LIMNOLOGY
and
OCEANOGRAPHY

ASLO

Limnol. Oceanogr. 60, 2015, 765–776
© 2015 Association for the Sciences of Limnology and Oceanography
doi: 10.1002/lno.10054

Light and nutrient effects on the settling characteristics of the sea ice diatom *Nitzschia frigida*

C. F. Aumack* A. R. Juhl
Lamont-Doherty Earth Observatory of Columbia University, 61 Route 9W, Palisades, New York

Abstract

Sea ice-algae contribute significantly to Arctic primary production and play an important role in the life histories of planktonic and benthic consumers after the algae are released from the sea ice habitat. Following export from the ice, the extent to which fresh algal material is available to planktonic or benthic consumers is dependent on residence time in the water column, initially related to particle settling rate. Laboratory experiments using isolated *Nitzschia frigida*, a common sea ice diatom, were conducted to ascertain the effects of nutrient (N, P, and Si) and light limitation on settling characteristics of the algal material. While settling characteristics of N- and P-limited cultures were not significantly different from controls grown under light and nutrient-replete conditions, significant differences from the controls were found for light and Si limitation. Differences between treatments were evidenced by changes in the proportion of each population that had particular settling rates, rather than by changes in the range of settling rates measured within a treatment. Thus, fast (> 20 m d^{-1}) and slow-sinking particles (< 2 m d^{-1}) were found in all cultures, but compared to the controls, a larger percentage of fast-sinking particles were observed under Si limitation while a larger percentage of slow-sinking material was observed under light limitation. While *N. frigida* is just one member of the sea ice algal assemblage, its prevalence in Arctic land-fast sea ice means these results may be representative of the broader Arctic nearshore ice-algae community. As such, abiotic conditions within Arctic sea ice, such as nutrient availability and depth of overlying snow (which affects the light field in the ice), could influence the amount of algae-derived material available to different components of the underlying marine food web.

The interstitial and undersurface environments of sea ice support a diverse community of organisms that thrive in this physically and chemically dynamic habitat (Horner 1976; Cota and Smith 1991; Arrigo et al. 2010). These sea ice assemblages, typically dominated in biomass by diatoms (Hsiao 1980; Gradinger 1999; von Quillfeldt et al. 2003), contribute greatly to annual primary production of polar regions. In the Arctic, several studies have estimated that the sea ice community can contribute 15-20% of annual marine primary production (Legendre et al. 1992; Gosselin et al. 1997; Arrigo and Thomas 2004). In nearshore, land-fast sea ice, ice-algae production peaks in early spring when water column phytoplankton production is minimal (Horner and Schrader 1982; Hsiao 1988; Cota and Smith 1991). The timing of peak ice-algae production thus lengthens the period of annual autotrophic production into the ice-covered, pre-open water season (Horner and Alexander 1972; Cota et al. 1991; Arrigo and Thomas 2004). Although ice-algae production rates fluctuate annually (Horner and Schrader 1982; Melnikov et al. 2002; Arrigo et al. 2008), their importance to the underlying communities is such that many Arctic marine organisms have adapted life cycles to take advantage of ice-derived organic material (Runge et al. 1991; Bluhm et al. 2010; Daase et al. 2013) prior to the spring phytoplankton bloom that typically occurs after ice breakup.

Dissolved and particulate organic material generally accumulates within sea ice in a predictable seasonal sequence, especially within first-year, land-fast sea ice. Through early spring, as surface irradiances increase, there is corresponding algal growth in the ice. This bloom is especially apparent in the bottom 10 cm of the ice near the ice-seawater interface (Meguro et al. 1967; Smith et al. 1990; Riedel et al. 2008). Later in spring, but before substantial ice melt or break up, organic material is lost from first-year ice in rapid export pulses that may only last a few days (Fortier et al. 2002; Juhl and Krembs 2010; Juhl et al. 2011). Although the mechanisms are not fully understood, export events often coincide with increased light, temperature, ice porosity, and ablation of the ice bottom (Apollonio 1961; Mundy et al. 2005; Nishi

*Correspondence: caumack@ldeo.columbia.edu

Table 1. Nutrient and irradiance conditions used for *N. frigida* incubations prior to settling experiments. Vitamins and trace metals were started at L1 recipe concentrations.

Culture	Nitrogen (mol L^{-1})	Phosphorus (mol L^{-1})	Silicate (mol L^{-1})	Irradiance (μmol photons m^{-1} s^{-1})
Control	8.82×10^{-4}	3.62×10^{-5}	1.06×10^{-4}	25-30
N-limited	3.91×10^{-5}	3.62×10^{-5}	1.06×10^{-4}	25-30
P-limited	8.82×10^{-4}	3.53×10^{-6}	1.06×10^{-4}	25-30
Si-limited	8.82×10^{-4}	3.62×10^{-5}	1.88×10^{-6}	25-30
PAR-limited	8.82×10^{-4}	3.62×10^{-5}	1.06×10^{-4}	2-5

and Tabeta 2007). Once released, organic material from the ice is either consumed in the water column (Tremblay et al. 1989; Michel et al. 1997), initiates ice-edge algal blooms (Michel et al. 1993; Haecky et al. 1998; Yamamoto et al. 2014), or settles on the benthos where it is subsequently either grazed or buried in the sediments (McMahon et al. 2006; Renaud et al. 2007; Morata et al. 2011). While particulate organic matter consumed by pelagic heterotrophs may still reach the benthos as a viable food resource in the form of fecal pellets or settled molts/carcasses (Wassmann 1997; Goutx et al. 2007; Elliott et al. 2010), the amount of carbon reintroduced post ingestion can be diminished (Møller et al. 2003). Furthermore, decomposition and digestive processes significantly impact the overall nutritional quality of material that has been ingested (Lovvorn et al. 2005; Goutx et al. 2007; Morata et al. 2011), ultimately altering the relative value of material reaching the benthos directly and rapidly, vs. material settling out post ingestion and/or post decomposition that occurred during transit through the water column.

Whether organic material freshly exported from sea ice is primarily consumed in the plankton or the benthos is initially dependent on the settling rate of the material released, influencing the residence time ice-derived material remains suspended in the water column. Settling rates are unlikely to be uniform though, and changes in the sea ice community's settling characteristics may correspond to a number of biotic and abiotic changes within the ice. The very-limited previous research in the Arctic has indicated that overlying snow depths (Riedel et al. 2006) and seasonal bloom progression (Michel et al. 1993) can influence microalgal sinking rates upon release from the ice, though the mechanisms underlying these two influences are unknown. In other studies, phytoplankton physiology has proven to have significant effects on their settling rates. This includes physiological changes caused by altered nutrient availability (Bienfang et al. 1982; Bienfang and Harrison 1984*b*), internal inorganic ion concentrations (Anderson and Sweeney 1977), light availability (Steele and Yentsch 1960), cell age (Smayda and Boleyn 1966), and life history stages (Gross and Zeuthen 1948; Eppley et al. 1967). Changes in cell or colony size and shape, which can be influenced by growth conditions (e.g., Takabayashi et al. 2006) can also affect settling rates (Smayda and Boleyn 1966, Smayda 1970). Nevertheless, little work has been conducted on the settling rates of ice-algae post export from the ice habitat, despite high variability of light and nutrients within land-fast Arctic sea ice (Welch and Bergman 1989; Gosselin et al. 1990; Krembs and Engel 2001).

In this paper, we describe the effects that nutrient (N, P, and Si) and light limitation have on settling rates of the sea ice diatom, *Nitzschia frigida*, in controlled laboratory culture experiments. *N. frigida* was chosen to be representative of the ice algae found in land-fast sea ice because it has been prevalently reported within the sea ice assemblage across nearshore Arctic fast ice (Suzuki et al. 1997; Michel et al. 2002; Ratkova and Wassmann 2005) and it often is the most abundant algal species within land-fast sea ice near Barrow (Horner and Alexander 1972). If the regulation of diatom buoyancy is inherently linked to mechanisms associated with growth and photosynthesis, than light/nutrient availability in sea ice could drastically influence the settling properties of ice algae after release from the ice. Subsequently, this could have indirect effects on the ultimate fate of sea ice-derived material by altering the proportion reaching the benthos vs. being consumed in the water column.

