MICROALGAL FUNCTIONAL TRAITS

Opinion Paper

Analysis of morphological traits as a tool to identify the realized niche of phytoplankton populations: what do the shape of planktic microalgae, Anna Karenina and Vincent van Gogh have in common?

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Abstract Understanding the dynamics of phytoplankton assemblages in various and variable aquatic ecosystems is of paramount importance, given the strategic supporting services offered by these organisms. Such knowledge is implicitly based on the analysis of the realized niche of the different populations, i.e. of the sets of conditions within which populations show a positive growth. The range of phytoplankton morphological traits variability is evolutionarily selected to maximize the ecological performance of species while they are entrained in the spectrum of turbulent flows. In addition, most phytoplankton species exhibit high morphological plasticity that can further optimize their performance under reduced environmental variability. Although this plasticity is well known, it is seldom considered in phytoplankton studies. Morphological analysis could therefore be used as a tool to estimate the environmental variability within which a species can persist and, ultimately, the niche width of phytoplankton populations. This opinion paper tries to answer the questions: to what extent can the morphological variability of phytoplankton offer a synthesis of the environmental variability of aquatic ecosystems?. Do the morphological traits contain sufficient information to describe the width of the realized niche of phytoplankton species? What can we do to fill eventual gaps in our knowledge?

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Introduction

Paraphrasing the incipit of Anna Karenina,[1] the famous novel by Leo Tolstoy, we could say "Happy phytoplankton species are all alike; each unhappy phytoplankton species is unhappy in its own way". In fact, for a phytoplankton population "to be happy" (i.e. to persist and reproduce in a given environment), several aspects/factors must be fulfilled: e.g. optimal amounts of resources (light and a variety of macro- and micronutrients) under suitable mixing conditions of the water column, as well as appropriate values of water temperature, pH, conductivity/salinity, etc. A deficiency of even one of these aspects can be enough to make a phytoplankton species unable to persist and reproduce (and thus "unhappy"). In the synthesis, competitive and evolutionary success does not depend on some particular, positive condition, instead, it is the absence of any negative condition that allows a species to thrive.

The niche theory has been one of the most appealing in ecology and has undergone several modifications and refinements. According to the Grinnellian niche concept (Grinnell, 1917), the niche is shaped largely by abiotic attributes of the habitat where a (animal) species lives along with its behavioural adaptation. The Eltonian niche is largely centred around foraging strategies of (animal) species with focus on the biotic environment (Elton, 2001, originally published in 1927). G. E. Hutchinson (1957) combined the Grinnellian and Eltonian approaches and introduced a kind of "qualitative mathematics" (later translated into statistical terms by MacArthur, 1958) into the niche theory by defining niche as "n-dimensional hypervolume" in the environmental hyperspace. He introduced terms like niche breadth, niche partitioning and niche overlap. Without going into the details of later developments of Hutchinson's concepts it is fair to mention that it was criticized for several reasons. For example, Riegler & Peters (1995) classified it as typical nontheory because niche of a

species can never be described fully since the number of axes of the *n*-dimensional hypervolume is not defined and therefore additional axes can be added. Nevertheless, recent developments in phytoplankton ecology support the usefulness of the Hutchinsonian niche theory, if we concentrate on the most relevant axes and the most relevant attributes (like size and shape) of a species or even group of biota (traits, functional groups).

But let's get back to phytoplankton. The aspects that collectively contribute to making phytoplankton species "happy" can be imagined, according to Hutchinson (1957), as the axes of a hypervolume representing the fundamental niche of a species. This is the niche commonly measured in the lab from unialgal cultures, excluding biological interactions with other species. In natural ecosystems, biological interactions (competition, predation, parasitism) generally reduce the breadth of the fundamental niche, while still allowing growth under suboptimal conditions. The subset of actual physical and chemical conditions registered in the environment, and the modulating effect of biological interactions under which a species still shows a positive growth, represent its realized niche. It follows that, depending on the portion of the fundamental niche involved and, on the number and extent of biological interactions, species often occupy slightly different realized niches in different ecosystems (Marrone et al., 2022).

The analysis of the realized niche of the different phytoplankton populations is of paramount importance, given the strategic supporting ecosystem services that these organisms provide (B-Béres et al., 2022; Lengyel et al., 2022; Naselli-Flores & Padisák, 2022) and the impacts that human activities exert on the characteristics of their niches (Salmaso et al., 2012). However, phytoplankton ecologists tend to seek easy, single-factor explanations to describe the structure of phytoplankton populations and their success in their studied environment commonly using "axes" defined by parameters widely used in water quality monitoring. Many studies on phytoplankton are centred on singular aspects like resource requirements in terms of nutrients, light, temperature, pH, grazers avoidance, etc., and often, in papers on phytoplankton ecology we read: «TN (or TP) is the most important variable shaping phytoplankton… Light is the driver of phytoplankton growth… Temperature or dissolved oxygen is an essential factor favoring the

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[1] The "Anna Karenina principle" was used for the first time in 1997 by Jared Diamond in his popular book *Guns, Germs, and Steel* (Diamond, 1997, Chap. 9), to describe the factors that favoured the domestication of a few wild animals. Later, it has been used to describe numerous ecological patterns (for further details: https://en.wikipedia.org/wiki/Anna_Karenina_principle).

