



Life in suspension and its impact on phytoplankton morphology: an homage to Colin S. Reynolds

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Abstract The amazing morphological diversity of phytoplankton has to be considered an evolutionarily driven compendium of strategies to cope with the strong variability and unpredictability of the pelagic environment. Phytoplankton collects unicellular and colonial photosynthetic organisms adapted to live in apparent suspension in turbulent water masses. Turbulence represents a key driver of phytoplankton dynamics in all aquatic ecosystems and phytoplankton morphological variability is the evolutionary response of this group of photosynthetic organisms to the temporal and spatial scales of variability of turbulence. This paper reviews the existing literature on the

effects exerted by turbulence on phytoplankton populations and is aimed at showing how deeply turbulence contributes to the shape and size structure of phytoplankton assemblages. Our aim is to explore how turbulence governs phytoplankton access to resources and, at the same time, how the shape and size structure of phytoplankton represent the evolutionary way in which this group of organisms has optimised its survival in the highly dynamic aquatic environment. The paper is intended to serve as an homage to the (phytoplankton) ecologist Colin S. Reynolds. His life-long work highlighted how profoundly the ecology of phytoplankton depends on the physical constraints governing the movements of the water masses in which phytoplankton evolved and lives.

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Introduction

Contributing about half of the global primary production, phytoplankton represents the real “green lung” of the Planet (e.g. Smayda, 1970; Falkowski 1994; Litchman et al., 2015) although its standing stock accounts for only a negligible fraction (< 1%) of the global photosynthetic biomass (Field et al., 1998; Sigman & Hain, 2012). To better understand the links

existing between phytoplankton biomass and its productivity, a main focus of scientific papers over the last ~ 60 years has been the roles of resource availability (nutrients and light) and the effect of grazers on phytoplankton structure. If indeed nutrients, light and predators represent primary constraints to phytoplankton growth in an isotropic environment, it would be legitimate to ask: why evolution/competition has not driven phytoplankton toward being composed by a few species all showing similar sizes and shapes (possibly small and spherical)? As pointed out by Sommer et al. (2017a, b), it is too simplistic to equate small size with metabolic advantages.

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

The way in which water masses move within inland lentic ecosystems strongly depends on their exposure to wind, on their morphology (e.g. shoreline development, bathymetry, surface area, volume, extension of the tributaries, etc.) and on the effects of local climate as expressed by their geographic location (Imberger, 1998) and land use (Katsiapi et al., 2012). In lotic ecosystems, the velocity of the unidirectional flow can

change at various points along the river course and it is generally related to a variety of meteorologically driven and morphological factors such as water discharge, the gradient of the slope that the river moves along, the width and depth of the channel and the amount of friction caused by rough edges within the river bed (e.g. Julien, 2002; Bukaveckas, 2010). The complex physical processes governing water motion in an aquatic ecosystem are therefore subjected to the intrinsic and local features of water bodies: these further contribute to increase the variability of the physical scenario (e.g. Elliott et al., 2001; Padisák et al., 2010b). Phytoplankton is evolutionarily equipped to cope with this variability and much of the features it developed are expressed in the extent of morphological plasticity within populations, formed by highly variable, unicellular organisms eventually grouped in aggregates with various number of cells.

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

Colin S. Reynolds (London, 1942—Kendal, 2018) dedicated a substantial part of his professional career to investigate the adaptations of phytoplankton species and assemblages with regard to the acquisition of resources while suspended in water and subjected to its motions. He showed that much of the ecological success of phytoplankton depended on their morphology, evolutionarily forged to optimise their access to resources in a turbulent world (Reynolds, 1984a, 1997, 2006). The spectrum of shapes and sizes of phytoplankton is therefore the result of adaptive selection addressed at maximising the chances to survive under variable environmental conditions (Naselli-Flores & Barone, 2011 and literature therein). These morphological features determine the degree of entrainment of phytoplankton organisms in the water motion. Furthermore, these features impact their ability to exploit resources, constitute an efficient shield against grazing, and ultimately drive their ecology by allowing populations to grow (Reynolds, 1984b).

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

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

Why are there so many different phytoplankton morphologies?

Phytoplankton, according to a widely accepted definition, is an ecological group of unicellular and colonial photosynthetic microorganisms (not a taxonomic group, due to the distant phylogenetic origins of its members) adapted to live in apparent suspension in turbulent water masses (Reynolds, 2006). This definition implies that through trying to exert a control on their position and rate of movement in the water column (i.e. its entrainment in the turbulent motion), phytoplanktonic populations are able to acquire the resources they need to persist in a turbulent environment. Since water on Earth is in continuous motion, and the extent of this motion is variable, phytoplankton has to be evolutionarily adapted to life in a wide range of hydrodynamic conditions. Moreover, the polyphyletic origin of phytoplankton may reflect the existence of convergent forces in evolution that moulded these organisms into planktic existence (Reynolds, 2006).

