Can diatom girdle band pores act as a hydrodynamic viral defense mechanism?

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Received: 9 November 2018 / Accepted: 12 April 2019 / Published online: 28 May 2019
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Abstract

Diatoms are microalgae encased in highly structured and regular frustules of porous silica. A long-standing biological question has been the function of these frustules, with hypotheses ranging from them acting as photonic light absorbers to being particle filters. While it has been observed that the girdle band pores of the frustule of *Coscinodiscus* sp. resemble those of a hydrodynamic drift ratchet, we show using scaling arguments and numerical simulations that they cannot act as effective drift ratchets. Instead, we present evidence that frustules are semi-active filters. We propose that frustule pores simultaneously repel viruses while promoting uptake of ionic nutrients via a recirculating, electroosmotic dead-end pore flow, a new mechanism of “hydrodynamic immunity”.

Keywords Diatom frustule · Girdle band pores · Drift ratchet · Electroosmosis

PACS 05.40.-a · 87.10.Mn · 87.16.dp

1 Introduction

Diatoms are single-celled, photosynthesizing, microscopic algae [1] that surround their cell membrane with a rigid, porous, silica-based shell known as a frustule [2] (Fig. 1). They inhabit

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Fig. 1 Schematic of a generic centric diatom [3] – reproduced with permission of The Royal Society of Chemistry. The diameter of the frustule of *Coscinodiscus* sp. is in the range of approximately 80–150 μm [2, 4]

the upper layer of marine environments and experience large population blooms in the presence of sufficient sunlight and nutrients to facilitate photosynthesis [1].

Diatoms are classed as non-swimming phytoplankton, as, unlike their competitors (bacteria and other phytoplankton), they do not possess their own propulsion system to actively seek out nutrients or light [5]. This means that geophysical flows completely govern their movements and they spend the vast majority of their time in the more turbulent upper mixed layer/euphotic zone of aquatic environments [5, 6], as illustrated in Fig. 2.

The frustule of the centric diatom species, *Coscinodiscus* sp., is cylindrical and is comprised of two distinct porous regions; the valves and girdle band section, shown in Fig. 3a and b, respectively.

The girdle band is the mid-section of the frustule, whereas the caps of the cylinder are known as the valves. These two regions have distinctly shaped pores, the significance of which is not yet understood. One side of the girdle band pore is open to the surrounding ocean environment, while the other is bound by the diatom cell membrane (green membrane shown in Fig. 2). Among other proposed functions, it has been suggested that diatoms use their

Fig. 2 Different types of flow conditions experienced by pelagic diatoms from the macro- to nanoscale [3] – Reproduced with permission of The Royal Society of Chemistry

Fig. 3 SEM of the diatom, *Coscinodiscus waiselii*. **a** Valve structure and **b** girdle band structure

porous silica frustule to control, sort, and separate nutrients from harmful entities such as colloids, pollutants, poisons, and pathogens [4, 5, 7]. It has been suggested that the architecture of the frustule could play an important role with respect to such separation, yet the mechanism for this has not been identified. Losic et al. [8] recognized that the girdle band pores are geometrically similar to those of the *hydrodynamic drift ratchet* shown in Fig. 4a [9–11], suggesting that selective mass transfer could involve ratcheting. Consequently, this paper will focus on establishing whether these girdle band pores can act as an effective drift ratchet to filter nutrients from harmful entities like viruses. Losic et al. [8] did not identify the valve pores as being geometrically similar to a drift ratchet nor are they geometry similar to previously established drift ratchet pores, so only girdle band pores are investigated here.

A hydrodynamic drift ratchet is a series of ratchet-shaped axisymmetric pore units that are often placed in parallel to form a membrane (Fig. 4a) [9, 10, 11]. Under the action of oscillating fluid flow, each pore can generate rectified motion of micro-particles, even though there may be no net displacement of the fluid flow. These particles can migrate through the pore due to the combined effects of Brownian motion and particle-wall hydrodynamic interactions [9, 15, 16]. In the absence of comprehensive research into the elasticity of the cell membranes of diatoms, we may either assume that the cell membrane is elastically deformable or is rigid. In the unlikely latter case, the impervious (to water) cell membrane would form a dead-end channel through which fluid could not flow, preventing a drift ratchet mechanism. While in the former case, the impervious, deformable diatom cell membrane would allow zero-mean oscillatory fluid flow, and so could facilitate the drift ratchet mechanism.

The possibility of identifying the drift ratchet mechanism in diatoms is intriguing from both an engineering and biological perspective. Biologically, this would be the first identified example of a hydrodynamic drift ratchet in nature and will contribute a great deal to our understanding of how these microorganisms survive in their environment. Furthermore, there

Fig. 4 **a** SEM of a massively parallel silica membrane with asymmetric pores – reprinted with permission from *Nature* [11]. **b** SEM of girdle band pores of diatom *Coscinodiscus* sp. [8]. **c** SEM of girdle band pores of diatom *Coscinodiscus* sp. [12]. **d** SEM of girdle band pores of diatom *Coscinodiscus* sp. (scale unknown) – reproduced with permission of The Royal Society Interface [13]. **e** SEM of girdle band pores of diatom *Coscinodiscus* sp. – reprinted with permission from American Chemical Society [14]

is the potential to use this and future knowledge gained regarding drift ratchet mechanisms to improve the performance and efficiency of man-made separation and sorting devices [3]. Also, previously studied drift ratchet membranes are comprised of around 15–30 ratchet-shaped elements in series. Thus, these membranes are often analyzed by neglecting end effects and idealizing them as an infinite series of periodic elements. In contrast, the diatom frustule is comprised of a smaller (diameter and length), differently shaped single drift ratchet element, and so it is unknown whether such architecture can act as an efficient drift ratchet.

