

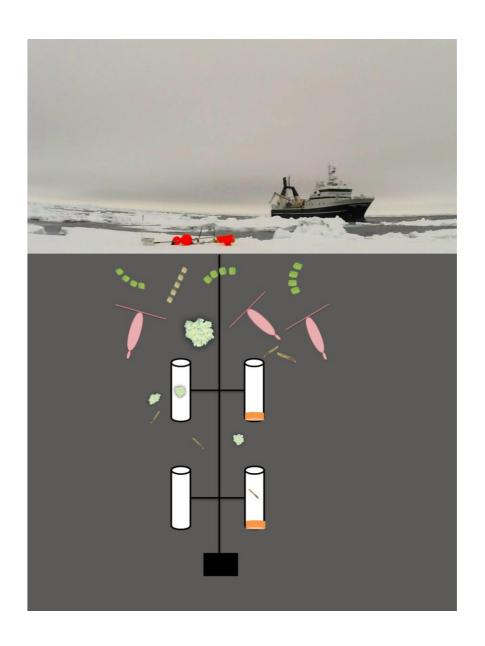
Faculty of Biosciences, Fisheries and Economics Department of Arctic and Marine Biology

Potential drivers of the downward carbon and particle flux in Arctic marine ecosystems under contrasting hydrographical and ecological situations

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Ingrid Wiedmann

A dissertation for the degree of Philosophiae Doctor – July 2015





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ONCE YOU HAVE A TASTE FOR THE OCEAN, $\mbox{THE INTOXICATION LASTS A LIFE LONG.}$ $\mbox{TREVOR NORTON}$

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ABSTRACT

In Arctic marine ecosystems, hydrography, nutrient concentrations and ecological interactions of plankton change with season, which, in turn, affects the downward flux of particulate organic carbon (POC). Climate warming induces further changes, but detailed predictions of the future downward POC flux in Arctic regions are challenging due to the poor mechanistic understanding of potential drivers.

Here, short-term sediment traps, partly modified with gel-containing jars (gel traps), were deployed under contrasting hydrographical and ecological situations in the Barents Sea and Adventfjorden, Svalbard. In this way, the downward POC and the particle flux (≥ 0.05 mm equivalent spherical diameter determined in an image analysis, ESD_{image}) was quantified in a parallel manner, and POC sedimentation could be aligned with characteristics of sinking particles (e.g., size, POC: volume ratio) and be used to refine the understanding of potential drivers of the downward POC flux.

In the Barents Sea, three stations were investigated along a north-south gradient of stratification, turbulent mixing and phytoplankton bloom stage (late peak bloom, late bloom, post bloom, respectively). The highest downward POC flux (260-670 mg POC m⁻² d⁻¹) occurred at the ice-free, weakly stratified and deeply mixed southernmost station. Sinking particles were here < 1.00 mm ESD_{image} and the particle volume flux was low (30-90 m: 40-130 x 10³ mm³ m⁻² d⁻¹), resulting in a high POC: volume ratio of the sinking material. It is assumed that the high upward nitrate flux stimulated new production in the mixing layer, and that the produced biomass enhanced the downward POC flux in two ways. On the one hand, the biomass was fast transported to deeper layers by vertical mixing and on the other hand, zooplankton grazed and repackaged biomass into fast-sinking pellets, which matched the observed POC: volume ratio.

The seasonal study in Adventfjorden was conducted during winter, spring and autumn. The highest POC flux was found during autumn (mid-September, 770-1530 mg POC m⁻² d⁻¹), when glacial run-off occurred. High volume flux (2150-6190 x 10³ mm³ m⁻² d⁻¹) and large sinking particles (0.05-3.62 mm ESD_{image}) with a low POC: volume ratio were associated with this flux at two sampling depths. According to Stokes' Law, large particles tend to sink fast, and thus they may have caused a high downward POC flux despite the low POC: volume ratio. Further, entrained terrestrial POC apparently enhanced the downward POC flux in the fjord. The high downward flux was most likely also promoted by ballasting effects by

entrained lithogenic material as well as the formation of large aggregates by flocculation processes or pteropods, but further detailed investigation of these drivers is needed.

In conclusion, it is illustrated here that a high downward POC flux in Arctic marine ecosystems may occur during the phytoplankton bloom, but can also take place in deep-mixed waters during a post bloom situation or coastal regions affected by glacial run-off. The present study further shows that high POC downward flux is not necessarily caused by large sinking particles or a high sinking particle volume, but may also occur in form of small particles with a high POC: volume ratio.

TABLE OF CONTENTS

	ABSTRACT	i
	LIST OF PAPERS.	2
1	Introduction.	3
2	BACKGROUND	
2.1	SEASONALITY OF THE DOWNWARD POC FLUX IN ARCTIC MARINE ECOSYSTEMS	6
2.2	FORMATION, MODIFICATION AND CHARACTERISTICS OF SINKING PARTICLES	9
3	OBJECTIVES.	14
4	SAMPLING AREA AND METHODS	
4.1	BARENTS SEA	15
4.2	Adventfjorden	16
4.3	METHODS	17
5	RESULTS AND DISCUSSION	
5.1	SUSPENDED AND SEDIMENTED BIOMASS IN A SEASONAL CONTEXT	20
5.2	SEASONAL AND SPATIAL VARIATION IN SINKING PARTICLES' CHARACTERISTICS	
	(SIZE COMPOSITION AND POC: VOLUME RATIO)	25
5.3	POTENTIAL DRIVERS OF THE DOWNWARD POC AND PARTICLE FLUX	
5.3.1	VERTICAL TURBULENT MIXING	28
5.3.2	UPWARD NITRATE FLUX.	30
5.3.3	Phytoplankton	33
5.3.4	ZOOPLANKTON	34
5.3.5	GLACIAL RUN-OFF.	36
6	CONCLUSION: DRIVERS OF HIGH POC FLUXES IN THE BARENTS SEA AND	
	Adventfjorden	39
7	Outlook	43
	REFERENCES	44
R∩v 1·	WHAT IS A PARTICLE?	11
Rox 2.	Challenges in Particles Image Analysis	19

LIST OF PAPERS

PAPER I

Wiedmann I, Reigstad M, Sundfjord A, Basedow S (2014) Potential drivers of sinking particle's size spectra and vertical flux of particulate organic carbon (POC): Turbulence, phytoplankton and zooplankton. *Journal of Geophysical Research: Oceans*, 119: 6900-6917. doi: 10.1002/2013JC009754.

PAPER II

Wiedmann I, Tremblay JE, Sundfjord A, Reigstad M, Upward nitrate flux and downward particulate organic carbon (POC) flux along a gradient of stratification and turbulent mixing in an Arctic shelf sea, Barents Sea.

(Manuscript formatted to the standards of Journal of Geophysical Research: Oceans).

PAPER III

Wiedmann I, Reigstad M, Marquardt M, Vader A, Gabrielsen T M, Seasonality of vertical flux and sinking particle characteristics in an ice-free high Arctic fjord – different from sub-Arctic fjords?

(Submitted after revision to Journal of Marine Systems).

1 Introduction

The present scenario of climate warming causes considerable changes in the Arctic hydrographical environment (Carmack and McLaughlin, 2011; IPCC, 2013; Lique, 2015), its marine ecosystems (Kahru et al., 2011; Wassmann et al., 2011; Arrigo and van Dijken, in press), and the ability of the Arctic seas to function as a carbon sink (Wassmann and Reigstad, 2011). Especially the latter is challenging to predict, because it is controlled by various changing physical and biological factors, as illustrated by the following examples:

A reduced and weakened sea-ice cover exposes the Arctic seas to greater wind mixing and surface stress (Rainville et al., 2011; Martin et al., 2014). Direct mechanical wind mixing and wind-induced shelf upwelling potentially replenishes nutrient concentrations in the euphotic zone during the productive summer season (Sakshaug and Slagstad, 1992; Carmack et al., 2004; Spall et al., 2014). Pulsed nutrient renewal like this has been simulated in a mesocosm study, and there it caused an enhanced downward flux of biomass (chlorophyll *a* and particulate organic carbon) (Svensen et al., 2002).

At the same time, the Arctic surface waters tend to freshen due to increased melting of the sea-ice cover, stronger glacial melt water run-off and changes in the hydrological cycle (Arendt et al., 2002; Carmack and McLaughlin, 2011; Bamber et al., 2012). This strengthens the water column stratification and restricts both the downward mixing of biomass and the upward nutrient flux into the surface layer (Carmack and McLaughlin, 2011). Low nutrient concentrations in the surface favor small phytoplankton cells (< 2 µm) as it has been observed in the Canadian Arctic (Li et al., 2009; Li et al., 2013). The high surface: volume ratio of these cells gives them a competitive advantage for the nutrient uptake under these conditions. Small cells also tend to have lower sinking velocities than large cells (Richardson and Jackson, 2007), and a shift in the phytoplankton community toward smaller cells may cause a decline in the downward biomass flux.

Zooplankton is a major regulating factor of the downward biomass flux (Turner, 2002; Turner, 2015). In case of a warming Arctic with earlier ice-break up and earlier phytoplankton spring blooms (Kahru et al., 2011; Arrigo and van Dijken, in press), a temporal mismatch of the primary production peak and the maximum abundance of certain life stages of the Arctic copepod *Calanus glacialis* may occur (Søreide et al., 2010). Sinking of ungrazed autotrophic biomass could enhance the downward biomass flux, but the impact of northwards moving

species, such as temperate zooplankton and fish species (Slagstad et al., 2011; Dalpadado et al., 2012; Fossheim et al., 2015), is still rather unclear.

Glacial run-off from land increases in some parts of the Arctic (Bamber et al., 2012). It has been suggested that entrained nutrients locally stimulated primary production in a Greenlandic fjord (Jensen et al., 1999). In the case that the produced biomass is not utilized by grazers, it may enhance the downward biomass flux. Lithogenic material, entrained with the glacial run-off, has a high density and a high sinking velocity (De La Rocha and Passow, 2007) and it may ballast sinking of organic aggregates and enhance the downward biomass flux.

These examples illustrate that predicting the downward biomass flux in a future (warmer) Arctic is challenging due to a variety of influencing factors as well as the high temporal and spatial variability in the Arctic (Wassmann et al., 2004). Studies covering different seasons, hydrographic situations and contrasting Arctic marine ecosystems are therefore needed to further develop the mechanistic understanding and improve predictions of the (future) downward biomass flux.

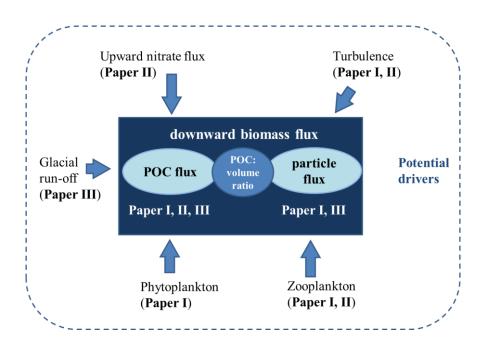


Figure 1: Schematic overview illustrating the structure of the present study. Downward biomass flux was here studied as POC flux and particle flux (interlinked via the POC: volume ratio) and different potential drivers of the fluxes were examined. Detailed information on the downward POC and particle flux and its potential drivers can be found in **Paper I-III** (see List of papers).