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

A first attempt to define a boundary between “small” and “big” organisms was made, about a century ago, by Thompson (1917). Trying to explain how physical forces govern the growth and shape of

organisms, he separated organisms into two types: “small” organisms in which physical forces acted mainly on their surface, and “big” organisms in which the forces acted proportionally on their body mass. Since all the living organisms move in a fluid (air or water), the boundary between these two groups of organisms can be assessed by computing their Reynolds Number (Re), i.e. the ratio between the inertial (gravity) and the viscous (drag or fluid resistance) forces that act on a body moving in a fluid, a unitless number (for more details see Naselli-Flores & Barone, 2011). In particular:

$$Re = (\rho ul)\eta^{-1} = (ul)v^{-1}$$

where u is velocity of the fluid [m s^{-1}], l [m] is the length dimension available for the dissipation of energy (usually the depth of the flow or the linear dimension of an object) and v [$\text{m}^2 \text{s}^{-1}$] is the kinematic viscosity of the fluid, i.e. the absolute viscosity of the fluid (η) [$\text{kg m}^{-1}\text{s}^{-1}$] with its density (ρ) [kg m^{-3}] divided out. Any combination of velocity, viscosity and length scale that results in the same Re will result in a geometrically similar flow regime, as characterised by the ratio of inertial to viscous forces. Thus, doubling the length scale will result in a flow regime that can also be realised by doubling velocity or by halving kinematic viscosity (Humphries, 2007).

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

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

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

The reliability of velocity estimated with the Stokes' equation is high, even for actively swimming

dinoflagellates (Sommer, 1988; Kamykowski et al., 1992), as confirmed by sophisticated measurements performed by Walsby & Holland (2006). However, early observations exist highlighting that phytoplankton settling rates often diverge from what is predicted by the Stokes' equation, which was established to calculate sinking velocity of spherical particles (e.g. Smayda & Boleyn, 1965; Eppley et al, 1967). The deviation from predictions, since long ago (Ostwald, 1902 in Margalef, 1957), has been attributed to the “bizarre” morphologies often shown by different phytoplankton species, characterised by expansions and protuberances, and to their effectiveness in increasing the role of viscous forces on cell surface and ultimately in modulating the sinking velocity of phytoplankton (e.g. Padisák et al., 2003; Chindia & Figueredo, 2018). This deviation can be computed by including the Stokes' equation, a dimensionless species-specific variable called coefficient of form resistance (Φ_r). Φ_r represents the factor by which the directly measured sinking velocity of the particle (w_s measured) differs from that of a sphere (w_s sphere) of equivalent volume and density, in the same fluid:

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

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

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

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

Of the six variables appearing in the Stokes' equation, one (g) can be considered a constant; two (ρ and η) depend on water temperature and salinity,

and the other three (cell or colony size, cell density and coefficient of form resistance) are species-specific biological characteristics and thus subjected to adaptation and to evolutionary modification through natural selection. In particular, the fact that some organisms may sink faster than the equivalent sphere allow to think that they are adapted to exploiting resources under turbulent conditions quite differently from those organisms sinking more slowly than the equivalent sphere, which have therefore to be able to show different adaptive strategies. Therefore, minimising sinking velocity is actually not the main goal of phytoplankton. Instead, maximising the opportunities for suspension under variable turbulent conditions should be considered the primary evolutionary target of this group of organisms.

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

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

The evidence that phytoplankton species show different physiological characteristics per se does not answer the question “why are there so many different morphologies in phytoplankton?”. It is therefore important to point out that several trade-offs exist between morphological (i.e. size and shape of single cells and colonies) and physiological traits of phytoplankton, and that morphology, through modulating

the physiological pathways of protein synthesis, photosynthesis and nutrient uptake, deeply impacts growth and metabolism of the different phytoplankton populations (Litchman & Klausmeier, 2008 and literature therein).

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

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

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

An additional explanation lies in the way in which water masses move. When a fluid is moved by a force acting on it, small portions of that fluid will tend to stick to themselves and to the particles eventually suspended in that fluid. Viscosity represents the magnitude of this tendency and will depend on the physicochemical nature of the fluid itself (Vogel, 1994). Following Reynolds (2006), if a mild force (τ) is applied to the surface of a fluid (e.g. wind blowing on the surface of a water body), the interaction between these two fluids (air and water) will result in the linear dragging of the water molecules at the air–water interface in the same direction of the wind. The movement will be progressively transmitted to the

