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RESEARCH ARTICLE

# A trait database for Phytoplankton of temperate lakes

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**Abstract** – Phytoplankton is a choice ecological indicator of lake ecological quality. Microalgae composing this biological compartment display a large diversity of morphological, physiological and ecological features, which are useful for understanding the interactions they have with other biotic and abiotic elements. Such kind of information together with classical Utermöhl phytoplankton analyses are useful for lake management and basic science. We present here a reference database of morphological (cell and colony sizes, biovolumes, mobility apparatus, colony formation), functional (functional groups of Reynolds, Padisak and Kruk, zooplankton edibility groups), physiological (trophic capacities) and ecological traits (Brettum index values) of more than 1200 taxa often observed in temperate lakes. This database, maintained since the 70's until nowadays by the authors of this paper is now realized open access in Zenodo (<https://zenodo.org>; DOI: [10.5281/zenodo.1164834](https://doi.org/10.5281/zenodo.1164834)) and also as supplementary material on the journal website. The paper presents an overview of its content.

**Keywords:** Biovolume / functional groups / microalgae / morphological traits / taxonomy

## 1 Introduction

Phytoplankton is the most often used ecological indicator of lakes ecological quality because its biomass and species composition are directly affected by anthropogenic activities. In many cases human activities is at the origin of eutrophication phenomena and they have a well know impact of phytoplankton (Pinay *et al.*, 2017). More than 170 publications were published on the impact of eutrophication of phytoplankton in the Web Of Science until 2017, which is a proof of the interest about this topic. Compared to benthic microalgae, there are ten times more published studies about phytoplankton (Cantonati and Lowe, 2014). Indeed, phytoplankton gives a good picture of the overall ecological quality of a lake (*e.g.* Thackeray *et al.*, 2013) and for such reason it has a long legacy especially in the routine monitoring of large lakes surrounded by dense populations. It is also a required ecological indicator for lakes and larges rivers of US federal (Copeland, 2016) and European transnational (European Commission, 2000) legislations.

Large peri-alpine lakes in Western Europe are an excellent illustration of this situation. This is in particular the case of the largest deep lake in Western Europe, Lake Geneva situated on the border between France and Switzerland. More than 950 000 people now inhabit its catchment area and it suffered strong eutrophication in the 60's–70's. After the first efforts in the 70's to limit pollution and its impact of the lake, the trophic

status of Lake Geneva gradually changed until nowadays, since it is now in on a meso-oligotrophic status (*e.g.* Anneville *et al.*, 2017). To measure the benefit of restauration actions of ecological quality in this lake, phytoplankton has been monitored every two weeks (or every month during winter season) with the same sampling methodology since 1974 (Rimet *et al.*, 2009): an integrated sample between 0 and 18-m depth is carried out above the deepest point. Then samples were analyzed under microscope (counting, determinations) following a given methodology (Utermöhl, 1958), now standardized at European level (Afnor, 2006).

Since the 60's–70's, scientific reports were delivered to lake Geneva managers. Phytoplankton is an important item of these reports and even if the taxonomic inventories were produced using the same methodology –and this enable a good comparability throughout the years- they were presented using different traits from a decade to another; which is due to the evolution of knowledge about microalgae ecology. For instance in the 70's, reports were simply presenting monthly phytoplankton biomasses and species richness (*e.g.* Lang, 1975). Then in the 80's, the authors (*e.g.* Revaclier *et al.*, 1988) of these reports started to use the relative biomasses of algal classes and of size classes (*e.g.* nanophytoplankton/micro-phytoplankton) since these traits are good descriptors of trophic level (*e.g.* Thunmark, 1945; Nygaard, 1949) and of edibility for zooplankton (Makarewicz *et al.*, 1998). In the 90's, authors of the reports (*e.g.* Pelletier *et al.*, 1997) used ecological information about nutrient preferences of algal classes and species from literature and information about colony shape (*e.g.* filamentous/coenobial/mucilaginous) which

