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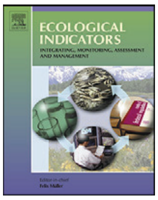

Taxonomic or ecological approaches? Searching for phytoplankton surrogates in the determination of richness and assemblage composition in ponds

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ABSTRACT

In the context of the global decline in biodiversity there is a pressing need for simple methods to assess biodiversity and community composition. Identification of phytoplankton to species level is difficult, expensive and time-consuming and requires high levels of expertise. Thus, the search for parsimonious predictors of organism diversity based on simplified taxonomy or approaches representing community structure, has received much attention. Few studies have focused on identifying surrogates for predicting both phytoplankton richness and community composition. Here we examined the suitability of several taxonomic and ecological classifications in summarising phytoplankton diversity and community structure from 87 stratified-random selected Andalusian artificial ponds. Taxa based approaches at genus and family level, as well as functional groups predicted relatively well both phytoplankton richness and assemblage composition. Size classes could be used as a reasonable predictor of richness and environmental conditions, but it was a weak predictor of community composition. The morphology-based approach was the poorest proxy for richness patterns and environmental conditions, but more suitable than the size class approach as a proxy for assemblage composition.

1. Introduction

The rapid loss of biodiversity during recent decades, especially in freshwater ecosystems (Dudgeon et al., 2006; Strayer and Dudgeon, 2010), has resulted in an increased focus on how to effectively monitor biodiversity. As species level identification involves increased costs in terms of time, money and expertise, the search for suitable biotic surrogates describing diversity patterns has become a priority in conservation planning (Margules and Pressey, 2000). The use of biodiversity surrogates in the assessment of the ecological status of freshwater water bodies has been widely reported (review in Heino, 2010). Approaches using reduced taxonomic resolution are the most common surrogates for individual taxa in both terrestrial (Balmford et al., 2000; Cardoso et al., 2004; Villaseñor et al., 2005) and aquatic ecosystems (Bilton et al., 2006; Carneiro et al., 2010; Cottingham and Carpenter, 1998; Heino and Soininen, 2007). Additionally, proxies based on ecological criteria have proved good predictors of the structure of plant communities (Lavorel et al., 1997), birds (French and Picozzi, 2002), insects (Didham et al., 1996) and zooplankton (Barnett et al., 2007; Hansen and Bjørnsen, 1997) in response to shifts in the environmental conditions.

Phytoplankton studies have seen a reduction in species level identification. Evidence of chaotic behaviour in plankton communities at species level (Benincà et al., 2008; Scheffer et al., 2003) and the development of novel techniques, such as the measurement of pigments (Havskum et al., 2004) or the computer assisted taxonomy (Gaston and O'Neill, 2004), have led to the decrease in the number of publications with species level identification, emphasising the need for evaluating surrogates used to describe biodiversity and ecological function of lakes and ponds.

An overview of surrogates for phytoplankton as ecological assessment tools reveals a variety of proxies ranging from indicator groups (*e.g.* Soininen et al., 2009), the higher taxa approaches

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Abbreviations: FG, functional groups; MBFGs, morphology-based functional groups; SCs, size classes.

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(Carneiro et al., 2010; Cottingham and Carpenter, 1998; Heino and Soininen, 2007) and the use of ecological classifications such as the functionality-based approach (Padisák et al., 2009; Reynolds et al., 2002), a functional approach that captures morphology, *e.g.* Kruk et al. (2010) and classifications based on body size, *e.g.* Rojo and Rodríguez (1994).

Ecological classification systems usually employ size and other morphological characteristics of algae. Body size is one of the most important traits of an organism, determining the type and the strength of its ecological interactions (De Roos et al., 2003). The ecological relevance of size structured communities (SC), first reported in marine ecosystems (Platt and Denman, 1977; Rodríguez and Mullin, 1986) has also been highlighted for freshwaters, *e.g.* Rojo and Rodríguez (1994). Phytoplankton functional groups (FG; Reynolds et al., 2002) include several categories with similar morphology, environmental sensitivity and tolerance. The classification has been continuously expanded to represent all possible phytoplankton assemblages found in freshwater and saline ecosystems (review in Padisák et al., 2009). A more recent morphology-based functional grouping (MBFG), focussing on the organisms' morphology (including physiological and functional characteristics), proved useful when predicting the effect of environmental conditions on phytoplankton assemblages (Kruk et al., 2010, 2011).

In addition to the phytoplankton classification system, the determination of the optimal numerical resolution of biological data sets is necessary to carry out effective monitoring plans. Although biovolume is considered one of the most relevant traits when analyzing phytoplankton community dynamics (Hillebrand et al., 1999; Wetzel and Likens, 2000), the use of density accounts may simplify the process of biomonitoring programs (Carneiro et al., 2010) since some difficulties have been reported regarding the search of accurate geometric formulae on certain algal shapes (Sun and Liu, 2003).

Pond ecosystems differ in limnology in many ways from lakes (Oertli et al., 2002; Søndergaard et al., 2005), and in lowland areas they are often also linked to and therefore strongly affected by agricultural use (Davies et al., 2008; Hazell et al., 2004; Williams et al., 2004). Furthermore, agricultural ponds have a paradoxical nature in that they must reconcile biodiversity conservation with severe management practices based on crops production efficiency (Abellán et al., 2006; Casas et al., 2011a). In an effort to assess ponds ecological quality, recent studies have determined the performance of various biodiversity surrogates (Gioria et al., 2010; Kadoya et al., 2011; Menetrey et al., 2011).

To our knowledge, no studies have sought to identify surrogate groups of phytoplankton as potential biodiversity indicators for pond systems and more generally, in aquatic ecosystems, only few have compared the performance of the different surrogate variables for both richness and community composition. Here we present a data set of 87 small water bodies in Southern Spain with contrasting nutrient status to compare five different phytoplankton classifications to the species-level identification: two lower taxonomic resolutions (genus, family) and three ecological approaches, based on functional traits (FG, MBFG) or size classes spectra (SC). The aim was to detect the degree of congruence between phytoplankton species and the various surrogate classifications with focus on the environment–biological relationships.

2. Materials and methods

2.1. Study area

We selected 87 out of the 16,545 artificial permanent ponds in Andalusia, Southern Spain, covering an area of nearly 90,000 km^2 (Fig. 1). Since environmental heterogeneity is high in this region, we adopted a stratified-random procedure for pond selection. The selection accounted for variation in geographical, agricultural management and pond typology in the region. Information on these criteria and environmental characteristics of Andalusian ponds is given by Casas et al. (2011b).

