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## RESEARCH ARTICLE

# Structures of coexisting marine snow and zooplankton in coastal waters of Svalbard (European Arctic)

Emilia Trudnowska<sup>1,\*</sup>, Katarzyna Błachowiak-Samołyk<sup>1</sup>, and Lars Stemmann<sup>2</sup>

How plankton and particles are arranged spatially and the configurations of their co-occurrence shape the rates of organic matter production, utilization, and export within marine systems. The aim of this study was to examine whether the composition of marine snow (particles and aggregates >500 µm) and its coexistence with zooplankton change with depth layer, level of zooplankton dominance, chlorophyll fluorescence, and turbidity across the coastal-offshore gradients of hydrographically different Arctic fjords. The distribution and concentrations of zooplankton and marine snow were assessed *in situ* using an underwater vision profiler (UVP) in Svalbard waters during summer 2019. UVP counts of marine snow drastically outnumbered zooplankton at glacial stations, whereas zooplankton dominated offshore and in upper water layers, even in coastal waters. The most common compositional structure was dominance by an elongated morphotype of marine snow, often co-occurring with small dark (opaque) particles below 40 m depth, implying that these were the typical forms exported directly from surface layers. The other widespread type of structuring was dominance of UVP counts by copepods. They often coexisted with a flake morphotype of marine snow associated with high chlorophyll fluorescence. Structuring dominated by dark morphotypes was observed mainly near glaciers and in deep fjord basins. The highest amount of marine snow, represented by a high degree of dark morphotype, was observed in Hornsund, the most Arctic-type fjord. A *Phaeocystis*-associated agglomerated morphotype of marine snow occurred scarcely and only in more Atlantic-influenced fjords. A bimodal distribution pattern, with one abundance peak at the surface and another in deeper layers (>80 m) was observed offshore and in Kongsfjorden. This study emphasizes the high potential of UVPs for tracking links between plankton and detritus directly in their natural environment, and that variation in their co-occurrence may provide a proxy for the state of a pelagic ecosystem.

**Keywords:** Arctic, Marine snow, Zooplankton, Morphology, Underwater imaging, Environmental gradients, UVP, Coastal waters, Coexistence

## Introduction

The way plankton and particles are distributed and related to each other in the natural environment fundamentally shapes the marine realm. How their co-occurrence changes across various gradients is critical to understanding ecosystem functionality and carbon export processes. Typically, knowledge of how the concentrations of plankton and particles differ horizontally and vertically provides background information for the production, utilization, and export of organic matter within marine systems. Knowing the relative shares of these 2 fundamental components of aquatic systems, living (plankton) and largely

non-living (particles/detritus/marine snow/aggregates) forms, and recognizing their individual compositions are also crucial. The increasing awareness that zooplankton is usually greatly outnumbered by marine snow (Forest et al., 2012; Stemmann and Boss, 2012) and that there is a strict connection between plankton activity and creation of those aggregates (Laurenceau-Cornec et al., 2015; Turner, 2015; Trudnowska et al., 2021) has redirected research of the pelagic realm toward a more comprehensive perception of its composition. Owing to the development of new technologies, simultaneous and analogous analyses of both constituents are now at hand to complement previous approaches that considered them independently in separate studies.

A previous study presented how a simple clustering method can be applied effectively to distinguish a few ecologically meaningful morphotypes of marine snow and that the concentration and vertical distribution of those different categories of marine snow change during sequential phases of the phytoplankton bloom (Trudnowska et al., 2021). In brief, 5 morphotypes of marine

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snow were distinguished: dark, elongated, flake, fluffy, and agglomerated. The dark morphotype is characterized by a small size, a rather circular shape, the highest opacity, and high vertical export efficiency (Trudnowska et al., 2021; Rogge et al., 2022). With its constant presence and generally high concentrations, it has the widest spectrum of possible sources, from aggregates of ice algae when under the ice to fragments of fecal pellets and any compact aggregate. Sources of the elongated morphotype are mostly linked with fecal pellets, large diatom chains, filaments, or cnidarian tentacles. Flake and fluffy morphotypes are representative of typically perceived marine snow, appearing as rather circular and light flocs that mostly appear together with the accumulation of phytoplankton biomass, with the flake type being more compact and the fluffy type being larger but lighter. The agglomerated morphotype of marine snow is characterized by having the largest size and a heterogeneous structure. Most likely, the formation of such agglomerates is enhanced by sugars produced as phytoplankton senesce and decay, especially after blooms of species forming mucilaginous colonies, such as *Phaeocystis* spp.

An interesting area to track interactions between different morphotypes of marine snow and zooplankton is across the coastal–offshore gradient, including in Arctic regions (Ashjian et al., 2005; Forest et al., 2012; Trudnowska et al., 2020b). In the Svalbard Archipelago, pronounced horizontal environmental gradients occur along most of the fjords due to the discharge of fresh and turbid glacial waters from numerous glaciers that are retreating intensively (Bourgeois et al., 2016; Szeligowska et al., 2020; Trudnowska et al., 2020b). However, fjords of the Svalbard Archipelago are experiencing climate warming and Atlantification at various rates and to various extents (Strzelewicz et al., 2022); consequently, zooplankton communities differ clearly in terms of their taxonomic composition and size structure even across fjords of the same island (Gluchowska et al., 2016; Ormańczyk et al., 2017; Trudnowska et al., 2020c). For example, Hornsund, situated on the southwestern tip of Spitsbergen, is the fjord most influenced by the cold and fresh coastal Sørkapp Current and thus has the most Arctic-type characteristics (Strzelewicz et al., 2022). Hornsund has 14 glaciers that have experienced substantial retreat and mass volume loss over the last decades, increasing the input of freshwater into the fjord (Błaszczuk et al., 2018). The lack of a distinct sill at the entrances of Kongsfjorden and Isfjorden leads to easy exchange of the waters, mostly in the form of advection of Atlantic waters (Svendsen et al., 2002; Nilsen et al., 2008; Wiencke and Hop, 2016). However, one of the innermost arms of Isfjorden, Billefjorden, has a shallow sill (50 m) at the entrance that typically inhibits water mass exchange, resulting in its Arctic characteristics and ability to serve as a refugium for local zooplankton populations (Søreide et al., 2022). Therefore, hydrographical conditions in the main basin of Isfjorden are in a state of dynamic equilibrium between Arctic and Atlantic water masses (Skogseth et al., 2020). Although Kongsfjorden has the most northern location, it is typically considered the most boreal, as it receives twice as much Atlantic water as

Hornsund (Promińska et al., 2017). Some of the Atlantic-origin waters may even continue above the shallow (20 m deep) sill into the inner basin of Kongsfjorden, where very high concentrations of particles have been recorded in recent years (Trudnowska et al., 2022).

Because ocean structuring is shaped by the interaction of multiple forces, the distribution of particles and plankton is patchy and may span multiple planes. Among the most important physical and biological factors, chlorophyll fluorescence may have an important effect in shaping the structuring of particles and plankton in the oceans (Trudnowska et al., 2022), as it is a commonly used proxy of primary production (Duveiller and Cescatti, 2016; Smith et al., 2018). The other important factor, especially in coastal waters, is water turbidity, as it represents an important stressor causing water darkening that has numerous ecological consequences for marine systems (Aksnes et al., 2009; Opdal et al., 2019; Mustaffa et al., 2020; Trudnowska et al., 2020b; Blain et al., 2021). High loads of suspended particles have direct effects not only on light, living, and feeding conditions but also on the aggregation process of organic matter produced by phytoplankton, resulting in the formation of heterogeneous flocs of marine snow (Tansel, 2018; van der Jagt et al., 2018). Elevated turbidity is expected to increase in response to climate-induced changes such as increased eutrophication and intensified glacier and river discharges and flooding or storm events (Syvitski et al., 2005; Roleda et al., 2008). Therefore, of great interest is to test whether environmental factors other than hydrography, such as levels of chlorophyll fluorescence, water turbidity, and the presence of zooplankton, can also have a direct impact on the composition of marine snow.