growth of Cyanobacteria, Chlorophyta and Bacillariophyta… The pH has significantly negative relationships with Cyanobacteria, Chlorophyta and Bacillariophyta… A high salinity is an adverse factor for (freshwater) phytoplankton…etc.». Ecophysiological studies involving more than two variables (commonly light and temperature) are rare but exist (e.g. Lengyel et al., 2015). While contributing to deepen our knowledge on the extension of individual axes of the hypervolume occupied by a species, these results (i) only seldom do consider phytoplankton responses in relation to the interactions of multiple variables (Machado et al., 2022); (ii) do not fully keep in account the distinctive characteristics of phytoplankton, i.e. to be a collective of organisms adapted to live in apparent suspension in open waters (Naselli-Flores et al., 2021a). This apparent suspension can be fully achieved only by organisms of small dimensions (< 0.2 mm), and whose intrinsic movements are frequently too feeble to overcome the velocity and direction of much of the spectrum of water movements (Reynolds, 2006). Their small size implies that these organisms are subjected to physical forces different from those to which larger organisms are subjected (see Naselli-Flores et al., 2021a). In fact, due to their small dimension phytoplankton organisms live at low Reynolds numbers (Purcell, 1977), i.e. phytoplankters are scarcely subjected to inertia (which acts proportionally to their volume/size) and strongly to water viscosity (which acts proportionally to their surface/shape). Viscosity can be defined as the effect of water «stickiness» on the organisms and largely govern the lifestyle of phytoplankton and its entrainment in water motion (Naselli-Flores & Barone, 2011) since, as stated by Purcell (1977) "At low Reynolds numbers you can't shake off your environment. If you move you take it along".

Phytoplankton organisms developed many adaptive strategies, largely based on the variability of their size and shape (Litchman & Klausmeier, 2008) in order to be sheltered or to take advantage of turbulent flow features as regard, e.g. their access to resources and/or escape from grazers (Reynolds, 1997). For a given volume/size, sheltering or taking advantage depend on the characteristics of the turbulent flow and on the interactions between water viscosity, which varies with temperature and phytoplankton surface area, which varies among and within species. Morphological variability is, therefore, of fundamental importance in determining whether a certain shape (associated to a certain species or group of species) can persist in the specific turbulent conditions that affect a waterbody. We can say that the spectrum of morphological variability commonly observed in phytoplankton is evolutionarily addressed to match with the spectrum of turbulent conditions of water masses observable on our planet. Along with size, the shape of a species therefore represents an important morphological characteristic to be considered when analysing phytoplankton assemblages, and the relationships between species and the environmental conditions that define their realized niche (Naselli-Flores, 2014).

In this opinion paper, we discuss the role that morphological traits have in the ecology of phytoplankton and try to support the idea that morphological analysis of phytoplankton can represent a useful tool to estimate the niche width of phytoplankton populations and, ultimately, the patterns of environmental variability within which a species can persist.

Niche dimensions and morphological traits of phytoplankton: where are we now?

Quantitatively defining multidimensional ecological niches of phytoplankton and determining the influences of environmental factors on niches of individual species (and functional groups) is not an easy task because of the contemporary multidimensionality of environmental changes and of the nonlinear and nonadditive responses of phytoplankton to these changes (Litchman et al., 2012; Xu et al., 2022). Accordingly, a relatively small number of studies attempted to describe the niche characteristics of phytoplankton species in the past, and the number of considered niche dimensions has increased as the knowledge about the ecological requirements of phytoplankton has progressed (see Amorim & Moura, 2022), and especially after recognition that physical constraints of growth or even existence are often of greater importance than nutrient availability (Zohary et al., 2010).

Traits are characteristics that can be measured at individual level and whose value (e.g. "small" or "big", "long" or short") can increase the fitness of an organism to its environment. They are genetically controlled and include physiological, behavioural,
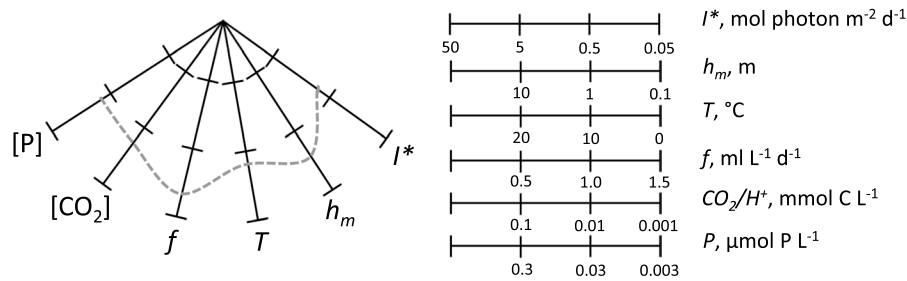
Fig. 1 Graphical development of the habitat template for a hypothetical phytoplankton species (grey dashed contour is fitted to show maximum growth rate) and based on six variables, all but T and f plotted on a log scale: integrated underwater irradiance (I^*), mixed depth of the water column (h_m), water temperature (T), filtration capacity of herbivores (f), acidity or alkalinity as availability of free carbon (CO_2/H^+), and external concentration of phosphorus required to saturate the maximum growth rate (P). The axes are scaled to be comparable to each other and oriented to show the best net performance to the left (i.e. towards the focal root of the hexacle). Redrawn and modified from Reynolds (1997)

