



Multi-year mesozooplankton flux trends in Kongsfjorden, Svalbard

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Received: 20 December 2022 / Revised: 25 March 2024 / Accepted: 26 March 2024
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Abstract

We conducted this study to investigate the relationship between environmental stressors and mesozooplankton fluxes in inner Kongsfjorden, Svalbard. The ongoing Arctic amplification, characterized by phenomena such as increased temperatures, glacial and watershed runoff, and diminishing ice cover, poses significant challenges to marine ecosystems. Our multi-year time-series analysis (2010–2018) of mesozooplankton, collected from a moored automatic sediment trap at approximately 87 m depth, aims to elucidate seasonal and interannual variations in fluxes within this Arctic fjord. We integrate meteorological, hydrological, and chemical datasets to assess their influence on zooplankton populations. Principal component analysis reveals the impact of seawater characteristics on mesozooplankton fluxes and composition, while two-way ANOVA highlights the role of seasonality in driving variations in our dataset. We observe a decrease in swimmer fluxes following the maxima mass flux event (from 2013 onwards), coupled with an increase in community diversity, possibly attributed to copepod decline and functional diversity. Notably, sub-Arctic boreal species such as *Limacina retroversa* have been detected in the sediment trap since 2016. Our continuous multi-year dataset captures the physical, chemical, and biological dynamics in this extreme environment. With Arctic amplification in Kongsfjorden and increasing submarine and watershed runoff, we anticipate significant shifts in mesozooplankton communities in the medium to long-term. This underscores the urgency for further research on their adaptation to changing environmental conditions and the potential introduction of alien species.

Keywords Arctic · Kongsfjorden · Mesozooplankton · Swimmers · Sediment trap · Time-series data

Introduction

Since 1994, the air temperature in Ny-Ålesund (Svalbard) has risen by a rate of 1.6 ± 0.7 °C^{-decade} (Maturilli et al. 2015); its increase has been even higher ($+ 3.0$ °C^{-decade}) from 2010 onwards (Mazzola et al. 2016), mainly during the

winter seasons ($+ 3.2$ °C^{-decade}, Maturilli & Kayser 2017). Due to the influence of meridional advection (Dahlke and Maturilli 2017), changes in the atmospheric moisture have also occurred (Maturilli and Kayser 2017) with a subsequent increase in rainfall events, especially during the winter months. A greater riverine discharge has contributed to enhanced water stratification, leading to more frequent two-layer conditions. Furthermore, the fjord experiences the influence of Atlantic Water (AW), as some veins reach its innermost part (De Rovere et al. 2022) through the intrusion of the West Spitsbergen Current (WSC) core from the Fram Strait. An intensification of AW inflow has been observed in the Arctic Ocean (AO) (Svendsen et al. 2002; Beszczynska-Möller et al. 2012; Polyakov et al. 2017; Tesi et al. 2021), with consequences on the hydrodynamics of Kongsfjorden (Svendsen et al. 2002). Data from the last decade show that Kongsfjorden is transitioning to an Atlantic-type fjord, which is characterized by depleted sea ice conditions and regular surface AW intrusions both in summer and winter seasons (De Rovere et al. 2022). This greater intrusion

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of AW strengthens the water stratification and leads to an increase in the abundance of allochthonous plankton (Hop et al. 2002; Arnkværn et al. 2005; Daase and Eeiane 2007; Dalpadado et al. 2016; Gluchowska et al. 2016). A change in the phytoplankton composition has also been observed within Kongsfjorden (Lalande et al. 2016a, b a) with a shift from a dominance of diatoms to small-sized phytoplankton (e.g., nanoflagellates) under warmer water conditions. Such changes in this area could lead to a reorganization of the ecosystem, as the fraction of carbon produced by zooplankton grazing on phytoplankton and organic detritus (secondary production) serves as food for larger organisms in the ocean, including fish and mammals (Le Quéré et al. 2016).

Combining multiple studies on zooplankton within Kongsfjorden gives us a better understanding of how they interact with their environment. One study from 1998 to 1999 showed us that copepods, especially smaller species like *Oithona similis* and *Pseudocalanus minutus*, as well as larger species like *Calanus finmarchicus* and *Limacina helicina*, were the most common (Lischka and Hagen 2016). Ocean currents have been shown to affect the number of zooplankton moving through the Fram Strait, and found that copepods rich in carbon, like *C. finmarchicus*,

were abundant (Basedow et al. 2018). Even in winter, copepods, especially *Calanus* species, were still dominant in the waters around Svalbard (Dvoretzky and Dvoretzky 2020; Dvoretzky et al. 2023). The influence of AW on zooplankton in Kongsfjorden varies depending on local ocean conditions, as recent research has shown (Gluchowska et al.). Understanding these patterns helps us determine how seasonal changes, the environment, and ocean currents shape the zooplankton community in Kongsfjorden.

The aim of our study is to present continuous high-resolution zooplankton fluxes in Kongsfjorden over a multi-year period (2010–2018), using data collected from an automatic sediment trap moored in the inner fjord (refer to Fig. 1). The mooring MDI (Mooring Dirigibile Italia) is strategically positioned between the glacier termini and the sill, receiving influences from both glacial meltwater and Atlantic Water (AW) (Svendsen et al. 2002; Cottier et al. 2005). Utilizing trap-collected zooplankton samples (swimmers) instead of traditional net-collected plankton facilitates continuous and prolonged sample acquisition in extreme study areas (Makabe et al. 2010). We analyze the temporal variability in zooplankton fluxes and communities. In addition, we correlate these variations with

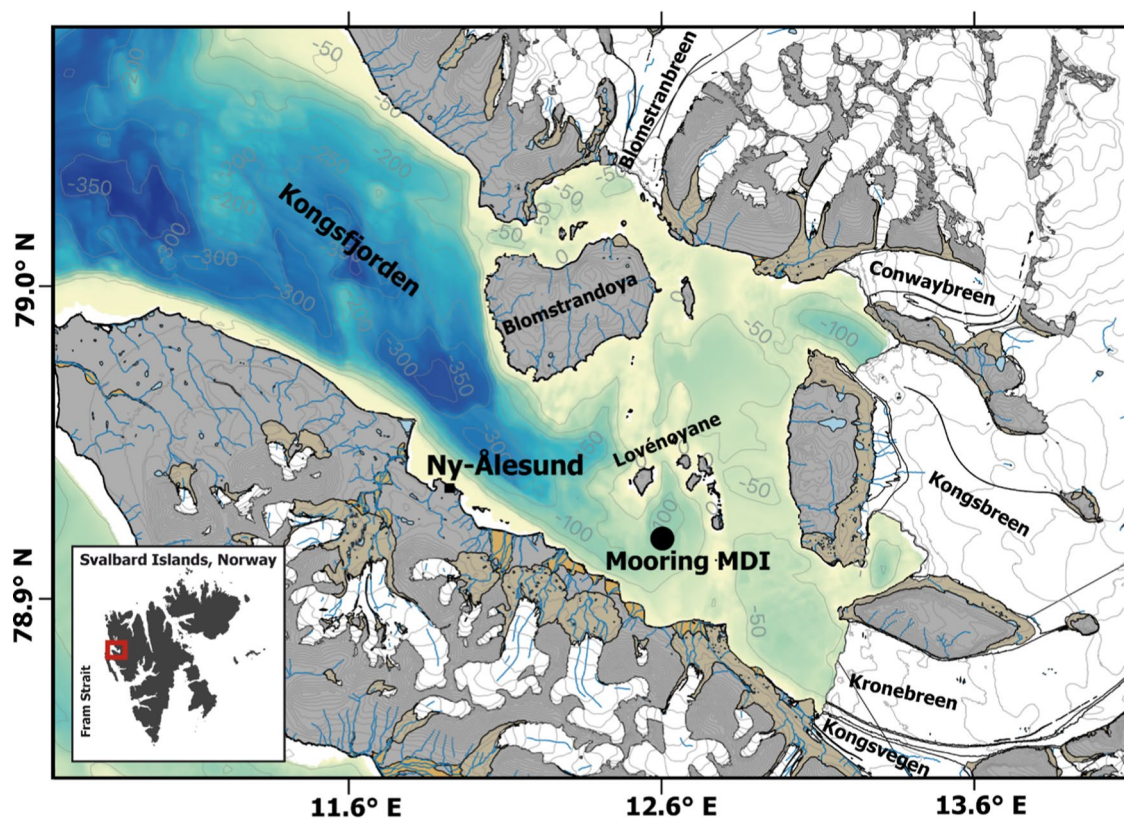


Fig. 1 Lower left corner, a map of Svalbard with a red rectangle showing the location of Kongsfjorden. Kongsfjorden, with a color map displaying the bathymetry of the fjord, and the main glacier

fronts (Kongsvegen, Kronebreen, Kongsbreen, Conwaybreen, Blomstrandbreen). The black point “Mooring MDI” indicates the location of the Mooring Dirigibile Italia (MDI)

environmental factors to discern environmental-mediated changes in zooplankton dynamics.