2.2. Data collection

Ponds were sampled in late spring 2007, when the majority of organisms have their maximum biological activity and water level remains relatively high. The means and ranges of environmental variables are listed in Table 1. Pond area was measured using ortho-image interpretation (B/W 1:20,000; years 2001–2002). Water samples for chemistry analyses and phytoplankton samples were gathered from two randomly selected locations in each pond, from which we integrated depth profiles from both pelagic and littoral parts. The water was collected with a 15-cm-diameter Plexiglass tube sampler of 2-m length (Knoechel and Campbell, 1992). Conductivity and pH were measured *in situ* with a Multiparameter Probe (HANNA HI9828). A 1 L subsample of water was taken to be analysed in the laboratory for alkalinity, silicate concentration (SRSi), total suspended solids (TSS), total nitrogen (TN), total phosphorus (TP), nitrate (NO_3—N), nitrite (NO_2—N), ammonia (NH_4—N) and soluble reactive phosphorus (SRP) following procedures described in APHA (1992). Dissolved inorganic nitrogen (DIN) was calculated as the sum of nitrate, nitrite and ammonia. Planktonic chlorophyll *a* was determined by the trichromatic method using alkaline acetone extracts (Wetzel and Likens, 2000).

Phytoplankton samples (250 mL) were immediately fixed in acetic Lugol's solution (4% final concentration). Phytoplankton samples were allowed to settle in counting chambers before examination with a Carl Zeiss Axiovert 35 inverted microscope, according to the technique of Utermöhl (1958). A volume from 5 to 50 ml was settled, depending on the phytoplankton biomass. Identification was carried out to species level where possible. Smaller taxa were counted at 1000× or 400× magnification, whereas larger ones were counted at 200× and 100× magnification. At least 100 cells or setting units (colonies, filaments) of the most frequent species were counted in order to get reliable abundance estimates. Counting continued until species reached an asymptotic value, when no more new species were encountered for 10 units.

Individual biovolume was calculated according to fitted geometric forms (Hillebrand et al., 1999), taking linear measures of 25 individuals, when possible (Rojo and Rodríguez, 1994). Specific biomass [mg (C fresh weight) L^{-1}] was estimated from the product of the population and mean unit volume of each species (Edler, 1979), using a specific density of phytoplankton cells of 1 mg mm^{-3}.

Zooplankton samples were filtered through a 40 μm net and preserved in a 4% formaldehyde solution. A constant volume of 10 L was filtered, counted and identified to species level. In the analysis we only included total zooplankton density and cladoceran density, being the grazers with typical highest impact on phytoplankton biomass and composition (Lampert et al., 1986).

The percentage cover of submerged aquatic vegetation (%SAV) was determined along two randomly selected transects from the shore to the centre. For further details about sampling procedures and laboratory analyses see Casas et al. (2011b).

2.3. Data analyses

Phytoplankton density (individual mL^{-1}) and biomass (pg C mL^{-1}) data were identified according to Komárek and Fott (1983) for Chlorophyceae, Komárek and Anagnostidis (2008) for cyanoprokariota, Krammer and Lange-Bertalot (1991) for diatoms,

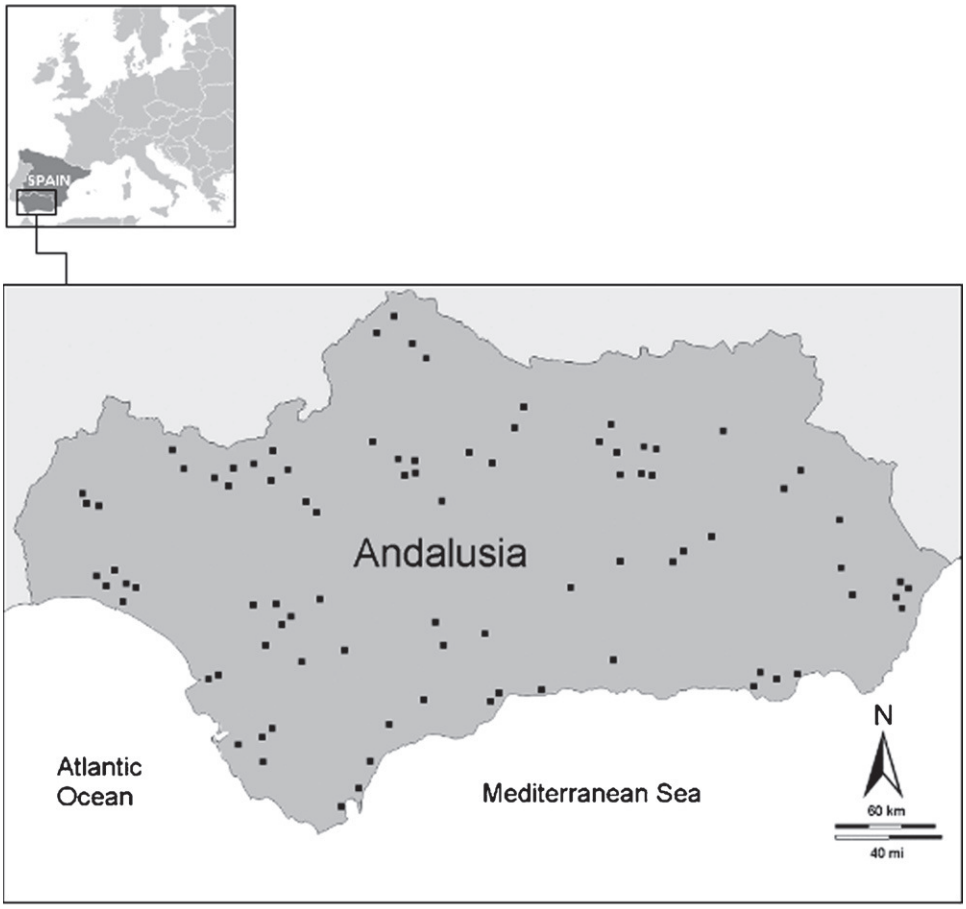

Fig. 1. Map showing the 87 studied ponds throughout Andalusia (southern Spain).

