of Atlantic water in the northern North Atlantic and Nordic seas toward Arctic. Geophys. Res. Lett. **29**: 1896. doi: 10.1039/2002/GL015002

Oziel, L., and others. 2020. Faster Atlantic currents drive poleward expansion of temperate phytoplankton in the Arctic Ocean. Nat. Commun. **11**: 1705. doi:10.1038/s41467-020-15485-5

Pagès, F., H. E. González, and S. R. González. 1996. Diet of the gelatinous zooplankton in Hardangerfjord (Norway) and potential predatory impact by *Aglantha digitale* (Trachymedusae). Mar. Ecol. Prog. Ser. **139**: 69–77. doi: 10.3354/meps139069

Pertsova, N. M., K. N. Kosobokova, and A. A. Prudkovsky. 2006. Population size structure, spatial distribution, and life cycle of the hydromedusa *Aglantha digitale* (O.F. Müller, 1766) in the White Sea. Okeanologiya **46**: 249–258. doi:10.1134/S0001437006020093

Piechura, J., and W. Walczowski. 1995. The Arctic front: Structure and dynamics. Oceanologia **37**: 47–73.

Polyakov, I. V., and others. 2020. Borealization of the Arctic Ocean in response to anomalous advection from sub-Arctic seas. Front. Mar. Sci. **7**: 491. doi:10.3389/fmars.2020.00491

Purcell, J. E., J. R. White, D. A. Nemazie, and D. A. Writgh. 1999. Temperature, salinity and food effects on asexual reproduction and abundance of the scyphozoan *Chrysaora quinquecirrha*. Mar. Ecol. Prog. Ser. **180**: 187–196. doi:10.3354/meps180187

Richardson, A. J. 2008. In hot water: Zooplankton and climate change. ICES J. Mar. Sci.s **65**: 279–295. doi: 10.1093/icesjms/fsn028

Rossi, S., C. Gravili, G. Milisenda, M. Bosch-Belmar, D. De Vito, and S. Piraino. 2019. Effects of global warming on reproduction and potential dispersal of Mediterranean cnidarians. Eur. Zool. J. **86**: 255–271. doi:10.1080/24750263.2019.1631893

Runge, J. A., P. Pepin, and W. Silvert. 1987. Feeding behavior of the Atlantic mackerel *Scomber scombrus* on the hydromedusa *Aglantha digitale*. Mar. Biol. **94**: 329–333. doi:10.1007/BF00428238

Russell, F. S. 1938. The Plymouth offshore medusa fauna. J. Mar. Biolog. Assoc. UK **22**: 411–439.

Schlichtholz, P., and I. Goszczko. 2006. Interannual variability of the Atlantic water layer in the West Spitsbergen Current at 76.5° N in summer 1991–2003. Deep Sea Res. Part I Oceanogr. Res. Pap. **53**: 608–626. doi: 10.1016/j.dswr.2006.01.001

Shiota, T., A. Yamaguchi, R. Saito, and I. Imai. 2012. Geographical variations in abundance and body size of the hydromedusa *Aglantha digitale* in the northern North Pacific and its adjacent seas. Bull. Fish. Sci. Hokkaido Univ. **62**: 63–69.

Skagseth, Ø., K. A. Orvik, and T. Furevik. 2004. Coherent variability of the Norwegian Atlantic Slope Current derived from TOPEX/ERS altimeter data. Geophys. Res. Lett. **31**: L14304. doi:10.1029/2004gl020057

Skjoldal, H. R., J. M. Aarflot, E. Bagøien, Ø. Skagseth, J. Rønning, and V. S. Lien. 2021. Seasonal and interannual variability in abundance and population development of *Calanus finmarchicus* at the western entrance to the Barents Sea, 1995–2019. Prog. Oceanogr. **195**: 102574. doi:10.1016/j.pocean.2021.102574

Stempniewicz, L., and others. 2021. Advection of Atlantic water masses influences seabird community foraging in a high-Arctic fjord. Prog. Oceanogr. **193**: 102549. doi: 10.1016/j.pocean.2021.102549

Takahashi, D., and T. Ikeda. 2006. Abundance, vertical distribution and life cycle patterns of the hydromedusa *Aglantha digitale* in the Oyashio region, western subarctic Pacific. Plankton Benthos Res. **1**: 91–96. doi:10.3800/pbr.1.91

Tsuruta, A. 1963. Distribution of plankton and its characteristics in the oceanic fishing grounds with special reference to their relation to fishery. J. Shimonoseki Coll. Fish. **12**: 13–214.

