

1 **Effects of cell motility and morphology on the**
2 **rheology of algae suspensions**

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7 **Abstract** Algae have been proposed as a source of biofuels and high value
8 chemical products, but if this potential is to be fully realised, it is crucial to
9 understand the factors affecting the suspension rheology. Suspensions of three
10 algae species, *Tetraselmis chuii*, *Chlorella sp.* and *Phaeodactylum tricoratum*,
11 were sheared in a rotational rheometer in order to characterise their rheology
12 and examine the effects of cell concentration, motility and morphology. The
13 volume fraction ranged from 0.05 to 0.2, and the shear rate from 20 to 200 s⁻¹.
14 The rheology measurements are fitted to the Herschel-Bulkley model, and the
15 intrinsic viscosity is estimated using both Einstein's equation and the Krieger-
16 Dougherty model, which are found to perform well for low concentrations.
17 The intrinsic viscosity of *T. chuii* suspensions is shown not to be constant,
18 but decreases with strain rate, indicating that the suspension viscosity is less
19 sensitive to the cell concentration at high strain rates. The rate of decline is
20 constant for strain rates below approximately 100 s⁻¹, after which it continues
21 to decline linearly but at a slower rate. It is speculated that this transition at

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100 s⁻¹ is related to the appearance of flocculation at low strain rates. The effect of the cell motility on the rheology of *T. chuii* suspensions is investigated by comparing the rheology of motile and passive cells. The shear-thinning behaviour is absent and the effective viscosity is considerably lower for the passive cell suspensions, indicating that the motility of the *T. chuii* cells causes them to align to resist the flow. In contrast, the *C. sp.* suspensions exhibit shear-thickening behaviour, which has not previously been reported. Finally, the influence of the effective aspect ratio on the cell suspensions is examined by comparing the intrinsic viscosity of all three species. The algal species with the largest aspect ratio, *P. tricornutum*, has the largest intrinsic viscosity, while the smallest aspect ratio strain, *C. sp.*, has the smallest viscosity. However, it is shown that the increase in viscosity of motile compared to non-motile *T. chuii* suspensions cannot be attributed to a change in the effective aspect ratio of individual cells due to the motion of the flagella alone.

Keywords Algae suspension · effective viscosity · non-Newtonian · cell motility · cell morphology

1 Introduction

Increased levels of energy demand over the past century and the global reliance on fossil fuels have led to staggering levels of CO₂. There is an urgent need to develop sustainable energy technologies, and microalgae have long been mooted as a potential solution. The potential of algae as an energy source is further increased by the possibility of using genetically modified species with higher lipid content (Radakovits et al, 2010). As microalgae are responsible for up to half of the carbon fixation on the Earth (Fields et al, 1998), they also present the possibility for effective carbon capture schemes to combat climate change. However, in spite of the theoretical potential of microalgae as a global energy source, many major challenges remain, including the efficiency of conversion of solar energy into fuels compared to other crops (Walker, 2009) and their requirement for limited resources, such as phosphorous and freshwater (Borowitzka and Moheimani, 2013). As a result, the commercial use of microalgae has tended to be limited to producing high-value chemicals for niche markets (Borowitzka, 2013), for which the economies of scale are not prohibitive.

The main costs involved in the production of microalgae products arise not in the cultivation, for which there are well-established systems, but in the harvesting and downstream processing of the biomass (Grima et al, 2003). If the potential of microalgae is to be fully realised, several challenges must be overcome, including the development of more efficient downstream processes, which will require a greater understanding of the rheological properties of algal suspensions.

The rheology of suspensions depends on both the nature of the suspended particles (e.g. volume fraction, particle shape) and the interactions between the particles themselves and the fluid flow (Mueller et al, 2009). Suspensions

65 of solid particles have been extensively studied and they are well understood
66 and described theoretically, e.g. using Einstein's equation or the Krieger-
67 Dougherty semi-empirical formula, whereas those of more complex particles,
68 e.g. deformable or active particles such as algae, are less well understood.

69 *Chlorella* is one of the most common non-motile genus of microalgae stud-
70 ied rheologically. Wu and Shi (2008) studied *Chlorella pyrenoidosa* and ob-
71 served Newtonian behaviour for cell volume fractions of up to $\phi = 0.15$,
72 but above this concentration the viscosity increased dramatically and could
73 not be described by Einstein's equation. At higher cell concentrations ($\phi >$
74 0.175) a yield stress behaviour was observed described by the Herschel-Bulkley
75 model. Zhang et al (2013) examined suspensions of freshwater and marine
76 *Chlorella sp.* and observed shear-thinning behaviour at all volume fractions
77 ($\phi = 0.08 - 0.04$), while Wileman et al (2012) found suspensions of *Chlorella*
78 *vulgaris* (and suspensions of another non-motile green algae, *Nannochloropsis*
79 *sp.*) were Newtonian for $\phi < 0.02$. They found that another non-motile species,
80 *Phaeodactylum tricornutum* did not exhibit any non-Newtonian behaviour at
81 any volume fraction examined ($\phi = 0.005 - 0.08$).

82 Soulies et al (2013) performed a thorough investigation of suspensions of *C.*
83 *vulgaris* for a wide range of volume fractions. The cells were roughly spherical
84 with a mean diameter of $1.98 \mu\text{m}$ and were shown to aggregate at high volume
85 and in the absence of flow. Three distinct regimes were identified: a Newto-
86 nian one was observed for $\phi \leq 0.115$; a shear thinning one for volume fractions
87 between $\phi = 0.115$ and 0.25 , which was attributed to the microstructure of
88 the suspensions; and the formation of flocs at low values of applied stress. A
89 yield stress regime for volumes above 0.25 was observed which was attributed
90 to larger scale aggregate formation. The authors also observed thixotropic-like
91 behaviour in the intermediate and high concentration regimes, which illus-
92 trates the rich rheological phenomena of algae suspensions.

93 The rheology of algal suspensions becomes even more complex when the
94 algae are motile, where the motion of the flagella can have very significant effect
95 on both the microscale and bulk rheology (Foffano et al, 2012; Giomi et al,
96 2010). The majority of algal blooms in oceans and lakes are motile (around
97 90% of strains which produce harmful blooms can swim (Smayda, 1997)), and
98 the motility of green algae has fascinated the fluid dynamics community in
99 recent years (Goldstein, 2015). Flagellated organisms can exhibit two types of
100 swimming behaviour depending on the configuration of their flagella: they can
101 be pullers, i.e. they pull the fluid in front of their body, or pushers, i.e. push
102 the fluid behind their bodies.

103 Hatwalne et al (2004) analysed the dynamics of active fluids, and predicted
104 that the presence of pushers will *lower* the bulk viscosity of the suspension,
105 while puller algae will act to *increase* the viscosity. This has been supported by
106 Sokolov and Aranson (2009), who measured the shear viscosity of suspensions
107 of *Bacillus subtilis* cells (a pusher species), and found that the viscosity was
108 reduced by a factor of up to 7, compared to suspensions of non-motile cells.
109 Similarly, Rafai et al (2010) and Mussler et al (2013) studied the rheology
110 of suspensions of *Chlamydomonas reinhardtii*, a $10\mu\text{m}$ puller type microswim-

mer, and found that the viscosity of suspensions of active cells was higher than that of suspensions of dead cells, as predicted by Hatwalne et al (2004). Using the Krieger-Dougherty rheology model, Rafai et al (2010) found that the intrinsic viscosity was 4.5 for live cells, but only 2.4 for dead cells. Imaging of cell suspensions revealed different behaviour in a shear flow with the active cells resisting rotation and remaining aligned with the flow nearly 70% of the time. The authors postulated that the motility may induce shear-thinning behaviour by the motion of the flagella increasing the effective aspect ratio of the cells, or by reducing the cells' ability to rotate in response to the flow at high strain rates. However, a further study by the same group (Mussler et al, 2013) concluded that none of the above two hypotheses can fully describe the observed increase in viscosity.

Adesanya et al (2012) examined the rheology of suspensions of live and dead *Scenedesmus obliquus* cells, which have a motile phase (Trainor, 1965), and found that when the cells were motile the suspensions had a higher viscosity and exhibited enhanced viscoelastic behaviour. They suggested that this was caused by greater interaction between motile cells, including the tangling of flagella of different cells.

