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PRIMARY RESEARCH PAPER

Enhanced ecological indication based on combined planktic and benthic functional approaches in large river phytoplankton ecology

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Abstract The occurrence of benthic diatoms in large river plankton is considered to be highly stochastic. Accordingly, the widely applied phytoplankton functional group concept sensu Reynolds (FG) classifies all benthic diatom taxa together. Based on data of a high-frequency 1-year long phytoplankton survey of the Pearl River (China), we tested whether the combination of the FG system with various trait-based classifications of benthic diatoms enhances our ability in predicting the community composition from the local environment. Using the Self-Organizing Map approach, we identified characteristic community compositions based on (i) taxonomic data, (ii) the FG approach, and (iii) the FG system combined with trait-based functional approaches of benthic diatoms: size structure, ecological guilds, and eco-morphological groups. All combined functional approaches enabled better predictions for the community composition than the taxonomic data or the FG system alone. The most reliable approach was the combination of the FG system with ecological guilds of benthic diatoms. Therefore, the occurrence of benthic diatoms in large river phytoplankton can be assessed ecologically in a meaningful way based on combined planktic and benthic functional classifications. The application of this approach seems to be highly relevant in large river

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phytoplankton ecology, ecological modelling, or in ecological status indication.

Keywords Benthos · Diatoms · Ecological guilds · Functional groups · Functional traits · Potamoplankton

Introduction

Upstream river sections have slight seasonality and relatively constant environmental conditions (Vannote et al., 1980), where the short water residence time selects for benthic algal dominance (Leitão & Lepretre, 1998; Leland, 2003; Ács et al., 2006). Therefore, benthic diatoms are present in all seasons in upstream rhithral river sections (Abonyi et al., 2012; Bolgovics et al., 2017). Further downstream, however, their occurrence depends highly on alterations of the physical environment, especially in the river flow. The further in distance from the source, the higher seasonality overcomes in structuring the community composition of river phytoplankton (Abonyi et al., 2012). Euplanktic algae are only expected to develop in the middle sections of large rivers due to favorable conditions (Reynolds & Descy, 1996). In middle and downstream river sections, however, the occurrence of benthic diatom taxa is considered to be highly stochastic.

According to Reynolds et al. (2002), characteristic species associations do occur in the phytoplankton, according to more or less well-defined sets of environmental conditions. The phytoplankton functional group (FG) approach was originally developed for lake phytoplankton, and did not include benthic algae. Later, an additional functional group including meroplanktic taxa (codon MP) was proposed for lake phytoplankton (Padisák et al., 2006). Borics et al. (2007) implemented the FG approach in river phytoplankton ecology, and proposed supplementary FGs for benthic taxa including codon TB for benthic diatoms. The FG approach sensu Reynolds (Reynolds et al., 2002) has now been applied widely to better understand mechanisms shaping the community composition of river phytoplankton (Devercelli, 2006; Stanković et al., 2012; Stević et al., 2013; Abonyi et al., 2014; Borics et al., 2014). However, some limitations have also been highlighted. Abonyi et al. (2012) argued that the FG approach did not separate between natural and human-induced dominance among benthic diatoms, nor did penalize invasive species. The need for a more detailed functional classification of pennate diatoms has also been emphasized in the context of the understanding potamoplankton community structuring along large rivers (Abonyi et al., 2014).

One of the most frequently applied functional classifications of benthic diatoms is the diatom ecological guild system (Passy, 2007), modified by Rimet and Bouchez (2012). The recognition of redundancy in the ecological characteristics of diatom taxa has led to the development of this approach. The diatom ecological guild concept classifies diatom taxa based on functional and/or morphological traits, which approach also provides basis for recently developed ecological status assessment methods (Tapolczai et al., 2016). Diatom ecological guilds make possible the identification of key environmental factors affecting the functional community composition (Rimet & Bouchez, 2011; Stenger-Kovács et al., 2013; B-Béres et al., 2014; Marcel et al., 2017). The advantage of such approaches lies in their relatively simple application, which enables users to avoid some obvious limitations arising from uncertainties in taxonomic identification (Berthon et al., 2011; B-Béres et al., 2014). Functional and/or morphological traits of diatoms have also been applied successfully to assess ecological changes in benthic algal assemblages (Berthon et al., 2011; Kókai et al., 2015; Lengyel et al., 2015; B-Béres et al., 2016; Lange et al., 2016). Accordingly, diatom functional approaches that express relevant functional characteristics of taxa may enhance potentially our ability to interpret ecological processes in a meaningful way. Such ecological processes may include functional community responses due to colonization (B-Béres et al., 2016) or community responses to various types of environmental pressures (Law et al., 2014; B-Béres et al., 2017).

In the large River Pearl (China), benthic diatoms can contribute largely to the community composition of phytoplankton (Wang et al., 2014). Therefore, the River Pearl as a large lotic ecosystem may provide a reliable basis to test combined planktic and benthic algal functional approaches. Our study tests whether the use of refined functional groups for benthic diatoms (under codon TB) based on cell size, diatom ecological guilds, or eco-morphological groups enhances our ability in relating the phytoplankton community composition of the River Pearl to local environmental variables. We hypothesize that such combinations of the FG planktic system and trait-based functional approaches of benthic diatoms enable better predictions for the phytoplankton community composition from the local environment than the taxonomic classification or the original FG approach (all benthic diatom taxa together in codon TB) alone.