In the present study, I focus on the downward biomass flux and its potential drivers during contrasting scenarios of stratification, season and biological setting (bloom/ not-bloom) in an Arctic shelf sea (Barents Sea) and an Arctic fjord (Adventfjorden, western Svalbard). The downward flux was quantified as (1) flux of particulate organic carbon (POC > 0.7 μ m, Figure 1) and (2) particle flux (particles \geq 50 μ m equivalent spherical diameter, ESD_{image}, collected in "gel traps" and quantified in an image analysis, Figure 1). Both fluxes could be interlinked by the POC: volume ratio of the particles (**Paper I, III**). Small-scale turbulence (**Paper I)**, upward nitrate flux (**Paper II**), phyto-/ zooplankton abundance (**Paper I, III**) and glacial run-off (**Paper III**) were examined as potential drivers of the downward flux.

2 BACKGROUND

2.1 SEASONALITY OF THE DOWNWARD POC FLUX IN ARCTIC MARINE

ECOSYSTEMS

Sun light penetrates the surface ocean and stimulates autotrophic biomass production in the euphotic zone (> 1% surface irradiance). Buesseler and Boyd (2009) described this surface layer as the zone, "where the 'strength' of the biological pump is set". The abundance and composition of the autotrophs in this layer determine how much biomass is produced by photosynthetic processes.

Heterotrophic grazers utilize the produced biomass and can often be found associated with a subsurface Chl *a* maximum or somewhat below it in the upper twilight zone (< 1 % surface irradiance) (Longhurst and Glen Harrison, 1989; Checkley Jr. et al., 2008), causing a strong biomass attenuation (Olli et al., 2002; Reigstad et al., 2008; Olli, 2015). In other words, the ecological interactions of primary producers and consumers in the upper twilight zone define "the 'efficiency' of the biological pump" (Wassmann et al., 2003; Buesseler and Boyd, 2009).

The downward POC flux in Arctic marine ecosystems is affected by the alternation between the polar night during winter (e.g. 78°N: from mid-November to end of January) and the period of midnight sun during the summer (e.g. 78°N: from mid-April to late August). This causes strong seasonal changes in light, temperature and environmental conditions, which, in turn, influence hydrography, phyto-/ zooplankton abundance and composition. The ecological interaction of these parameters then determines the downward POC flux.

A compilation of POC fluxes (200 m) from both long-term and short-term deployed sediment traps in Arctic regions with and without seasonal ice-cover illustrates a high spatial variability, especially depending on the ice break-up. Nevertheless, it also shows that there is a seasonal cycle in the downward POC flux, and that more POC tends to sink out during the productive summer period than in winter (January to April, Figure 2).

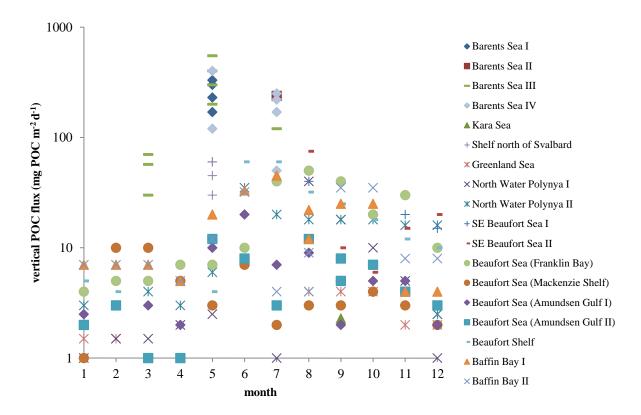


Figure 2: Compilation of downward POC flux measurements at 200 m from the Barents Sea (Barents Sea I: Andreassen and Wassmann, 1998; Barents Sea II: Coppola et al., 2002; Barents Sea III: Olli et al., 2002; Barents Sea IV: Reigstad et al., 2008), the Kara Sea (Wassmann et al., 2004), the shelf north of Svalbard (Andreassen et al., 1996), the Greenland Sea (Noji et al., 1999), the North Water Polynya (Hargrave et al., 2002), the Beaufort Sea (Beaufort Shelf: O'Brien et al., 2006; Beaufort Sea (Franklin Bay): Forest et al., 2008; Beaufort Sea (Mackenzie Shelf, Amundsen Gulf I+II): Lalande et al., 2009; SE Beaufort Sea I+II: Forest et al., 2013), and Baffin Bay (Lalande et al., 2009). Please note the log scale on the y-axis.

The seasonal changes in the hydrography, ice cover and plankton dynamics cause variations of the downward POC flux throughout the year. Convection, brine formation and wind cause deep-mixing in Arctic seas during winter (Yang et al., 2004; Ingvaldsen and Loeng, 2009). Nitrate, the primary limiting nutrient in the Arctic (Tremblay and Gagnon, 2009) is replenished in the euphotic zone, if these mixing processes penetrate below the nitracline. Since microalgae are light-limited during the winter and deep convectional mixing counteracts the biomass build-up (Behrenfeld, 2014), their concentrations remain low (Eilertsen and Degerlund, 2010; Vader et al., 2014).

Ice algae blooms are observed under the sea ice cover in April and May (Ji et al., 2013). When the ice breaks up, the algal cells are released into the water column. They form an

important food source for pelagic grazers, but also contribute to the downward POC flux (Tremblay et al., 1989; Tamelander et al., 2009).

In seasonally ice-covered regions, the phytoplankton spring bloom takes place dependent on latitude and ice break-up between May and August (Leu et al., 2011 and citations therein). In contrast, it can already be observed in April/ May in ice-free high latitude regions. The bloom is commonly dominated by diatoms and the prymnesiophyte *Phaeocystis pouchetii* in northern Norway, the Barents Sea, and waters around Svalbard (Degerlund and Eilertsen, 2010). Senescent diatom cells and resting stages are frequently observed after the peak bloom stage (Eilertsen et al., 1981; Hegseth and Sundfjord, 2008). They have a high sinking velocity (Eppley et al., 1967; Sugie and Kuma, 2008) and commonly cause a substantial POC sedimentation associated with the bloom (Thompson et al., 2008; Rynearson et al., 2013).

The strong nitrate drawdown during the first part of the bloom (Dugdale and Goering, 1967; Kristiansen et al., 1994) causes a decline in the nitrate concentrations in the euphotic zone. This induces a gradual shift from the nitrate based new production to a regenerative production, based on ammonium, urea or other biogenic nitrogen compounds (Kristiansen et al., 1994). Small autotrophic cells (< 10 μ m, Hodal and Kristiansen, 2008) become abundant, which are better adapted to take up nutrients at low concentrations due to their higher surface to volume ratio.

While mesozooplankton species like *Metridia longa* and some small omnivorous/detritivorous taxa (e.g. *Oithona* spp., *Pseudocalanus* spp.) actively graze throughout the year (Hirche and Kosobokova, 2011; Tommasi et al., 2013; Darnis and Fortier, 2014), the life cycle of e.g. *Calanus* spp. is adapted to the timing of the microalgae bloom (Søreide et al., 2010; Melle et al., 2014). This taxon goes into diapause during winter, but the timing of different life cycle stages is adjusted to the peak bloom of ice algae and phytoplankton. Accordingly, *Calanus* spp. may exert a strong grazing pressure and reduce the downward POC flux, but this repackaging of organic material into fast-sinking fecal pellets may also increase the sinking velocity of the sedimenting biomass (Thompson et al., 2008; Wexels Riser et al., 2008).

Wassmann et al. (1991) proposed a conceptual model of nutrient concentration and phyto-/zooplankton biomass throughout the year. It describes a major POC sedimentation linked to the weak temporal coupling of the phytoplankton peak bloom and the zooplankton maximum abundance during summer (Figure 3). Throughout the last 15 years, some more details of the

Arctic marine ecosystem were revealed, such as weak downward POC flux during winter (Forest et al., 2008) and the contribution of ice algae to the POC sedimentation (Tamelander et al., 2009; Søreide et al., 2013). These aspects are included in a new version of the conceptual model of the Arctic pelagic ecosystem and the downward POC flux (Wassmann and Reigstad, 2011), but the basic pattern is still the same with the highest downward POC flux taking place linked to the phytoplankton spring bloom.

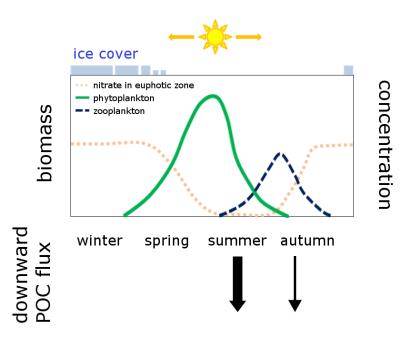


Figure 3: Conceptual understanding of the Arctic pelagic ecosystem with seasonal ice cover (with nitrate concentration, phyto-/ and zooplankton biomass) and the associated downward POC flux throughout the year (modified from Wassmann et al., 1991; Wassmann and Reigstad, 2011).

2.2 FORMATION, MODIFICATION AND CHARACTERISTICS OF SINKING PARTICLES

The intensity of the downward POC flux has been determined by (1) in-situ pumps and a settling model (Bishop and Edmond, 1976; Liu et al., 2009), (2) deployment of sediment traps (Zeitschel et al., 1978), filtration of the collected material and analysis of the filters (Ehrhardt, 1983)(**Paper I-III**), as well as (3) using disequilibria of particle-reactive tracers like ²³⁴Th, ²¹⁰Po, or ²¹⁰Pb with their soluble parent element in the water column (Moran, 2004; Stewart et al., 2007; Gustafsson and Andersson, 2012).

All of these methods determine a downward bulk flux, but POC is not a "single amorphous category […] of undefined behavior and uniform property" (De La Rocha and Passow, 2007). The particles of organic carbon have distinct characteristics like shape, composition, density,

and sinking velocity, which crucially determine the downward POC flux (De La Rocha and Passow, 2007; Passow et al., 2014; Durkin et al., in press).

An increasing number of "particle studies" has been conducted during the last years (Lundsgaard et al., 1999; Waite et al., 2000; Ebersbach and Trull, 2008; Ebersbach et al., 2011; Laurenceau-Cornec et al., 2015; Durkin et al., in press; Nowald et al., in press). All these investigations used short-term sediment traps modified with gel-containing jars, which allowed collecting sinking particles with a largely conserved three dimensional structure. Despite the increasing number of studies, the terminology of the term "particle" is still challenging and strongly dependent on the research discipline (Box 1).

In the present work, a "particle" is used as an umbrella definition for particulate material $\geq 50~\mu m~ESD_{image}$ and includes algal and detrital aggregates, fecal pellets, and conglomerates of these units.

Stokes' Law tightly connects particles size and sinking velocity (Mann and Lazier, 2006) and suggests that small particles sink slowly and large particles sink fast. Following this argumentation, aggregation of small particles into larger ones increases the sinking velocity and the downward biomass flux. Two mechanistic concepts of aggregation were described by Kiørboe (2001): aggregation via physical coagulation (Figure 4a) and a zooplankton mediated pathway (Figure 4b).