By taking advantage of the possibility of capturing the coexistence of zooplankton and marine snow in their natural environment using the same method, which is non-invasive for fragile marine organisms and aggregates and accomplished with underwater vision profiler (UVP) imaging, we tested how the compositional structure of marine snow and its coexistence with zooplankton may differ across various gradients. Regional scaling was set horizontally across 3 sections representing the west Spitsbergen fjords that experience gradually different hydrographic conditions (Hornsund, Isfjorden, and Kongsfjorden) to examine whether the structuring of co-occurring marine snow and zooplankton differs from the typical Arctic toward more boreal-like fjord systems because of their different plankton communities and glacier impacts. The coastal–offshore gradient was tested by grouping stations into glacial sites that are in close proximity to marine-terminating glaciers in innermost fjord basins, a Torellbreen site with glacier terminating on shelf, a site with river impact, sites in the main basins of fjords, and sites in offshore waters to test how various sources of turbidity may cause variations in the compositional structuring of marine realms. We hypothesized that offshore waters would be zooplankton-dominated and populated by marine snow characteristic of biological production, while coastal, inner basins of fjords would be detritus-dominated with aggregates characteristic of turbid waters. Vertically, several water layers were considered, assuming

that surface water layers provide completely different conditions than mid- and deep layers because of the elevated productivity but also turbidity. We also aimed to examine more closely how the structuring of zooplankton and marine snow may vary not only spatially, but also between waters characterized by high, medium, and low levels of zooplankton, chlorophyll fluorescence, and turbidity. We considered that evaluating the compositional structuring of marine snow morphotypes and their coexistence with zooplankton would provide new insight into our understanding of the marine realm. As this comprehensive approach is both possible and amenable to standardization given new imaging technologies and simple statistical clustering, it may represent a new qualitative parameter of ecological and carbon cycling importance.

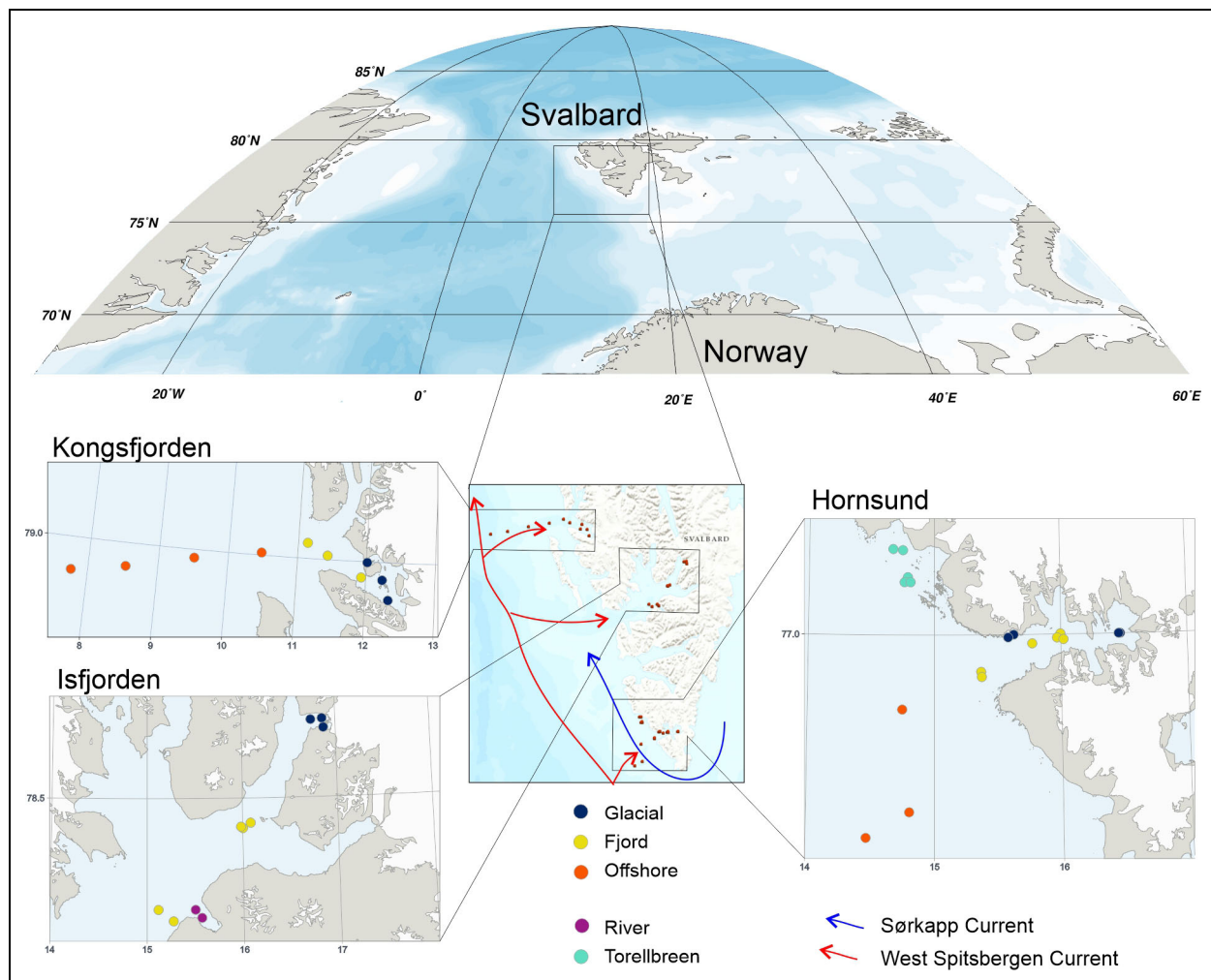
## Materials and methods

### Field campaign and sites

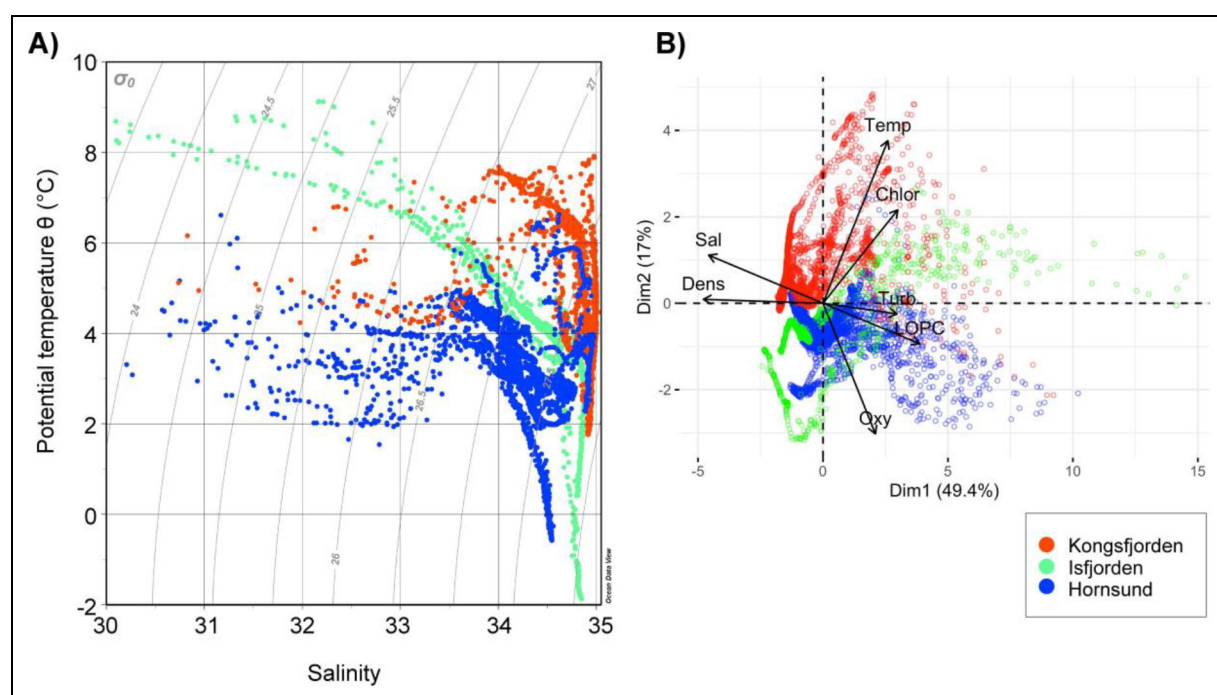
The measurements were performed at 38 stations during the summer of 2019 (between July 26 and August 11) onboard the RV *Oceania* in the area of the western Spitsbergen, the

