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23

Abstract

24 We model how phytoplankton exopolymeric substances (EPS) may change pycnocline thickness δz
25 through control by Richardson number Ri . Shear stress τ_{forced} is imposed across the pycnocline, giving a
26 shear rate $\delta u / \delta z$, where δu is cross-pycnocline velocity difference, modulated by viscosity η . In natural
27 waters viscosity is composed of two components. The first is Newtonian, perfectly dispersed viscosity due
28 to water and salts. The second is non-Newtonian, and depends on phytoplankton abundance raised to an
29 exponent between +1.0 and +1.5. It is also generally shear-thinning, depending on $(\delta u / \delta z)^P$, where P is
30 negative. In suspensions of microbial aggregates viscosity depends also on (length scale) ^{d} . Published
31 measurements of EPS rheology in a culture of *Karenia mikimotoi* are input. These measurements were
32 made at 0.5 mm, so they can be scaled to $\delta u / \delta z$ if d is known for this EPS over the appropriate range of
33 length scales. The model shows that $\delta u / \delta z$ is very sensitive to d . At values of $d < -0.2$ or -0.3 , however,
34 high concentrations of *K. mikimotoi* (<31 million L⁻¹) have no significant effect on δz at ambient values
35 (>1 cm). Future investigations of pycnocline dynamics should include measurements of rheological
36 properties, and particularly d .

37 KEYWORDS: Rheology, phytoplankton, pycnocline, thin layer, exopolymeric substance,
38 biogeochemistry

39

41 **1. Introduction**

42 A companion paper (Jenkinson, submitted to this volume) reviews the state-of-the-art of the rheology and
43 rheometry of natural waters. Thin layers (TLs) of dense phytoplankton often occur associated with density
44 discontinuities, or pycnoclines, in coastal seas (Bjørnsen et al., 1993; Dekshenieks, 2001; Alldredge et al.,
45 2002, GEOHAB, 2008), oceans and lakes. Since dense phytoplankton is often associated with increased
46 viscosity as well as elasticity of the seawater or lake water (Jenkinson, submitted to this volume, and
47 references therein), the question arises whether the phytoplankton in such TLs may alter pycnocline
48 characteristics through the rheological affects of their secreted extracellular polymeric substances (EPS).
49 We begin this investigation by modeling the possible effects of increased viscosity on pycnocline
50 thickness. Published values are used for the viscosity and elasticity of seawater (Jenkinson, 1993b;
51 Jenkinson and Biddanda, 1995) and phytoplankton cultures (Jenkinson, 1986, 1993a). Recent findings that
52 the effects of length scale on rheological properties of heterogeneous suspensions of microbial flocs can
53 be modeled using a power law (Jenkinson and Wyatt, 2008) are applied to a natural-water situation for the
54 first time The aim of using this model is to help identify appropriate targets for future research on TL and
55 pycnocline dynamics.

56 In this paper, the model is presented, some results for seemingly appropriate values of pycnocline
57 parameters, and densities of the harmful algal bloom (HAB) dinoflagellate *Karenia mikimotoi*, that occurs
58 widespread, often forming TLs in relation to pycnoclines (Bjørnsen et al., 1993). Rheological
59 measurements in cultures and seawater have been measured at a length scale only of 0.5 mm, and it is
60 shown that whether rheological effects can modify the values of pycnocline thickness that actually occur,
61 will depend critically on the length scale exponent d . Since this model has so far no field data with which
62 to validate it, we then discuss appropriate targets for future investigation.

63 **2. Model setup and examples**

64 The aim of this model is not to predict the dynamics of thin layers or pycnoclines. It is to suggest how thin
65 layers or pycnoclines may be sensitive to modification by algal EPS, particularly those of *Karenia*
66 *mikimotoi*.

67 We build the model with a standard set of parameters, ready to change each parameter separately for
68 numerical experiments (Table 1). This is a 1-D 3-layer equilibrium model of a pycnocline (Fig. 1) in
69 which Richardson number Ri determines the thickness.

70 There are three layers: an upper and a lower mixed layer, with a stratified pycnocline between them. The
 71 mixed layers are turbulent, with a turbulent eddy viscosity A_z of 10^{-1} to 10^2 Pa.s in the vertical plane
 72 (Massel, 1999), several orders of magnitude greater than the viscosity in the pycnocline, that comprises
 73 only molecular viscosity η . There exists a difference in density $\delta\rho$ between the upper and the lower mixed
 74 layers, which we vary around a standard value of 1 kg.m^{-3} , and this produces a uniform vertical gradient
 75 $\delta\rho/\delta z$ in the pycnocline, where δz is the thickness of the pycnocline. The mean density of the water ρ is all
 76 layers is set to 10^3 kg.m^{-3} , and we ignore the 0.1% or so variation induced by $\delta\rho$.