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are also good indicators of microalgae nuisances. For instance, filamentous algae, like *Mougeotia gracillima* in lake Geneva, when blooming, clog professional fishermen nets and this reduce their fishing catch (Tapolczai *et al.*, 2016), or can form toxic blooms like the cyanobacteria *Planktothrix rubescens* in lake Bourget (Kerimoglu *et al.*, 2017). In the 2000s, rather precise notions of ecological niches of species appeared in the reports (e.g. Druart *et al.*, 2004) coming from the scientific literature (e.g. Anneville *et al.*, 2002) for instance the ecological niche of *Stephanodiscus* species (*alpinus*, *neo-astraea*) is described as they occur in meso-eutrophic lakes during winter when the water column is mixed. After 2007, use of functional groups described in Reynolds *et al.* (2002) explaining the seasonal and long-term evolution of phytoplankton communities (e.g. Rimet and Druart, 2009) appeared because they summarize with robustness phytoplankton ecology and are good indicators of lake ecological quality and functioning. Furthermore, biotic indices like the Brettum index (Brettum, 1989; Dokulil *et al.*, 2005) and information about mixotrophic capacities of species were used to assess the trophic evolution of the lake.

The authors of this paper have regularly updated a database of traits during more than 50 years with species they observed in the large peri-alpine lakes in France (Geneva, Annecy, Bourget, Aiguebelette) but also in high altitude lakes in the French Alps (Feret *et al.*, 2017) and various other lakes (e.g. Lac du Der, Lac de Nantua, Lac de Miribel ...). This database encompass more than 1200 taxa and more than 50 traits of various types (types according to the definitions of Violle *et al.*, 2007): functional traits, performance traits, Ecological traits performances.

The objective of this paper is to describe this database, hosted on a Windows Excel® spreadsheet, released open-access with this publication in Zenodo (<https://zenodo.org>; DOI:10.5281/zenodo.1164834) and also as supplementary material on the journal website. It is hereafter called Appendix 1.

## 2 Methodology

### 2.1 Cell and colony sizes and biovolumes

Appendix 1 gives for each taxon its cell dimensions, length, width, thickness (also called in some cases “hidden” dimension) and its best fitting geometric shape. Cell (and colony) dimensions origin is given in the column “Notes on biovolumes”. Nine different geometrical shapes are used (ellipse, cuboid, tube, double cone, triaxial ellipsoid, sphere, cone, rhomboid prism, prism) which is much smaller than the 43 different shapes given in the European standard for the determination of phytoplankton biovolumes (European Standardization Committee, 2014).

If the geometrical shape selected corresponds exactly to the shape of the cell, a multiplicative factor of “1” is applied to the geometrical formula to get the final taxon biovolume. This is the case of a *Chlorella vulgaris* cells in Figure 1a, which shape are a perfect sphere and therefore the biovolume of one cell is corresponding to the formula of a sphere with a multiplicative factor of “1”.

But in some cases, the best fitting geometrical shape do not correspond exactly to the cell shape and therefore the

biovolume is over estimated. In such case, this multiplicative factor is below 1 and is applied in order to reduce the estimation of the taxon biovolume. This factor is based on a subjective estimation (after a careful observation under microscope) the space the cell occupies in the geometrical shape. For instance, we consider that the best fitting shape of *Cymbella* C. Agardh species is a box. But shape of *Cymbella* is not exactly corresponding to a box. Therefore a multiplicative factor of 0.7 is applied to get a correct estimation of the biovolume of *Cymbella* species since it is smaller than a box. Figure 1b illustrates this situation.

The surface area of the cell is calculated on the basis of the geometrical shapes formula. Similarly, if the geometrical shape do not correspond exactly to the cell shape, the surface area obtained with the geometrical formula will be divided by a subjectively estimated factor (called “dividing factor” in Appendix 1).

