CrossMark

PRIMARY RESEARCH PAPER

A trait-based approach to summarize zooplankton–phytoplankton interactions in freshwaters

**Maite Colina · Danilo Calliari ·
Carmela Carballo · Carla Kruk**

Abstract Assessing zooplankton grazing on phytoplankton is crucial to understand, model, and predict the structure and dynamics of pelagic communities. Our hypothesis is that phytoplankton consumption by zooplankton in freshwater lakes can be well represented by clustering phytoplankton species into morphology-based functional groups (MBFG) and zooplankton species into broad taxonomic units: cladocerans, calanoid copepods, and rotifers. We characterized zooplankton potential grazing on MBFG based on an extensive literature review of experimental data including clearance and ingestion rates. Rotifers show greater potential grazing upon small- and medium-sized species (MBFG I and IV) and presented a Type III trait-based functional response. Cladocerans also show greater potential impact upon MBFG IV but a Type II response. Both groups maintained their respective feeding response regardless of the type of food available, indicating poor food selectivity. Copepods consumed different MBFGs, but a clear Type II pattern was observed when feeding on MBFGs V and VI. Prediction intervals indicated a greater variability in cladocerans' and copepods' response. This approach is a step to summarize and characterize grazing to the future quantification of ecosystem models. Further efforts should be done to include information about different larval stages and phytoplankton traits not directly related to morphology.

Keywords Zooplankton · Phytoplankton · Trait-based functional responses · Functional traits

Handling editor: Mariana Meerhoff

M. Colina (✉) · D. Calliari · C. Carballo · C. Kruk
Ecología Funcional de Sistemas Acuáticos, Universidad de la República, Iguá 4225, C.P. 11400 Montevideo, Uruguay
e-mail: maitecolina@gmail.com

M. Colina · C. Carballo · C. Kruk
Sección Limnología, Instituto de Ecología y Ciencias Ambientales, Universidad de la República, Iguá 4225, C.P. 11400 Montevideo, Uruguay

M. Colina · D. Calliari · C. Carballo · C. Kruk
Centro Universitario de la Región Este, Rocha y Facultad de Ciencias, Universidad de la Republica, Ruta nacional No 9 intersección con ruta No 15 Rocha, Montevideo, Uruguay

D. Calliari
Oceanografía y Ecología Marina, Facultad de Ciencias, Universidad de la República, Iguá 4225, C.P. 11400 Montevideo, Uruguay

Introduction

Determination of zooplankton grazing over phytoplankton is a key issue to understand, model, and

🅐 Springer

predict the dynamics and structure of pelagic communities (Reynolds, 2006; Lampert & Sommer, 2007). In this manner, matter and energy fluxes to higher trophic levels (Lehman, 1988; Sommer, 2008) and into the detritivore pathway (Turner, 2002) can be estimated. Knowledge on food preferences, grazing rates, and patterns may also serve to improve biomanipulation of harmful phytoplankton blooms (Fussmann & Blasius, 2005; Anderson et al., 2010).

The wide range of feeding strategies in zooplankton (Litchman et al., 2013), coupled with the high diversity of phytoplankton species (Reynolds, 2006) compromises the construction of general models and the predictability of zooplankton grazing fluxes and their impact over different phytoplankton communities (Segura et al., 2012; Litchman et al., 2013). Functional traits of both zooplankton (e.g., food preferences, functional response) and phytoplankton (e.g., palatability, quality as food) can affect grazing fluxes (DeMott, 1982; Hansen, 1994; Reynolds, 2006; Barnett et al., 2007). Therefore, one way to summarize that variability without losing too much information about driving processes is using trait-based approaches and clustering organisms into functional groups (Hulot et al. 2000; Hubbell, 2005; Litchman & Klausmeier, 2008).

Rotifers, cladocerans, and calanoid copepods are the main metazoan consumers of freshwater phytoplankton and have relevant differences in relation to grazing behavior (Barnett et al., 2007; Litchman et al., 2013). Rotifers prefer small-sized phytoplankton; cladocerans have a wider spectrum of prey sizes, while copepods usually feed on larger prey (Hansen, 1994; Reynolds, 2006; Lampert & Sommer, 2007). Rotifers and cladocerans typically have a more passive suspension feeding behavior and thus lower prey selectivity (Hansen, 1994; Reynolds, 2006). Differently, copepods are more selective based on the presence of chemoreceptors and mechanoreceptors and a complex feeding apparatus (Koehl & Strickler, 1981; Hansen, 1994; Barnett et al., 2007; Fuchs & Franks, 2010).
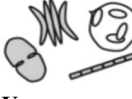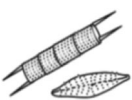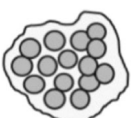
Different morphological and physiological traits of phytoplankton affect their quality as food and their palatability to zooplankton (Reynolds, 2006). Morphological traits affecting grazing include maximum linear dimension (MLD) (Bergquist et al., 1985), and the presence of mucilage and siliceous exoskeletons (Hamm et al., 2003), while physiological traits may

include, for example, toxin production (Kurmayer et al., 2003; Wang et al., 2013; Sarnelle et al., 2010).

Morphology-based functional groups (MBFG) of phytoplankton are an attempt to cluster species into a small number of morphologically and physiologically coherent groups (Kruk et al., 2010). That classification scheme is based on the robust correlation between key physiological and morphological traits of phytoplankton individuals and has proven successful to explain and model community dynamics under different scenarios (Kruk et al., 2011; Caroni et al., 2012; Kruk & Segura, 2012; Segura et al., 2012; Petar et al., 2014; Salmaso et al., 2015). Several of the traits that characterize each of the seven MBFG are relevant features known to affect susceptibility of phytoplankton to zooplankton grazing. MBFG summarize well differences in size among phytoplankton (Table 1). Phytoplankton organism's size determines to a significant degree their susceptibility to different groups of zooplankton, according to optimal size range of prey for each zooplankton group. For example, MBFGs IV and V can be considered optimal prey for large cladocerans. Other morphological traits like the presence of mucilage or formation of filaments, also well summarized within MBFG (Table 1), pose difficulties for organisms with filter type feeding behavior. For cladocerans, filaments (i.e., III) and mucilaginous organisms (i.e., VII) can clog the feeding apparatus (Rothhaupt, 1990; Sarnelle et al., 2010). On the other hand, calanoid copepods are able to manipulate their food and are less affected by these morphological traits (Lampert & Sommer, 2007). MBFG might also account for some physiological traits like toxin production; MBFGs III and VII are composed by several potentially toxic cyanobacteria (Table 1), and large VII are associated to toxic strains (Kurmayer et al., 2003; Wang et al., 2013).

