Hydrobiologia
DOI 10.1007/s10750-008-9645-0

REVIEW PAPER

Use and misuse in the application of the phytoplankton functional classification: a critical review with updates

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Received: 2 September 2008 / Revised: 29 October 2008 / Accepted: 3 November 2008

Abstract Since its publication, the article 'Towards a functional classification of the freshwater phytoplankton' (Reynolds et al., J Plankton Res 24: 417–428, 2002), has attracted the attention of dozens of phytoplankton ecologists worldwide. These numerous applications of the functional classification to describe phytoplankton patterns in various aquatic ecosystems allowed the recognition of some uncertain features of this concept originating from various reasons. In this article, we attempt to facilitate the application of the functional classification, by providing a detailed description of the typical misplacements and by modifying some of the original habitat templates and species allocations. Furthermore, we discuss in this review those coda that were additionally described after the publication of the original article, and attempt giving an overview, as complete as possible, of the state of art.

Keywords Functional groups · Codon · Phytoplankton · Water Framework Directive

Handling editor: K. Martens

Electronic supplementary material The online version of this article (doi:10.1007/s10750-008-9645-0) contains supplementary material, which is available to authorized users.

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Introduction

The article 'Towards a functional classification of the freshwater phytoplankton' published in 2002 by Reynolds and coauthors has received a great deal of attention from phytoplankton ecologists, as indicated by the 130 citations that it collected by August 2008 (Web of Science). 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 more or less well-defined functional traits. Indeed, this approach proved to be more useful for ecological purposes than the previously applied taxonomic grouping (Kruk et al., 2002; Salmaso & Padisák, 2007). The apparent simplicity of the functional group approach coincided with the needs of the implementation of the Water Framework Directive (EC Parliament and Council, 2000) and two articles were published describing indices based on the functional grouping (Padisák et al., 2006; Borics et al., 2007). Moreover, as most

Published online: 25 November 2008

of the apparently easy approaches, it may also originate misinterpretations if the theoretical bases of the functional classification are disregarded.

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. Splitting species into different functional groups requires a deep knowledge of the autoecology of single species or species groups. If the functional group approach becomes widely used in monitoring programmes carried out by environmental agencies, there is the risk of misplacing species and coming to wrong conclusions. As we will demonstrate in this article, even experienced phytoplankton ecologists may place species in inadequate groups. This is generally due to two main reasons: one is that not all the functional groups are defined with the same level of accuracy and this may sometime generate confusion among the users. The second reason seems to be linked to pre-concepts of the users. Therefore, we felt it necessary to critically review the existing literature and to check whether the grouping of species reflected the autoecological features of organisms. The experience that accumulated in the last 6 years allows us to evaluate whether the original descriptions (Reynolds et al., 2002) are sufficiently clearly defined or if they need further clarification, and/or the eventual setting of subgroups.

In order to fulfil our goals, we searched for citations of Reynolds et al. (2002) in 'Web of Science' and 'Scholar Google'. Then, we selected the related articles, i.e. those applying the functional group approach. From these, only the articles which clearly used and related the coda to the respective species were considered. Our search, until August 2008, resulted in 130 citations in the Web of Science and 143 in Scholar Google. Of these, 67 articles were closely related to the application of the functional approach to phytoplankton. However, only those which clearly assigned assemblage codons to the species (63 articles) were used in this review. The complete list of selected papers is available as an electronic attachment to this article. In this attachment, we did not change the original species placements by the authors, however, we annotated those cases where, in our opinion, the given species needed to be placed in a different codon.

Screening the functional approach codon by codon

Codon **A** (Reynolds et al., 2002)

Habitat template: clear, deep, base poor lakes, with species sensitive to pH rise.

Described representatives: *Urosolenia* spp. (Huszar & Reynolds, 1997; Melo & Huszar, 2000); Antenucci et al., 2005; Silva et al., 2005; Sarmento et al., 2006; Borges et al., 2008; Souza et al., 2008); *Rhizosolenia* spp. (Borics et al., 2007); *Brachysira vitrea* (Huszar & Reynolds, 1997; Melo & Huszar, 2000); *Acanthoceras* spp. (Townsend, 2006); *Thalassiosira* spp. (Becker et al., 2008); *Cyclotella comensis* (Borics et al., 2007); *C. glomerata* (Borics et al., 2007); *C. baicalensis*, *C. ornata*, *C. minuta* (Fietz et al., 2005); *C. rhomboideo-elliptica* (Zhang et al., 2007); *C. wuethrichiana* (Leitão et al., 2003); *C. stylorum* (Çelik & Ongun, 2008); *Cyclotella* sp. (Soares et al., 2007); *Cyclostephanos* spp. (Fietz et al., 2005; Sarmento et al. 2006).

Typical misplacements: some authors included in this group all the *Cyclotella* species, even those that are not typical for clear, base poor lakes such as *C. bodanica*, *C. kuetzingiana*, *C. ocellata*, *C. comta*, *C. stelligera*. In one case, a misinterpretation of the habitat characteristics was noted which resulted in the placement of *Mallomonas* sp. (codon **E**) in this codon. Moreover, a low taxonomical resolution was in some cases observed and items like 'non-identified centrales', '*Cyclotella* spp.', '*Stephanodiscus* spp.' can be included in this group only if the given aquatic habitat clearly fits the environmental features of the codon.

Codon **B** (Reynolds et al., 2002)

Habitat template: mesotrophic small- and medium-sized lakes with species sensitive to the onset of stratification.

Described representatives: *Aulacoseira islandica* (Salmaso, 2002, Dokulil & Teubner, 2003), *A. subarctica* (Borics et al., 2007); *A. italica* (Dokulil & Teubner, 2003; Devercelli, 2006; Nabout et al., 2006); *A. hergozii* (Nabout et al., 2006) *Stephanodiscus neoastraea*, *S. rotula* (Borics et al., 2007); *S. meyerii* (Fietz et al., 2005); *S. minutulus* (Leitão et al., 2003; Dokulil & Teubner, 2003); *Cyclotella bodanica* (Huszar et al., 2003); *C. comta* (Padisák et al., 2003a; Borics et al., 2007; Hajnal & Padisák, 2008); *C. operculata* (Dokulil & Teubner, 2003); *C. kuetzingiana* (Gurbuz et al., 2003); *C. ocellata* (Gurbuz et al., 2003; Naselli-Flores & Barone, 2003); *Cyclotella/Discostella stelligera* (Lopes et al., 2005; Borges et al., 2008); small *Cyclotella* spp. (Salmaso, 2002).

Typical misplacements: some authors included in this group some centric diatoms typical for other coda like *Cyclotella meneghiniana* which is typical for codon **C** or *Aulacoseira granulata*, typical of the **P** codon. Taxonomical resolution was low in some cases (e.g. *Aulacoseira* sp.; *Cyclotella* sp.; Centrales spp.) and would not allow attributing these organisms to this codon unless the given aquatic habitat clearly fits the environmental features of the codon. In one case, all the species (*Fragilaria crotonensis*, dinoflagellates, *Ceratium hirundinella*, *Peridinium willei*, *Cryptomonas* sp. *Rhodomonas minuta*) co-occurring with the dominant **B**-species were considered to belong to codon **B** instead of placing them into their own coda. For unknown reasons, in some cases, genus like *Synedra* and *Erkenia* were attributed to the **B** codon.

Note: Inclusion of *Aulacoseira baicalensis* in codon **B** (Fietz et al., 2005) represents two main problems. One is that Lake Baikal does not fit the features of the B-habitat; the second is that this species is growing under fairly unusual environmental conditions: it is kept in suspension by convectional currents under thick ice cover (Kozhov, 1963). Such species (including *Stephanocostis chantaicus*, Scheffler & Padisák, 2000) would deserve to raise a separate codon, however, our present knowledge on their autoecology is too limited.

Modification to the habitat description: experience shows that species representing this codon also occur in large shallow lakes, therefore the suggested habitat description is mesotrophic, small- and medium-sized lakes to large shallow lakes with species sensitive to the onset of stratification.

Codon **C** (Reynolds et al., 2002)

Habitat template: eutrophic small- and medium-sized lakes with species sensitive to the onset of stratification.

Described representatives: *Aulacoseira ambigua* (Huszar et al., 2003; Morabito et al., 2003; Babanazarova & Lyashenko, 2007; Bovo-Scomparin & Train, 2008); *A. ambigua* var. *ambigua* f. *spiralis* (Borges et al., 2008); *A. distans* (Huszar et al., 2000; Marinho & Huszar, 2002; Devercelli, 2006; Bovo-Scomparin & Train, 2008); *Stephanodiscus* (Salmaso, 2002; Anneville et al., 2005; Sarmento et al., 2006; Wilhelm & Adrian, 2008); *S. rotula* (Morabito et al., 2003); *Cyclotella meneghiniana* (Kruk et al., 2002; Devercelli, 2006; Moura et al., 2007; Borics et al., 2007; Crossetti & Bicudo, 2008b); *C. ocellata* (Borics et al., 2007); *Asterionella formosa* (Salmaso, 2002; Albay & Akçaalan, 2003; Gurbuz et al., 2003; Morabito et al., 2003); *Asterionella* sp. (Huszar et al., 2003; Anneville et al., 2005; Sthapit et al., 2008).

