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Diatoms rapidly alter sinking behavior in response to changing nutrient concentrations

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Abstract

A diatom's sinking speed affects its depth in the water column, which determines its access to light and nutrients. Some large, centric diatom species perform an unsteady sinking behavior in which a cell's sinking speed oscillates over more than an order of magnitude on time scales of seconds. Diatoms are known to decrease mean sinking speeds and the magnitude of unsteady sinking following exposure to nutrient replete conditions over hours to days. Here we show that on shorter time scales of minutes to hours, nutrient deprived *Coscinodiscus wailesii* cells *increase* the mean and unsteadiness of their sinking when exposed to increased nutrient concentrations. Cultures exposed to nitrate or silicate-depleted media followed by a spike of the missing nutrient showed a sinking speed increase within the first 2 h that declined over the next 22 h. Phosphate deprived cultures did not respond similarly to a phosphate spike. In an experiment with an artificial nutricline in which cells encountered a sharp increase in nutrient concentrations over a distance of 10 cm, mean sinking speeds increased eight fold, and sinking unsteadiness increased significantly; these sinking speed changes occurred over 33 min. The contrasting short and long-term sinking behavior responses seen in this study demonstrates the importance of examining sinking behavior over multiple time scales. Initial fast and unsteady sinking upon encountering increasing nutrient concentrations may help diatoms take advantage of patchy nutrient distributions. Longer term, slow and steady sinking may be beneficial for maximizing light exposure and minimizing energy costs from unsteady sinking.

Sinking is an important determinant of a diatom population's spatial distribution and of an individual diatom's access to light and nutrients (Smayda 1970; Margalef 1978). Diatom sinking is also a major component of the global carbon cycle, with diatoms estimated to contribute up to 15% of global net primary production and 40% of particulate organic carbon export (Jin et al. 2006), but the contributions of different taxa of diatoms to carbon export are highly variable and are not well constrained (Tréguer et al. 2018).

It has long been known that population mean sinking speeds vary over time scales of hours to days (Smayda 1970), but little is known about the processes that regulate them. Proposed mechanisms include selective ion transport (Anderson and Sweeney 1977, 1978; Woods and Villareal 2008), production of organic osmolytes (Boyd and Gradmann 2002), carbohydrate ballasting (Lavoie et al. 2016), active water transport (Raven and Doblin 2014), and periodic cell expansion by cytoskeletal motors (Lavoie and Raven 2020). Sinking speeds respond to environmental conditions—including temperature (Bienfang and Szyper 1982), salinity (Bienfang and Szyper 1982), and irradiance (Bienfang et al. 1983; Granata 1991)—and to physiological conditions of the cells—including reproductive state (Waite and Harrison 1992) and nutrient exposure history (Bienfang 1981b; Bienfang et al. 1982).

Direct observation of the sinking behavior of individual cells, through videography, has revealed diatom sinking to be a more complex behavior than previously recognized (O'Brien et al. 2006; Miklasz and Denny 2010; Gemmell et al. 2016). Population mean sinking speeds are based on individual sinking speeds that can range over an order of magnitude. Furthermore, some species of large, centric diatoms, such as the *Coscindoscisus wailesii* examined in this study, exhibit unsteady sinking behavior, in which a cell varies its sinking speed over more than an order of magnitude repeatedly within tens of seconds (Gemmell et al. 2016). *C. wailesii* cells were shown to modulate the frequency and magnitude of unsteady sinking behavior in response to environmental and physiological conditions, sinking more slowly and steadily

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following long (hours to days) exposures to nutrient replete and dark conditions (Gemmell et al. 2016; Du Clos et al. 2019). Short-term responses to changes in light and nutrients had not been investigated prior to the present study.

Different sinking speeds and patterns have inherent tradeoffs; sinking faster (and possibly more unsteadily) can increase nutrient fluxes by thinning the diffusion boundary layer around a cell (Karp-Boss et al. 1996; Mann and Lazier 2006), but faster sinking also decreases residence time in the euphotic zone, and unsteady sinking requires energy in the form of ATP (Gemmell et al. 2016). Regulating sinking behavior over short time scales may allow diatoms to take advantage of patchy distributions of nutrients by temporarily increasing the mean and unsteadiness of their sinking speeds when nutrient concentrations are sufficient for increased nutrient uptake gains to outweighs the costs.

