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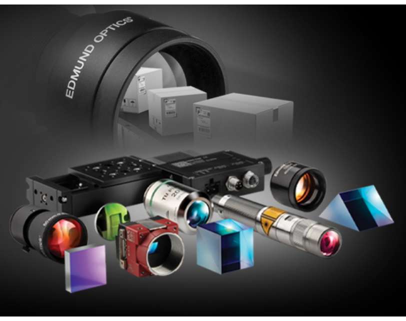

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ABSTRACT

The advancement of optical tweezers has revolutionized biological research, enabling precise manipulation of microscopic objects. In this study, we applied optical tweezers to diatom algae, known for their intricate silica frustules, achieving precise manipulation of their cells and chloroplasts. We demonstrated the ability to trap and move chloroplasts within cells of diatom *Coscinodiscus oculus-iridis* without causing damage, revealing the role of cytoplasm in maintaining organelle connectivity and facilitating motion. Using optical tweezers, we measured intracellular viscosity across different cytoplasmic regions, revealing a broad range influenced by local environment and cell-to-cell variability. These values reflect the viscosity of an equivalent continuous medium that would produce the same viscous friction coefficient for chloroplast movement. Although these data likely overestimate the true cytoplasmic viscosity—due to boundary layer interactions and the influence of cytoplasmic strands—they provide valuable insight into intracellular mechanics. Additionally, the achieved manipulation of entire diatom cells, including cells undergoing division, highlights the mechanical resilience of their silica frustules under external forces. These findings not only advance our understanding of diatom biology but also lay the groundwork for applications in biomimetic materials, photonic systems, and environmental research.

Optical tweezers, pioneered by Arthur Ashkin and colleagues in the 1980s and later recognized with the 2018 Nobel Prize in Physics, revolutionized micromanipulation in biology by enabling the non-contact trapping and manipulation of microscopic objects such as cells and subcellular organelles.[1–5] This technique allows for the measurement of femtonewton-scale forces and nanometer-precision positioning, providing powerful tools for probing biological systems across different scales.[6,7] The application of optical tweezers in biological research, especially in the single-cell analysis,[8,9] studies of cellular mechanics,[10–14] intercellular interaction,[15,16] intracellular processes,[17] and behaviors of organelles in their cellular context,[18,19] is immense. These tools are particularly powerful for manipulating organelles such as chloroplasts, enabling investigations of photosynthesis and intracellular dynamics. Previous studies have explored the effects of laser irradiation and optical trapping on various algal species, providing foundational insights into the interaction of laser light with cellular structures. For instance, Ashkin and Dziedzic[17] conducted experiments on *Spirogyra* and *Hydrodicton* using a laser at wavelength of 1064 nm, manipulating organelles and assessing potential damage. Similar laser-based manipulations were performed on *Spirogyra,*[20] as well as on *Micrasterias*, *Pleurenterium*, and *Closterium,*[21] with a focus on anatomical disturbances induced by the laser beam.

In our work, we advanced the application of optical tweezers to the study of diatoms, a group of microalgae characterized by their unique and intricate silica-based cell walls called frustules.[22] While optical manipulation of chloroplasts and entire cells has been previously demonstrated in plants[23,24] and algae,[17,25–27] this study extends the application of this technique specifically to diatoms. This distinction is particularly significant, as the structural and biomechanical properties of diatoms—such as their rigid, highly porous silica shells—

pose unique challenges for optical trapping. At the same time, these features provide opportunities to explore previously inaccessible aspects of cellular mechanics and photosynthetic dynamics in these ecologically and biotechnologically important microorganisms. These organisms are not only an important component of marine and freshwater ecosystems, making great contributions to the global biogeochemical cycle, but their intricate and highly ordered porous frustules inspire biomimetic materials science applications.[28] Chloroplasts, the cellular organelles responsible for photosynthesis, play a critical role in converting light energy into chemical energy, driving the metabolic processes that sustain diatom growth and ecological function. Understanding how light interacts with chloroplasts, and how chloroplasts are spatially arranged and move within the cell, is fundamental to advancing our knowledge of diatom biology and optimizing their potential applications in biotechnology. The unique structural properties of diatoms, when combined with the capabilities of optical tweezers, might thus help reveal previously unexplored aspects in both applied physics and biological disciplines.