Turrell, W. R., B. Hansen, S. Hughes, and S. Østerhus. 2003. Hydrographic variability during the decade of the 1990s in the Northeast Atlantic and southern Norwegian Sea. ICES Mar. Sci. Symp. **219**: 111–120.

Walczowski, W. 2013. Frontal structures in the West Spitsbergen Current margins. Ocean Sci. **9**: 957–975. doi: 10.5194/os-9-957-2013

Walczowski, W., J. Piechura, I. Goszczko, and P. Wieczorek. 2012. Changes in Atlantic water properties: An important factor in the European Arctic marine climate. ICES J. Mar. Sci. **69**: 864–869. doi: 10.1093/icesjms/fss068

Walczowski, W., A. Beszczyńska-Möller, P. Wieczorek, M. Merchel, and A. Grynczel. 2017. Oceanographic observations in the Nordic Sea and Fram Strait in 2016 under the IOPAN long-term monitoring program AREX. Oceanologia **59**: 187–194. doi: 10.1016/j.oceano.2016.12.003

Warton, D. I. 2005. Many zeros does not mean zero inflation: Comparing the goodness-of-fit of parametric models to multivariate abundance data. Environ. **16**: 275–289. doi:10.1002/env.702

Wassmann, P., and others. 2015. The contiguous domains of Arctic Ocean advection: Trails of life and death. Prog. Oceanogr. **139**: 42–65. doi:10.1016/j.pocean.2015.06.011

Weydmann, A., N. C. Coelho, E. A. Serrao, A. Burzyñski, and G. A. Pearson. 2016. Pan-Arctic population of the keystone copepod Calanus glacialis. Polar Biol. **39**: 2311–2318. doi:10.1007/s00300-016-1898-x

Weydmann, A., J. Carstensen, I. Goszczko, K. Dmoch, A. Olszewska, and S. Kwaśniewski. 2014. Shift towards the dominance of boreal species in the Arctic: Inter-annual and spatial zooplankton variability in the West Spitsbergen Current. Mar. Ecol. Prog. Ser. **501**: 41–52. doi:10.3354/meps10694

Weydmann, A., W. Walczowski, J. Carstensen, and S. Kwaśniewski. 2018. Warming of subarctic waters accelerates development of a key marine zooplankton *Calanus finmarchicus*. Glob. Change Biol. **24**: 172–183. doi:10.1111/gcb.13864

Wickham, H. 2016. ggplot2: Elegant graphics for data analysis. Springer-Verlag.

Wickham, H., and others. 2019. Welcome to the tidyverse. J. Open Sour. Softw. **4**: 1686. doi:10.21105/joss.01686

Willcox, S., N. A. Moltschaniwskyj, and C. Crawford. 2007. Asexual reproduction in scyphistomae of *Aurelia* sp.: Effects of temperature and salinity in an experimental study. J. Exp. Mar. Biol. Ecol. **353**: 107–114. doi:10.1016/j.jembe.2007.09.006

Williams, R., and D. V. P. Conway. 1981. Vertical distribution and seasonal abundance of *Aglantha digitale* (O.F. Müller) (Coelenterata: Trachymedusae) and other planktonic coelenterates in the Northeast Atlantic Ocean. J. Plankton Res. **3**: 633–643. doi:10.1093/plankt/3.4.633

Acknowledgments

Present authors wish to express their gratitude to the past and present crew members of R/V *Oceania* and participants of all AREX expeditions without whom this study would have not been possible. Work of Maciej K. Mańko was financed by the Polish Ministry of Science and Higher Education through a Diamond Grant program (no. DI2014 020344). This study was supported by the National Science Centre, Poland with the DWINS Project (2016/21/N/ST10/02920) awarded to Małgorzata Merchel. The contribution of Agata Weydmann-Zwolicka was supported by the grant “HIDEA—Hidden diversity of plankton in the European Arctic” no. 2017/27/B/NZ8/01056 from the National Science Centre, Poland.