life history-related and morphological traits. Lewis (1976, 1977) was probably among the first who recognized the functional role of some phytoplankton morphological traits (surface area, volume and their ratio S/V) with respect to the nutrient gradient, and the possibility to use morphology to infer the niche characteristics of phytoplankton in Lake Lanao (Philippines). Two morphological traits (S/V, and the product of maximum linear dimension, m, and S/V, i.e. $m\,S/V$) were used by Reynolds (1988) to identify three main life strategies of phytoplankton (C–S–R) by putting in relation nutrients availability with S/V, a morphological descriptor of size and light availability with $m\,S/V$, a morphological descriptor of cell elongation (for more details see Naselli-Flores & Barone, 2011). As shown by Naselli-Flores & Barone (2007) in eutrophic waterbodies, the less the availability of light (as indicated by the increasing value of the ratio between mixing depth and euphotic depth), the greater is the tendency towards more elongated phytoplankton shapes. In addition, by investigating the relationships between morphological traits and the seasonal changes of niche characteristics, Kléparski et al. (2022) showed that elongation enhances buoyancy and confers a selective advantage in stratified low-nutrient waters typical of summer without changing phytoplankton S/V and therefore its ability to absorb nutrients.

The habitat template concept proposed by Reynolds (1997, p. 217; 2003) is among the first attempts to offer a graphical, quantitative description of the multidimensional niche of phytoplankton species. This author selected six diagnostic axes (but the method can embody any number of axes), each representing quantifiable environmental variables and expressed in comparable units, that govern the growth performances of phytoplankton species under controlled conditions, with respect to their requirements or tolerances. These axes, in the examples proposed by Reynolds, were arranged to form a kind of umbrella (a "hexacle") and, for given species, contours were constructed to link the intersections of the maximum growth rate on the respective axes (Fig. 1). These contour maps represent the habitat template of species and provide a projection on a bidimensional plane of the Hutchinson's hypervolume. Although simplified, the hexacle includes the main dimensions governing phytoplankton growth (Litchman et al., 2012).

A habitat shown typically to be constrained by light, or P or N or by any other variable, is more likely to be populated by species with the appropriate adaptations able to function there, even though this does not imply that those species will be there (Reynolds et al., 2002). Adaptations concern morphological, physiological and behavioural traits of phytoplankton organisms and are aimed at increasing the fitness of organisms to specific environmental conditions (Litchman & Klausmeier, 2008). These concepts are at the base of the functional classification of freshwater phytoplankton proposed by Reynolds (1980, 1997), and implemented by Reynolds et al. (2002) and Padisák et al. (2009). The Reynolds' functional classification reflects the principles used to identify the C–S–R life strategies of phytoplankton (as shown in Reynolds, 1997) and groups together species with
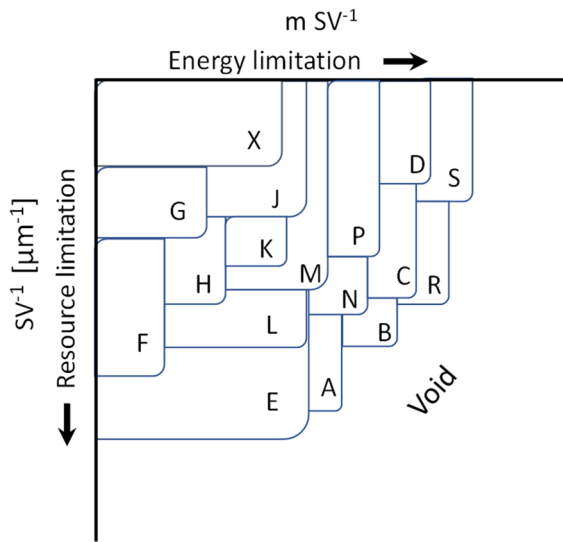
Fig. 2 Ordination of Reynolds' phytoplankton associations (as shown in Reynolds 1997) based on their morphological descriptors (*S/V* and *m S/V*) and according to gradients of decreasing light and decreasing nutrient accessibility limitation. This graph shows the link existing between the morphological grouping of phytoplankton into the C–S–R life strategies (Reynolds, 1997), and the functional coda as described in Reynolds et al. (2002). Redrawn from Reynolds (1997)

similar ecological features as a result of their morphological and physiological traits (Fig. 2). In particular, all species characterized by similar dimensions (*S/V*) and shape (*m S/V*) will be found close together in a C–S–R graph, and will identify an area within which it is possible to define a given functional group, and identify it by a unique codon (**A** or **X** or **J**, etc.). The method postulates that a certain degree of overlap exists among the different species and that these different species must possess traits that enable them to tolerate the constraining conditions of a factor deficiency more successfully than species without such traits. The overlapping of habitat templates and the sharing of traits allow species to co-exist and to give rise to stable and recognizable "floristic associations" even in different aquatic ecosystems (Reynolds, 1997; Salmaso et al., 2015). Thus, a key element of the functional type approach is that niches of species from the same functional type are more similar to each other, on average, than niches of species from different functional types (Irwin & Finkel, 2017).