Within the conceptual framework of trait-based ecology, it is also possible to use information at the population level to describe community level responses using explicit integration functions (sensu Violle et al., 2007). At the population level, consumption rate by a predator along a gradient of prey availability follows one of three basic Holling functional response types (Holling, 1959; Porter et al., 1983; Bämstedt et al., 2000). Type I Holling functional response describes a linear increase of ingestion rate with food. Type II functional response describes a linear increase at low prey numbers and progressive

223

Table 1 Morphological description and representative taxa of the seven phytoplankton morphology-based functional groups (MBFG)

MBFG	Description	Representative Taxa	μ_{max} (day^{-1})	V (μm^3)	MLD (μm)	Toxicity	Expected grazing susceptibility
I	Small organisms with high surface/volume	*Chlorella minutissima* *Monoraphidium minutum*	2.08	12.9	5	0	High(but might recover rapidly)
II	Small-flagellated organisms with siliceous exoskeletal structures	*Chromulina gyrans* *Dinobryon cylindricum*	0.54	626	7.3	0	Low
III	Large filaments with aerotopes	*Dolicospermum sp.* *Cylindrospermopsis raciborskii*	0.67	1541	90	1	Low
IV	Organisms of medium size lacking specialized traits	*Scenedesmus acutus* *Chlorella sp.*	1.49	1543	21.8	0	High
V	Unicellular flagellates of medium to large size	*Chlamydomonas reinhardii* *Rhodomonas sp.*	0.89	2444	11.6	1	Medium
VI	Non-flagellated organisms with siliceous exoskeletons	*Thalassiosira weissflogi* *Cyclotella sp.*	0,93	3143	34	0	Medium
VII	Large mucilaginous colonies	*Microcystis aeruginosa* *Aphanocapsa delicatissima*	0,94	43,152	19	1	Low

Average maximum grow rate (μ_{max}), volume (V), maximum linear dimension (MLD), potential toxicity, and expected grazing susceptibility. Data extracted from Kruk et al. (2010)

saturation as prey availability increases, while Type III response is characterized by a sigmoidal pattern. For zooplankton, ingestion by most species can be well represented by a Holling Type II functional response (Gentleman & Neuheimer, 2008). Here, we integrate the information of zooplankton individual species into major taxonomic groups to search for common functions describing their consumption over phytoplankton. We shall refer to these relations as "trait-based functional responses." In this manner, our objective is to characterize adults of rotifers, cladocerans, and calanoid copepods grazing on phytoplankton MBFG in freshwater bodies. We hypothesize that MBFG combined with major zooplankton taxonomic groups (rotifers, cladocerans, and calanoid copepods) represents a useful approach to predict phytoplankton susceptibility to grazing. We set to identify food preferences (reflected in clearance rates) and find integration functions ("trait-based functional responses") describing the relations between ingestion rates and food concentrations of each group of zooplankton on different MBFGs.

Materials and methods

Bibliography search

In order to characterize feeding patterns of rotifers, cladocerans, and calanoid copepods, a systematic bibliographic search was conducted, aimed at experimental information on ingestion and clearance rates of representative freshwater species of the three zooplankton groups upon different phytoplankton species and concentrations. This search covered peer-reviewed journals and was based on pre-established selection criteria. To ensure low heterogeneity of our data, only laboratory experiments performed with individual predator and prey species at comparable conditions were considered (temperature range, photoperiod, and zooplankton density) (Table 2). Data arising from in situ experiments or from laboratory experiments using species mixtures were not included. When possible, experiments designed to describe the functional response of zooplankton taxa were used. For data extracted from functional response experiments, in order to compare clearance and ingestion rates between zooplankton groups, as well as between MBFG for a given zooplankton group, only rates obtained under saturating food conditions were considered (i.e., maximum ingestion rates). For grazing experiments performed under single food concentration conditions, data were included for such comparisons if food levels could be reasonably ascribed to saturating or near saturating levels. For cladocerans, most data were actually derived

from functional response experiments; for rotifers, about half of the data corresponded to functional response experiments, while for copepods, most data were derived from single food level experiments.

In the case of phytoplankton, retrieved information included carbon content and morphology (presence of mucilage, organization level, and siliceous exoskeleton). Zooplankton species were classified into rotifers, cladocerans, and calanoid copepods, and phytoplankton into MBFG (Kruk et al., 2010). We analyzed 221 experiments (reported in 23 papers) similarly spread among the three zooplankton groups (Table 2). We found literature on experiments with representatives of all MBFG except MBFG II, and in the case of MBFG VI, information was not available for experiments with rotifers (Table 2).We only analyzed experiments with non-toxic strains to evaluate the effect of morphology on palatability, discarding possible effects of toxicity. Because nauplii and copepodid stages have different preferences and feeding behavior than adults, and information for such stages was scarce, as a result, we only analyzed experiments performed with adults.

Data analysis

To standardize and compare ingestion and clearance rates, as well as the food concentrations from different experiments, cell numbers were converted to carbon units (μgC l^{-1}) based on individual biovolume and taxon-specific carbon content (Montagnes et al., 1994; Menden-Deuer & Lessard, 2000).

Table 2 Summary of the information contained in the analyzed database including the total number of cases and citations per taxonomic zooplankton group, the number of citations per MBFG (I to VII), and the number of zooplankton and phytoplankton species

The temperature (°C) and density range (ind.ml^{-1}), as well as the photoperiod (daylight hours) of the selected experiments are included

Number of cases	Rotifers	Cladocerans	Copepods
Total experiments	67	91	63
Zooplankton species	10	17	10
Phytoplankton species	9	19	31
Articles included	6	13	10
I	25	4	5
II	–	–	–
III	9	6	25
IV	11	41	11
V	19	24	12
VI	–	10	8
VII	3	6	2
Temperature range (°C)	19–25	17–27	12–24
Photoperiod (daylight hours)	12, 16, 0 h	12, 16, 0 h	12, 16, 0 h
Zooplankton density (ind.ml^{-1})	0.03–125	0.01–0.3	0.016–0.05

Organism size (mm), clearance (ml ind^{-1} d^{-1}), and ingestion rates (µgC ind^{-1} d^{-1}) were compared among zooplankton groups and within MBFG for each group using Kruskal–Wallis and post hoc tests. We used nonparametric statistics since no normal distribution was found for the response variables ($P < 0.05$; Shapiro Test). In order to analyze the possible influence of publication bias, comparisons were repeated 30 times randomly for each group taking each time 1/3 of the individual data. The results obtained with the different subsets were compared using Kruskal–Wallis median test.

