

1 **Life in suspension and its impact on phytoplankton morphology. An homage to Colin S. Reynolds**

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11

12 **Abstract**

13 The amazing morphological diversity of phytoplankton has to be considered an evolutionarily-
14 driven compendium of strategies to cope with the strong variability and unpredictability of the
15 pelagic environment. Phytoplankton collects unicellular and colonial photosynthetic organisms
16 adapted to live in apparent suspension in turbulent water masses. Turbulence represents a key
17 driver of phytoplankton dynamics in all aquatic ecosystems and phytoplankton morphological
18 variability is the evolutionary response of this group of photosynthetic organisms to the temporal
19 and spatial scales of variability of turbulence. This paper reviews the existing literature on the
20 effects exerted by turbulence on phytoplankton populations and is aimed at showing how deeply
21 turbulence contributes to the shape and size structure of phytoplankton assemblages. Our aim is
22 to explore how turbulence governs phytoplankton access to resources and, at the same time, how
23 the shape and size structure of phytoplankton represents the evolutionary way in which this group
24 of organisms has optimized its survival in the highly dynamic aquatic environment. The paper is
25 intended to serve as an homage to the (phytoplankton) ecologist Colin S. Reynolds. His life-long
26 work highlighted how profoundly the ecology of phytoplankton depends on the physical
27 constraints governing the movements of the water masses in which phytoplankton evolved and
28 lives.

29 Keywords: planktic life, phenotypic plasticity, morphological variability, physical constraints, shape
30 structure, size, biotic interactions

31

32 **Introduction**

33 Contributing about half of the global primary production, phytoplankton represents the real
34 “green lung” of the Planet (e.g. Smayda, 1970; Falkowski 1994; Litchman et al., 2015) although its
35 standing stock accounts for only a negligible fraction (< 1%) of the global photosynthetic biomass
36 (Field et al., 1998; Sigman & Hain, 2012). To better understand the links existing between
37 phytoplankton biomass and its productivity, a main focus of scientific papers over the last ~60
38 years has been the roles of resource availability (nutrients and light) and the effect of grazers on
39 phytoplankton structure. If indeed nutrients, light and predators represent primary constraints to
40 phytoplankton growth in an isotropic environment, it would be legitimate to ask: why
41 evolution/competition has not driven phytoplankton toward being composed by a few species all
42 showing similar sizes and shapes (possibly small and spherical)? As pointed out by Sommer et al.
43 (2017), it is too simplistic to equate small size with metabolic advantages.

44 The evidence that this ecological group of photosynthetic organisms often shows a high
45 number of coexisting species, along with the high variability in their size and shape, led to the so
46 called “Paradox of the Plankton” (Hutchinson, 1961), which has been representing one of the
47 conceptual frameworks that moved ahead phytoplankton ecology (Dodds & Whiles, 2020). Among
48 the explanations proposed to solve the paradox, a large effort has been put in demonstrating that
49 the aquatic environment is far from being isotropic (Durham & Stocker, 2012). Anisotropy in
50 aquatic environments determines a lack of equilibrium (Margalef, 1978), largely due to the
51 intrinsic turbulent motion of water masses that represent the selective environments for
52 phytoplankton on Earth’s surface. Phytoplankton evolution responds to instability by providing a
53 large array of adaptive strategies addressed at facing variable environmental conditions mainly
54 driven by water movements (Glibert, 2016). Planet rotation, the gravitational effect of the Moon,
55 the wind blowing on the water surface, the establishment of temperature gradients both among
56 adjacent water layers and at a global scale (Hutter et al., 2011a), and convectional currents
57 generated by density differences (Lewis, 1973; Granin et al., 2000) all contribute to the motion of
58 water masses where phytoplankton is transported and has evolved (Finkel, 2007; Kozawa et al.,
59 2019).

60 The way in which water masses move within inland lentic ecosystems strongly depends on
61 their exposure to wind, on their morphology (e.g. shoreline development, bathymetry, surface
62 area, volume, extension of the tributaries, etc.), on the effects of local climate as expressed by

63 their geographic location (Imberger, 1998) and land use (Katsiapi et al., 2012). In lotic ecosystems,
64 the velocity of the unidirectional flow can change at various points along the river course and it is
65 generally related to a variety of meteorologically-driven and morphological factors such as water
66 discharge, the gradient of the slope that the river moves along, the width and depth of the
67 channel and the amount of friction caused by rough edges within the river bed (e.g. Julien, 2002;
68 Bukaveckas, 2010). The complex physical processes governing water motion in an aquatic
69 ecosystem are therefore subjected to the intrinsic and local features of water bodies: these
70 further contribute to increase the variability of the physical scenario (e.g. Elliott et al., 2001;
71 Padisák et al., 2010b). Phytoplankton is evolutionarily equipped to cope with this variability and
72 much of the features it developed is expressed in the extent of morphological plasticity within
73 populations, formed by highly-variable, unicellular organisms eventually grouped in aggregates
74 with various number of cells.

75 To explain vertical and horizontal patchiness of phytoplankton in the oceans (i.e. its
76 accumulation, blooming mechanisms, susceptibility to grazing, and geographic distribution),
77 several papers analysed the spatial distribution of phytoplankton in relation to the complex
78 patterns of vertical and lateral mixing at different space and time scales (e.g. Martin, 2003 and
79 literature therein; Behrenfeld & Boss, 2014 and literature therein; Mahadevan, 2016; Taylor, 2016;
80 Brereton et al., 2018; Spatharis et al., 2019). Moreover, the main evolutionary feature of
81 phytoplankton, i.e. being adapted to live in a three-dimensional moving fluid, has a central role in
82 giving phytoplankton access to the resources it needs for growth while moving (and being
83 transported) in the highly dynamic aquatic ecosystems (e.g. Reynolds, 1973; Reynolds, 1976a,
84 1976b; MacIntyre, 1998; Rodrigo et al., 1998; Naselli-Flores & Barone, 2000; Huisman et al., 2004;
85 Winder et al., 2009). However, today we are still far from a complete understanding of the
86 processes that govern planktic life in turbulent motion, even though our knowledge on the
87 evolutive role exerted by environmental variability on phytoplankton morphological traits has
88 increased in the last years (e.g. Reynolds et al., 2002; Kruk et al., 2010). According to Reynolds
89 (1998): “among phytoplankton ecologists, the concern focussed upon the importance of water
90 chemistry and upon the competition for nutrients has often outweighed the attention afforded to
91 the physical quality of the environment”.

92 Colin S. Reynolds (London, 1942 – Kendal, 2018) dedicated a substantial part of his
93 professional career to investigate the adaptations of phytoplankton species and assemblages with
94 regard to the acquisition of resources while suspended in water and subjected to its motions. He

95 showed that much of the ecological success of phytoplankton depended on their morphology,
96 evolutionarily forged to optimize their access to resources in a turbulent world (Reynolds, 1984a;
97 1997; 2006). The spectrum of shapes and sizes of phytoplankton is therefore the result of adaptive
98 selection addressed at maximising the chances to survive under variable environmental conditions
99 (Naselli-Flores & Barone, 2011 and literature therein). These morphological features determine
100 the degree of entrainment of phytoplankton organisms in the water motion. Furthermore, these
101 features impact their ability to exploit resources, constitute an efficient shield against grazing, and
102 ultimately drive their ecology by allowing populations to grow (Reynolds, 1984b).

103 The scientific contributions of Colin S. Reynolds have influenced profoundly not only modern
104 phytoplankton ecology but also ecosystem theory. As an homage to CS Reynolds, this paper
105 attempts to review the literature on the role of phytoplankton morphological variability and its
106 adaptive value addressed to i) fit the spectrum of turbulent conditions generated by water
107 motions, ii) maximise resource exploitation while being entrained and transported in a moving
108 fluid, iii) reduce the impact exerted by herbivores. Papers dealing with both marine and
109 freshwater phytoplankton were considered since, as stated by Reynolds (2012a) “there is little
110 physical difference between seawater and fresh water, certainly not in the motions to which
111 either is subjected, nor, the clear taxonomic distinctions apart, in the evident adaptations of
112 species to exploit them”.

113 Here we will try to clarify how water motions modulate the ecology of phytoplankton and
114 how much its morphological variability is the result of adaptations evolutionarily addressed at
115 maximizing the chances to survive in a highly variable environment. An exhaustive treatment of
116 the physical laws governing water motions is beyond the scope of this paper.

117

118 **Why are there so many different phytoplankton morphologies?**

119 Phytoplankton, according to a widely accepted definition, is an ecological group of unicellular and
120 colonial photosynthetic microorganisms (not a taxonomic group, due to the distant phylogenetic
121 origins of its members) adapted to live in apparent suspension in turbulent water masses
122 (Reynolds, 2006). This definition implies that through trying to exert a control on their position and
123 rate of movement in the water column (i.e. its entrainment in the turbulent motion),
124 phytoplanktic populations are able to acquire the resources they need to persist in a turbulent
125 environment. Since water on Earth is in continuous motion, and the extent of this motion is

126 variable, phytoplankton has to be evolutionarily adapted to life in a wide range of hydrodynamic
127 conditions. Moreover, the polyphyletic origin of phytoplankton may reflect the existence of
128 convergent forces in evolution that moulded these organisms into planktic existence (Reynolds,
129 2006).

