Knowledge and Management of Aquatic Ecosystems (2015) 416, 36
© I. Battonyai et al., published by EDP Sciences, 2015
DOI: 10.1051/kmae/2015031

www.kmae-journal.org

Knowledge & Management of Aquatic Ecosystems

Journal fully supported by Onema

Relationship between gill raker morphology and feeding habits of hybrid bigheaded carps (*Hypophthalmichthys* spp.)

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Received July 6, 2015
Revised October 26, 2015
Accepted October 27, 2015

ABSTRACT

Key-words: *bigheaded carp, gill raker morphology, filter-feeding, food size, plankton*

Bigheaded carps and especially silver carp have been considered as an effective biological control for algal blooms, thus were introduced to several countries in the last decades, including Hungary. Our aim was to explore the feeding habits of bigheaded carps in Lake Balaton (Hungary), where the stock consists mainly of hybrids (silver carp × bighead carp). We examined the relationship between filtering apparatus (gill raker) morphology and size-distribution of planktonic organisms in the food. We failed to find any significant relationship between gill raker parameters and plankton composition in the filtered material. Bigheaded carps with various types of gill rakers consumed food within the same size-spectrum, independently of the rate of hybridization. However, the linkage between the proportion of different planktonic size classes in the water and in the diet of fish was detectable in case of both phytoplankton and zooplankton consumption, suggesting that the seasonally variable availability of different food items was an important factor in determining the food composition of bigheaded carps. We can deduce that bigheaded carps consume high amounts of zooplankton to meet their energy requirements, and the diet overlap among bigheaded carps and other planktivores may exert negative effects on native fish populations.

RÉSUMÉ

Relation entre la morphologie des branchiospines et les habitudes alimentaires d'hybrides de carpes à grosse tête (*Hypophthalmichthys spp*)

Mots-clés : *carpe à grosse tête,*

La carpe à grosse tête et en particulier la carpe argentée ont été considérées comme un moyen de contrôle biologique efficace contre la prolifération des algues, ainsi elles ont été introduites dans plusieurs pays dans les dernières décennies, dont la Hongrie. Notre objectif était d'étudier les habitudes alimentaires des carpes à grosse tête dans le lac Balaton (Hongrie), où le stock se compose principalement d'hybrides (carpe argentée × carpe à grosse tête). Nous avons

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morphologie des branchiospines, filtre, taille de nourriture, plancton

examiné la relation entre la morphologie de l'appareil de filtrage (branchiospines) et la distribution en taille des organismes planctoniques dans l'alimentation. Nous n'avons pas trouvé de lien significatif entre les paramètres des branchiospines et la composition du plancton dans le matériel filtré. Les carpes à grosse tête de différents types de branchiospines ont consommé des aliments de même distribution en taille, indépendamment du taux d'hybridation. Cependant, le lien entre la proportion des différentes classes de taille planctoniques dans l'eau et dans l'alimentation des poissons était détectable en cas de consommation mixte en phytoplancton et en zooplancton, ce qui suggère que la disponibilité variable selon les saisons des différentes sources alimentaires était un facteur important dans la détermination de la composition de la nourriture des carpes à grosse tête. Nous pouvons en déduire que les carpes à grosse tête consomment de grandes quantités de zooplancton pour répondre à leurs besoins en énergie, et le chevauchement de l'alimentation des carpes à grosse tête avec d'autres planctivores peut exercer des effets négatifs sur les populations de poissons indigènes.