Methods

Experiments quantified the effects of limiting N, P, Si, and irradiance on settling properties of laboratory cultures of the sea ice diatom, *N. frigida*. Control cultures were grown under replete nutrients and saturating light while the treatment cultures were grown under limiting conditions for one requirement (N, P, Si, or light) in different experiments (*see* Table 1 for treatment details). Settling experiments were conducted every three days during batch culture growth, ensuring increasing limitation of the treatment cultures through time.

All experiments used a monoalgal, non-axenic, clonal strain of *N. frigida* originally isolated by A. Juhl in May 2011 from melted sea ice samples collected near Barrow, AK. Stock cultures were maintained by serial transfer using sterile L1 medium (Guillard and Hargraves 1993) in a 4°C incubator

with continuous irradiance from cool-white fluorescent lights providing photosynthetically active radiation (PAR) of 25-30 μmol photons m^{-2} s^{-1}. Previous studies have found this PAR level saturating for *N. frigida* growth (Suzuki et al. 1997; Juhl and Krembs 2010). In culture and in the field, *N. frigida* grows as single cells and branched chains or colonies of various sizes. However, the distribution of chain lengths in different cultures was not assessed in these experiments.

Experiments

To conduct each series of settling experiments associated with each limitation treatment (N, P, Si, or light), nine 300-mL cultures were inoculated on day 0. Three of these nine cultures were used for settling experiments on days 3 and 15 each, such that $n = 3$ settling experiments were conducted at the beginning and ending points of the growth period. Statistical analyses therefore focused on these two time points. In addition, settling experiments were also conducted on days 6, 9, and 12 to assess the temporal trend in settling characteristics for each limitation treatment, assuming that limitation increased in successive dates. However, for days 6, 9, and 12, only a single culture ($n = 1$) was sacrificed for each day's settling experiments. Two sets of control cultures were handled in a parallel manner, such that $n = 6$ control settling experiments were conducted on days 3 and 15, with $n = 2$ on days 6, 9, and 12.

The experimental setup used a homogenous sample (*sensu* Bienfang et al. 1977) or homogenous suspension (type a) approach (*sensu* Chancelier et al. 1998) to measure settling velocities. The height of the columns was 0.375 m, with a diameter of 9.0 cm. All experiments were conducted in a walk-in incubator set at 4°C (± 0.5°C) with no direct lighting on the columns. All cultures and dilution water, as well as the settling columns and all other equipment used were housed in the incubator for at least 24 h before conducting each experiment to ensure that temperatures were consistent at the beginning and through each experiment (Peperzak et al. 2003). For each settling experiment, a selected culture was added to 6 L of filtered seawater (0.2 μm) that was then mixed and transferred to three 2-L settling columns. Once culture material was added to the settling columns, they were capped and left undisturbed for 30 min, 90 min, or 180 min. Water remaining after filling the settling columns was used to determine the initial chlorophyll-*a* (hereafter referred to as "chlorophyll") concentrations in the settling columns. After each time period, water was carefully pumped off of the top of the column except for the bottom 300 mL. The bottom 300 mL was then collected and used to determine the amount of chlorophyll that had settled to the bottom layer of the columns. Each settling column was only sampled for a single time point, but the entire time course of settling was tracked by combining observations from the replicate columns. The expectation was that as algal material settled through time, the chlorophyll concentrations in the bottom layer would increase, or conversely, that the amount remaining in suspension would decline through successive time points. Chlorophyll samples were filtered onto 25-mm Whatman GF/F filters. After extraction in 100% methanol, chlorophyll concentrations were determined fluorometrically using a Turner Designs fluorometer according to UNESCO (1994).

The percentage of chlorophyll remaining in suspension (P) through time (t) was plotted. The percentages in suspension after the 30 min and 180 min time points were used as the basis for statistical comparisons between treatments (*see* statistical analyses section below). In addition, summarizing the data in terms of absolute settling velocities followed Owen (1976). The plot of P vs. t was fit with a curve including upper and lower 95% confidence intervals. For any time t along the curve, a corresponding settling velocity w_s ($= h/t$, where h is the height of the water column) was calculated and $I(w_s)$, the cumulative percentage of the particle population with a settling rate less than any given value of w_s was estimated as

$$I(w_s) = P - (t)\mathrm{d}P/\mathrm{d}t \quad (1)$$

(Jones and Jago 1996; Malarkey et al. 2013). Equation 1 was then solved for $I(w_s)$ across a range of w_s values using a spreadsheet implementation of the original graphical procedure described by Owen (1976) with the values for Eq. 1 deriving from the curve fit to P vs. t. The cumulative percentage of the population with settling rates greater than w_s was simply $100\% - I(w_s)$. Upper and lower 95% confidence intervals for the settling velocity distributions were calculated in the same way, using the equations for the confidence intervals around the curve fit to P vs. t.

Statistical analysis

Statistical comparisons between treatments and controls were based on the percent of chlorophyll remaining in suspension after the 30 min and 180 min time points during individual settling experiments. We use these data, as opposed to the settling velocity spectra, as the basis for statistical comparisons because the data on material remaining in suspension were less derived than the calculated spectra. Data describing the percent remaining in suspension at different time points were also more readily analyzed using common statistical methods. After the completion of all settling trials, results from control experiments on different dates were statistically compared to each other using t-tests comparing days 3 and 15 to test whether control settling characteristics remained consistent during culture growth. Statistical comparisons between controls and treatments were based on two-way analysis of variance (ANOVA), using time in culture (days 3 and 15) and the respective limitation treatment as the factors.

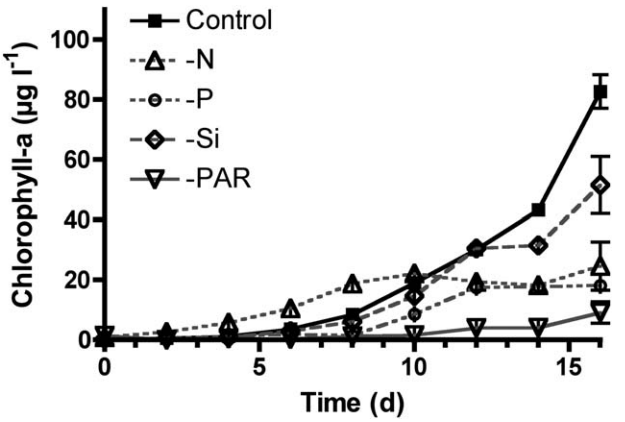


Fig. 1. Average growth curves of *N. frigida*, in terms of chlorophyll concentration over time, for control (nutrient-replete and light-saturated) cultures vs. cultures limited by N, P, Si, or light availability (PAR). Data from day 16 show the mean ± 1 standard error. Standard errors for earlier dates were proportionally similar but not shown for the sake of clarity.

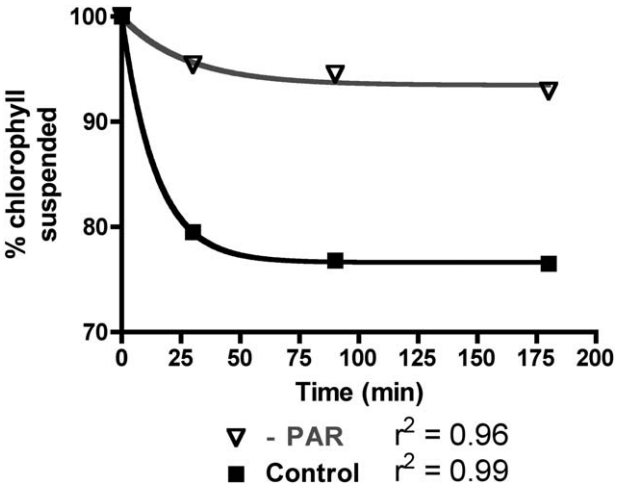


Fig. 2. Exponential decay curves indicating the percent of chlorophyll remaining suspended as a function of time during settling experiments for two *N. frigida* cultures grown for 15 days under either control or light-limited conditions.

Results

Figure 1 shows average growth curves, in terms of chlorophyll concentration over time, in the control cultures and four limitation treatments. In each treatment, the effectiveness of the respective nutrient/light limitation is seen in lower yield by the end of the experiment. The exponential growth rate of the control cultures was approximately 0.36 d^{-1} over the 15-day incubation period, consistent with previously published data for *N. frigida* under similar temperature and irradiance levels (Suzuki et al. 1997; Juhl and Krembs 2010).