Huber-Pestalozzi (1968) for Dinophyceae and Cryptophyceae, Ettl (1978) for Xantophyceae, Starmach (1985) for Chrysophyceae and Wolowski and Hindák (2005) for Euglenophyceae. Species were aggregated in genus and family levels. Subsequently, species, or genera if possible, were clustered in 31 different functional groups (Reynolds et al., 2002). A phytoplankton morphology-based functional classification from Kruk et al. (2010) was used to aggregate the different taxa into 7 groups. Biomass size spectra were produced for each pond. The size class (SC) approach constructed phytoplankton size spectra by grouping phytoplankton biomass into $\log_2$ size classes producing 39 size classes. Normalised biomass was required since the width of size classes varies through the spectra. The normalised size spectrum was calculated by dividing the biomass in a size class by the width or range of each size class, as described by Platt and Denman (1977).

There were a total of 6 different phytoplankton classification schemes: species, genus, family, functional group (FG), morphological-based functional group (MBFG), size class (SC). Both biomass and density data were available for each classification, except for SC, in which numerical data on individual mL^{-1} are not suited by definition (Platt and Denman, 1977). Taxa strongly associated to benthic and periphytic communities were excluded. Only those phytoplankton species that occurred at >1% of sites were considered.

Pearson's correlation coefficient was calculated to test the relationships between pairs of richness data of each classification

Table 1
Summary of variables measured of the ponds included in the study, indicating abbreviations, units, mean, median, minimum and maximum values.

Variable	Abbreviation	Units	Mean	Median	Min	Max
Alkalinity	Alk	µeq/L	120	94	15	415
Chlorophyll *a*	Chl *a*	µg/L	39.1	8.2	0.1	489.2
Cladoceran	Clad	Ind/L	14	1	1	427
Dissolved inorganic nitrogen	DIN	µmol/L	272	57	4	2728
Conductivity	Cond	µS/m	2.09	0.99	0.08	24.00
pH	pH		8.5	8.4	7.0	10.7
Pond area	Area	m^2	18,290	7362	99	179,301
Pond maximum depth	Zmax	m	6.3	5.8	1.5	17.0
Soluble reactive silica	SRSi	µg/L	4804	3872	53	18,116
Soluble reactive phosphorous	SRP	µmol/L	9.05	2.08	0.05	133.50
Submerged aquatic vegetation	%SAV	%	22	5	0	100
Total nitrogen	TN	µg/L	3473	1550	100	28,200
Total phosphorus	TP	µg/L	327	106	8	3528
Total suspended solids	TSS	µg/L	22.8	13.5	1.2	160.1
Total zooplankton	TZoo	Ind/L	310	41	1	6424

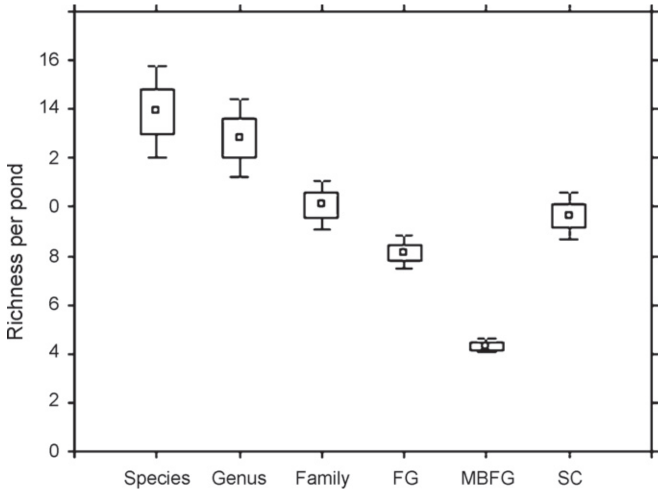

Fig. 2. Richness mean values per pond ($n = 87$) for each classification scheme. Dots indicate mean values, boxes represent standard error and whiskers show confident intervals ($\alpha = 0.05$).

scheme, compared to the highest resolution. Generalised Linear Models (GLM) with the appropriate error structure (McCullagh and Nelder, 1989) – quasipoisson or negative binomial accounting for the heteroscedasticity of the data – (Venables and Ripley, 2002) were employed to identify the optimal model explaining taxa richness for the various proposed classifications. All the variables were included originally in a full model, including quadratic functions of nutrients as nutrient-richness relationships may be unimodal. Backward selection was used to find the optimal models. The explained variance by the model was given by deviance (D^2), an analogue to the coefficient of determination R^2. The statistical significance of each model was assessed by F and χ^2-tests, for quasipoisson and negative binomial distributions respectively (Zuur et al., 2009). Residuals of the final models were examined to check for normality of data and absence of overdispersion. GLM were performed in R, using {MASS} package (Venables and Ripley, 2002; R Development Core Team, 2010).

Correspondence Analyses (CA) were performed to investigate the main gradients of variation in the various phytoplankton assemblages. All the environmental variables except pH were $\log_{10}(x + 1)$ transformed. Biological data were square-root transformed, following recommendations for data with Poisson distributions (Legendre and Legendre, 1998).

The level of concordance between the species CA and the CA from the other classifications was tested with Procrustes rotation analyses (Gower, 1971). The degree of concordance between the ordination results of two data sets was assessed with the Procrustes sum of squares and the Procrustes root mean square error. Significance of Procrustes analyses was checked with PROTEST randomisation test (9999 permutations; Jackson, 1995). The analysis was carried out using the {Vegan} package, which produces a correlation-like statistic r – where 1 is perfect accord and 0 the complete absence of any accord – and an associated P value (Oksanen et al., 2008; R Development Core Team, 2010). The residuals of Procrustes analyses were examined to identify the points of discord between the ordinal results of the different classifications.

