

Invited review

Fight on plankton! Or, phytoplankton shape and size as adaptive tools to get ahead in the struggle for life

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Abstract – A renewed interest in investigating the relationships existing between body size and environmental variables is pervading ecological studies. Phytoplankton has a long tradition as model system in studies of community ecology and several research concepts were developed using these organisms. In this paper we try to review the relevance of analyzing the morphological features of phytoplankton in ecology. Starting with a brief account of allometric relationships existing in phytoplankton, we i) examine the physical context in which phytoplankton grow, and ii) highlight the role of their size in nutrient uptake, and that of their shape in light harvesting. Moreover, the way in which the morphology of phytoplankton organisms cope with the hydrodynamical conditions of a given water-body are considered. In addition, we also included a paragraph on the role of grazing in moulding the size and the shape structure of phytoplankton assemblages. An account on the main research currents about the role of morphology in the definition of morpho-functional traits of phytoplankton is offered. All these approaches, which can be viewed as complementary of taxonomy, both molecular and “traditional”, are promising tools to better understand the functioning of aquatic ecosystems and may offer a vast array of new perspectives in the field of aquatic ecology and phytoplankton research as well as a simplified tool to perform water quality monitoring.

floating / grazing / light harvesting / maximum linear dimension / morphological traits / nutrient uptake / sinking / surface / volume

Résumé – Les relations qui existent entre la taille des organismes et les variables environnementales suscitent un intérêt croissant dans les études écologiques. Le phytoplancton a une longue tradition en tant que modèle pour les études écologiques des communautés et plusieurs concepts de recherche ont été développés à partir de ces organismes. Dans cet article, nous essayons d'examiner la pertinence des analyses des traits morphologiques dans l'écologie du phytoplancton. Après un bref exposé sur les relations allométriques au sein du phytoplancton, nous examinons le contexte physique dans lequel celui-ci croît et nous mettons l'accent sur le rôle de sa taille vis-à-vis de l'absorption des nutriments et de sa forme quant à la capture de la lumière. Nous évaluons aussi la manière dont les morphologies des organismes phytoplanctoniques font face aux conditions hydrodynamiques d'une masse d'eau. De plus, nous incluons un paragraphe décrivant

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comment le broutage façonne les structures de taille et de forme des assemblages phytoplanctoniques. Un compte rendu des principales recherches actuelles concernant l'incidence de la morphologie sur les traits morpho-fonctionnels du phytoplancton est également proposé. Toutes ces approches, qui peuvent être considérées comme des compléments à la taxinomie tant moléculaire que « traditionnelle », sont des dispositifs prometteurs pour mieux appréhender le fonctionnement des écosystèmes aquatiques et peuvent offrir un vaste panel de perspectives dans le domaine de l'écologie aquatique et de la recherche sur le phytoplancton, tout comme un outil simplifié dans la réalisation des suivis de la qualité de l'eau.

absorption des nutriments / broutage / capture de la lumière / dimension linéaire maximum / enfoncement / flottement / traits morphologiques / surface / volume

INTRODUCTION

Body size is widely recognized to be an important feature related to physiological and ecological performances of organisms and the interest in body size related issues has a history as long as scientific thinking. Greek philosophers and naturalists were attracted by the widespread presence in Nature of constantly repeated morphological patterns. The so called “golden ratio”, for instance, has been again and again found to govern the shape of a variety of life-forms: from the spirals of shells to the disposition of the leaves around the branches or the position of apple seeds inside the fruit (Douady & Couder, 1992). In ecology, the importance of body size was early recognized by Alfred Wallace (1858), who was amongst the first who noted that the variability in size of organisms, or part of them, may enhance the survivorship of a given species, and by Elton (1927, reprinted in 2001), who identified its relevance to trophic interactions. However, the modern debate on the physiological and ecological implications of body size find its roots in the elegant writings of Robert Henry Peters (1983). This publication indirectly created, and was followed by, a renewed interest in the issues related to body size (e.g. Hildrew *et al.*, 2007). Organisms range in body sizes over about 22 orders of magnitude, from the smallest self-reproducing bacteria such as *Mycoplasma* weighing 10^{-13} g to giant sequoia trees weighing 10^9 g (Brown *et al.*, 2007). This wide range of body size in ecological communities is emerging as the key to predict features of ecological systems, such as the number and diversity of organisms (Hillebrand & Azovsky, 2001; Blackburn & Gaston, 2003).

The fascination with body size represents probably the key issue in ecology and hundreds of authors have been involved in studying its meaning and effects at different levels. With regard to aquatic ecosystems, the implications of body size on i) species interactions and population dynamics were analyzed by Hutchinson (1959), Brooks & Dodson (1965), Paine (1974), Leibold & Wilbur (1992), Morin (1995; 1999); ii) distributions of biomass, abundance and energy use across species, were investigated in the work from Sheldon & Parsons (1967), Sheldon *et al.* (1972, 1977), Cyr & Peters (1996) and Kerr & Dickie (2001); iii) structure of food webs includes work from Lindeman (1942), Odum (1956), Hutchinson (1959), Carpenter & Kitchell (1988), Sprules & Bowerman (1988) and Cohen *et al.* (2003); iv) nutrient relations and ecological stoichiometry are

reported in Redfield (1958), Schindler (1974), Wetzel (1984), Sterner & Elser (2002) and more recently were reviewed by Klausmeier *et al.* (2008).

Most of the studies on body size, however, were carried out on organisms “easy to handle” and the bulk of investigations only rarely has faced single species of microorganisms. This has been partly due to inherent difficulties in achieving precise measurements and to the fact that physical laws acting on “big organisms” are different from those governing the life of “small organisms”. However, all living organisms are subject to physical laws and processes and these determine their physiological requirements, act on their form and mould it.

The importance of shape was first described by D.W. Thompson in his masterpiece “On growth and form” (1942, but originally published in 1917). In this book, the author provided the first mathematical analysis of biological processes and suggested that the possibilities of “shapes” among living organisms are limited when compared to what Physics makes available; nevertheless, these are enough to determine at least three conditions as different as those permitting life to mammals, insects and bacteria. He also faced the problem of scales and separated those organisms where physical forces act either directly at the surface of their body, or otherwise in proportion to their surface, from those where these forces, and above all gravity, act on all particles and result in a force proportional to the mass or volume of the body. In synthesis, he pointed out the necessity to distinguish among the forces acting on organisms living at low and high Reynolds numbers.

Among the organisms living at low Reynolds numbers, phytoplankton offers an amazing morphological diversity and all those involved in phytoplankton research have commonly observed that these organisms are present in various shapes and may express a quite high variability, both intra- and inter-specific, in their morphology. These features have been traditionally used just for taxonomic classification of organisms. Lewis (1976) was one of the first recognizing the ecological value of morphological descriptors in phytoplankton in relation to uptake of light and nutrients and, as a result of, natural selection and competition. A few years later Margalef (1978) used life-forms as a determinant of seasonal succession of phytoplankton suggesting that morphological variability has an adaptive value directed toward the best fitting to environmental template. More recently, Reynolds (1997, 2006 and literature therein), summarizing a life-long work, explained in detail how the diverse ecological strategies adopted by phytoplankton can be related to differences in their morphology, which thus acquire a fundamental adaptive value.

In the last years, morphological and functional analysis of phytoplankton traits has become more and more popular especially because of the need to find descriptors easy to handle for the management purposes as requested by the different directives emanated by several countries to monitor the quality of their water-bodies. Trait-based approaches, which include morphological analysis of species involved, are being increasingly used in phytoplankton ecology to explain and predict species distributions along environmental gradients (e.g. Reynolds *et al.*, 2002; Weithoff, 2003; Litchman *et al.*, 2007, 2010; Naselli-Flores *et al.*, 2007a; Litchman & Klausmeier, 2008; Padisák *et al.*, 2009; Kruk *et al.*, 2010).

With this paper we are attempting the task to summarize the course of scientific research in the last decades and to highlight the most recent findings on the importance of size and shape of phytoplankton in describing the ecological characteristics of the aquatic ecosystems in which they develop.

A BRIEF ACCOUNT OF ALLOMETRIC RELATIONS

As stated by Brown *et al.* (2007), “nearly all characteristics of organisms, from their structure and function at molecular, cellular and whole-organism levels to ecological and evolutionary dynamics, are correlated with body size”. The relationship between an organism’s size (BS) and another of its characteristics (y) is usually expressed by the simple power formula:

$$y = aBS^b$$

The line described by this equation is a straight one only when $b = 0$ (and thus $y = a$) or when $b = 1$ (and thus $y/BS = a$). These two conditions rarely apply in nature and thus organism’s size and y (whatever it may represent) increase at different rates. For this reason the relations between y and BS are called *allometric* (ἄλλος: other; μέτρον: measure). The variation of y with BS is called *scaling* of that characteristic to body size: cats and tigers are built to the same design but on a different scale and the characteristics of the cat have to be scaled up to produce a tiger. Allometric relationships are the rules by which this scaling is achieved. On the other hand, a change in size which does not lead to change in proportion (isometric growth) is governed by the square-cube law. An organism which doubles in length isometrically will find that the surface area available to it will increase fourfold, while its volume and mass will increase by a factor of eight. This can present structural and physiological problems to organisms since a doubling in length would imply an eight times increase of biologically active tissue to be supported. Deviations from isometric growth are thus forced by physiological factors. Many biochemical processes (such as the respiration rate, or the maximum reproduction rate) show scaling, mostly associated with the ratio between surface area and mass in the animal. Overall metabolic rate in animals is generally accepted scaling to mass to a power 0.75, known as Kleiber’s law (Kleiber, 1947). This law derives from the observation that an organism’s metabolic rate scales to the 3/4 power of the organism’s mass. The puzzle why empirically estimated values of b are typically close to multiples of 1/4 has been longstanding. Recent theoretical advances in biological scaling and metabolism suggest that these pervasive quarter-power exponents are due to the fractal-like design of the networks and surfaces that supply energy and materials used by cells in biological metabolism (West *et al.*, 1997, 1999). A further advance was achieved by adding the exponential effect of temperature as a key parameter to the basic formula $y = aBS^{3/4}$, then transformed in:

$$P = P_0 M^{3/4} e^{-E/kT}$$

where P is the whole organism metabolic rate or production at a given time and P_0 its initial value, M is body size, E is the activation energy, k is Boltzmann’s constant (8.62×10^{-5} eV/K), and T is absolute temperature in degrees Kelvin (Savage *et al.*, 2004). These findings allowed Brown *et al.* (2004) to formulate the Metabolic Theory of Ecology (MTE), which posits that the metabolic rate of organisms is the fundamental biological rate that governs most observed patterns in ecology. This theory is based on an interpretation of the relationships between body size, body temperature, and metabolic rate across all organisms, including phytoplankton. Savage *et al.* (2004) presented data which related maximal growth rate (r_{max}) of unicellular eukaryotic algae, temperature and body size as $\mu\text{g}^{1/4}$. However, the general interspecific nature of allometric datasets may confound the existing relationships between size and physiological and ecological attributes. This is

partly due to the little known influence of single species. The relatively few studies that have documented intraspecific allometric variation have shown departures from the universal patterns (reviewed by Glazier, 2005) and de Castro & Gaedke (2008), by analyzing productivity of phyto- and zooplankton in Lake Costance, concluded that the MTE has little predictive power for the metabolism of freshwater phytoplankton. Some argue that such intraspecific variation in b is simply a consequence of a narrowed range in organism sizes (West *et al.*, 2001; West & Brown, 2005). This variation could be ecologically important (Glazier, 2005), but there is no way of assessing this given the limited number of studies that quantify allometric relationships within species.

As regard phytoplankton, their wide size range, which span over seven orders of magnitude by mass and four orders by length (Reynolds, 2006), as well as the fact that they are responsible for approximately half of the world's primary production (Field *et al.*, 1998), has generated significant interest in understanding how the size of these algae can influence their physiology and ecology (e.g. Chisholm, 1992; Finkel & Irwin, 2000; Irwin *et al.*, 2006; Beardall *et al.*, 2009). The 3/4 power law for phytoplankton was earlier recognized beyond laboratory cultures of freshwater chlorophytes (Agusti & Kalff, 1989). Later, Li (2002) provided macroecological perspectives on North Atlantic phytoplankton communities and found that trends of abundance in picophytoplankton (0.2-2 μm) and nanophytoplankton (2-20 μm) was related to assemblage mean-cell size according to the 3/4 power law of allometric scaling in biology. More in general, phytoplankton cell size has been shown to be related to chlorophyll a content (Geider *et al.*, 1986; Marañón *et al.*, 2007), macronutrient content (Paasche, 1973; Furnas, 1978), and growth rate (Durbin, 1977; Geider *et al.*, 1986; Costello & Chisholm, 1981; Nielsen, 2006; Vuorio *et al.*, 2009; Wilson *et al.*, 2010).

In the oceans, phytoplankton community structure is shaped by physical processes of advection and turbulence (Cullen *et al.*, 2002) and there is a direct influence of mesoscale (10-100 km) vertical motion on the slope of the phytoplankton size-abundance spectrum (Rodríguez *et al.*, 2001). In other words, hydrodynamic processes linked to up- and downward water motion, as well as the degree of mixing and stratification strongly contribute to determine the size distribution of phytoplankton. However, the importance of physical forces in promoting the vertical size distribution of freshwater phytoplankton, as described later for the oceans, was much earlier recognized and analyzed in details by Reynolds (1984a, 1997, 2006 and literature therein).

