Biogeosciences
Discussions

Cells of matter and life – towards understanding the internal structure and spatial patchiness of particles and plankton distribution in the Arctic fjords

Emilia Trudnowska[1], Katarzyna Dragańska-Deja[2], Sławomir Sagan[2], Katarzyna Błachowiak-Samołyk[1]

[1]Marine Ecology Department, Institute of Oceanology Polish Academy of Sciences, Sopot, Poland
5   [2]Departemnt of Marine Physics, Institute of Oceanology Polish Academy of Sciences, Sopot, Poland

Correspondence to: Emilia Trudnowska (emilia@iopan.pl)

Abstract. Nothing is homogenous, neither the oceans, nor the distribution pattern of particles and plankton, both in the water column and within their patches. Here we analyse and map the spatio-temporal distribution patterns and the internal structure of 94 patches of various size fractions of particles and plankton studied in two Arctic fjords over six summer seasons. Observed patches generally occupied only the minor part of the studied upper water column (on average 12%), and frequently occurred as multi-fraction forms. They varied among years and regions in terms of their position in a water column, size, shape, and structure. Consequently, we propose completely novel insight into their internal structure, by classifying them according to their shapes and the location of their cores. We distinguished seven types of patches: Belt, Triangle, Diamond, Flare, Fingers, Flag, and Rosette. The observed increasing role of the smallest size fractions (steepening size spectra slopes) over years implies that Atlantic water advection played the crucial role on compositional dynamics on temporal scale. The recurring feature of the elevated concentrations of particles and plankton near glacier fronts suggest that it, together with local biological production, is the strongest mechanism generating patchiness on the local scale. Even though we significantly extended our comprehension of the phenomenon of patchiness, it still remains an ambiguous matter, when, why, and if the mechanistic or ecological forcing prevails in shaping the patterns of particles and plankton distribution. Regardless of the mechanism, our results show that particles and plankton are not purely dye-like passive objects and that the type of their structuring in a water column may have only short term and local validity.

1 Introduction

Distribution of particles and plankton in the oceans is highly patchy. Those 'clouds of matter' are fundamental 'cells' for trophic interactions and organic carbon cycling (Benoit-Bird et al., 2011; Brentnall et al., 2003; Godø et al., 2012; Priyadarshi et al., 2019). The identification of the phenomenon of patchiness (distribution of concentration hotspots) is not new to ecological plankton studies (Levin and Segel, 1976; Mackas et al., 1985; Wiebe et al., 1968), but in fact it is still hardly recognized and documented. The possibility to document and observe the patchiness has opened just recently, thanks to the high resolution automatic instruments such as underwater cameras, laser counters and acoustic methods (Davis et al., 2005; Geoffroy et al., 2017; Möller et al., 2012; Trudnowska et al., 2012, 2016). However, in most cases the patches of only one type or fraction of particles or plankton could be designated, mostly due to the methodological constraints, as every single method is limited to specific type/size of objects (Martin, 2003; Woodson et al., 2007). The simultaneous application of the

combination of various instruments, dedicated to different size fractions of particles and plankton, opens up the possibility of
traceability of the full composition of those 'cells of matter and life' (Forest et al., 2012; Lombard et al., 2019; Stemmann et
al., 2008; Szeligowska et al., 2020; Trudnowska et al., 2018). Moreover, such an approach gives an unique possibility to check,
if those patches are multi-fractioned or rather composed of monospecific size fractions. The existence of mono- vs. multi-
fraction patches are extremely interesting to explore further, whether those are randomly or physically gathered objects, or the
biologically rich hotspots that accumulated together in an active way.

A co-distribution of plankton and particles in marine realm is a derivative of many physical and biological processes
that all occur at different spatio-temporal scales (Mahadevan, 2016; Pinel-Alloul, 1995; Trudnowska et al., 2020a). As the
environmental conditions are typically not homogenous, especially in coastal regions, they must provide a mosaic of distinct
habitats that can be occupied by a characteristic set of particle types and plankton species. The attempts to study patchiness
patterns of particles and plankton patchiness together with underlying physical and biophysical fields suggested that the
observed heterogeneity at different spatial and temporal scales can be interpreted as the interactions between ocean turbulence
and predator-prey encounter rates (Lovejoy et al., 2001; Schmitt and Seuront, 2008; Seuront et al., 2001), or can be strictly
related to such physical features as ocean fronts and eddies (Durham and Stocker, 2012; Greer et al., 2016; Trudnowska et al.,
2016), vertical thermal stratification (Greer et al., 2013; McManus et al., 2005; Steinbuck et al., 2009), river input (Ehn et al.,
2019; Matsuoka et al., 2012), or the contact with sea ice (Trudnowska et al., 2018). Despite those numerous studies neither the
mechanisms favouring generation of patches, nor the processes underlying plankton distribution within patches, are yet not
clearly recognized (Menden-Deuer, 2012).

Although patches of particles and plankton are very common in marine systems, we know very little about their size,
composition and internal structure (Currie et al., 1998). To date, empirical measurements of particles and plankton patch
structures are still not carried out, as they require in-depth exploration with various dedicated techniques and sophisticated
approaches. All the more, the combination between the internal structure of the patches together with the framework for the
dominating forcing for marine particles and plankton to become accumulated and/or to actively accumulate are still the great
unknown. Those processes are especially complicated and dynamic in the Arctic fjord systems, where the advected warm,
saline and biologically rich Atlantic waters collide with the outflow of cold, fresh and turbid waters from the melting glaciers
(Halbach et al., 2019; Trudnowska et al., 2014, 2020a). Such strong hydrographical gradients set a perfect scene for both
horizontal and vertical partioning of water by both plankton and particles. It results in high spatial variability in distribution
patterns of particles and plankton and thus in spatial gradients in primary and secondary production (Piwosz et al., 2009;
Trudnowska et al., 2014). The inter-annual variability of the intensity of water advection is also an important driving force, as
it can even surpass the effect of local processes (Szeligowska et al., 2020). Indeed, the progressing "Atlantification" of west
Spitsbergen fjords is highly modifying the community compositions of protists (Kubiszyn et al., 2014; Smoła et al., 2017) and
zooplankton (Gluchowska et al., 2016; Trudnowska et al., 2020b), influencing finally the overall food web interactions in the
fjords (Csapó et al., 2021; Vihtakari et al., 2018; Węsławski et al., 2017).

65   In this study we answer the call for the insight studies at the interactions between ocean physics and ecology in structuring marine ecosystems (Lévy et al., 2018). We follow the patterns of patchiness of a wide spectrum of particles and plankton over several summer seasons in two Arctic fjords in order to ask a few crucial questions: 1) Does the distribution of particles and plankton patches differ over time and space? 2) How many percent of the water column is occupied by the patches of particles and plankton? 3) Are patches of various size fractions of particles and plankton co-occurring, and if yes - why?
70   (mechanistic vs. ecological hypothesis) 4) Does the internal structure of particles and plankton patches differ?

2 Methods

2.1 Study area

       To study thoroughly a patchiness of particles and plankton, we used 11 transects investigated in two fjords of the western Spitsbergen, Kongsfjorden and Isfjorden (Fig. 1). Surveys were performed yearly during summer (late July – early
75   August). In Kongsfjorden, transects either started from the very outer parts from the West Spitsbergen Current domain (2014, 2017, 2019) or from more coastal parts of the shelf (2015, 2016, 2018)(Fig. 1), and spanned towards the innermost glacial bay. The sampling in Isfjorden was much more consistent over years as exactly the same lengths of the transects over 2015 – 2019 summer seasons were investigated. However, they were restricted to the fjord's interior. Data from Kongsfjorden has not been published before, whereas the background measurements from the Isfjorden transect were recently published (Szeligowska et
80   al., 2020). Both fjords are characterized by the advection of Atlantic origin water in the outer parts and by the freshwater runoff of several glaciers and glacier-fed rivers in the inner parts. They both are treated as natural laboratories for international monitoring of Spitsbergen marine environment (Wiencke and Hop, 2016).
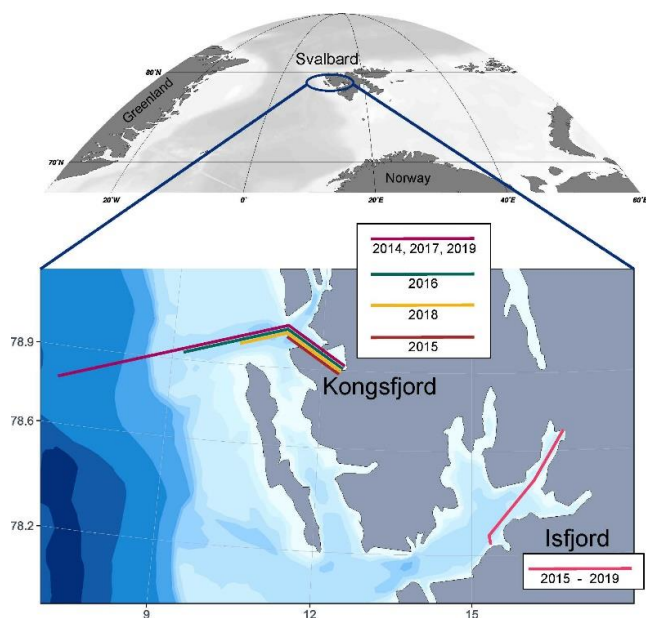

Figure 1: Map of the studied area: Kongsfjord and Isfjord (Svalbard). The ranges of transects in particular years are marked with colours.

2.2 Sampling

85

The high resolution measurements of wide size range of particles and plankton distribution were performed in an undulating mode between the surface and 50 m depth. The towed sampling platform was equipped with two laser-based optical counters: Laser In Situ Scattering and Transmissometry instrument (LISST-100X, type B, Sequoia Scientific, Inc., WA, United States) and a Laser Optical Plankton Counter (LOPC, Brooke Ocean Technology Dartmouth, Canada) and supplemented by a

90 conductivity-temperature-depth (CTD, SBE 911plus, Seabird Electronics Inc., United States) and a fluorometer (Seapoint Sensors Inc., United States) sensors. The concentrations of wide size range of particles and plankton (between 1 µm to 10 mm) were then summed over size-resolved fractions: Pico (1-3 µm), Nano (3-20 µm), Micro (20 – 200 µm), Small (200 – 500 µm), Medium (500 – 1 000 µm) and Large (1 000 – 10 000 µm).

2.3 Calculations and visualizations

95

Data were gridded over 1-m depth intervals and over 0.05 longitude for patches assignment and over 0.2 longitude for size spectra calculations. Size spectra were analysed as the regression fitted to the concentrations normalised to the widths of the size classes in the log-log space. Data points assigned as 'patches' were the ones that had higher concentrations than background (mean abundance + sd). The background was calculated separately for each transect. Therefore, the patch threshold is fjord- and year-specific. Individual patches were designated by the 2D kernel density estimation ('stat_density_2d' function

100 in R) applied to data points assigned as 'patches'. Then, the individual patches were selected from each other by the hierarchical clustering ('res.hc' function of "factoextra" package in R) of their x-y coordinates to group together only data points that lay close by and to eliminate the singular outlier observations.

