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1 **Zooplankton and sediment flux in two contrasting fjords reveal Atlantification of the**
2 **Arctic**

3

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20 **Abstract**

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

45 **Keywords:** Swimmers; Advection; Borealisation; Mooring; Kongsfjorden; Rijpfjorden

46

47 **1. Introduction**

48 The marine environment in the European Arctic is changing at an unprecedented rate,
49 and observed changes include increasing northward inflow of warm and saline Atlantic waters,
50 called Atlantification, and loss of sea ice (e.g., Spielhagen et al. 2011; IPCC, 2014; Polyakov
51 et al., 2017). These remarkable habitat shifts are coupled with changes in species diversity and
52 composition, such as northward range extension of Atlantic species into the Arctic (Berge et
53 al., 2005; Fleischer et al., 2007; Weydmann et al., 2014) and increases in primary and secondary
54 production (Arrigo et al., 2008; Slagstad et al., 2011; Carstensen et al., 2012). The progressive
55 retreat of sea ice cover induces changes in sedimentation rates and will consequently lead to
56 changes in the euphotic zone, and hence light available for the primary production, especially
57 in fjords (Zajączkowski et al., 2010). As a result, this might affect the onset of spring bloom,
58 which is the main food source for herbivorous zooplankton (Søreide et al., 2010; Kahru et al.,
59 2010), and in the worst case scenario, it can lead to the dramatic weakening of convective water
60 mixing during the polar night and strong limitation of spring/summer primary production in the
61 region (Łącka et al., 2019).

62 Sea ice coverage in some Svalbard fjords can last for 6–8 months, and these conditions
63 hamper the traditional net collection of zooplankton. Thus, most zooplankton studies have
64 focused on late spring - early autumn seasons only, limiting our knowledge about the seasonal
65 changes in zooplankton community. Sediment traps are often the only available method for
66 collecting zooplankton samples during the high Arctic late autumn - spring period, although
67 there are some limitations to using sediment traps to study zooplankton, including interpreting
68 results based only on qualitative data at one specific depth treated as a proxy of organisms'
69 position in the water column (Dezutter et al., 2019). Consequently, several year-round sediment

70 trap-derived observations on zooplankton fluxes have been reported from the Canadian Arctic
71 (Makabe et al. 2010; Matsuno et al. 2014; Dezutter et al. 2019), Fram Strait (Kraft et al., 2011;
72 Bauerfeind et al., 2014; Busch et al., 2015), and Kongsfjorden (Willis et al., 2006; Willis et al.,
73 2008).

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

85 Sediment flux in Arctic fjords is usually characterized by large seasonal, spatial and
86 interannual variability (Svendsen et al., 2002). Sedimentation seasonality in Svalbard fjords
87 used to be mainly dependent on the light regime (e.g., Zajączkowski et al., 2010). The early
88 spring light signal began meltwater runoff and organic matter supply. In summer, terrigenous
89 material was supplied from rivers and tidewater glaciers. The sediment flux decreased as
90 insolation weakened, and during the autumn/winter period, it was near basal levels. Recently,
91 in ice-free fjords, a decline in sedimentation seasonality, at least in its original form, has been
92 observed (e.g., Wiedmann et al., 2016; Morata et al., 2020). For instance, during the winter
93 season in ice-free Adventfjorden, mixing by thermal convection and wind is enhanced
94 compared to the previous ice-covered situation, and detrital material, which previously settled

95 to the bottom, is resuspended and laterally advected to the middle of the fjord, increasing winter
96 sedimentation rates (Wiedmann et al., 2016). Taking into account the further Atlantification of
97 the Arctic (i.e., intensified advection of Atlantic Water and shrinking sea ice) leading to warmer
98 and wetter winter conditions with a concomitant higher frequency of extreme weather events,
99 such as winter storms (Nilsen et al., 2016) and/or extreme precipitation events (e.g., Wickström
100 et al., 2020), unprecedented changes in the sedimentation regimes of Svalbard fjords might also
101 be expected in the near future.