Trait-based functional responses were constructed by pooling feeding data from the different species of zooplankton within each major taxonomic group and fitting the three Holling functional response types to the relationship between ingestion rate and food concentration. This was done for each zooplankton group, first considering all phytoplankton species together and secondly separating them according to their classification into MBFG, particularly for those MBFGs most cleared. The best models were chosen according to AIC (Akaike Information Criterion) (Akaike, 1974). AIC values differing by less than two units were considered as indicating that models' adjustment was equivalent (Burnham & Anderson, 2002). Equations fitted to describe trait-based functional responses were

Holling type I response

$$I = k \times C,$$

where k is a constant, slope of the linear trend, free parameter.

Holling type II (Michaelis–Menten equation)

$$I = \left(\frac{C}{kc + C}\right) \times I_{max},$$

kc is the half-saturation constant, i.e., the food concentration C when $I = 1/2 I_{max}$. I_{max} and C are free parameters.

Holling type III

$$I = \frac{I_{max}}{1 + ka \times e^{-kb \times C}},$$

where ka and kb are constants. I and C are free parameters.

In all cases, I is the ingestion rate (µgC ind^{-1} d^{-1}), C is the resource concentration (µgC l^{-1}), and I_{max} is the maximum ingestion rate (µgC ind^{-1} d^{-1}).

Prediction intervals were calculated to each fitted model. All analyses were performed in RStudio (R Core Team, 2013). For models, function "nlm" was used, and for prediction ranges, function "plotFit" from "investr" peakage was used.

Results

Maximum food concentrations used in the evaluated experiments varied from less than 10000 to more than 80,000 µgC l^{-1} (Fig. 1). For rotifers, the highest phytoplankton concentration was for experiments with MBFG I. In the case of cladocerans and copepods, the widest gradient concentrations corresponded to MBFG IV (Fig. 1).

Body size ($\chi_2^2 = 100.2$; $P < 0.001$), maximum clearance rates ($\chi_2^2 = 70.9$; $P < 0.001$), and ingestion rates ($\chi_2^2 = 37.9$; $P < 0.001$) differed significantly among zooplankton groups in the evaluated set of papers. Cladocerans and copepods were larger and developed significantly higher maximum clearance and ingestion rates than rotifers (Fig. 2).

Significant differences were also found between zooplankton groups in terms of food preferences and palatability on MBFG, as indicated by differential clearance and ingestion rates upon MBFGs. Rotifers ($\chi_4^2 = 34.8$; $P < 0.001$) ($\chi_4^2 = 24.1$; $P < 0.001$) and cladocerans ($\chi_5^2 = 34.5$; $P < 0.001$) ($\chi_5^2 = 34.8$; $P < 0.001$) had significantly different clearance and ingestion rates among MBFG. Rotifers cleared to a greater extent MBFG I and IV, but the highest ingestion occurred for MBFG I. In the case of cladocerans, MBFGs IV and VI were the most cleared groups, followed by MBFG V. MBFG VI, however, showed low ingestion rates. Clearance rates by copepods did not differ significantly among MBFG ($\chi_5^2 = 9.2$; $P = 0.1$). Clearance rates on MBFG I, II, V, and VI were highly variable, while clearance on MBFG IV was low. However, ingestion differed among MBFG ($\chi_5^2 = 10.4$; $P = 0.06$), being groups V and VI, the most ingested (Fig. 3). Comparison to evaluate possible article derived bias of clearance rates among groups using the entire database and randomly selected cases produced similar results (rotifers:
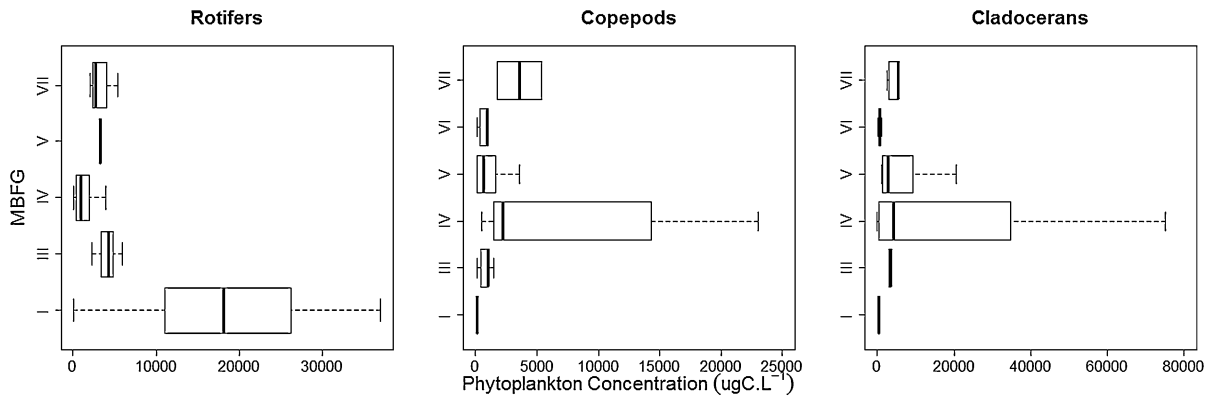
Fig. 1 Phytoplankton concentrations (µg C l^{-1}) in grazing experiments performed with rotifers, cladocerans, and calanoid copepod. Phytoplankton species are grouped into morphology-based functional groups (MBFG). *Box-plots* indicating the median, 1st and 3rd quartile with the dotted line representing the total range
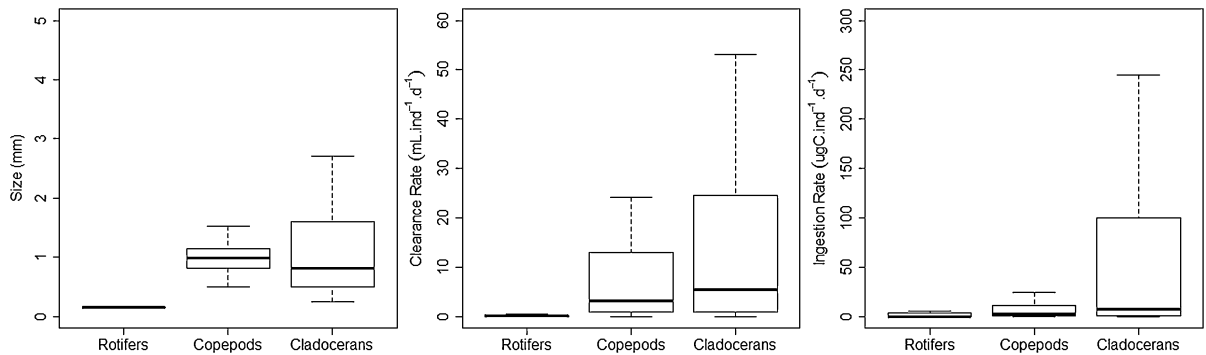