Indices of the spatial heterogeneity (Lloyd's crowding index, Lloyd's patchiness index) were calculated according to the previously published formulas (Pinel-Alloul, 1995). These indices are related to the variance (s2) and the mean (m) of

105 particles and plankton concentrations, and are based on the assumptions of the Poisson random distribution model, which corresponds to spatial homogeneity and variance to mean ratios.

Because quite different environmental conditions and spatial coverage of sampling concerned both studied areas, we decided to analyse the statistical trends separately for individual fjords. We analysed the cross correlations between patch characteristics (depth range, horizontal length, area, size spectrum), environmental settings (temperature, salinity, chlorophyll),

110 spatial heterogeneity indices (logarithms of variance/mean ratio, Lloyd's crowding and patchiness indices), and concentrations of particular size fractions of particles and plankton (log10()). In the dbRDA model we divided the explanatory variables into three groups: i) spatial (depth and horizontal part), ii) environmental (temperature, salinity, chlorophyll), and iii) size (vertical extension and area). We also tested over which ranges of those explanatory variables specific types of patches emerged by a density function of their occurrence.

115   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, R.; 2018. Ocean Data View, https://odv.awi.de). The other plots were made in R via the "ggplot" package.

3 Results

3.1 Distribution patterns

120   In Kongsfjorden, the cores of the warmest water (8°C) were localized far offshore and were distributed vertically even up to 40 and 50 m depth in 2014 and 2017, respectively (Fig. 2). Such a high seawater temperature was observed in the upper 20 m layer over most of the transect in 2019. and inside the fjord in 2015 and 2016 (Suppl. Fig. 1). A strong signal of cold (< 5°C) glacial meltwaters was observed in the surface 10-m layer of the innermost parts of the fjord each year except for 2019. However, in none of the studied seasons the pattern of hydrographical structure had any obvious reflection on the

125   distribution patterns of particles and plankton (Fig. 2 & Suppl. Fig. 1). The peaks of chlorophyll fluorescence were associated with concentration hotspots of the Nano, Micro and Small size fractions in 2014 and 2017, and only with the Nano fraction in 2016 and 2019. The Pico fraction was mostly concentrated near surface (upper 5 m) and over wider depth range only close to the glacier front. In the majority of cases very high concentrations of all particle and plankton size fractions were observed at the end of the transect, which was located in the glacial bay (Fig. 2 & Suppl. Fig. 1). The Medium and Large size fractions

130   were mostly decoupled in space with both chlorophyll fluorescence and other, smaller size fractions, apart from the glacial front parts. A distribution pattern was quite similar between Medium and Large size fractions in most investigated seasons, but totally different in 2015 and 2019, when Medium fraction was mainly concentrated in the lower, innermost part of the investigated transect, while Large fraction was scattered in form of small but numerous patches in a fjord and its entrance. Interestingly, in 2015 the Large size fraction was the only one which distribution reflected clearly the distribution of

135   chlorophyll fluorescence.

        In Isfjorden, the highest seawater temperatures were recorded in the upper 20 m layer, while the lowest were observed below 40 m at the end of the transect, near the glacier front (Fig. 2 in Szeligowska et al. 2020). Along this transect a shallow submesoscale eddy (approximately a few kilometres of diameter) was observed in 2016, 2017 and 2018. It was associated with a discontinuity of the chlorophyll fluorescence concentration peaks. In general, the fluorescence of chlorophyll was restricted

140   to the upper 20 m layer. Similarly as in Kongsfjorden, the hydrographical structuring and distribution pattern of chlorophyll fluorescence peaks had no obvious reflection on the distribution patterns of particles and plankton (Fig. 3 in Szeligowska et al. 2020). The high spatial compatibility was observed between Nano, Micro and Small size fractions in 2017 and 2018. The concentrations of all size fractions were much higher in 2018 than in other studied years.
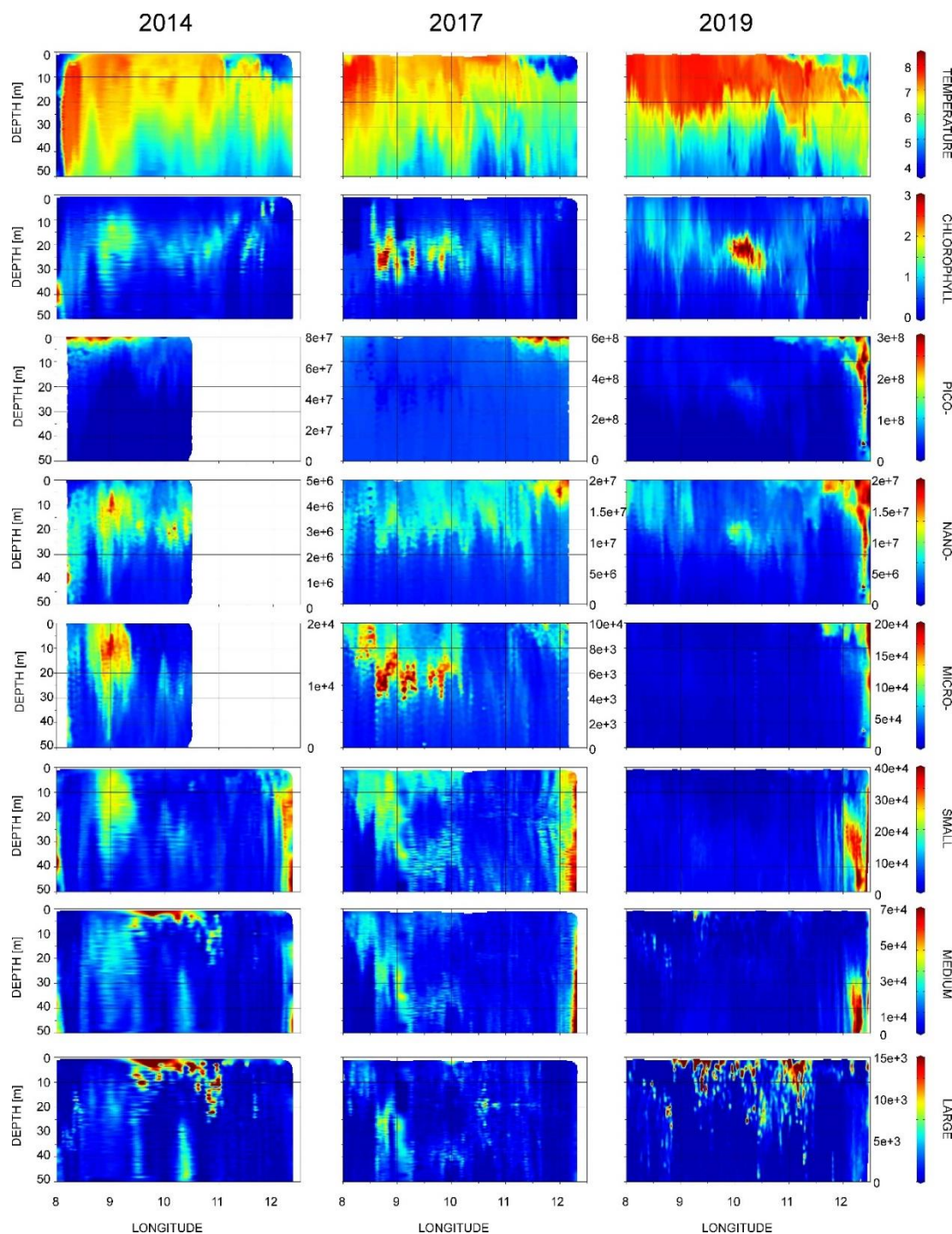
5

Figure 2: The section plots of the three exemplary years sampled in Kongsfjorden, presenting high resolution distribution of temperature, chlorophyll fluorescence and abundance of particles and plankton divided into six size fractions: Pico-, Nano-, Micro-, Small, Medium and Large.

3.2 Size spectra over time and space

In most cases a good compatibility between size spectra of LISST and LOPC measurements was observed (Suppl.
150   Fig. 2). The small divergence between the concentrations obtained by the two methods within the corresponding size fractions
was observed in 2018 in both Kongsfjorden and Isfjorden by the higher values provided by LISST.

In Kongsfjorden, the size spectra slopes differed significantly among years (2-way ANOVA, F = 27.8, p < 0.001) and
sub-regions (F = 5.0, p = 0.001). Also the interaction between the factor of Year and Region was statistically significant (F=2.7,
p=0.004). In general, flatter size spectra slopes were recorded during the first three years of the study and the spectra tended
155   to get steeper over time towards the last studied years (Fig. 3a). Especially flat size spectra slopes were recorded furthermost
offshore in 2014 and in the fjord's entrance in 2014 and 2015. The steepest particles and plankton size spectra were recorded
inside the fjord in 2018 and 2019.

In Isfjorden, the size spectra slopes differed significantly among years (2-way ANOVA, F = 64.67, p < 0.001), only
slightly among sub-regions (F = 5.46, p = 0.002), but the interaction between the factor of Year and Region was not statistically
160   significant (F=2.1, p=0.037). Flatter size spectra slopes were recorded in 2015 and 2017. The trend of spectra getting steeper
over time was observed over 2015-2016-2018 and 2017-2019 (Fig. 3b). The steepest particles and plankton size spectra were
recorded in 2018.
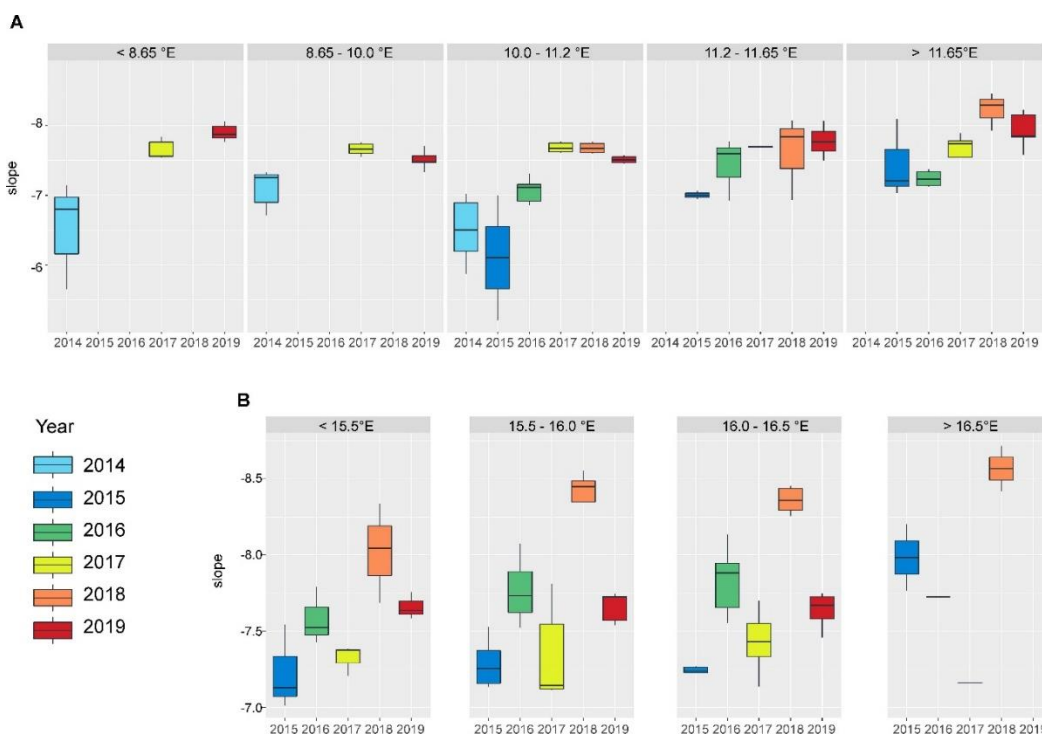
Figure 3: The box plots of size spectra slopes over inter-annual and spatial (over longitudinal steps) variability in A:
165   **Kongsfjorden and B: Isfjorden.**

7

3.3 Patch characteristics

The data points assigned as patches represented the minority of the studied space (the overall mean 12%)(Table 1). In Kongsfjorden, patches occupied slightly smaller fraction of data points, ranging from 1 to 22 % (12% mean), while in Isfjorden patches occupied from 5 to 25% (13% mean) of data points. Because of the extremely high concentrations of particles
170 and plankton near glacier front in Kongsfjorden in 2015 and 2018, only very few data points of the three smallest size fractions were assigned there as 'patches' (Table 1).