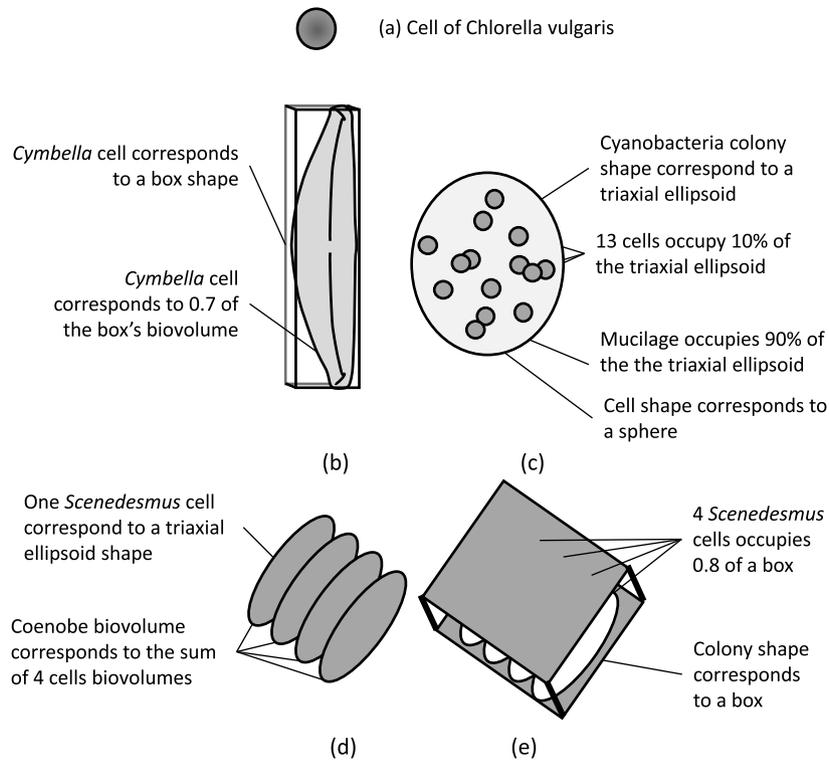
In the case of a colonial taxon, the number of cells in a colony is given. For instance, the mucilaginous Cyanobacteria in Figure 1c has 13 cells and the *Scenedesmus* Meyen has 4 cells (Fig. 1d, e). In Appendix 1, the colony biovolume is estimated using two ways:

- the first way is with the cumulated biovolume of the cells in a colony. For this, the biovolume of one cell is multiplied by the number of cells in a colony. For instance, the biovolume of one cell will be multiplied by 13 since there are 13 cells in the case of the mucilaginous cyanobacteria of Figure 1b. Figure 1d illustrates this for a *Scenedesmus* colony (or coenobe) composed by 4 cells;
- the second way is based on the colony sizes and shapes. For this, shapes and colony sizes (length, width, thickness) taking into account the mucilage, are given together with a multiplicative factor. This factor estimates subjectively the proportion of biovolume that cells occupy in the colony shape. For instance in Figure 1c, the biovolume of the colony will be calculated on the basis of a triaxial ellipsoid which size encompass the mucilage and will be multiplied by a factor of 0.1, since cells occupy approximately 10% and the mucilage approximately 90% of the colony. Figure 1e illustrates this for a *Scenedesmus* coenobe which fit 80% a box volume.

These two ways to calculate a biovolume have pro and cons. In the case of small colonies composed by a small number of cells, which are easily countable, the first way is preferred. On the other hand in the case of large colonies (e.g. colony of *Microcystis aeruginosa* (Kützing) Kützing of 100 µm), the number of cell is hardly countable, and the second way is preferred.

Finally, in Appendix 1, the surface area of the colony is given based on the colony sizes, shapes and dividing factor dedicated to colony.

