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NOTE

Effects of seawater viscosity and temperature on the movement of the marine dinoflagellate *Prorocentrum minimum*

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ABSTRACT: It is important to understand how planktonic dinoflagellate movements may be affected by environmental conditions, including those potentially influenced by climate change. Because of their small size, dinoflagellates can be expected to be highly sensitive to changes in viscosity; however, there is currently little understanding of how these organisms and other algae may be regulated by seawater viscosity. Previous work that has addressed the effects of seawater viscosity on single-celled plankton considered unnaturally large viscosity changes from a biomechanical perspective, sometimes without considering temperature effects. We studied the swimming of the dinoflagellate *Prorocentrum minimum*, a common coastal species, when exposed to environmentally relevant temperature and viscosity changes. *P. minimum* showed an additive response to seawater viscosity and temperature: cold temperature and high viscosity both slowed swimming speeds. However, seawater temperature and viscosity did not affect the movement direction or linearity of swimming of the dinoflagellates. We argue that temperature-related changes in movement may be partially regulated by a mechanical response to viscosity, which increases at cold temperature. We also propose possible future directions for laboratory and modelling studies.

KEY WORDS: Dinoflagellate · Plankton · Seawater viscosity · Temperature · Motility

1. INTRODUCTION

Motile prey, such as dinoflagellates, are preferred food species for many zooplankton (Atkinson 1996, Henriksen et al. 2007), and dinoflagellate swimming speeds may impact encounter rates with grazers (Kiørboe 2011a). Zooplankton can identify and leverage patches of prey cells (Herstoff 2019), and therefore dinoflagellate aggregation patterns can have cascading effects on the marine ecosystem.

When understanding how and why dinoflagellates respond to their environment, it is important to separate responses to temperature from responses to viscosity. Due to their small size (~5–100 µm), single-celled marine algae are characterized by low Reynolds numbers of $<10^{-2}$ ($Re = \rho uL/\mu$, where ρ is seawater density, μ is seawater dynamic viscosity, u is the speed of the organism, and L is the length of the organism). Thus, the viscosity of seawater may affect the motion of single-celled marine algae. At 0°C, the viscosity of 36‰ salinity seawater is 1.89×10^{-3} kg m^{-1} s^{-1}, whereas at 30°C, its viscosity is only 0.86×10^{-3} kg m^{-1} s^{-1} (Miyake & Koizumi 1948). Biogenic compounds, such as the mucus released by some bloom-forming algae, may also significantly increase seawater viscosity to

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double or triple its typical magnitude (Seuront et al. 2006). Thermohaline changes to seawater viscosity are Newtonian (independent of shear rate), whereas biogenic changes to seawater viscosity are non-Newtonian (dependent on shear rate) (Jenkinson & Biddanda 1995). Organisms with low Reynolds numbers, such as dinoflagellates, may be impacted by these natural changes in seawater viscosity.

Adaptation to seawater temperature and viscosity requires different evolutionary strategies: a thermal adaptation is metabolic (e.g. change to respiration rate), whereas a viscous adaptation is physical (e.g. change in size or strength). Due to their low Re environment, dinoflagellates are affected by viscosity, and therefore temperature-related responses may actually be responses to seawater viscosity. Laboratory experimentation is necessary to separate the viscous and thermal effects of temperature on dinoflagellates.

While previous research has focused on understanding how zooplankton respond to natural changes in seawater viscosity (e.g. Podolsky & Emlet 1993, Podolsky 1994, Bolton & Havenhand 1998, Bolton & Havenhand 2005, Larsen et al. 2008, Tyrell & Fisher 2019), there has been less work to understand how single-celled swimmers are affected by natural seawater viscosity changes (but see, e.g., Riisgård & Larsen 2009). Previous work on single-celled marine organisms has focused on unnaturally large viscosity changes from a biomechanical perspective, sometimes without considering temperature effects (e.g. Sohn et al. 2013, Orchard et al. 2016). Increasing seawater viscosity reduces flagellate swimming speeds (Beveridge et al. 2010, Sohn et al. 2013, Orchard et al. 2016), implying that some flagellate movement patterns may be regulated by seawater viscosity rather than by seawater temperature. However, further experiments are necessary to confirm this pattern. Additionally, further investigation of directional movement patterns is necessary to understand how cell aggregation may be affected by seawater temperature and viscosity.

