The role of filter-feeding Asian carps in algal dispersion

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Abstract

The gut contents of filter-feeding fish often contain considerable amounts of viable phytoplankton cells, thus these animals can act as vectors and may play an important role in the horizontal and vertical transport of algae. In this study, the potential role of the introduced filter-feeding Asian carps (hybrids of silver carp *Hypophthalmichthys molitrix* and bighead carp *H. nobilis*) in algal dispersion was studied in the oligo-mesotrophic Lake Balaton (Hungary). We examined the algal composition in the lake water, gut-contents (foregut and hindgut) and occasionally in the filtered suspensions collected directly from the gill rakers (filtering apparatus) of fish. Microscopic analyses revealed that the phytoplankton composition of the ingested food differed considerably from what we found in the lake water. Cryptophytes, dinoflagellates and euglenophytes were observed in both the lake water and

foregut samples, but were absent in the hindgut samples. However, in the cultured hindgut samples we found viable cells of several phytoplankton taxa (e.g., diatoms, blue-greens, desmids, volvocalean and chlorococcalean green algae), which managed to survive the physical and chemical digestion. Thus, it can be concluded that Asian carps can be potential vectors of phytoplankton and facilitate their dispersal. These results imply that the presence of these filter-feeding fish can alter the phytoplankton species composition and promote the dominance of taxa that are able to resist digestion.

Introduction

Capability of dispersion is among the most important features of all living organisms that enable them to colonize new habitats and increase their evolutionary success (Cox & Moore, 1993). Even though there are some endemic algal taxa typical for isolated areas, the majority of phytoplankton species have a widespread occurrence, which could be attributed mainly to their ability to travel over large distances. Algae are mainly dispersed passively by water currents, by air, by animals or by accidental human activities (Chrisostomou et al., 2009; Genitsaris et al., 2011; Padisák, 2004). There are some taxa (e.g., species in the Chlorophyta, Cyanobacteria, Chrysophyta groups), which are able to survive travelling in a humid medium (i.e., in aerosols or on the wet surfaces of animals), without developing specialized protective structures (Van Overeem, 1937; Brown et al., 1964). However, to cope with unfavorable external conditions, several phytoplankton species develop akinetes, cysts or thick-walled structures enabling algae to be effectively dispersed even on dry surfaces (Padisák, 2004).

Another possible way of active algal dispersal is the moving in aqueous media. This process does not involve the risk of dehydration, but if it occurs within the alimentary tract of a fish, algae are exposed to the effects of digesting fluids. Accordingly, the capability of

species to resist digestion is a significant factor in determining the survival and ultimately the dispersal success of algae (Miura & Wang, 1985; Vörös et al., 1997). Despite fish are less motile and able to travel slower than waterfowls for instance, they can also be important vectors of algae and serve as low-distance carriers in aquatic ecosystems.

To improve the water quality and increase fishery yields, filter-feeding silver carps (*Hypophthalmichthys molitrix*), bighead carps (*H. nobilis*), and their hybrids (collectively known as filter-feeding Asian carps) have been introduced into eutrophic lakes and rivers throughout the world since the early 1950s (Jennings 1988; Kolar et al. 2007). Consequently, Asian carps became key species in freshwater biomanipulation (Datta & Jana, 1998; Zhang et al., 2008; Zeng et al., 2014), and several studies were published on the ecological role of these fish, including their impacts on the functioning of aquatic food webs (Borics et al., 2013), or their capability to digest planktonic organisms (Spataru, 1977; Vörös et al., 1997; Herodek et al., 1989; Tátrai et al., 2006). The general approach regarding Asian carp stocking has changed considerably in the past decade, because a number of recent studies have demonstrated that the presence of these fish outside their native range involves ecological risks, including the deterioration of water quality and strong interspecific food competition with native fish species (Sampson et al., 2009; Lin et al., 2014).

Introduction of Asian carps to Hungarian waters started in the 1960s. They were stocked into small artificial ponds (Borics et al., 2000), as well as into natural lakes (Boros et al., 2014). During the decades, Asian carps became successful invaders in different types of aquatic habitats in Hungary and nowadays can be considered as the most efficient plankton consumers in the freshwaters of this region. Lake Balaton was stocked with Asian carps between 1972 and 1983. The stocking was stopped and banned thereafter because this intervention did not result in any significant improvement in water quality. Yet, the Asian

carp biomass is still high in the lake, constituting about 30% of the total fish biomass (Tátrai et al., 2009). The population is dominated by hybrid individuals (Boros et al., 2014).