The Reynolds' functional classification system implicitly recognizes morphological characteristics as "master traits" because of the large number of physiological and ecological features that are regulated by body shape and size (Reynolds, 2006; Glibert, 2019; Weithoff & Beisner, 2019), and because they represent both response and effect traits, i.e. they contemporarily reflect organisms' responses to environmental changes and represent individual features that affect ecosystem functioning (Kruk et al., 2021). In synthesis, they are reliable proxies for studying the environmental conditions of aquatic ecosystems and have been successfully used to develop a series of trait-based classification systems for phytoplankton (see the review by Salmaso et al., 2015 and literature therein).

Multidimensional environmental changes in field conditions can cause displacements in the local, realized niche of both species and functional groups. The analysis of natural populations often shows realized niches different both from each other and from the fundamental niche of the same species (e.g. see Zhang et al., 2022). These differences can be due to different biological interactions (Scheffer et al., 2003), and/or to the absence of part of the fundamental niche from the habitat studied. Any of these factors could change over space (in different environments) and time (in different periods of the annual succession). Thus, it can happen that several realized niches may occur for the same species as the environment changes. As an example, a displacement in the optimum of photosynthesis for *Aphanizomenon flos-aquae* Ralfs ex Bornet & Flahault was detected by Üveges et al. (2012) when studying the occurrence of a winter bloom of the species under ice and snow cover in Lake Stechlin. Optimum photosynthesis was above 20°C at irradiances above 150 µmol m^{-2} s^{-1}. However, net photosynthesis occurred at temperatures ranging between 2 and 5°C when light availability was in the range 7.5–30 µmol m^{-2} s^{-1}. Niche displacements were also observed by Nagy-László et al. (2020) when analysing the niche characteristics of functional groups sensu Reynolds et al. (2002) in rivers. According to these authors, the turbulent regime of rivers and their turbidity modify the niche characteristics of phytoplankton functional groups when they occur in lotic ecosystems.

Concerning ecophysiological experiments a side note is worth to mention. Most such unialgal experiments are aimed at exploring the optimum growth conditions (for temperature, light,

nutrients, pH, etc.) especially in biotechnological research where conditions for maximal production is the major target. Much less attention is paid for the tolerance margins. For example, the commonly applied temperature range is between 5 and 35°C and without exploring the maxima and minima at which the species is able to exhibit net photosynthesis. As well known from distribution areas of terrestrial plants, margins of areal distribution are often determined by climate-related variables being temperature one of the most important. Due to high heat capacity of water, the temperature climate of aquatic biota is much more restricted than that of terrestrial ones. Still, as the winter bloom of *A. flos-aquae* in Lake Stechlin depended on its cold and shade tolerance as shown in experiments by Üveges et al. (2012), experimental temperature decreased to 2°C. Such events may initiate cascading consequences at ecosystem level as shown in this case by extraordinarily high bacterial production after ice-break (Bižić-Ionescu et al., 2014). Additionally, tolerance limits determine whether a species can survive in extreme environments or not (Padisák & Naselli-Flores, 2021).

As pointed out by Reynolds (1997), the data to graph the hexacle of phytoplankton were (and still have been) only available for a small number of species/functional groups due to the paucity of autoecological studies for most phytoplankton species. However, an increasing number of papers has been produced in the last years aimed at linking habitat characteristics and morphological structure of phytoplankton (e.g., Naselli-Flores & Barone, 2000; Salmaso & Padisák, 2007; Kruk et al., 2010; Kruk & Segura, 2012; Stanca et al., 2013; Naselli-Flores, 2014; Abonyi et al., 2020; Ryabov et al., 2021; Pulina et al., 2022). These morphology-based efforts, while still numerically limited, reveal a renewed interest of phytoplankton ecologists in studying the relationships between the morphology of phytoplankton organisms and the dimensional structure of their niche. In addition, these studies are extremely useful as they offer new insights into the characterization of ecosystem functions and responses, especially considering the rapid changes affecting fresh and marine waters in the Anthropocene.

Morphological traits and their role in the establishment of phytoplankton niches: where are we going?

In the past 20 years, trait-based methods became widespread in analyses of spatial and temporal patterns of phytoplankton assemblages in both freshwater and marine ecosystems (e.g., Zingone et al., 2022; Paul et al., 2023). The extended use of such groupings can be explained by their joint feature: they allow to decrease the structural complexity of large phytoplankton datasets by decreasing the number of studied taxonomic categories (i.e. trait classifications are fed by a few groups of populations that share one or more traits instead of long lists of single populations) largely without losing functional attributes.

