



Zooplankton and sediment fluxes in two contrasting fjords reveal Atlantification of the Arctic

Agata Weydmann-Zwolicka^{a,*}, Paula Prątnicka^a, Magdalena Łącka^b, Sanna Majaneva^{c,d}, Finlo Cottier^{e,c}, Jørgen Berge^c

^a University of Gdansk, Institute of Oceanography, Department of Marine Plankton Research, Al. M. Piłsudskiego 46, 81 – 378 Gdynia, Poland

^b Institute of Oceanology, Polish Academy of Sciences, Powstańców Warszawy 55, 81-712 Sopot, Poland

^c The Arctic University of Norway, Department of Arctic and Marine Biology, NO- 9019 Tromsø, Norway

^d Norwegian University of Science and Technology, Department of Biology / Trondhjem Biological Station, NO-7491 Trondheim, Norway

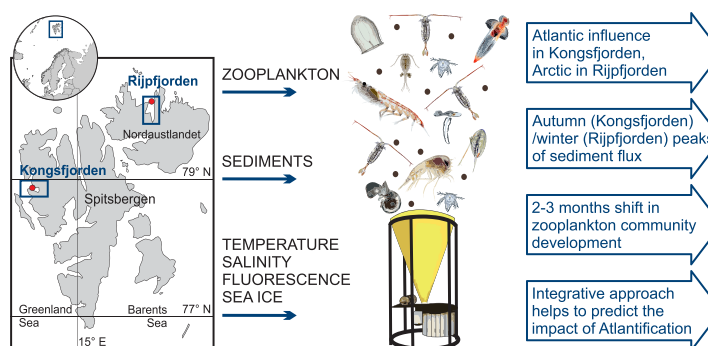
^e Scottish Association for Marine Science, Oban, United Kingdom



HIGHLIGHTS

- Sediment traps provided zooplankton and sedimentation data from high Arctic fjords.
- Atlantic conditions in the fjords influence all marine ecosystem components.
- Only integrating multiple information allows to assess Atlantification impact.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 16 November 2020

Received in revised form 25 January 2021

Accepted 29 January 2021

Available online 4 February 2021

Editor: Fernando A.L. Pacheco

Keywords:

Swimmers
Advection
Borealisation
Mooring
Kongsfjorden
Rijpfjorden

ABSTRACT

Svalbard fjords are facing a significant increase in Atlantic water inflow, which influences all ecosystem components, thus the objective of this study was to assess how recent Atlantification impacts the functioning of zooplankton community. For this purpose, two year-round operating sediment traps and associated hydrographic instruments, providing continuous time series of zooplankton and sediment fluxes, were deployed in the Atlantic-influenced Kongsfjorden and the typical high Arctic fjord Rijpfjorden. We used multivariate statistical methods to analyze how environmental variables, including the sediment fluxes, influence the zooplankton communities in the fjords. We found out that sedimentation rates were an order of magnitude higher in Kongsfjorden (reaching $39.7 \text{ g m}^{-2} \text{ d}^{-1}$ in December) and increased in autumn, while in Rijpfjorden, they peaked in late winter – early spring ($2.9 \text{ g m}^{-2} \text{ d}^{-1}$ in February). Such sediment flux patterns might result from the redeposition of sediments from shallower, subtidal areas and were probably connected to autumn/winter storms. According to multivariate analyses, zooplankton in Kongsfjorden were significantly influenced by water temperature, which explained 22% of their variation, and the flux of organic and mineral sediments explaining 15% and 7.8%, respectively; while in Rijpfjorden, it was sea ice (25.3%), water temperature (16.2%), salinity (8.1%), and mineral sedimentation (6.3%). The structure of zooplankton communities in both fjords was similar in winter; in Kongsfjorden, zooplankton kept developing through spring and summer, while in the Arctic Rijpfjorden, the community paused until the onset of phytoplankton bloom and sea ice break-up in summer, to finally achieve, in autumn, a similar species and development stage structure as summer in the Atlantic-influenced fjord. Our

* Corresponding author.

E-mail address: agata.weydmann@ug.edu.pl (A. Weydmann-Zwolicka).

study demonstrates how integrating multiple pieces of information can provide key insights into the relations between Atlantification, sediment flux, and zooplankton community, thus helping to assess the functioning of high Arctic ecosystems under climate change conditions.

© 2021 Elsevier B.V. All rights reserved.

1. Introduction

The marine environment in the European Arctic is changing at an unprecedented rate, and observed changes include increasing northward inflow of warm and saline Atlantic waters, called Atlantification, and loss of sea ice (e.g., Spielhagen et al., 2011; IPCC, 2014; Polyakov et al., 2017). These remarkable habitat shifts are coupled with changes in species diversity and composition, such as northward range extension of Atlantic species into the Arctic (Berge et al., 2005; Fleischer et al., 2007; Weydmann et al., 2014) and increases in primary and secondary production (Arrigo et al., 2008; Slagstad et al., 2011; Carstensen et al., 2012). The progressive retreat of sea ice cover induces changes in sedimentation rates and will consequently lead to changes in the euphotic zone, and hence light available for the primary production, especially in fjords (Zajaczkowski et al., 2010). As a result, this might affect the onset of spring bloom, which is the main food source for herbivorous zooplankton (Søreide et al., 2010; Kahru et al., 2010), and in the worst case scenario, it can lead to the dramatic weakening of convective water mixing during the polar night and strong limitation of spring/summer primary production in the region (Łącka et al., 2019).

Sea ice coverage in some Svalbard fjords can last for 6–8 months, and these conditions hamper the traditional net collection of zooplankton. Thus, most zooplankton studies have focused on late spring - early autumn seasons only, limiting our knowledge about the seasonal changes in zooplankton community. Sediment traps are often the only available method for collecting zooplankton samples during the high Arctic late autumn - spring period, although there are some limitations in using sediment traps to study zooplankton, including interpreting results based only on qualitative data at one specific depth treated as a proxy of organisms' position in the water column (Dezutter et al., 2019). Consequently, several year-round sediment trap-derived observations on zooplankton fluxes have been reported from the Canadian Arctic (Makabe et al., 2010; Matsuno et al., 2014; Dezutter et al., 2019), Fram Strait (Kraft et al., 2011; Bauerfeind et al., 2014; Busch et al., 2015), and Kongsfjorden (Willis et al., 2006; Willis et al., 2008).

Nevertheless, relatively little is known about seasonal changes in the zooplankton community and their relationship with the flux of sediments and advected water masses in high Arctic fjords, although shifts connected to the northward extension of boreal species' distribution ranges and the retreat of polar taxa are already observed around Svalbard (Węśławski et al., 2017; Hop et al., 2019; Grabowski et al., 2019). The contribution and proportion of Arctic and Atlantic species in zooplankton communities of Svalbard fjords respond to variations in the distribution and dynamics of the West Spitsbergen Current and Atlantic water masses (Daase and Eiane, 2007; Weydmann and Kwasniewski, 2008; Głuchowska et al., 2016), which change year-to-year, although the Atlantic impact is increasing, especially in west-facing fjords (Promińska et al., 2017; Cottier et al., 2019; Skogseth et al., 2020).

Sediment flux in Arctic fjords is usually characterized by large seasonal, spatial and interannual variability (Svendsen et al., 2002). Sedimentation seasonality in Svalbard fjords used to be mainly dependent on the light regime (e.g., Zajaczkowski et al., 2010). The early spring light signal began meltwater runoff and organic matter supply. In summer, terrigenous material was supplied from rivers and tidewater glaciers. The sediment flux decreased as insolation weakened, and during the autumn/winter period, it was near basal levels. Recently, in ice-free fjords, a decline in sedimentation seasonality, at least in its original form, has been observed (e.g., Wiedmann et al., 2016; Morata et al., 2020). For instance, during the winter season in ice-free Adventfjorden,

mixing by thermal convection and wind is enhanced compared to the previous ice-covered situation, and detrital material, which previously settled to the bottom, is resuspended and laterally advected to the middle of the fjord, increasing winter sedimentation rates (Wiedmann et al., 2016). Taking into account the further Atlantification of the Arctic (i.e., intensified advection of Atlantic Water and shrinking sea ice) leading to warmer and wetter winter conditions with a concomitant higher frequency of extreme weather events, such as winter storms (Nilsen et al., 2016) and/or extreme precipitation events (e.g., Wickström et al., 2020), unprecedented changes in the sedimentation regimes of Svalbard fjords might also be expected in the near future.

Zooplankton is usually treated as one of the sources of sedimentary material, through the flux of their fecal pellets and carcasses (Sampei et al., 2012; Darnis et al., 2017). We decided to check the opposite approach by using multivariate statistical methods to test how changes in the sediment flux influence the zooplankton community in high Arctic fjords in addition to other environmental variables, such as sea ice, temperature, salinity and fluorescence. Such an integrative approach, with a more complete dataset, may help to predict the future of high Arctic fjordic systems under the pressure of climate change and Atlantification more precisely.

The objective of this study was to assess how changes in oceanographic conditions influence the fluxes of zooplankton and sediments in high Arctic fjords, and how recent Atlantification impacts the functioning of fjordic systems. For this purpose, two year-round operating sediment traps and associated hydrographic instruments were moored in contrasting Svalbard fjords: Kongsfjorden, which is strongly influenced by waters of Atlantic origin and thus may serve as a model of the future Arctic environment, and Rijpfjorden, where Arctic conditions still predominate and which is usually ice-covered for a significant part of the year. The value of our study lies in the continuous collection of zooplankton samples from the ice-covered Rijpfjorden, which is practically inaccessible between late autumn and spring due to logistic difficulties.

Our integrative methodological approach, including an illustration of the study area with main ocean currents, the mooring scheme with the sensor arrangement and sediment trap, as well as the analytical methods, is presented in Fig. 1. The following **Materials and methods** sections correspond to the flowchart, while in the **Results** section, oceanographic conditions, sediment and zooplankton fluxes are presented first, followed by the results of multivariate statistical analyses based on these joint data.