Despite evidence of uneven phytoplankton distribution on vertical spatial scales ≥ 0.1 m (Cassie 1963; Mackas et al. 1985; Mitchell et al. 2008) studies of diatom sinking have generally examined sinking speed changes over hours to days, and prior to this study it was not known how rapidly these changes could occur. Here we show that *C. wailesii* sinking behavior responses to increases in ambient nutrient concentrations differ depending on the nutrient and whether short (2 h) or long-term (24 h) changes are examined. We also show that *C. wailesii* greatly increases the speed and unsteadiness of its sinking within 33 min when encountering a sharp increase in nutrient concentrations as it passes through a nutricline.

Methods

Diatom cultures

Cultures of *C. wailesii* (mean cell diameter: 102 ± 11 μm) were maintained in sterile L1 culture media (National Center for Marine Algae and Microbiota L1 media kit, MKL11000L; Guillard and Hargraves 1993). A 12 : 12 h light–dark cycle was maintained prior to and during experiments. All experiments were performed during the light phase of the cycle at room temperature.

Experimental setup

The experimental setup was similar to that described in Gemmell et al. (2016). Sinking of individual *C. wailesii* cells was filmed in a $10 \times 30 \times 3.5$ cm (width × height × depth) glass tank (Fig. 1).

Diatom sinking speeds are slow (on the order of 0.01–0.1 mm s^{-1}) and thus sensitive to ambient water velocities. To minimize convection currents in the filming vessel, salinity gradients were prepared using a method described by O'Brien et al. (2006). Two tanks were filled with low (32) and high (36) salinity water. The filming vessel was then slowly filled from the bottom using water from the low-salinity tank into which water from the high-salinity tank was continuously mixed, producing a gradual increase in salinity from top to bottom. Tests with fluorescein confirmed that salinity gradients produced in this way are stable for up to 1 h (Fig. S1).

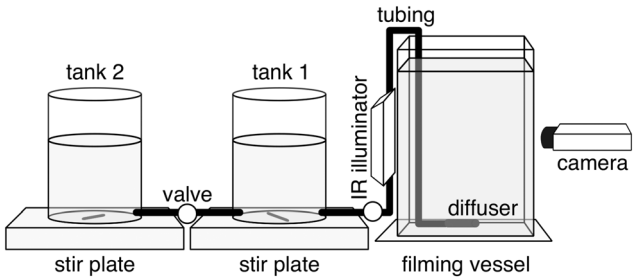

Fig 1. Diagram of experimental setup. Our system is based on a modified version of that described in O'Brien et al. (2006). Tanks 1 and 2 initially contains low (32) and high (36) salinity water. As the filming vessel is slowly filled from the bottom with water from tank 1, the salinity gradually increases due to mixing of water from tank 2. Sinking is recorded using bright-field illumination from an infrared illuminator.

Single-nutrient depletion experiments

To ensure nutrient-depleted conditions, culture media was removed by gently pouring the cultures through a 20 μm Nitex mesh. Cells were then quickly rinsed into a culture vessel containing low nutrient Gulf of Maine filtered surface seawater and incubated for 24 h to ensure depletion of any trace nutrients. Observation of cells under an inverted microscope showed no apparent visible damage to cells as a result of this manipulation. Cells were then transferred for 24 h to L1 culture media prepared without one of three macronutrients—nitrate, phosphate, or silicate—and incubated under these conditions for an additional 24 h. A "spike" of the "missing" nutrient was then added to the culture to bring the media up to replete conditions with respect to all nutrients (L1 final concentrations). Sinking behaviors were recorded at four time points: before transfer to single-nutrient deficient media, before addition of the nutrient spike, and 2 and 24 h after the spike (Fig. 2). For filming, small diatom samples were carefully transferred by pipette from the culture to the top of the water column within the filming vessel, and sinking behaviors were recorded in the center of the tank as described in Gemmell et al. (2016). To avoid biasing sinking speeds, the salinity of the subsample was matched to that of the top of the column and was carefully introduced just below the surface of the water column.

