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Storm events alter marine snow fluxes in stratified marine environments

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ABSTRACT

Marine snow is an important part of the biological pump and marine food web, and although previous research has provided a thorough understanding of the underlying mechanisms of marine snow dynamics in general, there is still a knowledge gap concerning extreme conditions, such as storm events. Storms are predicted to increase in magnitude and frequency in the future, and could potentially have a large impact on marine snow dynamics. For these reasons, we assessed the effects of storm events on marine snow dynamics in the Baltic Sea, an area chosen due to its well-studied and stable stratified conditions outside of meteorologically extreme events. The combination of *in-situ* imaging and biogeochemical environmental data from three different years facilitates an assessment of storm event impacts, while simultaneously excluding the possibility that patterns in particle distribution and abundances were due to other environmental influences. The results show that extreme meteorological events such as storms can increase the abundance of marine snow in stratified marine environments by a factor of 10 or more. The particles are distributed more widely and are larger, brighter, rounder and less complexly shaped. In non-extreme conditions, particles have been observed to deposit along the density gradients in thin-layer aggregations. This study indicates that storms can episodically disrupt these formations, thereby altering vertical flux and export potentials across stratification boundaries. In addition, we observed that marine snow abundances are drastically higher in the aftermath of storm events than under calm conditions, potentially due to the disaggregation of larger particles and lateral import of resuspended matter from shallower areas. In light of the increased frequency and magnitude of storms in the future due to climate change, our findings indicate that marine snow dynamics in stratified environments might be altered permanently.

1. Introduction

Marine snow, which is vertically fluctuating suspended particulate matter in the sea, plays an important role in oceanic particle flux dynamics and vertical carbon export (Carson, 1951; Shanks and Trent, 1980; Silver, 2015; Turner, 2015; Trudnowska et al., 2021). The sedimentation and potential subsequent burial of carbon compounds contained in marine snow aggregates is an essential component of the biological carbon pump (Turner, 2015), and can lead to long-term storage of organic carbon in the sediment (Macquaker et al., 2010). It also provides an important food source to benthic communities (see *e.g.* Fowler and Knauer, 1986). Nevertheless, our understanding of how vertical flux dynamics and aggregate characteristics may change under future conditions affected by climate change is limited. Assessing the impact of increasingly frequent meteorological extremes such as storm events is therefore increasingly urgent. *In-situ* observations at high temporal resolution around the time of a storm event, such as the ones presented here, are a great tool to further our understanding of marine snow dynamics in these conditions. It is known that marine snow aggregates in the open ocean predominantly consist of organic matter year-round, while coastal ocean conditions lead to seasonally variable aggregate compositions (Fettweis et al., 2012a). The latter is due to periodic organic matter input from phytoplankton blooms and physical mixing that can cause resuspension of benthic matter (Rühl et al., 2020). There are size-dependent differences in particle density and composition (Guidi et al., 2008; Fender et al., 2019), and carbon and nitrogen content (Alldredge, 1998) as well as associated microbial community compositions (Jackson and Weeks, 2008). Recent evidence shows that sinking speeds are driven more through particle density than size (Iversen and Lampitt, 2020), though the co-variance of a particle's size with its type and origin results in a weak, but measurable, relationship from which sinking speed may be estimated (Fender et al., 2019; Cael et al., 2021). Thus, the growth, or aggregation, and break-up, or disaggregation of marine snow has a strong potential of affecting vertical carbon flux. The

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process of aggregation can be affected by physical (*e.g.* coagulation: Jackson, 1990) and/or biological processes (*e.g.* microbial exopolymer production: Alldredge and McGillivary, 1991; Kiørboe, 2001). It has been shown that the aggregation of marine snow is also strongly dependent on ambient suspended matter concentrations. Disaggregation is similarly dependent on a range of environmental factors, including trophic interactions (*e.g.* zooplankton and fish feeding: Larson and Shanks, 1996; Kiørboe, 2000), microbially driven dissolution and remineralisation (Kiørboe, 2001), fluid shear (Alldredge et al., 1990), and the turbulence of the surrounding water from biogenic (Dilling and Alldredge, 2000; Goldthwait et al., 2004; Huntley and Zhou, 2004) and/or physical sources (Alldredge et al., 1990; Jackson et al., 1997). A full account of the mechanisms of marine snow aggregation and disaggregation dynamics can be found in Alldredge (1990).

Although aggregation and disaggregation are strongly linked to turbulent conditions, and measuring turbulence in the ocean is generally possible, there is a knowledge gap concerning the storm impacts on marine snow dynamics due to weather constraints on *in-situ* data collection (Schultze et al., 2020). Imaging methodologies may be a useful tool to provide information on marine snow during adverse meteorological conditions that would prohibit conventional sampling, as long as they are deployed autonomously or moored. Automated sensors and sensor platforms that can be deployed independently have only recently become widely available, thus opening the gates for a better understanding of the oceans under conditions under which sampling would previously have been impossible.

In stratified environments, storms can cause either temporary mixing across stratification boundaries, or even long-term break-up of stratification (*e.g.* Lass et al., 2003; Yang et al., 2004; Li et al., 2007). It has been shown that storm events can lead to vast increases in marine snow abundance due to their disaggregating properties (Jackson et al., 1997; Milligan and Hill, 1998), combined with the introduction of additional material through resuspension (Jago et al., 1993; Pusceddu et al., 2005; Ziervogel et al., 2016), including material with highly flocculating properties (Fettweis et al., 2012b). Storms can also affect marine snow sinking rates (Shanks, 2002), and increase suspended nutrient concentrations which can fuel plankton growth that would otherwise have been limited (Zhang et al., 2014; Schultze et al., 2020), thus fuelling the production of further biogenic matter that can be incorporated into marine snow. Here we focus primarily on the aggregating and disaggregating effects of turbulent conditions due to such storm events. Various models predict an increase in storm frequency and intensity in the future, due to climate change (Gräwe and Burchard, 2012; Räisänen, 2017; Myslenkov et al., 2018; IPCC, 2019), which would augment the vertical mixing potential in environments that are usually stratified, to an as yet unknown degree. Some predict a change in inflow frequency and magnitude in the future (Schimanke et al., 2014; Meier et al., 2017), while other studies argue that the evidence is inconclusive (*e.g.* Räisänen, 2017). The effects altered storm and/or inflow patterns could have on the distribution of marine snow throughout the water column have yet to be determined. Due to the critical role marine snow plays in the ecosystem, and considering the predicted increase in storm magnitude and frequency in the future (IPCC, 2019), the identification of storm effects on important environmental processes such as the sinking of marine snow is crucial.

In order to examine the effects of extreme events in any situation, the environmental physical and biological *status quo* needs to be known. One region in which this is the case is the Baltic Sea, as it has been studied for centuries and is known as a highly stable environment with a permanently stratified water column that can even be considered a natural mesocosm (Stigebrandt, 2001; Snoeijs-Leijonmalm et al., 2017). Furthermore, the thorough and consistent monitoring of the Baltic has yielded large amounts of data and publications of its biological, chemical and physical characteristics, which can be used to supplement data collected during campaigns that may not in themselves be comprehensive enough to yield reliable conclusions. Temporary seasonal stratification is common in many coastal and shelf-sea environments, such as for example the North Sea (van Leeuwen et al., 2015), Patagonia (Rivas and Piola, 2002) and Mediterranean (Santinelli et al., 2013). The principles of stratification are the same at all sites, regardless of the duration or permanence of the stratification: density differences between the water layers due to haloclines and/or thermoclines impede vertical mixing, thus altering and slowing the flux of particulates and solutes across the boundary. Because of this, we believe that the Bornholm Basin (BoB), also sometimes called Bornholm Deep, is an ideal study area for our observations and results might also be transferred to other marine ecosystems with stratified water columns.

Here, we tested whether meteorologically induced mixing caused by storm events has an impact on the distribution, abundance and/or physical characteristics of marine snow in stratified environments, by analysing three sets of imaging data, one of which was recorded in the immediate after-math of a storm event. By using imaging technology, we were able to produce temporally and spatially highly resolved marine snow abundance and property data, facilitating a more in-depth analysis of the particle flux dynamics than conventional sampling methods would have permitted. We found that both particle abundance and size are affected by the impacts of a storm.

2. Methods

2.1. Study site

The BoB is an area east of the island of Bornholm with a maximum depth of 106 m (Kullenberg, 1982), in the south-west of the central and largest basin in the Baltic Sea, the Baltic Proper (see Fig. 1A). Similar to the Baltic Sea in general, the BoB exhibits regular plankton blooms each year between April and May (Fennel, 1995; Fleming and Kaitala, 2006; Beusekom et al., 2009), in the late summer (July, August; see *e.g.* Lyngsgaard et al., 2017; Ostrowska et al., 2022), as well as in some winters (Laamanen, 1996; Granskog et al., 2006). There may be higher abundances of phytoplankton than zooplankton, leading to superfluous organic matter from phytoplankton blooms sinking instead of being consumed and processed near the surface (Kullenberg, 1982), especially during the summer blooms. According to the IOW time-series data, spring bloom sedimentation rates were lower than average in 2015 and very high in 2002 (Wasmund et al., 2003, 2016). Overall, secondary production is variable and better described near the coasts than in the basins (Ojaveer et al., 2010). The zooplankton community within the BoB tends to be dominated in terms of biomass by copepods, on which commercially important fish feed (Niermann and Greve, 1997; Möllmann et al., 2005; Möller et al., 2015).