Materials and methods

In this study we show time-series of paired physical, chemical, and biological datasets of Kongsfjorden waters. The dataset covers the period from September 2010 to July 2018. The first 6 years of the physical parameters and particle fluxes data (2010–2016) were already shown in D'Angelo et al. (2018). To be as accurate as possible, we decided to neglect the swimmers with averaged fluxes consistently $< 1 \text{ ind m}^{-2} \text{ d}^{-1}$ throughout the time-series, thus we considered only six dominant taxa and excluded data on chaetognaths and bivalvia larvae (Table S11). The taxonomical resolution differs between taxa; we used the order for amphipods, euphausiids and polychaetes, and identified to the genus level for copepods, pteropods and appendicularians. However, for multivariate analysis the same taxonomic rank is used between zooplankton groups.

Data and sample collection

A bathymetric and high-resolution seismic survey was performed in September 2010 with a Benthos DSP-662 CHIRP III (Aliani et al. 2016) to assess the bottom morphology and the surficial stratigraphy of the inner fjord, to select the best site for deploying the oceanographic mooring MDI.

The MDI site is in the innermost part of Kongsfjorden, Svalbard (Fig. 1), in a strategic area from both a hydrological and depositional point of view. Here, in fact, the AW water masses entering from the strait interact with the melt-water of the glacial fronts (De Rovere et al. 2022), and the area is characterized by high modern sediment accumulation (a rate of $\sim 1.2 \text{ cm y}^{-1}$ at MDI and even higher than 3 cm y^{-1} close to glacier fronts (Elverhoi et al. 1983; Aliani et al. 2004; Miserocchi et al. 2016).

In MDI (Aliani et al. 2016), a permanent mooring was deployed for the first time in September 2010 at $78^\circ 54.815 \text{ N}$, $12^\circ 14.899 \text{ E}$ at 103 m water depth, and then maintained annually. For safety purposes against the passage of icebergs and sea ice, the uppermost buoy was kept submerged, thus no information is available for surface water characteristics and dynamics. The MDI was equipped with a time-series Technicap sediment trap (12 receiving cups, model PPS4/3, 0.05 m^2 collection area) at 18 m above the sea bottom. The interval of rotation of the sediment trap varied between 8 and 90 days (Table SI2) depending on the seasonality. Shorter sampling periods were set during the summer seasons, as a greater variability in biological and physical–chemical conditions were expected as well as an augmented supply of suspended particulate materials. All programmed samples were

recovered, except those between August 3rd and September 11th, 2014, due to a technical failure of the sediment trap. The mooring was also equipped with a temperature and conductivity recorder (SBE16 SeaCAT) to acquire water temperature and salinity data near the bottom, at $\sim 87 \text{ m}$ below sea level. Values of solar radiation and air temperature of the region were extracted from the Amundsen-Nobile Climate Change Tower data set (Mazzola et al. 2016, <https://data.iadc.cnr.it>). The water temperature and salinity were measured on an average of 30-min intervals, whereas the solar radiation and air temperature were considered as daily mean values. Missing values for air temperature ($n=8$) were calculated based on monthly averages from the rest of the time-series. The utilization of sediment traps in zooplankton investigation has been a common practice since 1990. Oceanographers have employed sediment trap data analysis to evaluate the influence of environmental changes on zooplankton communities (Michaels et al. 1990; Matsuno et al. 2013; Makabe et al. 2016; Weydmann-Zwolicka et al. 2021). This kind of investigation permits a continuous overview of the meteorological, hydrological, and biological dynamics that have characterized the fjord during the multi-year sampling period (2010–2018).

Laboratory activities

Preliminary treatment

Prior to deployment, sample cups of the sediment trap were filled with a buffered 5% (v/v) formaldehyde solution in $0.45 \mu\text{m}$ filtered Arctic seawater, to prevent the degradation of organic matter (OM) during the deployment. The use of a formaldehyde solution appeared to be the most suitable compromise in terms of conservation effectiveness and preventing the degradation and fragmentation of the collected OM (Heussner et al. 1990; Lamborg et al. 2008). Samples recovered from the sediment trap were stored in the dark at 4°C until they were processed at the National Research Council—Institute of Marine Sciences (CNR-ISMAR) in Bologna, Italy, following the method of Chiarini et al. (2014). Samples were equally split into at least two subsamples (100 ml each). The first was used for total mass flux (TMF) determination. Samples were filtered through a pre-weighed $0.45 \mu\text{m}$ filter with a mixed cellulose esters Millipore membrane, rinsed with distilled water, dried at 50°C for 24 h, and weighed. The remaining subsamples were centrifuged for 10 min at 3000 rpm, the leachate was then removed, and the tube rinsed with demineralized water to remove any remaining salt and formalin residues from the samples. Samples were centrifuged again at 3000 rpm for 10 min. The water in excess was removed and the samples were freeze-dried. Finally, samples were gently ground to obtain a homogeneous powder for further chemical analysis.

Chemical analysis

We determined the contents of total carbon (TC), organic carbon (OC) and the stable isotope of organic carbon ($\delta^{13}\text{C}$) compositions using a Finnigan Delta Plus XP mass spectrometer directly coupled to a ThermoFisher Scientific Flash 2000 IRMS Element Analyzer via a ConFlo III interface for continuous flow measurements (Kristensen and Andersen 1987; Verardo et al. 1990; Tesi et al. 2007). The contents of OC and $\delta^{13}\text{C}$ were measured on freeze-dried samples after decarbonization with an acid treatment (HCl, 1.5 M). OM content was estimated as twice the OC content (Heussner et al. 1990). The average standard deviation of each measurement, determined by triplicate analyses of the same sample, was $\pm 0.07\%$ for OC. $\delta^{13}\text{C}$ was calculated as:

$$\delta^{13}\text{C} = \left[\frac{(^{13}\text{C}/^{12}\text{C})_{\text{sample}}}{(^{13}\text{C}/^{12}\text{C})_{\text{VPDB}}} - 1 \right] \times 10^3$$

Uncertainties were lower than $\pm 0.05\%$, as determined from at least three routine replicate measurements of the reference sample IAEA-CH7 (polyethylene, -32.15% vs. VPDB standard). Errors for replicate analyses of the standards were $\pm 0.20\%$. Biogenic silica was analyzed using a two-step 2.5 h extraction of 20 mg of freeze-dried sample with a 0.5 M Na_2CO_3 solution at 90°C , followed by the measurement of dissolved Si and Al contents in both leachates with a Perkin-Elmer Optima 3200RL Inductive Coupled Plasma Optical Emission Spectrometer (ICP-OES) at the University of Barcelona. The Si content of the first leachate was corrected by the Si/Al ratio of the second leachate to correct for the excess Si dissolved from aluminosilicates (Kamatani and Oku 2000; Fabr es et al. 2002; Ragueneau et al. 2005). Biogenic silica was transformed to opal by multiplying by 2.4 (Mortlock and Froelich 1989).

Mesozooplankton treatment and identification

Mesozooplankton were picked and identified as swimmers (zooplankton that actively swim into the sediment trap funnel). This procedure can provide insights into the temporal changes of zooplankton assemblages at a single site (Guidi-Guilvard et al. 2009). Makabe et al. (2016) conducted a comparison of sediment trap-collected zooplankton with net-collected counterparts in the Canadian Arctic and underscored the potential of sediment traps for ecological studies. The identification of specific zooplankton taxa correlated with environmental variables emphasized the utility of sediment traps in capturing nuanced ecological relationships. This study highlighted the feasibility of using sediment traps for ecological studies, particularly for certain taxa. The implications of these study suggested that sediment traps provide valuable information

on zooplankton fluxes, offering insights into ecological dynamics that complement traditional plankton net sampling.

The data, while not reaching species specificity, still capture trends and variations within the larger classifications of zooplankton orders. The sediment traps capture both actively swimming and passively sinking zooplankton (Michaels et al. 1990), potentially introducing bias into swimmer flux estimates. However, for our quantification, we selectively chose well-shaped organisms, prioritizing those likely involved in active swimming. Additionally, research indicates that factors such as ingestion by predators, turbulent mixing, and microbial degradation contribute to the removal of carcasses above trap depth. Notably, it has been shown that a significant portion of zooplankton carcasses remains in the upper water layer, rather than contributing to sinking (Dubovskaya et al. 2017). The swimmers were manually picked, counted, and identified through optical microscopy by wet sieving through two nylon meshes of 1 mm and 500 μm . Zooplankton with a size of $< 500 \mu\text{m}$ were excluded and not considered in the analysis. Taxonomic identification at highest possible resolution (down to genus) was obtained for three groups: copepods, pteropods, and appendicularians (Boxshall and Halsey 2004; Castellani and Edwards 2017). We identified two genera for pteropods, whereas for appendicularians, only one genus was identified. We report only the *Limacina retroversa* species until April 2019. Fluxes were calculated as fluxes of individuals (Ind. f.). The annual fluxes of individuals were calculated as follows:

$$\text{Tot.ind.peryear} = \text{Ind.f.} \times \text{durationofdeployment}, \quad (1)$$

where *Ind.f.* is *individual fluxes*, hence the number of identified items divided by the collection area of the sediment trap (0.05 m^2 for McLane traps) and multiplied by the number of deployment days.

