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Distinct change in zooplankton zoogeography in high-Arctic Isfjorden, Svalbard

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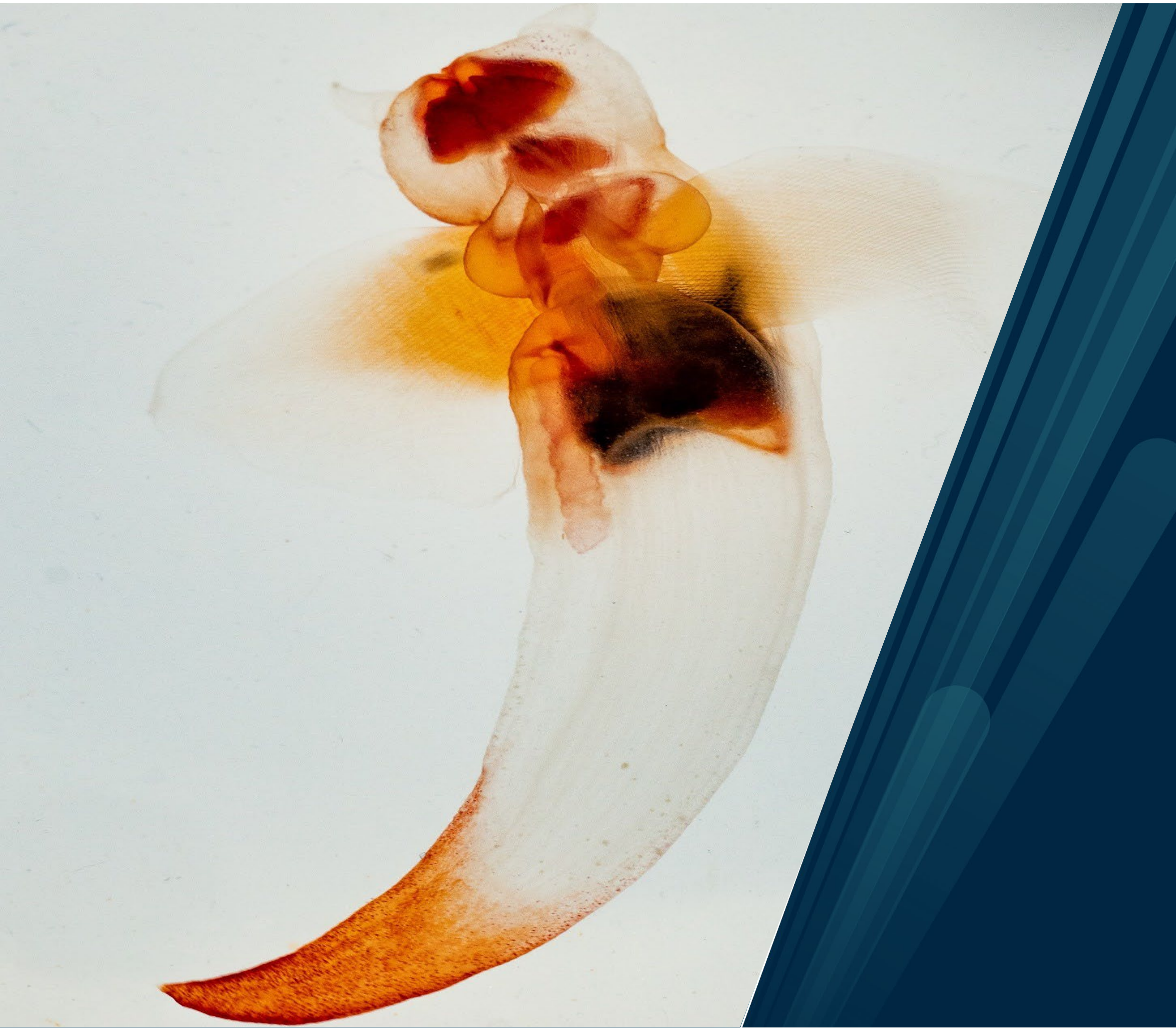

Abstract

Ongoing global warming in air and sea temperatures are changing the environment at a drastic pace. Arctic fjords are becoming warmer and fjord ice is decreasing and, in some cases, not forming. The zooplankton community is proposed to shift from an Arctic to a more boreal one – popularly termed "Atlantification" of the zooplankton community in the European Arctic. The extent and rate of change is challenging to determine due to the lack of longer zooplankton time series with sufficient species and zoogeographical resolution. The Isfjorden Marine Observatory Svalbard (IMOS) is a high-Arctic zooplankton time series with seasonal resolution along a transect from warm Atlantic influenced to cold Arctic water masses. Using zoogeography defined in the literature and customized for Isfjorden, determined from multivariate zooplankton and environmental analyses, in the period 2011-2022, zooplankton species were defined to be Arctic, widespread, Atlantic, or not defined. Multivariate and literature zoogeography revealed that there is ongoing Atlantification in Isfjorden, except in the innermost part (Billefjorden) which is protected by a shallow sill preventing Atlantic water masses from entering. A clear environmental and zooplankton zoogeographical gradient from the warmer fjord mouth to the inner cold Arctic sill fjord were found. According to literature zoogeography there are between ~34-45% Atlantic and widespread species in the outermost station, while in Billefjorden there are less than ~30%. According to the multivariate zoogeography there are 75-85% Atlantic species on the outermost station and 60% in Billefjorden. Many of the species defined in this thesis could be beneficial for management as it allows us to look at the whole zooplankton community and not only a few species for signs of Atlantification or Arctic resilience. Central is also an evaluation of data handling in modern science, and with the escalation of cloud storage, it is paramount to make data available. This increases any value data collected has and enables large-scale biological data analysis.

Keywords: Atlantification, Zoogeography, Zooplankton, European Arctic, Time series, Svalbard

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Finally, my supervisors Janne Søreide and Malin Daase, for taking a chance on me although this was an unconventional route.

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1 Introduction

In the Arctic marine ecosystem, boreal and sub-arctic species are becoming increasingly prevalent, known as borealization (Dalpadado et al., 2016; Fossheim et al., 2015; Vihtakari et al., 2018). This shift coincides with Atlantification - the transformation of Arctic water masses to resemble those of the Atlantic. These changes are primarily driven by global climate change, which has led to a consistent increase of Atlantic water in the European Arctic (Asbjørnsen et al., 2020; Carmack et al., 2015). Decadal trends reveal a declining sea ice cover, with the Arctic Ocean becoming ice-free, enhancing the similarities between Arctic and Atlantic waters (Asbjørnsen et al., 2020; Carmack et al., 2015).

With this increase in temperature, boreal species are expanding their thermal range, moving progressively north as favorable water temperatures allow them to survive and flourish (Born, 2020; Dalpadado et al., 2016; Fossheim et al., 2015; Hop, Wold, et al., 2019). Atlantification facilitates borealization and serves as a means for boreal species to disperse northwards. Many of these species are bound to their water mass and are consequently transported by the currents (Polyakov et al., 2020; Willis et al., 2006).

1.1 Zooplankton Community

Zooplankton are tiny animals or juvenile stages of larger animals that cannot swim against the current but can move vertically in the water column. They constitute an integral part of the Arctic marine ecosystem (Daase et al., 2021). They link primary production to higher trophic carnivores, like birds, filter-feeding whales and planktivorous fish (Descamps et al., 2022; Vihtakari et al., 2018). A change in the zooplankton community in the Arctic can have cascading effects throughout the food web that ultimately can have consequences for the stability of nature in the Arctic (Falk-Petersen et al., 2007).

The zooplankton community is highly influenced by its surrounding hydrography (Gluchowska et al., 2016); an increase in Atlantic water (AW) is a potential threat to endemic species and could shift the community from an Arctic towards a more boreal community composition (Dalpadado et al., 2020; Møller & Nielsen, 2020). Most studies on the borealization of zooplankton communities focus on a few species known to travel with either Arctic or Atlantic water masses, like *Calanus glacialis* and *Calanus finmarchicus*, respectively (Ershova, Kosobokova, et al., 2021). Some effects of zooplankton borealization are that the mean size of zooplankton is becoming smaller, and the diversity is increasing. Large, arctic zooplankton, with multi-year life cycles, are decreasing in numbers, which impacts the energy flux upwards in the system. Birds that feed on zooplankton must spend more time to gain the same energy as they must pick more zooplankton as they contain less energy on average (Descamps et al., 2022).

1.2 Description of the study area

Spitsbergen is the largest island of the Svalbard archipelago), located in the high European Arctic on the border between the North Atlantic and the Arctic Ocean (Figure 1). The bathymetry and prevailing currents determine the hydrography along the coast and in the fjords of the Svalbard archipelago. The hydrography of Spitsbergen's western coast is predominantly influenced by the warm and saline West Spitsbergen Current (WSC) and the colder and fresher coastal Sørkapp Current (SC). The WSC is a trailing arm of the North Atlantic Current, bringing warm and saline Atlantic water (AW) northwards. The SC is the trailing end of a current originating in the Arctic Ocean, bringing fresh and cold Arctic water (ArW) around the southern tip of Spitsbergen (Skogseth et al., 2020).

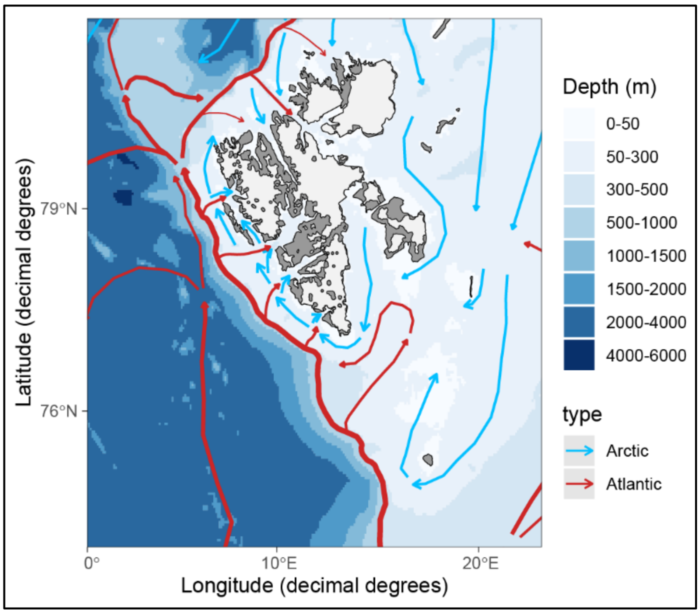

Figure 1: Overview map of Svalbard and the Arctic and Atlantic currents.

Isfjorden is the second-largest fjord of the Svalbard archipelago and hosts the two largest settlements in Svalbard. It has a broad and deep fjord entrance, and with the lack of a sill, it is prone to inputs from currents along Spitsbergen's coast (Nilsen et al., 2008; Skogseth et al., 2020). The AW flowing along Spitsbergen's shelf has become more prevalent in recent years, making Isfjorden warmer and more saline (Piechura & Walczowski, 2009). However, this is subject to intra-annual changes, and it has recently been shown that Isfjorden, in terms of water masses, has a strong seasonality in the presence of Atlantic or Arctic water masses (Skogseth et al., 2020). The range of marine-terminating glaciers and rivers along the fjord contribute a large amount of fresh and cold water to the fjord system influencing its hydrography (Nilsen et al., 2008). The outer parts of Isfjorden are highly influenced by the influx of water from the shelf; however, Billefjorden, one of the innermost fjord arms, is isolated from influx from the Isfjorden by two sills (70m and 50m depth) located before an inner basin of 190m (Nilsen et al., 2008). Billefjorden is highly influenced by fresh and cold water from rivers and glaciers, creating a fjord system of Arctic character with a seasonal ice cover (Nilsen et al., 2008). Isfjorden has since 2005 undergone a regime shift, where the whole fjord has had decreased ice-cover and is more prone to Atlantic influence (Muckenhuber et al., 2016; Skogseth et al., 2020)

1.3 Study aims and hypothesizes.

I want to investigate how the ongoing climate change influences the zooplankton communities in Isfjorden. In my approach, I use Isfjordens natural hydrography to my advantage, as it contains both open areas with large degree of Atlantic water influence and more protected parts where the Atlantic water does not penetrate. In addition, I would like to provide helpful information for managing the Arctic marine environment by identifying valid water mass indicator species for the Isfjorden system.

1.3.1 Aim 1:

Investigate any interannual changes in the relative abundance of the different zoogeographies in Isfjorden zooplankton.

H_{01}: There is no temporal trend in Isfjorden, and the relative abundances of Atlantic and Arctic species stay the same over time.

H_{A1}: Atlantic and Widespread species are increasing their relative abundance at the cost of Arctic species.

1.3.2 Aim 2:

Compare the zoogeographic composition in the outer and middle parts of Isfjorden, which are more exposed to an inflow of water from outside the fjord system, and with the innermost part of the Isfjorden system, Billefjorden, where the influx of water from the outer fjord system is highly reduced due to the presence of two shallow sills.

H_{02}: There is no difference in the relative zoogeographic abundance from the outer and middle part to the innermost part of Isfjorden.

H_{A2}: The outer and middle parts of Isfjorden show significantly higher relative abundances of Atlantic species compared to the innermost part.

1.3.3 Aim 3:

Examine the time series to find and identify species characteristic of the Atlantic or Arctic domain which can be used as indicators in long-term monitoring and environmental management in the High-Arctic.

H_{03}: No zooplankton species or families are characteristic of Atlantic or Arctic waters in Isfjorden.

H_{a3}: There are species or taxon which are Isfjorden-specific valid indicator species for Atlantification.

2 Materials & methods

2.1 Study area

This study is based on IMOS data from 2011 until 2022. Samples were collected at three stations in Isfjorden ranging from the innermost part of Isfjorden (BAB) to the middle part of Isfjorden (IsK), outside of Grønfjorden (IsG) (table 1, figure 2). On the southern side of the fjord mouth, there was a long-term mooring collecting temperature and salinity data.