In case of filamentous colonies, the biovolumes and surface areas of the colonies are given for an arbitrary length of 100 µm (usually the length of the filaments are longer). This is the case for filamentous Cyanobacteria, Chlorophyta, Xanthophyta. But, there are cases for which the biovolumes and surface areas of the colonies of filamentous taxa are not given for filaments of 100 µm. This is the case of Cyanobacteria taxa, which show short filaments (e.g. *Romeria* M. Koczwara). In



**Fig. 1.** Illustration of the biovolume calculations. (a) Case of a cell of *Chlorella vulgaris* which cell shape attribution in Appendix 1 is a sphere (a) Case of a cell of *Cymbella* which cell shape attribution in Appendix 1 is a box; a multiplicative factor of 0.7 is applied to the volume of the box to get the biovolume of the *Cymbella* cell. (b) Case of a mucilaginous Cyanobacteria colony. The first way to calculate the biovolume is to measure a cell dimension and calculate the biovolume of one cell based on a triaxial ellipsoid formula; the biovolume of one cell is multiplied by 13 (the number of cells in the colony) to get the colony biovolume. The second way is to measure the colony dimensions (taking into account the mucilage) and to calculate the biovolume of the colony based on a triaxial ellipsoid. Finally this volume is multiplied by a factor of 0.1 (the cell volume is estimated to be 10% of the mucilaginous colony) to get the colony biovolume. (c) and (d) give the case of a *Scenedesmus* coenobe biovolume calculation. The first way (c) to calculate the biovolume, is to measure the cell dimensions and to calculate its biovolume based on a triaxial ellipsoid ; then the cell biovolume is multiplied by 4 (4 cells in the coenobe) to get the coenobe biovolume. The second way (d) to calculate the biovolume, is to measure the coenobe dimensions; in this case the coenobe shape is associated to a box. The box volume is calculated. Since the coenobe volume is smaller than the box volume, the box volume is multiplied by a factor of 0.8 to get the coenobe volume (the coenobe volume is estimated to be 80% of the box).

this case, the average length of the colony (usually below 100  $\mu\text{m}$ ) of the taxon is used to calculate the biovolume and surface area of the colony. Similarly, the lengths of filaments of *Planctonema lauterbornii* Schmidle (Chlorophyta) are on average 50  $\mu\text{m}$ , therefore, biovolume and surface area of its colony given in Appendix 1 is calculated with a length of 50  $\mu\text{m}$ . In the case of filamentous diatoms (e.g. *Achnanthisidium catenatum* (Bily & Marvan) Lange-Bertalot, *Aulacoseira Thwaites*, *Fragilaria Lyngbye*, *Melosira C. Agardh* ...), the biovolume of the colony is not given because the lengths of the filaments can be very different from a sample to another. This is also the case of several Zygothyceae species (e.g. *Mougeotia gracillima* (Hassall) Wittrock, *Spondylosium Brébisson*) which can be filamentous but which are also often unicellular when the environment is turbulent. Therefore the colonial biovolume and surface area of these Zygothyceae taxa are not given.

The maximal length of the taxon is given in Appendix 1: if the taxon is unicellular, it is the maximal length of the cell, if it is colonial it is the maximal length of the colony. Finally, we give in Appendix 1 the "Reference biovolume" of each taxon,

which is the chosen biovolume (among the two possible biovolumes calculations for colonial taxa) for routine countings, did by the authors in the framework of the lake monitoring.

## 2.2 Morphological, metabolic and trophic traits

Several morphological traits are given in Appendix 1. The first one is the cell mobility apparatus is described if it is a flagella or a raphe system (for diatoms). These two kinds of mobility are far different: flagella enable cells to swim in water, raphe system enable diatoms to glide on a substrate. The second morphological trait given in Appendix 1 specifies if the algae is colonial, and if it is, it is precise if this is a filamentous colonial shape.