In this study, we employed optical tweezers to investigate the intracellular mechanics and organelle dynamics of the diatom species *Coscinodiscus oculus-iridis (Ehrenberg) Ehrenberg 1840*, a model organism known for its intricate silica frustules and remarkable properties.[22,28] The intracellular mechanics of diatoms was studied by measuring intracellular viscosity in distinct cytoplasmic environments. The dynamics of organelles within diatoms were studied by trapping and moving chloroplasts using optical tweezers, enabling precise manipulation without causing cellular damage. Additionally, we extended our manipulation techniques to whole diatom cells, including those undergoing division, demonstrating the mechanical resilience of their silica frustules under external forces. These experiments provided insights into both organelle dynamics and the overall mechanical behavior of diatom cells.

Figure 1 introduces the experimental setup and methodology employed to study and manipulate diatom algae and their chloroplasts using optical tweezers. In our setup, light from a light-emitting diode passing through the sample chamber was collected by an oil immersion objective lens with a numerical aperture of 1.3 and then directed into a video camera, which enabled real-time bright-field microscopy imaging of the sample and recording optical trapping and manipulation process. Images (a)–(e) on the left showcase sequential cross sections of *C. oculus-iridis* captured along the z-axis, providing a layered view of its internal structure from the top (a) to the bottom (e). This z-scanning approach enables the visualization of cellular components and their spatial arrangement within the frustule (see supplementary material, Video 1). Each cross section highlights unique details of the diatom's interior, demonstrating the distribution of chloroplasts and other cellular structures across different planes. The schematic on the right illustrates the custom-designed optical tweezers setup used in this study. The setup employs a focused single-mode 980-nm laser beam to trap and manipulate diatom cells and their organelles with high precision.

Optical tweezers enable the precise manipulation of chloroplasts within diatom cells by using a highly focused laser beam to exert optical forces on the targeted organelle. The chloroplast is trapped and moved by the gradient force generated by the laser, which attracts the chloroplast toward the region of highest light intensity, typically at the center of the laser focus.[23] This process occurs without causing damage to the surrounding cellular structures, making it an invaluable tool for studying intracellular dynamics in living cells.