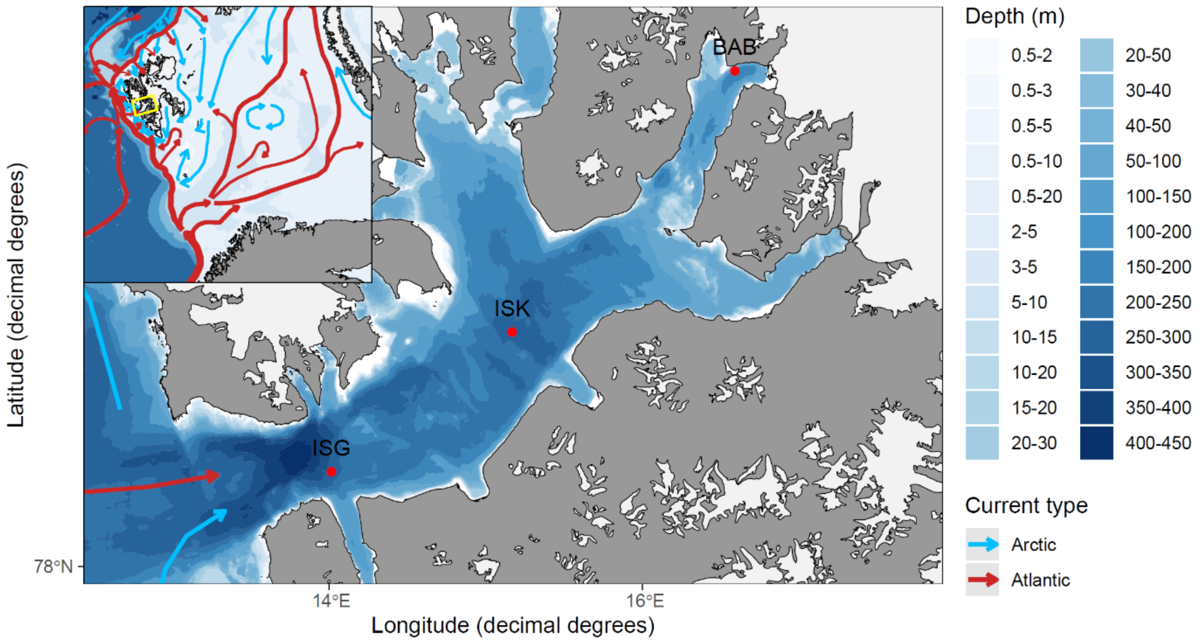

Figure 2: Map over study area with sampling stations.

Table 1:IMOS sampling sites with coordinates and depths.

Station name	Location	Latitude	Longitude	Bottom depth
BAB	Billefjorden/Adolfbukta	78°39.50	16°40.50	191 m
IsK	Karlskronadjupet	78°19.24	15°09.76	274 m
IsG	Isfjorden/Grønnfjorden	78°07.73	15°00.17	273 m

2.2 General sampling approach in IMOS

To monitor any long-term changes in the zooplankton community, the Isfjorden Marine Observatory Svalbard (IMOS) was established in Isfjorden (Isfjorden Marine Observatory Svalbard - Prosjektbanken, Research Council of Norway, 2015-2018). The proximity to permanent settlements and high research activity enables cost-effective opportunistic sampling. Several marine biology courses at UNIS often involve a teaching cruise creating sampling opportunities. Taking advantage of the infrastructure and logistics already in place, sampling several times a year is possible. The IMOS time series depends on opportunistic sampling done via preexisting cruises and during teaching cruises at UNIS. Therefore, the sampling protocol had to be as adaptable as possible to suit an extensive range of vessels and situations. Sampling is conducted from boats, research ships, and from sea-ice. The project flexibility is cost-effective, and sampling was conducted by students and well-rehearsed scientists using very standardized zooplankton sampling methods.

2.3 Zooplankton sampling

Zooplankton using either a closing WP2 net (Hydro-Bios Kiel, mesh size 180 µm, opening area 0.25 m^2) or a multi-zooplankton sampler (MPS) (Hydro-Bios Kiel, mesh size 180 µm, opening area 0.25 m^2). At the beginning of the IMOS time series, depth-stratified samples were taken. To ease the IMOS time series depth sampling, stratified samples were replaced with whole-column sampling with the WP2. Here, I only use depth-integrated data. The IMOS time series aims to have zooplankton samples throughout the year and establish a high-resolution time series over several years. Sampling intervals were at some stations monthly and at other stations seasonally (Appendix VI).

Zooplankton samples were preserved in a 4% formalin and seawater solution with borax or hexamine. Large gelatinous zooplankton were removed from the samples before preservation in formalin, as they disintegrated in formalin which makes analysis more time-consuming and could ruin samples. To ease the identification of zooplankton, samples were split into several subsamples depending on the density of the zooplankton. Depending on the volume of the subsample, and the amount of the subsample, this was then extrapolated to the number of individuals of a species per cubic meter. While the IMOS time series depends on opportunistic sampling, and many people are involved in the sampling effort, all taxonomic analyses were done by Kasia Dmoch (Oithona AS), increasing the data's comparability. To distinguish between *Calanus glacialis* and *Calanus finmarchicus* their prosome lengths were used. At IsK and IsG for stages CI and CII we used sizes from (Daase & Eiane, 2007), for CIII, CIV and CV we used (Daase et al., 2018). At BAB we used prosome lengths defined in Søreide et al., 2022.

2.4 Environmental data sampling

Water column hydrography was recorded at each sampling event using a CTD. A handheld SD 204 or 208, produced by SAIV, Bergen, was used from smaller boats or sampling from an ice platform in winter. From larger ships (RV Helmer Hanssen) the ship CTD was used (Seabird 911, USA).

2.5 Data management

In later years data management has become a more prevalent topic within biological sciences; the internet and artificial intelligence has had a quantum leap in innovation and functionality increasing the need to structure data. The collection of biological data provides several challenges; many are standardization issues. The way samples are collected makes it inherently hard to standardize; with millions of taxa names in biological sciences, just spelling species in the same way is challenging.

2.5.1 Universal format and machine readability

To make the data easy to work with and reliant on a standard, we used the Darwin core standard (DwC) (Wieczorek et al., 2012). DwC provides a flexible framework to compile biodiversity data. It is a data frame (DF) header vocabulary and provides the structure to build the Darwin core standard archive (DwC-A).

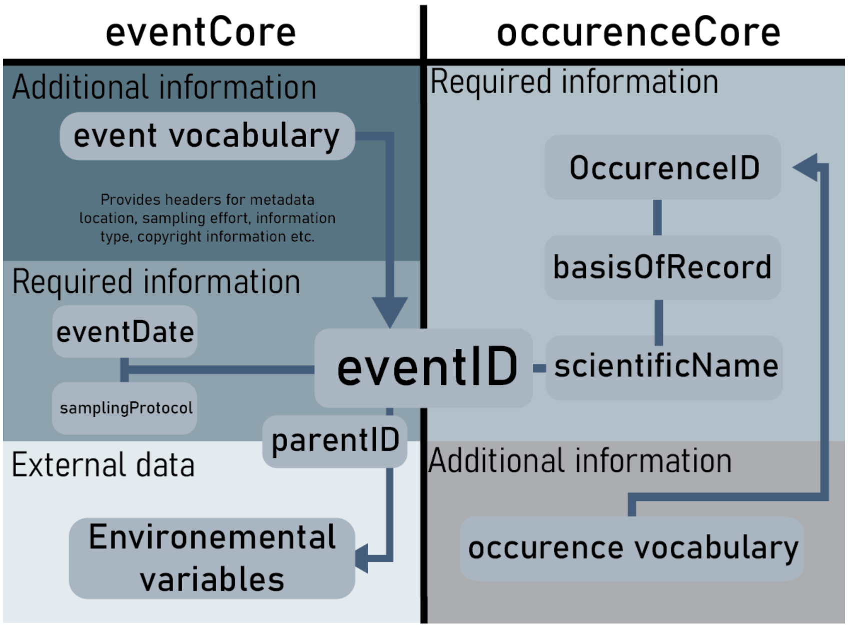

Figure 3: Illustration showing the relationship between the relevant terms in the DwC system.

In Figure 3 we can see the relationship between the terms used in DwC-A.

In IMOS, we only use a part of the DwC system; to use it, we first must look at our data. Our data consists of a series of sampling events (a net haul, for instance), which give us a series of occurrences (i.e., the number of species found in the net haul).
To make our data compliant with DwC and DwC-A, we need to use an eventCore and an occuranceCore. In the eventCore, it is required to provide a unique id (eventID), event date (eventDate), and a sample protocol reference (sampleProtocol). The eventID can be linked to a parent id (parentID) which can be used to connect all sampling events in, for instance, a research cruise together. The eventID is again linked to an occurenceID which links occurrences to events and occurrences to environmental data. The parentID can also link biodiversity data to environmental data stored outside DwC-A. When using the eventID and parentID correctly, it enables data to be easily connected; if the data is published, the DwC system allows data to be quickly sorted and categorized, which increases its value as it can be harvested for large-scale studies or times series which previously have not been linked as the data was intended for different projects.

A widespread tool to record environmental variables in zooplankton research is CTDs; they provide information about the water masses present at the sampling location and can be outfitted to record a range of valuable information. Data from the CTD cannot be stored in the DwC format but keeping it in a Network common data form (NetCDF) is standard practice. The NetCDF format is built to be self-describing, and much like the DwC format, headers are standardized, making the data easily combined and manipulated. One of the project goals of netCDF is to make the data archivable; they aim to achieve this by ensuring that all netCDF formats will be compatible with software released in the future.

Until now, CTD data in this IMOS has not been stored as netCDF and uploaded to an accessible platform. The opportunistic nature of IMOS includes different equipment, which records data, using different headers, and sometimes not calculating salinity from conductivity automatically. Some CTDs do not store the casts as different files, meaning you have to separate the different casts post-sampling. In some cases, this was not done right after the cruise, leaving it up to me to decide which cast is taken at a given time and date. The implication for our study is that not all CTD data was accessible, which is a detriment to our research.

2.6 Hydrography data handling and analysis

In addition to the CTD casts during the IMOS time series, we supplied additional CTD data from the UNIS hydrograpical database, stored in the NP database (*Norwegian Polar Data Centre*, n.d.; Skogseth et al., 2020) They are stored as NetCDF using global attributes and variable naming**.** This makes working with the data accessible, and large data frames are compiled using the Tidyverse and RNetCDF packages (Kelley et al., 2022; Wickham et al., 2019). As the database contains CTD cast done by different cruises and departments, we established geographic zones to filter for CTDs of interest. This was done using coordinate boxes. For BAB, we set the coordinate box behind the sill in the fjord to represent the overall hydrography more.

To unify the CTD data, we relied on the oce package (Kelley et al., 2022) to transform data from different CTD file formats into a universal format; we then used tidyverse (Wickham et al., 2019) to organize the CTD data into a tall format. The CTD data for the stations were subsequently plotted in a temperature-salinity (TS) plot using ggOceanPlots (ref). Water masses were displayed in the TS-plot; the water mass definitions are found in (Skogseth et al., 2020) and are the most recent water mass definitions for Isfjorden.

Using TS plots, I had to determine which water mass was present at each station where zooplankton was sampled. The TS plots were created using the ggOceanPlots package (Vihtakari, 2021); it uses the water mass definitions by Skogseth et al., 2020. In addition to the TS plot, I also plotted Temperature and Salinity. Using the information from the TS plots, I manually assigned which stations were Arctic-influenced or Atlantic-influenced. Due to missing data, many stations before 2015 and a few after 2015, we had to rely on the first-hand information of people sampling to determine stations as Arctic or Atlantic influenced (J. Søreide, 2023).

2.6.1 Mooring data

The Department for Arctic Geophysics (AGF) at UNIS has placed moorings at the southern entrance of Isfjorden for several years. The moorings have been placed there for most of the period in the IMOS time series. The data is accessible at the NP data portal (*Norwegian Polar*

Data Centre, n.d.) and is stored in the same way as the UNIS hydrograpical database in NetCDF files.

As mooring data gives a time series, they must be treated as several CTDs at the same station to make it usable with the oce package (Kelley et al., 2022). Data was averaged weekly across all depths to make processing less resource-demanding. This decreased the number of data points from more than 150000 points to ~500. The data was sorted into an oce section datatype and plotted over time.

I also plotted which water mass type was present at the mooring at any given time. To accomplish this, we used the water mass definitions in Skogseth et al., 2020 and defined the water mass at every point where we had temperature and salinity. The occurrence of each water mass was counted for every day, which then gave a percentage of water mass present at each station every day. This was plotted in a stacked bar plot, letting us identify the daily intrusion of different water masses into Isfjorden.

2.7 Zooplankton data handling and analysis

One of the tasks to make the IMOS data usable was to compile it all, organize it, and make it machine-readable. As several research teams collected the zooplankton samples, the scientific names entered varied slightly. Preserved zooplankton samples were analyzed irregularly and registered in different tables. To make data analysis more convenient, we rectified any species spelling mistakes and unified all data into a DwC format. To link the zooplankton data to the environmental data from the CTDs, we used date and location, even though, according to the DwC format, it would be optimal to use UUID for this.

For this thesis, only adult holoplankton was included in the analysis, and all species separated in different stages were summed up into one.

Zooplankton was classified into four zoogeographic groups, Arctic, Widespread, Atlantic, and Not defined (Beaugrand et al., 2002; *Home, Arctic Ocean Biodiversity*, n.d.; Hop, Wold, et al., 2019; Kosobokova et al., 2011; *WoRMS - World Register of Marine Species*, n.d.). This process was made easier by using a working master sheet from the Nansen Legacy project (*The Nansen Legacy*, n.d.), that had already defined most of the common zooplankton species, found around Svalbard (Appendix V).

2.7.1 Temporal relative abundance of zooplankton at each station

The zooplankton data in the IMOS times series is unevenly distributed throughout the year. For our purpose, we are trying to identify any longer-term changes. To balance out the effects of seasonality, I selected the months of late July to October every year, and used relative abundance data. To visualize the data, I plotted a scatterplot for each year, adding a line that follows the yearly averages to ease the reading of the plots.

2.7.2 Mean relative abundance of zooplankton between stations.

To compare the zoogeography among the stations, boxplot was used to display the mean relative abundance of each zoogeography divided by stations. Kruskal-Wallis test for comparison of means was used since the data were not normally distributed (Levene-test, $p < 0.05$). Pairwise Wilcox test was used to compare the means between each station if Kruskal-Wallis returned a significant p-value.