Since phytoplankton organisms are made up of one or a few cells similar to each other and grouped in a colony, it is on the size and shape of that cell(s) that natural selection primarily exerts its pressure. These morphological traits (and their combinations) are mainly aimed at regulating the entrainment of species in a gradient of turbulent water motions in order to maximize the uptake of energy and nutrients essential to their life. Morphological features of a species can change within the limits of maximum morphological variance characteristic for that species in the attempt to increase the fitness of individuals to a varying environmental scenario. This morphological variability is called "phenotypic plasticity" and represents the possibility for one single genotype to produce more than one morphotype (West-Eberhard, 1989). The phenotypic plasticity of a species can therefore contribute to make its realized niches unstable over space and time (Marrone et al., 2022). A recent example using six morphological traits of the dominant *Aulacoseira* species in the Pearl River Delta demonstrated that trait variation of *Aulacoseira* was more responsive to environmental changes than to interspecific interactions, and that the analysis of trait variation in phytoplankton species can improve our ability to forecast changes in ecosystem characteristics across environmental gradients (Hu et al., 2023). When the extent of any environmental parameter exceeds the morphological adaptive capacity of a single population, species replacement takes place offering further adaptation at a higher organization level (Naselli-Flores et al., 2007).
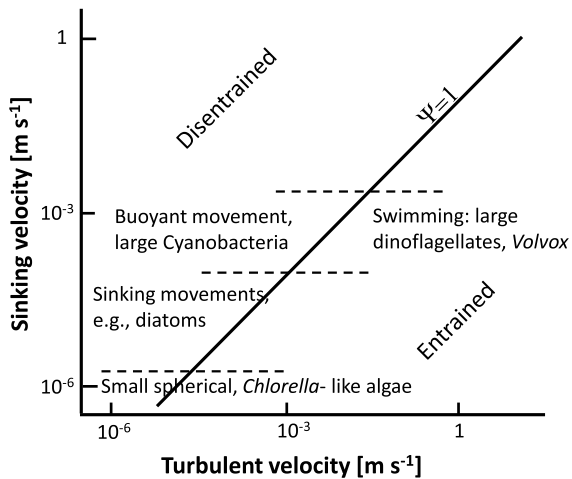
Fig. 3 The entrainment quotient (Y) as the ratio between the sinking velocity of phytoplankters and 15×the turbulent velocity of water masses. The larger is the alga (or, depending also on its shape, the lower is its form resistance factor), the higher is its sinking velocity, and the greater is the turbulent intensity required to entrain it. Redrawn from Reynolds (2006)

Thus, morphological traits largely contribute to make phytoplankton what it is: a group of organisms adapted to live in apparent suspension in turbulent water masses. According to Humphries & Imberger (1982), the effective entrainment (and disentrainment) depends on the ratio between the sinking velocity of the algae and the turbulent velocity of water masses (Fig. 3). Empirical judgement suggested that entrainment threshold occurs when turbulent velocity is 15×greater than the intrinsic motion of the particle. In any case, the larger is the alga and the greater its intrinsic settling (or flotation) velocity, then the greater is the extent of turbulence required to entrain it (for more details see Reynolds, 2006, p. 69). Several aspects of phytoplankton life depend on the degree of entrainment of cells and colonies. These include the possibility (i) to make thinner the diffusive boundary layer and to enhance the flux of nutrients from the medium into the cells, (ii) of being resuspended in better illuminated water layers and (iii) of decreasing encounter rates between phytoplankton and zooplankton (for more details see the review by Naselli-Flores et al., 2021a). Having the right shape and size with respect to the turbulent conditions of water masses

is therefore of paramount importance when living in apparent suspension in turbulent water masses.

Traits aimed at minimizing grazing impact

Morphological inducible defences in phytoplankton are attainable thanks to the phenotypic plasticity of species, may or may not be permanent throughout the individual's lifespan, and depends on biotic and abiotic stimuli from the environment (West-Eberhard, 1989). Escape from predation has been shown to be a powerful biotic stimulus exerting a selective pressure on phytoplankton morphology by favouring larger sizes, inducing the production of spines and bristles, and/or promoting cell clustering in colonial aggregates (for more details see Lürling, 2021). All these morphological changes have an ecological cost in terms of cell energetics, since they also influence the sinking velocity of phytoplankton and its entrainment in the turbulent water flow, possibly modifying the resource uptake (both light and nutrients) and, ultimately, interfering with species survival.

The information contained in the specific shape and size of phytoplankton therefore summarizes the contemporary and complex need for planktic algae to access resources (nutrients and light) and to minimize the effects of grazing as they are entrained in the water flow (Naselli-Flores & Barone, 2011).

Traits aimed at minimizing sinking loss

At decreasing turbulent intensity, to keep on benefitting from entrainment, algae have either to decrease their size or to increase the resistance to sinking exerted by their shape (Padisák et al., 2003). It is the morphology of phytoplankton and the "form resistance" generated by the different shapes that enhances the turbulent entrainment. Shape variability therefore controls the interactions between cell surface and water viscosity, and ultimately the way in which species respond to the environmental scenario. The "bizarre" shapes often exhibited by different phytoplankton species are characterized by a morphology that diverges from the spherical one and that involves, e.g., elongations on one or two planes, and/or the presence of expansions, setae and fibrils, spines, protuberances, papillae, mucilage, holes in coenobia (*Pediastrum*), etc. All these modifications affect the shape of both unicellular and colonial forms and are