In this paper, we investigate whether the girdle band pores structure can act as an effective drift ratchet using the numerical model validated in Herringer et al. [17]. To accomplish this, we revisit data published by Kettner et al. [9], who detailed how the ratchet mechanism is dependent on microparticle size, and we compare this to the case of diatom girdle band pores. Next, in Section 3.2, we assess whether a single ratchet-shaped unit, bound by two basins, function as a drift ratchet. Then, in Section 3.3, we investigate the effect of a diminishing ratio between advective and diffusive transport of particles in a drift ratchet and compare this to the case of a diatom girdle band pore. We did not directly simulate the girdle band pore as the time step needed to resolve the particle–wall interactions was too small and, therefore, computationally expensive. Finally, we investigate another possible sorting mechanism that the diatom may use.

2 Drift ratchet versus girdle band pores

We shall first investigate the physical differences between the pores of the girdle band and those in a typical drift ratchet membrane (Fig. 4). We also identify the major oceanic processes that may cause oscillatory flows within the girdle band pores of diatoms in their natural aquatic environment, and the implications of these for particle sorting.

2.1 Difference in size, shape, and configuration of the pores

As shown in Fig. 5 and Table 1, both the typical diameter and length of a ratchet element within the diatom girdle band pore are smaller to those of the drift ratchet pores studied previously [9, 10, 11]. Furthermore, the girdle band pores have only one or two repeating units in series, which is significantly less than the 15–30 ratchet units in series for the massively parallel drift ratchet membrane shown in Fig. 4a. Given the small number of repeating ratchet units, all simulations conducted herein involve fluid oscillation with an amplitude equal to one repeating unit length (called $1 \times$ amplitude). This means that a parcel of fluid on the centerline of the pore traverses the length of one repeating ratchet unit over half a period of fluid oscillation [9]. This is consistent with past hydrodynamic drift ratchet studies [9–11, 17].

Table 2 goes a step further than a simple geometric comparison between pores and shows a functional comparison between what girdle band pores of a diatom in a typical oceanic environment could experience and a previously studied hydrodynamic drift ratchet. The geometry of both pores is shown in Fig. 5. As mentioned previously, this comparison is made

Fig. 5 Schematic of the pore profile of **a** a typical drift ratchet studied by Kettner et al. [9] and **b** girdle band pore of *Coscinodiscus* sp. **c** Girdle band pore dimensions. All dimensions are in micrometers

Table 1 Comparison of the pore dimensions and parameters between the drift ratchet studied by Kettner et al. [9] and Matthias, Muller [11] and a girdle band pore

Geometric feature	Drift ratchet	Girdle band
Max. diameter	$\approx 4 \mu\text{m}$	$\approx 0.25 \mu\text{m}$
Min. diameter	$\approx 1.5 \mu\text{m}$	$\approx 0.1 \mu\text{m}$
Length of a repeating unit	$6 \mu\text{m}$	$0.5 \mu\text{m}$
No. of repeating units in series	17–33	1–2

using $1 \times$ amplitude fluid oscillation, with a similar particle-to-pore ratio and oscillation period for both cases. One notable difference is the smaller Péclet number for the girdle band pore, which indicates that the transport of a typical particle is dominated by diffusion rather than advection. We will discuss this comparison further in Section 3.3.

2.2 Fluid oscillation

Hydrodynamic drift ratchet pores use an oscillating fluid flow to achieve rectified particle transport. For diatom girdle band pores to act as a hydrodynamic drift ratchet, they must also experience a similar fluid oscillation. As the diatom cell membrane is assumed to be elastically deformable, such zero-mean oscillations can arise if oscillatory pressure fluctuations occur at the pore entrance. There are two main mechanisms that can generate such pressure fluctuations in the upper ocean: (i) turbulent fluctuations in the upper oceanic flow and (ii) pressure fluctuations arising from Jeffery orbits [18] of the diatom in this flow due to its elongated shape. There is the possibility of another source of fluid oscillations being acoustic pressure fluctuations in the ocean from wave movement [19], however this was not investigated in this study. To quantify the previously noted pressure fluctuations, we first assume that the timescales of the turbulent fluctuations (τ) and Jeffery orbit (T_{JO}) are separable for a linear shear field. In the case $T_{JO} \ll \tau$ fluctuations from the Jeffery orbits dominate behavior of the diatom, whereas if $T_{JO} \gg \tau$ then fluctuations due to turbulent eddies dominate.