77 Initially we consider the pycnocline without phytoplankton or its associated EPS. Eddies in this layer are
 78 damped by the stratification, so the only resistance to shearing is that due to molecular viscosity due to
 79 water and salt, η_w that is set at 10^{-3} Pa.s. Because of the large difference between the viscosity in the
 80 mixed layers A_z , shearing is neglected in the mixed layers, and assumed to take place only in the
 81 pycnocline. Vertical shear rate in the pycnocline,

$$82 \quad \dot{\gamma} = \tau / \eta_w \quad [\text{s}^{-1}] \quad (1)$$

83 The velocity difference between the top and base of the pycnocline,

$$84 \quad \partial u = \partial z \cdot \dot{\gamma} \quad [\text{m.s}^{-1}] \quad (2)$$

85 Pycnocline stability is governed by the Richardson number (Mann and Lazier, 2006),

$$86 \quad Ri = \frac{g \delta\rho / \delta z}{\rho (\delta u / \delta z)^2} \quad [\text{dimensionless}] \quad (3)$$

87 where g is the acceleration due to gravity.

88 When Ri becomes < 0.25 , turbulence is generated within the pycnocline, which entrains water in from one
 89 or both mixed layers, thus increasing its thickness (Mann and Lazier, 2006). In this equilibrium model, we
 90 fix a critical Richardson number $Ricr$ at 0.25. Substituting $Ricr$ for Ri in (3) and rearranging,

$$91 \quad \delta z = Ricr \cdot \rho \frac{(\delta u)^2}{g \cdot \delta\rho} \quad [\text{m}] \quad (4)$$

92 Turbulent energy dissipation rate ε in the oceans varies typically from 10^{-6} to $10^{-9} \text{ m}^2.\text{s}^{-3}$ (Mann and
 93 Lazier, 2006). Assuming a value for η of 10^{-3} Pa.s, this gives a corresponding value for $\dot{\gamma}$ of 1 to 0.03 s^{-1} ,
 94 corresponding to a value of shear stress τ of 10^{-3} to 3×10^{-5} Pa.

95 Now we add phytoplankton and its associated EPS, in this case *K. mikimotoi* (syn.: *Gyrodinium*
 96 *aureolum*). Jenkinson (1993a) measured the rheological properties of a culture of 4.4 cells. μL^{-1} of *K.*
 97 *mikimotoi* over a range of $\dot{\gamma}$ from 0.0021 to 8 s⁻¹. His results are reproduced in Fig 2. From measurements
 98 of Jenkinson's Fig.1, it may be deduced that the excess viscosity (due to EPS) varied with $\dot{\gamma}$ thus,

$$99 \quad \eta = \eta_W + \eta_E \quad [\text{Pa.s}] \quad (5)$$

$$100 \quad \eta_E = 1.27 \times 10^{-4} \cdot \dot{\gamma}^{-0.75} + 3.16 \times 10^{-4} \cdot \dot{\gamma}^{-0.18} \quad [\text{Pa.s}] \quad (6)$$

101 Like viscosity, shear stress can be similarly decomposed into the Newtonian part due to water and salts
 102 and an excess part due to EPS. So from (1),

$$103 \quad \tau_W = \eta_W \cdot \dot{\gamma} \quad , \quad \tau_E = \eta_E \cdot \dot{\gamma} \quad , \quad \tau = \eta \cdot \dot{\gamma} \quad [\text{Pa}] \quad (7)$$

104 Multiplying both sides of (6) by $\dot{\gamma}$ gives the excess shear stress for this culture

$$105 \quad \tau_E = 1.27 \times 10^{-4} \cdot \dot{\gamma}^{+0.25} + 3.16 \times 10^{-4} \cdot \dot{\gamma}^{+0.82} \quad [\text{Pa}] \quad (8)$$

106 Excess viscosity is generally proportional to a power of the concentration of the causative agent, whether
 107 this is a dissolved polymer (Ross-Murphy and Shatwell, 1993) or phytoplankton. For phytoplankton,
 108 Jenkinson and Biddanda (1995) found the power to be about 1.3. We assume the same power-law
 109 relationship between τ_E and *K. mikimotoi* concentration Km ,

$$110 \quad \tau_E = (1.27 \times 10^{-4}) \cdot (Km / 4.4)^{1.3} \cdot \dot{\gamma}^{+0.25} + (3.16 \times 10^{-4}) \cdot (Km / 4.4)^{1.3} \cdot \dot{\gamma}^{+0.82} \quad [\text{Pa}] \quad (9)$$

111 that simplifies to

$$112 \quad \tau_E = 1.85 \times 10^{-5} \cdot Km^{1.3} \cdot \dot{\gamma}^{+0.25} + 4.6 \times 10^{-5} \cdot Km^{1.3} \cdot \dot{\gamma}^{+0.82} \quad [\text{Pa}] \quad (10)$$

113 Spinosa and Lotito (2003) investigated the yield stress, or resistance to flow just enough to stop flow τ_y in
 114 sewage sludge in tubes of different diameters. Their data show that, for different sludge concentrations,

$$115 \quad \tau_y \sim L^d \quad [\text{Pa}] \quad (11)$$

116 where L is length scale, in this case tube diameter, and d is an exponent in this particular case close to -2.
 117 The particular value of d might be related to the fractal dimension of the aggregates' shape, size
 118 distribution, or both. Like sewage sludge aggregates, marine aggregates and transparent exopolymeric
 119 particles (TEP) are quasi-fractally hierarchical organic aggregates rich in EPS (Mari and Kiørboe, 1996).

