

Lateral supply and downward export of particulate matter from upper waters to the seafloor in the deep eastern Fram Strait



Catherine Lalande ^{a,*}, Eva-Maria Nöthig ^a, Eduard Bauerfeind ^a, Kristin Hardge ^a,
Agnieszka Beszczynska-Möller ^{a,2}, Kirsten Fahl ^a

^a Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Am Handelshafen 12, Bremerhaven 27570, Germany

ARTICLE INFO

Article history:

Received 21 December 2015

Received in revised form

21 April 2016

Accepted 25 April 2016

Available online 28 April 2016

Keywords:

Arctic Ocean

Fram Strait

West Spitsbergen Current

Sediment trap

Export

Flux

Lateral supply

ABSTRACT

Time-series sediment traps were deployed at 4 depths in the eastern Fram Strait from July 2007 to June 2008 to investigate variations in the magnitude and composition of the sinking particulate matter from upper waters to the seafloor. Sediment traps were deployed at 196 m in the Atlantic Water layer, at 1296 and 2364 m in the intermediate and deep waters, and at 2430 m on a benthic lander in the near-bottom layer. Fluxes of total particulate matter, particulate organic carbon, particulate organic nitrogen, biogenic matter, lithogenic matter, biogenic particulate silica, calcium carbonate, dominant phytoplankton cells, and zooplankton fecal pellets increased with depth, indicating the importance of lateral advection on fluxes in the deep Fram Strait. The lateral supply of particulate matter was further supported by the constant fluxes of biomarkers such as brassicasterol, alkenones, campesterol, β -sitosterol, and IP₂₅ at all depths sampled. However, enhanced fluxes of diatoms and appendicularian fecal pellets from the upper waters to the seafloor in the presence of ice during spring indicated the rapid export (15–35 days) of locally-produced large particles that likely contributed most of the food supply to the benthic communities. These results show that lateral supply and downward fluxes are both important processes influencing the transport of particulate matter to the seafloor in the deep eastern Fram Strait, and that particulate matter size dictates the prevailing sinking process.

© 2016 Elsevier Ltd. All rights reserved.

1. Introduction

The Fram Strait is a deep gateway between the northern North Atlantic and the Arctic Ocean. Warm Atlantic Water (3–4 °C) carried by the northward West Spitsbergen Current enters the Arctic Ocean boundary current on its eastern side (Beszczynska-Möller et al., 2012) and sea ice exits the Arctic Ocean by the southward East Greenland Current on its western side (Smedsrud et al., 2011). The Long-Term-Ecological Research (LTER) observatory HAUSGARTEN has been maintained for more than a decade in the eastern Fram Strait by the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research to monitor the impact of large-scale environmental changes on downward fluxes and benthic communities in this transition zone, approximately 120 km west of Spitsbergen (Fig. 1; Soltwedel et al., 2005, 2016).

* Corresponding author.

E-mail address: catherine.lalande@takuvik.ulaval.ca (C. Lalande).

¹ Present address: Takuvik Joint International Laboratory and Québec-Océan, Département de biologie, Université Laval, 1045 avenue de la Médecine, Québec, Québec, Canada G1V 0A6.

² Present address: Institute of Oceanology PAS, Physical Oceanography Department, Powst. Warszawy 55, 81-712 Sopot, Poland.

Long-term measurements of downward fluxes at the HAUSGARTEN central station showed that the annual export of particulate organic carbon (POC) at ~300 m is relatively constant in the eastern Fram Strait, ranging from 1.6 to 2.6 g m⁻² yr⁻¹ from 2000 to 2008 (Bauerfeind et al., 2009; Lalande et al., 2013). These long-term measurements also showed that the composition of the biogenic matter exported out of the upper ocean varies temporally depending on the temperature of the Atlantic Water inflow and on the presence of ice cover in the eastern Fram Strait, with enhanced fluxes of larger phytoplankton cells generally observed when sea ice is concurrently present with sunlight in the area (Bauerfeind et al., 2009; Hardge, 2012; Lalande et al., 2013). However, little is known on the magnitude and composition of particulate matter fluxes that actually reach the deep seafloor in the region.

Results from recent benthic studies conducted at HAUSGARTEN pointed toward the importance of organic matter supply for the deep-sea benthic community in eastern Fram Strait. Soltwedel et al. (2009, 2016) reported that large-scale distribution patterns of deep-sea megafauna at the long-term observatory were mainly controlled by food availability while water depth and seabed properties played a secondary role. The importance of food availability was further reflected in meiofauna distribution, with higher nematode and harpacticoid copepod densities observed with

increased organic content in sediments (Hoste et al., 2007). Moreover, a decrease in megafaunal densities observed from 2002 to 2007 at the central HAUSGARTEN station was partly attributed to a decrease in total organic carbon content in the sediments (Bergmann et al., 2011). These results identify supply of organic matter as a major factor shaping benthic distribution and density in the region and underscore the necessity of assessing how the magnitude and composition of fluxes are modified as particulate matter sinks toward the seafloor in the eastern Fram Strait.

In this study, sediment traps were deployed at 4 depths from July 2007 to June 2008 at the HAUSGARTEN central station to investigate spatial and temporal variations in the magnitude and composition of particulate matter fluxes from upper waters to the seafloor in the eastern Fram Strait. More precisely, fluxes of total particulate matter (TPM), particulate organic carbon (POC), particulate organic nitrogen (PON), biogenic particulate silica (bPSi), calcium carbonate (CaCO_3), diatoms, coccolithophores, zooplankton fecal pellet carbon (FPC), and biomarkers were measured at 196 m, 1296 m, 2364 m, and 2430 m (3 m above seafloor). The biomarkers sampled included brassicasterol (diatom biomarker), alkenones (coccolithophore biomarker), campesterol and β -sitosterol (terrestrial biomarkers), and IP₂₅ (sea ice diatom biomarker).

2. Material and Methods

2.1. Remote sensing

Daily averaged sea ice concentration for the area above the central station (78°30'–79°30' N; 2°30'–6°30' E) was obtained by analysis of Advanced Microwave Scanning Radiometer-EOS (AMSR-E) data provided by the National Snow and Ice Data Centre. The 89 GHz AMSR-E sensor and the ARTIST Sea Ice (ASI) algorithm were used, yielding a spatial resolution of 6.25×6.25 km (Spreen et al., 2008).

2.2. Mooring line and benthic lander

2.2.1. Current meters

Aanderaa current meters were deployed from July 2007 to July 2008 at 281, 1355, and 2530 m on a mooring line at the central station of the HAUSGARTEN observatory (water depth: 2540 m), and at 2430 m on a benthic lander near the mooring line (water depth: 2433 m) to record current speed, current direction and water temperature (Fig. 1; Table 1). Mean current speed, mean current direction, temperature, and the geographical origin of the sinking material collected in the sediment traps were illustrated in progressive vector diagrams with temperature (PVD-T; Fig. 2). The Eulerian measurements of currents at the mooring and lander locations were displayed in a Lagrangian way following the movement of water parcels with winter-centred deployment period (Fig. 2).

2.2.2. Sediment traps

Three modified automatic Kiel sediment traps with sampling areas of 0.5 m^2 and 20 collection cups (Kremling et al., 1996) were installed at 196, 1296, and 2364 m (176 m above seafloor) on the same mooring deployed at the central station from July 2007 to July 2008 (Fig. 1; Table 1). Collection cups for each sediment trap rotated at intervals ranging from 10 to 31 days depending on the season. Because the mooring line was recovered before the completion of the last rotation, measurements from the last collection cup were dismissed from the study. An additional smaller sediment trap with a sampling area of 0.25 m^2 and 13 collection cups rotating at intervals ranging from 15 to 39 days was mounted on the benthic lander and deployed approximately 3 m above the seafloor at 2430 m from July 2007 to July 2008 (Fig. 1; Table 1). Collection cups from each sediment trap were filled with filtered seawater adjusted to a salinity of 40 with NaCl and poisoned with HgCl_2 (0.14% final solution) to preserve samples during deployment and after recovery. It is important to note that the trap

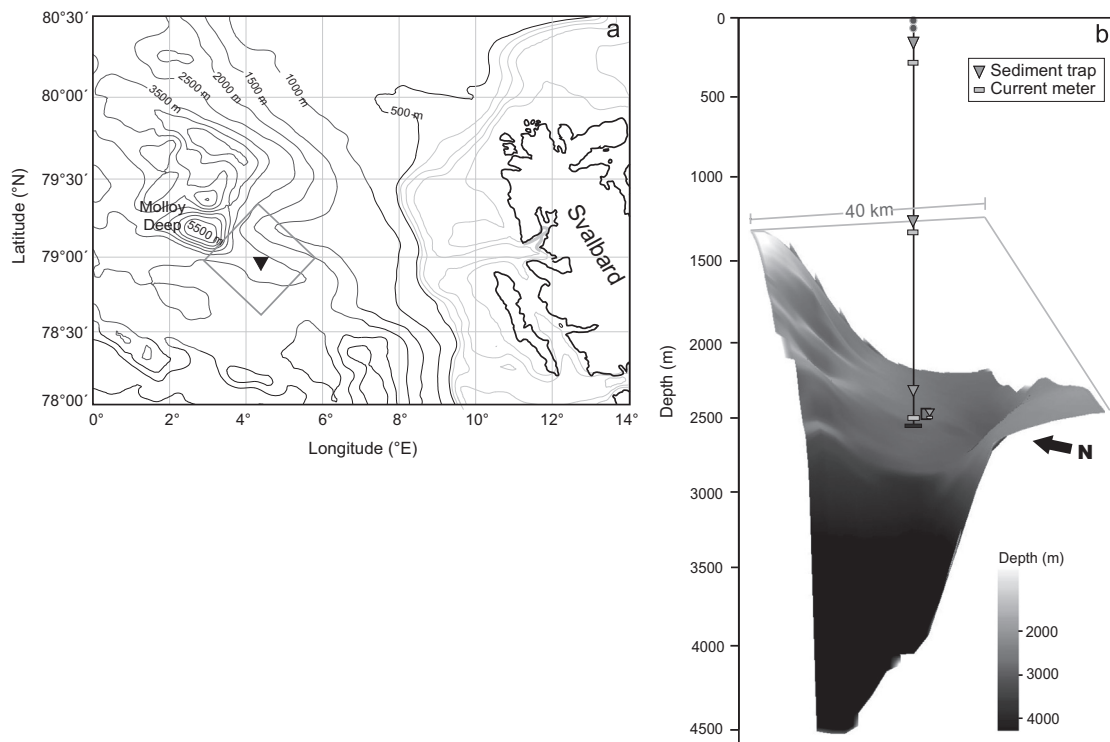


Fig. 1. (a) Map showing the location of the central station (triangle) at the HAUSGARTEN observatory west of Svalbard in the eastern Fram Strait (b) Diagram showing the depths of the sediment traps and current meters deployed on the mooring line at the central station and on the benthic lander near the central station in the context of the bottom topography at the observatory (not to scale; rectangle in panel a).