The total individual weighted mean was calculated as follows:

$$\text{Tot.Ind.weightedmean} = \frac{\text{Tot.ind.peryear}}{\text{Tot.days}}, \quad (2)$$

For the calculation of annual means the years 2010 and 2018 were excluded because the mesozooplankton data did not cover the entire year and could bias the calculated mean.

We also calculated the annual zooplankton diversity by measuring the Margalef Index (1958):

$$D = \frac{C - 1}{\ln N}, \quad (3)$$

where C is the number of the identified taxa (order level), and N is the total number of individuals (Danovaro et al. 2017).

Statistics

Data were quality controlled calculating the standard deviations of the weighted averaged values.

A two-way analysis of variance (ANOVA) was conducted to evaluate the impact of two categorical factors on a quantitative response variable, specifically examining the relationship between season, years, and zooplankton fluxes. The “aov” function within the R statistical software (version 3.6.2) (Chambers et al. 1992) was utilized for this analysis. In the process, the response variable and interacting factors were explicitly defined within a formula, allowing for a comprehensive exploration of the main effects and interaction terms.

A Principal Component Analysis (PCA) was carried out using the *vegan* (v. 2.4–2) package in R (Oksanen et al. 2016, R Core Team 2015) to assess the relationship between the environmental variables and the zooplankton fluxes. Environmental variables were tested for skewness (due to strong seasonal gradients), and heavily left or right skewed data were log transformed [$\log(x + 1)$] to stabilize variance (all data excluding radiation, salinity, air and water temperature). The $\delta^{13}\text{C}$ data were transformed to absolute values before being log transformed as above.

A Spearman’s rank correlation matrix (Fig. S11) was carried out in R studio, with libraries “dplyr”, “farway” and “corrplot” (Faraway 2016; Wei and Simko 2021; Wickham et al. 2021) on all environmental and sediment trap variables to look for significant correlations ($R^2 > 0.97$) and if any variables could be combined to reduce the number of principal components. We combined inorganic carbon and calcium carbonate, and organic carbon and organic matter. Variables used for the principal component analysis were: TMF, OC, $\delta^{13}\text{C}$, inorganic Carbon (Cin), opal, atmospheric temperature

(AirT), solar radiation (Rad), bottom water salinity (Sal) and bottom water temperature (WatT). Euclidean distances were used to determine spatial ranges within this data. Fluxes of zooplankton species were $\log(x + 1)$ transformed to reduce the influence of dominant taxa and normalized to a mean of 0 and standard deviation of 1, before being projected onto the resulting space of the PCA determined from environmental variables. To analyze the relationship between the light availability and zooplankton composition, the deployment periods were divided into polar night and polar day based on the solar radiation data (Table 1). When the solar radiation was $< 0 \text{ W m}^{-2}$ over the trap deployment this was considered polar night, and when radiation values were $\geq 0 \text{ W m}^{-2}$ these were attributed to the Polar day.

Results

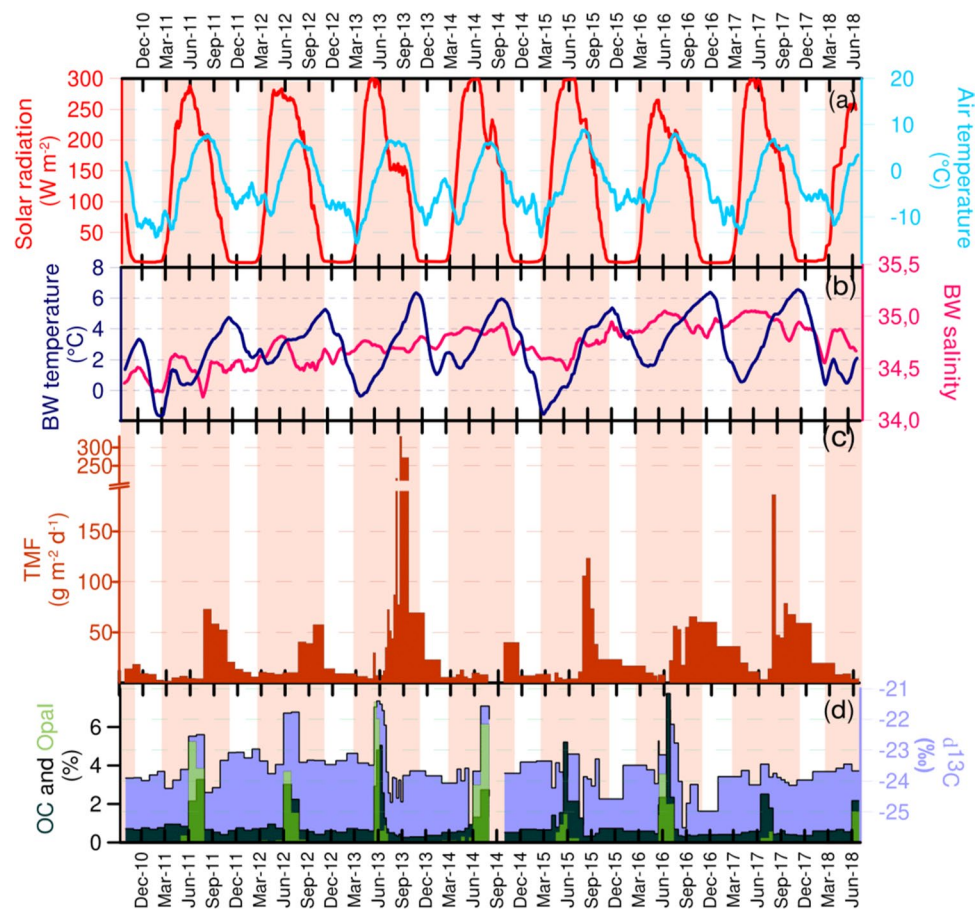
Physical parameters

Physical and chemical parameters with high-frequency temporal oscillations showed a superimposed 5-day running average (Fig. 2a, b). Solar radiation displayed a clear seasonal trend (Fig. 2a), with the highest values recorded in May 2015 (av. $\sim 455 \pm 120 \text{ W m}^{-2} \text{ d}^{-1}$ ($n = 84$)). Air temperature showed an increase overtime, with $R^2 = 0.053$ and $p = 0.013$ (Fig. 2a). The water temperature measured at $\sim 87 \text{ m}$ depth (Fig. 2b) also exhibited an increasing trend over the time scale ($R^2 = 0.096$ and $p = 0.0013$), with values of $\sim 6 \text{ }^\circ\text{C}$ recorded in October 2013 and November 2017. The lowest values of $-1.8 \text{ }^\circ\text{C}$ were recorded in February 2011 and 2015 (Fig. 2b). The practical salinity showed increasing trend within the time frame ($R^2 = 0.60$ and $p = < 0.0001$), with values staying higher than 35 in summers 2016 and

Table 1 Dates of mesozooplankton sampling design, according to the Polar seasons

Sampling period	Nr. of samples	Start date	End date	Nr. of days
Polar Night 2010–2011 (transition)	5	11-Sep-10	01-Feb-11	143
Polar Day 2011	8	01-Feb-11	01-Oct-11	237
Polar Night 2011–2012	4	01-Oct-11	01-Feb-12	123
Polar Day 2012	8	01-Feb-12	27-Sep-12	233
Polar Night 2012–2013 (transition)	3	27-Sep-12	31-Jan-13	126
Polar Day 2013 (transition)	17	31-Jan-13	01-Oct-13	234
Polar Night 2013–2014 (transition)	3	01-Oct-13	01-Apr-14	182
Polar Day 2014	6	01-Apr-14	03-Aug-14	124
Polar Night 2014–2015 (transition)	3	12-Sep-14	01-Feb-15	142
Polar Day 2015	10	01-Feb-15	1-Oct-15	219
Polar Night 2015–2016 (transition)	2	1-Oct-15	1-Apr-16	183
Polar Day 2016	3	1-Apr-16	16-Oct-16	191
Polar Night 2017 (transition)	2	16-Oct-16	1-Apr-17	167
Polar Day 2017	7	1-Apr-17	16-Sep-2017	160
Polar Night 2017–2018 (transition)	4	16-Sep-17	1-Apr-18	197

Fig. 2 Trends overtime (2010–2018) of the physical and chemical parameters measured at 34-m high (a) and ~87 m depth (b–d) in Kongsfjorden. **a** Air temperature and solar radiation from the Amundsen-Nobile Climate Change Tower in Ny-Ålesund; **b** bottom water temperature (WatT) and salinity from a SBE16 SEACAT moored on MDI; **c** Total mass flux from sediment trap on MDI; **d** Organic matter content (OC and opal in dark and light green, respectively), and $\delta^{13}\text{C}$ values (in purple) in the sediment trap samples. Light red bands depict the polar day periods. The values in **a** and **b** were shown as 5-day simple running averages



2017 (Fig. 2b). The peak values of meteorological, oceanographical, and chemical parameters consistently followed a seasonal trend, reaching their maxima during the warm season. The thermohaline parameters of seawater exhibited a discernible overall increasing trend over time. These detailed analyses underscore the seasonal and interannual variability of environmental variables, offering valuable insights into the dynamic nature of the study area.