Fig. 2 Size (mm), clearance rate (ml ind^{-1} day^{-1}), and ingestion rate (µgC ind^{-1} day^{-1}) for each zooplankton taxonomic group from the reviewed experiments. *Box plots* indicate the median, 1st and 3rd quartile, and the dotted line represents the total range

$20.0 < \chi^2_4 < 27.7$, $P < 0.001$, cladocerans: $18.2 < \chi^2_5 < 27.1$ $P < 0.01$; calanoids: $6.5 < \chi^2_5 < 8.7$, $P < 0.5$).

Consumption rates by rotifers and cladocerans were best described by Type III and Type II trait-based functional response models, respectively. For copepods, both Types I and II were selected as the best models (Fig. 4; only Type II adjustment shown).

For rotifers, Type III functional response model best fitted consumption both when all MBFGs were included in the dataset, and when only the most cleared MBFG (i.e., I) was included. In both cases, similar parameters were obtained, with a low I_{max} (4.7–4.8 µgCind^{-1} d^{-1}). For cladocerans, also similar Type II functional responses were obtained for all MBFGs pooled together and for the most cleared

MBFG (IV). However, for that case, when only MBFG IV was considered Type I and Type II responses similarly fitted the data. Results indicated higher I_{max} for cladocerans than for rotifers (Fig. 4). For both zooplankton groups, tests of other single MBFG did not result in significant fit to any functional response type. For copepods, it was not possible to fit a model combining all MBFGs. A model corresponding to a functional response Type II fitted copepods' ingestion on pooled and separated MBFG V and VI, although it was not different from a Type I response (Table 3). The relation between ingestion rates and other MBFG did not result in any significant functional response. Prediction intervals indicating the variability in trait-based functional responses were relatively narrow for rotifers and cladocerans and being wider for copepods (Fig. 4).
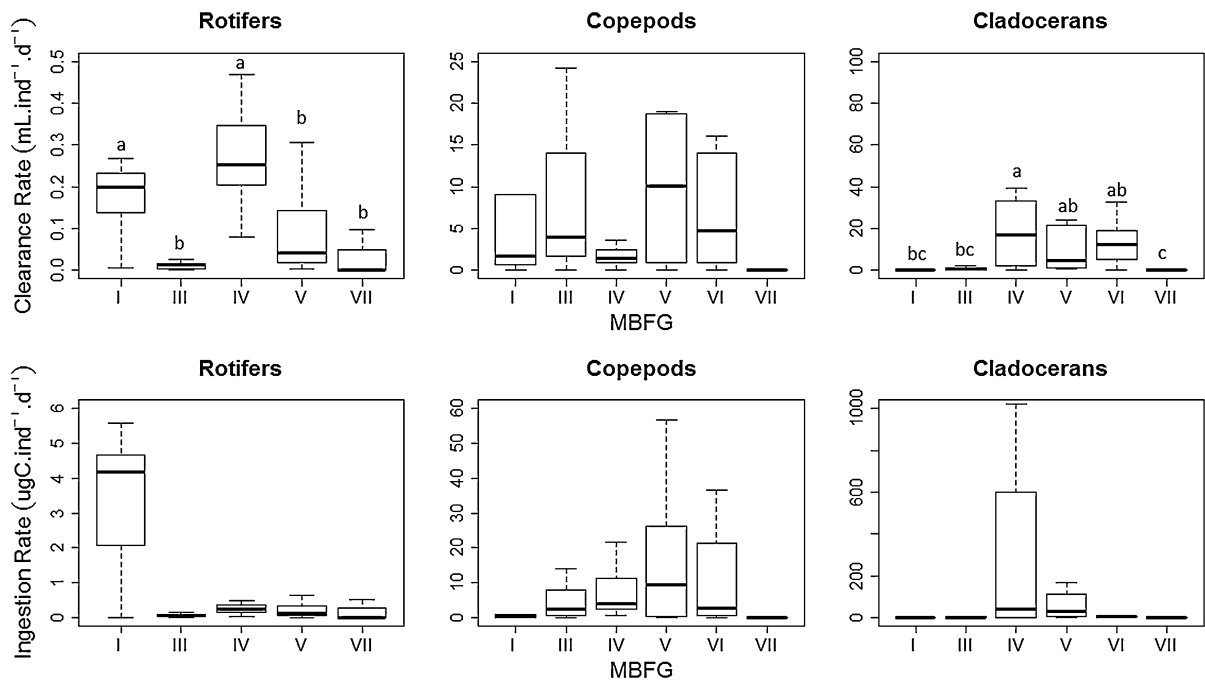
Fig. 3 Clearance rates (ml ind^{-1} day^{-1}) and ingestion rates (ml ind^{-1} day^{-1}) for each taxonomic group of zooplankton on each phytoplankton MBFG. *Box plots* indicate the median, 1st and 3rd quartile, and the dotted line represents the total range. For rotifers and cladocerans, significantly different groups according to clearance rate (post hoc analyses) are presented

Discussion

Present analysis indicates that functional responses of freshwater zooplankton grazing can be described by grouping zooplankton species into broad taxonomic groups and phytoplankton species into MBFG. Information at the individual level allowed us to construct trait-based functional relations at the community level. These results imply that at least some of the morphological features captured in the MBFGs (i.e., MLD, presence of mucilage) constitute important traits determining phytoplankton susceptibility to grazing, in agreement with previous studies (Reynolds, 2006; Lampert & Sommer, 2007).