Methods

Study area

The Pearl River, with a length of 2,320 km, a catchment area of 450,000 km^2, and an annual mean discharge of ~ 3,000 m^{3}s^{-1}, is the largest river in southern China. The river consists of three major tributaries: the West, the North, and the East Rivers, merging at the Pearl River Delta before entering into the South China Sea. The West River (2129 km), which runs through Guangdong and Guangxi provinces, is the largest tributary of the Pearl River with a catchment area of 345,700 km^2. The seasonal flow regime of the West River therefore shapes the hydrology characteristics of the Pearl River in all seasons.

The Zhaoqing section of the West River has an average width of 1,100 m, a maximum water discharge of 30,000 m^{3}s^{-1}, an annual mean flow speed of 0.3 ms^{-1}, and is the passage for the river flow entering the Pearl River Delta. The sampling station of this long-term monitoring is situated close to the wharf of the Zhaoqing Fishery Administration (23°2′40″ N, 112°27′5″ E), which is ~ 160 km above the Pearl River Estuary (Fig. 1). The water depth at the sampling site varies between 3 and 5 m.

Phytoplankton analysis and functional approaches

Phytoplankton samples were collected at 5-day intervals in all seasons in 2009. Each sample was collected ~ 0.5 m below the water surface using a HQM-1 sampler and fixed immediately with formaldehyde (5%). Phytoplankton samples were counted in a 1-ml Sedgewick-Rafte counting chamber using a Nikon Eclipse TS100 inverted microscope. In each sample, diatoms were identified from concentrated samples using dilute HCl and H_2O_2 (Kelly et al., 1998). We followed Van den Hoek et al. (1995) for the taxonomic identification of benthic diatom taxa.

Calculation of phytoplankton biomass was based on approximated geometrical forms according to Hillebrand et al. (1999). Phytoplankton taxa were classified into characteristic functional groups (FGs, coda) according to Reynolds et al. (2002), Borics et al. (2007), and Padisák et al. (2009). At first, all benthic diatom taxa were grouped together according to Borics et al. (2007) in one functional group, codon TB. Then, codon TB was detailed further according to different trait-based benthic diatom functional approaches.

Trait-based benthic diatom functional approaches

Benthic diatom taxa were classified based on the following functional approaches:

i. Using three diatom ecological guilds excluding planktic taxa according to Passy (2007) and Rimet and Bouchez (2012). According to their position in the benthic algal mats, the three guilds were 1) the low-profile (high reproduction rate, characteristic for low nutrient and light availability, and higher disturbance), 2) the high-profile (characteristic for high resource availability and low disturbance), and 3) the motile ecological guild (ability to choose the best microhabitat in a given circumstance);
ii. Using five size classes based on Berthon et al. (2011): S1: 5–99 μm^3, S2: 100–299 μm^3, S3: 300–599 μm^3, S4: 600–1499 μm^3, and S5: ≥ 1500 μm^3;
iii. Using fifteen ecological groups based on combined eco-morphological functional groups (CEMFGs) excluding planktic algae (B-Béres et al., 2016).

Environmental predictors

Additional 250 mL water samples were taken for nutrient analysis in parallel with the phytoplankton sampling. Water temperature was measured in situ. The monitoring of nutrients included orthophosphates (GB11893-89), total inorganic nitrogen (GB11894-

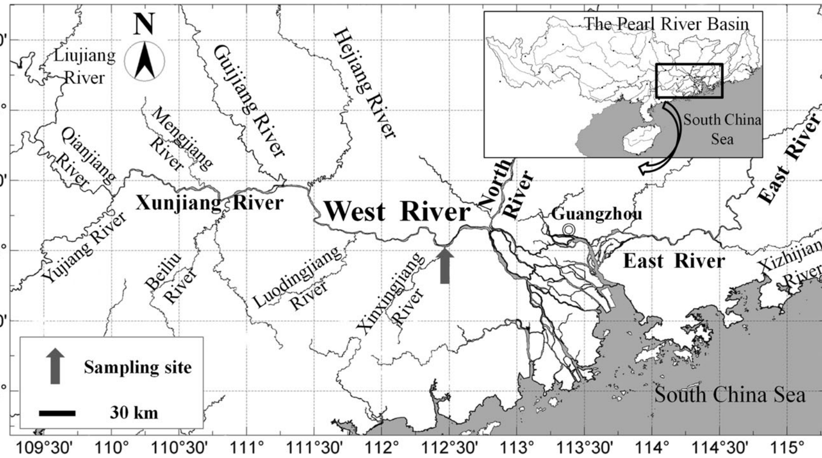

Fig. 1 Location of the long-term monitoring station following Zhaoqing section of the West River, China (23°2′40″N, 112°27′5″E)

89), nitrate (GB7480-87), nitrite (GB7493-87), and ammonium (GB7479-87) measured by a water flow injection analyzer (Skalar-SA1100, Netherland), as well as silicon (SL91.1-1994) measured spectrophotometrically (Shimadzu UV-2501PC, Japan). All chemical analyses were based on Chinese National Standards (Xu et al., 2014). Water discharge (http://xxfb.hydroinfo.gov.cn) and precipitation (http://weatheronline.co.uk) data were available online, both selected according to the phytoplankton sampling scheme.