Settling experiments

Figure 2 highlights raw data derived from two individual settling experiments shown as examples, depicting the percent of chlorophyll remaining suspended after 15 days of PAR limitation compared to a day 15 control culture. Data such as these were the basis for subsequent analyses. Exponential decay curves (as shown in Fig. 2) generally provided the best fit to settling experiment data, regardless of treatment. Statistical comparisons between treatments were based on the percent of chlorophyll remaining in suspension after 30 min and 180 min (i.e., the second and fourth data points for each curve in Fig. 2). Figures 3A,B summarize the results for all settling experiments at these two time points. Figure 3A shows the amount of chlorophyll left suspended in the settling column for each treatment after 30 min, with each group of bars representing one treatment (or the controls) and the bars within each grouping corresponding to experiments conducted on different days during the 15-day culture period. Figure 3B shows similar data for the 180-minute time points.

Focusing on results for the control cultures first, *t*-tests were used to test for differences in the percent of chlorophyll in suspension after the 30 min and 180 min time points during settling experiments conducted on days 3 and 15 ($n = 6$ for each day). No significant differences were found between days for either time point ($p > 0.4$ in each comparison), indicating consistent control settling characteristics at the beginning and end of the culture growth period. It should be noted that the decline in the percent of suspended chlorophyll from 30 min to 180 min on all days (i.e., comparing the upper and lower bar graphs) was expected and demonstrates that material was continually settling during individual experiments.

Significant differences were found when comparing the control culture results to those of the four limitation treatments. For each time point (30 min or 180 min), a two-way ANOVA, with treatment (control, N-, P-, Si-, and light-limited) and culture period (day 3 or day 15) as the factors, was used to test for differences between treatments and the controls. For both settling time durations, treatment had a significant effect ($p < 0.001$). Culture period did not have a significant effect for either the 30 min or 180 min time points ($p = 0.67$ and 0.87, respectively), though there was a significant interaction between factors (30 min. $p = 0.03$, 180 min. $p = 0.03$). Tukey post hoc tests were used for more detailed comparisons. While neither N- nor P-limitation had any significant effects ($p > 0.05$) on *N. frigida* settling characteristics on either day (relative to the controls), low Si and light treatments were significantly different from the controls on day 15 ($p < 0.03$ in each case). There was also a significant difference from the controls in the light-limited cultures on day 3, though only for the 30-min time point ($p = 0.012$), this difference was not significant at 180 min.

The data in Fig. 3A,B demonstrate that, after a 15-day growth period, irradiance levels and Si limitation had

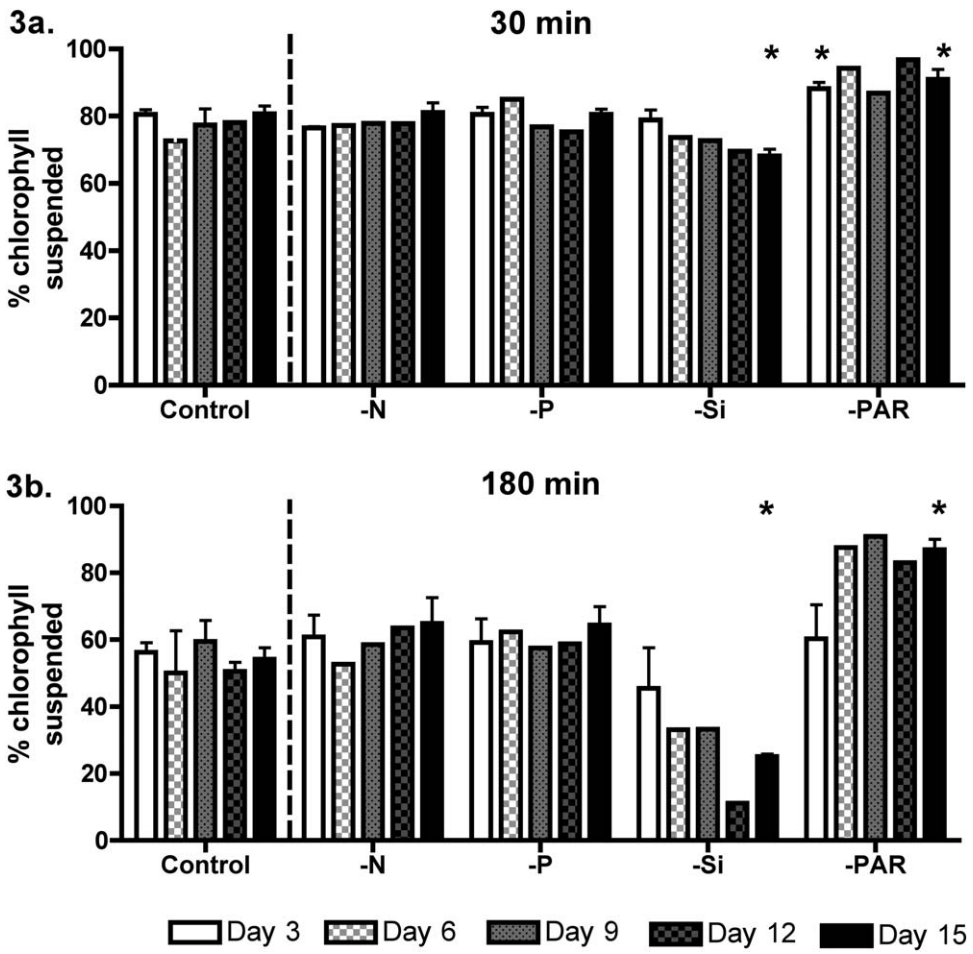


Fig. 3. Percent of chlorophyll left suspended in settling columns for control *N. frigida* cultures and parallel cultures grown under N, P, Si, or light (PAR) limitation after (A) 30 min and (B) 180 min. Individual columns within each grouping show results after 3 days, 6 days, 9 days, 12 days, and 15 days of culture growth. For the control cultures, $n = 6$ for days 3 and 15, and $n = 2$ for days 6, 9, 12. For treatment cultures, $n = 3$ on days 3 and 15 only, $n = 1$ on other days. Results for days with replicates are expressed as mean $\pm$ 1 standard error. The dashed line separates the control and treatment results. Significant differences ($p < 0.05$) in percent chlorophyll suspended (with respect to the controls) are highlighted with an asterisk.

significant effects on the settling characteristics of *N. frigida* while N and P-limitation did not. The relative differences between treatments constitute the primary finding of this study, but the results can be expressed in terms of absolute settling velocities to provide more context. Figure 4A shows three exponential curves describing the decline in suspended chlorophyll through time in the experiments conducted on day 15. Curves were fit using all day 15 data for control, Si, and light limited cultures and thus represent mean decay curves for each treatment. Similar data for the N and P-limited cultures were not plotted because, as demonstrated in Fig. 3, there were no significant differences from the controls on day 15 (or earlier). *See* Supporting Information (Figure S1a) for the comparison between mean decay curves for the N- and P-limited cultures relative to the controls. The best-fit equations from Figure 4A were used to calculate settling velocity spectra with upper and lower 95% confidence intervals for each treatment according to Eq. 1 (Fig. 4B). Since these spectra are based on the mean curve fits in 4A, they represent mean settling velocity spectra for the treatments shown. *See* Supporting Information (Figure S1b) for the mean settling velocity spectra of the N- and P-limited cultures.

The mean settling velocity spectra highlight the wide range of settling rates in each treatment. For example, $\sim$ 7% of particles in the controls had settling rates $\geq$ 20 m d^{-1}. The percent of control particles with settling rates $\geq$ 2 m d^{-1} was $\sim$30%, implying that $\sim$23% of particles had settling rates between 2 m d^{-1} and 20 m d^{-1}, and that $\sim$70% of particles sank $<$ 2 m d^{-1}. Despite the wide range of settling rates, differences between treatments were nevertheless apparent. For example, over 90% of particles in the light-limited treatment sank slower than 2 m d^{-1}, an increase of more than 20% compared to the mean value for the controls.