Table 1
Locations and sampling periods of the sediment traps deployments at the central HAUSGARTEN station and on a benthic lander near the central station from July 2007 to July 2008 in the eastern Fram Strait.

Sediment trap	Position		Trap depth (m)	Current meter depth (m)	Trap sampling period	Water depth (m)
	°N	°E				
Mooring/ upper trap	79°00.82	04°20.62	196	281	July 23 2007–June 30, 2008	2540
Mooring/ middle trap	79°00.82	04°20.62	1296	1355	July 23 2007–June 30 2008	2540
Mooring/ lower trap	79°00.82	04°20.62	2364	2530	July 23 2007–June 30, 2008	2540
Benthic lander	79°05.09	04°09.08	2430	2430	July 23 2007–June 30 2008	2433

installed on the benthic lander has different collection characteristics than traps deployed on the mooring line, which may introduce a bias when comparing the magnitude of the fluxes, but not their composition.

In the laboratory, swimmers (zooplankton actively entering the collection cups) were removed from samples with forceps and rinsed to retrieve all particles using a dissecting microscope. Samples were then split into subsamples for measurements of TPM, CaCO₃, POC, PON, bPSi, phytoplankton cells, zooplankton fecal pellets, and biomarkers. Subsamples for TPM measurements were filtered onto pre-weighed GF/F filters (nominal pore size: 0.7 μm), rinsed with distilled water to remove salt, dried at 60 °C, and weighed on a microbalance. The same filters were then soaked in 0.1 N HCl, rinsed with distilled water to remove residual CaCl₂ after treatment, and reweighed after drying at 60 °C. CaCO₃ values were calculated from the weight difference to total mass. Subsamples for POC and PON measurements were filtered onto GF/F filters (nominal pore size: 0.7 μm) pre-combusted at 500 °C for 4 h, soaked in 0.1 N HCl for removal of inorganic carbon and dried at 60 °C. POC and PON measurements were conducted on a Carlo Erba CHN elemental analyzer and should be considered as minimum values as they were not corrected for dissolution of organic material in the collecting cups. Subsamples for bPSi measurements were filtered on cellulose acetate filters (pore size: 0.8 μm), processed using the wet-alkaline method (pretreated 12 h at 85 °C in an oven), and extracted for 2 h at 85 °C in a shaking water bath (von Bodungen et al., 1991). The fraction of biogenic matter in the total particulate matter was calculated from: 2 × POC + CaCO₃ + opal (opal = 2.1 × bPSi), with the lithogenic fraction representing the difference between the total particulate matter and the biogenic matter fraction (von Bodungen et al., 1991).

Additional subsamples were used for the enumeration of phytoplankton cells by inverted microscopy according to the Utermöhl (1958) method for samples collected from July to November and from April to June. A minimum of 50–100 phytoplankton cells of the dominant groups was counted at 4 magnifications (100, 160, 250, and 400 ×) using phase contrast microscopy. Diatoms were grouped into full cells (containing plasma) and empty cells (valves only). As diatom walls are composed of bPSi and coccolithophores are made of CaCO₃ plates, bPSi and CaCO₃ were used as proxies for these phytoplankton groups.

Subsamples for biomarker analyses of brassicasterol, alkenones, campesterol, β-sitosterol, and IP₂₅ were extracted with dichloromethane/methanol (1:1, v/v) and dichloromethane using

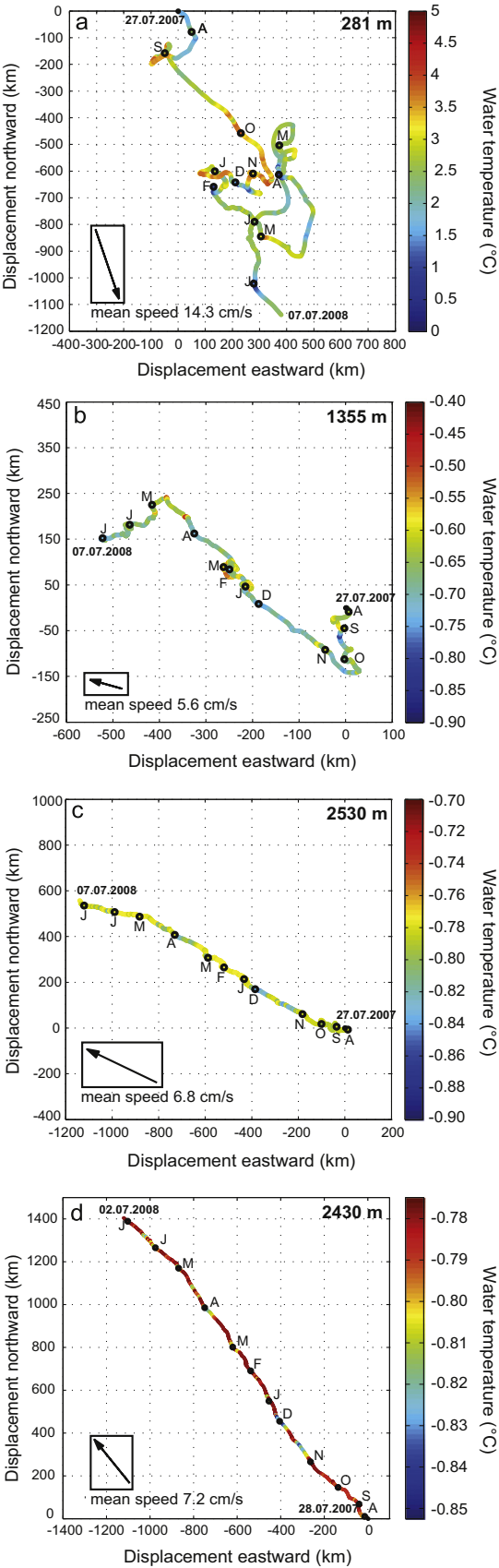


Fig. 2. Progressive vector diagrams (PVD-T) displaying mean current speed, mean current direction, and water temperature measured with current meters deployed on the mooring line at the nominal depths of (a) 281 m, (b) 1355 m, (c) 2530 m, and on the benthic lander at (d) 2430 m from July 2007 to July 2008 in the eastern Fram Strait. Each black dot represents a 1-month period. Note the different scales.

separating funnels. For quantification of the lipid compounds, the internal standards 7-hexylnonadecane, C_{36} *n*-alkane, and cholesterol- d_6 (cholest-5-en-3 β -ol- D_6) were added prior to further analytical steps. The different compounds (IP₂₅, alkenones, and sterols) were separated via open column chromatography (SiO₂) using *n*-hexane, dichloromethane/hexane (1:1 v/v), and ethyl acetate/*n*-hexane (20:80 v/v) as eluent. The alkenones ($C_{37:3}$ and $C_{37:2}$) were analysed by HP 6890 gas chromatograph (column: DB-1MS, 60 m length, 0.32 mm inner diameter, film thickness 0.25 μ m) using a temperature program as follows: 60 °C (1 min), 270 °C (rate: 20 °C/min), 320 °C (rate: 1 °C/min), 320 °C (20 min isothermal). The injection volume was 1 μ l (Cold Injection System: 60 °C, 105 °C (rate: 3 °C/s), 320 °C (rate: 10 °C/s), 320 °C (60 s isothermal)). The identification of the alkenones was carried out by retention time and comparison with an external standard. For further details see Fahl and Stein (1999).

The individual sterols brassicasterol (24-methylcholesta-5, 22E-dien-3 β -ol), campesterol (24-methylcholest-5-en-3 β -ol), and β -sitosterol (24-ethylcholest-5-en-3 β -ol) were silylated with 500 μ l BSTFA (bis-trimethylsilyl-trifluoroacet-amide) at 60 °C for 2 h. After extraction with hexane, analyses were carried out by gas chromatography-mass spectrometry (GC-MS) using an Agilent 6850 GC (30 m HP-5 MS column, 0.25 mm inner diameter, 0.25 μ m film thickness) coupled to an Agilent 5975 C VL mass selective detector. The GC oven was heated from 60 °C to 150 °C (rate: 15 °C/min) and at 3 °C/min to 320 °C (20 min isothermal) for sterols and at 10 °C/min to 320 °C (15 min isothermal) for IP₂₅, respectively. Helium was used as carrier gas. Individual compound identification was based on comparisons of their retention times with that of reference compounds and on comparisons of their mass spectra with published data (see Belt et al., 2007; Boon et al., 1979; Volkman, 1986). IP₂₅ was quantified using its molecular ion m/z 350 in relation to the abundant fragment ion m/z 266 of 7-hexylnonadecane and by means of an external calibration curve ($R^2 = 0.9989$) to balance the different responses of the used ions (for further details see Fahl and Stein, 2012). Brassicasterol (24-methylcholesta-5,22E-dien-3 β -o-Si(CH₃)₃), campesterol (24-methylcholest-5-en-3 β -o-Si(CH₃)₃), and β -sitosterol (24-ethylcholest-5-en-3 β -o-Si(CH₃)₃) were quantified as trimethylsilyl ethers using the molecular ions m/z 470, m/z 472, and m/z 486, respectively, in relation to the molecular ion m/z 464 of cholesterol- D_6 .

Subsamples were also used for the enumeration and measurement of zooplankton fecal pellets (5–200 pellets depending on the sample) using a dissecting scope. Copepod and appendicularian fecal pellets are the identifiable fecal pellets in the study area due to their peritrophic membranes preventing degradation of the pellets (Turner, 2002). The length and width of each fecal pellet were measured and pellet volumes were calculated according to the shape of the pellets, with cylindrical pellets being attributed to calanoid copepods and ellipsoidal pellets to appendicularians (González et al., 2000). Fecal pellet volumes were converted to fecal pellet carbon (FPC) using a volumetric carbon conversion factor of 0.057 mg C mm⁻³ for copepod pellets and 0.042 mg C mm⁻³ for appendicularian pellets (González et al., 1994; González and Smetacek, 1994).

Finally, TPM, POC, PON, bPSi, CaCO₃, diatom, coccolithophores, FPC, and biomarker fluxes were converted to daily fluxes for each collection period.

3. Results

3.1. Ice concentration

Ice was absent from the area at the beginning of the deployment period in July and August 2007 (Figs. 3, 4, 5, and 6). Low ice

concentrations (<20%) were recorded in September, October, December, and January, while ice was absent in November and from February to April 2008. Ice concentration rapidly increased at the end of April 2008 and ranged between 20 and 60% until the end of the deployment period in July 2008.

