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Effects of suspended sediments on copepods feeding in a glacial influenced sub-Arctic fjord

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We investigated the effect of suspended sediments on the vital rates of the copepods *Calanus finmarchicus*, *Pseudocalanus* sp. and *Metridia longa* in a Greenland sub-Arctic fjord. The fjord had a gradient of suspended particulate matter (SPM) with high concentrations ($>50\ \mathrm{mg\ L^{-1}}$) in the inner fjord due to glacial melt water runoff. Laboratory experiments showed that when feeding on the diatom *Thalassiosira weissflogii* specific ingestion rates were low at high concentrations of suspended sediment for *C. finmarchicus* ($>20\ \mathrm{mg\ L^{-1}}$) and *Pseudocalanus* sp. ($>50\ \mathrm{mg\ L^{-1}}$), while no effect was found for *M. longa*. For *C. finmarchicus*, a relatively constant fecal pellet production (FPP) and fecal pellet volume suggested ingestion of sediment, which probably led to reduction in egg production rates (EPRs) at high sediment concentrations. For *Pseudocalanus* sp., FPP decreased with increasing sediment concentrations, while no effect was observed on EPR. No significant difference was observed in FPP for *M. longa* feeding on the diatom *T. weissflogii* compared to the ciliate *Strombidium sulcatum*. The study shows that high sediment concentrations influence the capability of carbon turnover in *C. finmarchicus* and *Pseudocalanus* sp., while *M. longa* appears to be more tolerant to high sediment loads. Therefore, high concentrations of SPM could potentially influence the species composition of glacially influenced fjords.

KEYWORDS: grazing; copepoda; suspended sediment; Greenland

INTRODUCTION

Coastal planktonic organisms encounter, for periods, a wide range of suspended particulate matter (SPM) due to river runoff and re-suspension of sediments. Glacially influenced marine environments can temporally have high concentrations of SPM due to extensive glacial erosion of the bedrock that leads to a high sediment load in the runoff (Domack *et al.*, 1994; Hallet *et al.*, 1996). Marine organisms inhabiting these environments are, therefore, exposed to high loads of SPM. Most fjords in Greenland receive large amounts of melt water with high sediment concentrations from the Greenland Ice Sheet. The runoff is extensive during summer (Mortensen *et al.*, 2011), but plumes containing sediment can be observed by remote sensing even in winter when they are intensified by tidal re-suspension (Rysgaard *et al.*, 2008). At present, run off and SPM

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loads are expected to increase as a result of the melting of the Greenland Ice Sheet. The melting is advancing northwards along the northwestern coast of Greenland (Kahn *et al.*, 2010). Furthermore, the fact that circulation modes within fjords link to the outlet from Greenland ice Sheet glaciers (Mortensen *et al.*, 2011) highlights the urgent need of knowledge about fjord ecology and effects from melting of the Greenland Ice Sheet.

It is well documented that marine zooplankton ingest particles of low nutritional value, even mineral particles as inferred from both grazing experiments (Poulet, 1983; Paffenhöffer and Van Sant, 1985) and fecal pellet (FP) analysis (Bayliss and Syvitski, 1982; Turner, 1984; Urban *et al.*, 1992). Although ingested, inorganic material itself provides little food for zooplankton. On the other hand, relatively little information is available on whether or not the inert particles have an effect on the absorption of nutritional compounds, feeding strategy or food accessibility. Some protozooplankton seem to be well adapted to environments with high clay loads (Boenigk and Novarino, 2004). Flagellates discriminate against clay particles, while ciliates reject larger clay particles but incorporate smaller clay particles into food vacuoles and later excrete them without any significant negative effect on feeding, growth rate or maximal abundance (Boenigk and Novarino, 2004). Metazoans such as rotifers also seem to be well adapted to clay and silt loads, whereas silt alone can significantly negatively affect the ingestion of phytoplankton by cladocerans (Kirk, 1991). For this reason, filter-feeding cladocerans are often absent from glacial lakes and the macrozooplankton community is instead dominated by raptorial feeding copepods (Koenings *et al.*, 1990). Some copepod species are able to reject non-food particles (Paffenhöfer and Van Sant, 1985) by use of chemo- or mechanoreceptors either by perception at a distance or when particles are being handled (Koehl and Strickler, 1981; Paffenhöfer, 1998; Kiørboe, 2008). Other copepod species do ingest non-food particles, such as sediments of clay and silt particles (Paffenhöfer, 1972; White and Dagg, 1989; De Troch *et al.*, 2006). Ingested clay and silt particles take up space in the gut that otherwise could be occupied by more nutritious food particles and can therefore have a negative effect on the nutritional intake of the copepod (Paffenhöfer, 1972). On the other hand, sediment particles can absorb trace metals, organics and nutrients (Brown *et al.*, 2002) and serve as a substrate for bacteria (Syvitski and Lewis, 1980) and therefore indirectly end up being a nutritional source for the copepod (Lewis and Syvitski, 1983).

Previous studies have shown horizontal zonation of copepod species along the glacially influenced Godthåbsfjord (Southwest Greenland) (Arendt *et al.*, 2010a). There, the Atlantic species *Calanus finmarchicus* is most abundant in the mouth of the fjord and particularly in the offshore region, while *Pseudocalanus* sp. is most abundant in the central region of the fjord and *Metridia longa* in the inner parts of the fjord close to the glacial terminus. *Metridia longa* generally inhabits deep waters but migrates to the surface waters daily (Daase *et al.*, 2008). *Pseudocalanus* sp. are often found in surface plumes or fronts where freshwater plumes meet oceanic water and flocculation and aggregation of organic material takes place (Brown *et al.*, 2002; Dagg *et al.*, 2004). The dominance of *Pseudocalanus* sp. and *M. longa* in the Godthåbsfjord could therefore reflect the species ability to cope with high concentrations of SPM as suspended sediment. The distribution of *C. finmarchicus* is best related to the hydrography of the water flowing into the fjord from the adjacent shelf (Pedersen and Smidt, 2000; Arendt *et al.*, 2010a). However, why *Calanus* spp. has not established itself in the fjord receiving glacial melt water runoff is unclear. Based on the observed distribution pattern in the Godthåbsfjord, we hypothesize that species tolerance to high sediment concentrations may determine the distribution of these three copepod species along the glacially influenced fjord branch. The aim of this study was to investigate the species tolerance to natural concentrations of suspended sediments, in terms of grazing rate, fecal pellet production (FPP) and egg production rate (EPR).