Total mass flux

Overall, the trend for TMF followed a seasonal cycle with low fluxes during the winter and greater amounts in the late summer and fall (Fig. 2c). The highest value of TMF ($330 \text{ g d}^{-1} \text{ m}^{-2}$) was recorded in August 2013 (Fig. 2c). The TMF composition was mainly lithogenic (av. $\sim 74 \pm 3\%$), whereas the organic matter (OM) + Opal showed an average of $26 \pm 3\%$ ($n = 84$). The OC stayed in a range between 0.2 and 7.7% of the total flux and displayed a seasonal trend, with yearly peaks from May to June and a maximum value of 7.74% between the 26th of May and 16th June 2016 (Fig. 2d). The opal values also followed a seasonal cycle (Fig. 2d). Its magnitude was higher than OC during years 2011–2014, whereas it was lower than OC in years

2015–2018; its maximum was recorded in April–May 2013, with 7.31% (Fig. 2d). The isotopic signature $\delta^{13}\text{C}$ ranged between -25.9‰ in May 2014, and -21.4‰ in May 2013 (Fig. 2d). For less negative $\delta^{13}\text{C}$ values, OC contents were higher, suggesting greater contribution of marine OM. In 2013, when the highest total mass flux was detected, the OM reached the lowest summer values (0.21% OC and 0% opal—Fig. 2d), with -24.7‰ $\delta^{13}\text{C}$, exhibiting a signature associated with glacier detritic carbonate.

Mesozooplankton fluxes and taxa variability

Over the study period, more than 14,200 mesozooplankton individuals were identified from the sediment trap samples and classified into eight taxa (copepods, amphipods, euphausiids, pteropods, polychaetes, appendicularians, chaetognaths and bivalvia larvae). The most abundant taxon was copepods, with fluxes 10 times greater than other groups, often representing more than 90% of the trapped community (Fig. 3B). The highest flux of copepods was recorded in August 2011, with $504 \text{ ind m}^{-2} \text{ d}^{-1}$ (Fig. 3A, Table SII). Aside from the copepods, other taxa reaching high fluxes were amphipods ($220 \text{ ind m}^{-2} \text{ d}^{-1}$,

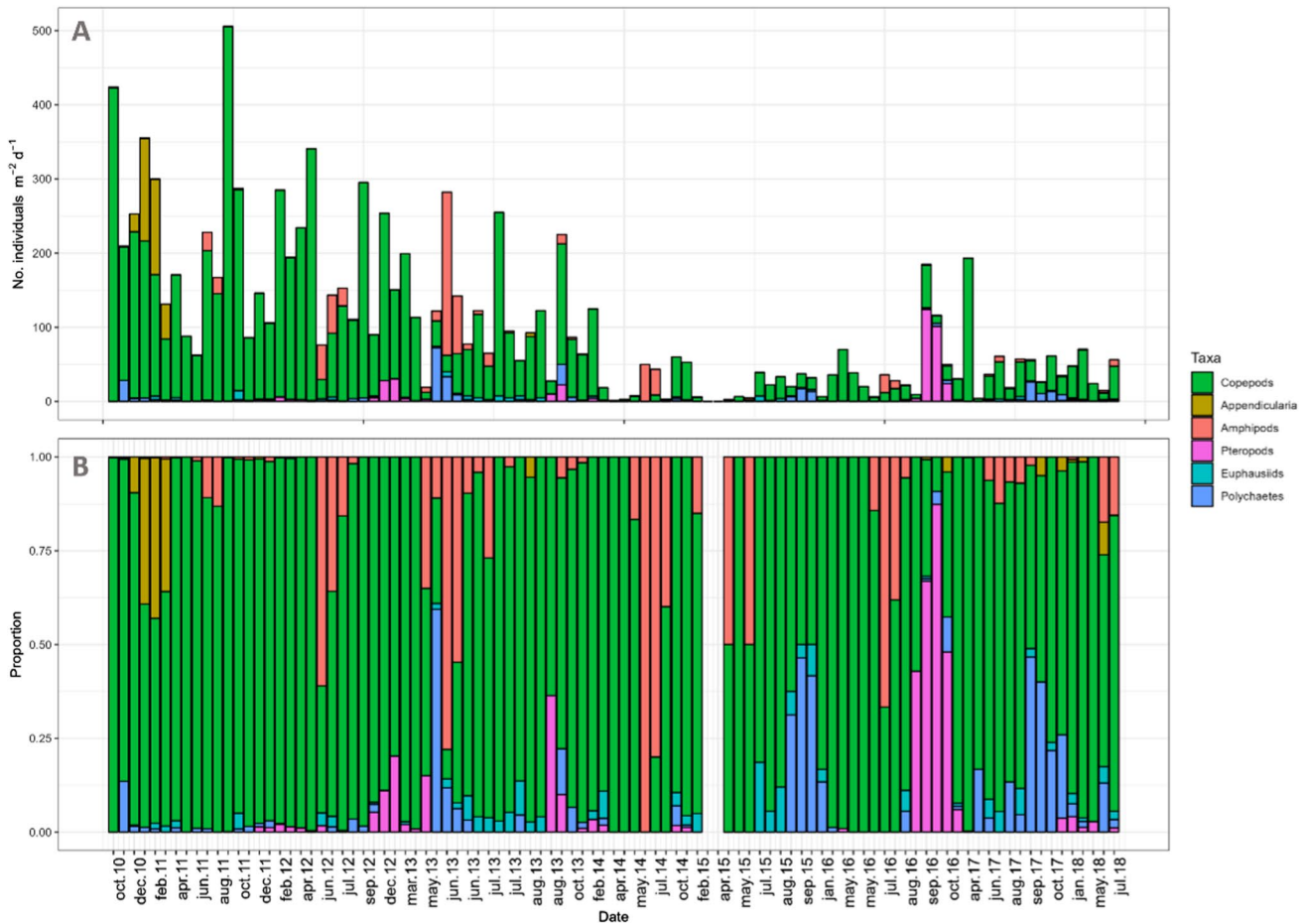


Fig. 3 **A** swimmers' total fluxes calculated as fluxes vs. time ($n. ind. m^{-2} d^{-1}$); **B** Percentages of taxa identified as swimmers within the multi-year time-series (October 2010–July 2018)

29th May–7th Jun 2013), appendicularians ($138 ind m^{-2} d^{-1}$, Dec 2010) (Fig. 3A), and pteropods ($124 ind m^{-2} d^{-1}$, 16th Aug–1st Sep 2016).

The mesozooplankton fluxes showed high variability between seasonality, specifically during polar night and polar day (Table 2). A two-way ANOVA revealed the statistical significance of both the main effects associated with seasons and zooplankton, along with their interactions. A significant influence of season was observed on zooplankton flux abundance ($F statistic = 26.14, df = 1, p < 0.05$). The statistical significance of the main effect of seasons suggested discernible variations in zooplankton attributable to changing seasons. Furthermore, the presence of a significant interaction term indicated that the joint impact of season and zooplankton was also statistically significant. In contrast, we determined there was no significant difference ($F statistic = 0.46, df = 1, p = 0.5$) between the years in terms of their effect on the zooplankton variables. Although the two-way ANOVA did not find statistical significance for the 'Year' factor, the observed decrease in zooplankton fluxes over time

suggested the potential influence of unaccounted factors or trends, such as the environmental variables.

The average of swimmers occurring from 2010 to 2014 was $173.19 \pm 106 ind m^{-2} d^{-1}$ ($n = 47$), while the numbers abruptly declined to $36.53 \pm 39.32 ind m^{-2} d^{-1}$ ($n = 51$) after that year (Table S11). Some of the mesozooplankton taxa showed seasonal cycles. The flux of amphipods for example, showed peaks each summer (aside from summer 2015), mostly in June and July (Fig. 3A), concurrently with peaks of OC and one-month delayed from opal maxima (see Figs. 2d and 3b). Most of the taxa peaked during the polar days, however we observed the occurrence of copepods and appendicularians during the polar night as well (up to 278 and 138 $ind m^{-2} d^{-1}$ in January 2012 and December 2010, respectively).

For the annual averages, we did not show the years 2010 and 2018 as they were not complete (Fig. 4). Copepods were the predominant taxon across the entire time-series but had a sudden decline after 2012. Their fluxes linearly decreased from September 2010 to July 2018 ($R^2 = 0.40$).