LIFE AT LOW REYNOLDS NUMBER

Life in water strongly conditions the shape and size of phytoplankton (Vogel, 1996). They need to access nutrients, whose diffusion, as discussed later, is limited by gradients (Raven, 1980) and have to harvest enough light to fulfill photosynthetic requirements, despite sinking.

The topic of sinking and floating was early considered by Hutchinson (1967) in a chapter on the hydromechanics of plankton and by Smayda (1970), who reviewed the issues on suspension of phytoplankton in the sea. These works highlighted the importance of relating the dimension of phytoplankton to the physical forces which govern the movements of a body in a viscous fluid.

The starting point of any discussion on this topic is the Reynolds number (Re): a ratio obtained by comparing the relative importance of inertial and viscous forces within a fluid. Reynolds number describes the way in which fluids will behave at different scales, and the flow regime within or around a given object or system. In particular, the effects of water velocity, viscosity and scale (size of the object of interest) on any biological object can be understood by considering the Reynolds number. This is given by:

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

where u is velocity [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 ν [$\text{m}^2 \text{s}^{-1}$] is the kinematic viscosity of the fluid [*i.e.* the absolute viscosity of the fluid (η) with its density (ρ) divided out]. Any combination of velocity, viscosity and scale that results in the same Re will result in a geometrically similar flow regime, as characterized by the ratio of inertial to viscous forces. Thus, doubling the length scale will result in a flow regime that can also be realized by doubling velocity or by halving kinematic viscosity (Humphries, 2007).

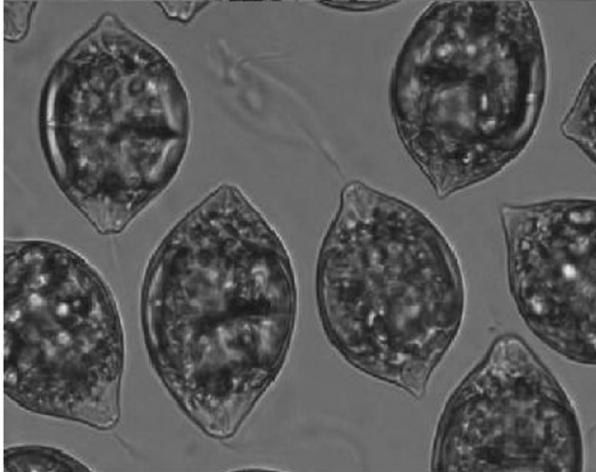
For biological objects and systems where size and speed are positively correlated (Vogel, 1996), high values of Re ($\gg 1$) indicate fast and more turbulent flow: inertial forces are in this case dominant, organisms are subjected to Eulerian dynamics, and gravity plays a major role. Conversely, low values of Re ($\ll 1$) indicate slow uniform (laminar) flow: viscous forces dominate and the organisms are subjected to Stokesian dynamics. This last condition is typical of microscopic organisms moving in aqueous solutions (Fig. 1). However, while high Re characterizes the flows at a human scale, the behavior of low Re flows are frequently counterintuitive. For instance, if a bacterium were suddenly to cease swimming, it would come to a halt in a distance much less than the diameter of a hydrogen atom (Berg, 1983). Reconstructing the cell's motion through water, Purcell (1977) equated the drag forces as being equivalent to those experienced by a human attempting to swim in molasses. Few species of planktic algae attain sizes greater than 3×10^{-4} m, while those that do so are often resident in weekly stratified or non-turbulent layers. The relative motion of a flagellate phytoplankton cell (e.g. *Chlamydomonas reinhardtii* P.A. Dangeard) with a diameter of $10 \mu\text{m}$, moving at a velocity of $10 \mu\text{m s}^{-1}$ has a Reynolds number of about 10^{-4} , considering the kinematic viscosity of water approximating to $10^{-6} \text{m}^2 \text{s}^{-1}$. If it stops swimming, it will progress for about 10nm ($10^{-2} \mu\text{m}$) in less than a μs . Although some very large unicellular species or colonies show values of $Re > 1$, the number is considerably lower than 0.1 for the majority of phytoplankton taxa (Walsby & Reynolds, 1980). This implies that phytoplankton will never be subjected to turbulence when moving into the water because their size is lower than the smallest eddy that can be generated in a water column (Reynolds, 1994). Moreover, algae move smoothly through the water without creating any turbulence. The relatively high viscosity of the medium, which could limit the rate of transport to cell wall, has important implications with regard to the ability to exchange gas and nutrient molecules. Re also governs the extent of sinking and entrainment of phytoplankton and their time-scale of circulation through a mixed layer, and thus the photoperiod and the possibility to harvest light in relation to light penetration in a water mass (Reynolds, 1989, 2006). The wide variety of strategies used by single phytoplankton species to fit these environmental constraints has been elucidated by analyzing the effects of their body size in the viscous range of the eddy spectrum, and their sinking speed (McNown & Malaika,



$L = 180 \text{ cm}$
 $u = 30 \text{ cm/s}$
 $Re = 540000$



$L = 2 \text{ cm}$
 $u = 2 \text{ cm/s}$
 $Re = 500$



$L = 0.020 \text{ mm}$
 $u = 0.010 \text{ mm/s}$
 $Re = 0.0002$

Fig. 1. Values of Reynolds number in organisms of different size calculated considering kinematic viscosity equal to $10^{-6} \text{ m}^2 \text{ s}^{-1}$ of . L: length of the organism; u: swimming velocity; Re: Reynolds number.

1950; Reynolds & Walsby, 1975; Reynolds & Wiseman, 1982; Reynolds, 1987, 1990, 1992, 1993a; Lüring & Van Donk, 2000).

FORM RESISTANCE AND VITAL FACTORS

At low Re (< 0.1) the passive sinking and floating velocities of a spherical body can be predicted by the Stokes equation:

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

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

When the shape of a phytoplanktic cell or colony differs from that of a sphere, Stokes equation can be modified by adding a dimensionless species-specific variable. This variable is called coefficient of form resistance (Φ_r) and expresses the factor by which the sinking velocity of the particle differs from that of a sphere of identical volume and density, in the same liquid. The relationship governing sinking velocity will be:

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

In the majority of cases, the value of the coefficient Φ_r is > 1 and the associated shape will tend to sink more slowly than the equivalent sphere. Only tear-drop shapes were shown to have $\Phi_r < 1$, thus sinking faster than a sphere (Padisák *et al.*, 2003a). Moreover, when the excess of density > 0 the organism will sink. When the excess of density < 0 the organism will float. The last eventuality commonly occurs in gas-vacuolated cyanobacteria and in the chlorophycean *Botryococcus braunii* Kützing, which can lower its density by producing isoprenoid triterpenes in the form of oil droplets (Metzger & Largeau, 2005).

The reliability of velocity estimated with the Stokes equation is quite high as confirmed by the sophisticated measurements performed by Walsby & Holland (2006) by using a density-stabilized sedimentation column scanned by a laser.

The degree of entrainment of algae in the turbulent motion of water masses (Ψ) is positively dependent upon their sinking or floating velocity (v') as calculated by Stokes' equation and negatively upon the shear velocity (u^*) according to the formula:

$$\Psi = v'/15u^*$$

Methods for an easy calculation of the shear velocity are shown in Denman & Gargett (1983) and in Moreno-Ostos *et al.* (2009), whereas the theoretical implications related to this physical quantity are shown in Reynolds (1997).

Humpries & Imberger (1982) showed that values of $\Psi < 1$ imply that phytoplankton distribution, in the water mass strongly depend on turbulent diffusion. This has been tested mainly with diatoms but also the dinoflagellate *Peridinium cinctum* (O.F. Müller) Ehrenberg was observed to fit the function (Regel *et al.*, 2004). Conversely, in case of buoyant cyanobacteria (with a negative v') the value of Ψ will reflect the balance between turbulent dispersion and colony density in determining whether a surface scum is likely to occur or not. Moreover,

the degree of entrainment influences the transport speed of a particle and its dispersion in a mixing water body. As shown by Reynolds (1994), a wind velocity of a few m s^{-1} imparts a speed to fully entrained phytoplankton which allows them to travel in the mixed layer in a few minutes. This time ($\sim 10^2$ s) is several 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 vertical distribution of phytoplankton organisms (Lucas *et al.*, 2009). It is thus only beyond the mixed layer or when the mixed layer contracts due to weakening of wind and/or increased solar heating that viscous forces overwhelm the entraining energy. Several issues related to phytoplankton (e.g. the development of diatom populations, the formation of both surface scums and deep chlorophyll maxima) rely upon the way in which the physical conditions of the water masses impinge the dimensional and temporal scales of phytoplankton (e.g. Huisman *et al.*, 2002, 2004; Regel *et al.*, 2004; Moreno-Ostos *et al.*, 2009).

The effect of form resistance was investigated by Conway & Trainor (1972) who showed that *Scenedesmus* strains with spines sank more slowly than others without spines. Smayda & Boleyn (1965) found that spineless preauxospore cells of the marine diatom *Rhizosolenia setigera* Brightwell sank faster than those with spines. In experiments when chitin fibres of *Thalassiosira weissflogii* (Grunow) G. Fryxell & Hasle were removed with chitinase, Walsby & Xypolyta (1977) showed that treated cells sank twice as fast as untreated ones.

Experimental measures of Φ_r were recently achieved by Padisák *et al.* (2003a), who established the value of the coefficient of form resistance for a variety of shapes using PVC models scaled up and moulded on different phytoplankton species. These algae were allowed to sink in an aquarium filled with glycerin. The excess of density between the PVC algae and the glycerin was comparable to that of real algae and water. This way, the authors could measure not only the value of the coefficient of form resistance for different species morphology but also evaluated the effects of colony size, coiling and symmetry. Even the presence/absence and typology of spines with regard to numbers, length and arrangement were considered. The paper offers not only an easy methodological procedure to measure Φ_r but it is also extremely useful in explaining some issues related to the ecological behavior of phytoplankton under different hydrodynamic and climatic regimes.

When discussing form resistance of phytoplankton species, it is difficult to avoid mentioning the so called “vital factor”. It has been demonstrated by a number of workers (Smayda & Boleyn, 1965; Eppley *et al.*, 1967; Smayda, 1970, 1974; Reynolds, 1973; Titman & Kilham, 1976; Wiseman & Reynolds, 1981) that dead or even living but senescent algae sink faster than viable cells, by factors of three to five, but without any visible alteration in shape, size or form-resistant structures.

Since this vital factor remained mysterious, Reynolds (1984a) concluded that it is advantageous to separate its contribution to Φ_r by investigating form resistance in killed cells (Fig. 2).

Living algae, especially green ones, can produce peculiar organic bristles protruding from the cell margins which are often hardly visible under the microscope and totally invisible in fixed material. In particular, some phytoplankton organisms produce chitin bristles often surrounding the cells which are likely an aid in flotation but could be also an antigrazing device. As an example, very often the coenobial green alga *Pediastrum* bear numerous bristles mainly originating from the marginal cells and radiating outwards (Figs 3-4).

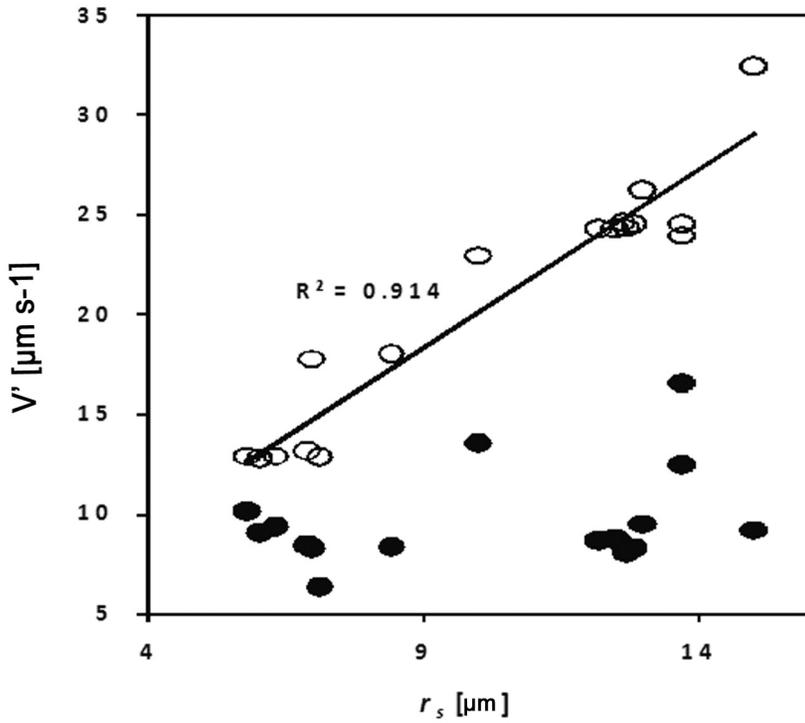
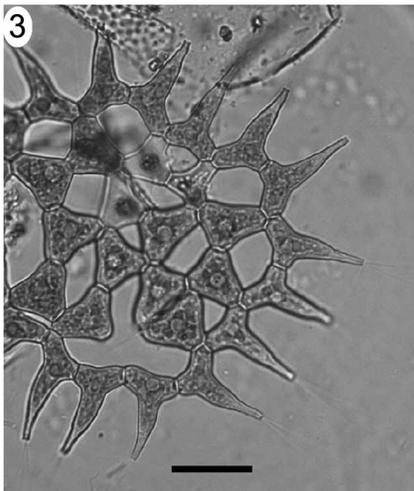
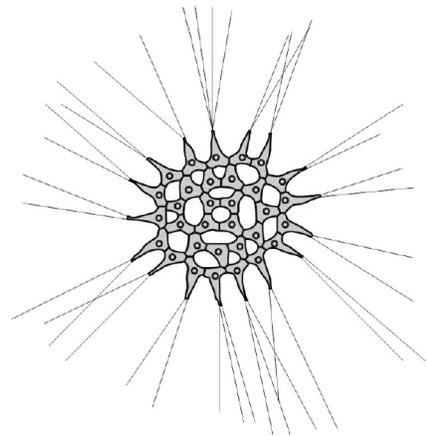


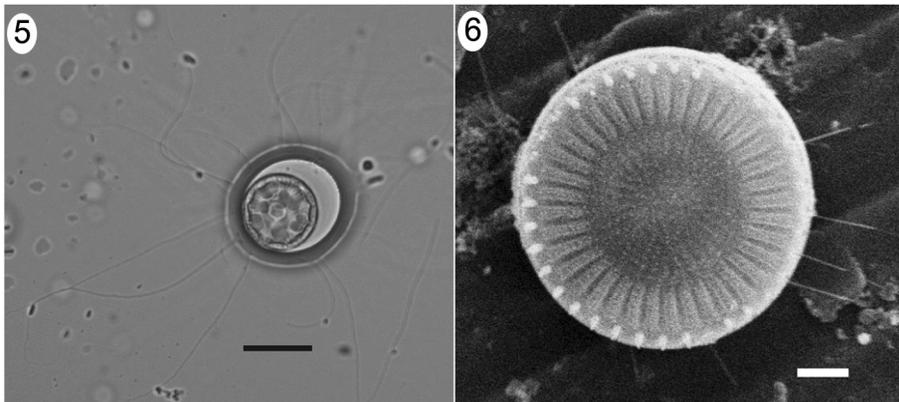
Fig. 2. Plot of the sinking velocities (v') of *Stephanodiscus rotula* against the radius (r_s) of a sphere of identical volume to the mean cell volume showing the effects of the "vital factor". Black circles represent live cells and no correlation is evident; empty circles represent the same cells killed by heat. In the latter case a strong positive correlation exists. Redrawn from Reynolds (1984).