130 The word “suspension” in the definition of phytoplankton echoes some rigorously defined
131 physical properties of water masses such as density, viscosity and flow. Moreover, since
132 phytoplankton rarely has exactly the same density as that of the medium in which it lives
133 (isopicnic), it will tend to sink or to float. The rate of these vertical movements depends also on
134 the size of the organisms and the “apparent suspension” (i.e. the state of being neutrally buoyant,
135 neither sinking nor floating) is therefore consistently achieved by “microscopic” organisms. To find
136 a shared consensus on what can be defined as being “truly microscopic” is therefore not trivial:
137 only those organisms which are small enough to be negligibly subjected to inertial forces (i.e. to
138 the gravity) should be considered microscopic. However, even among “microscopic” organisms a
139 wide dimensional spectrum exists, spanning over 4 orders of magnitude in maximum linear
140 dimension (from sub-microns to millimetres) and 7 orders of magnitude in volume (from about 10^{-1}
141 to $10^6 \mu\text{m}^3$). These differences in dimensions necessarily have an influence on the ecology of
142 these organisms.

143 A first attempt to define a boundary between “small” and “big” organisms was made,
144 about a century ago, by Thompson (1917). Trying to explain how physical forces govern the
145 growth and shape of organisms, he separated organisms into two types: “small” organisms in
146 which physical forces acted mainly on their surface, and “big” organisms in which the forces acted
147 proportionally on their body mass. Since all the living organisms move in a fluid (air or water), the
148 boundary between these two groups of organisms can be assessed by computing their Reynolds
149 Number (Re), i.e. the ratio between the inertial (gravity) and the viscous (drag or fluid resistance)
150 forces that act on a body moving in a fluid, a unitless number (for more details see Naselli-Flores &
151 Barone, 2011). In particular:

152
$$Re = (\rho u l) \eta^{-1} = (u l) \nu^{-1}$$

153 where u is velocity of the fluid [m s^{-1}], l [m] is the length dimension available for the dissipation of
154 energy (usually the depth of the flow or the linear dimension of an object), and ν [$\text{m}^2 \text{s}^{-1}$] is the
155 kinematic viscosity of the fluid, i.e. the absolute viscosity of the fluid (η) [$\text{kg m}^{-1}\text{s}^{-1}$] with its density
156 (ρ) [kg m^{-3}] divided out. Any combination of velocity, viscosity and length scale that results in the

157 same Re will result in a geometrically similar flow regime, as characterized by the ratio of inertial
158 to viscous forces. Thus, doubling the length scale will result in a flow regime that can also be
159 realized by doubling velocity or by halving kinematic viscosity (Humphries, 2007).

160 A relatively higher importance of viscous forces is typically recorded in those organisms
161 with a very small mass (i.e. inertial forces are negligible compared to viscous forces) and $Re \ll 1$,
162 as commonly showed by unicellular and colonial phytoplankters ($10^{-6} < Re < 10^{-2}$). These organisms
163 are all subjected to Stokesian dynamics, i.e. their sinking velocity, as early recognized by McNown
164 & Malaika (1950), can be computed using the Stokes' equation:

165
$$w_s = 2/9gr^2(\rho' - \rho) \eta^{-1} \quad [\text{ms}^{-1}]$$

166 where w_s [ms^{-1}] is the sedimentation velocity of the sphere, g [ms^{-2}] is the acceleration of gravity,
167 r [m] is the radius of the sphere, ρ' [kgm^{-3}] is the density of the sinking sphere, ρ [kgm^{-3}] is the
168 density of the fluid where sinking occurs, and [$\text{kgm}^{-1}\text{s}^{-1}$] is the viscosity of the fluid. The difference
169 $(\rho' - \rho)$ is also defined as "excess of density".

170 The reliability of velocity estimated with the Stokes' equation is high, even for actively
171 swimming dinoflagellates (Sommer, 1988; Kamykowski et al., 1992), as confirmed by sophisticated
172 measurements performed by Walsby & Holland (2006). However, early observations exist
173 highlighting that phytoplankton settling rates often diverge from what is predicted by the Stokes'
174 equation, which was established to calculate sinking velocity of spherical particles (e.g. Smayda &
175 Boleyn, 1965; Eppley et al, 1967). The deviation from predictions, since long ago (Ostwald, 1902 in
176 Margalef, 1958), has been attributed to the "bizarre" morphologies often shown by different
177 phytoplankton species, characterised by expansions and protuberances, and to their effectiveness
178 in increasing the role of viscous forces on cell surface and ultimately in modulating the sinking
179 velocity of phytoplankton (e.g. Padišák et al., 2003; Chindia & Figueredo, 2018). This deviation can
180 be computed by including in the Stokes' equation a dimensionless species-specific variable called
181 coefficient of form resistance (Φ_r). Φ_r represents the factor by which the directly measured sinking
182 velocity of the particle (w_s measured) differs from that of a sphere (w_s sphere) of equivalent
183 volume and density, in the same fluid:

184
$$\Phi_r = w_s \text{ measured} / w_s \text{ sphere}$$

185

186 Therefore, the relationship governing sinking velocity of phytoplankters will be:

187 $w_s = 2/9gr^2(\rho'-\rho) \Phi_r^{-1}\eta^{-1}$ [ms⁻¹]

188 Padišák et al. (2003), studied the systematic variability of the coefficient of form resistance
189 in selected phytoplankters and contributed to better understanding the effects of phytoplankton
190 morphology on sinking. These authors showed that for the majority of phytoplankters (both
191 unicellular and colonial), the value of Φ_r is > 1 , and the associated shape will tend to sink more
192 slowly than the equivalent sphere (e.g. a spherical particle of identical volume and density).
193 Moreover, colony formation and its morphology, although increasing the size of the
194 phytoplankton unit, can effectively contribute to increase the form resistance (see also Bienfang,
195 1982; Jaworski et al., 1988). Conversely, tear-drop shapes, often associated with small
196 phytoflagellates, were shown to have $\Phi_r < 1$, thus sinking faster than the equivalent sphere.

197 Of the six variables appearing in the Stokes' equation, one (g) can be considered a
198 constant; two (ρ and η) depend on water temperature and salinity, and the other three (cell or
199 colony size, cell density and coefficient of form resistance) are species-specific biological
200 characteristics and thus subjected to adaptation and to evolutionary modification through natural
201 selection. In particular, the fact that some organisms may sink faster than the equivalent sphere
202 allow to think that they are adapted to exploiting resources under turbulent conditions quite
203 differently from those organisms sinking more slowly than the equivalent sphere, which have
204 therefore to be able to show different adaptive strategies. Therefore, minimizing sinking velocity is
205 actually not the main goal of phytoplankton. Instead, maximising the opportunities for suspension
206 under variable turbulent conditions should be considered the primary evolutionary target of this
207 group of organisms.

208 In summary, the adaptations required to decrease sinking velocity include small size,
209 and/or excess of density close to that of water [$(\rho'-\rho) = 0$ or slightly positive], and/or mechanisms
210 for increasing frictional resistance with the water (i.e. expansions and protuberances),
211 independently from size and density. All these features are addressed at enhancing the
212 entrainability of phytoplankton by turbulent eddies. Conversely, other phytoplankters invested in
213 enhancing their ability to escape entrainment by turbulent eddies. This goal is achieved through a
214 negative excess of density [$(\rho'-\rho) < 0$], and/or relatively larger size (including formation of
215 colonies), and/or streamlining (i.e. tear-drop shapes), and/or bearing "propellers" (i.e. flagella) to
216 move rapidly through water.

217 However, it has been observed that healthy and physiologically active phytoplankton
218 organisms sink much slower than dead or moribund ones, without perceivable alteration in their
219 size and morphology (for more details see Naselli-Flores & Barone, 2011 and literature therein).
220 These differences have been related to the breakdown of active physiological mechanisms (vital
221 factor) yet unidentified but likely due to a rapid change in density that accompany physiological
222 death (Wiseman & Reynolds, 1981).

223 The evidence that phytoplankton species show different physiological characteristics *per se*
224 does not answer the question “why are there so many different morphologies in phytoplankton?”.
225 It is therefore important to point out that several trade-offs exist between morphological (i.e. size
226 and shape of single cells and colonies) and physiological traits of phytoplankton, and that
227 morphology, through modulating the physiological pathways of protein synthesis, photosynthesis
228 and nutrient uptake, deeply impact growth and metabolism of the different phytoplankton
229 populations (Litchman & Klausmeier, 2008 and literature therein).

230 The striking morphological variability, both intra- and interspecific, of unicellular and
231 colonial phytoplankton (see Naselli-Flores et al., 2007 and literature therein), has been early
232 recognised as a specific evolutionary feature allowing its living in apparent suspension in a variety
233 of hydrodynamic conditions (Hensen, 1887 in Smayda, 1970). The deep ecological implications of
234 phytoplankton morphological features in determining their competitive success led Lund (1959) to
235 state “It would therefore be useful if one could study their rate of sinking before embarking on
236 biochemistry” when talking about the role of buoyancy in the ecology of freshwater
237 phytoplankton.

238

239 *Is there an upper constraint to the maximum size of planktic algae?*

240 The microscopic dimensions of phytoplankton have been often explained by the need to uptake
241 nutrients from the surrounding medium over the cell surface. Furthermore, once inside the
242 organisms, nutrients have to be translocated to the site of use. These two constraints have a role
243 in determining the small size of cells and in pushing toward a relatively high surface-to-volume
244 ratio (Reynolds, 1984). However, this reason alone does not fully consider the wide range of
245 variability of phytoplankton size and shape, and the relatively low surface-to volume ratio, which
246 characterises the largest and spherical phytoplanktic organisms.