2. Materials and methods

2.1. Study area

The study was conducted in two fjords of the Svalbard Archipelago (Fig. 1), Kongsfjorden and Rijpfjorden, that have contrasting physical and biological characteristics. Kongsfjorden is an open fjord on the west coast of Spitsbergen, and its outer basin has a direct, deep connection to the West Spitsbergen Shelf by a deep glacial trough, Kongsfjordrenna (Svendsen et al., 2002). Therefore, the exchange and advection of water masses play significant roles in determining the physical and biological characteristics of the fjord (Hop et al., 2002). Kongsfjorden has been relatively ice-free since the 2005–2006 season (Cottier et al., 2007; Walczowski and Piechura, 2011; Johansson et al., 2020). The fjord is relatively rich in coexisting boreal and Arctic species, which respond to variations in the distribution and dynamics of the Atlantic origin water masses (Willis et al., 2006).

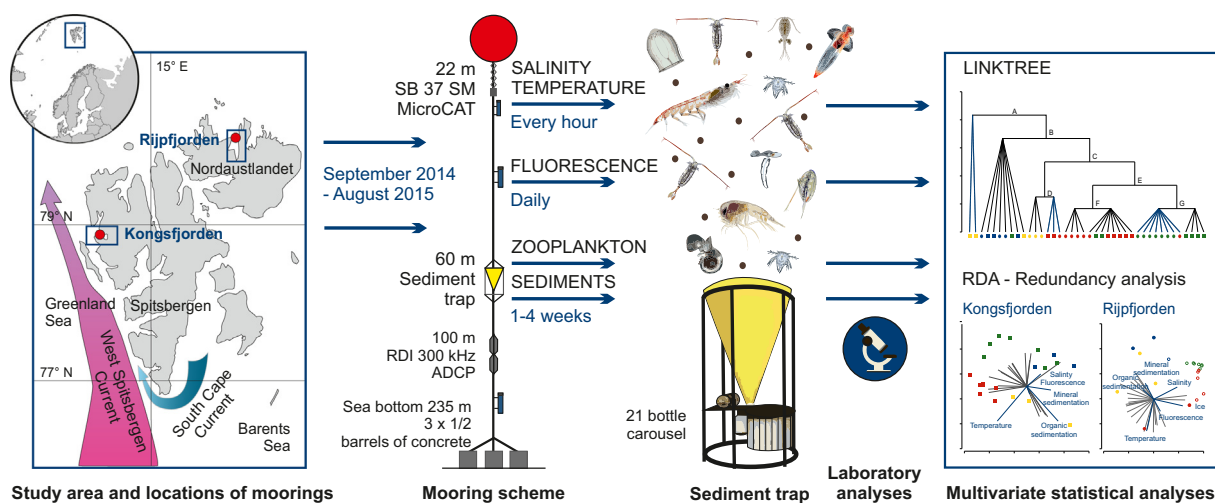


Fig. 1. The methodological approach: map of the study area with main ocean currents and red dots indicating the positions of moorings; the scheme of the mooring deployed in Rijpfjorden with targeted depths of the main sensors and sediment trap; sediment trap with zooplankton and sediments sampled; laboratory analyses of the zooplankton communities and sedimentation rates; joint multivariate statistical analyses of all data (zooplankton, sedimentation, water temperature, salinity, and fluorescence) derived from the devices attached to the moorings.

Rijpfjorden is located on the north-central shore of Nordaustlandet in the northeastern part of the Svalbard Archipelago (Fig. 1). It is north facing and open to the wide shelf through a broad mouth. In contrast to Kongsfjorden, Rijpfjorden is predominantly ice-covered for at least 6–8 months of the year and experiences oceanographic conditions that are more Arctic in character: colder and fresher (Johansson et al., 2020); as a consequence, the local zooplankton community is dominated by Arctic species. However, there is a periodic influence of warmer (>1 °C) water masses, which are thought to be highly modified Atlantic water carrying boreal species (Wallace et al., 2010; Weydmann et al., 2013; Hop et al., 2019).

2.2. Moorings, sediment traps and oceanographic data

Sediment traps (McLane Parflux 78H – 21 with a 21 bottle carousel and a 0.5 m² aperture) were deployed on single-point moorings in Kongsfjorden (78°57.760'N 11°47.835'E) at a depth of 60 m (bottom depth of 223 m), and in Rijpfjorden (80°17.661'N 22°18.230'E) at a depth of 60 m (bottom depth of 235 m) (Fig. 1). Sediment trap exposure times were programmed for different sampling periods (Table 1)

Table 1

Sediment trap sampling program in 2014 and 2015 in two high Arctic fjords: Kongsfjorden and Rijpfjorden.

Sample ID	Date from	Date to	Exposition time [days]
Oct	01.10.2014	01.11.2014	31
Nov	01.11.2014	01.12.2014	30
Dec	01.12.2014	01.01.2015	30
Jan	01.01.2015	01.02.2015	31
Feb	01.02.2015	01.03.2015	29
Mar1	01.03.2015	15.03.2015	14
Mar2	15.03.2015	29.03.2015	14
Mar3	29.03.2015	12.04.2015	14
Apr1	12.04.2015	26.04.2015	14
Apr2	26.04.2015	10.05.2015	14
May1	10.05.2015	24.05.2015	14
May2	24.05.2015	07.06.2015	14
Jun1	07.06.2015	21.06.2015	14
Jun2	21.06.2015	28.06.2015	7
Jun3	28.06.2015	05.07.2015	7
Jul1	05.07.2015	12.07.2015	7
Jul2	12.07.2015	19.07.2015	7
Jul3	19.07.2015	26.07.2015	7
Jul4	26.07.2015	09.08.2015	14
Aug	09.08.2015	23.08.2015	14

according to the season and primary and secondary production in the fjords. The trap sample bottles were pre-filled with filtered seawater adjusted with NaCl to 35 PSU to provide a density discontinuity relative to ambient seawater and to avoid diffusion of samples. To preserve deposited material, 4% formalin buffered with sodium borate, was added to the samples after deployment.

However, given the deployment depth of sediment traps (60 m), any changes in species abundance should realistically be considered only to reflect changes in zooplankton community composition in surface layers (0–60 m depth), especially when considering copepod developmental stages, which are known to seasonally migrate in the water column. Thus, we acknowledge that the presented results are likely to be biased towards species present in the upper water column, although zooplankton abundance used as a proxy of the position of the organisms in the water column may still provide important insight into their patterns of upward and downward migrations.

Temperature (T) and salinity (S) were recorded during the sediment trap deployment period with Seabird 37 Microcats moored at a depth of 22 m. Additional sensors measured fluorescence, and the presence or absence of sea ice was noted based on data from acoustic Doppler current profilers (ADCPs) (Hyatt et al., 2008). During the analyses, water masses in both fjords were classified based on Cottier et al. (2005) and Pérez-Hernández et al. (2017).

2.3. Laboratory analyses

All large zooplankton (chaetognaths, ctenophores, medusae, amphipods, euphausiids, and appendicularians) were sorted and carefully removed from the samples using small, soft forceps. The collected sediment was vacuum-filtered onto preweighed filters (MN GF5 with 0.4 µm openings) and rinsed with distilled water. The filters were air dried at 60 °C for 24 h, weighed to determine the sediment dry mass, combusted at 450 °C for 24 h, and then reweighed to obtain the amount of settled organic matter from weight loss (Zajaczkowski et al., 2010). The sedimentation rate was calculated for 7–31 days, depending on the season (Table 1).

The remaining zooplankton were passed through a 180 µm mesh sieve to obtain a mesozooplankton fraction, and then through a 60 µm mesh sieve to sort out the smaller organisms (juvenile stages and eggs). All organisms were identified under a stereomicroscope equipped with a calibrated ocular micrometer (Leica M125 C, Leica Imaging Systems GmbH). Developmental stages were determined for the larger genera, such as *Calanus*, *Metridia* and *Pseudocalanus*. *Calanus*

specimens were identified to a species based on morphology (Brodskii et al., 1983) and prosome lengths of individual copepodid stages (C1 – C5, and adults) according to Weydmann and Kwasniewski (2008). The remaining zooplankton were identified to the lowest taxonomic level possible. Only swimmers (zooplankton organisms that actively swam into the trap) (Matsuno et al., 2014) that showed no signs of decomposition, suggesting they were killed by the applied formaldehyde, were chosen for further analyses.

2.4. Multivariate statistical analyses

Since trap exposure time varied between the seasons (Table 1), we standardized the zooplankton and sedimentation data to a daily flux, expressed as individual $\text{m}^{-2} \text{day}^{-1}$ (zooplankton) and $\text{g m}^{-2} \text{day}^{-1}$ (sedimentation) according to Matsuno et al. (2014). Temperature, salinity and fluorescence data were calculated as means for the period of sediment trap exposure time. The presence or absence of sea ice was expressed as follows: 0 – sea ice absent, 0.5 – sea ice present for half of sediment trap exposure time, and 1 – sea ice present for the whole exposure time.

Multivariate statistical analyses of zooplankton community abundance data were carried out using the PRIMER 7 software package (Clarke and Warwick, 2001; Clarke and Gorley, 2015), with the PERMANOVA+ add on (Anderson et al., 2008). Due to possible disturbances connected with sediment trap deployment, the first samples (24.08.–2014–01.10.2014) were excluded from further analyses. The obtained zooplankton daily flux data were transformed [$n' = \log(n + 1)$] prior to further analyses, and similarities between samples were examined using the Bray-Curtis index. Due to the low abundances of some taxa, copepodite development stages were grouped as follows: C1–3, C4–5, and adult males and females.