To describe the typical geophysical fluid flow a diatom experiences, we consider the turbulence structure of the upper ocean flow. Geophysical turbulence in the upper ocean comprises superposed eddies of different sizes that are driven by unsteady forces including wind, currents, and waves [20]. The smallest eddy size is inversely proportional to the intensity of the turbulent kinetic energy [21], as characterized by the Kolmogorov length-scale η [22]:

$$\eta = \left(\frac{\nu^3}{\varepsilon} \right)^{\frac{1}{4}}, \quad (1)$$

Table 2 Comparison between parameters for a drift ratchet [9] and girdle band pores

	Drift ratchet [9]	Girdle band pore				
Period (s)	0.025	0.002	0.025	0.3	1	
Total number of fluid oscillations in 100 s	4000	50,000	4000	333	100	
Minimum pore diameter (μm)	1.58	0.1	0.1	0.1	0.1	
Thermal diffusion coefficient (μm ² s ⁻¹)	0.598	14.5	14.5	14.5	14.5	
Particle diameter (μm)	0.7	0.03	0.03	0.03	0.03	
Length of repeating units (μm)	6	0.5	0.5	0.5	0.5	
Ratio of particle diameter to minimum pore diameter	0.44	0.3	0.3	0.3	0.3	
Péclet number	4800	17	1.4	0.11	0.034	

where ν is the kinematic viscosity ($\text{m}^2 \text{s}^{-1}$) and ε is the kinetic energy dissipation rate ($\text{m}^2 \text{s}^{-3}$). Energy dissipation in the open ocean typically ranges from $10^{-5} \text{ m}^2 \text{s}^{-3}$ in the upper mixed layer of the ocean for wind speeds of $15\text{--}20 \text{ ms}^{-1}$, to $10^{-9} \text{ m}^2 \text{s}^{-3}$ in deeper parts [23]. From Eq. (1), the length-scale of the smallest eddies ranges between 1 and 10 mm [21, 24]. Some parts of the ocean reach an energy dissipation of approximately $10^{-4} \text{ m}^2 \text{s}^{-3}$ [25], where the Kolmogorov length drops to $300 \text{ }\mu\text{m}$. Below the Kolmogorov length-scale, the smallest eddies are dominated by viscous forces and thus the local flow can be described as a linear shear flow, with eddies transferring energy as heat via viscous dissipation [22]. As the size of even the smallest eddies is significantly larger than a typical diatom size ($\approx 150 \text{ }\mu\text{m}$), all diatoms in the upper ocean experience a locally laminar flow, which is well described as a local shear flow as illustrated by the linear velocity profile shown in Fig. 2 [3, 21, 26]. This velocity field can lead to translation and rotation of the diatom, which in turn could drive pressure fluctuations that lead to ratcheting in the girdle band pore. The time-scale of this laminar flow field is described by the Kolmogorov time [26–28]:

$$\tau = 2\pi \left(\frac{\nu}{\varepsilon} \right)^{\frac{1}{2}}, \quad (2)$$

which characterizes the correlation time of a local shear field until a new one is generated with a new magnitude and direction [28–30]. From the values above, the correlation time of a Kolmogorov eddy shear field in the ocean ranges over $0.6\text{--}200 \text{ s}$.

Prolate spheroids (like diatoms, as shown in Fig. 1) within a linear shear field undergo tumbling motions, known as a Jeffery orbit, in conjunction with a periodic translation (Fig. 6) [31, 32]. The unsteady linear shear field generated from the turbulence in the Upper Ocean can cause diatoms to undergo motion similar to a Jeffery orbit. The fluid flow resulting from these pressure fluctuations is viscous dominated (Stokesian, with very small Reynolds number $Re \approx 0.005\text{--}0.1$), hence these periodic flows respond instantaneously to the external forcing. Due to the unsteady nature of this flow as described by Eq. (2), diatoms will experience a variant of a Jeffery orbit. Pahlow et al. [31] comment that a prolate spheroid approximation for the representation of centric and pennate species of diatom in a shear flow experiencing Jeffery orbits is appropriate.

Fig. 6 Positional trajectory of a prolate spheroid within a linear shear field termed a Jeffery orbit [31]. This schematic shows two positions of the spheroid with the Jeffery orbit. The spacing of the black dots around the orbit represent the particle speed, with larger spacings indicating higher speed

The period of this orbit is then [21, 32]

$$T_{JO} = \frac{2\pi}{G} (r_a + r_a^{-1}), \quad (3)$$

where r_a is the aspect ratio (major to minor axis or minor to major axis) of the diatom cell and G the fluid shear rate. The characteristic shear rate in a Kolmogorov eddy is

$$G = \left(\frac{\varepsilon}{\nu} \right)^{\frac{1}{2}}, \quad (4)$$

which ranges from 0.5 to 12 s⁻¹ [23] in the upper ocean. For a typical diatom aspect ratio of $r_a = 0.5$, the period of orbit T_{JO} range over ≈ 1.3 –30 s. This rotational motion, in combination with the intermittency of the shear field in upper ocean turbulence, generates fluctuations in the local velocity and pressure fields at the diatom surface [31]. As shown in Fig. 7, for all considered values of energy dissipation rates the orbit period, T_{JO} , is much larger than the residence time of the linear shear field, τ , and therefore intermittency of the shear field provides the dominant fluctuations relevant for diatoms.