Distance-based Linear Models (distLM) were performed to investigate the relationship between the assemblage structure, described by a resemblance matrix, and the environmental variables (Legendre and Anderson, 1999). We used semimetric Bray–Curtis resemblance measure for the phytoplankton matrices and Euclidean distances for predictors. The selection criterion and selection procedure used were step-wise and Adjusted R^2

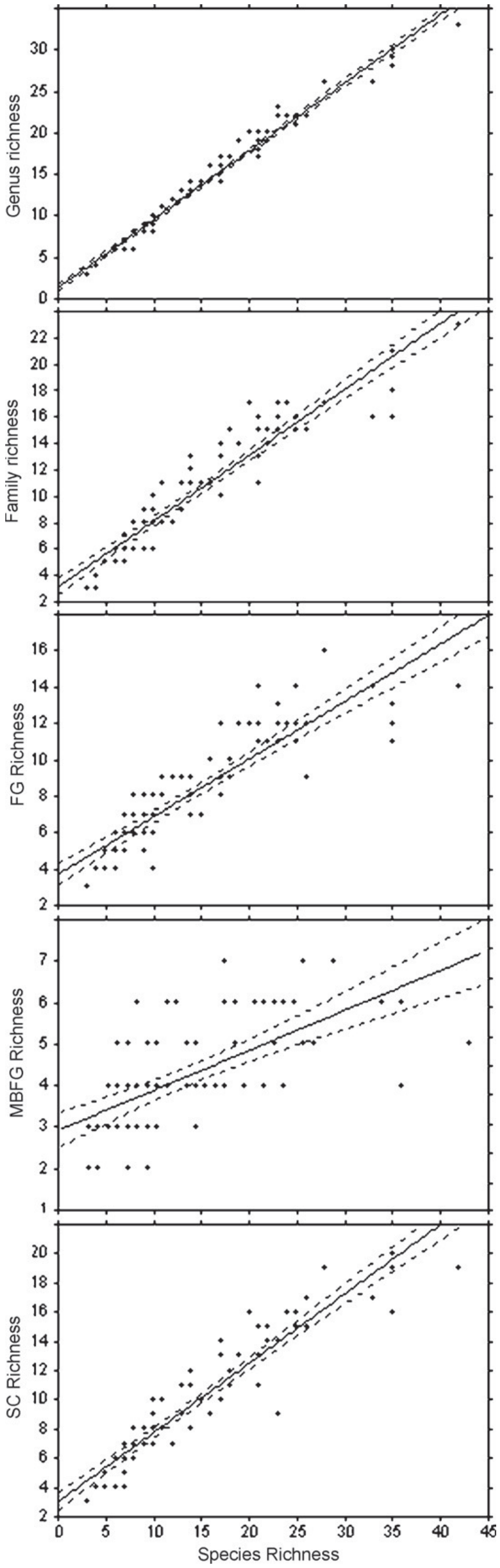

Fig. 3. Relationship between species richness and its potential surrogates. Dotted lines represent confidence intervals ($\alpha = 0.95$). In all cases $P < 0.001$.

Table 2
Results of GLM procedure, including the drop contribution of each explanatory variable (referred as the deviance reduction associated to dropping the variable from the final model), deviance D^2 (percentage explained by the model) and distribution of the variable response, for each classification scheme.

	Species	Genus	Family	FG	MBFG	SC
EC (−)	9.76^{***}	8.22^{***}	6.80^{**}	5.39^{*}	4.07^{*}	9.51^{**}
TP (+)	$2.47^{\cdot}$	3.28^{*}	$3.06^{\cdot}$	3.42^{*}	6.75^{**}	$2.83^{\cdot}$
DIN (−)	3.46^{*}	3.28^{*}	3.50^{*}	4.41^{*}	–	3.91^{*}
Chl *a* (−)	9.05^{*}	9.43^{***}	5.72^{**}	7.92^{**}	–	8.33^{**}
D^2	35.65	33.13	25.88	28.02	19.30	32.13

*** $P \leq 0.001$.
** $P < 0.01$.
* $P < 0.05$.
$^{\cdot}$ $P < 0.1$.

(9999 permutations). The most parsimonious model at species level using biomass data was used to calculate both R^2 – the proportion explained variation for the model – and Adjusted R^2 for the remaining taxonomic and ecological approaches. Highly collinear variables ($|r| > 0.8$) were excluded. We carried out distLM with PERMANOVA+ for PRIMER-E v6 (Clarke and Gorley, 2006).

3. Results

In total 293 phytoplankton species were identified in the 87 ponds, consisting of 132 genera and 58 families, with mean values of richness per pond of 14, 13 and 10 taxa respectively (Fig. 2). The ecological classifications included 27 of the 31 FG proposed by Reynolds et al. (2002), whereas all the 7 MBFG described by Kruk et al. (2010) were represented. The 39 phytoplankton size classes ranged from 0.7 to 1.2 × 10^5 μm^3. The detailed list of species and codes is included in Appendix A.

Significant positive correlations were obtained between species richness and the remaining taxonomic resolutions used (Fig. 3) being highly significant in most of cases ($r_{species–genus} = 0.99$; $r_{species–family} = 0.95$; $r_{species–FG} = 0.89$; $r_{species–SC} = 0.94$; $P < 0.001$) except for MBFG though significant ($r_{species–MBFG} = 0.65$, $P < 0.001$).

3.1. Generalised Linear Models

As the richness data showed overdispersion when Poisson distribution was applied ($\Phi > 1$), we used negative binomial distributions with the severely overdispersed data from taxonomic approaches (sp., gen., fam.), whilst the less overdispersed ecological proxies (SC, FG and MBFG) were fitted with quasi-Poisson distributions, both linked to logarithmic functions. Out of 14 non-collinear variables (Alk, Chl *a*, Cond, Clad, DIN, pH, Area, Zmax, SRSi, %SAV, TN, TP, TSS, Tzoo) only four variables (Chl *a*, Cond, TP, DIN) contributed significantly to the variation in taxa richness at species and genus level. Cond and TP were included in all taxonomical and functional approaches, whilst DIN and Chl *a* were not for MBFG. Taxa richness correlated negatively with Cond, DIN and TP, and positively to Chl *a* (Table 2). The highest deviance was obtained at the species and genus level ($D^2 = 35.6$ and 33.1 respectively). MBFG showed by far the lowest values ($D^2 = 16.7$). The relative importance of Cond in explaining the variance in richness decreased towards the highest aggregation level, varying from nearly 10% at species level to 4% for MBFG. Conversely, the contribution of TP increased 4% from species level to the lowest aggregation level. The contribution of DIN was similar for all classification approaches used (3.3–4.4%).

3.2. Correspondence Analyses and Procrustes rotations

The CA showed increasing percentages of variance explained with decreasing resolution in the phytoplankton as the total inertia, decreased 15-fold from species to MBFG (Table 3). The explained variance of the first two axes ranged from <10% at species level to close to 50% for the MBFG (Table 3), whilst the inertia for the first two axes decreased 50% from species to MBFG. Along the first two axes, the variance explained by density or biomass data differed slightly, being <1% for all taxonomical approaches, close to 2% for FG and >10% for the MBFG classification.