Typical misplacements: *Cyclostephanos* sp., member of codon **A**; members of codon **B** as *Cyclotella stelligera*, *Stephanodiscus minutulus*, *Cyclotella wuethrichiana*, *Aulacoseira islandica*; *Nitzschia acicularis*, *Nitzschia* sp. member of codon **D**; *Fragilaria crotonensis* and *Aulacoseira granulata* from codon **P**.

Codon **D** (Reynolds et al., 2002)

Habitat template: shallow turbid waters including rivers.

Described representatives: *Synedra/Ulnaria acus* (Kruk et al., 2002; Fietz et al. 2005; Fonseca & Bicudo, 2008; Hajnal & Padisák, 2008; Crossetti & Bicudo, 2008b); *Synedra ulna* (Townsend, 2006; Soares et al. 2007); *S. delicatissima* (Gurbuz et al., 2003); *S. nana* (Alves-de-Souza et al., 2006); *Synedra* sp. (Anneville et al., 2005; Antenucci et al., 2005; Moustaka-Gouni et al., 2007; Acuña et al., 2008); *Nitzschia acicularis* (Huszar et al., 2003; Fietz et al., 2005; Devercelli, 2006; Moustaka-Gouni et al., 2007); *N. agnita* (Townsend, 2006); *Nitzschia* spp. (Padisák et al., 2003a; Albay & Akçaalan, 2003; Anneville et al., 2005; Moura et al., 2007; Sthapit et al., 2008); *Fragilaria/Synedra rumpens* (Moura et al. 2007; Fonseca & Bicudo, 2008); *Encyonema silesiacum* (Soares et al., 2007). Probably, the above listed species belonging to the genera *Synedra* and *Nitzschia* are not the only members of the group but also several other small- or medium-sized planktonic species of these genera have to be listed in the codon **D**. Centric diatoms belonging to this group are *Stephanodiscus hantzschii* (Padisák et al., 2003a; Moustaka-Gouni et al., 2007); *Skeletonema potamos*, *S. subsalsum* (Devercelli, 2006); *Actinocyclus normannii* (Devercelli, 2006).

Typical misplacements: several *Cyclotella* species, which have to be listed in other coda; *Aulacoseira distans*, which belongs to codon **C** and *A. granulata* from codon **P**; various benthic or periphytic diatom taxa from codon **MP**.

Modification to the species sensitivities: according to the original description, members of this codon are sensitive to nutrient depletion. However, species like *Synedra* spp. with very low phosphorus half saturation constant belong to this group (Tilman, 1982). Thus, we suggest handling the nutrient depletion sensitivity with care.

Codon **N** (Reynolds et al., 2002)

Habitat template: continuous or semi-continuous mixed layer of 2–3 m in thickness. This association can be represented in shallow lakes where the mean depth is of this order or greater, as well as in the epilimnia of stratified lakes when the mixing criterion is satisfied.

Described representatives: *Cosmarium* spp., *Staurodesmus* spp., *Xanthidium* spp., (Kruk et al., 2002; Anneville et al., 2005; Antenucci et al., 2005; Soares et al., 2007; Sarmento & Descy, 2008); *Pleurotaenium* spp. (Reynolds et al., 2002). Probably, planktonic *Staurastrum* species (e.g. *S. leptocladum*) as well as *Teilingia* spp. and *Spondylosium* spp. also belong to this group, even though some hard-water species (*S. pingue*; *S. chaetoceras*; *S. planctonicum*) might belong to codon **P**. The other prominent representatives of this group are *Tabellaria* taxa (Huszar et al., 2003; Dokulil & Teubner, 2003; Anneville et al., 2005; Devercelli, 2006; Nabout et al., 2006; Sarmento & Descy, 2008).

With regard to this codon, misplacements are very rare.

Modification to the habitat description: originally, Reynolds et al. (2002) set this codon for environments located at lower latitudes or in the summer period in temperate lakes. We suggest restricting the distribution of codon **N** to the temperate environment because for the species at lower latitude a separate codon (**N**$_{\mathbf{A}}$) was described by Souza et al. (2008).

Codon **N**$_{\mathbf{A}}$ (Souza et al., 2008)

Habitat template: oligo-mesotrophic, atelomictic environments at lower latitudes with species sensitive to destratification.

Described representatives: small, isodiametric desmids as *Cosmarium*, *Staurodesmus*, *Staurastrum*, and unicells of filamentous desmids (Souza et al., 2008).

Codon **P** (Reynolds et al., 2002)

Habitat template: similar to that of codon **N** but at higher trophic states.

Described representatives: *Fragilaria crotonensis* (Salmaso, 2002; Dokulil & Teubner, 2003; Albay & Akçaalan, 2003; Gurbuz et al., 2003; Huszar et al., 2003; Leitão et al., 2003; Morabito et al., 2003; Naselli-Flores & Barone, 2005; Zhang et al., 2007; Sarmento & Descy, 2008); *Fragilaria* spp. (Leitão et al., 2003; Dokulil & Teubner, 2003; Anneville et al., 2005; Wilhelm & Adrian; 2008); *Aulacoseira granulata* (Huszar et al., 2000; Kruk et al., 2002; Salmaso, 2002; Morabito et al., 2003; Albay & Akçaalan, 2003; Naselli-Flores & Barone, 2003, 2005; Silva et al. 2005; Devercelli, 2006; Nabout et al., 2006; Moura et al., 2007; Zhang et al., 2007; Borics et al., 2007; Moustaka-Gouni et al., 2007; Becker et al., 2008; Sarmento & Descy, 2008; Bovo-Scomparin & Train, 2008; Borges et al., 2008; Hajnal & Padisák, 2008); *A. granulata* f. *curvata* (Devercelli, 2006); *A. granulata* var. *angustissima* (Devercelli, 2006; Moura et al., 2007; Borges et al., 2008); *Melosira lineata* (Devercelli, 2006); *Melosira* sp. (Moura et al., 2007); *Staurastrum chaetoceras* (Borics et al., 2007; Moustaka-Gouni et al., 2007), *S. pingue* (Sarmento & Descy, 2008); *S. planctonicum*, *S. gracile* (Albay & Akçaalan, 2003); *Staurastrum* sp. (Anneville et al., 2005; Antenucci et al., 2005; Moustaka-Gouni et al., 2007); *Closterium aciculare* (Salmaso, 2002; Morabito et al., 2003; Naselli-Flores & Barone, 2005; Sarmento & Descy, 2008); *C. acutum* (Moustaka-Gouni et al., 2007); *C. acutum* var. *variabile* (Devercelli, 2006); *C. gracile* (Kruk et al., 2002; Fonseca & Bicudo, 2008);

C. parvulum (Moura et al., 2007); *C. pronum* (Salmaso, 2002); *C. navicula* (Soares et al., 2007); *Closterium* sp. (Soares et al., 2007); *Closteriopsis acicularis* (Fonseca & Bicudo, 2008); *Spirotaenia condensata* (Soares et al., 2007).

Typical misplacements: *Pediastrum* spp. and *Coelastrum* spp. from codon **J**; *Aulacoseira italica* and *A. herzogii* from codon **B**; non-planktonic species like *Ulothrix* and *Navicula* spp., which belong to codon **MP**.

Codon **MP** (Padisák et al., 2006)

Habitat template: frequently stirred up, inorganically turbid shallow lakes.

Described representatives: *Surirella* spp., *Campylodiscus* spp., *Fragilaria construens* (Padisák et al., 2006); *Ulnaria ulna* (Bovo-Scomparin & Train, 2008); *Cocconeis* sp., *Gomphonema angustatum*, *Navicula cuspidata*, *Pleusosigma* sp. (Moura et al., 2007); *Nitzschia sigmoidea* (Hajnal & Padisák, 2008); *Navicula* spp. (Padisák et al., 2003a; Hajnal & Padisák, 2008); *Eunotia incisa* (Alves-de-Souza et al., 2006); *Ulothrix* (Salmaso, 2002; Anneville et al., 2005); Ulothrichales (Salmaso, 2002); *Lyngbya* sp. (Vardaka et al., 2005); *Oscillatoria sancta* (O'Farrel et al., 2003); *Oscillatoria* spp. (Kruk et al., 2002; Huszar et al., 2003; Anneville et al., 2005; Vardaka et al., 2005; Fazio & O'Farrell, 2005; Zhang et al., 2007); *Pseudanabaena galeata* (Kruk et al., 2002; Romo & Villena, 2005; Crossetti & Bicudo, 2008a); *P. catenata* (Allende & Izaguirre, 2003; Moura et al., 2007); *Cylindrospermum* cf. *muscicola* (Romo & Villena, 2005); *Chlorococcum infusorium* (Fonseca & Bicudo, 2008); *Achnanthes microcephala* (Çelik & Ongun, 2008); *Achnanthes* sp. (Anneville et al., 2005); *Desmidium laticeps* var. *quadrangulare* (Crossetti & Bicudo, 2008b). Moreover, this codon collects all the meroplanktonic (mostly diatoms) autotrophic organisms that can be accidentally found in phytoplankton samples. It includes metaphytic, periphytic and epilithic specimens drifted in the plankton.