INTRODUCTION

Bighead carp (*Hypophthalmichthys nobilis* R.) and silver carp (*H. molitrix* V.) are filter feeder fishes, native to the large lakes and rivers of eastern Asia (Jennings, 1988; Kolar *et al.*, 2007). These species and their hybrids (collectively referred as bigheaded carps) are planktivorous, detritivorous and opportunistic feeders (Lieberman, 1996; Kolar *et al.*, 2007). They have been introduced into lakes, rivers and reservoirs throughout the world. Kolar *et al.* (2007) reported that bighead carp has been imported or expanded its range into 72 countries, while silver carp has been introduced into or has spread along watercourses to at least 88 countries. Bigheaded carps are popular fish in aquacultures and have been considered as effective biological control agents for algal blooms (Cremer and Smitherman, 1980; Xie and Liu, 2001). However, recent studies have demonstrated that bighead and silver carps can adversely affect the water quality and native fish populations. For example, Borics *et al.*, (2000), Cooke *et al.* (2009) and Lin *et al.* (2014) reported that bigheaded carps contributed significantly to the development of high algal biomass and reduced water clarity, while Sampson *et al.* (2009) found considerable diet overlap among native fishes and bigheaded carps, which may cause decreased fitness in native fish populations. In addition, the combined stocking of these species caused a decline in the abundance of cladocerans and copepods in eutrophic lakes in China where bigheaded carps were introduced (Yang *et al.*, 1999; Shao *et al.*, 2001). Thus, these fishes constitute a considerable ecological threat to aquatic ecosystems where they are not native (Chick and Pegg, 2001; Xie and Chen, 2001; Cooke *et al.*, 2009). Accordingly, bigheaded carp introduction and stocking to natural waters have been stopped and banned in the last decades in several countries, including Hungary (Boros *et al.*, 2014).

Bigheaded carps use their filtering apparatus (gill raker) to harvest plankton and any other particles that match in size with their filtering capacity. Gill rakers are in two separate rows on each gill arch, forming a v-shaped cavity between them. There are two forms of filter-feeding in bigheaded carps: pump feeding and ram suspension feeding (Kolar *et al.*, 2007). During pump feeding, fish suck in water, which is pushed through the gill rakers by the buccal pump after closing the mouth. In some cases, fish exhibit ram suspension feeding, when they hold their mouths open and swim through the water, forcing water through the gill rakers. Subsequently, the filtered particles are trapped within the filtering apparatus, and the compressed filtrate is ingested (Dong and Li, 1994; Kolar *et al.*, 2007). Previous studies suggested that the feeding and filtering efficiency of bigheaded carps is primarily determined by the morphology, and more specifically, by the "mesh-size" of their gill rakers (Lieberman, 1996; Kolar *et al.*, 2007).

Bighead and silver carps can be easily distinguished by the distinctive morphology of their gill rakers. Bighead carp have long, thin gill rakers that are not fused (forming a comb-like structure), in contrast to the gill rakers of silver carps that are fused and form a sponge-like apparatus (Kolar *et al.*, 2007). In addition, there is a difference between the two species in the ratio between the area of filtering (gill raker) and respiratory (gill filaments) parts of the epibranchial organs; this ratio is about 1:1 in bighead carps, and varies between 2:1 and 3:1 in silver carps (Jirásek *et al.*, 1981; Kolar *et al.*, 2007). However, hybrid individuals often exhibit mixed morphological features, and gill rakers of hybrids are usually intermediate in their development between the two species (Kolar *et al.*, 2007). In some hybrids, gill rakers appear more like those of bighead carp, but are clubbed or wavy, sometimes with small branches. In the form that appears more like the filtering apparatus of silver carp, the rakers are incompletely fused, giving a ragged appearance (Kolar *et al.*, 2007).

Several studies have reported that comb-like gill rakers of bighead carp are specialized to filter larger particles than those of silver carp, and bighead carp is considered to be mainly zooplanktivorous (Burke *et al.*, 1986; Dong and Li, 1994; Kolar *et al.*, 2007). However, it has been shown that bighead carp can ingest particles even up to four times smaller than gill raker mesh-size (5−6 μm particles; Xie, 2001), and can switch to feeding on phytoplankton when zooplankton concentration is low (Lazareva *et al.*, 1977; Opuszynski *et al.*, 1991). Silver carp can filter and consume smaller particles than bighead carp, owing to the different morphology of their epibranchial organs. Most studies cite silver carp as primarily phytoplankton feeder, able to collect algae larger than 10 μm (Sieburth *et al.*, 1978; Hampl *et al.*, 1983; Smith, 1989; Vörös *et al.*, 1997), while others suggest that silver carp is able to collect even nanoplankton (<10 μm) (Cremer and Smitherman, 1980; Xie, 1999; Görgényi *et al.*, 2015). However, Spataru and Gophen (1985) revealed that the proportion of zooplankton in the diet of silver carps can be up to 50% in some cases, and several other studies have demonstrated that the presence of silver carp results in a zooplankton community dominated by smaller individuals (*e.g.*, Fukushima *et al.*, 1999; Lu *et al.*, 2002).