METHOD

The effects of suspended sediment on feeding and egg production of the three copepod species *Calanus finmarchicus*, *Pseudocalanus* sp. and *Metridia longa* were investigated at increasing concentrations of suspended sediment. The clearance rate (F), specific ingestion rate (SIR), FPP, FP volume and EPR were determined at a fixed concentration of the diatom *Thalassiosira weissflogii* (300 μg C L^{-1}) at six different concentrations of sediment suspensions. Additional experiments were performed for *M. longa* offered the ciliate *Strombidium sulcatum* as food at 40 μg C L^{-1} at four different sediment suspensions. All laboratory work was conducted at the Greenland Institute of Natural Resources.

SPM, field

Turbidity (FTU; Formazin Turbidity Units) and fluorescence were measured in the water column along a transect in the Godthåbsfjord in August 2008 (Fig. 1) using a Sea-Bird Electronics SBE19plus SEACAT

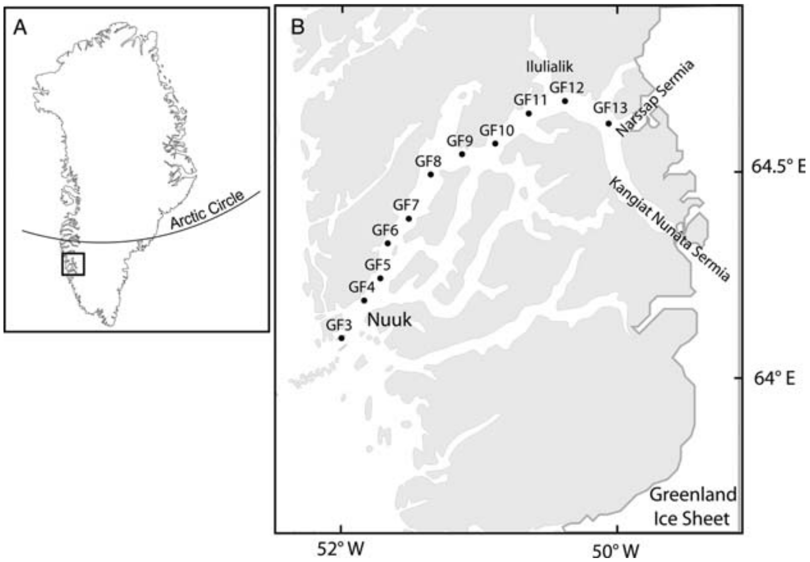

Fig. 1. (**A**) Greenland, and (**B**) the Godthåbsfjord system with station location.

Profiler CTD (conductivity, temperature and depth) equipped with a Seapoint Turbidity Meter and a Seapoint Chlorophyll Fluorometer. In January and August 2009, water was sampled near the outlet from Lake Tasersuaq (Stn GF11) and near the glacial terminus of Narssap Sermia (Stn GF13) for quantification of SPM (Figs 1 and 2A). Water samples were taken with 5 L Niskin bottles, from which 2000 mL were filtered on to pre-weighed GF/F filters. The filters were dried at 60°C for 24 h and weighed. At the same time, fjord water was sampled to determine concentration and particle size of SPM. Approximately 50 L of fjord water was sampled from both the surface plume at 1 m depth and from the subsurface plume at 100 m depth (indicated by crosses in Fig. 2A). The fjord water was allowed to settle for 2 weeks after which the supernatant was discharged. The precipitate was sieved through a 500 μm sieve to remove larger fractions and dried at 60°C for 3 days. The dry matter was then sieved through a 50 μm sieve, representing clay (grain size <2 μm) and silt (grain size 2−50 μm). Two stock solutions of natural SPM (SPM plume and SPM 100 m) were then made by suspending the dried material in demineralized water (Purelab Option, ELGA). The size frequency distribution in terms of number and volume of the stock solutions (1−50 μm) was measured with a Multisizer$^{\text{TM}}$ Model 3 (Beckman Coulter) equipped with a 100 μm orifice.

Experimental sediment stock

In March 2009, a block of ice originating from the Greenland Ice Sheet was collected from the inner part of the Godthåbsfjord (Fig. 1) near to the outlet glacier Kangiata Nunâta Sermia (Fig. 1B). The ice block was found trapped in the sea ice and contained high amounts of sediment, so-called black ice.

The ice block was brought to the laboratory where it was melted. The solution was treated as the SPM sampled in the water column (see above). A sediment stock solution of 20 g sediment L^{-1} was made for use in the laboratory experiments. The sediment stock solution was kept cold and dark until use.

Laboratory cultures

The diatom *Thalassiosira weissflogii* and the chlorophyte *Dunaliella tertiolecta* were grown in batch cultures in the L1 medium (Scandinavian Culture Centre for Algae and Protozoa) at 15°C in natural sea water of 34. Illumination was provided by cool fluorescent lamps at 75 $\mu E\ m^{-2}\ s^{-1}$ [measured using a LiCor 1411 (Li-Cor, NE, USA)] following a 12:12 h light:dark cycle. Cultures were kept in exponential growth by replacing one-third of the culture stock every day with new L1 medium. The heterotrophic ciliate *Strombidium sulcatum* was grown in batch cultures in 2 L polycarbonate bottles at 10°C in the dark and fed with *D. tertiolecta*. The carbon content of 131 pg carbon $cell^{-1}$ for *T. weissflogii* was obtained from Dutz *et al.* (Dutz *et al.*, 2008) measured on the same stock culture, whereas carbon content of 1220 pg carbon $cell^{-1}$ for *S. sulcatum* was obtained from Broglio *et al.* (Broglio *et al.*, 2003).