Most of the studies above, with the exception of Wileman et al (2012), have focussed on one type of microalgal species. In most cases a shear thinning behaviour with an increase in concentration has been observed and the effect of motility demonstrated. However, the effect of cell morphology has not been investigated despite the postulation that a hydrodynamic effective aspect ratio effect may be a major factor for flagellated algae. It is not clear, for example, why diatoms such as *P. tricornutum* which exhibit a high aspect ratio are found to maintain Newtonian behaviour Wileman et al (2012). In this study we consider three widely cultivated microalgal strains; we study the rheology of a motile algae species, *Tetraselmis chuii*, at different volume fractions and compare it to that of *Chlorella sp.* and *Phaeodactylum tricornutum* in order to investigate the effects of volume fraction, motility, cell size and morphology.

2 Materials and methods

2.1 Species and culture conditions

Tetraselmis chuii is an oval (approximately $10 \times 14 \mu\text{m}$) chlorophyte (green alga) commonly cultured commercially in the aquaculture industry. *Tetraselmis* species are highly motile and display four equally sized flagella, found in two pairs (Chengwu and Hongjun, 2002). *Chlorella sp.* is a spherical chlorophyte which is routinely cultured as a dietary supplement and utilised in bioremediation systems. *Phaeodactylum tricornutum* is a non-motile, unicellular diatom species which can display an oval or triradiate morphology under culture, but most commonly exists in fusiform morphology approximately $4 \times 10 \mu\text{m}$ in size (Tesson et al, 2009). A model diatom, *Phaeodactylum* is one of the first microalgae to have its genome sequenced, and has recently been genetically modified

153 to optimise omega-3 nutraceutical production (Hamilton et al, 2014). The se-
154 lection of these strains, therefore, allows comparisons to be made of similar
155 sized and/or shaped, unicellular algae displaying both motile and non-motile
156 characteristics, which are already or are becoming established in a variety of
157 industrial processes.

158 *Tetraselmis chuii* (CCAP 8/6), *Chlorella sp.* (CCAP 211/53) and *Phaeo-*
159 *dactylum tricornutum* (CCAP 1052/1A) were obtained from Culture Collec-
160 tion of Algae and Protozoa, SAMS. Microalgal cultures were grown in F/2
161 medium (Guillard and Ryther, 1962) at 18°C, 16:8 (light:dark) cycle and 30
162 $\mu\text{mol}/\text{m}^2\text{s}^2$ irradiance in 3.5 or 10 L bubble column photobioreactors (PML,
163 UK). F/2 medium was made using an aquatic salt mix (GroTech coral marine
164 easy mix) to 32 ppt and the addition of F/2 nutrients (Cell-hi F2P, Vari-
165 conAqua, UK). Microalgae were harvested by centrifugation at 200 *g* (3000
166 rpm) for 3 min in an Octafuge VI centrifuge and re-suspended in phosphate
167 buffered saline (PBS) at the desired volume fraction (either $\phi = 0.05, 0.1,$
168 0.15 or 0.2). A homogeneous sample of the algae suspension was achieved by
169 vigorous shaking.

170 Figure 1 shows cell images to illustrate the cell morphology and relative
171 sizes. In order to quantify the cell size distributions, cell images were acquired
172 and dimension information was extracted using ImageJ (Schneider et al, 2012).
173 The results are shown in Table 1 and the distributions of the major cell diam-
174 eter and aspect ratio in Figure 2.

175 In order to investigate the effect of cell motility, it was desirable to be
176 able to compare motile and non-motile suspensions of the same strain. *T.*
177 *chuii* cells become increasingly non-motile in stationary phase, presumably
178 due to lack of energy (light inhibition in dense cultures) and the availability
179 of nutrients. The reduced motility ('non-motile') suspension tested (at $\phi =$
180 0.1) was sampled from a stationary phase culture and reduced motility was
181 confirmed by observation under the microscope. It was shown that even though
182 the cell arrangement was extremely crowded, some cells were still capable of
183 spinning around, albeit it less fervently.

184 2.2 Rheology measurements

185 Rheological characterisation of algae suspensions was performed using a ro-
186 tational ARES rheometer (TA Instruments, New Castle, DE, USA) using a
187 Couette cell geometry. Steady Rate Sweep tests were performed for shear rates
188 ranging from 20 to 200 s^{-1} at room temperature and volume fractions ranging
189 from 5% to 20%.

190 During testing, the inner drum of the Couette cell rotates at a range of
191 pre-set speeds to provide the shear deformation to the algae sample. A shear
192 rate is thus generated and applied to the algae suspension. The torque exerted
193 by the rotating sample is detected by a transducer and converted to a wall
194 shear stress. The viscosity of the algae suspension is then obtained by:

$$\eta_{\text{eff}} = \frac{\tau}{\dot{\gamma}}, \quad (1)$$

195 where η_{eff} is the effective dynamic viscosity [Pa s] of the suspension, $\dot{\gamma}$ the
196 measured shear stress [Pa] and $\dot{\gamma}$ the applied shear rate [s^{-1}].

197 The inner drum has a diameter of $r_1 = 8.25$ mm and the outer cylinder has
198 a diameter of $r_2 = 8.5$ mm, leaving a radial gap of $d = 0.25$ mm. The depth
199 of the fluid in the drums was 13.5 mm. The Reynolds number is defined as

$$Re = \frac{\rho\omega r_1 d}{\eta_{\text{eff}}}, \quad (2)$$

200 where ρ is the density of the fluid and ω is the rotational velocity.

201 When the Reynolds number exceeds a critical value, the flow becomes
202 unstable (Esser and Grossmann, 1996), causing Equation 1 to break down and
203 the viscosity estimates to become unreliable. The maximum rotational velocity
204 employed in the experiments was 5.8 rad/s, and the lowest effective viscosity
205 encountered in any measurement was 0.89 mPa s. Assuming the density of the
206 suspensions was 1000 kg/m^3 , the largest Reynolds number encountered in any
207 experiment was $Re_{\text{max}} = 53.4$.

208 The critical Reynolds number at which the flow becomes unstable is given
209 by

$$Re_c = \frac{1}{0.1556^2} \frac{(1 + \beta)^2}{2\beta\sqrt{(1 - \beta)(3 + \beta)}}, \quad (3)$$

210 where $\beta = r_1/r_2 = 0.9706$ (Esser and Grossmann, 1996). This corresponds to
211 a critical Re_c of 241.8, which is almost an order of magnitude larger than that
212 encountered in the current study (even allowing for increases in the density of
213 the solutions due to the addition of algae cells), indicating that our results are
214 not affected by flow instabilities and remain valid at high strain rates.

215 As with all suspensions, the rheology measurements are susceptible to wall
216 slip, whereby the particles or cells tend to migrate away from the walls of the
217 rheometer, resulting in a low viscosity layer forming near the wall and reduc-
218 ing the apparent viscosity of the suspension. The wall slip phenomena have
219 been reviewed by a number of authors, e.g. Barnes (1995) and Hatzikiriakos
220 (2015). Despite having a potentially very significant effect, this factor is typi-
221 cally ignored (Buscall, 2010) or eliminated in rheological studies by modifying
222 wall roughness. Nevertheless, as Soulies et al (2013) note, wall slip is equally
223 likely to occur in industrial contexts such as photobioreactors and downstream
224 processing systems, and is an inherent mechanism by which algal suspensions
225 respond to shear. To evaluate the presence and extent of wall slip typically
226 requires the ability to image the fluid as it is being sheared in the rheometer
227 (Soulies et al, 2013) which is often not feasible, or the use of microfluidic ap-
228 proaches to image suspension flows under shear; the latter approach has been
229 followed in blood flow studies (Sherwood et al, 2012) as the cell depleted layer
230 is a key feature in the microcirculation. It is clear that more work is required
231 to understand the mechanism of slip and this is beyond the scope of this study.

3 Results

3.1 Rheology of *Tetraselmis chuii* suspensions

Figure 3 shows the measured shear stress and effective viscosity profiles of suspensions of *T. chuii* for various volume fractions. It is clear that the presence of *T. chuii* cells causes an increase in the observed stress (Figure 3(a)) and the effective viscosity (Figure 3(b)) of the fluid. The pure PBS ($\phi = 0$) shows Newtonian behaviour with shear stress increasing linearly with strain rate and the effective viscosity remaining constant. However, when *T. chuii* cells are suspended within the fluid, the effective viscosity falls with increasing strain rate, indicating shear-thinning behaviour. This non-Newtonian behaviour becomes progressively more pronounced as the cell concentration is increased; at $\phi = 0.05$, the suspension displays predominantly Newtonian-like properties, whereas from $\phi = 0.1$ onwards, non-Newtonian behaviour emerges and shear-thinning can be clearly observed, particularly at $\dot{\gamma} < 50 \text{ s}^{-1}$.