layer below and propagated downward, albeit at a lower velocity because part of the energy will be dissipated by the shear stress (due to viscosity) generated between these layers. The smooth sliding of each layer of water molecules over the one below is known as laminar flow. In this case, the mechanical energy introduced in the fluid is accommodated in an ordered structure of parallel layers moving in the same direction and showing a vertical gradient of horizontal velocities (u) [ms^{-1}] whose steepness is defined by the differential notation du/dz (i.e. the decrement of horizontal velocity for a small increment in the vertical direction z [m]). Persisting the condition of laminar flow, the ratio between the applied force τ [kgms^{-2}] per unit area and the velocity gradient corresponds to the absolute viscosity of the water, η . That is,

$$\eta = \tau(du/dz)^{-1} \text{ kg m}^{-1} \text{ s}^{-1}$$

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

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

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

Turbulence is a quite complex subject of Hydrodynamics (whose treating goes beyond the scope of this review) and its impact on the behaviour of planktic algae has remained obscure for a long time. The development of instrumentation and direct sensing of

turbulence began only in the second half of the last century (see Imberger, 1998). The results collected by this new generation of instruments were rapidly incorporated in physical limnology and oceanography (e.g. Imberger & Spigel, 1987; Imboden & Wüest, 1995; Wüest & Lorke, 2003; Hutter et al., 2011a; b, 2014; Baudena et al., 2019) and strongly contributed to a better characterisation of the phytoplankton environment and of the complex physical relationships between the movement of phytoplankton and that of the fluid in which it is contained (e.g. Guasto et al., 2012; Croze et al., 2013 and literature therein).

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

Moving in a constantly mixed environment

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

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

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

The degree of entrainment of phytoplankton depends on a quotient, Ψ [unitless], which represents

the boundary between a behaviour dominated by the turbulent diffusivity of water and a behaviour dominated by the speed of phytoplankton cells or colonies (as described by their sinking and floating velocity and/or by the velocity imparted by flagellar propulsion) in the medium (Humphries & Imberger, 1982). According to Reynolds (1994), it can be approximately computed according to the formula:

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

where w_s [ms^{-1}] is the sinking velocity of a particle and u^* [ms^{-1}] is the turbulent velocity of water. The latter can be related to the mean windspeed 10 m above the water surface (Denman & Gargett, 1983; Moreno-Ostos et al., 2009):

$$u^* = (\rho_a c_1 U_{10}^2 / \rho_w)^{0.5} \text{ (ms}^{-1}\text{)}$$

where ρ_a is the density of the air, ρ_w is the density of the water, U_{10} is the wind speed 10 m above the water surface and c_1 is a dimensionless coefficient for drag friction upon water (1.3×10^{-3}).

A value of $\Psi = 1$ represents the boundary between entrainment (particles are embedded in the turbulent motion) and disentrainment (particle properties dominate distribution). The smallest species of the picoplankton (cells $< 2 \mu\text{m}$) are almost perfectly entrained, whereas increasingly larger species of the nanoplankton (2 – $20 \mu\text{m}$) and microplankton (20 – $200 \mu\text{m}$) are likely to have higher sinking rates and to be liable to escape from turbulent eddies (Reynolds, 2012b). However, since w_s is generally 1 to 6 orders of magnitude less than u^* (Reynolds, 2006), under most of the hydrodynamic conditions experienced by a water body, phytoplankters are constantly redistributed in the turbulent water column and their trajectories will follow all the possible directions in the three-dimensional pelagic environment. This is true also for actively swimming dinoflagellates, whose spatial distribution is often patchier than that of non-motile species (Durham et al., 2013). Dinoflagellates establish vertical heterogeneity by migration during calm weather, then transport by water motions cause their patchy distribution (Alexander & Imberger 2009). The swimming behaviour shown by self-propelling algae when embedded in water motion was analysed in several studies to explain both the hydrodynamical aspects of algal motion and the dynamics of bloom formation (e.g. Kessler, 1985;

Pedley & Kessler, 1992; Reigada et al., 2003; Durham et al., 2009; O'Malley & Bees, 2011; Goldstein, 2015). In particular, actively swimming single cells are known to respond in a complex way to flow (e.g. Croze et al., 2013; Cencini et al., 2019) and their mean swimming direction largely depends on flow direction and intensity (gyrotaxis). In the absence of flow gradients, cells will tend to swim upwards on average (gravitaxis). More in general, the thrusts of the turbulent eddies can move phytoplankters upwards faster than they gravitate downwards and allow their sinking trajectories to re-initiate at a higher point in the turbulence field. However, as turbulence decays with depth, the role of sinking, floating and self-propelling velocities will increase with depth until a point where the entraining capacity is too weak to maintain entrainment. Some other particles will therefore be lost by sedimentation.

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

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

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

Last but not least, phytoplankters sink, float and swim in a moving medium (e.g. Reynolds & Walsby, 1975). The reciprocal movements of phytoplankters and of the water masses in which they are embedded have been demonstrated to have a role in the spatial distribution of phytoplankton at different scales (Font-Muñoz et al., 2017 and literature therein). In particular, the different circulation patterns of the water masses both at small (advection: 1–10 cm) and at larger scales (currents: 1–10 km) can be effective in shaping the spatial variability of phytoplankton size structure in the aquatic environment (Reynolds et al., 1993).