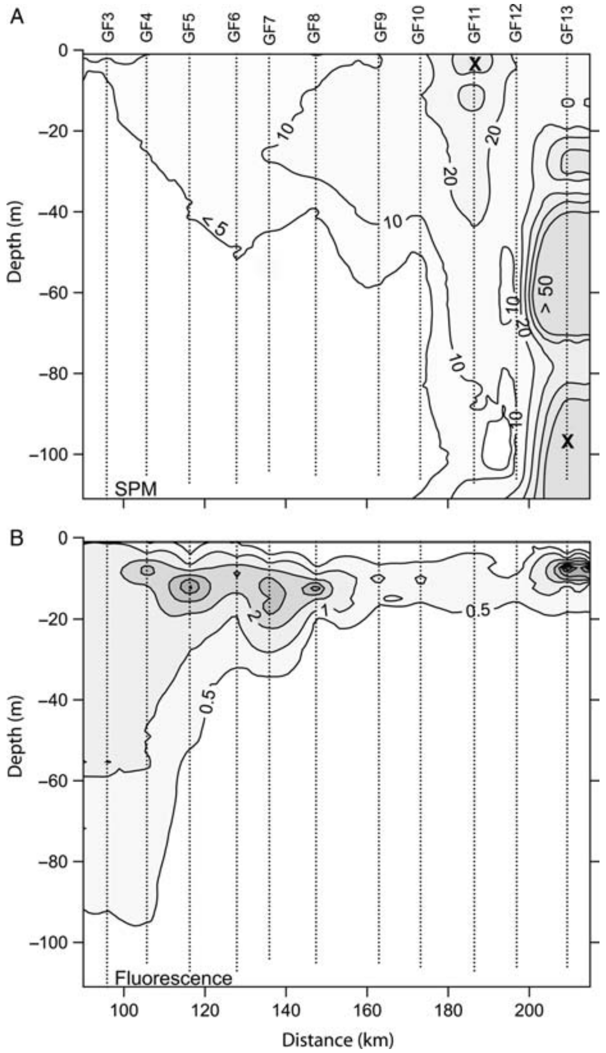

Fig. 2. (**A**) Vertical distribution of SPM along the Godthåbsfjord (marking represent samples for sediment stock solutions in the water column), and (**B**) fluorescence, dotted lines represent CTD casts.

Copepods

Copepods for the experiment were collected mid-May 2009 in the central part of the Godthåbsfjord Stn GF7 (Fig. 1B) by vertically towing a 200-μm WP-2 net equipped with a non-filtering cod end from 0 to 100 m. The samples were brought into the laboratory where living, healthy looking females (*Calanus finmarchicus*, *Pseudocalanus* sp. and *Metridia longa*) were picked and incubated in GF/C filtered sea water for 12 h at 5°C before being introduced to the experimental food and sediment concentrations.

Experimental setup

Food suspensions of 300 μg C L^{-1} *Thalassiosira weissflogii* were prepared with a series of the desired sediment concentrations of 0, 2.5, 5, 10, 20, 50 and 100 mg sediment L^{-1}, and 40 μg C L^{-1} of *Strombidium sulcatum* with sediment concentrations of 0, 20, 50 and 100 mg sediment L^{-1}. The food/sediment suspension was made in GF/F filtered seawater and was gently mixed before triplicate samples were taken for measurement of the initial Chlorophyll *a* (Chl *a*) concentrations. Each suspension was distributed between 18 530 mL polycarbonate bottles. Of these, three bottles without animals were run as controls, while a set of five bottles each received either two *Calanus finmarchicus* females, five *Pseudocalanus* sp. females or two *Metridia longa* females. The bottles were sealed without air bubbles and placed on a plankton wheel at 2 rpm at 5°C in the dark. Every 24 h, samples for Chl *a* (experiments with *T. weissflogii*) or cell counts (experiments with *S. sulcatum*) were taken, the remaining test suspension was gently sieved through a 450 μm mesh to retain copepods and hereafter sieved through a 20 μm mesh to collect eggs and FPs. Living copepods were transferred to bottles with new food and silt suspensions. Dead copepods were replaced by new individuals that had been treated and acclimated in the same way as the experimental copepods. The experiment was run for a total of 4 days.

Analytical procedures

In the experiments with *Thalassiosira weissflogii* as food, three samples of 50 mL were filtered onto 25 mm GF/C filters (pressure <0.2 bar) for Chl *a* analysis after each experimental day. Filters were extracted in 5 mL 96% ethanol for 18 h in the dark at 20°C before fluorescence was measured with a fluorometer (TD-700, Turner Designs, California, USA) calibrated against a pure Chl *a* standard (Turner Designs). In experiments with *Strombidium sulcatum*, four samples of 3 mL each were drawn from each of the suspensions and transferred to a micro titer plate with 3.5 mL chambers containing three drops of Lugol's solution. Samples were allowed to settle for 12 h before they were counted under an inverted microscope. Clearance rate (F) and ingestion rate (I) were calculated based on initial and final Chl *a* measurements (experiments with *T. weissflogii*) or cell counts (experiments with *S. sulcatum*) using the equation of Frost (Frost, 1972). Eggs and FPs were counted under a stereo microscope. Length and width of FPs and the prosome length of the copepods were measured using a calibrated ocular micrometer. The volume of FP was calculated assuming a cylindrical shape. The carbon content of the copepods was calculated using published length−weight regressions (given in Thor *et al.*, 2005). The carbon-SIR was calculated as the daily carbon ingestion divided by copepod carbon