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Figs 3-4. *Pediastrum simplex* var. *biwaense* Fukushima bristles. 3. LM image; the bar is 20 μm . 4. drawing from an LM picture.



Figs 5-6. Chitin fibrils in *Cyclotella meneghiniana* Kützing. **5.** fibrils in desiccated preparation; the bar is 20 μm ; **6.** SEM image; the bar is 3 μm .

These devices have lengths corresponding roughly to the diameter of the coenobium (Krienitz, 1990). Similar structures can also be observed in *Scenedesmus* (Trainor & Egan, 1988). Chitin fibrils radiating over 150 μm from the valve margin all around the cells are produced by some centric diatoms (Figs 5-6). These structures easily disintegrate when the cells are killed or even when they are merely senescent but their presence may significantly increase Φ_r and it is also probable that such flexible soft structures do not prevent grazing and therefore did not evolve for predation defense tool (Padisák *et al.*, 2003a).

Moreover, phytoplankton cells can regulate the size of their sap vacuoles or the production of oil reserve substances, which ultimately decrease their density. This is particularly true for the “heavy” diatoms (Reynolds, 2006).

Another important kind of vital contribution to form resistance might be the ability of the living organism to maintain the position that provides the highest form resistance. As reported in Padisák *et al.*, (2003a), this achievement could be reached by coupling asymmetry in spine distribution and motility as in *Mallomonas caudata* (Ivanov) Willi *et* Krieger.

Form resistance is of course not the only adaptive mechanism for enhancing flotation of plankton. Most flagellate phytoplankton species are quite efficient in vertical positioning and forms of individual species in euglenophytes, dinophytes, chlorophytes and chrysophytes are quite similar in the context of their probable form resistance (Sommer, 1988). Species of the first three groups are powerful swimmers. Conversely, chrysophytes are not so successful and most of their unicellular representatives inhabiting the epilimnia of stratified lakes are too small to be efficient swimmers. Colonies comprising many flagellated cells (like *Uroglenopsis americana* (Calkins) Lemmermann) cannot reach high unidirectional speed because flagellar movement of individual cells in the colony is not synchronized (Sandgren, 1988), as is the case in the superficially similar colonies of *Volvox aureus* Ehrenberg. In this way, it seems quite likely that the high morphological variability that is observed among the chrysoflagellates (like processes of *Bitrichia* or *Stephanoporos*, and silica spines in *Mallomonas*, *Chrysophaerella* or *Spiniferomonas*) were evolved to compensate their inefficient flotation.

Cyanoprokaryota have very effective mechanisms for regulating the buoyancy provided by their gas vesicles or aerotopes and respond to a variety of

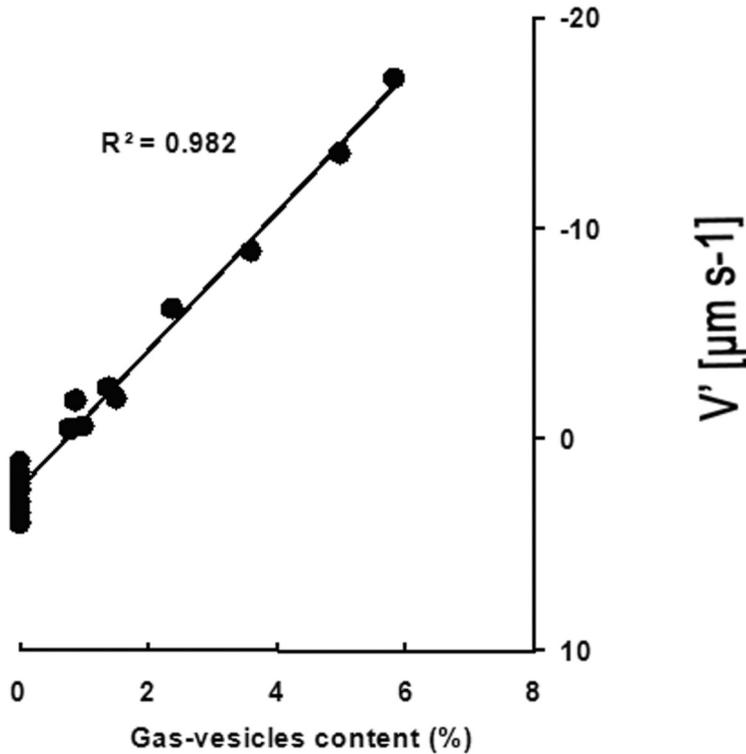


Fig. 7. Relationship between sinking/floating velocity (v') of the cyanobacterium *Dolichospermum* (*Anabaena*) *circinalis* and its gas-vesicles content as percentage of cell volume. Redrawn from Reynolds (2006).

environmental stimuli (Robarts & Zohary, 1984; Brookes *et al.*, 1999; Wallace & Hamilton, 1999; 2000; Wallace *et al.*, 2000; Naselli-Flores & Barone, 2003; Walsby *et al.*, 2006; Wilson *et al.*, 2010), which is proportionally scaled to the percentual proportion of these structures (Fig. 7). Although some authors tried to relate variation in coiling in planktic *Anabaena* Bory de Saint-Vincent *ex* Bornet *et* Flahault (now *Dolichospermum* Ralfs *ex* Bornet *et* Flahault) as an adaptive mechanism to travel faster in the water column (e.g. Booker & Walsby, 1979; Hickel, 1982), a recent work by Zapomělová *et al.* (2010) showed no effect of experimental conditions on trichome coiling, which could be a mechanism more effective to prevent grazing or to increase light harvesting (Zapomělová *et al.*, 2008).

Mucilage seems to be a flotation-aid, however the mechanisms are unclear since by decreasing the density of the organism also increases its size (Reynolds, 2007).

However, according to the Stokes' equation, the decrease of density, for example by mucilage secretion, is an ultimate tool for remaining in suspension: an organism with density equaling the density of the medium will float independently of size or shape (Padisák *et al.*, 2003a).

ENVIRONMENTAL CONSTRAINTS, BODY SIZE AND SHAPE

It may be evident to all those using identification keys, phytoplankton species generally show a rather wide range of size variation. For example, the spherical *Eremosphaera viridis* De Bary is reported to vary between 30 and 800 μm in diameter in the monograph on Chlorococcales by Komárek & Fott (1983) and in the needle-shaped *Closterium aciculare* T. West cell length can vary between 250 and 800 μm (Förster, 1982). As observed by Naselli-Flores & Barone (2000), environmental constraints may have a selective effect within the size range of single species. As an example, in a *Closterium aciculare* dominated lake, a decrease in light availability will first select the longest cells (with a higher coefficient of form resistance and thus sinking slower) already present in the population before causing their replacement by another species better adapted to darker conditions.

The morphological size range of phytoplankton span over four order of magnitude and is comparable to that of forest trees and herbs (Reynolds, 1994). No one would say that the ecological scales and requirements of an oak (e.g. *Quercus ilex* Linnaeus) are similar to that of a small orchid (e.g. *Ophrys apifera* Hudson) although both these species are common elements in the Mediterranean maquis. In the same way, picophytoplankton and the large dinoflagellate *Ceratium hirundinella* (O.F. Müller) Bergh may inhabit the same lake but are the expression of totally different ecological conditions. In other words, they belong to the same flora but are the expression of adaptive pressures resulting in different vegetation typologies.

This concept is not new to phytoplankton ecologists if at the beginning of the 70' of the last century Hecky and Kilham (1974), summarizing the results of a burning debate, wrote: "Phytoplankton are usually looked at as complex solutions with particular biochemical properties rather than as organisms acted upon by natural selection. If large and small phytoplankters were heuristically looked upon as elephants and mice and basic biological questions concerning form and function were asked, we are confident that the significance of size in the planktic environment would be more easily understood."

Grime (1974) offered a way to solve the debate by recognizing that there are three major determinants of vegetation – competition, stress and disturbance – and that each has invoked a distinct strategy on the part of the flowering plant. Later, he coauthored a book in which a functional approach to describe vegetation is described (Grime *et al.*, 1996). The book show how useful is to classify the external factors which affect the vegetation competitive processes into the two broad categories that he had called stress and disturbance. Those organisms with low tolerance to both stress and disturbance are called "Competitors", those well resisting to stress but liable to disturbance "Stress-tolerators", and those tolerating disturbance but sensitive to stress "Ruderals". From the initials of these three words the model was called C-S-R and it summarizes the three main strategies followed by terrestrial vegetation to counteract environmental constraints. How much is a coincidence that CSR correspond to the initials of the name of the renowned phytoplankton ecologist C.S. Reynolds is unknown. However, this author early understood the potentiality to transfer the concept developed for plants to phytoplankton and the ecological implications in coupling it to selected morphological descriptors, which could be related to the environmental conditions.

In adapting the Grime's concept to phytoplankton assemblages stress can identify a shortage of mineral nutrients whereas disturbance a shortage of light.

Since stress and disturbance influence growth, their effects on organisms can be searched by analyzing the variability of two selected morphological descriptors.

In particular, these are:

1) a size descriptor (the ratio between surface and volume of the organism or colony: sv^{-1} [mm^{-1}]), and

2) a dimensionless shape descriptor (obtained by multiplying sv^{-1} for the maximal linear dimension m of the same organism or colony).

Although these morphological descriptors could be considered as merely surrogates of a more detailed eco-physiological template, their fidelity in describing physiological properties of phytoplankton as well as the ecological condition which determine their dominance is remarkable as shown by the allometric relations found by Reynolds (1989; 1997) between i) the size descriptor and phytoplankton growth rates (under unlimiting nutrients availability) and ii) between the shape descriptor and specific rates of growth at markedly sub-saturating light intensities (under unlimiting light availability).

With regard to the first group of relations, maximum rates of increase in single-celled species of phytoplankton, at a constant temperature of 20°C, generally vary, from around $r_{20} = 0.2$ per day, sufficient to double the biomass ($\ln 2 = 0.693$) in 3.47 days, to 2.2 per day, sufficient to support one doubling in under 7.6 hours (Elliot *et al.*, 2010). Several authors have found that interspecific differences in growth rate are a function of algal size and morphology (e.g. Schlesinger *et al.*, 1983; Yang R.-J. *et al.*, 2006; Nielsen, 2006; Kruk *et al.*, 2010). Growth rates can be correlated with the surface area-to-volume ratios (size descriptor: sv^{-1}) of the algae (be that an individual cell or colony) and Reynolds (1989) demonstrated that in continuously light- and nutrient saturated cultures at 20°C:

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

The effect of temperature was also considered by Reynolds, who showed that, for different temperature values, the maximum daily replication rate (r_{θ}) at a given temperature (θ , °C) is:

$$\log r_{\theta} = \log r_{20} + \beta [1000/(273 + 20) - 1000/(273 + \theta)]$$

where

$$\beta = 3.378 - 2.505 \log(sv^{-1})$$

Despite colonial species may show different size-growth rate relationships from those of unicells (Nielsen, 2006), the equation was successfully used to describe the growth performance of very different planktic colonial forms as the diatom *Asterionella formosa* Hassall, the chrysophyte *Dinobryon sociale* Ehrenberg, the mucilage-swathed colonies of green algae like *Eudorina elegans* Ehrenberg and the cyanobacteria *Microcystis aeruginosa* (Kützing) Kützing and *Dolichospermum* spp. In these last cases, the representative surface-area and volume measurements adopted have to consider the complete colony unit, together with any bounding mucilage (Elliott *et al.*, 2007). Only the coenobial flagellate green alga *Volvox* has been found to depart from the general description (unless the inside surface of the hollow colony is included) and a separate model is available in Reynolds (1983).