In order to understand how trophic interactions are driven by environmental parameters, it is necessary to study how dinoflagellates respond to seawater viscosity at constant temperature and how these responses may affect trophic interactions. To better understand dinoflagellate movement patterns, we studied the swimming of *Prorocentrum minimum* at 2 temperatures and 2 viscosities. We hypothesized that *P. minimum* would demonstrate slower swimming and more linear movement when seawater viscosity was increased. Linear movement is defined as movement with a high net-to-gross displacement ratio (NGDR). We also hypothesized that seawater temperature would affect the vertical movement of dinoflagellates, which could have important implications for predation on dinoflagellates.

2. MATERIALS AND METHODS

2.1. Dinoflagellate cultures

Prorocentrum minimum (clone CCMP 696) cultures were used for all experiments. Cultures were maintained in sterile filtered (0.2 µm) seawater from Woods Hole, MA, USA (salinity 32–35‰) supplemented with f/2 nutrients (Guillard & Ryther 1962). Cells were kept on a 14 h light:10 h dark cycle at ambient temperature (18 to 21°C). Cell diameters were approximately 15 to 20 µm.

To acclimate *P. minimum* for experiments, cells were collected on a 5 µm polycarbonate membrane and resuspended in the proper treatment. Cells were acclimated for >17 h prior to recording videos. Experimental conditions and cell counts taken immediately prior to video recording are shown in Table 1.

2.2. Videography system

A high-speed microscale imaging system (HSMIS) was used to record 1024 × 1024-pixel resolution digital videos at 500 frames s^{-1}. The HSMIS consisted of a Photron FASTCAM SA3 120K monochrome video camera that was mounted horizontally with a 200 mm focal length objective lens plus an infinity-corrected, long-working-distance microscope objective (10 × 0.25 10.6 mm working distance) to yield a field-of-view of a vertically oriented area of ~1.6 × 1.6 mm (~80 × 80 cell diameters). The depth of focus (DoF) is calculated as (Nakano et al. 2005):

$$\mathrm{DoF} = \frac{n\,\lambda}{NA^2} + \frac{n\,e}{M\,NA} \quad (1)$$

where n is the refractive index of immersion medium (n = ~1.34 for seawater), λ is the wavelength of light (= 0.7 µm for the longest wavelength consisted in white light), NA is the numerical aperture of the microscope objective (= 0.25), M is the magnification of the microscope objective (= 10), and e is the pixel size, i.e. the smallest resolvable distance of the image sensor of the camera (= 17 µm). The calculated DoF is ~24 µm. A 1 W white LED light source was collimated

Table 1. Summary of conditions during *Prorocentrum minimum* videos in 2018

Video date (mo/d)	Temp (°C)	Viscosity ($\times 10^{-3}$ kg m^{-1} s^{-1})	No. of flasks	Initial cell density (cells ml^{-1})	No. of videos per flask	No. of cells tracked
6/5	10	1.441	1	6.5×10^3	4	6
6/7	10	1.441[a]	2	$2.5–4.5 \times 10^3$	3	17
6/12	20	1.351	2	5.0×10^3	3	11
6/14	20	1.327	3	$4.0–5.0 \times 10^3$	11–12	42
6/12	20	1.116	2	$3.0–4.0 \times 10^3$	3–4	13
6/15	20	1.090	3	$4.0–14 \times 10^3$	12	40

[a]Missing viscosity sample: substituted 6/5/2018 measurement (same treatment)

to provide backlit illumination in which light was shined toward the camera through a prepared flask placed in front of the microscope objective. The field-of-view was focused at the center of the flask, which was at least 1 cm (~500 cell diameters) away from flask walls. The HSMIS of different optical specifications has been previously used for quantitative microvideography and micro-particle image velocimetry of small protists and zooplankton (Jiang & Johnson 2017, Du Clos & Jiang 2018, Jiang et al. 2018, Jiang & Paffenhöfer 2020, Tyrell et al. 2020). The HSMIS has the advantage of achieving sharp imaging under low illumination.