One of the most important hydrographical features of the Baltic Sea is strong vertical density gradient due to a well-established halocline, below which the water has a higher salinity and lower oxygen concentrations than in the overlying water (Stigebrandt, 2001; Ojaveer et al., 2010; Broman et al., 2019). Vertical mixing across this halocline, which can typically be found at around 50 m depth in the BoB (Jakobsen, 1996), is minimal, and mostly dependent on wind (Kullenberg, 1977). However, oxygenated saline water does periodically enter the Baltic from the North Sea in so-called inflow events (Matthäus and Franck, 1992), which can lead to vertical mixing and the exchange of solutes across the halocline (Reissmann et al., 2009). Previous studies in the BoB recorded an accumulation of marine snow particles at the halocline boundary, with much higher particle concentrations at this depth than at any other depth (Möller et al., 2012, 2015). Inflow events in the BoB can disperse this otherwise strong and pronounced thin-layer accumulation, leading to a more even distribution of marine snow throughout the water column (Möller et al., 2015). This may be because of the resulting increase in halocline boundary surface area and decrease in depth of the halocline, both of which facilitate easier mixing through wind-driven turbulence (Kullenberg, 1982), or because of a general weakening in the vertical stratification through the lateral force of the

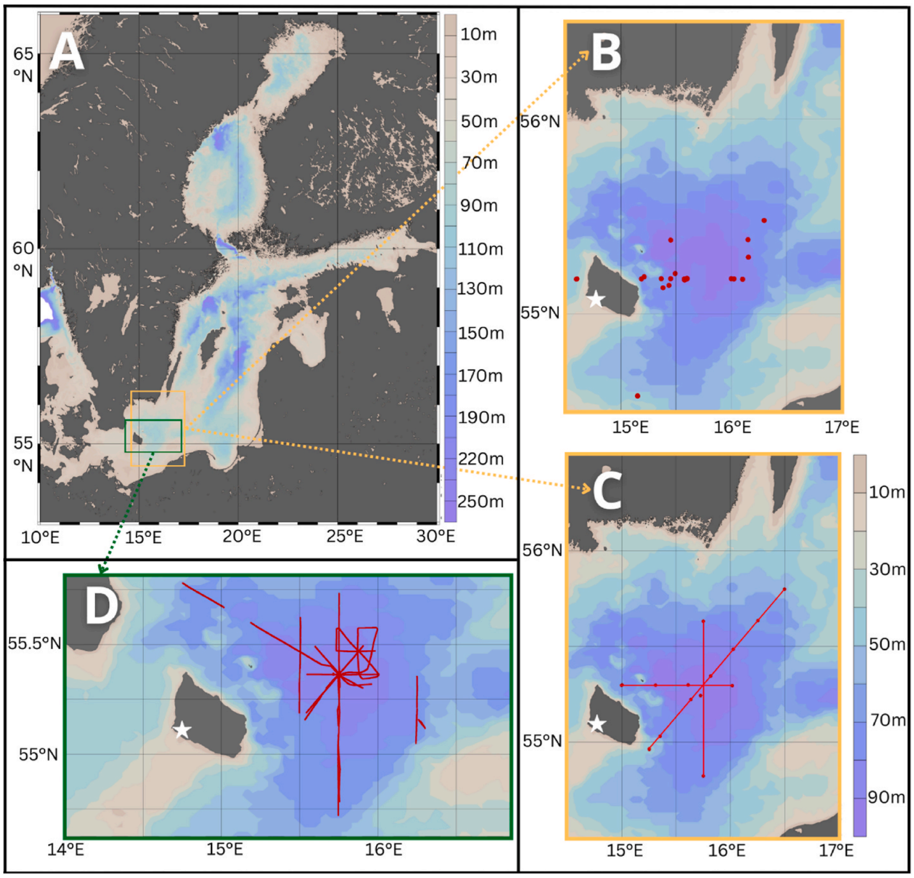

Fig. 1. A) Overview over the Baltic Proper with the Bornholm Basin area highlighted in a yellow rectangle; B) Record of all 2015 vertical profile stations in the Bornholm Basin (location in overview map indicated by yellow rectangle); C) Record of the 2015 transects through the Bornholm Basin (location in overview map indicated by yellow rectangle); D) Transects from the 2002/2003 cruises described in Möller et al. (2012), 2015 (location in overview map A indicated by green rectangle); The location of the weather station from which wind speed data were sourced is marked with a white star in the close-up maps (B,C and D); The colour bar alongside map C applies to maps B and D as well. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

in-flowing water (Mohrholz et al., 2006). In order to be able to examine whether the particulate distribution observed in 2015 was affected by the 2014/15 major inflow event (described *e.g.* in Gräwe et al., 2015; Rak, 2016; Mohrholz, 2018), additional data sets collected in the BoB in 2002 and 2003 were considered as a baseline. The 2002 data provide information on the *status quo* of marine snow abundance and distribution in the absence of major inflow or storm events, while the 2003 data represent conditions after an inflow but without storm event (see Möller et al., 2012, 2015).

Based on historical records from 1985 to 2015, January is typically the windiest month of the year in the Baltic, with average wind speeds of 40 km/h, while wind speeds in March and April average around 33 and 28 km/h respectively (DMI, 2021). According to Lass et al. (2003), wind-driven turbulence in Baltic environments can lead to an active erosion of the halocline if wind speeds exceed 50.4 km/h. Storm events have been shown to increase the magnitude and frequency of internal waves in the Baltic, resulting in turbulent transport across the halocline (Reissmann et al., 2009). In the presence of submesoscale structures such as fronts and filaments, vertical stratification may however be upheld despite the occurrence of mixing from strong wind (Chrysagi et al., 2021).

2.2. Data collection

Data collection was carried out over three years: on the 25.04.02–26.04.02 and 23.05.02–24.05.02, 18.04.03–22.04.03 and 18.05.03–19.05.03, and 29.03.15–08.04.15. In each instance, the peak to end period of the spring phytoplankton bloom was captured (see Fleming and Kaitala, 2006; Beusekom et al., 2009 for information on the 2002 and 2003 blooms). During the 2015 sampling period, data collection was accomplished despite adverse weather conditions, enabling the collection of records during and after a storm event with wind speeds up to 94.95 km/h (storm threshold = 88 km/h; DMI, 2021).

At the core of the 2015 campaign was a series of transects (see Fig. 1), along which a TRIAXUS remotely operated vehicle (Hansen and Hansen, 2003; Floeter et al., 2017) carrying a suite of different instruments was towed in a vertically undulating pattern, to collect horizontal and vertical water column measurements. In addition to the CTD sensor (conductivity, temperature and density; model SBE49; SeaBird Scientific, 2021), additional sensors measured turbidity (Turner C6 Cyclops 7; Turner Designs, 2021), dissolved oxygen (Aanderaa 4330 optode; Xylem, 2021), and chlorophyll *a* concentration (Turner C6 Cyclops 7; Turner Designs, 2021). Also attached to the TRIAXUS was a Video Plankton Recorder (VPR; Seascan Inc., 2015), which is a digital underwater camera system designed to capture *in-situ* colour images of plankton and particles (see examples in Appendix 1).

VPR images were collected at a frequency of 25 fps, capturing a 24 by 24 mm field of view with a camera resolution of 1028 by 1024 pixel. The resulting calibrated image volume was 44.726 ml. Lighting duration of the Xenon strobe accompanying the VPR was synchronised with its shutter speed. VPR recordings were transmitted to the surface to allow live viewing of incoming particle data via a fibre optic tow cable connection. Regions of interest (ROIs) were automatically detected in real-time by the Autodeck image analysis software based on contrast to the black background, depending on brightness, sharpness, texture and size thresholding settings (Seascan Inc., 2015). Each ROI was segmented from the image frame and individually saved and tagged with a unique identifier and time stamp, in order to merge images with the environmental variables recorded simultaneously. Furthermore, the shipboard acoustic split-beam echo sounder (Simrad EK60; Kongsberg, 2021) was used to measure acoustic backscatter as a function of depth, to determine particulate distribution, size and abundance in the water. We used transducer frequencies of 38, 70, 120, and 200 kHz. Absorption losses were calculated based on the Ainslie and McColm formula with set salinities of 7.5 and 36 ppt, roughly representing the respective conditions above and below the halocline (Ainslie and McColm, 1998). In addition, a stand-alone CTD was deployed in vertical profiles at a series of stations, supplementing the transects (see Fig. 1B; CTD model SSDA 183; Sea & Sun Technology, 2021).In order to quantify and evaluate the storm event and assess its strength, wind speed data were sourced from the closest weather station, at Bornholm Rønne airport (55.347°N, 14.4533°E; see Fig. 1) for the days between the March 20, 2015 and the April 11, 2015 (DMI, 2021). Whether or not a storm occurred on any given day was determined according to Qian and Saunders (2003), who define a storm as a period during which wind speeds are between seven and ten on the Beauford scale, constituting levels from “near-gale” (13.9–17.1 m/s) to “storm” (24.5–28.4 m/s) forces. To observe if storm-induced turbulence caused mixing down to and across the halocline we monitored the salinity and density depth gradients over time. Historical wind speed and direction data from the nearby Skillinge weather station (55.48 °N, 14.28 °E) was used to check conditions during the 2002/2003 sampling periods were normal, confirming that no extreme events had coincided with or directly preceded the sampling (data retrieved via windfinder.com).

Water column measurement data from 2002 to 2003 were available as also presented in the 2012 and 2015 Möller et al. publications, but the only variables available for this analysis were density, salinity and temperature as well as particle imaging data collected via VPR. A list of all data sets used in this study can be found in Appendix 2.

2.3. Data processing

VPR imaging data were manually classified to remove images of planktonic organisms, retaining only those of marine snow flocs. Images containing specimens too blurry to classify clearly, and those containing artefacts such as air bubbles introduced through the immersion of the VPR in the water, were also discarded. Overall, this excluded 10.88 % of the VPR images, meaning 89.12 % contained clearly identifiable marine snow particles.

EK60 data were processed using Echoview 12.1 (Echoview Software Pty Ltd, 2022), with focus on the Sv 200 kHz frequency as this was determined to capture the smallest features, such as marine snow aggregates, in the water column (Benoit-Bird and Lawson, 2016; Echoview Software Pty Ltd, 2022). Regions in which the data were of low quality were excluded, such as for example the top layer from the sea surface to between three and 10 m depth due to disturbances created by the ship itself, and the bottom-most metre to avoid capturing benthic features. The automatically detected seabed boundary was smoothed using the moving 5 ping median. Nautical Area Scattering Coefficient (NASC) data were extracted based on a grid of 10 m horizontal distance travelled by 1 m depth intervals between the lowered surface and raised bottom lines because the scattering intensity of marine snow is unknown, and can vary depending on its composition, meaning specific abundances could not be calculated and groups of particles may be misinterpreted as individuals. Additionally, even though the distinction of marine snow particles and organisms of similar backscatter intensity is not an option, the relative abundance of marine snow being much higher than that of organisms of the same size class facilitates the bulk approach.