We found clear significant differences in mean body size, clearance and ingestion rates, size range, and morphological traits of preferred food among the three zooplankton groups. Larger body sizes are related to higher clearance and ingestion rates, and to larger prey sizes (Hansen, 1994; Barnett et al., 2007; Kâ et al., 2012). Concordantly, we found larger body sizes and higher clearance and ingestion rates in cladocerans and copepods, compared to those of rotifers. Both microcrustaceans also preferred large-sized prey (IV, III, VI, and V). The three zooplankton groups differ in relation to foraging behavior (Litchman et al., 2013). Rotifers and cladocerans only consume prey retained by their feeding apparatus (Rubenstein & Koehl, 1977; Barnett et al., 2007). Else copepods select and manipulate prey (Reynolds, 2006; Lampert & Sommer, 2007). Those differences were reflected in a broader spectrum of MBFG consumed by copepods compared to that ingested by cladocerans and rotifers and in different functional responses among zooplankton groups. It was not possible to include consumption rates of different life stages, because of gaps in the available literature. This can be especially important for the calanoid group, where nauplii and copepodid stages have different preferences and behaviors than adults and can be abundant in freshwater bodies (Mauchline, 1998).

MBFG summarized well grazing susceptibility and palatability of phytoplankton. Species with similar morphologies have comparable susceptibility to grazing. This has been repeatedly shown before for individual traits, but few combined both continuous and categorical traits (i.e., Hulot et al., 2000). One advantage of using MBFG is that species within each
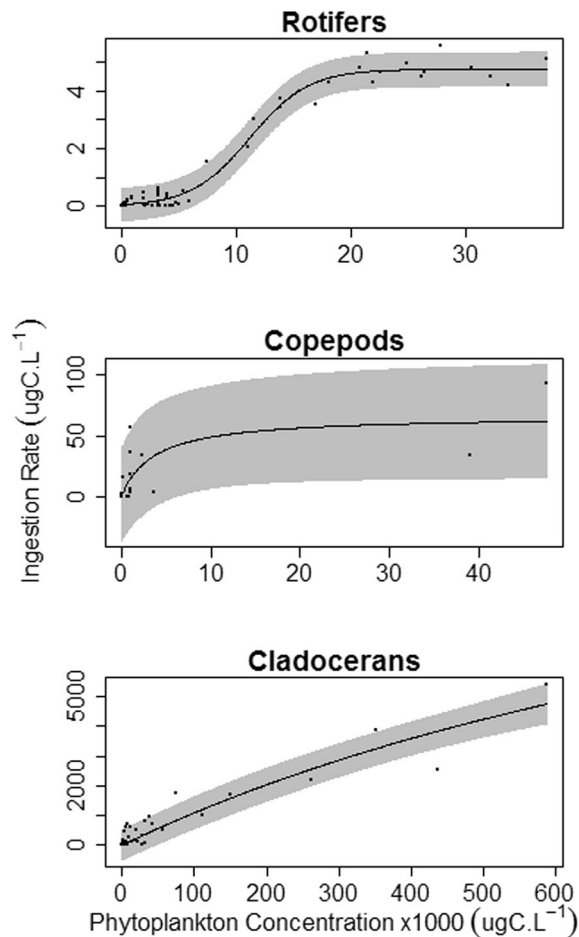
Fig. 4 *Data* and models fitted to the trait-based functional responses describing the relation between the ingestion rate (μgC ind^{-1} day^{-1}) and the phytoplankton concentration (μgC l^{-1}) for rotifers (Holling Type III) and cladocerans (Holling Type II) on all MBFG together and copepods on MBFGs V and VI. The gray area represents the prediction intervals

group are considered functionally similar and therefore potentially interchangeable. Therefore, information regarding some representatives of each group would allow to properly infer the zooplankton–phytoplankton interactions without the need to relay on detailed species by species information. Still, broader information regarding some MBFG with scarce representation might improve the results, as is the case of group VII. No results were obtained for MBFG II because no information was found in the literature.

Group IV was the most ingested and cleared by both zooplankton groups, rotifers and cladocerans. This

might result from a combination of particular morphologies: medium size and absence of structures which might hinder manipulation (i.e., mucilage, spines, silica walls) (Kruk et al., 2010) (Table 1). Additionally, some representative species from MBFG IV, like *Scenedesmus* sp have potentially high nutritional quality for cladocerans and rotifers (Rothhaupt, 1995) provided their high fatty acid contents (Ahlgren et al., 1990; Sterner et al., 1993; Boersma, 2000).

MBFG I was highly ingested and cleared by rotifers. This MBFG includes organisms of small size (MLD range 0.8–43.6 μm) without ingestion-limiting structures (Kruk et al., 2010) (Table 1). As a result, they might be considered a good food source for microphagous suspensivores. Cladocerans, however, showed low clearance rates over that MBFG. Clearance rates of cladocerans are normally highest over an optimum predator:prey size ratio of 50:1 (Hansen, 1994; Fuchs & Franks, 2010; Wirtz, 2012). The predator:prey ratio in our dataset (predator mean size/ prey mean size) regarding cladocerans preying on MBFG I is 140:1, that is, ca. 3 times higher than the expected optimal (Hansen, 1994). Organisms belonging to MBFG I are thus likely too small for cladocerans and are probably retained by the feeding apparatus with a low efficiency, their consumption implies high energy expenditure with a low energy returns (Rubenstein & Koehl, 1977). This should not be taken as asserting that cladocerans and rotifers do not (cannot) feed on very small-sized phytoplankton. Strictly speaking, clearance rates represent a metric of feeding efficiency (how easily the predators extract food particles from a volume of water); so, even if a grazer has a relatively low clearance rate ("preference") for small-sized algae, it may still develop high consumption rates if these algae are provided at very high concentrations.

MBFG VI clusters phytoplankton species of medium to large size, with silica exoskeleton and is comprised just by diatoms (Kruk et al., 2010) (Table 1); our database did not include species with spines. Cladocerans showed high clearance rates, but low ingestion rates upon MBFG VI. Indicating that, diatoms can be removed from water by cladocerans but are not successfully exploited as food. Silica walls protect the cells against mechanical pressure and provide a barrier against zooplankton grazing (Hamm et al., 2003). Copepods cleared and ingested VI

Table 3 Results of the different models applied to explain the functional relations between ingestion rate and phytoplankton concentrations of the zooplankton taxonomic groups

	Type I ΔAIC	Type II ΔAIC	Type III ΔAIC	Parameters for the best model	P value	% Std. error
Rotifers						
On all MBFG	106.5	102.6	0	$I_{max} = 4.7$	<0.01	0.15
				$ka = 11.1$	<0.01	0.6
				$kb = 2.9$	<0.01	0.3
Only on MBFG I	39.4	13.4	0	$I_{max} = 4.8$	<0.01	2.1
				$ka = 10.8$	<0.01	4.8
				$kb = 3.2$	<0.01	15.4
Cladocerans						
On all MBFG	25.6	0	26.6	$I_{max} = 5601$	<0.01	15.0
				$Kc = 337957$	<0.01	25.6
Only on MBFG IV	0.8	0	23.2	$Imax = 12950$	0.01	37.7
				$kc = 1034296$	0.06	52.1
Copepods						
On MBFG V and VI	0	0.2	341.2	$I_{max} = 66.3$	<0.01	22.7
				$kc = 3541.6$	0.1	60.0

ΔAIC values were calculated considering the model with the minimum AIC as 0. For rotifers and cladocerans, adjustments were performed over the whole set of species together and over the more palatable MBFG. Copepods' analyses were performed only considering MBFG V and VI. Parameters and their significant coefficients for the models with the lower AIC values are presented

representatives but without a clear orientation for them.