The dependence of phytoplankton specific rates of growth at sub-saturating light intensities (α_r) was found to be correlative of algal unit morphology (see Reynolds 1997 for an exhaustive explanation):

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

The value of $m sv^{-1}$ is least for sphere and is equal to 6 independently by any increase in diameter. As much the sphere is deformed in ellipsoidal or even rod-like or filamentous shapes as much greater is value of this shape descriptor. The evolutionary pressure promoting the relationship between growth rates at markedly sub-saturating light and the shape descriptor is likely due to the better exposition of chloroplasts to light in elongated, needle shaped phytoplankters (e.g. *Closterium aciculare*) compared to spherical or ellipsoidal ones with the same volume (e.g. small colonies of *Coelastrum reticulatum* (P.A. Dangeard) Senn or *Cryptomonas erosa* Ehrenberg).

As a consequence of these investigations, Reynolds (1995; 1997; 2006), by elegantly integrating Margalef's (1958) representation of the successional 'main sequence' from r- to K- selected plankton as a function of nutrients and turbulence (mixing) and the Grime's idea on C-S-R strategies developed his habitat template involving nutrient depletion and energy deprivation and showing the distributions of the strategic identities of phytoplankton (Fig. 8).

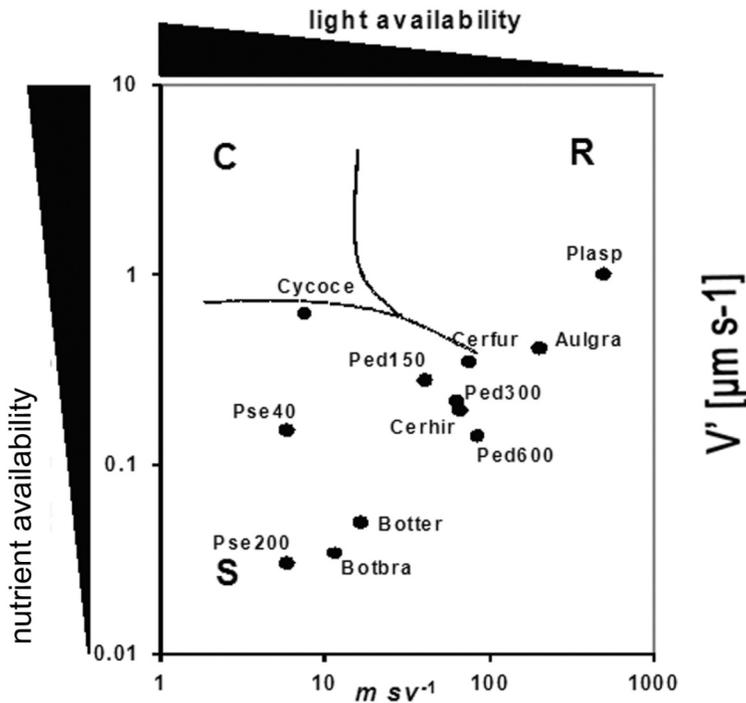


Fig. 8. Morphological ordination of some planktic algae recorded in Lake Arancio (Sicily, Italy) plotted against maximal linear dimension (m), surface area (s) and volume (v) of cells or colonies and the ecological C-, S-, and R-tendencies. Aulgra: *Aulacoseira granulata* (Ehrenberg) Simonsen; Cerfur: *Ceratium furcoides* (Levander) Langhans; Cycoce: *Cyclotella ocellata* Pantocsek; Cerhir: *Ceratium hirundinella* (O.F. Müller) Bergh; Pse40: colony 40 μm in diameter of *Pseudosphaerocystis lacustris* (Lemmermann) Nováková; Pse 200: colony 200 μm in diameter of *Pseudosphaerocystis lacustris* Botter: *Botryococcus terribilis* Komárek et Marvan; Botbra: *Botryococcus braunii* Kützing; Ped150: colony 150 μm in diameter of *Pediastrum simplex* Meyen; Ped300: colony 300 μm in diameter of *Pediastrum duplex* Meyen; Ped600: colony 600 μm in diameter of *Pediastrum* sp.; Plasp: *Planktothrix* sp. Redrawn from Naselli-Flores & Barone (2003).

Size and nutrient uptake

The smaller a cell, the greater is its surface-to-volume ratio. For example, a spherical cell 2 μm in diameter has a surface-to-volume ratio of approximately 3:1, while a spherical cell having a diameter of 20 μm has a surface-to-volume ratio of around 0.3:1.

A large surface-to-volume ratio, as seen in smaller prokaryotic cells, means that nutrients can easily and rapidly reach any part of the cells interior. In addition, small cells have a smaller diffusion boundary layer that limits nutrient transport since this is, at least for spherical cells, proportional to cell radius (Ploug *et al.*, 1999). Conversely, in the larger eukaryotic cell, the limited surface area when compared to its volume means nutrients cannot rapidly diffuse to all interior parts of the cell. That is why eukaryotic cells require a variety of specialized internal organelles to carry out metabolism, provide energy, and transport chemicals throughout the cell. However, intracellular nutrient concentrations are generally greater than those available in water. Thus nutrient uptake must occur against very great diffusion gradients and is regulated by sophisticated and high-affinity uptake/transport systems which are able to pull nutrients across the plasmalemma and retain them within the cell. In addition, phytoplankton display a variety of strategies to optimize their nutrient uptake such as alkaline phosphatases production, nitrogen fixation, mixotrophy and mucilage production which can help nutrient sequestration and processing, as well as give the capacity to take up nutrients through passing undamaged the gut of their grazers (Reynolds, 1997, 2007).

At high nutrient concentrations, under experimental conditions, phosphorus maximum uptake rates increase with increasing size of cells or colonies; these rates are more or less comparable once they have been normalized to the surface area of the interested cells or colonies (Reynolds, 1993b). Thus, a small *Chlorella* and a large *Microcystis* colony both show a maximum uptake rate for phosphorus (V_{max}) of about 10^{-18} mol P μm^{-2} s $^{-1}$.

However, in natural conditions resources are generally available at sub-optimal concentrations and species do differ in their affinities for nutrients at low concentrations, in their rates of assimilation and ultimately in their growth rates. At sub-optimal concentrations size becomes relevant, since a greater number of transport systems can be hosted on a larger surface. This, eventually coupled with nutrient storing metabolic pathways and/or mucilage bounding (both present in cyanobacteria) may increase the competitive success of large phytoplankton units under conditions of nutrients shortage but require a higher energy (light) supply (Stoyneva *et al.*, 2007; Morabito *et al.*, 2007).

Although a huge amount of literature has been produced investigating at what point interspecific competition for nutrients becomes important in determining selection of freshwater phytoplankton, no definitive or fully convincing answers were provided. This is partly due to the fact that nutrients limitation is seldom occurring and little direct evidence is available for instantaneous phosphorus limitation of primary production (Van Mooy *et al.*, 2009) and several observations are indicative of phytoplankton assemblages that are highly adapted to phosphorus scarcity (with phosphate at sub-nanomolar concentrations) and can simultaneously maintain both low cellular phosphorus requirements and effective rates of photosynthesis (e.g. Wu *et al.*, 2000; Thingstad *et al.*, 2005). As shown in the very information-rich review by Istvánovics (2008), phosphate turnover times are only a few hours, are very effective in maintaining primary production and follow the “highways of necessity” which are paved by

adaptation. As an example, when inorganic phosphorus is depleted, mixotrophic flagellates can start consuming P-rich bacteria with the additional benefit of eliminating competitors (Stibor & Sommer, 2003).

Nevertheless, several authors have faced the puzzle of phytoplankton competition in term of nutrients ratios and dozens of chemostat experiments under multiple-nutrient-limited growth conditions were performed in the 1970s and 1980s (Klausmeier *et al.*, 2004). Starting from the well known average atomic C:N:P ratio set by Redfield (1958) to be 106:16:1, a lot of work has been done trying to relate this internal ratio to the ratio of nutrients present in the water and identifying as “limiting” the nutrient which was present in quantities lower than predicted by the Redfield ratio (Sterner & Elser, 2002). These attempts often were carried out without considering that if the absolute value of an element cannot be considered limiting the same must apply to its ratio. Thus several papers have claimed at a supposed limiting effect of phosphorus on phytoplankton growth just because N:P was higher than 16:1 (or 7:1 by weight) and without considering the absolute value of the element, which very often was orders of magnitude higher than its real limiting effect.

As a consequence, indicator species for different nutritional levels have been presented for oligotrophic waters as well as for waters showing a higher trophic state (Lepistö *et al.*, 2004). Most of these species did not reveal to have a robust indicative value with respect to nutrients concentrations as demonstrated by the increased frequency with which cyanobacteria blooms are referred to occur in oligotrophic environments, often with SRP concentrations in the euphotic layer below the limit of detection (e.g. Naselli-Flores & Barone, 2000; Salmaso, 2000; Padišák *et al.*, 2003b; Salmaso & Padišák, 2007).

Moreover, it has to be considered that while phosphorus is still measurable in the water ($2 < [P] < 3 \mu\text{g P l}^{-1}$), active cells are not at that time deficient in their intracellular phosphorus content.

It has long been recognized that conditions exist under which phytoplankton stoichiometry diverges from the canonical Redfield ratio. According to Arrigo (2005), this highly variable and dynamic stoichiometry reflects the ability of bloom-forming phytoplankton, during exponential growth, to optimally increase their allocation of resources toward production of growth machinery, e.g. such as ribosomal RNA rich in both N and P, reducing their N:P ratio to ~8, far below the Redfield value of 16. However, when resources are scarce, slow-growing phytoplankton that can synthesize additional resource acquisition machinery, such as proteins and chlorophyll rich in N but low in P, are favoured. This allocation of resources results in optimal N:P ratios ranging from 36 to 45, depending on which resource is less available. Furthermore, nitrogen fixation can drive nutrient inventories away from the Redfield ratio (Karl *et al.*, 1997).

By applying the concept that phytoplankton compete for nutrients and are selected according to competitive advantage related to their availability we completely ignore the value and the meaning, easily visible under the microscope, of the astonishing morphological variability of phytoplankton. Conversely, why should not be only spherical phytoplankton? The spherical shape should favour nutrient uptake and intracellular diffusion and thus be selected as the best fitting shape under variable nutrients concentrations. However, phytoplankton does not only require mineral nutrients but also light and the underwater environment is governed by gradients as regard energy and nutrients availability. Selective pressures on micro-autotrophs are driven by the necessity to balance their light and nutrient requirements, which involve the necessity to continuously move and

search into the otherwise moving water masses. Moreover, as shown by Jäger *et al.* (2010) these selective pressures depend on the morphological features of a given water-body. According to these authors, the highest total biomasses are attained in turbulent waters at intermediate water column depths and in deep waters at intermediate turbulences. The reasons for this pattern are that in shallow waters, the most strongly limiting process is nutrient influx from the sediments; conversely, in deep waters, it is represented by the turbulent upward transport of nutrients to the photic zone.

Shape, water mixing and light availability

The morphological and climatic features to which a given water-body is subjected as important physical constraints in relations to size and shape of phytoplankton are being increasingly acknowledged by phytoplankton ecologists (Padisák *et al.*, 2010a; Zohary *et al.*, 2010). For whatever reason water masses move, they transport phytoplankton in an ever changing environment characterized by an uneven distribution of resources (nutrients and light) and changeable quantities of physical and chemical variables (e.g. pH, electrical conductivity, temperature, oxygen concentration). Phytoplanktic algae are sensitive to variation in these parameters and need to access resources to survive.

On a short time scale, several studies have demonstrated that forcing variables such as wind also modify the physical and chemical structure of lakes. From a few hours to a few days, the vertical structure can thus be changed, in particular the depth of the mixed layer, the intensity of mixing, the thermal gradient and the stratification state (Pennard *et al.*, 2007a). These changes take place on a similar time scale to the growth rate of phytoplankton and thus may affect the phytoplankton community over a few days (Nixdorf *et al.*, 2003).

With regard to light harvesting, phytoplankton shows a wide array of pigments which allow them to fully exploit the PAR radiation. However, light quantities may fluctuate considerably in relation to daytime, season and weather conditions. Furthermore, these fluctuations depend on geographic location, and exposition of water bodies as well as on their intrinsic morphological features and trophic state. This latter strongly conditions light absorption by water masses as described by the variability of the extinction coefficient in water bodies of different trophic state.

A vast amount of studies exists on allometric relationships between phytoplankton biomass and their photosynthesis performances and even the amount of chlorophyll *a* required to make an algal cell “optically-black” (100% of the light absorbed) can be calculated as a function of body size (Dubinky & Schofield, 2010). In general, a change in the size dependence of growth rate was detected depending on the severity of limitation by light (and nutrient) availability. Under conditions of growth-saturated resource supply, phytoplankton growth rate ($\text{mol C cell}^{-1} \text{time}^{-1}$) scales with cell volume with a size-scaling exponent of 3/4; light limitation reduces the size-scaling exponent to approximately 2/3, and nutrient limitation decreases the exponent to 1/3 as a consequence of the size-scaling of resource acquisition. Exponents intermediate between 1/3 and 3/4 occur under intermediate availability of light and nutrients and depend on the size-scaling of pigment photoacclimation and the size range examined (see Finkel & Irwin, 2000; Finkel, 2001; Finkel *et al.*, 2007; Mei *et al.*, 2009 and literature therein).

The importance of light gradients in shaping photosynthetic rates of phytoplankton was early studied by Talling (1957). However, the relations

existing between light availability, mixing depth and phytoplankton shape where elucidated much later (Reynolds, 1993a; Kirk, 1996).