Videos were recorded at 10 frames per second with an Edgertronic SC1 camera (Sanstreak Corp., San Jose, California) fitted with a Nikon 105 mm 1 : 1 macro lens and extension tubes, which produced an approximately 10×7 mm field of view near the center of the tank. Brightfield illumination was produced by an LED infrared illuminator. We determined that a recording time of 20 min was appropriate for these experiments as it was long enough to allow for a large number of individual sinking cells to be recorded and tracked but brief

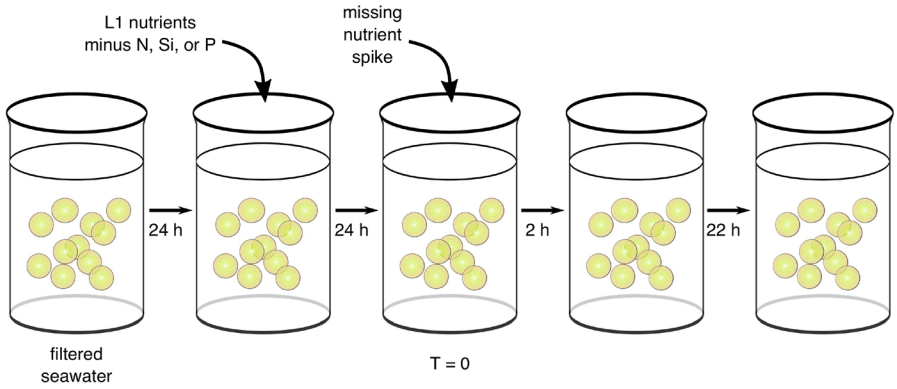

Fig 2. Schematic of time points used in single-nutrient depletion experiments. At each time point other than the first shown, diatoms were transferred to the filming vessel to record sinking behavior. Time zero is defined as the time when the nutrient spike was added.

enough that instabilities in the salinity stratified water column did not develop.

Nutricline experiment

Sinking behavior of nutrient replete cells was recorded above and below a laboratory created nutricline to determine whether *C. wailesii* sinking behavior responds rapidly to centimeter-scale changes in nutrient concentration. To form the nutricline, a salinity gradient was created as described above, but when the filming vessel was half full, nutrient solutions were added to both tanks. Nutrients were added in volumes sufficient to produce L1 concentrations in the lower half of the filming vessel. Fluorescein was added with the nutrients to locate the position of the nutricline (Figs. 3, S1).

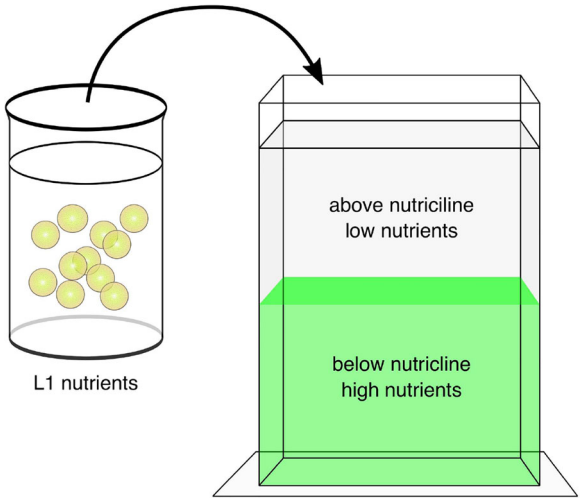

Fig 3. Schematic of the nutricline experiment. Diatoms were transferred to the top of a water column containing a nutricline with low nutrients in the top layer and high nutrients in the bottom layer (shaded green to indicate fluorescein, which was used as a tracer for the nutrients). Videos of sinking cells were simultaneously recorded above and below the nutricline with fields of view separated by 10 cm.

Videos were recorded as described for the single-nutrient depletion experiments except two cameras were used, one above and one below the nutricline. The top camera was mounted directly above the bottom camera with the fields of view of the two cameras separated by approximately 10 cm. As in the single-nutrient depletion experiments analyses were based on videos of the same duration from each camera for consistency. In this case videos covered 29 min following the first appearance of cells—the maximum duration that could be tracked with both cameras.

Analysis

All in-focus cells in the videos were tracked using the ImageJ package TrackMate (Tinevez et al. 2017). Tracks of less than 50 frames were discarded, yielding at least 69 cells tracked in each treatment. Additional analyses were performed with MATLAB 2018a (MathWorks, Nattick, Massachusetts). After manually verifying each track, a five-frame moving average was applied to reduce noise. Tracks were considered unsteady if a two-component Gaussian mixture model could be fit to a histogram of sinking speeds for each frame and the difference between the means of the two components was greater than 0.05 mm (Fig. 4).

Parameters of sinking speed could not be transformed to meet normality assumptions of parametric tests, so nonparametric tests were used. For the single nutrient depletion experiments, Kruskal–Wallis tests followed by multiple comparison tests were used to test for differences between time points for each nutrient ($\alpha = 0.05$). For the nutricline experiment, Mann–Whitney *U*-tests were used to test for differences between tracks above and below the nutricline ($\alpha = 0.05$).