Conflict of Interest

None declared.

Submitted 21 August 2021
Revised 25 February 2022
Accepted 13 May 2022

Associate editor: Thomas Kiørboe

Chapter 10. 1. Supplementary files

This document consists of the following parts: 1) results of PERMANOVA analyses 2) results of the forward selection of model using likelihood ratio test, 3) diagnostics of the final generalized linear mixed model, 4) summary of the model results (model coefficients).

1) PERMANOVA

Tab. S1. Full results of PERMANOVA for differences in *Aglantha digitale* abundance (**A.**) and population structure (**B.**) between years, latitudinal groups, the West Spitsbergen Currents branches, and their combinations.

A.	**Abundance of *Aglantha digitale***						
	Df	**Sums of squares**	**MS**	**F.model**	**R^2**	**Pr (>F)**	**Significance**
Year	11	2.294	0.209	1.984	0.212	0.042	*
Group	2	0.714	0.357	3.400	0.066	0.017	*
Branch	1	1.030	1.030	9.805	0.095	0.003	**
Year × Group	20	2.110	0.105	1.004	0.195	0.477	
Year × Branch	10	1.378	0.138	1.311	0.127	0.215	
Group × Branch	2	0.161	0.080	0.764	0.015	0.532	
Year × Group × Branch	6	0.308	0.051	0.489	0.028	0.896	
Residuals	27	2.837	0.105		0.262		
Total	79	10.832			1.000		

B.	***Aglantha digitale* population structure**						
	Df	**Sums of squares**	**MS**	**F.model**	**R^2**	**Pr (>F)**	**Significance**
Year	11	4.665	0.424	1.627	0.188	0.004	**
Group	2	0.969	0.484	1.858	0.039	0.046	*
Branch	1	1.705	1.705	6.538	0.069	0.001	***
Year × Group	20	4.867	0.243	0.933	0.197	0.639	
Year × Branch	10	3.385	0.338	1.298	0.137	0.085	
Group × Branch	2	0.721	0.360	1.382	0.029	0.175	
Year × Group × Branch	6	1.407	0.234	0.899	0.057	0.635	
Residuals	27	7.040	0.261		0.284		
Total	79	24.757			1.000		

2) Model selection

For a detailed description of the predictors used in the model see the Materials and methods section of the paper. In short, abundance of jellyfish (counts) was split between small (bell height < 5 mm) and large (bell height > 5 mm) specimens, and the size class was then encoded as a dummy variable (*Size*) with a reference level set to large specimens. Abundance of jellyfish was then modelled using a series of predictors, which included: *Latitude* (standardized continuous variable), *Depth* (standardized continuous variable), *Salinity* (standardized continuous variable) and *Temperature* (standardized continuous variable). Predictors were added to the model sequentially, in the order that followed theoretical expectations of their importance in structuring *A. digitale* abundance and population structure. Additionally, all models included: an *offset* (log volume of sample), and two random effects, sampling site-based RE_{site} and year-based RE_{year}. In order to estimate different responses of small and large jellyfish to a given predictor, models included interaction terms between each predictor and the variable *Size*. Obtained coefficients were interpreted followingly: coefficients associated with each predictor pertained to large jellyfish, except for the coefficient for the dummy variable *Size* that was associated with small jellyfish. Then, in order to calculate model coefficients for small jellyfish, those predictor-associated coefficients were added to the coefficient of the interaction of a given predictor and the dummy variable. Lastly, since the chosen model was a negative binomial generalized linear mixed model, all coefficients were exponentiated to facilitate their interpretation.