Typical misplacements: *Aulacoseira granulata*, *A. ambigua* which respectively belong to coda **P** and **C**; *Urosolenia eriensis*, which is typical of codon **A**.

Modification to habitat description: in all types of lakes, littoral diatoms are drifted to the plankton. We suggest including these sporadic occurrences (*Navicula* spp., *Gomphonema* spp., *Epithemia* spp., *Cymbella* spp.) to codon **MP** independently of lake type.

Codon **T** (Reynolds et al., 2002)

Habitat template: persistently mixed layers, in which light is increasingly the limiting constraint and thus optically deep, mixed environments including clear epilimnia of deep lakes in summer.

Described representatives: *Geminella* spp. (Morabito et al., 2003; Borics et al., 2007); planktonic *Mougeotia* spp. (Huszar & Reynolds, 1997; Melo & Huszar, 2000; Salmaso, 2002; Morabito et al., 2003; Anneville et al., 2005; Romo & Villena, 2005; Sarmento et al., 2006; McIntire et al., 2007; Zhang et al., 2007); *Tribonema* spp. (Morabito et al., 2003; Anneville et al., 2005; Borics et al., 2007; McIntire et al., 2007); *Planctonema lauterbornii* (Leitão et al., 2003; Devercelli, 2006); *Mesotaenium chlamydosporum*, *Mesotaenium* sp. (Huszar & Reynolds, 1997; Melo & Huszar, 2000).

Typical misplacements: needle-shaped planktonic *Closterium* spp. belonging to codon **P** and occasionally *Tabellaria* spp. from group **N**.

Codon $\mathbf{T_C}$ (Borics et al., 2007)

Habitat template: eutrophic standing waters, or slow-flowing rivers with emergent macrophytes.

Described representatives: epiphytic cyanobacteria as *Oscillatoria* spp. (Borics et al., 2007; Soares et al., 2007); *Phormidium* spp., *Lyngbya* spp., *Rivularia* spp. (Borics et al., 2007); *Leptolyngbya* cf. *notata* (Soares et al., 2007); *Gloeocapsa punctata* (Soares et al., 2007).

Codon $\mathbf{T_D}$ (Borics et al., 2007)

Habitat template: mesotrophic standing waters, or slow-flowing rivers with emergent macrophytes.

Described representatives: epiphytic and metaphytic desmids, filamentous green algae and sediment dwelling diatoms (Borics et al., 2007).

Modification to habitat description: we suggest including habitats with submerged macrophytes in this codon.

Codon $\mathbf{T_B}$ (Borics et al., 2007)

Habitat template: highly lotic environments (streams and rivulets).

Described representatives: epilithic diatoms like *Didymosphaenia geminata*, *Gomphonema* spp., *Fragilaria* spp., *Achnanthes* spp., *Surirella* spp. and also several species belonging to the genera *Nitzschia* and *Navicula* (Borics et al., 2007); Pennales, *Gomphonema parvulum*, *Melosira varians* (Soares et al., 2007).

Codon **S1** (Reynolds et al., 2002)

Habitat template: turbid mixed environments. This codon includes only shade-adapted cyanoprokaryotes.

Described representatives: *Planktothrix agardhii* (Padisák & Reynolds, 1998; Kruk et al., 2002; Salmaso, 2002; Mischke & Nixdorf, 2003; Morabito et al., 2003; Naselli Flores & Barone, 2003; Nixdorf et al., 2003; Crossetti & Bicudo, 2005; Padisák et al., 2006; Babanazarova & Lyashenko, 2007; Pinto et al., 2007; Yéprémian et al., 2007; Fonseca & Bicudo, 2008; Crossetti & Bicudo, 2008a, 2008b; Hajnal & Padisák, 2008); *Planktothrix* sp. (Silva et al., 2005; Wilhelm & Adrian, 2008; *Geitlerinema unigranulatum* (Fonseca & Bicudo, 2008; Crossetti & Bicudo, 2008a, 2008b); *G. amphibium* (Moura et al., 2007); *Geitlerinema* sp. (Huszar et al., 2000; Romo & Villena, 2005); *Limnothrix redekeii* (Mischke & Nixdorf, 2003; Morabito et al., 2003; Nixdorf et al., 2003; Vardaka et al., 2005; Babanazarova & Lyashenko, 2007; Borics et al., 2007; Moustaka-Gouni et al., 2007); *L. planctonica* (Kruk et al., 2002; Devercelli, 2006; *L. amphigranulata* (Mischke & Nixdorf, 2003; Nixdorf et al., 2003); *Pseudanabaena limnetica* (Huszar & Reynolds,1997; Melo & Huszar, 2000; Salmaso, 2002; Mischke & Nixdorf, 2003; Nixdorf et al., 2003; Padisák et al., 2003a, b; Babanazarova & Lyashenko, 2007); *Pseudanabaena* sp. (Vardaka et al., 2005); *Planktolyngbya limnetica* (Padisák et al., 2003a; Romo & Villena, 2005; Vardaka et al., 2005; Pinto et al., 2007; Babanazarova & Lyashenko, 2007; Alves de Souza et al., 2006; Hajnal & Padisák, 2008); *P. contorta* (Borics et al., 2007); *P. circumcreta* (Vardaka et al., 2005); *Planktolyngbya* spp. (O'Farrel et al., 2003; Antenucci et al., 2005; Burford & O'Donohue, 2006; Souza et al., 2008); *Lyngbya* sp. (Vardaka et al., 2005; Souza et al., 2008); *Jaaginema subtilissimum* (Huszar et al., 2000; Vardaka et al., 2005); *Jaaginema quadripunctulatum* (*Oscillatoria quadripunctulata*) (Huszar & Reynolds,1997; Melo & Huszar, 2000); Limnothrichoideae (Salmaso, 2002); *Phormidium* sp. (Huszar et al., 2000); *Isocystis pallida*, *Leptolyngbya tenue*, *L. antarctica* (Allende & Izaguirre, 2003); *L. fragilis* (O'Farrel et al., 2003).

Typical misplacements: rarely occur. Those that were found include non-planktonic Oscillatoriales (**MP**).

Note: **S1** species may occur in deep layer maxima of tropical lakes. If so, these species should be grouped in codon **R** as *Planktothrix rubescens*.

Codon **S2** (Reynolds et al., 2002)

Habitat template: warm, shallow and often highly alkaline waters.

Described representatives: *Spirulina* spp. (Fazio & O'Farrell, 2005; Moura et al., 2007; Souza et al., 2008); *Arthrospira platensis* (Vardaka et al., 2005).

Typical misplacements: in this codon are frequently included Oscillatoriales species from non-alkaline or deep waters.

Modification to representative species: originally *Raphidiopsis mediterranea* was included in this codon. However, it frequently occurs in not highly alkaline environments. Moreover, its taxonomy, and especially its relationship to *Cylindrospermopsis raciborskii* has not been clarified yet and the co-occurrence or subsequent occurrence of these two species is very frequent (e.g. Mohamed, 2006; Fonseca & Bicudo, 2008). Therefore, we suggest including *Raphidiopsis mediterranea* in codon $\mathbf{S_N}$.

Codon $\mathbf{S_N}$ (Reynolds et al., 2002)

Habitat template: warm mixed environments.

Described representatives: *Cylindrospermopsis raciborskii* (Padisák & Reynolds, 1998; Huszar et al., 2000; Marinho & Huszar, 2002; Nixdorf et al., 2003; Padisák et al., 2003a; Stoyneva, 2003; Silva et al., 2005; Vardaka et al., 2005; Crossetti & Bicudo, 2005, 2008a, b; Burford & O'Donohue, 2006; Padisák et al., 2006; Soares et al., 2007; Moura et al., 2007; Moustaka-Gouni et al., 2007; Pinto et al., 2007; Hajnal & Padisák, 2008); *C. catemaco* (Huszar et al., 2000; Komárková & Tavera, 2003); *C. philippinensis* (Huszar et al., 2000; Komárková & Tavera, 2003); *Cylindrospermopsis* sp. (Bouvy et al., 2003; Antenucci et al., 2005; Sarmento et al., 2006); *Anabaena minutissima* (Borics et al., 2007); *Raphidiopsis* *mediterranea* (Kruk et al., 2002; Moura et al., 2007); *Raphidiopsis/Cylindrospermopsis* (Fonseca & Bicudo, 2008); *Raphidiopsis* sp. (Bouvy et al., 2003; Sthapit et al., 2008).

Observed misplacements: *Aphanizomenon gracile* from codon **H1**; *Pseudanabaena limnetica* from codon **S1**; *Cylindrospermum muscicola* from codon **MP**.