To estimate nutrient flux enhancement due to sinking for each treatment we calculated the Sherwood number (*Sh*). The Sherwood number is the ratio between the fluxes of nutrient to a sinking cell and a stationary one, a measure of the nutrient flux advantage of sinking due to depletion of the diffusion limiting boundary layer surrounding a cell (Karp-Boss et al. 1996). Sherwood numbers were calculated using the

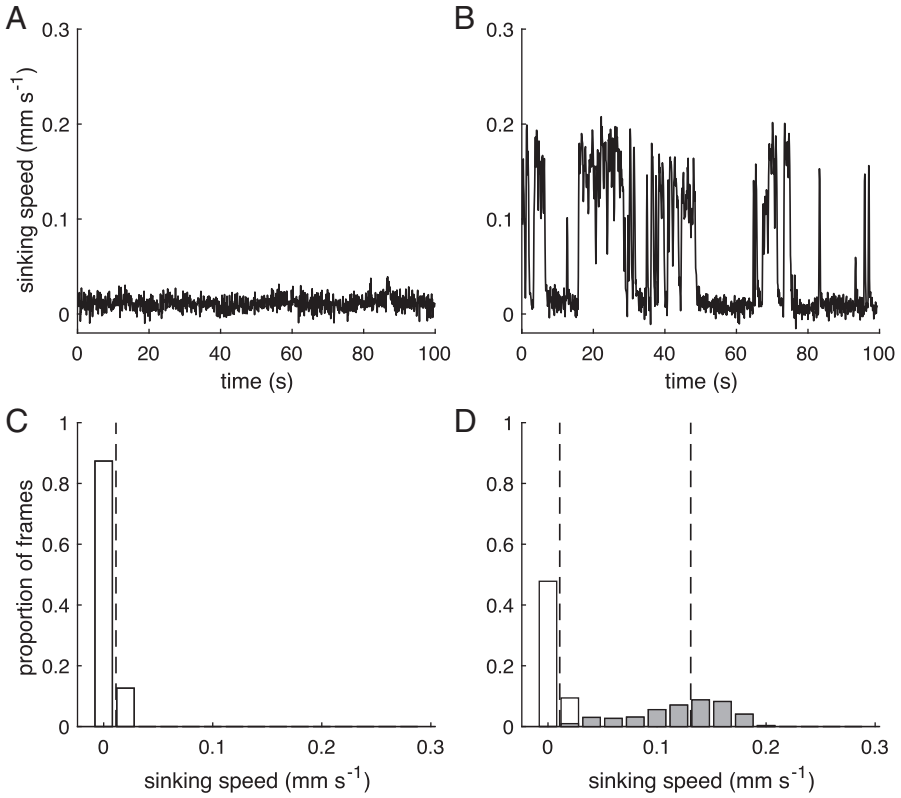

Fig 4. Steady and unsteady sinking behavior. Traces of instantaneous sinking speed during (**A**) steady and (**B**) unsteady sinking behavior. (**C** and **D**) distributions of instantaneous sinking speed over the time period shown. For steady sinking (**C**) the mean sinking speed is indicated by a dashed line. For unsteady sinking (**D**) the two components of a Gaussian mixture model and their means are shown. Tracks were considered unsteady if a two-component Gaussian mixture model could be fit to a histogram of sinking speeds for each frame and the difference between the means of the two components was greater than 0.05 mm s^{-1}.

equation for low Reynolds number sinking in Karp-Boss et al. (1996, their Eq. 18):

$$Sh = \frac{1}{2}\left[1 + (1 + 2Pe)^{\frac{1}{3}}\right] \quad (1)$$

Pe is the Péclet number, the dimensionless ratio of advective and diffusive transport:

$$Pe = \frac{Va}{D} \quad (2)$$

where V (m s^{-1}) is sinking speed, a is cell radius (m), and D is the diffusion coefficient of the nutrient of interest, which we take to be 1×10^{-9} m^2 s^{-1}, an approximation for small molecules in water (Haynes 2014).

Results

Single nutrient depletion experiment

Diatoms were filmed prior to addition of the single-nutrient deficient media, prior to the nutrient spike (time 0), and 2 and 24 h after the nutrient spike. The number of individual cells tracked ranged from 69 to 492, with only two time points having fewer than 138 cells–24 h pre-spike for the phosphate-depleted (n = 71) and silicate-depleted (n = 69) treatments. Results are reported below in terms of medians and interquartile ranges (IQR) of sinking speed parameters.