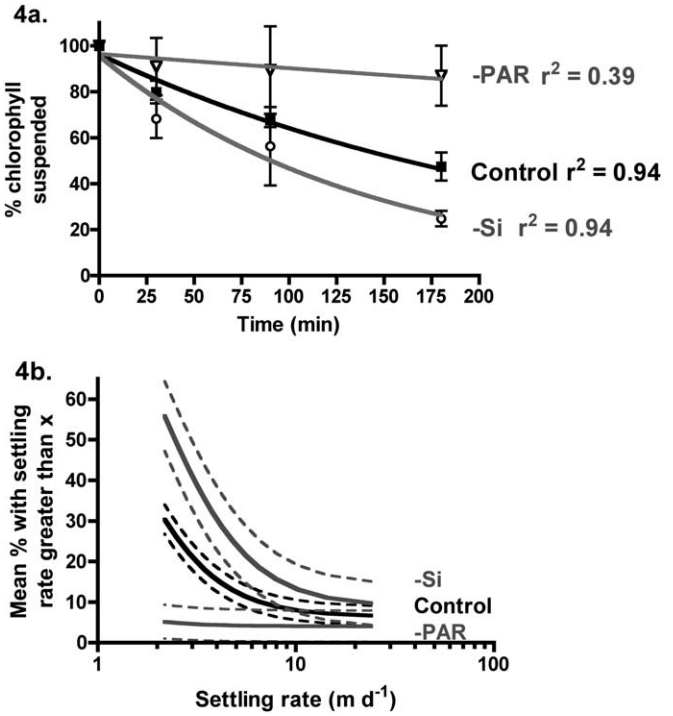


Fig. 4. (A) Mean and 95% confidence intervals for the percent chlorophyll suspended through time during settling experiments conducted on day 15 for control *N. frigida* cultures vs. cultures grown under Si or PAR limitation. The best-fit exponential curves (and corresponding r^2 values) shown were fitted using all respective data points within a treatment. The equations for the three curves in Fig. 4A were then used to calculate mean settling velocity spectra, with upper and lower 95% confidence intervals (dashed curves) of the percentages for each treatment (B). The curves for each treatment show the mean proportion of particles with a sinking rate greater than the corresponding rate on the *x*-axis.

Discussion

This is the first study of the settling characteristics of an ice alga grown under controlled conditions. Our findings demonstrate that light and nutrient limitation can have significant effects on the sinking characteristics of *N. frigida*. While fast (> 20 m d^{-1}) and slow (< 2 m d^{-1}) sinking particles were present in all treatments, a higher fraction of slow-sinking algal particles were present during light-limited growth, and a higher fraction of fast-sinking algal particles were present during Si-limitation (compared to respective controls). Because of changes in aggregation probability, one might expect that differences in biomass, per se, could alter settling characteristics of a culture. However, evidence from the control cultures demonstrated that settling characteristics of *N. frigida* did not change over time, despite more than an order of magnitude increase in biomass from days 3 to 15. This suggests that any changes in sinking rates in the treatments were the result of either physiological changes within the cells or changes in colony size or shape, rather than the biomass differences between control and treatment cultures. Because *N. frigida* is a common species of the landfast sea ice assemblage during the seasonal ice-algae bloom, both in terms of abundance and biomass (Suzuki et al. 1997; Michel et al. 2002; Ratkova and Wassmann 2005), these results may be representative of the broader Arctic nearshore ice-algae community. Although algae are just one component of the material that fluxes out of the sea ice (Juhl et al. 2011), they are likely an important trophic resource for both benthic and planktonic Arctic consumers (Runge et al. 1991; McMahon et al. 2006; Daase et al. 2013).

Given only a few prior studies of ice algae settling characteristics, what is known appears consistent with our results, although earlier studies used field samples of mixed assemblages with uncontrolled environmental histories. Riedel et al. (2006) and Michel et al. (1993) used the SETCOL method (Bienfang 1981) to measure the effects of the seasonal bloom progression and overlying snow depths on mean settling rates of field-collected Arctic ice-algae material. One major effect of deeper overlying snow is a decrease in light availability for ice algae (Maykut and Grenfell 1975; Mundy et al. 2007; Aumack et al. 2014), and Riedel et al. (2006) described significantly lower mean settling rates for algal particles collected in the field under thicker snow/lower light conditions, consistent with our laboratory results. Michel et al. (1993) found that mean settling rates of ice-algae particles increased with the seasonal progression of the under ice bloom. Again consistent with our laboratory experiments, Michel et al. (1993) hypothesized that the increase in settling rates they observed could be related to increasing Si-limitation during bloom progression, though they lacked direct evidence.

The SETCOL approach used by Michel et al. (1993) and Riedel et al. (2006) provided only an estimate of mean settling rates, rather than settling velocity spectra. The mean rates for field-collected Arctic ice algae in those two studies ranged from 0.1 m d^{-1} to 2.7 m d^{-1}, a range that certainly overlaps with the spectra measured in this study. In contrast, Riebesell et al. (1991) highlighted fast sinking rates for Antarctic ice algae (> 100 m d^{-1}). Rather than indicating a difference between Arctic and Antarctic ice algae, the discrepancy between studies is more likely related to methodological differences. Our observations show that fast- and slow-sinking particles can both come from the same culture. By focusing on mean settling rates, the Michel et al. (1993) and Riedel et al. (2006) studies were not able to separately quantify the contribution of fast-sinking particles. Meanwhile, the Riebesell et al. (1991) study focused on the fastest-sinking particles because their approach included an aggregation step prior to measuring settling rates. By highlighting the continuous, broad distribution of settling rates even within a unialgal ice-algae culture, our study bridges perceived discrepancies when comparing earlier results.

Given limited information on variability of ice diatom settling rates, comparisons to phytoplankton studies may be useful, with the caveat that comparable research on

phytoplanktonic diatoms has generally focused on centric diatoms (e.g., Smayda 1970; Bienfang et al. 1982; Waite et al. 1992*a*) rather than pennates (like *N. frigida*) that dominate nearshore sea ice. In addition, many studies of diatom settling rates have used dead cells (e.g., Smayda 1974; Durkin et al. 2013). Settling rates of dead cells may not directly pertain to those of live cells (Smayda 1970, Waite et al. 1997), so comparison to those studies is problematic.

The changes in settling characteristics described here for light-limited *N. frigida* are consistent with several earlier studies of centric, planktonic diatoms. Lower mean sinking rates under low light have been described for *Thalasiosira pseudonana*, *Chaetoceros gracilis*, and *C. flexuosum* (Culver and Smith 1989; Waite et al. 1997). Similarly, settling rates of *Coscinodiscus concinnus* decreased in the dark part of the daily light : dark cycle (Granata 1991). Light quality (red, white, or blue) has also been show to affect mean sinking rates of some centric diatoms (Fisher et al. 1996). Although apparently common in diatoms, lower settling rates under low light is not universal since opposing or equivocal results have been reported for *T. weissfloggii* and *Ditylum brightwellii* (Bienfang et al. 1983; Waite et al. 1997). Compiling across studies, changes in settling rates of live cells in response to light conditions were not consistently explained by changes in cell volume, cellular carbon, nitrogen, silica, or carbohydrate content (Bienfang et al. 1983; Culver and Smith 1989; Waite et al. 1997). Nevertheless, a physiological basis for the response is likely because settling rates of metabolically inactivated cells were more strongly related to predictions based on cell volume than were those for healthy, live cells (Waite et al. 1992*b*; Waite et al. 1997).

In this study, neither N nor P limitation appeared to have any significant effects on the sinking characteristics of *N. frigida*. There have been no conclusive trends across studies concerning either N- or P-limitation effects on settling rates of phytoplanktonic diatoms, and it thus appears that the relationships between settling rates and limitation of these nutrients are species specific (Titman and Kilham 1976; Bienfang et al. 1982; Bienfang and Harrison 1984*b*). For instance, Titman and Kilham (1976), Bienfang (1982), and Waite et al. (1992*a*) found that settling rates of certain centric diatoms responded to either N or P limitation, but settling in other species, similar in origin, were unaffected. In species that did respond to nutrient stress, the physiological basis for changes in settling rate was highlighted by concomitant decreases in settling rate with increasing intracellular N pools and a lack of correspondence with chain length or aggregate formation (Waite et al. 1992*a*).