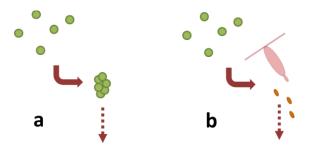


Figure 4: Aggregate formation by a) physical coagulation (collision and adhesion of particles) and b) zooplankton mediated (modified from Kiørboe, 2001).

Box 1: What is a "particle"?

Hill (1998) describes various important roles for particles in the sea and states that the "understanding of particles is a keystone of overall understanding of the seas". However, he leaves us without a clear definition of the term "particle". A short and certainly incomplete compilation of literature indicates that it is frequently used in different fields of marine geology and marine biology. The upper size limit for a particle is not defined (even jellyfish may be regarded as particles in a Lagrangian tracking model, Lee et al., 2013), and also the lower limit is somewhat blurry, but set at the transition stage of particulate and dissolved material (Azam and Malfatti, 2007).

In a geological framework, "particle" is used as an umbrella term for "sand and silt grains, clay casts, mineral-bearing fecal pellets, flocculates, and agglomerates" (Syvitski and Murray, 1981). The sub-categories "aggregates", "agglomerates" and "flocculates" are then defined by the type of compound material (inorganic or organic) as well as the force holding the units together (surface tension, electrostatic, cohesive forces).

In the field of marine biology, less focus is put on the combining forces, but particles are defined by size and origin.

In biogeochemical work, "particle flux" is often used synonymously with the downward flux of particulate organic material (POM) or particulate organic carbon (POC) (e.g. Andreassen et al., 1996). Particulate material is here defined in contrast to dissolved material, which passes through standard filters with a pore size of e.g. 0.7 µm (GF/F Whatmann Filters). In contrast, studies determining the POC flux based on the ²³⁴Th method often use 53 µm or 70 µm to distinguish between suspended material and sedimenting particles (Le Moigne et al., 2013). Studies using optical plankton or particle counters (e.g. LOPC: Herman et al., 2004; UVP: Stemmann et al., 2008), define "particle" in a somewhat different way, and so do groups working with short-term sediment traps modified with gel-jars ("gel traps"). Particles here often range "from individual cells through chains to assemblages of highly degraded detritus forming aggregates; they can be formed by biological processes such as cell division and fecal pellet production or indirectly by coagulation of particles due to differential settling and turbulence" (Stemmann and Boss, 2012). Dependent on the applied instruments and sampling/ analysis technique different particle size ranges are included (> 11 μ m, Durkin et al., in press; \geq 50 μ m, **Paper I, III**; > 73 µm, McDonnell and Buesseler, 2010; > 150 µm, Ebersbach and Trull, 2008).

The coagulation theory describes physical coagulation as a two-step process: Particles collide in the water column, and the collision rate primarily depends on the particle abundance (Jackson, 1990), differential sinking velocities (Alldredge, 2001) and turbulent mixing (McCave, 1984; Kiørboe et al., 1990). As a second step, some 'natural glue' ensures coagulation after collision. This can either be sticky phytoplankton cells or adhesive extracellular polymeric substances, which are excreted by microalgae or bacteria associated with them (Kiørboe and Hansen, 1993; Thornton, 2002; Gärdes et al., 2011). As particles

stick together after collision, larger aggregates are formed. The coagulation theory has also been verified by experiments in beakers (Kiørboe et al., 1990), roller tanks (compiled in Jackson, 2015) and mesocosm experiments (Kiørboe et al., 1994). Therefore, it is a common way to explain an enhanced POC export e.g. during the phytoplankton spring bloom, when the number of particles in the water column is high.

Algal aggregates are a special type of aggregate, because they mainly consist of one type of original particles. Alldredge and Silver (1988) coined in contrast the term 'marine snow' for conglomerates (> 0.5 mm diameter) of algal cells and other units, such as detritus, bacteria, and fecal pellets. Particles observed in the present work (**Paper I, III**) sometimes resembled the composition of marine snow, but they were smaller. To prevent confusion, these particles were not labelled "marine snow", but termed "aggregates" (**Paper III** Table 3) or "other" (**Paper I** Table 5), whereas the latter implys that they were not classified as fecal pellets or phytoplankton aggregates.

The sinking velocity and the downward POC flux can alternatively be increased, when "ballast" material with high specific weight (e.g., lithogenic matter, coccolithophores) is incorporated into (algal) aggregates and marine snow (reviewed in De La Rocha and Passow, 2007; Engel et al., 2009; Iversen et al., 2010). This is described by the "ballasting hypothesis" (De La Rocha et al., 2008), but the concept is still under discussion. A high contribution of lithogenic material has for example been shown to enhance the sinking velocity of the aggregate, but also it also increased aggregate break-up, which, in turn, reduces the sinking velocity due to the smaller particles size (Hamm, 2002; Passow et al., 2014).

Large, fast-sinking particles, which enhance the downward POC flux, are alternatively formed by zooplankton-mediated aggregation (Kiørboe, 2001, Figure 4b). Pteropods and larvaceans mediate particle formation by collecting bacteria and algal cells in their mucus feeding webs or houses, which are regularly lost or rejected and sink out as marine snow (Kiørboe, 2001). Crustacean plankton, such as copepods or krill, feed on small particles (e.g. algal cells) and re-package them into dense fecal pellets, which sink few tens to several hundreds of meters per day (Turner, 2002).

At the same time, copepods and krill also fragment fecal pellets (coprohexy) when rejecting them (Dilling and Alldredge, 2000; Iversen and Poulsen, 2007). The fragments, smaller in size, have a lower sinking velocity and are more exposed to microbial degradation processes

(Svensen et al., 2012; Giering et al., 2014). Accordingly, the "retention filter" in the upper twilight zone contributes both to the biomass attenuation in the upper twilight zone (Wexels Riser et al., 2001), but also enhances the downward POC flux by producing fast-sinking fecal pellets.

This chapter only describes the most basic lines of particle formation and modification, but it still illustrates that the term "sinking particles" integrates a variety of different types of particles and that these particles are formed and modified in size, shape and composition in numerous ways.

3 OBJECTIVES

In this thesis two different Arctic marine ecosystems, an Arctic fjord (Adventfjorden, western Svalbard) and an Arctic shelf sea (Barents Sea) were studied under contrasting hydrographical and ecological settings (i.e., bloom vs. non-bloom phase) to investigate the following questions:

- (1) Is the highest downward flux of POC and particles (collected by deployment of gel traps and \geq 50 μ m ESD_{image}) associated with the phytoplankton spring bloom? (Paper I, III)
- (2) Are turbulence (**Paper I**), upward nitrate flux (**Paper II**), phytoplankton composition and abundance (**Paper I, III**), zooplankton composition and abundance (**Paper I, III**), and the influence of glacial run-off (**Paper III**) potential drivers of the downward POC flux in these regions?

4 SAMPLING AREA AND METHODS

The present work was part of the "Conflux" project in the central Barents Sea (**Paper I, II**) and the Isfjorden-Adventfjorden (IsA) field campaign in Adventfjorden, western Svalbard (**Paper III**).

4.1 BARENTS SEA

The Barents Sea is with $1.5 \times 10^6 \text{ km}^2$ the largest Arctic shelf sea (Jakobsson et al., 2004). It has a mean depth of 200 m and is bordered by the Svalbard Archipelago, Franz Josef Land, Novaya Zemlya and the Norwegian mainland (Figure 5). Fresh and cold Arctic derived water (salinity S = 34.3-34.8, temperature T < 0.0 °C, Loeng, 1991) enters the Barents Sea from the north (eastern) edge and a seasonal ice-cover is found in the region. Saline and relatively warm Atlantic water (S > 35.0, T > 3.0 °C, Loeng, 1991) flows into the Barents Sea through the Barents Sea Opening between the Norwegian mainland and the Bear Island. This water is the oceanic main heat source for the region (Årthun et al., 2012), causing a permanently ice-free southern Barents Sea. Arctic and Atlantic derived water masses meet in the topographically steered Polar Front in the central Barents Sea. Lighter Arctic derived water covers here warmer and more saline Atlantic water.

Data presented in this thesis (**Paper I, II**) followed a stratification, turbulent mixing and bloom gradient along the 30°E longitude from the northernmost station M1 (78°N) in stratified ice-covered Artic derived waters (Figure 5) through the Polar Front (M2, 77°N) to the southernmost station M4, located in the deep-mixed ice-free Atlantic derived waters (75°N).

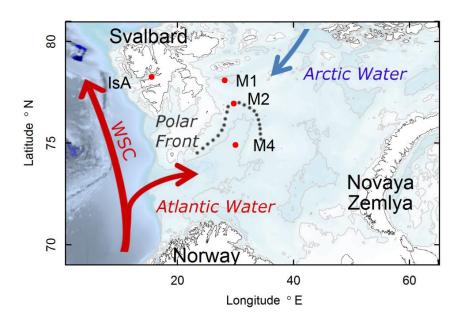


Figure 5: Map indicating the sampling stations in the Barents Sea (M1, M2, M4, **Paper I, II**) and in Adventfjorden, Svalbard (IsA, **Paper III**). Warm and saline derived Atlantic water meets Arctic derived water in the Polar Front in the Central Barents Sea. The West Spitsbergen Current (WSC) brings warm and saline Atlantic derived water to the western coast of Svalbard.

4.2 ADVENTFJORDEN

The sampling station IsA (Figure 6) was located in the mouth of the high Arctic Adventfjorden, which is a small side branch in the Isfjorden system. Since neither Adventfjorden nor Isfjorden has a sill, both fjords are strongly influenced by warm and saline water derived from the West Spitsbergen Current. The IsA station (~80 m) was permanently ice-free during our nine-month study between December 2011 and September 2012 (Table 1). During summer and autumn Adventfjorden is affected by sediment-loaded glacial melt water run-off (Advent River, Longyear River, Węsławski et al., 1999), which also influenced the present work during September 2012. Data presented here were collected during field periods covering three seasons. The field period in mid-December, mid-January and late January, was denoted as Winter I, II, III, respectively. The field sampling in late April, mid-May and late May are termed Spring I, II, III, respectively, and the mid-September investigation is denoted as Autumn I (Table 1).

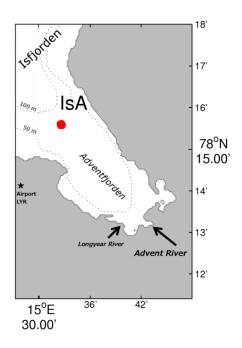


Figure 6: Detailed map of the sampling station IsA in the mouth of Adventfjorden, a side fjord of the Isfjorden system at the western coast of Svalbard (see Figure 5). Modified from **Paper III** Figure 1. Depth lines following Zajączkowski et al. (2010).