In this study, we aimed at examining the potential role of filter-feeding Asian carps in algal dispersion. More specifically, we studied the algal composition in the lake water, in the gut contents (foregut, hindgut) and occasionally in the filtrated suspension (collected from the gill rakers of Asian carps), focusing on the identification of algae species that remain viable after passing through the alimentary tract.

We hypothesized that algae having thick gelatinous substance around the cells or robust cellulose cell wall can cope successfully with the different physical and chemical digesting processes. We also hypothesized that smaller-sized taxa are more exposed to digesting effects of intestinal fluids, because of their larger surface to volume ratio. Thus, we expected that their survival rate in the alimentary tract is smaller compared to that of larger-sized taxa.

Methods

Study area

Lake Balaton (latitude: 47° 3' 50"- 46° 42' 6", longitude: 17° 14' 58"- 18° 10' 28") is the largest shallow lake in Central Europe, located in Hungary. The lake has a surface area of 596 km^2 and an average depth of about 3 meters (Istvánovics et al., 2007). The lake had been suffering from serious eutrophication and cyanobacterial blooms for several decades, but the water quality has since improved due to the restoration efforts, and now the lake is oligo-mesotrophic (Tátrai et al., 2008).

Collection of fish, gut content and gill raker filtrate samples and lake water for microscopic analyses

To explore the feeding habits of Asian carps, five samplings were conducted between April−October 2013. Fish were sampled from the eastern basin of Lake Balaton with 12 cm mesh-size gill nets. Altogether 46 Asian carps were collected (9−12 fish per sampling). Fish were transported to the laboratory after catching (within 30 min) and were dissected immediately to obtain the foregut and hindgut contents. Foregut samples were collected from the anterior end of intestines (a 10 – 15 cm long section starting from the oesophagus), while hindgut samples were collected from the posterior end of the alimentary tract (0 – 15 cm from the anus). Alternatively, when we did not find sufficient amount of material in the foreguts, gill raker filtrate samples were collected from the sulcus of the epibranchial organ, which is a groove within the gill arch where the filtered matter is concentrated before ingestion. The compressed filtrates were scraped off from the inner surface of gill rakers with a flat stick (Fig. 1). The collected samples were stored in dry and cold place until sample processing, which was performed within 1 hour. All samples for microscopic phytoplankton analyses were preserved in diluted Lugol's solution, while samples for culturing were stored in sterile vessels and were not treated with any chemicals. These samples were kept in darkness at 0−4°C for no longer than 24 h before culturing.

To determine phytoplankton species composition in Lake Balaton, water samples were collected from the entire water column with a tube-sampler at each fish sampling date. Three subsamples were taken at different locations of the study area, typically in the proximity of the fishing net. These three samples were mixed right after samplings.

Subsamples for additional zooplankton and detritus analyses were also preserved in Lugol's solution, but these results are not detailed in this study.

Analysis of phytoplankton composition

Phytoplankton samples

The preserved phytoplankton samples were placed in 5 mL sedimentation chambers (Hydrobios, Kiel) and were left to settle for 24 h. The identification of phytoplankton species was carried out using Zeiss Axioimager A2 research microscope. Determination of relative percentage abundances were performed with an inverted microscope (ZEISS Axiovert-40 CFL), following Utermöhl's (1958) method. In all cases, a minimum of 400 specimens per sample were counted at 400× magnification. For the characterization of phytoplankton, both abundance and occurrence data were used. Identification of species was performed according to Ettl, 1978; Förster, 1982; Hofmann et al., 2011; Huber-Pestalozzi, 1950, 1955, 1961; Komárek & Anagnostidis, 1998, 2005; Komárek & Fott, 1983; Krammer, 2003; Krammer & Lange-Bertalot, 1986-1991; Popovsky & Pfiester, 1990 and Starmach, 1985.

Gut contents

Phytoplankton was identified using an inverted microscope (ZEISS Axiovert-40 CFL). Samples of suitable density were placed in 1 ml counting chambers (Hydrobios, Kiel) and allowed to settle for at least 24 hours. High-density samples were diluted with distilled water (10×, 20×, 25× dilutions were applied, depending on the density). Estimations of cell concentrations and identifications were made either by counting the whole chamber at 400× magnification or by counting two or more transects. At least 400 individuals were counted. The identified taxa were classified into 12 main groups, following the taxonomic categorization of Van den Hoek et al. (1995) (Table 1). Diatoms and blue-green algae were not homogenous regarding their morphology, so these taxa were divided into further subgroups. To study the importance of size on the survival during the passage through the

digestive tract, phytoplankton taxa were categorized into 3 groups based on their longest diameter (<10 μm, 10−40 μm and >40 μm).