Phytoplankton access to resources while entrained and disentrained in water motion

The pelagic environment is characterised by a great heterogeneity with regard to resource distribution and availability, as well as with regard to the direction and intensity of water movements (Reynolds, 1997). The water movements, generally much larger than the value of molecular diffusivity, largely contribute to re-distribution of heat (Jassby & Powell, 1975) and nutrients (Robarts & Ward, 1978) within and across the upper mixed layer of a given water body. There, light is attenuated with depth and varies in relation to the hour of the day, the season, the geographic location, the meteorological conditions, the trophic state, the inorganic seston and humic material contents. Nutrients accessible for a phytoplanktic organism are often patchily distributed, even at the scale of a few millimetres, and their concentrations generally

increase with depth (Padisák & G-Tóth, 1991; Reynolds, 2006). The movements of water masses at different spatial and temporal scales influence and modulate the availability of light and nutrients for phytoplankton: they can transport nutrients from the deep layers to the euphotic zone and can enhance the (re)suspension of phytoplankton in the illuminated layers (Mahadevan, 2016). Moreover, since physical factors can modify the growth (and loss) rates of phytoplankton, they can also modify the competitive abilities of phytoplankton and reshape the composition of assemblages (Seip & Reynolds, 1995; Padisák et al., 2010b).

Temperature is largely considered a powerful driver of phytoplankton size structure in different aquatic ecosystems (e.g. López-Urrutia & Morán, 2015; Rasconi et al., 2015; Pulina et al., 2018; Rugema et al., 2019; Abonyi et al., 2020) due to the multiple constraints it imposes on cell growth. Water temperature exerts a direct influence on metabolic rates and biochemical processes of phytoplankton (e.g. Chisholm, 1992) and, consequently, it has an important role in determining the rates of resource uptake (both nutrients and light) by phytoplankton (Borowitzka et al., 2016). Moreover, temperature affects the duration of stratification and the thickness of the surface mixed layer, with different and independent consequences to phytoplankton growth (Winder & Sommer, 2012). Falkowski & Oliver (2007) suggested that, at a global scale, higher temperatures are causing a decreased turbulent mixing in the upper part of the oceans, and a consequent reduction of nutrient availability, which is leading to an altered size structure of phytoplankton assemblages. Last but not least, temperature also affects two variables (density and absolute viscosity of water) directly linked to phytoplankton sinking, floating and swimming, and ultimately to its entrainment in water motion (Zohary et al., 2017).

By regulating its entrainment in the external medium through species selection and/or phenotypic plasticity, phytoplankton has to accommodate for two vital necessities: to gain enough light and enough nutrients to sustain net production. Although a geometrical trade-off exists between size and shape (Litchman & Klausmeier, 2008; Stanca et al., 2013), phytoplankton size and structure is considered to be largely driven by nutrient availability (e.g. De Senerpont Domis et al., 2013; Peter & Sommer, 2013;

Marañón et al., 2015; Mousing et al., 2018), whereas light availability can have a strong influence in determining the shape of phytoplankton organisms (e.g. Naselli-Flores & Barone, 2007). Disentrainment (by increasing sinking velocity or by active swimming) may therefore represent an advantage with regard to nutrient supply, since it facilitates the movement of the organisms towards deeper layers where nutrient concentrations are higher. At the same time, it brings organisms away from the upper layers where the light conditions are more favourable. Different species have therefore adopted different strategies to manage and regulate their positioning in the water column. Each strategy represents the attempt to maximise the chances to survive in the challenging pelagic environment. Moreover, phytoplankton species are characterised by a relatively high degree of phenotypic plasticity (Naselli-Flores & Barone, 2011). This morphological variability can be considered as a tool to cope with environmental changes. Zohary et al. (2017) noted that many phytoplankton species, of diverse taxonomic phyla, commonly found in Lake Kinneret, Israel, all year-round (even though with different abundances) had larger cells or colony size in winter, and smaller in summer. Similar results were obtained by Naselli-Flores (Fig. 1, previously unpublished data) for two phytoplankton species from Sicily (Italy). Pulina et al. (2019) analysed long-term variability of single phytoplankton species and assemblage size structure in Mediterranean reservoirs. They found assemblages with smaller mean cell size in summer and larger mean size in winter. Literature surveys allowed Sommer et al. (2017a, b) and Zohary et al. (2020) to conclude that marine and freshwater phytoplankton become smaller in size with increasing water temperatures. This occurred at the species and community levels. Based on computations of Stokes' sinking velocity, Zohary et al. (2017) hypothesised that the seasonal changes in intra-specific cell or colony size they observed could represent an adaptation that enabled species to overcome temperature-dependent changes in water density and viscosity. These changes are summarised in Fig. 2 where the theoretical relationships between phytoplankton size and sinking velocity are shown. In the figure, the curves represent the sinking velocities attained by spherical algae of different sizes (but with the same cell density of 1.15 g cm^{-3}) in the temperature range $10\text{--}30^\circ\text{C}$: when temperature increases (and the related