In this study, our aim was to explore the feeding habits of bigheaded carps in Lake Balaton, where the stock consists mainly of hybrid individuals. Hybrids can be characterised with variously mixed phenotypical features, including the morphology of their gill rakers. We hypothesized that the proportion of small planktonic organisms would be higher in the filtered material of hybrids that resemble to silver carp, as this species is specialised to consume mainly phytoplankton. In turn, we expected that the proportion of larger planktonic organisms would increase with the increasing dominance of bighead carp characteristics in the filtering apparatus. Moreover, we expected that the seasonally variable availability of planktonic organisms would determine the food composition of bigheaded carps, but to different extents in individuals with silver and bighead carp traits.

MATERIALS AND METHODS

> *SAMPLING AREA*

Lake Balaton is a large shallow lake in Central Europe, situated in the western part of Hungary. It is an oligo-mesotrophic lake, with a surface area of 596 km^2 and an average depth of about 3 m. Lake Balaton is a unique system with a very high suspended particulate load and is one of the few large natural lakes where bigheaded carps are present in large abundance and are not still being stocked. These conditions are rarely encountered elsewhere in the world.

Bigheaded carps were introduced to Lake Balaton in the early 1970s, and since then they form a massive stock in the lake, despite the stocking was stopped and banned in 1983. The last extensive fish survey in 2008 showed that bigheaded carps constitute about one-third of the total fish biomass in the lake (Tátrai *et al.*, 2009), thus they might have an important role in any fish-mediated ecological processes (including bottom-up and top-down effects). In addition, despite the relatively low productivity and consequently scarce food resources in Lake Balaton, bigheaded carps grow intensively and their condition factor is relatively high compared to other ecosystems (Boros *et al.*, 2014).

Table I
Main parameters of the 26 studied bigheaded carps. SL – standard body length; W – wet mass; Gill raker category – occurrence of comb-like and spongy structures in the gill rakers, denoted with a category number (see explanation in the Materials and methods chapter); NPUA – number of pores per unit (1 cm^2) area on the gill raker, standard error in the brackets; FRR – filtering to respiratory part ratio of the gill raker.

Sampling month	*SL* (cm)	*W* (kg)	Gill raker category	NPUA (SE)	FRR
May	94	19.1	2	5.83 (1.15)	1.29
	86	12.2	3	6.17 (1.75)	0.90
	91	11.2	3	5.83 (1.26)	1.31
	98	21.4	3	5.67 (2.93)	0.97
June	89	13.4	3	8.42 (2.20)	1.15
	94	17.7	3	6.92 (1.39)	1.37
	95	17.7	3	10.58 (2.42)	1.00
	78	11.2	4	11.67 (3.97	1.27
	81	11.8	3	9.50 (2.09)	1.09
	101	22.1	3	8.17 (1.60)	1.10
	85	14.1	2	10.67 (2.44)	1.02
	88	15.1	3	4.58 (2.69)	0.82
	84	12.3	4	9.00 (2.30)	1.08
Sep.	103	22.0	2	0	0.69
	102	24.2	1	0	0.66
	106	25.1	1	0	0.98
	89	12.5	4	7.67 (3.48)	1.30
	94	15.7	3	6.42 (1.63)	0.87
	94	21.1	4	6.83 (1.98)	1.28
	90	12.8	3	3.50 (2.62)	1.14
Oct.	111	30.5	2	0	0.90
	98	18.2	4	5.83 (1.94)	1.21
	90	13.8	4	10.83 (3.43)	1.09
	91	13.2	4	8.17 (2.21)	1.42
	85	12.8	4	8.79 (2.86)	1.38
	87	14.6	4	8.21 (2.67)	1.23