3.2. Current speed, current direction, and water temperature

The mean current speed recorded at the upper current meter (14.3 cm s⁻¹) was 2–3 times higher than mean current speeds recorded by the 3 deeper instruments (5.6–7.2 cm s⁻¹; Fig. 2). A large temporal variation in current direction was observed at the upper current meter, while current direction was more stable at the middle current meter (1355 m) and nearly constant at the lower current meter (2530 m) and benthic lander (2430 m), 10 m and 3 m above seafloor, respectively. Mean currents were in a SSE direction at the upper current meter, in a WNW direction at the middle and lower current meters, and in a NW direction at the benthic lander. Water temperatures were higher and displayed larger temporal variations in the upper layer than in the intermediate and deep waters (Fig. 2). Water temperatures ranged between 0.63 and 3.90 °C at the upper current meter, between –0.81 and –0.48 °C at the middle current meter, between –0.84 and –0.77 °C at the lower current meter, 10 m above seafloor, and between –0.84 and –0.78 °C at the benthic lander, 3 m above seafloor (Fig. 2).

3.3. Particle fluxes

Annual fluxes of most parameters measured from July 2007 to June 2008 were lowest at the upper trap and highest at the benthic lander trap 3 m above seafloor (Table 2; Figs. 3–6). More precisely, annual fluxes of TPM, biogenic matter, lithogenic matter, POC, PON, bPSi, CaCO₃, and FPC increased with depth, with the exception of lower annual fluxes of POC and PON observed at the lower trap than at the middle trap (Table 2; Figs. 3–5).

Enhanced daily TPM fluxes were observed in August, December, and from April to June at the upper trap, in April and May at the middle trap, and in May and June at the benthic lander trap, while no clear peaks in TPM fluxes were observed at the lower trap apart from February (Fig. 3b). TPM fluxes were generally low during winter except near the seafloor where they were higher than at shallower depths and remained fairly constant throughout fall and winter (Fig. 3(b)). The proportion of biogenic matter in the annual TPM flux was highest at the upper trap, decreased with depth to a nearly equal contribution of biogenic and lithogenic matter at the middle trap, and further decreased to low proportions of biogenic matter at the lower and benthic lander traps (Table 2; Fig. 3(b)). Enhanced POC and PON fluxes were observed in August and April or May at the upper and middle traps but this seasonal pattern faded with depth and POC and PON fluxes remained <20 mg C m⁻² d⁻¹ and <3 mg N m⁻² d⁻¹ respectively at the lower and benthic lander traps, except for 2 peaks observed in March and May at the seafloor (Fig. 3c). Similar to TPM fluxes, winter POC and PON fluxes were higher near the seafloor than at shallower depths (Fig. 3(c)). Large variation in the C/N ratios of the sinking particulate matter was observed at the upper trap, with the highest C/N ratios observed in September and October, while C/N ratios remained fairly constant throughout deployment at the other 3 depths and <10 at the middle and lower traps (Fig. 3(d)). Mean C/N ratios of the sinking material were higher near the seafloor and in upper waters than at the intermediate depths (Table 2).

Enhanced bPSi fluxes were observed at the end of August and at the end of May at the upper trap, and at the beginning of September and from the end of May to the end of June at the middle and lower

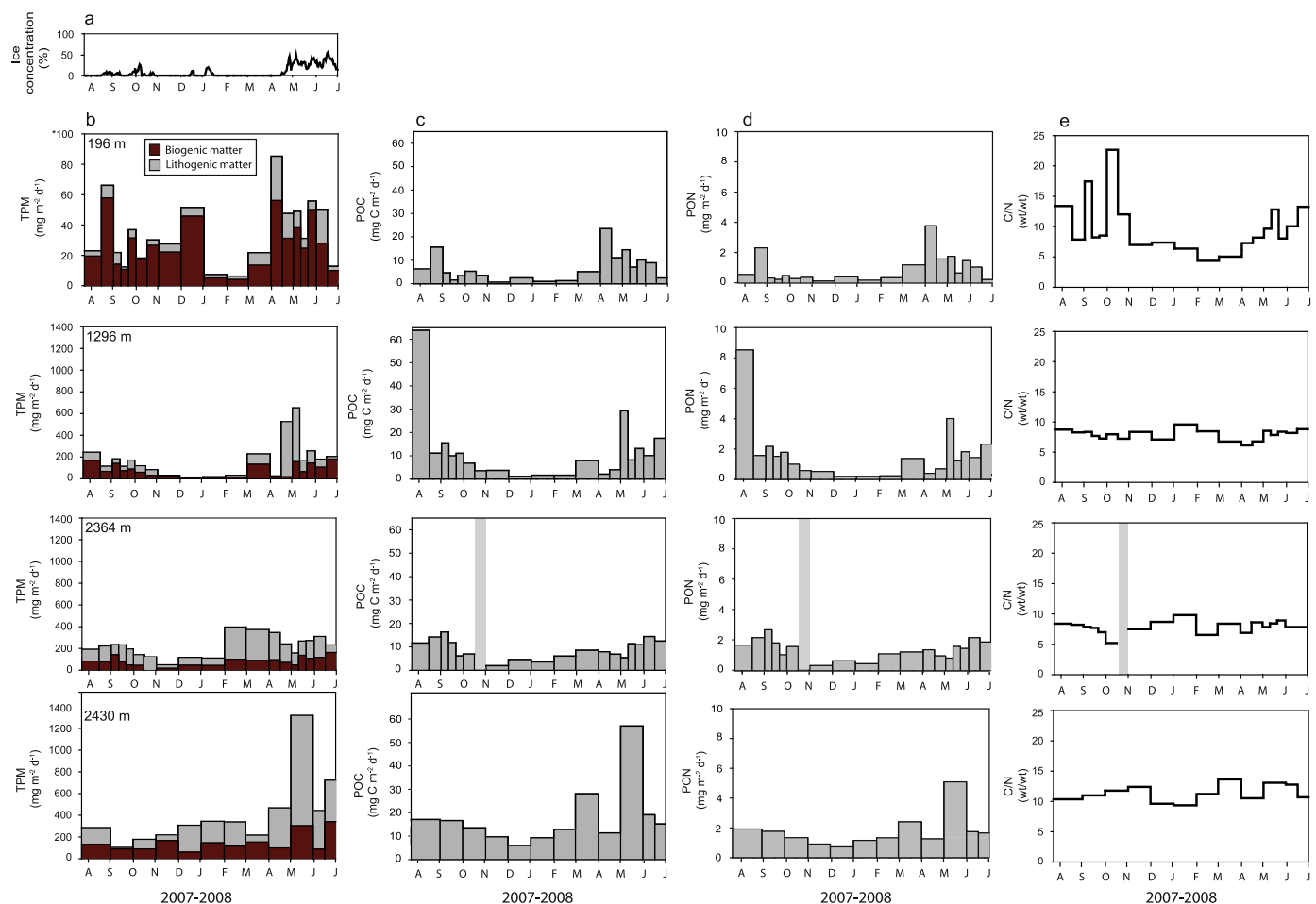


Fig. 3. (a) Daily averaged sea ice concentration for the area above the central station, (b) TPM fluxes including the proportion of biogenic and lithogenic matter, (c) POC fluxes, (d) PON fluxes, and (e) C/N ratios (weight/weight) of the sinking particulate matter obtained at 4 depths from July 2007 to June 2008 in the eastern Fram Strait. *indicates different scales.

traps (Fig. 4b). No increases in bPSi fluxes were observed at the end of summer near the seafloor but enhanced bPSi fluxes were observed in May and at the end of June (Fig. 4b). In addition, enhanced bPSi fluxes were observed in March at the middle and lander traps and from February to April at the lower trap (Fig. 4b). bPSi fluxes were also higher during winter near the seafloor than at the other 3 depths sampled (Fig. 4b). In accordance with bPSi (a diatom proxy), peaks in diatom cell fluxes were observed at the end of August and at the end of May at the upper trap, and at the beginning of September and from the end of May to the end of July at the middle and lower traps, with a slight difference in timing between enhanced bPSi and diatom fluxes in September at the lower trap (Fig. 4c). Diatom fluxes and the proportion of empty diatom cells in the diatom fluxes increased with depth (Fig. 4c). In contrast to bPSi fluxes, no clear peaks in CaCO_3 fluxes were observed at the upper trap where they remained $\leq 10 \text{ mg m}^{-2} \text{d}^{-1}$ (Fig. 4d). CaCO_3 fluxes $> 40 \text{ mg m}^{-2} \text{d}^{-1}$ were observed in March, at the beginning of May, and at the end of June at the middle trap (Fig. 4d). CaCO_3 fluxes increased at the lower trap but remained $< 40 \text{ mg m}^{-2} \text{d}^{-1}$, whereas CaCO_3 fluxes $> 60 \text{ mg m}^{-2} \text{d}^{-1}$ were observed in November, January, March and at the end of June at the benthic lander (Fig. 4d). Coccolithophore fluxes increased with depth but displayed different peaks than CaCO_3 fluxes (Fig. 4e). *Emiliana huxleyi* and *Coccolithus pelagicus* composed the coccolithophore fluxes, with *C. pelagicus* dominating the annual coccolithophore flux at the upper trap and *E. huxleyi* dominating at the middle, lower and lander traps (data not shown).

Brassicasterol fluxes were high at the end of July, in August, and from March to June at the upper trap, whereas they were high from the end of July to October and in May and June at the middle, lower, and benthic lander traps (Fig. 5(b)). Annual brassicasterol fluxes had similar values at the upper, middle, and lower traps but were lower near the seafloor (Table 2, Fig. 5b). Fluxes of alkenones displayed a similar seasonal pattern to brassicasterol with higher fluxes observed from the end of July to October and in May and June at the upper trap, middle and lower traps (Fig. 5c). Alkenone fluxes decreased and displayed less variation near the seafloor (Table 2, Fig. 5c). Terrestrial biomarker (campesterol and β -sitosterol) fluxes peaked at the end of August and at the end of May at the upper trap and in August, September, November, May, and June at the middle trap and lower traps, except for November at the lower trap (Fig. 5d). Similar to brassicasterol and alkenones, annual terrestrial biomarker fluxes decreased and displayed less variation near the seafloor (Fig. 5(d)). IP_{25} was completely absent from the upper trap but was present at all other depths sampled, with higher fluxes observed in March at the middle, lower, and lander traps (Table 2, Fig. 5(e)). IP_{25} fluxes increased from the middle to the lower trap, but decreased and displayed less variation at the benthic lander trap, similar to the other biomarkers (Fig. 5(e)).