In order to characterise this shear thinning effect and identify how it varies with volume fraction, the experimental data in Figure 3(a) was fitted to the Herschel-Bulkley model:

$$\tau = \tau_y + K\dot{\gamma}^n, \quad (4)$$

where τ_y is the yield stress [Pa s], K the consistency [Pa s^{*n*}] and n the flow index, with $n < 1$ for shear-thinning fluids. When the yield stress is exceeded, the viscosity of a Herschel-Bulkley fluid is given by:

$$\eta = K|\dot{\gamma}|^{n-1} + \tau_y|\dot{\gamma}|^{-1}. \quad (5)$$

It should be noted that even in the case of fluids that exhibit quasi-Newtonian behaviour ($n \approx 1$), the effective viscosity will be greater at low strain rates if the yield stress is greater than zero (due to the $\tau_y|\dot{\gamma}|^{-1}$ term).

The estimated Herschel-Bulkley parameters found are listed in Table 2, and the solid lines in Figures 3(a) and 3(b) represent the corresponding estimates of the shear stress and effective viscosity (Equations 4 and 5), respectively. The uncertainties in the estimates of the Herschel-Bulkley parameters are represented by their standard deviations, which are also listed in Table 2. There is some variation in the estimated values of the yield stress, which may be a result of the limited number of measurements at low strain rates. The flow index is approximately equal to unity for $\phi < 0.1$. As the *T. chuii* concentration is increased further, n declines, indicating progressive shear-thinning behaviour, while the yield stress is also reduced and the consistency increases. These results are broadly consistent with the studies of Wu and Shi (2008), Wileman et al (2012) and Soulies et al (2013), who observed Newtonian behaviour in suspensions of various *Chlorella* species at low volume fractions, and shear-thinning behaviour above a critical value in the range $\phi = 0.02 - 0.15$.

270 The shear-thinning nature of algae suspensions has been reported in the
 271 literature (Rafai et al, 2010; Adesanya et al, 2012; Soulies et al, 2013) and
 272 is a well known aspect of particle suspensions. It is attributed to cell inter-
 273 actions and microstructural changes of the suspension (Adesanya et al, 2012;
 274 Soulies et al, 2013) or to highly localised viscous heating of the suspension at
 275 high volume fractions (Mueller et al, 2009). Soulies et al (2013) reported the
 276 existence of flocs in the shear thinning regime for *Chlorella* suspensions both
 277 with and without shearing. In order to investigate the presence of flocculation,
 278 suspensions of *T. chuii* at $\phi = 0.05$ were tested in the rheometer at different
 279 shear rates applied for 20 seconds each and samples were studied under the
 280 microscope post-shearing (Figure 4). Some cell aggregation was observed in
 281 the micrographs obtained at 10 s^{-1} , which might explain the shear thinning
 282 behaviour at low shear rates (Figure 4(b)), whereas no cell aggregation was
 283 evident at high shear rates (Figures 4(c) and 4(d)). It should be noted that
 284 these images were taken after the shearing had stopped and it was not possible
 285 to acquire images *in situ*.

286 The rheological properties of suspensions of solid spherical particles in the
 287 dilute regime (i.e. $\phi \leq 0.05$) have been characterised by Einstein's equation:

$$\eta = \eta_0 (1 + \alpha\phi), \quad (6)$$

288 where η_0 is the viscosity of the suspending medium, and α is the intrinsic
 289 viscosity ($\alpha = 2.5$ for passive, rigid, spherical particles). The model is known
 290 to work well in the dilute regime, whereas at higher concentrations the Krieger-
 291 Dougherty model is often used (Mueller et al, 2009):

$$\eta = \eta_0 \left(1 - \frac{\phi}{\phi_m}\right)^{-\alpha\phi_m}, \quad (7)$$

292 where ϕ_m is the maximum packing volume fraction. This factor is often treated
 293 as a free variable that can be fitted to experimental data. However, given the
 294 limited number of data points at low concentrations, we take $\phi_m = 0.62$,
 295 following the approach of Rafai et al (2010).

296 Figures 5(a) and 5(b) compare the experimental data to Einstein's equation
 297 and the Krieger-Dougherty model, respectively, for a range of strain rates. As
 298 can be seen, both equations fail to match the observed viscosity at all strains
 299 for $\phi > 0.1$ (in each case α was found by applying the best-fit to the data
 300 for $\phi \leq 0.1$). The breakdown of the Krieger-Dougherty model is particularly
 301 evident at the highest volume fraction. On the basis of solid particle suspension
 302 theory (Mueller et al, 2009), the volume fraction presented here ($\phi = 0.05-0.2$)
 303 corresponds to the semi-dilute regime, and the poor performance of Equations
 304 6 and 7 is well known.

305 It is interesting to note that the best-fit lines of the Einstein and Krieger-
 306 Dougherty equations in Figure 5 are not the same at all strain rates, i.e.
 307 the intrinsic viscosity varies with $\dot{\gamma}$. In order to examine this dependence, the
 308 parameters were evaluated for both equations at a range of strain rates, and are
 309 presented in Figure 6. The trends are qualitatively the same: α declines linearly

310 for $\dot{\gamma} < 100 \text{ s}^{-1}$, at higher strain rates it also declines linearly but at a less
311 steep gradient. This indicates that the degree to which the cell concentration
312 affects the rheology is dependent on the strain rate: at low strain rates the
313 rheology is strongly dependent on the cell concentration (i.e. α is high), while
314 at high strain rates the concentration has a weak effect on the viscosity (low
315 α). The clear change in the dependency of α on $\dot{\gamma}$ at $\dot{\gamma} = 100 \text{ s}^{-1}$ suggests
316 that there is a change in the physical mechanism by which the suspended cells
317 affect the fluid rheology. It seems likely that this is related to the appearance
318 of flocs at low shear rates (Figure 4(b)), and their absence in the micrographs
319 acquired for $\dot{\gamma} \geq 100 \text{ s}^{-1}$ (Figures 4(c) and 4(d)), as the tendency to form
320 flocs at low strain rates induces a significant increase in the observed viscosity.
321 Other potential factors include the presence of extracellular polysaccharides
322 and cell deformability.

323 The Krieger-Dougherty model and the Einstein equation were developed
324 for suspensions of passive, rigid spheres. However, the *T. chuii* cells are neither
325 passive or rigid; they are motile and can respond to the flow, thereby affecting
326 the rheology. In order to study this effect, the rheological characteristics of
327 suspensions of motile and non-motile *T. chuii* cells were measured.

328 Figure 7(a) compares the variation in the measured stress with strain rate,
329 for motile and non-motile suspensions at different volume fractions, with the
330 corresponding viscosity profiles shown in Figure 7(b). It is clear that the motil-
331 ity of cells is associated with a significant increase in viscosity.

332 The data in Figure 7(a) was fitted to the Herschel-Bulkley model, and the
333 lines in Figures 7(a) and 7(b) correspond to the estimated stress and viscosity
334 profiles (Equations 4 and 5, respectively). The estimates of the consistency and
335 flow index for each case are presented in Figure 8(a) and 8(b), respectively. As
336 noted previously, increasing the concentration of motile *T. chuii* cells causes a
337 dramatic increase in the consistency of the suspension and a drop in the flow
338 index (i.e. the suspension exhibits increasing shear-thinning behaviour). In
339 contrast, when the *T. chuii* cells are non-motile, both K and n remain largely
340 constant as the volume fraction is increased. The flow index remains at $n \approx 1$
341 (with some scatter due to the fitting process), indicating that the addition of
342 non-motile cells does not lead to significant shear-thinning behaviour (although
343 the effective viscosity may be larger near $\dot{\gamma} = 0$ due to the effects of the yield
344 stress).