2.7.3 Correspondence analysis and Isfjorden-specific zoogeographic origin

The variation in the relative abundance of all species at all stations over time and how it was related to different water masses found at the station was explored by Correspondence analysis (CA) on arcsin transformed relative species data. The CA was plotted using the vegan package in R using the CCA function and the envfit function to plot the water masses (Oksanen et al., 2019). With the correspondence analysis, the aim was to explore the relationship between the stations and the species/taxa. The grouping will reveal if there are differences and likenesses between stations and species. All species/taxa with less than three observations were considered as outliers and removed.

From the CA, I visually defined each species as Arctic or Atlantic depending on its proximity to AW or ArW. The zoogeography was then linked to all species found in the IMOS time series. To investigate the Isfjorden specific zoogeography, I compared the literature-based zoogeography with the new Isfjorden specific multivariate zoogeography definitions.

2.7.4 Relative abundance of the most abundant species

To properly understand the data and which species drive the relative abundance of the different zoogeographies, I created a basic overview of species present at the stations yearly. To select the ten most abundant species, I summed up all species and selected the top 10 most abundant species, and the remaining species were grouped into the others category. For each year in the study, I chose a month between July-October, which was then visualized using a filled stacked bar plot using tidyverse. For each year and station, this gave me the relative abundance of all the selected species.

3 Results

3.1 Hydrography

3.1.1 Temperature and salinity at the entrance of Isfjorden

Looking at the mooring data, we can see that summer temperatures were 0.5-1.4°C higher from 2014 to 2018 compared to 2019-2022. Salinity has similar trends, whereas before 2013 and after 2019 (Figure 4), salinities were generally a bit lower. Translated to water masses this shows that Isfjorden was more influenced by Atlantic/transformed Atlantic water in the beginning (2014-2018) than in the later years (2019-2022) (Figure 4).

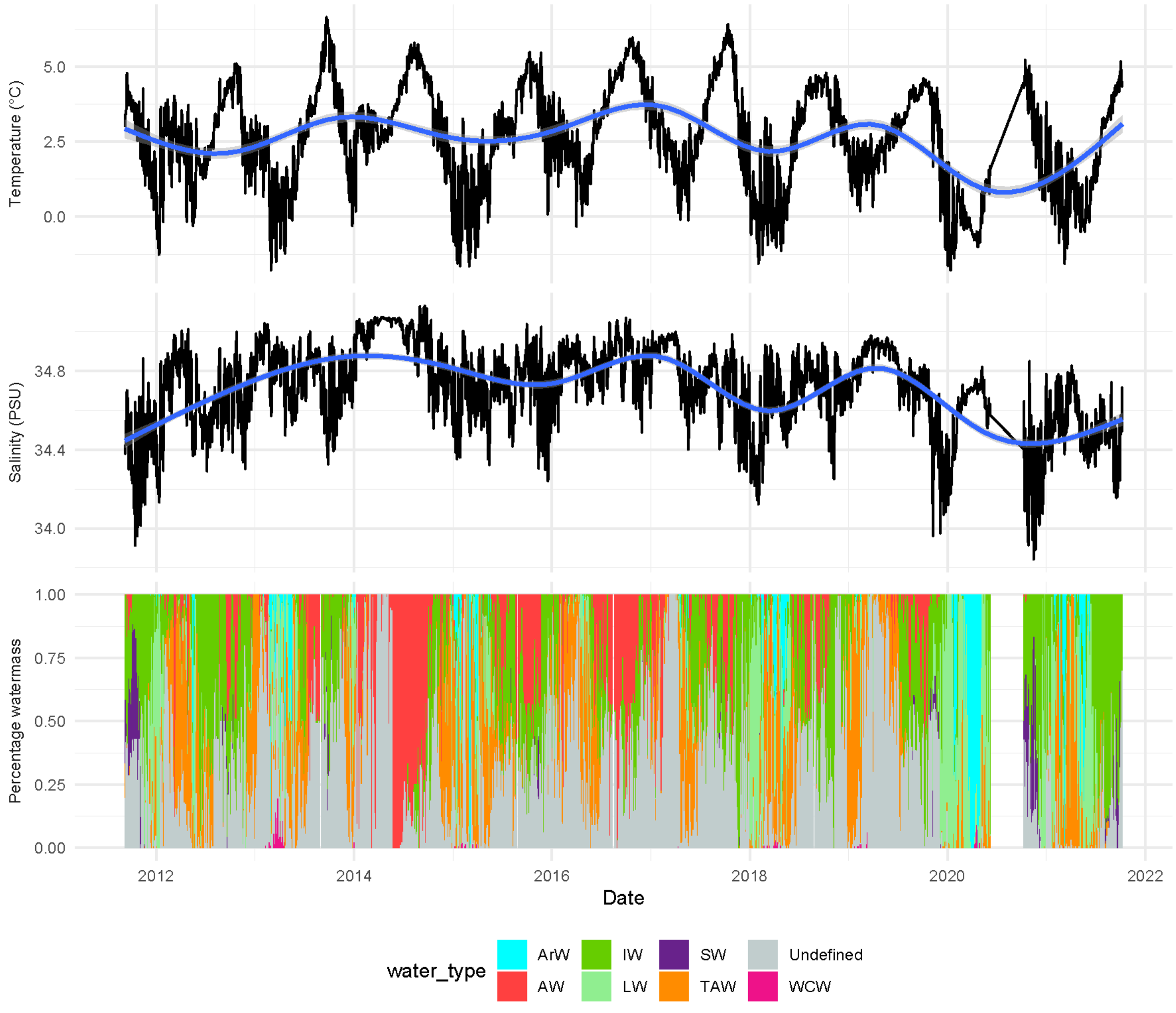

Figure 4: Temperature, salinity, and water mass composition at the Isfjorden South Mooring. The uppermost plot shows the mean temperature (°C) at the mouth of Isfjorden from 2011 to 2021. The middle plot shows salinity (PSU) from 2011 to 2021, the lowermost plot shows the percentage of water mass present each day, according to

Skogseth et al. 2020): Arctic Water (ArW), Atlantic Water (AW), Transformed Atlantic Water (TAW), Intermediate Water (IW), Surface Water (SW), Local Water (LW) and undefined.

3.1.2 CTD Hydrography

The CTD casts taken when sampling zooplankton, supplied with additional CTD data from the UNIS hydrographical database (UNIS HD; Skogseth et al., 2019) showed a relatively stable cold (~0.3°C to ~0.1°C) water column mean temperature at BAB from 2010 to 2022 (Table 3). The middle (IsK) and outer (IsG) was much warmer (>3°C). From 2010 to 2022, IsK showed an increase in mean water column temperature from ~3.1°C to ~3.5°C, while IsG an increase from ~3.4°C to ~4.0°C (Figure 5). I can see that at IsK the spread of the points was high, indicating that IsK has a higher variability in temperature, compared to both BAB and IsG.

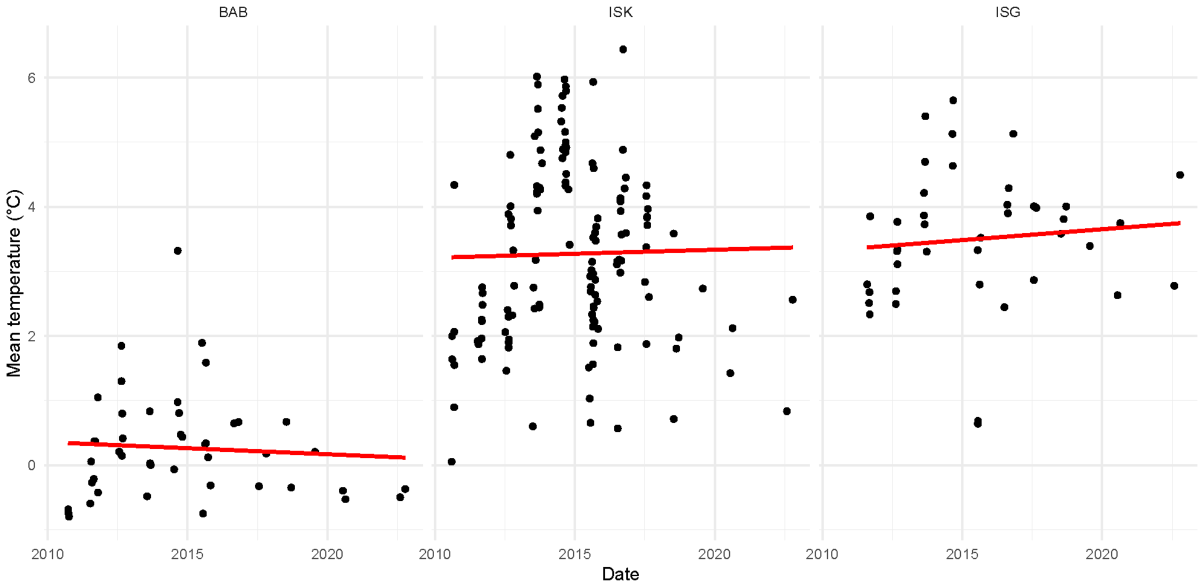

Figure 5: Mean temperature (averaged from five meters to the bottom) at the station's BAB, IsK, and IsG in the study period 2011-2022 in Isfjorden, Svalbard.

3.2 Zoogeographic changes in Isfjorden

3.2.1 Temporal and mean changes in relative zoogeographic abundance

The relative abundance of the different zoogeographies over time was visualized using a scatter plot, with lines indicating the yearly averages (Figure 6). Overall, widespread species were most common (on average 28-48%), followed by taxa “not defined” (on average 22-38%). Considering Arctic and Atlantic species, there was a higher percentage of Arctic species at BAB (on average 23%) compared to IsK (on average 19%) and especially IsG (on average 8%). Atlantic species were more prevalent than Arctic species at IsK (on average 18%) and IsG (on average 16%). In the warmer years 2013-2018 the widespread, and to some degree the Atlantic species displayed increased relative abundance. From 2018 – 2022 when the summer temperature was lower, widespread species decreased, while the not defined group increased in relative abundance.

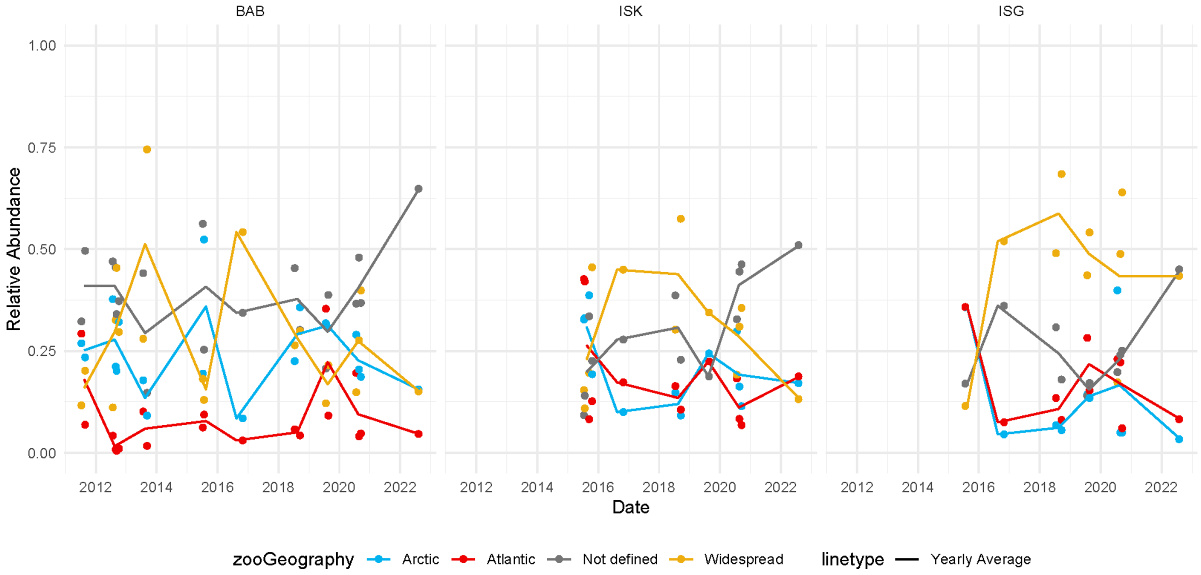

Figure 6: Changes in the relative abundance of literature zoogeography for BAB (2011-2022) and the outer stations IsK and IsG (2015-2022) in Isfjorden, Svalbard.

A closer look at the in relative zoogeography composition averaged for all years (Figure 7) shows that the relative composition of Arctic species is highest at BAB, slightly lower at IsK and distinct lower at IsG (paired Wilcox, p=0.027) (Table 3). Widespread and Atlantic species showed the reverse pattern. Significant lower proportions of widespread species were observed at BAB versus IsK (paired Wilcox, p= 0.005) and at BAB versus IsG (paired Wilcox, p=0.016) (Table 1). For Atlantic species significant differences in proportions was only found at BAB versus IsG (paired Wilcox, p=0.016) (Table 3). Not defined species exhibit a gradient from High to Low for BAB to IsG, with only a significant difference observed between BAB and IsG (Paired Wilcox, p=0.0072) (Table 3).