247 An additional explanation lies in the way in which water masses move. When a fluid is
248 moved by a force acting on it, small portions of that fluid will tend to stick to themselves and to
249 the particles eventually suspended in that fluid. Viscosity represents the magnitude of this
250 tendency and will depend on the physicochemical nature of the fluid itself (Vogel, 1994). Following
251 Reynolds (2006), if a mild force (τ) is applied to the surface of a fluid (e.g. wind blowing on the
252 surface of a water body), the interaction between these two fluids (air and water) will result in the
253 linear dragging of the water molecules at the air-water interface in the same direction of the wind.
254 The movement will be progressively transmitted to the layer below and propagated downward,
255 albeit at a lower velocity because part of the energy will be dissipated by the shear stress (due to
256 viscosity) generated between these layers. The smooth sliding of each layer of water molecules
257 over the one below is known as laminar flow. In this case the mechanical energy introduced in the
258 fluid is accommodated in an ordered structure of parallel layers moving in the same direction and
259 showing a vertical gradient of horizontal velocities (u) [ms^{-1}] whose steepness is defined by the
260 differential notation du/dz (i.e. the decrement of horizontal velocity for a small increment in the
261 vertical direction z [m]). Persisting the condition of laminar flow, the ratio between the applied
262 force τ [kgms^{-2}] per unit area and the velocity gradient corresponds to the absolute viscosity of the
263 water, η . That is,

$$264 \quad \eta = \tau(du/dz)^{-1} \quad [\text{kgm}^{-1}\text{s}^{-1}]$$

265 Absolute viscosity of water inversely varies with temperature and directly with salinity.

266 Biological factors, as the secretion of exopolymers from both phytoplankton and bacteria
267 can contribute to increase viscosity on a small scale (Decho, 1990; Jenkinson & Sun, 2010),
268 whereas morphological features of phytoplankton such ornamentations of the cell wall (e.g.
269 papillate surface), spines, bristles and protuberances (and their distribution on the surface of cells
270 and colonies) may contribute to increase the effects of viscosity at an individual scale (Padisák et
271 al., 2003). Moreover, temperature-dependent variations in density and viscosity of water are
272 known to control ciliary activity and swimming behaviour in several zooplankton species (e.g.
273 Larsen et al., 2008; Larsen & Riisgård, 2009; Moison et al., 2012; Simoncelli et al., 2019).

274 Viscosity is therefore a measure of the resistance offered by the water to the motion
275 induced, at different spatial scales, by buoyancy, swimming, tide, wind or Coriolis effects. If
276 mechanical energy introduced in the aquatic system is higher than that the molecular structure of
277 the fluid is able to accommodate in a laminar flow, turbulence will develop.

278 Turbulence is a quite complex subject of Hydrodynamics (whose treating goes beyond the
279 scope of this review) and its impact on the behaviour of planktic algae has remained obscure for a
280 long time. The development of instrumentation and direct sensing of turbulence began only in the
281 second half of the last century (see Imberger, 1998). The results collected by this new generation
282 of instruments were rapidly incorporated in physical limnology and oceanography (e.g. Imberger &
283 Spiegel, 1987; Imboden & Wüest, 1995; Wüest & Lorke, 2003; Hutter et al., 2011a; 2011b; 2014;
284 Baudena et al., 2019) and strongly contributed to a better characterisation of the phytoplankton
285 environment and of the complex physical relationships between the movement of phytoplankton
286 and that of the fluid in which it is contained (e.g. Guasto et al., 2012; Croze et al., 2013 and
287 literature therein).

288 When turbulence develops, the energy is not dissipated through an ordered system of
289 parallel layers of water sliding one on each other but through cascades of gyratory structures,
290 called eddies, that have smaller and smaller dimensions as they proceed downward (or upward –
291 the motion is not necessarily unidirectional) the vertical direction. The progressively smaller
292 dimensions of the eddies are due to the dissipation of energy as heat. Of course, viscosity is still
293 effective among the small portions of the fluid but the intensity of the energy imparted to the fluid
294 overwhelms viscosity effects and the motion of the fluid will assume complex and quite chaotic
295 patterns; there is however an end point of the eddy spectrum where energy is dissipated enough
296 to allow viscous forces to overwhelm inertia. Reynolds (1998) calculated that even in the most
297 dissipative conditions the smallest eddy has a diameter of about 0.2-0.4 mm. To avoid mechanical
298 damages caused by turbulence and to take advantage of the viscosity of mobile water masses (e.g.
299 to be constantly embedded in a laminar flow), planktic algae must be smaller than the smallest
300 eddy. In fact, unicellular organisms rarely exceed 200 μm , larger colonies generally growing in only
301 very calm or stratified water layers. The smallest eddy size therefore places a physical constraint
302 to the upper limit of size that planktic algae may attain.

303

304 *Moving in a constantly mixed environment*

305 The word “plankton”, coined in 1887 by the German physiologist Viktor Hensen from Greek
306 *πλαγκτόν*, means “wanderer” and reflects the basic characteristic of these organisms that “go with
307 the flow”, where the water movements (i.e. the turbulent motion) drift them. However, it tells us
308 little about the trajectories followed by individual phytoplankters when they are embedded and

309 transported in water motion. Furthermore, it does not contribute to understanding the conditions
310 of life at the spatial scales appropriate to the different species. Actually, the time scale of
311 phytoplankton growth falls between $10^5 - 10^6$ s (Reynolds, 1990), which corresponds to the time
312 scale of sub-mesoscale turbulent processes (Mahadevan, 2016). In particular, as shown by
313 Reynolds (1994), a wind velocity of 8 m s^{-1} on the water surface creates a turbulence that imparts
314 a speed to fully entrained phytoplankton which allows the cell to travel a 5 m deep mixed layer
315 and to regain its initial position in about 10 minutes. This time ($\sim 10^2$ s) is three-four orders of
316 magnitude lower than the time required by phytoplankton cells to replicate ($10^5 - 10^6$ s) or to
317 develop a stable population ($10^6 - 10^7$ s) and clearly attest the dominance of mixed-layer
318 advection in the spatial distribution of phytoplankton organisms. In other words, the transport
319 time (the flow velocity of water masses, often indicated as flushing time or residence time)
320 influences algal growth and loss rates (e.g. Reynolds & Wiseman, 1982), and biomass
321 accumulation (e.g. Lucas et al., 2009 and literature therein).

322 To assess the trajectories followed by phytoplankton species and their displacement in the
323 mixed layer as they are transported in the water motion is a complex issue (Clifton et al., 2018). By
324 simplifying, it can be related to the velocity fluctuations of turbulence along horizontal and vertical
325 axes in the three-dimensional water mass. The variable resulting from the combination of the
326 different velocities is called turbulent intensity $(u^*)^2$ and its square root u^* , which has the
327 dimension of velocity (m s^{-1}), is known as turbulent velocity or shear velocity. Turbulent velocity
328 varies significantly in time and space. However, as discussed above, independently from the value
329 of turbulent velocity, phytoplankton live in an immediate spatial environment that is wholly
330 viscous. At the same time, it is liable to be transported far and quickly in the turbulent field, with
331 varying intensities and frequency. As pointed out by Reynolds (2006), phytoplankton lives in
332 viscous packets, rapidly moving in any of three dimensions. The extent by which phytoplankton is
333 efficiently embedded in these viscous packets determines its degree of entrainment in water
334 motion.

335 The degree of entrainment of phytoplankton depends on a quotient, ψ [unitless] which
336 represents the boundary between a behaviour dominated by the turbulent diffusivity of water and
337 a behaviour dominated by the speed of phytoplankton cells or colonies (as described by their
338 sinking and floating velocity and/or by the velocity imparted by flagellar propulsion) in the
339 medium (Humphries & Imberger, 1982). According to Reynolds (1994), it can be approximately
340 computed according to the formula:

341

$$\psi \approx w_s/15u^*$$

342 where w_s [ms^{-1}] is the sinking velocity of a particle and u^* [ms^{-1}] is the turbulent velocity of water.

343 The latter can be related to the mean windspeed 10 m above the water surface (Denman &

344 Gargett, 1983; Moreno-Ostos et al., 2009):

$$345 \quad u^* = (\rho_a c_f U_{10}^2 / \rho_w)^{0.5} \quad [\text{ms}^{-1}]$$

346 where ρ_a is the density of the air, ρ_w is the density of the water, U_{10} is the wind speed 10m above

347 the water surface and c_f is a dimensionless coefficient for drag friction upon water (1.3×10^{-3}).

348 A value of $\psi = 1$ represents the boundary between entrainment (particles are embedded in

349 the turbulent motion) and disentrainment (particle properties dominate distribution). The smallest

350 species of the picoplankton (cells $< 2\mu\text{m}$) are almost perfectly entrained, increasingly larger

351 species of the nanoplankton ($2\text{--}20\mu\text{m}$) and microplankton ($20\text{--}200\mu\text{m}$) are likely to have higher

352 sinking rates and to be liable to escape from turbulent eddies (Reynolds, 2012b). However, since

353 w_s is generally 1 to 6 orders of magnitude less than u^* (Reynolds, 2006), under most of the

354 hydrodynamic conditions experienced by a water body, phytoplankters are constantly

355 redistributed in the turbulent water column and their trajectories will follow all the possible

356 directions in the three-dimensional pelagic environment. This is true also for actively swimming

357 dinoflagellates, whose spatial distribution is often patchier than that of non-motile species

358 (Durham et al., 2013). Dinoflagellates establish vertical heterogeneity by migration during calm

359 weather, then transport by water motions cause their patchy distribution (Alexander & Imberger

360 2009). The swimming behaviour shown by self-propelling algae when embedded in water motion

361 was analysed in several studies to explain both the hydrodynamical aspects of algal motion and

362 the dynamics of bloom formation (e.g. Kessler, 1985; Pedley & Kessler, 1992; Reigada et al., 2003;

363 Goldstein, 2015; Durham et al., 2009; O'Malley & Bees, 2011). In particular, actively swimming

364 single cells are known to respond in a complex way to flow (e.g. Croze et al., 2013; Cencini et al.,

365 2019) and their mean swimming direction largely depends on flow direction and intensity

366 (gyrotaxis). In the absence of flow gradients, cells will tend to swim upwards on average

367 (gravitaxis). More in general, the thrusts of the turbulent eddies can move phytoplankters

368 upwards faster than they gravitate downwards and allow their sinking trajectories to re-initiate at

369 a higher point in the turbulence field. However, as turbulence decays with depth, the role of

370 sinking, floating and self-propelling velocities will increase with depth until a point where the

371 entraining capacity is too weak to maintain entrainment. Some other particles will therefore be
372 lost by sedimentation.