2.3. Experimental treatments

The 3 experimental treatments used 0.2 µm-filtered water (salinity of 32–35‰) collected from Woods Hole, MA. Treatments were (1) 10°C seawater, (2) 20°C seawater, and (3) 20°C seawater with 0.12% w/v polyvinylpyrrolidone (PVP, Sigma-Aldrich), a non-toxic polymer. Addition of 0.12% w/v PVP enabled manipulation of seawater viscosity without affecting temperature or seawater density (Podolsky & Emlet 1993, Riisgård & Larsen 2007, Tyrell & Fisher 2019).

These 3 treatments allowed for the determination of the separate effects of temperature and viscosity according to the following comparisons: (1) 10°C treatment compared to 20°C high viscosity treatment showed the effect of temperature, (2) 20°C treatment compared to 20°C high viscosity treatment showed the effect of viscosity, and (3) 10°C treatment compared to 20°C treatment showed the effect of a natural temperature change.

Seawater samples were taken from each experiment and stored at 4°C in the dark until analysis of viscosity. The kinematic viscosity of the experimental water was measured at the appropriate temperature using an Ubbelohde viscometer (Sigma-Aldrich UBBEL02UKC) and the equation supplied by the manufacturer. The capillary of the viscometer had a diameter of 0.36 mm and a length of 10.5 cm. The hydrostatic pressure drop was approximately 0.004 atm, varying by a fraction of a percent depending on the density of the seawater. Kinematic viscosity was converted to dynamic viscosity using the equation: dynamic viscosity = density × kinematic viscosity. Dynamic viscosity is a measure of the resistance to flow (units: force × time × area^{-1}), while kinematic viscosity synthesizes both the dynamic viscosity and the density of the fluid into 1 metric (units: length^2 × time^{-1}).

2.4. Experimental measurements and analysis

Immediately prior to videoing, flasks were inverted to resuspend cells. We took a total of 93 videos of flasks containing $2.5–14 \times 10^3$ dinoflagellate cells ml^{-1} (Table 1). This helped minimize the chances we would re-record the same *P. minimum* cell. Videos were recorded according to the following procedure: a live video feed was monitored. When a cell swam across the field of view, the previous 10.9 s of footage was captured by manually triggering the camera. The footage was then edited to include only the period of time during which 1 or more cells were swimming, and it was saved. The saving process took ~5–10 min, after which the procedure was repeated. Most videos contained multiple swimming cells. The maximum video length was 10.9 s, and only 1 video was shorter than the maximum length, with a length of 2.8 s.

Sections of video containing 1 *P. minimum* cell moving in the plane of focus were analyzed. Cell coordinates were obtained using ImageJ and corrected for background movement by subtracting the movement of a randomly selected background parti-

cle that was not swimming. (The field of view was illuminated by a low-power light spot of a slightly larger size. There were, however, still chances that weak convective currents could arise as background movement.) The cell's coordinates were smoothed using a fourth-order Savitsky-Golay filter with a 23-point window (Jiang & Kiørboe 2011), and these smoothed coordinates were used for subsequent calculations.

Cell displacements (distance traveled during the video) in the vertical and horizontal directions, and the total displacement (vector sum of vertical and horizontal), were all calculated in 3 ways: net displacement was calculated as the difference in position in the first and last frames of the swimming period; the absolute value (magnitude) of the net displacement was also calculated; and gross displacement was calculated between each 2 coordinate points and summed for the entire period. The cell's angle of net displacement (in the standard coordinate system, i.e. $0 < \theta < \pi$ is upward movement) was calculated from the net displacement in the vertical and horizontal directions.