Statistical analysis

Similar phytoplankton samples based on the taxonomic, the FG approach sensu Reynolds, and the FG approach combined with various trait-based functional classifications of benthic diatoms were grouped together using the Self-Organizing Map (SOM) method in the SOM toolbox (Alhoniemi et al., 2000) in MATLAB™. SOM is a neural network approach, which has been applied widely in order to identify similar potamoplankton compositions based on community data (Várbíró et al., 2007; Abonyi et al., 2014). In SOM, samples with similar phytoplankton community compositions were grouped into the same or neighboring neuron (cluster) using the Ward's linkage method, the unified distance matrix (U-matrix, Ultsch, 1993) approach, and the Davies–Bouldin index (Davies & Bouldin, 1979). The relationships between SOM clusters and environmental variables were assessed using Linear discriminant analysis (LDA) in the 'ade4' package (Chessel et al., 2004; Dray et al., 2007; Dray & Dufour, 2007) in R. We used 1000 permutations in Monte Carlo test in order to assess the significance level of environmental variables in affecting SOM clusters. We used the Kruskall–Wallis test to highlight significant differences in environmental variables among SOM clusters, and then used multiple comparison tests in the 'pgirmess' R package (Giraudoux, 2015). We also compared the variance explained by the local environment in the phytoplankton community structure based on each specific approach (taxonomic and functional ones) using different numbers of SOM clusters identified (see Supplement Table S.1). Our results are discussed based on the highest values in the variance explained by the local environment, and therefore based on the most reliable number of SOM clusters for the taxonomic and then for each specific combination of the functional approaches.

Results

SOM clusters based on the taxonomic approach

Based on the taxonomic composition of phytoplankton, four SOM clusters were defined (Fig. 2a1, a2). The taxonomic composition of clusters was similar between clusters C1 and C3 to some extent, but was considerably different between clusters C2, C3, and C4 (see Supplementary Table S.2). Cluster C1 was characteristic for autumn, while C2 and C4 were characteristic for summer phytoplankton. Cluster C3 was characteristic for winter and spring (Table 1). All