Culturing

The hindgut material consists of various inorganic particles, dead and living organic compounds. Besides the microscopic investigation of this material is a really challenging task, viability of the organisms cannot be demonstrated by this method. Thus, the hindgut samples were cultured. It is important to note, that there is no “general” culturing medium which would be suitable to check the viability of all the phytoplankton groups in the hindgut. Therefore, prior to the investigations, we made preliminary studies, and tested several media (Jaworski’s, Allen’s media, diatom-, euglena specific media, BG-11), among which the BG-11 was found to be the best for our purposes. Although BG-11 gives an advantage to cyanobacteria, other taxa (Chlorococcalean green algae and diatoms) grew much better in this medium than in other offered genera-specific media. In addition, the species that proved to be viable in this medium were identical with those we observed during the microscopic observations of the hindgut material. To study the viability of cells in the hindguts, 100 μl aliquots of hindgut samples were inoculated to blue-green medium (BG-11) and nitrogen free (BG) medium (Stanier et al., 1971). Each sample were grown in microtiter plate (with 24 well) in 2 ml volume. Samples were incubated at 28°C and at 80 μmol m^{-2} s^{-1} light intensity for 10 days. After finishing the incubation for the microscopic analyses, the samples were fixed with Lugol’s solution.

Statistical analyses

Kolmogorov-Smirnov tests and Levene’s tests were used to estimate the normality of response variables and the homogeneity of variances. One-way ANOVA tests were used to compare the number of taxa in the three types of samples. When criteria of normality and

174 homogeneity did not meet, Kruskal-Wallis ANOVA was applied. We used the STATISTICA
175 8.0 software for the statistical analyses, and decisions about the statistical significances were
176 set at $p = 0.05$ level. Differences between the three sample types were examined with non-
177 metric multidimensional scaling ordination (NMDS), based on Jaccard similarity index. The
178 significant segregation of groups was tested by ANOSIM. We used PAST 3 software package
179 for the analyses (Hammer et al., 2001).
180
181 **Results**

182 *Phytoplankton composition of Lake Balaton*
183 A total of 100 phytoplankton species were identified in the water samples taken from Lake
184 Balaton, among which the *Cyclotella ocellata* had the highest relative abundance.
185 *Chrysochromulina parva* and *Rhodomonas* cf. *minuta* also were abundant in the lake's
186 phytoplankton samples (these results are not shown here).
187 Phytoplankton species were divided into 12 groups. Pennate diatoms and Chlorococcales spp.
188 had the highest number of species in April, May, June and October. In September, colonial
189 blue-greens and chlorococcalean green algae were the most species-rich taxa (Table 1).
190 Regarding the species richness, there were no considerable differences in the numbers of
191 species during the five sampling months (higher number of tychoplanktonic pennate diatoms
192 was probably the consequence of water column mixing).
193 Regarding the relative abundances of counted units (cells or colonies) (Fig. 2), blue-greens,
194 Chrysophyceae, diatoms, Cryptophyta, Chlorococcales and Volvocales occurred in relatively
195 high percentage (>10%) in Lake Balaton samples, while the relative abundance of Dinophyta,
196 Euglenophyta and Desmidiales were less than 5%. In April and June, Diatoms (April: 38.3%,
197 June: 40.8%) and Chlorococcales (April: 33.9%, June: 32.4%), in May Chlorococcales (27 %)
198 and Cryptophyta (26.4%), while in September and October diatoms (September: 56.7%,

October: 40.6%) and blue-greens (September: 19.3 %, October: 16.6%) had the highest relative abundance in the water column samples.

Foregut contents

In the samples taken from the foreguts, 138 phytoplankton species were found, among which (similarly to the water samples) the most frequent was the *Cyclotella ocellata*. Besides this, *Aulacoseira* sp. and *Chroococcus* sp. were also common species in the foreguts.

Pennate diatoms and chlorococcalean green algae had the greatest number of species in each month of the study period (Table 2). As for the total numbers of taxa, only slight differences were found, and similarly to the Lake Balaton samples the highest number of species was observed in June.