largest island of the Svalbard archipelago (**Figure 1**). During summer in the Arctic, there is daylight throughout the day and night hours. Most stations (36 of the 38) were sampled during “day” hours. The 2 stations sampled during the “night” (22:16;00:23) did not show any anomalies compared to the rest of the dataset. Vertical profiles of the UVP5 (Hydroptic, France, described by Picheral et al., 2010) were preceded by vertical casts of a platform equipped with a set of sensors: Laser Optical Plankton Counter (LOPC; Brooke Ocean Technology Dartmouth, Canada), conductivity-temperature-depth probe (CTD; SBE 911plus, Sea-Bird Electronics Inc, USA), fluorometer and turbidity meters (Seapoint Sensors Inc, USA), and oxygen sensor (Sea-Bird Electronics, Inc); that is, the LOPC-CTD-F-T-O platform.

West Spitsbergen is a region where warm saline Atlantic waters carried by the West Spitsbergen Current (WSC) mix with cold fresh Arctic Waters carried by the coastal Sørkapp Current (SC) and with riverine and glacial waters (Nilsen et al., 2008; Cottier et al., 2010; Sundfjord et al., 2017). The 3 studied fjords (Hornsund, Isfjorden, Kongsfjorden) have different shapes, bathymetries, and amounts of rivers and



**Figure 1. Maps of the study area, station locations, and dominant ocean currents.** Svalbard Archipelago, with close-ups of specific sections of the 3 investigated fjords: Kongsfjorden, Isfjorden, and Hornsund. These fjords represent 3 different hydrographical regimes, from more Arctic-type (Hornsund) to more progressively Atlantic-influenced (Isfjorden, then Kongsfjorden). Stations representing defined sites (glacial, fjord, offshore, river, Torellbreen) are marked with different colors. The offshore–coastal gradient can be followed by the color-coded stations.



**Figure 2. Scaling of hydrography.** (A) T-S plot of the 1-m averaged data from profiles in the 3 studied regions: Hornsund (blue), Kongsfjorden (green), and Isfjorden (red). Contour lines indicate density ( $\sigma_0$ ). (B) PCA scaling of measurements provided by the LOPC-CTD-F-T-O platform deployed in the 3 regions: concentrations of particles (LOPC), temperature (Temp), salinity (Sal), density (Dens), chlorophyll fluorescence (Chlor), turbidity (Turb), and oxygen (Oxy).

glaciers that all influence their local hydrographic conditions, which are the most Arctic-type in Hornsund, while Isfjorden and especially Kongsfjorden are to a greater extent under the influence of the warm Atlantic water.

The stations were arranged along 3 sections, one for each studied fjord, to survey the glacier-fjord-offshore gradient, plus a site where glacier discharge is directly on shelf (Torellbreen) and a site where a land-terminating glacier discharges in the form of a river (**Figure 1**). The assignment of stations to specific sites was made a priori, based on their affiliation with monitoring programs and considering their locations, fjord topography, and ocean bathymetry. The appropriateness of such grouping was confirmed by analyzing LOPC-CTD-F-T-O profiles (**Figure 2**). Accordingly, in Kongsfjorden, 4 stations represented the offshore site, 3 stations were located in the main fjord basin, and 3 stations were located in a glacial bay. In Isfjorden, 3 stations represented the glacier-fed regime, whereas 5 stations were located in the main fjord basin, and 2 stations were under the influence of river discharge. In Hornsund area, 3 stations represented the offshore oceanic conditions, 5 stations were located on the shelf in close proximity to the Torellbreen glacier, and the other 4 glacier-influenced stations were located inside the fjord, where its main basin was sampled at 6 stations (**Figure 1**).

## Data analyses

### Environmental background and depth layers

The measurements provided by the LOPC-CTD-F-T-O platform (the concentrations of particles derived via LOPC, temperature, salinity, chlorophyll fluorescence, turbidity,

and oxygen) were averaged over 1-m depth intervals. These high-resolution results were visualized in a T-S diagram and analyzed by principal component analysis (PCA; Rstudio, libraries “FactoMineR” and “factoextra”) to understand how the input environmental variables vary from the mean with respect to each other and to determine if there are relationships between them. Finally, the water temperature, salinity, turbidity, and LOPC counts were interpolated along profiles using Ocean Data View Software.

### UVP data categorization

First, all the vignettes taken by the UVP were uploaded to the Ecotaxa web application (<https://ecotaxa.obs-vlfr.fr/>), where their categorization was predicted automatically based on deep learning algorithms. Later, all the vignettes were classified manually, either by approving the automatic prediction or by changing the category into the proper one. Overall 960,526 vignettes were collected during the campaign, among which numerous artefacts were discarded (600,476), including pictures of turbid waters (120,877). Ultimately, 360,050 images were processed for this study, containing both detritus (270,551) and living organisms (89,499). The concentrations of marine snow and zooplankton were first calculated over 5-m depth intervals for which the imaged volume of water was provided and then averaged over defined water layers.

### Marine snow composition and morphological traits

The categorization of marine snow into morphotypes was based on PCA scaling of 24 morphological traits, superimposed on the morpho-space created in the original study describing this method (Trudnowska et al., 2021)



for use with the ecologically meaningful and tested categories. Four of the most meaningful morphological traits were selected according to their high explanatory power of the axes of the PCA (Rstudio, libraries “FactoMineR” and “factoextra”) to present the characteristics of each morphotype. Size is represented by the perimeter, opacity by the mean grey value, shape by circulation, and heterogeneity by the mean position of variability extent in opacity ( $[(\text{max} - \text{mean})/\text{range of grey intensity}]$ ).

To check if the composition of marine snow differed not only spatially but also across waters of various biophysical characteristics, we grouped data according to high, medium, and low levels of numerical importance of zooplankton, intensities of chlorophyll fluorescence, and turbidity. The distinction of the 3 levels was based on the quantiles of their data distribution, that is, the first quantile (0%–25%) represented low values of percentage of zooplankton in UVP counts ( $<7\%$ ), chlorophyll fluorescence ( $<0.02$ ), and turbidity ( $<0.006$ ), the medium level included values that fell into the 25%–75% quantiles, and the high level included data points with values above the third quantile ( $>75\%$ ) of the data distribution, with zooplankton percentages  $>50\%$ , chlorophyll fluorescence  $>0.1$ , and turbidity  $>0.28$ .