Table 1. Percentage of the data points representing patches of particular size fractions in subsequent summer seasons.

	Size fraction	2014	2015	2016	2017	2018	2019
Kongsfjord	Pico	15	1	12	6	2	6
	Nano	16	2	7	18	4	13
	Micro	15	2	10	11	5	7
	S	12	18	13	21	22	9
	M	20	8	8	19	17	5
	L	10	12	8	15	14	9
Isfjord	Pico		12	13	16	5	8
	Nano		13	17	21	14	25
	Micro		8	10	13	18	5
	S		11	10	17	21	9
	M		7	8	11	15	10
	L		11	9	14	14	13

On average, the concentrations within patches exceeded the background (mean + sd) by a factor of 1.6 (Suppl. Table).
175 This was slightly greater for the three smallest size fractions (1.8 in Kongsfjorden and 1.5 in Isfjorden) than for the larger size fractions (1.5 in Kongsfjorden and 1.4 in Isfjorden).

Each year, the highest concentrations of most of the size fractions were observed in recurring patches in the innermost part of the fjord (Fig. 4a). In most cases the patches of the Pico, Micro and Small size fractions occupied the whole investigated depth range at the end of the transect. The Pico fraction patches were mostly confined to the upper 10-m depth layer, but their
180 location was not repetitive over studied years (Fig. 4a). The huge Nano fraction patch was extended over the whole transect in 2017, with deeper location offshore and shallower inside the fjord. The patches of the Micro and Small size fractions were located either offshore or inside the fjord, but none at the entrance to the fjord (10-11°E). The Large size fraction had the

highest number of patches and demonstrated the most variable distribution pattern among all studied fractions in Kongsfjorden

(Fig. 4a). The similar, offshore location of Micro, Small and Medium size fractions was observed in 2014 and 2017, and of

185   Nano and Large size fractions between 2014 and 2019, which resulted in the multi-fraction patches occurring offshore in 2014

and 2017 and in most of the studied seasons at the end of the transect (Suppl. Fig. 3a).
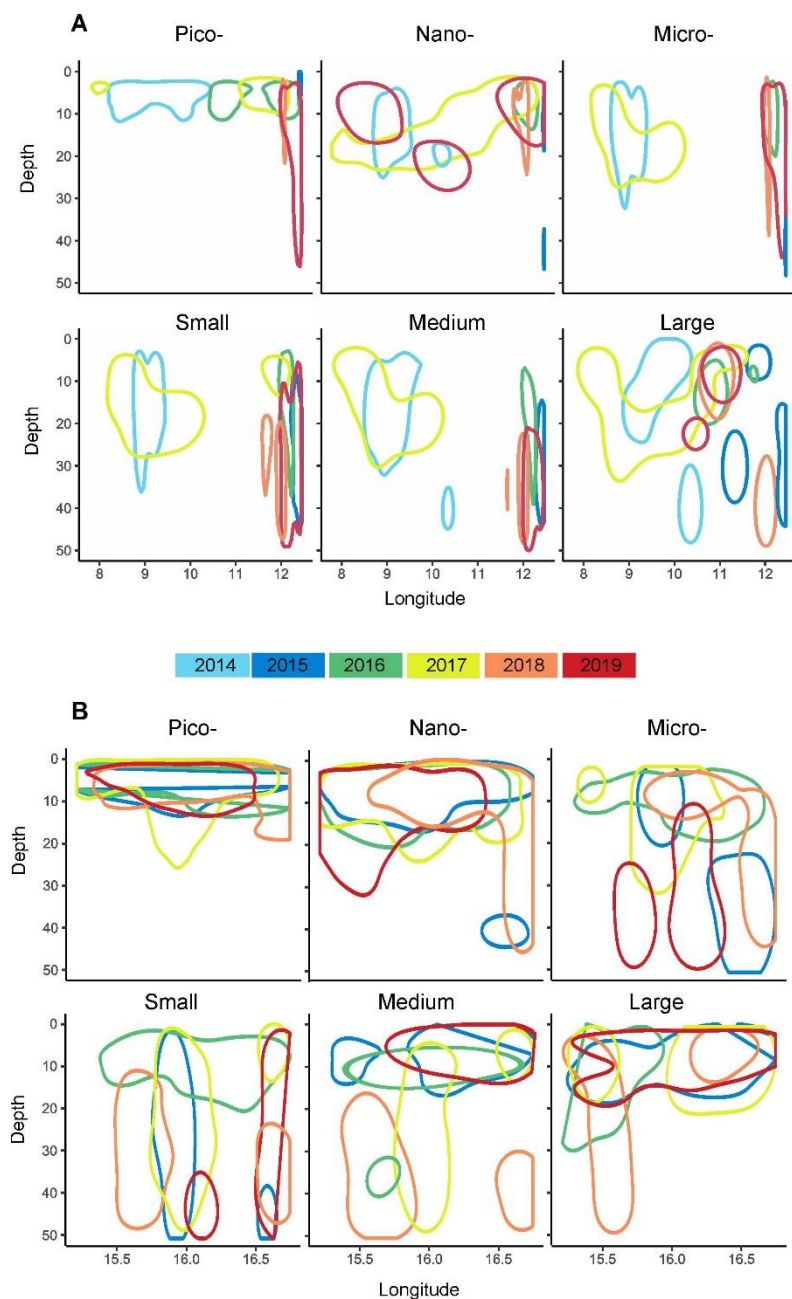

Figure 4: Distribution of patches of particular size fractions (separate panels) in particular years (colours), using function stat_density_2d. A: Kongsfjorden, B: Isfjorden

190   In Isfjorden, Pico patches were mostly confined to the upper 10 m layer and extended over the whole investigated transect, while Nano patches were mostly concentrated in the upper 20 m layer (Fig. 4b). In some years patches of the Micro, Small and Medium size fractions were located also in deeper parts of the investigated water column (e.g. Nano, Micro and Small fraction in 2014; Small, Medium and Large fractions in 2018). Interestingly, the effect of the glacier influence at the end of the transect was reflected mostly by the distribution pattern of just the Small size fraction, and only in 2018 also by

195   peaks of the Nano and Micro size fractions (Fig. 4b). The patches consisting of two and three size fractions were most common in Isfjorden in 2017 and 2018 and were spreading over substantial part of the studied water column, while multi-fraction ones occurred sporadically in the very upper water layers (Suppl. Fig. 3b).

        Overall, we distinguished 94 patches, and when analysing them we realized that they differ significantly in their shapes and structure, depending on the fact, where their core was located. In consequence, we distinguished 7 functional types

200   of patches : Belt, Triangle, Diamond, Flare, Fingers, Flag, and Rosette (Fig. 5). Each analysed patch was ascribed to specific type and the location of its core (the highest kernel density situated either in the central part, on the border, or in the corner). The most common shapes of the designated patches were the Flare (19%) and Triangle (18%) types (Suppl. Table). Belt and Diamond (15% of patches each) were the second dominant types. Belt and Flag (12% of patches) were mostly observed in the innermost parts of both transects. Many patches (34%) had their cores in the central parts (especially Diamond and Rosette

205   (11 % of all patches) types). In other cases they had their cores near surface (23% with upper corner and 15% with upper border), occasionally also at the bottom of the patch (9 cases), or did not have any obvious centre of aggregation (15 cases)(Suppl. Table).
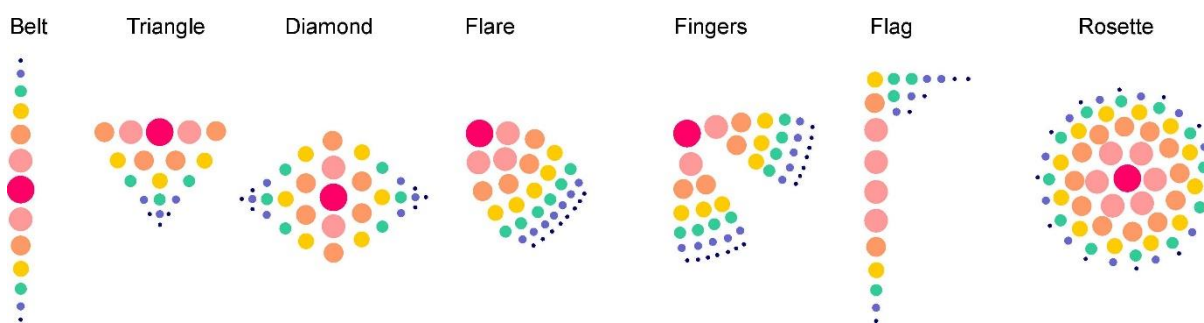
Figure 5: Types of patches basing on their shape, structure and the location of the Kernel density.

210

        We distinguished 8 patches of the Pico fraction in Kongsfjorden (mostly near glacier) and 5 patches of this fraction in Isfjorden (mostly extending through the surface of the whole transects) (Supplementary Table). They were generally small (on average 0.3, min. 0.1, max 0.7 km^2), mostly in a shape of a Triangle or Flare, and characterized by very steep size spectra slopes of the LISST measurements (on average -8.9), but of rather flat slopes of LOPC measurements (on average -7.4). The

215   Pico fraction patches were associated with low values of chlorophyll fluorescence, especially in Kongsfjorden (on average 0.19).