Regarding the relative abundances of counted units (cells or colonies) of the foregut samples, blue-greens, Chrysophyceae, diatoms and Chlorococcales species were dominant. Relative abundance of Dinophyta, Euglenophyta, Desmidiales, Volvocales and Cryptophyta taxa were less than 5%. Diatoms (April: 54.4%, May: 68.1%, June: 49.8%, September: 49.9%, October: 60.1 %) and blue-greens (April: 26.8%, May: 15.7%, June: 29.1%, September: 33%, October: 27.1 %) were present in the highest percentage in the foregut samples (Fig. 3).

Significant difference ($p > 0.05$) was found in the number of taxa between the Lake Balaton and the foregut samples (Fig. 4 a,b). More specifically, the taxa numbers of pennate diatoms, colonial blue-greens, Chlorococcales, Dinophyta and Euglenophyta species were higher in the foreguts. All other groups showed similar species richness in the lake and in the foregut samples.

Although there were several species which were found exclusively in Lake Balaton samples, surprisingly much more species were found in the foreguts, which were not found in the lake water samples (Table 3).

Hindgut samples

In the cultured hindgut samples, 149 viable phytoplankton species were identified (Table 3). Nine of these species occurred in the cultured samples in all months of the study (*Aulacoseira ambigua, Cyclotella ocellata, Fragilaria construens, Microcystis aeruginosa, Microcystis flos-aquae, Monoraphidium griffithii, Oocystis marssonii, Pediastrum boryanum* and *Scenedesmus denticulatus*). We found 60 taxa, which were detected neither in the foregut, nor in the Lake Balaton, but were found in the hindgut samples (Table 3). As to the species richness of the larger algae groups, there were no considerable differences in the numbers of species during the study period. Pennate diatoms, chlorococcalean green algae and colonial blue-greens had the greatest number of species in each months (Table 4).

Significant difference was detected ($p<0.05$) in the number of species of colonial blue-greens, chlorococcalean green algae, Chrysophyceae and Cryptophyta groups between the Lake Balaton and hindgut samples (Fig. 4 a,b). When foregut and hindgut samples were compared, significant differences ($p <0.05$) were detected in the number of species in case of pennate diatoms, colonial blue-greens, Chlorococcales, Dinophyta, Euglenophyta and Cryptophyta groups (Fig. 4 a,b).

By comparing the taxa richness of the Lake Balaton and the hindgut samples, we found that pennate diatoms and chlorococcalean green algae were the most species-rich groups in both types of samples. However, the hindgut samples contained almost twice as many green algae and colonial blue-green species than the lake water samples (Fig. 5).

The proportion of groups in the foregut and hindgut samples differed remarkably from each other. Towards the hindgut, the number of chlorococcales and volvocalean green algae and both colonial and filamentous blue-green algae increased significantly ($p<0.05$). Cryptophyta and Dinophyta species were not detectable in the hindgut samples (Fig. 5).

The NMDS ordination of samples also showed a clear separation of the three groups, thereby indicated significant differences in the algal composition between the three sample types (ANOSIM, $p < 0.001$) (Fig. 6).

Size categories

The three groups of samples contained an almost identical number of species in the small-sized taxa (Fig. 7). Taxa numbers in the middle and large-sized groups showed similar patterns, and both differed considerably in taxa numbers from the small-sized group.

Discussion

Due to the extensive global stocking that started in the 1950s, nowadays filter-feeding Asian carps have a widespread occurrence in the temperate regions all around the world, inhabiting almost all types of aquatic ecosystems. If we assume that planktivorious fish can be potential vectors of phytoplankton dispersal, then two questions should be answered: what kinds of algae are filtered, and what are digested by Asian carps? Both questions were examined profoundly in preceding studies. For instance, Porter (1973) divided phytoplankton to 3 distinct groups from the point of fish nutrition: non-available; available but non-digestible; and available and digestible. As for the availability, several studies addressed this topic, focusing mostly on the phytoplankton content of the foreguts. These studies have yielded controversial results. Some of them support the notion that silver carps cannot ingest algae smaller than 10 µm (Hampl et al., 1983; Smith, 1989; Vörös et al., 1997), while others suggest that silver carps are able to collect even nannoplankton (< 10 µm) (Cremer & Smitherman, 1980; Xie, 1999). This latter can be explained by the fact that gill rakers of silver carps are coated with mucus that facilitates filtering particles smaller than the gill-raker spacings (Lazzaro, 1987; Northcott & Beveridge, 1988). Our results support this finding,

because we found algae smaller than 10 µm both in the foregut (*Nitzschia* sp., *Oocystis* sp., *Phacus skujae, Rhodomonas minuta, Tetraedron minutum, Xanthophyceae* sp., *Centrales* sp., *Chlorococcales* sp., *Chrysophyceae* sp., *Cyclotella pseudostelligera*) and in the hindgut (*Achnanthes minutissima, Centrales* sp., *Chlorella* sp., *Chlorococcales* sp., *Choricystis minor, Chrysophyceae* sp, *Cyclotella pseudostelligera, Fragilaria pinnata, Lagerheimia balatonica, Monoraphidium irregulare, Trachydiscus* sp.*)*.