effective in increasing the role of viscous forces on the cell surface, and in modulating the sinking rate of different phytoplankton species, and consequently their entrainment in the turbulent flow (Naselli-Flores et al., 2021a). According to Huisman et al. (2002), phytoplankton can positively grow in the euphotic zone within a "turbulent window" characterized 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 depth of the mixed layer is therefore another crucial point for phytoplankton (e.g., Lindenschmidt & Chorus, 1998) and can influence its taxonomic and morphological structure (Lofton et al., 2022). It is in the very low-turbulence environments of boundary layers and tight metalimnetic gradients where velocities may fall to $< 10^{-3}$ m s^{-1}, that entrainment is critically lost and phytoplankton sinks to a greater depth (Wheeler et al., 2019). Thus, the criterion for continued suspension, and for minimizing sedimentation losses, is not whether the system is stratified but the probability of encountering boundary layers; roughly, this relates to how deep the turbulent mixed layer is and to how many thermoclines (boundary layers) develop within the euphotic zone (Reynolds, 2012). This criterion can contribute to explain why high temperatures (e.g., in summer or due to global warming) tend to select smaller phytoplankton dimensions with lower sinking velocities, and favour a better entrainment of organisms, maximizing the chances of resuspension and minimizing sedimentation losses. Turbulent mixing and depth of the mixed layer can also contribute to generate spatial segregation of water masses and give rise to a variety of realized niches for planktic Cyanobacteria characterized by different morphological attributes (Selmeczy et al., 2016).

Traits aimed at coping with physical variability of aquatic ecosystems

The depth of the mixed layers largely depends on temperature and even shallow water bodies can undergo summer thermal stratification (Borics et al., 2015; Søndergaard et al., 2022) with significant consequences on the size structure of their phytoplankton (Naselli-Flores, 2003).

In lakes where day–night temperature differences generate epilimnetic daily, convective mixing during the stratified period (partial atelomixis; Barbosa & Padisák, 2004) depth of the mixed layer (which also depends on wind intensity and direction, and on the size of the lake) largely determines the presence or absence of small diatoms. In lakes with deep mixing depth (approx. deeper than 30 m) diatoms are characteristic as in many African, high latitude lakes. Typical example is Lake Hayq, Ethiopia with dominance of *Navicula* and *Fragilaria* (Fetahi et al., 2014). With mixing depths 10–15 m diatoms like *Pantocsekiella ocellata* K. T. Kiss & Ács and desmids co-dominate (typical example: Lake Ziahurén, Mexico; Martinez-Almeida & Tavera, 2005), while at mixing depths shallower than about 10 m only desmids can proliferate since the heavier diatoms cannot compensate their high sinking loss by growth rate (examples: Lake Carioca and Lake Dom Helvécio, Brasil; Barbosa & Padisák, 2004; Souza et al., 2008). Desmids dominated in these two South American lakes: small, isodiametric (*Staurastrum*, *Staurodesmus*, *Cosmarium*) in one of them and elongated (*Closterium*, *Pleurotaenium*) in the other. In both cases, species were selected by drivers other than atelomixis, e.g., light climate and trophic state (Barbosa et al., 2013).

Water temperature also 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 nutrients uptake and light harvesting (Borowitzka et al., 2016). Due to the multiple metabolic constraints that it imposes to phytoplankton growth, temperature has often been considered a powerful driver of phytoplankton size structure in several aquatic ecosystems (e.g. Falkowski & Oliver, 2007; Morabito et al., 2007; Winder et al., 2009; López-Urrutia & Morán, 2015; Zohary et al., 2021).

Although worthy of consideration, less investigated is the role played by temperature on the density and viscosity of water, and how changes in these physicochemical properties impact the morphology (size and shape) and the entrainment of individual phytoplankters. Zohary et al. (2017) recorded the seasonal phenotypic plasticity over 8 years for a significant number of both unicellular and colonial planktic algae in Lake Kinneret. These belonged to different phylogenetic groups, persisted throughout the year (although with different abundances) and were characterized by different sizes. Since no influences due to nutrient or light availability were detected, the

Fig. 4 *The Starry Night* by Vincent van Gogh (taken from: https://commons. wikimedia.org/wiki/File: Van_Gogh_-_Starry_ Night_-_Google_Art_Proje ct.jpg)

authors hypothesized that this pattern could be due to the seasonal variation in density and viscosity of water linked to the seasonality of water temperatures. Such morphological plasticity could therefore represent a response of planktic algae to compensate the seasonal differences in density and viscosity of water masses and to regulate their sinking velocity, and ultimately their entrainment in turbulent flows throughout the year. Combination of deep mixing and higher specific gravity of water explains why marine eukaryotic phytoplankton is, in general, bigger than freshwater phytoplankton. However, it has been still not fully understood how the large, heavy, e.g. the endemic *Aulacoseira baikalensis* (Wisłouch) Simonsen and *A. skvortzowii* M.B. Edlund, Stoermer & C.M. Taylor may keep their populations recurrent while relying only on convectively generated turbulence under ice (Popovskaya et al. 2006; Jewson et al, 2009; Cael & Strong, 2018) in Lake Baikal. Another example is the rather enigmatic *Phacotus* with its thick loricae (whose synthesis is very expensive in terms of cell energetics), making the cell heavy and fast sinking (compensation by flagellar movement also consumes cell energy) and without preventing the cell being grazed (Schlegel et al., 1998). Still, the species is widespread and its existence demonstrates that or

our understanding has been limited especially, in this case, regarding specific gravity, size and shape.