Results from Procrustes analyses reflected a lower degree of concordance between density and biomass in taxonomic classifications (r PROTEST < 0.5) than in ecological approaches (r PROTEST > 0.7; Table 4). In all cases, the fit between density and biomass data sets produced low P values, showing no statistical differences when both data sets were rotated for each approach. However, when rotations were performed between species and each proxy, the lower Procrustes sum of squares and higher PROTEST r revealed a greater degree of congruence when biomass data were used ($r > 0.221$, $P < 0.05$) regarding densities ($r > 0.177$, $P < 0.05$) for all the proxies. The degree of concordance between the ordinal results of the species and SC and MBFG approaches was significantly lower than that between the species–genus, –family and –FG (Table 5).

The plots of Procrustes residuals from the rotations between species and the remaining approaches revealed that the majority of sites with large residuals were characterised by having low richness in the taxonomical proxies in comparison to ecological approaches, which showed higher dispersion in the distribution of the residuals along the richness axis (Fig. 4).

Table 3
Summary of the contribution to variance and inertia of each classification approach explained by 2 first axes in Correspondence Analyses (CA), considering both density and biomass data (999 permutations).

	Density					Biomass					
	Species	Genus	Family	FG	MBFG	Species	Genus	Family	FG	MBFG	SC
% E.V.[a], axis 1	4.18	6.64	8.13	13.28	25.37	4.53	6.06	8.01	12.62	30.81	10.50
% E.V.[a], axis 2	3.74	5.31	6.37	11.62	21.85	3.65	4.70	6.49	10.18	25.93	9.79
% C.V.[b], axes 1,2	7.91	11.95	14.49	24.91	47.22	8.18	10.75	14.50	22.81	56.75	20.29
Inertia, axes 1,2	1.52	1.27	0.95	1.05	0.67	1.57	1.12	1.01	0.92	0.64	1.18
Total inertia	19.22	10.67	6.53	4.22	1.42	19.21	10.37	6.93	4.06	1.13	5.82

[a] Percentage of explained variance.
[b] Cumulative percentage of variance.

Table 4
Summary of Procrustes analyses, PROTEST *r* correlation-like statistic and significance referred to the concordance between density and biomass Correspondence Analyses (CA) of each approach.

	PSS[a]	PRMSE[b]	*r*[c]	*P*
Species	92.53	1.03	0.452	0.011
Genus	75.13	0.93	0.430	0.001
Family	95.14	1.05	0.373	0.001
FG	42.90	0.70	0.716	0.001
MBFG	66.29	0.87	0.763	0.001

[a] Procrustes sum of squares.
[b] Procrustes root mean squared error.
[c] PROTEST *r* correlation-like statistic between density and biomass.

Table 5
Summary of Procrustes analyses, PROTEST *r* correlation-like statistic and significance referred to the concordance between the Correspondence Analyses (CA) of each of the phytoplankton approach, rotated at species level.

	Density				Biomass			
	PSS[a]	PRMSE[b]	*r*[c]	*P*	PSS[a]	PRMSE[b]	*r*[c]	*P*
Species–genus	93.90	1.04	0.439	0.012	85.14	0.99	0.466	0.001
Species–family	108.01	1.11	0.267	0.011	75.59	0.93	0.553	0.001
Species–FG	102.72	1.09	0.342	0.004	82.80	0.98	0.489	0.001
Species–MBFG	112.66	1.14	0.177	n.s.	103.53	1.09	0.221	0.037
Species–SC	–	–	–	–	106.05	1.10	0.159	n.s.

[a] Procrustes sum of squares.
[b] Procrustes root mean squared error.
[c] PROTEST *r* correlation-like statistic between species and each classification approach.