Another key factor of dispersion is the digestibility of algae, which plays also an important role in the success of biomanipulation and in the growth of fish. The high number of viable species found in the hindgut samples and their large morphological diversity imply that algae developed various types of adaptations that help their survival in the digestive tract. Several studies argued that the digestibility of phytoplankton by filter-feeding fishes is variable and depends on the structure and composition of the algal cell walls (Moriarty, 1973; Moriarty & Moriarty, 1973). Some studies showed that colonial and filamentous blue-greens species that produce extracellular mucilage are able to remain viable after passing through the alimentary tract of filter-feeding fishes (Miura & Wang, 1985; Vörös et al., 1997; Datta & Jana, 1998; Lewin et al., 2003). Moreover, Gavel et al. (2004) demonstrated that larger *Microcystis* colonies were disintegrated during the passage through the digestive system of fish, but individual cells remained viable due to their mucilaginous coating. These results might serve as an explanation for the large number of viable blue-greens in the hindgut samples.

The thick cellulose cell wall might also protect algae from digestion. Bitterlich (1985) suggested that silver carps may not be able to meet their energy requirements consuming phytoplankton alone, most probably because the digestibility of some phytoplankton taxa is low (Dong et al. 1992) and gut fluids of silver carps lack cellulase enzyme to break down algal cell walls (Kolar et al. 2007). Thus, phytoplankton species with thicker cellulose cell walls are more likely to survive the passage through the guts. Among the viable taxa we found

299 in the hindgut samples, chlorococcalean green algae and members of Xanthophyceae group
300 have this type of cell-wall structure. Several studies demonstrated that viable cells of blue-
301 greens, chlorococcalean green algae and Xanthophyceae not simply survived the passage
302 through the digestive system of fish, but were able to take-up phosphorus from the gut
303 content, which enhanced their growth after returning to water (Lewin et al., 2003; Kolmakov
304 et al., 2006; Jancula et al., 2008). This can be explained by the fact that both the gelatinous
305 cover and the thick cellulose cell wall can act as selective sieves, allowing small ionic
306 compounds to enter, but impede the penetration of large molecules, such as digestive enzymes
307 (Porter, 1976).
308 Although we hypothesized that the size of algae is an important feature, which ultimately
309 determines the survival success during the passage through the digestive system, we found no
310 relationship between survival rates of the algae and their cell sizes. However, the number of
311 viable phytoplankton taxa increased in the larger cell-sized categories after digestion (Fig. 7).
312 This increment was not typical for Dinoflagellatae, Euglenophyceae and Cryptophyta, even
313 though most of these taxa consist of larger-sized species. The number of viable taxa from
314 these groups decreased considerably as the digested material reached the hindgut. Despite the
315 fact that these groups have different phylogenetic origin, they share common characteristics
316 regarding their cell wall structure (intracellular coverings can be found in each of the
317 enumerated taxa). It means that the structures, which make the cells more or less rigid, i.e.,
318 flattened cellulose-containing vesicles (Dinoflagellates), protainaceous plates (Cryptophytes)
319 and the protainaceous pellicle (Euglenophytes), are formed beneath the outermost plasma
320 membrane (Okuda, 2002). It seems that this otherwise evolutionary successful type of inner
321 cell covering does not facilitate the survival of algal cells in the digestive systems of fish.
322 However, investigation of potential dispersion of algae from the aspect of digestibility is
323 not necessarily the most relevant approach. It is indisputable, that digestibility largely

determines the amount of viable cells in the faeces of fish, i.e., the number of cells that can inoculate new habitats. Nevertheless, under favourable conditions, even a single cell can proliferate and build large populations in a new habitat. Thus, in the present context, the most important question is: which taxa are able to survive the passage through the digestive system of fish? Our investigations demonstrated that viable cells can be observed in the hindgut contents from each size group and each taxonomic group, except those algal groups that possess intracellular cell coverings.