The steady-state light intensity at the bottom of the water column has been termed “critical light intensity” (Huisman & Weissing, 1994). The critical light intensity is species specific and plays a crucial role when phytoplankton species compete for light. Theory predicts that the species with lowest critical light intensity should be the superior light competitor (Weissing and Huisman, 1994) and competition experiments have confirmed this prediction (Huisman *et al.*, 1999). Following the concepts relating light availability and mixing time showed in Reynolds (1993a), Huisman (1999) highlighted that the ratio of euphotic depth to mixing depth (z_{eu}/z_{mix}), which changes with a change in population density, can be used to make quantitative predictions since it provides sufficient information to reconstruct the light gradient.

It is interesting to note that researchers mainly working on light limited environments generally prefer to use the inverse of the above quoted ratio: the mixing depth to euphotic depth ratio (z_{mix}/z_{eu}). This happens probably because in dark environments z_{mix}/z_{eu} is a descriptor that better depicts the underwater light climate of a given water body since it also indicates the proportion of time that an alga has to spend at critical light intensities once it is entrained in the mixed water column (Naselli-Flores & Barone, 2007). The degree of entrainment of phytoplankton species largely depends on their sinking velocity and on the value of their coefficient of form resistance, which ultimately regulate the degree of entrainment of phytoplankton in the water motion. A further step in this reasoning is thus that the shape of phytoplankton determines their fitness to the environmental conditions with regard to mixing regime and light availability.

The concepts related to mixing depth to euphotic depth ratio have been successfully used to explain cyanobacteria buoyancy regulation (Walsby *et al.*, 2006 and literature therein) and dominance (e.g. Dokulil & Teubner, 2000; Fabbro & Duivenvoorden, 2000; Naselli-Flores, 2003). Moreover, their morphological variability as regard colony size and shape can be explained in terms of adaptation to varying values of z_{mix}/z_{eu} (Naselli-Flores & Barone, 2003; Wilson *et al.*, 2010).

In particular, when $z_{mix}/z_{eu} = 1$, cells are constantly illuminated and photosynthesis is continuous during the daylight period. If the mixing depth becomes greater than the depth of light penetration, phytoplankton spends a proportion of their daylight period in the dark when photosynthesis cannot occur but respiration can. Phytoplankton growth has been found to be negative when mixing depth exceeds four times the euphotic depth (Talling, 1971). Reynolds (1984a) also showed that assuming a constant respiration rate of 10% of maximum photosynthetic rate, net growth cannot occur when $z_{mix}/z_{eu} > 3$. Starting from these observations, Bormans *et al.* (2005) found that in an Australian stratified impoundment during the summer months, buoyant cyanobacteria had a clear advantage over other phytoplankton groups to stay in the well-lit surface-mixed layer and the ratio $z_{mix}/z_{eu} \sim 3$ was well correlated with the first onset of cyanobacterial growth.

Cyanobacteria can thus cope with low light not only thanks to their peculiar photosynthetic pigments but also because of their light-mediated mechanisms of buoyancy regulation, which enable them to be disentrained from downward vertical motions. Dominance of cyanobacteria under low light has been found to be due to a variety of environmental conditions characterized by a poor light availability both due to surface-covering by floating plant (O’Farrell *et al.*, 2009;) and their removal (Bicudo *et al.*, 2007), post-flood turbidity (Bormans *et al.*,

2005; Cardoso & Marques, 2009), irregular stratification patterns (Padisák *et al.*, 2003b; Salmaso & Padisák, 2007) or to light attenuation decrease as a consequence of increased trophic state (Naselli-Flores & Barone 1998; Caputo *et al.*, 2008).

More in general, an increase in the value of $z_{\text{mix}}/z_{\text{eu}}$ can be achieved by a decrease of the euphotic depth and/or an increase in the mixing depth of a water body. Data on morphological response of phytoplankton to reduced underwater light availability have been shown by O'Farrel *et al.* (2007), Fonseca & Bicudo (2009), Allende *et al.* (2009) and Loverde-Oliveira *et al.* (2009), whereas Pannard *et al.*, (2007a; 2007b) have shown how the effects of wind events, by deepening the mixing depth, can cause a change in the size structure of phytoplankton both in natural and experimental conditions.

Further mechanisms that influences the mixing depth to euphotic depth ratio, which were recognized to impact phytoplankton composition and structure are related to water-level fluctuations (Naselli-Flores, 2003; Zalocar de Domitrovic, 2003; Zohary, 2004; Naselli Flores & Barone, 2005; Alster *et al.*, 2010), hydrological regulation (Naselli-Flores, 2000; Tolotti *et al.*, 2010) and flood pulses (Oliveira & Calheiros, 2000; Mihaljević *et al.*, 2010).

A mechanism involving both the deepening of the mixing depth and the contraction of the euphotic depth was described in details for man-made lake under Mediterranean climate. Actually, these environments are subjected to climate-driven seasonal water level fluctuations to which water-management procedures superimpose. As a consequence of summer water withdrawal (addressed to irrigate and provide drinking water), deep stratifying reservoirs are emptied and start circulating in mid-summer. This causes a deepening of the mixing zone and the establishment of an atelomictic thermal pattern, which promote a faster recycling of nutrients from the sediments (Naselli-Flores, 1998, 1999). Consequently, nutrients pulses occur, which enhance phytoplankton production and biomass accumulation with a reduction of the euphotic depth. In these environments, $z_{\text{mix}}/z_{\text{eu}}$ variations were recognized as the primary factor influencing size-structure of phytoplankton (Barone & Naselli-Flores, 1994; Naselli-Flores & Barone, 2003) and were found to play a major role in determining the specific composition of the assemblages (e.g. Barone & Naselli-Flores, 2003; Naselli-Flores *et al.*, 2007b; Hoyer *et al.*, 2009).

In addition, Naselli-Flores & Barone (2007) have shown that the morphological descriptor of phytoplankton ($m \text{ sv}^{-1}$) is allometrically related to the variations of the mixing depth euphotic depth ratio. In particular, these authors identified two main morphological modifications through which phytoplankton respond to light deficiency. The first of these mechanisms takes place when the $z_{\text{mix}}/z_{\text{eu}}$ ratio ranges between 1.5 and 3.0 and implies a morphological shift towards more attenuated shapes. Needle shaped *Closterium* spp., long chain forming *Aulacoseira granulata* (Ehrenberg) Simonsen, filamentous greens (e.g. planktic species of *Mougeotia*) or blue-greens (e.g., *Planktothrix agardhii* (Gomont) Anagnostidis and Komárek), are all good light-harvesting taxa and are characterized by a reduced entrainment in the water column circulation. Their morphology (needle shaped or cylindrical), at a constant value of the diameter, shows little variation in the surface-volume ratio compared to a sphere. Thus, to maximize exposition of chloroplasts to light they have to show the most elongated shape by maintaining the shortest diameter. According to Reynolds (1999) they can be defined R-selected "acclimating species", i.e. adapted to invest in the most efficient light conversion. These organisms develop well in environment where light can be a limiting resource for species showing a lower surface-volume ratio

(e.g., large spherical shapes) but where nutrients are easily available. Nevertheless, at very high $z_{\text{mix}}/z_{\text{eu}}$ values (i.e. > 3), this mechanism does not seem to represent a successful strategy. When water transparency strictly depends on the amount of phytoplankton biomass, it is important to consider that, once entrained in the mixing column, if all the phytoplanktic algae have the same shape and size, they would be on the average subject to the same light conditions and have the same probability to harvest light. A value of $z_{\text{mix}}/z_{\text{eu}} > 3$ means that phytoplankton while travelling in the mixed water column, spend just one third (or even one tenth in the worst case recorded in Sicilian reservoirs) of their lifetime in suitable light conditions. This time span is likely not enough, even for elongated forms, to sustain photosynthetic needs as compared to respiratory ones. Under this condition, the S-strategy represents an advantage. Large unicells or large colonies, through motility or the ability to control buoyancy, may regulate their position in the water column (Naselli-Flores & Barone, 2003; Peltomaa & Ojala, 2010). The striking success of gas-vacuolated cyanobacteria in eutrophic environments with $z_{\text{mix}}/z_{\text{eu}}$ values exceeding 3 is likely to be searched in their buoyancy, and thus in their low entrainment in water mixing.

Climate change effects on phytoplankton composition and size structure

It is impossible not to briefly mention climate among the factors that can influence the hydrology of water bodies and their mixing/stratification patterns as well as the incidence and duration of ice-cover and the hypolimnetic temperature (Dokulil *et al.*, 2010). Global climatic patterns, regularly driven by Sun's magnetic field (Baker, 2008), were shown to promote cyclic cyanobacteria bloom during the years of drought caused by El Niño in a subtropical Australian reservoir (Harris & Baxter, 1996). Cyclic droughts, with a periodicity of about 11 years, also occur in the Mediterranean Basin where they produce analogous responses in phytoplankton composition (Naselli-Flores & Barone, 2005). More recently, Devercelli (2010) highlighted a direct influence on the size structure of phytoplankton assemblages in the Middle Paraná River during extreme flood events in three different mesoclimatic periods: El Niño, La Niña, and neutral. The author demonstrated that floods during these different periods lead to development of clearly distinct communities through a cascade of variables. As summarized by Reynolds & Descy (1996), phytoplankton composition in large rivers is primarily driven by physical factors strongly related to discharge (e.g. flow velocity, water level, solid load and its consequence on transparency). However, the distinct patterns observed by Devercelli (2010) are largely related to the connectivity of the main river flow to its lateral waters through different wash-in of nutrients when the surrounding lands are flooded (El Niño) or completely dry (La Niña). Moreover, a compositional change from diatoms dominated communities (Centis *et al.*, 2010) to increasing contribution of other phytoplankton groups seems to be likely if discharge of the River Adige (Italy) will further decrease as climate change models predict (Salmaso & Zignin, 2010). A wide array of variation in the phenological responses of populations inhabiting aquatic ecosystems can be described as climatic-induced (Adrian *et al.*, 2006).

A different pattern was shown by Winder *et al.* (2009), who found that lake warming and increased stratification select for small-celled diatoms of the genus *Cyclotella* in Lake Tahoe. The results achieved by these authors show that within the diverse group of diatoms, small-sized species with a reduced sinking velocity were able to adapt to a decrease in mixing intensity, further supporting the hypotheses that abiotic drivers affect the size structure of planktic

communities. The actual climate warming was found to exhibit a selection pressure on diatom cell size analogous to that already observed in palaeoecological studies (Falkowski & Oliver, 2007).

Although a few data are still available, some evidences exist that climate change can promote pseudo-eutrophication events (see Paerl & Huisman, 2009; Nöges *et al.*, 2010) and, by altering the hydraulic balance in shallow lakes, cause a shift between a clear macrophyte-dominated state and a turbid algae-dominated one (Barone *et al.*, 2010). A further consequence of the ongoing climate change can be considered the increasing rate of successful invasions by algal species previously restricted to the tropics into lakes of the temperate zone (Cellamare *et al.*, 2010).

As already postulated by Hutchinson (1959), climate may limit productivity in aquatic ecosystems (Naselli-Flores & Rossetti, 2010). The ongoing climate change has been shown to affect phytoplankton also in a top-down perspective. Preston & Rusak (2010) found a strong inverse relationship between ice-off date and *Daphnia* density in Wisconsin lakes, which had important effects on aquatic productivity by altering the size-selective grazing.

As shown in George (2010), the research until now carried out on climate change effects have demonstrated that small changes in the physical characteristics of a lake can have a disproportionate effect on its chemistry (e.g. an intensified recycling of phosphorus) and biology (e.g. enhanced cyanobacterial blooms). The monitoring of phytoplankton size structure, due to the fast response to these changes, may thus become an early-warning tool to prevent water quality deterioration.

THE ROLE OF GRAZING

A synthesis on the major role exerted by grazing on phytoplankton shapes is offered by Smetacek (2001), who wrote: “planktonic evolution is ruled by protection and not competition. The many shapes of plankton reflect defence responses to specific attack systems.”

The studies carried out by Jaroslav Hrbáček at the end of the 50' of the last century, offered the opportunity to Brooks & Dodson (1965 and literature therein) to introduce one of the most famous ecological theories for freshwater: the size selective hypothesis. The theory was originally developed to demonstrate the importance of planktivorous fish in determining the structure of a zooplankton community and it was aimed at explaining the co-occurrence of different size and species of zooplankton and fish. However it also underlined that the most dramatic phytoplankton loss process is due to grazing and opened the way to several works investigating the size selection operated by zooplankton on phytoplankton.

Grazing refers to herbivory interactions involving various herbivores that consume archaea, bacteria and algae. The types of herbivores present depend on the aquatic system. In freshwater systems herbivores tend to be protists, rotifers, and crustaceans; the last two groups essentially represent the true zooplankton. A general account on freshwater planktic herbivores is offered by Gliwicz (2003). Larger, more conspicuous herbivores include oligochaete worms, dipteran larvae, limpets, mussels, crabs, insects and fish.

Protists cover a wide range of sizes, from 2 μm to 200 μm long, and may consume archaea, bacteria, algae and other protists. Most of these organisms use the process of endocytosis to engulf prokaryotes and small algae into cellular digestion structures known as food vacuoles. Such feeders are known as phagotrophs; they often have specialized structures that aid in consuming prey and typically lack rigid cell coverings that would interfere with prey engulfment. Phagotrophic protists occur as photosynthetic (mixotrophic) or non-photosynthetic flagellates (heterotrophic), ciliates, or amoebae, distinguished by their type of mobility and food gathering.