Zooplankton composition was investigated using linkage tree analysis (LINKTREE) with a series of similarity profile (SIMPROF) tests, which allowed for the divisive clustering of samples constrained by inequalities in one or more environmental variables (in this case: water temperature, salinity, organic and mineral sedimentation rates, fluorescence, and presence/absence of sea ice) (Clarke et al., 2008). In this way, the collection of 40 samples with characteristic zooplankton community composition was divided into smaller groups, where each division had an 'explanation' regarding the threshold on environmental

variables. The following set conditions gave the best linkage tree illustration: minimum group size = 2, minimum split size = 5, minimum split $R = 0.49$. To further investigate the groups obtained by LINKTREE, a similarity percentage (SIMPER) analysis was used to determine the contribution of certain zooplankton taxa/developmental stages to the within-group similarity. Thus, this analysis investigated the distinct clusters of zooplankton taxa separated by threshold responses for given environmental variables.

To analyze the relationships between the flux of zooplankton taxa and environmental variables, such as: water temperature, salinity, fluorescence, sea ice, and sedimentation rates of both, mineral and organic fractions, as well as to provide quantitative measures of variation explained by these predictor variables, a distance-based linear model (DISTLM) routine was applied and illustrated by distance-based redundancy analysis (dbRDA) diagrams (Anderson, 2006). To build the models, all specified predictor variables were included using a forward selection procedure, and the selection criterion was based on R^2 values. After testing several models for each fjord, the best ones were chosen based on the highest R^2 values. Because predictor variables jointly affect species composition in marine environments, we showed only the results of sequential tests (Legendre and Anderson, 1999).

3. Results

3.1. Oceanographic conditions

In Kongsfjorden, at the beginning of the sampling period in October 2014, water above the sediment traps had a temperature of approximately 3.7 °C and a salinity of 34.6, likely influenced by Atlantic water (Fig. 2). In November, the water temperature decreased to 2.7 °C, while salinity increased to 34.7, and until the end of January, the water was characteristic of Transformed Atlantic Water (TAW). From February 2015 to May 2015, cold water masses characteristic of Local Winter Water (LWW) were observed, with temperatures ranging between –0.5 °C and 0.8 °C. Towards the end of May, the temperature slightly increased to 1.4 °C, probably through warm water inflow from the shelf area and local warming. These water masses dominated until mid-July when an abrupt decline in salinity to 33.3 occurred, suggesting the influence of fresher Surface Waters (SW).

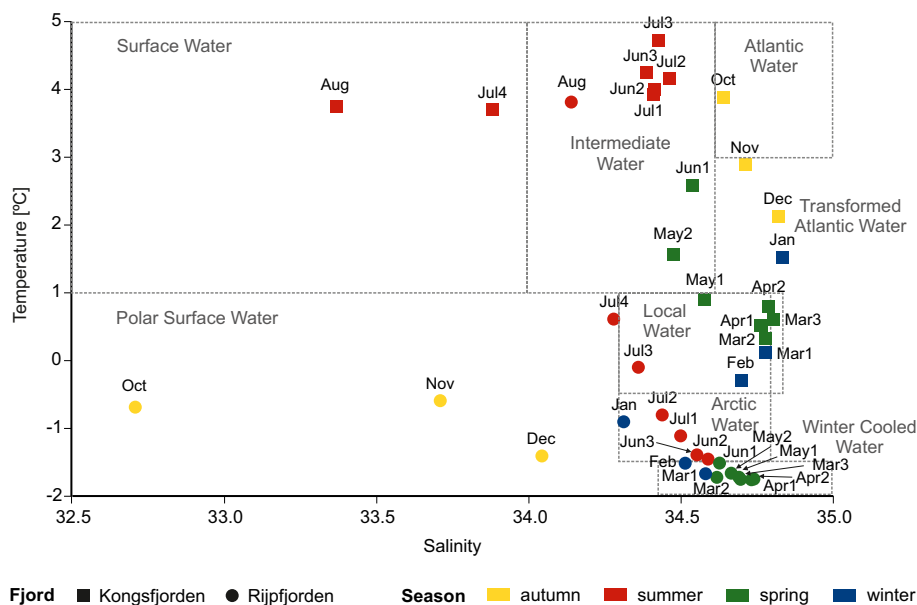


Fig. 2. Temperature and salinity diagram from Rippfjorden and Kongsfjorden between October 2014 and August 2015. Water masses are distinguished based on Cottier et al., 2005 and Pérez-Hernández et al., 2017.

Seasonal changes in oceanographic conditions observed in Rijpfjorden were different from those observed in Kongsfjorden (Fig. 2). Generally, Rijpfjorden was under the influence of colder (-0.9°C to -1.8°C) water masses, with salinities of 34.4 to 34.7, particularly from February to the middle of July. Winter Cooled Water (WCW) dominated the fjord during this period as a result of sea ice cover. After July, the surface temperature abruptly increased to 3.7°C in August, which was the warmest month. Freshwater discharge from glacial melt was observed in October 2014 and caused the formation of fresher Polar Surface Water with a salinity of 32.7, which gradually became more saline in the early winter months.

The presence or absence of sea ice was among the main differences between the fjords. According to ADCP data, Kongsfjorden was ice-free during the observation period, while in Rijpfjorden sea ice cover was present most of the time: from mid-October to late-October, then between mid-November to late-November 2014, and from mid-February to late-July 2015 (Fig. 3). In contrast, the measured fluorescence values in Kongsfjorden were much higher, with almost basal levels observed from October 2014 to April 2015, followed by two distinct peaks in May and June–July, and a gradual decrease after that period (Fig. 3). In Rijpfjorden, some activity was noted in October 2014, followed by close to zero values until May 2015, when the first fluorescence peak was observed along with two subsequent peaks in June–July and August.

3.2. Sediment flux

The difference in sediment fluxes between the fjords was an order of magnitude, with the highest sedimentation rates observed in Kongsfjorden (reaching $38\text{ g m}^{-2}\text{ d}^{-1}$ in December), whereas in Rijpfjorden the maximum sedimentation rates reached $2.86\text{ g m}^{-2}\text{ d}^{-1}$ in February (Fig. 3). In Kongsfjorden, sediment flux was quite similar between the remaining autumn and winter months (ca. $6\text{ g m}^{-2}\text{ d}^{-1}$), with the contribution of organic material constituting between 4 and 7%. The sedimentation rates in Kongsfjorden decreased considerably in the

spring and summer months (between 0.01 and $1\text{ g m}^{-2}\text{ d}^{-1}$), with a concomitant increase in organic material contribution (reaching 23.8% in May).

In Rijpfjorden, significant differences in the sediment flux were observed between the autumn and winter months, with the highest sedimentation rates observed between January and March $1.5\text{--}2.8\text{ g m}^{-2}\text{ d}^{-1}$; Fig. 3). The sedimentation rates decreased considerably towards the spring and summer months (reaching $0.01\text{ g m}^{-2}\text{ d}^{-1}$ in late May). Similar to Kongsfjorden, the highest contribution of organic material in Rijpfjorden was measured in the spring and summer seasons: 22.3% in May and reaching 25.9% in July; however, in winter months, organic material constituted up to 17%.

3.3. Zooplankton flux

The most common zooplankton species in all sediment trap-derived samples were the small, cosmopolitan copepod *Oithona similis*, the two sibling *Calanus* species, *C. finmarchicus* and *C. glacialis*, as well as the pteropods *Limacina helicina* and *L. retroversa*. Seasonally, meroplankton were also noted in high numbers, especially *Bivalvia* veligers, as well as the eggs and nauplii of copepods, and Euphausiacea eggs (Fig. 3). In Kongsfjorden, the lowest zooplankton flux was noted between November and mid-April (Fig. 3). From early spring until early summer, copepod eggs and nauplii were the most abundant, with increasing fluxes in this period, while the subsequent summer samples were dominated by *Bivalvia* veligers, forming the Kongsfjorden peak flux in June. In Rijpfjorden, high numbers of *O. similis* contributed mostly to the autumn peak of zooplankton flux, which was followed by the lowest numbers of all taxa occurring in winter, between December and February. The eggs and nauplii of copepods were observed from March to mid-July, and dominated the zooplankton community during this period, largely contributing to the maximum summer flux in mid-July. The subsequent samples collected in the end of July and in August were dominated by *Bivalvia* veligers (Fig. 3).

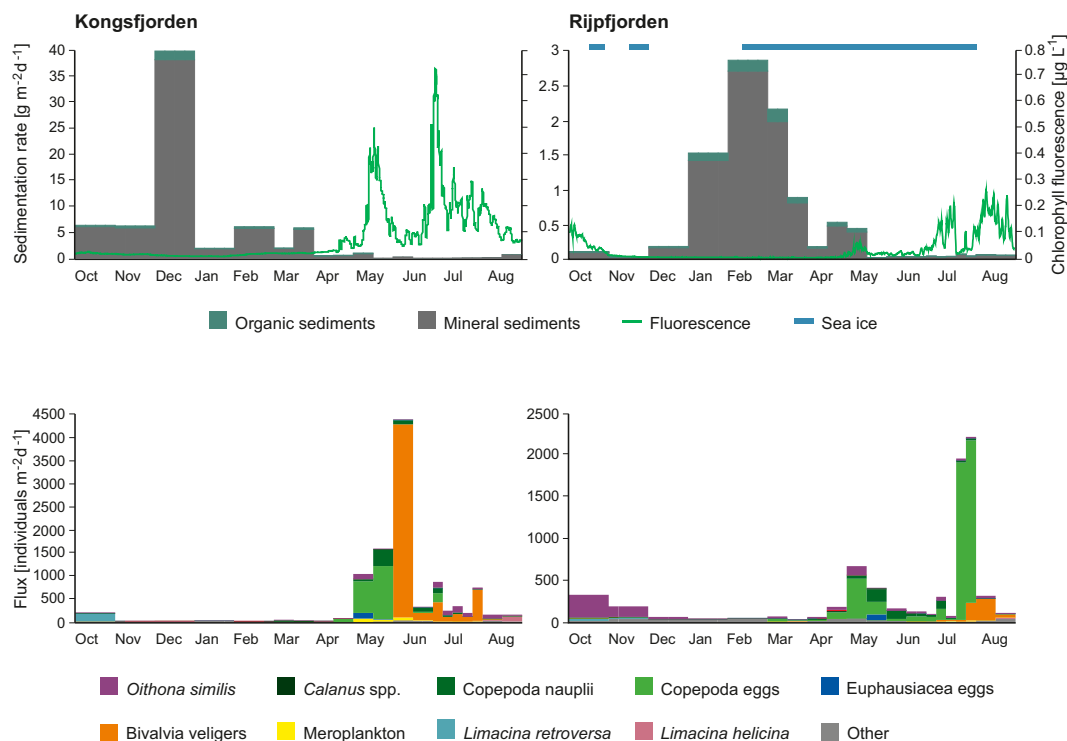


Fig. 3. Sedimentation rates, fluorescence and sea ice (upper diagrams); fluxes of the most abundant zooplankton taxa in sediment traps (lower diagrams) from Kongsfjorden and Rijpfjorden between October 2014 and August 2015. Note the differences in scales between the fjords.