Availability of algae to fish, i.e., which algae can be filtered effectively by Asian carps, also seemed to be an important question for us when planning this study. We can conclude that the plankton filtering of fish is apparently but not exclusively a size selective process, and even the smallest (< 10 μm) components of the phytoplankton can be found in the diet of Asian carps. Moreover, we established that there were taxa, which were not found in the lake water samples, but were observed in both foregut and hindgut content samples in variable proportions. Asian carps are able to filter several orders of magnitude larger water volume a day than what a researcher can check during a conventional sample analysis and this may explain the presence of more species in gut contents. These results support the view that distribution of phytoplankton size classes found in the hindgut does not reflect the menu offered to the herbivores but the leftovers after feeding (Sommer & Stibor, 2002).

Because of the rapid downstream transport of algae (Hudon et al., 1996), colonization of the riverine ecosystems seems to be difficult for the newly arriving phytoplankton taxa. Although in the shallow areas the rivers are capable of retaining planktonic organisms (Reynolds, 2000), upstream dispersal needs the contribution of active vectors. Although, to our knowledge, there are no reports on the role of fish in algal dispersion in riverine systems, Asian carps can be effective vectors. Large population of these fish can develop in rivers and because of their feeding habits they have to come considerable distances independently of the

flow direction. These fish can not only inoculate side arms, oxbows and other connecting water bodies, but can also modify the composition of the prevailing planktonic communities of these waters and thus can help the newcomers in the establishment populations.

In conclusion, we demonstrated that filter-feeding fish can harvest and disperse all algal taxa that are available in the ambient water, except for those few groups that possess intracellular cell coverings. However, this latter finding still requires further confirmation by additional experimental studies.

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Tables

Table 1.

Number of identified phytoplankton species in samples collected from Lake Balaton at the vicinity of the nets used for fishing Asian carp on 5 occasions (April, May, June, September, October) during 2013.

	April	May	June	September	October
Pennate diatoms	11	9	20	4	11
Centric diatoms	4	6	6	4	5
Filamentous blue-greens	1	5	4	4	6
Colonial blue-greens	5	4	5	8	3
Chlorococcales	12	16	19	12	13
Volvocales	0	1	1	0	1
Dinophyta	2	1	0	1	0
Desmidiales	0	1	2	4	2
Crysophyceae	2	2	1	1	1
Cryptophyta	2	1	2	1	2
Euglenophyta	2	1	0	1	0
Xanthophyceae	0	1	1	0	0
Total number of species	**41**	**48**	**61**	**40**	**44**

Table 2

Number of identified phytoplankton species collected from the foreguts (the anterior end of intestines of the fish) of Asian carps on 5 occasions (April, May, June, September, October) during 2013.

	April	May	June	September	October
Pennate diatoms	21	17	30	25	26
Centric diatoms	4	5	8	10	7
Filamentous blue-greens	3	6	6	6	5
Colonial blue-greens	8	8	8	10	8
Chlorococcales	17	21	29	22	27
Volvocales	0	0	1	1	0
Dinophyta	2	3	2	3	1
Desmidiales	2	2	2	3	4
Crysophyceae	2	0	1	0	0
Cryptophyta	1	2	1	0	1
Euglenophyta	9	4	6	4	10
Xanthophyceae	0	0	0	1	0
Total number of species	**69**	**68**	**94**	**85**	**89**

558

559 **Table 3**

560 The list of all species, which occurred in the Lake Balaton, in the foregut and in the hindgut

561 samples during the 5 month (April, May, June, September, October) of 2013.

Name of the species	Lake Balaton	Foregut	Hindgut
Acanthoceras zachariasii		X	
Aphanizomenon gracile		X	X
Achnanthes minutissima			X
Achnanthes sp.		X	
Amphora calumetica	X	X	
Amphora ovalis		X	X
Amphora sp.			X
Amphora veneta	X	X	
Anabaena sp.			X
Aphanizomenon issatschenkoi	X		X
Aphanizomenon sp.		X	X
Aphanocapsa holsatica	X	X	
Aphanocapsa incerta			X
Aphanocapsa conferta			X
Aphanocapsa delicatissima			X
Aphanocapsa planctonica	X		
Aphanocapsa sp.	X	X	X
Aphanothece sp.	X	X	X
Aulacoseira ambigua	X	X	X
Aulacoseira granulata	X	X	X
Aulacoseira granulata var. *angustissima*	X	X	X
Aulacoseira sp.	X	X	X
Botryococcus braunii		X	
Caloneis sp.	X	X	