4.3 METHODS

Hydrographical data on temperature, salinity and density were measured by CTD casts and data were processed following standard procedures. Hydrography microstructure (small-scale current shear) was quantified in the Barents Sea with a loosely tethered turbulence drop sonde (Paper I, II). These data were used to determine the mixing layer, which is defined as the actively mixed surface layer with a vertical diffusivity > 10^{-4} m² s⁻¹ during the time of data acquisition (Brainerd and Gregg, 1995; background vertical diffusivity of 10⁻⁴ m² s⁻¹ defined following Paper I Figure 4b and Sundfjord et al., 2007). In contrast, the "mixed layer" describes the weakly stratified water layer above the pycnocline (Brainerd and Gregg, 1995). Suspended chlorophyll a (Chl a), POC and the atomic carbon to nitrogen ratio (C/N) were determined from sea water collected with Niskin bottles and analyzed according to standard procedures (Paper I-III). Zooplankton abundance in the Barents Sea was estimated using a Laser Optical Plankton Counter (LOPC, Paper I). In addition, zooplankton was identified and quantified in microscopic studies (Barents Sea: Svensen et al., in prep., C. Svensen, pers. comm., Paper I; Adventfjorden: Stübner et al., in rev., E.I. Stübner, pers. comm., Paper III). Short-term sediment trap arrays (Paper I, II: free floating or anchored on an ice floe, Paper III: anchored at the bottom) were deployed for ~ 24 h to study the biogeochemical flux of Chl

a and POC as well as the C/N ratio of sinking material. Deployment depths were chosen to cover the transition from the lower euphotic zone (1% surface irradiance) to the upper twilight zone. This depth interval has been described to be the zone of the highest POC attenuation (Martin et al., 1987; Olli, 2015). Sediment traps were deployed between 20 m and 200 m in the Barents Sea (Paper I, II; 20 m and 30 m only included in the present summary to allow comparison between the fjord and shelf sea data, but not included in the papers) and between 20 m and 60 m in Adventfjorden (Paper III). To limit collection of resuspended bottom material, the lowest trap was deployed approximately 20 m above the seafloor. Downward particle flux (Paper I, III) was examined by deploying sediment trap cylinders modified with gel containing glass jars, denoted as "gel traps" in the following (conceptual idea of gel traps, Lundsgaard, 1995; Lundsgaard et al., 1999; image analysis following Ebersbach and Trull, 2008; modification from acrylamidegels to commercially available gels, Thiele et al., 2015; Wiedmann et al., 2014). Gel traps were deployed at 30, 40, 60, and 90 m in the Barents Sea (Paper I) and at 20, 30, 40 and 60 m in Adventfjorden (Paper III). Gels were photographed and an image analysis was conducted. Only particles $\geq 50 \mu m ESD_{image}$ were included in the analysis, because a very low light reflection of smaller particles at the used magnification (15 x) would have caused underestimation of the number of particles < 50 µm ESD_{image} (Jackson et al., 2005). The image analysis gave information on the size composition, origin and structure of the sinking particles, which cannot be grasped in an estimation of the downward biomass bulk flux. However, some challenging steps are linked to the image analysis (Box 2).

Box 2: Challenges in Particle Image Analysis

Extracting particles from images requires a threshold level, which sets the border between the background and the particle (Figure 7). A good estimation of this threshold is necessary, because it keeps over- or underestimation of the (two-dimensional) particle size to a minimum. In the present work, I used two different approaches to determine the threshold. In Paper I, I determined the threshold using the "plot profile function" of the program ImageJ (Paper I Figure 2). The intermediate grey value between the background and the particle was chosen by eyeballing and then used for all images of one gel. This worked well for the gels deployed in the Barents Sea, because most particles had a compact form (Paper I Figure 7). They could even be distinguished from the background under not absolute optimal illumination, such as at the edges of the glass, where some reflection occurred. For the fine, detrital particulate material in Adventfjorden (Paper III Figure 6a, b), the AutoThresholding function of ImageJ was the better choice. This automatically set an optimal threshold for the analysis of each image, which was accepted or manually adjusted after visual inspection. Among the AutoThresholding functions, the Otsu clustering algorithm gave the best result and was therefore applied in Paper III.

The second challenging step in the image analysis is the conversion from the twodimensional particle area to the three-dimensional particle volume. I presumed here an ellipsoidal volume for the particles and chose the third dimension being equal to the minor axis, which reflected the elongated form of most particles.

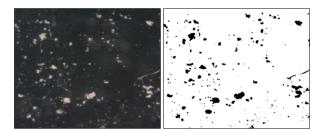


Figure 7: Original image of particles in the gel (left, black background, white particles) and after applying a thresholding process to the image (right, white background, black particles.

5 RESULTS AND DISCUSSION

5.1 SUSPENDED AND SEDIMENTED BIOMASS IN A SEASONAL CONTEXT

Investigations along a north-south transect in the Barents Sea and during a nine months seasonal study in Adventfjorden resulted in contrasting snap-shot pictures of the situation in the water column, defined by hydrography, nutrient concentrations, suspended biomass (Chl *a*, POC, phytoplankton) and downward POC flux. Here, these snap-shots are put in a seasonal context with the help of parallel conducted zooplankton studies (Svensen et al., in prep.; Stübner et al., in rev.; E.I. Stübner pers. comm.) and literature.

During winter, high nitrate surface concentrations were found in Adventfjorden, accompanied by low Chl *a* concentrations in the whole water column (Table 1, **Paper III** Figure 3). It is assumed that nitrate was replenished by convective mixing and wind mixing previous to mid-December (Winter I), which resulted in the high nitrate surface concentrations. Low Chl *a* concentrations during winter (Table 1, **Paper III** Figure 3) have previously been reported from other high-latitude regions (Węsławski et al., 1991; Eilertsen and Degerlund, 2010; Iversen and Seuthe, 2011; Vader et al., 2014). In Adventfjorden they were rather caused by limited primary production (negligible irradiance levels during the polar night) than by top-down regulation, because zooplankton abundance was low during winter (approx. 100 ind. m⁻³, Stübner et al., in rev.). Based on the high nitrate concentrations, the low Chl *a* concentrations and the low zooplankton abundance, the situations observed during mid-December, mid-January and late January (Winter I, Winter II and Winter III, respectively) was regarded to reflect a typical Arctic winter conditions.

Low downward POC fluxes have been reported from Arctic shelf seas during winter or the pre-bloom phase (Olli et al., 2002; Forest et al., 2008), but studies in an Arctic fjord show that moderate downward POC fluxes may occur in these embayments during winter (25-750 mg POC m⁻² d⁻¹; Wassmann, 1984; Noji et al., 1993; Zajączkowski et al., 2010). Moderate fluxes were also observed in Adventfjorden during the polar night (Winter II, 195-410 mg POC m⁻² d⁻¹, Figure 8), potentially caused by resuspension of bottom material, lateral advection to the middle of the fjord and subsequent sedimentation (Noji et al., 1993).

Table 1: Concentrations of suspended nitrate, chlorophyll *a* (Chl *a*) and particulate organic carbon (POC) as well as the depth of the sub-surface Chl *a* maximum (SCM) and the classification of the field periods in the Barents Sea (**Paper I-II**) and Adventfjorden (**Paper III**).

	Date	Nitrate concentration (µM) (1)	Chl a concentration (mg Chl a m ⁻³) ⁽²⁾ and depth of SCM (m)	Range of suspended POC (mg m ⁻³) (2)	Season/ ecological category
Barents Sea (BS)					_
M1 (northern BS)	22.06.11	2.8	0.2-4.3 (40 m)	160-390	late peak bloom
M2 (Polar Front)	24.06.11	1.9	0.06-1.4 (44 m)	130-320	late bloom
M4 (southern BS)	27.06.11	0.8	0.03-1.6 (45 m)	130-360	post bloom
Adventfjorden					
Winter I	14.12.11	2.8	0.04 (60 m)	43-50	winter
Winter II	18.01.12	-	0.06 (60 m)	92-144	winter
Winter III	28.01.12	7.2	0.0-0.1 (15 m)	65-73	winter
Spring I	27.04.12	4.5	0.6-2.1 (5 m)	238-324	early bloom
Spring II	10.05.12	1.5	3.2-4.2 (25 m)	235-400	peak bloom
Spring III	30.05.12	0	0.6-1.6 (60 m)	246-635	late bloom
Autumn I	19.09.12	2.6	0.3-0.4 (5 m)	94-137	autumn

⁽¹⁾ Nitrate concentration at 30 m in the Barents Sea, at 25 m in Adventfjorden

Spring bloom scenarios were investigated at three stations in the Barents Sea and during three sampling episodes in Adventfjorden.

In the Barents Sea, the stations were located along a north-south transect. Drift ice cover decreased from the northernmost station M1 (30 % sea ice) to station M2 in the Polar Front (20 % sea ice) and station M4, which was located in ice-free waters. The different stages in sea ice melt resulted in a moderately and strongly halocline driven water column stratification at the two northernmost stations, respectively. A weak, thermocline driven stratification was found in the deep-mixed waters at the southernmost station (**Paper I** Figure 3).

Associated with the north-south transect, a conceptual model of the spring bloom development has been established (Sakshaug et al., 1991; Wassmann et al., 2006; Sakshaug et al., 2009). It suggests an earlier bloom stage in the north and a later one in the south.

This bloom gradient was also observed during the present study. The integrated nitrate concentration declined from north to south (integrated to 40 m, M1: 7.04 mmol nitrate m⁻², M2: 5.43 mmol nitrate m⁻², M4: 2.31 mmol nitrate m⁻²) and implied a minor nitrate drawdown, and thus an earlier phytoplankton bloom stage, at M1 in the north than at M4 in the south. The change in the phytoplankton composition, from a diatom dominated ice edge bloom (cells > 10 μ m) in the north to a prevailing *Phaeocystis* community (cells ~5 μ m,

 $^{^{(2)}}$ Chl a and POC concentrations measured between sub-surface and 60 m

Paper I Table 3) in the south, pinpoints the same, because it has been proposed that the peak bloom stage in the Barents Sea is dominated by large cells, while small cells prevail during the early and late bloom (Hodal and Kristiansen, 2008). Taking into account these findings, M1 in the north was classified as a typical late peak bloom situation and M2 in the Polar Front as a late bloom situation (Table 1). Classification of M4 was challenging. The deep mixing layer (25 m, **Paper I** Table 3) and the comparable higher Chl *a* concentrations at 5 m (M4: 0.6 mg Chl *a* m⁻³ versus M1: 0.4 mg Chl *a* m⁻³ and M2: 0.2 mg Chl *a* m⁻³, **Paper I** Figure 5) contradicted previously reported traits of a post bloom stage, such as a strongly stratified water column and negligible Chl *a* surface concentration (Leu et al., 2006; Hodal et al., 2012). Nevertheless, M4 was here classified as a post bloom situation, because of the deep nitracline and the more advanced late spring to summer zooplankton composition, dominated by microzooplankton, small mesozooplankton species, and high abundances of mesozooplankton eggs and nauplii (Svensen et al., in prep.).