345 The fact that the cell motility increases the bulk viscosity of the suspension
346 implies that the *T. chuii* cells align to resist the flow, or the motion of the
347 flagella may affect rheology by changing the effective aspect ratio of the cells.
348 The latter effect will be discussed in Section 4. This behaviour is typical of
349 puller type swimming algae (Hatwalne et al, 2004; Rafai et al, 2010). This
350 information suggests that when processing *T. chuii* suspensions in industrial
351 contexts, it may be beneficial to induce a reduction in motility by UV radiation
352 exposure or chemical treatment, thereby lowering the viscosity, and reducing
353 the energy requirements.

354 Meanwhile, the different trends in Figure 8(b) suggest that the pronounced
355 shear-thinning behaviour is a direct result of the cell motility; at high strain

356 rates the cells cannot align to resist the flow (and increase the viscosity) as
 357 effectively as at lower strain rates.

358 3.2 Effect of algal species

359 In order to understand the role of *T. chuii* morphology on the suspension
 360 rheology, we also examined the rheology of suspensions of the different algal
 361 species described in Section 2.1. A *Phaeodactylum tricornutum* suspension was
 362 examined at a volume fraction of $\phi = 0.1$, and suspensions of *Chlorella sp.* were
 363 examined at $\phi = 0.1$ and 0.2 . The variations in the stress and effective viscosity
 364 for each case are presented in Figure 9.

365 The *Phaeodactylum* suspension shows clear shear-thinning behaviour (Fig-
 366 ure 9(a)), with a viscosity profile quite similar to that of the *T. chuii* sus-
 367 pension at $\phi = 0.1$. Wileman et al (2012) did not observe any non-Newtonian
 368 behaviour at slightly lower volume fractions ($\phi = 0.005 - 0.08$), which sug-
 369 gests that there is a critical value at which suspensions of *P. tricornutum*
 370 become non-Newtonian, as has been observed for *Chlorella* (Wileman et al,
 371 2012; Soulies et al, 2013; Wu and Shi, 2008).

372 The *Chlorella* suspensions exhibit some particularly interesting behaviour.
 373 Figures 9(a) and 9(b) show that, similar to other cases, the viscosity falls
 374 dramatically with strain rate, as occurs for shear-thinning fluids. This is in
 375 agreement with the work of Zhang et al (2013), examining suspensions of
 376 *Chlorella sp.*, and the work of Soulies et al (2013), examining suspensions
 377 of *Chlorella vulgaris*, who found that the rheology was shear-thinning at $\phi =$
 378 0.165 , but Newtonian (or very weakly shear-thickening) at $\phi = 0.082$. However,
 379 upon closer inspection of the variation in shear stress (Figures 9(a) and 9(b)),
 380 it is apparent that the suspension is in fact shear-thickening, as the rate of
 381 increase in stress with strain is greater at high strain rates. This can be seen
 382 in Figure 9(c) for $\dot{\gamma} > 100 \text{ s}^{-1}$. It has been noted previously that the viscosity
 383 of many suspensions initially decreases with strain rate before going through
 384 a transition in which it increases (Barnes, 1989; Stickel and Powell, 2005),
 385 although this tends to only occur at high cell concentrations.

386 The parameters of the Herschel-Bulkley model for the *Chlorella* data are
 387 summarised in Table 3. At both volume fractions, the *Chlorella* suspensions
 388 have a relatively large yield stress; this leads to the high effective viscosity
 389 observed at low strain rates, via the $\tau_y |\dot{\gamma}|^{-1}$ term in the Herschel-Bulkley
 390 expression for η (Equation 5). The point at which the effective viscosity begins
 391 to increase with strain rate is found by differentiating Equation 5, and is equal
 392 to

$$\dot{\gamma}_{\text{crit}} = \left(\frac{\tau_y}{K(n-1)} \right)^{1/n}. \quad (8)$$

393 These values are listed in Table 3, and are consistent with the measure-
 394 ments presented in Figures 9(b) and 9(d) (and shown in detail in Figure 10(a)).
 395 At low strain rates, the yield stress term in Equation 5 is very large, and the

396 shear thinning effects are not clearly visible. However, it is clear from Figure
397 10(b) that the shear stress has a super-linear ($n > 1$) dependence of strain
398 rate. This super-linearity is not a result of uncertainties in the fitting process,
399 as for both *Chlorella* suspensions, the standard deviation in the estimates of
400 the flow index is small (Table 3).

401 4 Discussion

402 It was shown in Figure 6 that the estimates of the intrinsic viscosity of *T.*
403 *chuii* suspensions vary considerably with strain rate; over the range examined
404 ($\dot{\gamma} = 20 - 200 \text{ s}^{-1}$) α decreased by 38% when calculated using the Krieger-
405 Dougherty model, and by over 50% when using the Einstein equation. To the
406 best of the authors' knowledge, the strain-dependence of the intrinsic viscosity
407 of algae suspensions has not previously been noted in the literature. However,
408 it may explain some of the variation in the intrinsic viscosity measured in
409 previous studies. Zhang et al (2013) reported intrinsic viscosities of 24.7 and
410 16.1 for dilute ($\phi \leq 0.04$) suspensions of freshwater and marine *Chlorella sp.*,
411 respectively, found using the Krieger-Dougherty model at a strain rate of 6
412 s^{-1} . Soulies et al (2013) studied *Chlorella vulgaris*, and chose to fit their data
413 to the Quemada (1998) model, which is the same as Equation 7, with the
414 exponent set to -2 , i.e. $\alpha\phi_m = 2$. Using this approach and measurements at
415 high strains rates ($\dot{\gamma} \approx 50 - 500 \text{ s}^{-1}$), they found $\phi_m = 0.637$, which corre-
416 sponds to $\alpha = 3.14$. The difference of almost an order of magnitude between
417 the estimates of the intrinsic viscosity found in the two studies may arise from
418 the different algae species or the differing experimental conditions, such as
419 the greater presence of polymeric material in the experiments of Zhang et al
420 (2013) (who used Bold's basal and F/2 medium for the freshwater and marine
421 suspensions, respectively, while Soulies et al (2013) used Hunter's solution).
422 However, the observation of higher intrinsic viscosity estimates at low strain
423 rates in these studies is consistent with the results shown in Figure 6, where
424 the variation in α cannot be attributed to changes in the suspending medium,
425 and indicates that the intrinsic viscosity of algal suspensions may be inherently
426 strain rate-dependent.

427 An interesting finding of this study is evidence of shear-thickening be-
428 haviour in *Chlorella sp.* suspensions at high strain rates (Figure 10), which
429 could not be attributed to uncertainties in the estimation of the flow index
430 (Table 3), and has not previously been reported in the literature. Zhang et al
431 (2013) examined the rheology of suspensions of *Chlorella sp.*, but presented
432 only the variation in effective viscosity rather than the shear stress, making
433 it difficult to ascertain whether the high viscosity they observed at low strain
434 rates was a result of shear-thinning behaviour, or a result of a high yield stress.
435 However, our findings are clearly in contrast to those of Soulies et al (2013)
436 and Wileman et al (2012), who found *Chlorella* suspensions were strongly
437 shear-thinning for $\phi > 0.1$.

438 It is not clear why the opposite trend is observed in this work. A possi-
 439 ble factor may relate to the presence of extracellular polysaccharides (EPS)
 440 into the suspending medium. As a chlorophyte, *Chlorella* is a strong producer
 441 of starch (Bailey and Neish, 1954), and starch solutions are well known to
 442 have shear-thickening rheology (Barnes et al, 1989); thus if the starch were
 443 to somehow enter the suspending medium, perhaps as a result of cell damage
 444 at high strain rates, this could explain the clear shear-thickening behaviour
 445 observed here. However, Kaplan et al (1987) found that after several days,
 446 only about 10% of the polysaccharide produced by *Chlorella stigmatophora*
 447 dissolved into the suspending medium, with the rest remained bound to the
 448 cell. Alternatively, the shear-thickening behaviour here may be a result of
 449 thixotropic behaviour, as was observed in the study of Soulies et al (2013).
 450 Further work is planned to investigate these possibilities.