The following models were tested:

Model1: Abundance ~	Size + Temperature + (Size × Temperature) + RE_{site} + RE_{year} + offset
Model2: Abundance ~	Size + Temperature + (Size × Temperature) + Salinity + (Size × Salinity) + RE_{site} + RE_{year} + offset
Model3: Abundance ~	Size + Temperature + (Size × Temperature) + Depth + (Size × Depth) + RE_{site} + RE_{year} + offset
Model4: Abundance ~	Size + Temperature + (Size × Temperature) + Depth + (Size × Depth) + Latitude + (Size × Latitude) + RE_{site} + RE_{year} + offset

Statistically significant improvement of the model performance was found with increasing model complexity, except for addition of Salinity (Model2) that was found to be insignificant. Thus the final model (Model4) included the following predictors: Temperature, Depth and Latitude. Exact results of the model comparison through the likelihood ratio test are following:

Model2 (AIC = 1216.2) against Model1 (AIC = 1214.1); $\chi^2 = 1.924$, df = 2, p = 0.382
Model3 (AIC = 1169.9) against Model1 (AIC = 1214.1); $\chi^2 = 48.218$, df = 2, p < 0.001
Model4 (AIC = 1163.7) against Model3 (AIC = 1169.9); $\chi^2 = 10.171$, df = 2, p = 0.006

3) Final model diagnostics

Model diagnostics was run using *DHARMA* package (Hartig 2022) in R (v. 4.0.4), following the authors’ guidelines (Fig. S1).