A conceptual model described by Sakshaug et al. (1991) proposes a major biomass sedimentation along the ice edge of the Barents Sea and a prevailing top-down regulation in the ice-free waters further south, channeling the produced biomass rather into the food web than contributing to export. In this study, we deployed short-term sediment traps in the marginal ice zone of the Barents Sea (M1, M2) and they indicated a downward POC flux of 150-370 mg POC m⁻² d⁻¹ (Figure 8). This met previous spring and summer data on downward fluxes observed in the region (Andreassen and Wassmann, 1998; Olli et al., 2002; Reigstad et al., 2008).

Contrasting the conceptual model of Sakshaug and co-workers (1991), the highest downward POC flux was not found along at the ice edge, but observed in the ice-free southern Barents Sea (M4: 261-600 mg POC m⁻² d⁻¹, Figure 8). This has occasionally been reported before during spring and summer (Olli et al., 2002; Reigstad et al., 2008), but mechanisms causing the high flux during the post bloom situation remained poorly understood.

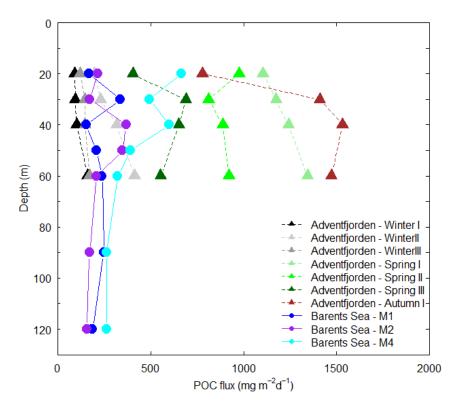


Figure 8: Downward POC flux estimated by deployment of short-term sediment traps (for ~24 h) in the Barents Sea (**Paper II**) and Adventfjorden (IsA, **Paper III**).

As observed in the Barents Sea, a decline of the suspended nitrate concentrations (25 m) was also found in Adventfjorden throughout spring (Table 1). The Chl *a* concentrations peaked during Spring II in mid-May and the maximum concentrations were similar to those observed during the late peak bloom in the Barents Sea (Spring II: 4.2 mg Chl *a* m⁻³, M1: 4.3 mg Chl *a* m⁻³, Table 1). Nitrate and Chl *a* concentrations in Adventfjorden were also comparable to previously measured spring bloom concentrations in Adventfjorden (Zajączkowski et al., 2010) and the ice-free Kongsfjorden, Svalbard (Iversen and Seuthe, 2011). Due to the highest Chl *a* concentration, Spring II was identified as peak bloom stage, while Spring I and Spring III were classified as early bloom and late bloom, respectively.

In Adventfjorden, the early bloom stage was associated with a high downward POC flux, and the intensity of the flux declined toward the peak bloom and late bloom stage (Figure 8). The downward POC flux exceeded the present spring bloom observations from the Barents Sea (Figure 8) and literature data from ice-free fjords in northern Norway (Keck and Wassmann, 1996; Reigstad and Wassmann, 1996; Reigstad et al., 2000; Zajączkowski et al., 2010), and Conception Bay, Canada (Thompson et al., 2008), but was comparable to fluxes found in a

study in the Barents Sea (Olli et al., 2002). Along these lines, the high downward POC flux associated with the spring bloom in Adventfjorden matched the situation described by the conceptual model of an Arctic marine ecosystem (Figure 3).

The autumn situation in Adventfjorden was characterized by replenished nitrate concentrations (Table 1), which was used as an indicator that water column stratification broke down previous to Autumn I. However, the Chl *a* concentrations remained low (5-60 m: 0.2-0.4 mg Chl *a* m⁻³, **Paper III** Figure 3) and no autumn bloom was observed, such as it has been reported from the autumn situation in Kongsfjorden (Iversen and Seuthe, 2011) and the Barents Sea (Hegseth, 1997). Due to lacking data on primary production, it was not possible to evaluate if the low Chl *a* concentrations were caused by low primary production or high loss rates by the moderately abundant zooplankton community (7 x 10³ ind. m⁻³, Stübner et al., in rev.). Based on the nitrate and Chl *a* concentrations, Autumn I was classified as a typical Arctic autumn situation, though the downward POC flux in Adventfjorden (Figure 8) exceeded previous studies in the same fjord in October (Zajączkowski et al., 2010) as well as autumn studies conducted in north/ western Norwegian fjords (Wassmann, 1984; Keck and Wassmann, 1996) and Hudson Bay, Canada (Lapoussière et al., 2013).

The concentration of suspended biomass (Chl a, POC) and downward POC fluxes observed in the Barents Sea and Adventfjorden were largely comparable to literature data. The snapshot sampling episodes conducted here are therefore regarded to represent typical Arctic winter, spring and autumn situations. The peak bloom and late bloom situation was investigated both in the Barents Sea and Adventfjorden. Though comparable concentrations of suspended biomass were found, the downward POC flux was higher in Adventfjorden. The conceptual understanding of the Arctic sedimentation pattern (Figure 3) suggests that the major sedimentation event is associated with the phytoplankton spring bloom. This was observed during the early bloom situation in Adventfjorden. However, the highest downward POC flux in the Barents Sea was found during the post bloom situation in deep mixed, icefree waters (M4) and the highest POC flux in Adventfjorden occurred during autumn (Autumn I, Figure 8).

5.2 SEASONAL AND SPATIAL VARIATION IN SINKING PARTICLES' CHARACTERISTICS (SIZE COMPOSITION AND POC: VOLUME RATIO)

The deployment of short-term sediment traps modified with gel-containing jars allows investigating characteristics of sinking particles such as the microbial community associated with sedimenting marine snow (Thiele et al., 2015), the sinking velocity of particles (McDonnell and Buesseler, 2010), or the contribution of different particle types to the downward flux (Ebersbach et al., 2011). In the present work, I focused on the size distribution of sinking particles, the volume flux (Figure 9) and the link between the downward particle flux and the POC flux (Figure 9).

Following Stokes' Law, very low sinking velocities have been estimated for small particles (few μ m, McCave, 1975) and these particles have often been regarded as "non-sinking". In the present image analysis (**Paper I, III**), particles < 50 μ m ESD_{image} were not included. Their light reflection was very low at the used magnification (15 x), most likely causing an underestimation of the particle number (Jackson et al., 2005). Nevertheless, particles < 50 μ m ESD_{image} were very abundant in the gels deployed in the Barents Sea and Adventfjorden, which matches the results of other field and model studies (\geq 11 μ m, Durkin et al., in press; \geq 2 μ m ESD, Richardson and Jackson, 2007; \geq 43 μ m, McDonnell and Buesseler, 2010). However, a comparison with literature also shows that abundance of small sinking particles varies spatially. Ebersbach and Trull (2008) deployed gel traps around the Kerguelen Plateau and chose to exclude particles < 150 μ m ESD from their image analysis because of the low abundance and statistical challenges.

The particle coverage in gels is determined by the particle abundance and the size of the particles. Both factors vary with location and season. Gel trap deployment for ~24 h during mid-December (Winter I) resulted in densely covered, but not overloaded, gels. In contrast, the deployment time had to be shortened during spring and autumn (Barents Sea: 4-5 h, Adventfjorden: 2 h) to prevent particle overload in the gels, which would have made them unusable in the image analyses.

In this context, a comparison with literature is remarkable: Gel traps were deployed in the southern Ocean (Austral spring and summer) (Ebersbach and Trull, 2008; McDonnell and Buesseler, 2010; Ebersbach et al., 2011; Laurenceau-Cornec et al., 2015; Durkin et al., in press). They were deployed at greater depth than in the present study (100-500 m vs. 20-90 m). A lower particle abundance must be assumed for greater depth, and thus a longer

deployment time is possible. Nevertheless, it is remarkable that the gels could be deployed for up to three days in the Southern Ocean without particle overload, while a 4-5 h deployment time was appropriate in the Barents Sea. This pinpoints in my opinion a certain difference between the system in the southern Ocean and an Arctic shelf sea, which may be subject to future investigations.

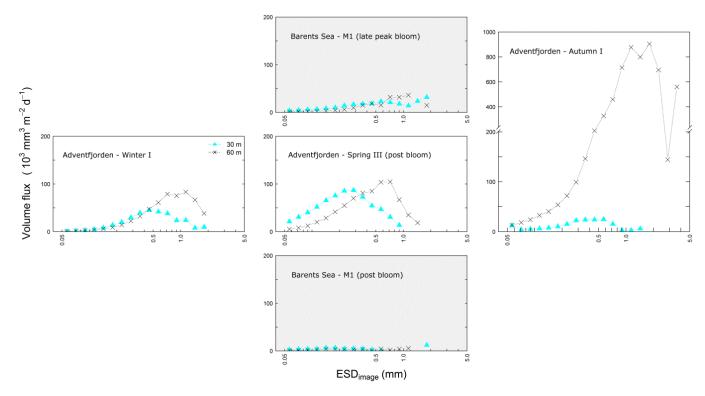


Figure 9: Particle volume flux in the Barents Sea (grey shaded; top: M1; bottom: M4, **Paper I**) and Adventfjorden (left: Winter I; middle: Spring III; right: Autumn I; **Paper III**). The area under the curve corresponds to the total volume of sinking particles. Data from M2 (late bloom, Barents Sea) and Spring II (peak bloom in Adventfjorden) were not included, because the volume flux spectra were very similar to M1 and Spring III, respectively.

In volume flux spectra, the area under the curve corresponds to the total sinking volume, which is the sum of the volume of all sinking particles at a certain depth. In addition, the spectra give an indication on the contribution of different sized particles to the downward volume flux. Comparing the two regions investigated here (Barents Sea, Adventfjorden) indicates that the downward volume flux generally was lower in the Barents Sea (Figure 9). The spectra further show that the volume flux tended to be higher at 60 m than at 30 m. This meets predictions of the coagulation theory (Jackson, 1990; Kiørboe et al., 1990), which suggests that larger particles could be expected at greater depth.

The highest downward POC flux in the Barents Sea (M4, Figure 8) was associated with the lowest particle volume flux of the present study (40-130 x 10³ mm³ m⁻² d⁻¹ Figure 9). In contrast, the highest POC flux in Adventfjorden occurred during Autumn I at 40 m and 60 m in form of the highest particle volume found during the present study (2150-6190 x 10³ mm³ m⁻² d⁻¹, Figure 9). Interlinking the downward particle volume flux with the POC flux showed substantially different POC: volume ratios. They ranged over almost three orders of magnitude (Figure 10, note log scale on x-axis).

The POC: volume ratios found in Adventfjorden and the Barents Sea corresponded well with ratios established for diatom aggregates (Alldredge, 1998) and fecal pellets of the copepod species *C. finmarchicus* and *C. glacialis* (Reigstad et al., 2005; Wexels Riser et al., 2007). Also, the POC: volume ratio matched the visual inspection. The gels deployed in the southern Barents Sea and the Polar Front contained predominantly fecal pellets (**Paper I** Table 5), and had the highest POC: volume ratio in the present study (Figure 10). In Adventfjorden, fine detrital material prevailed in the gels during Winter I and the two deepest sampling depths of Autumn I (Figure 10), and it must be assumed that it had a low POC: volume ratio.