To determine particle properties such as size, eccentricity, fractal dimension and solidity of imaged entities, the MATLAB “regionprops” package (The MathWorks Inc, 2022) was applied, adjusted to the respective field of view and sampling volumes of each sampling event. Eccentricity describes any deviation from a perfectly circular shape, and plays a role in particle sinking speed. Solidity was included as a visual indicator of particle density, as no direct measurements are available of this variable. The fractal dimension is calculated using the MATLAB “boxcount” routine, which uses a black and white image and counts the number N of boxes of size R needed to cover the nonzero elements of the image. The box sizes are powers of two, *i.e.* $R = 1, 2, 4 \ldots 2^P$, where 2^P is the largest size to fit into the original image. The fractal dimension is calculated as a double-logarithmic fit to the result of N versus R. Major axis length (MAL) and minor axis length (MIL) were used to estimate true particle sizes based on randomly sampled visual checks as these parameters are regularly used for automated functional trait analyses of plankton imaging data (*e.g.* Orenstein et al., 2022).

2.4. Statistical analysis

As a first statistical assessment of the depth-dependence of particle abundances and physical properties, simple correlations were used, after first checking the data for normal distribution using Shapiro-Wilk tests. Pearson’s correlation coefficient was chosen for this purpose to best explore the potential of linearity of the relationship between associated variables (Pearson, 1895; Schober and Schwarte, 2018). Temporal and spatial variability in particle abundance and properties was assessed through Analysis of Variance (ANOVA; Girden, 1992) and subsequent Tukey’s HSD post-hoc tests (Tukey, 1977).

Weighted Mean Depth (WMD, see Frost and Bollens, 1992) and Brunt-Väisälä frequencies (see *e.g.* Jacobsen and Norrbin, 2009) were calculated to aid the assessment of vertical particle distribution maxima and stratification strength.

In order to investigate the multidimensional cause-effect relationships between environmental variables and marine snow abundance and physical properties, several multivariate gradient analysis methods were used. Orthogonal partial least squares discriminant analyses (OPLS-DA; Bylesjö et al., 2006) were used to determine the relative importance of primary and orthogonal determinants of variability. Through this approach, a loss of information on potentially important secondary, tertiary, *etc.* factors could be avoided. Averaging the data along a spatial gradient (in 1 m depth bins) prior to OPLS-DA facilitated faster and more concise modelling of marine snow abundance with depth as a response to the environmental predictors. To assess the impact of extreme events, temporal variability in the data, such as the comparisons of marine snow particle abundance and physical properties in relation to time passed since a storm event occurred, was investigated. To this end, the data were sorted according to their temporal gradients, and analysed using OPLS-DA as described above. Potential differences in impact between the water masses above, within, and below the halocline were assessed similarly, by grouping the data accordingly. Variables that contributed significantly to the fit of each of the models were identified as having variable influence of projection (VIP) values, representing loading weights of the model components and a quantification of the variability of model response due to the components, larger than 1 (Mehmood et al., 2012).

To assess the (dis-)aggregation potential through a change in particle abundances and size ranges between two sampling days in the same area, an “Aggregation Factor” (AF) was developed. This is to be considered a strictly qualitative assessment, as aggregation and disaggregation could not be directly, nor quantitatively, measured. The most important variables for the AF are particle abundances and sizes, as the former decreases and the latter increases when aggregation takes place, and vice versa in the case of disaggregation. Solidity and fractal dimension were also considered as both typically increase slightly in line with aggregation. However, their potential to be indicative of change is not imperative, which is why Solidity and Fractal Dimension were included in the calculation only to a lesser extent, by halving them. To normalize the variables, they were transformed logarithmically.

$$AF = \log(-A_{day1} * MAL_{day1} * 1/2(S_{day1} * FC_{day1})) - \log(-A_{day2} * MAL_{day2} * 1/2(S_{day2} * FC_{day2}))$$

In which A = Abundance per litre, MAL = Major Axis Length in μm, S = Solidity on a scale from 0 to 1 and FC = Fractal complexity, which is without unit. All values used describe averages within the respective depth bin. The AF is calculated as a change from one day (day1) to another (day2), although the two days do not have to be directly following one another so that the time period over which potential aggregation or disaggregation is assessed can span more than 24 h. A positive AF indicates that aggregation may have taken place, while a negative AF shows potential disaggregation. AF was calculated for each 1 m depth bin, as well as for the water column as a whole, to avoid mistaking vertical movement of aggregates between days for depth-specific aggregation or disaggregation.

All statistical analyses were carried out in cran R (R Core Team, 2020).

3. Results

3.1. Environmental conditions and water column stratification

Wind speed and direction data from Skillinge weather station showed that the sampling periods in 2002 and 2003 had not been preceded by, or intersected with, stronger than average wind speed events. In the 2002 sampling period, maximum wind speeds of 13.9 km/h were reached (mean wind speed 4.559 km/h), while in 2003 the maximum speed was 13.8 km/h with a mean of 4.792 km/h. In 2015, wind speeds exceeded the storm threshold only once during the sampling period, on the 30th of March, but the threshold of potential vertical mixing across the halocline (Lass et al., 2003) was exceeded more frequently and for longer periods of time (see Fig. 2). During the storm, as well as over the majority of the sampling period, the wind predominantly originated in the West and Northwest, which means that parts of the BoB were sheltered by the island (see wind directions indicated in Fig. 2).

The characteristic permanent halocline for the BoB, which separates top and bottom water layers, was well pronounced at a depth of roughly 55 m throughout the sampling period, including the period immediately following the storm event. Below the halocline, not only higher salinity levels but also corresponding higher temperatures (4–5 °C above; 7–8 °C below) and lower oxygen saturation levels (93.5–93 % above, 91.9–92.5 % below) were recorded, which is characteristic of the BoB at this time of year. Turbidity was more uniform throughout the water column, but higher in the bottom boundary layer near the sea floor in deep BoB regions. The established halocline separation of water masses remained stable at around 50–55 m, suggesting that there had been no mixing of the two water masses in the period between the 29th of March and the April 8, 2015 (see salinity profiles in Fig. 2 and density profiles in Appendix 3). Chlorophyll maxima were broad, ranging from 10 to about 40 m, and Chlorophyll ranges varied slightly with 1.255–5.690 mg/l on the 4th, 1.023–6.218 mg/l on the 5th and 1.594–6.834 mg/l on the April 8, 2015 (see Fig. 3).

3.2. Marine snow particle abundance, distribution and properties

In post-storm conditions, such as those recorded in 2015, particle abundances above the halocline were drastically higher than those recorded in 2002 and 2003 (at the time recorded around 55 and 42 m depth respectively, see Fig. 3 and Möller et al., 2012, 2015). Marine snow particles were most widely and evenly distributed throughout the water column on the April 5, 2015, when overall abundance was also higher, and least on the 8th, when abundance was generally lower and particles had accumulated atop the halocline boundary. The latter was also the particle distribution pattern, which out of the three sampling days in 2015, most closely resembled the more stable 2002 conditions (see Fig. 3).

Variability in particle abundance and size between the three sampling days was significant within depth bins (for full results see Appendix 4). No comparison in particle size could be made with the 2002 or 2003 data, as no particle size data were available from those years and the original images were not available to base calculations on.

Particle abundance Weighted Mean Depths (WMD, see Frost and Bollens, 1992) were 37.663 m on the 4th, 38.927 m on the 5th and 33.844 m on the 8th of April. Based on the respective differences in these values between dates, there was an increase in WMD from the 4th to the 5th, and a decrease in WMD from the 5th to the April 8, 2015. A calculation of the Brunt-Väisälä frequency based on the gravitational acceleration (9.8 m s^{-2}), measured density and depth throughout the water column (see formula in Jacobsen and Norrbin, 2009) showed that the water column was most stable below the halocline, and least stable above it (see Table I). Conditions were the least stable above and within the halocline on the 5th, and below the halocline on the April 4, 2015. The 8th of April was the overall 'calmest' day (see Table 1).

There was no specific correlation between marine snow abundance and depth (see Appendix 5), but particle properties as measured through VPR imaging varied with depth, and especially between the area above

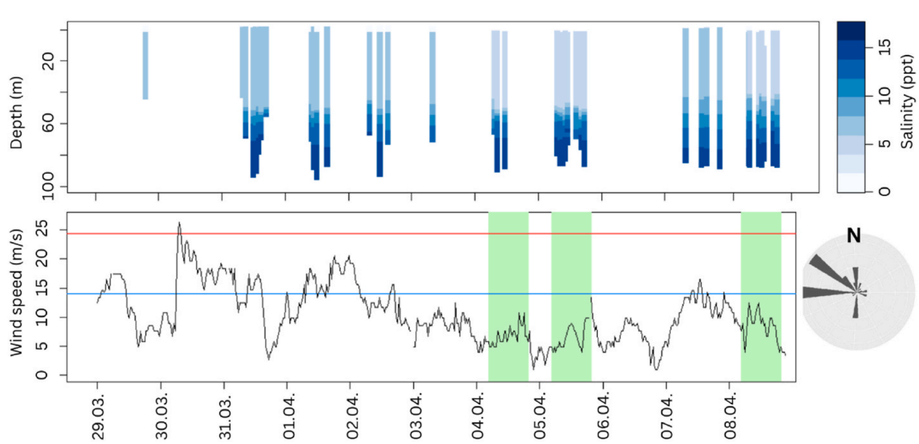

Fig. 2. Salinity measurements from rosette and TRIAXUS hauls (top), and wind speed in 30-min increments (bottom) between the 29th of March and the April 8, 2015; in the bottom graph, the storm threshold (see DMI, 2021) is marked through the red horizontal line, halocline mixing threshold (see Lass et al., 2003) is marked as a blue horizontal line and days on which imaging data were collected (4th, 5th and 8th of April) are marked with green vertical sections; Wind direction frequencies throughout the 2015 sampling period are indicated in the polar histogram on the right of the wind speed plot. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