Average cell speeds in the vertical and horizontal directions, and the total speed (vector sum of vertical and horizontal), were calculated from these 3 displacement measurements (net, absolute value [magnitude] of net, and gross displacements) by dividing by the length of time of the swimming period. Cell speed was also calculated in a fourth way: the cell's coordinates were smoothed using a fourth-order Savitsky-Golay filter with a 23-point window (Jiang & Kiørboe 2011), and speed was calculated by taking the first derivative of the cell's position with respect to time.

The linearity (NGDR) was also calculated in the vertical, horizontal, and total directions. Two videos contained footage of a cell that was interrupted by a temporary visual obstruction of the cell's position (e.g. crossing paths with another cell or particle); in such cases, the cell's movements in the 2 unobstructed video sections were combined into 1 measurement so that the cell was not double-counted.

2.5. Statistics

We analyzed our data with the non-parametric Kruskal-Wallis test to determine whether median measurements differed by treatment group. Due to the large number of statistical tests, we assessed statistical significance at a Bonferroni-corrected level of $p < 0.0022$. When treatment had statistical effect, post-hoc groupwise comparisons were done with paired Wilcoxon rank sum tests with a Bonferroni correction. Statistics were run in *R* version 4.0.1 using the native *stats* package.

3. RESULTS AND DISCUSSION

Swimming speed was affected by treatment, typically with an additive effect of viscosity and temperature (Kruskal-Wallis test, $p < 0.0022$; Fig. 1,Tables 2

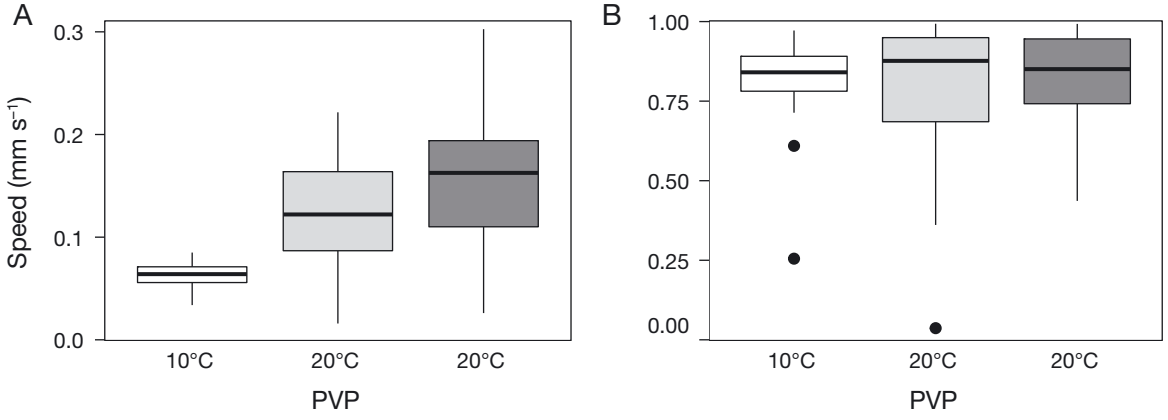

Fig. 1. *Prorocentrum minimum* (A) swimming speed and (B) linearity of swimming. Swimming speed was calculated according to the Savitsky-Golay method (Jiang & Kiørboe 2011), and linearity is based on the total displacement. PVP: polyvinylpyrrolidone. Measurements taken at 10°C (white), 20°C with high viscosity (light gray), or 20°C (dark gray). All groups had statistically different swimming speeds, while linearity did not differ by group (Kruskal-Wallis test for group effect; groupwise comparison with paired Wilcoxon rank sum tests with Bonferroni correction). The lower bound of the box is the 25% quartile; the middle horizontal line is the median; the upper bound of the box is the 75% quartile. Vertical lines extend to the minimum and maximum data points, excluding outliers. Outliers defined as data points that were >1.5 × IQR above the 75% quartile, or >1.5 × IQR below the 25% quartile (IQR = interquartile range, 75% quartile – 25% quartile)