Table 2 Averaged fluxes of swimmers identified in the sediment trap samples during the Polar days and nights within the 8-year time-series

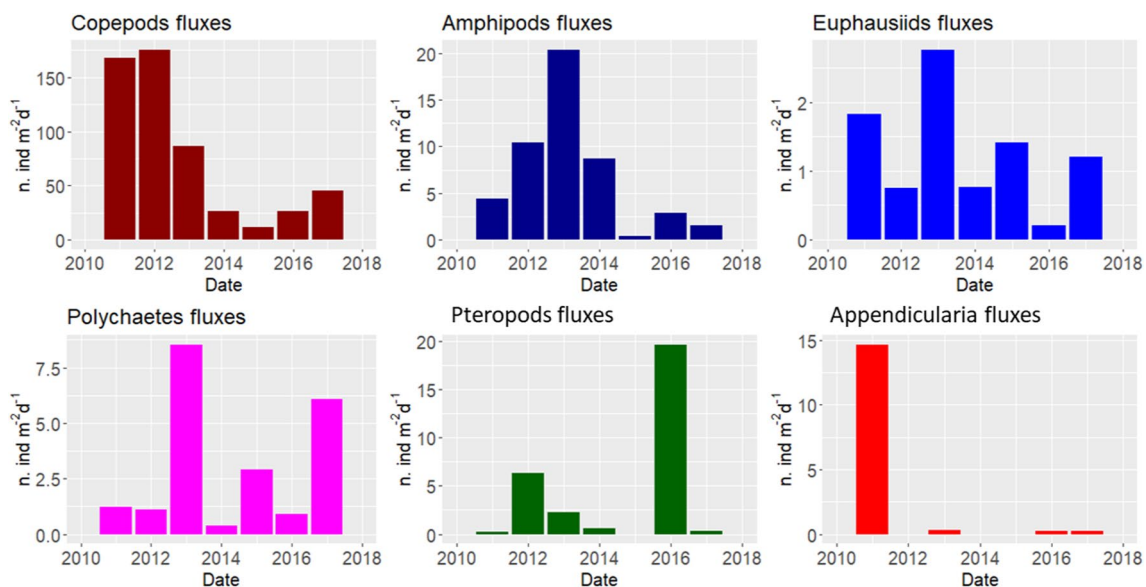
Sampling periods	Averaged fluxes of individuals (ind. m ⁻² d ⁻¹)
Polar Night 2010–2011 (transition)	51.39 ± 100.3
Polar Day 2011	34.19 ± 77
Polar Night 2011–2012	26 ± 61
Polar Day 2012	32.24 ± 72
Polar Night 2012–2013 (transition)	27.5 ± 57.3
Polar Day 2013 (transition)	20.61 ± 41
Polar Night 2013–2014 (transition)	11.52 ± 26.3
Polar Day 2014	3 ± 6.5
Polar Night 2014–2015 (transition)	6.62 ± 0.50
Polar Day 2015	3 ± 0.3
Polar Night 2015–2016 (transition)	3.53 ± 0.09
Polar Day 2016	8.82 ± 1.16
Polar Night 2017 (transition)	18.64 ± 0.5
Polar Day 2017	6.20 ± 0.57
Polar Night 2017 – 2018 (transition)	8.94 ± 0.5

The minimum values were recorded in 2015 (annual average of $\sim 12 \pm 11$ ind m⁻² d⁻¹ ($n = 13$)) and had a slight recovery in 2016 with a mean of 26 ± 19.58 ind m⁻² d⁻¹ ($n = 13$). A steady increase in copepods was also seen in 2017 and 2018 (av. 42.48 ± 45 ind m⁻² d⁻¹ ($n = 15$)). Amphipods showed an increase in fluxes until 2013 (maxima 220 ind m⁻² d⁻¹), followed by an abrupt decrease, with almost none detected during 2015. Euphausiids displayed an oscillatory trend, with enhanced fluxes recorded every two years. Polychaetes

showed the highest fluxes during years 2013 and 2017 (6 ± 8 ind m⁻² d⁻¹), however few individuals were detected overall. Pteropods (mostly, *Limacina helicina*, veligers and juveniles) showed two peaks, in 2012 and 2016 with $\sim 7 \pm 10$ and 20 ± 42 ind m⁻² d⁻¹, respectively. From 2010 to 2016 the only species occurring in our samples was *L. helicina*, however, after 2016 we started to record the occurrence of *L. retroversa* in the sediment trap samples. Appendicularians (i.e., *Oikopleura vanhoeffeni*, Hopcroft 2021) displayed the maximum occurrence in December 2010 and its annual average showed a single peak in 2011, reaching $\sim 15 \pm 38$ ind m⁻² d⁻¹. Overall, each taxon generally displayed a downward annual average from 2013 onwards, apart from pteropods (Fig. 4).

Biodiversity of the trapped zooplankton

The mean annual value of the Margalef Index (Margalef 1958; Danovaro et al. 2017) is 0.5 ± 0.3 ($n = 9$) throughout the multi-year time-series (Table S13), with the highest annual average of 0.7 ± 0.2 ($n = 97$) recorded in year 2017, and the lowest in year 2012 (0.4 ± 0.2 , $n = 97$). During 2018 the Margalef index recorded an annual average of 0.9 ± 0.5 ($n = 4$), however this year included only data from January to July. Copepods, already known for playing a central role in Arctic marine food webs by dominating the zooplankton assemblage of many Norwegian fjords (Arnkværn et al. 2005; Daase and Eieane 2007), represented more than 90% of the zooplankton trapped within the multi-year sampling period. We identified five different genera from this taxon: *Metridia* spp. (43.6%), *Calanus* spp. (24.7%), *Aetideidae*

**Fig. 4** Inter-annual mean fluxes of the main mesozooplankton taxa. Years 2010 and 2018 are not displayed, as not complete

(3.2%), *Pseudocalanus* spp. (1.6%) and *Euchaetidae* (0.4%) (Fig. 5) as well as some unidentified specimens (26.5%).

Environmental factors affecting the swimmer community

During the multi-year time-series, Kongsfjorden experienced changes in environmental parameters as seen in Fig. 2 (e.g., meteorological events and thermohaline characteristics of the water masses). To demonstrate if and how this affected the biota distribution, we measured the relationships with the physical, chemical, and biological datasets through a Spearman's rank correlation (Fig. S11) and a multivariate analysis (PCA, Fig. 6). The results showed that in Kongsfjorden the most influential factors affecting the zooplankton community were, the seasonal shift between polar day and night, the seawater Salinity with copepods ($r_s = -0.53$, $n = 84$, $p < 0.01$), the opal flux with amphipods ($r_s = 0.49$, $n = 84$, $p < 0.01$). This data overall confirms the outcomes of a recent study hold in Kongsfjorden (Weydmann-Zwolicka et al. 2021). A principal component analysis (PCA) was performed on samples ($n = 97$). The PCA was computed based on the best fitting environmental dataset (Fig. S11). There were 8 principal components (PCs) in total, with Axis1 (PC1) and Axis2 (PC2) accounting for 65% of the original variance. The coefficients of variables with PC1 and PC2 are shown in Table 3. PC1 (36.1%) was strongly correlated to the polar day (radiation, air T, Opal, OC and $\delta^{13}\text{C}$). PC2 (28.9%) was strongly correlated to the thermohaline parameters (water T and salinity), and to the lithogenic/detrital material. The environmental variables were set as active, while swimmer fluxes were projected as supplementary variables into the resulting factorial space generated by the environmental variables. To compare the physical datasets to fluxes of taxa, we used cross correlation analyses followed

by Spearman rank (SP) tests. Each dataset (factorial axis and swimmer fluxes) was treated as a stationary time-series, and paired correlations in deployment-period increments were computed from 0 to 90 d. As PC2 represented the shift between spring and summer time, including higher availability of food for deep-living organisms, any correlation of swimmer fluxes in the positive values of this axis could represent an association with the spring phytoplankton bloom (e.g., as shown between amphipods and opal flux, Fig. S11).

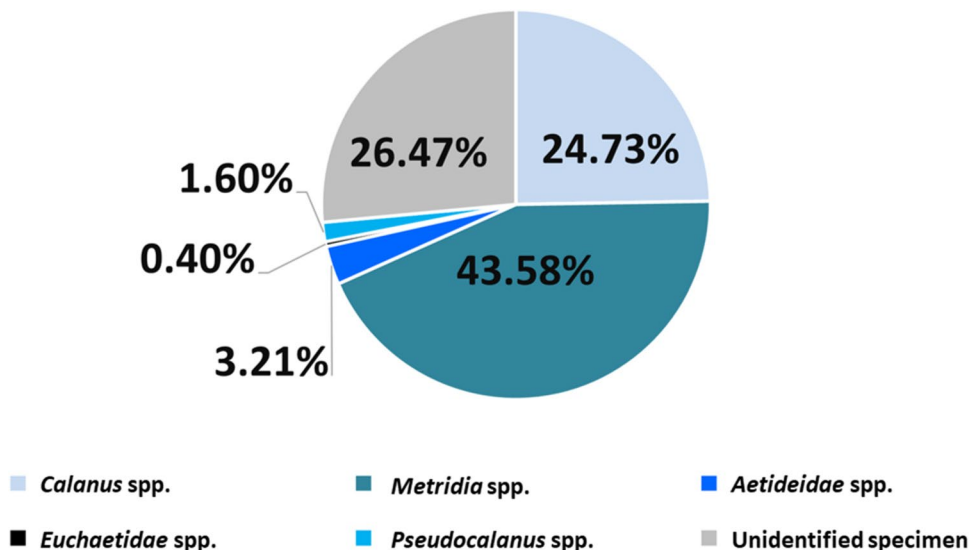
Discussion

Biodiversity of the trapped community

Although the deployment of a single moored sediment trap at ~87 m could not reflect spatial or vertical changes in zooplankton community composition, it could give information on the occurrence of mesozooplankton in the overlaying layers (0–87 m depth), especially when considering developmental stages, since the community is migrating in the water column (Weydmann-Zwolicka et al. 2021). Despite the bias towards species occurring in the upper water column of the inner Kongsfjorden, our dataset provides important insights of the mesozooplankton population across the multi-year time-series.