373 Since entrainment depends on w_s , it is not surprising that phytoplankters adaptively show a
374 great variability of size, and an array of shapes that allow them to modulate their sinking velocity
375 through increasing/decreasing form resistance.

376 In addition, phytoplankters also developed tools to vary, more or less effectively, their cell
377 density in the attempt to reduce the excess of density and avoid sedimentation losses (e.g.
378 Peperzak et al., 2003). The density of phytoplanktic cells depends on their content in proteins,
379 carbohydrates, nucleic acids (all more dense than water) and lipids (less dense than water).
380 Although these components were found to be positively correlated with cell volume and taxon-
381 specific (Hitchcock, 1982), the mechanisms deployed by phytoplankton to reduce cell density are
382 shared by species phylogenetically distant, most likely as a result of evolutionary convergence
383 (Reynolds, 2006). These include mucilage production (e.g. Reynolds, 2007), lipid accumulation (e.g.
384 Walsby & Reynolds, 1980), ionic (e.g. Kahn & Swift, 1978) and other osmolytes regulation (e.g.
385 Boyd & Gradmann, 2002), and, in cyanobacteria, production of gas-vesicles (e.g. Reynolds et al.,
386 1987; Walsby, 1994). Other “heavy” constituents as silica and carbonate impregnated into the cell
387 walls can affect sinking. However, in diatoms, the thickness of the frustule was found to be
388 negatively scaled with size. This can contribute to mitigate the effects of a larger size on sinking
389 velocity (Miklasz & Denny, 2010).

390 The sinking behaviour of a single phytoplankton population can differ significantly from the
391 average sedimentation rate shown by the whole phytoplankton assemblage (Riebesell, 1989). This
392 is in large part due to the fact that assemblages are generally composed by species with
393 morphologies that respond differently to environmental stimuli, and that many of them eventually
394 live in relatively low numbers under sub-optimal conditions (Padisák, 1992). The high variability
395 intrinsically imparted by water turbulence to the pelagic environment (which also include a
396 variability in the re-distribution of the resources needed to phytoplankton growth) allows these
397 species to eventually gain advantage (and reach dominance) when the average physical conditions
398 of the water masses change (Padisák et al., 2010a).

399 Last but not least, phytoplankters sink, float and swim in a moving medium (e.g. Reynolds
400 & Walsby, 1975). The reciprocal movements of phytoplankters and of the water masses in which
401 they are embedded have been demonstrated to have a role in the spatial distribution of

402 phytoplankton at different scales (Font-Muñoz et al., 2017 and literature therein). In particular,
403 the different circulation patterns of the water masses both at small (advection: 1-10 cm) and at
404 larger scales (currents: 1-10 km) can be effective in shaping the spatial variability of phytoplankton
405 size structure in the aquatic environment (Reynolds et al., 1993).

406

407 *Phytoplankton access to resources while entrained and disentrained in water motion*

408 The pelagic environment is characterised by a great heterogeneity with regard to resources
409 distribution and availability, as well as with regard to the direction and intensity of water
410 movements (Reynolds, 1997). The water movements, generally much larger than the value of
411 molecular diffusivity, largely contribute to re-distribution of heat (Jassby & Powell, 1975) and
412 nutrients (Robarts & Ward, 1978) within and across the upper mixed layer of a given water body.
413 There, light is attenuated with depth and varies in relation to the hour of the day, the season, the
414 geographic location, the meteorological conditions, the trophic state, the inorganic seston and
415 humic material contents. Nutrients accessible for a phytoplanktic organism are often patchily
416 distributed, even at the scale of a few millimetres, and their concentrations generally increase
417 with depth (Padisák & G-Tóth, 1991; Reynolds, 2006). The movements of water masses at
418 different spatial and temporal scales influence and modulate the availability of light and nutrients
419 for phytoplankton: they can transport nutrients from the deep layers to the euphotic zone and can
420 enhance the (re)suspension of phytoplankton in the illuminated layers (Mahadevan, 2016).
421 Moreover, since physical factors can modify growth (and loss) rates of phytoplankton, they can
422 also modify the competitive abilities of phytoplankton and re-shape the composition of
423 assemblages (Seip & Reynolds, 1995; Padisák et al., 2010b).

424 Temperature is largely considered a powerful driver of phytoplankton size structure in
425 different aquatic ecosystems (e.g. López-Urrutia & Morán, 2015; Rasconi et al., 2015; Pulina et al.,
426 2018; Rugema et al., 2019; Abonyi et al., 2020) due to the multiple constraints it imposes on cell
427 growth. Water temperature exerts a direct influence on metabolic rates and biochemical
428 processes of phytoplankton (e.g. Chisholm, 1992) and, consequently, it has an important role in
429 determining the rates of resource uptake (both nutrients and light) by phytoplankton (Borowitzka
430 et al., 2016). Moreover, temperature affects the duration of stratification and the thickness of the
431 surface mixed layer, with different and independent consequences to phytoplankton growth
432 (Winder & Sommer, 2012). Falkowski & Oliver (2007) suggested that, at a global scale, higher

433 temperatures are causing a decreased turbulent mixing in the upper part of the oceans, and a
434 consequent reduction of nutrient availability, which is leading to an altered size structure of
435 phytoplankton assemblages. Last but not least, temperature also affects two variables (density
436 and absolute viscosity of water) directly linked to phytoplankton sinking, floating and swimming,
437 and ultimately to its entrainment in water motion (Zohary et al., 2017).

438 By regulating its entrainment in the external medium through species selection and/or
439 phenotypic plasticity, phytoplankton has to accommodate for two vital necessities: to gain enough
440 light and enough nutrients to sustain net production. Although a geometrical trade-off exists
441 between size and shape (Litchman & Klausmeier, 2008; Stanca et al., 2013), phytoplankton size
442 structure is considered to be largely driven by nutrient availability (e.g. Peter & Sommer, 2013; De
443 Senerpont Domis et al., 2013; Marañón et al., 2015; Mousing et al., 2018), whereas light
444 availability can have a strong influence in determining the shape of phytoplankton organisms (e.g.
445 Naselli-Flores & Barone, 2007). Disentrainment (by increasing sinking velocity or by active
446 swimming) may therefore represent an advantage with regard to nutrient supply, since it
447 facilitates the movement of the organisms towards deeper layers where nutrient concentrations
448 are higher. At the same time, it brings organisms away from the upper layers where the light
449 conditions are more favourable. Different species have therefore adopted different strategies to
450 manage and regulate their positioning in the water column. Each strategy represents the attempt
451 to maximise the chances to survive in the challenging pelagic environment. Moreover,
452 phytoplankton species are characterised by a relatively high degree of phenotypic plasticity
453 (Naselli-Flores & Barone, 2011). This morphological variability can be considered as a tool to cope
454 with environmental changes. Zohary et al. (2017) noted that many phytoplankton species, of
455 diverse taxonomic phyla, commonly found in Lake Kinneret, Israel, all year-round (even though
456 with different abundances) had larger cells or colony size in winter, and smaller in summer. Similar
457 results were obtained by Naselli-Flores (Fig. 1, previously unpublished data) for two phytoplankton
458 species from Sicily (Italy). Pulina et al. (2019) analysed long-term variability of single
459 phytoplankton species and assemblage size structure in Mediterranean reservoirs. They found
460 assemblages with smaller mean cell size in summer and larger mean size in winter. Literature
461 surveys, allowed Sommer et al. (2017) and Zohary et al. (2020) to conclude that marine and
462 freshwater phytoplankton become smaller in size with increasing water temperatures. This
463 occurred at the species and community levels. Based on computations of Stokes' sinking velocity,
464 Zohary et al. (2017) hypothesised that the seasonal changes in intra-specific cell or colony size

465 they observed could represent an adaptation that enabled species to overcome temperature-
466 dependent changes in water density and viscosity. These changes are summarised in Figure 2
467 where the theoretical relationships between phytoplankton size and sinking velocity are shown. In
468 the figure, the curves represent the sinking velocities attained by spherical algae of different size
469 (but with the same cell-density of 1.15 g cm^{-3}) in the temperature range $10 - 30 \text{ }^\circ\text{C}$: when
470 temperature increases (and the related water density and viscosity decrease), smaller
471 cells/colonies have to be selected to keep a given sinking velocity constant.