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

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

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

125

126 **2. Materials and methods**

127 **2.1. Study area**

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

138 Rijpfjorden is located on the north-central shore of Nordaustlandet in the northeastern
139 part of the Svalbard Archipelago (Fig. 1). It is north facing and open to the wide shelf through
140 a broad mouth. In contrast to Kongsfjorden, Rijpfjorden is predominantly ice-covered for at
141 least 6–8 months of the year and experiences oceanographic conditions that are more Arctic in
142 character: colder and fresher (Johansson et al., 2020); as a consequence, the local zooplankton
143 community is dominated by Arctic species. However, there is a periodic influence of warmer

144 (>1°C) water masses, which are thought to be highly modified Atlantic water carrying boreal
145 species (Wallace et al., 2010; Weydmann et al., 2013; Hop et al., 2019).

146

147 **2.2. Moorings, sediment traps and oceanographic data**

148 Sediment traps (McLane Parflux 78H – 21 with a 21 bottle carousel and a 0.5 m²
149 aperture) were deployed on single-point moorings in Kongsfjorden (78°57.760'N 11°47.835'E)
150 at a depth of 60 m (bottom depth of 223 m), and in Rijpfjorden (80°17.661'N 22°18.230'E) at
151 a depth of 60 m (bottom depth of 235 m) (Fig. 1). Sediment trap exposure times were
152 programmed for different sampling periods (Table 1) according to the season and primary and
153 secondary production in the fjords. The trap sample bottles were prefilled with filtered seawater
154 adjusted with NaCl to 35 PSU to provide a density discontinuity relative to ambient seawater
155 and to avoid diffusion of samples. To preserve deposited material, 4% formalin buffered with
156 sodium borate, was added to the samples after deployment.

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

165 Temperature (T) and salinity (S) were recorded during the sediment trap deployment
166 period with Seabird 37 Microcats moored at a depth of 22 m. Additional sensors measured
167 fluorescence, and the presence or absence of sea ice was noted based on data from acoustic

168 Doppler current profilers (ADCPs) (Hyatt et al., 2008). During the analyses, water masses in
169 both fjords were classified based on Cottier et al. (2005) and Pérez-Hernández et al. (2017).

170

171 **2.3. Laboratory analyses**

172 All large zooplankton (chaetognaths, ctenophores, medusae, amphipods, euphausiids,
173 and appendicularians) were sorted and carefully removed from the samples using small, soft
174 forceps. The collected sediment was vacuum-filtered onto preweighed filters (MN GF5 with
175 0.4 μm openings) and rinsed with distilled water. The filters were air dried at 60°C for 24 h,
176 weighed to determine the sediment dry mass, combusted at 450°C for 24 h, and then reweighed
177 to obtain the amount of settled organic matter from weight loss (Zajączkowski et al., 2010).
178 The sedimentation rate was calculated for 7-31 days, depending on the season (Table 1).

179 The remaining zooplankton were passed through a 180 μm mesh sieve to obtain a
180 mesozooplankton fraction, and then through a 60 μm mesh sieve to sort out the smaller
181 organisms (juvenile stages and eggs). All organisms were identified under a stereomicroscope
182 equipped with a calibrated ocular micrometer (Leica M125 C, Leica Imaging Systems GmbH).
183 Developmental stages were determined for the larger genera, such as *Calanus*, *Metridia* and
184 *Pseudocalanus*. *Calanus* specimens were identified to a species based on morphology (Brodskii
185 et al., 1983) and prosome lengths of individual copepodid stages (C1 – C5, and adults)
186 according to Weydmann and Kwaśniewski (2008). The remaining zooplankton were identified
187 to the lowest taxonomic level possible. Only swimmers (zooplankton organisms that actively
188 swam into the trap) (Matsuno et al., 2014) that showed no signs of decomposition, suggesting
189 they were killed by the applied formaldehyde, were chosen for further analyses.