Notes:

1. For *Cylindrospermopsis* spp. other than *C. raciborskii*, high level of shade tolerance has not been tested in laboratory experiments. Therefore, their inclusion in this codon has not been yet proved. In case they are less shade tolerant than *C. raciborskii*, they will have to be moved to group **H1**.
2. Exceptionally, *C. raciborskii* may occur in deep layer maxima of tropical lakes (Padisák et al., 2003b). If so, it should be grouped in codon **R** as *Planktothrix rubescens*.

Codon **Z** (Reynolds et al., 2002)

Habitat template: metalimnia or upper hypolimnia of oligotrophic lakes.

Described representatives: originally, this codon was set to allocate unicellular prokaryote picoplankton as *Synechococcus* spp., *Cyanobium* spp., etc., occurring in deep oligotrophic lakes. By examining the produced literature, the habitat features corresponded to this template in a very few cases only. More often, these supposed species are reported inhabiting oxbows, saline lakes, highly eutrophic, shallow lakes, humic environments, mesocosms with floating plants, wetlands and so on. Moreover, unicellular prokaryotic picoplankton cannot be identified at even generic level by the commonly applied microscopic methods (epifluorescence). Therefore, the only justifiable cases in literature are those discussed by Fietz et al. (2005) in Lake Baikal, Lopes et al. (2005) in a tropical oligotrophic reservoir, McIntire et al. (2007) in Crater Lake, Sarmento et al. (2006) in Lake Kivu and by Callieri et al. (2006) in Lake Maggiore.

Typical misplacements: as written above, picoplankton from environments, which do not fit the habitat template is very frequently placed in this codon, instead of **K** codon.

Codon $\mathbf{Z_{MX}}$ (Callieri et al., 2006)

Habitat template: deep, subalpine oligotrophic lakes.

This codon includes *Synechococcus* spp. and *Ceratium hirundinella* and is based on a hypothetised predator–prey interaction between these two taxa coming from inverse linear relationships between them. However, this hypothesis would require the absence of spatial segregation of the populations. In fact, *Synechococcus* is often observed in deep chlorophyll maxima in oligotrophic lakes, whereas *C. hirundinella* exhibits a very characteristic diurnal migration pattern within the epilimnion. This situation largely excludes the predator–prey relationships. A second reason for proposing this codon was the supposed low-light preferences of the above mentioned species. Nevertheless, it is widely recognised that *Synechococcus* is a shade adapted species and *C. hirundinella* requires substantially more light (Padisák et al., 2003b). This, in our opinion, provides a second reason for not to accept the codon $\mathbf{Z_{MX}}$ and to place *Synechococcus* in codon **Z** and *C. hirundinella* in the appropriate subgroup of codon **L**.

Codon **X3** (Reynolds et al., 2002)

Habitat template: shallow, well mixed oligotrophic environments.

Described representatives: *Koliella* spp. (Padisák et al., 2006; Fietz et al., 2005); *Chrysococcus* spp. (Fietz et al., 2005; Hajnal & Padisák, 2008); *Chlorella* spp. from oligotrophic environments (Souza et al., 2008); eukaryotic picoplankton (Fietz et al., 2005; Pinto et al., 2007; Hajnal & Padisák, 2008; Sarmento & Descy, 2008); *Chromulina* spp., *Ochromonas* spp. (Salmaso, 2002; Allende & Izaguirre, 2003); *Chrysidalis* sp. (Allende & Izaguirre, 2003); *Schroederia antillarum*, *S. setigera* (Devercelli, 2006).

Typical misplacements are very rare: in one case, colonial cyanobacteria with picoalgal cell size were placed in this group instead of in the codon **K**, and in another case, the small green algae *Chlorella minutissima* and *Chrocystis minor* were placed in this group instead **X1**.

Codon **X2** (Reynolds et al., 2002)

Habitat template: shallow, meso-eutrophic environments.

Described representatives: *Plagioselmis*/*Rhodomonas* (Dokulil & Teubner, 2003; Barone & Naselli-Flores, 2003; Leitão et al., 2003; Padisák et al., 2003a; Fietz et al., 2005; Romo & Villena, 2005; Devercelli, 2006; Moustaka-Gouni et al., 2007; Hajnal & Padisák, 2008; Sarmento & Descy, 2008); *Chrysocromulina* sp. (Anneville et al., 2005; Padisák et al., 2003a; Moustaka-Gouni et al., 2007; Sarmento & Descy, 2008; Wilhelm & Adrian, 2008); *Carteria complanata* (Devercelli, 2006); *Chlamydomonas depressa*; *C. microsphera*; *C. passiva*; *C.* cf. *muriella* (Devercelli, 2006); *C. planctogloea*; *C. sordida* (Lopes et al., 2005); *Chlamydomonas* spp. from meso-eutrophic environments (Kruk et al., 2002; Allende & Izaguirre, 2003; Leitão et al., 2003; Lopes et al., 2005; Devercelli, 2006; Pinto et al., 2007; Soares et al., 2007); *Pedimonas* sp., *Pteromonas variabilis*; *Pyramimonas tetrarhynchus*, *Spermatozoopsis exultans* (Devercelli, 2006); *Monas* (Anneville et al., 2005); *Spermatozoopsis* sp. (Borics et al., 2007); *Scourfeldia cordiformis* (Alves-de-Souza et al., 2006); *Katablepharis*, *Kephyrion; Pseudopedinella, Chrysolykos* (Anneville et al., 2005); *Coccomonas* sp. (Lopes et al., 2005; Devercelli, 2006); *Ochromonas* sp. (Allende & Izaguirre, 2003, 2005); *Chroomonas* sp. (Kruk et al., 2002; Burford & O'Donohue, 2006); *Cryptomonas pyrenoidifera* (Huszar & Reynolds, 1997; Melo & Huszar, 2000; Soares et al., 2007); *Cryptomonas brasiliensis* (Devercelli, 2006; Alves-de-Souza, 2006; Soares et al., 2007).

Typical misplacements are frequent and include silica scaled flagellates from codon **E**.

Note: Positioning of *Chlamydomonas* spp. depends on species and habitat template. Some species are better allocated in **X3**, or even in **G**.

Codon **X1** (Reynolds et al., 2002)

Habitat template: shallow, eu-hypertrophic environments.

Described representatives: *Monoraphidium contortum* (Mazzeo et al., 2003; O'Farrell et al., 2003; Romo & Villena, 2005; Devercelli, 2006; Moura et al., 2007; Fonseca & Bicudo, 2008); *M. convolutum* (Devercelli, 2006); *M. griffithii* (Devercelli, 2006; Moura et al., 2007; Moustaka-Gouni et al., 2007); *M. minutum* (O'Farrell et al., 2003; Romo & Villena, 2005; Devercelli, 2006); *M. circinale* (O'Farrell et al., 2003; Moura et al., 2007; Pinto et al., 2007); *M. pseudomirabile* (Fietz et al., 2005); *M. dybowskii*, *M. pseudobraunii*, *M. tortile* (Lopes et al., 2005); *M. arcuatum* (Lopes et al., 2005; Moura et al., 2007; Moustaka-Gouni et al., 2007); *M. pusillum* (Moura et al., 2007); *M.* cf. *nanum* (Moustaka-Gouni et al., 2007); *Monoraphidium* spp. (Kruk et al., 2002; Antenucci et al., 2005; Pinto et al., 2007; Burford & O'Donohue, 2006; Padisák et al., 2006); *Ankyra* spp. (Salmaso, 2002; Leitão et al., 2003); *Chlorolobium* sp. (Devercelli, 2006); *Didymocystis bicellularis* (O'Farrell et al., 2003); *Ankistrodesmus* spp. (Huszar & Reynolds, 1997; Melo & Huszar, 2000; Antenucci et al., 2005; Burford & O'Donohue, 2006; Moura et al., 2007; Fonseca & Bicudo, 2008; Hajnal & Padisák, 2008); *Chlorella vulgaris* (Huszar et al., 2000; Kruk et al., 2002; Moura et al., 2007; Fonseca & Bicudo, 2008); *Chlorella homosphaera* (Huszar & Reynolds, 1997; Melo & Huszar, 2000) *Chlorella* spp. (Devercelli, 2006; Pinto et al., 2007); *Pseudodidymocystis fina* (Fonseca & Bicudo, 2008); *Keryochlamys styriaca* (Romo & Villena, 2005); *Ochromonas* cf. *viridis* (Fazio & O'Farrell, 2005); *Choricystis minor* (Alves-de-Souza et al., 2006); *Chroricystis cylindraceae* (Huszar & Reynolds, 1997; Melo & Huszar, 2000); *Schroederia* sp. (Fazio & O'Farrell, 2005); *Schroedriella setigera* (Kruk et al., 2002).

Typical misplacements are very frequent: small green algae from oligotrophic environments belonging to codon **X3**, **F** codon species as *Micractinium* and *Oocystis*, **J** codon species as *Scenedesmus*, **P** codon species as *Closteriopsis acicularis*, species from codon **Lo** as *Synechocystis aquatilis*, *Cosmarium* from **N** codon and *Planktolyngbya* from **S1**. In addition, the inclusion in this codon of non-planktonic algae (**MP**) is frequent.