> SAMPLING AND SAMPLE PROCESSING

Bigheaded carps were collected from the eastern basin of the lake by the local fishery company (Balaton Fish Management Non-Profit Ltd) between May–October 2013, using 12 cm knot-to-knot mesh-size gillnets. A total of 58 large bigheaded carps were captured during the course of the year, among which we found 26 individuals that had sufficient quantities of filtrate (*i.e.*, the material captured in the gill rakers) samples for microscopic analyses (Table I). Filtrate samples were collected with a flat stick directly from the inner grooves of the gill rakers, where the filtered material is compressed before ingestion. Further information on the methods of filtrate sample collection can be found in the study of Vitál *et al.*, (2015). This study has demonstrated that filtrate samples are more appropriate for the determination of food composition of bigheaded carps, compared to foregut samples. Consequently, we used gill raker filtrates for the analysis of phytoplankton and zooplankton composition in the food.

To determine phytoplankton species composition in Lake Balaton, water column samples were collected around the fishing nets with a tube sampler at each fish sampling dates. Zooplankton samples were also taken from the entire water column around the nets (subsamples were taken at 50 cm depth intervals from the surface to the benthic water layers and were mixed and merged), using a Schindler-Patalas sampler (34 L volume) equipped with 60 μm mesh-size plankton netting.

Filtrate and lake water samples for microscopic analysis of phytoplankton composition were preserved in Lugol's solution, while samples for zooplankton analysis were stored in 70% ethanol at 4 °C until processing. Phytoplankton identification was carried out using a Zeiss Axiovert-40 CFL inverted microscope at 400 × magnification, while zooplankton were counted with a binocular microscope at 40 × magnification. Phytoplankton individuals found in the

Table II
Categorization of filtering-to-respiratory part ratio (FRR) and the number of pores per unit area (NPUA) values, measured in the gill rakers of bigheaded carps.

	FRR	*n*		NPUA	*n*
I	0.66–0.69	2	**I**	0	5
II	0.82–0.9	4	**II**	3.5–4.6	2
III	0.97–1.02	4	**III**	5.7–6.9	8
IV	1.08–1.15	6	**IV**	8.2–9.5	7
V	1.21–1.31	7	**V**	10.6–11.7	4
VI	1.37–1.42	3			