190

191

192 **2.4. Multivariate statistical analyses**

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

200 Multivariate statistical analyses of zooplankton community abundance data were carried
201 out using the PRIMER 7 software package (Clarke and Warwick, 2001; Clarke and Gorley,
202 2015), with the PERMANOVA+ add on (Anderson et al., 2008). Due to possible disturbances
203 connected with sediment trap deployment, the first samples (24.08.-2014-01.10.2014) were
204 excluded from further analyses. The obtained zooplankton daily flux data were transformed
205 [$n' = \log(n+1)$] prior to further analyses, and similarities between samples were examined using
206 the Bray-Curtis index. Due to the low abundances of some taxa, copepodite development stages
207 were grouped as follows: C1-3, C4-5, and adult males and females.

208 Zooplankton composition was investigated using linkage tree analysis (LINKTREE)
209 with a series of similarity profile (SIMPROF) tests, which allowed for the divisive clustering
210 of samples constrained by inequalities in one or more environmental variables (in this case:
211 water temperature, salinity, organic and mineral sedimentation rates, fluorescence, and
212 presence/absence of sea ice) (Clarke et al., 2008). In this way, the collection of 40 samples with
213 characteristic zooplankton community composition was divided into smaller groups, where
214 each division had an 'explanation' regarding the threshold on environmental variables. The
215 following set conditions gave the best linkage tree illustration: minimum group size = 2,
216 minimum split size = 5, minimum split R = 0.49. To further investigate the groups obtained by
217 LINKTREE, a similarity percentage (SIMPER) analysis was used to determine the contribution

218 of certain zooplankton taxa/development stages to the within-group similarity. Thus, this
219 analysis investigated the distinct clusters of zooplankton taxa separated by threshold responses
220 for given environmental variables.

221 To analyze the relationships between the flux of zooplankton taxa and environmental
222 variables, such as: water temperature, salinity, fluorescence, sea ice, and sedimentation rates of
223 both, mineral and organic fractions, as well as to provide quantitative measures of variation
224 explained by these predictor variables, a distance-based linear model (DISTLM) routine was
225 applied and illustrated by distance-based redundancy analysis (dbRDA) diagrams (Anderson,
226 2006). To build the models, all specified predictor variables were included using a forward
227 selection procedure, and the selection criterion was based on R^2 values. After testing several
228 models for each fjord, the best ones were chosen based on the highest R^2 values. Because
229 predictor variables jointly affect species composition in marine environments, we showed only
230 the results of sequential tests (Legendre and Anderson, 1999).

231

232 **3. Results**

233 **3.1. Oceanographic conditions**

234 In Kongsfjorden, at the beginning of the sampling period in October 2014, water above
235 the sediment traps had a temperature of approximately 3.7°C and a salinity of 34.6, likely
236 influenced by Atlantic water (Fig. 2). In November, the water temperature decreased to 2.7°C ,
237 while salinity increased to 34.7, and until the end of January, the water was characteristic of
238 Transformed Atlantic Water (TAW). From February 2015 to May 2015, cold water masses
239 characteristic of Local Winter Water (LWW) were observed, with temperatures ranging
240 between -0.5°C and 0.8°C . Towards the end of May, the temperature slightly increased to
241 1.4°C , probably through warm water inflow from the shelf area and local warming. These water

242 masses dominated until mid-July when an abrupt decline in salinity to 33.3 occurred, suggesting
243 the influence of fresher Surface Waters (SW).

244 Seasonal changes in oceanographic conditions observed in Rjipfjorden were different
245 from those observed in Kongsfjorden (Fig. 2). Generally, Rjipfjorden was under the influence
246 of colder (-0.9°C to -1.8°C) water masses, with salinities of 34.4 to 34.7, particularly from
247 February to the middle of July. Winter Cooled Water (WCW) dominated the fjord during this
248 period as a result of sea ice cover. After July, the surface temperature abruptly increased to
249 3.7°C in August, which was the warmest month. Freshwater discharge from glacial melt was
250 observed in October 2014 and caused the formation of fresher Polar Surface Water with a
251 salinity of 32.7, which gradually became more saline in the early winter months.