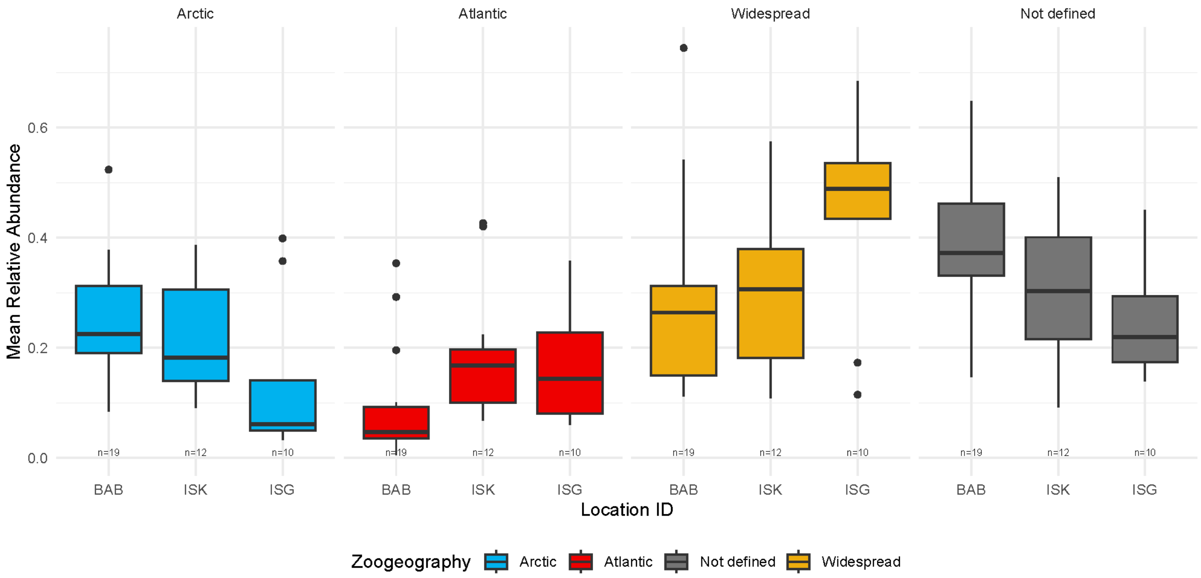

Figure 7: Boxplots depicting the mean relative abundance of each zoogeographic group at three stations BAB, IsK, IsG for the years 2015-2022 in Isfjorden, Svalbard.

3.3 Multivariate defined zoogeography.

Isfjorden specific zoogeography determined from own data using multivariate statistics on zooplankton and hydrography data (Figure 8) showed two main gradients: a strong seasonal gradient along axis 1 (CA1, 27.8%) from June to August/September, and a zoogeographic gradient along axes 2 (CA2 16.6%) with mainly Atlantic/widespread-related species gathered above the CA2 zero line, while the more Arctic-related species gathered below the zero line. The species located at the center were more equally distributed and showed no distinct seasonal and environmental (water mass) preferences. The more Atlantic-influenced stations were more apparent in late summer/fall. The zoogeography was determined for all the taxa (Supplementary table 2: Table over species and their respective zoogeographies), except the ones not included in the CCA which comprised of taxa with three or fewer observations in the entire dataset (Supplementary table 1: Table over species removed from CA analysis.).

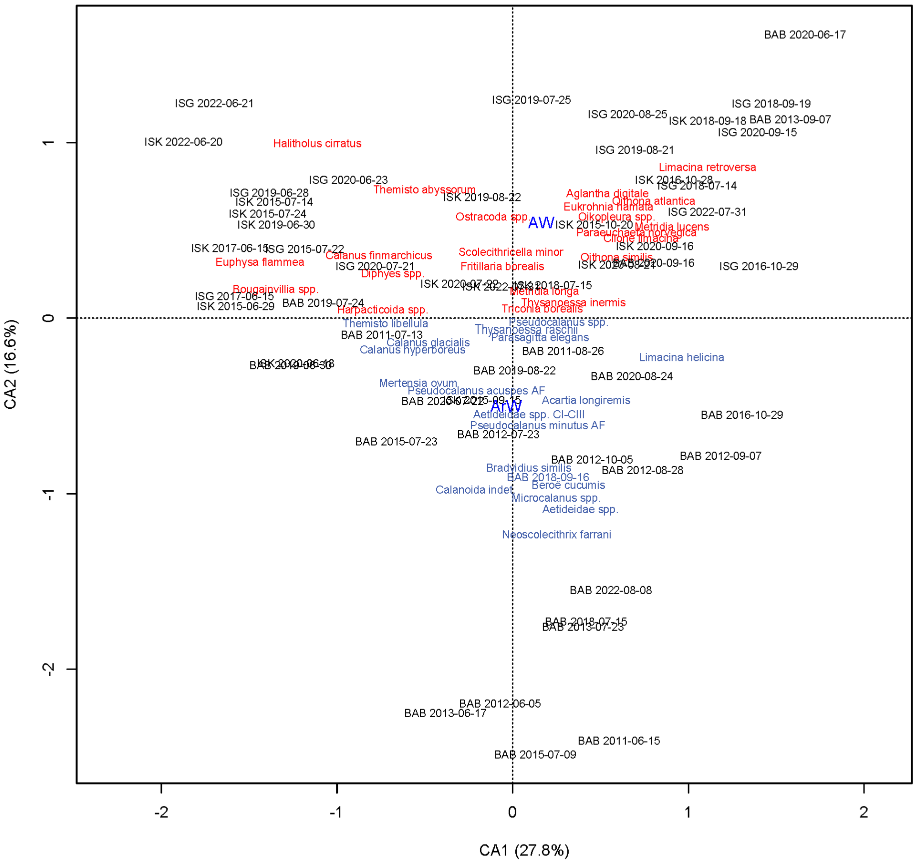

Figure 8: Correspondence analysis of zooplankton community data in Isfjorden, Svalbard, 2011 to 2022. Two factorial environmental variables, Atlantic water (AW) and Arctic water (ArW) placed according to best fit. Species names are separated by color, blue I defined to Arctic species, while red Atlantic/widespread species.

3.3.1 Isfjorden specific zoogeography patterns

Based on the new Isfjorden specific zoogeography, distinct patterns in zoogeography were seen across the transect (Figure 9). BAB was alternating between Arctic and Atlantic zoogeographies being dominant. During the last three years, however, Atlantic species were dominant. At IsK and IsG, the dominant relative zoogeography was Atlantic with an increasing dominance trend in the later years.

Figure 9: Relative abundance of multivariate zoogeography for the innermost part of the fjord (BAB; 2011-2022) and the outermost region (IsK and IsG; 2015-2022), Isfjorden, Svalbard.

Figure 10 shows the mean proportions of Isfjorden specific zoogeography for years when data from all their stations exists (2015-2022), only taking in consideration summer/autumn data (Late July-October) to downscale variability due to seasonality. Here a clear gradient from the inner (BAB) to the outer stations (IsK and IsG) can be seen. The Not Defined (ND) taxa were very low and showed no distinct patterns.

The arctic species significantly decreased from BAB to IsG (paired Wilcox, p=6.262e-05), while Atlantic species significantly increase from BAB to IsG (paired Wilcox, p=6.262e-05). Between the two outer stations, there is a just barely significant difference between IsK and IsG (p=0.05032) for Arctic or Atlantic relative abundance.

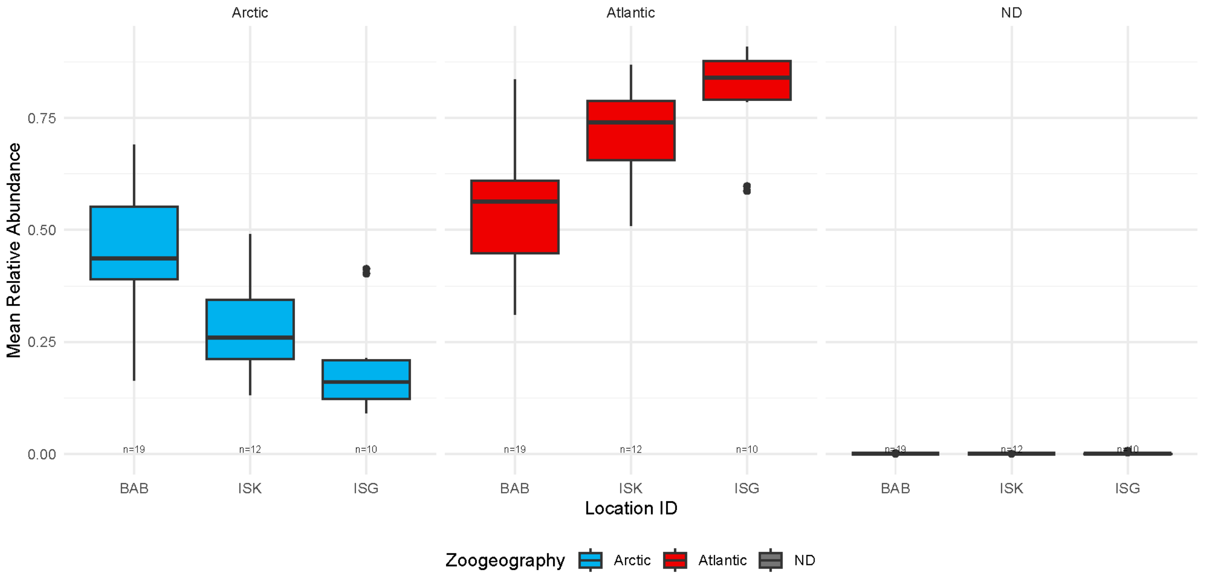

Figure 10: Boxplots depicting the relative abundance of Isfjorden specific zoogeographic for zooplankton at the three stations (BAB, IsK, IsG), Isfjorden, Svalbard, 2015-2022.

3.4 Species abundance

The total abundance (Figure 11) shows that the five taxa; *O. similis*, *Pseudocalanus* spp., *Microcalanus* spp., *C. glacialis* and *C. finmarchicus* comprised more than half of all species found in Isfjorden, independent of station location. In the years 2011 to 2015 total zooplankton abundances were overall high (783.384 – 2.640.619 ind m^{-2}), overall higher in years 2015-2022 (150.791-2.829.196 ind. m^{-2}). This was primarily driven by large variability in *C. glacialis* and *C. finmarchicus*, followed by variability in *O. similis*, *Pseudocalanus* spp. and *Microcalanus* spp., the latter being much more abundant at BAB than elsewhere especially in years 2011-2015. Overall, *C. finmarchicus* was much more prevalent in the outer stations, while *Calanus glacialis* was commonly more abundant at BAB. In October 2012, the total abundance was almost an order of magnitude higher than the rest. The same occurred in July and September 2015 at IsK, and July 2015 at IsG. I can see that these abundances are driven by *Calanus glacialis,* and *Calanus finmarchicus* and to a certain extent *Pseudocalanus spp*.

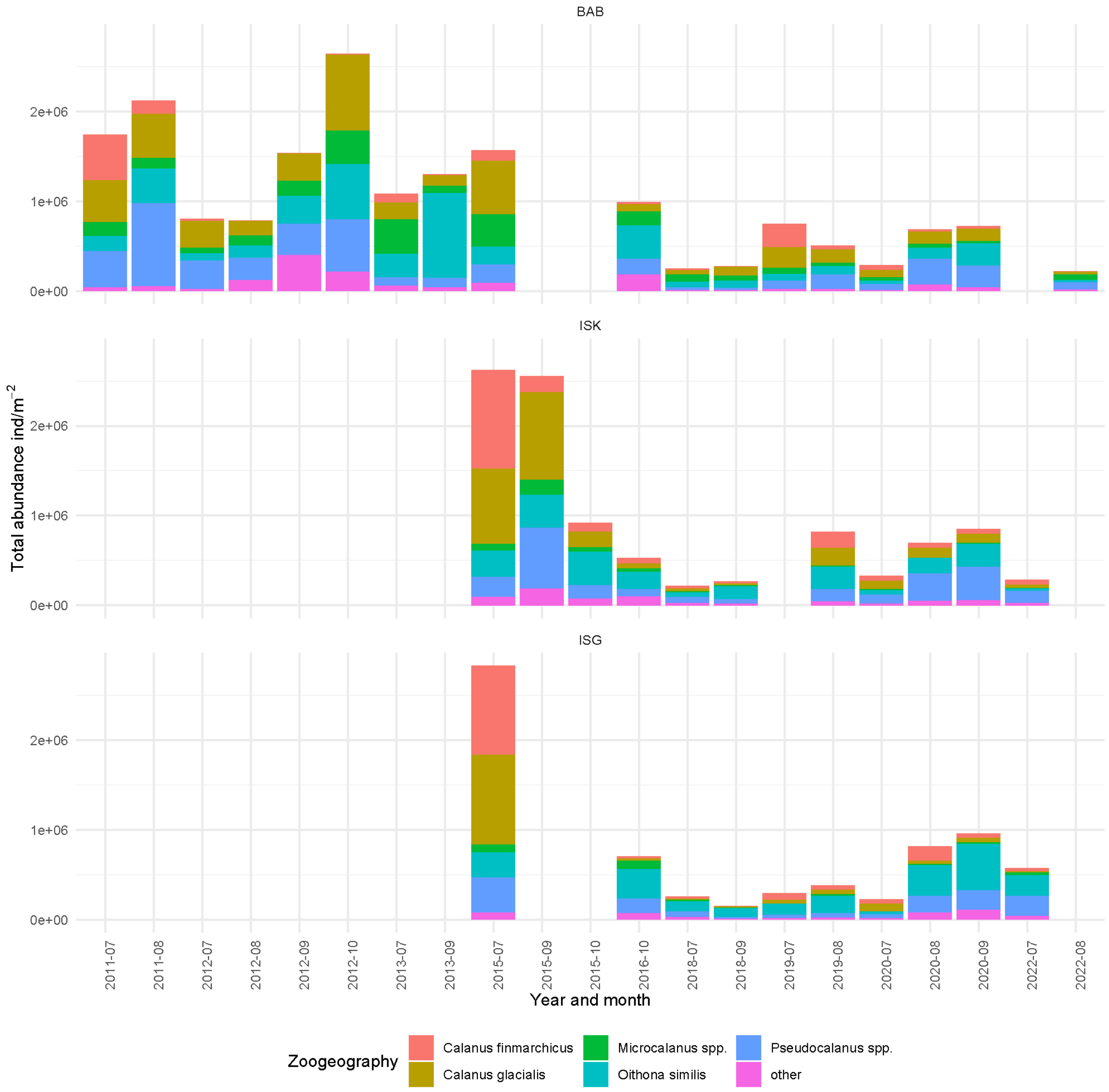

Figure 11: Stacked barplot showing the absolute abundance at BAB, IsK and IsG, Isfjorden, Svalbard, July to October, 2011-2022.

Table 2 of the most abundant species gives us an overview of the zoogeography changes when applying the multivariate approach (Table 2). From the multivariate zoogeography (Figure 10) was Pseudocalanus spp. and Oithona similis defined to be Atlantic, while Microcalanus spp. and Limacina helicina Arctic.

Table 2: Top ten species/taxa in Isfjorden, Svalbard (IMOS-transect), with both their literature-defined and multivariate zoogeography defined zoogeography.