Cladocerans also showed a preference for MBFG V. This group includes medium- to large-sized flagellates (Kruk et al., 2010) (Table 1). MBFG V also clusters species of high nutritional quality due to their high content of poly-unsaturated fatty acids (PUFAs) (Brett et al., 2006). It has been argued that frequent changes in swimming direction in flagellated organisms might decrease encounter rates with zooplankton predators (Stocker & Durham, 2009). However, the present evidences from laboratory experiments indicate that such feature did not limit their consumption by cladocerans. In this analysis, large representatives of MBFG V (i.e., *Ceratium*) were not included as there are not usually consumed by zooplankton, and no experimental data were available (Ahlgren et al., 1990; Santer, 1996). This should be considered when applying the present results. No information of large-flagellated colonies (i.e., *Pandorina*, *Volvox*) was included as these organisms were not originally considered in the MBFG classification (Kruk et al., 2010).

According to our database, copepods did not have clear preferences for any MBFG, showing similar clearance and ingestion rates over several MBFGs (III,

IV, V, and VI). The presence of mechanoreceptors, chemoreceptors, and specialized muscles to manipulate prey might enable them to feed on a greater diversity of phytoplankton groups (Mauchline, 1998; Barnett et al., 2007; Litchman et al., 2013).

MBFGs III and VII include blooming and potentially toxic species. Predicting grazing pressure over these groups might be useful to design biological control strategies and prevent noxious blooms (Boon et al., 1994; Perrow et al., 1997). Group VII is characterized by large colonies with mucilage that are not palatable to most zooplankton (Rolland & Hans, 1987), upon this MBFG, clearance and ingestion rates were zero or close to zero for all zooplankton groups. For MBFG VII, the largest and denser colonies can be related to toxins production (Kurmayer et al., 2003; Wang et al., 2013); palatability upon this morphology can be a useful indicator. Group III comprises long filaments with aerotopes. The organisms in this group have a low vulnerability to consumption due to their large size and potential toxicity (Kruk et al., 2010). However, some species from MBFG III were cleared and ingested by copepods. This coincides with field studies showing that copepods might graze well on species classified into that MBFG (Rolland, 1988; Burns & Hegarty, 1994). Cladocerans like *Daphnia*

would be strongly affected by blooms of MBFG III due to the obstruction of their filtering apparatus by long and large filaments, their greater susceptibility to toxins and the generally low nutritional value of species within this MBFG (Rolland & Hans, [1987](); Sarnelle et al., [2010]()). A potential biological control of this toxic MBFG might focus on increasing the abundance of zooplankton groups that prey on them (Boon et al., [1994]()). Calanoid copepods seem to be the most adequate group for that purpose as they have high clearance rates and, according to literature, might not be as negatively affected as cladocerans (Koski et al., [2002]()).

Ecosystem effect of phytoplankton and zooplankton interactions will depend on the structure of the fish community. According to the Size Efficiency Hypothesis (Brooks & Dodson, [1965]()), in a system dominated by planktivorous fish, the zooplankton community will be mainly composed by small zooplankton species of rotifers and cladocerans. On the other hand, with low planktivorous fish abundance, large zooplankton species are expected to be dominant (large cladocerans and calanoid copepods). In the first scenario, species from MBFG I and IV will be more cleared, while MBFGs III, VI, or V will be mostly grazed in the second.

For MBFG II (comprising only Chrysophyceae), it was not possible to find information matching our selection criteria. However, phytoplankton of MBFG II was considered a good food source for cladocerans and calanoids according to Lehmalz & Sandgren ([1985]()). These authors found that under the presence of *Uroglena* sp., zooplankton biomass was kept constant indicating that phytoplankton was used as food.

The Type III trait-based functional response best described the relationship between rotifers ingestion rates and phytoplankton concentration (all MBFG pooled), and a similar pattern had been earlier described for rotifers individual species (Fussmann et al., [2005]()). Sigmoid functional responses have been associated with the learning ability of the predator (Real, [1977]()), a feature not usually expected for zooplankton (Jeschke et al., [2004]()). That pattern may also result from a shift in the predator search behavior at low food concentrations, so that encounter rate with food particles progressively increases with minor increments in food concentration when that is present at very low levels (Real, [1977]()). Such simple behavioral change in reaction to perceived food level seems

a more realistic explanation for this result when considering only one species. Here, where several species of predators and preys are included, the Type III pattern might arise from the overlay of several responses of different phytoplankton and rotifer species combinations. For Cladocerans, the Type II response produced the best fit when all phytoplankton species were included. Type II response suggests a higher competitive capacity of cladocerans at low food concentrations in contrast to Type III (Porter et al., [1983](); Martinez, [2000]()). Development of a trait-based functional response Type II and significantly higher absolute rates by cladocerans indicates a strongly higher grazing pressure by cladocerans compared to rotifers. Considering only the most palatable MBFG for cladocerans, Type II and I responses performed equally well. This might be the result of the high variability of the data analyzed. For both rotifers and cladocerans (separately), the fitted response was very similar when using all MBFG pooled together and when only the most palatable MBFG was considered. Such results lead us to suppose that rotifers and cladocerans develop similar foraging behavior independently of the food presented. This is supported by other authors who describe a low selective character of cladocerans and rotifers (Barnett et al., [2007](); Litchman et al., [2013]()).

For copepods, the best trait-based functional responses (Type II and I) were found for MBFGs V and VI but not when including all MBFGs. These results may arise due to a more selective foraging behavior by copepods, as well as the combination of different copepod species with different preferences in our dataset. The features that make copepods able to manipulate different phytoplankton morphotypes contribute to their capacity to select food (Mauchline, [1998](); Barnett et al., [2007](); Litchman et al., [2013]()).