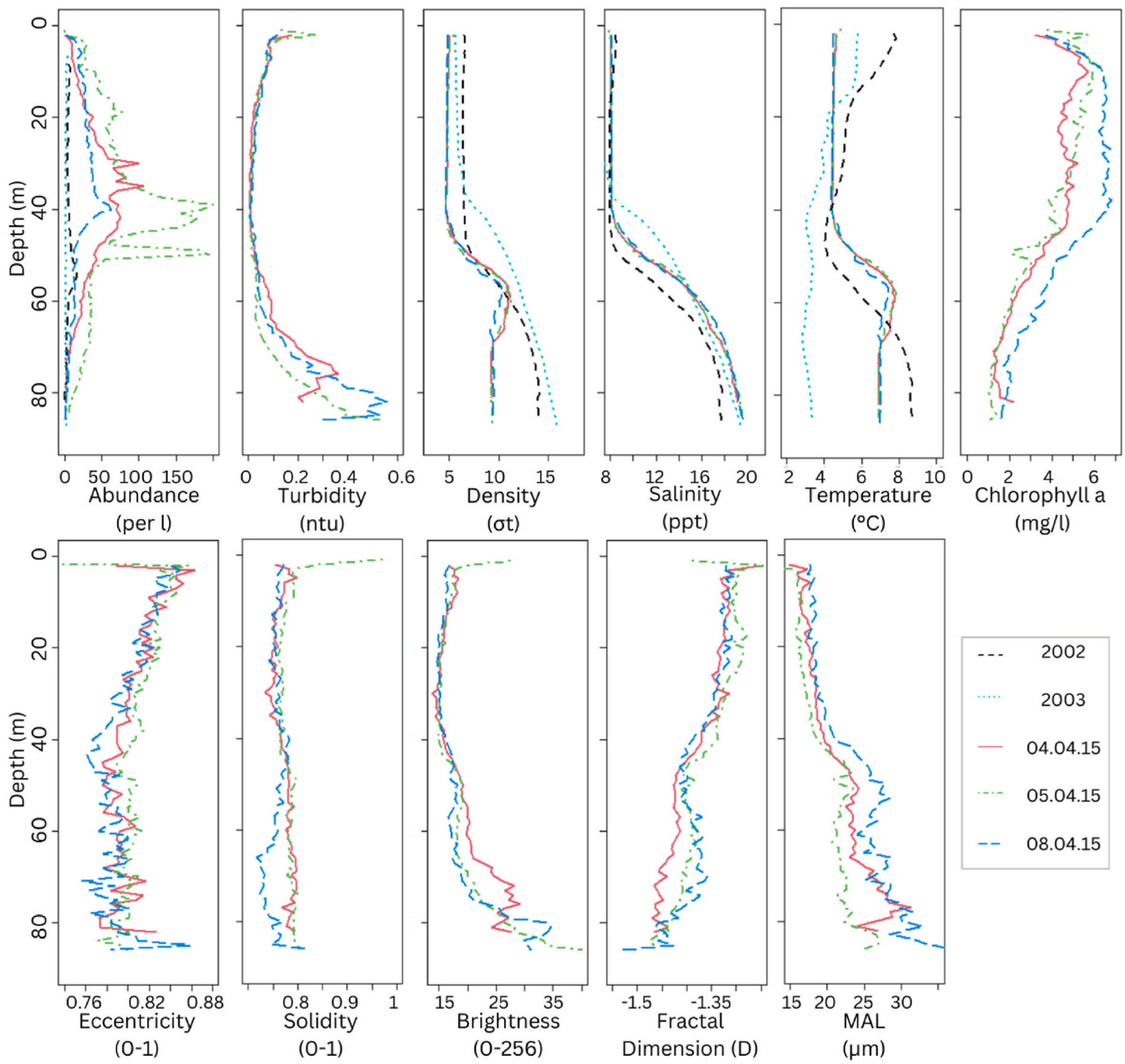

Fig. 3. Vertical profiles with daily averages of on the three Triaxus sampling days (4th, 5th and April 8, 2015) as well as the averages from the 2002 and 2003 sampling days respectively (dates in Section 2.2); Top row from left to right: 1) particle abundance (including data from 2002 to 2003), 2) turbidity, 3) density (including data from 2002 to 2003), 4) salinity (including data from 2002 to 2003), 5) temperature (including data from 2002 to 2003 and 6) Chlorophyll *a* concentration; Bottom row from left to right: 1) eccentricity, 2) solidity, 3) brightness, 4) fractal dimension, 5) size in MAL (major axis length); Line legend to the bottom right of the figure.

Table 1
Brunt-Väisälä frequencies for the water bodies above, within and below the halocline on each of the sampling days of the 2015 campaign.

Date	Complete water column	Above halocline	Inside halocline	Below halocline
April 04, 2015	2.326 rad s^{-1}	3.170 rad s^{-1}	1.230 rad s^{-1}	0.972 rad s^{-1}
April 05, 2015	2.765 rad s^{-1}	4.075 rad s^{-1}	1.255 rad s^{-1}	0.934 rad s^{-1}
April 08, 2015	2.211 rad s^{-1}	3.123 rad s^{-1}	1.163 rad s^{-1}	0.922 rad s^{-1}

and below the halocline (for detailed correlation results see Appendix 5). Particles below the halocline were larger, brighter, rounder, and less complex (see Fig. 3). OPLS analyses indicated that the halocline division of the water column (as indicated by the salinity and temperature gradients, see Fig. 3) was an important driver of particle abundance, brightness, fractal dimension and size. The assignment of one of three different parts of the water column to each data point (0–50 m = above, 50–60 m = inside, and 60 m – bottom = below the halocline; also used for Brunt-Väisälä frequency calculations, see Table 1) illustrates this further, as the indicated location respective to the halocline was a strong driver of variability in all of the factors listed above, while sheer depth of measurement impacted merely on fractal dimension and size of the particles. Chlorophyll *a* concentration was also an influential predictor of variation in both particle abundance and physical properties. The eccentricity of imaged particles was the only physical characteristic which appeared to be unconnected to any of the recorded environmental variables, which rendered meaningful OPLS analyses impossible in this case. The complete results of all OPLS models can be found in Appendix 6.

The overall AF between the 4th and the 5th of April was indicative of a slight disaggregation (depth-averaged AF = −0.20288), as particles decreased in size, solidity and complexity while increasing in abundance. Between the 4th and the 8th as well as between the 5th and the 8th of April on the other hand, the opposite was true (depth-averaged AF = 0.179264 and 0.382142 respectively; see Fig. 4).

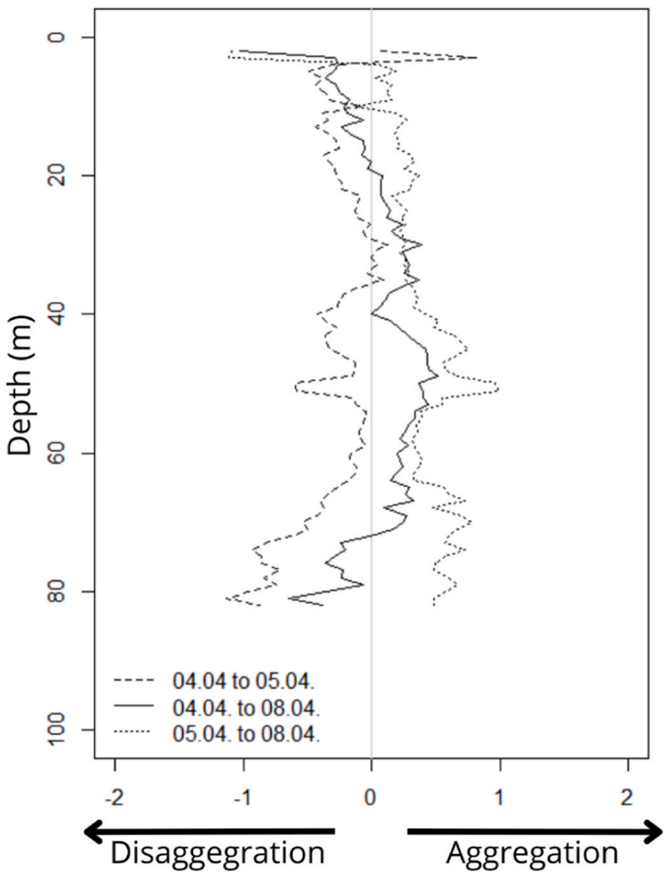

Fig. 4. Qualitative Aggregation Factor (AF) values throughout the water column, calculated in 1 m depth steps for all three days of sampling in 2015; positive values indicate potential aggregation; negative values indicate potential disaggregation.

Despite NASC values being generally higher and more variable below the halocline than above (see Fig. 3), Echosounder recordings did not reflect the observed particle distribution patterns with depth as recorded via VPR. There was also a lot of variability in the recorded NASC between, and even within days (see Appendix 7).

It is likely that the discordance of particle distributions determined via Echosounder and VPR is due to differences in physical properties and size ranges of particles most easily picked up the two sensors. While the VPR detected visually notable particles between 2.138 and 98.074 μm Equivalent Spherical Diameters (ESD) in size, the Echosounder focuses on those of contrastive density to the surrounding sea water, and likely omits particles smaller than 500 μm (Echoview Software Pty Ltd, 2022). Based on visual inspection of the imaging data, most of the marine snow flocs present are too small and consist of loosely packed detritus, and are therefore unlikely to differ much from the surrounding water in density (see Appendix 1). Because of this, and because entities registered via Echosounder cannot be clearly identified as marine snow particles, we excluded the Echosounder data from further analyses in relation to the VPR images. A big advantage of the Echosounder however, was that recordings could be made during the storm period too. During this time, while the ship was sheltering from the high winds by sampling shallower waters immediately to the east of Bornholm, unusually high NASC values were recorded all throughout the water column (see Fig. 5, top left).

4. Discussion

Marine snow is a vital component of the biological carbon cycle and the basis of pelagic and benthic food webs. Although we have a good understanding of its dynamics in general, there are clear knowledge gaps concerning the effects of meteorological extremes, which are predicted to increase in strength and frequency in the future, due to climate change. Here we investigated the impact of storms on marine snow in stratified environments, observed changes to particle distribution, as well as an increase in abundance and decrease in particle size after a storm, thus affecting particulate matter fluxes.