472 Compared to freshwater, seawater shows higher density and viscosity values at a given
473 temperature. Differences in the size distribution of marine and freshwater diatoms are known,
474 with marine diatoms larger than freshwater species (Litchman et al., 2009). However, these
475 differences were explained in terms of nutrient fluctuations and differences in the depth of the
476 mixed layer rather than as a consequence of the higher density and viscosity of seawater. A
477 decrease in cell size of microphytoplanktonic organisms was also registered in correspondence of
478 increased ice-melting (and decreased salinity) episodes in Antarctica (Teixeira de Lima et al.,
479 2019). Unfortunately, to our knowledge, no data exist on the effects exerted by viscosity and
480 density on the size structure of marine and freshwater phytoplankton. Nevertheless, larger or
481 smaller specimens are alternatively selected by environmental pressure and their size change, as
482 suggested by Zohary et al. (2017), could be addressed at counteracting the changes in density and
483 viscosity of the water and at adjusting their sinking velocities in order to achieve a similar access to
484 resources in the different physical scenario set by seasonal and environmental variations in the
485 density and viscosity of water. To our knowledge, the effects of temperature on the morphology
486 of single phytoplankton species were rarely investigated (e.g. Bailey-Watts & Kirika, 1981; De
487 Miranda et al., 2005; Jung et al., 2013) and, apart from Zohary et al. (2017), no other works exist in
488 the literature on the potential effects of temporal and spatial variation in water density and
489 viscosity on phytoplankton. However, it is well known that the increase in density and viscosity
490 along the water column during thermal stratification is responsible for the spatial segregation of
491 morphologically different phytoplankton species, and for the eventual establishment of the so
492 called “deep chlorophyll maximum” (e.g. Selmečzy et al., 2016) as one extreme case, as well as
493 surface scums of cyanobacteria (e.g. Zohary & Robarts, 1990; Paerl & Otten, 2013) at the other
494 extreme.

495 Indirect evidences of the effects exerted on phytoplankton by temperature-dependent
496 variation of water viscosity and density are abundant in the literature. A direct influence of

497 temperature on the size structure of phytoplankton assemblages was found by Mousing et al.
498 (2014), who showed a global decrease in the relative contribution of large cells to phytoplankton
499 assemblages as temperature increases regardless of ambient nutrient availability. Analogous
500 results were shown by Winder et al. (2009) who recorded a compositional shift in the diatom
501 assemblage of Lake Tahoe, independently from nutrient concentrations and addressed at
502 favouring smaller species, as a consequence of increased temperatures due to global warming.
503 Several authors found similar patterns (smaller phytoplanktonic organisms in warmer periods) using
504 paleolimnological records to compare different climate periods over geological and centennial
505 time scales (e.g. Smol et al., 2005; Finkel et al., 2005; Mousing et al., 2017).

506 As regard phytoplankton assemblage composition, the role of higher temperature and
507 lower density and viscosity of water, along with an atelomictic thermal pattern, was discussed by
508 Barbosa & Padisák (2002) to explain the replacement of diatoms by desmids, frequently observed
509 in some large tropical lakes with deep epilimnia (Descy & Sarmento, 2008). According to these
510 authors, the low density and viscosity of the water in shallow epilimnia would increase the sinking
511 velocity of diatoms enough to cause an excessive loss by sedimentation, making the lighter but
512 also shade-adapted desmids more suitable to small and warmer waters. As demonstrated by Salas
513 de Leon et al. (2016), tropical lakes stratify and mix more easily, and at lower depths than
514 temperate ones in response to changes in wind intensity and to reversals in the heat flux.

515 Climate-driven physical properties of water can therefore play a role in determining the
516 composition and structure of phytoplankton. Analogous results were shown by Rugema et al.
517 (2019) by studying long-term, non-seasonal dynamics of phytoplankton in Lake Kivu, confirming
518 what was shown by Ptacnik et al. (2003): specific sedimentation loss rates can be higher in shallow
519 mixed layers (as those occurring in tropical lakes, especially under atelomictic conditions) than in
520 deep ones because the probability of resuspension increases with increasing mixing depth. To
521 prevent settling out of the upper mixed layer, natural selection will therefore favour
522 phytoplankton organisms with lower sinking rates. However, presence of non-buoyant
523 phytoplankton like diatoms and desmids in epilimnia appears paradoxical at first sight. Diatoms
524 sink relatively fast because of cell density reasons (specific gravity of diatom frustules is about 2 g
525 cm⁻³; Smol et al., 1984) and small desmids because of their low form resistance ($\Phi_r < 1$; Padisák et
526 al., 2003). In this case, fast sinking within the epilimnion is beneficial since cells can reach the
527 nutrient rich density gradient (which anyhow slows sinking down) and the climate driven nocturnal
528 mixing (atelomixis) resuspends the cells having a temporary “rest” on the density gradient (Souza

529 et al., 2008). This strategy is useful as long as growth rate can exceed or at least compensate
530 sinking loss and reminds us that sedimentation properties and nutrient uptake strategies are
531 closely linked to each other.

532

533 *Nutrient uptake and entrainment in water motion*

534 Phytoplankton size is conveniently described by the ratio between the surface and the volume (sv^{-1})
535 of the organism (unicell or colony). Size influences several metabolic patterns of phytoplankton,
536 ultimately addressed at optimizing the growth of the populations. Reynolds (1989) showed that
537 maximum growth rates at 20 °C, r_{20} , and sv^{-1} , in continuously light- and nutrient-saturated
538 cultures, are scaled according to the formula:

$$539 \quad r_{20} = 1.142(sv^{-1})^{0.325}$$

540 Not surprisingly, growth rates are higher in smaller species, which are also characterised by lower
541 sinking velocities (Fig. 3). Conversely, larger cells and colonies characterised by lower growth rates
542 will show higher sinking velocity. This different behaviour is strictly associated to the different life
543 strategies (C-S-R) that characterise large and small sized phytoplankton (see below and Reynolds,
544 1995).

545 Evidently, all the nutrients needed by phytoplankton to grow have to be drawn from the
546 surrounding water. There, nutrient concentrations (typically in the range 2-50 $\mu\text{mol N L}^{-1}$ and 0.1-
547 5 $\mu\text{mol P L}^{-1}$) are 5-6 orders of magnitude lower than those occurring within the cells ($\approx 2.8 \text{ mol N}$
548 L^{-1} and $\approx 0.18 \text{ mol P L}^{-1}$; see Reynolds, 2006). Therefore, phytoplankton has to overcome a steep
549 chemical gradient to perform nutrient uptake and this requires a complex system of
550 transmembrane proteins to capture, bind and transport specific molecules into and within
551 phytoplankton cells as well as a high amount of energy (Reynolds, 2006). This cellular mechanism
552 can only be effective over a short distance beyond the cell but sufficient to influence the
553 concentration of nutrients within the boundary layer adjacent to the cell (Pasciak & Gavis, 1975;
554 Sommer, 1988; Estrada & Berdalet, 1997), up to creating, in the absence of water flow or algal
555 movement, a depletion zone (the so called “concentration boundary layer” or “diffusive boundary
556 layer”, see Kiørboe, 2008) in its immediate vicinity (Bonachela et al., 2011). Both microturbulence
557 and phytoplankton motion (either swimming or passive sinking/floating) can therefore make the
558 diffusive boundary layer thinner (Arin et al., 2002; Peters et al., 2006) and increase the fluxes of

559 nutrients into the cells above the fluxes that would be experienced by one cell that is not motile
560 with respect to the adjacent medium (Munk & Riley, 1952; Ploug et al., 1999; Kiørboe et al., 2001;
561 Guasto et al., 2012). However, Riebesell & Wolf-Gladrow (2002) showed that, for particles moving
562 in the water at low Reynolds numbers, a distinction has to be made between i) very small cells
563 (e.g. *Chlorella* or small centric diatoms) deeply entrained in the turbulence spectrum and ii) larger
564 or actively swimming cells or colonies ($Re > 10^{-3}$). By considering the rate of solute diffusive
565 transport, the concentration gradient from the medium to the algal surface and the thickness of
566 the diffusive boundary layer, these authors demonstrated that in the first group of organisms the
567 benefit of increasing water fluxes (i.e. the dependence on turbulence) around the cell is quite
568 marginal, whereas it becomes increasingly important for larger organisms. It was also shown that
569 the nutrient concentration threshold below which cells cannot sustain a given growth rate
570 increases rapidly with cell size (Chisholms, 1992). An increase in the relative movement between
571 the organisms and the water masses allow large organisms to overcome the biophysical constraint
572 given by i) the thickening of the diffusion boundary layer around the cell, and by ii) the reduction
573 in nutrient diffusion per unit of cell volume (Marañón, 2014). Moreover, large elongated cells and
574 multi-celled trichomes can also show an increased nutrient flux per unit cell volume due to the
575 increased surface-to-volume ratio (Pahlow et al., 1997; Karp-Boss & Boss, 2016). These results
576 confirmed the earlier observations made by Walsby & Reynolds (1980) who analysed the trade-
577 offs between sinking and uptake rates in diatoms and suggested that under chronically low
578 nutrient concentrations, large organisms depend much more on turbulence than smaller ones to
579 maximise nutrient acquisition.

580 It is therefore the trade-off between entrainment and nutrient availability that determines
581 the competitive success of a species, rather than the absolute value of nutrient concentrations.
582 This trade-off also plays an important role in the seasonal succession of freshwater phytoplankton.
583 As shown by Reynolds (1988; 1995; 1997), small spherical or quasi-spherical organisms (volume <
584 $10^3 \mu\text{m}^3$) are good competitors under deep mixing and high nutrient availability (as in winter, early
585 spring in temperate lakes) whereas a reduced nutrient availability, and lower mixing conditions (as
586 in late spring, summer) will favour larger ($10^4 < \text{volume} < 10^6 \mu\text{m}^3$), spherical or subspherical, more
587 stress-tolerant ones. These two groups respectively well fit the features of *r*- and *K*-selected
588 organisms, as applied to plankton by Kilham & Kilham (1980).