Copepod FPC fluxes increased in August–September and in May–June at the upper trap and slightly increased during the same periods at the middle trap (Fig. 6b). Enhanced copepod FPC fluxes were also observed during May and June at the lower trap, but no

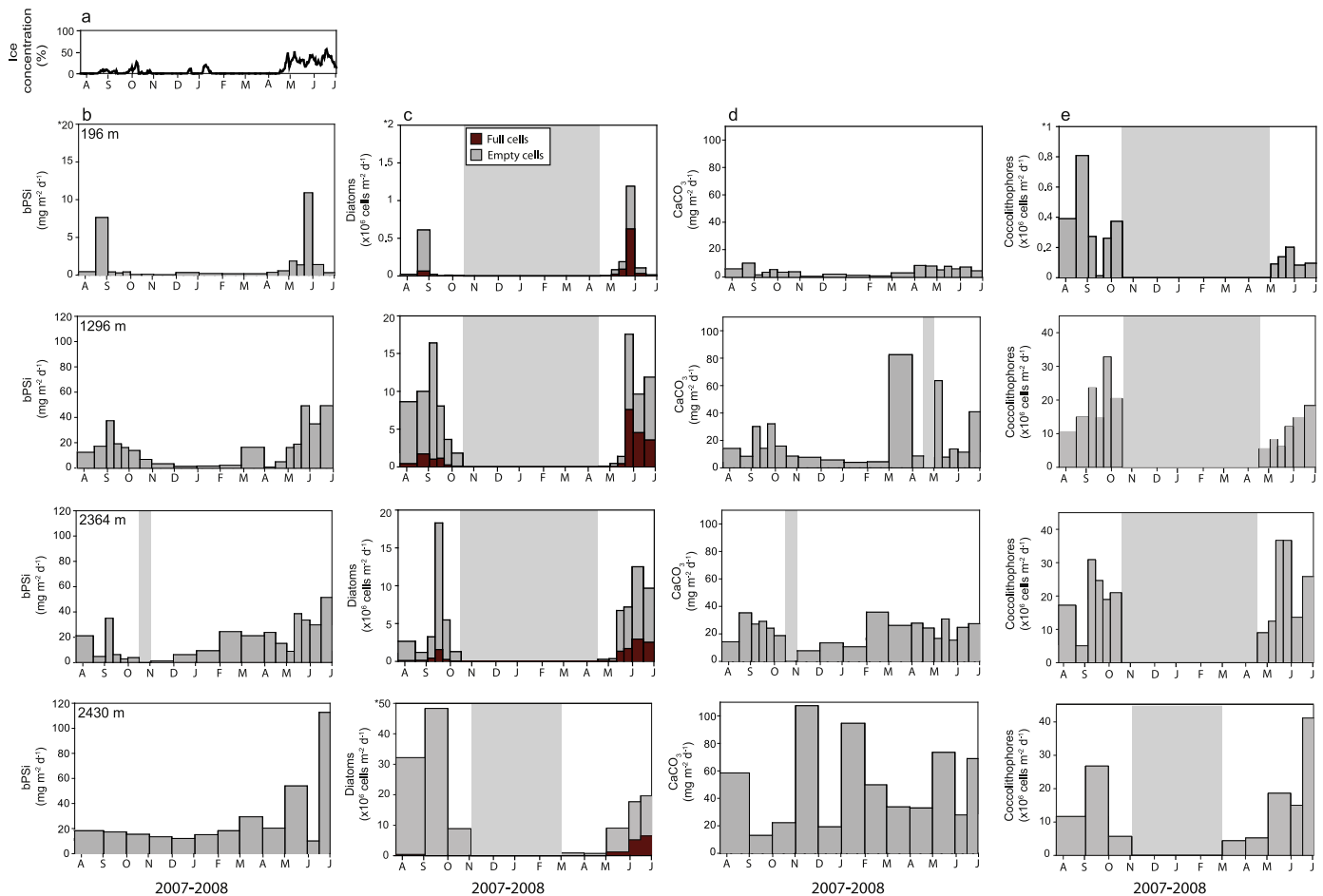


Fig. 4. (a) Daily averaged sea ice concentration for the area above the central station, (b) bPSi fluxes, (c) diatom fluxes, (d) CaCO_3 fluxes, and (e) coccolithophore fluxes obtained at 4 depths from July 2007 to June 2008 in the eastern Fram Strait. *indicates different scales.

clear increase was observed during August–September at that depth (Fig. 6b). Copepod FPC fluxes remained low throughout deployment near the seafloor (Fig. 6b). Meanwhile, enhanced appendicularian FPC fluxes of larger fecal pellets were observed at the end of May at the upper trap, at the beginning of June at the middle and lower traps and at the end of June at the lander trap (Fig. 6b–c). Appendicularian FPC fluxes were low at the end of summer – beginning of fall except for enhanced fluxes observed at that time only at the middle and lower traps (Fig. 6b). Average copepod and appendicularian fecal pellet volumes were smaller at the upper trap than at the 3 other depths but displayed similar volumes at the middle, lower, and benthic lander traps (Table 2; Fig. 6c). While the largest copepod fecal pellets were collected at different times of the year for each depth sampled, the average volume of appendicularian fecal pellets was largest in May at the upper trap, at the beginning of June at the middle and lower traps, and at the end of June at the benthic lander trap (Fig. 6c).

4. Discussion

Particulate matter fluxes were measured in a trough leading to the Molloy Deep (water depth: 5669 m) located ~20 km north of an array of oceanographic moorings that has been maintained to monitor the transport of mass, heat, and freshwater through Fram Strait (Beszczynska-Möller et al., 2012; Schauer et al., 2004). Results from these oceanographic moorings indicate that our study region is influenced by the offshore branch of the West

Spitsbergen Current, carrying Atlantic Water northward in a less-coherent way than in the West Spitsbergen Current core above the upper slope (Beszczynska-Möller et al., 2012; Schauer et al., 2004). The quasi-permanent, topographically-steered cyclonic gyre around the Molloy Deep may also occasionally impact our study area. The eastern Fram Strait between 3 and 6°E is characterized by extended periods of flow reversals associated with a re-circulating branch of the West Spitsbergen Current. Mesoscale features such as anticyclonic eddies and westward-propagating meander-like features dominate the variability of currents in this area (Beszczynska-Möller et al., 2012; Schauer et al., 2004). Ice conditions are typically irregular in the region, and were irregular during the deployment period of 2007–2008 with more ice present in summer than in winter, as the amount of ice exported out of the central Arctic Ocean depends on the southward ice-drift velocity regulated by geostrophic winds (Smedsrud et al., 2011). Particle fluxes obtained during this study will be discussed in the context of these variable ice conditions and oceanographic features in the eastern Fram Strait.

4.1. Atlantic Water layer

The upper trap was located in the warm Atlantic Water layer, as indicated by the highest temperatures $> 2^\circ\text{C}$ recorded by the upper current meter (Fig. 2). As expected for the region, several flow reversals and a mean southeastward current direction related to the cyclonic circulation around the Molloy Deep were recorded at the upper depth during the deployment period (Fig. 2). The high mean current speed and the shifts in current direction indicate

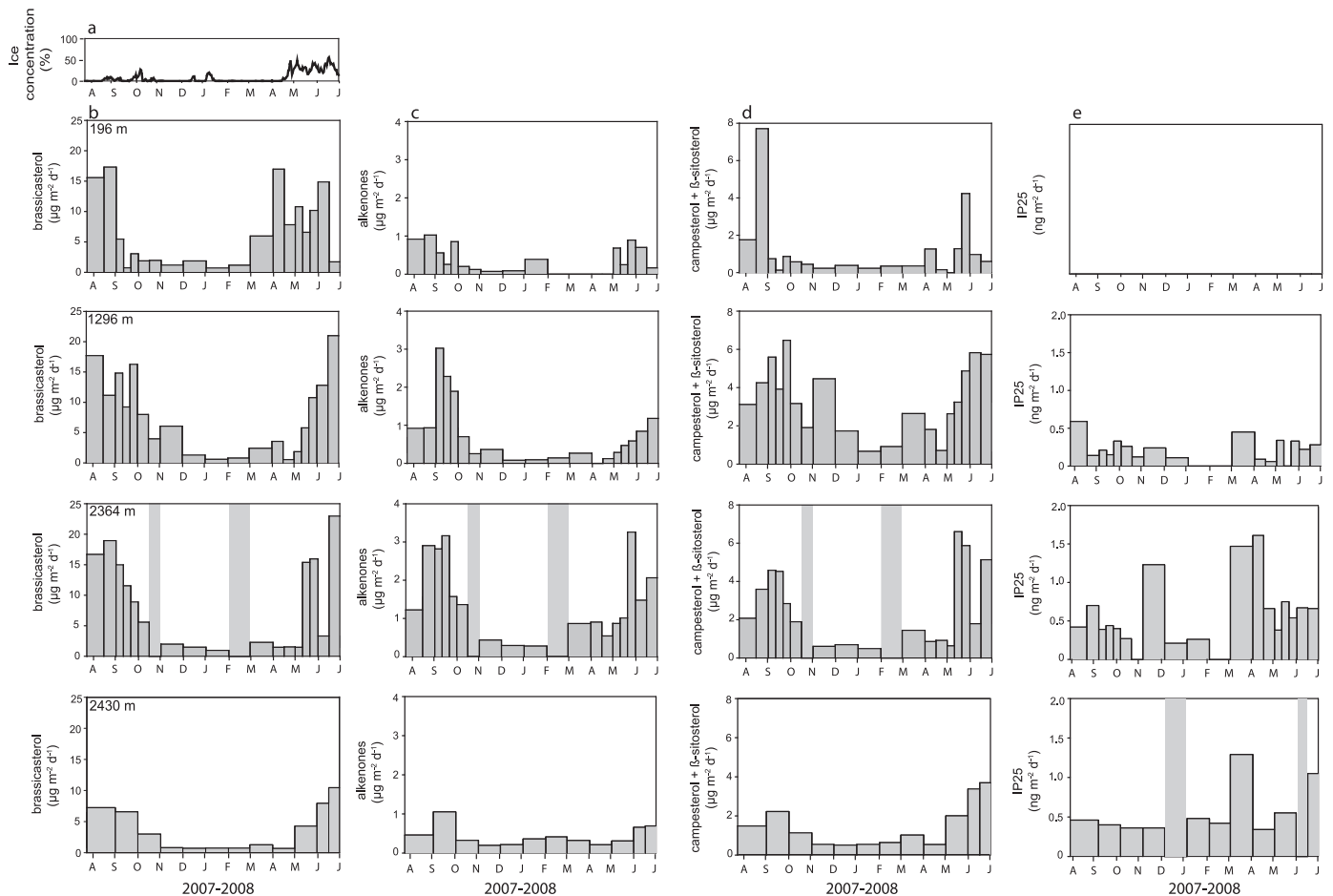


Fig. 5. (a) Daily averaged sea ice concentration for the area above the central station, (b) brassicasterol fluxes, (c) alkenone fluxes, (d) terrestrial biomarkers (campesterol fluxes, and (e) IP₂₅ fluxes obtained at 4 depths from July 2007 to June 2008 in the eastern Fram Strait. * indicates different scales.