There were 8 patches of the Nano fraction distinguished in Kongsfjorden and 6 in Isfjorden. They were situated in the innermost as well as in the central parts of the transects. Patches of the Nano fraction occasionally extended over large areas (up to 2.8 km^2, 0.7 km^2 on average) and occurred in a high diversity of shapes (the mixture of Triangles, Flares, Diamonds

220   and Rosettes) (Supplementary Table). Similarly as patches of the Pico fraction, they were characterized by steep size spectra slopes of the LISST measurements (on average -8.7), but of rather flat slopes of LOPC measurements (on average -7.5). The Nano fraction patches were associated with elevated values of chlorophyll fluorescence, especially in Kongsfjorden (on average 0.67).

There were 6 patches of Micro fraction designated in Kongsfjorden (among which 4 in the innermost part) and 9 in

225   Isfjorden (mostly in the central parts of the transect) (Supplementary Table). Only 3 of them were larger (0.8, 1.0, 1.4 km2) than the overall mean (0.5 km^2). The most frequent Micro patches were in the shape of Belt and Diamond. In Kongsfjorden they were mostly characterized by flat size spectra slopes (-8.0), while in Isfjorden by steep ones (-8.9). Only two of the Micro fraction patches were characterized by the high chlorophyll fluorescence (approx. 1), while most of them were associated with low chlorophyll (on average 0.25).

230   Among 17 distinguished patches of the Small size fraction, 8 were found in Kongsfjorden (mostly located in the inner glacial bay). They were of rather medium size (on average 0.6 km^2) and in a shape of the Flag (Supplementary Table). The size spectra slopes of the particles and plankton found within the patches of the Small size fraction were flatter in Kongsfjorden (-8.1) and steeper in Isfjorden (-8.6) than the overall mean. Similarly as for the Micro fraction, only two patches of Small size fraction were characterized by the high chlorophyll fluorescence (approx. 1), while most of them were associated with low

235   chlorophyll (on average 0.20).

Overall, 17 patches of the Medium size fraction were distinguished, among which 8 were found in Kongsfjorden, where they were characterized by extremely steep size spectra slopes in 2014 and 2015 (-10.2) and of moderate slopes in the other years (on average -8.2) (Supplementary Table). They either covered large areas (>1.5 km^2), or were really small (on average 0.2 km^2), and represented mostly shapes of Fingers, Diamonds or Flares. In Kongsfjorden, the patches of the Medium

240   size fraction were typically associated with waters of the elevated salinity.

We distinguished 18 patches of the Large size fraction, half of which was larger than the overall mean. The most frequent shape of the Large size fraction was Flare (Supplementary Table). They had various localizations of the occurrence. They were characterized by the relatively flat size spectra slopes in Kongsfjorden, (-7.51 on average), and steeper ones in Isfjorden (-8.48 on average), resulting in rather large mean size of the particles (2.4 μm), especially detected by the LOPC

245   (240 μm). In Kongsfjorden they were associated with rather high salinity waters (34.14), while in Isfjorden with fresh waters (31.84). In both fjords they occurred in waters of the elevated chlorophyll fluorescence (0.5).

The highest ratio between the variance and mean concentrations and thus the highest values of indices of spatial heterogeneity were observed in the patches of the Pico size fraction and the values of all the indices clearly decreased with size (Fig. 6). The largest difference was observed between the Nano and Micro size fractions, whereas only subtle decreasing

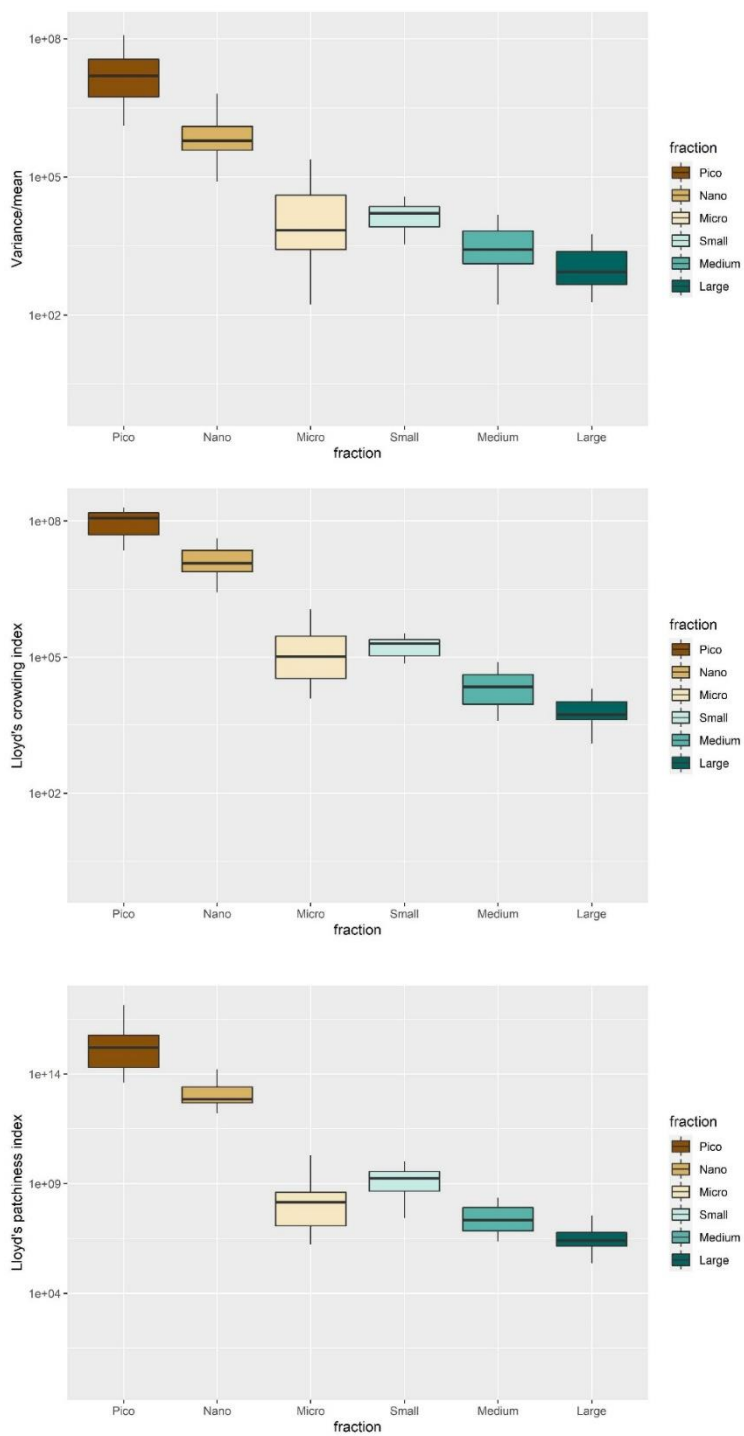250   trend was observed for the larger size fractions.

Figure 6: Mean indices of spatial heterogeneity applied to patches of specific size fractions of particles and plankton.

3.4 What correlates with patches?

255 Some types of the patches frequently occurred in the very narrow temperature ranges, e.g., numerous Belt patches of the Pico
fraction were observed in relatively cold (4°C) water while many Flag patches of the Nano fraction were occurring in relatively
warm (6°C) water (Fig. 7a). A domination of the Belt patches within water temperatures of 4-6 °C was also observed in the
case of the Small and Large size fractions. Triangle patches were more common in warm waters, especially in the case of the
Micro and Large size fractions. Diamond patches of the Small, Medium and Large size fractions were mostly confined to the
260 higher salinity (34) waters (Fig. 7b). The other salinity-specific types of the patches were: Belt type in the case of the Pico
fraction (two peaks between 32 and 24), Rosette type of the Nano fraction (observed only in the salinity of 35), and Flare type
of the Micro fraction patches (frequently present in waters with salinity slightly higher than 33). Similarly as in the case of the
temperature, the Belt type of the Pico fraction and the Flag type of the Nano fraction patches were restricted to the very narrow:
low (0.15) and relatively high (0.35) chlorophyll ranges (Fig. 7c). The other patch types specific to low-chlorophyll levels
265 were: Belt (Micro and Medium size fractions), Flare (Micro fraction), Diamond (Small and Medium size fractions), and Flag
(Small fraction). Contrary, the Triangle and Diamond types of the Large size fraction patches occurred mostly in water with
elevated chlorophyll.
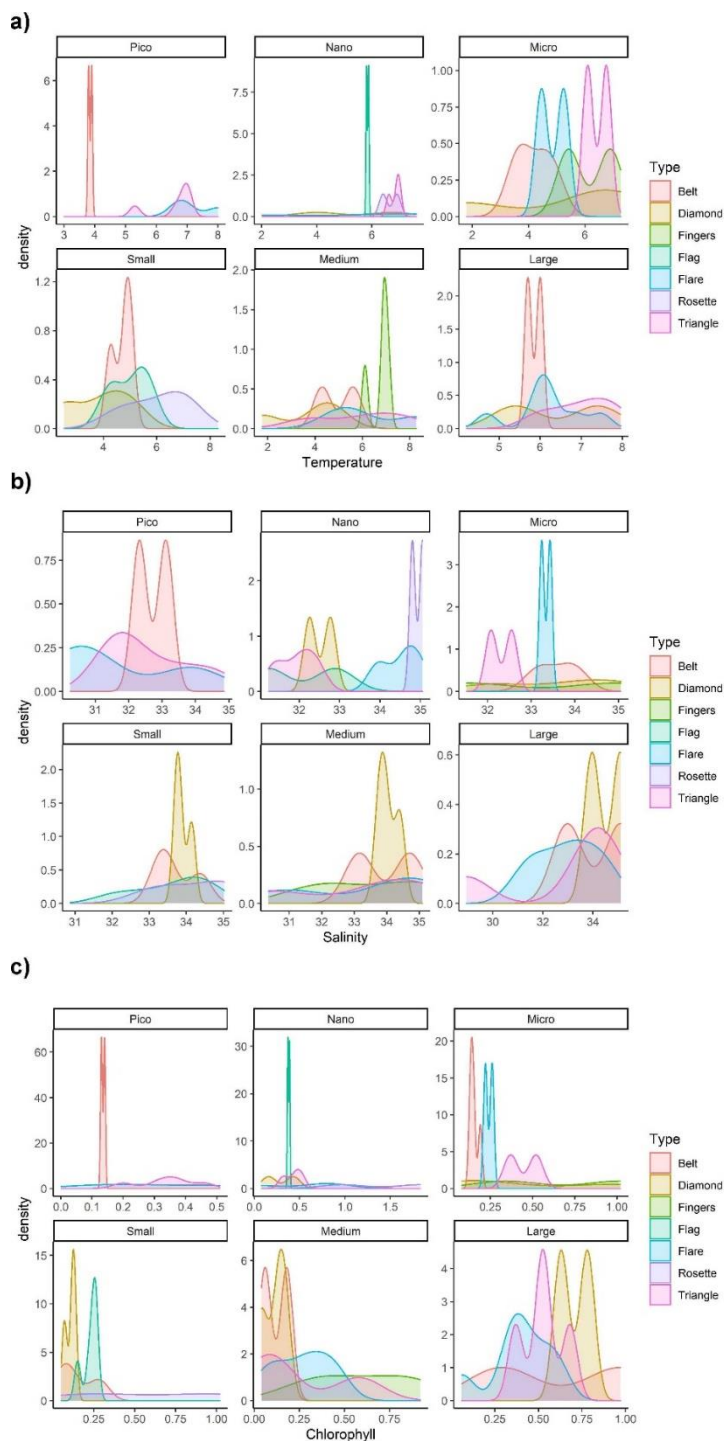
Figure 7: The frequency of occurrence of various size fractions and types of patches over environmental settings of water: a) temperature, b) salinity, and c) chlorophyll.