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

261

262 **3.2. Sediment flux**

263 The difference in sediment fluxes between the fjords was an order of magnitude, with
264 the highest sedimentation rates observed in Kongsfjorden (reaching $38\text{ g m}^{-2}\text{ d}^{-1}$ in December),
265 whereas in Rjipfjorden the maximum sedimentation rates reached $2.86\text{ g m}^{-2}\text{ d}^{-1}$ in February
266 (Fig. 3). In Kongsfjorden, sediment flux was quite similar between the remaining autumn and

267 winter months (ca. $6 \text{ g m}^{-2} \text{ d}^{-1}$), with the contribution of organic material constituting between
268 4 and 7%. The sedimentation rates in Kongsfjorden decreased considerably in the spring and
269 summer months (between 0.01 and $1 \text{ g m}^{-2} \text{ d}^{-1}$), with a concomitant increase in organic material
270 contribution (reaching 23.8% in May).

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

278

279 **3.3. Zooplankton flux**

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

292 period largely contributing to the maximum summer flux in mid-July. The subsequent samples
293 collected in the end of July and in August were dominated by *Bivalvia veligers* (Fig. 3).

294

295 **3.4. Influence of environmental variables on the zooplankton community**

296 LINKTREE, coupled with SIMPROF tests (Fig. 4) and the subsequent SIMPER
297 analysis (Table 2), revealed 8 characteristic groupings of samples and allowed us to relate them
298 to differences in environmental variables. The first, and thus the most important, split A, in the
299 divisive clustering was between the samples from November and December from Kongsfjorden
300 and the remaining samples. The samples in this first subdivision (group I) were characterized
301 by the organic sedimentation rates higher than $0.186 \text{ g m}^{-2} \text{ d}^{-1}$ and high contributions of *L.*
302 *retroversa* (27%), *Oikopleura* spp. (17.2%) and *Metridia longa* copepodites in the fourth and
303 fifth stages (C4-5, 15.1%). The second division, B, separated group II, with mineral
304 sedimentation rates higher than $0.706 \text{ g m}^{-2} \text{ d}^{-1}$, which included mainly winter samples from
305 both fjords, and in which the presence of *O. similis* was the most significant (23.5%), although
306 older developmental stages of other copepods were also important. Split C was based on
307 salinity, where samples with salinities <34.1 , were further divided into two groups (split D)
308 based on temperature or fluorescence. Group III included all autumn samples from Rjipfjorden
309 and was characterized by temperatures lower than 0.73°C and high contributions of *O. similis*,
310 *L. retroversa*, *Microcalanus* spp., and *Bivalvia veligers*. Group IV consisted of late summer
311 samples from both fjords, when water temperatures were higher than 3.56°C , and the
312 zooplankton community consisted of 25.1% *L. helicina*, 24.6% *O. similis*, and 15.9% *Bivalvia*
313 *veligers*. Split E was based on the salinity threshold of 34.6, and was followed by two
314 subsequent divisions: F and G. The first division was between July and August samples from
315 Rjipfjorden (group V), which were characterized by temperatures lower than 0.24°C , as well as
316 high contributions of Copepoda eggs (28.6%) and *O. similis* (21.9%); and mid-May to mid-July

317 samples from Kongsfjorden that had temperatures higher than 0.47°C and in which *Bivalvia*
318 veligers and *O. similis* jointly constituted 54.5% of the zooplankton community (group VI).
319 The second allowed us to separate most of the spring samples from both fjords into two groups.
320 Group VII included the samples from Rjipfjorden that were collected when sea ice was present
321 and temperatures were lower than 1.6°C and were dominated by the eggs and nauplii of
322 copepods. The remaining samples, which were all from Kongsfjorden, formed group VIII, with
323 temperatures higher than 0.37°C and absence of sea ice, as well as a very high contribution of
324 Copepoda eggs (34.4%) and a substantial proportion of *O. similis* and Cirripedia larvae.