4.1. Physical drivers of marine snow dynamics

Although the extreme meteorological conditions throughout the sampling period appear to have had little effect on the physical and chemical stratification in the BoB, differences in the abundances and properties of the marine snow particles were observed between sampling days. The differences in Brunt-Väisälä frequencies between the different layers of the water column over all three days indicate that although the water column was gaining in stability towards the end of the sampling period (8th of April), stratification had not been compromised at the beginning (4th of April). In addition, the abundance depth profiles recorded in 2015 deviated greatly from those recorded in 2002. Conditions between the two time periods varied in terms of both inflow-strength and extreme weather conditions. Although no direct measurements of the pre-storm conditions could be taken in 2015, determining which of the two factors is more critical in explaining the different marine snow patterns is possible, as the environmental conditions and marine snow abundances and properties of 2015 were unlike those recorded in 2003, even though inflow events were recorded in both years prior to sampling. The lack of temperature gradient along the density and salinity stratification in 2003 (see Fig. 3) is likely a result of the inflow event that had happened that year, but since the particle dynamics are much more dependent on salinity and density than on temperature, this is not of consequence in the context of this study.

It has been shown that inflow events generally have little effect on suspended matter concentrations in the Baltic (Lund-Hansen and Christiansen, 2013). Storms on the other hand, can lead to resuspension, which in turn increases the particle loads in the water and promotes sedimentation (Eckhéll et al., 2000; Stigebrandt, 2001). Particularly in shallow areas, frequent resuspension is common throughout the year, whereas basins such as the BoB experience resuspension for less than three percent of each year (Christiansen et al., 1997). As the high NASC values scattered throughout the water column near Bornholm show, a likely source of additional particles in the water column in 2015, compared to abundances measured in 2002, is storm-induced resuspension and subsequent horizontal particle transport from near-by shallower areas (Håkanson and Eckhéll, 2005). The exact locations of the particles' sources are not known, as environmental measurements were only taken in the BoB itself, which, due to its depth, was likely beyond the reach of wind and wave induced critical resuspension thresholds for the muddy sediments typically found in the Baltic (Danielsson et al., 2007). Lateral transport may have caused the introduction of particulate matter from near Bornholm, or from other shallow areas within the Baltic. Particle transport models show that the relocation of matter from shallow and coastal areas to deep basins through resuspension is generally likely, and can contribute to long term carbon export and storage (Almroth-Rosell et al., 2011). There are also other disruptions, such as mechanical ones caused by demersal fishing gear that can dislodge sedimentary carbon stores at the site of resuspension (Pusceddu et al., 2005; Epstein et al., 2022), and thus increase the importance of protecting depositional sites such as the Bornholm Basin as natural long-term carbon stores. In the case of the sampling period investigated here, this is however not a likely contributor to the increase in particle numbers in the water, as seen in the AIS records. Meteorologically induced and mechanically induced resuspension from fisheries are unlikely to coincide in any way, as fishing efforts are impeded by storms (Heck et al., 2021).

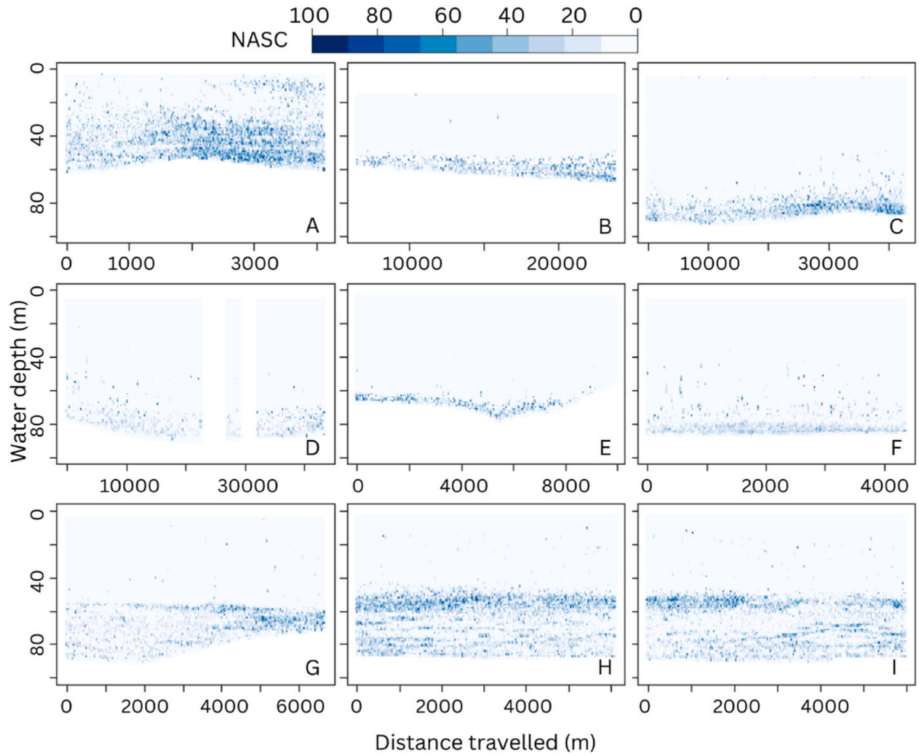

Fig. 5. Backscatter coefficients as recorded via Echosounder between the 29th of March and the April 8, 2015 (Figures correspond to days as follows: A = 29.03; B = 31.03; C = 01.04.; D = 02.04.; E = 03.04.; F = 04.04.; G = 05.04.; H = 07.04.; I = 08.04.).

4.2. Biological drivers of marine snow dynamics

Pelagic chlorophyll concentration on the other hand, proved to be one of the drivers of marine snow abundance and physical properties in 2015, so it can be assumed that this was another source of particulate matter input into the water column. Phytoplankton blooms are a well-known contributor to marine snow in most marine environments, including the Baltic (Turner, 2002; Cisternas-Novoa et al., 2019; Trudnowska et al., 2021). This could not be compared directly between the 2015 and 2002/03, due to a lack of environmental data from the earlier years. It is however known that data collection in both years also occurred during the spring bloom season between March and May during which Chlorophyll concentrations are typically at their peak (Stoń-Egiert and Ostrowska, 2022). The slight difference in bloom timing between 2002/03 and 2015 is attributable to the milder weather during the 2014/15 winter (Wasmund et al., 1998, 2016). The uncharacteristically even temperature profile recorded in 2003 is likely to have affected the plankton bloom in that year (see also Möller et al., 2012). Based on information from the annual biological assessment of the Baltic Sea reports (Wasmund et al., 2003, 2004, 2016), the 2002 and 2003 spring blooms were dominated by *Skeletonema costatum* (Greville, 1865), while the 2015 bloom featured mainly *Mesodinium rubrum* (Lohmann, 1908), followed by *Chaetoceros similis* (Cleve, 1896). This interannual variability in phytoplankton community species composition is not unusual, and may have contributed to variability in the marine snow composition (see *e.g.*, Guidi et al., 2009). All three species are known mucilage producers (Passow, 1991; Genitsaris et al., 2019), and *Skeletonema*-dominated communities have been associated with high flocculation indices (Kiørboe et al., 1994; Thornton and Thake, 1998). However, the sedimentation rates between the species vary, with Mesodinium featuring particularly low rates (Passow, 1991). According to the annual survey reports, post-bloom sedimentation was particularly fast in 2002 (Wasmund et al., 2003), and sedimentation rates were lower than average in 2015 (Wasmund et al., 2016). Based on this, the seasonal variability in organic matter production from phytoplankton blooms cannot be conclusively excluded as an additional cause of the differences in marine snow abundance between 2002/03 and 2015.

4.3. (Dis-)Aggregation dynamics

In addition to the influx of particles from external sources, the high likelihood of marine snow particle disaggregation throughout storm events might be considered (see *e.g.* Jackson et al., 1997; Milligan and Hill, 1998). The combination of lower abundances and larger particle sizes on the April 8, 2015, compared to the other two days, could be indicative of an on-going re-aggregation, following the disaggregating impact of the storm. In meteorologically stable conditions, the vertical distribution of particles in a stratified environment is influenced mostly by the presence, strength and location of the density gradient in the water column (see *e.g.* Alldredge et al., 2002; Möller et al., 2012). The irregular depth distributions recorded on all three days in 2015 therefore point towards a disturbance of the particles settled upon the density boundary, as does the variability in WMD. As indicated by conditions on the 8th being most similar to those of 2002, it is likely that re-settlement takes place within days to weeks after a storm. According to Alldredge et al. (1990), disaggregation of marine snow particles is highly likely through storm-induced turbulence. By taking particle sizes into account in combination with abundances, we can see that the Aggregation Factor indicates aggregation between the 4th/5th and April 8, 2015. This is therefore most likely a re-aggregation of marine snow flocs that had be disaggregated throughout the storm period.

There are additional factors that may impact particulate aggregation and disaggregation processes, such as the biogenic production of transparent extracellular polymer (TEP) gels. TEP-driven aggregation is affected by UV radiation and temperature as well as changes in ambient pH and salinity due to freshwater input (Ortega-Retuerta et al., 2009; Wetz et al., 2009; Mari et al., 2012; Chen et al., 2021). Thus, the lower UV input and temperatures in combination with potentially large amounts of rain (directly or through delayed fluvial input) can amplify the storm's mechanical disruption of particles through biochemical processes of disaggregation.

Other processes that may have storm-unrelated effects on aggregation dynamics include, amongst others, physical coagulation (Jackson, 1990), trophic interactions (*e.g.* Kiørboe, 2000), microbial interactions (Kiørboe, 2001), biogenic turbulence (*e.g.* Huntley and Zhou, 2004) and local phytoplankton community species composition (Riebesell, 1991; Guidi et al., 2009).

4.4. Considerations regarding data limitations

It should be noted that, while comprehensive, the data set available for this study is limited in biological and biochemical parameters, as well as in terms of temporal coverage. If data had been collected right before and during, instead of only after, the investigated storm event in 2015, the storm's effects could have been investigated better. Similarly, if a wider range of environmental parameters had been recorded alongside the imaging data, it would have been helpful for the identification of driving forces of aggregation and disaggregation. It should be noted, that the limited data availability is mainly a product of the circumstances and timing of the sampling: extreme meteorological conditions are limiting to the ship-board deployment of samplers and sensors. For example, as can be seen in Fig. 1, the profiling samplers and the TRIAXUS were not deployed in exactly the same spots. This is due to the need for calmer conditions for the deployment of the rosette sampler, while the towed equipment could be used more widely, even during periods of high winds. Due to the thus limited nature of the data immediately available to us from the sampling campaigns, information from published sources had to be consulted to be able to draw conclusions. This is suboptimal as the comparability of sampling circumstances cannot be ascertained in all instances. However, the Baltic is a particularly well-studied area, so that large amounts of information from surveys and studies are available. Hence, through the consideration of the earlier publications, conclusions drawn from the results presented in section 3 can be considered viable. However, future observations from platforms that are less sensitive to meteorological extremes, such as moorings and autonomous vehicles, are needed to further close the important knowledge gaps highlighted throughout this study.