Si limitation had pronounced effects on the settling characteristics of *N. frigida* in this study, leading to a higher percentage of fast-sinking particles than the controls or other treatments. These results compare favorably to Bienfang and Harrison (1982, 1984*a,b*) who found that Si limitation caused higher mean settling rates in several diatom species and that Si-deprivation had more pronounced effects on settling characteristics than other nutrient limitation treatments. These results for Si limitation are somewhat counterintuitive. Recent research has shown that phytoplanktonic diatoms with excess Si can become more heavily silicified (Durkin et al. 2013; Martin-Jézéquel et al. 2000), which leads to faster sinking of dead cells (Durkin et al. 2013). However, this study and others (Bienfang et al. 1982; Bienfang and Harrison 1984*b*) indicate faster sinking of living, Si-limited diatoms. This phenomenon could be a response to physiological modifications in response to Si stress, potentially related to changes in the cell cycle. Under continual Si stress, the duration of the G_2 phase increases as growth becomes Si limited, while the cellular carbon content increases (Flynn and Martin-Jézéquel 2000; Martin-Jézéquel et al. 2000). Increased cellular carbon should increase sinking rate unless balanced by other physiological processes (Bienfang and Harrison 1984*a*; Thompson et al. 1991). Additionally, Si limitation leads to a loss of setae which could also increase sinking potential (Raven and Waite 2004).

Inconsistent and variable results of Si limitation on diatom settling rates, as with limitation from other nutrients or light (discussed above), reflect the complex physiological control of settling rates. Numerous authors have pointed out that while maximum diatom settling rates are related to cell volume and composition as predicted by Stoke's law, physiological processes allow the cells to greatly reduce their settling rates from the potential maximum (e.g., Anderson and Sweeney 1977; Villareal 1988; Waite et al. 1997), even allowing for positive buoyancy (Villareal 1988; Villareal 1992). In the context of this study, we can see that changes in the settling characteristics of populations occurred through alterations in the proportions of cells exhibiting particular settling properties (e.g., fast or slow settling) while maintaining a broad overall range.

For a colonial diatom such as *N. frigida*, changes in colony or chain size and shape must also be considered as a potential explanation for differences in settling velocities between treatments. Smayda (1970) concluded that cell size, per se, was not related to settling velocities for chain forming diatoms, though there was a general increase in settling velocities as the cell number per chain increased. However, this trend was not uniform across species. For example, *Skeletonema costatum* chains decreased settling velocity with increasing cell number (Smayda 1970). Similarly, subsequent culture and field studies have found that chain length or aggregate size were not related to measured diatom sinking rates (Waite et al. 1992*a*, 1997, Peperzak et al. 2003). Nevertheless, changes in the number of cells per *N. frigida* colony, or the shapes of the colonies, may have varied between treatments in our experiments and could play a role, together with physiological responses at the level of the individual cell, in explaining the changes in settling velocity spectra observed in response to light and Si limitation.

As a methodological comment, the approach to quantifying settling velocities we applied in this study was based on the description of Owen (1976), which has a history of use in quantifying settling of particulates in estuarine water columns and in the context of sewage treatment (Kowalski et al. 1999; Crump and Baross 2000; Pejrup and Mikkelsen 2010). In our application, it is technically very similar to the SETCOL method (Bienfang 1981) that has been more widely used in studies of phytoplankton settling rates, with the exception that one needs sequential samples through time during a settling experiment to use the Owen approach, easily accomplished in our case by using replicate settling columns. One advantage of the Owen approach is that it provides a settling rate spectrum, which is more informative than the single mean settling rate that results from the SETCOL method. SETCOL is also subject to artifact when the population of particles being studied has a wide range of settling rates. In that situation, the plot of P vs. t (or any measure of settled particles through time) would be nonlinear (as in Figs. 1, 4), violating a key SETCOL assumption (Bienfang 1981). When particle accumulation at the bottom is nonlinear through time, the mean settling rate estimated according to the SETCOL protocol changes with the duration of the settling experiment. Longer settling experiments result in progressively lower mean settling rates and the calculated mean settling rate is always an underestimate relative to the true mean for the population of particles (Johnson and Smith 1986; Pitcher et al. 1989; Peperzak et al. 2003). The approach used in this study avoids this common artifact. It should be noted that Bienfang (1981) described this caveat of the SETCOL approach, suggesting that it be best applied to particle fields with uniform settling rates, and also described methods for calculating the distribution of phytoplankton settling velocities from the time series of settled particles through time in settling columns (Bienfang et al. 1977; Bienfang 1979; Bienfang 1980). However, the caveats of SETCOL, and the alternate methods Bienfang developed have not been widely appreciated in phytoplankton research.

Nearshore land-fast sea ice contributes greatly to productivity of Arctic coastal marine communities, though ice algae are largely isolated from planktonic and benthic consumers until accumulated material is exported from the ice. The degree to which exported particles are consumed in the water column or benthos is initially related to their settling properties. Although the data presented here are based on laboratory experiments using only one species, the prevalence of *N. frigida* in land-fast Arctic sea ice, as well as the correspondence of these results with earlier field studies, indicates that these data may reflect in situ trends. If so, settling velocities of ice algae exported from sea ice are highly variable, though with predictable influences of in situ light levels and nutrient availability. Although the regulation of diatom sinking rates is physiologically complex, increased ability to predict how ice algae sinking rates change in response to environmental conditions improves current understanding of the connection and importance of ice-based primary production to other components of the Arctic marine ecosystem.

References

Anderson, L. W., and B. M. Sweeney. 1977. Diel changes in sedimentation characteristics of *Ditylum brightwelli*: Changes in cellular lipid and effects of respiratory inhibitors and ion-transport modifier? Limnol. Oceanogr. **22**: 539-552. doi:10.4319/lo.1977.22.3.0539.

Apollonio S. 1961. The chlorophyll content of Arctic sea ice. Arctic **14**: 197-200. doi:10.14430/arctic3674.

Arrigo, K. R., T. Mock, and M. P. Lizotte. 2010. Primary Producers and Sea Ice. p. 283-326. In D. Thomas and G. Dieckmann [eds.], Sea Ice. Wiley-Blackwell.

Arrigo, K. R., and D. N. Thomas. 2004. Large scale importance of sea ice biology in the Southern Ocean. Antarct. Sci. **16**: 471-486. doi:10.1017/S0954102004002263.

Arrigo, K. R., G. Van Dijken, and S. Pabi. 2008. Impact of a shrinking Arctic ice cover on marine primary production. Geophys. Res. Lett. **35**: L19603. doi:10.1029/2008GL035028.

Aumack, C. F., A. R. Juhl, and C. Krembs. 2014. Diatom vertical migration within land-fast Arctic sea ice. J. Marine Syst. **139**: 496-504. doi:10.1016/j.jmarsys.2014.08.013.

Bienfang, P. K. 1979. A new phytoplankton sinking rate method suitable for field use. Deep-Sea Res. **26**: 719-729. doi:10.1016/0198-0149(79)90043-8.

Bienfang, P. K. 1980. Phytoplankton sinking rates in oligotrophic waters off Hawaii, USA. Mar Biol. **61**: 69-77. doi:10.1007/BF00410342.

Bienfang, P. K. 1981. SETCOL-a technologically simple and reliable method for measuring phytoplankton sinking rates. Can. J. Fish. Aquat. Sci. **38**: 1289-1294. doi:10.1139/f81-173.

Bienfang, P., and P. Harrison 1984*a*. Sinking-rate response of natural assemblages of temperate and subtropical phytoplankton to nutrient depletion. Mar. Biol. **83**: 293-300. doi:10.1007/BF00397462.

Bienfang, P., and P. Harrison. 1984*b*. Co-variation of sinking rate and cell quota among nutrient replete marine phytoplankton. Mar. Ecol.-Prog. Ser. **14**: 297-300. doi:10.3354/meps014297.

Bienfang, P., P. Harrison, and L. Quarmby. 1982. Sinking rate response to depletion of nitrate, phosphate and silicate in four marine diatoms. Mar. Biol. **67**: 295-302. doi:10.1007/BF00397670.

Bienfang, P., E. Laws, and W. Johnson. 1977. Phytoplankton sinking rate determination: technical and theoretical aspects, an improved methodology. J. Exp. Mar. Biol. Ecol. **30**: 283-300. doi:10.1016/0022-0981(77)90037-5.

Bienfang, P., J. Szyper, and E. Laws. 1983. Sinking rate and pigment responses to light-limitation of a marine diatom-implications to dynamics of chlorophyll maximum layers. Oceanol. Acta **6**: 55-62.

Bluhm, B. A., R. R. Gradinger, and S. B. Schnack-Schiel. 2010. Sea ice meio- and macrofauna, p. 357-394. In D. Thomas and G. Dieckmann [eds.], Sea Ice. Wiley-Blackwell.