The functional response of a predator species can be highly variable against different types of prey (Besiktepe & Dam, [2002]()). However, we were able to construct explicitly formulations to scale-up from individual traits to community functions (sensu Violle et al., [2007]()) combining different predator and prey species. The similarly with functional responses at the species level supports the application of these trait-based functional responses to summarize trophic relationships between freshwater phytoplankton and zooplankton species. Albeit these responses showed noisy in some cases, reflected in prediction intervals

(Fig. 4). We believe that this variability within each zooplankton group can be explained including body size and feeding behavior diversity as new variables. In these sense, the groups with higher variability were copepods (due to their high feeding behavior diversity) and cladocerans (due to their high body size range).

In summary, current analysis indicates that grazing behavior of freshwater zooplankton might be well described by organizing consumer species into major taxonomic groups and phytoplankton into MBFG. However, the approach has limitations related to the structure of the database analyzed. Further effort should be undertaken to include information of nauplii and copepodid life stages and of some poorly represented MBFG as is the case of VII and II. These limitations might be overcome by performing more grazing experiments for individual species or by evaluating the potential interchangeability of the species within each zooplankton and phytoplankton group. In this scenario, the relevance of traits as a better representation of biological interactions might defeat the practical limitation of performing all the required individual experiments (Hulot et al., 2000; Hubbell, 2005; Litchman & Klausmeier, 2008). Experiments with natural communities combining different groups and time series analysis should also increase the present results validity. The quantification of trait values describing phytoplankton–zooplankton fluxes (i.e., the parameters of trait-based functional responses) is an important step toward the formulation of quantitative ecosystem models and to new hypotheses (Litchman et al., 2013). A further prospect is to analyze the relationship between body size and consumption rates within each zooplankton group.

References

Ahlgren, G., L. Lundstedt, M. Brett & C. Forsberg, 1990. Lipid composition and food quality of some freshwater phytoplankton for cladoceran zooplankters. Journal of Plankton Research 12: 809–818.

Akaike, H. A. I., 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19: 716–722.

Anderson, T. R., W. C. Gentleman & B. Sinha, 2010. Influence of grazing formulations on the emergent properties of a complex ecosystem model in a global ocean general circulation model. Progress in Oceanography 87: 201–213.

Bämstedt, U., D. J. Gifford, X. Irigoien, A. Atkinson & M. Roman, 2000. Feeding. In Harris, R., P. Wiebe, J. Lenz, H. R. Skjoldal & M. Huntley (eds), ICES zooplankton methodology manual. Academic Press, San Diego: 297–399.

Barnett, A. J., K. Finlay & B. E. Beisner, 2007. Functional diversity of crustacean zooplankton communities: towards a trait-based classification. Freshwater Biology 52: 796–813.

Bergquist, A. M., S. R. Carpenter & J. C. Latino, 1985. Shifts in phytoplankton size structure and community composition during grazing by contrasting zooplankton assemblages. Limnology and Oceanography 30: 1037–1045.

Besiktepe, S. & H. G. Dam, 2002. Coupling of ingestion and defecation as a function of diet in the calanoid copepod *Acartia tonsa*. Marine Ecology Progress Series 229: 151–164.

Boersma, M., 2000. The nutritional quality of P-limited algae for *Daphnia*. Limnology and Oceanography 45: 1157–1161.

Boon, P. I., S. E. Bunn, J. D. Green & R. J. Shiel, 1994. Consumption of cyanobacteria by freshwater zooplankton: implications for the success of "top-down" control of cyanobacterial blooms in Australia. Marine and Freshwater Research 45: 875–887.

Brett, M. T., C. Müller-Navarra, A. P. Ballantyne, J. L. Ravet & C. R. Goldman, 2006. Daphnia fatty acid composition reflects that of their diet. Limnology and Oceanography 51: 2428–2437.

Brooks, J. & S. Dodson, 1965. Predation, body size and composition of plankton. Science 150: 28–35.

Burnham, K. P. & D. R. Anderson, 2002. Model Selection and Multimodel Inference. A Practical Information Theoretic Approach. Springer, New York.

Burns, C. W. & B. Hegarty, 1994. Diet selection by copepods in the presence of cyanobacteria. Journal of Plankton Research 16: 1671–1690.

Caroni, R., G. Free, A. Visconti & M. Manca, 2012. Phytoplankton functional traits and seston stable isotopes signature: a functional-based approach in a deep, subalpine lake, Lake Maggiore (N. Italy). Journal of Limnology 71: 84–94.

DeMott, W. R., 1982. Feeding selectivities and relative ingestion rates of *Daphnia* and *Bosmina*. Limnology and Oceanography 27: 518–527.

Fuchs, H. & P. Franks, 2010. Plankton community properties determined by nutrients and size-selective feeding. Marine Ecology Progress Series 413: 1–15.

Fussmann, G. F. & B. Blasius, 2005. Community response to enrichment is highly sensitive to model structure. Biology Letters 1: 9–12.

Fussmann, G. F., G. Weithoff & T. Yoshida, 2005. A direct, experimental test of resource versus consumer dependence. Ecology 86: 2924–2930.

Gentleman, W. C. & A. B. Neuheimer, 2008. Functional responses and ecosystem dynamics: how clearance rates explain the influence of satiation, food-limitation and acclimation. Journal of Plankton Research 30: 1215–1231.

Hamm, C. E., R. Merkel, O. Springer, P. Jurkojc, C. Maier, K. Prechtel & V. Smetacek, 2003. Architecture and material properties of diatom shells provide effective mechanical protection. Nature 421: 841–843.

Hansen, B., 1994. The size ratio between planktonic predators and their prey. Limnology and Oceanography 39: 395–403.

Holling, H. S., 1959. Some characteristics of simple types of predation and parasitism. The Canadian Entomologist 91: 385–398.

Hubbell, S. P., 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. Functional Ecology 19: 166–172.

Hulot, M., G. Lacroix, L. M. Francoise & M. Loreau, 2000. Functional diversity governs ecosystem response to nutrient enrichment. Nature 405: 340–344.

Jeschke, J. M., M. Kopp & R. Tollrian, 2004. Consumer-food systems: why type I functional responses are exclusive to filter feeders. Biological Reviews of the Cambridge Philosophical Society 79: 337–349.

Kâ, S., J. M. Mendoza-Vera, M. Bouvy, G. Champalbert, R. N'Gom-Kâ & M. Pagano, 2012. Can tropical freshwater zooplankton graze efficiently on cyanobacteria? Hydrobiologia 679: 119–138.

Koehl, M. A. R. & J. R. Strickler, 1981. Copepod feeding currents: food capture at low Reynolds number. Limnology and Oceanography 26: 1062–1073.