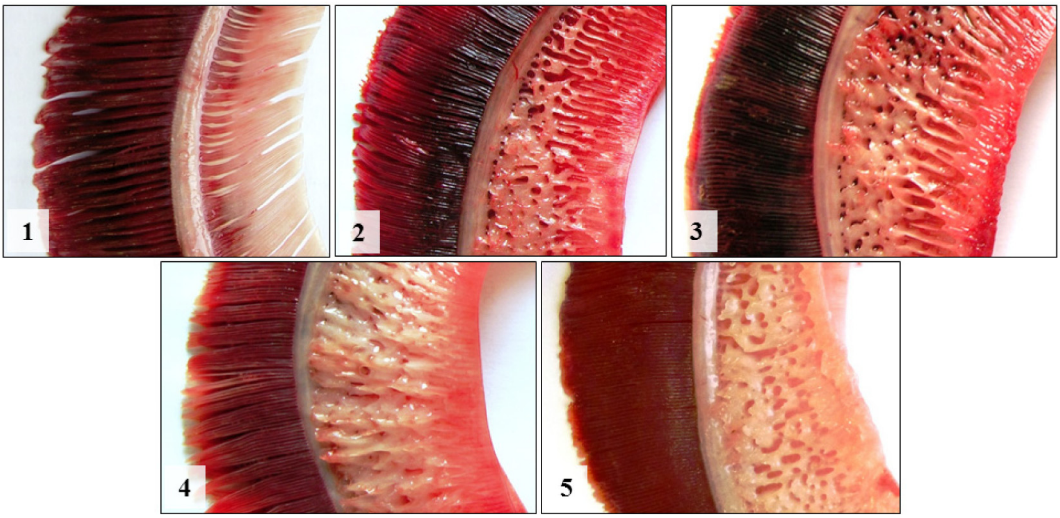

Figure 1
Various types of gill rakers are found in the bigheaded carps sampled from Lake Balaton, including comb-like (1/1), mixed (1/2; 1/3; 1/4) and sponge-like (1/5) structures.

filtered material were divided into three size categories (<10 μm; 10–40 μm; >40 μm), as well as zooplankton (<0.4 mm; 0.4–1.3 mm; >1.3 mm).

The gill rakers of bigheaded carps were categorized according to the following three parameters: (a) morphological characteristics (*i.e.* comb-like, sponge-like and intermediate types); (b) the number of pores per unit (1 cm^2) area (NPUA) on the outer surface of gill rakers (in three replicates per gill raker; NPUA = 0 in comb-like gill rakers); (c) the filtering-to-respiratory part ratio (FRR) of the epibranchial organs, measured in the midline of gill rakers and gill filaments. NPUA values were divided into five groups and FRR values into six groups (Table II). Morphological characteristics of the gill rakers was evaluated visually, and gill rakers were categorized as follows: (1) typical for bighead carp, *i.e.*, comb-like (Figure 1/1); (2) hybrid gill raker with bighead carp dominance (Figure 1/2); (3) intermediate in development between bighead and silver carp (Figure 1/3); (4) hybrid gill raker with silver carp dominance (Figure 1/4); (5) typical for silver carp, *i.e.*, sponge-like (Figure 1/5).

> STATISTICAL ANALYSES

To explore the relationship between gill raker morphology and size-distribution of planktonic organisms in the filtered material (*i.e.*, the filtering efficiency of fish), MANOVA (multivariate analysis of variance) test was used. We made separate models for phytoplankton and zooplankton for assessing the relationships with gill raker morphology. The size categories of food items were added as response (dependent) variables, while structure of gill rakers (1–5 category number; see above), the NPUA, FRR, and sampling date were added as factors (categorical variables) to the models. Subsequently, ANOVA (analysis of variance) was

Table III
Results of the MANOVA models on the relationship between different factors (sampling date, filtering to respiratory part ratio, number of pores per unit area, gill raker structure) and the size-distribution of the filtered phytoplankton and zooplankton.

	Wilks' λ	*F*	effect *df*	error *df*	*P*
Phytoplankton					
Intercept	0.09	46.42	2	9	<0.01
Sampling date	0.20	3.74	6	18	0.01
FRR	0.36	1.21	10	18	0.35
NPUA	0.43	1.19	8	18	0.36
Gill raker structure	0.49	1.30	6	18	0.31
Zooplankton					
Intercept	0.05	92.49	2	9	<0.01
Sampling date	0.29	2.52	6	18	0.05
FRR	0.42	0.98	10	18	0.49
NPUA	0.42	1.22	8	18	0.34
Gill raker structure	0.35	2.05	6	18	0.11

used to reveal significant relationships between variables, in cases where the effect of any of the factors proved to be significant ($P < 0.05$). MANOVAs were performed with the StatSoft Statistica 7.0 software. In addition, similarity percentage (SIMPER) tests (Clarke, 1993) were used to assess the importance of different food item size categories in explaining potential differences between the filtrate and Lake Balaton samples. SIMPER analyses were performed with the Past 2.17 software package (Hammer *et al.*, 2001).