Chancelier, J. P., G. Chebbo, and E. Lucas-Aiguier. 1998. Estimation of settling velocities. Water Res. **32**: 3461-3471. doi:10.1016/S0043-1354(98)00114-6.

Cota, G., L. Legendre, M. Gosselin, and R. Ingram. 1991. Ecology of bottom ice algae: I. Environmental controls and variability. J. Marine Syst. **2**: 257-277. doi:10.1016/0924-7963(91)90036-T.

Cota, G. F., and R. E. Smith. 1991. Ecology of bottom ice algae: II. Dynamics, distributions and productivity. J. Marine Syst. **2**: 279-295. doi:10.1016/0924-7963(91)90037-U.

Crump, B. C., and J. A. Baross. 2000. Characterization of the bacterially-active particle fraction in the Columbia River estuary. Mar. Ecol.-Prog. Ser. **206**: 13-22. doi:10.3354/meps206013.

Culver, M. E., and W. O. Smith. 1989. Effects of environmental variation on sinking rates of marine phytoplankton. J. Phycol. **25**: 262-270. doi:10.1111/j.1529-8817.1989.tb00122.x.

Daase, M., S. Falk-Petersen, Ø. Varpe, G. Darnis, J. E. SØreide, A. Wold, E. Leu, J. Berge, B. Philippe, and L. Fortier. 2013. Timing of reproductive events in the marine copepod *Calanus glacialis*: a pan-Arctic perspective. Can. J. Fish. Aquat. Sci. **70**: 871-884. doi:10.1139/cjfas-2012-0401.

Durkin, C. A., S. J. Bender, K. Y. K. Chan, K. Gaessner, D. Grünbaum, and E. V. Armbrust. 2013. Silicic acid supplied to coastal diatom communities influences cellular silicification and the potential export of carbon. Limnol. Oceanogr. **58**: 1707-1726. doi:10.4319/lo.2013.58.5.1707.

Elliott, D. T., C. K. Harris, and K. W. Tang. 2010. Dead in the water: The fate of copepod carcasses in the York River estuary, Virginia. Limnol. Oceanogr. **55**: 1821-1834. doi:10.4319/lo.2010.55.5.1821.

Eppley, R. W., R. W. Holmes, and J. D. Strickland. 1967. Sinking rates of marine phytoplankton measured with a fluorometer. J. Exp. Mar. Biol. Ecol. **1**: 191-208. doi:10.1016/0022-0981(67)90014-7.

Fisher, A. E., J. A. Berges, and P. J. Harrison. 1996. Does light quality affect the sinking rates of marine diatoms? J. Phycol. **32**: 353-360. doi:10.1111/j.0022-3646.1996.00353.x.

Flynn, K. J., and V. Martin-Jézéquel. 2000. Modelling Si–N-limited growth of diatoms. J. Plankton Res. **22**: 447-472. doi:10.1093/plankt/22.3.447.

Fortier, M., L. Fortier, C. Michel, and L. Legendre. 2002. Climatic and biological forcing of the vertical flux of biogenic particles under seasonal Arctic sea ice. Mar. Ecol.-Prog. Ser. **225**: 1-16. doi:10.3354/meps225001.

Gosselin, M., L. Legendre, J.-C. Therriault, and S. Demers. 1990. Light and nutrient limitation of sea-ice microalgae (Hudson Bay, Canadian Arctic). J. Phycol. **26**: 220-232. doi:10.1111/j.0022-3646.1990.00220.x.

Gosselin M., M. Levasseur, P. A. Wheeler, R. A., Horner, and B. C. Booth. 1997. New measurements of phytoplankton and ice algal production in the Arctic Ocean. Deep-Sea Res. II **44**:1623-1644. doi:10.1016/S0967-0645(97)00054-4.

Goutx, M., S. G. Wakeham, C. Lee, M. Duflos, C. Guigue, Z. Liu, B. Moriceau, R. Sempéré, M. Tedetti, and J. Xue. 2007. Composition and degradation of marine particles with different settling velocities in the northwestern Mediterranean Sea. Limnol. Oceanogr. **52**: 1645. doi:10.4319/lo.2007.52.4.1645.

Granata, T. C. 1991. Diel periodicity in growth and sinking rates of the centric diatom *Coscinodiscus concinnus*. Limnol. Oceanogr. **36**: 132-139. doi:lo.1991.36.1.0132.

Gradinger, R. 1999. Vertical fine structure of the biomass and composition of algal communities in Arctic pack ice. Mar. Biol. **133**: 745-754. doi:10.1007/s002270050516.

Gross, F., and E. Zeuthen. 1948. The buoyancy of plankton diatoms: a problem of cell physiology. P. Roy. Soc. Lond. B Bio. **135**: 382-389. doi:10.1098/rspb.1948.0017.

Guillard, R., and P. Hargraves. 1993. *Stichochrysis immobilis* is a diatom, not a chrysophyte. Phycologia **32**: 234-236. doi:10.2216/i0031-8884-32-3-234.1.

Haecky, P., S. Jonsson, and A. Andersson. 1998. Influence of sea ice on the composition of the spring phytoplankton bloom in the northern Baltic Sea. Polar Biol. **20**: 1-8. doi:10.1007/s003000050270.

Horner, R. 1976. Sea ice organisms. Oceanography and Marine Biology, An Annual Review **14**: 167-182.

Horner, R., and V. Alexander. 1972. Algal populations in Arctic sea ice: an investigation of heterotrophy. Limnol. Oceanogr. **17**: 454-458. doi:10.4319/lo.1972.17.3.0454.

Horner, R., and G. Schrader. 1982. Relative contributions of ice algae, phytoplankton, and benthic microalgae to primary production in nearshore regions of the Beaufort Sea. Arctic: 485-503. doi:10.14430/arctic2356.

Hsiao, S. 1988. Spatial and seasonal variations in primary production of sea ice microalgae and phytoplankton in Frobisher Bay, Arctic Canada. Mar. Ecol-Prog. Ser. **44**: 275-285. doi:10.3354/meps044275.

Hsiao, S. I. 1980. Quantitative composition, distribution, community structure and standing stock of sea ice microalgae in the Canadian Arctic. Arctic **33**: 768-793. doi:10.14430/arctic2595.

Johnson, T., and W. Smith. 1986. Sinking rates of phytoplankton assemblages in the Weddell Sea marginal ice zone. Mar. Ecol-Prog. Ser. **33**: 131-137. doi:10.3354/meps033131.

Jones, S. E, and C. F. Jago. 1996. Determination of settling velocity in the Elbe estuary using Quisett tubes. J. Sea Res. **36**: 63-67. doi:10.1016/S1385-1101(96)90772-8.

Juhl, A. R., and C. Krembs. 2010. Effects of snow removal and algal photoacclimation on growth and export of ice algae. Polar Biol. **33**: 1057-1065. doi:10.1007/s00300-010-0784-1.

Juhl, A. R., C. Krembs and K. M. Meiners. 2011. Seasonal development and differential retention of ice algae and other organic fractions in first-year Arctic sea ice. Mar. Ecol-Prog. Ser. **436**: 1-16. doi:10.3354/meps09277.

Kowalski, R., J. Reuber, and J. Köngeter. 1999. Investigations into and optimisation of the performance of sewage detention tanks during storm rainfall events. Water Sci. Technol. **39**: 43-52. doi:10.1016/S0273-1223(99)00006-2.

Krembs, C., and A. Engel. 2001. Abundance and variability of microorganisms and transparent exopolymer particles across the ice–water interface of melting first-year sea ice in the Laptev Sea (Arctic). Mar. Biol. **138**: 173-185. doi: 10.1007/s002270000396.

Legendre, L. S. F. Ackley, G. S. Dieckmann, B. Gulliksen, R. Horner, T. Hoshiai, I. A. Melnikov, W. S. Reeburgh, M. Spindler, C. W. Sullivan. 1992. Ecology of sea ice biota. Polar Biol. **12**: 429-444. doi:10.1007/BF00243114.

Lovvorn, J. R., L. W. Cooper, M. L. Brooks, C. C. De Ruyck, J. K. Bump, and J. M. Grebmeier. 2005. Organic matter pathways to zooplankton and benthos under pack ice in late winter and open water in late summer in the north-central Bering Sea. Mar. Ecol-Prog. Ser. **291**: 135-150. doi: 10.3354/meps291135.