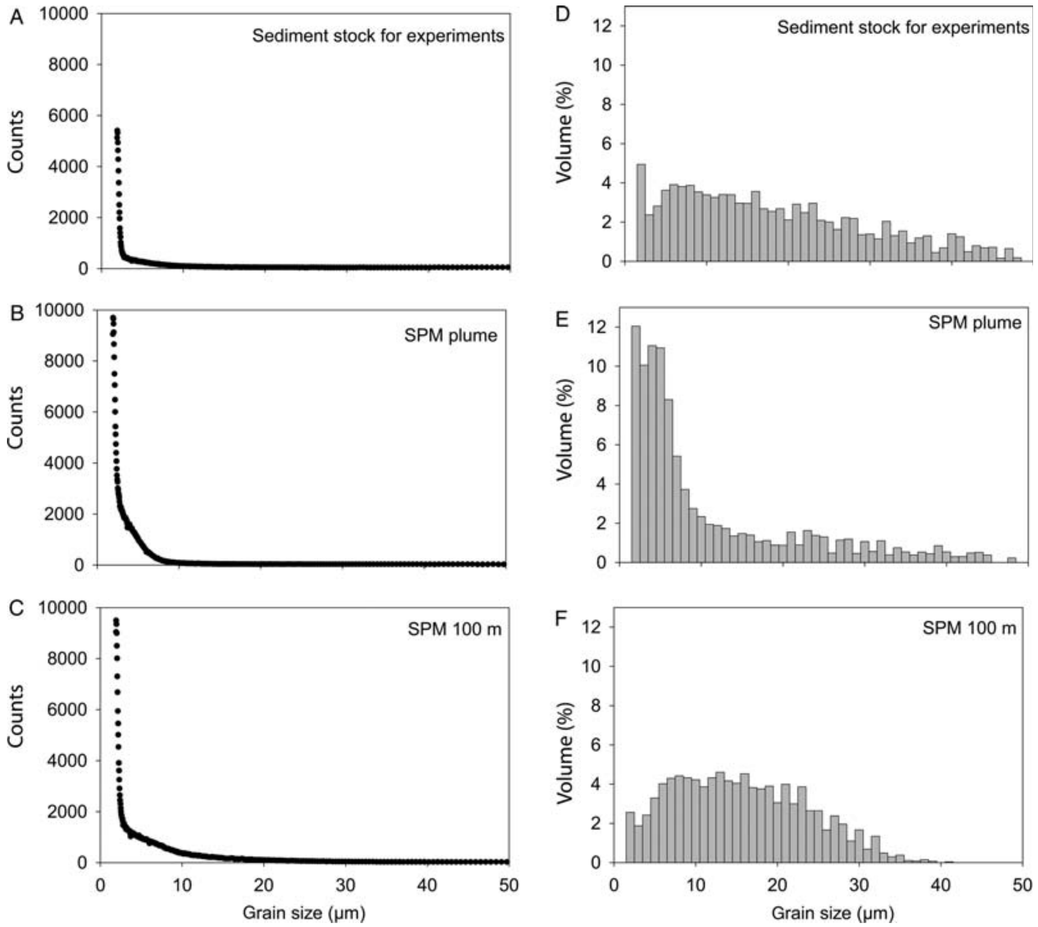

Fig. 3. (**A–C**) Concentration (counts) and (**D–F**) distribution of total volume (%) as function of grain size (μm) (2–50 μm) in the stock solutions; sediment stock used in the experiments (from melted ice), SPM plume (sampled in the fjord Stn GF11, 1 m) and SPM 100 m (sampled in the fjord Stn GF13, 100 m).

content (SIR, μg C day^{-1} μg C^{-1} gives the rate day^{-1}). The influence of increasing sediment concentrations on SIR was fitted to functions in Solver Excel, and statistical analysis and nonparametric Wilcoxon test were performed using JMP® 8.0.1.

RESULTS

SPM, field

Concentrations of SPM ranged from 4.2 to 48.3 mg L^{-1} in the water samples from 2009. The SPM had a positive correlation with the *in situ* turbidity measurements (FTU) ($R^2 = 0.94$, $F = 323.11$, $P < 0.0001$) and therefore concentrations of SPM (mg L^{-1}) were estimated from the FTU measurements following a linear relationship (Domack *et al*., 1994):

$$\mathrm{SPM} = 2.66\,\mathrm{FTU} + 5.45 \qquad (1)$$

The FTU measurements on the transect sampled in 2008 were accordingly converted to concentrations of SPM (mg L^{-1}) (Fig. 2A). The field study showed that the concentrations of SPM can be very high in subsurface plumes close to the outlet glaciers (>50 mg L^{-1}) and in the surface water near the outlet of Lake Tasersuaq at Stn GF11 (>40 mg L^{-1}). The concentrations of SPM decreased towards the fjord mouth to less than 5 mg L^{-1} (Fig. 2A). In contrast, the fluorescence increased towards the fjord mouth (Fig. 2B). We therefore assume that the high concentration of SPM close to the glacial outlet and its decrease towards the fjord mouth largely reflect the inorganic mineral load of seawater and not the phytoplankton concentration, which is by definition part of the SPM.

Stock solutions

Particle size distributions (2–50 μm) in terms of concentration and total volume (%) of the three SPM 'stock

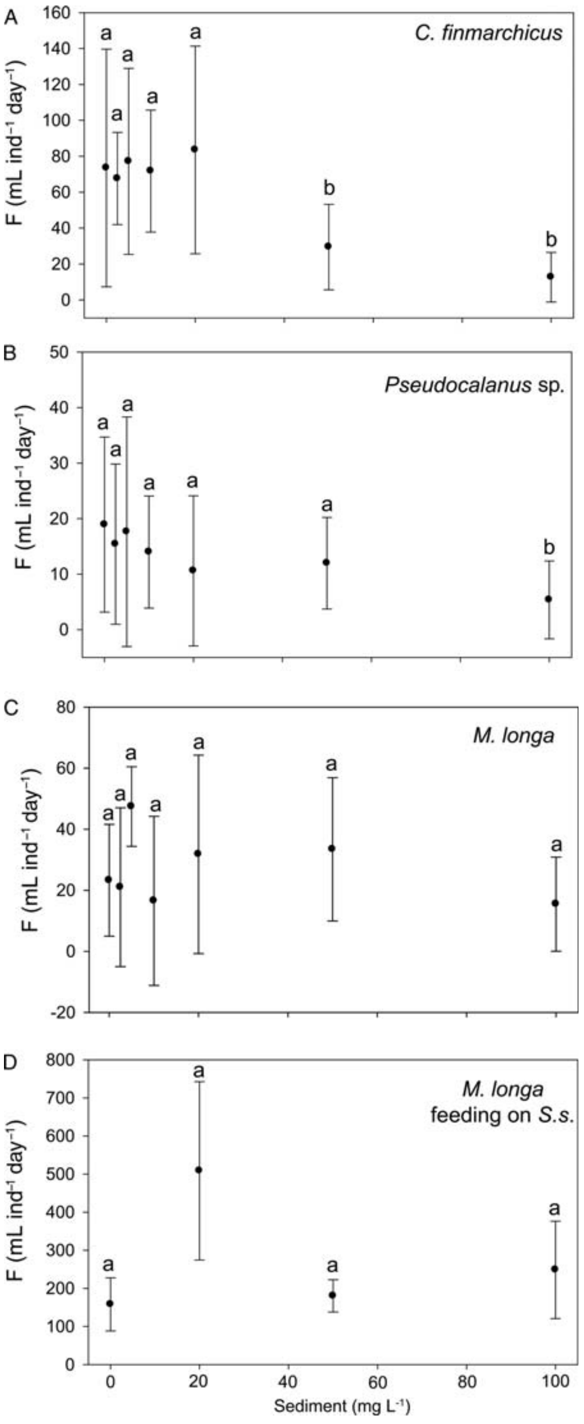

Fig. 4. Clearance rate F (mL ind^{-1} day^{-1}) ± standard deviation, for (**A**) *Calanus finmarchicus*, (**B**) *Pseudocalanus* sp. and (**C** and **D**) *Metridia longa* at variable sediment concentrations when feeding on *Thalassiosira weissflogii* or *Strombidium sulcatum*. Different letters denote treatments that are significantly different from each other ($P < 0.05$).

solutions'; sediment stock (melted ice), SPM surface plume and SPM 100 m (Fig. 2A) are shown in Fig. 3. For all three samples, clay (2–3 μm) was the most abundant particle size (Fig. 3A–C). In terms of volume, 90% of the sediment stock solution was made of silt grains (>5 μm), while 93% of the total volume was made of silt grains in the stock solution SPM 100 m. Fine clay material made up larger part of the SPM surface plume stock solution, hereof 33% of total volume were clay particles and 67% of the total volume were silt grains.