Another mechanism that could cause pressure fluctuations in diatom pores is gravitational settling through the water column. Diatoms can self-regulate their buoyancy in response to external signals, as well as forming chains and growing spines to alter their sinking rates [7, 33]. Many studies [34–37] have investigated the bulk sinking rates of larger diatoms, however experiments by Gemmell et al. [38] have shown that diatom sinking is a dynamic process, and that larger diatoms control their instantaneous descent rate to within 200–300 ms. Gemmell et al. [38] observe variations in the instantaneous sinking rate in the range 10–750 μms^{-1} for *Coscinodiscus waiselii* depending on nutrient depletion/repletion. This instantaneous change in sinking rate could be a source for pressure fluctuations driving a drift ratchet through the girdle band pores. In the following section, we assess the propensity for these mechanisms inducing pressure fluctuations to impart rectified particle motion in the girdle band pore.

Fig. 7 Relationship between Jeffery orbit period and the correlation time for turbulent linear shear field for various aspect ratio of diatom. The red shaded section represents aspect ratios where the period of the Jeffery orbit is dominant over the correlation time for turbulent shear

3 Results / Discussion

3.1 Effect of particle size on drift ratchet performance

To determine whether the girdle band pores of a diatom could operate as a hydrodynamic drift ratchet, we assess the effect of particle size on the performance of a drift ratchet and apply these results to the case of a diatom girdle band pore. Figure 8 shows the magnitude of the drift velocity of particles in a drift ratchet as a function of the ratio of particle size to minimum pore diameter, with a maximum around a ratio of 0.35. For very small particles (corresponding to negligible Péclet number Pe), diffusion dominates over advection, and so the relatively weak advective flow leads to reduced particle drift. Conversely, as the particles increase in size relative to the pore, they reach a physical limit of the minimum pore diameter and cannot travel through the drift ratchet. Even in the absence of this restriction, in the limit of very large Pe , the motion of a particle is almost fully reversible along a streamline over one flow period and hence no drift occurs. As such, maximum drift occurs between these limits, and in Fig. 8 we observe significant rectified transport over the diameter ratio 0.2–0.6.

These results can then be applied to the range of particles encountered by diatoms in their environment. Diatoms live in the euphotic zone of marine environments and uptake/process inorganic nutrients and trace elements required for a variety of differing cell functions, as outlined by Rosengarten and Herring [39].

In ionic form, these chemical species move through the pores of the silica frustule before being taken up by the cell membrane [40]. The size of these ions is typically 1–2 nm, yielding a ratio of ion to minimum pore diameter (~ 100 nm) over the range ≈ 0.01 –0.02 (Table 1). The predicted drift velocity of these nutrient and elements is negligible, as depicted by the thin green band in Fig. 8. Diatoms are also exposed to harmful entities such as viruses, bacteria, pollutants, and poisons. The typical size of viruses which can infect diatoms are of the order of 25–220 nm [41], corresponding to a particle to pore size ratio of 0.25–2.2 (red band in Fig. 8), and of these particles with size ratio in the range 0.25–0.7 could experience significant drift. While the analysis above is based upon the assumption of drift ratchet comprised of an infinite number of ratchet-shaped pore units in series, diatom girdle and pores are typically comprised of only 1–2 ratchet-shaped units in series. We shall assess the impact of such finite numbers of units in the following Section.

Fig. 8 Effect of particle size on drift velocity data from Kettner et al. [9] for a drift ratchet with fluid oscillations of 40 Hz and fluid viscosity that of water. *Red* Ratio of typical virus size to minimum girdle band pore diameter. *Green* Ratio of nutrient ions to minimum girdle band pore diameter. The negative drift velocity represents the direction through the pore the particles are drifting with the coordinate system defined in Fig. 5

3.2 Particle drift in a single ratchet pore

To determine whether the single ratchet-shaped unit in the girdle band pores can produce significant particle drift, we performed a 2D planar simulation of particle transport in single ratchet-shaped element between two infinite fluid reservoirs. A zero-mean oscillating flow was imposed between these reservoirs (Fig. 9) and the pore shape was the same as that of a typical drift ratchet (Fig. 5a).

The oscillatory fluid velocity $v_{fluid}(\mathbf{x}(t), t)$ in the ratchet pore is solved via the computational fluid dynamics (CFD) package COMSOL. From this flow field, we model evolution of the position $\mathbf{x}(t) = (x(t), z(t))$ of a particle (where $x(t)$, $z(t)$, respectively, are the longitudinal and transverse directions) within the pore via the stochastic Langevin equation

$$\frac{d\mathbf{x}}{dt} = v_{fluid}(\mathbf{x}(t), t) + \boldsymbol{\eta}(t), \quad (5)$$

where $\boldsymbol{\eta}(t) = \sqrt{2D_{fs}}\boldsymbol{\gamma}$ [9] represents Brownian motion. Here $\boldsymbol{\gamma}$ is a delta-correlated Gaussian white noise, which satisfies $\langle \gamma_i(t) \rangle = 0$ and $\langle \gamma_i(t)\gamma_j(t') \rangle = \delta(t-t')\delta_{ij}$ [9], and D_{fs} is the free space particle diffusion coefficient

$$D_{fs} = \frac{k_B T}{6\pi\mu R}, \quad (6)$$

where k_B is the Boltzmann constant, T is the temperature, μ is the dynamic viscosity and R is the particle radius. Following earlier studies [9, 16, 17], the particle–wall interactions are modeled via an elastic ballistic reflection condition. While the detailed particle–wall hydrodynamics are not captured by this boundary condition, we have shown [17] that this qualitatively captures the action of the pore wall in generating rectified particle motion.