RESULTS

We did not find any significant relationship between the measured gill raker parameters (occurrence of comb-like and sponge-like structures on the gill rakers, number of pores per unit area, filtering-to-respiratory part ratio) and phytoplankton and zooplankton size-distribution in the filtered material (Table III). Thus, our results suggest that the feeding habits of bigheaded carps were not determined primarily by the morphology of gill rakers. We found that the various types of gill rakers were able to harvest plankton with similar efficiency. It has to be noted that the overall sample size was relatively low in our study and we could not collect all gill raker types at each sampling months. In addition, some fish possessed gill rakers typical for silver carp (Figure 1/5), but we failed to find sufficient amount of filtrate samples in these structures for food composition analysis.

Nevertheless, our results show that sampling date and accordingly the seasonal difference in the availability of food resources in the ambient water had a significant influence on the food-spectrum of bigheaded carps, regarding both phytoplankton and zooplankton consumption (Table III). The proportion of small ($<$10 μm) algae in the filtered material was found to be significantly higher in June and October, compared to that in May (Figure 2). The proportion of medium-sized (10–40 μm) algae was significantly higher in October than in all other sampling months. However, such type of seasonality was not detectable in the case the largest algae ($>$40 μm) present in the food. Although the MANOVA test revealed significant relationship between sampling date and phytoplankton size-distribution in the food (Table III), the proportion of the small algae was not the highest in the filtered matter when the ratio of small algae increased in the ambient water (in September). Similarly, we found mismatch in the peak proportions of medium-sized phytoplankton in the food (peaked in October) and in Lake Balaton (peaked in May and June) (Figure 2).

Regarding seasonality in zooplankton consumption, significant differences were also found in the small ($<$0.4 mm) and medium-size (0.4–1.3 mm) categories, but not in case of the largest ($>$1.3 mm) zooplankters. The proportion of small zooplankton in the food was significantly lower in June, corresponding to the period when the ratio of the smallest zooplankton was

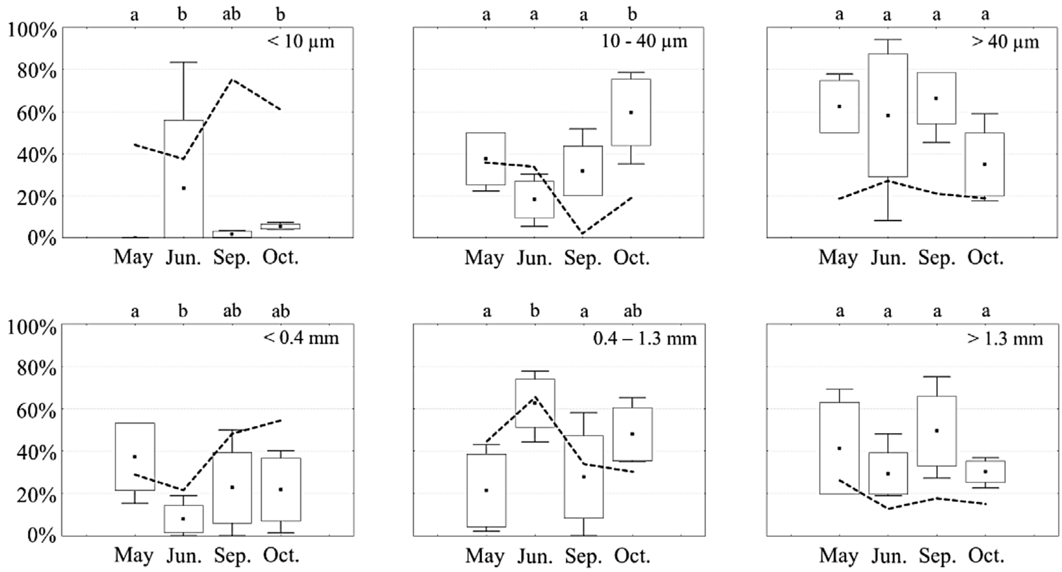

Figure 2
Box-plots of seasonal differences in the phytoplankton (upper plots) and zooplankton (lower plots) size-distribution in the diet of bigheaded carps. Boxes marked by the same letters do not differ significantly ($P < 0.05$*). Dashed lines indicate the proportion of each phytoplankton and zooplankton size classes in lake water samples.*