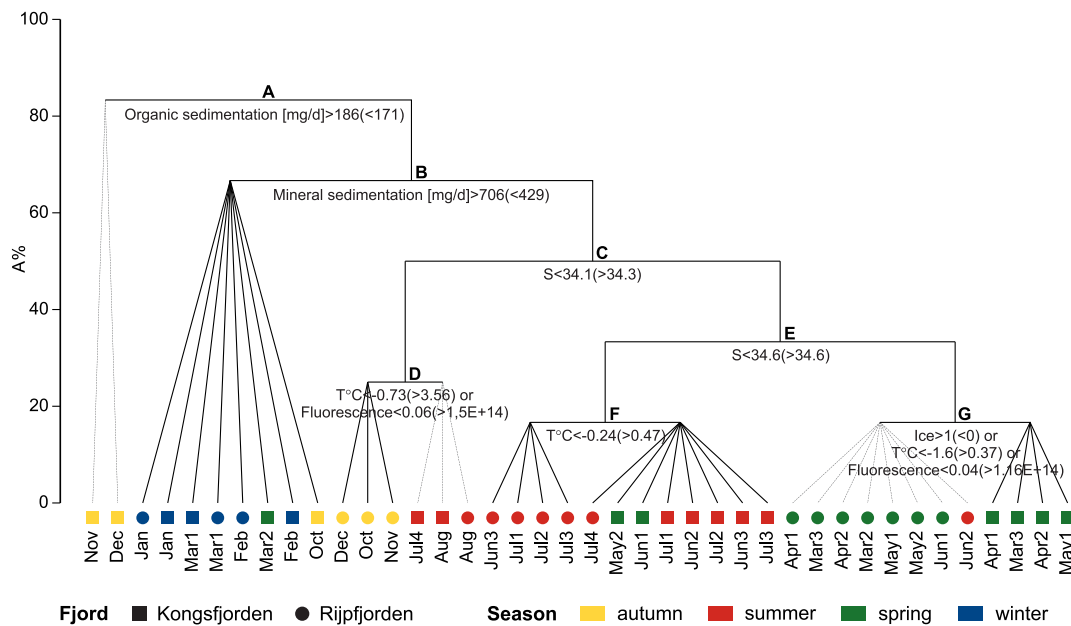


Fig. 4. Linkage tree analysis (LINKTREE) showing binary partitioning of samples (groups I – VIII) obtained by seven splits (A-G) with the corresponding thresholds of temperature (T), salinity (S), organic and mineral sedimentation rates, fluorescence, and presence or absence of sea ice.

3.4. Influence of environmental variables on the zooplankton community

LINKTREE, coupled with SIMPROF tests (Fig. 4) and the subsequent SIMPER analysis (Table 2), revealed 8 characteristic groupings of samples and allowed us to relate them to differences in environmental variables. The first, and thus the most important, split A, in the divisive clustering was between the samples from November and December from Kongsfjorden and the remaining samples. The samples in this first subdivision (group I) were characterized by the organic sedimentation rates higher than $0.186 \text{ g m}^{-2} \text{ d}^{-1}$ and high contributions of *L. retroversa* (27%), *Oikopleura* spp. (17.2%) and *Metridia longa* copepodites in the fourth and fifth stages (C4–5, 15.1%). The second division, B, separated group II, with mineral sedimentation rates higher than $0.706 \text{ g m}^{-2} \text{ d}^{-1}$, which included mainly winter samples from both fjords, and in which the presence of *O. similis* was the most significant (23.5%), although older developmental stages of other copepods were also important. Split C was based on salinity, where samples with salinities <34.1 , were further divided into two groups (split D) based on temperature or fluorescence. Group III included all autumn samples from Rjipfjorden and was characterized by temperatures lower than $0.73 \text{ }^{\circ}\text{C}$ and high contributions of *O. similis*, *L. retroversa*, *Microcalanus* spp., and *Bivalvia veligers*. Group IV consisted of late summer samples from both fjords, when water temperatures were higher than $3.56 \text{ }^{\circ}\text{C}$, and the zooplankton community consisted of 25.1% *L. helicina*, 24.6% *O. similis*, and 15.9% *Bivalvia veligers*. Split E was based on the salinity threshold of 34.6, and was followed by two subsequent divisions: F and G. The first division was between July and August samples from Rjipfjorden (group V), which were characterized by temperatures lower than $0.24 \text{ }^{\circ}\text{C}$, as well as high contributions of Copepoda eggs (28.6%) and *O. similis* (21.9%); and mid-May to mid-July samples from Kongsfjorden that had temperatures higher than $0.47 \text{ }^{\circ}\text{C}$ and in which *Bivalvia veligers* and *O. similis* jointly constituted 54.5% of the zooplankton community (group VI). The second allowed us to separate most of the spring samples from both fjords into two groups. Group VII included the samples from Rjipfjorden that were collected when sea ice was present and temperatures were lower than $1.6 \text{ }^{\circ}\text{C}$ and were dominated by the eggs and nauplii of copepods. The remaining samples, which were all from Kongsfjorden, formed group VIII, with temperatures higher than $0.37 \text{ }^{\circ}\text{C}$ and absence of sea ice, as well as a very high contribution of Copepoda eggs (34.4%) and a substantial proportion of *O. similis* and Cirripedia larvae.

The models that were based on the results of sequential tests obtained by DISTLM analyses showed large differences between the fjords (Table 3, Fig. 5). In Kongsfjorden ($R^2 = 0.56$), only the temperature and sedimentation rates of both the organic and mineral fractions significantly affected the variation of the zooplankton flux. Temperature had the largest explanatory power, and alone explained 22% of zooplankton variability, while both types of sedimentation, organic and mineral, explained an additional 15% and 7.8%, respectively. In Rjipfjorden ($R^2 = 0.65$), the most important environmental predictor was sea ice, which explained 25.3% of zooplankton variation, with temperature being the second-most influential, and responsible for 16.2%. The remaining significant environmental variables were salinity (8.1%) and the mineral sedimentation rate (6.3%).

Based on dbRDA plots (Fig. 5), the seasonal distribution of samples, which form aggregations characteristic for a certain season, as well as a clear negative correlation between the abundances of most zooplankton taxa and both fractions of sedimentation, which eigenvectors point in opposite directions, can be observed in the studied fjords. In Kongsfjorden, the samples from November and December were characterized by the highest sedimentation rates and correlated increasing abundances of *M. longa* C2–C5, *Eualus gaimardii*, and *Aglantha digitale* (Fig. 5a). In the period between January and March, illustrated by the characteristic group of samples, high numbers of *Calanus glacialis* and *C. finmarchicus* females and eggs were noted. In spring (April – beginning of June), the increased flux of young developmental stages, including the nauplii of copepods, *C. finmarchicus* and *C. glacialis* copepodites of stages C1 and C2, as well as the larvae of euphausiids, decapods, and echinoderms, were observed. Summer (samples from mid-June to August) was characterized by increasing water temperatures and the flux of *Fritillaria borealis*, *C. finmarchicus* C3, *Bivalvia veligers* and *O. similis*. Interestingly the zooplankton community from October seemed to be more similar to the summer one than to the samples collected from November and December.

In Rjipfjorden, the samples from the period when sea ice cover was permanently present (March – beginning of July) were grouped together, and were characterized by a high salinity and a low number of taxa (Fig. 5b). Copepoda eggs and nauplii appeared after the ice break up in July. The larval stages of Polychaeta, Echinodermata, and *Bivalvia*, as well as *Mertensia ovum*, *L. helicina*, *Triconia borealis*, and *C. finmarchicus* C3 and C4, were present in August, which was connected

Table 2

SIMPER list of zooplankton taxa contributing mostly to similarities within the groups obtained by LINKTREE (see Fig. 4), with a cutoff at 50% for the log-transformed data.