Species	**Literature zoogeography**	**Multivariate zoogeography**
Acartia longiremis	Widespread	Arctic
Calanus finmarchicus	Atlantic	Atlantic
Calanus glacialis	Arctic	Arctic
Limacina helicina	Widespread	Arctic
Metridia longa	Widespread	Atlantic
Microcalanus spp.	Not defined	Arctic
Oithona atlantica	Atlantic	Atlantic
Oithona similis	Widespread	Atlantic
Pseudocalanus minutus AF	Widespread	Arctic
Pseudocalanus spp.	Not defined	Atlantic

4 Discussion

4.1 Hydrography and Zoogeography

Isfjorden has undergone large changes in its hydrography. Since 1987 there has been a distinct increase in summer temperature of 0.6±0.1°C per decade (Skogseth et al., 2020). Coupled with an increase in salinity, this is a clear evidence of increased AW advection (Skogseth et al., 2020). A major change took place in the winter 2005 when special weather systems and ocean densities opened the door for Atlantic water to penetrate into Isfjorden (Nilsen et al. 2008; Skogseth et al. 2020). Since then, proper sea ice has not formed in the Isfjorden (Muckenhuber et al. 2016). From the mooring data (Figure 4), the peak temperature was higher in 2014-2018 than in the years before and after. Indicating stronger influence of Atlantic water in the years 2014-2018. High seasonal variability in temperature is observed. During winter, the temperature commonly sinks close to zero and sometimes below in April which is the month with coldest sea temperatures (Skogseth et al. 2020). The warmest sea temperatures are normally seen in late summer and fall. A closer look at the mean temperature for July-October (Figure 5) showed that BAB had relatively stable summer sea temperatures while IsK and IsG were steadily increasing. In Billefjorden there is a water layer below 50-70m that has stable Arctic conditions with negative temperatures, throughout the year (Søreide et al., 2022). The upper layer, which is above the sill, exhibits seasonal variation, and sometimes hosts traces of Atlantic influenced water especially in summer/late fall. This is likely due to the shallow sill in Billefjorden which acts as a physical barrier and only allow water exchange in the upper 50 m. The mooring provides valuable information on fluctuations in Atlantic influence. For the outermost stations, which are influenced the most by water intrusion into Isfjorden, we only have zooplankton data from 2015 to 2022, which coincided with a more substantial Atlantic influence period. A summer study in 2007 along the entire Isfjorden shows similar zoogeography pattern as this study (Gluchowska et al. 2016) with a distinct higher proportion of boreal and boreal-Arctic zooplankton in the outer Isfjorden compared to inner Billefjorden.

Kongsfjorden, like Isfjorden, lacks a sill at the entrance of the fjord. Which leaves it open for Atlantic influence from the west Spitsbergen current. From 1996 to 2014 the summer temperature in Kongsfjorden has also been steadily increasing with 1°C per decade (Cottier et al., 2022), due to stronger intrusion of Atlantic influenced water masses combined with less extensive winter cooling (Tverberg et al., 2019). Kongsfjorden is much smaller than Isfjorden and has only a small inner glacial bay that is somewhat protected against Atlantic water mass intrusion (Hop et al., 2023).

For the multivariate approach to define zoogeography, the CTD data was not available for every sampling event in Billefjorden (BAB). The rather stable hydrography in Billefjorden in this and earlier studies (e.g. Arnkværn et al. 2005; Søreide et al. 2022) which also was supported from the data available in the UNIS hydrographical data base (Skogseth et al. 2020) this innermost fjord was defined as Arctic water despite some CTD data was missing for some of the sampling events. In Billefjorden (stn. BAB) sea temperatures below -1°C is found year-round in the bottom layer (Søreide et al., 2022), an act as an Arctic refuge for Arctic species (ref). At IsG and IsK the water masses were defined as either Arctic or Atlantic from the TS-plots, after the water mass definitions from Skogseth et al., 2020. From the water mass definitions, we defined AW and TAW as Atlantic, whereas ArW and WCW were defined as Arctic. There were situations where IW was the dominant water mass, which is a mix of water masses, based on its temperature and salinity profiles, IW was put as either Arctic or Atlantic. This was done be evaluating traces of other water masses present in the TS plot, if there was mainly IW with traces of ArW and WCW, the water masses were defined to Arctic. If it was IW and traces of AW or TAW it was defined to Atlantic. This process is to a large extent subjective and introduces some uncertainty as to whether the water masses truly are influenced by Arctic influenced, but supportive CTD data from the hydrographical databases guided the decisions. Traditionally zoogeography is defined by the species core center of distribution (.)In the Isfjorden-specific zoogeography, zoogeography was decided from a much smaller geographical area covering a shorter environmental gradient than zoogeographical distributions in the literature (e.g. Norwegian Sea to the high-Arctic). For this Isfjorden specific study, however, it was a useful approach, as this study can be used as a decadal baseline from which the future zooplankton composition can be compared to. Although several groups do help you distinguish more subtle differences, we have seen that especially boreo-arctic and arctic groups tend to correlate with Arctic water masses, while widespread and boreal groups associate with Atlantic water masses (Gluchowska et al., 2016). This can indicate that having split the zoogeography into two separate groups, in many cases is sufficient, especially in this specific study focusing on Atlantification and the impact of climate change.

4.2 Changes in relative zoogeography in Isfjorden

The outer stations were the most affected by warmer Atlantic water which also was reflected by the relative zooplankton composition with a high relative abundance of Atlantic and widespread tax dominating. Within the same fjord, a somewhat Atlantic influenced system (IsK and IsG) can be compared to a "purer" Arctic, local system (BAB). Looking at the relative abundance of the literature-defined zoogeographies, large differences along the Arctic to Atlantic gradient could be seen. While Arctic species at BAB seem to be in somewhat of a tête-à-tête with widespread species. Widespread species seem to gain an overhand of the relative abundance at the outer stations, especially on IsG furthest out (Figure 6). Gluchowska et al., 2016 found similar results for Isfjorden in 2007, which was right after the regime shift to a more Atlantic fjord (Skogseth et al. 2020). They found a gradient where Arctic relative abundance increases the further away from the mouth they are sampled. While Ubiquitous species decrease in relative abundance, but there Atlantic and Boreo-Arctic species remain stable. They also found that across Kongsfjorden, Isfjorden and Hornsund the zooplankton community in Isfjorden was somewhat in the middle of the three fjords when it comes to being influenced by Atlantic water (Gluchowska et al., 2016). Kongsfjorden and Isfjorden both have relatively deep, open entrances making it more prone to influence from the deep and warm west Spitsbergen current. Hornsund with its shallow entrance, is mainly influenced by the shallow coastal current, making it a more Arctic environment, much like BAB.

The significant differences in mean relative abundance show that BAB is more Arctic than the outer stations. Although not all differences were significant, we can say that BAB is a refuge for Arctic species, which is not the case for the much warmer IsK and IsG which also were reflected in the dominant zoogeographical composition there (Table 3). This is similar to what seen in Kongsfjorden (Hop et al., 2023) and Hornsund (Weslawski et al. 2017), which also have an Arctic cold refuge in the innermost part of the fjords due to glacial bays here. BAB however, is deeper than those in the two other fjords, housing a large local population of *C. glacialis* (Arnkværn et al. 2005; Søreide et. al. 2022) and data from 2011 to present show a rather stable zoogeographical composition these years (Figure 7), even though the mooring data shows increased intrusion and higher peak summer temperatures (Figure 4, Appendix I). It is important to note that Atlantic species were in higher relative abundance the last three years at BAB, possibly indicating that BAB is undergoing a shift. The not defined group relative abundance was high for literature-based zoogeography since the numerous genuses

Pseudocalanus and *Microcalanus* were not identified to species level. Pseudocalanus comprises of three species in Svalbard: The Arctic *P. acuspes* and *P. minutes* and the boreal *P. moultoni* (Ershova et al. 2021). In Isfjorden high percentage of *P. moltouni* has been observed while the Arctic *P. acuspes* prevail in the inner Billefjorden (Ershova et al. 2021; Astad, 2022). The Pseudocalanus was defined as Atlantic in the Isfjorden specific zoogeography (Figure 10) indicate that the boreal *P. moultoni* dominate in numbers here. *Microcalanus* spp. seem to have a high relative abundance at BAB (Figure 11). Primarily two *Microcalanus* species exist in the Arctic; *M. minutes* and *M. pusillus* (Mazzocchi et al. 1995), both considered to be deeper dwelling with a preference for colder water (Søreide et al. 2022).

Applying my zoogeography defined by the CA, we can see that these trends and differences between Arctic vs. Widespread and Atlantic species are accentuated because we grouped them as Atlantic or Arctic. There is a much more apparent gradient from the outermost station to the innermost station (Figure 9, Figure 10). The overall picture stays similar at BAB, with Arctic and Atlantic species exchanging dominance from 2011-2019, however in the last three years of the study Atlantic species have been consecutively dominant. This can indicate that BAB is getting more influenced by Atlantic water, but it is too early to draw any conclusions since few data from 2021 and 2022. Looking at the outer stations, there is a large separation of Arctic and Atlantic species. Species previously in the Not defined group are now also part of either Arctic or Atlantic. *Microcalanus spp.,* which was not defined in the literature, zoogeography is more arctic, while *Pseudocalanus spp.* is now defined as Atlantic. Since *Pseudocalanus* spp. comprise of both Arctic and Atlantic species there is a need to species determine *Pseudocalanus* in future studies to capture the rate of Atlantification. Because these two families were divided into the Atlantic and Arctic, BAB remains in "balance" regarding zoogeographic relative abundance. There is a caveat, since *Pseudocalanus spp.* if defined to species level, could either be Atlantic or Arctic. *Pseudocalanus acuspes*, is regarded as Arctic, and is present in Isfjorden. *P. minutus* is regarded as cosmopolitan with no preference to Atlantic nor Arctic water. *P. moultoni* is regarded as a boreal species (Astad, 2022) and found abundantly in Isfjorden (Ershova, Nyeggen, et al., 2021). Microcalanus abundances have previously been attributed to *Microcalanus pygmaeus*, however other species could be occurring in low numbers (Søreide et al., 2022), without knowing which exact species is present, they could be attributed to each water mass. Both taxa *Microcalanus spp.* and *Pseudocalanus spp.* have high relative abundances, their separation zoogeographically could impact the overall relative zoogeographic abundance in this study. *Metridia longa* has been shown to be marginalized in the increasing atlantifying Arctic (Daase & Eiane, 2007). However, it has also been shown to be thriving in more boreal systems (Diel, 1991) indicating that an Atlantic affiliation in Isfjorden is not unreasonable. *Oithona similis* is regarded as a cosmopolitan and occurs in high abundances year-round. It is predicted that *Oithona similis* will thrive in a warming Arctic, so an increase in its abundance can be used as an indication of increased Atlantic influence.

The overall impression is that increased Atlantic inflow severely affects the relative abundance of zooplankton and that Isfjorden is indeed undergoing borealization. With the IMOS data, I can confidently say that BAB is more stable cold, and much less affected by Atlantic inflow. In contrast, the outer stations are severely affected by the Atlantic inflow. Both zoogeographic approaches show these differences, so we can accept H_{a2} and reject H_{02}. This provides evidence that the outer and middle parts of Isfjorden show significantly higher relative abundances of Atlantic zooplankton species than the innermost part (Figure 7, Figure 10, Table 3, Table 4). Regarding the temporal trends, I cannot show any significant increases in the relative abundance of Atlantic species nor any significant decrease in Arctic species. Looking at the yearly averages, there are indications of both (Figure 6, Figure 9). However, I cannot confidently reject H_{01} and accept H_{a1}. Still, with continued sampling of these three stations, it will be possible to identify a statistical linear relationship where Atlantic and widespread species will become increasingly dominant.

Kongsfjorden zoogeographic changes have been observed by using popular Atlantic indicating species like *Calanus finmarchicus*, *Oithona atlantica*, *Thyssanoessa longicaudata* and *Themisto abyssorum* which in warmer years have higher biomass (Hop, Wold, et al., 2019). Surprisingly, C. *glacialis* seems to have stable abundance, indicating that they are resistant to warming in the temperature window so far seen (Hop, Wold, et al., 2019). There is also a gradient in Kongsfjorden where the abundance and biomass per m^{-3} is increasing from the shelf areas to the inner basin for both Atlantic and Arctic species (Hop, Wold, et al., 2019). It is apparent that the Atlantic species since around 2010 are increasing and have in manycases become more dominant over Arctic species (Vihtakari et al. 2018; Hop, Wold, et al., 2019).

The total abundance of zooplankton (Figure 11) shows that there in general has been somewhat of a decrease in the total abundance at BAB. There are some notable exceptions in the total abundance, especially at BAB October 2012, July and September 2015 at IsK and July 2015 at IsG. There can be multiple reasons for this, none of which we have any proof. There could be exceptionally high productivity in that summer, with high mortality rates as the total abundance returns to more normal levels later in the year. Or there can be methodological issues that are the root of the cause. Before 2015 samples were depth stratified, with either a closing WP2 or Multinet. To make sampling more efficient IMOS switched to water column sampling with WP2. This switch could have caused some confusion in the extrapolation of samples, and they can have been estimated abnormally high. This could also explain the difference we are seeing at BAB comparing before and after 2015.

Comparing BAB to the outer stations we cannot see any difference in productivity, indicating that the Atlantic influence is neither decreasing nor increasing it. This could possibly have been expected as boreal systems tend to be more productive overall.

4.3 Arctic and Atlantic indicator species

The zoogeographic definition of the zooplankton in Isfjorden is limited to water mass definitions using temperature and salinity, not its origin. I could not assume if the species are widespread or Atlantic since studying such a small geographical and environmental range. Our zoogeography is limited to Isfjorden and is helpful in answering questions regarding Atlantic influence and borealization. Traditionally the borealization of Arctic fjords has been shown by selecting zooplankton species, and my zoogeography is an attempt to expand the selection of species for monitoring borealization in Isfjorden and potentially other Arctic fjords. Several species defined as widespread and not defined in literature were now separated into Arctic and Atlantic (Table 2). This enabled us to get a clearer understanding of how the borealization of Isfjorden. Notable species in my zoogeography newly defined as Atlantic are *Metridia longa, Oithona similis,* and *Pseudocalanus spp*. At the same time, Arctic-defined species are *Limacina helicina, Acartia longiremis*, *Microcalanus spp*., and *Pseudocalanus minutus AF.* The species in Table 2 are the most abundant and comprise more than 90% of the species found in IMOS for July-October. Following these select species and their abundances will likely give a more accurate indication of borealization than just following *C. glacialis* and *C. finmarchicus*. They are highly correlated to Arctic and Atlantic waters. They are traditionally separated by size, with a subsample confirmed by molecular methods. This introduces uncertainty in the individuals at the borders of their prosome size, there have been errors up to 80% when separating *C. glacialis* and *C. finmarchicus* (Gabrielsen et al., 2012). Using several species as an indicator of Atlantic influence creates a more robust framework to follow the impact of the ongoing climatic shift on the Arctic zooplankton communities. My zoogeography is simpler to understand from the plots and is tailored to investigate the impact of Atlantic inflow, which is a key factor when it comes to understanding the impact of climate change on the marine environment in the Arctic.