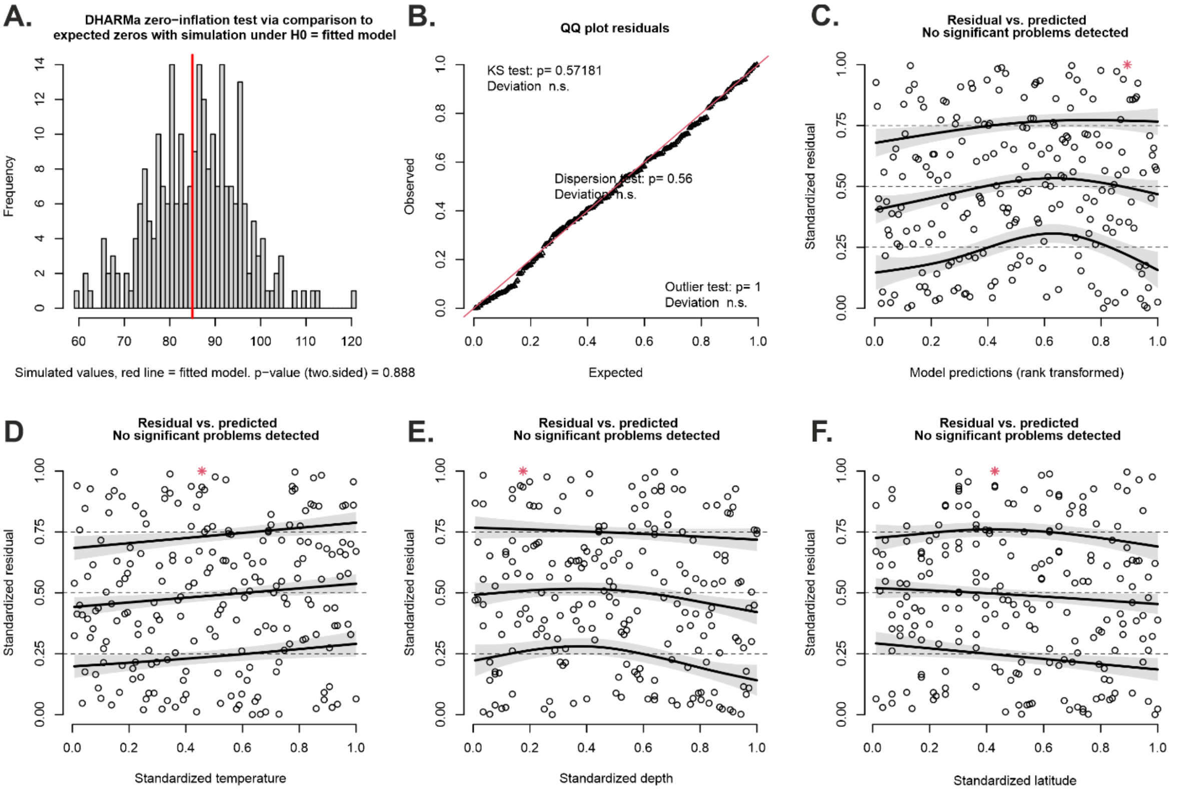

Fig. S1. Model diagnostics. **A.** Frequency of observed zeros against expected zeros with overlayed *p*-value of the test of evenness of these two frequencies. **B.** QQ-plot of the observed against expected values with overlayed results of tests for uniformity (KS test; H0 overall distribution conforms to the expectations), dispersion (Dispersion; H0 observed dispersion equals simulated dispersion), and outliers (Outlier; H0 number of observed outliers equals the number of expected outliers). **C.-F.** Scaled residuals against model predictions with quantile regressions at 0.25, 0.50, 0.75 quantiles and with outliers marked with red stars, separately given for the full model (**C.**), and particular predictors: standardized temperature (**D.**), depth (**E.**), and latitude (**F.**). Note that plot titles and axis labels have been adjusted in graphical software.

4) Summary of model results

Tab. S2. Exponentiated coefficients of the Model4, given separately for small and large jellyfish.

	Large jellyfish (bell height > 5 mm)	**Small jellyfish** (bell height < 5 mm)
	Exponentiated coefficient	*Exponentiated coefficient*
Intercept	0.047	
Size		3.352
Temperature	1.233	1.657
Depth	0.902	0.175
Latitude	0.458	0.520

References

1. Hartig, F. 2022. DHARMa: Residual diagnostics for hierarchical (multi-level mixed) regression models. R package version 0.4.5. http://florianhartig.github.io/DHARMa/
2. Hilbe, J. M. 2011. Negative Binomial Regression (second edition). Cambridge University Press. doi: 10.1017/CBO9780511973420

Chapter 10. 2. Author contribution statement

We hereby confirm, that the specific contributions to the publication:

Mańko M. K., Merchel M., Kwaśniewski S., Weydmann-Zwolicka A. 2022. Atlantification alters the reproduction of jellyfish *Aglantha digitale* in the European Arctic. Limnology and Oceanography. doi: 10.1002/lno.12170

were as follows:

Mańko Maciej Karol – 70%

conceptualization and design of the study, laboratory work, statistical analyses, preparation of figures 1, 3, 4, 6 and coordination of other figure design (Fig. 2, and 5), writing of the first draft of the manuscript, revision and editing, funding acquisition, corresponding author

Merchel Małgorzata – 5%

analysis of hydrological data, participation in writing of the subsection *Arctic-Atlantic gateway* of the *Materials and Methods* section, figure preparation (Fig. 2), revision and commenting on the first draft, funding acquisition

Kwaśniewski Sławomir – 5%

field work coordination, curation of sample collection, revision and commenting on the first draft

Weydmann-Zwolicka Agata – 20%

conceptualization and design of the study, supervision, participation in the statistical analysis, figure preparation (Fig. 5, and 6), revision and commenting on the first draft, funding acquisition

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Chapter 11. Acknowledgements

First and foremost, I want to thank my supervisor, **Agata Weydmann-Zwolicka** for all the time that she devoted to this project, but also for guiding my career development. It would have not been possible to finish either of the papers nor the thesis without her guidance, expertise, patience but also willingness to help with the last minute corrections.

Special thanks are also due to my coauthors **Gosia, Marta** and **Sławek**, who have all contributed significantly to this work, and were always there, whenever I needed some more help with the data. Sławek deserves additional words of gratitude for our long-lasting collaboration, which has started already during writing the Diamond Grant proposal, has continued over all these years, and will hopefully lead to exciting new projects in the future!