All particles were initially placed at the left opening of the pore, and the flow cycle was such that the initial fluid velocity was from left to right in Fig. 9. The magnitude of the fluid oscillation was such that a fluid element along the pore centerline traversed one pore length over a complete cycle of the oscillating flow. To identify whether a finite single ratchet-shaped

Fig. 9 Schematic of the numerical simulation of the finite drift ratchet pore, bound by two basins

pore will exhibit particle drift, we compare its performance to that an infinite two-dimensional pore (with all other properties the same) and two-dimensional finite straight pore (Fig. 10).

To quantify particle transport in these geometries, we compute the ratio of axial dispersion D_e to the free space particle diffusion coefficient

$$\frac{D_e}{D_{fs}} = \frac{\left[\frac{\langle z^2(t_{run}) \rangle - \langle z(t_{run}) \rangle^2}{2t_{run}} \right]}{D_{fs}}, \quad (7)$$

and the average drift velocity

$$v_e = \frac{\langle z(t_{run}) \rangle}{t_{run}}, \quad (8)$$

and the results are summarized in Table 3. Here $z(t_{run})$ is the axial displacement of a particle along the axis of the drift ratchet pore over time t_{run} , and the angled brackets represent an ensemble average over 100 simulations of different particles.

As expected, we do not observe particle drift in the straight-walled pore due to symmetry of the geometry and reversibility of Stokes flow. Moreover, the pore comprising of only one ratchet unit does not exhibit significant drift velocity, indicating it is unlikely that the girdle band pores can act as a drift ratchet, or for that matter the pores of a diatom frustule valve. In the following section, we further test this conclusion by considering the impact of Péclet number upon the drift mechanism.

3.3 Effect of Péclet number on drift

In a previous study [15], we established that the ratchet mechanism is effective over a finite range of Péclet number (Pe), which defines the relative timescale of advection to diffusion. As discussed in Section 3.1, particle drift does not occur in either limits of very large or small Péclet number, and so we observe maximum particle drift at a finite Péclet number between

Fig. 10 **a** Finite two-dimensional and **b** infinite two-dimensional hydrodynamic drift ratchet pore. **c** Finite two-dimensional straight pore

Table 3 Drift velocity and ratio of effective to free-space diffusion coefficient for the case of a 2D finite drift ratchet and straight-walled pores bound by two basins. Compared to an infinite two-dimensional drift ratchet pore

	A. Finite 2D drift ratchet	B. Infinite 2D drift ratchet	C. Finite 2D straight pore
D_e/D_{fs}	1.2	5.0	1.3
v_e ($\mu\text{m s}^{-1}$)	9×10^{-4}	- 0.24	6×10^{-3}

these limits. We have simulated an infinite drift ratchet pore over a range of Péclet numbers and compared these values to those characteristic values in a girdle band pore in marine environments as summarized in Table 2. The shape of the drift ratchet pore modeled is shown in Fig. 5. We define the Péclet number as

$$Pe = \frac{VL}{D_{fs}} \quad (9)$$

where the mean particle velocity $V = 2L/T_{ff}$ and L is the fluid displacement along the pore axis over half a period of fluid oscillation $T_{ff}/2$. In addition to the free-space diffusivity D_{fs} , we also consider a spatially varying diffusion coefficient D_{hyd} , which accounts for the reduced particle mobility due to hydrodynamic lubrication forces as the particle approaches the pore wall Herringer et al. [17]. As shown in Fig. 11, our computations confirm the hypothesis that there exists a finite Péclet number that maximizes drift velocity, and the drift mechanism is significant only at intermediate values of Pe .

As shown in Fig. 11 and Table 2, the characteristic Péclet numbers in a girdle band pore (green-shaded area of Fig. 11) are several orders of magnitude smaller than those that generate significant particle drift. These results indicate that under normal conditions in the upper ocean, mass diffusion within the girdle band pore is too fast for diatoms to use the drift ratchet mechanism to sort and separate particles. These results, along with those from Section 3.3, indicate that it is highly unlikely that the diatom girdle band pores can effectively utilize the drift ratchet mechanism.

The finding that the diatom girdle band pores of *Coscinodiscus* sp. cannot use the drift ratchet mechanism to selectively transport matter can be expanded to other species of diatom, and to different pore structures in the frustule (e.g., valve pores) using the Péclet number. The

Fig. 11 Relationship between the Péclet number and the drift velocity (yellow points) from computational simulations of particle transport in a drift ratchet. The green-shaded area represents the approximate range of Péclet numbers experienced by a 30-nm-sized particle in a diatom girdle band pore in the upper ocean

small scale of frustule pores presented in Table 4 means that variations in pore shape between different areas of the same diatom frustule and variations between diatom species will still experience a low Péclet number. This low Péclet number means diffusion dominated particle-fluid flow, which is not conducive for generating a drift ratchet. Furthermore, a lack of repeating pore units in series also mean significant drift is not possible in the girdle band pore. As such, we conclude that it is highly unlikely that the diatom girdle band pore acts as a hydrodynamic drift ratchet to filter out pathogens and viruses from nutrients.