Keratella quadrata (Müller, 1786) and *Brachionus calyciflorus* Pallas, 1766 are examples of common freshwater rotifers that are known to consume algal food. Rotifers are mainly filter feeders that feed on smaller organisms (< 12 μm), but a few specialists feed by raptorial capture of large algae such as dinoflagellates and euglenophytes (Figs 9-11).

Freshwater planktic crustaceans comprise two distinct groups: the cladocera and the copepods. The two major ways in which crustaceans feed are filter feeding and raptorial feeding.

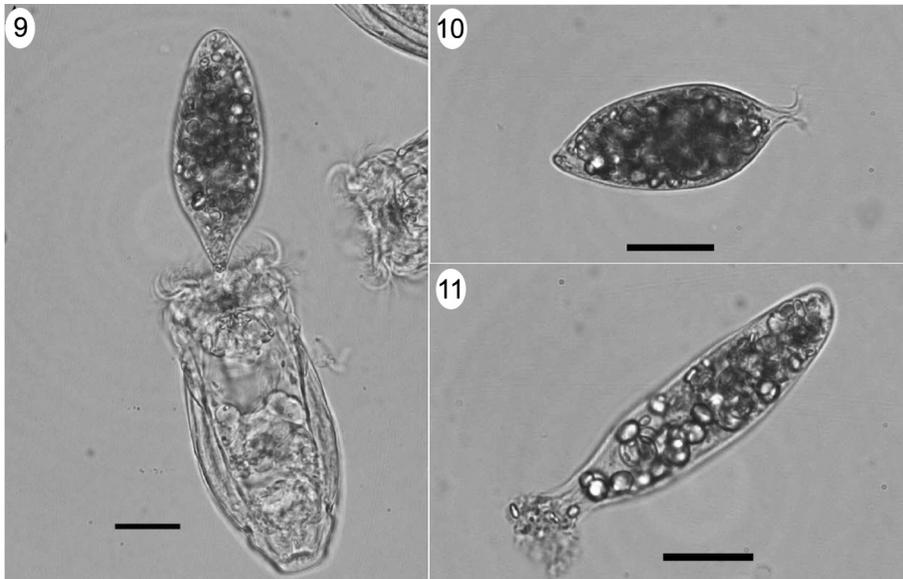
During filter feeding, cladocerans as *Daphnia* and *Bosmina* and some copepods use specialized feeding structures to filter phytoplankton from larger volumes of water and sweep food into the mouth. All the cladocerans inhabiting an eutrophic lake can filter about five times the volume of that lake in one day, though filtering rates are lower in oligotrophic waters (Sommer *et al.*, 2001). In addition, *Daphnia* may be able to detect the odour of preferred food such as the green alga *Scenedesmus*. *Daphnia* uses this ability to find patches of water that are relatively rich in edible algae, thus effectively avoiding patches of less-desirable algae. Cladocerans are nonselective filter feeders and the lower limit for filterable cell size is determined by the size of the mesh formed by the plumose setae on the thoracic legs. This net-like mesh ranges from 0.16 to 4.2 μm in different species. Most cladocerans have an upper limit for phytoplankton cell size of around 20 to 30 μm (Lampert & Sommer, 2007).

In raptorial feeding, copepods and some cladocerans use feeding appendages to pick up pieces of algal food, taste it, and select types that are high in nutritional quality, digestible, and nontoxic. The upper end of the algal size range that can be consumed by crustaceans is determined by the opening width of the mandibles or the carapace gape. This is about 50 μm for copepods and some large cladocerans (Lampert & Sommer, 2007). In particular, copepods, particularly significant in marine food webs, feed by raptorial capture and are selective within a size range from about 20 μm to an upper limit of 50 to > 100 μm , depending on copepod species.

In freshwaters, cladocerans and copepods have contrasting effects; cladocerans consume small phytoplankton cells, flagellates and ciliates, and copepods feed on large phytoplankton and medium-sized ciliates.

Phytoplankton defences against grazers

Phytoplankton has evolved various morphological, biochemical and behavioural defence mechanisms against grazing of zooplankton. At the predator's species level, size and shape remain first-order determinants of prey suitability (Tillmann, 2004). Some algal species produce life stages (e.g. colonies, chains) or cellular features (e.g. horns, spines) that are resistant to herbivore attack. The presence of mucilage is clearly important in promoting a maximum size (e.g. the blue-green *Microcystis*) Gelatinous chlorophytes may be readily



Figs 9-11. **9.** Raptorial capture of *Euglena* sp. by a rotifer; **10-11.** specimens of *Euglena* sp. damaged by grazing. The bars are 20 μm .

ingested but are poorly digested by zooplankters like *Daphnia* passing unharmed through the grazer's gut (Porter, 1975). Others, as dinoflagellates, startle herbivores with brilliant light flashes or produce chemical deterrents or toxins as cyanobacteria and dinoflagellates. However, no single defense system functions perfectly against the whole range of potential predators. Some members of nearly major algal groups display both very small cell size and rapid cell division (on the order of hours to day), thereby generating large populations. Herbivores are unable to find and consume all such cells, and thus some are able to generate new populations when growth conditions allow. The ability of phytoplankton to grow in the cold season, when populations of herbivores are relatively low, can be another way to avoid or diminish grazing pressure.

The specific grazing defences can be constitutive, i.e. permanent, or induced. Induced defences include changes in morphology (e.g. formation of spines, colonies), biochemistry (e.g. production of toxins), in behaviour (e.g. aggregation, escape) and in life history characteristics (e.g. reduced recruitment rate). Several flagellated algal species regulate their recruitment rate from the sediment depending on the presence or absence of grazers in the water column (Hansson, 1996, 2000).

Some changes in defensive traits in the field can be explained by clonal replacement provided with constitutive defenses as conditions change (Yoshida *et al.*, 2003), but there is also a remarkable evidence for phenotypic plasticity.

Phenotypic plasticity is the ability of a single genome to produce one or more alternative form of morphology in response to environmental condition (West-Eberhard, 1989). Widespread in nature, often involves ecologically relevant behavioral, physiological, morphological and life-historical traits (Miner *et al.*, 2006). In particular, Kishida *et al.* (2009), in a recent review on inducible morphological plasticity in predator-prey interaction, have argued that studies

focusing on morphological plasticity can provide significant insights that complement studies on plasticity in other traits such as behaviour and life history.

As discussed earlier, size is the most important single characteristic affecting the ecology of phytoplankton. As phytoplankton become larger, their volumes increase as the cube of their radius, while their surface areas increase in proportion to only the square of the radius. Consequently, as algal species become larger, their surface area-to-volume ratio (sv^{-1}) becomes smaller, especially if they retain a spherical shape. Many of the adaptations that reduce sinking rates (e.g. chitin fibrils and bristles) and increase the sv^{-1} ratio also perform anti-grazer role. Grazers such as protists, rotifers, and crustaceans consume small cells more readily than large cells. The size of phytoplankton cell, colony, or filament therefore determines in part the susceptibility to particular grazers.

Given the importance of size-selective predation in structuring pelagic food webs, it has been argued that species that can significantly alter their sizes or modify their shape should be selected to use chemical information from consumers (or attacked conspecifics) to induce phenotypes with reduced susceptibility to consumers (Long *et al.*, 2007).

Phytoplankton sizes and shapes induced by grazers

Inducible defences, which describe the specific case of plastic changes in prey traits in response to predation risk, appear to be particularly common in natural systems. These adaptive changes reduce phytoplankton mortality due to herbivory, while the energetic cost of the response is lowered by the fact that the defence can be attuned depending on the presence of predators.

As recently reviewed by van Donk (2007), it has been shown for several phytoplankton species that herbivorous zooplankton can induce these defence mechanisms by releasing infochemicals.

The role of infochemicals

In an ideal aquatic environment, selection pressure should exist for small organisms since these have the most efficient uptake of nutrients and light and lowest sinking losses. By contrast, the high mortality of small phytoplankton through grazing exerted by protozoan and metazoan would strongly select phytoplankton traits that reduce this mortality. Thus, an effective way to resist grazing could be represented by a dramatic increase in cell or colony size. However, this kind of morphological modification would confront phytoplankton with conflicting allometries of selection pressures (Lüring, 1999). Since algae are small relative to their predators, they hardly survive an encounter with a grazer. Therefore, to elicit a defensive strategy, it may be useful to detect a grazer at distance and before encountering it.

All organisms exchange constantly chemicals with their environment and some of those chemicals that are essential in the biology of a grazer may prove to be potential indicators of danger once they become detectable by algae. These chemicals are referred to as infochemicals or semiochemicals and according to Dicke & Sabelis (1988), are defined as 'chemicals that in a natural context, convey information between two individuals, evoking in receiving organisms a behavioural or physiological responses that is adaptively favourable to one or both organisms.

Pheromones are infochemicals that relay information between organisms of the same species while the transfer of allelochemicals is interspecific. Allelo-

chemicals not only have a role in foraging, but are also important in detecting natural enemies.

Kairomones are a class of allelochemicals that benefit the receiver but do not benefit the sender and are commonly involved in interactions between predator and prey. This group of allelochemical has received extensive attention because the changes in behavior, morphology, and life history that they elicit are often easily characterized (Lass & Spaak, 2003; Pohnert *et al.*, 2007; van Donk, 2007). Kairomones frequently mediate predator-prey interactions whereby prey chemically detects the presence of potential predators. In particular, kairomones produced by zooplankton such as *Daphnia* elicit adaptive responses in phytoplankton. Unicellular green algae belonging to the genera *Scenedesmus* and *Desmodesmus* exposed to kairomones produced by *Daphnia* and other zooplankton species form colonies and, in some species, long rigid spines, both of which increase resistance to grazing (Hessen & Van Donk, 1993; Lürling, 2003a).

The chemical nature of *Daphnia* kairomones is not well resolved (Lürling & Von Elert, 2001; Van Holthoorn *et al.*, 2003), but recently aliphatic sulphates have been identified as a candidate class of *Daphnia* chemicals known to induce morphological defences in phytoplankton (Yasumoto *et al.*, 2008 and literature therein). In particular, infochemicals that could induce morphological changes of *Scenedesmus gutwinskii* var. *heterospina* Bodrozközy were isolated from *Daphnia pulex* Leydig, 1860 and elucidated as aliphatic sulfates. It remains unclear whether these compounds have the same effects on other *Scenedesmus* species, and whether other *Daphnia* species, or even other herbivorous zooplankton species release the same or similar colony-inducing compounds.

The structural similarity between the aliphatic sulphates, the natural *Daphnia* kairomones, and the synthetic anionic surfactants allows to presume that synthetic anionic surfactants may behave as info-disruptors generating the same morphological reaction in algae. The term info-disruptors denotes the chemically different substances that distort the nature and perception of the “smellscape” in which organisms interact. This suggests that mimicry of the natural signal results in the same physiological outcome (Lürling & Scheffer, 2007).

Largely ignored in kairomone research is the response of individuals to kairomones produced by organisms that are not direct consumers, but that may indicate the presence of a consumer, such as the relationship between fish kairomones and phytoplankton. There is evidence (Kim *et al.*, 2003) that the cryptomonad *Plagioselmis prolunga* var. *nordica* Novarino, Lucas *et* Morral produce longer tails in the presence of the silver carp *Hypophthalmichthys molitrix* (Valenciennes, 1844). However, these experiments were conducted in mesocosms that also contained zooplankton, and thus the morphological response in *P. prolunga* may have been a direct effect of changes in zooplankton density and not related to the presence of fish kairomone.

Nevertheless, in experimental microcosms the unicellular green alga *Chlamydomonas reinhardtii* appears to alter vertical migration patterns in response to kairomones produced by both zooplankton (*Daphnia*) and planktivorous fish (Latta *et al.*, 2009).

Effects of infochemicals on the morphology of phytoplankton species

The influence of zooplankton infochemicals on the morphology of the closely related green algae *Scenedesmus* (nonspiny) and *Desmodesmus* (spine armored), formerly both belonging to the genus *Scenedesmus*, has been intensively studied (e.g. Hessen & van Donk, 1993; Lürling & van Donk, 1997;

Verschoor *et al.*, 2004). Individual strains of various *Scenedesmus* species can grow as unicells or form colonies (coenobia) of four or eight cells. The cells can also vary in the number and size of the spines (Van Donk, 2006).

It is well known that many algal species isolated as clones from the field change their morphology or growth form after several generations in laboratory cultures, suggesting that some unknown factor triggers their 'typical' or consistent appearance in the field. For example, colonies like *Microcystis* grow as single cells, and flakes of *Aphanizomenon* grow as single filaments. It is, however, difficult to determine if the observed effect is caused by selective grazing on small flakes and single cells or an active response to the grazers' presence (Van Donk, 2006).

The presence of infochemicals from grazers has been shown to induce changes in the cell size, colony formation and spine or bristles induction in a range of species from both genera, revealing a high phenotypic plasticity (Lürling, 2003a). *Scenedesmus* plasticity is, however, not only shaped by the activity of grazers. Several factors are known that may influence the growth and morphological development in *Scenedesmus* and among them nutrient availability, light and temperature are important ones (Trainor, 1998).