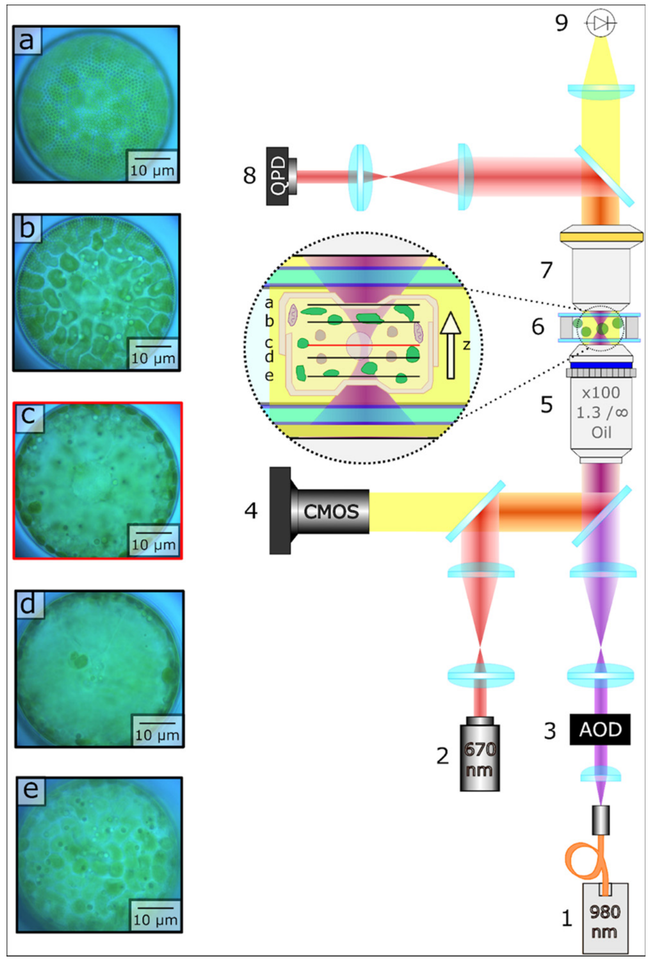

FIG. 1. Illustration of the optical tweezers setup used for manipulating diatom algae and their chloroplasts. (a)–(e) Bright-field microscopy images of diatom cell cross sections captured sequentially along the z-direction, from the top (a) to the bottom of the cell (e). The images on the left (a)–(e) correspond to the magnified area with the indicated cross sections of the diatom cell, highlighting its internal structure and arrangement of cellular components. The schematic diagram on the right depicts the detailed optical tweezers configuration: 1—980 nm trapping laser, 2—670 nm detecting laser, 3—acousto-optic deflector (AOD), 4—video camera, 5—objective lens, 6—sample chamber, 7—condenser lens, 8—quadrant photodiode (QPD), and 9—light-emitting diode (LED).

Figure 2 demonstrates the application of optical tweezers for manipulating chloroplasts within diatom algae, highlighting their spatial mobility and structural interactions. This experimental approach is a significant advancement in the study of diatom cellular dynamics, providing insight into how these photosynthetic organelles function within the cell. The bright-field microscopy time-sequenced images in Figs. 2(a1)–2(e1) show the trajectory of a single chloroplast being manipulated over a 4-s interval (see supplementary material, Video 2). This manipulation demonstrates the precise control achievable with optical tweezers, allowing the movement of organelles within their

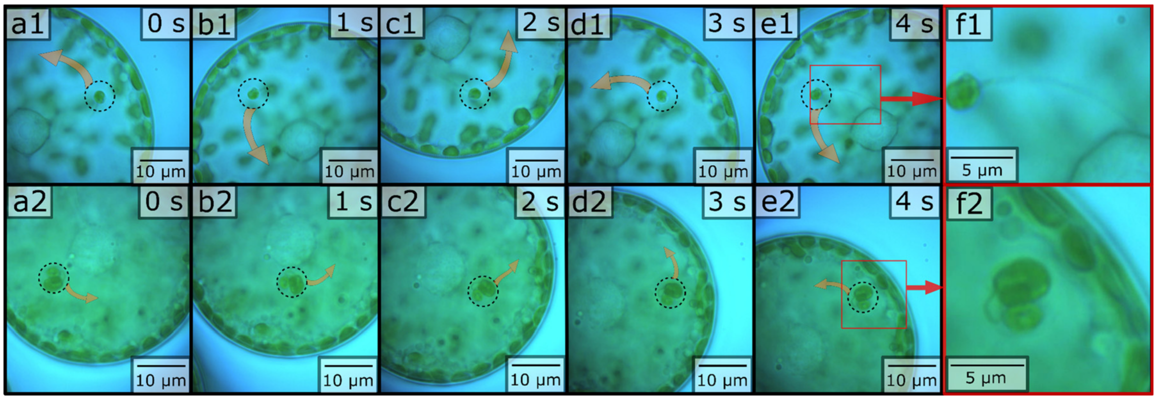

FIG. 2. Time-lapse sequence of bright-field microscopy images demonstrating the manipulation of chloroplasts within the diatom alga *C. oculus-iridis* using optical tweezers. Panels (a1)–(e1) depict the movement of a single chloroplast, while (a2)–(e2) show the manipulation of chloroplast aggregates over a 4-s interval. Each column represents a specific time point (0, 1, 2, 3, 4 s). Arrows indicate the trajectory of the manipulated chloroplasts, and dashed circles highlight the regions of interest. Magnified views in (f1) and (f2) correspond to the red boxed regions in (e1) and (e2), respectively, showing the cytoplasmic strand connecting the nucleus and the trapped chloroplast (f1) and a detailed view of the grouped chloroplasts (f2).

natural cellular environment without disrupting other cellular components. The sequence in Figs. 2(a2)–2(e2) extends this concept to the manipulation of chloroplast aggregates, showcasing the ability to move clusters of chloroplasts with similar precision (supplementary material, Video 3). The dashed circles and arrows in each panel indicate the region of interest and the direction of movement, respectively, illustrating the controlled trajectory of these organelles.