LINKTREE Group	Samples	Fjord	Taxa	Average abundance	Average similarity	Sim/SD	Contribution [%]	Cumulative [%]
I	Nov	KF	<i>Limacina retroversa</i>	1.46	17.2		27.05	27.05
	Dec		<i>Oikopleura</i> spp.	1.37	10.91		17.16	44.21
			<i>Metridia longa</i> C4–5	0.78	9.59		15.08	59.29
II	Oct	KF	<i>Oithona similis</i>	1.8	9.24	2.02	23.54	23.54
	Jan		<i>Microcalanus</i> spp.	0.87	3.87	2.14	9.85	33.39
	Feb		<i>Metridia</i> adult	0.58	2.39	1.1	6.08	39.47
	Mar1		<i>Calanus glacialis</i> female	0.91	2.38	0.45	6.06	45.52
	Mar2		<i>Metridia longa</i> C4–5	0.62	1.88	0.77	4.79	50.31
	Jan	RF						
	Feb							
Mar1								
III	Oct	RF	<i>Oithona similis</i>	4.62	18.21	14.79	27.49	27.49
	Nov		<i>Limacina retroversa</i>	2.27	7.2	2.16	10.87	38.36
	Dec		<i>Microcalanus</i> spp.	1.7	5.8	2.85	8.75	47.12
IV		KF	<i>Bivalvia veliger</i>	1.69	5.55	4.86	8.38	55.49
	Jul4		<i>Limacina helicina</i>	3.53	14.6	7.18	25.09	25.09
	Aug	RF	<i>Oithona similis</i>	3.51	14.32	4.86	24.62	49.71
	Aug		<i>Bivalvia veliger</i>	2.59	9.27	2.91	15.92	65.63
V	Jun3	RF	Copepoda egg	5.67	19.39	3.16	28.57	28.57
	Jul1		<i>Oithona similis</i>	3.27	14.86	4.48	21.89	50.47
	Jul2							
	Jul3							
VI	May2	KF	<i>Bivalvia veliger</i>	5.71	19.97	6.44	31.86	31.86
	Jun1		<i>Oithona similis</i>	3.97	14.21	3.28	22.66	54.52
	Jun2							
	Jun3							
	Jul1							
	Jul2							
	Jul3							
VII	Jul4	RF						
	Mar2		Copepoda egg	4	17.76	4.56	31.28	31.28
	Mar3		Copepoda nauplius	3.2	13.1	1.8	23.07	54.35
	Apr1							
	Apr2							
	May1							
	May2							
VIII	Jun1							
	Jun2							
	Mar3	KF	Copepoda egg	4.96	15.26	3.27	34.38	34.38
	Apr1		<i>Oithona similis</i>	2.41	6.16	2.92	13.87	48.26
	Apr2		Cirripedia larva	2.27	3.7	0.89	8.34	56.59
May1								

to the increasing temperature based on the same direction of their eigenvectors. The sample from October seemed to be distinct from the remaining ones, and was characterized by the high abundances of older developmental stages of *Pseudocalanus* spp. (C4–C5), as well as *M. longa* C2–C5, *Paraeuchaeta* spp., *Oikopleura* spp., *L. retroversa*, *Themisto libellula*, *Thysanoessa inermis*, and *Monoculodes borealis*. The samples from December and January grouped together and were characterized by the increasing mineral sedimentation rate and the related high abundances of *Aetideopsis* spp., *Paraeuchaeta norvegica* and the adults of *M. longa*.

4. Discussion

The integrative approach proposed in our study allowed us to provide key insights into the relations between Atlantification, sediment flux, zooplankton composition and, thus, high Arctic fjordic ecosystem functioning. Main environmental differences between the studied fjords, including sea ice that was present only in Rjppfjorden, and sedimentation rates that were an order of magnitude higher in Kongsfjorden, together with seasonal differences, and water temperature, had the greatest impact on zooplankton communities present in

Table 3

The significance of tested environmental variables on the zooplankton communities in Kongsfjorden and Rjppfjorden, with the proportion of variation in zooplankton explained by each predictor, based on the results of DistLM sequential tests for environmental variables. Significant predictors are given in bold.

Fjord	Variable	R ²	SS(trace)	Pseudo-F	P	Proportion of explained variation [%]	Cumulative total [%]	Res. df
Kongsfjorden	Temperature	0.220	10,375	5.07	0.003	22.0%	22.0%	18
	Organic sedimentation	0.370	7092.8	4.05	0.002	15.0%	37.0%	17
	Fluorescence	0.431	2883.7	1.72	0.099	6.1%	43.1%	16
	Mineral sedimentation	0.509	3696.8	2.39	0.03	7.8%	50.9%	15
	Salinity	0.557	2230.9	1.49	0.216	4.7%	55.7%	14
	Ice	0.253	7909.9	6.11	0.001	25.3%	25.3%	18
	Temperature	0.416	5070.4	4.73	0.001	16.2%	41.6%	17
Rjppfjorden	Salinity	0.497	2519.8	2.57	0.007	8.1%	49.7%	16
	Mineral sedimentation	0.560	1960.5	2.14	0.037	6.3%	56.0%	15
	Organic sedimentation	0.612	1648.8	1.91	0.065	5.3%	61.2%	14
	Fluorescence	0.652	1240.7	1.49	0.184	4.0%	65.2%	13

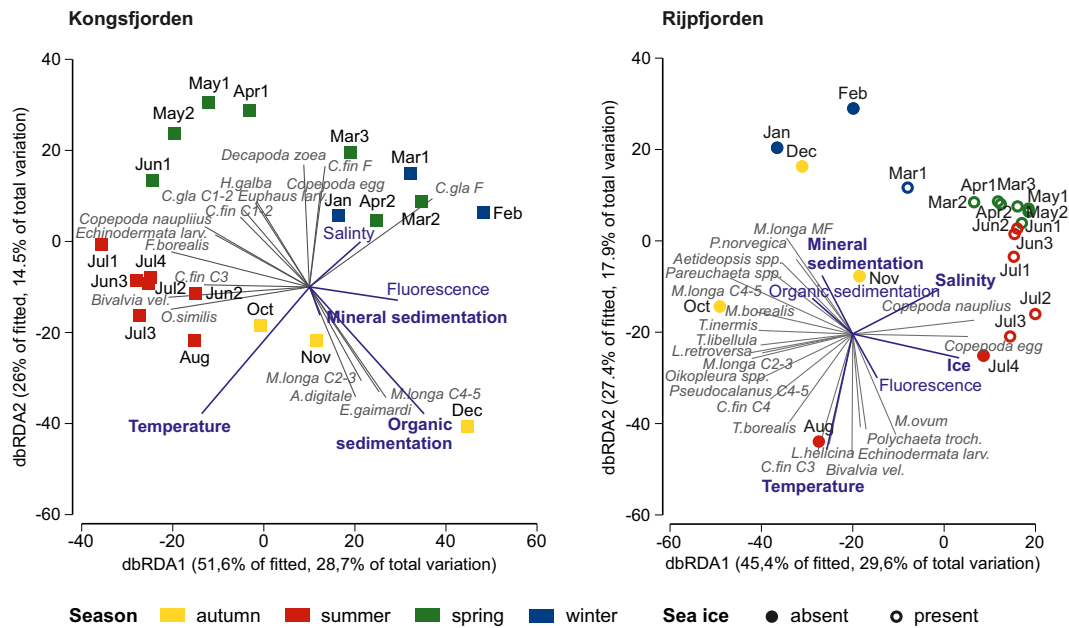


Fig. 5. The ordination of samples with environmental variables and zooplankton taxa based on dbRDA. Significant environmental variables, according to DistLM routine, are given in bold. The vectors show taxa with Pearson's correlations >0.5 .

the upper parts of the water column in these high Arctic fjords. Pronounced seasonal changes in the flux and composition of zooplankton communities in Rijpfjorden and Kongsfjorden were characterized by different significances of tested environmental variables and ca. 2–3 month shifts in seasonal development of certain taxa between the two fjords at the end of the observation period.

In Kongsfjorden, the most influential factors affecting the zooplankton community were water temperature, which explained 22% of its variability, and sedimentation rates of both organic (15%) and mineral fractions (7.8%). During the year-round observation period, this fjord was under the influence of advected relatively warm and saline Atlantic waters, which were observed in October 2014. These water masses also reached Rijpfjorden and significantly reinforced the zooplankton community in a boreal pelagic snail *Limacina retroversa*, which is a typical species for the subarctic region and spawns exclusively in Norwegian Sea, but is migrating also further north with the West Spitsbergen Current (Kacprzak et al., 2017). In the Fram Strait, *L. retroversa* shifted its distribution northwards, at the same time replacing the cold water *Limacina helicina* (Busch et al., 2015). Our observations confirmed the domination of the boreal species in the high Arctic in recent times. Other characteristic boreal species connected to the Atlantic water masses in Kongsfjorden were the jellyfish *Aglantha digitale*, and different developmental stages of the copepod *Metridia longa*. The expansion of *Aglantha digitale* into the Arctic is promoted by recent Atlantification (Mańko et al., 2020). Significantly, autumn was the period of the highest sedimentation rates in Kongsfjorden, which peaked in December (reaching ca. $40 \text{ g m}^{-2} \text{ d}^{-1}$).

Winter zooplankton communities, although generally characterized by very low zooplankton fluxes, were also similar in both fjords, and thus formed one group in LINKTREE (group II). Apart from the high abundances of the cosmopolitan copepod *O. similis*, the taxa primarily contributing to this group were older developmental stages of *M. longa*, which remained active in the upper water column during autumn and winter (Båmstedt and Ervik, 1984), and the females of *C. glacialis*, a typical Arctic copepod. These findings are comparable to the observations from sediment traps moored in Kongsfjorden in the previous years (Willis et al., 2008), and from the Canadian Beaufort Sea (Forbes et al., 1992), where the same species dominated in the winter samples. Interestingly, winter sedimentation rates were also comparable between the fjords, although their trends were contrasting; in

Kongsfjorden the sedimentation flux decreased after its maximum in December, while in Rijpfjorden the highest values were observed between January and March.