Clearance rate

There were no significant differences in clearance rates (F, mL ind^{-1} day^{-1}) at the tested sediment concentrations over the four experimental days ($P > 0.05$, $n \geq 18$, Wilcoxon test). Clearance rate, F, is therefore pooled over the whole experimental period for each copepod species at each sediment concentration. Clearance rate of *Thalassiosira weissflogii* by *Calanus finmarchicus* and *Pseudocalanus* sp. decreased with increasing sediment concentrations, whereas no significant effect of sediment on F was observed for *Metridia longa* (Fig. 4). The strongest reduction in F for *C. finmarchicus* was found between 20 and 100 mg sediment L^{-1} ($P < 0.01$, $n = 38$, Wilcoxon test), whereas no difference in F was observed at either of the incubations at 0–20 mg sediment L^{-1} or at 50 and 100 mg sediment L^{-1} (Fig. 4A). Clearance rate varied between 67.6 ± 25.7 and 83.5 ± 57.8 mL ind^{-1} day^{-1} for *C. finmarchicus* exposed to 0–20 mg sedimentL^{-1}, whereas F decreased to <12.0 ± 13.7 mL ind^{-1}day^{-1} for the incubation with 50 and 100 mg sediment L^{-1}. A significant reduction in F for *Pseudocalanus* sp. was found at the highest sediment concentration of 100 mg sediment L^{-1} ($P < 0.02$, $n = 143$, Wilcoxon test). F decreased from 11.9 ± 15.8–18.9 ± 15.8 mL ind^{-1} day^{-1} at 0–50 mg sediment L^{-1} to 5.3 ± 7.0 mL ind^{-1} day^{-1} at 100 mg sediment L^{-1}; however, there was no difference in F when exposed to 0–50 mg sediment L^{-1} (Fig. 4B). Clearance rate for *M. longa* varied between 15.5 ± 15.4 mL ind^{-1} day^{-1} at 100 mg sediment L^{-1} and 47.4 ± 13.1 mL ind^{-1} day^{-1} at 5 mg sediment L^{-1} without any significant difference between the experiments (Fig. 4C). F was significantly higher when *M. longa* was feeding on *Strombidium sulcatum* compared to the rates when feeding on *T. weissflogii* ($P < 0.01$, $n = 34$, Wilcoxon test; Fig. 4D). Clearance rate was highly variable when feeding on *S. sulcatum* and varied between 158.0 ± 69.8 and 508.6 ± 234.0 mL ind^{-1} day^{-1}, but the difference in F on the ciliates was not significant between the four silt concentrations.

Specific ingestion rate

Carbon-SIR (Fig. 5) was calculated directly as a function of the clearance rate F and, as the same individual copepods were used during the four experimental days,

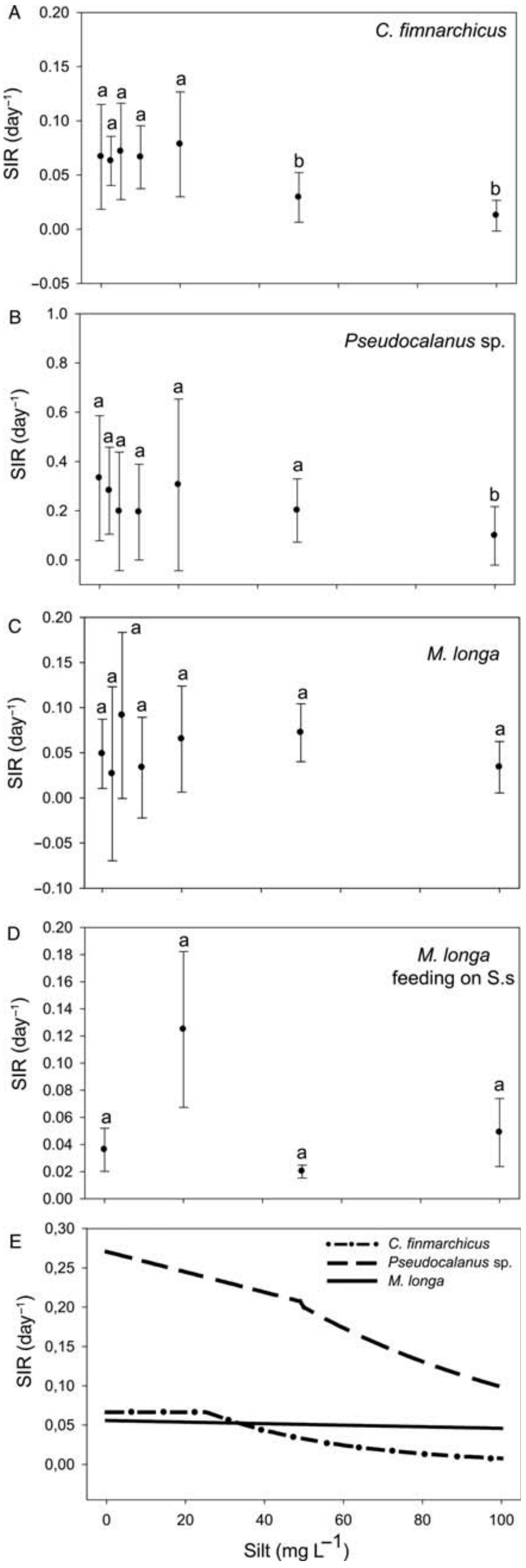

Fig. 5. SIR ±standard deviation, for (**A**) *Calanus finmarchicus*, (**B**) *Pseudocalanus* spp. and (**C** and **D**) *Metridia longa* at variable sediment concentrations when feeding on *Thalassiosira weissflogii* or *Strombidium sulcatum*. Different letters denote treatments that are significantly different from each other ($P < 0.05$). (**E**) Function fit of SIR for *Calanus finmarchicus*, *Pseudocalanus* spp. and *Metridia longa* at variable sediment concentrations when feeding on *Thalassiosira weissflogii*.