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

335 Based on dbRDA plots (Fig. 5), the seasonal distribution of samples, which form
336 aggregations characteristic for a certain season, as well as a clear negative correlation between
337 the abundances of most zooplankton taxa and both fractions of sedimentation which
338 eigenvectors point in opposite directions, can be observed in the studied fjords. In
339 Kongsfjorden, the samples from November and December were characterized by the highest
340 sedimentation rates and correlated increasing abundances of *M. longa* C2-C5, *Eualus*
341 *gaimardii*, and *Aglantha digitale* (Fig. 5a). In the period between January and March, illustrated

342 by the characteristic group of samples, high numbers of *Calanus glacialis* and *C. finmarchicus*
343 females and eggs were noted. In spring (April - beginning of June), the increased flux of young
344 developmental stages, including the nauplii of copepods, *C. finmarchicus* and *C. glacialis*
345 copepodites of stages C1 and C2, as well as the larvae of euphausiids, decapods, and
346 echinoderms, were observed. Summer (samples from mid-June to August) was characterized
347 by increasing water temperatures and the flux of *Fritillaria borealis*, *C. finmarchicus* C3,
348 *Bivalvia veligers* and *O. similis*. Interestingly the zooplankton community from October
349 seemed to be more similar to the summer one than to the samples collected from November and
350 December.

351 In Rjipfjorden, the samples from the period when sea ice cover was permanently present
352 (March - beginning of July) were grouped together, and were characterized by a high salinity
353 and a low number of taxa (Fig. 5b). Copepoda eggs and nauplii appeared after the ice break up
354 in July. The larval stages of Polychaeta, Echinodermata, and *Bivalvia*, as well as *Mertensia*
355 *ovum*, *L. helicina*, *Triconia borealis*, and *C. finmarchicus* C3 and C4, were present in August,
356 which was connected to the increasing temperature based on the same direction of their
357 eigenvectors. The sample from October seemed to be distinct from the remaining ones, and was
358 characterized by the high abundances of older developmental stages of *Pseudocalanus* spp.
359 (C4-C5), as well as *M. longa* C2-C5, *Pareuchaeta* spp., *Oikopleura* spp., *L. retroversa*,
360 *Themisto libellula*, *Thysanoessa inermis*, and *Monoculodes borealis*. The samples from
361 December and January grouped together and were characterized by the increasing mineral
362 sedimentation rate and the related high abundances of *Aetideopsis* spp., *Pareuchaeta norvegica*
363 and the adults of *M. longa*.

364

365 4. Discussion

366 The integrative approach proposed in our study allowed us to provide key insights into
367 the relations between Atlantification, sediment flux, zooplankton composition and, thus, high
368 Arctic fjordic ecosystem functioning. Main environmental differences between the studied
369 fjords, including sea ice that was present only in Rjipfjorden, and sedimentation rates that were
370 an order of magnitude higher in Kongsfjorden, together with seasonal differences, including
371 water temperature, had the greatest impact on zooplankton communities present in the upper
372 parts of the water column in these high Arctic fjords. Pronounced seasonal changes in the flux
373 and composition of zooplankton communities in Rjipfjorden and Kongsfjorden were
374 characterized by different significances of tested environmental variables and ca. 2 – 3 month
375 shifts in seasonal development of certain taxa between the two fjords at the end of the
376 observation period.

377 In Kongsfjorden, the most influential factors affecting the zooplankton community were
378 water temperature, which explained 22% of its variability, and sedimentation rates of both
379 organic (15%) and mineral fractions (7.8%). During the year-round observation period, this
380 fjord was under the influence of advected relatively warm and saline Atlantic waters, which
381 were observed in October 2014. These water masses also reached Rjipfjorden and significantly
382 reinforced zooplankton community in a boreal pelagic snail *Limacina retroversa*, which is a
383 typical species for the subarctic region and spawns exclusively in Norwegian Sea, but is
384 migrating also further north with the West Spitsbergen Current (Kacprzak et al. 2017). In the
385 Fram Strait, *L. retroversa* shifted its distribution northwards, at the same time replacing the cold
386 water *Limacina helicina* (Busch et al. 2015). Our observations confirmed the domination of
387 boreal species in the high Arctic in recent times. Other characteristic boreal species connected
388 to the Atlantic water masses in Kongsfjorden were the jellyfish *Aglantha digitale*, and different
389 developmental stages of the copepod *Metridia longa*. The expansion of *Aglantha digitale* into