Clear differences between the structure of zooplankton communities in Kongsfjorden and Rijpfjorden appeared in spring, along with higher water temperatures in the former and the formation of sea ice in the latter. Characteristically, in Kongsfjorden this was the period of both, increasing zooplankton flux, and the contribution of organic material in sediments. In the Atlantic-influenced fjord, the zooplankton spring community developed continuously, with the peak of eggs and subsequent nauplii of Copepoda, young copepodites of *C. finmarchicus* and *C. glacialis*, larval stages of euphausiids, as well as meroplankton, including Echinodermata and Cirripedia larvae. The presence of Cirripedia larvae, together with an increase in fluorescence, indicates phytoplankton bloom in this area, as cirripedians are known for releasing their larvae with increased food availability (Crisp and Spencer, 1958; Walczyńska et al., 2019). Similarly, Euphausiacea eggs were found in large numbers in the fjord, what corresponds with the previous observations of Hegseth and Tverberg (2013) on the relationship of increasing chlorophyll *a* concentrations and presence of younger stages of *Thysanoessa inermis* in April in Kongsfjorden.

Rijpfjorden, in contrast, had been covered by sea ice since mid-February, which led to the formation of cold and rather homogenous water, with temperatures of ca. $-1.8 \text{ }^\circ\text{C}$. The zooplankton community was dominated by the eggs and nauplii of copepods, mainly *Calanus* spp., that, along with the first fluorescence peak in the beginning of May, may also indicate the ice algal bloom, which is also the main food source for females completing their gonad maturation process (Søreide et al., 2010; Weydmann et al., 2013).

The 2–3 month shift in seasonal development of zooplankton community between the investigated fjords was clearly visible in summer. The peak of *Bivalvia veligers*, which were the most contributing taxa to the Kongsfjorden early summer community (group VI), was already observed in mid-May. In Rijpfjorden, the water temperature gradually increased during this period, and with the sea ice breakup at the end of July, the subsequent phytoplankton bloom allowed for rapid changes in the zooplankton community. Therefore, the community abundance peak was observed at that time, which was mainly due to the high densities of copepod eggs and nauplii, as well as the increased numbers of meroplankton, including Echinodermata and Polychaeta larvae.

Although Echinodermata larvae can peak several times, depending on the genus-specific spawning strategy, they are usually observed within a month after the spring bloom and are often highly correlated with chlorophyll *a* biomass (Starr et al., 1990; Stübner et al., 2016; Weydmann-Zwolicka et al., 2021). In light of seasonal shifts between the fjords, a key observation of this work is that the late summer community from Kongsfjorden (group IV) grouped closely to the Rjippfjorden autumn community (group III) and showed a similar age structure and taxonomic composition, characterized by an increasing flux of boreal taxa.

Remarkably, sedimentation rates of both organic and mineral fractions were connected to the most important first two splits of zooplankton samples in LINKTREE, which emphasizes the influence of sedimentation on pelagic communities in the fjords. Interestingly, although the flux of mineral sediments significantly affected zooplankton in both fjords, explaining 6.3% (Rjippfjorden) and 7.8% (Kongsfjorden) of their variability, organic sedimentation was significant only in the latter fjord and reached 15% of the explained variation in that location. However, the seasonal measurements of sedimentation rates significantly differed from the typical seasonality of sedimentation known from Arctic fjords (e.g., Zajączkowski et al., 2010; Wiedmann et al., 2016), because they show the highest sedimentation rates during autumn and winter months, when there is no sediment supply from glaciers and rivers. Therefore, we suggest that the high sediment amount captured by the sediment traps resulted from the redeposition of sediments from shallower, subtidal areas and was connected to the autumn/winter storms. In general, the Svalbard area is characterized by a stormy period from December to February, followed by a decrease in spring and a calm period from June to mid-August (Stopa et al., 2016). Additionally, the acceleration of wind speeds and wave heights was recently observed in the Nordic Seas (Stopa et al., 2016), resulting in a higher frequency and total duration of extreme winter events (Wojtyśiak et al., 2018). The winter waves entering the mouths of the fjords erode the shallow-bottom sediments and distribute them in the water column. Due to the lack of a freshwater layer, which usually occupies the fjord surface during the melting period, sediments may sink immediately (Zajączkowski et al., 2010), partly reaching the exposed sediment traps.

It would be interesting to include more environmental predictors into the performed statistical analyses to explain more variability in the zooplankton communities from high Arctic fjords, although it can be difficult, or even impossible, to collect additional data, especially during the Polar Night or when fjords are covered by sea ice. For example, it would be worth to test the influence of wind speed on the studied zooplankton communities, especially knowing that diminishing Arctic sea ice promotes stronger surface winds (Mioduszeński et al., 2018), and that wind speed was a significant predictor in the seasonal study on the copepods from the Baltic Sea (Musiałik-Koszarowska et al., 2019). Light intensity is another environmental predictor that affects fjordic meroplankton (Weydmann-Zwolicka et al., 2021), and thus it would be worth testing its influence also on the whole zooplankton community. Generally, the more environmental variables, the better statistical models describing variability in biological communities can be obtained, so we believe that our study, which includes the fluxes of organic and mineral sediments into multivariate analyses of the zooplankton community, is a good example of applying integrative approach in predicting the future of high Arctic fjordic systems under the pressure of climate change and Atlantification.

5. Conclusions

The properties of water masses, especially temperature, as well as the presence of sea ice and sediment flux, had the greatest impact on the variations in the surface zooplankton flux in the Svalbard fjords in our study. Moreover, these environmental variables were also the ones that contributed the most to the differences between the fjords

and thus influenced the zooplankton communities. The most striking difference was the presence of sea ice only in Rjippfjorden, which was associated with the dominating cold water masses and the delay of a pelagic algal bloom until July, thus causing the 2–3 month shift in the zooplankton community development compared to the Atlantic-influenced Kongsfjorden. If Kongsfjorden is representative of a future high Arctic environment, one may expect less or no sea ice and increased temperature and sedimentation rates in late autumn – early winter. These factors will lead to the progressing development of the zooplankton community during spring, which may result in the mismatch between phytoplankton bloom and the youngest developmental stages of herbivorous Arctic species (Søreide et al., 2010). Increased Atlantification of Svalbard fjords would impose changes in the composition and distribution of zooplankton species (Willis et al., 2006, 2008; Wallace et al., 2010; Weydmann et al., 2013) and consequently in higher trophic levels (Kwaśniewski et al., 2012; Vihtakari et al., 2018).

The unexpected pattern of seasonal sediment fluxes, with the peaks in autumn (Kongsfjorden), and winter (Rjippfjorden) might have resulted from the redeposition of sediments from shallower, subtidal areas and was probably connected to the autumn/winter storms, which are likely to increase with climate change. Thus, seasonal timing of organic and mineral sediment fluxes should be taken into account when trying to predict the future of Arctic coastal ecosystems in the era of climate change and increased inflow of Atlantic water masses.

A shift from Arctic to Atlantic conditions in high Arctic fjords will influence whole ecosystems, including their abiotic components, such as weather conditions, presence of sea ice, water temperature, sediment flux, and species composition, from zooplankton to top predators. Therefore, only integrating multiple pieces of information can provide key insights into the relations between Atlantification, sediment flux, and zooplankton composition, thus helping to predict the functioning of high Arctic fjordic ecosystems under climate change conditions.

Abbreviations

ADCP	Acoustic Doppler current profiler
C1 – C5	Copepodite stages (from the first to the fifth one)
DISTLM	Distance-based linear model
dbRDA	Distance-based redundancy analysis
LINKTREE	Linkage tree analysis
LWW	Local Winter Water
S	Salinity
SIMPROF	Similarity profile test
SIMPER	Similarity percentages analysis
SW	Surface waters
T	Temperature
TAW	Transformed Atlantic water
WCW	Winter cooled water

CRedit authorship contribution statement

Agata Weydmann-Zwolicka: Conceptualization, Formal analysis, Investigation, Writing – original draft, Supervision, Project administration, Funding acquisition. **Paula Prątnicka:** Formal analysis, Writing – original draft. **Magdalena Łącka:** Formal analysis, Writing – original draft. **Sanna Majaneva:** Writing – review & editing. **Finlo Cottier:** Conceptualization, Methodology, Writing – review & editing, Funding acquisition. **Jørgen Berge:** Conceptualization, Methodology, Resources, Writing – review & editing, Funding acquisition.

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

This research project was supported by the grant No. 2015/19/B/NZ8/03937 from the National Science Centre, Poland. The work was also financially supported by the Norwegian Research Council project Arctic ABC (project no. 244319). Contribution to manuscript preparation by Finlo Cottier was supported by Arctic PRIZE research project (NE/P006302/1), part of the Changing Arctic Ocean programme funded by the UKRI Natural Environment Research Council (NERC). Magdalena Łącka participation in this study was supported by the National Science Centre in Poland project no. 2019/33/B/ST10/00297. We would like to thank prof. Piotr Kukliński and prof. Marek Zajączkowski for their comments to the manuscript.