14

In Kongsfjorden, water temperature and chlorophyll correlated negatively with concentrations of all size fractions except the Large one (Fig. 8). Low salinity was favourable only for the Pico, Nano and Micro size fractions. Higher water
275   temperature, salinity and chlorophyll enhanced the formation of the larger patches (significant positive correlations with their size), but with lower indices of spatial variability (Fig. 8). In Isfjorden, a different pattern of significant correlations between patch parameters was observed, with almost no correlations found with spatial heterogeneity indices and only few significant relations with environmental settings (e.g., Micro, Small and Medium size fractions correlated negatively with water temperature and chlorophyll, whereas the Pico and Large size fractions correlated negatively with salinity and positively with
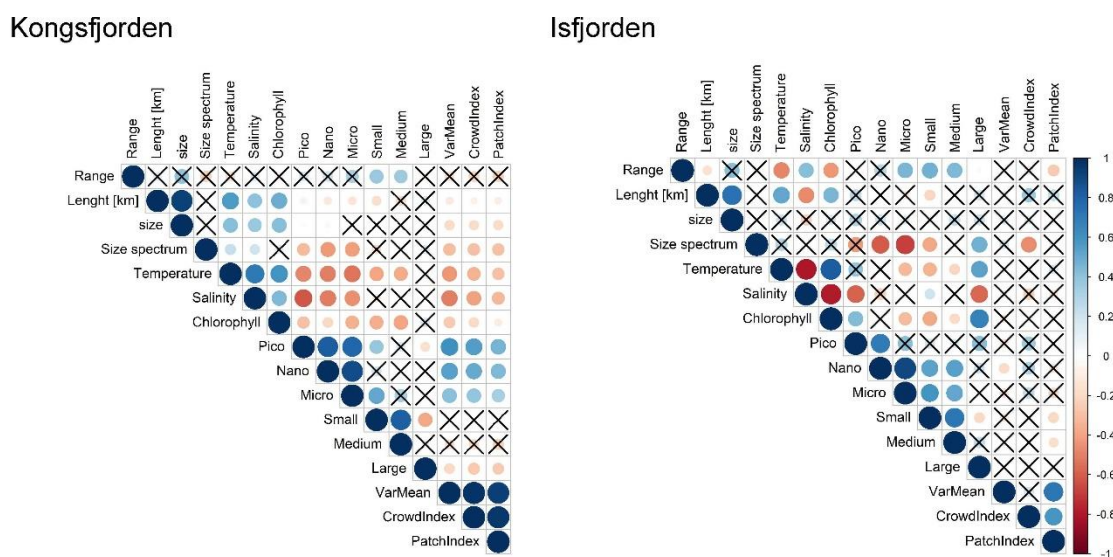280   chlorophyll (Fig. 8)).

Figure 8: Correlations between patch characteristics (depth range, horizontal length, area, size spectrum), environmental settings (temperature, salinity, chlorophyll) and spatial heterogeneity indices (logarithms of variance/mean ratio, Lloyd's crowding and patchiness indices), and concentrations of particular size fractions of
285   **particles and plankton (log10()) in two investigated fjords (Kongsfjorden and Isfjorden). Non-significant (p > 0.005) correlations are marked with X.**

In both regions approximately half of the variation in size-resolved particle and plankton concentrations was explained by the studied patch characteristics (51% in Kongsfjorden and 45% in Isfjorden)(Fig. 9). In Kongsfjorden, the most important
290   factor in the model of all the explanatory variables considered together, was location of the patch (34% of variation), whereas in Isfjorden the environmental variables explained the highest amount of the observed variation (21%). However, when running the separate models for the individual sets of the parameters, it turned out that in Kongsfjorden the environmental variables explained almost the same percent of the observed variation (29%) as spatial constraints (33%)(Fig. 9). The fact that the location of the patch (if in the glacial bay, main fjord or offshore waters) was more significant in Kongsfjorden than in Isfjorden
295   is not surprising as different spatial scales and environmental ranges were studied in both fjords.

Kongsfjorden

Isfjorden
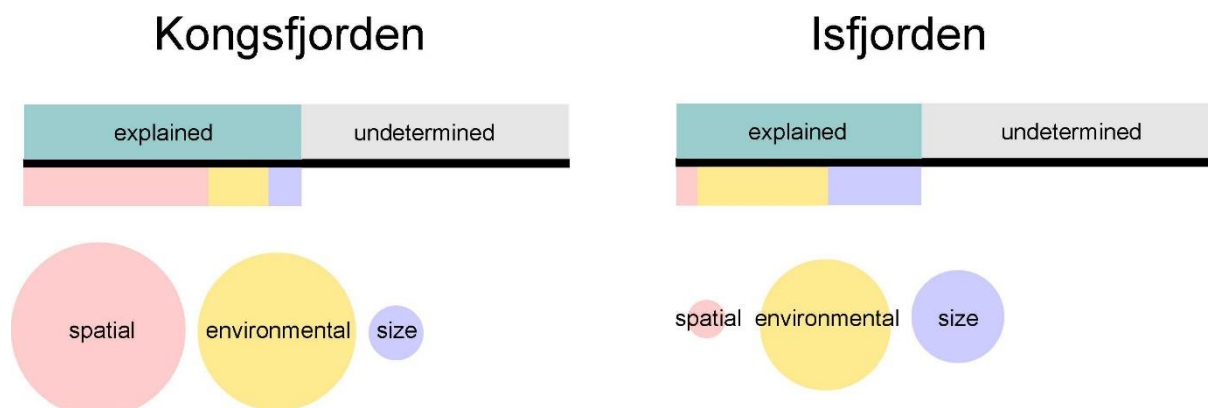
Figure 9: A schematic presentation of the RDA results. The bars indicate to the percentages explained by studied patch characteristics, when all explanatory variables were considered together, whereas the size of the circles indicates their roles in the independent analyses of the spatial patch locations (vertical and horizontal coordinates of patch presence), environmental settings (temperature, salinity, chlorophyll), and size of the patch (vertical range and area).

4 Discussion

4.1 Multiple agents are shaping the patterns of patchiness

The patchy distribution of particles and plankton is a derivative of a complex set of multi-stage and multi-dimensional processes. First, to build a patch, the plankton organism and/or a particle has somehow get to the place, or to be produced there. Then, it has to sustain at a certain depth layer (if it is a motile plankton it may migrate to the favourable layer, if it is a particle its buoyancy decides), where it interacts with other organisms/particles (e.g. it can be eaten or it has to feed itself). It may also become aggregated (e.g. by the mucous produced by phytoplankton) as disaggregated (e.g., by wave action or sloppy feeding). Meantime, some independent processes, as e.g. wind/tidal mixing or any other unpredictable trajectories of water circulation, may relocate it, either individually, or with the entire lens of objects. At each step of its residence in a given parcel of the water several agents**,** representing the physical and biological forces, are acting simultaneously (Martin, 2003; Pinel-Alloul, 1995) and the interactions among them often result in an overlaid effect (Borcard et al., 1992; Borcard and Legendre, 2002; Levin and Segel, 1976), seriously complicating our understanding of their distribution patters. Even though we extended our comprehension of patchiness phenomenon by analysing thoroughly 94 patches of various size fractions of particles and plankton that existed in comparable environmental conditions (two Arctic fjords) over several years of the study, it still remains an ambiguous matter when, why, and which of the mechanisms (mechanistic vs. ecological) prevails in shaping the patterns of particles and plankton distribution. Since no explicit conclusions could be made, this study rather opens up new gates for further research providing some initial in-depth observations than provides the final solution to the puzzle.

Biogeosciences
Discussions
Open Access
EGU

4.2 The interplay between local and oceanic processes

320   Traditionally, the variance related to the distribution patterns of patches was partitioned into effects of local environmental gradients, spatial structure and undetermined variance (Pinel-Alloul, 1995). To make matters more complicated, the dominating mechanisms vary depending on the scale, location or time of the year (Martin, 2003), e.g., the relative importance of the biotic processes increases inversely with scale (Pinel-Alloul, 1995), because the physical processes act naturally at different timescales than plankton growth and activity (Mahadevan, 2016). Also the local processes and ocean

325   circulation operate on very different scales, making it extremely difficult to elucidate their relative contributions on particles and plankton distributions (Kuhn et al., 2019). In the case of the patches analysed in this study, the local environmental variables were the most crucial in the case of the fjord, where smaller spatial scale was investigated (Isfjorden), whereas the spatial effect was privileged when the larger distance and thus wider spectrum of environments was considered (Kongsfjorden). However, as both fjords are opened and prone to intensive Atlantic water advection, which definitely re-shapes plankton

330   communities (Basedow et al., 2004; Kubiszyn et al., 2014; Skogseth et al., 2020; Trudnowska et al., 2020b), this large scale oceanic circulation process is of importance in both studied regions. Whereas as the dominating local process the influence of melting glaciers was clearly recognized, resulting in the recurring high particles and plankton accumulations in the innermost glacial bays, which is typical for the summer melting period (D'Angelo et al., 2018; Kanna et al., 2018; Meire et al., 2017; Szeligowska et al., 2020; Trudnowska et al., 2020a). Since the summertime in the Arctic is also a time of intense biological

335   production and plankton activity (Kubiszyn et al., 2017; Svensen et al., 2019; Trudnowska et al., 2014), the local ecological selection must have also been acting, playing important role in shaping the observed patchy distribution patterns and high concentrations of plankton.

4.3 Mechanistic vs. Ecological hypothesis

    Simultaneous, fine-resolution measurements of undulating sampling platforms equipped with laser counters advance

340   our so far limited insights of both the physical processes and associated biological distributions (Basedow et al., 2014; Szeligowska et al., 2020; Trudnowska et al., 2014), and thus improve our understanding of the mechanisms included in habitat partitioning by various fractions of particles and plankton (Currie et al., 1998; Greer et al., 2015). However, as only half of the variation was explained by the studied explanatory variables, the considered relations turned out to be much weaker than intuitively expected, pointing towards the interference of some other driving forces. Those were either mechanistic constraints

345   that could not by detected by hydrographic measurements, or some ecological interactions that are in general immeasurable. In a biological context, the favourable character of the local community is shaped by a great variety of aspects that determine the type, diversity and relative availability of potential mates, food sources, predators, and competitors (Mackas et al., 1985). The other argument towards the importance of the other, local dynamics of populations is that, again contrary to the expectations, the development and persistence of patches was not strictly associated with the existence of strong environmental

350   spatial gradients observed in both fjords. The determined by us environmental cues (temperature, salinity, chlorophyll),

explained only 20-30% of overall studied variation. Therefore the controversially exploited statement that below 1-mm body size "everything is everywhere, but the environment selects" (Finlay, 2002; De Wit and Bouvier, 2006) is most probably overrating the influence of the environment. Our results show that particles and plankton are not purely dye-like passive tracers of advection and/or local hydrographical water structuring. Moreover, as shown by differences in the correlations strengths

355 and directions between the two studied regions, it is important to note that the correlations may have only short term and local validity.