589

590 *Access to light when travelling in the water column*

591 The ability to harvest and process light at low irradiance levels is enhanced by small size or by the
592 attenuation of larger size in one or two planes (Reynolds, 2006; Naselli-Flores & Barone, 2011).
593 These morphological traits characterise phytoplankton organisms with a high photon affinity that
594 can therefore photosynthesize with high capacity at low ambient light (Reynolds, 1997; Padisák et
595 al., 2003). Moreover, as recently shown by Durante et al. (2019), who reviewed the data on sinking
596 velocity of phytoplankton species available in the literature, cell shape changes as size increases
597 and cylindrical shapes can get much larger than spherical or subspherical cells though maintaining
598 a similar sinking rate.

599 Since morphological traits related to small spherical and large cylindrical shapes are
600 typically shown by both small r- and elongated K-selected species, they were placed by Reynolds
601 et al. (1983) in a strategic group created *ad hoc* (w-selected species, investing in efficient light
602 conversion; see also Reynolds, 2003).

603 The relationships existing between phytoplankton specific growth rates at sub-saturating
604 light intensities (α_r) and cell morphology were discussed by Reynolds (1997) who found that:

605
$$\alpha_r = 0.257(msv^{-1})^{0.236}$$

606 where m is the maximal linear dimension. The product of m and sv^{-1} well describes the attenuation
607 in a solid and its departure from a spherical shape. Its value is actually minimal (6) for the spherical
608 shape and progressively increases as it is attenuated in one or two planes, up to reaching a
609 filamentous shape (see Naselli-Flores & Barone, 2011 for further details). Elongated shapes are
610 generally characterised by a coefficient of form resistance up to 2.3-5.1 times higher than that of
611 the equivalent sphere (Reynolds, 1984) and, for cylindrical shapes, their sinking velocity may
612 depend on initial filaments' orientation (Holland, 2010). Padisák et al. (2003), by using PVC models
613 for reproducing the shapes of different phytoplankton species and allowing them to sink in a
614 glycerine medium, showed that sinking velocity of elongated (cylindrical) shapes is also positively
615 related to the length/width ratio of the cylinders and to their degree of coiling (tightly coiled
616 filaments sink faster than loosely coiled ones). These results confirmed earlier observations carried
617 by Booker & Walsby (1979) who noted that cyanobacterial filaments with helical shapes sank
618 faster than straight filaments of comparable length. Several morphological features, which affect
619 the sinking velocity and modify the entrainment of phytoplankton organisms in the turbulent
620 motion, can be expressed within the extent of phenotypic plasticity of a given population in

621 response to the selective pressure of environmental constraints. When these constraints
622 overcome the range of phenotypic plasticity of a species, the species will be replaced by another
623 having a shape better fitting the new environmental conditions.

624 The reduced sinking velocity shown by elongated shapes allows them to persist in the
625 upper part of the mixed layers of the water column where light availability is higher. Adopting this
626 strategy can be particularly helpful in the more productive environments, characterised by
627 reduced light availability and by nutrient concentrations above limiting thresholds (e.g.
628 Zapomělová et al. 2008; Naselli-Flores, 2014).

629 However, the environmental template sets the rules and, as shown by Reynolds et al.
630 (1986), under stagnant conditions sinking may represent a short-term benefit to escape the
631 damaging photo-inhibition caused by oxidative stress of excessive insolation near the water
632 surface.

633 In well-mixed environments, a “critical light intensity” was defined as the species-specific
634 minimal light intensity needed for the species to grow under a constant light supply (Huisman &
635 Weissing, 1994). Accordingly, the species showing the lowest value of critical light intensity will
636 constitute better competitors under light-limited conditions (Weissing & Huisman, 1994; Huisman
637 et al., 1999). A further consequence is that establishment of a highly shade adapted species [like
638 *Raphidiopsis raciborskii* (Wołoszyńska) Aguilera, Berrendero Gómez, Kastovsky, Echenique &
639 Salerno in any appropriate ecosystem] may build up much higher biomass per square meter than
640 its also N-fixing counterparts (e.g. *Aphanizomenon* or *Dolichospermum*). However, phytoplankton
641 entrained in the turbulent water motion is exposed to a fluctuating light regime while being
642 transported up and down in the water column. The frequency of such fluctuations, at a given
643 location and season, is directly related to the amount of kinetic energy imparted to water masses
644 by wind intensity (Reynolds, 1987). The relationships between light attenuation and the time
645 required to fully travel (and be repositioned) along a well-mixed water column (in the order of 10^3
646 s during vigorous wind mixing in a water column 5 m deep), will depend on the depth of the
647 mixing zone and will have implications in the selection of phytoplankton species (Reynolds, 1993).
648 The ratio between euphotic and mixing depth (z_{eu}/z_{mix}) was therefore selected as a good predictor
649 of phytoplankton performance under fluctuating light conditions (Huisman, 1999).

650 To explain how phytoplankton can manage to persist, and eventually bloom, in the
651 illuminated water layers, Huisman et al. (2002 and literature therein) proposed a population

652 dynamic theory of sinking phytoplankton that considered balancing between light-dependent
653 growth rates, mortality rates, sinking rates, and turbulent-diffusion rates. These authors described
654 the existence of a “turbulent window” that allows phytoplankton to grow in the euphotic zone.
655 The window is characterised by intermediate turbulence levels allowing phytoplankton organisms
656 to avoid both sedimentation losses and dilution beyond their growth capacity, while being
657 passively transported within the mixed layer. The interplay between the depth of the mixing zone
658 (z_{mix}) and that of the euphotic layer (z_{eu}) was further analysed by Huisman & Sommeijer (2002) and
659 by Huisman et al. (2004 and literature therein), who showed that changes in the z_{mix}/z_{eu} ratio
660 (primarily caused by a lower turbulent diffusivity) are key factors in determining the species
661 structure of phytoplankton assemblage. Naselli-Flores (2000) reached similar conclusions by
662 studying phytoplankton dynamics in Mediterranean reservoirs. In fact, the z_{mix}/z_{eu} ratio indicates
663 the proportion of time a phytoplankton organism may spend at critical light intensities once it is
664 entrained in the mixed water column (Naselli-Flores & Barone, 2007). As shown by Reynolds
665 (1984), assuming a constant respiration rate of 10% of maximum photosynthetic rate, net growth
666 of entrained phytoplankton cannot occur when $z_{mix}/z_{eu} > 3$ due to the insufficient extent of the
667 aggregated photoperiod. A significant relationship between z_{mix}/z_{eu} and msv^{-1} is shown in Naselli-
668 Flores & Barone (2007) and in Naselli-Flores (2011) attesting the selective tendency toward an
669 attenuated shape as z_{mix}/z_{eu} ranges between 1.5 and 3.0. In shallow, optically-deep water bodies,
670 as those characterised by a high algal turbidity, low flow conditions and values of the ratio higher
671 than 3 were found to promote the dominance of gas-vacuolated cyanobacteria that float to the
672 surface shading eukaryotic phytoplankton (e.g. Naselli-Flores, 2003; Bormans et al., 2005). In these
673 cases, buoyancy regulation represents an efficient strategy to persist in the illuminated layer and
674 to monopolise light resources, while shading and outcompeting phytoplankton species more
675 dense than water. In water bodies subjected to low wind speeds where shallow diurnal mixed
676 layers form, those cyanobacteria are further advantaged by maintaining position within the
677 diurnal mixed layer, while non-buoyant species depend on turbulent mixing to re-suspend them to
678 the euphotic zone (Robarts & Zohary, 1984).

679 Reynolds et al. (1983) have shown that stratification within the euphotic zone positively
680 affects large flagellates and buoyant cyanobacteria such as *Microcystis* spp., which require and
681 also tolerate a high dose of light to grow. Conversely, deep mixing favours negatively buoyant
682 diatoms and desmids (that otherwise would be lost from suspension) provided that the reduction
683 of the average light intensity is sub-critical to their net growth. Based on these findings, deep

684 mixing has proved to be effective in hampering cyanobacterial growth, especially that of
685 *Microcystis* spp. and *Dolichospermum* spp., in stratifying water bodies (Visser et al., 2016 and
686 literature therein). Deep mixing and high flow conditions negatively affect these cyanobacteria
687 since they promote i) an increase of the z_{mix}/z_{eu} , ii) an increase of the frequency of exposure to
688 light levels below the critical intensity, and iii) the growth of competitors better adapted to deep
689 mixing (Xiao et al., 2018). Similar results were shown by Naselli-Flores & Barone (2005) in a
690 *Microcystis*-dominated Mediterranean reservoir: in summer the reservoir experienced a strong
691 dewatering (up to 90 % of the water volume stored in early spring) due to its use for irrigation
692 purposes, which transformed a quite deep lake into a shallow one (Naselli-Flores, 2003) with an
693 immediate development of a dense *Microcystis* bloom. To prevent the repetition of this event, in
694 the following years the summer water-withdrawal was managed to establish a stable thermocline
695 at depth of 5-6 m and to maintain it throughout the summer. The resulting upper mixed layer was
696 much deeper than the intermittent microstratification caused by atelomixis in the “shallow lake”
697 phase, with a diurnal thermocline development located within the upper 50 cm of depth. As a
698 consequence, a strong reduction of cyanobacteria was recorded in the reservoir when dewatering
699 was managed to maintain a stable summer thermocline. This effect was accompanied by lower
700 values of z_{mix}/z_{eu} , which favoured green algae (e.g. *Pediastrum* s.l., *Hariotina*, *Coelastrum*,
701 *Scenedesmus*) sensitive to settling into the low light layers (see Reynolds et al., 2002). Hence, two
702 opposing approaches can exert similar results on the composition of phytoplankton assemblages:
703 the first is aimed at decreasing the thermal stability while the second at enhancing thermal
704 stability. Both resulted in the reduction of light resources for cyanobacteria. These observations
705 are in agreement with the results shown by Wu et al. (2019) who found that the effects of
706 turbulence on the formation of cyanobacteria scums can vary according to the extent of
707 turbulence itself, and to the way in which mixing regimes influence resource availability (both light
708 and nutrients) in the water column.