390 the Arctic is promoted by recent Atlantification (Mańko et al., 2020). Significantly, autumn was
391 the period of the highest sedimentation rates in Kongsfjorden, which peaked in December
392 (reaching ca. 40 g m⁻² d⁻¹).

393 Winter zooplankton communities, although generally characterized by very low
394 zooplankton fluxes, were also similar in both fjords, and thus formed one group in LINKTREE
395 (group II). Apart from the high abundances of the cosmopolitan copepod *O. similis*, the taxa
396 primarily contributing to this group were older developmental stages of *M. longa*, which
397 remained active in the upper water column during autumn and winter (Båmstedt and Ervik,
398 1984), and the females of *C. glacialis*, a typical Arctic copepod. These findings are comparable
399 to the observations from sediment traps moored in Kongsfjorden in the previous years (Willis
400 et al., 2008), and from the Canadian Beaufort Sea (Forbes et al. 1992), where the same species
401 dominated in the winter samples. Interestingly, winter sedimentation rates were also
402 comparable between the fjords, although their trends were contrasting; in Kongsfjorden the
403 sedimentation flux decreased after its maximum in December, while in Rijpfjorden the highest
404 values were observed between January and March.

405 Clear differences between the structure of zooplankton communities in Kongsfjorden
406 and Rijpfjorden appeared in spring, along with higher water temperatures in the former and the
407 formation of sea ice in the latter. Characteristically, in Kongsfjorden this was the period of both,
408 increasing zooplankton flux, and the contribution of organic material in sediments. In the
409 Atlantic-influenced fjord, the zooplankton spring community developed continuously, with the
410 peak of eggs and subsequent nauplii of Copepoda, young copepodites of *C. finmarchicus* and
411 *C. glacialis*, larval stages of euphausiids, as well as meroplankton, including Echinodermata
412 and Cirripedia larvae. The presence of Cirripedia larvae, together with an increase in
413 fluorescence, indicates phytoplankton bloom in this area, as cirripedians are known for
414 releasing their larvae with increased food availability (Crisp and Spencer, 1958; Walczyńska et

415 al., 2019). Similarly, Euphausiacea eggs were found in large numbers in the fjord, what
416 corresponds with the previous observations of Hegseth and Tverberg (2013) on the relationship
417 of increasing chlorophyll *a* concentrations and presence of younger stages of *Thysanoessa*
418 *inermis* in April in Kongsfjorden.

419 Rjipfjorden, in contrast, had been covered by sea ice since mid-February, which led to
420 the formation of cold and rather homogenous water, with temperatures of ca. -2°C. The
421 zooplankton community was dominated by the eggs and nauplii of copepods, mainly *Calanus*
422 spp., that, along with the first fluorescence peak in the beginning of May, may also indicate the
423 ice algal bloom, which is also the main food source for females completing their gonad
424 maturation process (Søreide et al., 2010; Weydmann et al., 2013).

425 The 2 – 3 month shift in seasonal development of zooplankton community between the
426 investigated fjords was clearly visible in summer. The peak of *Bivalvia* veligers, which were
427 the most contributing taxa to the Kongsfjorden early summer community (group VI), was
428 already observed in mid-May. In Rjipfjorden, the water temperature gradually increased during
429 this period, and with the sea ice breakup at the end of July, the subsequent phytoplankton bloom
430 allowed for rapid changes in the zooplankton community. Therefore, the community abundance
431 peak was observed at that time, which was mainly due to the high densities of copepod eggs
432 and nauplii, as well as the increased numbers of meroplankton, including Echinodermata and
433 Polychaeta larvae. Although Echinodermata larvae can peak several times, depending on the
434 genus-specific spawning strategy, they are usually observed within a month after the spring
435 bloom and are often highly correlated with chlorophyll *a* biomass (Starr et al., 1990; Stübner et
436 al., 2016; Weydmann-Zwolicka et al., 2021). In light of seasonal shifts between the fjords, a
437 key observation of this work is that the late summer community from Kongsfjorden (group IV)
438 grouped closely to the Rjipfjorden autumn community (group III) and showed a similar age
439 structure and taxonomic composition, characterized by an increasing flux of boreal taxa.