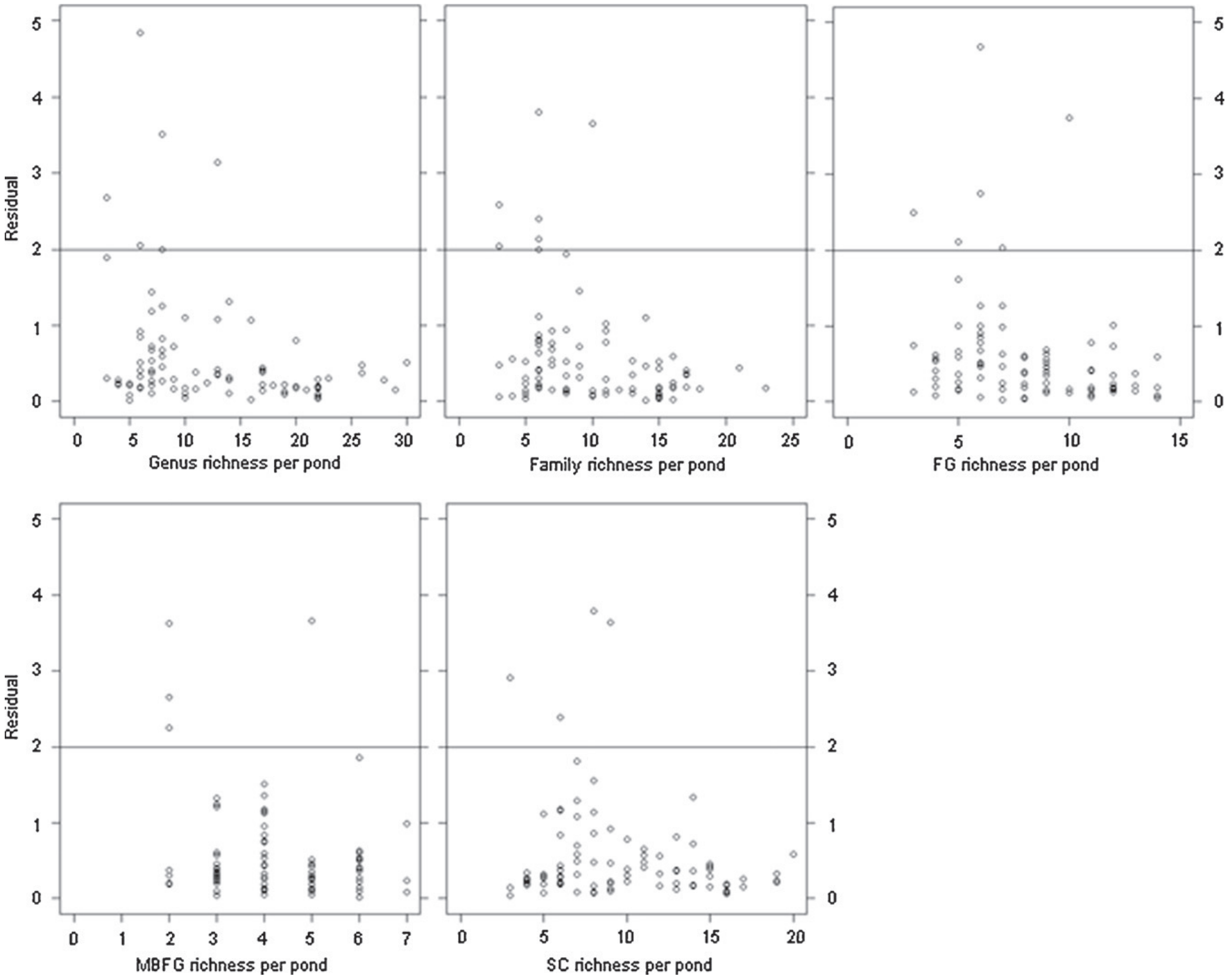

Fig. 4. Plots of richness for each approach against residuals from Procrustes superimpositions between species and each proxy (biomass data). Values above the horizontal line show residuals > 2 SD.

Table 6
Summary of contribution to variance of each variable in the six phytoplankton classifications evaluated, total explained variance for the models (R^2) and their correspondent adjusted fractions (Adj R^2), for both density and biomass data. Variables were selected from the most parsimonious model using distance-based Linear Model analysis (distLM) for biomass species dataset. Significance (9999 permutations).

	Density					Biomass					
	Species ($n = 293$)	Genus ($n = 132$)	Family ($n = 58$)	FG ($n = 27$)	MBFG ($n = 7$)	Species ($n = 293$)	Genus ($n = 132$)	Family ($n = 58$)	FG ($n = 28$)	MBFG ($n = 7$)	SC ($n = 39$)
SRSi	1.96***	2.07**	2.20**	2.03*	1.03	2.16***	2.60***	2.45**	2.55**	0.60	1.50
Chl *a*	2.27***	3.01***	3.79***	4.89***	8.58***	2.08***	3.20***	4.19***	5.00***	8.52***	2.95***
Cond	1.62**	1.87**	2.16**	2.05*	1.98$^{\cdot}$	1.65**	1.81**	2.34**	1.99*	1.50	1.41
SAV	1.82**	1.58*	1.60$^{\cdot}$	1.26	1.24	1.61**	1.41$^{\cdot}$	1.45$^{\cdot}$	1.13	0.72	1.59$^{\cdot}$
TP	1.41*	1.54*	1.41	0.83	1.35	1.52*	1.49***	1.35$^{\cdot}$	0.85	0.70	1.29
R^2 model	0.091	0.101	0.112	0.111	0.131	0.090	0.105	0.118	0.115	0.121	0.089
Adj R^2 model	0.035	0.045	0.057	0.059	0.091	0.034	0.050	0.063	0.063	0.079	0.010

*** $P \leq 0.001$.
** $P < 0.01$.
* $P < 0.05$.
$^{\cdot}$ $P < 0.1$.
$^{\cdot\cdot}$ $P > 0.1$.

3.3. Distance-based Linear Models

The explained variance by distance-based Linear Models (distLM) showed a similar trend as the unconstrained analyses (CA), increasing towards the lowest aggregation level proxy (Tables 3 and 6). The proportion of variance explained by the environmental variables varied less than 5% from species to MBFG, with MBFG being the approach that explained the highest amount of variance, 13% and 12% for density and biomass datasets, respectively (Table 6).

Species biomass ordination included SRSi, Chl *a*, Cond, SAV and TP as significant structuring variables ($P < 0.05$). Only Chl *a* was significant in all the classifications, increasing its value from the highest (species level) to the lowest resolution (MBFG). SRSi and Cond were significant for the three taxonomic approaches and FG. SAV and TP were significant only at species and genus level (Table 6), decreasing their weight towards the lower resolutions.

We observed that total variance explained (R^2) and partitioned variance of predictors were similar for biomass and density data sets, varying less than 2%. MBFG and SC approaches were the least concordant proxies compared to species level, including only one significant variable in the fitted model (Chl *a*). By contrast, genus level was the proxy that best fitted with the species model. Family level and FG included the same three significant variables (Chl *a*, SRSi, Cond), showing similar results ($R^2 = 0.11$; Table 6).

4. Discussion

Our results revealed that higher taxonomic levels (genus, family) were the best surrogates for species richness, which is in accordance with previous studies on taxonomic resolution for different groups of organisms, such as fungi (Balmford et al., 2000), plants (Villaseñor et al., 2005), invertebrates (Bilton et al., 2006; Heino and Soininen, 2007; Lovell et al., 2007) and even phytoplankton (Carneiro et al., 2010; Passy and Legendre, 2006). In contrast to other investigations (*e.g.* Heino and Soininen, 2007) all the taxonomic-based assemblages we used responded similarly to the environmental drivers. We found a clear negative correlation between phytoplankton taxa richness and conductivity, concurring with other studies on lentic systems (Brucet et al., 2009; Flöder and Burns, 2004; Waterkeyn et al., 2008).

It has been suggested that the relationship between different taxonomic levels and species is strongly congruent in regions with phylogenetically “shallow-rooted” assemblages, *i.e.* with low species:genus and species:family ratios, whilst the congruence diminishes in regions with phylogenetically “deeply rooted” assemblages resulting from high degrees of adaptive radiation (Hawkins and Norris, 2000). Our data had low species:genus, genus:family and species:family ratios (1.06, 1.21 and 1.29 respectively), as a high number of genus and families were monospecific. These ratios coincide with those obtained by Carneiro et al. (2010) for phytoplankton in tropical latitudes, but are considerably lower than the values obtained by Heino and Soininen (2007) for diatoms in boreal streams. Unlike this latter study, variation in richness at the different taxonomic level was attributable to the same environmental gradients, indicating a phylogenetic shallowness in the sampled ponds.

The ecological approaches showed different response patterns. Whilst FG was a reliable predictor of both richness– and assemblage–environment relationships, the SC and MBFG approaches showed a weak relationship to the key variables controlling community and richness, respectively. Moreover, the environmental variables determining variation in assemblages of the ecological approaches differed from those obtained at species level. The key importance of eutrophication related variables were, however, common for all proxies, coinciding with previous studies of various organisms group in Andalusian ponds (Casas et al., 2011b; F. Fuentes-Rodríguez, unpublished data; León et al., 2010).