120 However, in places where the rheologically active polymer in the sea is more diffuse, then d is likely
 121 closer to zero, but the effect of length scale on seawater rheological properties has not yet been
 122 investigated. The rheological data in Jenkinson (1993a) were all obtained using Couette flow with a
 123 measuring gap of 0.5 mm. Therefore to model the effect of d (for simplicity assumed to be the same over
 124 all values of $\dot{\gamma}$) on excess viscosity, we take the appropriate *in situ* length scale to be δz , applying a
 125 "correction" relative to the value of L equal to $(\delta z/L)^d$ thus:

$$126 \quad \tau_E = (1.85 \times 10^{-5} \cdot Km^{1.3} \cdot \dot{\gamma}^{+0.25} + 4.6 \times 10^{-5} \cdot Km^{1.3} \cdot \dot{\gamma}^{+0.82}) \cdot (\delta z/L)^d \quad [\text{Pa.s}] \quad (12)$$

127 We take the appropriate value of $\dot{\gamma}$ to be the shear rate vertically through the pycnocline, $(\delta u/\delta z)$, so that

$$128 \quad \tau_E = (1.85 \times 10^{-5} \cdot Km^{1.3} \cdot (\delta u/\delta z)^{+0.25} + 4.6 \times 10^{-5} \cdot Km^{1.3} \cdot (\delta u/\delta z)^{+0.82}) \cdot (\delta z/L)^d \quad [\text{Pa.s}] \quad (13)$$

129 τ_E thus depends on Km , $\delta u/\delta z$, δz and d . The resistance to shearing by the water phase (water + salt),

$$130 \quad \tau_W = \eta_W \cdot (\delta u/\delta z) \quad [\text{Pa}] \quad (14)$$

131 where η_W is independent of both shear rate and length scale and is assumed to be 0.001 Pa.s. We have
 132 taken respective values for $\delta \rho$ and ρ to be 1 and 1000 kg.m⁻³. Combining (5) and (14),

$$133 \quad \tau = \tau_W + \tau_E \quad [\text{Pa}] \quad (15)$$

134 To run the model, let us first consider an example of no plankton ($Km = 0$ cells. μL^{-1}) and a forced shear
 135 stress across the pycnocline $\tau_{forced} = 0.0001$ Pa. Here the value of d makes no difference to the outcome.
 136 The computation proceeds in two steps.

137 In step 1, values are put in for a forced shear stress τ_{forced} and a value is guessed for δz . We solve for $\tau =$
 138 τ_{forced} and read off the corresponding value for pycnocline shear rate $\delta u/\delta z =$ (Fig. 3a).

139 In step 2, δz is now calculated in two ways, firstly from (2), using a range of values for δu , and secondly
 140 from (4) (where δz is called $\delta z z$), using the same range of values for δu . Here when $\delta z = \delta z z$, δz is read off
 141 as well as a new value for δu . (Fig. 3b). As confirmation, Ri , calculated from (3), equals $Ricr$ always at the
 142 same value of δu as when $\delta z = \delta z z$. In the present case, τ equals τ_W since in the absence of phytoplankton
 143 and EPS, τ_E is zero

144 Iteration now proceeds by repeating step 1, putting in the value of δz obtained in step 2, and so on, until
145 the values remain unchanged. In this case $\delta z = 4.0$ m, $\delta u = 0.4$ m.s⁻¹, $\dot{\gamma}$, or $\delta u / \delta z, = 0.1$ s⁻¹, $\eta = \eta_w = 10^{-3}$
146 Pa.s, and the buoyancy frequency $N^2 = 2.5 \times 10^{-3}$ rad.s⁻¹.

147 Now let us add phytoplankton EPS to the model with $Km = 4.4$ cells. μ L⁻¹ and $d = 0$ (rheological properties
148 independent of length scale) and, as before, $\tau_{forced} = 0.0001$ Pa. The results are shown in Fig. 3c, d. In Fig.
149 3c. While the contributions, τ_{Hi} , τ_{Lo} , τ_E , τ_W and τ_{are} each shown, the co-ordinate of $\tau \cdot \dot{\gamma}$ is retained for input
150 to step 2. After iteration, this simulation with phytoplankton EPS gives $\delta z = 50.0$ m, $\delta u = 1.43$ m.s⁻¹, $\dot{\gamma}$, or
151 $\delta u / \delta z, = 0.029$ s⁻¹, $\eta = 3.5 \times 10^{-3}$ Pa.s, and $N^2 = 2.0 \times 10^{-4}$ rad.s⁻¹.

152 The code is available at <http://assoc.orange.fr/acro/TL/SupInfo.html> .

153

154 **3. Results**

155 In our model pycnocline, the Richardson number Ri controls its thickness. With no extra viscosity from
156 phytoplankton EPS, Fig. 4a illustrates that δz shows a linear relationship with $\delta\rho$, and is proportional to
157 the square of τ_{forced} .