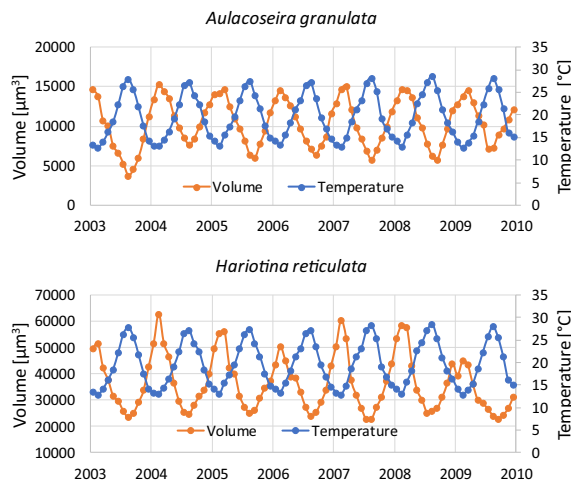


Fig. 1 Temporal trends of water temperature and phytoplankton size, expressed as volume per colony, of two phytoplankton species (*Aulacoseira granulata* (Ehrenberg) Simonsen and *Hariotina reticulata* P. A. Dangeard) recorded in Lake Arancio (Sicily, Italy) over an 8-year period. Temperature was measured with a YSI 556 MPS multiprobe; methods for phytoplankton colony volume calculations are those in Zohary et al. (2017)

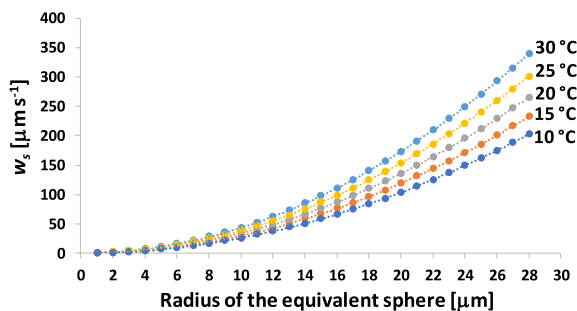


Fig. 2 Relationships between phytoplankton size and sinking velocity (w_s) computed according to Stokes' equation in the temperature range 10–30 °C for spherical shapes with a cell density of 1.15 g cm⁻³. When temperature changes (and the related water density and viscosity), smaller cells/colonies have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

water density and viscosity decrease), smaller cells/colonies have to be selected to keep a given sinking velocity constant.

Compared to freshwater, seawater shows higher density and viscosity values at a given temperature. Differences in the size distribution of marine and freshwater diatoms are known, with marine diatoms larger than freshwater species (Litchman et al., 2009). However, these differences were explained in terms of nutrient fluctuations and differences in the depth of the mixed layer rather than as a consequence of the higher

density and viscosity of seawater. A decrease in cell size of microphytoplanktic organisms was also registered in correspondence of increased ice-melting (and decreased salinity) episodes in Antarctica (Teixeira de Lima et al., 2019). Unfortunately, to our knowledge, no data exist on the effects exerted by viscosity and density on the size structure of marine and freshwater phytoplankton. Nevertheless, larger or smaller specimens are alternatively selected by environmental pressure and their size change, as suggested by Zohary et al. (2017), could be addressed at counteracting the changes in density and viscosity of the water and at adjusting their sinking velocities in order to achieve a similar access to resources in the different physical scenario set by seasonal and environmental variations in the density and viscosity of water. To our knowledge, the effects of temperature on the morphology of single phytoplankton species were rarely investigated (e.g. Bailey-Watts & Kirika, 1981; De Miranda et al., 2005; Jung et al., 2013) and, apart from Zohary et al. (2017), no other works exist in the literature on the potential effects of temporal and spatial variation in water density and viscosity on phytoplankton. However, it is well known that the increase in density and viscosity along the water column during thermal stratification is responsible for the spatial segregation of morphologically different phytoplankton species, and for the eventual establishment of the so-called deep chlorophyll maximum (e.g. Selmečzy et al., 2016) as one extreme case, as well as surface scums of cyanobacteria (e.g. Zohary & Robarts, 1990; Paerl & Otten, 2013) at the other extreme.