The highest fluxes of swimmers recorded in our samples was reached by copepods with $\sim 505 \text{ ind m}^{-2} \text{ d}^{-1}$. This was not surprising, as previous literature has shown an even higher predominance of these organisms in Kongsfjorden, at different depths (e.g., Hop et al. 2019; Weydmann-Zwolicka et al. 2021). Our data (Table S11) suggested a high number of taxa occurred in the inner Kongsfjorden at ~87 m depth. This is consistent with previous studies (e.g., Zaborska et al. 2016; Ormanczyk et al. 2017) that

Fig. 5 Percentage of the species of Copepods in the sediment trap samples



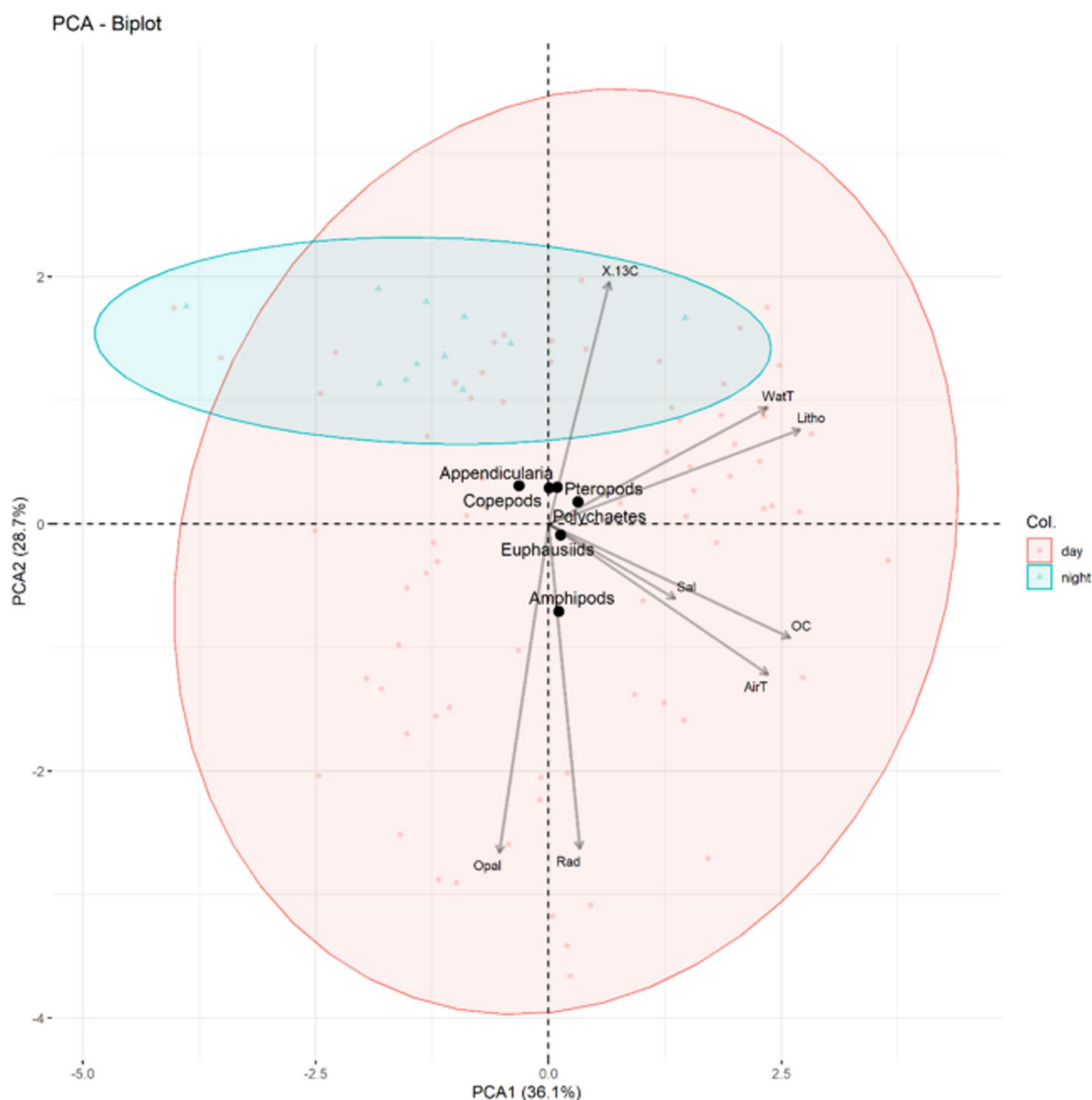


Fig. 6 Principal Component Analysis (PCA) of zooplankton and environmental variables in Kongsfjorden. Appendicularia, copepods, pteropods, polychaetes, euphausiids, amphipods. The legend of the environmental variables is the following: *OC* organic carbon, *Litho*

Lithogenic material, *X.13C* $\delta^{13}\text{C}$, opal, *Rad* solar radiation, *Sal* bottom water salinity, *WatT* bottom water temperature, *AirT* atmospheric temperature

reported high biomass and biodiversity within this fjord, in both the water column and sediments. The annual average of the biodiversity index showed an increasing trend, over the complete years (2011–2017) ($R^2 = 0.55$, $p < 0.05$, $n = 7$) (Fig. 7), suggesting a statistically significant relationship between time and the Margalef index, indicating that as time progresses, there may be a tendency for the Margalef index to rise. This increase could be explained by the reduction in copepods, opening more functional diversity for other zooplankton taxa to be found. Copepods have a widespread diet, so their reduction could provide more functional availability for other species.

A possible driver leading to enhanced biodiversity in Kongsfjorden could be AW intrusion (Arrigo et al. 2008; Slagstad et al. 2011; Carstensen et al. 2012; Beszczynska-Möller et al. 2012; Polyakov et al. 2017; Hop et al. 2019; Weydmann-Zwolicka et al. 2021). The shelf inflow modifies the thermohaline and chemical characteristics of Kongsfjorden waters, moreover, it could introduce allochthonous species into Kongsfjorden, causing the death of the autochthonous non-dominant populations, and simultaneously, the enrichment of taxa (Willis et al. 2006; Kraft et al. 2013). In our study, this was observed for *L. retroversa*. It is known to be a typical species of the sub-Arctic boreal region and

Table 3 PCA analysis of zooplankton and environmental variables at Kongsfjorden. PC1 and PC2 explain 68.3% of the variance observed (36.1% for PC1 and 28.9% for PC2)

Parameter	PC1	PC2
OC	0.49	-0.20
X.13C	0.12	0.42
Opal	-0.10	-0.57
AirT	0.45	-0.26
Rad	0.06	-0.56
Sal	0.26	-0.13
WatT	0.45	0.20
Litho	0.51	0.16

Highest coefficients for each PC are shown in bold. Organic carbon (OC), $\delta^{13}\text{C}$, Cin, opal, air temperature (AirT), solar radiation (Rad), bottom water salinity (Sal), bottom water temperature (WatT) and Lithogenic material (Litho)

to spawn between the Norwegian Sea and the eastern Fram Strait (Bauerfeind et al. 2014; Lischka and Riebesell 2017), however, recent studies have shown that it is migrating further north with the West Spitsbergen Current (Kacprzak et al. 2017) and northwards in the Fram Strait, replacing the cold-water *L. helicina* (Busch et al. 2015). This is documented by the emergence of *L. retroversa* in our samples from 2016 to 2019 (Fig. 8). The highest flux was recorded in January 2019 ($> 5 \text{ ind m}^{-2} \text{ d}^{-1}$) and likely an increase of organisms in further samples is expected. Previous literature (Weydmann-Zwolicka et al. 2021) showed the occurrence of *L. retroversa* in October 2014 from sediment trap samples collected at 60 m depth in the outer Kongsfjord. This would

suggest a progressive intrusion of this species into the inner fjord.

Main drivers of swimmer fluxes in the inner Kongsfjord at ~87 m depth

The primary factors influencing the abundance fluxes of swimmers in our dataset were determined to be atmospheric and marine physical parameters, along with opal concentrations. For most taxa (excluding polychaetes), the shift between polar day and polar night emerged as the major driver of occurrences.