158 At our standard value for τ_{forced} of 0.0001 Pa, and -0.2 for d , Fig. 4b shows how *K. mikimotoi*
159 concentration Km progressively increases δz , by over 3 times when $Km = 10$ cells μL^{-1} . The two lower
160 curves, for $Km = 0.1$ and 0.316 cells μL^{-1} , cannot be distinguished, and even the curve for $Km = 1$ cell μL^{-1}
161 is barely distinguishable. The relative effect is higher at lower values of τ_{forced} . (Supplementary Table 1
162 <http://assoc.orange.fr/acro/TL/091011SupTab1.xls>). Fig. 4b also shows that the effect of Km on δz
163 decreases as δz itself increases, This is because the negative value of d lessens the functional value of
164 viscosity η as pycnocline thickness increases

165 Fig. 4c shows the effect of d on relationship between δz and $\delta\rho$, in relation to that when $Km = 0$. When Km
166 is the standard value 4.4 cells μL^{-1} and d is zero, and over the range of length scales of interest here, the
167 EPS would be perfectly dispersed. (Water and its viscosity η_w are also perfectly dispersed). Such perfect
168 dispersion of EPS would give thickening independent of length scale, and this is why the curve for $d = 0$ is
169 parallel to that for $Km = 0$. For negative values of d , in contrast, as δz increases, η_E decreases, so the
170 curves tend down towards that for $Km = 0$.

171 **4. Discussion**

172 There have recently appeared complaints of models that show "failure to fail", for instance in plankton
173 trophic models (Franks, 2009), while in the field of rheology, Woodcock (2009) bemoans, "computer
174 modeling with many-parameter models is neither 'theory' nor 'experiment'!. Moreover, it's not research,
175 it[']s 'animation'!". The present model, in contrast, aims to suggest which parameters are critical to
176 pycnocline dimensions, and under which conditions, and which are not. Our aim is not to animate, but to
177 help focus the attention of future research.

178 Previous work (Jenkinson 1986, 1993b) modeled, and attempted to predict, the effect of the shear-thinning
179 exponent of phytoplankton EPS on isotropic turbulence. As explained by Jenkinson (submitted to this
180 volume), however, a 10-fold increase in Newtonian viscosity (sucrose solution) imposed for calibration of
181 those experiments did not significantly change the size of turbulent eddies, possibly because the 3-L
182 container constrained a harmonic system of eddies (Jenkinson 2004b).

183 Later work (Jenkinson et al., 2007; Jenkinson and Wyatt, 2008) pointed out that data presented by Spinosa
184 and Lotito (2003) indicated that the yield stress in suspensions of microbial flocs is strongly length-scale-
185 dependent. This implies that EPS thickening in natural waters is likely to depend not only on the shear-
186 thinning exponent of the polymers P , but also on the length-scale exponent d and, of course, the EPS
187 abundance and type.

188 P has already been measured in the sea (Jenkinson 1993b, Jenkinson and Biddanda, 1995) and in
189 phytoplankton cultures (Jenkinson, 1986, 1993a) as mentioned above, while the effect of P on isotropic
190 turbulence has also been modeled (Jenkinson, 1986, 1993b, 2004a). The present model, therefore, has kept
191 P constant and investigates the effects of changing d and the concentration Km of a *K. mikimotoi* bloom,
192 whose rheological properties correspond to a culture measured by Jenkinson (1993a) at a known length
193 scale. Comparison of Fig. 4b to Fig. 4c shows that for an imposed shear stress τ_{forced} , changing d from 0 to
194 -0.2 changes pycnocline thickness δz by a factor of 10 or more, while a hefty bloom with Km of 10 million
195 cells L^{-1} , and $d = -0.2$, increases δz only ~ 5 times more than with no phytoplankton.

196 It is important to note that for values of d of -0.4 or more negative, the effect of blooms on pycnocline
197 thickness is practically negligible at realistic values of δz , say 1 cm or more, even for blooms of high
198 concentration. To understand whether EPS thickening may be affecting δz *in situ*, effort should be given
199 to measuring d in different blooms and cultures. As mentioned, a value for d of 0 corresponds to a
200 perfectly dispersed polymer solution, so by changing the flocculation parameters of its EPS, a bloom
201 organism may have the potential to radically change its local environment over a wide range of scales.
202 Simple changes in molecular properties may thus be under strong, and perhaps competing, evolutionary
203 pressures related to niche engineering by bloom species (Jenkinson and Wyatt, 1992; 1995, 2008; Wyatt
204 and Ribera d'Alcalà, 2006). Marine snow and TEP (Alldredge et al., 2002) are common in pycnoclines,
205 and probably form an important component in the allometric floc-size continuum, thus probably
206 influencing d .