The trace of cytoplasm disturbances is clearly visible in the form of a cytoplasmic strand formed by manipulation [Fig. 2(f1)]. The thickness of the cytoplasmic strand, as measured in Fig. 2(f1), is $0.4 \pm 0.3\,\mu$m, which is validated by transmission electron microscopy (TEM) images (Fig. S1, supplementary material). The cytoplasmic strand acts as a flexible tether, enabling the chloroplast to follow the trajectory imposed by the optical tweezers. This tethering ensures that the chloroplast remains integrated within the cellular network, preserving its interactions with other organelles and its role in photosynthesis. Additionally, the elasticity of the cytoplasmic strand allows the organelle to move within certain spatial limits without detachment, highlighting the mechanical adaptability of the intracellular environment.[29]

Figure 2(f2) highlights the arrangement and grouping of chloroplasts, shedding light on their potential collaborative roles in optimizing photosynthesis. Figure S2 in the supplementary material shows the trapping and manipulation of a chloroplast within a small diatom cell using optical tweezers. The efficiency and stability of optical trapping are influenced by the refractive index (RI) mismatch between the trapped object and its surrounding medium. In our setup, the medium is artificial seawater (RI $\approx$ 1.33),[30,31] while the diatom frustule has an effective RI of $\sim$1.35–1.38,[32] with higher values reported for *Coscinodiscus* species ($\sim$1.43–1.45).[33] Cytoplasm and vacuoles have RI $\sim$1.36–1.39[32] and chloroplasts have RI $\sim$1.403–1.436.[32] This RI contrast ($\Delta n \approx 0.07$–0.12) enables stable trapping of both chloroplasts and whole diatoms. However, due to their larger size and complex geometry, whole diatoms ($\sim$10–50 μm) require higher laser power (>10 mW) than chloroplasts ($\sim$2–5 μm), which can be trapped with $\sim$8–10 mW. In all cases, chloroplasts adopted a stable orientation within the trap, with no notable in-plane rotation or tumbling during measurements. The use of moderate laser powers, safely within the biological tolerance for near-infrared trapping, resulted in no observable photodamage—no chlorophyll bleaching, loss of green coloration, or visible changes in organelle size or shape.

It is known that the chloroplast movement is provided by specific actin microfilaments called chloroplast actin (cp-actin) filaments.[34] Earlier,[21] it has been shown that using various lasers it is possible to move organelles in the cells of the microalgae *Micrasterias denticulata* and *Pleurenterium tumidum* with various consequences. Since the movement of chloroplasts and small vesicles is normally mediated by actin filaments, when they were exposed to a laser, normal movement was restored within a short time. Thus, we assume that actin microfilaments are the primary factor responsible for the elastic properties of the cytoplasmic strand formed through manipulation with optical tweezers.

Using optical tweezers, we measured intracellular viscosity in both rarefied and dense cellular environments. Viscosity, a key mechanical property, reflects the resistance of the cytoplasmic medium to organelle movement and deformation. All measurements were carried out at room temperature of 20 °C as follows. A single chloroplast inside a diatom cell was captured by the optical trap with the laser power of 8.4 mW. Smaller diatom cells could also be manipulated at this power level. For larger diatoms ($\sim$50 μm in diameter), we used 30 mW, while manipulation of two connected diatom cells undergoing division was performed using a higher power of 35 mW. Small displacements of the chloroplasts were monitored using a quadrant photodiode (QPD in Fig. 1). This was achieved by detecting the scattering of an additional 670 nm laser beam from the trapped objects. In order to match the signal received from the QPD with the actual chloroplast displacements, a calibration procedure was carried out by shifting the optical trap to a known distance using an AOD and measuring the resulting change in the QPD signal. This established the conversion factor between the QPD output and the real displacements.

By analyzing the chloroplast's thermal motion, which manifests itself in the displacement of the particle from the equilibrium position in the optical trap $x(t)$, the spatial probability density $p(x)$ and the normalized autocorrelation function $NACF(\tau) = \frac{\langle x(t)\,x(t+\tau)\rangle}{\langle x^2(t)\rangle}$ ($\langle\ \rangle$ denotes averaging over time) of the chloroplast displacements from the equilibrium position were determined. Assuming the displacement follows a Boltzmann distribution, the optical trap potential $U(x)$ was then extracted as

$$U(x) = -k_B T\, ln\left(\frac{p(x)}{p_0}\right), \tag{1}$$

where $k_B T$ is the thermal energy, p_0 is a normalization constant. The effective optical trap stiffness k was then obtained by fitting the measured potential to a harmonic potential well, $U(x) \approx \frac{kx^2}{2}$. Then, the hydrodynamic drag coefficient γ was extracted by fitting the autocorrelation function of a particle to an exponential decay,[35]

$$NACF(\tau) = e^{-\frac{k}{\gamma}\tau}. \tag{2}$$

The typical potential and autocorrelation function for a trapped chloroplast are shown in supplementary material, Fig. S3.