Carteria sp.	X		
Centrales sp.	X	X	X
Ceratium hirundinella	X	X	
Characium sp.			X
Chlamydomonas simplex			X
Chlamydomonas sp.	X	X	
Chlorella sp.			X
Chlorococcales sp.		X	X
Choricystis minor			X
Chroococcus limneticus	X	X	X
Chroococcus minimus		X	X
Chroococcus planctonicus		X	X
Chroococcus turgidus	X	X	X
Closterium aciculare	X	X	X
Closterium acuminatum	X		
Closterium acutum			X
Closterium acutum var. *variabile*	X	X	X
Cocconeis sp.	X	X	
Coelastrum astroideum			X
Coelastrum microporum			X
Coelastrum pseudomicroporum			X
Coelastrum reticulatum		X	X
Cosmarium humile		X	
Cosmarium sp.	X	X	
Cryptomonas sp.	X		
Cryptophyta sp.	X	X	
Crysochromulina parva	X	X	X
Crysophyceae sp.	X	X	X
Cyanocatena sp.			X
Cyanodichtyon sp.		X	X
Cyclotella bodanica	X	X	
Cyclotella meneghiniana	X	X	
Cyclotella ocellata	X	X	X
Cyclotella pseudostelligera	X	X	X
Cylindrospermopsis raciborskii			X
Cylindrospermopsis sp.	X		
Cymatopleura elliptica		X	X
Cymatopleura solea		X	X
Cymbella silesiaca			X
Cymbella elliptica		X	
Cymbella minuta	X	X	X
Cymbella sp.	X		X
Dactyosphaerium jurisii	X	X	X
Dactyosphaerium sociale	X	X	X
Dictyosphaerium chlorelloides			X
Dictyosphaerium pulchellum	X	X	X
Dictyosphaerium tetrachotomum		X	X
Dinophyta sp.		X	
Diploneis parma	X	X	X

Dysmorphococcus sp.		X	
Entomoneis costata	X		
Eucapsis sp.			X
Euglena acus		X	
Euglena allorgei		X	
Euglena oblonga	X		
Euglena deses		X	
Euglena gracilis		X	
Euglena limnophila		X	
Euglena mutabilis		X	
Euglena oxyouris		X	
Euglena pisciformis		X	
Euglena spirogyra			X
Euglena texta		X	
Euglena variabilis		X	
Euglenoid sp.	X	X	X
Eunotia sp.	X	X	
Eutetramorus fottii	X	X	X
Eutetramorus glabrum			X
Fragilaria capucina		X	X
Fragilaria construens	X	X	X
Fragilaria nitzschoides			X
Fragilaria parasitica		X	
Fragilaria pinnata			X
Fragilaria sp.	X	X	X
Fragilaria ulna	X	X	X
Fragilaria ulna var. *acus*			X
Francea sp.	X		
Gloeotila sp.		X	
Gomphonema olivacea	X	X	X
Gomphosphaeria sp.			X
Gyrosigma sp.	X	X	X
Kirchneriella dianae		X	
Kirchneriella irregularis	X	X	X
Kirchneriella obesa			X
Komvolophoron sp.			X
Lagerheimia balatonica	X		X
Lepocinclis fusiformis		X	
Lepocinclis ovum var. dimido-minor		X	
Merismopedia minutissima	X		X
Merismopedia tennuis	X	X	
Micractinium pusillum	X	X	X
Microcoleus sp.			X
Microcystis aeruginosa		X	X
Microcystis viridis	X	X	X
Microspora sp.		X	
Monoraphidium contortum	X	X	X
Monoraphidium griffithii	X	X	X
Monoraphidium irregulare			X

Monoraphidium komarkovae		X	X
Navicula radiosa		X	
Navicula reticulata	X	X	X
Navicula rhynchocephala			X
Navicula sp.	X	X	X
Neidium sp.		X	
Nephrochlamys sp.	X		X
Nephrochlamys subsolitaria			X
Nitzschia acicularis	X	X	X
Nitzschia amphibia			X
Nitzschia dissipata	X	X	
Nitzschia constricta	X	X	X
Nitzschia graciliformis			X
Nitzschia gracilis			X
Nitzschia hantzschiana		X	X
Nitzschia hungarica			X
Nitzschia linearis	X	X	
Nitzschia lorenziana	X	X	X
Nitzschia palea			X
Nitzschia sigmoidea	X	X	X
Nitzschia sp.	X	X	X
Oocystis lacustris		X	X
Oocystis marsonii	X	X	X
Oocystis parva	X	X	X
Oocystis solitaria	X	X	X
Oocystis sp.	X	X	X
Oscillatoria sp.	X	X	X
Pandorina smithii			X
Pediastrum boryanum	X	X	X
Pediastrum duplex	X	X	X
Pediastrum simplex		X	
Peridinium cinctum	X		
Phacotus lenticularis		X	X
Phacotus sp.			X
Phacus dangeardii		X	
Phacus megapyrenoides	X		
Phacus skujae		X	
Phacus sp.		X	
Phacus wettsteinii		X	
Phormidium autumnale		X	X
Phytomonadina sp.			X
Pinnularia viridis			X
Pinnularia sp.	X	X	X
Planktolyngbya capillaris		X	
Planktolyngbya circinale	X	X	X
Planktolyngbya limnetica	X	X	X
Planktonema lauterbornii	X	X	X
Planktosphaeria gelatinosa		X	
Pseudanabaena sp.	X	X	X