### Coexistence structuring

To verify which morphotypes of marine snow tend to occur together as well as to verify whether zooplankton presence tends to relate to the occurrence of specific morphotypes of marine snow, we performed hierarchical clustering (function *hclust*). This clustering procedure was applied to distinguish the dominant structures of coexistence. It was based on the compositional dataset built by concentrations of 5 morphotypes of marine snow (dark, elongated, fluffy, flake, agglomerated), copepods, and other zooplankton quantified at specific depth layers at each station: 10 m layers over 0–100 m, 20 m layers over 100–200 m, the 200–250 m layer, and from  $>250$  m to bottom. The outcome of the clustering was visualized in the form of a heatmap (Rstudio, library “pheatmap”), where data points characterized by similar structuring were grouped together, and the higher the numerical importance of the included marine snow and zooplankton categories, the higher the intensity of the color according to the scale below. Each cluster, representing specific coexistence structuring, was attributed by a specific color. This color coding was used to plot the location of specific clusters over stations and depth layers.

To verify whether the occurrence of specific coexistence structures was related to environmental variables, DistLM (distance-based linear model) routines were run. In this way, we analyzed and modeled the relationship between distinguished coexistence structures (multivariate data cloud built by logarithm of the concentrations of 5 morphotypes of marine snow [dark, elongated, fluffy, flake, agglomerated], copepods, and other zooplankton, converted into a resemblance matrix) and explanatory variables (temperature, salinity, chlorophyll fluorescence, turbidity, and LOPC counts of particles). The forward selection procedure was used to determine the best

combination of predictor variables for explaining variation in observed coexistence structures. In this method the predictor variable with the highest explanatory power is chosen first, followed by the variable that, together with the first, improves the selection criterion the most, and so on (Anderson et al., 2008).

The relationships between patterns in coexistence structures and a set of explanatory variables were presented by a constrained ordination: distance-based redundancy analysis (dbRDA). In the dbRDA, the locations of points are the centroids of data points of specific coexistence structuring, and the lines indicate the direction of their relation with specific explanatory variables. Moreover, compositional structuring was tested across spatial factors (region, site, layer) by PerMANOVA. PerMANOVA, DistLM, and dbRDA were performed in Primer6 and PERMANOVA+ software.

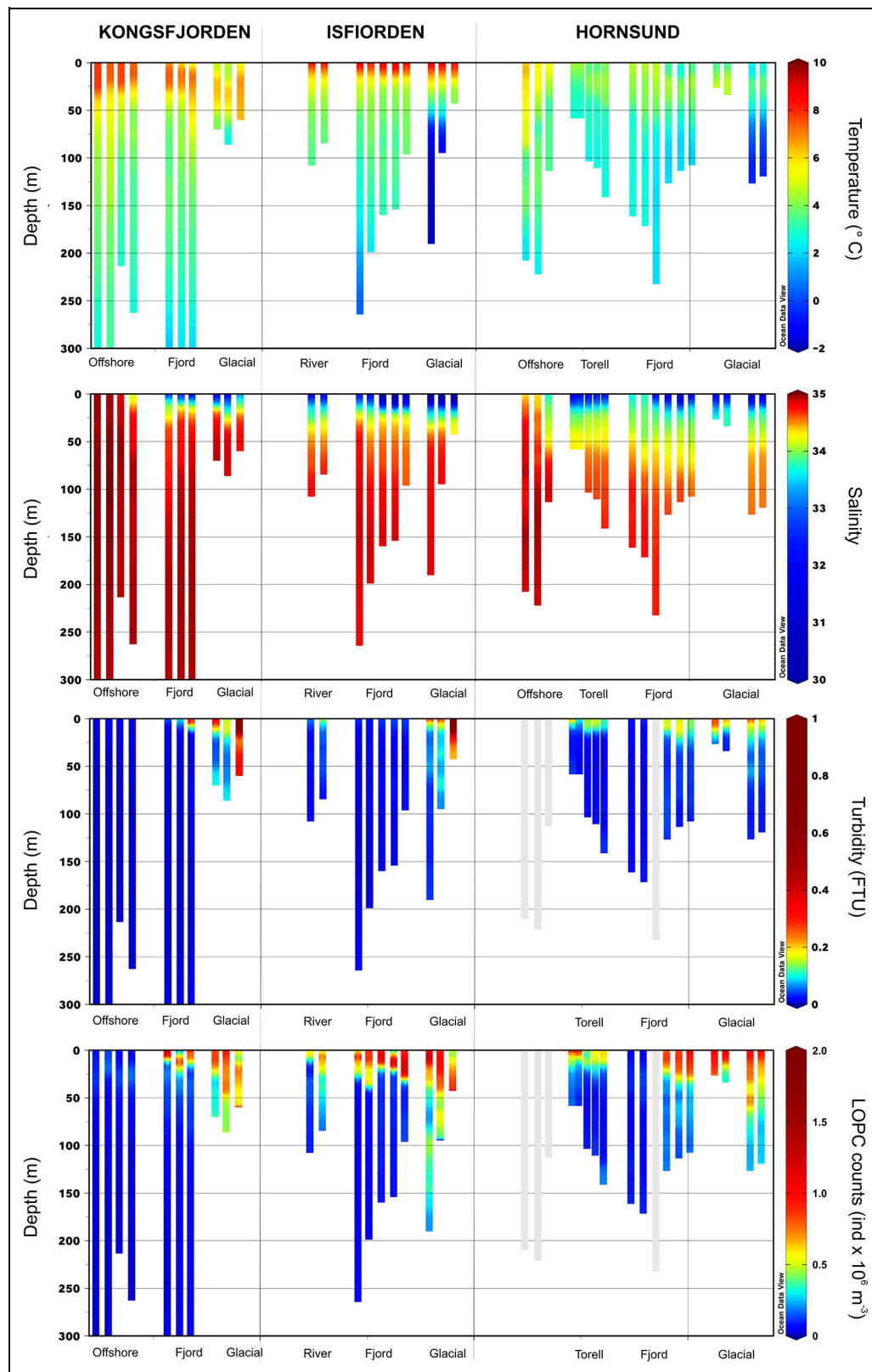
A map of the study area was prepared with the PlotSvalbard package in R, created by Vihtakari (2019). Section plots of the distribution patterns were prepared in the Ocean Data View software, with the application of Diva interpolation (Schlitzer, 2021). The other plots were created in R via the “ggplot2” package.

## Results

### Environmental structuring

Among the 3 fjords investigated, Hornsund was the coldest one with the lowest salinity, Kongsfjorden was the warmest with the highest salinity, and in Isfjorden, an intermediate hydrographical regime was observed (**Figure 2**). PCA scaling showed that temperature scaled positively with chlorophyll fluorescence (**Figure 2**). Turbidity scaled positively with LOPC counts and negatively with salinity and density along the first PCA axis (i.e., the lower the salinity, the more turbid the waters). Turbidity also scaled negatively with temperature and chlorophyll on the second axis of the PCA (i.e., the higher the turbidity, the lower the chlorophyll fluorescence).

The coldest waters ( $<0^{\circ}\text{C}$ ) were observed at glacial stations of the Isfjorden and Hornsund regions (**Figure 3**). The depth range of lowered salinity ( $<34$ ) was the greatest ( $>50$  m) in the Hornsund region. In the Kongsfjorden and Isfjorden regions, the low salinity layer was restricted to the upper 20-m depth layer. The highest turbidity levels were observed at the innermost, glacial stations of the Kongsfjorden and Isfjorden regions. In Hornsund, the elevated turbidity ( $>0.1$  formazin turbidity units, FTU) was also spreading to the fjord main basin. Along each of the sections, the counts of the LOPC were the highest at the glacial stations over the whole water column. At the fjord site, the LOPC counts were also elevated, but only within the upper 25–50 m (**Figure 3**). Higher temperatures (approximately  $7^{\circ}\text{C}$ ) were observed in the upper 50-m layers, while lower temperatures (approximately  $3^{\circ}\text{C}$ ) were observed in the lower parts of most of the stations. The highest salinity was observed throughout the studied depth range of the offshore stations of Kongsfjorden but also in deeper parts of its fjord site, as well as at depths of the offshore stations of Hornsund region (**Figure 3**).