References

- Anderson, M.J., 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62, 245–253. <https://doi.org/10.1111/j.1541-0420.2005.00440.x>.
- Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth, UK.
- Arrigo, K.R., Van Dijken, G., Pabi, S., 2008. Impact of shrinking Arctic ice cover on marine primary production. *Geophys. Res. Lett.* 35, L19603. <https://doi.org/10.1029/2008GL035028>.
- Båmstedt, U., Ervik, A., 1984. Local variations in size and activity among *Calanus finmarchicus* and *Metridia longa* (Copepoda, Calanoida) overwintering on the west coast of Norway. *J. Plankton Res.* 6, 843–857. <https://doi.org/10.1093/plankt/6.5.843>.
- Bauerfeind, E., Nöthig, E.M., Pauls, B., Kraft, A., Beszczyńska-Möller, A., 2014. Variability in pteropod sedimentation and corresponding aragonite flux at the Arctic deep – sea long – term observatory HAUSGARTEN in the eastern Fram Strait from 2000–2009. *J. Mar. Syst.* 132:95–105. DOI:<https://doi.org/10.1016/j.jmarsys.2013.12.006>.
- Berge, J., Johnsen, G., Nilsen, F., Gulliksen, B., Slagstad, D., 2005. Ocean temperature oscillations enable reappearance of blue mussel *Mytilus edulis* in Svalbard after 1000 yr absence. *Mar. Ecol. Prog. Ser.* 303, 167–175. <https://doi.org/10.3354/meps303167>.
- Brodskii, K.A., Vyshkvartseva, N.V., Kos, M.S., Markhatseva, E.L., 1983. Copepods (Copepoda: Calanoida) of the seas of the USSR and adjacent waters. Vol. 1. Keys to the fauna of the USSR No 135. (In Russian).
- Busch, K., Bauerfeind, E., Nöthig, E.M., 2015. Pteropod sedimentation patterns in different water depths observed with moored sediment traps over a 4 – year period at the LTER station HAUSGARTEN in eastern Fram Strait. *Polar Biol.* 38, 845–859. <https://doi.org/10.1007/s00300-015-1644-9>.
- Carstensen, J., Weydmann, A., Olszewska, A., Kwasniewski, S., 2012. Effects of environmental conditions on the biomass of *Calanus* spp. in the Nordic Seas. *J. Plankton Res.* 34, 951–966. <https://doi.org/10.1093/plankt/fbs059>.
- Clarke, K.R., Gorley, R.N., 2015. PRIMER v7: user manual/tutorial. PRIMER-E, Plymouth.
- Clarke, K.R., Warwick, R.M., 2001. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. 2nd edn. PRIMER-E, Plymouth.
- Clarke, K.R., Somerfield, P.J., Gorley, R.N., 2008. Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. *J. Exp. Mar. Biol. Ecol.* 366, 56–69. <https://doi.org/10.1016/j.jembe.2008.07.009>.
- 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. *J. Geophys. Res.* 110, C12. <https://doi.org/10.1029/2004JC002757>.
- Cottier, F., Nilsen, F., Inall, M.E., Gerland, S., Tverberg, V., Svendsen, H., 2007. Wintertime warming of an Arctic shelf in response to large – scale atmospheric circulation. *Geophys. Res. Lett.* 34. <https://doi.org/10.1029/2007GL029948>.
- Cottier, F., Skogseth, R., David, D., Berge, J., 2019. Temperature time series in Svalbard fjords. A contribution to the “Integrated Marine Observatory Partnership (iMOP)”, in: Orr et al. (Eds): *SESS report 2018*. Longyearbyen, Svalbard Integrated Arctic Earth Observing System, pp. 108–118.
- Crisp, D.J., Spencer, C.P., 1958. The control of the hatching process in barnacles. *Proc R Soc London B Biol Sci* 149, 278–299. <https://doi.org/10.1098/rspb.1958.0069>.
- Daase, M., Eiane, K., 2007. Mesozooplankton distribution in northern Svalbard waters in relation to hydrography. *Polar Biol.* 30, 969–981. <https://doi.org/10.1007/s00300-007-0255-5>.
- Darnis, G., Hobbs, L., Geoffroy, M., Grenvald, J.C., Renaud, P.E., Berge, J., Cottier, F., Kristiansen, S., Daase, M., E. Søreide, J., Wold, A., Morata, N., Gabrielsen, T., 2017. From polar night to midnight sun: Diel vertical migration, metabolism and biogeochemical role of zooplankton in a high Arctic fjord (Kongsfjorden, Svalbard). *Limnol. Oceanogr.* 62:1586–1605. DOI:<https://doi.org/10.1002/lno.10519>.
- Dezutter, T., Lalonde, C., Dufresne, C., Darnis, G., Fortier, L., 2019. Mismatch between microalgae and herbivorous copepods due to the record sea ice minimum extent of 2012 and the late sea ice break-up of 2013 in the Beaufort Sea. *Prog Oceanogr* 173: 66–77. DOI:<https://doi.org/10.1016/j.pocean.2019.02.008>.
- Fleischer, D., Schaber, M., Piepenburg, D., 2007. Atlantic snake pipefish (*Entelurus aequoreus*) extends its northward distribution range to Svalbard (Arctic Ocean). *Polar Biol.* 30, 1359–1362. <https://doi.org/10.1007/s00300-007-0322-y>.
- Forbes, J.R., Macdonald, R.W., Carmack, E.C., Iseki, K., O'Brien, M.C., 1992. Zooplankton retained in sequential sediment traps along the Beaufort Sea shelf break during winter. *Can J Fish Aquat Sci* 49, 663–670.
- Gluchowska, M., Kwaśniewski, S., Promińska, A., Olszewska, A., Goszczko, I., Falk-Petersen, S., Hop, H., Węśławski, J.M., 2016. Zooplankton in Svalbard fiords on the Atlantic – Arctic boundary. *Polar Biol.* 39:1785–1802. DOI:<https://doi.org/10.1007/s00300-016-1991-1>.
- Grabowski, M., Jabłońska, A., Weydmann-Zwolicka, A., Gantsevich, M., Strelkov, P., Skazina, M., Węśławski, J.M., 2019. Contrasting molecular diversity and demography patterns in two intertidal amphipod crustaceans reflect Atlantification of High Arctic. *Mar. Biol.* 166, 155. <https://doi.org/10.1007/s00227-019-3603-4>.
- Hegseth, E.N., Tverberg, V., 2013. Effect of Atlantic water inflow on timing of the phytoplankton spring bloom in a high Arctic fjord (Kongsfjorden, Svalbard). *J. Mar. Syst.* 113–114, 94–105. <https://doi.org/10.1016/j.jmarsys.2013.01.003>.
- Hop, H., Pearson, T., Hegseth, E.N., Kovacs, K.M., Wiencke, C., Kwaśniewski, S., Eiane, K., Mehlum, F., Gulliksen, B., Włodarska-Kowalcuk, M., Lydersen, C., Węśławski, J.M., Cochran, S., Gabrielsen, G.W., Leakey, R.J.G., Lønne, O.J., Zajączkowski, M., Falk-Petersen, S., Kendall, M., Wängberg, S.A., Bischof, K., Voronkov, A.Y., Kovaltchouk, N.A., Wiktor, J., Poltermann, M., di Prisco, G., Papucci, C., Gerland, S., 2002. The marine ecosystem of Kongsfjorden, Svalbard. *Polar Res.* 21:167–208. DOI:<https://doi.org/10.3402/polar.v21i1.6480>.
- Hop, H., Assmy, P., Wold, A., Sundfjord, A., Daase, M., Duarte, P., Kwasniewski, S., Gluchowska, M., Wiktor, J.M., Tatarek, A., Wiktor Jr., J., 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). *Front. Mar. Sci.* 6, 181. <https://doi.org/10.3389/fmars.2019.00181>.
- Hyatt, J., Visbeck, M., Beardsley, R.C., Brechner Owens W., 2008. Estimating sea-ice coverage, draft, and velocity in Marguerite Bay (Antarctica) using a subsurface moored upward-looking acoustic Doppler current profiler (ADCP). *Deep-Sea Res II* 55:351–364. DOI:<https://doi.org/10.1016/j.dsr2.2007.11.004>.
- IPCC, 2014. *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)). IPCC, Geneva, Switzerland, 151 pp.
- Johansson, A.M., Malnes, E., Gerland, S., Cristea, A., Douglis, A.P., Divine, D.V., Pavlova, O., Lauknes, T.R., 2020. Consistent ice and open water classification combining historical synthetic aperture radar satellite images from ERS-1/2, Envisat ASAR, RADARSAT-2 and Sentinel-1A/B. *Ann. Glaciol.* 61, 40–50. <https://doi.org/10.1017/aog.2019.52>.
- Kacprzak, P., Panasiuk, A., Wawrzynek, J., Weydmann, A., 2017. Distribution and abundance of pteropods in the western Barents Sea. *Oceanol. Hydrobiol. Stud.* 46 (4), 393–404. <https://doi.org/10.1515/ohs-2017-0039>.
- Kahru, M., Brotas, V., Manzano – Sarabia, M., Mitchell, B.G., 2010. Are phytoplankton blooms occurring earlier in the Arctic? *Glob Change Biol* 17:1733–1739. DOI: <https://doi.org/10.1111/j.1365-2486.2010.02312.x>.
- Kraft, A., Bauerfeind, E., Nöthig, E.M., 2011. Amphipod abundance in sediment trap samples at the long – term observatory HAUSGARTEN (Fram Strait, ~79°N/4°E). Variability in species community patterns. *Mar. Biodivers.* 41, 353–364. <https://doi.org/10.1007/s12526-010-0052-1>.
- Kwaśniewski, S., Gluchowska, M., Walkusz, W., Karnovsky, N.J., Jakubas, D., Wojczulanis-Jakubas, K., Harding, A.M.A., Goszczko, I., Cisek, M., Beszczyńska-Möller, A., Walczowski, W., Węśławski, J.M., Stempniewicz, L., 2012. Interannual changes in zooplankton on the West Spitsbergen shelf in relations to hydrography and their consequences for the diet of planktivorous seabirds. *ICES J. Mar. Sci.* 69, 890–901. <https://doi.org/10.1093/icesjms/fss076>.
- Łącka, M., Cao, M., Rosell-Melé, A., Pawłowska, J., Kucharska, M., Forwick, M., Zajączkowski, M., 2019. Postglacial paleoceanography of the western Barents Sea: implications for alkenone-based sea surface temperatures and primary productivity. *Quat. Sci. Rev.* 224, 105973. <https://doi.org/10.1016/j.quascirev.2019.105973>.
- Legendre, P., Anderson, M.J., 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecol Monogr* 69, 1–24.
- Makabe, R., Hattori, H., Sampei, M., Ota, Y., Fukuchi, M., Fortier, L., Sasaki, H., 2010. Regional and seasonal variability of zooplankton collected using sediment traps in the southeastern Beaufort Sea, Canadian Arctic. *Polar Biol.* 33, 257–270. <https://doi.org/10.1007/s00300-009-0701-7>.
- Mańko, K.M., Gluchowska, M., 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. <https://doi.org/10.1016/j.pocean.2020.102414>.
- Matsumo, K., Yamaguchi, A., Fujiwara, A., Onodera, J., Watanabe, E., Imai, I., Chiba, S., Harada, N., Kikuchi, T., 2014. Seasonal changes in mesozooplankton swimmers collected by sediment trap moored at a single station on the Northwind Abyssal Plain in the western Arctic Ocean. *J. Plankton Res.* 36, 490–502. <https://doi.org/10.1093/plankt/fbt092>.
- Mioduszewski, J., Vavrus, S., Wang, M., 2018. Diminishing Arctic Sea ice promotes stronger surface winds. *J. Clim.* 31, 8101–8119. <https://doi.org/10.1175/JCLI-D-18-0109.s1>.
- Morata, N., Michaud, E., Poullaouec, M.A., Devesa, J., Le Goff, M., Corvaisier, R., Renaud, P.E., 2020. Climate change and diminishing seasonality in Arctic benthic processes. *Philos T R Soc A* 378 (2181), 20190369. <https://doi.org/10.1098/rsta.2019.0369>.
- Musialik-Koszarowska M., Dzierzbicka-Głowacka L., Weydmann A., 2019. Influence of environmental factors on the population dynamics of key zooplankton species in the Gulf of Gdańsk (southern Baltic Sea). *Oceanologia* 61:17–25. DOI:10.1016/j.oceano.2018.06.001.
- 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(4): 1209–1230. DOI:10.1175/JPO-D-15-0058.1.
- Pérez-Hernández, M.D., Pickart, R.S., Pavlov, V., Våge, K., Ingvaldsen, R.B., Sundfjord, A., et al., 2017. The Atlantic water boundary current north of Svalbard in late summer. *J Geophys Res Ocean* 122:2269–2290. DOI:10.1002/2016JC012486.