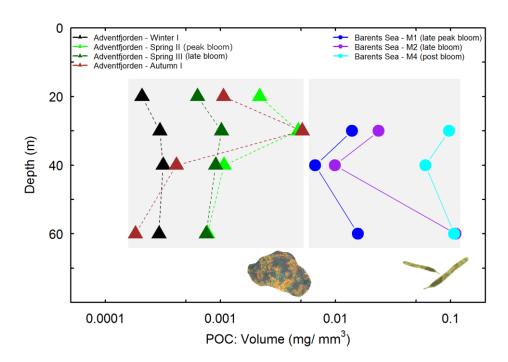


Figure 10: POC: volume ratio for sinking particles (\geq 50 μ m ESD_{image}) collected in the gel traps, which were deployed in the Barents Sea (filled circles, **Paper I**) and Adventfjorden (triangles, **Paper III**). The algae aggregate and fecal pellets close to the x-axis indicate literature values of the respective particles type (Alldredge, 1998; Reigstad et al., 2005; Wexels Riser et al., 2007).

The differences in the POC: volume ratio between the Barents Sea and Adventfjorden were remarkable. To my knowledge, these ratios have not been determined from gel traps. However, several studies aimed to estimate the downward POC flux from size spectra of suspended particles, which were determined with different types of optical instruments (e.g. underwater video profiler, UVP, Guidi et al., 2008; particle camera, ParCam, Iversen et al., 2010; video plankton recorder, VPR, McDonnell and Buesseler, 2010). Guidi et al. (2008) presented a global equation to link optically determined particle spectra to the downward POC flux, but later studies indicated that temporal and spatial calibration of this equation is necessary to achieve a good estimate of the downward flux (Iversen et al., 2010; McDonnell and Buesseler, 2010; Nowald et al., in press). Despite the different approach in the present work, the results here point in the same direction. Sinking particles have distinctly different POC: volume ratios, dependent on location, season and depth (e.g. Figure 10, Autumn I), and the downward POC flux may only be determined from the particle flux if the predominant particle type and/ or composition of particles is known and taken account.

Deployment of gel traps and a subsequent image analysis revealed that the particle size composition in the Barents Sea and Adventfjorden differed with location and season. It was remarkable, that the low particle volume flux in the deep-mixed southern Barents Sea and the high particle volume flux in Adventfjorden during September (40 m, 60 m) were both associated with a high downward POC flux. This indicates that the POC: volume ratio of different types of particles (e.g. fecal pellets, algal aggregates, detritus) varied considerably.

5.3 POTENTIAL DRIVERS OF THE DOWNWARD PARTICLE AND POC FLUX

The downward POC flux and sinking particles characteristics, such as size composition and the POC: volume ratio, varied between locations, seasons and depths in the present study. In the following, potential drivers of the downward POC and particle flux are examined to improve the understanding of the downward flux regulation.

5.3.1 VERTICAL TURBULENT MIXING

Shear rate is a measure of turbulent mixing and it affects particle size. An enhanced shear rate increases the collision rate of particles and thus promotes formation of larger particles, but a too high shear rate also fragments large particles into smaller ones. The shear rate accordingly

impacts the downward POC flux, because larger/ smaller particles are assumed to have a higher/ lower sinking velocity and enhance/ reduce the downward POC flux.

During the present study, shear rates of $0.02\text{-}13.11~\text{s}^{-1}$ were observed in the Barents Sea (**Paper I**, Figure 5), which generally matches previous observations (Sundfjord et al., 2007). Shear rates $> 2.8~\text{s}^{-1}$ appear to fragment larger particles (Alldredge et al., 1990), but these intensities were only observed in the upper 11-12 m of M2 and M4.

Assuming that the background shear rate in the Barents Sea was ca. 0.03 s⁻¹ (found at the deep layers of all three stations), the depth layer of enhanced shear rate (background shear: 0.03 s⁻¹ < enhanced shear rate < threshold for fragmentation: 2.8 s⁻¹) was located between 0-28 m at M1, 11-78 m at M2 and 13-38 m at M4. Because the depth distribution of high Chl *a* concentrations coincided with the depth interval of enhanced shear rates, particle aggregation was most likely stimulated at all three stations

The promoted aggregate formation raises the question if the observed particle maximum size in the Barents Sea data matched the theoretical maximum size. Jackson (1990) suggested that the Kolmogorov length scale, calculated based on the kinematic viscosity v of seawater (10^{-2} cm² s⁻¹, Moum and Lueck, 1985, cited in Jackson, 1990) and the shear rate γ by the equation

Kolmogorov length scale =
$$\sqrt{\frac{v}{\gamma}}$$
 (1),

could give a coarse indication of the theoretical maximum particle diameter. Using this shear rates from the Barents Sea indicates a theoretical particles maximum size of 5 mm ESD. All particles found in the deployed gels were ≤ 3.2 mm ESD_{image} and thus well below this crude upper size limit.

Apart from promoting aggregate formation, vertical turbulent mixing may have also enhanced the downward POC flux by active down-mixing of organic biomass. The upper mixing layer (vertical diffusivity $> 10^{-4} \text{ m}^{-2} \text{ s}^{-1}$) reached down to 13 m, 17 m and 25 m at M1, M2 and M4, respectively (Figure 11). Stronger stratification and the partial ice-cover at M1 and M2 probably dampened the effect of wind mixing (7-13 m), while the weakly stratified water column at M4 (pycnocline at 35-40 m) was more prone to deep wind-induced mixing.

Indications of an enhanced down-mixing of biomass were found at M4 in the southern Barents Sea. The sedimenting biomass at 60 m had a C/N ratio of 7.5, which suggested that little degraded biomass was sinking out. *P. pouchetii* dominated the phytoplankton community, and this phytoplankton taxon has been reported to sink slowly (approx. 1 m d⁻¹, Osinga et al., 1996; Reigstad and Wassmann, 2007) in comparison to for example diatoms, which may sink up to several meters per day (Smayda and Boleyn, 1966a; Smayda and Boleyn, 1966b). Thus, the vertical transport of recently produced *P. pouchetii* cells was potentially driven by wind-induced downward mixing.

Deep vertical mixing probably enhanced the downward POC flux in the weakly stratified southern Barents Sea in two ways: (1) Enhanced shear rate (higher than the background shear, but lower than the threshold of fragmentation) may have stimulated aggregate formation in the depth layer of the high particle abundance (~15-30 m depth), resulting in larger, faster sinking particles. (2) Vertical deep mixing most likely caused an active downwards transport of otherwise slowly sinking P. pouchetii cells.

5.3.2 UPWARD NITRATE FLUX

Vertical turbulent mixing (section 5.3.1) as well as phytoplankton composition (section 5.3.3) have a direct effect on the downward particle and POC flux. Enhanced shear rate or the amount of excreted transparent exopolymer particles by diatoms, for example, promotes particle coagulation, increases the abundance of large particles with a higher sinking velocity and, in turn, increases the downward POC flux. In contrast, the upward nitrate flux has an indirect effect on the downward POC flux, because it stimulates the whole ecosystem and may only potentially, via a multistep process explained in the following, enhance the downward particle and POC flux.

Due to the weakly stratified water column in the southern Barents Sea, M4 was more prone to wind effects and had a deeper mixing layer with vertical diffusivity $> 10^{-4}$ m⁻² s⁻¹ than M1 and M2 (Figure 11). This affected also the upward nitrate flux, which is determined by the vertical diffusivity and the depth gradient of the nitrate concentration (**Paper II** equation 2).

The upward nitrate flux into the base of the mixing layer at M4 (25 m: 5.39 mmol nitrate m⁻² d⁻¹) was one order of magnitude higher than the flux at M2 (base of

mixing layer 17 m: 0.35 mmol nitrate m⁻² d⁻¹) and two orders higher than the flux at M1 (base of mixing layer 13 m: 0.04 mmol nitrate m⁻² d⁻¹, Figure 11). The three investigated stations illustrate thus a gradual change in water column stratification and upward nitrate flux along the north-south transect in the central Barents Sea. In the following, however, I will focus on upward nitrate flux as a driver of the downward POC flux under the most "extreme" situations, i.e. M1 and M4, because also the nitrate uptake rate was determined there.

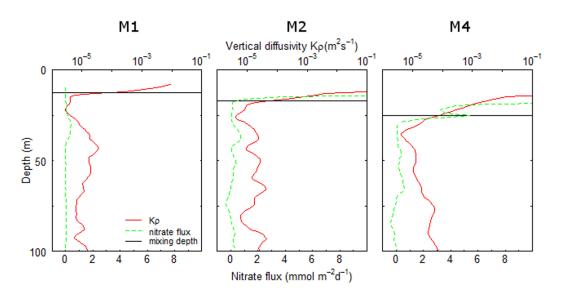


Figure 11: Vertical diffusivity and nitrate flux (upward: positive values, downward: negative values) in the upper 100 m of station M1 (left), M2 (middle) and M4 (right) in the central Barents Sea.

At M1, the low upward nitrate flux negligibly contributed to the nitrate stock in the mixing layer (ca. $< 0.5 \% d^{-1}$). Similar observations were reported from the subpolar North Atlantic during summer (Painter et al., 2014). Model calculations were set up to investigate the development of the nitrate stock in the mixing layer over several days. They were based on he observed upward nitrate flux and the nitrate uptake rate measured in this depth interval (**Paper II**). This model indicated that the nitrate stock continuously decreased in the mixing layer, because the nitrate uptake rate always exceeded the upward nitrate flux into the layer.

Sakshaug and Slagstad (1992) suggested, based on observed wind patterns, that strong wind events occur roughly every ten days in the southern Barents Sea. This was used as a basis for the model simulations for M4. Model runs were set up in a way that a period of 1-3 days of enhanced upward nitrate flux into the base of the mixing layer (5.29 mmol nitrate m⁻² d⁻¹) was followed by a 7-9 days relaxation period (upward nitrate flux: 0.3 mmol nitrate m⁻² d⁻¹,

equaling the average upward nitrate flux in the layer 50-70 m at M4, **Paper II** Table 4). The upward nitrate flux before the assumed relaxation period considerably exceeded the nitrate uptake rate (> 3 fold, **Paper II** Figure 3d, h), causing almost a doubling of the nitrate concentration in the mixing layer after three days. Thus, repetitive strong wind events (Sakshaug and Slagstad, 1992) potentially replenish the nitrate stock in the surface layer also during the productive early summer.