**Figure 3. Environmental background data across the sections of each region studied.** Profiles of temperature, salinity, turbidity, and the abundance of particles and plankton assessed via Laser Optical Plankton Counter (LOPC) at each station grouped by sites. Light grey bars indicate missing data.

#### **Marine snow versus zooplankton**

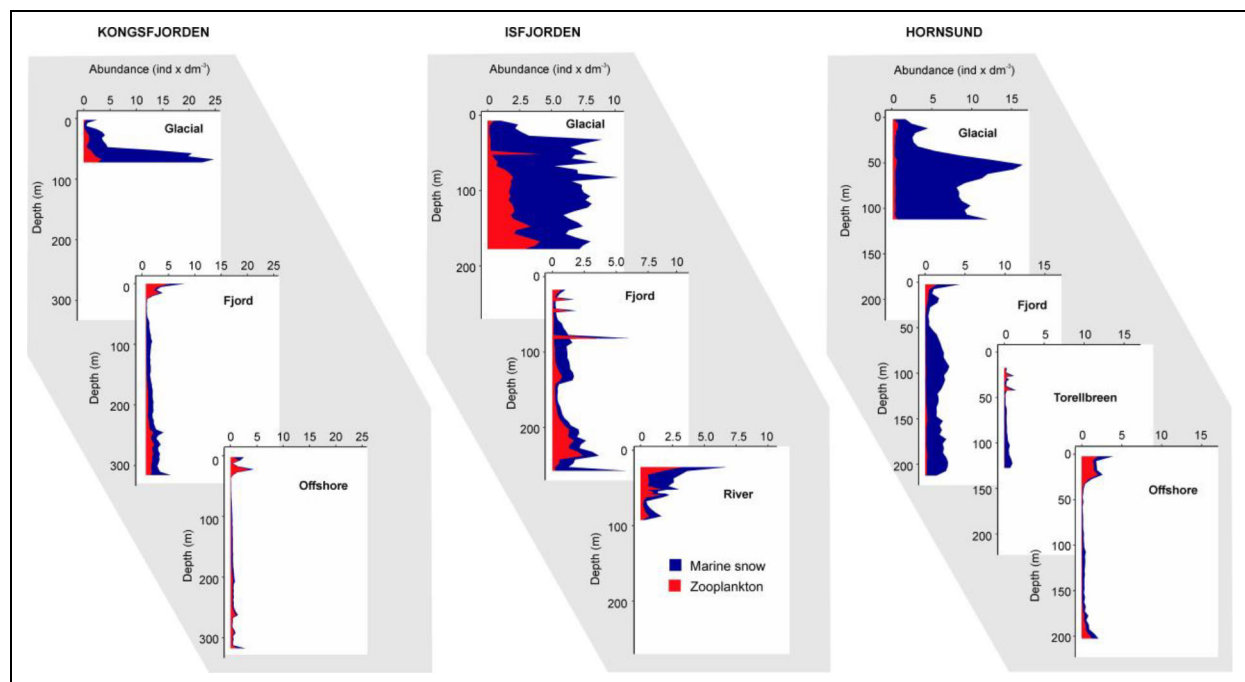
Overall, marine snow constituted 75% of UVP vignettes. Regarding concentrations within regional sections, their sites and water layers, zooplankton shares varied from 3%

to 75% (**Table 1**). The lowest contribution of zooplankton to overall UVP counts was observed at glacial stations, especially below 20 m depth. Among the main fjord basin stations, in Hornsund, the lowest relative amount of

**Table 1. The percentage of zooplankton in relation to concentration of marine snow (ind  $\text{dm}^{-3}$ ) derived via UVP across sections of the 3 fjords, their associated sites and depth layers**

Studied Fjord	Depth Layer (m)	Associated Sites				
		Offshore	Fjord	Glacial	River	Torellbreen
Kongsfjorden	0–20	61	63	14	— <sup>a</sup>	—
	20–50	55	34	17	—	—
	50–200	36	16	11	—	—
	>200	59	41	—	—	—
Isfjorden	0–20	—	70	17	75	—
	20–50	—	36	3	46	—
	50–200	—	34	27	40	—
	>200	—	49	—	—	—
Hornsund	0–20	64	39	17	—	60
	20–50	41	23	7	—	24
	50–200	20	5	3	—	16
	>200	60	9	—	—	—

<sup>a</sup>Site not relevant (not sampled) for the section.

**Figure 4. Depth profiles of marine snow versus zooplankton.** Abundance (ind  $\text{dm}^{-3}$ ) of zooplankton (red) and marine snow (navy blue) over depth profiles in sites across sections of the 3 investigated fjords.

zooplankton to marine snow was observed. The offshore waters, in both the Kongsfjorden and Hornsund sections, were characterized by the dominance of zooplankton in UVP images near the surface and in the lowest depth layers, while lower zooplankton ratios were observed between 50 and 200 m (Table 1).

The highest overall abundances assessed via UVP were observed at the glacial stations of each section (Figure 4). High concentrations were also observed at the fjord site of

the Hornsund region, especially below 50 m. Additionally, higher abundances were recorded at the river station than at the fjord stations of Isfjorden, especially in the upper 50 m. The vertical pattern of zooplankton distribution was bimodal, with peaks near the surface and near the bottom at the fjord site of the Kongsfjorden section and at all offshore stations. In Isfjorden, the highest concentrations of zooplankton were recorded at the glacial stations and at greater depths (>200 m) of the fjord site (Figure 4).



Generally, copepods dominated the UVP counts of zooplankton. They constituted 93% of the zooplankton in Kongsfjorden, 89% in Hornsund, and 87% in Isfjorden. Occasionally, their main predators (jellies and chaetognaths) were also observed, especially in Isfjorden. Singular larger crustaceans (e.g., amphipods, decapods, and krill) were observed mostly in the deeper layers.

### **Composition of marine snow**

Five morphotypes were distinguished to characterize the composition of marine snow (**Figure 5**). The agglomerated morphotype represented the largest aggregates among the defined categories that were also characterized by high lightness and heterogeneity of their internal structure (**Figure 5C**). Fluffy aggregates were also very light in grey level intensity and heterogeneous, but much smaller than the agglomerated morphotype. Flake particles were small, quite light, and typically circular in shape. The elongated forms were characterized by low circularity, medium size, and a wide range of lightness. The dark morphotype consisted of small, dark, homogeneous, and often circular particles (**Figure 5C**).

The dataset was almost devoid of the agglomerated morphotype of marine snow. It occurred only in Isfjorden (**Figure 5A**). Flake and fluffy morphotypes dominated within the upper layers (<20 m) at each investigated fjord section and site. Their dominance was observed deeper at the offshore stations than at the fjord and glacial stations. The elongated morphotype was an important contributor to the overall marine snow abundance mostly below the surface layer (depth >20 m or >50 m), mainly in the fjord site but also on the shelf of Hornsund (offshore and Torellbreen sites). The dark morphotype of marine snow was most abundant below the surface at the glacial stations, regardless of the investigated region, as well as at the fjord sites of Kongsfjorden and Hornsund. They were also highly significant representatives of marine snow below 20 m at the Torellbreen and river sites (**Figure 5A**).

When the highest relative importance of zooplankton was observed in UVP counts, the marine snow was composed mainly of the fluffy and flake morphotypes. The numerical importance of these 2 morphotypes decreased across the 3 decreasing levels of the ratio between zooplankton and marine snow (**Figure 5B**). At the medium level of the relative share of zooplankton and marine snow, the dark and elongated morphotypes clearly dominated (potentially representing fecal pellets, when their amounts were similar to the amount of zooplankton producing them). When the UVP counts were heavily dominated by marine snow, the dark morphotype dominated.