Note: in case of doubts, non-gelatinous (very thin mucilage coats), non-motile, roughly isodiametric chlorococcaleans, even those forming coenobia, are advised to be placed into codon **J**.

Codon $\mathbf{X_{Ph}}$ (this article)

Habitat template: small, even temporary, calcium rich, well illuminated, alkaline lakes.

Described representatives: *Phacotus lenticularis* (Padisák et al., 2003a; Borics et al., 2007; Hajnal & Padisák, 2008); *Phacotus sp.* (Anneville et al., 2005).

Notes:

1. Establishment of this codon is due to the very high calcium carbonate demand of this species to build up its lorica.
2. Originally described as $\mathbf{Y_{Ph}}$ (Padisák et al., 2003a). This codon is here renamed as $\mathbf{X_{Ph}}$, due to the small size of its only described representative.

Codon **E** (Reynolds et al., 2002)

Habitat template: usually small, shallow, base poor lakes or heterotrophic ponds.

Described representatives: *Dinobryon* spp. (Salmaso, 2002; Dokulil & Teubner, 2003; Huszar et al., 2003; Padisák et al., 2003a; Anneville et al., 2005; Fietz et al., 2005; Devercelli, 2006; Alves-de-Souza et al., 2006; McIntire et al., 2007; Zhang et al., 2007; Hajnal & Padisák, 2008). *Mallomonas* spp. (Mazzeo et al., 2003; Anneville et al., 2005; Antenucci et al., 2005; Lopes et al., 2005; Devercelli, 2006; Moustaka-Gouni et al., 2007); *Epipyxis* sp. (Devercelli, 2006); *Salpingoeca* sp. (Padisák et al., 2003a); *Erkenia* (Anneville et al., 2005); siliceous Chrysophyceae (Devercelli, 2006).

Typical misplacements: 'unidentified, small chrysophyceans' and *Ochromonas* are commonly placed into this codon instead of **X2**; *Synura* was moved to the newly established $\mathbf{W_S}$ codon.

Codon **Y** (Reynolds et al., 2002)

Habitat template: this codon, mostly including large cryptomonads but also small dinoflagellates, refers to a wide range of habitats, which reflect the ability of its representative species to live in almost all lentic ecosystems when grazing pressure is low.

Described representatives: *Cryptomonas* spp. (Huszar et al., 2000; Kruk et al., 2002; Marinho & Huszar, 2002; Albay & Akçaalan, 2003; Barone & Naselli-Flores, 2003; Huszar et al., 2003; Leitão et al., 2003; O'Farrel et al., 2003; Dokulil & Teubner, 2003; Padisák et al., 2003a; Anneville et al., 2005; Crossetti & Bicudo, 2005; Fazio & O'Farrell, 2005; Fietz et al., 2005; Romo & Villena, 2005; Silva et al., 2005; Alves-de-Souza et al., 2006; Devercelli, 2006; Nabout et al., 2006; Townsend, 2006; Moura et al., 2007; Moustaka-Gouni et al., 2007; Soares et al., 2007; Borges et al., 2008; Bovo-Scomparin & Train, 2008; Crossetti & Bicudo, 2008a, 2008b; Fonseca & Bicudo, 2008; Hajnal & Padisák, 2008; Sarmento & Descy, 2008; Wilhelm & Adrian, 2008); *Glenodinium* spp. (Dokulil & Teubner, 2003; Fietz et al., 2005; Anneville et al., 2005); small *Gymnodinium* spp. (Kruk et al., 2002; Padisák et al., 2003a; Anneville et al., 2005; Moura et al., 20057; Fonseca & Bicudo, 2008; Souza et al., 2008; Hajnal & Padisák, 2008; Sarmento & Descy, 2008; Crossetti & Bicudo, 2008b); *Teleaulax* sp. (Alves-de-Souza et al., 2006); *Komma caudata* (Marinho & Huszar 2002).

Misplacements are rare and include *Rhodomonas*/*Plagioselmis* and small *Cryptomonas* from codon **X2**; some authors, generically referring to cryptophytes, assign the entire phylum to codon **Y**. Moreover, quite often *Gymnodinium* spp. are sorted into coda $\mathbf{L_O}$ or $\mathbf{L_M}$.

Codon $\mathbf{Y_{Ph}}$ (Padisák et al., 2003a) → Codon $\mathbf{X_{Ph}}$

Codon **F** (Reynolds et al., 2002)

Habitat template: clear, deeply mixed meso-eutrophic lakes.

Described representatives: *Botryococcus braunii* (Huszar et al., 2003; Naselli-Flores & Barone, 2003; O'Farrell et al., 2003; Moustaka-Gouni et al., 2007; Fonseca & Bicudo, 2008; Hajnal & Padisák, 2008; Souza et al., 2008); *B. terribilis* (Kruk et al., 2002; Naselli-Flores & Barone, 2003); *B. neglectus* (Kruk et al., 2002); *B. protuberans* (Moura et al., 2007); *Botryococcus* (Antenucci et al., 2005); *Oocystis lacustris* (Kruk et al., 2002; Albay & Akçaalan, 2003; Lopes et al., 2005; Moura et al., 2007; Stoyneva et al., 2007); *O. parva* (Mazzeo et al., 2003; Devercelli, 2006); *O. borgei* (Gurbuz et al., 2003; Huszar et al., 2003; Albay & Akçaalan, 2003); *O. marina* (Padisák et al., 2003a); *Oocystis* spp. (Huszar et al., 2000; Anneville et al., 2005; Antenucci et al., 2005; Devercelli, 2006; Padisák et al., 2006; Sarmento et al., 2006; Moustaka-Gouni et al., 2007); *Kirchneriella pseudoaperta*, *K. pinguis* (Lopes et al., 2005); *K. lunaris*, *K. obesa* (Moura et al., 2007); *Kirchneriella* sp. (Anneville et al., 2005); *Coenochlorys*/*Sphaerocystis* spp. (Kruk et al., 2002; Leitão et al., 2003; Anneville et al., 2005; Antenucci et al., 2005; Devercelli, 2006; Padisák et al., 2006; Stoyneva et al., 2007); *Pseudospaherocystis lacustris* (Naselli-Flores & Barone, 2003); *Lobocystis planctonica* (Padisák et al., 2003°, 2006; Stoyneva et al., 2007); *Lobocystis* sp. (Sarmento et al., 2006); *Dictyosphaerium* spp. (Anneville et al., 2005; Antenucci et al., 2005; Devercelli, 2006; Sarmento et al., 2006; Moura et al., 2007); *Eutetramorus* spp. (Kruk et al., 2002; Huszar et al., 2003; Devercelli, 2006; Becker et al., 2008); *Nephroclamys* spp. (Devercelli, 2006); *Nephrocytium* sp. (Becker et al., 2008); *Willea wilhelmii* (Huszar et al., 2003); *Elakatothrix* spp. (Antenucci et al., 2005; Fietz et al., 2005; Lopes et al., 2005); *Eremosphaera tanganykae* (Stoyneva et al., 2007); *Planktosphaeria gelatinosa* (Kruk et al., 2002; Padisák et al., 2006); *Micractinium pusillum* (Devercelli, 2006; Moura et al., 2007; Fonseca & Bicudo, 2008); *Treubaria triappendiculata* (Kruk et al., 2002; Padisák et al., 2003a); *Fusola viridis, Coenococcus* (Devercelli, 2006); *Strombidium* sp. (Sarmento et al., 2006); *Dimorphococcus* spp. (Borics et al., 2007).

Typical misplacements: erratic inclusions of small flagellates belonging to different coda or of colonial chlorophytes belonging to codon **J** were found.

Note: in several papers just the genus *Oocystis*, *Elakatothrix* or *Kirchneriella* are mentioned without reference to the species. These placements can be correct, but only if the given taxon forms coenobia.

Codon **G** (Reynolds et al., 2002)

Habitat template: nutrient-rich conditions in stagnating water columns; small eutrophic lakes and very stable phases in larger river-fed basins and storage reservoirs.

Described representatives: *Volvox* spp. (Borics et al., 2007), *Eudorina* spp. (Anneville et al., 2005; Borics et al., 2007); *Pandorina* spp. (Huszar et al., 2003; Padisák et al., 2003a; Anneville et al., 2005; Fazio & O'Farrell, 2005; Borics et al., 2007); *Carteria* sp. (Anneville et al., 2005).

Only one misplacement was detected: *Tetraedron* sp. from codon **J**.

Codon **J** (Reynolds et al., 2002)

Habitat template: shallow, mixed, highly enriched systems (including many low-gradient rivers).