Svensen et al. (2002) conducted a mesocosm experiment under boreal summer conditions and found that a pulsed nutrient repletion (every nine days) enhanced the downward biomass flux. Despite this indication, it is challenging to link the upward nitrate flux to the downward POC flux in this study due to the time lag between the upward and the potential downward flux. A conceptual model from the Fram Strait suggested a lag of up to 60 days between primary production and vertical export in the upper 200 m (Forest et al., 2010), and a somewhat longer time window must be assumed between the upward nitrate flux, a stimulating factor of the primary production, and the downward POC flux. Station work here was conducted within ~27 h, and a mechanistic link between the upward nitrate flux and downward POC flux can therefore only be inferred. In the upper 26 m, the nitrate uptake rate was slightly higher during the post bloom situation at M4 than during the late peak bloom at M1 (Paper II 3c, d). Using the nitrate uptake rate as a proxy for nitrate based new primary production (Dugdale and Goering, 1967), it is suggested that new production was stimulated at M4. No particularly high Chl a concentrations were however observed and it is assumed that some produced phytoplankton biomass was down-mixed by the enhanced vertical mixing (section 5.3.1). In addition, the biomass was probably utilized by the abundant zooplankton community (Svensen et al., in prep.), which, in turn, enhanced the downward POC flux by production of fast-sinking fecal pellets (detailed discussion in section 3.5.4).

The upward nitrate flux into the base of the mixing layer of M4 was one order of magnitude higher than into the corresponding depth at M2 and even two orders of magnitude higher than at M1. Model calculations suggest that the strong upward nitrate flux replenished the nitrate stock in the mixing layer at M4, while it contributed negligible to the replenishment of the nitrate stock at M1. It is assumed that the enhanced upward nitrate flux stimulated new production at M4. The produced biomass was probably downmixed by the vertical mixing processes or repackaged into fast-sinking fecal pellets. In both instances it increased the downward POC flux.

5.3.3 PHYTOPLANKTON

Phytoplankton composition potentially drives the downward POC flux by the sinking velocity of the cells or the potential to form aggregates. Both factors vary with the prevailing taxon and the physiological stage (Smayda, 1970, Kiørboe and Hansen, 1993).

Diatoms potential increase the downward POC flux in two ways: Their cells have been described to sink fast, especially as senescent cells or resting stages (Smayda and Boleyn, 1966a; Smayda and Boleyn, 1966b; Eppley et al., 1967; Bienfang, 1981). Also, some diatom genera, such as *Chaetoceros* and *Thalassiosira*, have been reported to produce sticky cells, excrete adhesive substances or occur associated with bacteria, which excrete these sticky substances (Kiørboe and Hansen, 1993; Hansen and Kiørboe, 1997; Thornton, 2002; Gärdes et al., 2011). The production of this "natural" glue promotes aggregate formation, and enhances the downward flux.

Chaetoceros spp. and Thalassiosira spp. were abundant during the spring bloom in the Barents Sea and in Adventfjorden (SCM, M1: ~421 x 10³ cells L⁻¹, **Paper I** Table 3; SCM, Spring I: 270 x 10³ cells L⁻¹, Kubiszyn et al., in prep.) and aggregates were frequently found in the gels deployed at M1 (**Paper I** Table 5). No gel trap data were available from Spring I, because the gels were completely covered after a too long deployment time and unsuitable for particle enumeration and characterization. A molecular biological analysis (18S rDNA) of the water in the sediment traps however indicates that diatoms contributed substantially to the downward flux (M. Marquardt, pers. comm.). Thus, it is inferred that diatoms enhanced the downward POC flux at both locations.

The prymnesiophyte *P. pouchetii* is another common spring bloom species in high latitudes (Degerlund and Eilertsen, 2010). It dominated during the post bloom scenario (M4) and toward the end of the bloom in Adventfjorden (SCM, M4: 1,810 x 10³ cells L⁻¹, **Paper I** Table 3; SCM 24.5.2012: 1,340 x 10³ cells L⁻¹, no data available during Spring III, Kubiszyn et al., in prep.). *P. pouchetii* cells have a low stickiness (Passow and Wassmann, 1994), tend to sink slowly (with 2.7-5.0 m d⁻¹, Reigstad and Wassmann, 2007) and may thus not substantially contribute to the downward POC flux. Its colonies were not observed in the gels deployed at the two sampling sites, and its single cells were too small to be included in the analysis. Neither was *P. pouchetii* identified by the 18S rDNA analysis as a dominant

contributor to the downward flux in Adventfjorden (Spring III). It is therefore presumed that *P. pouchetii* was not a driver of the downward POC flux.

Diatoms dominated the phytoplankton late peak bloom at the ice edge in the Barents Sea and the early bloom situation in Adventfjorden. Diatom aggregates were frequently observed in the gel deployed at the ice edge and diatom DNA dominated in the sediment traps in Adventfjorden during the early bloom (18S rDNA analysis, M. Marquardt, pers. comm.). The prymnesiophyte Phaeocystis pouchetii was in contrast most abundant in the ice-free waters of the southern Barents Sea (M4) and probably during the late spring bloom in Adventfjorden. Its cells were not observed in the gels at M4, presumably because of their small size. The 18S rDNA analysis suggested that they neither contributed substantially to the downward flux in Adventfjorden (M. Marquardt, pers. comm.). It is accordingly suggested that a high diatom abundance enhanced the downward POC flux, while high numbers of P. pouchetii did not promote it.

5.3.4 ZOOPLANKTON

Zooplankton attenuates POC in the upper water column, but dependent on the dominant species (e.g. copepods, meroplankton, pteropods) the downward POC flux is affected in different ways. Preferred prey size of zooplankton varies (Hansen et al., 1994; Wirtz, 2012) as well as timing of the peak abundance (Stübner et al., in rev.; Arashkevich et al., 2002; Arendt et al., 2013; Kwasniewski et al., 2013), and sinking velocity of fecal pellets (Turner, 2015).

Calanoid copepods, such as *C. finmarchicus* and *C. glacialis*, were abundant in the Barents Sea (Svensen et al., in prep.). They were characterized to be mainly suspension feeders (Wexels Riser, 2007), and it was therefore examined here if the grazers' depth distribution was associated with the SCM. Phytoplankton depth distribution was determined by vertical fluorescence profiles and the *Calanus* spp. depth allocation was quantified by LOPC profiles, a non-invasive optical technique. This revealed that the vertical zooplankton distribution was highly variable in the upper 100 m in the Barents Sea and that *Calanus* spp. was not associated with the SCM (**Paper I** Figure 6). Instead, reduction and modification of sinking biomass appeared to take place over a wide vertical range, as it has also been reported by Norrbin et al. (2009) for the waters around Svalbard.

Zooplankton biomass increased along the north-south transect in the Barents Sea (Svensen et al., in prep.). At station M4 in the southern Barents Sea, the highest *Calanus* spp. biomass was found (Svensen et al., in prep.) and also the abundance of fecal pellets was highest in the gel traps (**Paper I** Table 5). Enhanced upward nitrate flux at M4 probably stimulated primary production (section 5.3.2) and increased copepod feeding rates (Turner and Ferrante, 1979). Wexels Riser et al. (2007) observed in experiments with older stages of *C. finmachicus*, *C. glacialis* and *C. hyperboreus* that rather the production of larger fecal pellets sizes was promoted than the production of a higher number of pellets. According to Stokes' Law, these larger fecal pellets would have higher sinking velocities and potentially enhanced the downward POC flux at M4.

The gels deployed at M4 (40 m, 60 m, 90 m) also contained substantial amounts of unidentifiable material. Due to the high POC: volume ratio of the sinking material, it is assumed the unidentifiable material partly consisted of fragmented fecal pellets. Handling, rejection or swimming activities by crustacean zooplankton can cause fecal pellet breakage (Dilling and Alldredge, 2000; Iversen and Poulsen, 2007). This will reduce the sinking velocity of the fragmented pellets compared to unbroken ones. The slower sinking prolongs the period in the pelagic zone and exposes the pellet fragments for a longer time to zooplankton grazing and other degradation processes by dinoflagellates or bacteria (Svensen et al., 2012; Svensen et al., 2014). These processes probably caused the high POC attenuation at M4 (**Paper II** Figure 4), but the high POC: volume ratio of fecal pellets and their fragments still caused a high downward POC flux.

During spring, the zooplankton community in Adventfjorden was dominated (40-70 %) by meroplankton nauplii and larvae (approx. 16 x 10³ ind. m⁻³, Stübner et al., in rev.). Their high abundances probably caused a major grazing pressure especially of small cells (Sommer et al., 2000) though the ingestion rate of meroplankton has been estimated to be lower than e.g. for copepods (Hansen et al., 1997). Thus, it is here assumed, that meroplankton mainly contributed to POC attenuation in the water column by their grazing and decreased the downward POC flux. The active downward migration during meroplankton settling at the seafloor probably has an effect on the downward POC flux, but this was not investigated here.

During Autumn I, a substantial number of pteropods (*Limacina* sp.) was found in the gels deployed in Adventfjorden. It could not be determined if the animals were actively swimming

down and trapped in the gels, passively sinking or if they were dead when reaching the gel. Accordingly, they were not included in the image analysis, though major sedimentation events of this suspension feeder have been reported from the Fram Strait (Meinecke and Wefer, 1990; Bauerfeind et al., 2009) and the Norwegian Sea (Bathmann et al., 1991). Lost or rejected mucous feeding nets of pteropods have been described to promote aggregate formation (Bathmann et al., 1991; Noji et al., 1997), and they may potentially explain the high abundance of the large particles found in the gels deployed in Adventfjorden during September (Autumn I, Figure 8, **Paper III** Figure 6).

In the Barents Sea, no direct correlation was found between the SCM or the zone of the strongest POC attenuation and the zooplankton depth distribution. However, the highest zooplankton abundance coincided with the highest number of fecal pellets in the gel traps in the southern Barents Sea (M4). Apart from fecal pellets, also unidentified material was found here below 30 m, probably fragmented fecal pellets with a lower sinking velocity compared to unbroken ones. Due to their high POC: volume ratio, it is suggested that they nevertheless enhanced to the downwards POC flux.

The role of zooplankton taxa as drivers of the downward POC flux in Adventfjorden is more unclear. High meroplankton abundances during spring potentially attenuated POC in the water column, while lost or rejected feeding webs of pteropods may have promoted formation of large particles, which were found during autumn.

5.3.5 GLACIAL RUN-OFF

Adventfjorden is affected by glacial run-off between June and September (Węsławski et al., 1999), and entrained sediment-loaded meltwater could be a potential driver of the high downward POC flux (780-1530 mg POC m⁻² d⁻¹, Figure 8) found during mid-September (Autumn I).

Hood et al. (2015) proposed that entrained glacial run-off is generally high in terrestrial dissolved and particulate organic carbon. Sedimenting material collected in the short-term sediment traps in Adventfjorden during Autumn I had a high C/N ratio of 13-15 (**Paper III** Table 3). This suggests sinking of either very degraded marine material or a mixture of marine and entrained terrestrial material (Bianchi, 2006), which was brought to the sampling location in the middle of Adventfjorden by the meandering melt water plume.

A second sediment trap deployment was not affected by the plume and indicated C/N ratios of 7-9 of the sinking material (**Paper III**). It is inferred that the first deployment was affected by the melt water plume and a mixture of marine and terrestrial material was collected in the trap cylinders.

The particle size spectra showed that large detrital particles were sinking out at 40 m and 60 m (Figure 10). Their low POC: volume ratio resembled the probably resuspended particles observed during winter. The major glacial run-off probably induced estuarine circulation in Adventfjorden, and a strong current at the bottom potentially resuspended detrital material from the seafloor and enhanced the downward POC flux at the deeper sampling depths during Autumn I.