4.4 Suggestions for future changes to IMOS

The zooplankton data is of high quality, and the sampling protocol works well. It is important to stress that Oithona AS should continue to do the analysis, as this is a lifeline for continuity in the time series. However, for long term consistency, there is a future in metabarcoding. If we manage to be able to quantify the data from molecular methods this would enable a much more exact identification of species, and we would not be limited by having certain species identified to taxon only. This would have several benefits and would potentially enable us to track how populations are changing genetically and that IMOS in the future is not reliant on certain individuals for identification consistency. Two major considerations going forward in IMOS are, firstly the overall sampling strategy could be revised somewhat, and this is dependent on the aim of the project. If the aim is to support management, it would be an advantage that the sampling effort is equalized between the years, and that the summer and fall months are sampled, preferably up to two times a month. I can see however that IsK and IsG show similar development, and for cost and time saving only IsK could be sampled, in addition to BAB. This could be valuable data for management, and to track changes caused by increased Atlantic pressure. Secondly, storage of CTD data needs revision. There is a lack of protocol, which understandably is since CTDs are normally operated by a technician onboard the research vessel. However, it should be noted that the person in charge of sampling must ensure that the data gets downloaded, and headers get standardized, and immediately uploaded to a secure common storage upon return. For handheld CTD devices that do not automatically split the different casts, it is imperative that this is done by the personnel sampling as this can be a close to impossible task for the researchers to do later.

The IMOS data is valuable for management as it contains data for over a decade, and continuation of the project enables us to tell the story of how the Arctic is affected due to climate change. The opportunistic framework of IMOS is commendable, but it requires a stricter system for data storage to fully reach its potential. This is where the Darwin Core data management comes in, following DwC makes sure that the data is future proof, and if uploaded, accessible by all interested parties. I would recommend in addition to a revised CTD protocol to write a data policy, so that data is stored and made available, as soon as it is collected. Isfjorden contains all the necessary qualities which make it an excellent model system for Spitsbergen, with both open areas influenced by outside water, and silled system, remaining more Arctic.

With data sharing becoming increasingly common within science, it could be of high interest to coordinate sampling strategies in Svalbard fjords (e.g. Gluchowska et al., 2016; Hop, Assmy, et al., 2019). Although there are strong synergies between different institutions already, collective sampling could present valuable data for management, and enable more frequent data and that from several fjords for better monitoring the Atlantification of high-Arctic zooplankton communities in the European Arctic.

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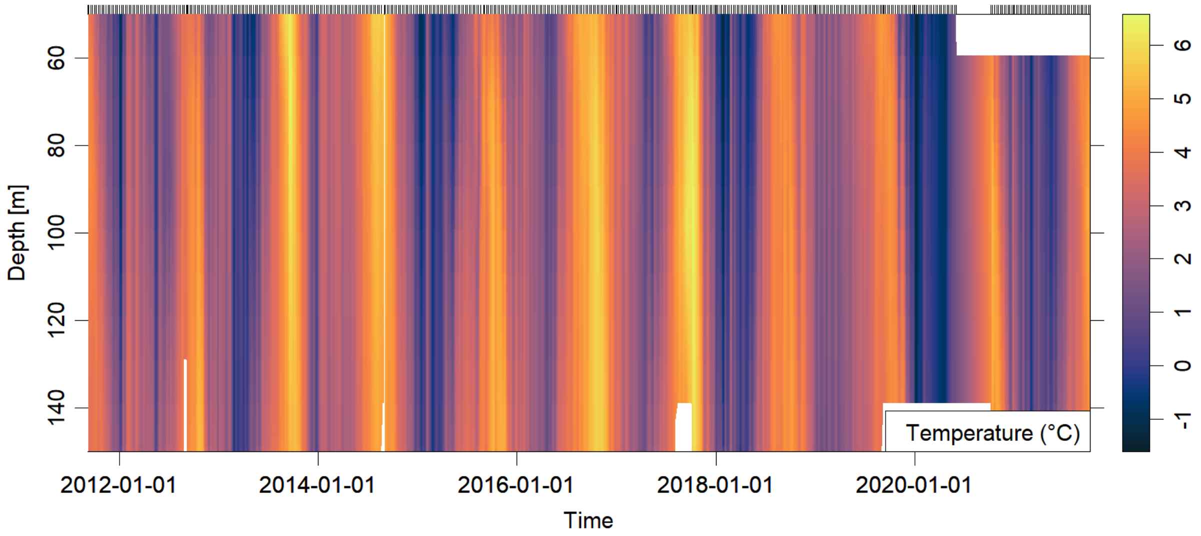
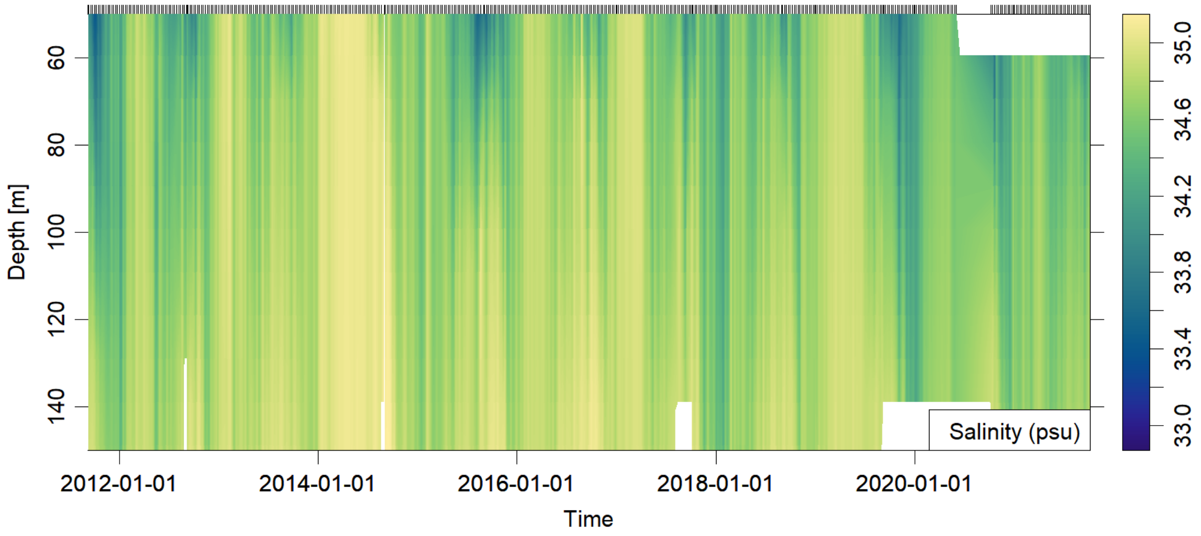
6 Appendix

6.1 Appendix I: Mooring section plots





6.2 Appendix II: R script for plotting mooring data

```
#read NetCDF files and compile to dataframe
{
  library(RNetCDF)
  library(tidyverse)
  library(lubridate)
  library(ggOceanPlots)
  library(readxl)
  library(writexl)
  setwd("directory address ")
  # Get the list of NetCDF files in the directory
```

```
  file_list <- list.files(pattern = "\\.nc$")
  # Initialize an empty list to store the individual datasets
  dataset_list <- list()
  dataset_list1<- list()
  dataset_list2 <- list()

  # Iterate over each file
  for (file in file_list) {
    # Open the NetCDF file
    data <- open.nc(file)

    # Extract the variables
    temp <- var.get.nc(data, "TEMP")
    depth <- var.get.nc(data, "MPRES")
    time <- var.get.nc(data, "TIME")
    sal <- var.get.nc(data, "PSAL")
    vel <- var.get.nc(data,"UVEL")
    # Close the NetCDF file
    close.nc(data)

    # Convert variables to data frames
    temp <- as.data.frame(temp)
    sal <- as.data.frame(sal)
    depth <- round(depth)
    vel <-as.data.frame(vel)

    # Convert time to POSIXct format using lubridate
    base_date <- as.POSIXct("1950-01-01T00:00:00Z", tz = "UTC")
    time_minutes <- base_date + round(as.numeric(time) * 24 * 60) * 60
    time <- as.data.frame(time_minutes)

    # Transpose the temperature data frame and set column names
    temp <- t(temp)
    colnames(temp) <- depth
    sal<-t(sal)
    colnames(sal)<- depth
    vel <- t(vel)
    colnames(vel)<-depth

    # Combine temperature and time data frames
    temp <- cbind(temp, time)
    sal <- cbind(sal, time)
    vel <-cbind(vel,time)

    # Append the current dataset to the list
    dataset_list <- c(dataset_list, list(temp))
    dataset_list1 <- c(dataset_list1,list(sal))
    dataset_list2 <- c(dataset_list2,list(vel))
  }

  {# Combine all datasets into one
    combined_dataset <- bind_rows(dataset_list)
    combined_dataset <- combined_dataset[, c("time_minutes", setdiff(names(combined_dataset),
"time_minutes"))]
    #pivot the dataset so it works with tidyverse
    combined_dataset <- combined_dataset%>%
      pivot_longer('13':'148',names_to = "depthInMetres",values_to = "temperatureCelsius")
    combined_dataset <- combined_dataset[complete.cases(combined_dataset), ]

    combined_dataset1 <- bind_rows(dataset_list1)
    combined_dataset1 <- combined_dataset1[, c("time_minutes", setdiff(names(combined_dataset1),
"time_minutes"))]
    #pivot the dataset so it works with tidyverse
    combined_dataset1 <- combined_dataset1%>%
      pivot_longer('13':'148',names_to = "depthInMetres",values_to = "practicalSalinity")
    combined_dataset1 <- combined_dataset1[complete.cases(combined_dataset1), ]
```

```
    combined_dataset2 <- bind_rows(dataset_list2)
    combined_dataset2 <- combined_dataset2[, c("time_minutes", setdiff(names(combined_dataset2),
"time_minutes"))]
    #pivot the dataset so it works with tidyverse
    combined_dataset2 <- combined_dataset2%>%
      pivot_longer('13':'148',names_to = "depthInMetres",values_to = "velocity")
    combined_dataset2 <- combined_dataset2[complete.cases(combined_dataset2), ]
  }

  mooring<-full_join(combined_dataset,combined_dataset1)
  mooring<-full_join(mooring, combined_dataset2)
  #removing unneccessary data
  rm(combined_dataset)
  rm(combined_dataset1)
  rm(combined_dataset2)
  rm(dataset_list)
  rm(dataset_list1)
  rm(dataset_list2)
  rm(sal)
  rm(temp)
  rm(time)
  rm(base_date)
  rm(data)
  rm(depth)
  rm(file)
  rm(file_list)
  rm(time_minutes)
  rm(vel)
}

#Average data over depths and per week
{
mooring$depthInMetres<-as.numeric(mooring$depthInMetres)
mooring <- mooring%>%
    filter(depthInMetres>=45&
             depthInMetres<=150)
mooring<-mooring%>%
  rename(eventDate=time_minutes)
mooring$eventDate <- floor_date(mooring$eventDate, unit = "day")

watermasses <- mooring%>%
  mutate(month = week(eventDate),
         year = year(eventDate))
#applying water mass definitions accordin to R. Skogseth et al. (2020)
watermasses <- watermasses %>%
  drop_na(temperatureCelsius, practicalSalinity) %>%
  mutate(water_type = case_when(
    temperatureCelsius >= 3 & practicalSalinity >= 34.9 ~ "AW",
    temperatureCelsius >= 1 & practicalSalinity >= 34 & practicalSalinity <= 34.7 ~ "IW",
    temperatureCelsius >= 1 & practicalSalinity < 34 ~ "SW",
    temperatureCelsius <= 0 & practicalSalinity >=34.3 & practicalSalinity <=34.8 ~ "ArW",
    temperatureCelsius < -0.5 & practicalSalinity >= 34.4 ~ "WCW",
    temperatureCelsius <1 & practicalSalinity >= 32 ~ "LW",
    temperatureCelsius >= 1 & temperatureCelsius <= 3 & practicalSalinity >=34.7 &
practicalSalinity<=34.9 ~ "TAW",
    TRUE ~ "Undefined"
  ))
#remove unneccessary df
rm(mooring)
}

#plotting temperature, salinity and percentage water mass
{
water<-watermasses%>%
  select(eventDate,water_type)%>%
```

```
  mutate(unit="water_mass")

#plot water temperature and salinity over time

  mooring <- watermasses%>%
  select(-c(velocity,month,year,water_type))%>%
  group_by(eventDate)%>%
  summarize(temperatureCelsius=mean(temperatureCelsius),
            practicalSalinity=mean(practicalSalinity))%>%
  pivot_longer("temperatureCelsius":"practicalSalinity", names_to = "unit",values_to="values")


ggplot()+
  geom_line(data=mooring,aes(x=eventDate, y=values))+
  geom_smooth(data=mooring,aes(x=eventDate, y=values))+
  geom_bar(data=water,aes(x=eventDate,fill=water_type),position="fill")+
  scale_fill_manual(values=c("ArW"="cyan1","AW"="brown1","IW"="chartreuse3","LW"="lightgreen",

"SW"="darkorchid4","TAW"="darkorange","Undefined"="azure3","WCW"="deeppink2"))+
  facet_wrap(~factor(unit,levels=c("temperatureCelsius","practicalSalinity","water_mass")), scales =
"free_y",
             ncol=1,
             strip.position = "left",
             labeller = as_labeller(c(temperatureCelsius="Temperature (°C)",practicalSalinity="Salinity
(PSU)",water_mass="Percentage watermass") ) )  +
  xlab("Date")+
  ylab(NULL)+
  labs(title="Temperature, Salinity and percentage of watermass at Isfjorden South Mooring")+
  theme_minimal()+
  theme(strip.background = element_blank(),
        strip.placement = "outside",
        legend.position = "bottom")
}
```

6.3 Appendix III: R Script for plotting zooplankton data

This script is Hardcoded and should work as long as you use standard names, defined in DwC and in the sheets defining zoogeography use zooGeography for literature zoogeography and zooGeographyCA for your own zoogeography. The data entered is in n*m-3 using darwincore terms.