In the 24 h after the addition of the single-nutrient deficient media, mean sinking speed and the standard deviation of sinking speed (an indicator of unsteadiness) decreased significantly in the nitrate deficient treatment, and the standard deviation of sinking speed decreased significantly in the silicate treatment (Fig. 5A,D). Mean and unsteady sinking speeds in the phosphate and silicate-depleted treatments did not change significantly over this time period.

In the first 2 h after the nutrient spike, in the nitrate deficient treatment mean sinking speed doubled from 0.04 (IQR 0.04) to 0.08 (IQR 0.11) mm s^{-1} ($p < 0.001$), the standard deviation of sinking speed increased significantly ($p < 0.001$; Fig. 5A,D), and the proportion of cells exhibiting unsteady sinking increased from 0.25 to 0.40. In the silicate deficient treatment, mean sinking speed increased significantly from 0.09 (IQR 0.09) to 0.13 (IQR 0.15) mm s^{-1} during this period, similarly to cells in the nitrate deficient treatment, but standard deviation of sinking speed did not change significantly (p = 0.87; Fig. 5B,E); the proportion of cells sinking unsteadily

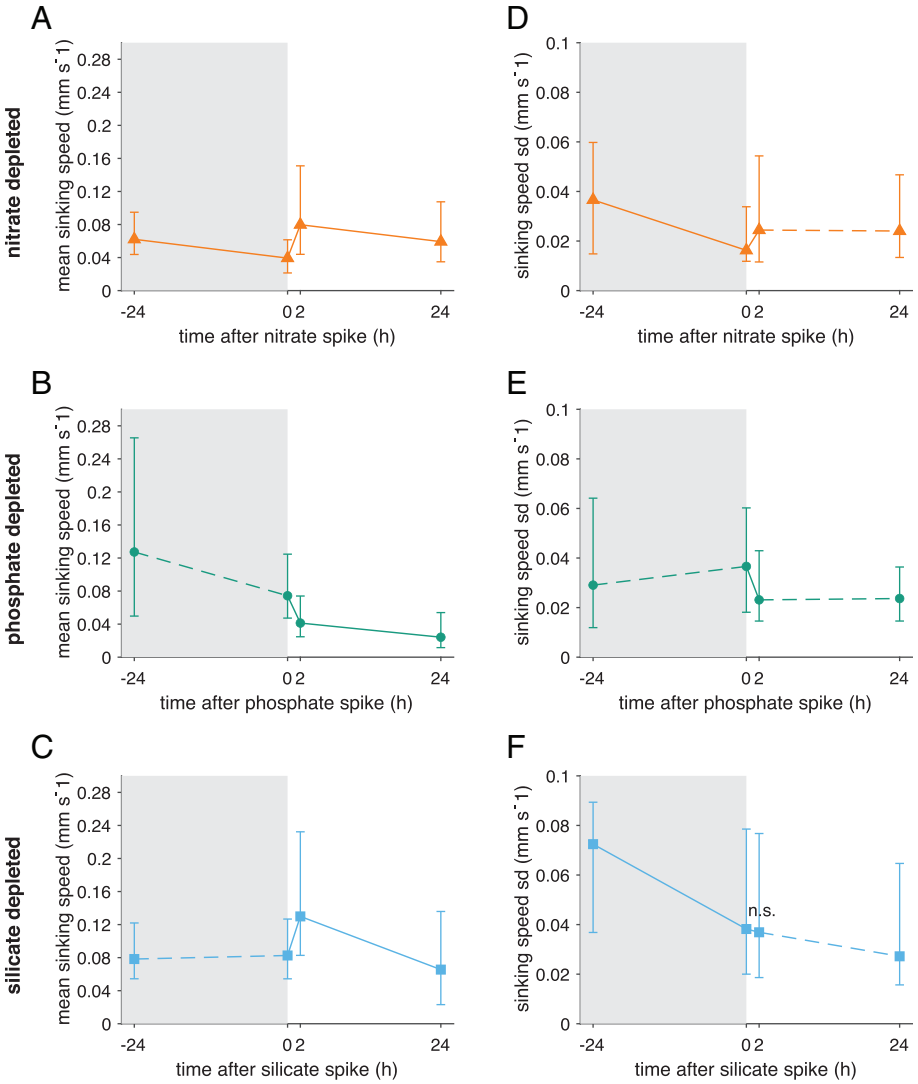

Fig 5. Results from individual nutrient depletion experiments. Sinking parameters for cultures exposed to media deficient in nitrate, phosphate, or silicate at $T = -24$ h and a spike of the missing nutrient at $T = 0$. The gray region represents the time before the nutrient spike. Medians and interquartile ranges of (**A**–**C**) individual mean sinking speeds and (**D**–**F**) standard deviation of individual sinking speeds for each of the three nutrient treatments. Solid lines indicate significant differences between neighboring time points. Diatoms in nitrate-depleted and silicate-depleted treatments sank significantly faster, and diatoms in the phosphate-depleted treatments sank significantly more slowly, 2 h after a spike of the missing nutrient.