Indirect evidences of the effects exerted on phytoplankton by temperature-dependent variation of water viscosity and density are abundant in the literature. A direct influence of temperature on the size structure of phytoplankton assemblages was found by Mousing et al. (2014), who showed a global decrease in the relative contribution of large cells to phytoplankton assemblages as temperature increases regardless of ambient nutrient availability. Analogous results were shown by Winder et al. (2009) who recorded a compositional shift in the diatom assemblage of Lake Tahoe, independently from nutrient concentrations and addressed at favouring smaller species, as a consequence of increased temperatures due to global warming. Several authors found similar patterns (smaller phytoplanktic organisms in warmer periods) using paleolimnological records to compare different

climate periods over geological and centennial time scales (e.g. Finkel et al., 2005; Smol et al., 2005; Mousing et al., 2017).

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

Climate-driven physical properties of water can therefore play a role in determining the composition and structure of phytoplankton. Analogous results were shown by Rugema et al. (2019) by studying long-term, non-seasonal dynamics of phytoplankton in Lake Kivu, confirming what was shown by Ptacnik et al. (2003): specific sedimentation loss rates can be higher in shallow mixed layers (as those occurring in tropical lakes, especially under atelomictic conditions) than in deep ones because the probability of resuspension increases with increasing mixing depth. To prevent settling out of the upper mixed layer, natural selection will therefore favour phytoplankton organisms with lower sinking rates. However, the presence of non-buoyant phytoplankton-like diatoms and desmids in epilimnia appears paradoxical at first sight. Diatoms sink relatively fast because of cell density reasons (specific gravity of diatom frustules is about 2 g cm^{-3} ; Smol et al., 1984) and small desmids because of their low form resistance ($\Phi_r < 1$; Padisák et al., 2003). In this case, fast sinking within the epilimnion is beneficial since cells can reach the nutrient-rich density gradient (which anyhow slows sinking down) and the climate-driven nocturnal mixing (atelomixis) resuspends the cells having a temporary “rest” on the density gradient (Souza et al., 2008). This strategy is useful as long as growth rate can exceed or at least compensate sinking loss and reminds

us that sedimentation properties and nutrient uptake strategies are closely linked to each other.

Nutrient uptake and entrainment in water motion

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

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

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

Evidently, all the nutrients needed by phytoplankton to grow have to be drawn from the surrounding water. There, nutrient concentrations (typically in the range $2\text{--}50 \mu\text{mol N l}^{-1}$ and $0.1\text{--}5 \mu\text{mol P l}^{-1}$) are 5–6 orders of magnitude lower than those occurring within the cells ($\approx 2.8 \text{ mol N l}^{-1}$ and $\approx 0.18 \text{ mol P l}^{-1}$; see Reynolds, 2006). Therefore, phytoplankton has to overcome a steep chemical gradient to perform nutrient uptake and this requires a complex system

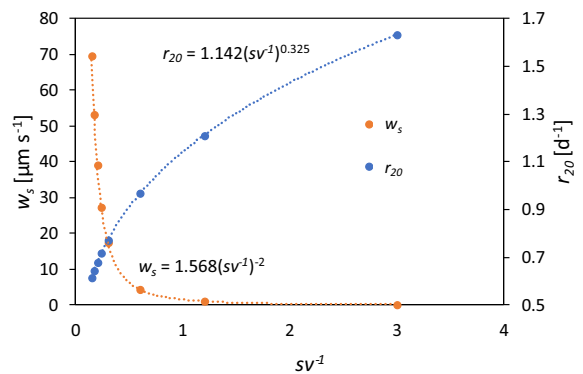


Fig. 3 Variability of sinking velocity of phytoplankton (w_s) and its maximum growth rates at 20°C (r_{20}), as a function of size, expressed here as the surface-to-volume ratio (sv^{-1})

of transmembrane proteins to capture, bind and transport specific molecules into and within phytoplankton cells as well as a high amount of energy (Reynolds, 2006). This cellular mechanism can only be effective over a short distance beyond the cell but sufficient to influence the concentration of nutrients within the boundary layer adjacent to the cell (Pasciak & Gavis, 1974; Sommer, 1988; Estrada & Berdalet, 1997), up to creating, in the absence of water flow or algal movement, a depletion zone (the so-called concentration boundary layer or diffusive boundary layer, see Kiørboe, 2008) in its immediate vicinity (Bonachela et al., 2011). Both microturbulence and phytoplankton motion (either swimming or passive sinking/floating) can therefore make the diffusive boundary layer thinner (Arin et al., 2002; Peters et al., 2006) and increase the fluxes of nutrients into the cells above the fluxes that would be experienced by one cell that is not motile with respect to the adjacent medium (Munk & Riley, 1952; Ploug et al., 1999; Kiørboe et al., 2001; Guasto et al., 2012). However, Riebesell & Wolf-Gladrow (2002) showed that, for particles moving in the water at low Reynolds numbers, a distinction has to be made between (i) very small cells (e.g. *Chlorella* or small centric diatoms) deeply entrained in the turbulence spectrum and (ii) larger or actively swimming cells or colonies ($Re > 10^{-3}$). By considering the rate of solute diffusive transport, the concentration gradient from the medium to the algal surface and the thickness of the diffusive boundary layer, these authors demonstrated that in the first group of organisms, the benefit of increasing water fluxes (i.e. the dependence on turbulence) around the cell is quite marginal, whereas it becomes increasingly important for larger organisms. It was also shown that the nutrient concentration threshold below which cells cannot sustain a given growth rate increases rapidly with cell size (Chisholms, 1992). An increase in the relative movement between the organisms and the water masses allows large organisms to overcome the biophysical constraint given by (i) the thickening of the diffusion boundary layer around the cell and by (ii) the reduction in nutrient diffusion per unit of cell volume (Marañón, 2014). Moreover, large elongated cells and multicelled trichomes can also show an increased nutrient flux per unit cell volume due to the increased surface-to-volume ratio (Pahlow et al., 1997; Karp-Boss & Boss, 2016). These results confirmed the earlier observations made by Walsby &