This work was made possible because of the hard work and commitment of the **crew members** of the R/V *Oceania* and other participants of the AREX expeditions, who have spent months in the Arctic sampling zooplankton. Special thanks are also due to **Emilia Trudnowska**, who together with Marta led the mesopelagic sampling of the Fram Strait in 2012, and to my **colleagues** at the Division of Marine Plankton Research and at other units of the Faculty of Oceanography and Geography who have made this journey a great experience.

Last but not least, I want to thank **Olga,** my **Family** and **Friends**, not only for their undying support, but also for being understanding about my late hours of work, absence at many important events, and all those long-term leaves. Thank you!

Chapter 12. Funding

This work was primarily financed by:

Diamond Grant DI2014 020344

awarded to Maciej Karol Mańko by the Polish Ministry of Education and Science

and benefited from additional funding from:

- National Science Centre in Poland
    - grant no. 2017/27/B/NZ8/01056, *HIDEA - Hidden diversity of plankton in the European Arctic*, awarded to Agata Weydmann-Zwolicka
    - grant no. 2016/21/N/ST10/02920, *DWINS*, awarded to Małgorzata Merchel
    - grant no. 2017/25/B/NZ8/01100, *Tax4Fun*, awarded to Sławomir Kwaśniewski
- Polish Ministry of Education and Science
    - grant no. W37/Svalbard/2012, *KongHau_ZOOM*, awarded to the Institute of Oceanology of the Polish Academy of Sciences
    - Outstanding Young Scientist Scholarship, awarded to Marta Głuchowska
- University of Gdańsk
    - grant no. 538-6250-B104-18, Research Projects for PhD students and early career scientists, awarded to Maciej Karol Mańko

Chapter 13. Academic Curriculum Vitae

Academic career

2019 – present	University of Gdańsk, research-teaching assistant
2016 – present	University of Gdańsk, graduate school
2014 – 2016	University of Gdańsk, Master degree program
2011 – 2014	University of Gdańsk, Bachelor degree program

Published works

1. **Mańko M.K.**, Merchel M., Kwaśniewski S., Weydmann-Zwolicka A. 2022, Oceanic fronts shape biodiversity of gelatinous zooplankton in the European Arctic. *Frontiers in Marine Science* 9: 941025 (IF: 4.912, ME&S points: 100)
2. **Mańko M.K.**, Merchel M., Kwaśniewski S., Weydmann-Zwolicka A. 2022, Atlantification alters the reproduction of jellyfish *Aglantha digitale* in the European Arctic. *Limnology and Oceanography* (IF: 4.745, ME&S points: 140)
3. **Mańko M.K.**, Głuchowska M., Weydmann-Zwolicka A. 2020, Footprints of Atlantification in the vertical distribution and diversity of gelatinous zooplankton in the Fram Strait (Arctic Ocean). *Progress in Oceanography* 189: 102414 (IF: 4.060, ME&S points: 140)
4. Błaszczyk A., Panasiuk A., **Mańko M.** 2020, Plankton nets [In:] Szymczak E. (ed.) Introduction to the interdisciplinary research in the Baltic Sea, ISBN 978-83-945891-1-0. *In Polish*
5. Weydmann-Zwolicka A., Panasiuk A., **Mańko M.** 2020, Baltic zooplankton – sampling and conservation methods [In:] Szymczak E. (ed.) Introduction to the interdisciplinary research in the Baltic Sea, ISBN 978-83-945891-1-0. *In Polish*
6. Błaszczyk A., **Mańko M.**, Panasiuk A. 2020, Plankton nets [In:] Szymczak E. (ed.) Advanced methods of the interdisciplinary research in the Baltic Sea, ISBN 978-83-945891-2-7. *In Polish*
7. Weydmann-Zwolicka A., **Mańko M.**, Panasiuk A. 2020, Zooplankton diversity of the Gulf of Gdańsk [In:] Szymczak E. (ed.) Advanced methods of the interdisciplinary research in the Baltic Sea, ISBN 978-83-945891-2-7. *In Polish*
8. **Mańko M.K.**, Pugh P.R. 2018, *Agalma clausi* (Bedot, 1888) (Siphonophora: Physonectae) – complementary description with notes on species distribution and ecology. *Zootaxa* 4441: 311-331 (IF: 0.972, ME&S points: 20)