Table 2. *Prorocentrum minimum* swimming summary. Table entries are means ± 2 SE; number in parentheses is the median. dis.: displacement, i.e. distance travelled during the video

Measurement	Treatment		
	10°C (23 cells)	20°C PVP (53 cells)	20°C (53 cells)
Time in focus (s)	5.45±1.22 (4.63)	2.63±0.60 (1.76)	2.51±0.50 (1.94)
Size (µm)	20.29±1.34 (20.53)	16.84±0.53 (16.83)	16.77±0.60 (16.85)
Net horizontal dis. (mm)	0.01±0.07 (–0.02)	–0.0008±0.04 (0.007)	–0.04±0.09 (0.0006)
Net vertical dis. (mm)	0.10±0.11 (0.012)	0.10±0.07 (0.07)	0.10±0.08 (0.09)
Magnitude of net horizontal dis. (mm)	0.12±0.04 (0.09)	0.10±0.03 (0.07)	0.21±0.07 (0.13)
Magnitude of net vertical dis. (mm)	0.22±0.07 (0.19)	0.19±0.05 (0.12)	0.23±0.06 (0.14)
Magnitude of net total dis. (mm)	0.28±0.07 (0.26)	0.24±0.05 (0.16)	0.34±0.08 (0.24)
Gross horizontal dis. (mm)	0.18±0.04 (0.15)	0.15±0.03 (0.13)	0.25±0.07 (0.16)
Gross vertical dis. (mm)	0.25±0.07 (0.22)	0.21±0.05 (0.14)	0.26±0.06 (0.20)
Gross total dis. (mm)	0.34±0.08 (0.29)	0.29±0.06 (0.21)	0.41±0.09 (0.30)
Horizontal linearity (unitless)	0.67±0.13 (0.75)	0.63±0.10 (0.73)	0.76±0.09 (0.93)
Vertical linearity (unitless)	0.81±0.11 (0.97)	0.81±0.07 (0.97)	0.82±0.07 (0.98)
Total linearity (unitless)	0.81±0.06 (0.84)	0.79±0.06 (0.88)	0.82±0.04 (0.85)
Angle of net dis.[a] (radians)	0.99π±0.24π (0.87π)	0.77π±0.14π (0.62π)	0.90π±0.15π (0.75π)
Net horizontal speed (mm s^{-1})	0.001±0.01 (–0.004)	–0.003±0.02 (0.005)	–0.01±0.03 (0.0003)
Net vertical speed (mm s^{-1})	0.01±0.02 (0.007)	0.03±0.02 (0.04)	0.03±0.03 (0.05)
Magnitude of net horizontal speed (mm s^{-1})	0.03±0.01 (0.02)	0.05±0.01 (0.04)	0.08±0.02 (0.06)
Magnitude of net vertical speed (mm s^{-1})	0.04±0.01 (0.04)	0.08±0.01 (0.07)	0.09±0.02 (0.08)
Magnitude of net total speed (mm s^{-1})	0.05±0.01 (0.05)	0.10±0.01 (0.09)	0.13±0.02 (0.14)
Gross horizontal speed (mm s^{-1})	0.04±0.01 (0.03)	0.07±0.01 (0.06)	0.10±0.01 (0.10)
Gross vertical speed (mm s^{-1})	0.05±0.01 (0.05)	0.09±0.01 (0.09)	0.11±0.01 (0.10)
Gross total speed (mm s^{-1})	0.06±0.005 (0.07)	0.12±0.01 (0.12)	0.16±0.02 (0.16)
Savitsky-Golay total speed (mm s^{-1})	0.06±0.01 (0.06)	0.12±0.01 (0.12)	0.16±0.02 (0.16)

[a]Angle of net displacement in the standard coordinate system, i.e. $0 < \theta < \pi$ is upward

& 3). Notably, swimming speeds at 20°C were typically double the swimming speeds at 10°C, consistent with the canonical temperature coefficient (Q_{10}) of 2 (Ikeda et al. 2001). Cell displacement, angle of swimming, and linearity were not affected by treatment (Kruskal-Wallis test, $p > 0.0022$; Fig. 1, Tables 2 & 3). A sample video of *Prorocentrum minimum* movement can be viewed in Video S1 in the Supplement at www.int-res.com/articles/suppl/a086p021_supp/.