the copepod carbon content did not vary over time. Therefore, the statistics of SIR followed the statistics for F. SIR of *Calanus finmarchicus* varied from 0.06 ± 0.02 to 0.08 ± 0.05 day^{-1}, whereas it decreased to 0.03 ± 0.02 and 0.01 ± 0.01 day^{-1} at sediment concentrations of 50 and 100 mg sediment L^{-1}, respectively (Fig. 5A). SIR of *Pseudocalanus sp.* was clearly the highest of the three copepod species, with up to 0.33 ± 0.25 day^{-1} (Fig. 5B). *Metridia longa* showed no general response in SIR with rising sediment concentration (Fig. 5C), SIR varied from 0.03 ± 0.06 to 0.09 ± 0.09 day^{-1}. SIR of *M. longa* was in the same range when feeding on *S. sulcatum* 0.05 ± 0.05 day^{-1} (all data) compared to when *T. weissflogii* was offered as food (Fig. 5C and D), still with no significant differences when exposed to the various sediment concentrations.

SIR for the three copepod species feeding on *T. weissflogii* at increasing sediment concentrations is illustrated in Fig. 5. The best fit to the data showed an exponential decrease in SIR for *C. finmarchicus* and *Pseudocalanus* sp., while the slope was not significant for *M. longa*. Therefore, an average of SIR at all sediment concentrations is shown. When the SIRs of all three species are shown in same figure (Fig. 5E), this clearly demonstrates that *Pseudocalanus* sp. has the highest SIR of the three species at all sediment concentrations. *Metridia longa* showed the lowest SIR at sediment concentrations $<$20 mg sediment L^{-1}, whereas *C. finmarchicus* showed lowest SIR at sediment concentrations $>$20 mg sediment L^{-1} (Fig. 5E).

Fecal pellet production

There were no significant differences in FPP of any of the species (FPP, fecal pellets fem^{-1} day^{-1}) at each of the sediment concentrations tested over the four experimental days ($P > 0.05$, $n = 20$, Wilcoxon test). The FPP is therefore pooled over the whole experimental period for each copepod species at each sediment concentration (Table I). There were no significant differences in FPP of *Calanus finmarchicus* or *Metridia longa* feeding on *T. weissflogii* (all data). In contrast, a significant effect was observed in *Pseudocalanus* sp. FPP ($P < 0.01$, $n = 160$, Wilcoxon test). FPP was low in the control experiment (0 mg sediment L^{-1}), increased at

Table I: FPP (fecal pellets fem^{-1} day^{-1}) for the three copepod species Calanus finmarchicus, Pseudocalanus sp. and Metridia longa at the different sediment concentrations (mg L^{-1}) feeding on Thalassiosira weissflogii (T. w) or Strombidium sulcatum (S. s)

	C. finmarchicus		*Pseudocalanus* sp.		*M. longa*		*M. longa*	
Sediment (mg L^{-1})	FPP *T. w*	± SD (*n*)	FPP *T. w*	± SD (*n*)	FPP *T. w*	± SD (*n*)	FPP *S. s*	± SD (*n*)
0	52.4	31.8 (40)	20.5	14.1 (37)	6.7	4.6 (32)	15.2	5.5 (10)
2.5	58.7	16.1 (20)	56.7	16.0 (20)	5.7	3.5 (20)		
5	49.4	18.5 (20)	57.6	13.7 (20)	9.9	5.1 (20)		
10	60.8	16.2 (20)	72.4	25.5 (19)	6.3	4.4 (20)		
20	54.4	25.9 (20)	62.0	26.0 (20)	6.6	4.4 (20)	8.1	4.8 (10)
50	43.6	14.3 (19)	34.4	18.2 (20)	9.1	2.3 (12)	5.7	3.8 (8)
100	46.6	16.5 (20)	41.1	24.6 (20)	8.8	2.0 (12)	7.4	5.2 (10)

Values are means over the four experimental days (± standard deviation (SD), *n* number of replicates).

2.5–20 mg sediment L^{-1}, but decreased when females were exposed to 50 and 100 mg sediment L^{-1} (Table I). In the control experiment (0 mg sediment L^{-1}), a significant difference was observed in the FPP of *M. longa* when fed *S. sulcatum* compared to *Thalassiosira weissflogii* (Table I) ($P < 0.05$, $n = 41$, Wilcoxon test). On the other hand, there was no significant difference in the FPP from the two food items when exposed to sediment concentrations above 20 mg sediment L^{-1} (Table I). FP volume (μm^3) increased with increasing sediment concentration for *C. finmarchicus* and *M. longa*, while there was no general trend for the pellets of *Pseudocalanus* sp. (Fig. 6A–C). There was a significant difference ($P < 0.01$, $n = 138$, Wilcoxon test) of FP volume for *C. finmarchicus* when feeding at 0 and 100 mg sediment L^{-1} and for *M. longa* feeding at 5 and 50 mg sediment L^{-1}($P < 0.01$, $n = 122$, Wilcoxon test). FP volumes were significantly higher at 2.5 mg sediment L^{-1} than for any of the other sediment concentrations ($P < 0.05$, $n = 138$, Wilcoxon test). There was no relationship between excretion measured as total FP volume (μm^3 fem^{-1} day^{-1}) and ingestion (μg C fem^{-1} day^{-1}) when *T. weissflogii* was fed to the three copepod species (*C. finmarchicus*, $r^2 = 0.01$; *Pseudocalanus* sp., $r^2 = 0.02$; *M. longa*, $r^2 = 0.04$). No difference was observed in FP volume when *M. longa* fed on *T. weissflogii* compared to *Strombidium sulcatum* (Fig. 6C).