that the particles collected in the upper trap had a wide range of geographical origins but were mostly produced northwest of the mooring location. As sinking speeds of biogenic particles may range from 5 to 200 m d⁻¹ (Turner, 2002), particles collected in the upper trap may have been produced 12–480 km away from the mooring location. Lower fluxes in the upper trap than at the other depths sampled may have been the result of a higher mean current velocity at that depth, potentially reducing the collection efficiency. However, the fact that some parameters had values in a similar range and pattern at the upper depth to the other depths sampled (POC, PON, FPC, biomarkers) while other parameters had values several orders of magnitude lower at the upper depth than at the other depths sampled (TPM, coccolithophores) suggests actual lower fluxes in the upper trap and not a collection efficiency bias. Frequent flow reversals at the upper depth also suggest the occurrence of eddies during the deployment period (Fig. 2). Particulate matter fluxes measured at a high-temporal resolution (every 4 days) at 340 m at a nearby location in the eastern Fram Strait showed a shift in the composition of the fluxes at the onset of an ice-edge eddy (Lalande et al., 2011). Such eddy-induced shifts were not clearly apparent in the fluxes measured during the present study, probably due to the lower temporal resolution of measurements.

Particle fluxes obtained at 196 m from July 2007 to June 2008 displayed pronounced seasonal variation for nearly all parameters sampled, with higher fluxes observed in summer and spring reflecting biological productivity in surface waters, similar to observations made during previous years at the same mooring location (Bauerfeind et al., 2009; Lalande et al., 2013). As anticipated,

the proportion of biogenic matter in TPM fluxes was higher in the upper trap than at the other depths sampled, reflecting the proximity to surface productivity in upper waters (Fig. 3). Peaks of bPSi and diatom fluxes at the end of August and at the end of May suggest enhanced diatom biomass at these times, with both peaks occurring in the presence of ice in the area (Fig. 4). Ice melt and the proximity of the ice edge may have promoted the onset of diatom production as a result of strongly-stratified surface waters (Fortier et al., 2002; Lalande et al., 2007; Peinert et al., 2001). The absence of the sea ice diatom biomarker IP₂₅ (Belt et al., 2007) in the upper trap may reflect an increase in pelagic diatom production rather than the release of diatoms enclosed in the ice (Michel et al., 1997). The enhanced flux of diatoms at the end of August was associated with a peak in the flux of coccolithophores, further indicating suitable conditions for phytoplankton growth in surface waters in the preceding days and/or weeks. Increased fluxes of brassicasterol (diatom biomarker; Goad and Withers, 1982; Kanazawa et al., 1971; Volkman, 2006) and alkenones (coccolithophore biomarker; Volkman et al., 1995) also support the increased fluxes of diatoms and coccolithophores at the end of summer and in spring (Fig. 5). Extended periods of increased brassicasterol fluxes compared to brief peaks in bPSi and diatom fluxes may reflect the detection of brassicasterol even when diatoms are destroyed or dissolved (Fahl and Stein, 2012). Nevertheless, fluxes of bPSi, diatoms, brassicasterol, coccolithophores, and alkenones displayed the same increasing trend at the end of summer and in spring. The peaks in phytoplankton growth at the end of August and at the end of May were matched by the highest FPC fluxes, dominated by copepod fecal pellets at the end of August and

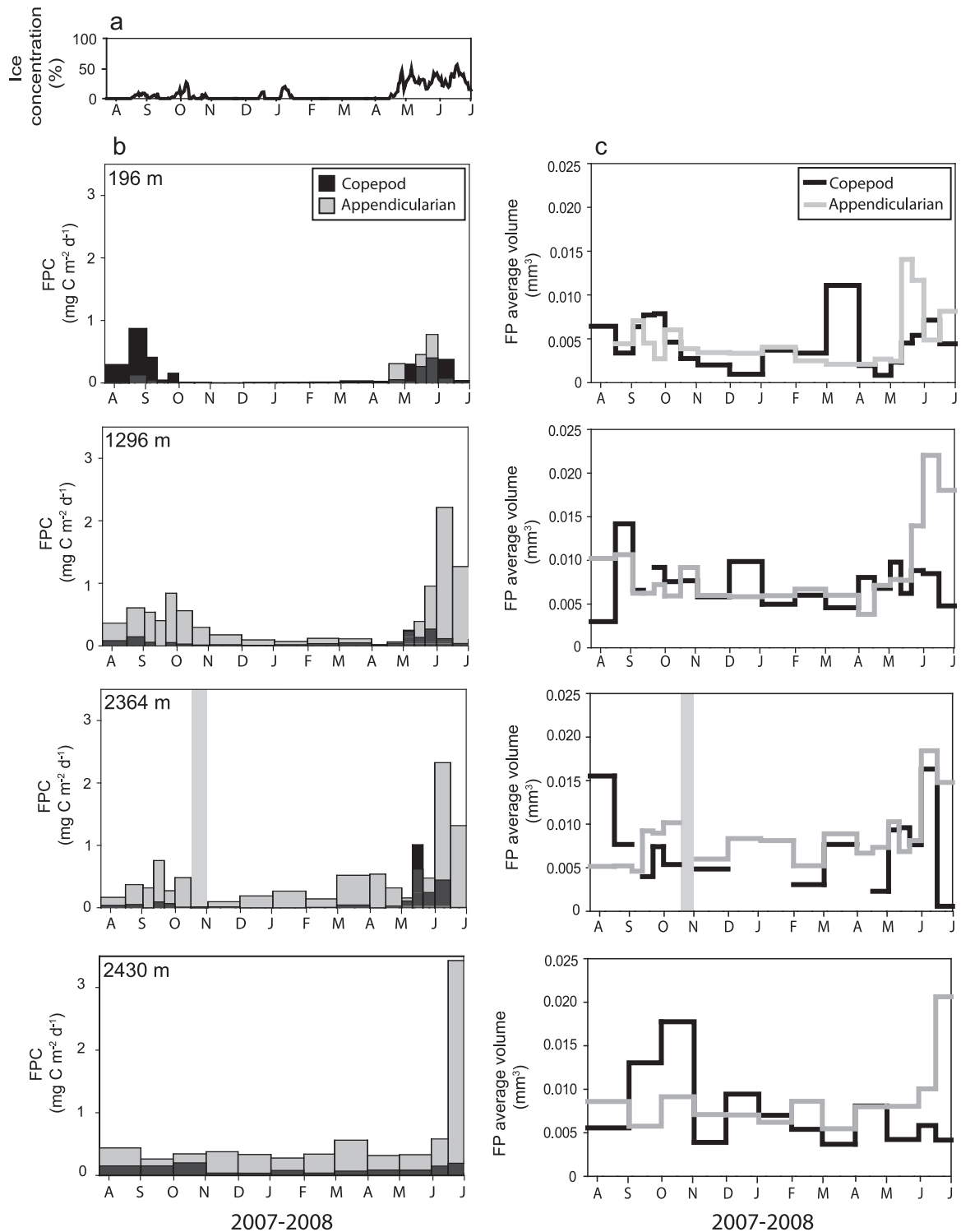


Fig. 6. (a) Daily averaged sea ice concentration for the area above the central station, (b) FPC fluxes, and (c) FP average volumes obtained at 4 depths from July 2007 to June 2008 in the eastern Fram Strait. *Indicates different scales.

appendicularian fecal pellets at the end of May (Fig. 6), indicating that a match between phytoplankton production and zooplankton grazing led to increased fluxes at the upper depth. The increase in copepod fecal pellet fluxes at the end of May reflected the ontogenetic migration of overwintering copepods towards the surface at that time, also observed at a nearby location at the end of May in 2003 (Lalande et al., 2011). A large proportion of copepods were also observed to remain in surface waters until September in the eastern Fram Strait (Lalande et al., 2013; Svensen et al., 2011),

explaining the increase in copepod fecal pellet fluxes at the end of summer when phytoplankton cell fluxes increased.

Interestingly, peaks in phytoplankton and FPC fluxes were associated with peaks of campesterol and β -sitosterol (terrestrial biomarkers; Huang and Meinschein, 1976; Volkman, 1986), reflecting an increased input of terrestrial matter at both the end of August and May (Fig. 5). Terrestrial matter is often incorporated into ice during freeze-up on the shallow Arctic shelves and is then transported with the Transpolar Drift towards Fram Strait (Eicken

Table 2
Annual fluxes of TPM, biogenic matter, lithogenic matter, POC, PON, bPSi, CaCO₃, FPC, brassicasterol, terrestrial biomarkers (campesterol + β -sitosterol), and IP₂₅ obtained at 4 depths from July 2007 to July 2008 in the eastern Fram Strait.

Sediment trap	Depth (m)	TPM (g m ⁻² y ⁻¹)	POC (g C m ⁻² y ⁻¹)	PON (g N m ⁻² y ⁻¹)	C/N (weight)	bPSi (g m ⁻² y ⁻¹)	CaCO ₃ (g m ⁻² y ⁻¹)	FPC (g m ⁻² y ⁻¹)	FPC volume (μ m ⁻³)	Biogenic (g m ⁻² y ⁻¹)	Lithogenic (g m ⁻² y ⁻¹)	Biogenic/Lithogenic (%)	Brassicasterol (mg m ⁻² y ⁻¹)	Alkenones (mg m ⁻² y ⁻¹)	Campesterol and β -sitosterol (mg m ⁻² y ⁻¹)	IP ₂₅ (μ g m ⁻² y ⁻¹)
Mooring/upper trap	196	11.2	2.0	0.3	10.6	0.4	3.8	0.07	4.8	8.6	2.6	77/23	2.00	0.11	0.35	0
Mooring/middle trap	1296	44.5	3.8	0.5	8.0	4.9	5.2	0.16	8.3	23.4	21.1	53/47	2.34	0.20	1.06	0.07
Mooring/lower trap	2364	77.3	2.7	0.4	7.9	5.9	8.2	0.17	7.9	26.0	51.3	34/66	2.30	0.41	0.69	0.26
Benthic lander	2430	139.6	6.3	0.6	11.4	8.7	18.5	0.21	8	49.7	89.9	36/64	1.17	0.15	0.46	0.16

et al., 2000; Wegner et al., 2005). The elevated fluxes of terrestrial biomarkers observed in the upper trap in the presence of drifting ice in the region likely reflected the release of ice-exported terrestrial matter as it melted in Fram Strait. Such releases of ice-raftered material have previously been observed in 1989 and 1990 at ~1100 m at a nearby location in Fram Strait, with large amounts of quartz grains ranging from silt- to fine sand-size collected from melting sea ice (Hebbeln, 2000; Hebbeln and Wefer, 1991). The absence of ice-exported diatoms reflected by the absence of IP₂₅ when enhanced ice-exported terrestrial matter fluxes were observed suggests that sea ice diatoms were released from the under-ice before reaching Fram Strait, whereas terrestrial matter was still enclosed in the ice.