4.5. Conclusion and future prospects

The effects current storm events have on marine snow in stratified environments, causing a clear increase in suspended matter abundance, severe particle disaggregation and change in their vertical distribution, are likely to be altered by changing conditions in the future due to climate change for several reasons. Firstly, the magnitude & frequency with which storms occur is predicted to increase (IPCC, 2019). This could cause stronger fluxes from shallow to deep areas and disrupt the re-aggregation of marine snow as well as settlement of resuspended particulate matter (see *e.g.* Madsen et al., 1993; Dobrynin et al., 2010; Ziervogel et al., 2016). The longer particulate organic matter remains in suspension, the less nutritional value it retains by the time it reaches the seafloor (Lee et al., 2004). This may be detrimental to benthic communities that rely on organic matter input from marine snow as a food source (see *e.g.* Evrard et al., 2012). Prevalence of resuspended over biologically created particulate matter could further affect the utility of marine snow as a food source to both pelagic and benthic consumers (*e.g.* Newell et al., 2005). There are also on-going trends of decreasing phytoplankton diversity and biomass, which are likely to intensify in the future and the latter of which will further reduce the organic matter supply to the water column (Andersson et al., 2015; Henson et al., 2021; Stoń-Egiert and Ostrowska, 2022). A secondary storm effect are changes in phytoplankton community composition and biochemical composition due to alterations of salinity caused by increased rainfall quantities (Reeder et al., 2022; Barrillon et al., 2023). In some cases, even zooplankton community composition can be affected by these storm impacts (Topor et al., 2022). Predicted changes in temperature and nutrient supply are likely to further affect plankton diversity, promoting the more resilient and opportunistic species (Meier et al., 2022). Other elements that may change in the future include stratification strength (Meier et al., 2022), inflow frequency (Meier et al., 2017), salinity levels and temperature (IPCC, 2019). The combinations of all these factors are likely to result in changes to the abundance and composition of marine snow, and as a consequence in carbon flux.

As the carbon balance is shifting due to climate change related processes, improving our understanding of carbon pathways through the environment is a vital tool in the protection of the environment. To this end, measurements made at high temporal resolutions with automated sensors and imaging techniques such as the ones applied in this study are a valuable asset to monitor changing conditions throughout extreme events. Although direct measurements throughout the entire evolution of a storm (before, during and after) are necessary to fill in the missing details in this particular case, the methods applied shown here have plenty of potential for short-term observations and resolving episodic events as well. Sampling in extreme weather conditions can be difficult or even impossible, which is why moored instrument carriers, floats, ROVs, AUVs and the like, with a wide range of automated sensors attached to them, should ideally be used to collect the data. Our results already indicate that storm events can affect the abundance, distribution and aggregation of marine snow, which in turn has an impact on vertical organic matter and carbon flux. With the addition of a wider range of biological, physical and chemical parameters, cause-effect relationships can be explored in more detail and the impacts of present and future storminess can be assessed more accurately. We therefore strongly recommend the execution of further, more comprehensive studies on this subject.

CRediT authorship contribution statement

Saskia Rühl: Writing – original draft, Visualization, Formal analysis, Data curation, Conceptualization. **Klas Ove Möller:** Writing – review & editing, Supervision, Funding acquisition, Data curation.

Declaration of competing interest

Our manuscript is an original work and is not being submitted to or published by any other journal. No part of it is under consideration for another publication and none of the authors have conflicts of interest to disclose concerning this publication. All authors have approved of this manuscript at the time of submission. The funding body financially supporting the study was not directly involved in the study design, data collection, or write-up process.

Data availability

The authors are in the process of publishing the data used in this study.

Acknowledgements

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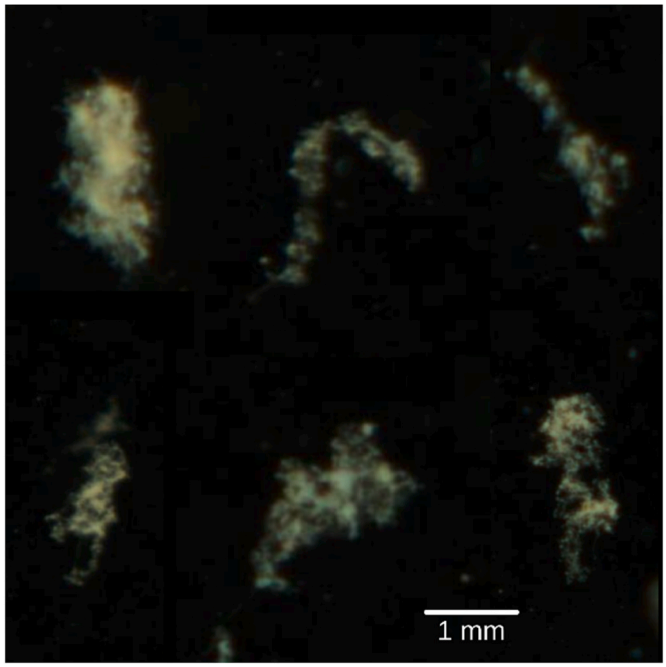
Appendices.

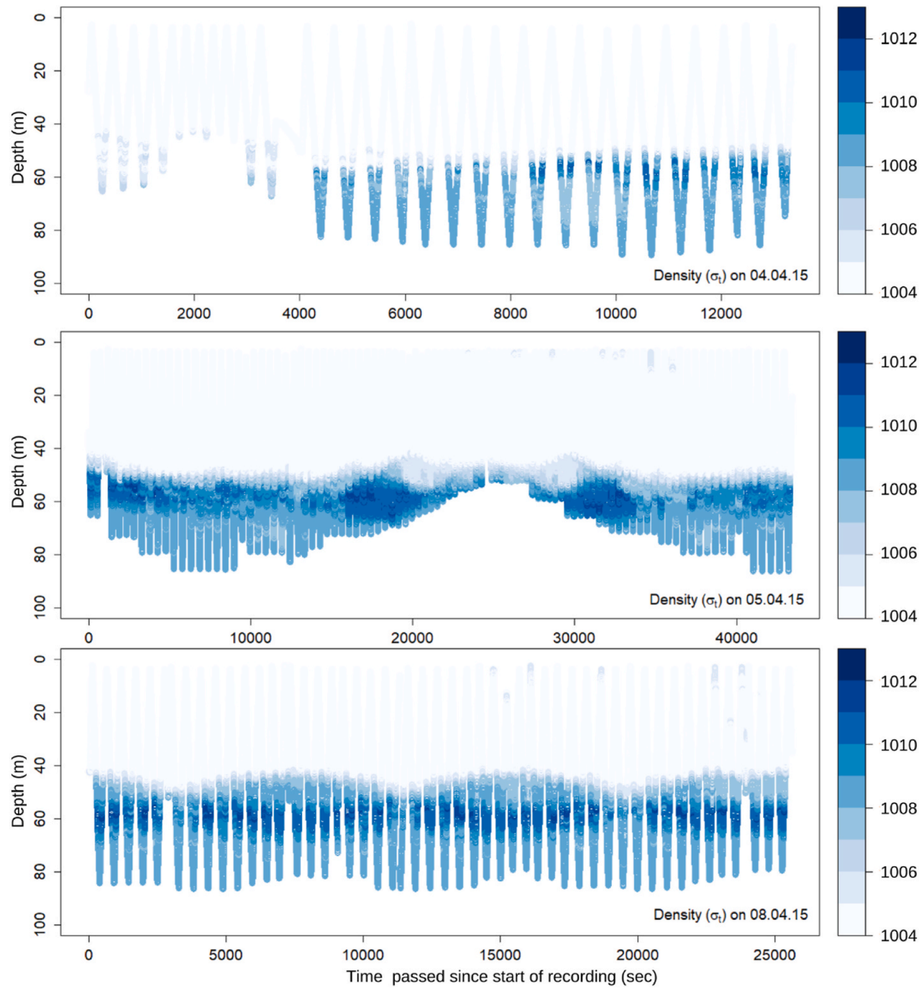
Appendix 1. Examples of VPR images of marine snow aggregates



Appendix 2. List of data sets and parameters included in this study, with associated dates of availability and data sources

Data set/parameter	Data type/measuring instrument	Dates	Source
Wind speed	Meteorological	29th of March to April 8, 2015	Rønne-Bornholm Weather station
Particle imaging	Video Plankton Recorder	4th, 5th and April 8, 2015	Sampled *in-situ* during AL453 campaign
		April–May 2002	Sampled *in-situ* during AL200 and HE168 campaigns, data from Möller et al., (2012), 2015 publications
		April–May 2003	Sampled *in-situ* during AL219 and AL220 campaigns, data from Möller et al., (2012), 2015 publications
Acoustic backscatter	Echosounder	29th of March to April 8, 2015	Sampled *in-situ* during AL453 campaign
Density	CTD Rosette	29th and March 31, 2015; 1st, 2nd, 3rd, 7th and April 8, 2015	Sampled *in-situ* during AL453 campaign
		April–May 2002	Sampled *in-situ* during AL200 and HE168 campaigns, data from Möller et al., (2012), 2015 publications
		April–May 2003	Sampled *in-situ* during AL219 and AL220 campaigns, data from Möller et al., (2012), 2015 publications
Salinity	CTD Rosette	29th and March 31, 2015; 1st, 2nd, 3rd, 7th and April 8, 2015	Sampled *in-situ* during AL453 campaign
		April–May 2002	Sampled *in-situ* during AL200 and HE168 campaigns, data from Möller et al., (2012), 2015 publications
		April–May 2003	Sampled *in-situ* during AL219 and AL220 campaigns, data from Möller et al., (2012), 2015 publications
Temperature	CTD Rosette	29th and March 31, 2015; 1st, 2nd, 3rd, 7th and April 8, 2015	Sampled *in-situ* during AL453 campaign
		April–May 2002	Sampled *in-situ* during AL200 and HE168 campaigns, data from Möller et al., (2012), 2015 publications
		April–May 2003	Sampled *in-situ* during AL219 and AL220 campaigns, data from Möller et al., (2012), 2015 publications
Density	Triaxus CTD	4th, 5th and April 8, 2015	Sampled *in-situ* during AL453 campaign
Salinity	Triaxus CTD	4th, 5th and April 8, 2015	Sampled *in-situ* during AL453 campaign
Temperature	Triaxus CTD	4th, 5th and April 8, 2015	Sampled *in-situ* during AL453 campaign
Turbidity	Triaxus CTD	4th, 5th and April 8, 2015	Sampled *in-situ* during AL453 campaign
Chlorophyll *a* concentration	Triaxus CTD	4th, 5th and April 8, 2015	Sampled *in-situ* during AL453 campaign