If we were to depict the dominating source of the biological forcing, the only factors we could measure are the chlorophyll fluorescence levels and cross-correlations among size fractions. Because only the concentrations of the Large size fraction correlated significantly with chlorophyll just in Isfjorden, this indicates that in general the concentration hotspots of

360 smaller size fractions of particles and plankton were not strictly phytoplankton-specific and that we could rather observe the relationship between herbivorous grazers (as the Large fraction is mostly represented by *Calanus* copepods (Balazy et al., 2018, 2019)) and food availability (expressed as high chlorophyll levels). The spatial compatibility of distribution patterns of various size fractions resulted in a multi-fraction form of patches, which in general were not associated with any specific hydrographical structure, which points towards the ecological hypothesis, e.g. in form of a mechanism of gathering in the

365 concentration hotspots of the potential prey (Holliday et al., 2003). But despite the high degree of correlation between spatial patterns of the neighbouring size fractions, the combinations of pairs/groups of the corresponding size fractions was very variable, which indicates that under some conditions there were in force mechanisms favourable for a specific set of particles or plankton fractions, but absolutely neutral or unfavourable for other fractions.

Regardless of the mechanisms shaping the patterns of particles and plankton patchiness, their location was not

370 repeatable in subsequent years on the same transects, except for the recurring feature of high concentrations observed near glacier fronts. The patches varied clearly among years either in terms of their position, size, shape, and structure. They occupied the minor part of the studied water column (on average 12%, ranging from several percentages up to 25%), which is of similar order as observed on the west Spitsbergen shelf (2-17%, (Trudnowska et al., 2016)), and in East Sound fjord in USA (12% (Menden-Deuer, 2012), but much less than observed in St. Lawrence Estuary in Canada (80% (Currie et al., 1998).

375 **4.4 Size structure of particles and plankton**

The trend of an increasing role of the smallest size fractions (steepening size spectra slopes) over years was consistent in the two studied regions, at least until 2018. Such shift in plankton size structure towards the proliferating importance of Pico fraction is now a widely recognized effect of the progressing climate warming in the Arctic (Li et al., 2009; Metfies et al., 2016; Nöthig et al., 2015). Meanwhile, the steepest size spectra slopes observed in 2018 could be related also to some other,

380 albeit various mechanisms: e.g., the resuspension of sediments or disaggregation of marine aggregates due to the stormy weather, activity of eddies, or by the observed bloom of *Phaeocystis pouchetii* and high concentrations of copepods nauplii, as observed in Isfjorden (Szeligowska et al., 2020). The observed spatial and inter-annual variability in size spectra must have shaped different states of the pelagic communities, as probably were driven by the shifts in dominating size fractions of

particles and plankton. Indeed, the switched relative roles between Pico and Nano fractions were observed in Kongsfjorden in

385   2017 in form of the preference of the Pico fraction for regenerated nitrogen and a higher proportion of the Nano fraction in the relatively cold and turbid surface water in the inner basin (Kim et al., 2020). Differences in size structure may also indicate differences in particles and plankton phenology, as a result of e.g., the seasonal succession from larger diatoms to smaller dinoflagellates, meroplankton blooms or different developmental stage composition of the dominating copepods (Balazy et al., 2019; Szeligowska et al., 2020; White et al., 2015).

390   We expected that the planktonic food web structure inside the glacial fjord will be clearly different from the one outside, as often observed in Arctic regimes (Tang et al. 2011), but size spectra approach applied in this study does not confirm so. Moreover, an effect of the glacial/riverine inputs on the laser-derived size spectra in comparison to the offshore waters was much weaker than expected and observed in other studies (Trudnowska et al., 2014, 2020a; Xi et al., 2014). The observed higher variability in particle size distribution over time than over space was indicated also by others (D'Angelo et al., 2018;

395   Jouon et al., 2008; Szeligowska et al., 2020), which suggests that particles remain similar over relatively large spatial scales, but differentiate with years and/or seasons.

The other interesting feature to analyse is the relation between abundance and body size and its role played in determining the formation of patches. The observed by us extension of the patches of the smaller size fractions was frequently much wider than of the larger ones, which agrees with the rule that dispersal scales show a negative correlation with body size,

400   where less abundant large-bodied communities have significantly shorter dispersal scales than more abundant small-bodied plankton (Villarino 2018). We observed also a clear negative trend between size and all the indices of spatial heterogeneity applied, where the smaller the size fraction the higher the crowding/patchiness index was, implying that not only the spatial extension is wider for smaller fractions, but also their gathering rates are greater.

4.5 Patch structure

405   As shown by the very first studies of patchiness, the abundance patch does not necessarily coincide with the same compositional patch, as it may be formed either by a bloom of a different species or a group of species (Mackas, 1984), resulting in a taxonomically heterogeneous patches (Greer et al., 2016). We may only assume that the observed by us patches differed compositionally, basing on highly different parameters describing size spectra of particles and plankton within the patches, even of the same size fractions, and our general ecological knowledge of the plankton composition observed during

410   summer in studied regions. The planktonic dominants representing the particular size fractions may vary in both studied regions depending on the year and season, but typically dinoflagellates (Bhaskar et al., 2020) or diatoms (Piwosz et al., 2009) dominate the summer community structures of protists in Kongsfjord, while *Phaeocystis pouchetii* dominate in Isfjord (Kubiszyn et al., 2017), together with Cryptophytes and Ciliates (Szeligowska et al., 2020). Zooplankton in turn is mainly dominated in both fjords by copepods, such as *Oithona* and *Calanus* (Gluchowska et al., 2016; Hop and Wiencke, 2019; Szeligowska et al., 2020;

415   Trudnowska et al., 2020b). Phytoplankton patches are expected to be more monospecific than zooplankton ones (Mackas, 1984). Also the spatial patterns are different between patches of phytoplankton and zooplankton (Mackas et al., 1985), and

Biogeosciences
Discussions

between different size classes of those (Kuhn et al., 2019; Trudnowska et al., 2016), which may explain why we observed different distribution patterns of various size fractions (e.g. the Pico fraction was mostly confined to the upper few meters while having wide horizontal distribution, whereas the Micro and Small fraction patches extended frequently over wide vertical

420   ranges, but had much smaller horizontal range).

Among the fundamental problems facing studies of patchiness are concerns how to properly detect, designate, define and describe individual patches. While the first two challenges are now well resolved by new *in situ* technologies and calculation possibilities, the portrayal of the patches has mostly been limited to the information about the particles or plankton concentrations and spatial extension of those hot spots (Brentnall et al., 2003; Greer et al., 2016; Pinel-Alloul, 1995;

425   Trudnowska et al., 2016), and assumed a circular patch structure to calculate patch area and other properties (Currie et al., 1998). Hence, so far we know almost nothing about the internal structure of the patches! Inspired by the comment that patches observed at a given spatial resolution may, on examination at a higher resolution, be seen to be patchy themselves so that there may be a kind of hierarchy within patches (Pinel-Alloul, 1995), we analysed each patch individually, by focusing on the isolated patches and 'mapping' their internal structures. Even though some older observations imply that plankton is totally

430   randomly distributed within patches (Currie et al., 1998), in most cases we could clearly depict the core (kernel density) of particular patches. Consequently, we propose a novel classification of patches, depending on their shape the location of their cores (either in the central part, in the corner or at the border).

Even though no clear trends between the types of the patches and the studied parameters emerged, we do encourage further studies to test if the type of the patch determines its origin, fate, role, or functionality. The interesting spectrum of the

435   observed shapes of the particles and plankton patches may be the result of both the active gathering types of the planktonic organisms (e.g., Rosette, Diamond, Triangle, Flare), by the hydrographical structuring (e.g., Belt, Flag), or the irregularities in the water velocity, which may stretch/squeeze, twist and distort them in many various ways (e.g., Fingers) (Mackas et al., 1985). While the horizontal thin layers (up to few meters thickness and horizontal extensions overs many kilometres) are among the best studied patchy forms (McManus et al., 2005), typically containing densities far greater than those above or

440   below the layer (Dekshenieks et al., 2001; Durham and Stocker, 2012), the observed by us thin vertical layers (narrow horizontally, by vertically extended over the studied water column depth range, such as Belt and Flag types), are something not reported so far, most probably specific to the waters near glacier fronts. The observation that particles and plankton organisms are variously organized in space, both in the ocean and within their individual aggregations, opens a new avenue for our understanding of the mechanisms governing those 'cells of matter and life'. Determining the processes that mediate

445   the co-occurrence of particles, protists, and zooplankton will help assess impacts of patchiness on the marine food webs and geophysics.

Code availability: on request from the corresponding author

Data availability: on request from the corresponding author

Competing interest: None

450 **Author contribution:** ET: conceptualization, data curation, formal analysis, investigation, methodology, software, visualization, writing – original draft preparation. KDD & SS: data curation, writing – review & editing. KBS: funding acquisition, project administration, writing – review & editing.

455 **References**

Balazy, K., Trudnowska, E., Wichorowski, M. and Błachowiak-Samołyk, K.: Large versus small zooplankton in relation to temperature in the Arctic shelf region, Polar Res., 37(1), doi:10.1080/17518369.2018.1427409, 2018.

Balazy, K., Trudnowska, E. and Błachowiak-Samołyk, K.: Dynamics of Calanus copepodite structure during little auks' breeding seasons in two different Svalbard locations, Water (Switzerland), 11(7), doi:10.3390/w11071405, 2019.

460 Basedow, S. L., Eiane, K., Tverberg, V. and Spindler, M.: Advection of zooplankton in an Arctic fjord (Kongsfjorden, Svalbard), Estuar. Coast. Shelf Sci., 60(1), 113–124, doi:10.1016/j.ecss.2003.12.004, 2004.

Basedow, S. L., Zhou, M. and Tande, K. S.: Secondary production at the Polar Front, Barents Sea, August 2007, Elsevier B.V., 2014.

Benoit-Bird, K. J., Kuletz, K., Heppell, S., Jones, N. and Hoover, B.: Active acoustic examination of the diving behavior of
465 murres foraging on patchy prey, Mar. Ecol. Prog. Ser., 443, 217–235, doi:10.3354/meps09408, 2011.