Reynolds (1980) who analysed the trade-offs between sinking and uptake rates in diatoms and suggested that under chronically low nutrient concentrations, large organisms depend much more on turbulence than smaller ones to maximise nutrient acquisition.

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

Access to light when travelling in the water column

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

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

The relationships existing between phytoplankton specific growth rates at sub-saturating light intensities

(α_r) and cell morphology were discussed by Reynolds (1997) who found that:

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

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

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

However, the environmental template sets the rules and, as shown by Reynolds et al. (1986), under stagnant conditions, sinking may represent a short-

term benefit to escape the damaging photo-inhibition caused by oxidative stress of excessive insolation near the water surface.

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

To explain how phytoplankton can manage to persist, and eventually bloom, in the illuminated water layers, Huisman et al. (2002 and literature therein) proposed a population dynamic theory of sinking phytoplankton that considered balancing between light-dependent growth rates, mortality rates, sinking rates and turbulent diffusion rates. These authors described the existence of a “turbulent window” that allows phytoplankton to grow in the euphotic zone. The window is characterised by intermediate turbulence levels allowing phytoplankton organisms to avoid both sedimentation losses and dilution beyond their growth capacity, while being passively transported within the mixed layer. The interplay between

the depth of the mixing zone (z_{mix}) and that of the euphotic layer (z_{eu}) was further analysed by Huisman & Sommeijer (2002) and by Huisman et al. (2004 and literature therein), who showed that changes in the $z_{\text{mix}}/z_{\text{eu}}$ ratio (primarily caused by a lower turbulent diffusivity) are key factors in determining the species structure of phytoplankton assemblage. Naselli-Flores (2000) reached similar conclusions by studying phytoplankton dynamics in Mediterranean reservoirs. In fact, the $z_{\text{mix}}/z_{\text{eu}}$ ratio indicates the proportion of time a phytoplankton organism may spend at critical light intensities once it is entrained in the mixed water column (Naselli-Flores & Barone, 2007). As shown by Reynolds (1984a, b), assuming a constant respiration rate of 10% of maximum photosynthetic rate, net growth of entrained phytoplankton cannot occur when $z_{\text{mix}}/z_{\text{eu}} > 3$ due to the insufficient extent of the aggregated photoperiod. A significant relationship between $z_{\text{mix}}/z_{\text{eu}}$ and msv^{-1} is shown in Naselli-Flores & Barone (2007) and in Naselli-Flores (2011) attesting the selective tendency toward an attenuated shape as $z_{\text{mix}}/z_{\text{eu}}$ ranges between 1.5 and 3.0. In shallow, optically deep water bodies, as those characterised by a high algal turbidity, low flow conditions and values of the ratio higher than 3 were found to promote the dominance of gas-vacuolated cyanobacteria that float to the surface shading eukaryotic phytoplankton (e.g. Naselli-Flores, 2003; Bormans et al., 2005). In these cases, buoyancy regulation represents an efficient strategy to persist in the illuminated layer and to monopolise light resources, while shading and out-competing phytoplankton species more dense than water. In water bodies subjected to low wind speeds where shallow diurnal mixed layers form, those cyanobacteria are further advantaged by maintaining position within the diurnal mixed layer, while non-buoyant species depend on turbulent mixing to resuspend them to the euphotic zone (Robarts & Zohary, 1984).

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

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

Biotic interactions and water motion

Understanding how bacterio-, phyto- and zooplanktons interact when being passively transported across the pelagic environment is not trivial. The existence

and functioning of aquatic ecosystems depend on these interactions that convey energy fluxes and promote biogeochemical cycles. Intuitively, members of these ecological groups, due to differences in their size and modes of propelling through the water, are differently subjected to water motion. Moreover, fluid dynamics affects plankton growth and its spatial distribution, but at the same time, plankton behaviour influences fluid motion across a range of scales, through excretion of exopolymers (Prairie et al., 2012), feeding (Jiang et al., 1999) and swimming (Simoncelli et al., 2018, 2019).