Metabolic types are given for each taxon. Three different categories are given to algal classes and their subsequent taxa: autotrophic, mixotrophic and heterotrophic. Several taxa in Appendix 1 are heterotrophic, this can sound surprising since phytoplankton should be composed exclusively by

photosynthetic taxa. This is not the case because a few taxa were formerly considered as photosynthetic, whereas recent studies show they were not. This is the case for instance of the genus *Salpingoeca* H.J. Clark considered to be part of Chrysophyceae (a photosynthetic algal class) in [Bourrelly \(1981\)](#), whereas it is part of Choanoflagellates (an autotrophic protist class). These classes were attributed after consideration of various literature references (e.g. [Jones, 2000](#); [Stickney et al., 2000](#); [Salmaso and Padisak, 2007](#); [Tittel et al., 2009](#)). These taxa are traditionally counted in phytoplankton whereas they are not photosynthetic.

The Brettum index is a biotic index, calculated on phytoplankton communities, adapted to large and deep alpine lakes to assess phosphorus concentration (modified after [Brettum, 1989](#); [Dokulil et al., 2005](#)). To calculate this index, two different traits are used. The first is a species biomass in the sample (performance trait) and the second is the presence probability of the species along the phosphorus gradient (ecological performance). [Appendix 1](#) gives the trophic traits of the species integrated in this index: they are composed by 6 classes of phosphorus concentrations in which are given the presence probability of the species. The presence probabilities are ranking from 0 (species absent) to 10 (very high probability that the species is present). This index is routinely used to assess phosphorus level in large peri-alpine lakes in France (e.g. [Jacquet et al., 2017](#); [Rimet et al., 2016](#)).

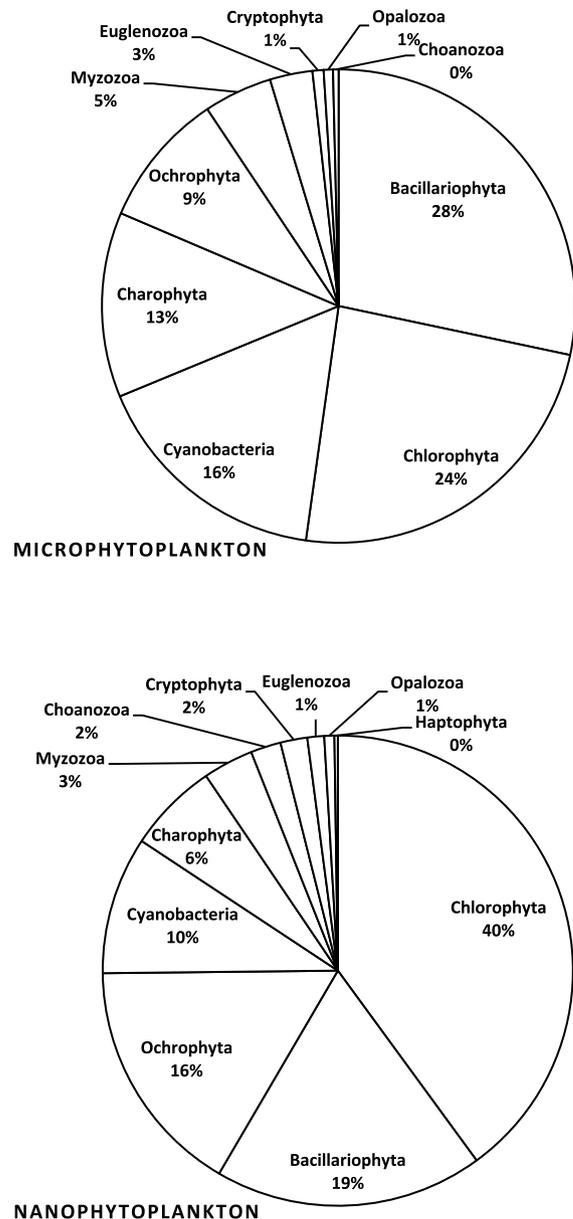
### 2.3 Functional and morphological classifications