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

461 It would be interesting to include more environmental predictors into the performed
462 statistical analyses to explain more variability in the zooplankton communities from high Arctic
463 fjords, although it can be difficult or even impossible to collect additional data, especially
464 during the Polar Night or when fjords are covered by sea ice. For example, it would be worth

465 to test the influence of wind speed on the studied zooplankton communities, especially knowing
466 that diminishing Arctic sea ice promotes stronger surface winds (Mioduszewski et al., 2018),
467 and that wind speed was a significant predictor in the seasonal study on the copepods from the
468 Baltic Sea (Musialik-Koszarowska et al., 2019). Light intensity is another environmental
469 predictor that affects fjordic meroplankton (Weydmann-Zwolicka et al., 2021), and thus it
470 would be worth testing its influence also on the zooplankton community. Generally, the more
471 environmental variables, the better statistical model describing variability in biological
472 communities can be obtained, so we believe that our study that includes the fluxes of organic
473 and mineral sediments into multivariate analyses of the zooplankton community, is a good
474 example of applying integrative approach in predicting the future of high Arctic fjordic systems
475 under the pressure of climate change and Atlantification.

476

477 **5. Conclusions**

478 The properties of water masses, especially temperature, as well as the presence of sea
479 ice and sediment flux, had the greatest impact on the variations in the surface zooplankton flux
480 in the Svalbard fjords in our study. Moreover, these environmental variables were also the ones
481 that contributed the most to the differences between the fjords and thus influenced zooplankton
482 communities. The most striking difference was the presence of sea ice only in Rijpfjorden,
483 which was associated with the dominating cold water masses and the delay of a pelagic algal
484 bloom until July, thus causing the 2-3 month shift in zooplankton community development
485 compared to the Atlantic-influenced Kongsfjorden. If Kongsfjorden is representative of a future
486 high Arctic environment, one may expect less or no sea ice and increased temperature and
487 sedimentation rates in late autumn – early winter. These factors will lead to the progressing
488 development of the zooplankton community during spring, which may result in the mismatch
489 between phytoplankton bloom and the youngest developmental stages of herbivorous Arctic

490 species (Søreide et al., 2010). Increased Atlantification of Svalbard fjords would impose
491 changes in the composition and distribution of zooplankton species (Willis et al., 2006, 2008;
492 Wallace et al., 2010; Weydmann et al. 2013) and consequently in higher trophic levels
493 (Kwaśniewski et al., 2012; Vihtakari et al., 2018).

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

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

507

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517

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753 **TABLES**

754 **Table 1** Sediment trap sampling program in 2014 and 2015 in two high Arctic fjords:
755 Kongsfjorden and Rijpfjorden.

756

757 **Table 2** SIMPER list of zooplankton taxa contributing mostly to similarities within the groups
758 obtained by LINKTREE (see Fig. 4), with a cutoff at 50% for the log-transformed data.

759

760 **Table 3** The significance of tested environmental variables on zooplankton communities in
761 Kongsfjorden and Rijpfjorden, with the proportion of variation in zooplankton explained by
762 each predictor, based on the results of DistLM sequential tests for environmental variables.
763 Significant predictors are given in bold.

764 **FIGURES**

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

771

772 **Fig. 2** Temperature and salinity diagram from Rjipfjorden and Kongsfjorden between October
773 2014 and August 2015. Water masses are distinguished based on Cottier et al. 2005 and Pérez-
774 Hernández et al. 2017.

775

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

780

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

785

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