The data is automatically calculated to m-2 if the depth interval is listed.

#R Script for all zooplankton plots

```
{
setwd("directory adress")
library(tidyverse)
library(lubridate)
library(readxl)
library(writexl)

zoo <- read_excel("IMOS.xlsx")
zoo <-zoo%>%pivot_longer("Acartia longiremis":"Triconia borealis", names_to="scientificName",values_to
="indm2")

#collapsing and summarising the data so it is indm2 and not depth seperated anymore
```

```
aggregated_data <- zoo %>%
  group_by(eventDate,locationID,decimalLatitude,decimalLongitude,scientificName) %>%
  summarize(
    total_species = sum(indm2, na.rm = TRUE),
    max_depth = max(maximumDepthInMeters, na.rm = TRUE)
  )

aggregated_data <- aggregated_data %>%
  group_by(eventDate,locationID,decimalLatitude,decimalLongitude,scientificName) %>%
  summarize(
    total_species = sum(total_species, na.rm = TRUE),
    max_depth = max(max_depth, na.rm = TRUE)
  ) %>%
  mutate(
    indm2 = total_species * max_depth
  )
#selecting the data we want to keep
zoo <- aggregated_data%>%
  select(eventDate, locationID,decimalLatitude,decimalLongitude,scientificName,indm2)
#removing unneccesary dataframe
rm(aggregated_data)
#Attaching information about the different species in dataset
meta1 <- read_excel("Zooplankton_species_data.xlsx")
meta2 <- read_excel("Spec_multi.xlsx")
meta <- left_join(meta1,meta2)
zoo<- left_join(zoo,meta)
rm(meta,meta1, meta2)
#making sure the date format is uniform and in the lubridate format
zoo <- zoo %>%
  mutate(Date = ymd(eventDate))
#filtering out everything except holoplankton and adults
zoo <- zoo %>%
  filter(meroHoloPlankton=="holoplankton")
zoo <- zoo%>%
  filter(larvae=="adult")
#attaching additional station metadata
zoo <- zoo %>%
  mutate(stationType = case_when(
    locationID == "BAB" ~ "innermost",
    locationID %in% c("IsG", "IsK") ~ "outermost"))
}
#here you select which month you want to look at 1=January, 2=Februare etc.
#The month you select is included (>=)

startmonth <- 7
endmonth <- 10

{
#creating df containging only literature zoogeography and calculating relative abundance
zoolit <- zoo %>%
  filter((month(eventDate) >= startmonth ) &
           month(eventDate) <= endmonth)%>%
  group_by(eventDate, locationID) %>%
  mutate(total_indm2_by_event_location = sum(indm2)) %>%
  group_by(eventDate, locationID, zooGeography, total_indm2_by_event_location) %>%
  summarise(sum_indm2 = sum(indm2),
            relative_abundance = sum_indm2 / first(total_indm2_by_event_location))
#creating df containing only multivariate zoogeography and calculating relative abundance
zooca <- zoo %>%
  filter((month(eventDate) > startmonth ) &
           month(eventDate) <= endmonth)%>%
  group_by(eventDate, locationID) %>%
  mutate(total_indm2_by_event_location = sum(indm2)) %>%
  group_by(eventDate, locationID, zooGeographyCA, total_indm2_by_event_location) %>%
  summarise(sum_indm2 = sum(indm2),
            relative_abundance = sum_indm2 / first(total_indm2_by_event_location))
```

```
#removing unnecessary Nas created by the combination of different zoogeographies
zooca <- zooca %>%
  drop_na()

#calculating yearly averages for literature zoogeography
yearly_averages_lit_fall <- zoolit%>%
group_by(year = year(eventDate), zooGeography, locationID) %>%
  summarize(avg_relative_abundance = mean(relative_abundance, na.rm = TRUE), .groups = 'drop')
#calculating yearly averages for multivariate zoogeography
yearly_averages_ca_fall <- zooca %>%
group_by(year = year(eventDate), zooGeographyCA, locationID) %>%
  summarize(avg_relative_abundance = mean(relative_abundance, na.rm = TRUE), .groups = 'drop')
#removing unnecessary DF
rm(zoo)
}
#scatterplot with yearly averages for literature zoogeograhy
zoolit %>%
  ggplot(aes(x = eventDate, y = relative_abundance, color = zooGeography)) +
  geom_point() +
  geom_line(data = yearly_averages_lit_fall, aes(x = as.POSIXct(as.Date(paste(year, "-08-15",
sep=""))), y = avg_relative_abundance, linetype = "Yearly Average")) +
  ylim(0,1) +
  facet_grid(~as.factor(locationID)) +
  labs(x = "Date",
       y = "Relative Abundance",
       title = "Zoogeographic relative abundance (July-October)",
       subtitle = "Literature zoogeography") +
  scale_color_manual(values = c("Arctic" = "deepskyblue2",
                              "Widespread" = "darkgoldenrod2",
                              "Atlantic" = "red2",
                              "Not defined" = "grey46")) +
  scale_linetype_manual(values = c("Yearly Average" = "solid")) +
  theme_minimal()+
  theme(legend.position = "bottom")
#scatter and lineplot for multivariate zoogeography
zooca %>%
  ggplot(aes(x = eventDate, y = relative_abundance, color = zooGeographyCA)) +
  geom_point() +
  geom_line(data = yearly_averages_ca_fall, aes(x = as.POSIXct(as.Date(paste(year, "-08-15", sep=""))),
y = avg_relative_abundance, linetype = "Yearly Average")) +
  ylim(0,1) +
  facet_grid(~as.factor(locationID)) +
  labs(x = "Date",
       y = "Relative Abundance",
       title = "Zoogeographic relative abundance (July - October)",
       subtitle = "Multivariate zoogeography") +
  scale_color_manual(values = c("Arctic" = "deepskyblue2",
                              "Widespread" = "darkgoldenrod2",
                              "Atlantic" = "red2",
                              "Not defined" = "grey46")) +
  scale_linetype_manual(values = c("Yearly Average" = "solid")) +
  theme_minimal()+
  theme(legend.position = "bottom")
#boxplot for literature zoogeography
zoolit %>%
  ggplot(aes(x = factor(locationID,levels=c("BAB","IsK","IsG")), y = relative_abundance, fill =
zooGeography)) +
  geom_boxplot() +
  facet_grid(~ factor(zooGeography, levels=c("Arctic", "Atlantic","Widespread","Not defined"))) +
  geom_text(aes(label=paste0("n=", ..count..)), y=0.01, stat='count', colour="black", size=2) +
  labs(x = "Location ID", y = "Mean Relative Abundance",
       fill="Zoogeography", title = "Relative abundance of zoogeography (July-October)",
       subtitle="Literature zoogeography") +
  scale_fill_manual(values = c("Arctic" = "deepskyblue2", "Widespread" = "darkgoldenrod2", "Atlantic" =
"red2", "Not defined" = "grey46")) +
  theme_minimal()+
```

```
  theme(legend.position = "bottom")
#boxplot for multivariate zoogeography
zooca %>%
  ggplot(aes(x = factor(locationID,levels=c("BAB","IsK","IsG")), y = relative_abundance, fill =
zooGeographyCA)) +
  geom_boxplot() +
  facet_wrap(~ factor(zooGeographyCA), nrow = 1) +
  geom_text(aes(label=paste0("n=", ..count..)), y=0.01, stat='count', colour="black", size=2) +
  labs(x = "Location ID", y = "Mean Relative Abundance", fill="Zoogeography",
       title = "Relative abundance of zoogeography (July-October)",
       subtitle="Multivariate zoogeography") +
  scale_fill_manual(values = c("Arctic" = "deepskyblue2", "Atlantic" = "red2", "ND" = "grey46")) +
  theme_minimal()+
  theme(legend.position = "bottom")

#testing mean differences (literature zoogeography), change the zoogeography in zoolit$zooGeography ==
""
kruskal <- zoolit[zoolit$zooGeography == "Atlantic", ]
hist(kruskal$relative_abundance)
kruskal.test(relative_abundance~locationID,data=kruskal)
pairwise.wilcox.test(kruskal$relative_abundance,kruskal$locationID)

#testing mean differences (multivariate zoogeography), change the zoogeography in zooca$zooGeography ==
""
kr <- zooca[zooca$zooGeographyCA == "Atlantic", ]
hist(kr$relative_abundance)
kruskal.test(relative_abundance~locationID,data=kr)
pairwise.wilcox.test(kr$relative_abundance,kr$locationID)
```

6.4 Appendix IV: R script for plotting CTD data

```
{
library(ncdf4)
library(tidyverse)
library(lubridate)
library(broom)
library(cowplot)
library(readxl)
setwd("working directory adress")
# Directory path containing the netCDF files
directory_path <- "path to CTD unis hydrography"
ctd1 <- read_excel("your ctd data")


# Define the three coordinate boxes along with their corresponding station names
box1 <- list(lat_min = 78.54, lat_max = 78.71, lon_min = 16.23, lon_max = 17.10, station = "BAB")
box2 <- list(lat_min = 72.24, lat_max = 78.44, lon_min = 14.24, lon_max = 15.67, station = "IsK")
box3 <- list(lat_min = 78.04, lat_max = 78.26, lon_min = 13.15, lon_max = 14.31, station = "IsG")

# Combine the boxes into a list
boxes <- list(box1, box2, box3)

# Create an empty list to store the data frames for each box
box_data_list <- list()

# Get a list of netCDF files in the directory
file_paths <- list.files(path = directory_path, pattern = "\\.nc$", full.names = TRUE)

# Iterate over each netCDF file
for (file_path in file_paths) {
  # Read the netCDF file
  nc_data <- nc_open(file_path)

  # Check if the required variable names exist in the file
  required_variables <- c("LATITUDE", "LONGITUDE", "TEMP")
```

```
  if (!all(required_variables %in% names(nc_data$var))) {
    message("Skipping file: ", file_path)
    nc_close(nc_data)
    next
  }

  # Extract latitude, longitude, and temperature
  latitude <- ncvar_get(nc_data, "LATITUDE")
  longitude <- ncvar_get(nc_data, "LONGITUDE")
  temperature <- ncvar_get(nc_data, "TEMP")
  depth <- ncvar_get(nc_data, "PRES")

  # Extract the date from the file name
  file_name <- basename(file_path)
  date <- str_extract(file_name, "\\d{8}")
  formatted_date <- as.Date(date, format = "%Y%m%d")

  # Check if the coordinates fall within any of the boxes
  for (box in boxes) {
    in_box <- latitude >= box$lat_min & latitude <= box$lat_max &
      longitude >= box$lon_min & longitude <= box$lon_max

    if (any(in_box)) {
      # Create a data frame with latitude, longitude, temperature, and date
      box_data <- data.frame(latitude[in_box], longitude[in_box], temperature[in_box], depth[in_box])
      box_data$date <- formatted_date

      # Add the station name to the data frame
      box_data$station <- box$station

      # Add the box's data frame to the list
      box_data_list[[box$station]] <- bind_rows(box_data_list[[box$station]], box_data)
    }
  }

  # Close the netCDF file
  nc_close(nc_data)
}

# Combine all the box data frames into a single data frame
combined_data <- bind_rows(box_data_list)

ctd <- combined_data%>%
  select(station,date, temperature.in_box., depth.in_box.)%>%
  distinct()
ctd <- ctd %>%
  rename(locationID = station, eventDate = date, temperature= temperature.in_box., depth =
depth.in_box.)
ctd$depth <- as.double(ctd$depth)


ctd1 <- ctd1 %>%
  mutate(eventDate = parse_date_time(eventDate, orders = c("dmy", "mdy", "ymd")))

ctd <- bind_rows(ctd,ctd1)
ctd <- ctd %>%
  filter(depth >= 5)%>%
  group_by(locationID, eventDate) %>%
  summarise(average_temperature = mean(temperature))

}

ctd%>%
  filter((month(eventDate) >= 7 ) &
           month(eventDate) <= 10)%>%
  ggplot(aes(x = eventDate, y = average_temperature))+
```

```
geom_point()+
geom_smooth(method=loess,se=F, color ="red")+
labs(x = "Date",
     y = "Temperature",
     title = "Mean temperature at stations for July-October",
     subtitle = "from 5 metres to bottom") +
facet_grid(~factor(locationID, levels=c("BAB","IsK","IsG")))+
theme_minimal()
```

6.5 Appendix VI: Table over species removed for correspondence analysis.

Supplementary table 1: Table over species removed from CA analysis.