In [Appendix 1](#), two functional classifications are given, the one of [Reynolds et al. \(2002\)](#) thereafter modified by [Padisak et al. \(2009\)](#). In the sense of these authors, a functional group gathers species that live in the same kind of habitat. These groups can be made of polyphyletic species but which developed sometimes different kind of adaptations, which enable taxa to be present in the same kind of habitat ([Tapolczai et al., 2016](#)). Nevertheless, species belonging to the same group are not necessarily found in association in the same place at the same time, for instance simply because they may compete and exclude each other.

The classification of [Reynolds et al. \(2002\)](#) is made of 31 groups, where the habitat is mostly described in terms of water stability, nutrient level, depth, light intensity, water-body size. For instance, the functional group A gathers species living in lakes characterized by oligotrophic transparent waters, often mixed and with a neutral pH. Typical representatives given in [Reynolds et al. \(2002\)](#) are listed in [Appendix 1](#).

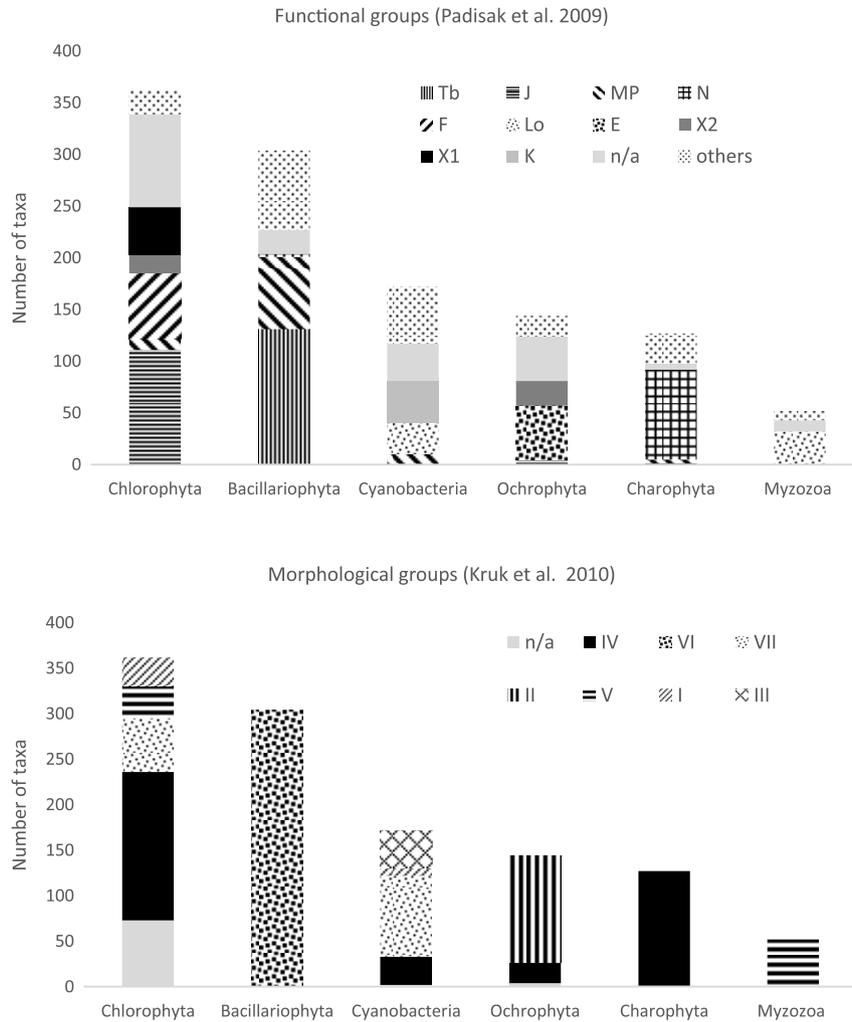
The classification of [Padisak et al. \(2009\)](#) is more extensive and encompass much more taxa. It is made of 40 groups (called codons). For each group, [Padisak et al. \(2009\)](#) also describe the habitat similarly to [Reynolds et al. \(2002\)](#), but add some particular habitats, like frequently stirred up shallow lakes (codon MP), slow flowing rivers (codon Tc), lotic habitats (codon Tb).