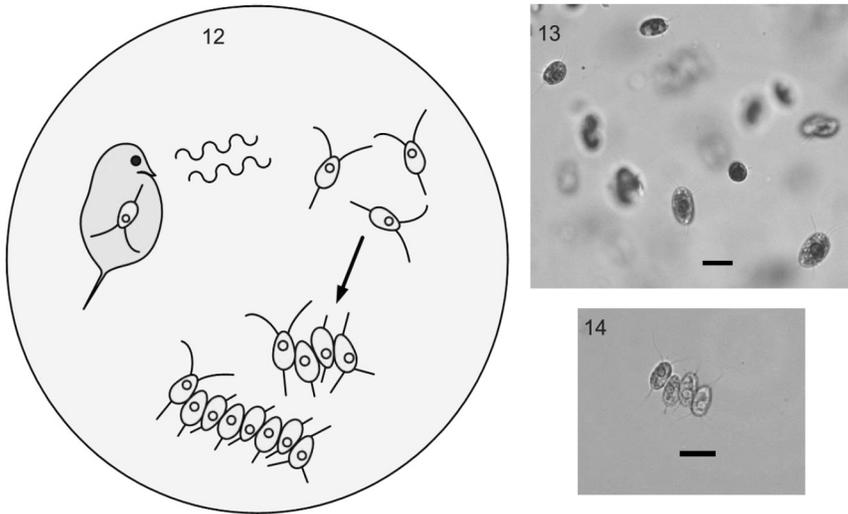
The phenotypic response of *Scenedesmus/Desmodesmus* spp. was the first experimental proof that there was a chemical signal from grazers that induces morphological changes in phytoplankton. Hessen and van Donk (1993) were the first to show that a chemical factor released by the cladoceran *Daphnia magna* Straus, 1820 was able to induce colonies in the spine-armored *Scenedesmus subspicatus* Chodat, now *Desmodesmus subspicatus* (R. Chodat) E. Hegewald *et al.* Schmidt. In response to the presence of grazing-released infochemicals by *D. magna*, this alga formed four- to eight celled coenobia with more rigid and longer spines. The response also occurred when *Desmodesmus* was exposed to grazing-released infochemicals of the rotifers *Brachionus* and *Keratella* (Lürling & Van Donk 1997; Van Donk *et al.* 1999). Different taxa of herbivorous zooplankton species are capable of colony induction in *Scenedesmus*, and average colony size has been found to be proportional to the actual grazing pressure (Verschoor *et al.*, 2004).

In Mediterranean temporary ponds it has been frequently observed (unpublished data) that the absence of herbivores in the early phase of filling (early autumn) or at the end of the emptying phase (June/July) is accompanied by dense *Desmodesmus* blooms mainly formed by unicells (Figs 12-14).

Lampert *et al.* (1994) found an identical response in the spineless *Scenedesmus acutus* Meyen, now *Scenedesmus obliquus* (Turpin) Kützing. In the presence of filtered medium from a *Daphnia* culture, *S. obliquus* formed numerous eight-celled colonies. In the absence of *Daphnia*-infochemical, the chlorophyte remained unicellular and formed only four-celled coenobia when cultures reached stationary phase.

The phenomenon is not restricted to *Scenedesmus/Desmodesmus* and because of the enormous plasticity in phytoplankton, numerous species may eventually turn out not only to respond to abiotic but to biotic agents as well. Van Donk *et al.* (1999) examined the effect of *Daphnia* infochemicals on the morphology of fifteen strains of chlorophytes, two strains of diatoms and three strains of cyanobacteria. *Daphnia*-induced colony formation, which was restricted to chlorophytes was, in addition to the genus *Scenedesmus*, also observed in the coenobial *Coelastrum*.

The infochemical that induces colony formation in *Scenedesmus* appears to be released by actively feeding zooplankton (Lampert *et al.*, 1994; Von Elert & Franck, 1999). Starved animals or animals fed with ingestible but non-digestible



Figs 12-14. **12.** *Daphnia-Desmodesmus* interactions. **13.** *Desmodesmus intermedius* (Chodat) Hegewald, unicells stained with Lugol. **14.** *D. intermedius* coenobium. The bars are 10 μ m.

beads are ineffective in inducing colonies (Lürling, 1999). The production of the *Daphnia*-infochemical is also related to the amount of food processed. Therefore the infochemicals does seem to originate from the interaction of grazers with their algal food. Fink (2001, in Van Donk, 2007) hypothesized that bacteria in the gut of *Daphnia* may release the infochemicals.

Although large *Daphnia* release these infochemicals, inducible colony formation did not prove to be an effective defence against these zooplankters (Lampert *et al.*, 1994; Lürling & Van Donk, 1997), since large *Daphnia* may still be able to ingest relatively large colonies. It has therefore been suggested that inducible colony formation should be most effective against small herbivores (Van Donk *et al.*, 1999). Colony formation might be an effective defence against grazing by smaller *Daphnia* species, such as *D. cucullata* Sars, 1862. This “cooperation” between large *Daphnia* and *Scenedesmus* can thus be advantageous for both since the formation of larger *Scenedesmus* colonies at the same time protect these algae from the grazing exerted by small herbivores but do not significantly interfere with their edibility by large ones. This could be considered a case of coevolution of induced responses, i.e., the evolution of induced prey defenses that benefit the predator as well as the prey (Tollrian & Harvell, 1999).

It must be considered that although colony formation has adaptive benefits, it also involves costs. In planktic algae, colony formation appeared to have direct photosynthetic costs (Verschoor, 2005). In addition, colony formation increases sedimentation rates but also reduces the surface to volume ratio of *Scenedesmus*. Hence, they could lower their light or nutrient uptake rates. Even so, no differences in growth rates (Hessen & Van Donk, 1993; Lampert *et al.* 1994; Lürling & van Donk, 2000) have been found between unicells and colonies of *Scenedesmus* and the only costs that have been demonstrated unambiguously for *Scenedesmus* colonies are increased sedimentation rates (Lürling & van Donk, 2000). Therefore, the phenomenon of grazer-induced colony formation in

Scenedesmus can be interpreted as an inducible defense at the expense of higher sinking losses. Sinking, however, could also be interpreted as an escape in time (Lürling & Von Elert, 2001). *Scenedesmus* is capable of surviving prolonged periods of darkness; in this condition, colonies disintegrate and unicells may serve as inocula for subsequent blooms.

Although colony formation apparently does not affect light harvesting capacity, light is an essential prerequisite for autotrophic growth and, hence, light is an important requirement for formation and maintenance of colonies. Sedimentation of induced colonies may thus cause *Scenedesmus* to settle to depths with lower light intensity, where it disintegrates and loses its defensive properties (Lürling, 2003b). In natural systems, the light quality and quantity varies both spatially (e.g., with depth) and temporally: daylight intensity is never constant and every light period (day) is followed by a dark period (night), which puts important constraints on *Scenedesmus* colony formation in the field.

Another factor which varies dynamically under field conditions is the concentration of the infochemicals. Most research on infochemical-induced colony formation in *Scenedesmus* has been performed using standard bioassays with fixed infochemical concentrations. In natural ecosystems, the population density of herbivores varies dynamically, causing continuously varying concentrations of herbivore-released infochemicals. Furthermore, biodegradation causes the infochemical signal to weaken over time. The combination of herbivore population dynamics and environmental degradation will thus create highly dynamic infochemical concentrations and gradients, resulting in dynamic patterns of colony formation and disintegration (Lürling & Van Donk, 1997).

A recent article by Verschoor *et al.* (2009) investigated the dynamics of *Scenedesmus* colony formation and disintegration in response to the density of the herbivorous rotifer *Brachionus calyciflorus* in large-scale mesocosms. After a peak of herbivory, these authors noted that the 'ghost of herbivory past', i.e. the remaining infochemicals, continued to induce colony formation, causing an additional lengthening of colony disintegration times and associated fitness costs (higher sedimentation loss rates). This indicated that costs of colony formation were not only important during the induction phase, but could be even more important during the relaxation phase.

The production of chemicals inducing the colony formation in *Scenedesmus* is not restricted to grazers. One of the strategies employed by microorganisms to eliminate competitors is the release of inhibiting compounds, a process known as allelopathy. A review about allelopathy in phytoplankton and the biochemical, ecological and evolutionary aspects, is given by Legrand *et al.* (2003). In biofilms, the competition between microorganisms for light, nutrients and space is extreme. Moreover, planktic algae can be considered as competitors insofar as they decrease the available light for the benthic algae. Leflaive *et al.* (2008) demonstrated that a benthic/epiphytic green alga, *Uronema confervicolum* Lagerheim, produces allelopathic compounds that induce oxidative stress and growth inhibition in the planktic *Desmodesmus quadrispina* Chodat. Some of these compounds can also trigger the formation of colony in *D. quadrispina*. As colonies have higher sedimentation rates than unicells, their induction by *U. confervicolum* might decrease shading.

Other green algae show different induced morphological responses against grazing pressure. The green alga *Chlamydomonas reinhardtii* usually occurs in cultures as single, biflagellated cells. However, *C. reinhardtii* is known for its ability to form gelatinous and palmelloid stages that arise as a result of an interaction with its environment. The palmelloid stage seems to enhance

C. reinhardtii cells resistance to grazing. Exponentially growing unicellular *C. reinhardtii* formed palmelloid colonies rapidly when cultured together with the rotifer *Brachionus calyciflorus* (Lürling & Beekman, 2006).

In a study on genotype versus phenotype variability in *Chlorella* and *Micractinium* Luo *et al.* (2006) demonstrated that bristle formation by the green alga *Micractinium pusillum* Fresenius is induced by culture medium of the rotifer *Brachionus calyciflorus*. Grazing experiments with *Brachionus* showed the rotifer preferably feeding on non-bristled cells. Nevertheless, the dominance of colonies versus solitary cells in the *Micractinium* culture was not correlated with the “*Brachionus* factor”. These results suggest that morphological characteristics like formation of bristles represent phenotypic adaptations to a more general pattern of conditions in the ecosystem. Pröschold *et al.* (2010) have recently discussed the polymorphism and polyphyly of bristle formation in Chlorellaceae.

Accordingly, a study on factors controlling the colonial structure of *Pediastrum tetras* (Ehrenberg) Ralfs (now *Stauridium tetras* (Ehrenb.) E. Hegewald) shows that infochemicals by *Daphnia magna* not induce colony formation in this alga but only a slight increase in the density of the largest colonies compared to the control treatment (Rojo *et al.*, 2009). In addition, *Daphnia* infochemicals appear not induce colony formation and not influence significantly growth rate and the colony size of the gelatinous green alga *Sphaerocystis Schroeteri* Chodat (Kampe *et al.*, 2007).

Some studies on cyanobacteria reported that colony formation in the *Microcystis aeruginosa* could be induced by cladocerans (Jang *et al.*, 2003; Ha *et al.*, 2004) or flagellates (Burkert *et al.*, 2001). Recently, Becker (2010) highlighted the possible role of infochemicals in the morphology changes in *Microcystis*. In particular, cell aggregate formation of the cyanobacterium increases in presence of spent *Daphnia* medium. However, in other reports (Hessen & Van Donk, 1993; Yang *et al.*, 2006) no colonial algae were found when *M. aeruginosa* was cultivated with cladocerans.

Yang *et al.* (2009) suggested that infochemicals released from flagellate *Ochromonas* sp. fed with *Microcystis aeruginosa* may be a trigger for colony formation. From experiments, the authors observed that the colonial *M. aeruginosa* did not occur immediately after cultivation with filtered cultures of flagellates. Moreover, it did not result from the adhesion of already existing single cells but from the incomplete loosening of daughter cells in cell division and the size of colonial *M. aeruginosa* in these experiments were smaller than that induced by the grazing of flagellates directly (Yang Z. *et al.*, 2006). These results are similar to those showing colony formation in *Scenedesmus* as induced by filtered cultures of zooplankton (Lürling & van Donk, 1997). The colony formation in *Microcystis aeruginosa* appear thus to be a predator-induced defense which could reduce predation risk from flagellates.

Current data suggest that *Daphnia* infochemicals generally have a weak influence on growth rate, microcystin production and colony formation of *Microcystis* strains as compared to the inter-strain variability, while existing inducible effects are highly strain-specific (van Grembergh *et al.*, 2009). In marine phytoplankton Bergkvist (2008) showed that grazer-induced paralytic shellfish toxins production is a grazer-specific response in the dinoflagellate *Alexandrium minutum* Halim, and its potential ecological importance will thus depend on the composition of the zooplankton community, as well as the intrinsic toxin-producing properties of the *A. minutum* population.

The mixotrophic nanoflagellate *Ochromonas* sp. appears also to induce the aggregation of the single cells of phycocyanin-rich freshwater *Cyanobium* sp.

into microcolonies characterized by hundreds of tubes (spinae). Spinae production, previously unknown for the freshwater *Cyanobium* species, suggests that picocyanobacterial life strategies are more flexible than previously thought (Jezberová & Komárková, 2007).

In marine environment a striking example about the role of grazers' infochemicals on phytoplankton size and shape is represented by the bloom-forming phytoplankton *Phaeocystis* (Tang, 2008).

The two primary forms of most *Phaeocystis* species are solitary, flagellate cells of 4-6 μm and hollow, spherical, mucilaginous colonies that can reach up to 30,000 μm in diameter. When *Phaeocystis globosa* Scherffel chemically senses its neighbors being attacked by ciliates that feed on small foods, it shifts shape and grows as colonies too big for ciliates to consume. In contrast, when its neighbors are attacked by copepods that feed on larger foods, it suppresses colony formation and grows as single cells too small to interest copepods. The species *P. globosa* senses grazer-associated chemical cues, senses the type of consumer attacking conspecifics, and responds adaptively to these grazer-specific cues with opposing shifts in phenotype. Copepod associated cues suppress, whereas ciliate-associated cues enhance, colony formation. These consumer-specific responses should be adaptive given that copepods feed preferentially on colonies and ciliates grow faster on diets of solitary cells (Long *et al.*, 2007). Therefore this signal appears non-species specific (Tang, 2003). Thus, this phytoplankton species not only senses that neighbors are being attacked, but also identifies the attacker and responds with opposing phenotypic shifts depending on the identity of the attacker. In addition, the presence of grazers has been shown to induce *P. globosa* and *P. antarctica* Karsten to form significantly larger colonies (Tang *et al.*, 2008).