Appendix 3. Temperature dependent water density, calculated from TRIAXUS CTD measurements made during tow-yo hauls on the 4th (top), 5th (middle) and 8th (bottom) of April 2015



Appendix 4. ANOVA and Tukey HSD results

Tested variables	df	F	Pr(<F)	p
Abundance 04.04. *vs* 05.04.	79	94.9	3.97e-15	<0.001
Abundance 04.04. *vs* 08.04.	79	129.9	<2e-16	<0.001
Abundance 05.04. *vs* 08.04.	79	57.06	6.85e-11	<0.001
MAL 04.04. *vs* 05.04.	79	305.5	<2e-16	<0.001
MAL 04.04. *vs* 08.04.	79	662.5	<2e-16	<0.001
MAL 05.04. *vs* 08.04.	79	457	<2e-16	<0.001

Appendix 5. Correlation results

Tested variables	Type	t	df	p-value	cor
04.04.15, Depth *vs* MAL	Pearson's	13.869	79	<2.2e-16	0.8419377
05.04.15, Depth *vs* MAL	Pearson's	21.545	84	<2.2e-16	0.9202004
08.04.15, Depth *vs* MAL	Pearson's	25.468	82	<2.2e-16	0.9422126
04.04.15, Depth *vs* Eccentricity	Pearson's	−8.1352	79	4.753e-12	−0.6751682
05.04.15, Depth *vs* Eccentricity	Pearson's	−1.0948	84	0.2767	−0.1186071
08.04.15, Depth *vs* Eccentricity	Pearson's	−6.0221	82	4.661e-08	−0.5537577
04.04.15, Depth *vs* Solidity	Pearson's	7.2749	79	2.218e-10	0.6333805
05.04.15, Depth *vs* Solidity	Pearson's	0.26514	84	0.7916	0.02891662
08.04.15, Depth *vs* Solidity	Pearson's	−2.7311	82	0.007726	−0.2887541

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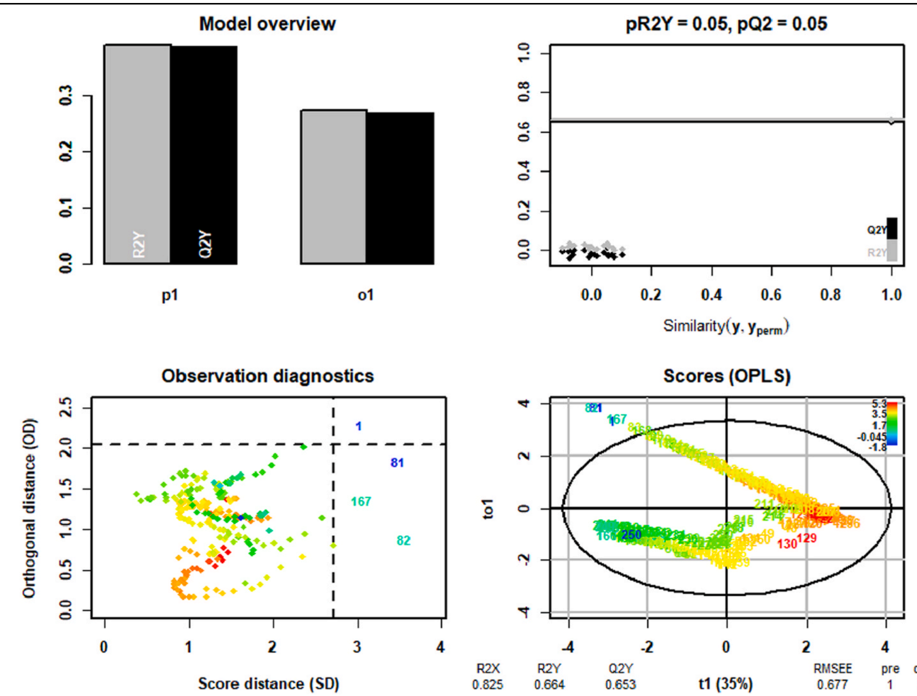
Tested variables	Type	t	df	p-value	cor
04.04.15, Depth *vs* Brightness	Pearson's	11.842	79	<2.2e-16	0.7997848
05.04.15, Depth *vs* Brightness	Pearson's	7.7075	84	2.328e-11	0.6436195
08.04.15, Depth *vs* Brightness	Pearson's	9.3687	82	1.331e-14	0.7190269
04.04.15, Depth *vs* Fractal dimension	Pearson's	−28.997	79	<2.2e-16	−0.956094
05.04.15, Depth *vs* Fractal dimension	Pearson's	−21.87	84	<2.2e-16	−0.9222854
08.04.15, Depth *vs* Fractal dimension	Pearson's	−14.198	82	<2.2e-16	−0.8431104
04.04.15, Depth *vs* Abundance	Pearson's	−1.9664	78	0.05281	−0.2173322
05.04.15, Depth *vs* Abundance	Pearson's	−1.9336	84	0.05654	−0.2064243
08.04.15, Depth *vs* Abundance	Pearson's	−6.5891	82	3.968e-09	−0.5883705

Appendix 6. OPLS Results

Model number and response variable	Predictor variables	VIP score	Model output
1 Abundance	Depth	0.0109111289774758	
	Temperature	0.978864862893056	
	Salinity	**1.09957073371875**	
	Oxygen concentration	0.877893347482074	
	Chlorophyll *a* concentration	**1.02992541135576**	
	Location respective to Halocline	**1.0962985086591**	
	Date	0.249411136586236	



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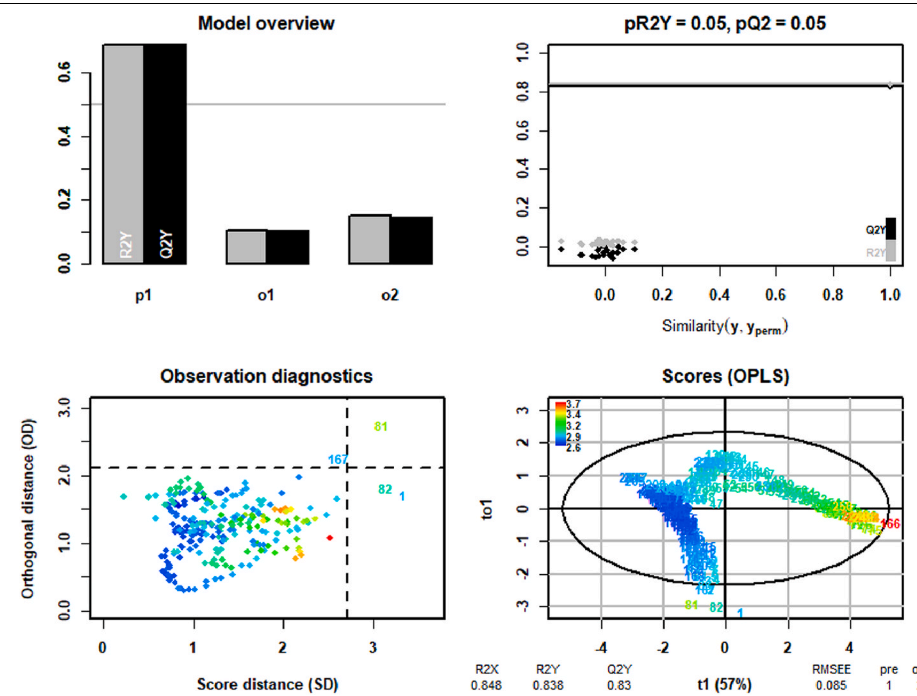
Model number and response variable	Predictor variables	VIP score	Model output
2 Brightness	Depth	0.666072839683398	
	Temperature	**1.02422342235661**	
	Salinity	**1.17985420881352**	
	Oxygen concentration	0.985611560524427	
	Chlorophyll *a* concentration	**1.20329452435879**	
	Location respective to Halocline	**1.14591023216706**	
	Date	0.107577139555124	

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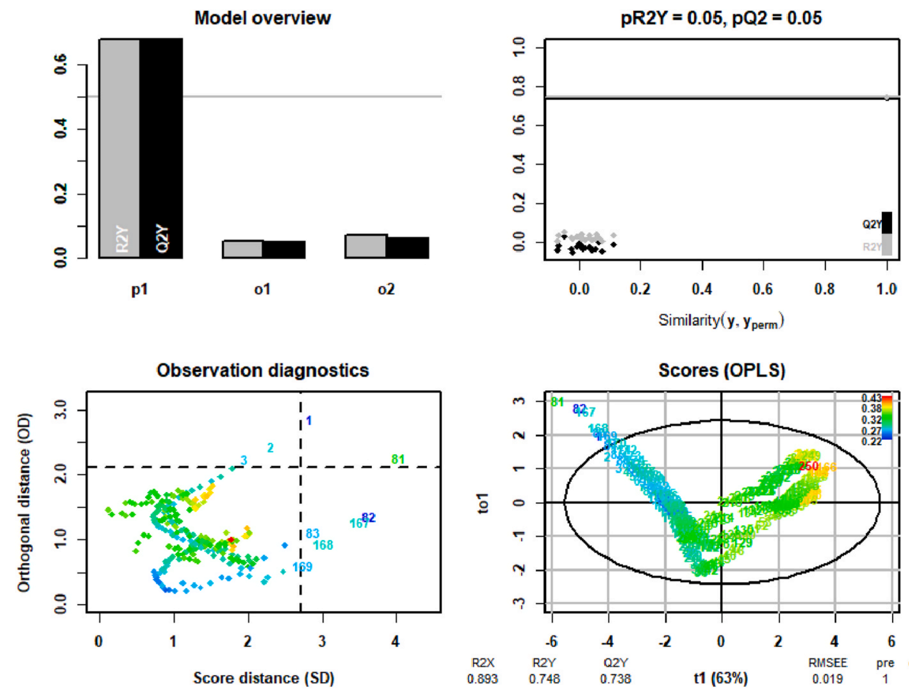
Model number and response variable	Predictor variables	VIP score	Model output
3 Fractal Dimension	**Depth**	**1.15194362793865**	
	Temperature	**1.11404603135995**	
	Salinity	**1.16181004045552**	
	Oxygen concentration	**1.13314008736184**	
	Chlorophyll *a* concentration	**1.09919061997553**	
	Location respective to Halocline	**1.12809126263408**	
	Date	0.082597093713237	