709

710 **Biotic interactions and water motion**

711 Understanding how bacterio-, phyto- and zooplankton interact when being passively transported
712 across the pelagic environment is not trivial. The existence and functioning of aquatic ecosystems
713 depend on these interactions that convey energy fluxes and promote biogeochemical cycles.
714 Intuitively, members of these ecological groups, due to differences in their size and modes of

715 propelling through the water, are differently subjected to water motion. Moreover, fluid dynamics
716 affects plankton growth and its spatial distribution, but at the same time plankton behaviour
717 influences fluid motion across a range of scales, through excretion of exopolymers (Prairie et al.,
718 2012), feeding (Jiang et al., 1999) and swimming (Simoncelli et al., 2018; 2019).

719 As regard bacteria, they occupy all habitats of aquatic (and non-aquatic) ecosystems
720 including the sediments (even the deep ocean thermal chimneys), the water column, and the
721 surface of all the other members of the biological compartment. Bacteria in plankton are found in
722 the mucilage of cyanobacterial species, where they establish symbiotic relationships (e.g.
723 Brunberg, 1999; recently recognized as global functional interactome, see Hooker et al., 2019),
724 and in the gut of zooplankton (Grossart et al., 2010). Stratification patterns can create abrupt
725 differences between the upper and lower layers of the water column and promote the
726 development of distinctive, specialized prokaryotic assemblages (Salcher et al., 2011) or at least
727 disperse them. Climate change may promote the incidence of such events (Kasprzak et al., 2017).
728 Although bacteria show high morphological variability (e.g. van Teeseling et al., 2017) it is unlikely
729 that this could represent an adaptive response to the pelagic environment [but see Faivre et al.,
730 (2008 and Raschdorf et al. (2013)]. Their size, and the very low Reynolds Number at which they
731 live, can however represent an advantage since it keeps them in suspension (Lauga, 2016) and/or,
732 depending on the depth of a water body, it can favour re-suspension (Amalfitano et al., 2017),
733 promote their motion (Koch & Subramanian, 2012), and allow their dispersion in all the biotic
734 components of the aquatic ecosystem (Eckert et al., 2020).

735 In an attempt to explain the morphological variability of phytoplankton, Jiang et al. (2005)
736 presented a model showing that in the absence of grazers, phytoplankton should evolve towards
737 picoplanktic size. According to this model, the interactions between phytoplankton and
738 zooplankton over geological time scales may have contributed to the high variability in size shown
739 by phytoplankton. The basic assumption of this model was partially contradicted by another
740 model recently developed by Woodward et al. (2019) showing that water flow can keep planktic
741 predators and preys separated as they are transported in the water motion. Inertial drift can drive
742 crustacean zooplankton out of the turbulent eddies allowing phytoplankton within the eddies to
743 escape grazing control, and eventually favouring the formation of water blooms. As it was
744 evidenced, crustacean zooplankton is more subjected to inertia (G.-Tóth et al., 2011) than
745 phytoplankton and even small differences in inertia and/or buoyancy between predators and
746 preys can significantly affect their encounter rates. To overcome the problem, several planktic

747 herbivorous crustaceans use their body appendages to generate microcurrents to convey the algal
748 particles to their mouth (e.g. Jiang et al., 1999; Lampert, 2001). A side effect of the
749 microturbulence generated by zooplankton (biomixing) at millimetric scale could cause the
750 thinning of the diffusive boundary layer and increase nutrient uptake by phytoplankton (see
751 Prairie et al., 2012 and literature therein). However, the role of biomixing at larger scales (i.e.
752 disruption of thermal stratification) has been controversial (e.g. Dekshenieks et al., 2001; Visser,
753 2007; Subramanian, 2010; Prairie et al., 2010).

754 However, crustaceans are not the only players with the role of “consumer” in the planktic
755 compartment of the pelagic food webs. Since the work by Azam et al. (1983) who highlighted the
756 importance of the microbial loop in sustaining primary production in all the aquatic environments,
757 a huge amount of literature has investigated the interactions among bacteria, heterotrophic
758 flagellates and phytoplankton (including mixotrophic species), and the importance of the role they
759 exert in ecosystem functioning (e.g. Fenchel, 2008; Nakano, 2014; Mitra et al., 2016; Naselli-Flores
760 & Barone, 2019). As shown by Reigada et al. (2003), if one group of planktic organisms is “lighter”
761 than the other, some degree of separation between predators and prey can occur. Accordingly,
762 the comparable size of the organisms forming the microbial loop has probably a role in gathering
763 them together and in strengthening their trophic interactions by minimizing the patchy
764 distribution of trophic resources generally occurring in a nutritionally diluted environment
765 (Conover, 1968).

766 It is well known that the impact of grazers has evolutionarily produced an array of
767 phytoplankton defence tools, involving biochemical, behavioural and morphological mechanisms
768 addressed at reducing grazing losses (see Van Donk et al., 2011 for a review). As reviewed in
769 Naselli-Flores & Barone (2011), several defence morphological mechanisms are not constitutive
770 but are induced by the grazing activity exerted by herbivores by release of infochemicals and
771 allelopathic substances. Infochemicals were demonstrated to be effective in promoting colony
772 formation, changes in cell size and/or induction to grow spines and bristles (e.g. Lüring, 2003;
773 Tang et al., 2008). The induction of these morphological changes requires re-allocation of
774 resources and can have a cost in terms of growth rates. Changes in size (e.g. as it happens when
775 single cells aggregate to form colonies) can cause an increase in the sedimentation rates affecting
776 the persistence in the illuminated layers and the gathering of nutrients, due to the decreased
777 surface-to-volume ratio (e.g. Verschoor, 2005).

778 Developing defences against grazing is part of the adaptations required by the organisms
779 living in apparent suspension. The evolutionary interactions between phytoplankton and
780 zooplankton certainly have had a role in determining the present spectrum of sizes and shapes
781 shown by phytoplankton organisms (Jiang et al., 2005). However, it is often difficult to disentangle
782 the effects exerted on phytoplankton morphology while being transported in the water motion
783 regarding three fundamental necessities: i) to access adequate amount of resources, ii) to
784 minimize sedimentation losses, and iii) to escape from herbivores. The amazing morphological
785 diversity of phytoplankton has therefore to be considered an evolutionarily-driven compendium of
786 strategies to cope with the strong variability and unpredictability of the pelagic environment.
787 Escape of parasites, like chytrids, by disruption of colonies, sinking fast and being reanimated
788 during the next complete mixing may represent another strategy of population survival.

789

790 **Perspectives: where research should be addressed**

791 Global warming, among others, is causing an increase of water temperature, which has multiple
792 effects on phytoplankton growth by directly influencing its metabolism and the temperature-
793 dependent physical properties of its fluid environment (Prairie et al., 2012). Temperature acts
794 directly and indirectly on phytoplankton in several ways and disentangling the single effect caused
795 by temperature variations is not an easy task. Direct effects are those impacting phytoplankton
796 metabolic rates (and resulting in an alteration of biogeochemical cycles; see Toseland et al., 2013).
797 Indirect effects include, as an example, warming of the surface waters leading to shallowing of the
798 upper mixed layer (Gray et al., 2019), and temperature-dependent changes in density and viscosity
799 of water which affect fluid dynamics and the entrainment of phytoplankton into the water motion
800 (Zohary et al., 2017). Literature on whether climate change is deepening or shallowing the
801 thermocline (therefore the depth of the upper mixed layer) is controversial: either deepens or
802 makes it shallower (see Selmeczy et al., 2016); influence seems to be highly lake-specific (and
803 model specific). However, existing data are consistent in that climate change has a profound effect
804 on stratification patterns cascading throughout the whole pelagic scenario (e.g. Pareeth et al.,
805 2016 and literature therein).

806 Although several interdisciplinary papers coupling biological and physical aspects of
807 phytoplankton ecology are available in the scientific literature, we are still far from a complete
808 understanding of the structuring impacts of (micro)turbulence on plankton. This is certainly linked

809 to the complexity of effects exerted on plankton dynamics by the physical properties of the fluid at
810 different spatial (from millimetres to kilometres) and temporal (from a few seconds to seasons)
811 scales and by the inherent difficulties in coupling phytoplankton ecology and fluid mechanics.
812 Methodological and technological advances along with closer interactions between physicists and
813 biologists have begun to reveal the importance of flow–microorganism interactions and the
814 adaptations of microorganisms to flow (Berman & Shteinmann, 1998; Koch & Subramanian, 2011;
815 Ng et al., 2011; Prairie et al., 2012; Wheeler et al., 2019). In addition, it is important to recall that
816 phytoplankton morphology is evolutionarily shaped. However, phytoplankton shape structure,
817 compared to phytoplankton size structure, is only seldom considered in the literature.
818 Morphological variability among species as well as natural intrapopulation variability, can lead to
819 variability in metabolic and functional traits, which may impair our full understanding of the
820 ecological trajectories followed by natural phytoplankton assemblages (Bestion et al., 2018).
821 Investigations aimed at finding the links between cell morphology (and its ornamentations:
822 papillae, protuberances, arms, spines, bristles), sinking velocity of phytoplankton, metabolic traits
823 and flow conditions of aquatic ecosystems would therefore help in better understanding the
824 structure and distribution patterns of phytoplankton in aquatic ecosystems, and its role in
825 determining the ecosystem functioning. Although time-consuming, morphological analysis of
826 phytoplankton, both addressed at evaluating the modifications in its size structure along time and
827 at recording seasonal size changes of single species, represent an important tool to investigate the
828 ecological dynamics of aquatic ecosystems (Naselli-Flores, 2014). It would be therefore important
829 to invest more efforts in collecting and analysing morphological data on phytoplankton and
830 include such analyses in the scientific literature dealing with phytoplankton dynamics, especially
831 when long-trend data sets are presented.