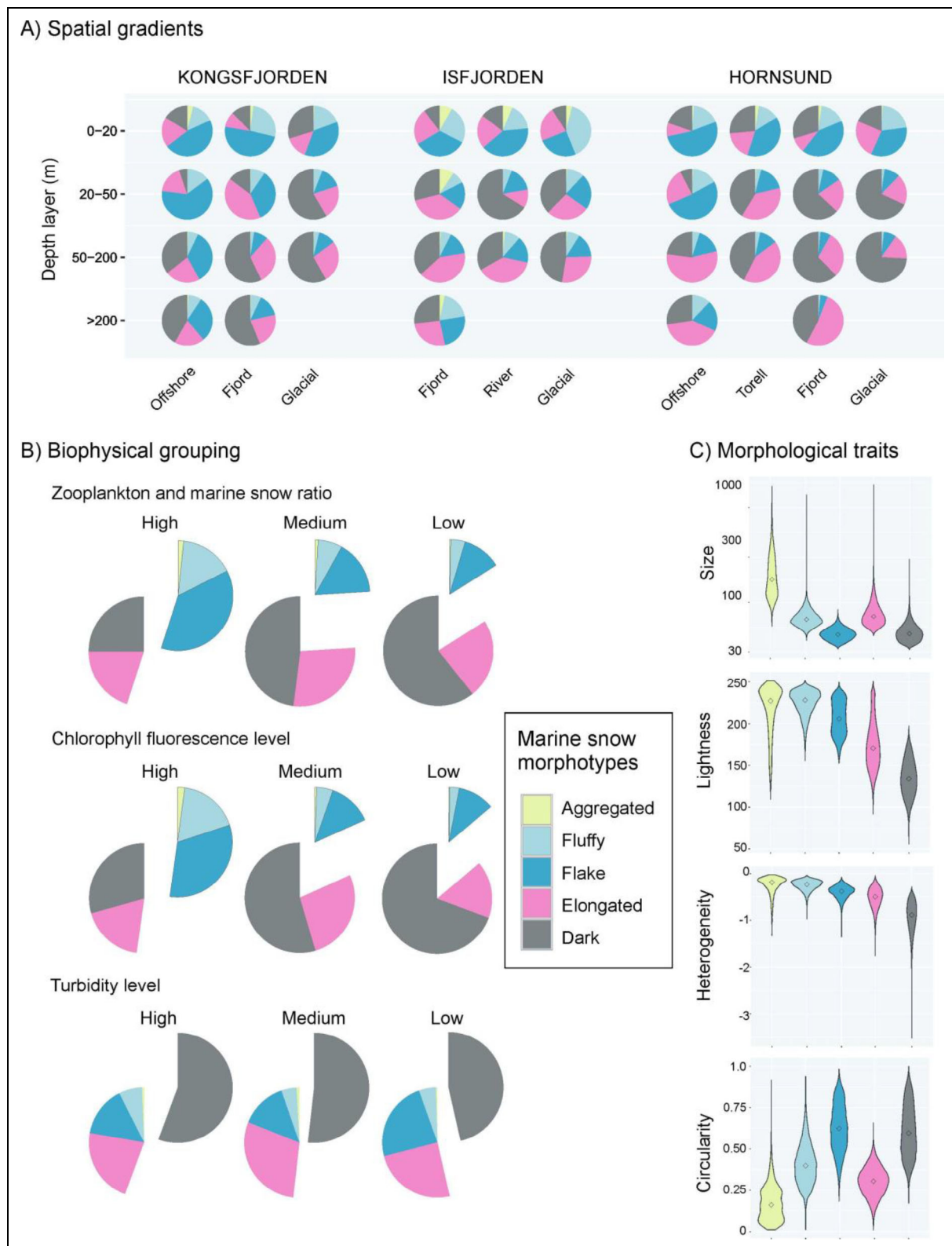
A similar trend was observed across 3 levels of chlorophyll fluorescence, with the highest numerical importance of fluffy and flake morphotypes occurring at high chlorophyll fluorescence levels and their lowest numerical importance occurring at low fluorescence levels. This interesting feature showed the opposite trend of the dark particles, whose importance was the lowest in the high chlorophyll fluorescence levels, and increased toward the lower chlorophyll activity (**Figure 5B**).

The dark type of marine snow dominated at all turbidity levels, with only a slightly decreasing percentage contribution from highest to lowest turbidity level. The high contribution of the flake morphotype in low turbidity waters can be an indication of the importance of fresh phytoplankton material in clear waters (**Figure 5B**).

### **Coexistence of marine snow morphotypes and zooplankton**

The structural compositions of marine snow morphotypes and their co-occurrence with copepods and other zooplankton groups were analyzed to define which of those categories occurred together. Via the hierarchical cluster analysis, 7 distinct groups (clusters) were defined that were characterized by the highest intergroup similarity in compositional structuring (**Figure 6A**). The most common type of composition was the coexistence of the elongated and dark morphotypes of marine snow. This compositional structure was observed below 30–40 m at most of the stations (shown in purple in **Figure 6B**). The compositional structures characterized by the high occurrence of copepods were also frequent. These structures were observed in the upper layers of most of the stations, as well as in the deepest parts of the offshore sites (shown in yellow in **Figure 6B**). Dominance by the dark morphotype was also common (third largest cluster), observed mostly at depths of the glacial and fjords sites, especially in Hornsund (shown in grey in **Figure 6B**). Structural compositions characterized by the coexistence of copepods with either flake, elongated, or dark morphotypes were observed, especially in the Kongsfjorden region, below 80 m and at similar depths of some stations in the Isfjorden region (shown in orange in **Figure 6B**). The compositions shaped by fluffy and flake morphotypes or other zooplankton groups occurred only at singular specific sites, such as at upper water layers of inner coastal stations.

Compositional structures varied significantly across regions, sites, and depth layers (PerMANOVA  $p < 0.001$  for each factor and their interactions). The analyzed environmental factors together explained only 22% of the observed variance in the compositional structuring of marine snow morphotypes co-occurring with zooplankton. Even though each tested explanatory variable was statistically significant ( $p = 0.001$  in the DistLM model), their individual relationships within a tested data cloud were not high, with the highest explanatory power (8%) found for the LOPC counts, the second highest for temperature and salinity (5% each), and the lowest for chlorophyll fluorescence and turbidity (2% each). Despite high overall variability, data points representing copepod-based communities scaled mostly positively with temperature and chlorophyll fluorescence in the dbRDA plot (**Figure 6C**). The compositional structure characterized by the high importance of the fluffy and flake morphotypes scaled positively with LOPC counts. Dark morphotype-based structures (shown in grey and purple in **Figure 6C**) scaled with salinity and turbidity.