9. Walczyńska S.K., **Mańko M.K.**, Weydmann A. 2018, DNA barcoding and Arctic Ocean biodiversity – a climate change perspective. [In:] Jungblut S., Liebich V., Bode M. (eds.) *YOUMARES 8 – Oceans across boundaries: Learning from each other*. Springer, ISBN 978-3-319-93283-5
10. Purcell J.E., Juhl A.R., **Mańko M.K.**, Aumack C.F. 2017, Overwintering of gelatinous zooplankton in the coastal Arctic. *Marine Ecology Progress Series* 13: 1-6 (IF: 2.292, ME&S points: 35)
11. **Mańko M.K.**, Weydmann A., Mapstone G.M. 2017, A shallow-living Rhodaliid siphonophore: citizen science discovery from Papua New Guinea. *Zootaxa* 4324: 189-194 (IF: 0.972, ME&S points: 20)
12. **Mańko M.K.**, Słomska A.W., Jażdżewski K. 2017, Siphonophora of the Gulf of Aqaba (Red Sea) and their associations with crustaceans. *Marine Biology Research* 13: 480-485 (IF: 1.161, ME&S points: 25)
13. Słomska A. W., Panasiuk-Chodnicka A. A., Żmijewska M. I., **Mańko M.K.** 2015, Variability of Salpa thompsoni population structure in the Drake Passage (Southern Ocean) in summer season 2010. *Polish Polar Research* 36: 391-404 (IF: 1.275, ME&S points: 20)
14. **Mańko M.K.**, Panasiuk-Chodnicka A. A., Żmijewska M. I. 2015, Pelagic coelenterates in the Atlantic sector of the Arctic Ocean - species diversity and distribution as water mass indicators. *Oceanological and Hydrobiological Studies* 44: 466-479 (IF: 0.670, ME&S points: 15)
15. **Mańko M.K.** 2015, Current grading systems and methods of progress verification as seen by students. [In:] Bolałek J., Sadoń-Osowiecka T., Szymczak E. (eds.) *Good academic practices in environmental sciences*. Libron, Kraków, ISBN 978-83-65148-31-5. *In Polish*
16. **Mańko M.K.**, Turowicz A. 2015, Activities of the Student Research Group of Oceanographers as a chance for self-development. [In:] Bolałek J., Sadoń-Osowiecka T., Szymczak E. (eds.) *Good academic practices in environmental sciences*. Libron, Kraków, ISBN 978-83-65148-31-5. *In Polish*
17. Panasiuk-Chodnicka A. A., Żmijewska M. I., **Mańko M.K.** 2014, Vertical migration of Siphonophora (Cnidaria) and their productivity in the Crocker Passage, the Antarctic. Polish Polar Research 35: 115-131 (IF: 0.788, ME&S points: 15)

Research grants

- Research internship grant. National Science Centre, Etiuda7, 2019/32/T/NZ8/00130, in collaboration with Steven Haddock (Monterey Bay Aquarium Research Institute, California, USA)
- *Evolution of the new life cycle stage in calycophoran siphonophores (Cnidaria): integrative eco-evo-devo approach*. National Science Centre, Preludium15, 2018/29/N/NZ8/01305, in collaboration with Lucas Leclère (Institute de la Mer de Villefranche, France)
- *Morphological and molecular description of the eudoxid-stage of the unknown polar calycophoran siphonophore*. University of Gdańsk, Research Projects for PhD students and early career scientists, 538-6250-B104-19, in collaboration with Aino Hosia (University of Bergen, Norway)
- *EUDOX: Calycophoran eudoxid – a highest level of zooids' functional specialization*? European Marine Biology Resource Centre, OOV–EMBRC FR–AAP2018–2180, in collaboration with drs Catriona Munro and Casey Dunn (Yale University, USA)
- *Gelatinous zooplankton as climate change indicator in the European Arctic*. Ministry of Education and Science, Diamond Grant, DI2014 020344, under supervision of Agata Weydmann-Zwolicka (University of Gdańsk, Poland)
- *Review of genus* Agalma *(Physonectae: Siphonophora) with an emphasis on cormidial arrangements, colony level development and zooid morphometric variation within the geographical ranges of each valid species*. European Commission, Synthesys, GB-TAF-5264, in collaboration with Gill Mapstone (Natural History Museum, London, UK)