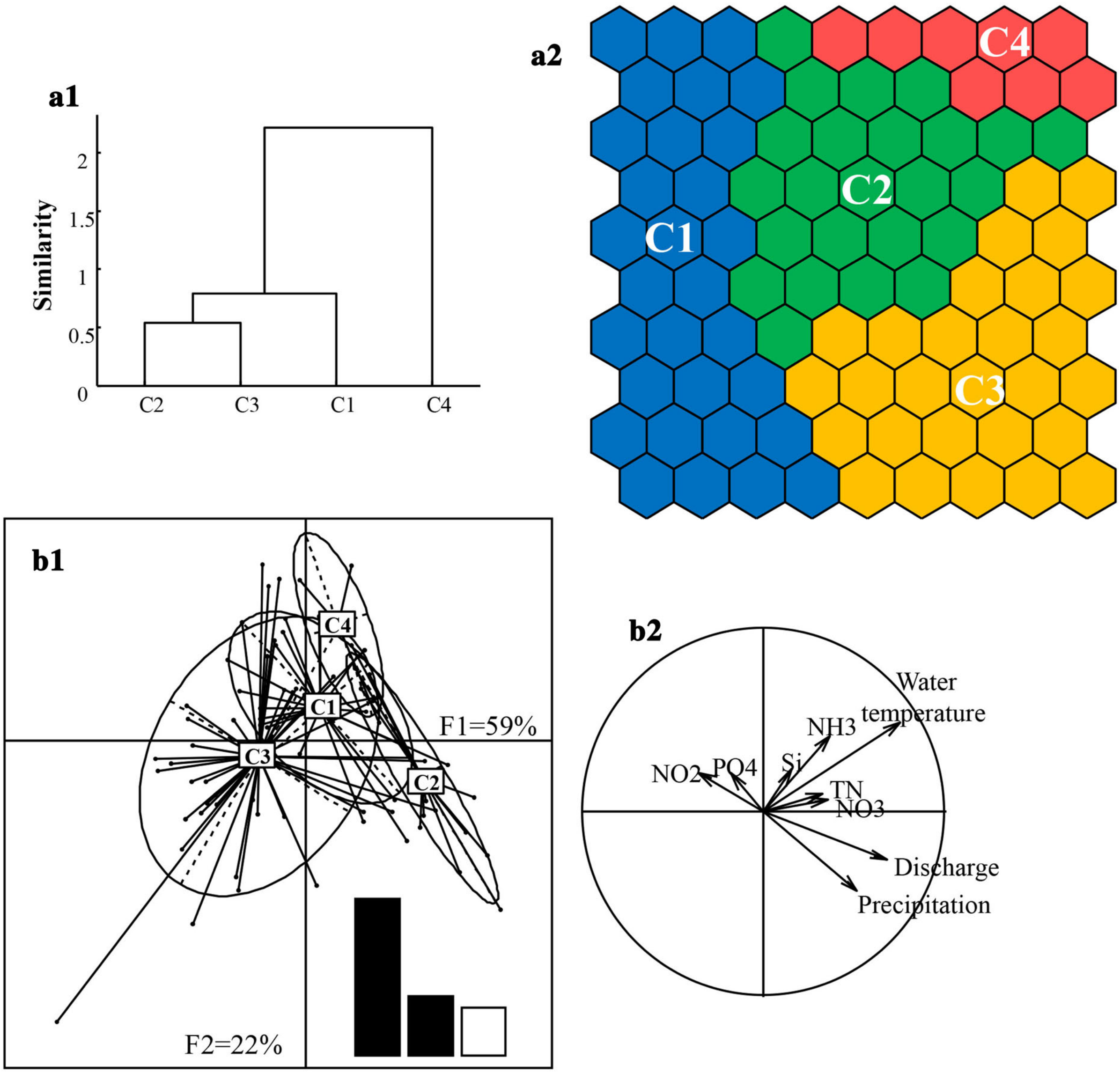

Fig. 2 Self-Organizing Map (SOM) clusters based on similarities in the taxonomic composition of the Pearl River phytoplankton, 2009. Samples with similar taxonomic composition belonged to the same cluster. When 4 clusters (C1–C4) were created, the best relationship with environmental parameters was approached. (a1) Similarity levels between the four SOM clusters identified; (a2) the distribution of clusters on SOM; (b1) the distribution and overlap of SOM clusters; (b2) the correlation of SOM clusters with main environmental predictors based on Linear Discriminant Analysis

clusters were characterized by the biomass dominance of *Aulacoseira granulata* (Ehrenb.) Simonsen. However, species composition of secondary taxa varied greatly among SOM clusters. Green algae, Cyanobacteria, and Euglenophyta diversified further the phytoplankton community composition in C2 and C4, while in C the dominance of *Melosira varians* Agardh was characteristic.

All environmental parameters predicted all SOM clusters significantly according to the Monte Carlo test ($P < 0.001$, in all cases). SOM clusters were highly overlapping, among which cluster C1 overlapped the most with the other three ones (Fig. 2b1).

Environmental constraints explained 64.2% variance in the phytoplankton taxonomic composition. The prediction rates for clusters were 48% (C1), 62%

Table 1 Characteristics of Self-Organizing Map (SOM) clusters defined based on similarities in the taxonomic composition of phytoplankton in the Pearl River, 2009

SOM clusters	C1	C2	C3	C4
Number of samples	21	13	43	4
Overlapping period	Apr–Dec	Jun–Sep	Jan–Dec	Aug–Sep
Dominant seasons	Autumn	Summer	Winter & Spring	Summer
Dominant species	*Aulacoseira granulata*	*A. granulata*	*A. granulata*; *Melosira varians*	*A. granulata*

(C2), 74% (C3), and 50% (C4). Clusters C2 and C3 were the most related to the first ordination axis (Fig. 2b1, b2), with water temperature, water discharge, and precipitation as the most important predictors of the phytoplankton community composition.

SOM clusters based on the FG approach sensu *Reynolds*

Four SOM clusters were defined (Fig. 3a1, a2) based on the phytoplankton FG composition sensu Reynolds (Reynolds et al., 2002). The FG composition was almost the same in F2 and F4 clusters, but was considerably different between F1, F2, and F3 clusters (see Supplementary Table S.2). Cluster F1 was characteristic for autumn and winter; in contrast, the other three clusters (F2, F3, and F4) were all specific for summer samples (Table 2). While the codon P (eutrophic, planktic diatoms with the ability for chain formation, i.e., *A. granulata*) was characteristic in all SOM clusters, codon TB (benthic diatoms) was dominant only in cluster F1. The taxonomic composition of codon TB, however, changed considerably along the year (Table 2). Although *M. varians* was the dominant member of benthic diatoms in all SOM clusters, the composition of other benthic diatom taxa differed significantly among clusters (*Cymbella* sp. in F2; *Surirella minuta* Brébisson ex Kützing, *S. robusta* Ehrenberg in F3; *Pleurosigma* sp., *Navicula* sp., *Cymbella affinis* Kützing, *Amphora ovalis* (Kützing) Kützing in F4; see Table 2).

All environmental parameters predicted all SOM clusters significantly according to the Monte Carlo test ($P < 0.001$, in all cases). All clusters except cluster F3 overlapped each other to some extent.

Environmental constraints explained 71.6% variance in the phytoplankton FG composition. The variance explained in each cluster was 95% (F1), 63% (F2), 50% (F3), and 14% (F4). The clusters F1 and F2 were related the most to the first ordination axis (Fig. 3b1, b2), in which case water discharge and precipitation appeared to be the most important predictors. Cluster F3 was related to the second ordination axis, with water temperature and orthophosphates as the most important predictors.

SOM clusters based on combined FGs sensu *Reynolds and benthic diatom ecological guilds*

Based on the FG approach of phytoplankton sensu Reynolds (Reynolds et al., 2002), and detailed benthic diatom compositions based on the diatom ecological guild concept, three SOM clusters were defined (Fig. 4a1, a2). While codon P was the dominant functional group in all SOM clusters, codon TB (benthic diatoms) was dominant only in cluster G1 (Table 3). The benthic diatom composition based on the ecological guild concept, however, differed considerably between the three SOM clusters. Dominance of the high-profile guild was characteristic in all clusters owing to the presence of *M. varians*; the low-profile guild was characteristic only in G2, and the motile guild in G3 (Table 3).