the lowest in Lake Balaton (Figure 2). In turn, we found significantly higher ratios of medium-sized zooplankton in the diet in June, when the proportion of zooplankton of this size was the highest in the water. Significant seasonal differences were not typical for large (>1.3 mm) zooplankton in the food of bigheaded carps (Figure 2).
The SIMPER test showed that lake water and filtrate samples differed more typically in their phytoplankton composition, compared to their zooplankton composition (Table IV). In general, the smaller components of phytoplankton occurred more frequently in the lake water compared to that in filtrate samples, thus bigheaded carps exhibited a certain degree of selectivity for larger food items (*i.e.*, for >40 μm phytoplankton).

DISCUSSION

In this study, we analysed the size-selective feeding habits of bigheaded carps, as a function of gill raker morphology and seasonality. We expected that hybrid bigheaded carps with silver carp-like or intermediate type gill rakers would consume smaller plankton in higher proportion compared to individuals with bighead carp-like gill rakers. In addition, it was also hypothesized that the presence of different food resources in the ambient water (seasonal differences in food availability) has a significant effect on the food size-spectrum of bigheaded carps.
The assumption of seasonal differences in the food composition of bigheaded carps is supported by our results. The linkage between the proportion of different planktonic size classes in the water and in the diet of fish was detectable in case of both phytoplankton and zooplankton, being more typical for the latter. Previous studies reported that silver carps can filter and consume smaller particles than bighead carp (Cremer and Smitherman, 1980; Spataru *et al.*, 1983; Shapiro, 1985; Kolar *et al.*, 2007), while others pointed out that silver carp are able to collect algae larger than 10 μm (Hampl *et al.*, 1983; Smith, 1989; Vörös *et al.*, 1997).
However, similarly to Cremer and Smitherman (1980) or Xie (1999), we have also found that a smaller but still considerable fraction of the algae in the food of bigheaded carps was smaller than 10 μm, suggesting that these fish are able to filter and consume even nanoplankton. Based on the previously reported feeding habits of silver and bighead carps, we expected that beside the distribution and availability of different planktonic size classes in the lake water,

Table IV
SIMPER analysis of dissimilarity between size categories of phytoplankton and zooplankton in filtrate and Lake Balaton samples.

	Sampling month	Size-category	Contribution	Cumulative %	Mean % in filtrate	Mean % in Lake Balaton	Overall dissimilarity
Phytoplankton	May	< 10 μm	22.46	45.52	0	44.9	49.34
		>40 μm	21.87	89.86	62.4	18.7	
		10–40 μm	5	100	37.6	36.4	
	Jun.	>40 μm	18.23	43.01	58.2	27.2	42.38
		<10 μm	15.96	80.66	23.6	38.2	
		10–40 μm	8.19	100	18.2	34.6	
	Sep.	<10 μm	37.14	50	1.8	76.1	74.28
		>40 μm	22.61	80.44	66.4	21.1	
		10–40 μm	14.53	100	31.8	2.7	
	Oct.	<10 μm	28.04	49.80	5.5	61.6	56.30
		10–40 μm	19.98	85.28	59.6	19.6	
		>40 μm	8.28	100	34.9	18.8	
Zooplankton	May	0.4–1.3 mm	11.69	41.39	21.4	44.8	28.23
		>1.3 mm	8.92	72.99	41.3	26.3	
		<0.4 mm	7.62	100	37.3	28.9	
	Jun.	>1.3 mm	8.39	43.16	29.4	12.6	19.45
		<0.4 mm	6.82	78.27	7.9	21.6	
		0.4–1.3 mm	4.22	100	62.7	65.8	
	Sep.	>1.3 mm	15.91	42.41	49.5	17.7	37.50
		<0.4 mm	13.09	77.31	22.7	48.4	
		0.4–1.3 mm	8.51	100	27.8	34	
	Oct.	<0.4 mm	16.43	49.97	21.8	54.7	32.88
		0.4–1.3 mm	8.86	76.93	48	30.3	
		>1.3 mm	7.58	100	30.2	15	