Moving in a moving medium: reciprocal movements of plankton and water masses

A further aspect that increases the variability and complexity of phytoplankton niches is related to the reciprocal (vertical vs. horizontal) movements of planktic organisms (due to sinking, floating and/ or swimming which depend on their morphological features) and of the water masses in which they are entrained. These have a role in the spatial distribution of phytoplankton at different scales (Font-Muñoz et al., 2017 and literature therein) and in determining the spatial variability of phytoplankton size structure (Reynolds et al., 1993), often in counterintuitive ways (Durham et al., 2013). About 25 years ago, Peters & Redondo (1997) wrote "the complete understanding of turbulence is still one of the last frontiers in physics". Since then, several methodological and technological advances have started to reveal the importance of flow–microorganism interactions and the adaptations of microorganisms to flow (e.g. Guasto et al., 2012; Prairie et al., 2012; Goldstein, 2015; Wheeler et al., 2019; Mackay et al., 2022). Understanding

how the shape and size of phytoplankton couple with hydrodynamic aspects of turbulent flows is a promising research line to disclose new axes of the multi-dimensional niche of phytoplankton (e.g. see Arnott et al., 2021 and literature therein), and deserves further scientific efforts and closer interactions between physicists and biologists. However difficult, the resolution of problems associated with a complete understanding of turbulence is within the reach of human understanding if the famous painter Vincent van Gogh, in his painting "The Starry Night" (performed on June 18th, 1889), was able to intuitively perceive and paint swirls of turbulence (Fig. 4) that fit well with Kolmogorov's mathematical description of turbulent flow (Kolmogorov, 1941; Ball, 2006; Aragón et al., 2008).

Estimation of phytoplankton morphological descriptors

Due to the wide size range covered by phytoplankton organisms, the inadequacy of cell counts as a measure of phytoplankton abundance is evident, and a biomass estimate is fundamental for comparing data collected in different environments. The assumption that phytoplankton is isodense with water allows to express the biovolume values in terms of biomass (as fresh weight) but the use of the same models and formulas to perform the computation is essential. Therefore, efforts to compile geometric models for computing phytoplankton volume and surface area date back more than half a century (Kovala & Larrance, 1966), and attempts were made to standardize phytoplankton biovolume calculations due to its importance as a biomass estimate (Rott, 1981). A consensus was reached with the paper by Hillebrand et al. (1999) who proposed a standardized set of equations for biovolume and surface area calculations from linear dimensions measured under the microscope: for over 20 years these equations have enabled phytoplankton ecologists to calculate the volume of phytoplankton populations and estimate their biomass in a comparable way. However, an accurate geometric analysis of phytoplankton goes beyond the simple calculation of the biovolume since several physiological attributes of phytoplankton are related to its morphological characteristics (Hillebrand et al., 2022).

It is important to remark that "size" alone is not a sufficient descriptor of phytoplankton performance, especially when it is estimated only by considering just a single morphological descriptor as length, volume or the ratio between surface area and volume: a needle-shaped *Closterium aciculare* T. West 400 μm long and 6 μm wide has a surface area-to-volume ratio almost identical to that of a spherical *Chlorella*-like cell 6 μm in diameter: the latter is considered a small phytoplankter, whereas the first is considered a large one. The volume of the same *C. aciculare* is equal to that of a spherical cell 20 μm in diameter but the equivalent sphere as regard the surface area has an almost double diameter. In all these examples, the effect of viscosity on the cell due to their shapes can be quite different as well as the cell entrainment in the turbulent flow, and its ecological responses to environmental constraints. Phytoplankton shape has a strong adaptive value but, unfortunately, appropriate and objective descriptors are not available in literature and shape complexity lacks unequivocal definition (Sukumar et al., 2008). A shape descriptor estimating cell or colony elongation is given by the product of maximum linear dimension and *S/V*. For spherical shapes, this descriptor is equal to six and progressively increases with the extent of elongation along one or two planes, but this computation in many cases is not enough to effectively describe shape variability of phytoplankton organisms. The application of the principles of geometric morphometrics (Mitteroecker & Gunz, 2009) to phytoplankton morphological analysis is a promising tool for better understanding how the shape structure of phytoplankton is related to its realized niche (Borics et al., 2023).

Geometric analysis is also useful to elucidate important evolutionary aspects of phytoplankton (Ryabov et al., 2021) as well as its community organization and adaptive mechanisms (Roselli & Basset, 2015). This idea pervades much of the work carried out by Colin S. Reynolds and numerous references addressed to the topic are available in this author's extensive scientific production (for a complete list see the Supplementary Material contained in the paper by Naselli-Flores et al., 2021b).