Removed species
Aeginopsis laurentii
Apherusa sp.
Ctenophora sp.
Gaidius tenuispinus
Hyperoche medusarum
Microsetella norvegica
Mysidae sp.
Oncaea sp.
Pelagobia sp.
Plotocnidae borealis
Siphonophora indet.
Tomopteris helgolandica
Amphipoda indet.
Bougainvillia superciliaris

Evadne nordmanni
Heterorhabdus norvegicus
Meganyctiphanes norvegica
Monstrilloida spp.
Oithona nana
Paraeuchaeta spp.
Pleuromamma robusta
Sarsia spp.
Thysanoessa longicaudata

6.6 Appendix VII:

6.6.1 Table over literature zoogeography and multivariate zoogeography

In table references are as follows: 1. Kosobokova et al., 2011, 2. (*WoRMS - World Register of Marine Species*, n.d.), 3. (*Home, Arctic Ocean Biodiversity*, n.d.) and 4. Beaugrand et al., 2002

Supplementary table 2: Table over species and their respective zoogeographies

scientificName	**Zoogeography**	**Reference**	**Multivariate zoogeography**
Acartia longiremis	Widespread	4; 1, 2	Arctic
Acartia sp.	Not defined		ND
Aeginopsis laurentii	Widespread	1, 2	ND
Aetideidae spp.	Not defined		Arctic

Aetideopsis minor	Widespread	1	ND
Aetideopsis rostrata	Arctic	1	ND
Aetideus armatus	Atlantic	4	ND
Aglantha digitale	Arctic	1	Atlantic
Amphipoda indet.	Not defined		ND
Anomalocera patersoni	Atlantic	2	ND
Anthozoa indet.	Not defined		ND
Apherusa glacialis	Arctic	1	ND
Apherusa sp.	Not defined		ND
Appendicularia indet.	Not defined		ND
Atolla sp.	Not defined		ND
Augaptilidae indet.	Not defined		ND
Augaptilus glacialis	Arctic	1	ND
Beroë cucumis	Widespread	1	Arctic
Boreomysis arctica	Widespread	1	ND
Boroecia borealis	Widespread	1	ND
Boroecia maxima	Widespread	2	ND
Bosmina sp.	Not defined		ND
Botrynema ellinorae	Arctic	1	ND
Bougainvillia spp.	Not defined		Arctic
Bougainvillia superciliaris	Widespread	2	ND

Bradyidius similis	Arctic	1	Arctic
Calanoida indet.	Not defined		Arctic
Calanus finmarchicus	Atlantic	4; 1	Atlantic
Calanus glacialis	Arctic	4	Arctic
Calanus hyperboreus	Arctic	4	Arctic
Calanus spp.	Not defined		ND
Centropages hamatus	Atlantic	2	ND
Centropages spp.	Not defined		ND
Centropages typicus	Atlantic	2	ND
Cephalopoda indet.	Not defined		ND
Chaetognatha indet.	Not defined		ND
Chiridiella abyssalis	Widespread	1	ND
Chiridius obtusifrons	Widespread	1	ND
Clione limacina	Widespread	1	Atlantic
Copepoda indet.	Not defined		ND
Crossota norvegica	Widespread	2	ND
Ctenophora indet.	Not defined		ND
Cumacea sp.	Not defined		ND
Cyclocaris guilelmi	Widespread	1	ND
Cyclopina schneideri	Atlantic	?	ND
Cyclopoida indet.	Not defined		ND

Decapoda indet.	Not defined		ND
Dimophyes arctica	Arctic	3	ND
Diphyes spp.	Not defined		Atlantic
Disco sp.	Not defined		ND
Discoconchoecia elegans	Widespread	1	ND
Eggs indet.	Not defined		ND
Eukrohnia hamata	Widespread	1	Atlantic
Eukrohnia sp.	Not defined		ND
Euphausiacea indet.	Not defined		ND
Euphysa flammea	Arctic	3	Atlantic
Eusergestes arcticus	Widespread	2	ND
Eusirus holmii	Arctic	1	ND
Eusirus sp.	Not defined		ND
Evadne nordmanni	Atlantic		ND
Facetotecta indet.	Not defined		ND
Fritillaria borealis	Widespread	2	Atlantic
Gaetanus brevispinus	Widespread	1	ND
Gaetanus tenuispinus	Widespread	1	ND
Gaidius tenuispinus	Widespread	1	ND
Gammaracanthus loricatus	Arctic	1	ND
Gammaridea indet.	Not defined		ND

Gammarus wilkitzkii	Arctic	1	ND
Gilia reticulata	Widespread	1	ND
Halitholus cirratus	Arctic	3	Atlantic
Halitholus pauper	Widespread	3	ND
Haloptilus acutifrons	Widespread	1	ND
Harpacticoida spp.	Not defined		Arctic
Heterorhabdus compactus	Not defined		ND
Heterorhabdus norvegicus	Widespread	4; 1	ND
Homeognathia brevis	Atlantic		ND
Homeonema spp.	Not defined		ND
Homoeonema platygonon	Widespread	1	ND
Hydrozoa indet.	Not defined		ND
Hymenodora glacialis	Widespread	1	ND
Hyperia galba	Atlantic	?	ND
Hyperia medusarum	Atlantic	?	ND
Hyperiidae indet.	Not defined		ND
Hyperoche medusarum	Atlantic	?	ND
Isopoda indet.	Not defined		ND
Jaschnovia brevis	Arctic	1	ND
Lepidepecreum umbo	Atlantic	?	ND
Limacina helicina	Widespread	1	Arctic

Limacina retroversa	Widespread	2	Atlantic
Limnocalanus macrurus	Atlantic	?	ND
Lubbockia glacialis	Widespread	1	ND
Lucicutia polaris	Widespread	1	ND
Marrus orthocanna	Widespread	2	ND
Meganyctiphanes norvegica	Atlantic	1	ND
Mertensia ovum	Widespread	1	Arctic
Mesaiokeras spitsbergensis	Arctic	?	ND
Metridia longa	Widespread	4; 1	Atlantic
Metridia lucens	Atlantic	1	Atlantic
Microcalanus spp.	Not defined		Arctic
Microsetella norvegica	Widespread	1	ND
Mitrocomella sp.	Not defined		ND
Monstrilloida spp.	Not defined		ND
Munnopsis typica	Atlantic	?	ND
Mysidae sp.	Not defined		ND
Mysis oculata	Atlantic	?	ND
Nanomia cara	Arctic	?	ND
Nematoda indet.	Not defined		ND
Nemertea indet.	Not defined		ND
Neomormonilla minor	Atlantic		ND

Neoscolecithrix farrani	Atlantic		Arctic
Neoscolecithrix sp.	Not defined		ND
Obelia sp.	Not defined		ND
Oikopleura spp.	Not defined		Atlantic
Oithona atlantica	Atlantic	1	Atlantic
Oithona nana	Not defined		ND
Oithona similis	Widespread	1	Atlantic
Oithona sp.	Not defined		ND
Oncaea parila	Arctic	1	ND
Oncaea pumilis	Arctic	?	ND
Oncaea sp.	Not defined		ND
Onisimus glacialis	Arctic	1	ND
Onisimus nanseni	Arctic	1	ND
Onisimus spp.	Not defined		ND
Ostracoda spp.	Not defined		Atlantic
Pachyptilus pacificus	Not defined		ND
Pandalus borealis	Widespread	2	ND
Paradisco nudus	Atlantic	?	ND
Paraeuchaeta barbata	Widespread	1	ND
Paraeuchaeta glacialis	Widespread	1	ND
Paraeuchaeta norvegica	Atlantic	4; 1	Atlantic

Paraheterorhabdus compactus	Widespread	1	ND
Parasagitta elegans	Atlantic	1	Arctic
Pasiphaea tarda	Widespread	2	ND
Pelagobia sp.	Not defined		ND
Pertsovius fjordicus	Atlantic	?	ND
Pisces indet.	Not defined		ND
Pleuromamma robusta	Atlantic	4; 1	ND
Plotocnidae borealis	Atlantic	3	ND
Plotocnide borealis	Atlantic	2	
Podon leuckartii	Widespread	2	ND
Pontophilus norvegicus	Widespread	2	ND
Pseudocalanus acuspes AF	Arctic	1,2	Arctic
Pseudocalanus minutus AF	Widespread	1	Arctic
Pseudocalanus spp.	Not defined		Atlantic
Pseudochirella spectabilis	Arctic	1	ND
Pseudomma truncatum	Widespread	2	ND
Pseudosagitta maxima	Widespread	3	ND
Rathkea octopunctata	Atlantic	?	ND
Rhincalanus nasutus	Widespread	1,2	ND
Rythabis atlantica	Atlantic		ND
Sabinea septemcarinata	Atlantic	2	ND

Sarsia princeps	Widespread	2	ND
Sarsia spp.	Not defined		ND
Scaphocalanus brevicornis	Widespread	1	ND
Scaphocalanus magnus	Widespread	3	ND
Scina borealis	Widespread	1	ND
Scolecithricella minor	Atlantic	4	Atlantic
Scolecitrichidae indet.	Not defined		ND
Scyphozoa indet.	Not defined		ND
Siphonophora indet.	Not defined		ND
Siphonostomatoida indet.	Not defined		ND
Spinocalanus antarcticus	Arctic	1	ND
Spinocalanus elongatus	Arctic	1	ND
Spinocalanus horridus	Widespread	1	ND
Spinocalanus longicornis	Widespread	1	ND
Spinocalanus polaris	Arctic	1	ND
Spinocalanus spp.	Not defined		ND
Stephos lamellatus	Not defined	?	ND
Temora longicornis	Widespread	2	ND
Temorites brevis	Widespread	1	ND
Tharybidae indet.	Not defined		ND
Tharybis groenlandicus	Widespread	1,2	ND

Themisto abyssorum	Widespread	1	Atlantic
Themisto libellula	Widespread	1	Arctic
Themisto spp.	Not defined		ND
Thysanoessa inermis	Widespread	1	Atlantic
Thysanoessa longicaudata	Atlantic	1	ND
Thysanoessa raschii	Widespread	1	Atlantic
Tomopteris helgolandica	Atlantic	1	ND
Tomopteris spp.	Not defined		ND
Triconia borealis	Widespread	1	Atlantic
Triconia conifera	Atlantic	2	ND
Tunicata indet.	Not defined		ND
Undeuchaeta spectabilis	Not defined		ND
Undinella oblonga	Widespread	1	ND
Xantharus siedleckii	Arctic	?	ND
Xanthocalanus polarsternae	Arctic	1	ND
Xanthocalanus sp.	Not defined		ND

6.7 Appendix VIII: Table over zooplankton samples and method

Supplementary table 3: Table over zooplankton samples and method

eventDate	samplingProtocol	locationID
17/05/2011	WP 200µm	BAB

15/06/2011	WP 200µm	BAB
13/07/2011	WP 200µm	BAB
26/08/2011	WP 200µm	BAB
12/12/2011	WP 200µm	BAB
05/06/2012	MPS	BAB
23/07/2012	WP 200µm	BAB
28/08/2012	WP 200µm	BAB
07/09/2012	MPS	BAB
05/10/2012	MPS	BAB
07/11/2012	WP 200µm	BAB
04/12/2012	MPS	BAB
10/01/2013	MPS	BAB
04/02/2013	MPS	BAB
13/03/2013	WP 200µm	BAB
07/04/2013	WP 200µm	BAB
25/04/2013	WP 200µm	BAB
07/05/2013	WP 200µm	BAB
17/06/2013	WP 200µm	BAB
23/07/2013	WP 200µm	BAB
07/09/2013	WP 200µm	BAB

XX

13/05/2015	MPS 180µm	BAB
14/05/2015	MPS 180µm	IsK
29/06/2015	MPS 180µm	IsK
09/07/2015	WP2 180µm	BAB
14/07/2015	WP2 180µm	IsK
22/07/2015	WP2 180µm	IsG
23/07/2015	MPS 180µm	BAB
24/07/2015	MPS 180µm	IsK
15/09/2015	MPS 180µm	IsK
20/10/2015	MPS 180µm	IsK
02/11/2015	WP2 180µm	IsG
03/12/2015	MPS 180µm	BAB
28/10/2016	WP2 180µm	IsK
29/10/2016	WP2 180µm	BAB
29/10/2016	WP2 180µm	IsG
15/06/2017	WP2 180µm	IsG
15/06/2017	MPS 180µm	IsK
19/11/2017	MPS 180µm	IsK
20/11/2017	WP2 180µm	BAB
14/07/2018	WP2 200µm	IsG

15/07/2018	WP2 200µm	BAB
15/07/2018	WP2 200µm	IsK
16/09/2018	WP2 200µm	BAB
18/09/2018	WP2 200µm	IsK
19/09/2018	WP2 200µm	IsG
17/06/2020	WP2 200 µm	BAB
22/07/2020	WP2 200 µm	BAB
24/08/2020	WP2 200 µm	BAB
16/09/2020	WP2 200 µm	BAB
23/06/2020	WP2 200 µm	IsG
21/07/2020	WP2 200 µm	IsG
25/08/2020	WP2 200 µm	IsG
15/09/2020	WP2 200 µm	IsG
11/05/2020	WP2 200 µm	IsK
18/06/2020	WP2 200 µm	IsK
22/07/2020	WP2 200 µm	IsK
21/08/2020	WP2 200 µm	IsK
16/09/2020	WP2 200 µm	IsK
15/05/2019	WP2 200 µm	BAB
30/06/2019	WP2 200 µm	BAB

24/07/2019	WP2 200 µm	BAB
22/08/2019	WP2 200 µm	BAB
16/05/2019	WP2 200 µm	IsG
28/06/2019	WP2 200 µm	IsG
21/08/2019	WP2 200 µm	IsG
25/07/2019	WP2 200 µm	IsG
16/05/2019	WP2 200 µm	IsK
30/06/2019	WP2 200 µm	IsK
22/08/2019	WP2 200 µm	IsK
08/08/2022	WP2 180um	BAB
20/06/2022	Bongo 180 um	IsK
31/07/2022	Bongo 180 um	IsK
21/06/2022	Bongo 180 um	IsG
31/07/2022	Bongo 180 um	IsG

6.8 Appendix IX: Significance tables

Supplementary table 4: Statistical significance (p-values) of the Kruskal-Wallis and pairwise Wilcox test for the relative abundance of zoogeographic groups (Arctic, Widespread, Atlantic, Not defined) at three stations (BAB, IsK, IsG).

	Arctic	**Widespread**	**Atlantic**	**Not Defined**
	P-value	P-value	P-value	P-value
Kruskal-Wallis	0.02343*	0.05088~	0.002433*	0.01066*
IsK-BAB	0.412	0.459	0.005*	0.1696
IsG-BAB	0.027*	0.082	0.016*	0.0072*
IsG-IsK	0.085	0.101	0.674	0.3136

*Significant ~barely not significant

Supplementary table 5: Statistical significance (p-values) of the Kruskal-Wallis and pairwise Wilcox test for the relative abundance of multivariate zoogeographic groups (Arctic, Widespread, Atlantic, Not defined) at three stations (BAB, IsK, IsG).

	Arctic	**Atlantic**	**ND**
	P-value	P-value	P-value
Kruskal-Wallis	6.262e-05*	6.262e-05*	0.7408
IsK-BAB	0.00098*	0.00098*	
IsG-BAB	0.00026*	0.00026*	
IsG-IsK	0.05032~	0.05032~	

*Significant ~barely not significant