Bhaskar, J. T., Parli, B. V. and Tripathy, S. C.: Spatial and seasonal variations of dinoflagellates and ciliates in the Kongsfjorden, Svalbard, Mar. Ecol., (January), 1–12, doi:10.1111/maec.12588, 2020.

Borcard, D. and Legendre, P.: All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices, Ecol. Modell., 153(1–2), 51–68, doi:10.1016/S0304-3800(01)00501-4, 2002.

470 Borcard, D., Legendre, P. and Drapeau, P.: Partialling out the Spatial Component of Ecological Variation Author, Ecology, 73(3), 1045–1055, 1992.

Brentnall, S. J., Richards, K. J., Brindley, J. and Murphy, E.: Plankton patchiness and its effect on larger-scale productivity, J. Plankton Res., 25(2), 121–140, doi:10.1093/plankt/25.2.121, 2003.

Csapó, H. K., Grabowski, M. and Węsławski, J. M.: Coming home - boreal ecosystem claims Atlantic sector of the Arctic,
475 Sci. Total Environ., 771, 144817, doi:10.1016/j.scitotenv.2020.144817, 2021.

Currie, W. J. S., Claereboudt, M. R. and Roff, J. C.: Gaps and patches in the ocean: A one-dimensional analysis of planktonic distributions, Mar. Ecol. Prog. Ser., 171, 15–21, doi:10.3354/meps171015, 1998.

D'Angelo, A., Giglio, F., Miserocchi, S., Sanchez-Vidal, A., Aliani, S., Tesi, T., Viola, A., Mazzola, M. and Langone, L.:

Multi-year particle fluxes in Kongsfjorden, Svalbard, Biogeosciences, 15(17), 5343–5363, doi:10.5194/bg-15-5343-2018,
480   2018.

Davis, C. S., Thwaites, F. T., Gallager, S. M. and Hu, Q.: A three-axis fast-tow digital Video Plankton Recorder for rapid surveys of plankton taxa and hydrography, Limnol. Oceanogr. Methods, 3(2), 59–74, doi:10.4319/lom.2005.3.59, 2005.

Dekshenieks, M. M., Donaghay, P. L., Sullivan, J. M., Rines, J. E. B., Osborn, T. R. and Twardowski, M. S.: Temporal and spatial occurrence of thin phytoplankton layers in relation to physical processes, Mar. Ecol. Prog. Ser., 223, 61–71,
485   doi:10.3354/meps223061, 2001.

Durham, W. M. and Stocker, R.: Thin phytoplankton layers: Characteristics, mechanisms, and consequences, Ann. Rev. Mar. Sci., 4, 177–207, doi:10.1146/annurev-marine-120710-100957, 2012.

Ehn, J. K., Reynolds, R. A., Stramski, D., Doxaran, D., Lansard, B. and Babin, M.: Patterns of suspended particulate matter across the continental margin in the Canadian Beaufort Sea during summer, Biogeosceinces, 16, 1583–1605, 2019.

490   Finlay, B. J.: Global dispersal of free-living microbial eukaryote species, Science (80-.)., 296(5570), 1061–1063, doi:10.1126/science.1070710, 2002.

Forest, A., Stemmann, L., Picheral, M., Burdorf, L., Robert, D., Fortier, L. and Babin, M.: Size distribution of particles and zooplankton across the shelf-basin system in southeast Beaufort Sea: Combined results from an Underwater Vision Profiler and vertical net tows, Biogeosciences, 9(4), 1301–1320, doi:10.5194/bg-9-1301-2012, 2012.

495   Geoffroy, M., Cottier, F. R., Berge, J. and Inall, M. E.: AUV-based acoustic observations of the distribution and patchiness of pelagic scattering layers during midnight sun, ICES J. Mar. Sci., 74(9), 2342–2353, doi:10.1093/icesjms/fsw158, 2017.

Gluchowska, M., Kwasniewski, S., Prominska, A., Olszewska, A., Goszczko, I., Falk-Petersen, S., Hop, H. and Weslawski, J. M.: Zooplankton in Svalbard fjords on the Atlantic–Arctic boundary, Polar Biol., 39(10), 1785–1802, doi:10.1007/s00300-016-1991-1, 2016.

500   Godø, O. R., Samuelsen, A., Macaulay, G. J., Patel, R., Hjøllo, S. S., Horne, J., Kaartvedt, S. and Johannessen, J. A.: Mesoscale eddies are oases for higher trophic marine life, PLoS One, 7(1), 1–9, doi:10.1371/journal.pone.0030161, 2012.

Greer, A. T., Cowen, R. K., Guigand, C. M., Mcmanus, M. A., Sevadjian, J. C. and Timmerman, A. H. V.: Relationships between phytoplankton thin layers and the fine-scale vertical distributions of two trophic levels of zooplankton, J. Plankton Res., 35(5), 939–956, doi:10.1093/plankt/fbt056, 2013.

505   Greer, A. T., Cowen, R. K., Guigand, C. M. and Hare, J. A.: Fine-scale planktonic habitat partitioning at a shelf-slope front revealed by a high-resolution imaging system, J. Mar. Syst., 142, 111–125, doi:10.1016/j.jmarsys.2014.10.008, 2015.

Greer, A. T., Woodson, C. B., Smith, C. E., Guigand, C. M., Cowen, R. K. and Koski, M.: Examining mesozooplankton patch structure and its implications for trophic interactions in the Northern Gulf of Mexico, J. Plankton Res., 38(4), 1115–1134, doi:10.1093/plankt/fbw033, 2016.

510   Halbach, L., Vihtakari, M., Duarte, P., Everett, A., Granskog, M. A., Hop, H., Kauko, H. M., Kristiansen, S., Myhre, P. I., Pavlov, A. K., Pranik, A., Tatarek, A., Torsvik, T., Wiktor, J. M., Wold, A., Wulff, A., Steen, H. and Assmy, P.: Tidewater Glaciers and Bedrock Characteristics Control the Phytoplankton Growth Environment in an Arctic Fjord, Front. Mar. Sci.,

22

6(May), 254, doi:10.3389/fmars.2019.00254, 2019.

Holliday, D. V., Donaghay, P. L., Greenlaw, C. F., McGehee, D. E., McManus, M. M., Sullivan, J. M. and Miksis, J. L.:

515   Advances in defining fine- and micro-scale pattern in marine plankton, Aquat. Living Resour., 16(3), 131–136, doi:10.1016/S0990-7440(03)00023-8, 2003.

Hop, H. and Wiencke, C.: The Ecosystem of Kongsfjorden, Svalbard., 2019.

Jouon, A., Ouillon, S., Douillet, P., Lefebvre, J. P., Fernandez, J. M., Mari, X. and Froidefond, J. M.: Spatio-temporal variability in suspended particulate matter concentration and the role of aggregation on size distribution in a coral reef lagoon,

520   Mar. Geol., 256(1–4), 36–48, doi:10.1016/j.margeo.2008.09.008, 2008.

Kanna, N., Sugiyama, S., Ohashi, Y., Sakakibara, D., Fukamachi, Y. and Nomura, D.: Upwelling of Macronutrients and Dissolved Inorganic Carbon by a Subglacial Freshwater Driven Plume in Bowdoin Fjord, Northwestern Greenland, J. Geophys. Res. Biogeosciences, 123(5), 1666–1682, doi:10.1029/2017JG004248, 2018.

Kim, B. K., Joo, M., Jung, J., Lee, B. and Ha, S.-Y.: In Situ Rates of Carbon and Nitrogen Uptake by Phytoplankton and the

525   Contribution of Picophytoplankton in Kongsfjorden, Svalbard, Water, 12, 2903 [online] Available from: www.mdpi.com/journal/water, 2020.

Kubiszyn, A. M., Piwosz, K., Wiktor, J. M. and Wiktor, J. M.: The effect of inter-annual Atlantic water inflow variability on the planktonic protist community structure in the West Spitsbergen waters during the summer, J. Plankton Res., 36(5), 1190–1203, doi:10.1093/plankt/fbu044, 2014.

530   Kubiszyn, A. M., Wiktor, J. M., Wiktor, J. M., Griffiths, C., Kristiansen, S. and Gabrielsen, T. M.: The annual planktonic protist community structure in an ice-free high Arctic fjord (Adventfjorden, West Spitsbergen), J. Mar. Syst., 169, 61–72, doi:10.1016/j.jmarsys.2017.01.013, 2017.

Kuhn, A. M., Dutkiewicz, S., Jahn, O., Clayton, S., Rynearson, T. A., Mazloff, M. R. and Barton, A. D.: Temporal and Spatial Scales of Correlation in Marine Phytoplankton Communities, J. Geophys. Res. Ocean., 124(12), 9417–9438,

535   doi:10.1029/2019JC015331, 2019.

Levin, S. A. and Segel, L. A.: Hypothesis for origin of planktonic patchiness, Nature, 259, 1976, 1976.

Lévy, M., Franks, P. J. S. and Smith, K. S.: The role of submesoscale currents in structuring marine ecosystems, Nat. Commun., 9(1), 4758, doi:10.1038/s41467-018-07059-3, 2018.

Li, W. K. W., McLaughlin, F. A., Lovejoy, C. and Carmack, E. C.: Smallest algae thrive as the arctic ocean freshens, Science

540   (80-.)., 326(5952), 539, doi:10.1126/science.1179798, 2009.

Lombard, F., Boss, E., Waite, A. M., Uitz, J., Stemmann, L., Sosik, H. M., Schulz, J., Romagnan, J. B., Picheral, M., Pearlman, J., Ohman, M. D., Niehoff, B., Möller, K. O., Miloslavich, P., Lara-Lopez, A., Kudela, R. M., Lopes, R. M., Karp-Boss, L., Kiko, R., Jaffe, J. S., Iversen, M. H., Irisson, J. O., Hauss, H., Guidi, L., Gorsky, G., Giering, S. L. C., Gaube, P., Gallager, S., Dubelaar, G., Cowen, R. K., Carlotti, F., Briseño-Avena, C., Berline, L., Benoit-Bird, K. J., Bax, N. J., Batten, S. D., Ayata,

545   S. D. and Appeltans, W.: Globally consistent quantitative observations of planktonic ecosystems, Front. Mar. Sci., 6(MAR), doi:10.3389/fmars.2019.00196, 2019.

Lovejoy, S., Currie, W. J. S., Tessier, Y., Claereboudt, M. R., Bourget, E., Roff, J. C. and Schertzer, D.: Universal multifractals and ocean patchiness: Phytoplankton, physical fields and coastal heterogeneity, J. Plankton Res., 23(2), 117–141, doi:10.1093/plankt/23.2.117, 2001.

550   Mackas, D. L.: Spatial autocorrelation of plankton community composition in a continental shelf ecosystem, Limnol. Oceanogr., 29(3), 451–471, doi:10.4319/lo.1984.29.3.0451, 1984.

Mackas, D. L., Denman, K. L. and Abbott, M. R.: Plankton patchiness: biology in the physical vernacular., Bull. Mar. Sci., 37(2), 653–674, 1985.