Malarkey, J., C. Jago, R. Hübner, and S. Jones. 2013. A simple method to determine the settling velocity distribution from settling velocity tubes. Cont. Shelf Res. **56**: 82-89. doi:10.1016/j.csr.2013.01.018.

Martin-Jézéquel, V., M. Hildebrand, and M. A. Brzezinski. 2000. Silicon metabolism in diatoms: implications for growth. J. Phycol. **36**: 821-840. doi:10.1046/j.1529-8817.2000.00019.x.

Maykut, G. A., and T. C. Grenfell. 1975. The spectral distribution of light beneath first-year sea ice in the Arctic Ocean. Limnol. Oceanogr. **20**: 554-563. doi:10.4319/lo.1975.20.4.0554.

McMahon, K. W., W. G. Ambrose, Jr., B. J. Johnson, M. Sun, G. R. Lopez, L. M. Clough, and M. L. Carroll. 2006. Benthic community response to ice algae and phytoplankton in Ny Ålesund, Svalbard. Mar. Ecol-Prog. Ser. **310**: 1–14. doi:10.3354/meps310001.

Meguro, H., K. Ito, and H. Fukushima. 1967. Ice flora (bottom type): a mechanism of primary production in polar seas and the growth of diatoms in sea ice. Arctic **20**: 114-133. doi:10.14430/arctic3287.

Melnikov, I. A., E. G. Kolosova, H. A. Welch, and L. S. Zhitina. 2002. Sea Ice biological communities and nutrient dynamics in the Canada Basin of the Arctic Ocean. Deep-Sea Res. Pt. I **49**: 1623-1649. doi:10.1016/S0967-0637(02)00042-0.

Michel, C., L. Legendre, and S. Taguchi. 1997. Coexistence of microalgal sedimentation and water column recycling in a seasonally ice-covered ecosystem (Saroma-ko Lagoon, Sea of Okhotsk, Japan). J. Marine Syst. **11**: 133-148. doi: 10.1016/S0924-7963(96)00034-6.

Michel, C., L. Legendre, J.-C. Therriault, S. Demers, and T. Vandevelde. 1993. Springtime coupling between ice algal and phytoplankton assemblages in southeastern Hudson Bay, Canadian Arctic. Polar Biol. **13**: 441-449. doi: 10.1007/BF00233135.

Michel, C., T. G. Nielsen, C. Nozais, and M. Gosselin. 2002. Significance of sedimentation and grazing by ice micro- and meiofauna for carbon cycling in annual sea ice (northern Baffin Bay). Aquat. Microb. Ecol. **30**: 57-68. doi: 10.3354/ame030057.

Møller, E. F., P. Thor, and T. G. Nielsen. 2003. Production of DOC by *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* through sloppy feeding and leakage from fecal pellets. Mar. Ecol-Prog. Ser. **262**: 185-191. doi:10.3354/meps262185.

Morata, N., M. Poulin, and P. E. Renaud. 2011. A multiple biomarker approach to tracking the fate of an ice algal bloom to the sea floor. Polar Biol. **34**: 101-112. doi: 10.1007/s00300-010-0863-3.

Mundy, C., D. Barber, and C. Michel. 2005. Variability of snow and ice thermal, physical and optical properties pertinent to sea ice algae biomass during spring. J. Marine Syst. **58**: 107-120. doi:10.1016/j.jmarsys.2005.07.003.

Mundy, C., J. Ehn, D. Barber, and C. Michel. 2007. Influence of snow cover and algae on the spectral dependence of transmitted irradiance through Arctic landfast first-year sea ice. J. Geophys. Res-Oceans. **C3**: 112. doi:10.1029/2006JC003683.

Nishi, Y., and Tabeta, S. 2007. Effects of atmospheric heat input on the release of organic carbon from sea ice. J. Marine Syst. **67**: 155-169. doi:10.1016/j.jmarsys.2006.10.004.

Owen, M. W. 1976. Determination of the settling velocities of cohesive muds. Hydraulics Research Station, Wallingford, Report No. IT **161**: 1-8.

Pejrup, M., and O. A. Mikkelsen. 2010. Factors controlling the field settling velocity of cohesive sediment in estuaries. Estuar. Coast. Shelf S. **87**: 177-185. doi:10.1016/j.ecss.2009.09.028.

Peperzak, L., F. Colijn, R. Koeman, W. Gieskes, and J. Joordens. 2003. Phytoplankton sinking rates in the Rhine region of freshwater influence. J. Plankton Res. **25**: 365-383. doi:10.1093/plankt/25.4.365.

Pitcher, G., D. Walker, and B. Mitchel-Innes. 1989. Phytoplankton sinking rate dynamics in the southern Benguela upwelling system. Mar. Ecol-Prog. Ser. **55**: 261-269. doi: 10.3354/meps055261.

Ratkova, T. N., and P. Wassmann. 2005. Sea ice algae in the White and Barents seas: composition and origin. Polar Res. **24**: 95-110. doi:10.1111/j.1751-8369.2005.tb00143.x.

Raven, J. A., and A. M. Waite. 2004. The evolution of silicification in diatoms: inescapable sinking and sinking as escape? New Phytol. **162**: 45-61. doi:10.1111/j.1469-8137.2004.01022.x.

Renaud, P. E., A. Riedel, C. Michel, N. Morata, M. Gosselin, T. Juul-Pedersen, and A. Chiuchiolo. 2007. Seasonal variation in benthic community oxygen demand: a response to an ice algal bloom in the Beaufort Sea, Canadian Arctic? J. Marine Syst. **67**: 1-12. doi:10.1016/j.jmarsys.2006.07.006.

Riebesell, U., I. Schloss, and V. Smetacek. 1991. Aggregation of algae released from melting sea ice: implications for seeding and sedimentation. Polar Biol. **11**: 239-248. doi:10.1007/BF00238457.

Riedel, A., C. Michel, and M. Gosselin. 2006. Seasonal study of sea-ice exopolymeric substances on the Mackenzie shelf: implications for transport of sea-ice bacteria and algae. Aquat. Microb. Ecol. **45**: 195-206. doi:10.3354/ame045195.

Riedel, A., C. Michel, M. Gosselin, and B. Leblanc. 2008. Winter–spring dynamics in sea-ice carbon cycling in the coastal Arctic Ocean. J. Marine Syst. **74**: 918-932. doi:10.1016/j.jmarsys.2008.01.003.

Runge, J. A., J. C. Therriault, L. Legendre, R. G. Ingram, and S. Demers. 1991. Coupling between ice microalgal productivity and the pelagic, metazoan food web in southeastern Hudson Bay: a synthesis of results. Polar Res. **10**: 325-338. doi:10.1111/j.1751-8369.1991.tb00657.x.

Smayda, T. J. 1970. The suspension and sinking of phytoplankton in the sea. Oceanogr. Mar. Biol. Annu. Rev. **8**: 353-414.

Smayda, T. J. 1974. Some experiments on the sinking characteristics of two freshwater diatoms. Limnol. Oceanogr. **19**: 628-635. doi:10.4319/lo.1974.19.4.0628.

Smayda, T. J., and B. J. Boleyn. 1966. Experimental observations on the flotation of marine diatoms. III. *Bacteriastrum hyalinum* and *Chaetoceros lauderi*. Limnol. Oceanogr. **11**: 35-43.[10.4319/lo.1966.11.1.0035][Not Given in Reference].

Smith, R. E., W. G. Harrison, L. R. Harris, and A. W. Herman. 1990. Vertical fine structure of particulate matter and nutrients in sea ice of the high Arctic. Can. J. Fish. Aquat. Sci. **47**: 1348-1355. doi:10.1139/f90-154.

Steele, J., and C. Yentsch. 1960. The vertical distribution of chlorophyll. J. Mar. Biol. Assoc. UK. **39**: 217-226. doi:10.1017/S0025315400013266.

Suzuki, Y., S. Kudoh, and M. Takahashi. 1997. Photosynthetic and respiratory characteristics of an Arctic ice algal community living in low light and low temperature conditions. J. Marine Syst. **11**: 111-121. doi:10.1016/S0924-7963(96)00032-2.