Classifications based on FG *sensu* Reynolds et al. (2002), usually provide reliable predictions of environmental conditions in various aquatic ecosystems, such as lakes, reservoirs and wetlands (Anneville et al., 2005; Becker et al., 2010; Caputo et al., 2008; O’Farrell et al., 2003; Romo and Villena, 2005), and can be more effective than taxonomic approaches, *e.g.* Huszar and Caraco (1998). The original FG classification has been refined and applied to other habitats, evincing the validity of this approach as an effective tool for the assessment of phytoplankton community structure (summarised in Padisák et al., 2009). In keeping with the work of Carneiro et al. (2010), we found a strong relationship between FG and species, genus and family assemblages (data not shown), suggesting a high dependence of FG on taxonomy. The higher aggregation level in FG is appealing, but it must be emphasised that the grouping of species into FG coda is not less time consuming than grouping them into higher taxonomic levels, even for experts.

The SC approach was expected to report rather similar results as MBFG, due to the importance of cell size as a morphological trait related to the physiology of algae (Naselli-Flores et al., 2007; Reynolds, 2006; Rodríguez et al., 1990; Rojo and Rodríguez, 1994). Although SC was confirmed as a reliable predictor of local richness, it seems that cell size *per se* is not a good surrogate for phytoplankton community structure in ponds. Despite the fact that grazing pressure is considered to be important in structuring size distribution of phytoplankton (McCauley and Briand, 1979; Sterner, 1989), none of the zooplankton variables we included contributed significantly to the variation in the tested approaches, including SC. Andalusian ponds are mostly used for irrigation and/or livestock farming purposes (Casas et al., 2011b), and the intense management practices (Abellán et al., 2006; Casas et al., 2011a) may have affected zooplankton through dilution, since the cladoceran concentration is even lower than in subtropical waterbodies (Kruk et al., 2011; Meerhoff et al., 2007). Moreover, key-grazers amongst zooplankton are often controlled heavily by fish in lakes and permanent ponds in warm areas leading to low grazing pressure on phytoplankton (Brucet et al., 2009; Havens et al., 2009; Meerhoff et al., 2007), though no effect of fish was seen on macroinvertebrate richness in our ponds (F. Fuentes-Rodríguez, unpublished data).

Apart from organism size, other morphological features, such as the presence of aerotopes, flagella or mucilage, have been shown to yield useful information about phytoplankton assemblages, which is included in the MBFG approach (Kruk et al., 2010). This intuitive and summarising approach, however, appears to have limitations as a species richness surrogate. In contrast to Kruk et al. (2011), MBFG did not capture the influence of environmental variables as accurately as FG. A possible explanation may be that the MBFG system was developed for lakes, and may not describe equally well the often variable and extreme pond systems, characterised by large variations in morphometry, residence time and anthropogenic pressure (Casas et al., 2011a; Oertli et al., 2002; Søndergaard et al., 2005).

The disparity in the relationship between Procrustes residuals and richness increased with nutrient state. Systems with low richness had high nutrient loadings, mostly from recycled wastewater (Casas et al., 2011b). This is also reflected in the Chl *a* and DIN-richness relationships. Primary productivity, expressed in our study by Chl *a* and nutrients, is considered an important key of diversity (Oksanen et al., 1981; Tilman, 1993). The productivity–diversity relationship of phytoplankton has been extensively studied (Chase and Leibold, 2002; Declerck et al., 2007; Jeppesen et al., 2000; Mittelbach et al., 2001). Some empirical studies show that elevated nutrient loading and concentrations reduce algal species diversity (Proulx et al., 1996; Romo and Villena, 2005) whilst others have found a unimodal relationship with nutrients (Jeppesen et al., 2000). We found a negative relationship to DIN for both taxonomic and ecological proxies, in accordance with classical studies (Margalef, 1968). Whilst the role of phosphorous as a key structuring variable in freshwater ecosystems has been well known for decades (Schindler, 1977; Tilman, 1982), recent studies have highlighted the important role of nitrogen for structuring shallow ecosystems (González Sagrario et al., 2005; James et al., 2005; Moss et al., in press) including – directly and indirectly – their phytoplankton composition and abundance (González Sagrario et al., 2005; Jeppesen et al., 2011).

Contrary to studies in temperate shallow ecosystems (Declerck et al., 2005; Jeppesen et al., 1998; Muylaert et al., 2010), phytoplankton richness was not related to the submerged aquatic vegetation cover. Additionally, our phytoplankton assemblages included macrophyte cover as a predictor only at species and genus levels. The weak effect of submerged aquatic vegetation on phytoplankton biomass has also been reported in warm water bodies (Meerhoff et al., 2007; Muylaert et al., 2010), suggesting a higher sensitivity of these ecosystems to external changes *e.g.* increased nutrient loadings (Meerhoff et al., 2007). The negative correlation between Chl *a* and SAV (data not shown) supports the theory of alternative stable states (Scheffer, 1998), in which planktonic Chl *a* points towards eutrophication in our ponds.

The low variance explained by all classification approaches when predicting the community compositions underlies the unpredictability of phytoplankton assemblages, as chaos may play a role in plankton dynamics (Benincà et al., 2008; Scheffer et al., 2003). Planktonic Chl *a* was significant at all taxonomic and ecological levels, revealing the suitability of all the proxies to capture the main drivers of the phytoplankton assemblages. However, weaker environment–assemblage relationships were less obvious at less-aggregated approaches, since only one out of five key environmental variables was significant at MBFG, despite the highest explained variance in the approaches. In view of our results, we do not recommend the use of ecological and family level approaches for predicting environmental-assemblages relationships, since the higher explained variance is obtained at the expense of information about the community structure. Thus, surrogates should be applied with some caution and selected to match the goal of the study.

Simplifying the numerical resolution reduces time and effort in biomonitoring aquatic ecosystems. Algal assemblage metrics based on planktonic cell densities are good indicators for both water quality and stressors, since estimating densities is less vulnerable to analytical errors than biovolume metrics (Reavie et al., 2010), but most often biomass data have been used. In contrast to previous studies (Carneiro et al., 2010; Kruk et al., 2010), a better fit between ordinations using biomass as opposed to density data, was found using the Procrustean superimpositions approach at species level. However, once the environmental variables were included in the analyses through distLM, our results indicated that time can be saved by analysing phytoplankton densities, since they provided similar patterns to biomass data.