- 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., Yuli, A., 2017. Greater role for Atlantic inflows on sea-ice loss in the Eurasian Basin of the Arctic Ocean. *Science* 356:285–291. DOI: <https://doi.org/10.1126/science.aai8204>.
- Promińska, A., Cisek, M., Walczowski, W., 2017. Kongsfjorden and Hornsund hydrography – comparative study based on a multiyear survey in fjords of west Spitsbergen. *Oceanologia* 59:397–412. <https://doi.org/10.1016/j.ocean.2017.07.003>.
- Sampei, M., Sasaki, H., Forest, A., Fortier, L., 2012. A substantial export flux of particulate organic carbon linked to sinking dead copepods during winter 2007–2008 in the Amundsen Gulf (southeastern Beaufort Sea, Arctic Ocean). *Limnol Oceanogr* 57:90–96. DOI: <https://doi.org/10.4319/lo.2012.57.1.0090>.
- Skogseth, R., Olivier, L.L.A., Nilsen, F., Falck, E., Fraser, N., Tverberg, V., Ledang, A.B., Vader, A., Jonassen, M.O., Søreide, J., Cottier, F., Berge, J., Ivanov, B.V., Falk-Petersen, S., 2020. Variability and decadal trends in the Isfjorden (Svalbard) ocean climate and circulation – an indicator for climate change in the European Arctic. *Prog Oceanogr* 187. <https://doi.org/10.1016/j.pocean.2020.102394>.
- Slagstad, D., Ellingsen, I.H., Wassmann, P., 2011. Evaluating primary and secondary production in an Arctic Ocean void of summer sea ice: an experimental simulation approach. *Prog. Oceanogr.* 90, 117–131. <https://doi.org/10.1016/j.pocean.2011.02.009>.
- Søreide, J.E., Leu, E., Berge, J., Graeve, M., Falk – Petersen, S., 2010. Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. *Glob. Chang. Biol.* 16:3154–3163. DOI: <https://doi.org/10.1111/j.1365-2486.2010.02175.x>.
- Spielhagen, R.F., Werner, K., Sørensen, S.A., Zamelczyk, K., Kandiano, E., Budeus, G., Husum, K., Marchitto, T.M., Hald, M., 2011. Enhanced modern heat transfer to the Arctic by warm Atlantic water. *Science* 331, 450–453. <https://doi.org/10.1126/science.1197397>.
- Starr, M., Himmelman, J.H., Theriault, J.C., 1990. Direct coupling of marine invertebrate spawning with phytoplankton blooms. *Science* 247, 1071–1074. <https://doi.org/10.1126/science.1197397>.
- Stopa, J.E., Arduin, F., Girard-Arduin, F., 2016. Wave climate in the Arctic 1992–2014: seasonality and trends. *Cryosphere* 10, 1605–1629. <https://doi.org/10.5194/tc-10-1605-2016>.
- Stübner, E.L., Søreide, J.E., Reigstad, M., Marquardt, M., Błachowiak-Samolyk, K., 2016. Year – round meroplankton dynamics in high – Arctic Svalbard. *J. Plankton Res.* 38, 522–536. <https://doi.org/10.1093/plankt/fbv124>.
- Svendsen, H., Beszczyńska-Møller, A., Hagen, J.O., Lefauconnier, B., Tverberg, V., Gerland, S., Børre Ørbøk, J., 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. <https://doi.org/10.1111/j.1751-8369.2002.tb00072.x>.
- Vihtakari, M., Welcker, J., Moe, B., Chastel, O., Tartu, S., Hop, H., Bech, C., Descamps, S., Gabrielsen, G.W., 2018. Black-legged kittiwakes as messengers of Atlantification in the Arctic. *Sci. Rep.* 8, 1178. <https://doi.org/10.1038/s41598-017-19118-8>.
- Walczowski, W., Piechura, J., 2011. Influence of the West Spitsbergen current on the local climate. *Int. J. Climatol.* 31, 1088–1093. <https://doi.org/10.1002/joc.2338>.
- Walczyńska, K.S., Søreide, J.E., Weydmann-Zwolicka, A., Ronowicz, M., Gabrielsen, T.M., 2019. DNA barcoding of Cirripedia larvae reveals new knowledge on their biology in Arctic coastal ecosystems. *Hydrobiol* 837, 149–159. <https://doi.org/10.1007/s10750-019-3967-y>.
- Wallace, M.I., Cottier, F., Berge, J., Tarling, G.A., Griffiths, C., Brierley, A.S., 2010. Comparison of zooplankton vertical migration in an ice – free and a seasonally ice – covered Arctic fjord: an insight into the influence of sea ice cover on zooplankton behavior. *Limnol. Oceanogr.* 55, 831–845. <https://doi.org/10.4319/lo.2010.55.2.0831>.
- Węślawski, J.M., Buchholz, F., Głuchowska, M., Weydmann, A., 2017. Ecosystem maturation process follows the warming of the Arctic fjords. *Oceanologia* 59, 592–602. <https://doi.org/10.1016/j.oceano.2017.02.002>.
- Weydmann, A., Kwasniewski, S., 2008. Distribution of *Calanus* populations in a glaciated fjord in the Arctic (Hornsund, Spitsbergen) – an interplay between biological and physical factors. *Polar Biol.* 31, 1023–1035. <https://doi.org/10.1007/s00300-008-0441-0>.
- Weydmann, A., Søreide, J.E., Kwaśniewski, S., Leu, E., Falk-Petersen, S., Berge, J., 2013. Ice-related seasonality in zooplankton community composition in a high Arctic fjord. *J. Plankton Res.* 35, 831–842. <https://doi.org/10.1093/plankt/ftb031>.
- Weydmann, A., Cartensen, 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. DOI: <https://doi.org/10.3354/meps10694>.
- Weydmann-Zwolicka, A., Balazy, P., Kuklinski, P., Søreide, J.E., Pała, W., Ronowicz, M., 2021. Meroplankton seasonal dynamics in the high Arctic fjord: comparison of different sampling methods. *Prog. Oceanogr.* 190, 102484. <https://doi.org/10.1016/j.pocean.2020.102484>.
- Wickström, S., Jonassen, M. O., Cassano, J. J., Vihma, T., 2020. Present Temperature, Precipitation, and Rain-on-Snow Climate in Svalbard. *J. Geophys. Res. Atmospheres* 125(14): e2019JD032155. DOI: <https://doi.org/10.1029/2019JD032155>.
- Wiedmann, I., Reigstad, M., Marquardt, M., Vader, A., Gabrielsen, T.M., 2016. Seasonality of vertical flux and sinking particle characteristics in an ice-free high arctic fjord—different from subarctic fjords? *J. Mar. Syst.* 154, 192–205. <https://doi.org/10.1016/j.jmarsys.2015.10.003>.
- Willis, K., Cottier, F., Kwaśniewski, S., Wold, A., Falk-Petersen, S., 2006. The influence of advection on zooplankton community composition in an Arctic fjord (Kongsfjorden, Svalbard). *J. Mar. Syst.* 61, 39–54. <https://doi.org/10.1016/j.jmarsys.2005.11.013>.
- Willis, K.J., Cottier, F.R., Kwaśniewski, S., 2008. Impact of warm water advection on the winter zooplankton community in an Arctic fjord. *Polar Biol.* 31, 475–481. <https://doi.org/10.1007/s00300-007-0373-0>.
- Wojtyśiak, K., Herman, A., Moskalik, M., 2018. Wind wave climate of west Spitsbergen: seasonal variability and extreme events. *Oceanologia* 60 (3), 331–343. <https://doi.org/10.1016/j.oceano.2018.01.002>.
- Zajaczkowski, M., Nygård, H., Hegseth, E.N., Berge, J., 2010. Vertical flux of particulate matter in an Arctic fjord: the case of lack of the sea-ice cover in Adventfjorden 2006–2007. *Polar Biol.* 33, 223–239. <https://doi.org/10.1007/s00300-009-0699-x>.