The described measurements gave us the values of the drag coefficient γ to be equal to $(34.6\pm0.8)\cdot 10^{-8}$ Pa·s·m, $(35.2\pm0.7)\cdot 10^{-8}$ Pa·s·m, and $(39.4\pm0.6)\cdot 10^{-8}$ Pa·s·m for a trapped chloroplast within a diatom cell as shown in Figs. 3(a)–3(c), respectively. Intracellular viscosity was estimated using Stokes' law, which describes the friction force F_S, acting on a spherical particle of radius r in a medium with dynamic viscosity η,

$$F_S = -\gamma\, v = -6\,\pi\,\eta\, v. \tag{3}$$

This gave approximate values of 34 ± 11 mPa·s, 39 ± 14 mPa·s, and 42 ± 14 mPa·s for the diatom cells shown in Figs. 3(a)–3(c), respectively. Additional measurements presented in Fig. S4 yielded intracellular viscosities of 3.5 ± 0.9, 7.3 ± 2.2, 64 ± 22, and 73 ± 20 mPa·s, further illustrating the variability across different cells and cytoplasmic regions. However, these values likely represent upper estimates, since the chloroplast was close to cell walls and other organelles, violating the assumption of an unbounded medium, because in reality the interaction of a trapped object with the medium's boundary leads to an increase in the effective hydrodynamic drag coefficient.[2] For example, viscosity of *Chlorella* cytoplasm is 5.2 mPa·s.[36] Additionally, adhesion to a cytoplasmic strand further increases the drag coefficient, which can also lead to overestimated viscosity. The present study, however, is intended chiefly as a proof-of-principle demonstration that optical tweezers can probe the mechanical micro-environment inside a living diatom. Currently, our measurements provide localized, point-based estimates of intracellular viscosity at the trapped chloroplast's position. Comprehensive spatial mapping would require introducing microscopic probes like, for example, inert tracer particles[37] or fluorescent latex beads[38] throughout the cytoplasm. However, in diatoms, this is highly challenging due to the rigid silica frustule that hinders probe delivery. Moreover, prolonged measurements at multiple locations are limited by concerns over cell viability and photodamage.

Figure 4 demonstrates the ability of optical tweezers to manipulate whole diatom cells, including dividing cells, which is crucial for understanding the dynamic interactions between diatom cells and their environment and highlights the versatility of optical tweezers as a tool for cellular studies. Figures 4(a1)–4(d1) present the side view of two diatom cells undergoing division (supplementary material, Video 4). Over the course of a 1-s interval, the cells are flipped, as indicated by the directional arrows. This manipulation reveals the mechanical properties of dividing cells, including their structural stability and how they respond to external forces. The ability to rotate dividing cells without causing structural damage demonstrates the gentle yet precise nature of optical tweezers. The flipping is the result of translational movement with abrupt direction changes that were applied while the diatom lies on the coverslip surface. Due to the friction between the diatom and the substrate, rapid lateral movements of the trap cause the diatom to roll over.

Figures 4(a2)–4(d2) illustrate the stable trapping and extended manipulation of a single large diatom cell, whose relative immobility results from the fixed position of the optical trap at the center of the field of view, rather than from any displacement of the neighboring diatom (supplementary material, Video 5). The optical trap can also move independently of the imaging field of view, as shown in Figs. 4(a3)–4(d3) (supplementary material, Video 6). Figure S5 shows the trapping and manipulation of a small diatom cell. The observed flipping and movement of diatom cells also align with studies investigating cell mobility and structural adaptation. Previous research has shown that diatom frustules exhibit remarkable mechanical strength and flexibility,[22] which are crucial for their survival in dynamic aquatic