451 The measurements of the suspensions of three different algae species allows
 452 the effect of cell morphology to be examined. Non-spherical particle suspen-
 453 sions behave differently to spherical ones; hydrodynamic and inter-particle
 454 interactions are different and more importantly non-spherical particles are ca-
 455 pable of orienting themselves with the flow (Mueller et al, 2009) rather than
 456 rotating freely as spheres do. Genovese (2012) showed that for a given vol-
 457 ume fraction the relative viscosity of non-spherical particles increases with
 458 increasing aspect ratio due to extra energy dissipation. Of the non-motile al-
 459 gal suspensions presented in Figure 9, the most viscous suspension is that of
 460 *P. tricornutum*, which has the largest aspect ratio ($r_p = 6.5$, Table 1), and the
 461 least viscous is that of *Chlorella*, which has the lowest aspect ratio ($r_p = 1$),
 462 suggesting a link between r_p and viscosity. Rafaï et al (2010) argued that the
 463 difference in the viscosity of motile and dead *C. rheihardtii* suspensions was
 464 caused by the moving flagella increasing the effective aspect ratio of the cells.
 465 The data of the motile and non-motile *T. chunii* cells, in conjunction with the
 466 other non-motile species, allows us to assess the role of motility and aspect
 467 ratio on the suspension rheology.

468 Figure 11 shows the intrinsic viscosity of the different suspensions as a
 469 function of the cell aspect ratio, at $\dot{\gamma} = 60 \text{ s}^{-1}$ and $\phi = 0.1$. Examining
 470 the non-motile cases (black symbols), there appears to be an approximate
 471 relationship of increasing intrinsic viscosity with aspect ratio, as was found by
 472 Mueller et al (2009) (for solid spheres, using the Quemada (1998) model) . The
 473 motile *T. chunii* suspension has a significantly higher intrinsic viscosity than
 474 the non-motile cases at a similar aspect ratio. If the only way by which the
 475 flagella (and the ability of the *T. chunii* cells to move) affects the suspension
 476 rheology is through an increase in the effective aspect ratio of the cells, then
 477 the trend in Figure 9 indicates that the *T. chunii* cells would be required to have
 478 an effective aspect ratio in the approximate range 6 – 8. The *T. chunii* flagella
 479 are approximately $12 \mu\text{m}$ in length, and are all positioned at the same point on
 480 the cell. If they are aligned to maximise the aspect ratio, the effective value is
 481 still only $r_{p,max} = (14.63 + 12)/9.591 = 2.78$ (Table 1). This is shown in Figure
 482 11 (open circle) and is still significantly above the trend line predicted by the
 483 non-motile cases. This indicates that while it is likely that the aspect ratio

484 plays a role in determining the suspension rheology, the increase in viscosity
485 associated with the cell motility cannot be attributed to an increase in the
486 effective aspect ratio alone. Other mechanisms by which the motility may
487 increase the viscosity include the greater diffusion of EPS into the suspending
488 medium in suspensions of live compared to dead cells, flocculation and the
489 preferential alignment of cells to oppose the flow, as discussed earlier.

490 5 Conclusions

491 The rheology of suspensions of three algal strains, *Tetraselmis chuii*, *Chlorella*
492 *sp.* and *Phaeodactylum tricornutum*, was examined using a rotational rheome-
493 ter for a range of volume fractions and strain rates. The measurements were
494 fitted to the Herschel-Bulkley model, while the effect of volume fraction on
495 the *T. chuii* suspensions was modelled using the Krieger-Dougherty and Ein-
496 stein equations, which both performed well for $\phi \lesssim 0.1$. The intrinsic viscosity
497 was found to decrease with strain rate, indicating that the rheology became
498 progressively less sensitive to the concentration of algal cells as the strain rate
499 was increased. The intrinsic viscosity of the cells declined linearly for $\dot{\gamma} \leq 100$
500 s^{-1} , where there was an inflection point, and at high strain rates it continued
501 to decline linearly but with a slower gradient. Micrographs of the $\phi = 0.05$
502 suspension acquired shortly after the viscosity measurements showed signs of
503 flocculation in the $\dot{\gamma} = 10 \text{ s}^{-1}$ case, but none in the $\dot{\gamma} = 100 \text{ s}^{-1}$ case, suggest-
504 ing that the change of behaviour in the intrinsic viscosity at 100 s^{-1} may be
505 related to presence/absence of flocculation. Other possible causes include the
506 presence of extracellular polysaccharides and the deformability of the *T. chuii*
507 cells.

508 The Herschel-Bulkley model clearly indicated that the *T. chuii* suspensions
509 were shear-thinning ($n < 1$). However, suspensions of non-motile *T. chuii* cells
510 did not show any signs of shear-thinning (i.e. n was approximately equal to
511 unity at all volume fractions), indicating that it is the motility of the cells
512 that is the cause of this non-Newtonian behaviour. In contrast, the *Chlorella*
513 suspensions indicated shear-thickening behaviour ($n > 1$). However, the yield
514 stress of the suspensions meant that the effective viscosity remained high at
515 low strain rates, and only started to increase with strain rate at $\dot{\gamma} \gtrsim 156 \text{ s}^{-1}$.

516 Finally, the viscosity profiles of all three algal strain suspensions were com-
517 pared. It was found that the viscosity tended to increase with the aspect ratio
518 of the algal cells, i.e. *Phaeodactylum* suspensions ($r_p = 6.47$) were the most
519 viscous, while *Chlorella* suspensions ($r_p = 1$) were the least so. It has been
520 speculated in the literature that the increased viscosity of motile suspensions
521 may be caused by an increase in the effective aspect ratio of the cells, due
522 to the motion of the flagella (Rafai et al, 2010). In order to assess to what
523 extent this is the case for the *T. chuii* suspensions, the viscosity of each strain
524 were compared as a function of r_p . It was shown that even if the flagella were
525 fully extended, the increase in aspect ratio is not sufficient to account for the

526 observed increase in viscosity. Therefore, the increased viscosity of motile *T.*
527 *chuii* cells requires that the cells preferentially align to resist the flow.

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532 References

- 533 Adesanya VO, Vadillo DC, Mackley MR (2012) The rheological characteriza-
534 tion of algae suspensions for the production of biofuels. *J Rheol* 56(4):925–
535 939
- 536 Bailey JM, Neish AC (1954) Starch synthesis in *Chlorella vulgaris*. *Can J*
537 *Biochem Phys* 32(4):452–464
- 538 Barnes HA (1989) Shear-thickening (“dilatancy”) in suspensions of nonaggre-
539 gating solid particles dispersed in Newtonian liquids. *J Rheol* (1978-present)
540 33(2):329–366
- 541 Barnes HA (1995) A review of the slip (wall depletion) of polymer solutions,
542 emulsions and particle suspensions in viscometers: its cause, character, and
543 cure. *J Non-Newton Fluid* 56:221–251
- 544 Barnes HA, F HD, Walters K (1989) *An Introduction to Rheology*, vol 3.
545 Elsevier
- 546 Borowitzka MA (2013) High-value products from microalgae—their develop-
547 ment and commercialisation. *J Appl Phycol* 25:743–756
- 548 Borowitzka MA, Moheimani NR (2013) Sustainable biofuels from algae. *Mitig*
549 *Adapt Strategies Glob Chang* 18:13–25
- 550 Buscall R (2010) Letter to the Editor: Wall slip in dispersion rheology. *J Rheol*
551 (1978-present) 54(6):1177–1183
- 552 Chengwu Z, Hongjun H (2002) Taxonomy and ultrastructure of five species of
553 *Tetraselmis* (*Prasinophyceae*) isolated from China seas. *Acta Oceanol Sin*
554 21(4):557–579
- 555 Esser AE, Grossmann S (1996) Analytic expression for Taylor-Couette stabil-
556 ity boundary. *Phys Fluids* 8(7):1814–1819
- 557 Fields CB, Behrenfeld MJ, Randerson P J T Falkowski (1998) Primary pro-
558 duction of the biosphere: integrating terrestrial and oceanic components.
559 *Science* 281(5374):237–240
- 560 Foffano G, Lintuvuori JS, Morozov AN, Stratford K, Cates ME, Marenduzzo
561 D (2012) Bulk rheology and microrheology of active fluids. *Euro Phys J E*
562 35(98):1–11
- 563 Genovese DB (2012) Shear rheology of hard sphere, dispersed and aggregated
564 suspensions, and filler-matrix composites. *Adv Colloid and Interfac* 171:1–16
- 565 Giomi L, Liverpool TB, Marchetti MC (2010) Sheared active fluids: Thicken-
566 ing, thinning, and vanishing viscosity. *Phys Rev E* 81(5):051,908
- 567 Goldstein RE (2015) Green algae as model organisms for biological fluid dy-
568 namics. *Annu Rev Fluid Mech* 47:343