remained constant at 0.51. In the phosphate deficient treatment, in contrast with the other two treatments, diatoms sank significantly more slowly and more steadily from the beginning to the end of this period. Mean sinking speed decreased from 0.09 (IQR 0.11) to 0.04 (IQR 0.05) mm s^{-1} ($p < 0.001$), the standard deviation of sinking speed decreased significantly ($p < 0.001$; Fig. 5C,F), and the proportion of cells sinking unsteadily decreased from 0.53 to 0.34.

Between the 2 and 24 h post-spike time points, mean sinking speeds decreased significantly for all three nutrient treatments ($p < 0.001$ for all treatments). Sinking unsteadiness did not change significantly during this time period for any of the three nutrient treatments.

Nutricline experiment

The median of mean sinking speed for cells below the nutricline (high nutrients) was approximately eight times that for cells above the nutricline (low nutrients): 0.08 (IQR 0.09) mm s^{-1} ($n = 72$) versus 0.01 (IQR 0.04) mm s^{-1} ($n = 153$); this difference was significant ($p < 0.001$; Fig. 6A). Cells below the nutricline also sank more unsteadily, with significantly higher standard deviations of sinking speed ($p < 0.001$; Fig. 6B) and more than triple the proportion of cell sinking unsteadily (0.72 versus 0.22). Assuming a sinking speed of 0.05 mm s^{-1}—the mean of the median sinking speeds above and below the nutricline—the 10 cm sinking distance over which these changes in sinking behavior occurred corresponds to approximately 33 min of sinking.

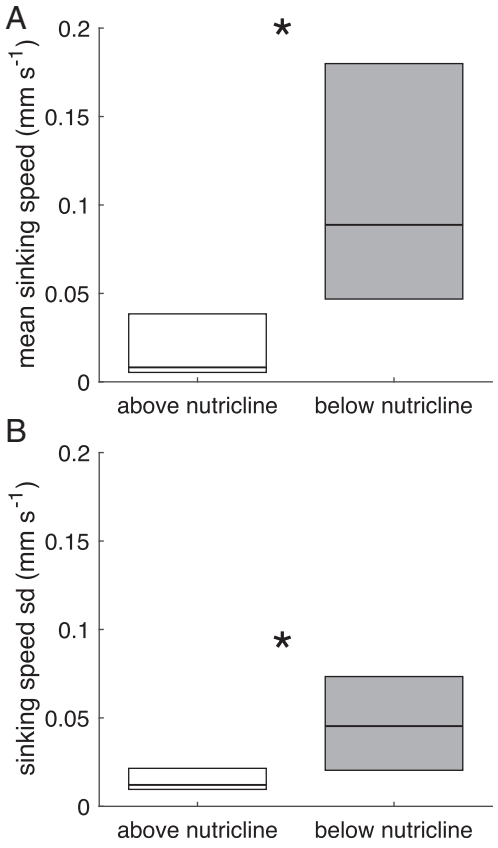

Fig 6. Sinking parameters for cells sinking above (low nutrients) and below (high nutrients) an artificial nutricline. Medians and interquartile ranges (IQR) of (**A**) individual mean sinking speed and (**B**) standard deviation of individual sinking speed. Asterisks indicate significant differences based on Mann–Whitney *U*-tests.

Discussion

It has long been known that nutrient concentrations affect diatom sinking speeds (e.g., Smayda and Boleyn 1965), but diatom sinking responds to nutrient history as well as ambient concentrations (Bienfang 1981b; Bienfang et al. 1982) because both external nutrient concentrations and internal nutrient pools affect buoyancy regulation, and the time scales over which changes in nutrient concentrations affect sinking behavior are not well known. This is particularly true for time scales less than a few hours due to the limited temporal resolution of past studies that used settling column methods (Bienfang 1981a).