Egg production rate

The EPR (egg fem^{-1} day^{-1}) varied over time in all incubations. The three first experimental days were considered as an acclimation period and EPR here is compared only at Day 4 in Table II. There was a significant difference ($P < 0.01$, $n = 35$, Wilcoxon test) in EPR for *Calanus finmarchicus* at the sediment concentrations 0 and 50 mg L^{-1} (22.9 ± 13.7 and 0.2 ± 0.4 eggs fem^{-1} day^{-1}, respectively), however no difference was observed in EPR between 0–20 mg sediment L^{-1} or 50–100 mg sediment L^{-1}. Egg production for *Metridia longa* was low; maximum EPR observed was 1.5 eggs fem^{-1} day^{-1}, with no significant differences between the sediment concentrations. The EPR of *M. longa* did not differ significantly when feeding on *Thalassiosira weissflogii* or *Strombidium sulcatum* (Table II). *Pseudocalanus* sp. females were carrying eggs during the four incubation days. There was no significant difference in numbers of eggs in the eggs sac at the different sediment concentrations at Day 4 (Table II). Survival of the copepod females was >95% at the end of the experiment (Day 4) for all concentrations of suspended sediments and copepod species.

DISCUSSION

The concentrations of SPM in the Godthåbsfjord measured >50 mg L^{-1} and turbidity measurements indicated that *in situ* concentrations could be even higher. Therefore, the level of suspended sediment in the laboratory experiments represents sediment loads that copepods can encounter in a fjord with a glacial outlet.

In situ SPM concentrations along the Godthåbsfjord were highly variable. High concentrations of more than 20 mg L^{-1} were observed in restricted areas near the glacier and the melt-water outflow (Stn GF13 and GF11, Fig. 2A). Concentrations of 20–10 mg L^{-1} were found from the inner parts to the central parts of the fjord (Fig. 2A), whereas the fjord mouth towards the off shore area had concentrations <5 mg L^{-1}. The analysis of the particle size distribution and concentration showed a strong similarity between the sediment stock solutions used in the experiment (melted ice block) and the SPM found in the fjord. In terms of particle

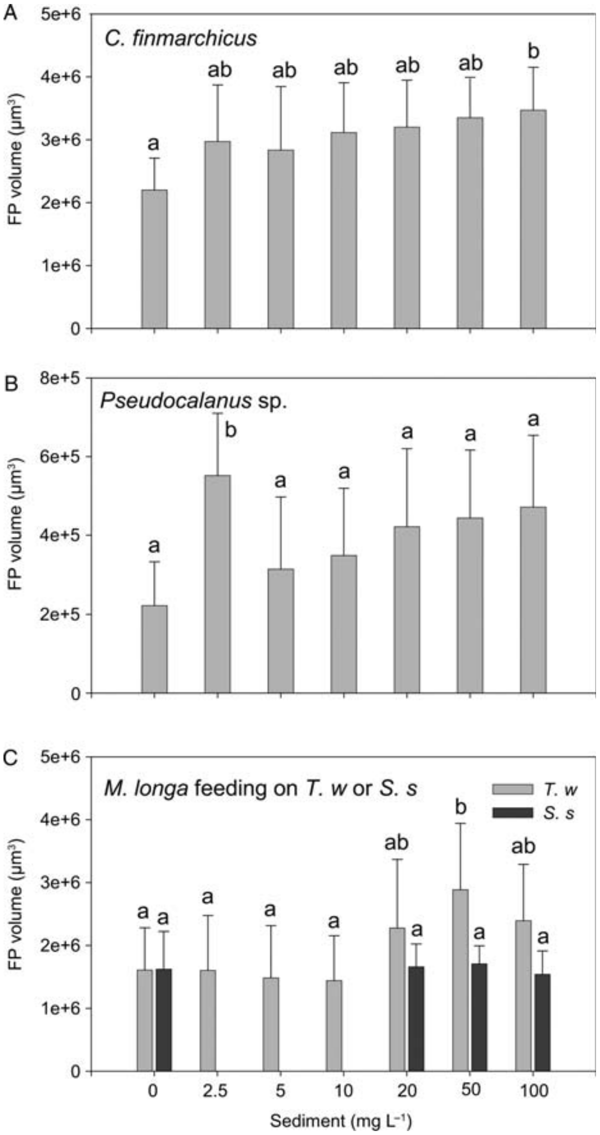

Fig. 6. Average FP volume for (**A**) *Calanus finmarchicus*, (**B**) *Pseudocalanus* sp. and (**C**) *Metridia longa* at variable sediment concentrations when feeding on *Thalassiosira weissflogii* (*T. w*) or *Strombidium sulcatum* (*S. s*). Whiskers indicate ±standard deviation. Different letters denote treatments that are significantly different from each other ($P < 0.05$).

abundance, clay grains (2–3 µm) had the highest concentration in the surface plume (Fig. 2A and E) due to the high sinking rate of large particles. However, in terms of total volume, silt grains dominated in all three stock solutions. In the field, the inorganic particles encountered by copepods might differ from these spectra. For instance, mineral particles are known to flocculate and aggregate (Stumm, 1990; Brown *et al.*, 2002) which results in increasing size of particles and higher sinking rates. In nature, copepods are therefore likely to encounter a variety of aggregate types, including organic material and particulate organic matter. Distinction between non-organic and organic particles was not made in the particle analysis and also could not be distinguished in the *in situ* turbidity (FTU) measurements. The correlation of SPM and FTU is less pronounced at FTU <3, which could be due to high proportion of organic material compared to sediment in the particle spectra. Therefore, direct correlations between suspended sediment and FTU measurements should be made with caution at low concentrations of SPM. However, in this study, the areal distribution of fluorescence and FTU was not similar (Fig. 2), which means that phytoplankton were not the primary source for the turbidity. Our measurements also do not take into account clay particles smaller than 1 µm, although these flocculate and therefore appear as larger size particles. At the highest *in situ* SPM concentrations found in the Godthåbsfjord, we would expect some effect on the feeding efficiency of the copepods. On the other hand, survival of all three copepod species was surprisingly high even at the highest concentrations of suspended sediments in the bottle incubations. This indicates that the copepods can handle very high sediment loads at least for a short period of time (here 4 days).