Described representatives: *Pediastrum* spp. (Kruk et al., 2002; Albay & Akçaalan, 2003; Anneville et al., 2005; Naselli-Flores & Barone, 2005; Borics et al., 2007; Moura et al., 2007; Moustaka-Gouni et al., 2007; Çelik & Ongun; 2008; Sarmento & Descy, 2008); *Coelastrum* spp. (Kruk et al., 2002; Salmaso, 2002; Albay & Akçaalan, 2003; Padisák et al., 2003a; Naselli-Flores & Barone, 2005; Devercelli, 2006; Moura et al., 2007; Borics et al., 2007; Moustaka-Gouni et al., 2007; Zhang et al., 2007; Becker et al., 2008; Hajnal & Padisák, 2008; Sarmento & Descy, 2008); *Scenedesmus* spp. (Kruk et al., 2002; Albay & Akçaalan, 2003; Padisák et al., 2003a; Antenucci et al., 2005; Crossetti & Bicudo, 2005; Romo & Villena, 2005; Devercelli, 2006; Nabout et al., 2006; Babanazarova & Lyashenko, 2007; Moura et al., 2007; Moustaka-Gouni et al., 2007; Soares et al., 2007; Fonseca & Bicudo, 2008; Sarmento & Descy, 2008;); *Golenkinia* spp. (Borics et al., 2007; Moura et al., 2007); *Actinastrum* spp. (Devercelli, 2006; Moura et al., 2007; *Goniochlorys mutica* (Padisák et al., 2003a); *Crucigenia* spp. (O'Farrell et al., 2003; Padisák et al., 2003a; Lopes et al., 2005; Devercelli, 2006; Moura et al., 2007; Fonseca & Bicudo, 2008); *Tetraedron* spp. (Anneville et al., 2005; Antenucci et al., 2005; Padisák et al., 2003a; Lopes et al., 2005; Moura et al., 2007; Zhang et al., 2007); *Tetrastrum* spp. (Padisák et al., 2003a; Nabout et al., 2006; Borics et al., 2007; Moura et al., 2007).

Typical misplacements: species of the genera *Micractinium*, *Treubaria*, *Lobocystis*, *Oocystis*, *Dictyosphaerium*, *Ankistrodesmus*, all belonging to codon **F**, are frequently listed in this codon. Moreover, some authors include in this codon items like 'coccal green algae', 'colonial green algae' or 'chlorophytes': this kind of misplacement cannot be resolved.

Codon **K** (Reynolds et al., 2002)

Habitat template: shallow, nutrient-rich water columns.

Described representatives: this association mainly includes small-celled (often picoalgal cell size), colonial, non gas-vacuolated Cyanoprokaryota of the genera *Aphanocapsa*, *Aphanothece* and *Cyanodictyon* (Huszar & Reynolds, 1997; Melo & Huszar, 2000; Kruk et al., 2002; Salmaso, 2002; Allende & Izaguirre, 2003; Huszar et al., 2003; Leitão et al., 2003; O'Farrell et al., 2003; Padisák et al., 2003a; Anneville et al., 2005; Fazio & O'Farrell, 2005; Silva et al., 2005; Burford & O'Donohue, 2006; Devercelli, 2006; Padisák et al., 2006; Moustaka-Gouni et al., 2007; Soares et al., 2007; Crossetti & Bicudo, 2008a, 2008b; Fonseca & Bicudo, 2008; Sarmento & Descy, 2008); *Synechococcus nidulans* (O'Farrel et al., 2003; Alves-de-Souza et al., 2006); *Synechococcus elongatus*, *S. elegans* (Huszar & Reynolds, 1997; Melo & Huszar, 2000); *Synechococcus* sp. (Devercelli, 2006; Moustaka-Gouni et al., 2007); *Synechocystis* spp. (O'Farrel et al., 2003); picoacyanobacteria (O'Farrel et al., 2003; Pinto et al., 2007); picoplankton (Mazzeo et al., 2003; Devercelli, 2006); *Chlorella minutissima* (Huszar et al., 2000; Kruk et al., 2002; Alves-de-Souza et al., 2006).

Typical misplacements: these comprise the inclusion in this codon of colonial cyanoprokaryotes with somewhat bigger cell sizes (e.g. *Coelosphaerium, Chroococcus, Eucapsis*). Also non-planktonic species (*Gloeocapsa punctata*) sometimes appear listed in this codon instead of **MP**.

Note: *Aphanocapsa* and *Aphanothece* colonies are often found late summer in the epilimnion of oligotrophic, deep lakes. These occurrences would find a better location in one of the **L** codon subgroups.

Codon **H1** (Reynolds et al., 2002)

Habitat template: eutrophic, both stratified and shallow lakes with low nitrogen content.

Described representatives: *Anabaena affinis* (Vardaka et al., 2005); *A. circinalis* (Vardaka et al., 2005; Borges et al., 2008; Bovo-Scomparin & Train, 2008); *A. crassa* (Becker et al., 2008); *A. flos-aquae* (Huszar et al., 2003; Vardaka et al., 2005; Moustaka-Gouni et al., 2007); *A. planctonica* (Kruk et al., 2002; Bovo-Scomparin & Train, 2008; Crossetti & Bicudo, 2008a, b; Fonseca & Bicudo, 2008); *A. perturbata*, *A. schermetievi* (Vardaka et al., 2005); *A. solitaria* (Huszar et al., 2003; Vardaka et al., 2005); *A. sphaerica* (O'Farrell et al., 2003), *A. spiroides* (Huszar et al., 2000; Kruk et al., 2002; Marinho & Huszar, 2002; Huszar et al., 2003; Stoyneva, 2003; Vardaka et al., 2005; Çelik & Ongun, 2008); *A. viguieri* (Vardaka et al., 2005; Moustaka-Gouni et al., 2007); *Anabaena* spp. (Anneville et al., 2005, Antenucci et al., 2005; Silva et al., 2005; Vardaka et al., 2005; Padisák et al., 2006; Sarmento et al., 2006; Soares et al., 2007; Zhang et al., 2007; Sthapit et al., 2008); *Anabaenopsis arnoldii* (Padisák et al., 2003a; Stoyneva, 2003); *A. cunningtonii* (Vardaka et al., 2005); *A. elenkinii* (Huszar et al., 2000; Vardaka et al., 2005); *A. tanganykae* (Vardaka et al., 2005); *Anabaenopsis* sp. (Kruk et al., 2002); *Aulosira* sp. (Fietz et al., 2005); *Aphanizomenon flos-aquae* (Kruk et al., 2002; Stoyneva, 2003; Vardaka et al., 2005; Zhang et al., 2007; Hajnal & Padisák, 2008); *A. gracile* (Kruk et al., 2002; Huszar et al., 2003; Mazzeo et al., 2003; Mischke & Nixdorf, 2003; Nixdorf et al., 2003; Stoyneva, 2003; Babanazarova & Lyashenko, 2007; Moustaka-Gouni et al., 2007; Crossetti & Bicudo, 2008a); *A. klebahnii* (Hajnal & Padisák, 2008); *A. issatschenkoi* (Padisák et al., 2003a; Vardaka et al., 2005; Moustaka-Gouni et al., 2007); *A. ovalisporum* (Padisák et al., 2003a); *A. aphanizomenoides*/*Anabaena aphanizomenoides*) (Vardaka et al., 2005; Devercelli, 2006; Moustaka-Gouni et al., 2007); *Aphanizomenon* spp. (Padisák & Reynolds, 1998; Burford & O'Donohue, 2006; Padisák et al., 2006; Wilhelm & Adrian, 2008).

Misplacements did not occur in this codon except sporadic inclusion of *Anabaena lemmermannii* from **H2**.

Note: *Anabaena solitaria* was originally listed in codon **H2** by Reynolds et al. (2002).

Codon **H2** (Reynolds et al., 2002)

Habitat template: oligo-mesotrophic, deep, stratifying lakes or mesotrophic shallow lakes, with good light conditions.

Described representatives: *Anabaena lemmermannii* (Salmaso, 2002; Vardaka et al., 2005; Borics et al., 2007); *Gloeotrichia echinulata* (Babanazarova & Lyashenko, 2007; Borics et al., 2007).

Modifications to typical representatives: we preferred to move *Anabaena solitaria* to codon **H1** because of its frequent occurrence in eu-hypertrophic lakes during periods of nitrogen shortage.

Codon **U** (Reynolds et al., 2002)

Habitat template: stratifying oligotrophic and mesotrophic lakes, where nutrient resources are exhausted in the upper layers but still available in the darker deep ones. The essential adaptation under these conditions is the combination of motility with large size.

There is only one described representative in this codon: *Uroglena* spp. (Anneville et al., 2005;

Sarmento & Descy, 2008). As a consequence, misplacements are rare and include *Monas* from codon **X2**.

Codon $\mathbf{L_O}$ (Reynolds et al., 2002)

Habitat template: deep and shallow, oligo to eutrophic, medium to large lakes.