Quadricoccus ellipticus		X	X
Rhodomonas minuta	X	X	X
Rivularia sp.			X
Romeria elegans	X	X	X
Scenedesmus acuminatus			X
Scenedesmus acutiformis			X
Scenedesmus acutus			X
Scenedesmus arcuatus			X
Scenedesmus armatus	X	X	X
Scenedesmus balatonicus	X		
Scenedesmus carinatus			X
Scenedesmus denticulatus			X
Scenedesmus dispar			X
Scenedesmus ecornis			X
Scenedesmus intermedius		X	X
Scenedesmus juvenilis	X	X	X
Scenedesmus maximus			X
Scenedesmus obtusos		X	X
Scenedesmus pleiomorphus			X
Scenedesmus quadricauda	X		X
Scenedesmus spinosus			X
Scenedesmus subspicatus			X
Schroederia robusta			X
Schroederia setigera	X	X	X
Schroederia sp.			X
Snowella lacustris			X
Snowella litoralis	X	X	X
Staurastrum chaetoceras	X	X	X
Stauroneis sp.	X	X	
Stephanodiscus hantzschii	X	X	
Stichococcus subtilis		X	X
Surirella brebissonii	X	X	
Surirella robusta	X	X	X
Synechococcus elongatus			X
Tetrachlorella sp.	X		
Tetraedron caudatum	X		
Tetraedron minutum		X	
Tetrastrum staurogeniaeforme	X	X	
Tetrastrum triangulare	X	X	X
Thalassiosira weissflogii			X
Trachelomonas oblonga	X		
Trachelomonas volvocina		X	
Trachydiscus lenticularis	X		
Trachydiscus sp.			X
Ulothrix tenerrima			X
Willea sp.		X	
Woronichinia naegeliana		X	X
Xanthophyceae sp.		X	

562

563 **Table 4**

564 Number of viable taxa which were observed in the cultured (BG-11) hindgut samples in the 5

565 sampling months (April, May, June, September, October) during 2013.

	April	May	June	September	October
Pennate diatoms	19	14	15	9	11
Centric diatoms	5	6	4	6	6
Filamentous blue-greens	6	5	5	7	8
Colonial blue-greens	12	13	11	10	12
Chlorococcales	26	30	33	19	29
Volvocales	0	1	1	1	2
Dinophyta	0	0	0	0	0
Desmidiales	0	0	1	2	3
Crysophyceae	0	1	0	0	0
Cryptophyta	0	0	0	0	0
Euglenophyta	0	0	1	1	1
Xanthophyceae	0	0	0	1	0
Total number of species	**68**	**70**	**71**	**56**	**72**

Legends for figures

Fig. 1

An image of the filtering apparatus (gill raker) of hybrid Asian carp showing the inner surface of the gill arch where the filtered material is collected and compressed prior to ingestion (filtered matter highlighted by the white ellipse).

Fig. 2

The relative abundances of counted units (cells or colonies) in Lake Balaton.

Fig. 3

Relative abundances of the counted units (cells or colonies) in the foregut contents.

Fig. 4 a, b

Occurrence of the various algal taxa in the three types of samples. Letters above the columns indicate the similarities and/or the significant differences between the groups. (Identical letters indicate the lack of significant differences based on Kruskal-Wallis tests).

Fig. 5

Comparison of the algal composition (based on the number of species) of Lake Balaton, the foregut and the hindgut samples.

Fig. 6

Non-metric multidimensional scaling (nMDS) plots showing the ordination of the three types of samples (Lake Balaton: □; foregut: **x;** hindgut: **o**), based on species occurrences and Jaccard similarity.

Fig. 7

The number of phytoplankton taxa in the three size categories (1. category: <10 µm; 2. category: 10-40 µm; 3. category: >40 µm).