207 In aquatic systems, biological and physico-chemical processes, such as diffusion, mixing and encounter,
208 are governed by water deformation, so viscosity and elasticity need to be measured and known at the
209 scales of each process under consideration. Measurement over a range of scales will furthermore allow d
210 to be determined, and to be extrapolated, with caution, to other length scales. Associated with such
211 measurements of physical properties, an intense research effort is needed to visualise water movement,
212 together with videos of flocculation and break-up of EPS flocs, turbulence, and organism trajectories in
213 3D over appropriate ranges of length, time and shear stress. *In situ* observations and measurements should
214 be the aim, and laboratory work only a step on the way towards it.

215 Finally, this is a proviso concerning the use of the Richardson number in modeling pycnoclines.
216 Dekshenieks et al (2001) measured Richardson number Ri on many occasions in a pycnocline in a shallow
217 fjord, and their Figs 4f and 7h show that while a tight lower bound of 0.25 to 0.23 existed for Ri , no upper
218 bound was apparent. Since Ri is linearly related to δz , a lower bound thus exists similarly for δz but no
219 upper bound. Previously Oakey and Elliott (1982) had worked in Shelf waters off Nova Scotia. Rather
220 similarly to Dekshenieks et al., they found high Ri , averaging ~ 10 , in mixed water below 20 m, but values
221 of $R < 0.25$ in the upper 10 m, where active turbulent events, thought to reduce stratification and hence Ri ,
222 were frequently observed. This implies that the lower limit of Ri is fairly tightly controlled by turbulence,
223 but that erosion of the pycnocline at high Ri is only a weak mechanism, so other causality for thick
224 pycnoclines, such as their history, may be more important. *In* the present model, Ri is determined only
225 indirectly by viscosity, through δz and δu . In the past, the critical value of Ri has been determined
226 empirically, without explicitly taking viscosity into account, so we do not know quantitatively the
227 mechanisms behind the control by Ri . It is important to know, and would be interesting to investigate,
228 whether viscosity has a *direct* effect on Ri , since if it does, η should appear explicitly in (3), corresponding
229 to the way in that case η would be controlling δz .

230 **5. Conclusions**

231 In natural waters, viscosity consists of the sum of two components. Newtonian, perfectly dispersed
232 viscosity is contributed by the water and salts. Non-Newtonian viscosity is contributed mainly by
233 dissolved and flocculated exopolymeric substances (EPS), related to shear rate by a mainly negative
234 exponent P , as well as to the plankton concentration raised to the power of another exponent, roughly
235 between +1 and +1.5. Based on work done on other microbe-rich suspensions, EPS viscosity is probably
236 related to length scale by a third, negative exponent d , but this has not yet been investigated for natural
237 waters.

238 Based on published values of how viscosity relates to shear rate in a culture of a *Karenia mikimotoi*
239 culture, we modeled how blooms of *K. mikimotoi* at different concentrations and for different values of d
240 would affect pycnocline characteristics. It was found that providing d is not more negative than about -0.2
241 or -0.3, the phytoplankton could affect pycnocline thickness several-fold, but below this value of d , even
242 high concentrations of the plankton would have no significant effect. This kind of model thus points out
243 the most critical parameters important for further investigations. In the present case, investigation if d , and
244 secondarily P , is required, as well as concentration dependence for different species of phytoplankton.

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302

303 **Legends**

304 Figure 1.-D 3-layer equilibrium model of a pycnocline in which the thickness is determined by Richardson
305 number Ri .

306 Figure 2. Rheological properties of a culture of $4.4 \text{ cells} \cdot \mu\text{L}^{-1}$ of *Karenia mikimotoi* (syn: *Gyrodinium* cf.
307 *aureolum*). Excess viscosity η_E and elastic modulus G' are plotted against shear rate. G' was found
308 between 10% and 50% of excess viscous modulus, $G''_E = \eta_E \cdot \dot{\gamma}$. (Slightly redrawn from Jenkinson,
309 1993a.)

310 Figure 3. Examples of output from model. a) For $Km = 0 \text{ cells} \cdot \mu\text{L}^{-1}$, $\tau_{forced} = 10^{-4} \text{ Pa}$, τ and τ_W (with
311 τ_{forced}) vs. $\dot{\gamma}$ (marked as $\gamma\dot{}$). Since $\tau = \tau_W$ the two lines are superimposed. After iteration, the values of
312 τ and $\dot{\gamma}$ are read off. b) As for a), but solution of δz and Ri as functions of δu . c) As for a) but with $Km =$
313 $4.4 \text{ cells} \cdot \mu\text{L}^{-1}$, $\tau_{forced} = 10^{-4} \text{ Pa}$ and $d = 0$. τ_{Hi} (dotted line), τ_{Lo} (dashed line), τ_E (dash-dotted line), τ
314 (upward curving thin continuous line), τ_W (straight thin continuous line) and τ_{forced} (horizontal line) vs. $\dot{\gamma}$
315 (as $\gamma\dot{}$). d) as for b) but with the same inputs as c).