5. Conclusions

We have shown that alternative taxonomic classifications of phytoplankton can be reliable predictors of species richness, richness-environment and assemblage–environment relationships in permanent artificial ponds from Southern Spain. Moreover, phytoplankton richness could be predicted reasonably well from FG and SC. Our study does, however, also highlight weaknesses in some of the classification systems. MBFG approach yielded poor prediction of richness patterns, but was more suitable than SC in explaining phytoplankton assemblages. Although the three proposed ecological classifications of phytoplankton explained more variance than using species level when studying assemblage–environment correlations, the lack of congruence between species and the morphological and functional proxies suggests that genus is the best surrogate of species. Furthermore, our indicate that analyses of density data may perhaps save costs and effort as they show similar capacity in predicting assemblage–environment relationships as when biomass data were used in our dataset. However, in case of a broader assessment of the ecological state of ponds, biomass data would be valuable.

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Appendix A.

List of species in alphabetical order with their corresponding FG codes, according to Reynolds (2006) and Padisák et al. (2009), as well as MBFG codes (Kruk et al., 2010). When 2 or more species from the same genus have identical FG and MBFG codes, they are referred as "*Genus spp*".

Species	FG	MBFG
Acanthosphaera zachariasii	J	IV
Actinastrum hantzschii	J	IV
Anabaenopsis spp	H1	III
Ankyra judayi	X1	IV
Aphanizomenon spp	H1	III
Aphanocapsa spp	K	I
Aphanothece spp	K	I
Arthrospira spp	S2	IV
Asterionella formosa	C	VI
Aulacoseira granulata	P	VI
Botryococcus spp	F	VII
Carteria sp	G	V
Ceratium hirundinella	L_O/L_M	V
Closteriopsis acicularis	P	IV
Closterium spp	P	IV
Coelastrum spp	J	IV
Coelomoron pusillum	LM	I
Coelosphaerium spp	Lo	I
Coenococcus sp	F	VII
Coenocystis cf tapasteana	F	VII
Colacium sp	W1	V
Cosmarium spp	N	IV
Crucigenia tetrapedia	J	IV
Crucigeniella spp	J	IV
Cryptoglena skujae	W1	V
Cryptomonas erosa	Y	V
Cryptomonas tetrapyrenoidosa	Y	V
Cryptomonas marssonii	Y	V
Cryptomonas parapyrenoidifera	X2	V
Cuspidothrix issatschenkoi	H1	III
Cyclotella atomus	B	VI
Cyclotella meneghiniana	C	VI
Cyclotella ocellata	C	VI
Cylindrospermum sp	MP	III
Chaetoceros sp	D	VI
Chlamydomonas spp	X3	V
Chlorella spp	X1	IV
Chlorotetraedron incus	J	IV
Chroococcus spp	Lo	VII
Chrysococcus sp	X3	II
Chrysochromulina parva	X2	II
Desmodesmus spp	J	IV
Dictyosphaerium spp	F	VII
Didymocystis spp	X1	IV
Dinobryon spp	E	II
Discostella spp	D	VI
Dolichospermum spp	H1	III
Dunaliella sp	X2	V
Elakatothrix genevensis	F	IV
Euastrum insulare	P	IV
Eudorina elegans	G	V
Euglena spp	W1	V
Follicularia sp	F	IV
Fragilaria spp	P	VI
Franceia ovalis	J	VII
Gloeotila spp	X2	IV
Golenkinia sp	J	IV
Goniochloris mutica	J	IV
Gonium pectorale	W1	V
Gymnodinium spp	W1	V
Hariotina spp	J	IV
Hyaloraphidium cf contortum	X1	IV
Kirchneriella spp	F	IV
Koliella spp	X3	IV
Komvophoron constrictum	S1	IV
Lagerheimia spp	J	VII
Lemmermaniella pallida	K	I
Lepocinclis ovum	W1	V
Lepocinclis steinii	W1	V
Leptolyngbya spp	S1	IV
Limnothrix sp	S1	IV
Melosira sp	P	VI
Merismopedia spp	Lo	I
Micractinium cf crassisetum	F	IV
Microcystis cf smithii	Lo/M	VII
Microcystis flos-aquae	M	VII
Monomastix sp	X2	VI
Monomorphina pyrum	W	V
Monoraphidium spp	X1	IV
Nephrocytium agardhianum	F	VII
Nephrochlamys spp	F	VII
Nephrodiella cf lunaris	X1	IV
Nitzschia spp	D	VI
Ochromonas sp	X3	II
Oocystidium cf marssonii	F	VII
Oocystis spp	F	VII
Pandorina morum	G	V
Pectodictyon cubicum	J	VII
Pediastrum spp	J	IV
Peridiniopsis spp	Lo	V
Peridinium spp	Lo	V
Phacotus minutum	Xph	VI
Phacus spp	W1	V
Phormidium sp	S1	IV
Planctonema lauterbornii	T	IV
Planktolyngbya spp	S1	IV
Planktosphaeria sp	F	IV
Planktothrix spp	S1	IV
Pleurosigma cf scalproides	D	VI
Pseudanabaena spp	S1	IV
Pseudopedinella sp	X2	II
Pseudoschroederia robusta	X3	IV
Pseudostaurastrum limneticum	X3	IV
Pseudostaurosira brevistriata	D	VI
Pyramimonas sp	X2	VI
Rhodomonas spp	X2	V
Scenedesmus spp	J	IV
Schroederia setigera	X3	IV
Selenastrum bibraianum	X1	IV
Spermatozopsis exsultans	X2	V
Sphaerollopsis sp	X2	V
Spirulina spp	S2	IV
Staurastrum spp	N	IV
Staurodesmus dejectus	N	IV
Stephanodiscus hantzschii	D	VI
Stephanodiscus parvus	C	VI
Strombomonas spp	W2	V
Synechococcus nidulans	K	I
Tetraedron spp	J	IV
Tetraplektron sp	X1	IV
Tetraselmis cordiformis	Y	V
Tetrastrum spp	J	IV
Thorakomonas sp	X2	VI
Trachelomonas spp	W2	V
Treubaria spp	F	IV
Ulnaria acus	D	VI
Willea vihelmii	F	IV
Woloszynskia sp	Lo	V
Woronichinia sp	Lo	I

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