Kruk, C. & A. Segura, 2012. The habitat template of phytoplankton morphology-based functional groups. Hydrobiologia 698: 191–202.

Koski, M., K. Schmidt, J. Engström-öst, M. Viitasalo, S. Repka & K. Sivonen, 2002. Calanoid copepods feed and produce eggs in the presence of toxic cyanobacteria Nodularia spumigena. Limnology and Oceanography 47: 878–885.

Kruk, C., V. L. M. Huszar, E. T. H. M. Peeters, S. Bonilla, L. Costa, M. Lürling, C. S. Reynolds & M. Scheffer, 2010. A morphological classification capturing functional variation in phytoplankton. Freshwater Biology 55: 614–627.

Kruk, C., E. T. H. M. Peeters, E. H. Van Nes, V. L. M. Huszar, L. S. Costa & M. Scheffer, 2011. Phytoplankton community composition can be predicted best in terms of morphological groups. Limnology and Oceanography 56: 110–118.

Kurmayer, R., G. Christiansen & I. Chorus, 2003. The abundance of microcystin-producing genotypes correlates positively with colony size in Microcystis sp. and determines its microcystin net production in Lake Wannsee. Applied and Environmental Microbiology 69: 787–795.

Lampert, W. & U. Sommer, 2007. Limnoecology. Oxford University Press, New York: 152–180.

Lehmalz, J. T. & C. D. Sandgren, 1985. Species-specific rates of growth and grazing loss among freshwater algae. Limnology and Oceanography 30: 34–46.

Lehman, J. T., 1988. Ecological principles affecting community structure and secondary production by zooplankton in marine and freshwater environments. Limnology and Oceanography 33: 913–945.

Litchman, E. & C. A. Klausmeier, 2008. Trait-based community ecology of phytoplankton. Annual Review of Ecology Evolution and Systematics 39: 615–639.

Litchman, E., M. D. Ohman & T. Kiorboe, 2013. Trait-based approaches to zooplankton communities. Journal of Plankton Research 35: 473–484.

Martinez, G., 2000. Conducta alimentaria de Daphnia ambigua Scourfield 1947, Moina micrura Kurz 1874 years Ceriodaphnia dubia Richard 1895 (Cladocera) frente a un gradiente de concentración de alimento. Revista Chilena de Historia Natural 73: 47–54.

Mauchline, J., 1998. The biology of calanoid copepods. Crustaceana 81: 763–764.

Menden-Deuer, S. & E. J. Lessard, 2000. Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. Limnology and Oceanography 45: 569–579.

Montagnes, D. J. S., J. A. Berges, P. J. Harrison & F. J. R. Taylor, 1994. Estimating carbon, nitrogen, protein, and chlorophyll a from volume in marine phytoplankton. Limnology and Oceanography 39: 1044–1060.

Perrow, M. R., M. Meijer, P. Dawidowicz & H. Coops, 1997. Biomanipulation in shallow lakes: state of the art. Hydrobiologia 342(343): 355–365.

Petar, Ž., G. U. Marija, K. B. Koraljka, P. M. Anđelka & P. Judit, 2014. Morpho-functional classifications of phytoplankton assemblages of two deep karstic lakes. Hydrobiologia 740: 147–166.

Porter, K. G., J. D. Orcutt & J. Gerritsen, 1983. Functional response and fitness in a generalist filter feeder, Daphnia Magna (Cladocera: Crustacea). Ecology 64: 735–742.

R Core Team, 2013. R: A Language and Environment for statistical computing. Vienna, Australia: R Foundation for 291 Statistical Computing.

Real, L. A., 1977. The kinetics of functional response. The American Naturalist 111: 289–300.

Reynolds, C. S., 2006. Ecology of phytoplankton. Cambridge University Press, New York: 250–292.

Rolland, S. F. I., 1988. Grazing on filamentous algae by herbivorous zooplankton. Freshwater Biology 20: 263–271.

Rolland, S. F. I. & W. P. Hans, 1987. Effects of colonial morphology on zooplankton utilization of algal resources during blue green algal (Microcystis aeruginosa) blooms. Limnology and Oceanography 32: 634–644.

Rothhaupt, K. O., 1990. Changes of the functional responses of the rotifers Brachionus rubens and Brachionus calyciflorus with particle sizes. Limnology and Oceanography 35: 24–32.

Rothhaupt, K. O., 1995. Algal nutrient limitation affects rotifer growth rate but not ingestion rate. Limnology and Oceanography 40: 1201–1208.

Rubenstein, D. & M. A. R. Koehl, 1977. The mechanism of filter feeding: some theoretical considerations. The American Naturalist 111: 981–994.

Salmaso, N., L. Naselli-Flores & J. Padisák, 2015. Functional classifications and their application in phytoplankton ecology. Freshwater Biology 60: 603–619.

Santer, B., 1996. Nutritional suitability of the dinoflagellate Ceratium furcoides for four copepod species. Journal of Plankton Research 18: 323–333.

Sarnelle, O., S. Gustafsson & L. A. Hansson, 2010. Effects of cyanobacteria on fitness components of the herbivore *Daphnia*. Journal of Plankton Research 32: 471–477.

Segura, A. M., C. Kruk, D. Calliari & H. Fort, 2012. Use of a morphology-based functional approach to model phytoplankton community succession in a shallow subtropical lake. Freshwater Biology 58: 504–512.

Sommer, U., 2008. Trophic cascades in marine and freshwater plankton. International Review of Hydrobiology 93: 506–516.

Sterner, R. W., D. D. Hagemeier, W. L. Smith, R. F. Smith, L. Smith & F. Smith, 1993. Phytoplankton nutrient limitation and food quality for Daphnia. Limnology and Oceanography 38: 857–871.

Stocker, R. & W. M. Durham, 2009. Tumbling for stealth? Science 325: 400–402.

Turner, J. T., 2002. Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms. Aquatic Microbial Ecology 27: 57–102.

Violle, C., M. L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel & E. Garnier, 2007. Let the concept of trait be functional! Oikos 116: 882–892.

Wang, X., M. Sun, M. Xie, M. Liu, L. Luo, P. Li & F. Kong, 2013. Differences in microcystin production and genotype composition among *Microcystis* colonies of different sizes in Lake Taihu. Water Research 47: 5659–5669.

Wirtz, K., 2012. Who is eating whom? Morphology and feeding type determine the size relation between planktonic predators and their ideal prey. Marine Ecology Progress Series 445: 1–12.