3.4 Hydrodynamic immunity

Given the findings above, we seek another explanation for the highly ordered structure of the diatom frustule. There have been many proposed explanations for the unique architecture of the diatom frustule, including: increasing or decreasing sinking rates through the water column [50, 7]; providing defense against predators, parasites and pathogens [7, 51, 52]; providing an acid-base buffer site for the catalysis of carbonic anhydrase [53, 54]; protecting sensitive organelles against damage from UV-A and UV-B exposure, scattering or focusing photosynthetic active radiation [55–58, 8, 59–65]. Other less familiar proposed functions include: countering the turgor pressure generated by the cell; helping to facilitate reproduction processes [2] and acting as a passive barrier, controlling, sorting and separating matter by acting as a filter [8]. These functions provide the diatom with advantages, so it can grow and survive in its environment. The sentence should read "However, none of these proposed functions have been confirmed and so the reason for the distinct shape of girdle band pores, and in a wider sense the configuration and architecture of the porous frustule, is still unknown.

The proposed hypothesis that girdle band pores operate as a hydrodynamic drift ratchet was originally suggested due to their geometric similarities [8], such that this mechanism allowed the diatom to separate and control the transport of nutrients towards the frustule while keeping deleterious entities away. However, our analyses in Sections 3.2 and 3.3 suggest that it is highly unlikely that girdle band pores operate as a hydrodynamic drift ratchet.

Considering these findings, we propose an alternate explanation for the girdle band pore shape that promotes the uptake of carbon dioxide into the frustule while excluding viruses.

Table 4 General pore sizes (valve and girdle band pores) across four diatom species and their corresponding Péclet numbers, using Eq. (9) assuming $T_H = 0.025$ s and $D_g = 14.5 \mu\text{m}^2 \text{s}^{-1}$ [4, 14, 42–49]

	<i>Rhizosolenia setigera</i> [42,43]	<i>Coscinodiscus</i> sp. [44–46,4,14]	<i>Thalassiosira eccentrica</i> [44,4,47]	<i>Aulacoseira</i> sp. [48,14,49]
Pore length (L)	≈ 91 nm	≈ 5 nm – 2 μm	≈ 8 – 200 nm	≈ 400 – 500 nm
Average Péclet number (Pe)	0.046	0.00014 – 22	0.00035 – 0.22	0.88 – 1.4
Images (citations adjacent to diatom species name)

Whilst viruses that could infect diatoms range in size from 25 to 220 nm [41], the minimum diameter of girdle band pores is ≈ 100 nm, hence there is a chance of infection from such small pathogens. Recent studies into the mechanics of diffusiophoresis and diffusioosmosis [66–68] in dead-end micro-channels [69–71] indicate that significant flows can arise in such geometries under appropriate conditions. As illustrated in Fig. 12, we hypothesize that electroosmosis arising from a concentration gradient of bicarbonate ions [69] between the fluid bulk and cell membrane can generate a significant recirculating flow within the girdle band pore. The concentration gradient induces an electric field resulting from the different tangential diffusion and convection fluxes of ionic pairs [72]. This flow simultaneously promotes carbon dioxide uptake within the frustule, while excluding larger viruses. We term this mechanism of virus defense, “hydrodynamic immunity”, as it originates from recirculating fluid flow through a dead-end pore resulting from electroosmosis. Regardless of the assumptions that the cell membrane is either elastically deformable or static, both allow recirculating flow to occur as a result of electroosmosis, however the effect of a deformable cell membrane on the electro-osmotic mechanism is not investigated in this paper.

As illustrated by Fig. 13, if the thickness of the inflow band (d), at the end of the girdle band pore that is open to the aquatic environment, is smaller than the diameter of a virus, then the virus is unlikely to enter the pore. However, the smaller bicarbonate ion species, may still enter the pore through the inflow region. These bicarbonate ions will be converted to carbon dioxide by an external carbonic anhydrase near the cell membrane [54, 73–78], which will then diffuse across the cell membrane to be used for photosynthesis.

The continual uptake of ions at the diatom cell membrane end of the girdle band pore maintains a concentration gradient along the pore, leading to electroosmosis.

Next, we discuss electroosmotic flow being induced in a diatom girdle band pore in more detail. As diatoms live in a soup of ions in the upper ocean, a high density of charged ions form an electric double layer (EDL) adjacent to the negatively charged amorphous silica of the girdle band pores shown in Fig. 12. The thickness of this layer is characterized by the Debye length κ^{-1} [79].

$$\kappa^{-1} = \sqrt{\frac{\epsilon_r \epsilon_0 k_B T}{\sum_i C_i^\infty (z_i e)^2}}, \quad (10)$$

The diagram illustrates a cross-section of a girdle band pore. On the left, a vertical line represents the 'Cell membrane / Sink'. The pore itself is a horizontal channel. An arrow labeled 'Electric Field' points from the right towards the left. A dashed line indicates the 'Inlet/outlet' region. A 'Virus' is shown as a yellow circle being excluded from the pore. A 'Surface charge' is indicated on the membrane. A legend on the right identifies the 'Concentration of bicarbonate ions (HCO₃⁻) and protons (H⁺)' and the 'Electric Double Layer (EDL)'. The EDL is shown as a layer of positive charges (red dots) near the negatively charged membrane (blue line).