The morphological classification of [Kruk et al. \(2010\)](#) is given in [Appendix 1](#). This classification is made on 8 groups characterized by differing morphological traits, such as presence of flagella, presence of siliceous features, presence of mucilage. These morphological groups are well correlated with functional properties such as growth rate, sinking rate.



**Fig. 2.** Number taxa in microphytoplankton and nanophytoplankton per Phyla present in the phytoplankton trait database ([Appendix 1](#)).

For each taxon given in [Appendix 1](#), its belonging to nanophytoplankton and microphytoplankton is also given. Nanophytoplanktonic taxa correspond to algae with a cell (or colony) whose maximal length is less than 20  $\mu\text{m}$  and their biovolume is less than 10 000  $\mu\text{m}^3$ ; microphytoplanktonic taxa have a maximal length greater than 20  $\mu\text{m}$  and/or a biovolume greater than 10 000  $\mu\text{m}^3$ . The attribution of taxa to nano or microphytoplankton is based on the values of the “reference biovolume” and the “maximal length of the algal object” given in [Appendix 1](#). Nanophytoplanktonic taxa have a high surface/volume ratio which facilitate nutrient uptake, given their small size they quickly reproduce and have a low sinking rate. On the other hand, nanophytoplankton species are easily grazed by zooplankton: they are more edible. Microphytoplanktonic taxa have a low sinking rate, a smaller surface/volume ratio and



**Fig. 3.** Number of taxa per Phyla (a) in the functional (Padisak *et al.*, 2009) and (b) in the morphological (Kruk *et al.*, 2010) groups. “n/a”: non-attributed taxa to functional and morphological groups, “others”: only the most frequent codons are represented, the other are gathered in “others”.

therefore a smaller nutrient uptake capacity. On the other hand, they are more resistant to zooplankton grazing: they are less edible (e.g. Mostajir *et al.*, 2001; Domaizon *et al.*, 2003; Tada *et al.*, 2003).

Finally, Appendix 1 gives a physiological trait, the organic carbon ratio (Wetzel and Likens, 2000) for each taxon. This ratio is an estimation of organic carbon content of algae, it correspond to the general ratio of cellular carbon to cell volume. In Appendix 1, it is given for each algal class and enable to estimate the organic carbon content of algae ( $\mu\text{g C}$ ) based on algal biovolume (in  $\mu\text{m}^3$ ). The phytoplankton biovolume is considered to have a density equivalent to water (so  $10^6 \mu\text{m}^3/\text{L} = 1 \mu\text{g}/\text{L}$ ), so phytoplankton carbon ( $\mu\text{g C}/\text{L}$ ) is the phytoplankton biomass ( $\mu\text{g}/\text{L}$ ) multiplied by the organic carbon ratio.

## 2.4 Taxonomy

Taxonomy of each taxon is given from Empire to infra-specific level according to Algaebase (Guiry and Guiry, 2014) in Appendix 1. The memberships of taxa to the different traits

cell and colony, functional and morphological groups were explored with simple descriptive statistics.

## 3 Results and discussion

A total of 1224 taxa is codified in Appendix 1. These taxa were encountered mostly during surveys carried out in the framework of the long term monitoring of the large sub-alpine lakes in France Lake Geneva (e.g. Rimet *et al.*, 2016), Lake Aiguebelette, Lake Annecy (e.g. Jacquet *et al.*, 2014), Lake Bourget (e.g. Kerimoglu *et al.*, 2017; Rivera *et al.*, 2017) but also low-land lakes like lac du Der (North East France, Rolland *et al.*, 2009) and other remote lakes (e.g. Martinet *et al.*, 2014). A majority of them belongs to Chlorophyta (30%), Bacillariophyta (25%), Cyanobacteria (14%) and Charophyta (*i.e.* Zygnemataceae, 10%).