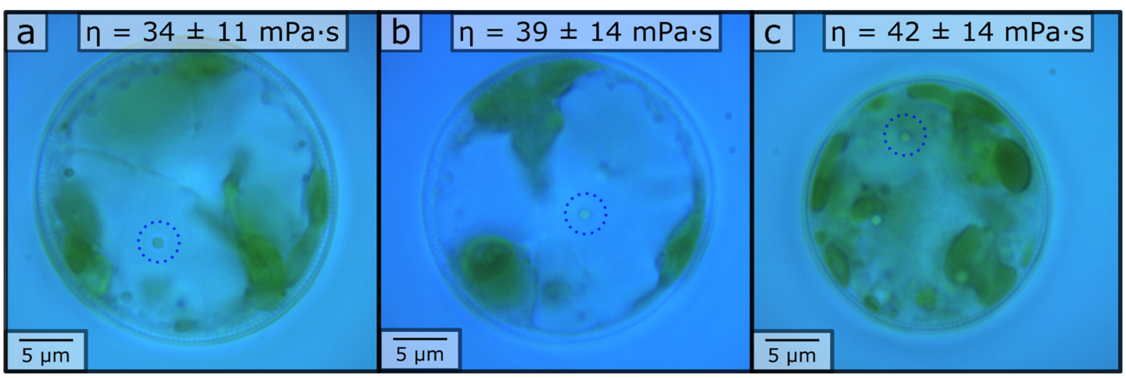

FIG. 3. Bright-field microscopy images showing optical trapping of chloroplasts inside *C. oculus-iridis* cells for intracellular viscosity measurements. Panels (a)–(c) show three different diatom cells, with dashed circles indicating the position of the trapped chloroplasts. The corresponding measured viscosity values (η) are indicated in each panel.