Mahadevan, A.: The Impact of Submesoscale Physics on Primary Productivity of Plankton, Ann. Rev. Mar. Sci., 8(1), 161–
555   184, doi:10.1146/annurev-marine-010814-015912, 2016.

Martin, A. P.: Phytoplankton patchiness: the role of lateral stirring and mixing, Prog. Oceanogr., 57(2), 125–174, doi:10.1016/s0079-6611(03)00085-5, 2003.

Matsuoka, A., Bricaud, A., Benner, R., Para, J., Sempéré, R., Prieur, L., Bélanger, S. and Babin, M.: Tracing the transport of colored dissolved organic matter in water masses of the Southern Beaufort Sea: relationship with hydrographic characteristics,
560   Biogeosciences, 9(3), 925–940, doi:10.5194/bg-9-925-2012, 2012.

McManus, M. A., Cheriton, O. M., Drake, P. J., Holliday, D. V., Storlazzi, C. D., Donaghay, P. L. and Greenlaw, C. F.: Effects of physical processes on structure and transport of thin zooplankton layers in the coastal ocean, Mar. Ecol. Prog. Ser., 301, 199–215, doi:10.3354/meps301199, 2005.

Meire, L., Mortensen, J., Meire, P., Juul-Pedersen, T., Sejr, M. K., Rysgaard, S., Nygaard, R., Huybrechts, P. and Meysman,
565   F. J. R.: Marine-terminating glaciers sustain high productivity in Greenland fjords, Glob. Chang. Biol., 23(12), 5344–5357, doi:10.1111/gcb.13801, 2017.

Menden-Deuer, S.: Structure-Dependent phytoplankton photosynthesis and production rates: Implications for the formation, maintenance, and decline of plankton patches, Mar. Ecol. Prog. Ser., 468, 15–30, doi:10.3354/meps09968, 2012.

Metfies, K., Von Appen, W. J., Kilias, E., Nicolaus, A. and Nöthig, E. M.: Biogeography and photosynthetic biomass of arctic
570   marine pico-eukaroytes during summer of the record sea ice minimum 2012, PLoS One, 11(2), 1–20, doi:10.1371/journal.pone.0148512, 2016.

Möller, K. O., John, M. S., Temming, A., Floeter, J., Sell, A. F., Herrmann, J. P. and Möllmann, C.: Marine snow, zooplankton and thin layers: Indications of a trophic link from small-scale sampling with the Video Plankton Recorder, Mar. Ecol. Prog. Ser., 468, 57–69, doi:10.3354/meps09984, 2012.

575   Nöthig, E. M., Bracher, A., Engel, A., Metfies, K., Niehoff, B., Peeken, I., Bauerfeind, E., Cherkasheva, A., Gäbler-Schwarz, S., Hardge, K., Kilias, E., Kraft, A., Kidane, Y. M., Lalande, C., Piontek, J., Thomisch, K. and Wurst, M.: Summertime plankton ecology in fram strait-a compilation of long-and short-term observations, Polar Res., 34(1), doi:10.3402/polar.v34.23349, 2015.

Pinel-Alloul, P.: Spatial heterogeneity as a multiscale characteristic of zooplankton community, Hydrobiologia, 300–301(1),
580   17–42, doi:10.1007/BF00024445, 1995.

Piwosz, K., Walkusz, W., Hapter, R., Wieczorek, P., Hop, H. and Wiktor, J.: Comparison of productivity and phytoplankton in a warm (Kongsfjorden) and a cold (Hornsund) Spitsbergen fjord in mid-summer 2002, Polar Biol., 32(4), 549–559, doi:10.1007/s00300-008-0549-2, 2009.

585   Priyadarshi, A., Smith, S. L., Mandal, S., Tanaka, M. and Yamazaki, H.: Micro-scale patchiness enhances trophic transfer efficiency and potential plankton biodiversity, Sci. Rep., 9(1), 1–9, doi:10.1038/s41598-019-53592-6, 2019.

Schmitt, F. G. and Seuront, L.: Intermittent turbulence and copepod dynamics: Increase in encounter rates through preferential concentration, J. Mar. Syst., 70(3–4), 263–272, doi:10.1016/j.jmarsys.2007.01.008, 2008.

Seuront, L., Schmitt, F. and Lagadeuc, Y.: Turbulence intermittency, small-scale phytoplankton patchiness and encounter rates in plankton: Where do we go from here?, Deep. Res. Part I Oceanogr. Res. Pap., 48(5), 1199–1215, doi:10.1016/S0967-

590   0637(00)00089-3, 2001.

Skogseth, R., Olivier, L. L. A., Nilsen, F., Falck, E., Fraser, N., Tverberg, V., Ledang, A. B., Vader, A., Jonassen, M. O., Søreide, J., Cottier, F., Berge, J., Ivanov, B. V. and Falk-Petersen, S.: Variability and decadal trends in the Isfjorden (Svalbard) ocean climate and circulation – An indicator for climate change in the European Arctic, Prog. Oceanogr., 187(July), 102394, doi:10.1016/j.pocean.2020.102394, 2020.

595   Smoła, Z. T., Tatarek, A., Wiktor, J. M. W., Wiktor, J. M. W., Kubiszyn, A. and Węsławski, J. M.: Primary producers and production in Hornsund and Kongsfjorden - Comparison of two fjord systems, Polish Polar Res., 38(3), 351–373, doi:10.1515/popore-2017-0013, 2017.

Steinbuck, J. V., Stacey, M. T., McManus, M. A., Cheriton, O. M. and Ryan, J. P.: Observations of turbulent mixing in a phytoplankton thin layer: Implications for formation, maintenance, and breakdown, Limnol. Oceanogr., 54(4), 1353–1368,

600   doi:10.4319/lo.2009.54.4.1353, 2009.

Stemmann, L., Eloire, D., Sciandra, A., Jackson, G. A., Guidi, L., Picheral, M. and Gorsky, G.: Volume distribution for particles between 3.5 to 2000μm in the upper 200m region of the South Pacific Gyre, Biogeosciences, 5(2), 299–310, doi:10.5194/bg-5-299-2008, 2008.

Svensen, C., Halvorsen, E., Vernet, M., Franzè, G., Dmoch, K., Lavrentyev, P. J. and Kwasniewski, S.: Zooplankton

605   Communities Associated With New and Regenerated Primary Production in the Atlantic Inflow North of Svalbard, Front. Mar. Sci., 6(June), 1–13, doi:10.3389/fmars.2019.00293, 2019.

Szeligowska, M., Trudnowska, E., Boehnke, R., Dąbrowska, A. M., Wiktor, J. M., Sagan, S. and Błachowiak-Samołyk, K.: Spatial Patterns of Particles and Plankton in the Warming Arctic Fjord (Isfjorden, West Spitsbergen) in Seven Consecutive Mid-Summers (2013–2019), Front. Mar. Sci., 7(584), doi:10.3389/fmars.2020.00584, 2020.

610   Trudnowska, E., Szczucka, J., Hoppe, L., Boehnke, R., Hop, H. and Blachowiak-Samolyk, K.: Multidimensional zooplankton observations on the northern West Spitsbergen Shelf, J. Mar. Syst., 98–99, 18–25, doi:10.1016/j.jmarsys.2012.03.001, 2012.

Trudnowska, E., Basedow, S. L. and Blachowiak-Samolyk, K.: Mid-summer mesozooplankton biomass, its size distribution, and estimated production within a glacial Arctic fjord (Hornsund, Svalbard), J. Mar. Syst., 137, 55–66, doi:10.1016/j.jmarsys.2014.04.010, 2014.

615 Trudnowska, E., Gluchowska, M., Beszczynska-Möller, A., Blachowiak-Samolyk, K. and Kwasniewski, S.: Plankton patchiness in the Polar Front region of the west Spitsbergen Shelf, Mar. Ecol. Prog. Ser., 560, doi:10.3354/meps11925, 2016.

Trudnowska, E., Sagan, S. and Błachowiak-Samołyk, K.: Spatial variability and size structure of particles and plankton in the Fram Strait, Prog. Oceanogr., 168, 1–12, doi:10.1016/j.pocean.2018.09.005, 2018.

Trudnowska, E., Dąbrowska, A. M., Boehnke, R., Zajączkowski, M. and Blachowiak-Samolyk, K.: Particles, protists, and
620 zooplankton in glacier-influenced coastal svalbard waters, Estuar. Coast. Shelf Sci., 242(April), 106842, doi:10.1016/j.ecss.2020.106842, 2020a.

Trudnowska, E., Stemmann, L., Błachowiak-Samołyk, K. and Kwasniewski, S.: Taxonomic and size structures of zooplankton communities in the fjords along the Atlantic water passage to the Arctic, J. Mar. Syst., 204, doi:10.1016/j.jmarsys.2020.103306, 2020b.

625 Vihtakari, M., Welcker, J., Moe, B., Chastel, O., Tartu, S., Hop, H., Bech, C., Descamps, S. and Gabrielsen, G. W.: Black-legged kittiwakes as messengers of Atlantification in the Arctic, Sci. Rep., 8(1), 1–11, doi:10.1038/s41598-017-19118-8, 2018.

Węsławski, J. M., Buchholz, F., Głuchowska, M. and Weydmann, A.: Ecosystem maturation follows the warming of the Arctic fjords, Oceanologia, 59(4), 592–602, doi:10.1016/j.oceano.2017.02.002, 2017.

White, A. E., Letelier, R. M., Whitmire, A. L., Barone, B., Bidigare, R. R., Church, M. J. and Karl, D. M.: Phenology of
630 particle size distributions and primary productivity in the North Pacific subtropical gyre (Station ALOHA) Angelicque, J. Geophys. Res. Ocean., 120, 7381–7399, doi:10.1002/2015JC010897.Received, 2015.

Wiebe, P. H., Wiebe, P. H. and Holland, W. R.: Plankton Patchiness: Effects on Repeated Net Tows, Limnol. Oceanogr., 13(2), 315–321, doi:10.4319/lo.1968.13.2.0315, 1968.

Wiencke, C. and Hop, H.: Ecosystem Kongsfjorden: new views after more than a decade of research, Polar Biol., 39(10),
635 1679–1687, doi:10.1007/s00300-016-2032-9, 2016.

De Wit, R. and Bouvier, T.: "Everything is everywhere, but, the environment selects"; what did Baas Becking and Beijerinck really say?, Environ. Microbiol., 8(4), 755–758, doi:10.1111/j.1462-2920.2006.01017.x, 2006.

Woodson, C. B., Webster, D. R., Weissburg, M. J. and Yen, J.: The prevalence and implications of copepod behavioral responses to oceanographic gradients and biological patchiness, Integr. Comp. Biol., 47(6), 831–846, doi:10.1093/icb/icm091,
640 2007.

Xi, H., Larouche, P., Tang, S. and Michel, C.: Characterization and variability of particle size distributions in Hudson Bay, Canada, J. Geophys. Res. Ocean., 119(3392), 3406, doi:10.1038/175238c0, 2014.