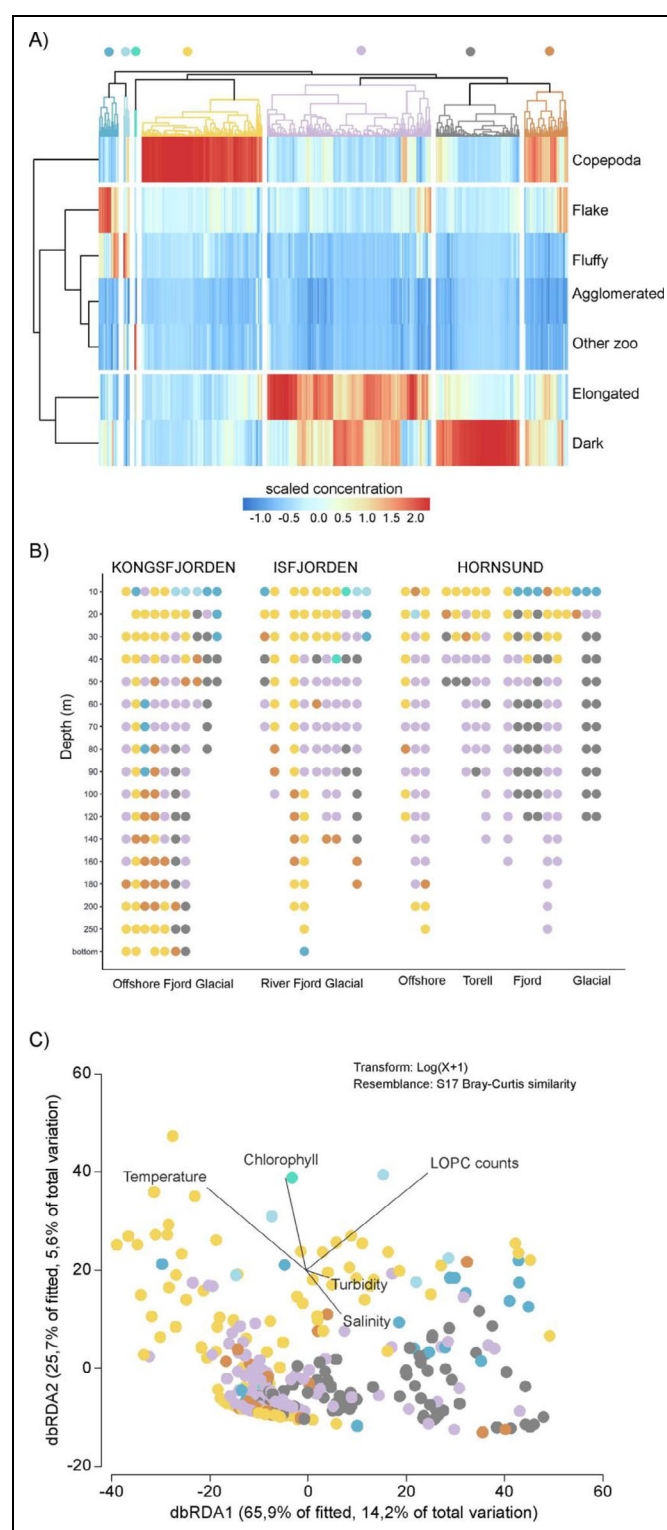


**Figure 5. Composition of marine snow by morphotype.** Shares of defined morphotypes of marine snow (color-coded, inset box) grouped by (A) depth layer, fjord region and site and (B) biophysical properties of high, medium and low (based on quantiles, 0%–25%, 25%–75%, and >75%, of their data distribution) zooplankton-to-marine-snow ratio and chlorophyll fluorescence and turbidity levels. (C) Violin plots of 4 ecologically meaningful morphological traits given in pixels (size, lightness, heterogeneity, and circularity) of marine snow across 5 morphotypes.

## Discussion

This study showed how an approach to utilizing UVP to study marine snow and zooplankton can be an effective

method to capture differences in their composition and co-existence across hydrographically different fjords and coastal–offshore gradients, vertically over the water



**Figure 6. Coexistence structures for marine snow morphotypes and zooplankton.** The clustering of similar compositions of marine snow and zooplankton at various depths in Svalbard waters over 3 offshore–coastal sections of the fjords Kongsfjorden, Isfjorden, and Hornsund. (A) The heatmap presents the concentrations of 5 morphotypes of marine snow, copepods (Copepoda), and other zooplankton (other zoo) arranged across the 7 clusters distinguished by hierarchical cluster analysis. The higher the numerical importance of the included marine snow and zooplankton categories, the higher the intensity of the color according to the color scale bar. Each cluster, representing specific coexistence structuring, was attributed by a specific color (colored dots across the top of the heat map). (B) The location of occurrence of specific clusters over stations and depths using the same color-coding of dots in panel A. (C) On the ordination plot (dbRDA), the location of points presents the centroids of data clouds of specific coexistence types and the lines indicate the direction of their relation with specific explanatory variables. Colors of data points correspond to colors of specific clusters marked in the dendrogram (A) and dot-plot (B).



The fact that the elongated morphotype of marine snow, coexisting with dark particles, mostly dominated in this study confirms that a spectrum of mechanisms causing their creation is broad (Verney et al., 2009; Meslard et al., 2018; Many et al., 2019; Trudnowska et al., 2021). Most likely, the elongated morphotype represents fecal pellets (Turner, 2002; Lalande et al., 2011; van der Jagt et al., 2020), especially when coexisting with zooplankton, as was the case in the offshore and fjord sites. Because dominance by the elongated particles was observed mainly below a depth of 40 m, we conclude that they were the dominant forms of matter exported directly from the surface layers. Because the dark morphotype

In the reference study that introduced morphotypes assessed via UVP, the creation of the agglomerated morphotype was explained by the presence of *Phaeocystis*

(Trudnowska et al., 2021), which typically forms mucilaginous colonies of increased stickiness (Engel et al., 2017; Tansel, 2018) and is occurring more commonly in Atlantic-influenced Svalbard areas (Kubiszyn et al., 2017; Dąbrowska et al., 2020). Indeed, this specific morphotype of marine snow was observed only in 2 fjords (**Figure 5A**), where Atlantic advection is prominent: Kongsfjorden and Isfjorden (Fahrbach et al., 2001; Saloranta and Haugan, 2004; Pavlov et al., 2013). Because such aggregates are positively buoyant, having decreased settling velocities (Azetsu-Scott and Passow, 2004; Prairie et al., 2013), they tend to stay suspended in the water column rather than effectively sinking (Passow and Wassmann, 1994; Olli et al., 2007; Trudnowska et al., 2020b; Trudnowska et al., 2021), which may explain why, in this study, they were observed only in the upper water layers. The formation of this morphotype of marine snow may also be expected in other sites and systems during the late stage of the phytoplankton bloom, as other phytoplankton groups can also produce sticky organic compounds when becoming senescent (Passow and Wassmann, 1994; Waite et al., 1995). Therefore, the lack of this morphotype indicated that, at the time of this study (end of July, beginning of August), no massive agglomeration of decaying organic matter was formed.

The Svalbard archipelago lies on the pathway of Atlantic Water heading toward the Arctic Ocean. This far north-reaching tongue of warm and saline Atlantic waters thus subjects the area of west Spitsbergen fjords to a high degree of Atlantification, albeit with considerable zonal variability in hydrography (Schauer et al., 2004; Polyakov et al., 2005). The observed gradual differences in hydrography across the 3 fjords investigated (**Figure 2**) is consistent with the established concept of Hornsund being a typical Arctic fjord and Kongsfjorden being a typical Atlantic fjord (Promińska et al., 2017). Hornsund is also the most glaciated fjord (Błaszczuk et al., 2018), with the highest concentrations of marine snow represented mostly by the dark morphotype (**Figure 5A**), while the other 2 fjords had much more organic typology of imaged objects.

Glacier retreat is an imminent consequence of exacerbating climate change that substantially impacts coastal Arctic marine ecosystems (Sommaruga, 2014; Sommaruga and Kandolf, 2014; Calleja et al., 2017; Szeligowska et al., 2021) by introducing high loads of freshwater, nutrients, and terrigenous particles. This combination results in a massive production of marine aggregates in glacier bays, as was also observed by their prominent abundances in each section investigated in this study (**Figure 4**). Moreover, the results of this study confirm that marine-terminating glaciers located in inner bays are much more efficient producers of local “snowstorms” of marine aggregates than glaciers that have their termini on the oceanic shelf (Torellbreen) because the matter produced there is immediately flushed by ocean currents (Trudnowska et al., 2020b). The same applies to the effect of land-terminating glaciers, with a discharge in the form of a stand-alone river (river stations), as their effect is mostly confined to the upper water layers (Szeligowska et al., 2021); therefore, strong stratification precludes vertical export, and the

produced aggregates are mostly transported horizontally at the surface plume.