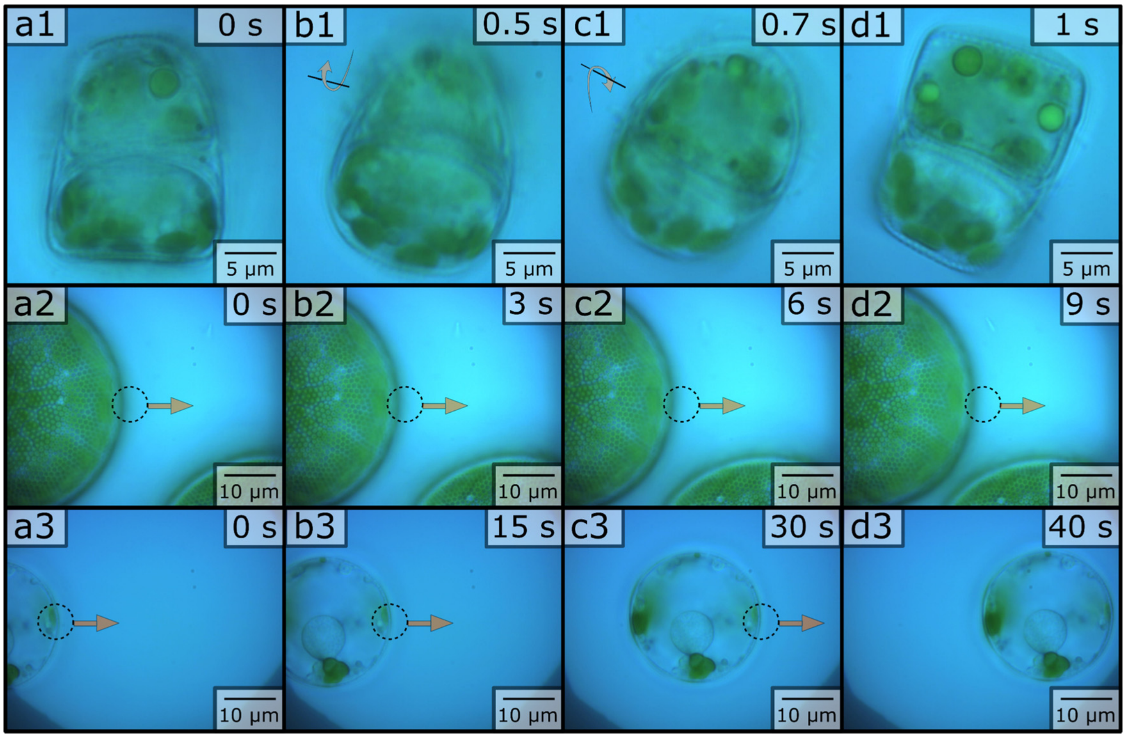

FIG. 4. Time-lapse bright-field microscopy images illustrating the manipulation of whole diatom cells using optical tweezers. Panels (a1)–(d1) present the side view of two diatom cells undergoing division. Over a 1-s interval (0, 0.5, 0.7, and 1 s), the cells are flipped, with arrows indicating the direction of rotation. Panels (a2)–(d2) display the trapping and movement of a single large diatom cell, captured at 0, 3, 6, and 9 s. The optical trap is immobile and located at the center while the cell movement is caused by the movement of the microscope stage. Panels (a3)–(d3) display the trapping and movement of a small diatom cell, captured at 0, 15, 30, and 40 s. The microscope stage is held fixed, and the movement of the cell occurs due to the displacement of the optical trap across the field of view. Dashed circles highlight the region where the optical trap is located, while arrows indicate the movement trajectory of the trapped cell.

environments. To experimentally evaluate cell integrity after exposure to the trapping and detection lasers, we performed viability assays using trypan blue staining; the methodology and results are described in the supplementary material and shown in Videos 7–10 of the supplementary material.

This study highlights the transformative potential of optical tweezers in advancing our understanding of diatom algae and their chloroplasts, providing valuable insights into intracellular dynamics and the optimization of photosynthesis. By effectively manipulating both individual chloroplasts and whole diatom cells, we demonstrated the capability of this tool to explore intracellular dynamics, photosynthesis optimization, and mechanical properties of diatoms. The observed motion of chloroplasts provides a deeper understanding of organelle positioning and intracellular interactions, with implications for enhancing light absorption efficiency in photosynthesis. Additionally, the study provided insights into the intracellular environment of diatom cells through viscosity measurements. Optical tweezers enabled measurement of intracellular viscosity across distinct cytoplasmic regions, revealing substantial variation driven by local structural density and differences between individual cells. These results contribute to the broader field of diatom research, bridging the gap between fundamental biology and applied sciences. The ability to study diatom cellular architecture and mechanical properties using optical tweezers without causing damage opens pathways for innovations in biomimetic materials, photonic devices, and environmental biotechnology.

See the supplementary material for details on materials and methods, TEM images of cell ultrastructure of *Coscinodiscus oculus-iridis*, time-lapse bright-field microscopy images showing the trapping and manipulation of a chloroplast within a small diatom cell, trapping potential and normalized autocorrelation analysis of chloroplast displacements, time-lapse bright-field microscopy images showing the trapping and manipulation of a small diatom cell, as well as chloroplasts for intracellular viscosity measurements, and experiments demonstrating the effect of optical trapping on diatoms and organelles.

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AUTHOR DECLARATIONS

Conflict of Interest

The authors have no conflicts to disclose.

Author Contributions

Evgeny S. Vavaev and Julijana Cvjetinovic contributed equally to this work.

Evgeny S. Vavaev: Formal analysis (equal); Investigation (equal); Methodology (equal); Visualization (lead); Writing – original draft (equal); Writing – review & editing (equal). **Julijana Cvjetinovic:** Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – original draft (lead); Writing – review & editing (lead). **Evgeny V. Lyubin:** Formal analysis (equal); Validation (equal); Writing – review & editing (equal). **Yekaterina D. Bedoshvili:** Investigation (supporting); Validation (supporting); Visualization (supporting); Writing – review & editing (equal). **Nickolai A. Davidovich:** Resources (supporting); Validation (supporting); Writing – review & editing (equal). **Pavlos Lagoudakis:** Supervision (equal); Validation (equal); Writing – review & editing (equal). **Andrey A. Fedyanin:** Resources (lead); Supervision (equal); Validation (equal); Writing – review & editing (equal). **Dmitry A. Gorin:** Funding acquisition (lead); Project administration (lead); Supervision (lead); Validation (equal); Writing – review & editing (equal).

DATA AVAILABILITY

The data that support the findings of this study are available within the article (and its supplementary material).

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