All environmental parameters predicted the SOM clusters significantly according to the Monte Carlo test ($P < 0.001$, in all cases). Environmental constraints explained 82.7% variance in the phytoplankton functional composition, where the variance explained in individual clusters were 88% (G1), 75% (G2), and 50% (G3), respectively. Clusters G1 and G2 were the most related to the first ordination axis F1 (Fig. 4b1, b2) with water discharge and precipitation as the most important predictors. Cluster G3 was the most related to the second ordination axis F2 (Fig. 4b1, b2) which was the most related to water temperature.

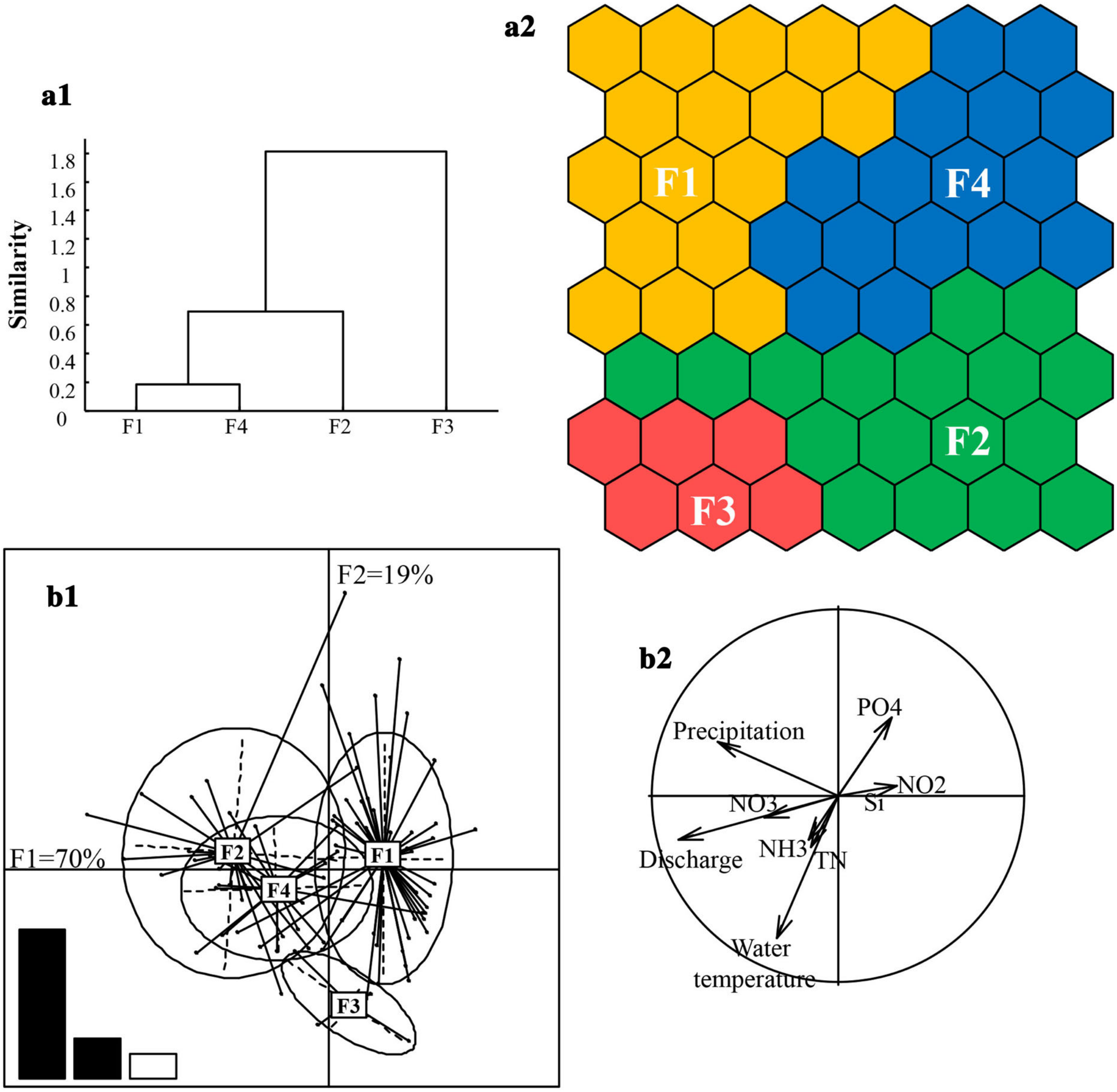

Fig. 3 Self-Organizing Map (SOM) clusters of phytoplankton in the Pearl River (2009) based on similarities in the phytoplankton functional group composition sensu Reynolds (Reynolds et al., 2002). Samples with similar functional groups belonged to the same cluster. When 4 clusters (F1-F4) were created, the best relationship with environmental parameters was approached. (a1) Similarity levels between the four SOM clusters identified; (a2) the distribution of clusters on SOM; (b1) the distribution and overlap of SOM clusters; (b2) the correlation of SOM clusters with main environmental predictors using Linear Discriminant Analysis