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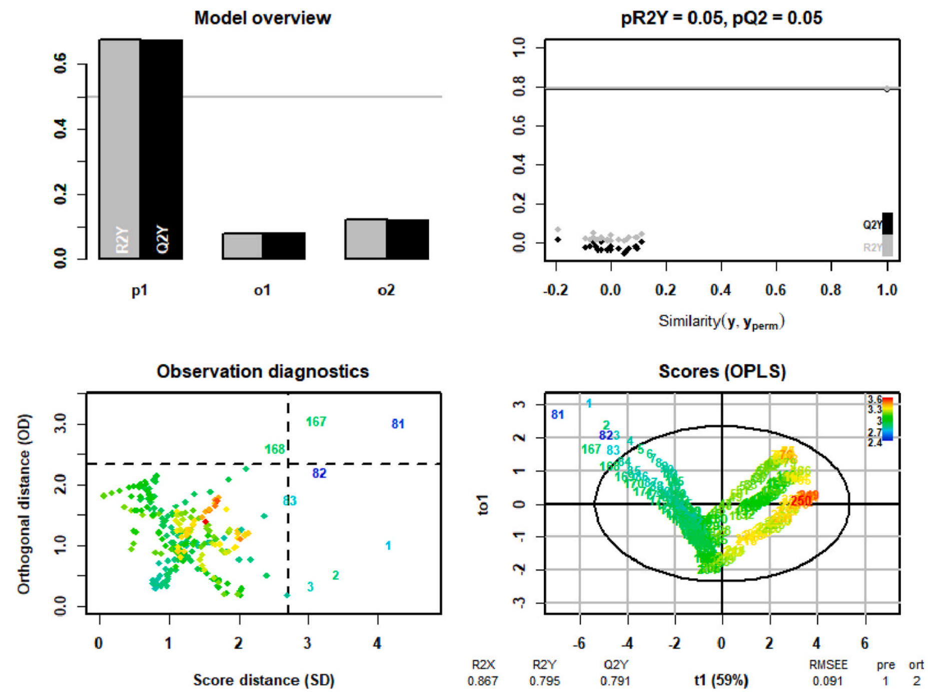
Model number and response variable	Predictor variables	VIP score	Model output
4 MAL	**Depth** **Temperature** **Salinity** **Oxygen concentration** **Chlorophyll *a* concentration** **Location respective to Halocline** Date	**1.21079891965533** **1.10350890035386** **1.17403760810915** **1.12201994928537** **1.0082775732919** **1.13707267170178** 0.142940107592823	

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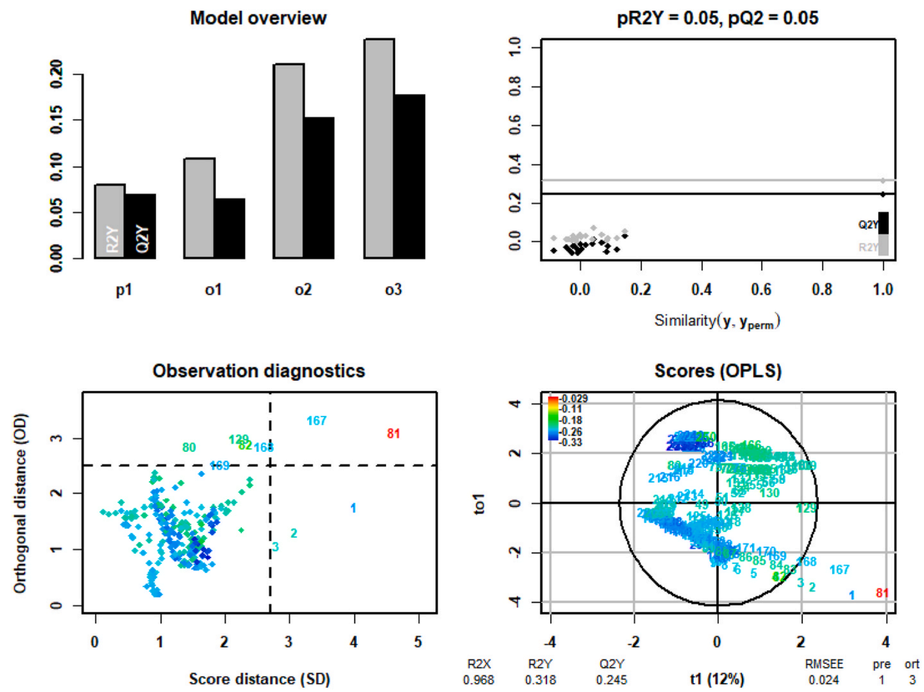
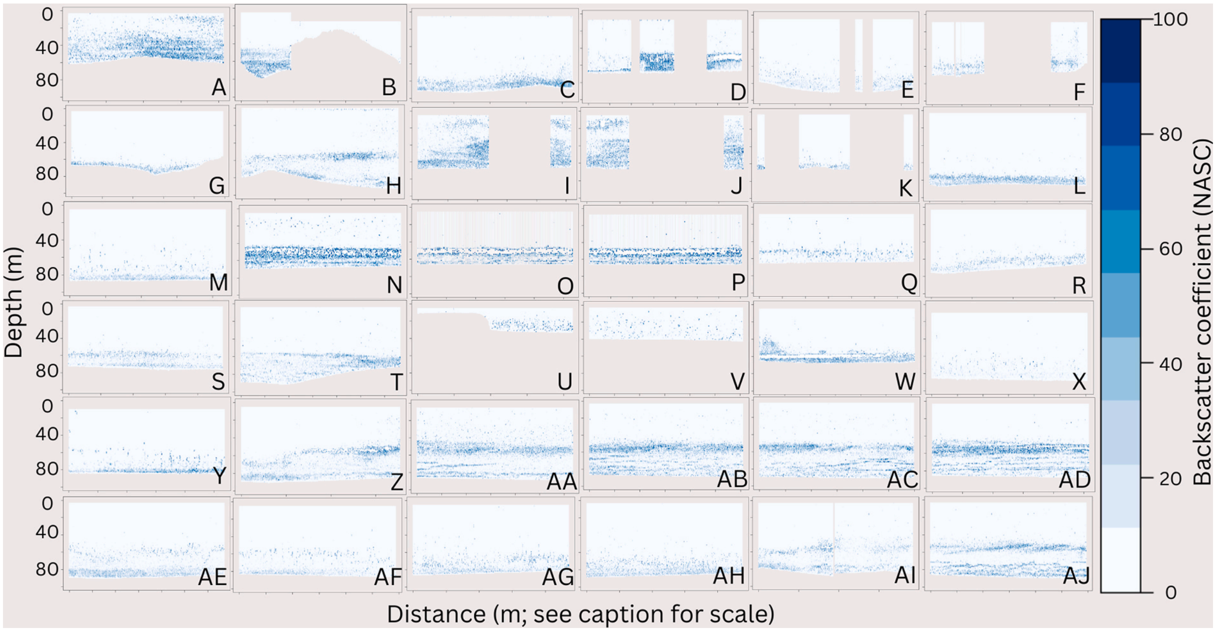
Model number and response variable	Predictor variables	VIP score	Model output
5 Solidity	Depth	0.549242071942379	
	Temperature	**1.10203556522676**	
	Salinity	0.772687456970199	
	Oxygen concentration	**1.05222371756094**	
	Chlorophyll *a* concentration	**1.42815434969219**	
	Location respective to Halocline	0.771997425553441	
	Date	**1.21598649578125**	

Appendix 7. Backscatter coefficients as recorded via Echosounder between the 29th of March and the April 8, 2015



Dates and distances covered as follows: A) 29.03.15, 0–4000 m; B) 30.03.2015, 0–12000 m; C) 01.04.15, 0–40000 m; D) 02.04.2015, 0–7000 m; E) 02.04.15, 0–40000 m; F) 02.04.15, 0–50000 m; G) 03.04.15, 0–10000 m; H) 03.04.15, 0–50000 m; I) 03.04.15, 0–10000 m; J) 04.04.15, 0–9000 m; K) 04.04.15, 0–13000 m; L) 04.04.15, 0–10000 m; M) 04.04.15, 0–4500 m; N) 04.04.15, 0–3000 m; O) 05.04.15, 0–1100 m; P) 05.04.15, 0–1400 m; Q) 05.04.15, 0–3500 m; R) 05.04.15, 0–20000 m; S) 05.04.15, 0–10000 m; T) 05.04.15, 0–6500 m; U) 06.04.15, 0–4000 m; V) 06.04.15, 0–3000 m; W) 07.04.15, 0–12000 m; X) 07.04.15, 0–6000 m; Y) 07.04.15, 0–2600 m; Z) 07.04.15, 0–20000 m; AA) 07.04.15, 0–6000 m; AB) 07.04.15, 0–6000 m; AC) 08.04.15, 0–6000 m; AD) 08.04.15, 0–5000 m; AE) 08.04.15, 0–13000 m; AF) 08.04.15, 0–6000 m; AG) 08.04.15, 0–9000 m; AH) 08.04.15, 0–10000 m; AI) 08.04.15, 0–40000 m; AJ) 08.04.15, 0–12000 m.

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