The limitation for all geometric models and equations proposed in the literature is that they do not consider the "ornamentations" (e.g. spines, bristles, papillate surfaces) of phytoplankton cells when calculating surface area and biovolume. These

morphological features, as shown by Padisák et al. (2003), can significantly contribute to decrease or increase the sinking velocity of phytoplankton cells (examples: forms of *Tetraedron* spp. or *Mallomonas* spp.), and therefore influence their entrainment in turbulent water masses. Some efforts to overcome this limit have been recently produced by using computer applications and automatic imaging systems, and these methods contributed useful information to clarify morphological responses of phytoplankton to environmental forcing (Sonnet et al., 2022). A geometric approach developed by Borics et al. (2021) further goes in this direction and reduces the uncertainties related to a reliable computation of morphological descriptors, paving the way for more accurate assessments of the relationships between phytoplankton and its environment. These authors created 3D realistic models of phytoplankton cells coupled with appropriate software tools to calculate their volume and surface area in a reliable and simple way. Surface area and volume calculator is freely available online at http://freshwater-ecology.com:3838/3D_Algae/.

The increasing number of approaches aimed at improving the ability to estimate phytoplankton shape and size show how phytoplankton ecologists are increasingly aware of the great importance of morphology in the ecological analysis of phytoplankton.

Final remarks

Addressing more research efforts towards a detailed description of the phytoplankton realized niches is of no minor importance given the role of phytoplankton organisms as niche constructors and biosphere engineers (Erwin, 2008; Uyeda et al., 2016)

Phytoplankton is made of unicellular or colonial organisms and their adaptations to the environmental constraints must involve those single cells (or colonies). Evolution has therefore shaped different phytoplankton cells to cope with the spectrum of physicochemical (i.e. related to water density and viscosity) and turbulent conditions of water masses that can develop on our planet (e.g., Finkel et al., 2007). Phytoplankton morphological traits contain an enormous amount of information relating to the adaptations that different species have developed to improve their survivorship chances (e.g., Hillebrand et al., 2022). This information, if adequately retrieved, can be used to identify the realized niche of phytoplankton species, as well as many other ecologically and evolutionarily relevant issues about phytoplankton.

Shape and size are strongly related to "Reproduction", "Resource acquisition" and "Predator avoidance" (i.e., Litchman & Klausmeier, 2008) but these relationships have to take place by regulating the entrainment of cells in the water motion. Entrainment largely depends on the species-specific coefficient of morphological resistance to sinking (Padisák et al., 2003), i.e., on the shape of microalgae, and on their size.

What we can do to fill gaps in our knowledge

An effort to improve the sensitivity of phytoplankton ecologists in recording the morphological variability of phytoplankton as regard both size and shape (finding the time to consider the morphological plasticity of species within and among samples) is highly desirable. In summary, to fulfil this task, we should:

i. implement measurement algorithms able to consider the ornamentation (e.g. papillae, spines) present on the surface of cells and colonies (see Borics et al., 2021);

ii. routinely measure cell and colony size in all the collected samples, and compute their surface area and volume using the most updated tools available in literature (e.g. http://freshwater-ecology.com:3838/3D_Algae/);

iii. use these variables to compute size (S/V) and shape ($m\,S/V$) descriptors of phytoplankton cells and colonies (as well as any other eventual morphological descriptor); and

iv. try to relate these descriptors to environmental variables (e.g. see Naselli-Flores, 2014).

In addition, even without recording turbulent velocity of water masses or any other hydrodynamic variable, information on characteristics, duration and depth of mixing, light extinction, flushing rates, depth of the euphotic zone, z_{mix}/z_{eu} (or anything else that indicates our awareness that phytoplankton is not "stuck" in fixed positions in the water) should be routinely measured since they are important to better understand the dynamics of phytoplankton species and to better appreciate their niche characteristics.

Furthermore, for a more precise definition of the realized niche, not only the optimal growth conditions of the species must be recorded, but also the suboptimal ones (i.e., all those conditions in which a species shows a positive growth, albeit small). Exploring the "niche dimensions" of species/traits/functional groups, however, need to take eco-physiological adaptations into consideration like ability for N_2 fixation (nostocalean species), storage of essential nutrients either in vegetative cells (polyphosphate bodies) or assimilation by resting stages (examples: *Gloeotrichia* and *Raphidiopsis*; Pettersson et al., 1993; Istvánovics et al., 2000) survival capacity while transferred among islands (water bodies) through the terrain (Naselli-Flores & Padisák, 2016) or physiological adaptation to extreme environments (Padisák & Naselli-Flores, 2021).

However, the approach regarding morphological features could significantly increase our understanding of the ecological needs of species and of their complex interactions with the environment. Especially, that a number of "niche dimensions" can be explored in batch- and throughflow cultures or in mesocosms of different size (N and P uptake, light-temperature dependence, grazing pressure, competition, etc.) but entrainment in the pelagic has remained a very hard issue to approach experimentally.

We also need to consider the appropriate time scale when studying phytoplankton since the occurrence of a windy day, the establishment of a temporary thermocline (Søndergaard et al., 2022), the very variable annual hydrological cycle of closed-basin lakes (Lengyel et al., 2019) or the lake–wetland habitats (Crossetti et al., 2007) may strongly alter the composition and succession pattern of phytoplankton assemblages and confound our analyses.

Finally, phytoplankton is not a "wanderer": different species populating different environments, and their eventual seasonal preferences, are selected by well-defined environmental constraints (Naselli-Flores et al., 2021a). Thus, these organisms perfectly know where they can or cannot go.

Data availability   n.a.

Declarations

Conflict of interest   The authors declare no conflict of interest.

Ethical approval   n.a.

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