316 Figure 4. Some examples of model output of pycnocline thickness δz plotted against density difference
317 across the pycnocline. Standard values of parameters (Table 2) are used except where stated to be
318 otherwise a) No phytoplankton. Values of shear stress across pycnocline τ_{forced} from lower to upper curves:
319 0.001, 0.000316, 0.0001, 0.0000316, 0.00001 Pa. b) *K. mikimotoi* concentrations, Km from lower to upper
320 curves 0.1, 0.316, 1, 3.16, 10 $\text{cells} \cdot \mu\text{L}^{-1}$; The curves for Km equal to 0.1 and 0.316 cannot be distinguished,
321 and serve also to illustrate the case for no phytoplankton. c) Different values of the exponent d defining
322 the relationship between viscosity and length scale. For the lowest curve, the case is given for $Km = 0$, and
323 for the other curves, the standard value of Km $4.4 \text{ cells} \cdot \mu\text{L}^{-1}$ is used, with d values of -0.1, -0.2, -0.3, -0.4.
324 Note the different vertical scales on the graphs, and that the lowest curve of Figs b and c corresponds to
325 the middle one of Fig a.

326

327

Fig 1

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Model of the water column (1-D, 3-layer, equilibrium)

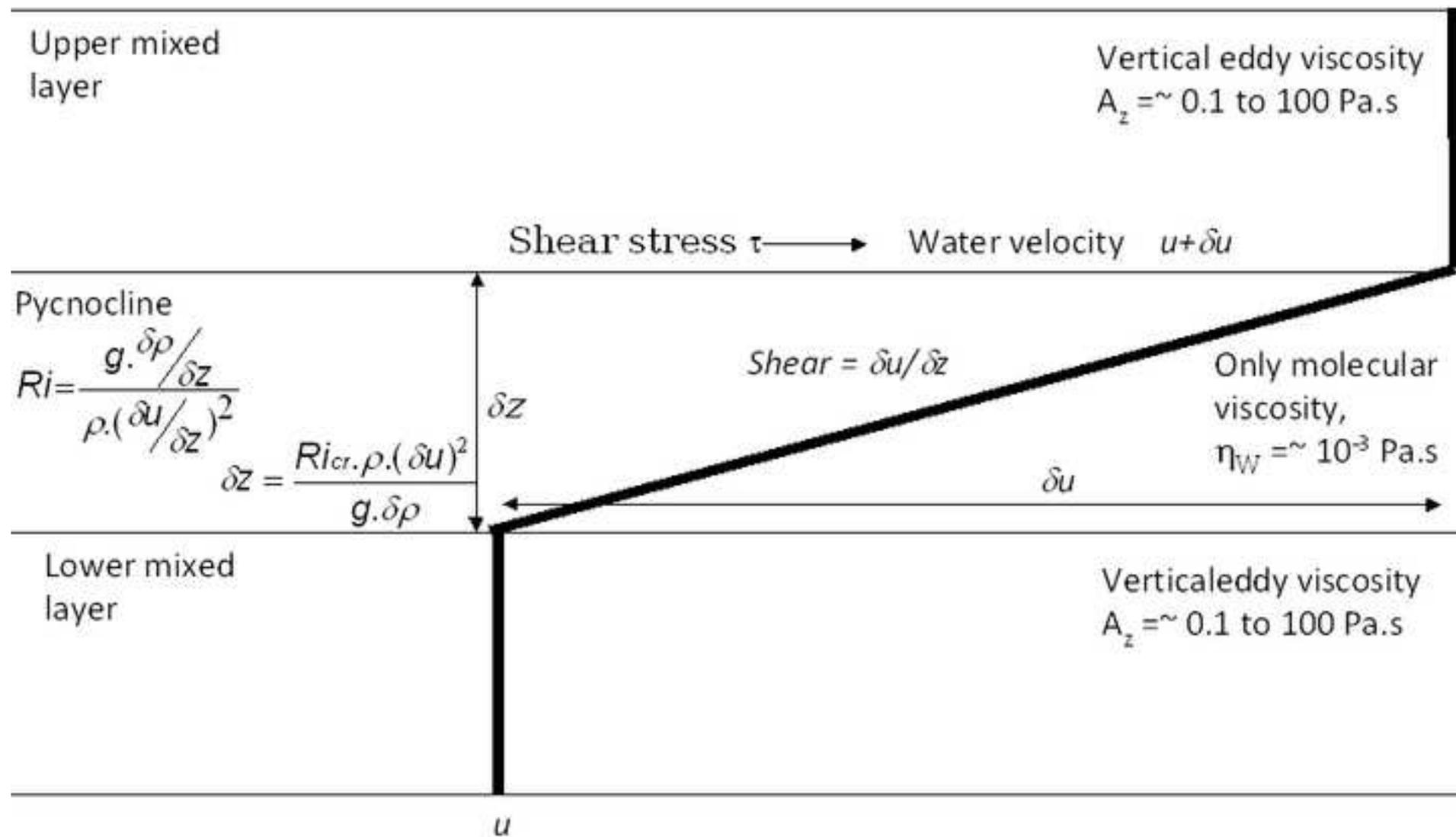


Fig 2

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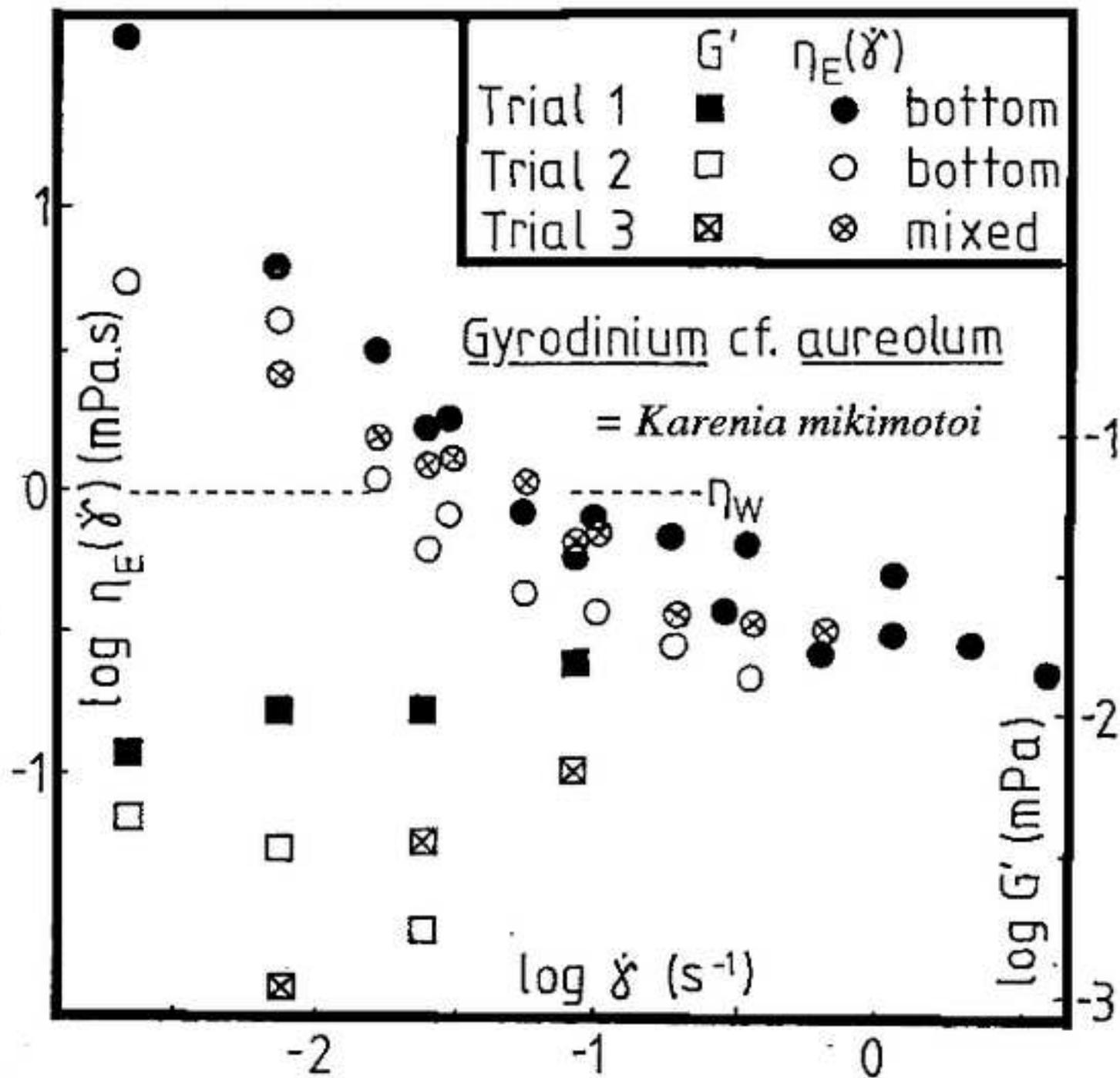