Most of our current knowledge about inducible defences performed by phytoplankton to counteract grazing has been obtained via experiments involving single predator-prey pairs. Studies of morphological plasticity are now moving to a new phase with increasing attention to the complexity of organismal design and how community-level properties (e.g., trophic complexity) can influence the plasticity of individuals. The inducible defences which affect predator handling times have been predicted to stabilise population dynamics. Experiments with bi- and tritrophic laboratory communities, consisting of undefended or inducibly defended *Scenedesmus*, *B. calyciflorus* and the carnivorous rotifer *Asplanchna brightwelli* Gosse, 1850, confirmed these theoretical predictions, both for the stabilising effect on population dynamics (Verschoor & Van der Stap, 2004), as well as for the dampening effect on the trophic cascade (Van der Stap *et al.*, 2008, 2009). This indicates that *Scenedesmus* colony formation, and more generally inducible defences by the release of infochemicals, have an effect on the structure and functioning of aquatic food webs (Van Donk, 2006).

The "smell of death" produces an ecology of fear that strongly, but indirectly, impacts populations, communities, and ecosystems. Unlike density-dependent interactions, these trait-mediated interactions act immediately, can affect hundreds or thousands of individuals instead of just those eaten, and can thus produce strong and cascading effects on aquatic communities and ecosystems (Hay, 2009).

MORPHO-FUNCTIONAL CLASSIFICATION OF PHYTOPLANKTON

According to the Gleasonian line of reasoning (Gleason, 1926), individual species respond independently to the environment, and community composition reflects this response of individual species. The environmental conditions favour groups of species that share similar adaptive features (Webb *et al.*, 2002). Such species are not necessarily taxonomically, and thus phylogenetically, related since even closely related taxa can differ widely in habitat use and phenotypic characteristics (e.g. Lüring, 2003b). However, each of them can be represented by an opportunely parameterized habitat template which can be helpful to distinguish the critical dimensions of aquatic habitat (Reynolds, 1987; 1997).

On the other hand, several scientists retain that communities are better, more reliable indicators of habitat conditions than are the presence or absence of component species. According to this consideration, the phytosociological approach (e.g. Braun-Blanquet, 1964) has developed a system of diagnosing and naming the very distinct associations of plant species that constitute vegetation. In essence, the associations are the basic functional units and terrestrial ecologists recognize types of system and predominant pathways of energy flow based wholly on their ability to abstract the average environmental conditions on the grounds of which kinds of (associations of) species are present. Although this approach is pragmatic and the idea of communities as functional entities (*sensu* Clements, 1916) is appealing, there is no obvious basis for such a classification of species, nor is there a reliable way of constructing a general classification that is independent of local biological and environmental characteristics. Actually, the inverse procedure, i.e. given a set of environmental conditions to forecast what species will be present, is not an easy task and largely remains under a probabilistic umbrella or is merely speculative (Reynolds, 2000).

As Naselli-Flores (2000) pointed out, similar phytoplankton assemblages may be encountered in lakes of supposedly quite different trophic states (based, for example, on OECD categories) and, conversely, lakes judged to be trophically similar may differ in the species structures they support. Sometimes, difficulties arise because of the proximity to a nutritional shift, as a consequence of a recent eutrophication or restoration. In such instances, existing species assemblages may persist for some time (e.g. Naselli-Flores *et al.*, 2003; Becker *et al.*, 2008). This ecological inertia can confound any judgement about the conditions that the species are supposed to characterize: trophic switches and compositional responses may become confused (Reynolds *et al.*, 2000). Only the quantitative responses of the phytoplankton biomass seem to be anywhere close to being predictable on the basis of the nutrient supplied. This much is, of course, very well known already. When it comes to species composition, no such convenient surrogate is demonstrable and Tilman (1996) had to write that despite an enormous investigative effort to understand the factors regulating species composition in the phytoplankton, the forces governing selection, dynamics, diversity and stability 'remain mysteries'.

A promising approach to solve the arcane is the possibility to group phytoplankton according to their functional attributes and several attempts have been made in this direction. As recently reviewed by Litchman & Klausmeier (2008), beside morphological features, functional traits also include considerations on physiological parameters related to light harvesting, nutrient uptake, nitrogen fixation, mixotrophy, temperature optima, reproductive traits and resting stage

production. In addition to resources acquisition and growth, relevant functional traits, as already discussed, also include the ability to avoid mortality through such processes as grazing and sedimentation. A further complication is related to the fact that most traits in organisms are not independent but are instead interrelated. Correlations between and among traits often represent trade-offs and complicate assessment of the selective pressures on traits.

Moreover, traits need to be measurable at the level of individuals, without reference to the environment (Violle *et al.*, 2007). Unfortunately, the current paucity of information on species-specific physiological traits in the phytoplankton (Weithoff, 2003) limits our ability to arrive at *a priori* functional classifications (Reynolds *et al.*, 2002; Mieleitner *et al.*, 2008; Padisák *et al.*, 2009). However, as already shown, physiological traits (specific growth rate, resource-uptake and light-interception properties) strictly depend on morphological and phenological features, and, as a result of adaptive mechanisms, govern ecological performance of phytoplankton (Reynolds, 1984b; Naselli Flores *et al.*, 2007a). Starting from the consideration that species adapted to a given ecological condition often show similar morphological features, and that these ecological conditions can be described by appropriate size and morphological descriptors, Reynolds (1997) formalized a trait-based functional classification of freshwater phytoplankton into groups identified by alpha-numeric “coda”. This classification, although not completely based on purely morphological traits represented a first attempt to emphasize the strong relationships existing between morphological traits, which are relatively simple to measure (see Hillebrand *et al.*, 1999), and physiology. This functional classification was later enlarged by Reynolds *et al.* (2002) and statistical analyses have been used to recognize, validate and label the coda (Kruk *et al.*, 2002; Tolotti *et al.*, 2005).

Since its publication, Reynolds’ functional classification has received a large consensus among phytoplankton ecologists, as reviewed by Padisák *et al.* (2009). The reason for its success probably lies in the fact that it may simplify to handle the long taxonomic lists traditionally produced by pooling the species with similar ecological characteristics into approximately three dozens of functional groups.

Two main ideas lie beneath the functional groups theory:

- 1) a functionally well-adapted species is likely to tolerate the constraining conditions of factor deficiency more successfully than individuals of a less well-adapted species;
- 2) a habitat shown typically to be constrained by light, P, or C or N or whatever, is more likely to be populated by species with the appropriate adaptations to be able to function there (this of course does not imply that those species will be there).

As a consequence, the term ‘functional group’ is sensitive to the sets of appropriate adaptive specialisms and the clusters of species that have them. However, the way in which species are split into different functional groups requires a deep knowledge of the autoecology of single species or species groups. However, a tight link between the morphology and autoecology of species can be also suggested by the fact that distribution in time and space, as well as demographic characteristics, is linked to phytoplankton morphological traits (Lewis, 1977; Cermeño *et al.*, 2006).

To overcome the problems inherent the use of functional traits, Kruk *et al.* (2010) proposed a purely morphological classification of freshwater phytoplankton. These authors, used cluster analysis to define seven species groups entirely based on morphological descriptors. Functional traits were not used for

this classification. By the way, they differed significantly among the clusters, suggesting that these clusters may indeed represent meaningful functional groups. This approach, up to now unique, could offer several advantages because of its objectivity, its independence from taxonomic affiliations, and the relative ease of its application to the majority of species for which physiological traits are unknown and are not readily determined.

PERSPECTIVES IN MORPHOLOGICAL ANALYSIS OF PHYTOPLANKTON

The morpho-functional approach has been retained to simplify the traditional taxonomical approach in the environmental biomonitoring. However, as underlined by Padišák *et al.* (2009), taxonomy cannot be replaced by a morpho-functional classification since the unequivocal link between any species and its traits is the basis for a correct inclusion of species into functional groups. Moreover, traditional taxonomy (based on phenotypes), although neglected in the last years and often totally substituted by more “modern” molecular approaches (Boero, 2010) has a fundamental value. In fact, molecular taxonomy is an essential aspect of taxonomy, but it does not solve all problems. We need to know both phenotypes and genotypes, and epigenetics is showing that the flow of information from genotype to phenotype is not a one-way road. As shown by Komárek (2010), we must tend to a classification method based on combined markers, in which molecular data (as an indisputable genetic basis) should be correlated with biochemical, ultrastructural, phenotypic and ecological data.

Moreover, microevolutionary processes are likely to affect phytoplankton dynamics owing to short generation times and large population numbers. Genetic shifts in trait values of a given species can easily occur over relatively short timescales (within a single growing season), often because of clonal selection (Kardinaal *et al.*, 2007). This can be particularly true for cyanobacteria as shown in the review on *Cylindrospermopsis* by Padišák (1997) but it has also been observed in several planktic green algae (Luo *et al.*, 2005). Grazing, competition, or changing environmental conditions can exert sufficient selective pressures to cause genetic shifts which could be proxied by analyzing the variations in morpho-functional traits.

One of the difficulties arising when using morpho-functional traits is the need to translate them into fitness. This implies that we need to understand what kind of relationships exists among traits and between traits and environmental variables. Thus if it can be clear enough to what extent the presence of a dominant population of cyanobacteria with heterocytes may underline a nitrogen limitation, and what is the threshold at which heterocytes formation start occurring, the relationships among e.g. the half-saturation constants for phosphorus uptake and for P-limited growth can not be easily related to morphology (Kruk *et al.*, 2010).

Although the number of investigations in this direction is constantly increasing, the achievement of this task is at its beginning and still a lot of work must to be done. Good and promising results were obtained by incorporating traits in a variety of models related to phytoplankton diversity, primary production, growth, competition, resistance to grazing, sinking and floating behavior, etc. (see Elliot *et al.*, 2010 and Litchman & Klausmeier, 2008).

There is no doubt that the correct interpretation of the dominant functional traits in phytoplankton assemblages can supply a powerful tool to clarify ecosystem functioning, relationships among species and, last but not least, to assess water quality. However, a standardized method to measure traits is still unavailable and the accuracy of cells/colonies measurements should be improved. The set up of automated systems based on object-oriented image analysis can substantially improve such time-consuming task (Zeder *et al.*, 2010). Moreover, a push ahead in this direction was given by Jorn Bruggeman (Centre for Integrative Bioinformatics, Vrije Universiteit of Amsterdam), who recently released a tool to estimate traits, which is available on the Internet at <http://www.ibi.vu.nl/programs/phylopars/phytoplankton.php>. This program, based on a recently introduced approach to the estimation of parameters with an evolutionary model (Bruggeman *et al.*, 2009) give results on traits of different freshwater phytoplankton taxa. These results account simultaneously for phylogenetic relationships between species, and approximate power law relationships (e.g., allometric scaling laws) between different traits. The web server takes an evolutionary perspective to the variability across phytoplankton taxa in order to estimate the size, maximum growth rate, phosphate affinity and susceptibility to predation of any phytoplankton taxon, starting from simple morphological features such as cell's length and diameter.

The wide success among phytoplankton ecologists of the morpho-functional classification proposed by Reynolds *et al.* (2002) is likely due to the fact that this kind of classification make easier to relate phytoplankton occurrence and environmental conditions of the investigated water bodies.

However, as shown by Kruk *et al.* (2010), the use of easily determined morphological criteria as an indicator for functional properties is a useful shortcut. Morphological descriptors as surface, volume and their ratio, as well as maximal linear dimension and its product with sv^{-1} can represent powerful predictors of physiological performances of phytoplankton and offer a valid interpretation of environmental conditions. Moreover, by broadening the list with the presence of aerotopes, flagella, mucilage, heterocytes and siliceous exoskeletal structures, fluctuations in the environmental conditions could be monitored just on the basis of the occurrence of such traits.

An attempt in this direction was performed by Naselli-Flores & Barone (2007), who could relate a variation in the product of maximum linear dimension and surface-volume ratio ($m\ sv^{-1}$) of the dominant phytoplankton species to the fluctuations of the ratio between the depth of the mixing zone and the euphotic zone ($z_{\text{mix}}/z_{\text{eu}}$). These authors also showed that it can be useful to track the seasonal succession of phytoplankton by using morphological traits and to relate such changes to the environmental condition of a freshwater ecosystem.

Actually, phytoplankton well integrate physical, chemical, and biological parameters of freshwater ecosystems and long-term data sets or the comparison of morphological structure of phytoplankton in different periods of time can offer good predictions on local climate change trends (Barone *et al.*, 2010). In addition, phytoplankton assemblages contain a high number of species, making data useful for statistical and numerical applications. Their response time is rapid, as is recovery time, with recolonization after a disturbance often more rapid than for other organisms.

Even the record of rare species contains a lot of information often discarded. As shown by Padišák *et al.* (2010b), rare species constitute the ecological memory of a given aquatic ecosystem, which can influence the present and future responses of the community. They thus could provide a powerful long-

term monitoring tool, once the processes governing the appearance and the relative importance of the different traits are fully understood.

Due to the variety of useful results obtained by applying the morpho-functional approach, we hope that phytoplankton research will expand its focus toward little known species in order to create a general data base of traits occurrence, which can further enlarge our knowledge on the functioning of ecosystems.

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