Fig. 12 Schematic of a generic electroosmosis case, induced by an ionic concentration gradient, for a dead-end girdle band pore [39]

Fig. 13 Schematic of the cross section of the inlet/outlet of the girdle band pore illustrated in Fig. 12. Inflow is represented by the horizontal hatching, while outflow is represented by the vertical hatching. “V” represents a virus, while “C” represents a carbonate ion

where ε_r is the dielectric constant of the fluid, ε_0 is the permittivity of a vacuum, k_B is the Boltzmann constant, T is the temperature, C_i the concentration of ionic species i , e is the charge of an electron and z_i is the valence of the ionic species i . Under typical conditions in the upper ocean, from Eq. (10) we estimate the thickness of the electric double layer to be of the order 1 nm. The EDL would therefore account for 4% of the girdle band pore minimum diameter (≈ 50 nm), hence the EDL may be considered infinitesimal [80].

To our knowledge, diatoms do not actively generate an external electric field that could interact with the EDL to generate fluid flow along a charged surface via electroosmosis. Rather, consumption of ionic species across the cell membrane produces a concentration gradient of ions from the bulk, passively inducing an electric field. This electric field is tangential to the concentration gradient and is driven by the difference in the diffusivity of two oppositely charged ion species diffusing down a concentration gradient while ensuring electro-neutrality [70, 81, 71, 69]. Bicarbonate (HCO_3^-) and protons (H^+) are expected to be the main ionic species in diatoms to contribute to this electric field, as they will be consumed at the cell membrane via conversion to carbon dioxide by the external carbonic anhydrase. However, further investigation into this theory may provide further insights into different ionic species responsible for this flow. As the girdle band pore is partially blocked by the cell membrane, fluid advection due to electroosmosis and chemiosmosis creates an annular recirculating flow as depicted in Fig. 12. Based on this mechanism, we proposed that the outflow in the centre of the pore helps keep viruses out of the frustule.

To test this hypothesis, we model electroosmotic flow in a girdle band pore and qualitatively evaluate the contribution of this flow to the expulsion of viruses. The electroosmotic flow in the pore is governed by Stokes flow driven by the electrostatic gradient $\mathbf{E} = -\nabla\psi$ (where ψ is the electrostatic potential [81]) arising from the interaction of the concentration gradient with the EDL:

$$\mu\nabla^2\mathbf{u} - \nabla p + \rho\mathbf{E} = 0 \quad (11)$$

$$\nabla \cdot \mathbf{u} = 0 \quad (12)$$

Here $\rho = (C_+ - C_-)Ze$ is the local space charge density, C_+ and C_- respectively are the local concentration of positive and negative ions, and from Coulomb's law $\nabla \cdot \mathbf{E} = 4\pi\rho/\varepsilon$, where ε is the permittivity of the fluid [81]. These equations can be combined to form Poisson's equation

$$\nabla^2 \psi = 4\pi(C_+ - C_-)Ze/\varepsilon \quad (13)$$

which describes distribution of the electrostatic potential. The advection-diffusion of an ionic species is then

$$\frac{\partial C_i}{\partial t} + \nabla \cdot \left(-D \nabla C - D \frac{Z_i e C_i}{kT} \nabla \psi + \mathbf{u} C \right) = R \quad (14)$$

$$D = \frac{2D_+ D_-}{D_+ + D_-}, \quad (15)$$

where D_+ and D_- are the particle diffusion coefficients of positive and negative ions, respectively, while R is a sink/source term.

In principle, Eqs. (11–15) must be solved to resolve the electric double layer after applying appropriate boundary conditions. However, this is both numerically intensive and unnecessary for an EDL of negligible thickness. In this case, the Helmholtz–Smoluchowski approximation [82] for an infinitesimally thin EDL may be implemented, which approximates the electroosmotic slip velocity over the EDL (hence alleviating the need to resolve the velocity profile within the EDL) as

$$\mathbf{u}_{Electro} = -\frac{\varepsilon_r \varepsilon_0 \zeta}{\mu} (\mathbf{E} - (\mathbf{E} \cdot \mathbf{n}) \mathbf{n}), \quad (16)$$

where ζ is the surface zeta potential.

Fig. 14 Contours of velocity magnitude and velocity vectors when osmotic flow is applied to a dead-end girdle band pore. From left to right the surface charge density is increased from 0.01 V/m to 10 V/m and applied to the pore wall

To determine the magnitude of electroosmotic flow in the girdle band pore and the significance of the proposed mechanism, we use the finite-element package COMSOL to solve for the slip velocity in Eq. (16) and then solve the Stokes flow equation. Figure 14 shows model predictions of the flow in an axisymmetric girdle band unit (shown in Fig. 5b) generated by the electroosmotic slip velocity (Eq. 16), while the pore dead-end was modeled as a no-slip boundary. The bottom boundary represents the pore entrance that was modeled as an open boundary to correctly resolve the mixed inflow and outflow boundary condition.

The results presented in Fig. 14 show that over the range of surface charge density modeled, the thickness of the inflow area is approximately constant. As the size of the smallest relevant viruses are of the order of 25 nm, therefore the ≈ 15 -nm-thick inflow section in Fig. 14 may be too small for a virus to enter the frustule. We must however acknowledge that our simulation does not consider the electric field generated from an ionic concentration gradient through the pore. Rather, we assume a constant surface charge density over the pore wall and apply the Helmholtz–Smoluchowski approximation to determine the slip velocity. In reality, the diatom induces an electric field through the generation of an ionic concentration gradient and future work would have to capture this.