Effects of increasing suspended sediment concentration on vital rates were observed for *Calanus finmarchicus* and *Pseudocalanus* sp., but not for *Metridia longa*. The three copepod species tested were likely impacted differently by the increasing sediment concentrations. In *C. finmarchicus* and *Pseudocalanus* sp. F, IR and SIR were significantly reduced at the highest sediment concentrations. For *C. finmarchicus*, a reduced ingestion of Chl *a* in conjunction with no effects on FPP and total FP volume suggests ingestion of sediment that replaced food particles in the gut. This was verified by direct observation of sediment particles occurring in FPs of *C. finmarchicus* (Arendt *et al.*, 2010b) indicating the low ability of this species to distinguish between food and non-food particles. Therefore, at high sediment concentrations, the ingestion of clay/silt likely reduced the food uptake and resulted in reduction of egg production by *C. finmarchicus*. At high sediment concentrations, both IR and FPP for *Pseudocalanus* sp. were reduced. However, a reduction in EPR for *Pseudocalanus* sp. was not observed despite the reduction in food uptake, probably due to time-lag differences in egg production between egg carrying *Pseudocalanus* and free spawning species such as *Calanus*. There was no impact on IR and FPP for *M. longa* when exposed to high sediment loads indicating a high ability to distinguish between

Table II: EPR (eggs female^{-1} day^{-1}) for Calanus finmarchicus and Metridia longa and eggs in egg sac of Pseudocalanus sp. feeding on Thalassiosira weissflogii (T. w) or Strombidium sulcatum (S. s) at different silt concentrations (mg L^{-1})

	C. finmarchicus		*Pseudocalanus* sp.		*M. longa*		*M. longa*	
Silt (mg L^{-1})	EPR *T. w*	± SD (*n*)	Egg fem^{-1} *T. w*	± SD (*n*)	EPR *T. w*	± SD (*n*)	EPR *S. s*	± SD (*n*)
0	22.9	13.7 (5)	1.2	2.3 (5)	0.0	0.3 (5)	0.2	0.5 (5)
2.5	20.4	7.7 (5)	1.0	1.4 (5)	0.0	0.0 (5)		
5	16.9	14.1 (5)	0.3	0.5 (5)	0.0	0.1 (5)		
10	19.2	8.5 (5)	3.2	4.9 (5)	0.0	0.2 (5)		
20	15.1	11.0 (5)	0.3	0.2 (5)	0.0	0.1 (5)	0.1	0.2 (10)
50	0.2	0.4 (5)	0.5	0.7 (5)	0.2	0.3 (5)	0.0	0.0 (8)
100	0.3	0.4 (5)	0.1	0.2 (5)	0.0	0.0 (5)	0.0	0.0 (10)

Values are given for experimental Day 4 (± standard deviation (SD), *n* number of replicates).

food and non-food particles for both food types tested (diatom or ciliates).

The significant impact of suspended sediment on vital rates was only observed at very high concentrations (>20 mg L^{-1} for *C. finmarchicus* and >50 mg L^{-1} for *Pseudocalanus* sp.). At lower sediment concentrations, ingestion, FPP and EPR of *C. finmarchicus* corresponded well with published data at food concentration of 300 µg C L^{-1} (Båmstedt *et al.*, 1999), while high SIR (>1 day^{-1}) rates have been reported for *Pseudocalanus* spp. (Paffenhöfer and Harris, 1976). The relatively high tolerance of the copepods to suspended sediments can be due to their ability to ingest particles of high nutritional quality even when particles of low value are more abundant (Paffenhöfer and Van Sant, 1985; Cowles *et al.*, 1988). We conclude that in accordance with results of other studies (Paffenhöfer, 1972; White and Dagg, 1989), *C. finmarchicus* ingests suspended sediments at the high concentrations but the ability of selective feeding seems to be impaired at high sediment concentration. Other studies have shown that the capability to feed selectively may be sensitive and reduced at low food concentrations (Paffenhöfer, 1972; Roman, 1984). This may explain the relatively high tolerance to suspended sediment in the present study where food concentration was high. *In situ* food concentrations are normally lower than in our experimental setup (Rysgaard *et al.*, 2008; Arendt *et al.*, 2010a) and we could expect that it would take more time and energy to search for food particles in mixtures with suspended sediment. Therefore, effects on copepod vital rates are probably more pronounced *in situ* in the Godthåbsfjord where food availability is generally lower than in our experimental setup. Furthermore, high sediment load could negatively affect primary production by reducing the light penetration and consequently indirectly negatively affect secondary production as previously reported from highly turbid estuaries or glacial lakes (Kirk, 1991; Lehman 1992; Gasparini *et al.*, 1999).

Metridia longa showed the same ingestion (F and SIR) at all sediment concentrations regardless of food type offered (diatom or ciliate) as single food type. The SIR did not differ in spite of a tenfold difference in food concentration (300 µg C L^{-1} for *T. weissflogii* versus 40 µg C L^{-1} for *S. sulcatum*). This might be due to a shift in feeding pattern from filter feeding to active hunting as suggested by Haq (Haq, 1967). The low EPR of *M. longa* observed in our study could be due to a low utilization efficiency known for this species as suggested by Hopkins *et al.* (Hopkins *et al.*, 1984) or due to cannibalism of the eggs (Plourde and Joly, 2008). *Metridia longa* is known to feed actively in winter (Hopkins *et al.*, 1984) where it feeds omnivorously on protozooplankton and has also been shown to exhibit coprophagy (Sampei *et al.*, 2009). Therefore, ecosystems that can offer some food during winter could provide a sufficient overwintering habitat for this species, which may explain the dominance of *M. longa* in the Godthåbsfjord over *Calanus*.

Increased melting of the Greenland Ice Sheet and, as a result, increased fresh water runoff is expected to occur in the future as a consequence of global warming (Kattsov and Källén, 2005). This would also increase the expected load of SPM into the fjord. However, concentrations >20 mg L^{-1} would only be expected to occur very close to the glacier melt water outlets. This study shows that high sediment concentrations influence the capability of carbon turnover for *Calanus finmarchicus* and *Pseudocalanus* sp., whereas *Metridia longa* is able to sustain stable carbon ingestion. Significant effects on the copepods were only observed at sediment loads >50 mg sediment L^{-1} which is expected to occur in confined areas. These results could prove to be useful in understanding the geographical distribution of copepod species in glacial marine environments. The species distribution shown in previous studies (Arendt *et al*., 2010a) cannot be explained solely by high loads of SPM. The observed pattern is rather a result of combined interaction of hydrographic conditions (Mortensen *et al*., 2011), differences in species fitness (Kiørboe, 2008), predation (Tang *et al*., 2011) and long-term influence of sediment plumes on the ecosystem (Dagg *et al*., 2004). However, it is evident that increased load of suspended sediments to the fjord due to increased runoff from the Greenland Ice Sheet will have an effect on the pelagic zooplankton feeding efficiency and production rates and therefore affect their survival in these waters.

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