Fig 3

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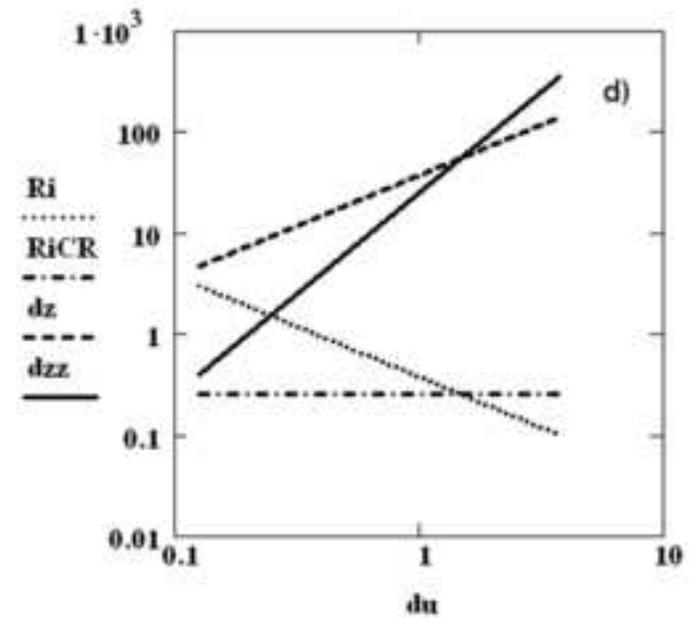
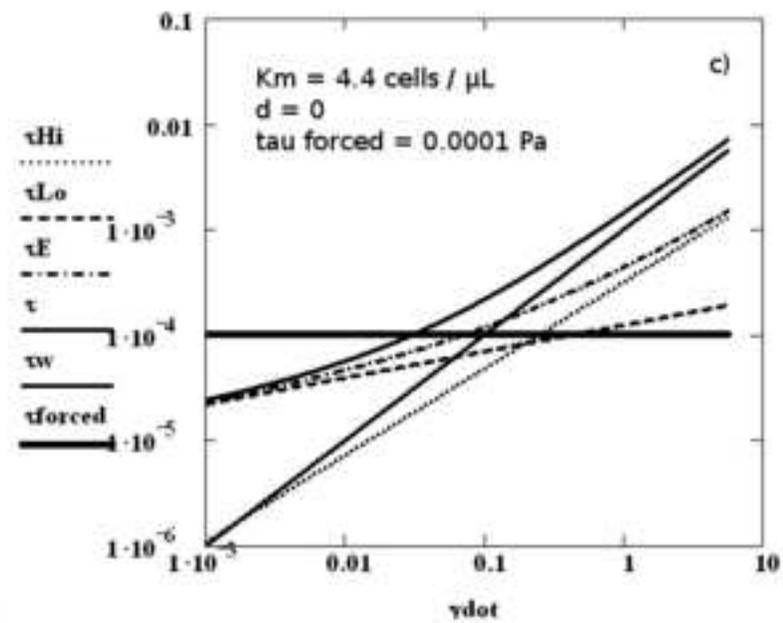
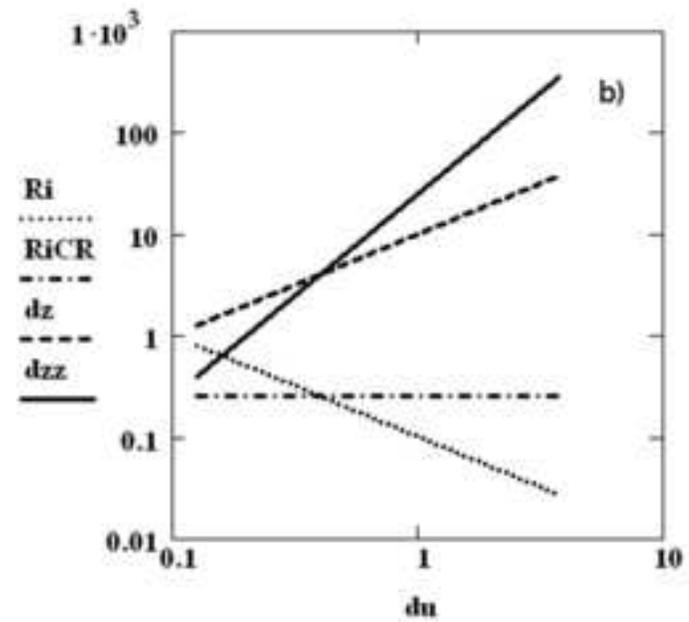
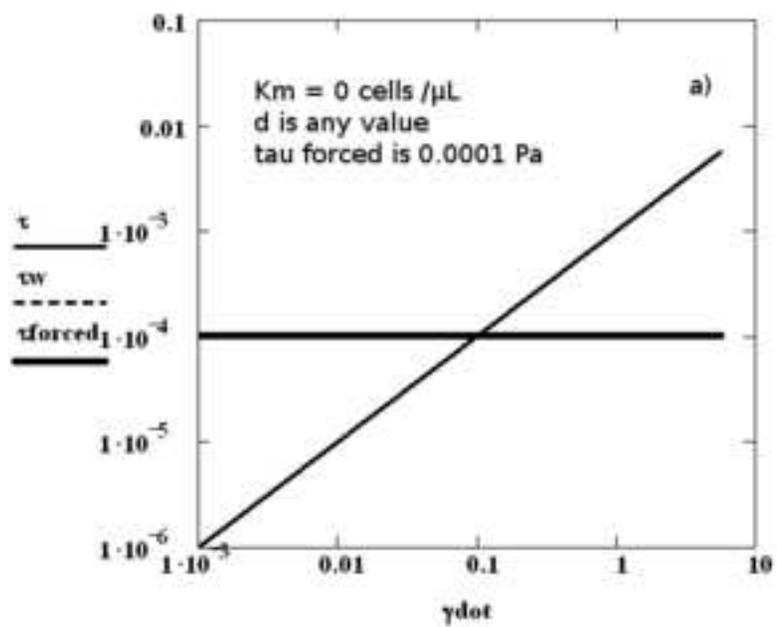


Fig 4

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