In this study, amphipods were associated to the light and warm temperature and showed a high correlation with opal concentrations ($r_s=0.47$, $n=84$, $p<0.05$, with solar radiation; $r_s=0.28$, $n=84$, $p<0.05$ with air T; $r_s=0.49$, $n=84$, $p<0.05$, with opal fluxes—Fig. SI1). This was consistent with previous literature (Orlova et al. 2015; Dalpadado et al. 2016), which asserted that the spawning of amphipods usually coincided with the main diatom bloom period, to benefit from a source of food. Moreover, in Poltermann (2001) high occurrences of diatoms were found from the gut content analysis of herbivorous-detritivorous amphipods. Notably, our findings suggest that since a future shift in phytoplankton dominance from diatoms towards nanoflagellates has been forecasted for Kongsfjorden (Hegseth and Tverberg 2013), a decline of herbivorous amphipod fluxes could be expected (Fig. 9). This highlights the importance of future taxonomical investigations on swimmers from MDI. Copepods, instead, showed an inverse correlation with the solar radiation, ($r_s=-0.35$, $n=84$, $p<0.05$, similar to

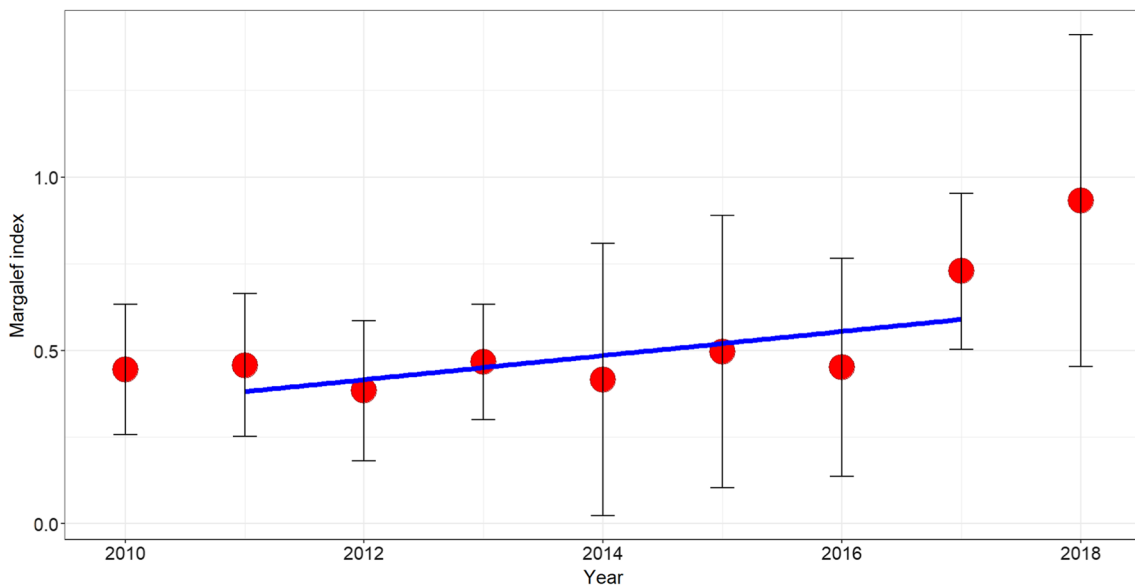


Fig. 7 Scatter plot of annual averaged Margalef Indexes along the time-series. The blue line represents the linear model over the years 2011–2017 ($R^2=0.55$, $p<0.05$, $n=7$)

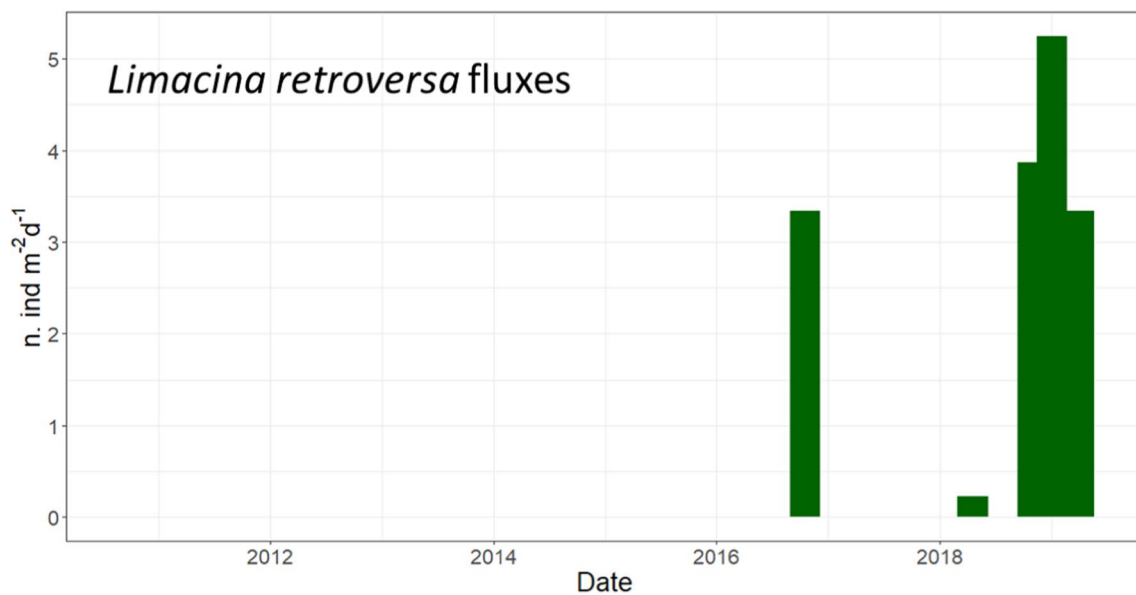


Fig. 8 *Limacina retroversa* fluxes in our samples over time

pteropods $r_s = -0.41$, $n = 84$, $p < 0.05$, and appendicularians $r_s = -0.35$, $n = 84$, $p < 0.05$, Fig. S11), suggesting that these species likely occupied the upper layers during the polar night. Prior studies (Ashjian et al. 2003; Lischka and Hagen 2005; Darnis and Fortier 2012; Berge et al. 2015a, b) have indicated that the omnivorous copepod *Metridia longa* and smaller omnivorous/detritivorous copepods exhibit year-round activity without extensive vertical migrations. These prevalent small omnivorous/detritivorous copepods, which dominate Arctic zooplankton numerically, significantly contribute to recycling organic carbon in the surface layer (Hopcroft et al. 2021). Copepods mainly occurred concurrently with the OM minima, during the polar night, confirming the behavior detected in Berge et al. (2015a, b) and Last et al. (2016). Here, they detected mostly *Oithona* and *Metridia* showing active zooplankton migration, during full moon periods (Hafker et al. 2017). Moreover, Grenvald et al. (2016), focusing on the polar night uncovered diel vertical migration patterns, highlighted the prevalence of copepod nauplii and small copepods, with *Thysanoessa* spp. playing a significant role. This behavior showed the adaptation strategies adopted by Arctic organisms to survive the dark winter period (e.g., diapause in Arctic copepods—Pond et al. 2011, Schmid et al. 2018). The light availability in Kongsfjorden is influenced not only by the seasonal changes but also by the turbidity of the water column. Piwosz et al. (2009) highlighted that the decrease in phytoplankton biomass and primary productivity towards the inner Kongsfjorden is attributed to light limitation, a condition exacerbated by elevated suspended sediments from summer melt-water input.

Another factor influencing the copepods fluxes appeared to be the salinity of the water masses ($r_s = -0.53$, $n = 84$,

$p < 0.05$, Fig. S11), suggesting that the higher occurrences of this taxon was triggered by fresher waters. In Weydmann-Zwolicka et al. (2021), they showed high correlation between the taxa and the thermohaline parameters as well, however, in the outer fjord the first physical forcing was the water temperature, instead of the salinity. With the increasing Arctic Atlantification documented in Tesi et al. (2021) and De Rovere et al., (2022) and persistent open-water conditions, the Kongsfjord copepod community is hence expected to decrease as a result of warmer and saltier water masses inflow, although the contribution of fresh meltwater from glaciers is also expected to increase due to global warming. Another example of connection between the communities and the thermohaline characteristics of the water column was the single-event occurrence of *Oikopleura vanhoeffeni* (appendicularians, stenothermal and stenohaline species; Choe and Deibel 2008) in 2011. It occurred in a single-event (with 128–138 ind m⁻² d⁻¹) simultaneously with the minima values of water temperature and salinity (−1.8 °C and 34.1, respectively). This thermohaline state is characteristic of the Winter Cooled Water formation (WCW) and describes the cold dense water mass sinking of surface waters toward the bottom (Cottier et al. 2005; De Rovere et al. 2022).