4.2. Intermediate and deep waters

The middle and lower traps were deployed well below the lower boundary of the Atlantic Water layer, delimited as 1 °C and found at a maximum depth of 700 m (Schauer et al., 2004; Fig. 2). Hydrographical conditions were similar in intermediate and deep waters, except for slightly higher water temperatures and more variable current directions observed in intermediate waters than in deep waters (Fig. 2). Still, the mean current direction and mean current speed were nearly the same at both depths and indicated that particles collected in the middle and lower traps originated from the southeast, with currents moving towards Molloy Deep.

Particulate matter fluxes were higher in intermediate waters than in upper waters, and higher in deep waters than in intermediate waters except for POC and PON fluxes. Increased annual fluxes of TPM, lithogenic matter, bPSi, CaCO₃, and FPC fluxes at the middle and lower depths identified lateral advection as the main process supplying particulate matter to intermediate and deep waters in the eastern Fram Strait (Figs. 3, 4, and 6). Diatoms and coccolithophores, the dominant identifiable phytoplankton groups at all depths, also displayed higher fluxes in deep waters than in upper waters. The increasing proportion of lithogenic matter with depth and the increased terrestrial biomarker fluxes suggest the downslope transport of particulate matter from the nearby Svalbard Archipelago, or farther south, into the trough leading to Molloy Deep. This hypothesis is supported by the recent observation of the northward transport of resuspended sediments previously deposited in the deep channel of Storfjordrenna along the upper slope west of Spitsbergen (Sanchez-Vidal et al., 2015).

The importance of lateral advection in the intermediate and deep waters of the eastern Fram Strait was further supported by a change in the dominant species of coccolithophores with depth. The cold-adapted species *C. pelagicus* dominated the coccolithophore fluxes in the upper waters whereas the smaller warm-water species *E. huxleyi* dominated in intermediate and deep waters (data not shown). The vertical distribution of coccolithophore species is supported by the lack of correlation between coccolithophore and alkenone fluxes in upper waters dominated by *C. pelagicus*, a species that does not produce alkenones (Fig. 7; Bendle et al., 2005; Conte et al., 1994). On the other hand, coccolithophore and alkenone fluxes were correlated in intermediate and deeper waters where the alkenone-synthesizing *E. huxleyi* dominated, although fluxes were not significantly correlated at the lower depth (Fig. 7). The dominance of *C. pelagicus* in upper waters is linked to the predominance of a southeastward current favouring the export of the cold-water species while the dominance of *E. huxleyi* in intermediate and deep waters is linked to north-westward water currents. Coccolithophore flux measurements obtained from sediment traps deployed from August 1983 to August 1985 in the Norwegian Sea region identified *C. pelagicus* as the dominant species of the coccolithophore fluxes at 2000 m in the Fram Strait while *E. huxleyi* was the dominant species at

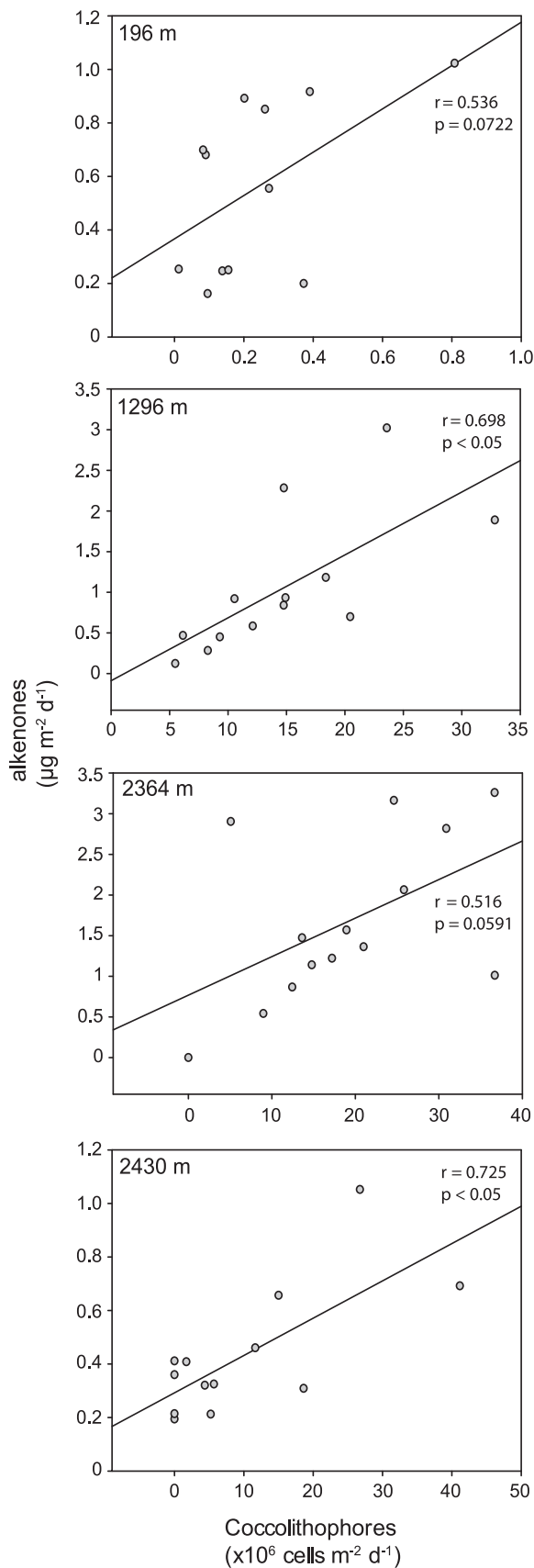


Fig. 7. Correlation between coccolithophore and alkenone fluxes at 4 depths in the eastern Fram Strait.

2600 m in the Lofoten Basin and at 1700 m near Bear Island, both located south of Fram Strait (Samtleben and Bickert, 1990). In addition, fluxes measured with sediment traps deployed from September 1990 to July 1992 at 500, 1000, and 300 m above bottom in the Norwegian and Greenland Seas showed a dominance of *E. huxleyi* in the Atlantic-influenced Norwegian Sea and of the cold-adapted *C. pelagicus* in the Arctic-influenced Greenland Sea, except for a dominance of *E. huxleyi* at 2300 m in the Greenland Sea implying the same origin of material at depth in the Norwegian and Greenland Seas (Andruleit, 1997). Measurements made in the Norwegian and Greenland Seas also displayed increased coccolithophore fluxes with depth, reflecting resuspension and lateral advection from surrounding slopes (Andruleit, 1997). Results from these previous studies and the present study emphasize the continuous supply of *E. huxleyi* from the warmer waters of the Nordic Seas toward the deep waters of Fram Strait and the Arctic Ocean. The proportion of *E. huxleyi* exported in the upper portion of the eastern Fram Strait appears to vary depending on the direction of surface currents, as a dominance of *E. huxleyi* was observed at 300 m at the same mooring location as in the present study in 2000–2001 and in 2004–2005 when currents measured above the sediment traps displayed mean northwestward direction or nearly no displacement, respectively (Bauerfeind et al., 2009). The extent of the lateral advection of *E. huxleyi* into the Arctic Ocean may have increased in recent years, as suggested by the measurements of a dominance of *E. huxleyi* in the deep waters of Fram Strait following the dominance of *C. pelagicus* at 2000 m in 1984–1985 (Andruleit, 1997; Samtleben and Bickert, 1990).

Although fluxes of biomarkers remained in a similar range from upper to deep waters, fluxes of alkenones and terrestrial biomarkers increased in intermediate and deep waters, indicating the increasing importance of small coccolithophore cells and particles of terrestrial origin in deep waters and reinforcing lateral transport as the dominant process for particle supply (Fig. 5). While the amounts of diatoms and coccolithophores and the fluxes of bPSi and CaCO_3 increased substantially between the upper and deep waters, fluxes of brassicasterol and alkenones remained similar or slightly increased only in deeper waters. These similar biomarker signatures in upper and deep waters may be due to a larger amount of smaller phytoplankton cells resulting in a similar amount of biomarkers, or may be due to continuous degradation and lateral transport apparently resulting in a constant downward flux, similar to observations made from sediment traps deployed at the Lomonosov Ridge (Fahl and Stein, 2012). Sterols are generally more susceptible to degradation than the more stable alkenones and IP_{25} , hence constant lateral advection led to higher alkenone and IP_{25} fluxes. Again, these biomarker fluxes likely reflected the transport of resuspended material originating from the Svalbard region or the Barents Sea with the intermediate or deep nepheloid layer. Alternatively, enhanced IP_{25} fluxes with depth may also be explained by the recirculation of Atlantic Water influenced by the topography of Molloy Deep (Schauer et al., 2004). Sea ice diatoms may have been released into the water column during melting farther north in the Arctic Ocean and carried back towards Molloy Deep within the recirculation loops north of Fram Strait, which may explain the absence of IP_{25} at the upper trap and the increasing IP_{25} fluxes in deep waters.

4.3. Above the seafloor

Given the proximity of the benthic lander trap to the seafloor, fluxes measured at that depth reflected resuspension of particulate matter within the bottom boundary layer in addition to downward export and lateral supply. Although TPM and lithogenic matter fluxes increased considerably in deep waters and probably partly reflected the advection of resuspended material, the contribution

of resuspended particulate matter to fluxes at the seafloor may be estimated from the difference between the annual TPM fluxes measured with the benthic lander and at the lower trap depth, which corresponded to nearly half of the fluxes ($\sim 60 \text{ g m}^{-2} \text{ y}^{-1}$; Table 2). However, higher fluxes near the seafloor may also partly reflect greater catchment efficiency of the benthic lander trap due to its smaller aperture compared to the aperture of the sediment traps deployed at the other depths (Gardner, 2000).