While detritus and terrestrial particles are mainly transported locally in the coastal Svalbard area and settle rather rapidly from their source (Ashjian et al., 2005; O'Brien et al., 2006), most organic components are advected via the West Spitsbergen Current (Sanchez-Vidal et al., 2015). Therefore, the offshore waters of Svalbard fjords are dominated by organic-type particles more so than mineral ones (Pavlov et al., 2015; Makarewicz et al., 2018; Trudnowska et al., 2018), which is in line with the results of this study, as mainly copepods and the flake morphotype of marine snow were imaged by the UVP in offshore waters (**Figure 6**). The vertical export of organic matter in offshore waters is often limited by intensive grazing of zooplankton (Olli et al., 2007). Only 2% of primary production is estimated to be exported to a depth of 300 m in this region (Forest et al., 2010). The hypothesis of effective grazing of zooplankton on freshly produced phytoplankton can be supported by observations of UVP images (**Figure 7**) that signify numerous copepods with spread antennae, implying that they were in active feeding mode (Ohman, 2019; Vilgrain et al., 2021). Those shelf locations are crucial feeding grounds of little auks, actively feeding on lipid-rich, large planktonic *Calanus glacialis* (Jakubas et al., 2013; Balazy et al., 2019); thus, offshore waters are probably more important for energy transfer to higher trophic levels than for vertical export of carbon, in contrast to the effective carbon burial that occurs inside fjords (Koziorowska et al., 2018; Zaborska et al., 2018; Włodarska-Kowalczyk et al., 2019; Cui et al., 2022).

The ratio between nonliving and living components of the pelagic realm may change substantially not only across shelf–offshore gradients (Ashjian et al., 2005; Forest et al., 2012) but also across depth gradient as shown in this study (**Figure 4**). Generally, depth is the most important factor structuring zooplankton communities in this region (Kosobokova and Hirche, 2000; Hirche and Kosobokova, 2007; Gluchowska et al., 2017). Typically, during summer when the Arctic region is experiencing continuous daylight (midnight sun), zooplankton are concentrated mostly within the surface layers to benefit from a short but intensely productive summer season. This concentrating in the surface layer was the case at the fjord and offshore sites. The second peak of copepod abundance that was observed at deeper Atlantic-influenced stations (offshore and fjord sites of Kongsfjorden and Isfjorden) can reflect the layered structuring of water masses (Promińska et al., 2017), that *Calanus* populations had already started to descend to depth (Svensen et al., 2011), or that zooplankton may exhibit a kind of vertical niche partitioning there, with taxa more adapted to surface and taxa typically dwelling deeper. Zooplankton tended to stay in deeper water layers near glaciers, most likely avoiding highly turbid surface layers with lowered salinity (Szeligowska et al., 2022), because both hydrographic and optical characteristics are of similar importance in driving fine-scale vertical selection of zooplankton in Svalbard (Trudnowska et al., 2015). Contrary to expectations, the composition of marine snow morphotypes did not differ in the



surface layers across sites representing the coastal–off-shore gradient of specific sections but did differ between sections (**Figure 5A**). The former implies that productive surface layers are similar across hydrographical regimes, regardless of the site.

While the relation between the occurrence and composition of phytoplankton and marine snow is anticipated and considered rather straightforward (Laurenceau-Cornec et al., 2015; Turner, 2015; Trudnowska et al., 2021), the perspective of the impact of zooplankton occurrence on marine snow quality is much less direct and thus still understudied (Möller et al., 2012; Taucher et al., 2018; Cawley et al., 2021). In this study, compositional structures clearly dominated by zooplankton were common, and those waters were often also populated mainly by the flake morphotype of marine snow (**Figure 6B**), implying their favorable association. Copepods have frequently been observed to follow the aggregates along the water column, presumably to feed on them (Garvey et al., 2007; Möller et al., 2012; Toullec et al., 2021). Feeding behavior on settling aggregates was even observed to dominate in this part of the Arctic, by filter-feeding copepods such as *Calanus* spp. and *Pseudocalanus* spp. (van der Jagt et al., 2020). Zooplankton feeding activity has been suggested to cause diel variations in aggregate abundances (Stemmann et al., 2000; Jackson and Checkley, 2011). Moreover, numerous field observations of zooplankton associated with marine snow suggest that aggregates may represent a substantial food source in addition to phytoplankton (Steinberg et al., 1994; Kiørboe, 2000; Jackson and Kiørboe, 2004; Möller et al., 2012), constituting a viable food choice even when other alternatives are present (Cawley et al., 2021). If we assume that the formation of the flake type of marine snow starts when primary production is high and that the aggregation process may make small phytoplankton cells more available to be eaten, a sort of trophic shortcut may indeed be perceived by the UVP (Lampitt et al., 1993; Cawley et al., 2021).

In contrast to favorable coexistence of zooplankton with the flake morphotype, zooplankton appeared to avoid waters where the dark morphotype of marine snow dominated, most likely widely representing the aggregates of lithogenic particles that dominate the suspended material in Svalbard fjords (Calleja et al., 2017). Living in turbid waters may be unfavorable, for example, due to clogged feeding appendages of tactile predators. High amounts of silt in seawater can be fatal for suspension-feeding copepods such as *Calanus* spp. (Arendt et al., 2011) because of lowered food intake efficiency (Kirk, 1991; Jönsson et al., 2011). Indeed, stable isotope analysis of the local *Calanus* population in the glacial bay of Hornsund showed that their diet consisted greatly of mineral particles compared to the populations feeding in clean waters, where the diet was diatom-based (Trudnowska et al., 2020a). However, for some reason they were also found to be very abundant and actively reproducing in waters at glacier fronts (Trudnowska et al., 2014; Trudnowska et al., 2020b).

### **New proxies to be further developed in ecological interpretations of the imaged pelagic realm**

Because the ratio between zooplankton and marine aggregates is very responsive to dynamically changing processes, such as reproduction and mortality rates in zooplankton, phases of phytoplankton bloom, external discharge of nonliving particles, or flocculation/defragmentation of aggregates, this percentage (**Table 1**) can be considered as an additional parameter describing the status of a particular marine system. The ability to measure detritus particles together with organisms *in situ* may help to identify the components of the pelagic realm that are particularly important in utilizing and biogeochemically transforming produced carbon. Because the composition of marine aggregates depends on the nature and type of the existing particles, as well as on the state of the phytoplankton bloom and the dominant species of microorganisms (Laurenceau-Cornec et al., 2015; Ehn et al., 2019; Toullec et al., 2021; Trudnowska et al., 2021), the composition of marine snow morphotypes can serve as an ecological indicator of the state of a pelagic system and ongoing processes within it.

Monitoring sensitive regions such as the Arctic coastal areas where a complex set of environmental factors drives strong physical and ecological gradients is an imperative. The routine deployment of imaging instruments, such as UVPs, can be beneficial for better understanding large-scale patterns and long-term trends in physical-biological coupling and ecosystem function through both observations and modeling. This study presents the ecological potential of a comprehensive assessment of living and nonliving components of the pelagic realm and various structurings of their coexistence as another ecological proxy that is now definable thanks to new technologies.

### **Data accessibility statement**

The UVP data that support the findings of this study can be acquired under CoastDark project at EcoTaxa (<https://ecotaxa.obs-vlfr.fr>). Other data are available from the corresponding author on request.

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## Competing interests

The authors declare no competing interest.

## Author contributions

Contribution to conception and design: ET, LS, KBS.

Acquisition of data: ET, KBS.

Analysis and interpretation of data: ET.

Drafting the article: ET.

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