SOM clusters based on the combinations of the FG approach and further ecological concepts of benthic diatoms

Compared to the taxonomic and the FG system sensu Reynolds alone, the combination of the FG classification with size classes and eco-morphological groups of benthic diatoms both increased the variance explained in the phytoplankton community composition from the local environment (80.2% and 76.5%, respectively). Among the combined planktic–benthic functional approaches, however, these latter two combinations were highly outperformed by the combination of the FG system with the diatom ecological

Table 2 Characteristics of Self-Organizing Map (SOM) clusters defined based on similarities in the phytoplankton functional group composition sensu Reynolds (Reynolds et al., 2002) in the phytoplankton of the Pearl River, 2009

SOM clusters	F1	F2	F3	F4
Number of samples	46	19	4	12
Overlapping period	All except July	Apr–Aug	Aug–Sep	May–July
Dominant seasons	Autumn & Winter	Spring & Summer	Summer	Summer
Dominant species	*Aulacoseira granulata*; *Melosira varians*	*A. granulata*	*A. granulata*	*A. granulata*
Dominant coda	P, TB	P	P	P
Dominant benthic diatoms	*M. varians*	*M. varians*, *Cymbella sp.*	*M. varians*, *Surirella minuta*, *Surirella robusta*	*M. varians*, *Pleurosigma sp.*, *Navicula sp.*, *Cymbella affinis*, *Amphora ovalis*

P: functional group P, TB: functional group TB

guild concept (see Supplementary Table S.1, Supplementary Figure S.1, and Figure S.2).

Discussion

We hypothesized that more detailed functional classification of benthic diatoms would enable better prediction for the phytoplankton community composition from local environmental predictors than the taxonomic or the FG approach sensu Reynolds (Reynolds et al., 2002) alone. Our results supported this hypothesis: all combined planktic–benthic functional approaches enhanced our ability in predicting the phytoplankton community composition compared to both the taxonomic and the FG approaches. The most successful approach was the combination of the FG system with detailed benthic diatom compositions based on the ecological guild concept (Passy, 2007; Rimet & Bouchez, 2012).

Following many decades along which phytoplankton ecology developed based exclusively on the taxonomic approach, recently, several functional approaches have been developed. Besides the functional trait concept, which focuses on characteristics of individuals that affect fitness directly or indirectly (Weithoff, 2003; Litchman & Klausmeier, 2008), functional group classifications have also been developed with the aim to better understand the mechanisms underlying the characteristic co-occurrences among phytoplankton taxa (Reynolds et al., 2002; Salmaso & Padisák, 2007; Kruk et al., 2010). Phytoplankton functional approaches classify taxa according to ecological similarities (functional redundancy), and therefore simplify the ecological information included in the taxonomic data (Salmaso et al., 2015). Our results, however, emphasize how the representation of functional differences among relatively similar taxa is also important (i.e., within benthic diatoms) as is the identification of ecologically relevant number of subgroups. Based on the Pearl River phytoplankton data set, we have shown that the combination of the FG system with functional approaches of benthic diatoms may be necessary to correspond the phytoplankton community composition and the local environment in a meaningful way. Therefore, instead of highlighting functional similarities (redundancy) among taxa, here we emphasize the importance of functional differences among benthic diatom taxa, even among those that occur in river plankton in a highly stochastic way.

Very few river phytoplankton studies have compared the performance of different functional approaches so far. Abonyi et al. (2014) showed that the FG approach sensu Reynolds might be able to highlight mechanisms responsible in assembling the phytoplankton community composition along the River Loire in a more reliable way than the MFG (Salmaso & Padisák, 2007) or the MBFG (Kruk et al., 2010) approaches. However, they also emphasized the