While fluxes of TPM, lithogenic matter, POC, bPSi, CaCO_3 , and FPC increased above seafloor, fluxes of brassicasterol, alkenones, campesterol and β -sitosterol and IP_{25} decreased and C/N ratios of the sinking particles increased, indicating the resuspension of refractory and possibly remineralized material (Figs. 3–6; Table 2). The constant mean current direction, reasonably low current speed, and the reduced or even absent seasonality in fluxes recorded $\sim 3 \text{ m}$ above seafloor suggest a constant input of resuspended material, except for a major resuspension event leading to increased TPM and POC fluxes in May 2008. Considering a sinking speed of 5 m d^{-1} estimated for smaller biogenic particles (Turner, 2002), the particulate matter collected at 2430 m may have been produced as far as 3000 km away from the benthic lander location.

Despite the major influence of lateral advection and resuspension on particle supply to the deep eastern Fram Strait, some fluxes reflected the influence of local processes. Due to their high sinking speed, diatom and fecal pellet fluxes may be used to trace the export of locally-produced biogenic matter (Billett et al., 1983; Eppley and Peterson, 1979; Turner, 2002). The export of large appendicularian fecal pellets can be traced from the upper waters to the seafloor, with peaks observed at the end of May in upper waters, at the beginning of June in the intermediate and deep waters, and at the end of June at the seafloor, indicating that these large, fast-sinking particles require 15–35 days to reach the seafloor at 2400 m (Fig. 6b,c). These peaks in appendicularian FPC fluxes were accompanied by similar peaks in diatom and bPSi fluxes, suggesting that this export event was triggered by appendicularians feeding on a diatom spring bloom and that diatoms were at least partly exported inside fecal pellets. Peaks of diatoms sinking from the surface to the seafloor were also observed at the end of August in upper waters, at the beginning of September in intermediate waters, in the middle of September in deep waters, and some time in September at the seafloor, showing that diatoms sank at a similar speed to appendicularian fecal pellets. This rapid export of diatoms during fall was matched with an increase in copepod fecal pellets at the end of August in upper waters but peaks in FPC fluxes were not subsequently observed at the lower depths. This absence of peaks in copepod fecal pellet fluxes at lower depths is likely due to the fragility and lowest sinking speed of copepod pellets in contrast to appendicularian pellets, and to possible coprophagy and coprorhexy during descent (Turner, 2002). Appendicularians, one of the most abundant mesozooplankton groups after copepods, have fecal pellet production rates substantially greater than those of copepods and appendicularian pellets are larger and more compact (Berline et al., 2011). Overall, the downward export of diatoms and appendicularian fecal pellets produced in surface waters during spring rapidly provided a fresh food supply for benthic communities.

4.4. Conclusion

The magnitude and composition of particulate matter fluxes measured using an approach combining biomarkers, microscopic observations, and standard flux measurements at 4 depths in the deep eastern Fram Strait identified lateral advection and resuspension as the main processes supplying particulate matter to the seafloor at the HAUSGARTEN observatory. Specifically,

biomarkers and microscopic observations provided added insight into the composition and the size of the sinking particles essential to the assessment of the importance of lateral supply. Increases in fluxes with depth due to lateral advection are not uncommon in the deep-sea and were observed at the Barents Sea continental slope (von Bodungen et al., 1995), in the Canada Basin (Hwang et al., 2008), at the Lomonosov Ridge (Fahl and Nöthig, 2007), in the Australian sector of the Southern Ocean (Trull et al., 2001), and in the Ross Sea (Collier, 2000). On the other hand, the rapid export of large diatoms and appendicularian fecal pellets traced from the upper waters to the deep waters in May–June reflected the influence of local processes on the export of biogenic matter to the seafloor in the eastern Fram Strait, specifically in the presence of ice. This is in agreement with results from several studies conducted in the deep-sea indicating a rapid downward transport of phytoplankton cells and/or fecal pellets (e.g. Billett et al., 1983; Boetius et al., 2013). This downward export of biogenic matter during spring likely represents the most important food supply for benthic communities at the HAUSGARTEN observatory. Indeed, lower fluxes of diatoms and fecal pellets measured in the upper waters of the observatory during the warm anomaly observed from 2005 to 2007 may have caused a decline in benthic megafauna abundance and density in the eastern Fram Strait (Bergmann et al., 2011; Lalande et al., 2013). This hypothesis is supported by the fact that suspension feeders accounted for nearly 100% of the megafauna density in 2007, while deposit feeders nearly disappeared in 2007 but had high densities in 2004 when ice was more frequently present in the region (Bergmann et al., 2011). These results imply that further warming in the eastern Fram Strait would lead to lower export fluxes of fast-sinking freshly-produced particulate matter, as suggested by Forest et al. (2010), and therefore to lower benthic megafaunal abundance dominated by suspension feeders. On the other hand, warm anomalies recorded in the Atlantic Water inflow observed concurrently with enhanced ice export in the Fram Strait (Beszczynska-Möller et al., 2012; Smedsrud et al., 2011) have the potential to increase fluxes of diatoms and terrestrial matter released from the melting ice. The actual impact of climate warming on downward export and lateral supply of particulate matter from upper waters to the seafloor in the deep eastern Fram Strait is therefore difficult to predict.

Acknowledgements

We thank the captain and crew of RV *Polarstern* expeditions ARKXXII/1c and ARKXXIII/2 for their excellent support during the deployment and recovery of the sediment traps at the HAUSGARTEN observatory. We thank L. Kaleschke for providing sea ice concentration data, C. Lorenzen, M. Ginzburg, N. Knüppel, S. Murawski, and W. Luttmner for laboratory work, and R. Martinez for providing the 3D map. This study was funded by the HGF MPG Joint Research Group on Deep Sea Ecology and Technology and the Polar Biological Oceanography Group of the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research. Data are available at <https://doi.pangaea.de/10.1594/PANGAEA.859549>, <https://doi.pangaea.de/10.1594/PANGAEA.855474>, <https://doi.pangaea.de/10.1594/PANGAEA.859547> and <https://doi.pangaea.de/10.1594/PANGAEA.859548>.

References

- Andrulleit, H., 1997. Coccolithophore fluxes in the Norwegian–Greenland Sea: seasonality and assemblage alterations. *Mar. Micropaleontol.* 31, 45–64.
- Bauerfeind, E., Nöthig, E.-M., Beszczynska, A., Fahl, K., Kaleschke, L., Kreker, K.,