Described representatives: *Peridinium cinctum* (Gurbuz et al., 2003; Fonseca & Bicudo, 2008; Crossetti & Bicudo, 2008b); *P. gatunense* (Lopes et al., 2005); *P. incospicuum* (Townsend, 2006; Souza et al., 2008); *P. umbonatum* (Romo & Villena, 2005); *P. willei* (Dokulil & Teubner, 2003; Niesel et al., 2007; Fonseca & Bicudo, 2008; Crossetti & Bicudo, 2008b); *Peridinium volzii* (Huszar et al., 2003); *Peridinium* spp. (O'Farrell et al., 2003; Anneville et al., 2005; Antenucci et al., 2005; Crossetti & Bicudo, 2005; McIntire et al., 2007; Moustaka-Gouni et al., 2007; Crossetti & Bicudo, 2008a; Hajnal & Padisák, 2008); *Peridiniopsis durandi* (Leitão et al., 2003); *P. elpatiewskyi* (Moustaka-Gouni et al., 2007); *Gymnodinium uberrimum* (Niesel et al., 2007); *G. helveticum* (Dokulil & Teubner, 2003); *Ceratium hirundinella* (Padisák & Reynolds, 1998; Salmaso, 2002; Dokulil & Teubner, 2003; Huszar et al., 2003; Callieri et al., 2006; Padisák et al., 2006; Hajnal & Padisák, 2008); *Ceratium cornutum* (Dokulil & Teubner, 2003); *Merismopedia glauca* (Fonseca & Bicudo, 2008; Crossetti & Bicudo, 2008b); *M. minima* (Moura et al., 2007; Pinto et al., 2007); *M. punctata* (Kruk et al., 2002; Moura et al., 2007); *M. tenuissima* (Huszar & Reynolds, 1997; Melo & Huszar, 2000; Kruk et al., 2002; Romo & Villena, 2005; Devercelli, 2006; Pinto et al., 2007; Fonseca & Bicudo, 2008, Crossetti & Bicudo, 2008b); *Merismopedia* spp. (O'Farrell et al., 2003; Burford & O'Donohue, 2006; Borics et al., 2007; Crossetti & Bicudo, 2008a); *Snowella lacustris* (Padisák & Reynolds, 1998; Padisák et al., 2006; Moustaka-Gouni et al., 2007; Hajnal & Padisák, 2008); *Woronichinia elorantae* (O'Farrell et al., 2003); *W. naegeliana* (Moustaka-Gouni et al., 2007); *Synechocystis aquatilis* (Huszar et al., 2000; Soares et al., 2007); *Woronichinia* sp. (Huszar et al., 2003; Borics et al., 2007); *Chroococcus limneticus*, *C. turgidus* (Moura et al., 2007); *C. minutus* (Allende & Izaguirre, 2003; Moura et al., 2007); *Chroococcus minor* (Nabout et al., 2006; Huszar & Reynolds, 1997; Melo & Huszar, 2000); *Coelosphaerium kuetzingianum* (Romo & Villena); *Coelosphaerium evidenter-marginatum* (Crossetti & Bicudo, 2008b); *Coelosphaerium* sp. (Kruk et al., 2002); *Eucapsis minuta* (Allende & Izaguirre, 2003); *Gomphosphaeria lacustris* (Dokulil & Teubner, 2003); *Radiocystis fernandoi* (Bovo-Scomparin & Train, 2008).

Typical misplacements: small dinoflagellates as *Glenodinium* spp. and small *Gymnodinium* spp. are often placed in this codon instead of codon **Y**.

Modifications to the typical representatives: we suggest considering in this codon, along with the above listed cyanobacteria, thecate dinoflagellates and some large *Gymnodinium* spp. like *G. uberrimum* and *G. helveticum*. This way, *Ceratium* spp. can also be sorted in this codon when they do not co-occur with *Microcystis*.

Codon $\mathbf{L_M}$ (Reynolds et al., 2002)

Habitat template: eutrophic to hypertrophic, small- to medium-sized lakes.

Typical representatives: *Ceratium hirundinella* and/or *C. furcoides* co-occurring with *Microcystis* spp. (Kruk et al., 2002; Naselli-Flores & Barone, 2003, 2005; Padisák et al., 2003a; Moustaka-Gouni et al. 2007; Sarmento & Descy, 2008); *Peridinium* cf. *cinctum*, *Gomphosphaeria* sp., *Coelomoron tropicalis* co-occurring with *Ceratium* and *Microcystis* (Kruk et al., 2002).

Typical misplacements: these are frequent and mainly occurring when only *Ceratium* spp. (codon $\mathbf{L_O}$) or only *Microcystis* spp. (codon **M**) are present.

Note: co-occurrence of *Ceratium* spp. and *Microcystis* spp. is obligatory to recognize the association $\mathbf{L_M}$.

Codon **M** (Reynolds et al., 2002)

Habitat template: eutrophic to hypertrophic, small- to medium-sized water bodies.

Typical representatives: all the *Microcystis* species (Huszar et al., 2000; Kruk et al., 2002; Marinho & Huszar, 2002; Dokulil & Teubner, 2003; Albay & Akçaalan, 2003; Mazzeo et al., 2003; Naselli-Flores & Barone, 2003, 2005; Vardaka et al., 2005; Padisák et al., 2003a; Stoyneva, 2003; Anneville et al., 2005; Antenucci et al., 2005; Crossetti & Bicudo, 2005, 2008a, b; Burford & O'Donohue, 2006; Devercelli, 2006; Sarmento et al., 2006; Babanazarova & Lyashenko, 2007; Moura et al., 2007; Moustaka-Gouni et al., 2007; Zhang et al., 2007; Borges et al., 2008; Çelik & Ongun, 2008; Fonseca & Bicudo, 2008; Hajnal & Padisák, 2008); *Sphaerocavum brasiliense* (Crossetti & Bicudo, 2008a, b; Fonseca & Bicudo, 2008).

Typical misplacements include chroococcaleans from $\mathbf{L_O}$ (*Radiocystis* spp.).

Codon **R** (Reynolds et al., 2002)

Habitat template: under stratification, in the metalimnion or upper hypolimnion of deep oligo-mesotrophic lakes.

Typical representatives: *Planktothrix rubescens* (Salmaso, 2002; Dokulil & Teubner, 2003; Morabito et al., 2003; Anneville et al., 2005); *P. mougeotii* (Morabito et al., 2003).

Typical misplacements: other Oscillatoriales (e.g. *Planktolyngbya limnetica*, *Isocystis pallida*, *Leptolyngbya tenue*, *L. antarctica*), which occur in the lake but not in deep layer maxima are often referred to this codon instead of **S1**, and the non-planktonic *Pseudanabaena catenata* of codon **MP**. Misunderstanding of the habitat template resulted in non understandable inclusions of a heterogeneous bunch of genera (e.g. *Chrysochromulina*, *Chrysolykos*, *Gymnodinium*, *Achnanthes*, *Tabellaria*, *Ceratium*, *Peridinium*, *Fragilaria*).

Note: apart from the typical representatives, any filamentous cyanoprokaryotic species can be included in this codon, if they occur in a deep layer maximum.

Codon **V** (Reynolds et al., 2002)

Habitat template: pronounced gradients in the redox potential that allow species of the purple and green sulphur bacteria to be the key autotrophs. Typically, in metalimnia of eutrophic stratified lakes or in monimolimnia of meromictic lakes.

Typical representatives: *Chromatium*, *Chlorolobium* (Reynolds et al., 2002)

Note: this association is never mentioned in the reviewed literature.

Codon **W1** (Reynolds et al., 2002)

Habitat template: ponds, even temporary, rich in organic matter from husbandry or sewages.

Typical representatives: Euglenoids (*Euglena* spp., *Phacus* spp., *Lepocinclis* spp.) except bottom-dwelling species (Kruk et al., 2002; O'Farrell et al., 2003; Padisák et al., 2003a; Devercelli, 2006; Nabout et al., 2006; Townsend, 2006; Moura et al., 2007; Moustaka-Gouni et al., 2007; Çelik & Ongun, 2008; Fonseca & Bicudo, 2008; Hajnal & Padisák, 2008). *Gonium* spp. (O'Farrell et al., 2003; Sarmento & Descy, 2008). *Vacuolaria tropicalis* (Crossetti & Bicudo, 2008b).

Typical misplacements: *Pandorina* spp. from time to time appears in this codon instead of codon **G**. Furthermore, *Strombomonas* and *Peridinium* were also listed in this codon instead of **W2** and $\mathbf{L_O}$, respectively.

Modification to typical representatives: we suggest removing *Synura* spp. as originally described typical species by Reynolds et al. (2002), because *Synura* occurs in organically rich sites, but this organic richness is largely caused by humic materials. For these species, a new codon $\mathbf{W_S}$ was established by Padisák et al. (2003a, b).

Codon **W2** (Reynolds et al., 2002)

Habitat template: meso-eutrophic ponds, even temporary, shallow lakes.

Typical representatives: bottom dwelling Euglenoids as *Trachelomonas* spp. (Padisák et al., 2003a; Antenucci et al., 2005; Crossetti & Bicudo, 2005, 2008a, 2008b;Townsend, 2006; Moura et al., 2007; Moustaka-Gouni et al., 2007; Soares et al., 2007; Becker et al., 2008; Fonseca & Bicudo, 2008) and *Strombomonas* spp. (Huszar et al., 2003).

No misplacements were observed in the reviewed literature.