- 569 Grima EM, Belarbi EH, Fernández FA, Medina AR, Chisti Y (2003) Recov-
570 ery of microalgal biomass and metabolites: process options and economics.
571 Biotechnol Adv 20(7):491–515
- 572 Hatwalne Y, Ramaswamy S, Rao M, Simha RA (2004) Rheology of active-
573 particle suspensions. Phys Rev Lett 92(11):118,101
- 574 Hatzikiriakos SG (2015) Slip mechanisms in complex fluid flows. Soft Matter
575 11(40):7851–7856
- 576 Kaplan D, Christiaen D, Arad S (1987) Chelating properties of extracellular
577 polysaccharides from *Chlorella* spp. Appl Environ Microb 53(12):2953–2956
- 578 Mueller S, Llewellyn EW, Mader HM (2009) The rheology of suspensions of
579 solid particles. In: P R Soc A, The Royal Society, p rspa20090445
- 580 Mussler M, Rafai S, Peyla P, Wagner C (2013) Effective viscosity of non-
581 gravitactic *Chlamydomonas reinhardtii* microswimmer suspensions. EPL-
582 Europhys Lett 101(5):54,004
- 583 Quemada D (1998) Rheological modelling of complex fluids. I. The concept of
584 effective volume fraction revisited. Eur Phys J-Appl Phys 1(1):119–127
- 585 Radakovits R, Jinkerson RE, Darzins A, Posewitz MC (2010) Genetic engi-
586 neering of algae for enhanced biofuel production. Eukaryot Cell 9(4):486–501
- 587 Rafai S, Jibuti L, Peyla P (2010) Effective viscosity of microswimmer suspen-
588 sions. Phys Rev Lett 104(9):098,102
- 589 Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25
590 years of image analysis”. Nat Methods 9:671–675
- 591 Sherwood JM, Dusting J, Kaliviotis E, Balabani S (2012) The effect of red
592 blood cell aggregation on velocity and cell-depleted layer characteristics of
593 blood in a bifurcating microchannel. Biomicrofluidics 6(024119)
- 594 Smayda TJ (1997) Harmful algal blooms: Their ecophysiology and general rel-
595 evance to phytoplankton blooms in the sea. Limnol Oceanogr 42(5.2):1137–
596 1153
- 597 Sokolov A, Aranson IS (2009) Reduction of viscosity in suspension of swim-
598 ming bacteria. Phys Rev Lett 103(14):148,101
- 599 Soulies A, Pruvost J, Legrand J, Castelain C, Burghelea TI (2013) Rheological
600 properties of suspensions of the green microalga *Chlorella vulgaris* at various
601 volume fractions. Rheol Acta 52(6):589–605
- 602 Stickel JJ, Powell RL (2005) Fluid mechanics and rheology of dense suspen-
603 sions. Annu Rev Fluid Mech 37:129–149
- 604 Trainor FR (1965) Motility in *Scenedesmus* cultures incubated in nature. B
605 Torrey Bot Club 92(5):329–332
- 606 Walker DA (2009) Biofuels, facts, fantasy, and feasibility. J Appl Phycol
607 21(5):509–517
- 608 Wileman A, Ozhan A, Berberoglu H (2012) Rheological properties of algae
609 slurries for minimizing harvesting energy requirements in biofuel production.
610 Bioresource Technol 104:432–439
- 611 Wu Zy, Shi Xm (2008) Rheological properties of *Chlorella pyrenoidsa* culture
612 grown heterotrophically in a fermentor. J Appl Phycol 20(3):279–282
- 613 Zhang X, Jiang Z, Chen L, Chou A, Yan H, Zou YY, Zhang X (2013) Influence
614 of cell properties on rheological characterization of microalgae suspensions,.

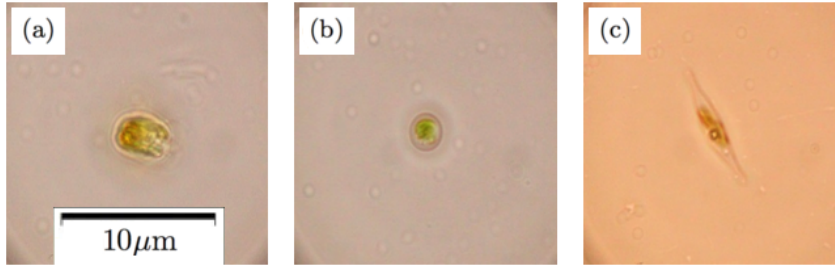


Fig. 1 Images of isolated cells illustrating cell morphology: *T. chuii* (a); *C. sp.* (b); and *P. tricornutum* (c).

Table 1 Cell sizes of samples tested.

Dimension	<i>T. chuii</i>	<i>C. sp.</i>	<i>P. tricornutum</i>
Average Major Diameter [μm]	14.63 ± 0.574	6.523 ± 2.422	23.968 ± 4.995
Average Minor Diameter [μm]	9.591 ± 1.955		3.817 ± 1.123
Aspect Ratio, r_p	1.539 ± 0.312		6.473 ± 2.514

Table 2 Yield stress, consistency and flow index found for different concentrations of motile *T. chuii*, and the standard deviation of the estimates.

ϕ	0	0.05	0.1	0.15	0.2
τ_y [mPa]	5.48	32.39	19.74	12.31	0
$\sigma(\tau_y)$ [mPa]	0.006	0.009	0.01	0.008	1×10^{-4}
K [mPa s n]	0.804	1.15	5.1	7.82	12.95
$\sigma(K)$ [mPa s n]	2×10^{-4}	4.9×10^{-4}	0.001	0.001	0.001
n	1.01	0.998	0.781	0.762	0.69
$\sigma(n)$	0.043	0.075	0.047	0.026	0.02

Table 3 Herschel-Bulkley parameters estimated from suspensions of *Chlorella sp.* presented in Figures 9(a) and 9(c). The uncertainties were calculated during the fitting process, and correspond to one standard deviation.

	$\phi = 0.1$	$\phi = 0.2$
τ_y [mPa]	50.56	80.1
$\sigma(\tau_y)$ [mPa]	0.005	0.002
K [mPa s n]	0.103	0.011
$\sigma(K)$ [mPa s n]	5×10^{-5}	6×10^{-6}
n	1.4	1.79
$\sigma(n)$	0.085	0.08
$\left(\frac{\tau_y}{K(n-1)}\right)^{1/n}$ [s $^{-1}$]	156.4	158.8

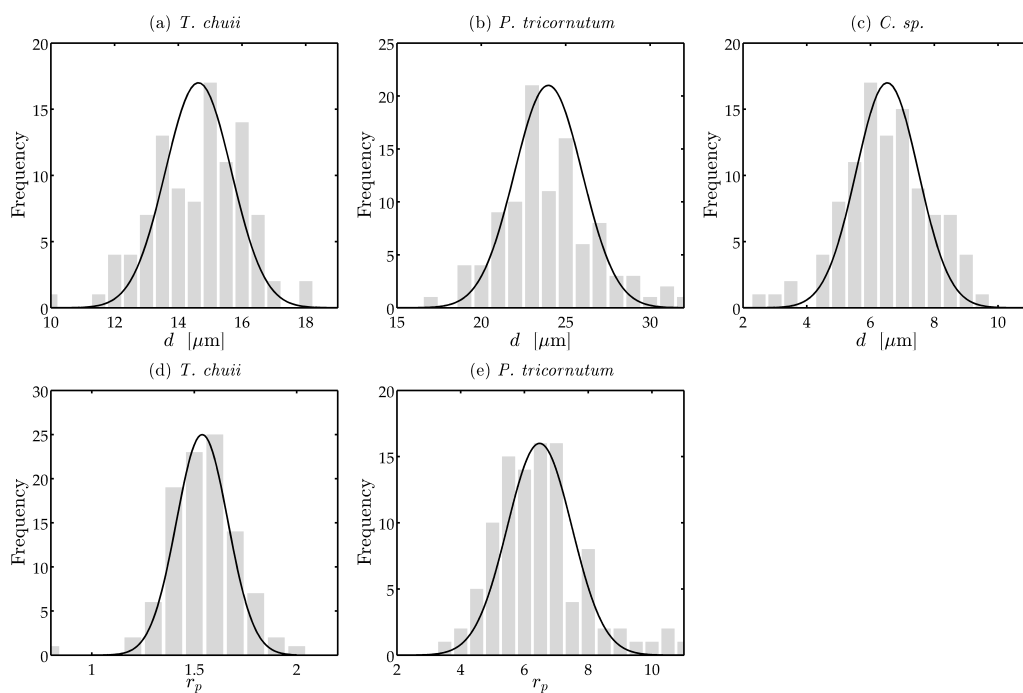


Fig. 2 Histograms of the maximum dimension of the cells (a-c) and the aspect ratio (d-e), for *T. chuii* (a, d); *P. tricorutum* (b, e); and *C. sp.* (c). The *C. sp.* are circular and have an aspect ratio of 1. For each strain, 100 cells were analysed. Black lines represent a best fit to a normal distribution.