After the highest mass flux event at the conclusion of August 2013, there was a significant decline in the flux of organisms. However, statistical tools did not reveal a direct correlation between taxa and lithogenic flux, as depicted in Fig. 6 and Fig. S11. One hypothesis to explain this phenomenon is that estuarine circulation facilitated the transportation of diverse marine zooplankton species with near-bottom currents toward the glacier front. This movement may have resulted in their demise as they were swept into

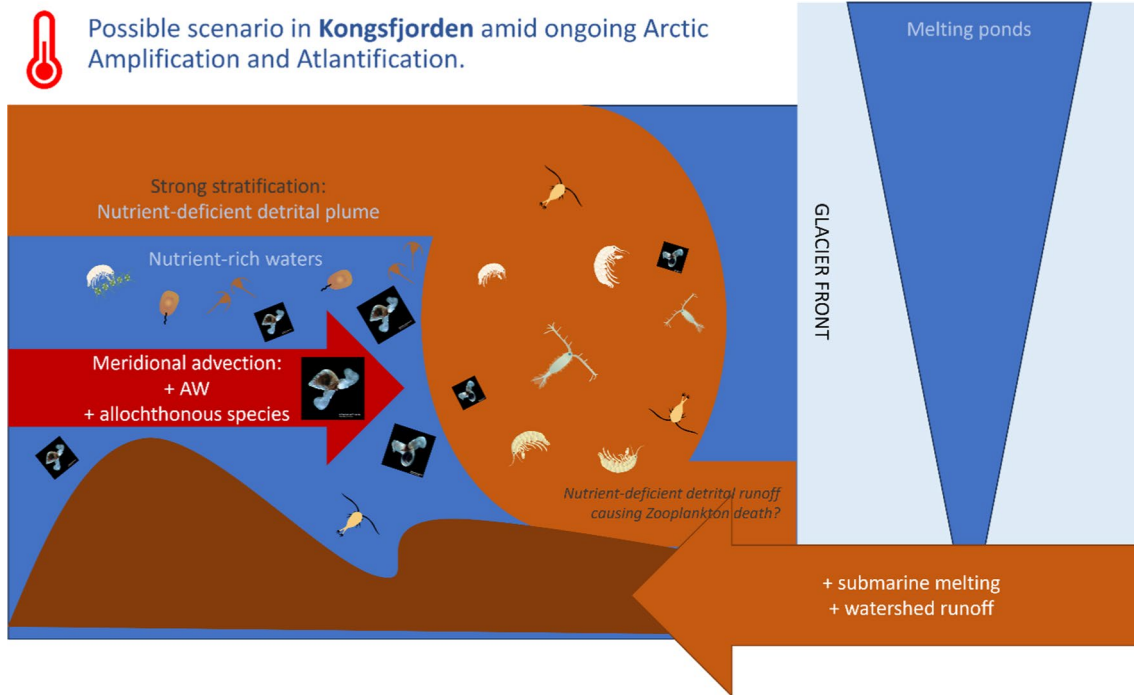


Fig. 9 Conceptual model of the possible future Kongsfjord realm during the polar day. Air temperature and moisture increasing (both in polar day and night); increase of meltwaters from watershed and submarine supply; strong stratification of the water column driven by the meridional advection (black arrow) characterized by increase of AW inflow and intrusion of allochthonous planktonic species, and meltwater plume (orange path). The result will be that the primary producers are shifting from siliceous (diatoms) to more small-size phytoplankton; the mesozooplankton community is changing in biodiversity, with the thrive of offshore boreal species. flagellated Dinoflagellate: Tracey Saxby, Integration and Application Network (ian.umces.edu/media-library).

Ceratium spp. (Dinoflagellate): Tim Caruthers, Integration and Application Network (ian.umces.edu/media-library). *Thalassiosira nordenskiöldii* (Diatom): Tracey Saxby, Integration and Application Network (ian.umces.edu/media-library). Amphipods: Tracey Saxby, Integration and Application Network (ian.umces.edu/media-library); Dieter Tracey, Water and Rivers Commission (ian.umces.edu/media-library). Copepods: Dieter Tracey, Water and Rivers Commission (ian.umces.edu/media-library). *L. retroversa* (Fleming, 1823): http://www.arcodiv.org/watercolumn/pteropod/Limacina_retroversa.html; *L. helicina* (Phipps, 1774): http://www.arcodiv.org/watercolumn/pteropod/Limacina_helicina.html

fresher surface waters, subsequently becoming a valuable food source for fish, seabirds, and mammals (Falk-Petersen et al. 1990; Lydersen et al. 2014).

In summary, the swimmers exhibited a robust correlation with the seasons, a finding corroborated by the two-way ANOVA, and this correlation was further associated with the characteristics of the water masses (refer to Fig. S11). It is crucial to note that in this study, factors influencing zooplankton fluxes, including predation pressure, food availability, and interactions among micro-, meso-, and macrozooplankton, were not considered.

Suggested scenario of a future Kongsfjord

In Fig. 9, we present a new conceptual model summarizing a possible future Kongsfjorden scenario. In the conceptual model we gathered previous literature and our results to pursue a unifying objective, to suggest a possible Kongsfjorden realm. High meridional advection accelerating the Atlantic Water (AW) masses eastward into the fjord, enhancing the

winter AW intrusion and warming the fjord waters (Maturilli et al. 2015; Maturilli and Kayser 2017; Payne and Roseler 2019). The glaciers Kongsbreen, Kronebreen, and Kongsvegen potentially retreating to land-terminating (Lindbäck et al. 2018; Payne and Roseler 2019), triggering insufficient macronutrients runoff to drive enhanced productivity (Hopwood et al. 2018). Furthermore, the glacial melting reduces light availability, thus primary production (Piwosz et al. 2009). Such phenomena are expected to trigger high detrital supply, leading to semi-permanent estuarine circulation, with subsequent nutrient-starved upwelling from the bottom water (D'Angelo et al. 2018). A change in the chemical and physical characteristics of the water masses, in addition to the intrusion of allochthonous species, could affect the mesozooplankton community. Recent studies showed inter-annual variability of the phytoplankton phenology in Kongsfjorden waters (Hegseth et al. 2019). This variability can be mainly attributed to variability in the magnitude and depth of AW inflow, sea ice cover and glacier melt-water discharge. A shift in the availability and composition of the

nutrients and, in turn, of the phytoplankton community (Willis et al. 2006; Svensen et al. 2011; Hegseth and Tverberg 2013; Węśławski et al. 2018) are expected to design a new Arctic fjord biota. Arctic species have already declined in Arctic fjords (Møller and Nielsen 2019).

Concluding remarks

This research successfully collected multi-year time-series data (2010–2018) in Kongsfjorden, an Arctic fjord of Svalbard. Our results provided useful information on the fluxes of swimming mesozooplankton, trapped in the sediment trap, within Kongsfjorden waters. We also demonstrated the influence of the alternation of day and night, along with highlighting the principal environmental factors that likely impact the vertical migration of the community. We acknowledge that our data lacks spatial and vertical resolutions, however it provides continuous information about the fluxes of mesozooplanktonic community within the water column otherwise sparsely discretely measured environment. This is an alternative method for collecting zooplankton data in continuous over multi-year time-series and can serve as baseline for more accurate sampling.

The waters were dominated by copepods; however, a decline of almost all the taxa was recorded after the fall 2013, concurrently with an intense plume event. Nevertheless, no direct correlation was detected between the lithogenic material and the swimmers' occurrences. The opal concentrations triggered the amphipods behavior, enhancing high occurrence of this taxon during June and July. Despite a decrease in the swimmers' fluxes, we recorded an increase of community diversity overtime, probably due to the copepods' reduction, which likely enriched functional diversity. We showed the intrusion from 2016 of the sub-Arctic boreal species *Limacina retroversa* at the expense of the cold-water *Limacina helicina*.

The principal environmental drivers correlated to swimmer fluxes included seasonal factors, such as solar radiation, periods of heightened productivity characterized by elevated opal concentrations, and the stratification caused by meltwater influx.

Our outcome showed for the first time a continuous multi-year data correlating the atmospheric, water column and zooplankton data in Kongsfjorden bay. This dataset serves as a valuable baseline for future targeted research. According to this study, a potential scenario for Kongsfjorden could involve an increase in biodiversity accompanied by a decrease in mesozooplankton abundance. However, taxonomical resolution is needed to further assess this scenario. This trend may be attributed to Arctic Amplification, resulting in heightened meltwater supply and increased influence from Atlantic Water.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00300-024-03251-y>.

Acknowledgements We would like to thank the CNR Arctic Station Dirigibile Italia and Kings Bay AS for logistic support. We greatly appreciated the collaboration with Dr. M. Mazzola for the meteorological data. We deeply acknowledge the captain of MS Teisten for assistance in the mooring deployment and recovery. We also thank Dr. Fabio Savelli (CNR- ISMAR) for the analysis of the organic compounds. This paper is a contribution of the Projects ARCA, FIKO, L-TEF and ENI-Artico. We express our gratitude to the anonymous reviewers for dedicating their time to review and provide constructive feedback on our manuscript. Their meticulous evaluation and insightful comments have significantly enhanced the quality of our research. We acknowledge and appreciate their efforts in contributing to the refinement and overall excellence of our study.

Author contributions A.D.: Conducted investigation, contributed to methodology, curated data, performed formal analysis, validated results, and wrote the original draft. K.M.: Performed Principal Component Analysis, contributed writing the original draft, and participated in its review and editing. J.R.: Analyzed copepod data and contributed to writing, review, and editing. I.C.: Contributed to methodology and participated in writing, review, and editing. S.M.: Conceptualized the study, contributed to methodology, curated data, validated results, and participated in writing, review, and editing. F.G.: Conceptualized the study, contributed to methodology, and participated in writing, review, and editing. P.G.: Contributed to methodology and participated in writing, review, and editing. L.L.: Conceptualized the study, contributed to methodology, curated data, validated results, and participated in writing, review, and editing; also provided supervision throughout the process. All authors read and approved the manuscript.

Data availability The authors confirm that the data pertaining to the swimmers in this study, supporting the findings, are accessible within the paper's Supplementary Material. For the sediment trap content of major constituents, please refer to D'Angelo et al. (2018) available at <https://doi.org/https://doi.org/10.5194/bg-15-5343-2018>. The meteorological and hydrological time-series are available upon request to Leonardo Langone (leonardo.langone@cnr.it).

Declarations

Conflict of interest We declare that there are no conflicts of interest regarding this research or this paper.

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