Our hypotheses were partially upheld. Seawater viscosity and temperature affected *P. minimum* swimming speed, but linearity of swimming and the angle of swimming were not affected (Kruskal-Wallis test, $p > 0.0022$; Fig. 1, Tables 2 & 3). The measured swimming speeds of *P. minimum* (Table 2) were approximately 3 times higher than those previously reported, and seawater viscosity had a much stronger effect on swimming speed than previously observed (Sohn et al. 2013); however, in line with previous research (Beveridge et al. 2010), viscosity accounted for ~40% of the temperature-induced decrease in swimming speed. Differences in swimming speed might be attributable to different nutrient conditions (f/2 in Sohn et al. 2013, versus no added nutrients in the present study) or possibly different cell densities (not reported in Sohn et al. 2013, vs. 2.5–14 × 10^3 cells ml^{-1} in the present study). Additionally, intraspecific variability in swimming speeds has also been observed in marine protists (Harvey et al. 2015) and could explain some of the variability.

P. minimum's slower swimming speeds at high viscosity and cold temperature may result in decreased encounter frequency with predators. The clearance rates of passive ambush feeders scale with the square of prey size and the square of prey speed (Kiørboe 2011a). Therefore, the decrease in *P. minimum* speed from 0.16 to 0.12 mm s^{-1} would decrease grazer clearance by 44%. At 10°C, *P. minimum* speed of 0.06 mm s^{-1} would decrease grazer clearance by 81%, even with the larger cell size.

However, most copepods, the most abundant mesozooplankton grazers in the oceans (Turner 2004), use a feeding-current feeding mechanism rather than an ambush mechanism (Kiørboe 2011b). When considering the clearance of copepods that use a feeding current, the characteristics of the prey are not as important and are typically not included in clearance estimates (Kiørboe 2011a). An 800 µm copepod feeding on *P. minimum* that is able to create a feeding

Table 3. Summary of statistics (Kruskal-Wallis test). Groupwise differences were determined with paired Wilcoxon rank sum tests with a Bonferroni correction; na: post-hoc test was not performed to determine groupwise differences. *p < 0.0022 (Bonferroni correction, 23 tests). dis.: displacement; PVP: polyvinylpyrrolidone

Metric		χ^2_2	p-value	Groupwise differences
Size (µm)		21.62	2.0×10^{-5}*	10°C larger than other 2 groups
Time in focus (s)		22.81	1.1×10^{-5}*	10°C in focus longer than other 2 groups
Net dis. (mm)	Horizontal	0.12	0.94	na
	Vertical	0.05	0.97	na
Absolute value of net dis. (mm)	Horizontal	7.62	0.022	na
	Vertical	1.38	0.50	na
	Total	4.36	0.11	na
Angle of net dis. (radians)		3.05	0.22	na
Gross dis. (mm)	Horizontal	7.15	0.028	na
	Vertical	2.21	0.33	na
	Total	5.03	0.081	na
Net speed (mm s^{-1})	Horizontal	0.02	0.99	na
	Vertical	3.18	0.20	na
Absolute value of net speed (mm s^{-1})	Horizontal	19.45	6.0×10^{-5}*	20°C faster than other 2 groups
	Vertical	16.46	0.00027*	10°C slower than other 2 groups
	Total	38.13	5.3×10^{-9}*	All groups different; 20°C>20°C+PVP>10°C
Gross speed (mm s^{-1})	Horizontal	36.04	1.5×10^{-8}*	All groups different; 20°C>20°C+PVP>10°C
	Vertical	30.24	2.7×10^{-7}*	10°C group slower than other 2 groups
	Total	47.64	4.5×10^{-11}*	All groups different; 20°C>20°C+PVP>10°C
Savitsky-Golay speed (mm s^{-1})		47.62	4.6×10^{-11}*	All groups different; 20°C>20°C+PVP>10°C
Linearity	Horizontal	6.637	0.036	na
	Vertical	2.001	0.37	na
	Total	0.51971	0.77	na