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

In an attempt to explain the morphological variability of phytoplankton, Jiang et al. (2005) presented a model showing that in the absence of grazers, phytoplankton should evolve towards picoplanktic size. According to this model, the interactions between phytoplankton and zooplankton over geological time scales may have contributed to the high variability in size shown by phytoplankton. The basic assumption of

this model was partially contradicted by another model recently developed by Woodward et al. (2019) showing that water flow can keep planktic predators and preys separated as they are transported in the water motion. Inertial drift can drive crustacean zooplankton out of the turbulent eddies allowing phytoplankton within the eddies to escape grazing control and eventually favouring the formation of water blooms. As it was evidenced, crustacean zooplankton is more subjected to inertia (G.-Tóth et al., 2011) than phytoplankton and even small differences in inertia and/or buoyancy between predators and preys can significantly affect their encounter rates. To overcome the problem, several planktic herbivorous crustaceans use their body appendages to generate microcurrents to convey the algal particles to their mouth (e.g. Jiang et al., 1999; Lampert, 2001). A side effect of the microturbulence generated by zooplankton (biomixing) at millimetric scale could cause the thinning of the diffusive boundary layer and increase nutrient uptake by phytoplankton (see Prairie et al., 2012 and literature therein). However, the role of biomixing at larger scales (i.e. disruption of thermal stratification) has been controversial (e.g. Dekshe-nieks et al., 2001; Visser, 2007; Prairie et al., 2010; Subramanian, 2010).

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

It is well known that the impact of grazers has evolutionarily produced an array of phytoplankton

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

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

Perspectives: where research should be addressed

Global warming, among others, is causing an increase of water temperature, which has multiple effects on phytoplankton growth by directly influencing its metabolism and the temperature-dependent physical properties of its fluid environment (Prairie et al., 2012). Temperature acts directly and indirectly on

phytoplankton in several ways and disentangling the single effect caused by temperature variations is not an easy task. Direct effects are those impacting phytoplankton metabolic rates (and resulting in an alteration of biogeochemical cycles; see Toseland et al., 2013). Indirect effects include, as an example, warming of the surface waters leading to shallowing of the upper mixed layer (Gray et al., 2019), and temperature-dependent changes in density and viscosity of water which affect fluid dynamics and the entrainment of phytoplankton into the water motion (Zohary et al., 2017). Literature on whether climate change is deepening or shallowing the thermocline (therefore the depth of the upper mixed layer) is controversial: either deepens or makes it shallower (see Selmečzy et al., 2016); influence seems to be highly lake-specific (and model specific). However, existing data are consistent in that climate change has a profound effect on stratification patterns cascading throughout the whole pelagic scenario (e.g. Pareeth et al., 2016 and literature therein).

Although several interdisciplinary papers coupling biological and physical aspects of phytoplankton ecology are available in the scientific literature, we are still far from a complete understanding of the structuring impacts of (micro)turbulence on plankton. This is certainly linked to the complexity of effects exerted on plankton dynamics by the physical properties of the fluid at different spatial (from millimetres to kilometres) and temporal (from a few seconds to seasons) scales and by the inherent difficulties in coupling phytoplankton ecology and fluid mechanics. Methodological and technological advances along with closer interactions between physicists and biologists have begun to reveal the importance of flow–microorganism interactions and the adaptations of microorganisms to flow (Berman & Shteinman, 1998; Koch & Subramanian, 2011; Ng et al., 2011; Prairie et al., 2012; Wheeler et al., 2019). In addition, it is important to recall that phytoplankton morphology is evolutionarily shaped. However, phytoplankton shape structure, compared to phytoplankton size structure, is only seldom considered in the literature. Morphological variability among species as well as natural intrapopulation variability can lead to variability in metabolic and functional traits, which may impair our full understanding of the ecological trajectories followed by natural phytoplankton assemblages (Bestion et al., 2018). Investigations aimed at finding the links

between cell morphology (and its ornamentations: papillae, protuberances, arms, spines, bristles), sinking velocity of phytoplankton, metabolic traits and flow conditions of aquatic ecosystems would therefore help in better understanding the structure and distribution patterns of phytoplankton in aquatic ecosystems, and its role in determining the ecosystem functioning. Although time-consuming, morphological analysis of phytoplankton, both addressed at evaluating the modifications in its size structure along time and at recording seasonal size changes of single species, represents an important tool to investigate the ecological dynamics of aquatic ecosystems (Naselli-Flores, 2014). It would be therefore important to invest more efforts in collecting and analysing morphological data on phytoplankton and include such analyses in the scientific literature dealing with phytoplankton dynamics, especially when long-trend data sets are presented.

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