A majority of the taxa are belonging to the micro-phytoplankton (65%). Microphytoplankton is mostly composed by Bacillariophyta (most taxa rich genera are *Cymbella*, *Fragilaria*, *Navicula* Bory, *Nitzschia* Hassall) and Chlorophyta (e.g. *Coelastrum* Nägeli, *Monoraphidium*

Komárková-Legnerová, *Scenedesmus*, *Ulothrix* Kützing) taxa. On the other hand, nanophytoplankton is mostly composed by unicellular Chlorophyta taxa (e.g. *Chlamydomonas* Ehrenberg, *Scenedesmus*) and unicellular diatoms (e.g. *Cyclotella* (Kützing) Brébisson, *Stephanodiscus* Ehrenberg, small *Navicula*, *Puncticulata* H. Håkansson) (Fig. 2).

Repartition of the different functional groups of Padisak *et al.* (2009) and Kruk *et al.* (2010) in the algal Phyla show a none phylogenetic distribution since taxa of a given phylum belong to different functional groups (Fig. 3). When focusing on functional groups of Padisak *et al.* (2009), most of Chlorophyta taxa belong to codon J (shallow, mixed, highly enriched systems) and codon F (clear, deeply mixed meso-eutrophic lakes). Diatom taxa belong mostly to codon Tb (highly lotic environments) and Mp (frequently stirred up, inorganically turbid shallow lakes). Indeed, a high proportion of diatom taxa of the database are mostly of benthic habitats and not specifically planktonic. Finally, Cyanobacteria taxa belong to codon K (shallow, nutrient-rich water columns) and Lo (summer epilimnia in mesotrophic lakes).

When focusing on functional groups of Kruk *et al.* (2010), most of Chlorophyta taxa belong to group IV (medium sized organisms lacking specialized traits as *Monoraphidium*, *Coelastrum*, *Scenedesmus* etc...) and VII (large mucilaginous colonies as *Oocystis* Nägeli, *Coenochloris* Korshikov etc ...). Diatoms all belong to group VI (non-flagellated organisms with siliceous exoskeletons). Cyanobacteria taxa mostly belong to group VII (large mucilaginous colonies as *Aphanothece* Nägeli, *Aphanocapsa* Nägeli ...).

Nowadays, this database is routinely used in monitoring reports and scientific studies to assess eutrophication of lakes (e.g. with the total biomass or with the Brettum index, see Jacquet *et al.*, 2014, Rimet, 2017), links with zooplankton and fish communities (e.g. with edible functional groups of nano/microphytoplankton classes see Rimet, 2017; Kerimoglu *et al.*, 2017) or global warming (e.g. Berthon *et al.*, 2014).

## 4 Perspectives

Such database is encompassing 1224 taxa, but for sure, it is far from being complete compared to the enormous diversity of microalgae. Indeed, diatoms encompass more than 100 000 extent species (Mann and Vanormelingen, 2013), Chlorophyceae more than 6500 described taxa and Cyanobacteria more than 4600 described taxa (Guiry and Guiry, 2014). This database surely encompasses the most frequently observed taxa in temperate lakes. But it would be definitely necessary to have a much more collaborative work around such topic in order to have similar trait database than the extensive trait databases existing for higher plants like the TRY database where more than a hundred of scientists collaborated together (e.g. Kattge *et al.*, 2011).

## Supplementary Material

Appendix 1.

The Supplementary Material is available at <https://www.limnology-journal.org/10.1051/limn/2018009/olm>.

**Acknowledgments.** We thank Orlane Anneville for pushing me to publish this database.

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