Exposure to high nutrient concentrations over periods ranging from 12 h to 6 d results in slower sinking speeds in *C. wailesii* (Bienfang et al. 1982; Gemmell et al. 2016; Du Clos et al. 2019). Similarly, we found that when cells were exposed to media replete in all nutrients for 24 h, sinking speeds slowed significantly between the 2nd and 24th hour in each of the three nutrient treatments (nitrate depleted, phosphate depleted, and silicate depleted; Fig. 5). However, in the nitrate-depleted and silicate-depleted treatments we observed a significant *increase* in sinking speed in the 2-h period immediately following the spike of the missing nutrient. The differential sinking behavior responses of *C. wailesii* to long and short-duration nutrient exposures demonstrate the importance of examining sinking behavior at multiple time scales. In the short term, when a cell experiences an increase in ambient nutrient concentrations it may quickly respond by sinking faster and more unsteadily, thus increasing nutrient fluxes. In the long term, after a cell has filled its internal nutrient stores it may slow its sinking speeds, maximizing light exposure and avoiding additional energy expenditure from unsteady sinking.

Cells in the phosphate-depleted treatment, in contrast with the other two nutrient treatments, showed a significant decrease in mean sinking speed in the 2 h following the phosphate spike; there are at least three possible explanations for the observed difference in responses. One possibility is that we missed a short-term sinking response that occurred less than 2 h after the addition of phosphate. Nishikawa et al. (2010) found that for *C. wailesii*, nitrate uptake rates were nearly constant for 6 h following nitrate addition but phosphate uptake rates declined much faster—within 60 min of phosphate addition. Another possibility is that *C. wailesii* does not respond or does not respond as strongly in the short term to the addition of phosphate as it does to the addition nitrate or silicate. This possibility seems unlikely, however, because Bienfang et al. (1982) found that *C. wailesii* cells in their phosphate-depleted treatment decreased their sinking speed more than cells in nitrate and silicate-depleted treatments 24 h after the addition of the missing nutrient. We observed a similar decrease in sinking speed 24 h after phosphate was added to our phosphate-depleted cultures, but it is unclear whether long and short-term responses are correlated. A third possibility is that diatoms in the phosphate-depleted treatment had not fully depleted their internal phosphate pools by the end of the 24 h incubation in phosphate-deficient media. The consistent decrease in sinking speed over the duration of the experiment, in that case, may simply represent a longer term response to the addition of the other nutrients. Further experiments including more time points could help clarify how time scales of short and long-term responses vary by nutrient.

In addition to a decrease in mean sinking speed, cells in the phosphate-depleted treatment also showed a decrease in unsteady sinking behavior 2 h after the phosphate spike, as opposed to the increase in unsteady sinking behavior seen in the nitrate-depleted treatment. Unsteady sinking requires ATP (Gemmell et al. 2016), and phosphate depletion can decrease ATP synthesis in diatoms (Alipanah et al. 2018), so it is possible that the phosphate-depleted cells in our study did not have sufficient ATP to sink unsteadily. An ATP deficit could also affect mean sinking speeds because unsteady sinking is correlated with higher mean sinking speeds.

The large magnitudes of the sinking speed increases within 2 h of a nutrient spike—approximately double the pre-spike speed for N and 1.6 times for Si—led to considerable increases in nutrient uptake fluxes to these cells. Sherwood number estimates based on the increased sinking speeds 2 h after the spike of N or Si correspond to additional nutrient flux benefits over steady sinking of 10%—from 1.4 to 1.5 for N and from 1.6 to 1.7 for Si (Fig. 7A).

Based on the results of the nutricline experiment, the sinking speed increases seen after 2 h may represent the tail end of a much stronger response to increased nutrient concentrations. In that experiment, cells sank eight times as fast after encountering a sharp increase in nutrient concentrations over a sinking distance of 10 cm—approximately 33 min sinking time—a sinking speed increase corresponding to a 50% increase in the nutrient flux compared to steady sinking, from Sh = 1.1 to 1.6 (Fig. 7B). These significant changes in sinking behavior occurred over time scales much shorter than those observed in previous studies.