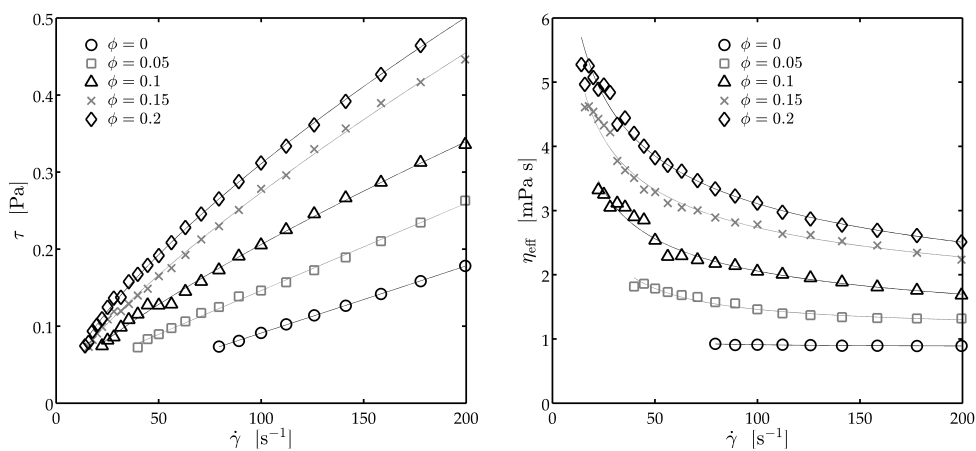


Fig. 3 Variation in shear stress (a) and effective viscosity (b) with strain rate, for different concentrations of *Tetreselmis chuii* suspended in PBS. Lines in (a) and (b) correspond to Herschel-Bulkley model fitting to the data.

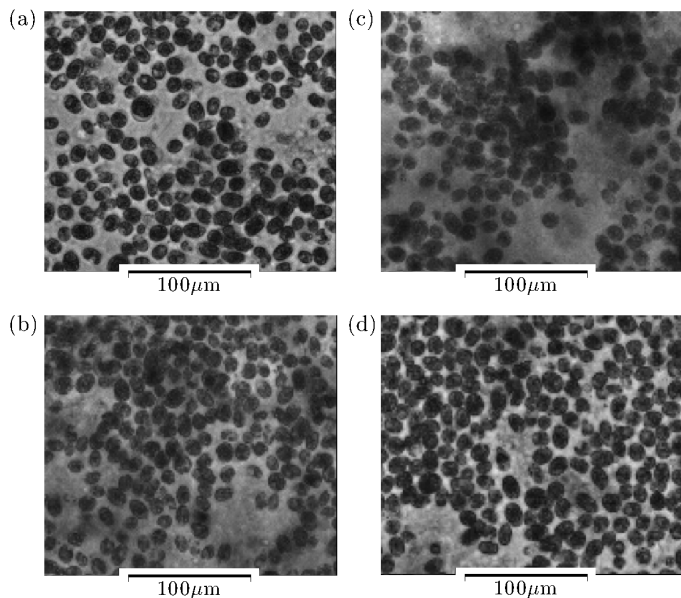


Fig. 4 Micrograph of $\phi = 0.05$ volume fraction *Tetraselmis chunii* suspension taken with $20\times$ magnification, 20 s after the suspension was sheared at rate of 0 s^{-1} (a), 10 s^{-1} (b), 100 s^{-1} (c), and (d) 1000 s^{-1} .

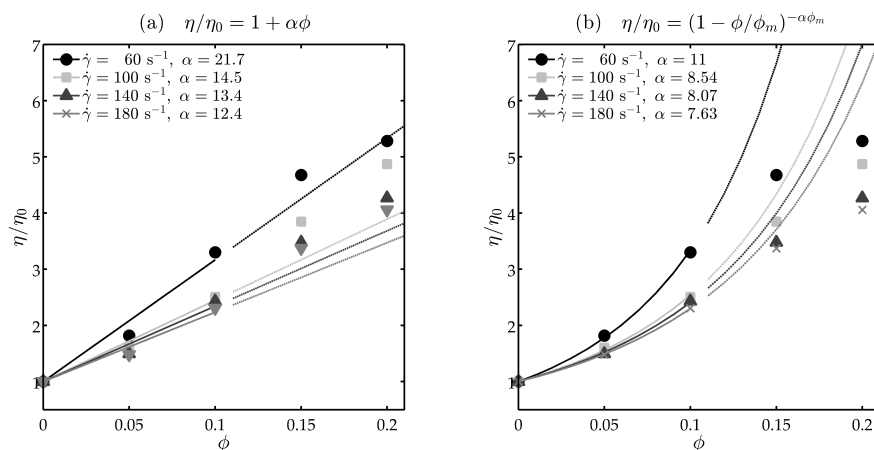


Fig. 5 Variation in effective viscosity of *T. chunii* suspensions as a function of concentration volume, measured at a range of shear rates. The lines in (a) show the best-fit of data to the Einstein's equation (Equation 6), while the lines in (b) represent the best fit to the Krieger-Dougherty model (Equation 7). The estimates of the intrinsic viscosity were calculated using the data for $\phi \leq 0.1$.

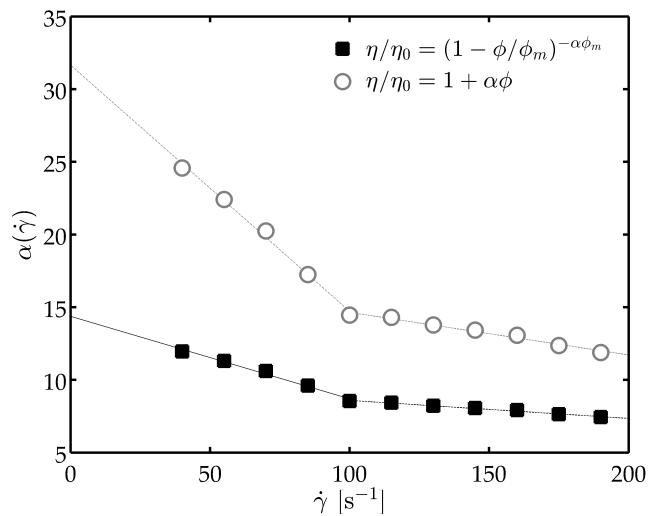


Fig. 6 Variation in the intrinsic viscosity estimated using the Einstein and Krieger-Dougherty equations with strain rate, for *T. chuii* suspensions.

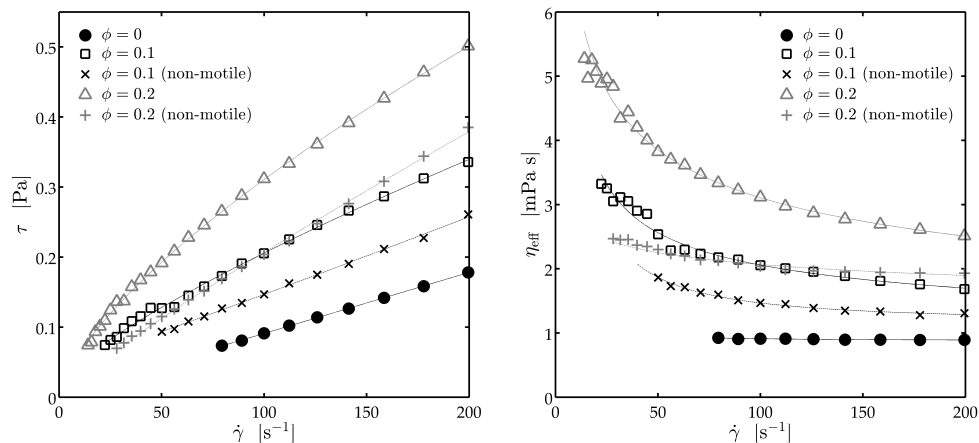


Fig. 7 Shear stress (a) and effective viscosities (b) of PBS and motile and non-motile *T. chuii* suspensions as a function of shear rate. The lines represent the best-fit of the data to the Herschel-Bulkley model (Equations 4 and 5).