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Figure captions

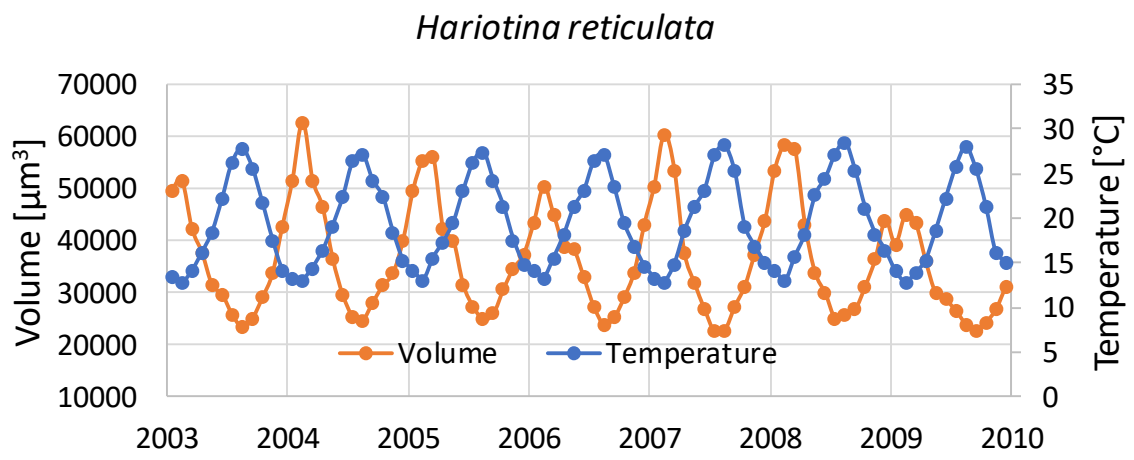
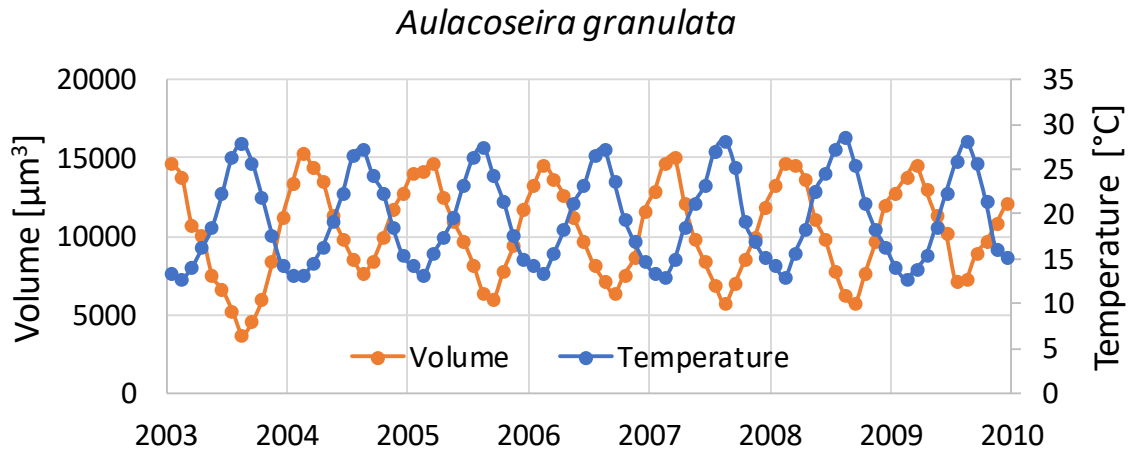
1348 Figure 1. Temporal trends of water temperature and phytoplankton size, expressed as volume per
1349 colony, of two phytoplankton species (*Aulacoseira granulata* (Ehrenberg) Simonsen and *Hariotina*
1350 *reticulata* P. A. Dangeard) recorded in Lake Arancio (Sicily, Italy) over an eight-year period.

1351 Temperature was measured with a YSI 556 MPS multiprobe; methods for phytoplankton colony
1352 volume calculations are those in Zohary et al. (2017).

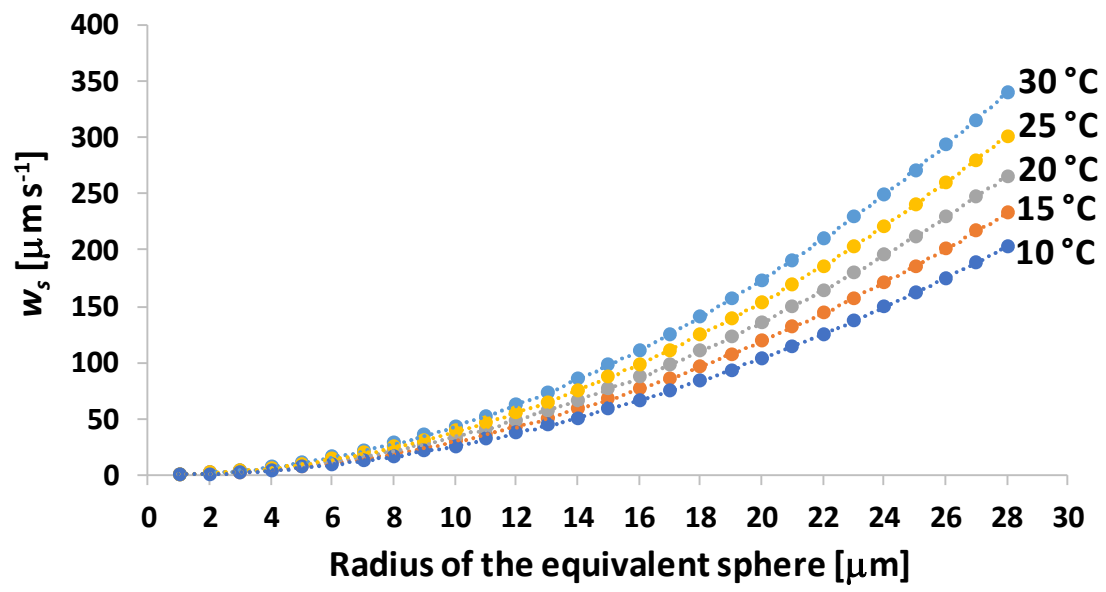
1353 Figure 2. Relationships between phytoplankton size and sinking velocity (w_s) computed according
1354 to Stokes' equation in the temperature range 10 – 30 °C for spherical shapes with a cell-density of
1355 1.15 g cm⁻³. When temperature changes (and the related water density and viscosity), smaller
1356 cells/colonies have to be selected to keep a given sinking velocity constant.

1357 Figure 3. Variability of sinking velocity of phytoplankton (w_s) and its maximum growth rates at 20
1358 °C (r_{20}), as a function of size, expressed here as the surface to volume ratio (sv^{-1}).

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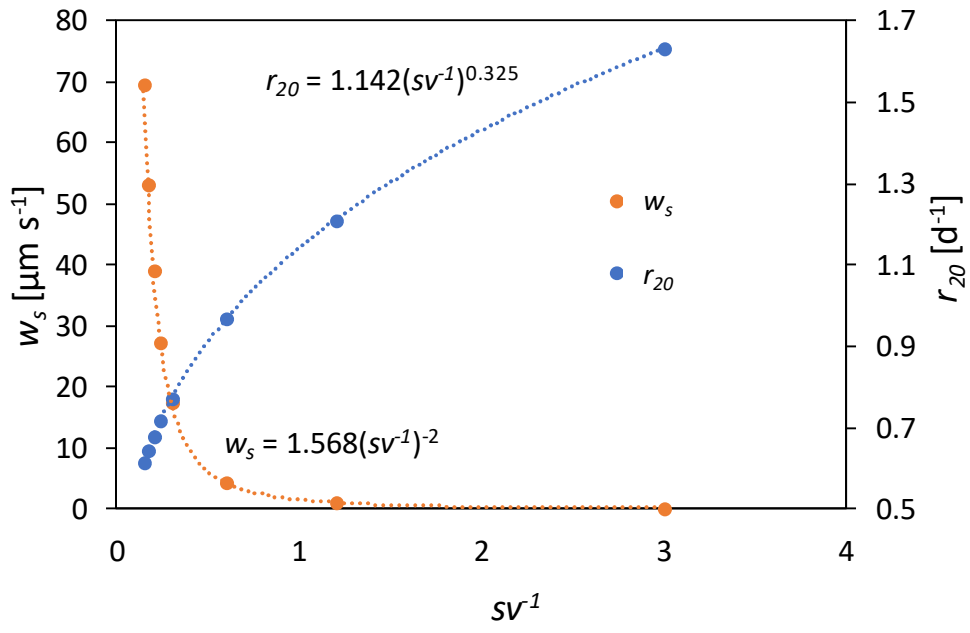
1360
 1361 Fig. 1
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 1365 Fig. 2

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1369 Fig. 3