Sinking inorganic material was not analyzed during the present study, but a downward flux of ~80 g particulate inorganic material (PIM) m⁻² d⁻¹ has been previously found during summer in Adventfjorden (Zajączkowski and Włodarska-Kowalczuk, 2007). The inorganic material may flocculate when entrained into sea water and enhance the downward flux by formation of large, faster sinking flocs, such as observed in laboratory experiments and field studies in fjords and estuaries (Kranck, 1973; Syvitski and Murray, 1981; Papenmeier et al., 2014; Sutherland et al., 2015). Entrained lithogenic material has a high specific weight and sinking velocity. In case it is incorporated into organic aggregates and fecal pellets, the lithogenic material may also enhance the sinking velocity of these particles (Syvitski and Murray, 1981; Passow and De La Rocha, 2006; Ploug et al., 2008; Iversen et al., 2010). Though these processes have not been addressed here, the present study indicated roughly 3 fold higher POC bulk sinking velocities during autumn (12-15 m d⁻¹) than during winter and spring (2-4 m d⁻¹ and 2-6 m d⁻¹, respectively, **Paper III** Table 2). This may not only have been an effect of the high POC: volume ratio of the particles at the shallower sampling depths (Figure 10) or the large size of the particles at the deeper sampling depths (Figure 9), but also a ballasting effect.

A high downward POC flux was observed in Adventfjorden during September, while a major glacial run-off from land occurred. Entrained terrestrial POC apparently enhanced the downward POC flux in Adventfjorden. Increasing effects on the downward POC flux by inorganic flocculation and ballasting of organic particles (by lithogenic material) are likely, but definite conclusions cannot be drawn from the data collected here. Glacial run-off probably induced estuarine circulation and caused re-suspension of large, detrital material with low POC: volume ratio from the seafloor, which enhanced the downward POC flux at the deepest sampling depths.

6 CONCLUSION: DRIVERS OF HIGH POC FLUX EVENTS IN THE BARENTS SEA AND ADVENTFJORDEN

In this study, the downward POC and particle (\geq 50 µm ESD_{image}) flux and their potential drivers were examined in Arctic marine ecosystems. The application of a space-for-time substitution by a north-south transect in the Barents Sea, an Arctic shelf sea, allowed the investigation of contrasting bloom scenarios. In addition, a seasonal study was conducted in the ice-free, but glacially impacted, Arctic fjord Adventfjorden, western Svalbard, to study the fluxes and their drivers during winter, spring and autumn.

The highest downward POC flux was observed during (1) a post bloom situation in the deeply mixed Barents Sea, (2) an early bloom situation in Adventfjorden, and (3) an autumn situation in Adventfjorden (Figure 8). The high downward POC flux took place in form of a minor particle volume flux (post bloom situation, Barents Sea), an intermediate particle volume flux (early bloom situation, Adventfjorden) and an intermediate (20 m, 30 m) to high (40 m, 60 m) particle volume flux (autumn, Adventfjorden, Figure 9), respectively. This pinpoints that different mechanisms drove the high downward POC flux in the Barents Sea and Adventfjorden.

High downward POC flux associated with vertical mixing and high zooplankton abundance. The post bloom situation in the southern Barents Sea (M4) occurred in a weakly stratified and deeply mixed water column. Strong winds, which are re-occurring in the region (Sakshaug and Slagstad, 1992), apparently induced the high upward nitrate flux into the mixing layer (5.39 mmol nitrate m⁻² d⁻¹). It is assumed that this stimulated the new primary production. The prymnesiophyte *P. pouchetii* was the dominant phytoplankton taxon and its small cells tend to sink slowly (Reigstad and Wassmann, 2007). Vertical mixing most likely enhanced the downward transport, because the low C/N ratio sedimenting material at 60 m (**Paper II** Figure 4) suggests sinking of recently produced biomass.

The abundant zooplankton community at M4 (Svensen et al., in prep.) utilized the produced biomass and repackaged it into fast-sinking fecal pellets, which were frequently found in the gel traps. Zooplankton however also formed a "retention filter" (Wexels Riser et al., 2001), and caused POC attenuation in the water column by for example fragmenting sinking material such as fecal pellets. Due to the high POC: volume ratio of the sinking material (Figure 10), also sinking of pellet fragments apparently enhanced the downward POC flux.

High downward POC flux associated with a diatom spring bloom

The second highest downward POC flux in the present study was found in Adventfjorden during an early bloom situation. It was the only scenario which was associated with the phytoplankton bloom, such as suggested by the conceptual model for the Arctic pelagic ecosystem (Figure 3). Diatoms were the dominating phytoplankton taxon in the water column during the early bloom, and 18S rDNA analyses (M. Marquardt, pers. comm.) indicated that they also prevailed in the sediment traps. Because the deployed gels from this sampling episode were not useable, it can only be speculated if diatom cells were sinking out in form of aggregates, which would enhance their sinking velocity (Iversen and Ploug, 2013). Alternatively, also the physiological state (e.g. senescent cells, nitrate limitation) of the cells may have caused a fast sinking of single cells, short chains or resting stages (Eppley et al., 1967; Smayda, 1970; Bienfang et al., 1982). The latter appears rather unlikely due to the previously defined situation of an early bloom stage, but cannot be disproven. This context illustrates well how gel traps can improve the understanding of an ecosystem, because an image analysis of the sinking material would show if single cells or aggregates were sinking out. Apart from the high diatom concentrations, also the low zooplankton abundance (4 x 10³ ind. m⁻³, E.I. Stübner, pers. comm.) contributed to the downward POC flux intensity, because the weak top-down regulation allowed biomass export rather than channeling biomass into the pelagic food web.

High downward POC flux associated with glacial run-off

The highest downward POC flux was observed in Adventfjorden during mid-September (Autumn I). During this time, Adventfjorden was affected by glacial run-off. It is indicated here, that a combination of factors related to the run-off enhanced the downward POC flux during this situation.

The present data imply that entrained terrestrial POC contributed to the downward POC flux. In addition, the bulk sinking velocity of POC was high (12-15 m d⁻¹, **Paper III** Table 3). Large particles with a low POC: volume ratio were found at 40 m and 60 m (Figure 10). It is assumed that these particles, potentially resuspended detrital material or marine snow formed from pteropod feeding nets, had a high sinking velocity due to their large size. At the shallower sampling depths, the POC sinking velocity was however also high. Here, mesozooplankton fecal pellets and aggregates with a comparable high POC: volume ratio (Figure 10) prevailed and probably contributed to the downward POC flux by their high POC content. In addition, ballasting of organic aggregates by entrained lithogenic material (with a

high specific weight and sinking velocity) or flocculation of entrained inorganic material is likely, but cannot be verified by data collected during the present study.

These three instances illustrate that different factors drove the downward POC flux in the ice-free Arctic Adventfjorden and the partially ice-covered Arctic shelf sea Barents Sea.

The conceptual model of the downward POC flux should therefore be extended (Figures 3 & 12). In this way it would point out that a high downward POC flux in Arctic marine ecosystem not only occurs coupled to a phytoplankton spring bloom. Instead, periods of high downward POC flux may also take place

- (1) during a post bloom situation in weakly stratified, deep-mixed waters, where pulsed upward nitrate flux stimulates new production, which, in turn, is utilized by an abundant zooplankton community and repackaged into fast-sinking pellets, or
- (2) in a coastal Arctic region (e.g., fjord, embayment), where high pteropod abundances coincide with glacial run-off, which entrains terrestrial POC and sediment-loaded melt water, whereas the latter may have an ballasting effect on organic aggregates.

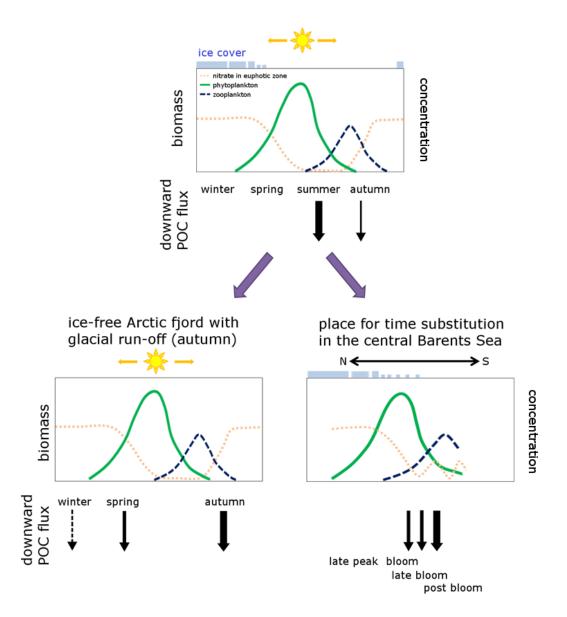


Figure 12: Conceptual understanding of the Arctic marine ecosystem with the major sedimentation event during late spring/ summer (top figure) and expansion of the conceptual model. Bottom left: Situation in the ice-free Arctic Adventfjorden with glacial run-off during autumn, which was associated with a high downward POC flux. Bottom right: Situation in the central Barents Sea, where a space for time substitution allowed investigation of different hydrographical and ecological situations (spring bloom scenarios) and the high downward POC flux in the weakly stratified southern Barents Sea, where wind mixing caused a pulsed upward nitrate flux.

7 Outlook

The downward POC flux in a future seasonally ice-covered Arctic is challenging to predict due to the strong spatial variability and the simultaneous changes of sea ice cover, water temperature, salinity, water column stratification, upward nitrate flux, phyto-/ zooplankton composition and other factors (e.g., Slagstad et al., 2011; Dalpadado et al., 2012; Coupel et al., 2015; Arrigo and van Dijken, in press).

Summer data from the last 30 years in the southern, ice-free Barents Sea show a weakly increasing salinity and declining stratification, as well as a slight increase in wind speed (Peralta-Ferriz and Woodgate, 2015). Thus, a high downward POC flux as found in the present study in the southern Barents Sea may also occur in the future. However, climatic warming in the Arctic will most likely strengthen the thermal stratification of the surface layers (Wassmann and Reigstad, 2011), limit the upward nitrate flux and favor smaller phytoplankton species with a lower sinking velocity. A decline has already been reported for the large ice-associated copepods *C. glacialis* and *C. hyperboreus* in the Barents Sea (Dalpadado et al., 2012), and thus a predominant regenerative system with minor POC export during summer is likely.

Though fjords make up a small part of Arctic ecosystems, they appear to be highly important for carbon burial (Smith et al., 2015). In a future, warmer Arctic glacial run-off will probably increase and thus also enhance the downward POC flux in the marine ecosystem. However, more run-off, potentially during a longer time of the year, will also enhance the turbidity of the water and reduce the irradiance level, which may decline the pelagic production.

The high uncertainty of these predictions leaves me with the conclusion that it is important to continue research on downward POC and particle flux in the Arctic, because this will improve our mechanistic understanding of the system and processes as well as it will provide a basis for more trustworthy predictions of the future Arctic marine ecosystem.

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