Codon $\mathbf{W_S}$ (Padisák et al., 2003a)

Habitat template: ponds, even temporary, rich in organic matter from decomposition of vegetal matter (humic environments), but not acidic.

Typical representatives: *Synura* spp. as *S. uvella*, *S. pettersonii* but not *S. sphagnicola*, which is not planktonic (O'Farrell et al., 2003; Padisák et al., 2003a; Sarmento & Descy, 2008).

Codon $\mathbf{W_0}$ (Borics et al., 2007)

Habitat template: rivers and ponds with extremely high organic contents, even septic for most aquatic biota.

Typical representatives: some species of *Chlamydomonas*, *Pyrobotrys*, *Chlorella*, *Polytoma* and *Oscillatoria chlorina*. This group may also include sulphur-bacteria as *Beggiatoa alba* (Borics et al., 2007).

Codon **Q** (Reynolds et al., 2002)

Habitat template: small acidic, humic lakes.

Typical representatives: *Gonyostomum* spp., *G. semen* (Willén, 2003; Findlay et al., 2005; Alves-de-Souza et al., 2006); *Heterosigma* cf. *akashiwo* (Alves-de-Souza et al., 2006).

Outcomes from literature screening and some recommendations

The critical reading of the selected literature dealing with functional groups of phytoplankton allows us to identify some problems linked with the use of the functional classification of the freshwater phytoplankton.

The article published by Reynolds et al. (2002) was preceded by a book by Colin Reynolds in 1997 with detailed description of habitat templates and corresponding associations. Probably, this is the reason why the authors of the article published in 2002 did not feel it necessary to provide again the detailed descriptions of habitats. After screening the available literature, the first that we noted is that most of the misplacements made by the users were due to a superficial reading of the article. Actually, many misplacements originate from inadequate coupling between the species and the codon. The aim of the 2002 article was not to sort the species into coda, but to offer, by indicating a few typical representatives, a method to attribute the species to the different coda. Nevertheless, we noticed that species not listed in the original article are very often attributed to a given codon because of taxonomic affinity or co-occurrence. This is not wrong a priori since algae forming a single functional group also have similar morphologies, as quantified by the dimensions of the algal 'units' (cells or colonies, as appropriate, together with any peripheral mucilage): selected morphological traits are powerful predictors of optimum dynamic performance (Naselli-Flores et al., 2007). But it is also true that algae also may show high infrageneric phenotypical variability (Naselli-Flores & Barone, 2007) and thus species belonging to the same genus find their best location in different coda. E.g. not all the *Cyclotella* species belong to codon **A**, or *Aulacoseira* spp. to codon **B**. Moreover, as it happens for several blue-green species, very similar morphologies may have very different ecological adaptations (e.g. *Planktothrix rubescens* and *P. agardhii*).

Some authors allocated all the taxa with sufficient biomass to the codon of the dominants. This practice has been a rather typical misinterpretation of the functional group approach. We always have to keep in mind that phytoplankton assemblages replace each other during a seasonal cycle; therefore co-occurrence different assemblages of more than one functional grops is rather a rule than an excepcion. Indeed, development of equilibrium/steady state assemblages is quite rare (see Naselli-Flores & Barone, 2003), especially in temperate climate. Consequently, investigators of temperate lakes have to face to transitional phases in the bulk of the cases. As can be concluded from the recentmost literature (Becker et al., 2008; Crossetti & Bicudo, 2008a, b; Fonseca & Bicudo, 2008; Souza et al., 2008), equilibria seem to be more frequent in tropical lakes, however, rules in the probablity of equilibrium development along latitudinal gradients needs further research.

Conversely, some coda were only provisionally described and this may have generated some confusion in the users. The best example to this is the placement of *Ceratium* spp. only in codon $\mathbf{L_M}$ (*Ceratium* + *Microcystis*) and not also in codon $\mathbf{L_O}$ where other large dinoflagellates are placed. This resulted in a number of misplacements (see Appendix—supplementary material). Authors very often sorted *Ceratium* spp. into the codon $\mathbf{L_M}$ in ecosystems where *Microcystis* does not occur at all. We tried to solve this problem by attributing a different set of representatives to codon $\mathbf{L_O}$, which now include all the large thecate dinoflagellates and even few very large *Gymnodinium*, without excluding them from the $\mathbf{L_M}$ codon since at higher trophic states *Ceratium* (and in some case other thecate dinoflagellates) occurs together with large masses of *Microcystis*. In synthesis, these three coda ($\mathbf{L_O}$, $\mathbf{L_M}$ and **M**) represent an eutrophication gradient without clear separations. Small dinoflagellates (*Glenodinium* spp., *Gymnodium* spp. etc.), as originally suggested by Reynolds et al. (2002), have to be placed in codon **Y** along with large cryptophytes.

It is fair to call the attention here to our insufficient knowledge on autecologies of most of diatom taxa. This lack makes particularly difficult to sort them into coda. Additionally, diatom dominated planktonic assemblages commonly prevail for a short time in either deep or shallow lakes, therefore, equilibrium conditions/habitat templates are difficult to define precisely.

Another problem is given by coda **K** and **Z**, both accommodating picoplankton. A frequently recorded mistake observed in the selected literature is due to an insufficient explanation of habitat characteristics in the table listing the trait-separated functional groups in the original article (Reynolds et al., 2002). Although in the text it is possible to read a detailed explanation of the habitat template of these coda, the consultation of the table only to allocate the species may generate doubts in the users and cause misplacements. Actually, picocyanobacteria can dominate under two conditions:

(a) metalimnia or upper hypolimnia (which are not mixed layers!) of oligotrophic lakes where they form a deep chlorophyll maximum (DCM). This environment is severely light deficient and relatively (compared to the respective epilimnia) nutrient rich. Typical example is Lake Stechlin (Padisák et al., 1997). The habitat template for codon **Z** is thus: undisturbed, upper hypolimnion or metalimnion of oligotrophic lakes;
(b) hypertrophic lakes which are also light deficient due to high density of phytoplankton (Vörös et al., 1991) or of inorganic seston (Padisák & Dokulil, 1994). However, in such lakes largely colony forming species dominate but cells of these colonies are of picoplanktonic size. Unicells are probably 'lost' cells only. Habitat for this group is turbid mixed layer of eutrophic or turbid shallow lakes, some with high conductivity. The above description fits to codon **K**. Thus, we warmly recommend the users of the functional classification to carefully consider the habitat template into which they allocate their picoplankton.

Another addition we accepted, directly comes from what already suggested by Reynolds et al. (2002) when they wrote: 'As yet, we have made no attempt to deal with tychoplanktonic entries from the periphyton or from the benthos, although to develop a scheme that included these life-forms in their own right is likely to be a worthwhile objective'. As a consequence, we listed the codon **MP** (Padisák et al., 2006), which comprises all the meroplanktonic, periphytic or epilithic which may be occasionally found in plankton samples.

Due to the strong influence that temperature imposes on the mixing patterns of the water columns, we acknowledged the recent establishment of a sub-codon ($\mathbf{N_A}$) to codon **N** (Souza et al., 2008). This may help in finding an appropriate location to the small isodiametric desmids sometimes with overwhelming dominance in oligo-mesotrophic, stratified, tropical lakes.

A further addition to the original set of coda comes from the recognition of the importance of planktonic species in fast flowing rivers that are otherwise not plankton environments. The recent implementation of the Water Framework Directive requires the recognition of hydromorphological modifications (e.g. reservoir construction) to the river channel. The best indicator under such conditions is the appearance of planktonic species downstream the dam. This need initiated the setting of three new coda ($\mathbf{T_B}$, $\mathbf{T_C}$ and $\mathbf{T_D}$) which makes possible to use the functional groups concept to the qualification of ecological status of running waters (Borics et al., 2007). A fourth group ($\mathbf{W_0}$) was set by these authors to allocate those species that occur in heavily polluted rivers and ponds. The $\mathbf{T_B}$, $\mathbf{T_C}$, $\mathbf{T_D}$ and $\mathbf{W_0}$) coda are suggested only for rivers but in artificial standing waters (sewage treatment ponds) they may be also helpful.

Last but not least, we would like to underline the importance of an appropriate taxonomic resolution when allocating the different taxa into the coda. Species of most algal divisions are distributed in more than one codon as well as different species of several genera. Therefore, as it is absolutely true that items like 'chlorophytes', 'centric diatoms', 'dinoflagellates', etc. cannot be properly placed in any codon. It is similarly valid that in some cases, the nude reference to, e.g. *Cyclotella* sp. may not ensure the belonging of the species to a given codon. We fully realize that identification is sometimes (many times) difficult or impossible: in such cases we suggest to provide a short morphological description, which, along with the habitat template, justifies the codon selection.

The unusually high number of references to the article by Reynolds et al. (2002) is the best indicator of the usefulness of the functional group concept in phytoplankton ecology. Our knowledge on the assemblage concept has been significantly enriched by the large number of contributions listed among the references of this article. This allowed identifying some consequent misunderstandings and hopefully clarifying some of them.

Acknowledgement This work was supported by the Hungarian National Science Foundation (OTKA No. K 75552).

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