- Klages, H., Soltwedel, T., Lorenzen, C., Wegner, J., 2009. Particle sedimentation patterns in the eastern Fram Strait during 2000–2005: results from the Arctic Long-Term Observatory HAUSGARTEN. *Deep Sea Res. Part I: Oceanogr. Res. Pap.* 56, 1471–1487.
- Belt, S.T., Massé, G., Rowland, S.J., Poulin, M., Michel, C., LeBlanc, B., 2007. A novel chemical fossil of palaeo sea ice: IP25. *Org. Geochem.* 38, 16–27.
- Bendle, J., Rosell-Melé, A., Ziveri, P., 2005. Variability of unusual distributions of alkenones in the surface waters of the Nordic seas. *Paleoceanography*. <http://dx.doi.org/10.1029/2004PA001025> (PA2001).
- Bergmann, M., Soltwedel, T., Klages, M., 2011. The interannual Variability of megafaunal (assemblages in the) Arctic deep sea: preliminary results from the HAUSGARTEN observatory (79°N). *Deep Sea Res. Part I: Oceanogr. Res. Pap.* 58, 711–723.
- Berline, L., Stemann, L., Vichi, M., Lombard, F., Gorsky, G., 2011. Impact of appendicularians on detritus and export fluxes: a model approach at DyFAMED site. *J. Plankton Res.* 33, 855–872.
- Beszczynska-Möller, A., Fahrbach, E., Schauer, U., Hansen, E., 2012. Variability in Atlantic water temperature and transport at the entrance to the Arctic Ocean, 1997–2010. *ICES J. Mar. Sci.: J. Cons.* 69, 852–863.
- Billett, D.S.M., Lampitt, R.S., Rice, A.L., Mantoura, R.F.C., 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature* 302, 520–522.
- Boetius, A., Albrecht, S., Bakker, K., Bienhold, C., Felden, J., Fernández-Méndez, M., Hendricks, S., Katlein, C., Lalande, C., Krumpen, T., Nicolaus, M., Peeken, I., Rabe, B., Rogacheva, A., Rybakova, E., Somavilla, R., Wenzhöfer, F., RV Polarstern ARK27/3 Shipboard Science Party, 2013. Export of algal biomass from the melting Arctic Sea ice. *Science* 339, 1430–1432.
- Boon, J.J., Rijpstra, W.I.C., Lange, F.D., de Leeuw, J.W., Yoshioka, M., Shimizu, Y., 1979. Black Sea sterol-a molecular fossil for dinoflagellate blooms. *Nature* 277, 125–127.
- Collier, R., Dymond, J., Honjo, S., Manganini, S., Francois, R., Dunbar, R., 2000. The vertical flux of biogenic and lithogenic material in the Ross Sea: moored sediment trap observations 1996–1998. *Deep-Sea Res. Part I: Oceanogr. Res. Pap.* 47, 3491–3520.
- Conte, M.H., Volkman, J.K., Eglinton, G., 1994. Lipid biomarkers of the haptophyta. In: Green, J.C., Leadbeater, B.S.C. (Eds.), *The Haptophyte Algae (The Systematics Association Special Volume)*. Clarendon, Oxford, UK, pp. 351–377.
- Eicken, H., Kolatschek, J., Freitag, J., Lindemann, F., Kassens, H., Dmitrenko, I., 2000. A key source area and constraints on entrainment for basin-scale sediment transport by Arctic sea ice. *Geophys. Res. Lett.* 27, 1919–1922.
- Eppey, R.W., Peterson, B.J., 1979. Particulate organic-matter flux and planktonic new production in the Deep Ocean. *Nature* 282, 677–680.
- Fahl, K., Stein, R., 1999. Biomarkers as organic-carbon-source and environmental indicators in the Late Quaternary Arctic Ocean: problems and perspectives. *Mar. Chem.* 63, 293–309.
- Fahl, K., Nöthig, E.M., 2007. Lithogenic and biogenic particle fluxes on the Lomonosov Ridge (central Arctic Ocean) and their relevance for sediment accumulation: vertical vs. lateral transport. *Deep-Sea Res. Part I: Oceanogr. Res. Pap.* 54, 1256–1272.
- Fahl, K., Stein, R., 2012. Modern seasonal variability and deglacial/Holocene change of central Arctic Ocean sea-ice cover: New insights from biomarker proxy records. *Earth Planet. Sci. Lett.*. <http://dx.doi.org/10.1016/j.epsl.2012.1007.1009>
- Forest, A., Wassmann, P., Slagstad, D., Bauerfeind, E., Nöthig, E.-M., Klages, M., 2010. Relationships between primary production and vertical particle export at the Atlantic-Arctic boundary (Fram Strait, HAUSGARTEN). *Polar Biol.* 33, 1733–1746.
- Fortier, M., Fortier, L., Michel, C., Legendre, L., 2002. Climatic and biological forcing of the vertical flux of biogenic particles under seasonal Arctic sea ice. *Mar. Ecol. Prog. Ser.* 225, 1–16.
- Gardner, W.D., 2000. Sediment trap sampling in surface waters: issues and recommendations. In: Hanson, R.B., Ducklow, H.W., Field, J.G. (Eds.), *The Changing Ocean Carbon Cycle: A Midterm Synthesis of the Joint Global Ocean Flux Study*. Cambridge University Press, New York, NY, pp. 240–281.
- Goad, L.J., Withers, N., 1982. Identification of 27-nor-(24R)-24-methylcholesta-5,22-dien-3 β -ol and brassicasterol as the major sterols of the marine dinoflagellate *Gymnodinium simplex*. *Lipids* 17, 853–858.
- González, H.E., Smetacek, V., 1994. The possible role of the cyclopoid copepod *Oithona similis* in retarding the vertical flux of zooplankton faecal material. *Mar. Ecol. Prog. Ser.* 113, 233–246.
- González, H.E., Gonzalez, S.R., Brummer, G.-J.A., 1994. Short-term sedimentation pattern of zooplankton, faeces and microplankton at a permanent station in the Bjornafjorden (Norway) during April–May 1992. *Mar. Ecol. Prog. Ser.* 105, 31–45.
- González, H.E., Ortiz, V.C., Sobarzo, M., 2000. The role of faecal material in the particulate organic carbon flux in the northern Humboldt Current, Chile (23°S), before and during the 1997–1998 El Niño. *J. Plankton Res.* 22, 499–529.
- Hargde, K., 2012. Sedimentation Pattern of Protists in the AWI-HAUSGARTEN (Fram Strait, Arctic Ocean). *Fachbereich Biologie, Chemie, Pharmazie*, vol. M.Sc. Freie Universität, Berlin, p. 94.
- Hebbeln, D., 2000. Flux of ice-rafted detritus from sea ice in the Fram Strait. *Deep Sea Res. Part II: Top. Stud. Oceanogr.* 47, 1773–1790.
- Hebbeln, D., Wefer, G., 1991. Effects of ice coverage and ice-rafted material on sedimentation in the Fram Strait. *Nature* 350, 409–411.
- Hoste, E., Vanhove, S., Schewe, I., Soltwedel, T., Vanreusel, A., 2007. Spatial and temporal variations in deep-sea meiofauna assemblages in the Marginal Ice Zone of the Arctic Ocean. *Deep Sea Res. Part I: Oceanogr. Res. Pap.* 54, 109–129.
- Huang, W.-Y., Meinschein, W.G., 1976. Sterols as source indicators of organic materials in sediments. *Geochim. Cosmochim. Acta* 40, 323–330.
- Hwang, J., Eglinton, T.L., Krishfield, R.A., Manganini, S.J., Honjo, S., 2008. Lateral organic carbon supply to the deep Canada Basin. *Geophys. Res. Lett.* 35, L11607.
- Kanazawa, A., Yoshioka, M., Teshima, S.-I., 1971. The occurrence of brassicasterol in the diatoms *Cyclotella nana* and *Nitzschia closterium*. *Bull. Jpn. Soc. Sci. Fish.* 37, 889–903.
- Kremling, K., Lentz, U., Zeitzschel, B., Schulz-Bull, D.E., Duinker, J.C., 1996. New type of time-series sediment trap for the reliable collection of inorganic and organic trace chemical substances. *Rev. Sci. Instrum.* 67, 4360–4364.
- Lalande, C., Bauerfeind, E., Nöthig, E., 2011. Downward particulate organic carbon export at high temporal resolution in the eastern Fram Strait: influence of Atlantic Water on flux composition. *Mar. Ecol. Prog. Ser.* 440, 127–136.
- Lalande, C., Bauerfeind, E., Nöthig, E.-M., Beszczynska-Möller, A., 2013. Impact of a warm anomaly on export fluxes of biogenic matter in the eastern Fram Strait. *Prog. Oceanogr.* 109, 70–77.
- Lalande, C., Grebmeier, J.M., Wassmann, P., Cooper, L.W., Flint, M.V., Sergeeva, V.M., 2007. Export fluxes of biogenic matter in the presence and absence of seasonal sea ice cover in the Chukchi Sea. *Cont. Shelf Res.* 27, 2051–2065.
- Michel, C., Legendre, L., Taguchi, S., 1997. Coexistence of microalgal sedimentation and water column recycling in a seasonally ice-covered ecosystem (Saroma-ko Lagoon, Sea of Okhotsk, Japan). *J. Mar. Syst.* 11, 133–148.
- Peinert, R., Bauerfeind, E., Gradinger, R., Haupt, O., Krumbholz, M., Peeken, I., Werner, I., Zeitzschel, B., 2001. Biogenic particle sources and vertical flux patterns in the seasonally ice-covered Greenland Sea. In: *The Northern North Atlantic: A Changing Environment*. Springer Verlag, Berlin, pp. 69–79.
- Samtleben, C., Bickert, T., 1990. Coccoliths in sediment traps from the Norwegian Sea. *Mar. Micropaleontol.* 16, 39–64.
- Sanchez-Vidal, A., Veres, O., Langone, L., Ferré, B., Calafat, A., Canals, M., Durrieu de Madron, X., Heussner, S., Mienert, J., Grimalt, J.O., Pusceddu, A., Danovaro, R., 2015. Particle sources and downward fluxes in the eastern Fram strait under the influence of the west Spitsbergen current. *Deep Sea Res. Part I: Oceanogr. Res. Pap.* 103, 49–63.
- Schauer, U., Fahrbach, E., Osterhus, S., Rohardt, G., 2004. Arctic warming through the Fram Strait: oceanic heat transport from 3 years of measurements. *J. Geophys. Res.* 109, C06026.
- Smetsrud, L.H., Sirevaag, A., Kloster, K., Sorteberg, A., Sandven, S., 2011. Recent wind driven high sea ice export in the Fram Strait contributes to Arctic sea ice decline. *Cryosphere* 5, 821–829.
- Soltwedel, T., Jaekisch, N., Ritter, N., Hasemann, C., Bergmann, M., Klages, M., 2009. Bathymetric patterns of megafaunal assemblages from the arctic deep-sea observatory HAUSGARTEN. *Deep Sea Res. Part I: Oceanogr. Res. Pap.* 56, 1856–1872.
- Soltwedel, T., Bauerfeind, E., Bergmann, M., Budaeva, N., Hoste, E., Jaekisch, N., Juterzenka, K.V., Matthiessen, J., Mokievsky, V., Nöthig, E.-M., Quéric, N.-V., Sablotny, B., Sauter, E., Schewe, I., Urban-Malinga, B., Wegner, J., Wlodarska-Kowalcuk, M., Klages, M., 2005. HAUSGARTEN: multidisciplinary investigations at a deep-sea, long-term observatory in the Arctic Ocean. *Oceanography* 18, 46–61.
- Soltwedel, T., Bauerfeind, E., Bergmann, M., Bracher, A., Budaeva, N., Busch, K., Cherkasheva, A., Fahl, K., Grzelak, K., Hasemann, C., Jacob, M., Kraft, A., Lalande, C., Metfies, K., Nöthig, E.-M., Meyer, K., Quéric, N.-V., Schewe, I., Wlodarska-Kowalcuk, M., Klages, M., 2016. Natural variability or anthropogenically-induced variation? Insights from 15 years of multidisciplinary observations at the arctic marine LTER site HAUSGARTEN. *Ecol. Indic.* 65, 89–102.
- Spren, G., Kaleschke, L., Heygster, G., 2008. Sea ice remote sensing using AMSR-E 89-GHz channels. *J. Geophys. Res.* 113, C02S03.
- Svensen, C., Seuthe, L., Vasilyeva, Y., Pasternak, A., Hansen, E., 2011. Zooplankton distribution across Fram Strait in autumn: are small copepods and protozooplankton important? *Prog. Oceanogr.* 91, 534–544.
- Trull, T.W., Bray, S.G., Manganini, S.J., Honjo, S., François, R., 2001. Moored sediment trap measurements of carbon export in the subantarctic and polar frontal zones of the Southern Ocean, south of Australia. *J. Geophys. Res.: Oceans* 106, 31489–31509.
- Turner, J.T., 2002. Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms. *Aquat. Microb. Ecol.* 27, 57–102.
- Utermöhl, H., 1958. Zur Vervollkommen der quantitativen Phytoplankton – Methodik. *Mitt. Int. Verh. Limnol.* 9, 1–38.
- Volkman, J.K., 1986. A review of sterol markers for marine and terrigenous organic matter. *Org. Geochem.* 9, 83–99.
- Volkman, J.K., 2006. Lipid markers for marine organic matter. In: Volkman, J.K. (Ed.), *Handbook of Environmental Chemistry*. Springer-Verlag, Berlin, Heidelberg, pp. 27–70.
- Volkman, J.K., Barrer, S.M., Blackburn, S.I., Sikes, E.L., 1995. Alkenones in *Gephyrocapsa oceanica*: implications for studies of paleoclimate. *Geochim. Cosmochim. Acta* 59, 513–520.
- von Bodungen, B., Antia, A., Bauerfeind, E., Haupt, O., Koeve, W., Machado, E., Peeken, I., Peinert, R., Reitmeier, S., Thomsen, C., Voss, M., Wunsch, M., Zeller, U., Zeitzschel, B., 1995. Pelagic processes and vertical flux of particles: an overview of a long-term comparative study in the Norwegian Sea and Greenland Sea. *Geol. Rundsch. (Int. J. Earth Sci.)* 84, 11–27.
- von Bodungen, B., Wunsch, M., Fürderer, H., 1991. Sampling and analysis of suspended and sinking particles in the northern North Atlantic. In: Hurt, D.C., Spencer, D.W. (Eds.), *Marine Particles: Analysis and Characterization*, Vol. *Geophysical Monograph Series American Geophysical Union*, vol. 63, pp. 47–53.
- Wegner, C., Hölemann, J.A., Dmitrenko, I., Kirillov, S., Kassens, H., 2005. Seasonal variations in Arctic sediment dynamics—evidence from 1-year records in the Laptev Sea (Siberian Arctic). *Glob. Planet. Change* 48, 126–140.