Conferences

Oral presentations: 18 (7 national, 11 international) with presentation awards at:

- V Jellyfish Bloom Symposium (2016, Barcelona, Spain)
- XIII Young Oceanographers Symposium (2014, Gdynia)
- VIII International Conference on Coelenterate Biology (2013, Eilat, Israel)

Posters: 7 (2 national, 7 international

Science communication

19.08.2021	Podcast on siphonophores, Science of the XXI Century (Borys Kozielski)
18.12.2018	Broadcast in the Polish Radio RDC on jellyfish research
20.10.2018	Role of polar scientist in the TV show DeFacto S10E11
2017	Scientific advisor of the mobile app – Svalbard Zooplankton Identification
21.11.2016.	Podcast on oceanography, Science of the XXI Century (Borys Kozielski)

Research internships

16.03 – 16.06.2022	Institute de la Mer de Villefranche-sur-Mer (France)
01.09 – 01.10.2021	Institute de la Mer de Villefranche-sur-Mer (France)
06.03 – 25.05.2021	Institute de la Mer de Villefranche-sur-Mer (France)
15.02 – 14.03.2020	Institute de la Mer de Villefranche-sur-Mer (France)
13.03 – 20.05.2018	Observatoire Océanologique de Villefranche-sur-Mer (France)
08.04 – 08.06.2017	Observatoire Océanologique de Villefranche-sur-Mer (France)
04.05 – 23.05.2015	Natural History Museum of London (United Kingdom)
10.02 – 10.05.2016	Observatoire Océanologique de Villefranche-sur-Mer (France)
26.03 – 02.05.2013	Observatoire Océanologique de Villefranche-sur-Mer (France)

At-sea experience

02.11 – 13.11.2018	Pacific Ocean, R/V Kilo Moana
21.06 – 15.08.2017	Arctic Ocean, S/Y Oceania
20.06 – 24.07.2016	Arctic Ocean, S/Y Oceania
08.04 – 15.04.2014	Baltic Sea, ORP Heweliusz
01.10 – 08.10.2013	Baltic Sea, ORP Heweliusz
27.03 – 05.04.2012	Baltic Sea, ORP Heweliusz

Teaching experience

Courses taught in Polish for students of Oceanography (BSc and MSc), Environmental protection (BSc), Aquaculture – Business and Technology (BSc):

> *Anthropogenic transformations of the marine environment, Biological oceanography Functioning of the polar ecosystems, Global change of marine ecosystems, Mariculture, Marine biogeography, Oceanographic field courses for BSc and MSc students, Statistics for oceanographers, Systematics and biology of cultured species*

15.12.2020 alumnus of the School of Academic Tutors

Scientific committees

2019 – present	*Association of Polar Early Career Scientists*, council member
2015 – present	*Hydrozoan Society*, regular member

Organizing committees

15 – 24.09.2019	*II Conference of Polish Oceanographers*, Gdynia, Poland
11 – 14.09.2018	*Youmares9*, Oldenburg, Germany
14 – 15.09.2017	*Youmares8*, Kiel, Germany
26.05.2017	*International Sopot Youth Conference*, Sopot, Poland

Awards

2nd degree Rector's Award for the scientific achievements 2018/2019

3rd degree Rector's Award for the scientific achievements 2017/2018, 2019/2020

University of Gdańsk doctoral scholarship – throughout doctoral school

Doctoral scholarship enhancement for scientific achievements – throughout doctoral school

Ministry of Education and Science Scholarship (2015/2016)

1st place in 2015 Poland's Best Student competition of the Independent Students Association