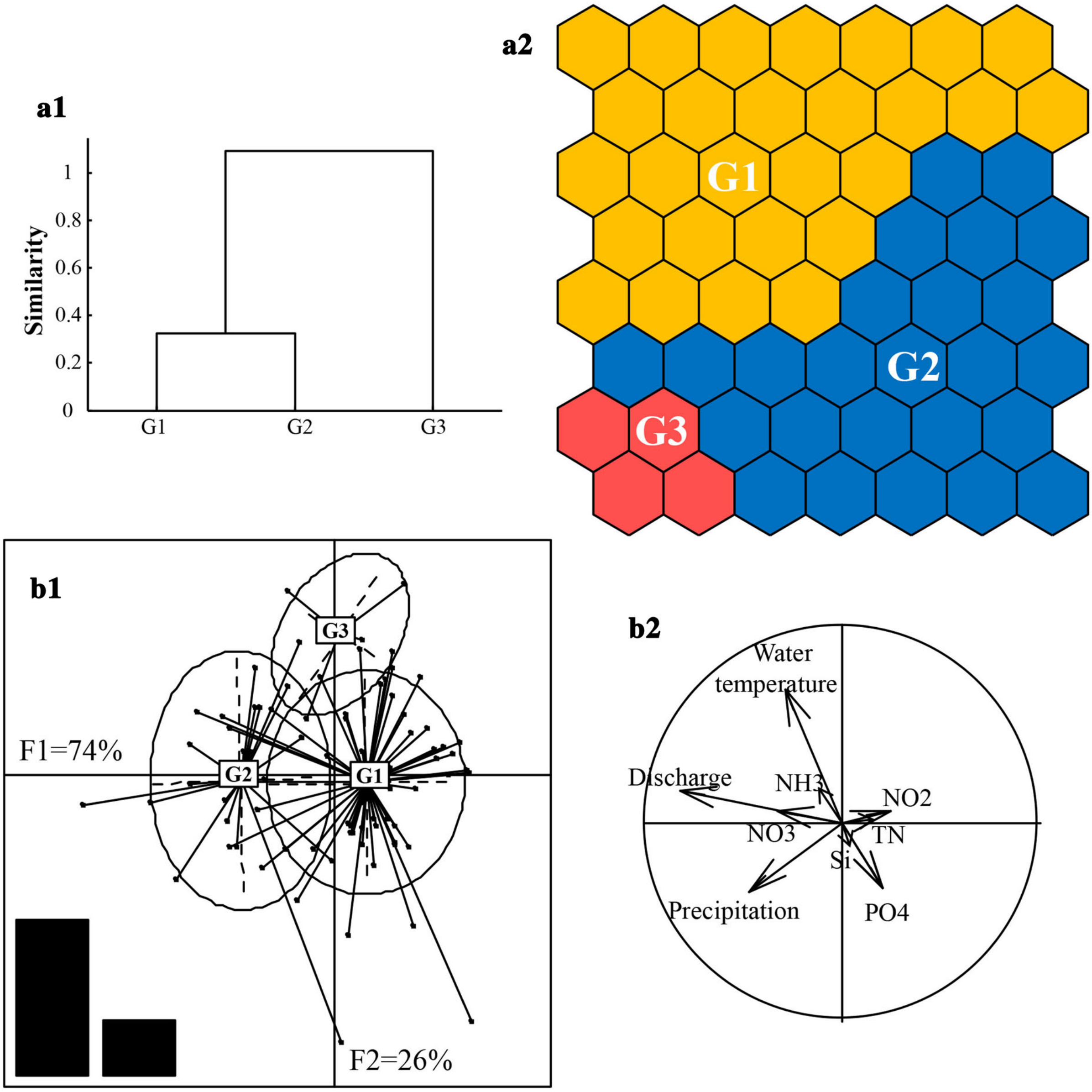

Fig. 4 Self-Organizing Map (SOM) clusters of phytoplankton in the Pearl River based on similarities in the combination of the functional group composition sensu Reynolds (Reynolds et al., 2002) and benthic diatom ecological guilds (Passy, 2007; Rimet & Bouchez, 2012). Samples with similar combination of the functional group approach sensu Reynolds (Reynolds et al., 2002) and benthic diatom ecological guilds belonged to the same cluster. When 3 clusters (G1-G3) were created, the best relationship with environmental parameters was approached. (a1) Similarity levels between the three SOM clusters identified; (a2) the distribution of clusters on SOM; (b1) the distribution and overlap of SOM clusters; (b2) the correlation of SOM clusters with main environmental predictors using Linear Discriminant Analysis

importance of a fine functional resolution among pennate diatoms. Here we showed that while several functional approaches were tested to further detail functional differences among benthic diatom taxa, they seemed not to be performing in the same manner.

In the Pearl River, diatoms and green algae contribute $\sim 75\%$ to total phytoplankton taxonomic richness (Wang et al., 2014). However, only a couple of them—mainly diatoms—are able to dominate with an occurrence frequency $> 50\%$. Phytoplankton

Table 3 Characteristics of Self-Organizing Map (SOM) clusters defined based on similarities in the combination of phytoplankton functional groups concept sensu Reynolds (Reynolds et al., 2002) and benthic diatom ecological guilds sensu Passy (2007) in the Pearl River phytoplankton, 2009

SOM clusters	G1	G2	G3
Number of samples	57	20	4
Overlapping period	All year	All year	Aug–Sep
Dominant seasons	Autumn & Winter	Summer	Summer
Dominant species	*Aulacoseira granulata*, *Melosira varians*	*A. granulata*	*A. granulata*
Dominant coda	P; TB	P	P
Dominant benthic diatoms	*M. varians*	*M. varians*, *Cymbella sp.*	*M. varians*, *Surirella minuta*, *Surirella robusta*
Dominant diatom ecological guilds	High-profile guild	High- and low-profile guilds	High-profile and motile guilds

P: functional group P, TB: functional group TB

biomass is often dominated by one single filamentous diatom species, *A. granulata*. However, seasonal alterations in water discharge may contribute to diversification in the taxonomic composition of potamoplankton, including various forms of benthic diatoms detached from the substrate. Hydrological factors alone, therefore, might contribute to changes in the diatom community composition to a greater extent than other physical or chemical factors might do (Wu et al., 2016; Tang et al., 2016).