As shown in Fig. 14, a localized recirculation region in the electroosmotic flow arises due the bulged shape of the girdle band pore. This localized region could be used as a vortical trap [83] to further retard uptake of viruses into the pore membrane, however further work is required to clearly elucidate and quantify the efficacy of this mechanism.

It is widely understood that an organic coating covers the surface of the silica frustule [84–86]. It is unknown how this coating could affect the presence of electroosmotic flow within the girdle band pore, or whether diatom can actively control this layer to control the magnitude of electroosmotic flow if present in the frustule pores.

To assess the prevalence of electroosmotic flow within the girdle band pore, we conduct an order of magnitude analysis of the relevant quantities. The uptake of ionic species by the diatom cell—whether nutrients for cell growth and repair or bicarbonate ions to facilitate photosynthesis—generates a concentration boundary layer around the diatom cell. As shown in Fig. 12, the boundary layer extends from the cell surface in through the girdle band pores over multiple cell radii into the cell's aquatic surroundings. Generally, for an osmotroph without a porous frustule, the diffusion-limited steady-state concentration profile over this boundary layer is [24, 28, 33].

$$\frac{(C(r)-C_0)}{(C_\infty-C_0)} = \frac{\left[\frac{r_0}{r}(C_0-C_\infty)\right] + C_\infty-C_0}{C_\infty-C_0}, \quad (17)$$

where r_0 and r are the cell radius and radial position respectively and $C(r)$, C_∞ and C_0 respectively are the species concentration at position r , in the bulk and at the cell surface [87]. For simplicity, the concentration gradient was assumed to be unaffected by the presence of the frustule. Future work would have to account for hindered diffusion through the diatom frustule to get a more accurate concentration gradient. Assuming spherical symmetry and the diffusion coefficient of ionic species is $D = 1 \times 10^{-11}$, the change in non-dimensional concentration over the thickness of a girdle band pore (≈ 700 nm) is 1.4×10^{-2} . This corresponds to a concentration gradient of 44 kmol/m^4 if the ambient ion concentration is 2.2 mol/m^3 and concentration at the cell surface is 0 mol/m^3 , assuming a perfect absorber cell [24, 28]. Keh and Ma [68] have specified that for an infinitesimal EDL, electroosmotic flow in an electrolyte solution with a concentration gradient of the

order of 100 kmol/m^4 along a surface with a zeta potential of $\approx 25 \text{ mV}$, (similar magnitude to the surface of a diatom girdle band pore [88]) results in a boundary flow of several micrometers per second. This supports the contention that the girdle band pores can generate electroosmotic flows of sufficient magnitude to warrant further detailed investigation into the validity of this mechanism as a method for effectively preventing viruses from entering the pores. If diffusioosmotic flows can occur for a concentration gradient of the order of 100 kmol/m^4 along a surface with a zeta potential of $\approx 25 \text{ mV}$, then there is a real possibility that the diatom case of 44 kmol/m^4 and a zeta potential of around 50 mV could give significant fluid flow relative to the size of the girdle band pore.

The transport phenomena; electrophoresis, chemiphoresis and chemiosmosis, may also be important but are beyond the scope of this paper.

4 Conclusions

Due to their resemblance to an engineered hydrodynamic drift ratchet, it has previously been postulated [8] that the girdle band pores of the diatom *Coscinodiscus* sp. could be the first example of a hydrodynamic drift ratchet in nature, and that this diatom uses this mechanism to prevent viruses from crossing the pore membrane. In this study, we have quantitatively shown that it is highly unlikely that the girdle band pores act as a drift ratchet, despite the fact that a hydrodynamic drift ratchet based on the girdle band pore geometry can generate rectified particle motion. We find this mechanism does not yield significant rectification in diatom girdle band pores because (i) the girdle band pore is so small that diffusive transport dominates over advection, rendering the ratchet mechanism ineffective, and (ii) the single ratchet-shaped pore unit present in the diatom frustule cannot generate significant particle rectification, whereas an infinite series of such pores can. Instead, we propose that the function of the highly ordered diatom girdle band pore is to use electroosmotic flow to provide protection against the uptake of viruses whilst promoting uptake of nutrients and trace elements. We have termed this mechanism *hydrodynamic immunity*. Basic numerical simulations and scaling arguments support this hypothesis, however more comprehensive experimental and computational analysis of the girdle band pores is required for complete validation. This represents a significant body of work, as the detailed interactions between the diatom frustule and their surrounding hydrodynamic, electrostatic and thermal environments are not yet clearly understood.

Acknowledgements J. G. Mitchell, from Flinders University, was instrumental in biological concepts in this manuscript and help draft the manuscript.

Author's contributions J. W. Herringer carried out the numerical modeling, participated in data analysis and drafted the manuscript; G. Rosengarten participated in numerical modeling, formulating the direction and concept of the paper, and drafted the manuscript; D. Lester participated in numerical modeling, formulating the direction and concept of the paper, and drafted the manuscript; G. E. Dorrington participated in formulating the direction and concept of the paper and drafted the manuscript.

Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflicts of interest.

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