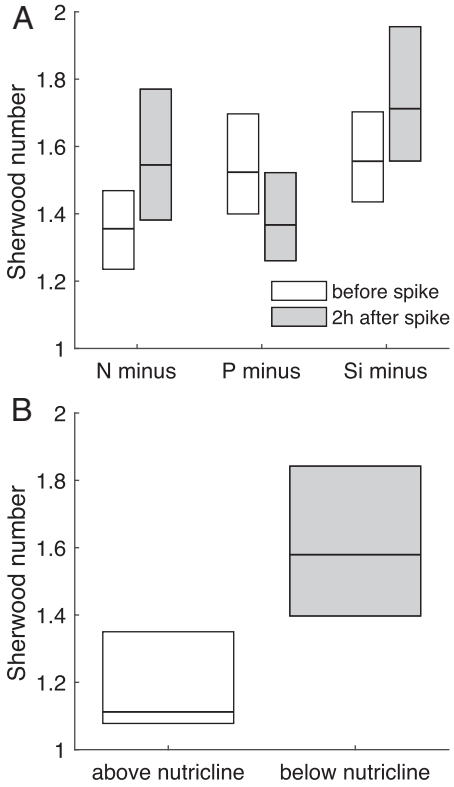

Fig 7. Sherwood numbers estimated from observed sinking speeds. Medians and interquartile ranges (IQR) of calculated Sherwood numbers from (**A**) the single nutrient depletion experiment, immediately before and 2 h after the nutrient spike and (**B**) nutricline experiment, above (low nutrients) and below (high nutrients) the nutricline. Sherwood numbers increased by approximately 0.1 following the nutrient spike for nitrate- and silicate-deficient treatments and increased by approximately 0.5 upon encountering the nutricline.

Increases in mean sinking speed were generally accompanied by more pronounced unsteady sinking behavior (except in the case of silicate depleted treatment). The greatest change in unsteady sinking behavior was seen in the nutricline experiment in which the standard deviation of sinking speed increased significantly, and the proportion of unsteady sinking cells more than tripled for cells below versus above the nutricline. Nutrient uptake is diffusion limited in diatoms, but steady sinking can partially relieve diffusion limitations for a large, fast sinking cell by thinning the diffusion boundary layer surrounding the cell (Lazier and Mann 1989; Karp-Boss et al. 1996). Unsteady sinking may further increase nutrient fluxes beyond the effects of steady sinking without requiring an increase in mean sinking speed that would cause the cells to sink from the euphotic zone more quickly (Gemmell et al. 2016).

We did not intend to replicate natural conditions in this study but rather to test the physiological limits of *C. wailesii*'s responses to changing nutrient conditions. Our results are ecologically relevant, however, because in many marine ecosystems, nutrient concentrations limit primary production (Howarth 1988) and nutrients are patchily distributed in space and time (Blackburn et al. 1998; Lunven et al. 2005). Laboratory studies have shown that the ability of phytoplankton to respond to changing nutrient concentrations varies between species with some species dominating under stable and others under fluctuating conditions (Turpin and Harrison 1979), and fluctuating nutrient environmental conditions have been cited as one explanation for the "paradox" of stable coexisting phytoplankton populations (Hutchinson 1961; Descamps-Julien and Gonzalez 2005). It has previously been shown experimentally that motile bacteria can exploit microscale nutrient patches (Stocker et al. 2008). Here we show that *C. wailesii*, while not motile, can similarly respond rapidly to changing nutrient concentration by altering its sinking behavior, presumably temporarily increasing nutrient uptake rates. Our results show that sinking behavior in *C. wailesii* can respond much more rapidly to changing nutrient conditions than has previously been recognized.

It is not known whether *C. wailesii* is unique among diatoms in its ability to change its sinking behavior rapidly in response to changing nutrient conditions or if this ability is more widespread. *C. wailesii* is somewhat unusual among diatoms because of its large cell size and its ability to sink unsteadily, which has only been documented in other large, centric diatoms to date (Gemmell et al. 2016), but it is unclear whether unsteady sinking ability is required for rapid alterations in *mean* sinking speed. *Coscinodiscus wailessi's* large cell size makes it more vulnerable to nutrient limitation and increases the nutrient uptake benefits it experiences from sinking (Karp-Boss et al. 1996). While *C. wailesii*'s distribution is not well documented, it has been described as occurring primarily in near-coastal areas where currents converge or impinge on shelf margins (Rincé and Paulmier 1986). These

environments have highly spatially and temporally variable nutrient concentration fields in which the ability to respond rapidly to changing nutrient concentrations is likely to be especially advantageous. *C. wailesii* is found in highest abundances during spring and fall blooms, in some cases dominating phytoplankton biomass during these periods (Edwards et al. 2001), and its ability to alter its sinking behavior in response to ambient nutrient conditions–as demonstrated here–as well as to changes in irradiance (Du Clos et al. 2019) may enable it to take advantage of high nutrient concentrations within a shallow mixed layer while minimizing losses due to sinking below the euphotic zone.

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