We showed that one main functional group (codon P: *A. granulata*) characterized the phytoplankton of the River Pearl in all seasons in 2009, but functional characteristics of secondary taxa altered substantially, especially among benthic diatoms. Such time- or discharge-related alterations in the functional community structure of benthic diatoms have already been highlighted in rivers located in the subtropical (Tang et al., 2016), and also in regions of the continental climate (Stenger-Kovács et al., 2013; B-Béres et al., 2014, 2016). According to B-Béres et al. (2017), seasonal patterns in the functional composition of benthic diatoms did not depend primarily on the location or typology of the watercourse, rather on more- or less-defined set of environmental conditions, including the overwhelming importance of hydrology (op. cit.). The occurrence of benthic diatoms belonging to the 'high-profile' ecological guild is often related to water discharge negatively, and so they occur primarily in low-flow conditions (Stenger-Kovács et al., 2013; B-Béres et al., 2016). On the other hand, the 'low' and 'motile' ecological guilds are both more susceptible to high water discharge, but their preferences in water temperature may differ. 'Motile' benthic diatoms prefer higher water temperatures than 'low-profile' ones. Accordingly, benthic diatom assemblages are often dominated by 'low-profile' taxa in spring and in early summer, while 'motile' taxa only become more important from summer to late autumn (B-Béres et al., 2017).

Here, we showed that functional shifts in phytoplankton and benthic diatoms of the Pearl River were related to seasonal differences in local environmental constraints, especially to alteration in water discharge. One of the most relevant functional characteristics in the Pearl River was reflected by the dominance of *M. varians*. This large, filamentous diatom is characteristic for low-flow periods in streams and rivers (Stenger-Kovács et al., 2013; B-Béres et al., 2014). In our case, however, its occurrence seemed to be related to disturbance effects by water discharge. Such effects, however, were also highlighted by alterations in the functional community composition of benthic diatoms with secondary importance. Diatom taxa belonging to the 'low-profile' ecological guild were characteristic in spring (*Cymbella* sp.) and early summer (*Am. ovalis*, *C. affinis*). Their sessile life forms enable them to adapt to physically disturbed conditions (e.g., high water discharge). However, 'motile' non-attached, solitary diatom taxa were rather characteristic from early summer (*Navicula* sp., *Pleurosigma* sp.) with high abundance until September (*S.*

minuta, *S. robusta*). The positive correlation between SOM clusters with the dominance of such diatom ecological guilds and water discharge may be interpreted as the functional response in community composition to physical disturbances (Passy, 2007; Rimet & Bouchez, 2012; Stenger-Kovács et al., 2013). Large benthic diatom taxa (including filamentous forms) or those belonging to the 'motile' ecological guild may dominate the benthic diatom community following flood events, as long as the physical disturbance is diminished (B-Béres et al., 2014).

Individual characteristics of benthic diatom functional approaches affected our SOM results in different ways. Therefore, these approaches represent different abilities in identifying mechanisms potentially underlying the taxonomic compositions observed. Although the cell size structure of benthic diatoms could also be a reliable ecological indicator of environmental conditions in lotic systems (Lengyel et al., 2015; Kókai et al., 2015; B-Béres et al., 2017), in our case, neither the combination of the FG system sensu Reynolds with the size structure of benthic diatoms nor with their eco-morphological groups were attractive. We argue, however, that this might be related to fact that mainly large species dominated the benthic diatom flora of the Pearl River. On the other hand, the outstanding performance of the combined planktic FG system sensu Reynolds and the benthic diatom ecological guild concept emphasizes its potential to indicate seasonal alterations in environmental conditions, especially in water discharge. Such an ability for ecological indication has already been revealed for individual benthic diatom functional approaches in the benthos (Passy, 2007; B-Béres et al., 2014). However, here, we show that functional differences among benthic diatoms may also be relevant indicators of hydrological constraints affecting the community composition of river phytoplankton. Based on our results, such reliable functional differences can be identified according to the diatom ecological guild concept. Accordingly, codon TB of benthic diatoms may be divided into TBL—'low-profile,' TBH—'high-profile,' and the TBM—'motile profile' sub-groups in future river phytoplankton studies.

Our results are the first to evidence that the occurrence of benthic diatoms in large river plankton is not random completely. Rather, benthic diatoms can also be detailed functionally in plankton studies based on an existing benthic diatom functional approach in a meaningful way. Therefore, the combination of planktic and benthic algal functional approaches seems to be highly relevant in river phytoplankton ecology, especially based on the phytoplankton functional group system sensu Reynolds and the diatom ecological guild concept.

Conclusion

Existing functional approaches of phytoplankton and benthic diatoms enable a better understanding of mechanisms potentially underlying alterations in community compositions in the plankton and in the benthos separately. Here we showed that the widely applied phytoplankton functional group concept sensu Reynolds (Reynolds et al., 2002) could be further detailed based on existing trait-based functional approaches of benthic diatoms in a meaningful way. Primarily, benthic diatoms dominate algal communities of streams and rhithral sections of large rivers. However, benthic diatoms do also occur in the river plankton further downstream. Here, we evidenced that the occurrence of benthic diatoms in large river phytoplankton is not random completely even in the middle or downstream river sections. Rather, their occurrence can be assessed ecologically by the combination of existing planktic and benthic algal functional approaches, especially based on the phytoplankton functional group system sensu Reynolds and the diatom ecological guild concept of benthic diatoms.

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Author contributions CW and XL collected the data; AA formulated the idea; AA and VBB classified algae according to functional approaches; CW performed statistical analysis; CW, VBB, and AA wrote the first draft of the manuscript and then all authors contributed to revisions substantially.

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