Takabayashi, M., K. Lew, A. Johnson, A. I. Marchi, R. Dugdale, F. P. Wilkerson. 2006. The effect of nutrient availability and temperature on chain length of the diatom, *Skeletonema costatum*. J. Plankton Res. **28**: 831-840. doi:10.1093/plankt/fbl018.

Thompson, P. A., P. J. Harrison, and J. S. Parslow. 1991. Influence of irradiance on cell volume and carbon quota for ten species of marine phytoplankton. J. Phycol. **27**: 351-360. doi:10.1111/j.0022-3646.1991.00351.x.

Titman, D., and P. Kilham. 1976. Sinking in freshwater phytoplankton: some ecological implications of cell nutrient status and physical mixing processes. Limnol. Oceanogr. **21**: 409-417. doi:10.4319/lo.1976.21.3.0409.

Tremblay, C., J. Runge, and L. Legendre. 1989. Grazing and sedimentation of ice algae during and immediately after a bloom at the ice-water interface. Mar. Ecol-Prog. Ser. **56**: 291-300. doi:10.3354/meps056291.

UNESCO, 1994. Protocols for the Joint Global Ocean Flux Study (JGOFS) Core Measurements, p. 119-122. In A. Knap, A. Michaels, A. Close, H. Ducklow, A. Dickson, [eds.], JGOFS Report No. 19, vi+170 pp.

Villareal, T. A. 1988. Positive buoyancy in the oceanic diatom *Rhizosolenia debyana* H. Peragallo. Deep-Sea Res. **35**: 1037-1045. doi:10.1016/0198-0149(88)90075-1.

Villareal, T. A. 1992. Buoyancy properties of the giant diatom *Ethmodiscus*. J. Plankton Res. **14**: 459-463. doi:10.1093/plankt/14.3.459.

von Quillfeldt, C. H., W. G. Ambrose, and L. M. Clough. 2003. High number of diatom species in first-year ice from the Chukchi Sea. Polar Biol. **26**: 806-818. doi:10.1007/s00300-003-0549-1.

Waite, A., P. K. Bienfang, and P. J. Harrison. 1992a. Spring bloom sedimentation in a subarctic ecosystem. Mar. Biol. **114**: 119-129. doi:10.1007/BF00350861.

Waite, A., A. Fisher, P. A. Thompson, and P. J. Harrison. 1997. Sinking rate versus cell volume relationships illuminate sinking rate control mechanisms in marine diatoms. Mar. Ecol-Prog. Ser. **157**: 97-108. doi:10.3354/meps157097.

Waite, A. M., P. A. Thompson, and P. J. Harrison. 1992b. Does energy control the sinking rates of marine diatoms? Limnol. Oceanogr. **37**: 468-477. doi:10.4319/lo.1992.37.3.0468.

Wassmann, P. 1997. Retention versus export food chains: processes controlling sinking loss from marine pelagic systems. Hydrobiologia **363**: 29-57. doi:10.1023/A:1003113403096.

Welch, H. E., and M. A. Bergmann. 1989. Seasonal development of ice algae and its prediction from environmental factors near Resolute, NWT, Canada. Can. J. Fish. Aquat. Sci. **46**: 1793-1804. doi:10.1139/f89-227.

Yamamoto, S., C. Michel, M. Gosselin, S. Demers, M. Fukuchi, and S. Taguchi. 2014. Photosynthetic characteristics of sinking microalgae under the sea ice. Polar Sci. **8**(4): 385-396. doi:10.1016/j.polar.2014.07.007.

Acknowledgments

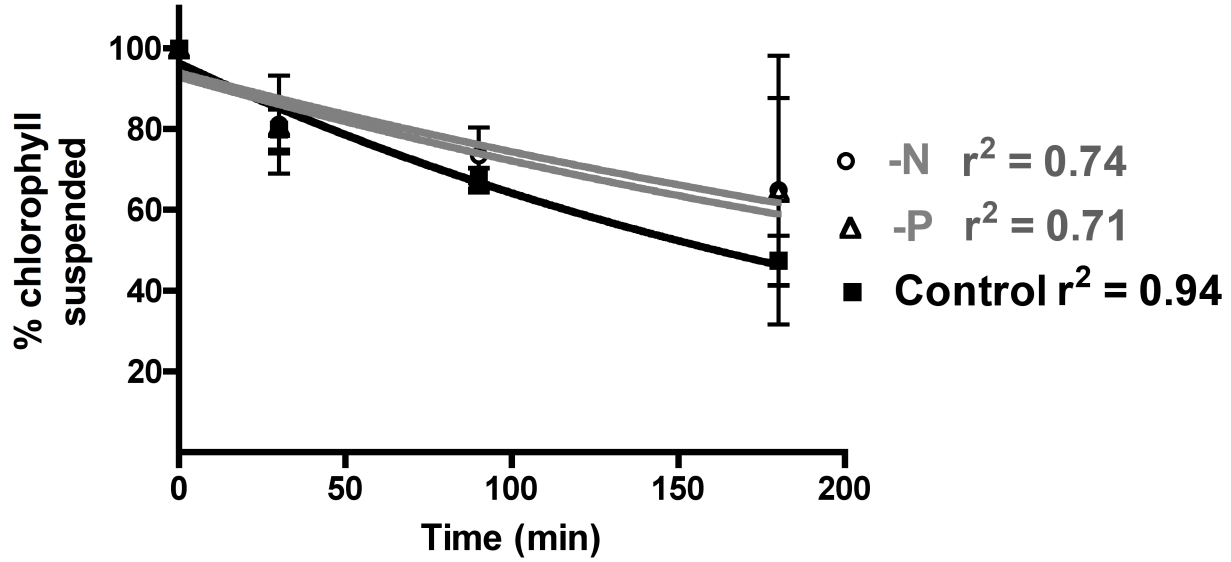
The authors wish to thank the editor and two anonymous reviewers for suggestions that greatly improved this manuscript. In addition, the authors thank Sheean Haley for transporting the large volumes of seawater needed for this project. This research was supported by a grant from the National Science Foundation (NSF) ARC10-23348 to A.R.J. In addition, C.F.A was partially supported by NSF Office of Polar Programs Post Doctoral Research Fellowship 1204166. This is contribution no. 7859 of Lamont-Doherty Earth Observatory.

Additional Supporting Information may be found in the online version of this article.

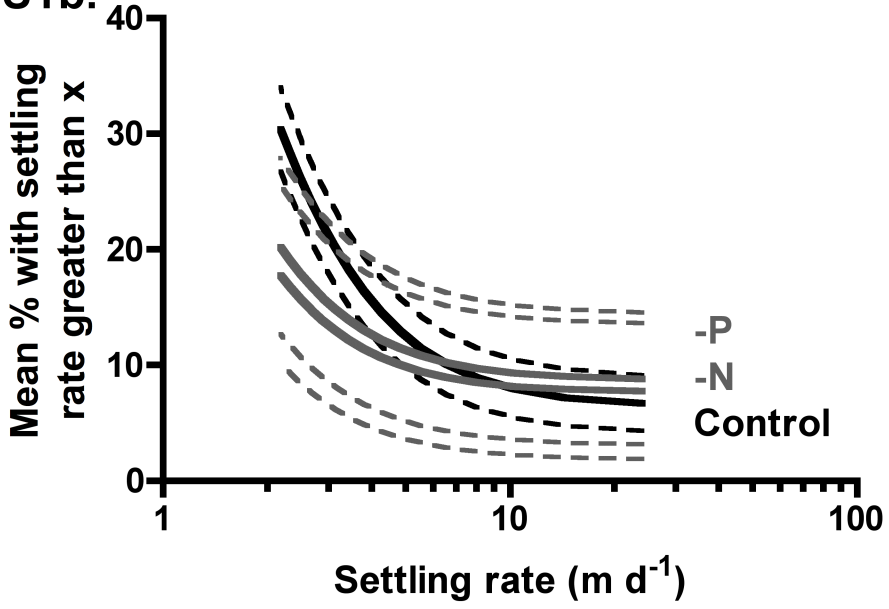
Submitted 8 June 2014
Revised 29 December 2014
Accepted 20 December 2014

Associate editor: John Albert Raven

S1a.


100
80
60
40
20
% chlorophyll suspended
0
50
100
150
200
Time (min)
-N r2 = 0.74
-P r2 = 0.71
Control r2 = 0.94

S1b.


40
30
20
10
0
Mean % with settling rate greater than x
1
10
100
Settling rate (m d-1)
-P
-N
Control