current with a speed of 2–4 mm s^{-1} (Tyrell et al. 2020) would be able to increase its specific clearance rate by a factor of 4–10 × 10^3 by utilizing a feeding-current feeding method rather than an ambush method and would presumably be unaffected by changes in prey swimming (as long as none of the prey swimming changes affected its ability to escape the copepod); even intermittent use of a feeding-current feeding method would greatly increase the copepod's specific clearance rate. Indeed, temperature does not affect copepod ingestion of *P. minimum* after accounting for viscosity (Tyrell & Fisher 2019). As *P. minimum* moves slowly compared to its copepod predators and does not appear to have an escape jump mechanism, changes in its swimming speed may not have a large impact on encounter rates. In order to further investigate the ecological relevance of flagellate swimming speed on tropic interactions, heterotrophs with compulsory ambush-feeding mechanisms should be investigated, including foraminifera, pteropods, and ciliates.

Cells at 10°C were in-focus for approximately twice as long as cells in the other 2 treatments (Tables 2 & 3); this is a reflection of their slower swimming speeds (Tables 2 & 3). All displacement in all directions was approximately similar, regardless of treatment (Kruskal-Wallis test, p > 0.0022; Tables 2 & 3); similarly, the angle of swimming was not affected by treatment (Kruskal-Wallis test, p > 0.0022; Tables 2 & 3). Therefore, seawater viscosity and temperature had no apparent effect on vertical, horizontal, or total movement patterns, angle of swimming, or linearity of swimming (Tables 2 & 3).

Cells in the 10°C treatment were larger than the other cells; however, any scaling of speed with cell size was obscured by the cold temperature-induced reduction in swimming speed. The larger cell size at cold temperature may be reflective of differing nutrient content, and the effect of temperature on nutrient content should be investigated in future studies.

Notably, there was no meaningful difference between the cell speeds calculated from the Savitsky-Golay derivative method and speeds calculated from the gross displacement method. Therefore, future research may benefit from utilizing the simpler gross displacement method.

We found no evidence of temperature- or viscosity-based swimming cues: cell displacement and angle of swimming did not vary in the different treatments (Kruskal-Wallis test, $p > 0.0022$; Tables 2 & 3). This contrasts with previous work showing that an increase in seawater viscosity of 0.2 cP (20% increase) promotes upward migration (Orchard et al. 2016) and that cold temperatures promote upward migration (Heaney & Eppley 1981). However, slower swimming speeds at cold temperature and high viscosity alone may lead to increased cell aggregation under these conditions (Heaney & Eppley 1981). Diel vertical migration in dinoflagellates is understood to be caused by a combination of phototaxis and geotaxis (Kamykowski et al. 1998), and future research should investigate the effects of seawater viscosity and temperature on phototaxis and geotaxis. Species-specific responses should also be investigated.

P. minimum is a mixotroph (Johnson 2015) and may alter its behavior according to the prey composition of its environment (Sheng et al. 2007). Because seawater viscosity may affect predation success (Podolsky 1994, Bolton & Havenhand 2005, Tyrell & Fisher 2019), seawater viscosity and prey community composition may have interactive effects on dinoflagellate movement patterns. Future research should investigate the interactive effects of prey type, seawater viscosity and temperature, and dinoflagellate movement.

In summary, the slower swimming speed of *P. minimum* at cold temperature can be partially explained as a response to viscosity, and therefore dinoflagellate adaptations to temperature must include physical adaptations to viscosity. Models that consider climate change-induced effects should consider how changes in dinoflagellate movement patterns may propagate into ecosystem-level effects.

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