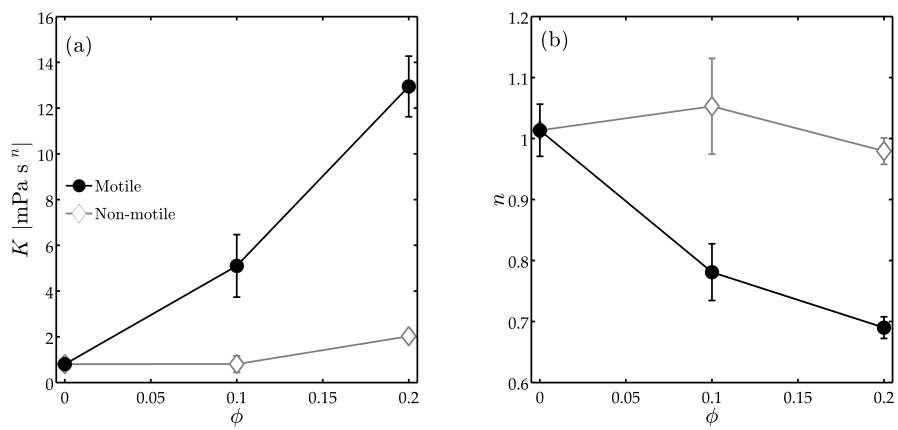


Fig. 8 Estimated consistency (a) and flow index (b) suspensions of motile and non-motile *T. chuii* cells at different volume fractions. The values were estimated by fitting the data in Figure 7 (a) to the Herschel-Bulkley model (Equation 4). The error bars correspond to one standard deviation.

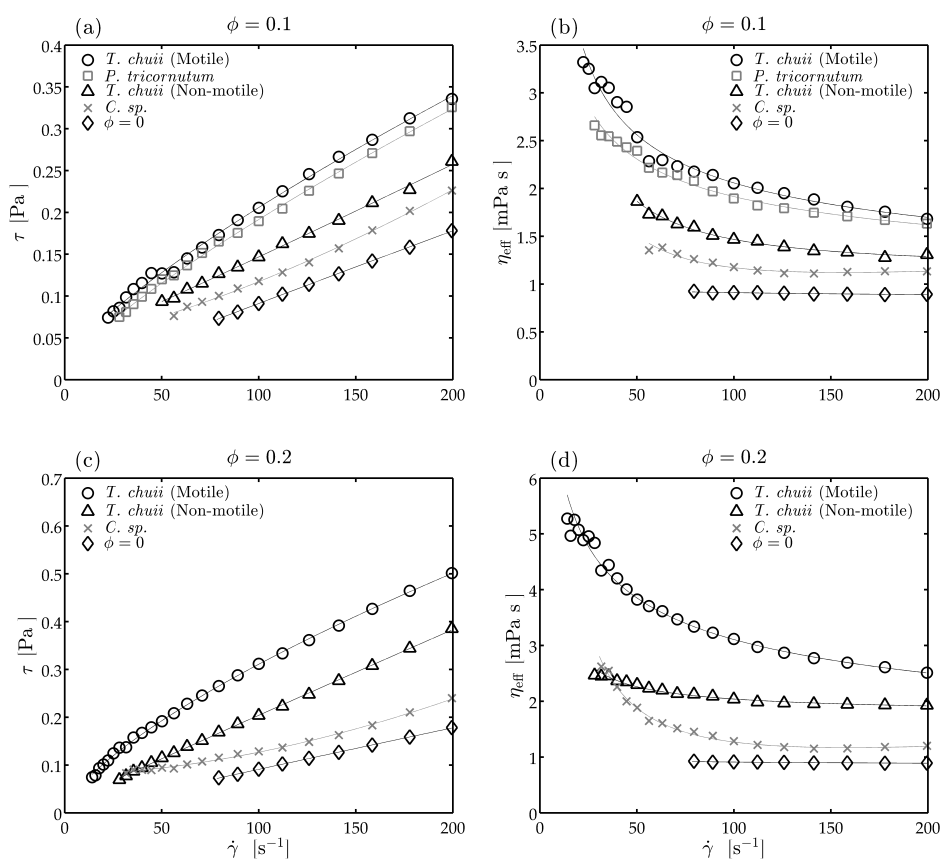


Fig. 9 Variation in the shear stress (a and c), and effective viscosity (b and d), as a function of strain rate, for suspensions of different algal strains and pure PBS. The data in (a) and (b) were acquired at $\phi = 0.1$, while the data in (c) and (d) were acquired at $\phi = 0.2$. The lines show the best-fit of the data to the Herschel-Bulkley model (Equation 4).

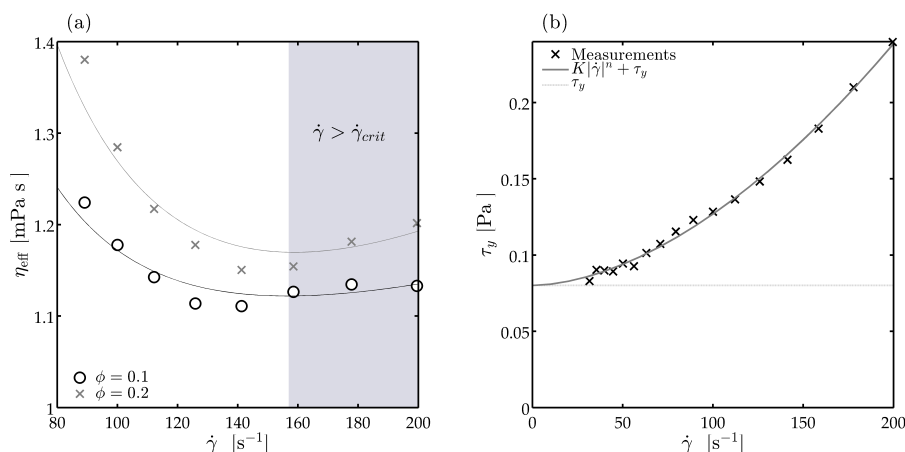


Fig. 10 Variation in the effective viscosity of *Chlorella sp.* suspensions at high shear rates (a) for two cell concentrations. The shaded region ($\dot{\gamma} > \dot{\gamma}_{crit}$) corresponds to the region where the effective viscosity is predicted to increase with strain rate, according to the Herschel-Bulkley model (Equation 5). The variation in the stress with strain rate for the $\phi = 0.2$ case is shown in (b), along with the estimated flow curves (Equation 4) and the contribution of the yield stress. The trend of increasing stress with strain rate (i.e. the shear-thickening behaviour) is particularly clear here.

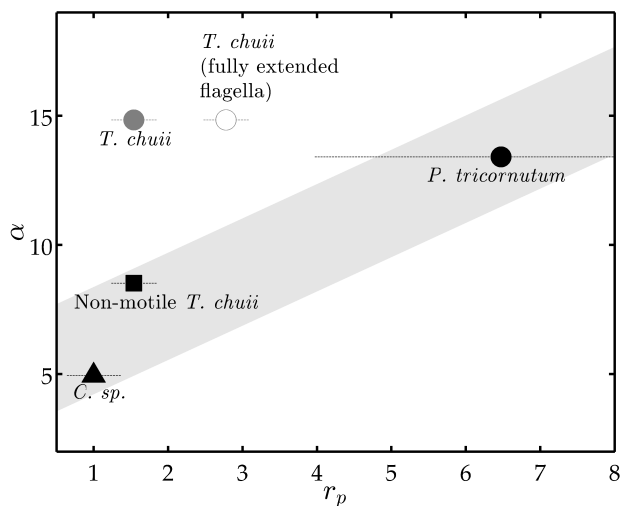


Fig. 11 Intrinsic viscosity, $\alpha = (\eta/\eta_0 - 1)/\phi$, for each algal suspension as a function of aspect ratio, for $\dot{\gamma} = 60 \text{ s}^{-1}$ and $\phi = 0.1$. The light grey line indicates a linear-fit to the non-motile data (black symbols).