the gill raker morphology would also affect the food composition. However, in contrast to our expectations and several reports in the literature, we did not find considerable relationship between any of the measured gill raker parameters and food composition of bigheaded carps. This suggests that in some ecosystems the feeding habits of these species may be less distinct than it was previously thought, and more specifically that bigheaded carps inhabiting Lake Balaton likely consume and utilize the same food resources, independently of the rate of hybridization. We have to acknowledge that the number of investigated bigheaded carps was relatively low in our study, and we could not collect all gill raker types at each sampling months, thus the results must be considered with some caution. Nevertheless, we believe that the general trends we found suggest that gill raker morphology is not the primary factor in determining the feeding habits of hybrid bigheaded carps in Lake Balaton.

In a recent study, Boros *et al.* (2014) pointed out that hybrid bigheaded carps in Lake Balaton consume significant amounts of inorganic matter, which can represent up to 80% of their gut contents (in dry mass). This suggests that bigheaded carps cannot discriminate small inorganic particles of no nutritional value from planktonic food, which means a lack of capability of quality-dependent food selectivity in these individuals. Also, Cremer and Smitherman (1980) found phytoplankton in the guts of silver carp in the same proportion as in lake water samples, suggesting no selectivity. The only evidence for some extent of food selectivity was that the proportion of larger algae was slightly higher in the gill raker filtrates than in the lake water samples. However, this kind of food selectivity was found to be independent of gill raker morphology in Lake Balaton. Although we did not find considerable relationship between the gill rakers' morphological parameters and the food composition of individuals in our study, it may be the case that the same relationship would be significant in other ecosystems where

the bigheaded carp stock consists of different-sized individuals and where the assemblage of the planktonic community is different than in Lake Balaton. Accordingly, we have to emphasize that we used relatively large fish in our study (see Table I). The food selectivity and feeding habits of smaller bigheaded carps may be different than those of the older and bigger individuals, as the morphology and mesh-size of gill rakers undergo some changes as the fish grows (Jirásek *et al.*, 1981; Hampl *et al.*, 1983). A good example for this is that all bigheaded carps start feeding on zooplankton after hatching and then switch to a mixed (phytoplankton and zooplankton) or phytoplankton-based diet as the ontogeny proceeds (Kolar *et al.*, 2007).
Bigheaded carps with various types of gill rakers (including those of comb-like, sponge-like, and intermediate forms) were found to consume similar-sized planktonic organisms in Lake Balaton and our results suggest that the most important determining factor of their food composition was the availability of planktonic organisms in the ambient water. Bigheaded carps in Lake Balaton consume both phytoplankton and zooplankton, but a significant fraction of the consumed algae survive the passage through the alimentary tract and are egested in a viable form, which means that these algae do not serve as nutritive components for bigheaded carps (Görgényi *et al.*, 2015). The reason of bigheaded carp stocking to Lake Balaton was to increase fishery yields and improve the water quality at the same time, because it was hypothesised that these fish (especially silver carp) would remove significant quantities of phytoplankton from the water column. However, our results show that hybrid bigheaded carps with silver carp traits seemingly do not consume smaller particles in higher proportions compared to bigheaded carps with comb-like gill rakers.
By considering the intensive growth and high condition factor of bigheaded carps in Lake Balaton (Boros *et al.*, 2014), and the fact that a reasonable fraction of the ingested phytoplankton passes through the alimentary tract without digestion and utilization (Vörös *et al.*, 1997; Görgényi *et al.*, 2015), we can deduce that bigheaded carps must consume high amounts of zooplankton to meet their energy requirements. This suggests a diet overlap among native planktivores (*e.g.*, the fingerlings of all other fish species) and bigheaded carps, which may lead to a strong interspecific competition and probably to reduced fitness in native fish populations in such a nutrient poor lake. Based on our results, we suggest and urge a more effective and targeted bigheaded carp removal from Lake Balaton to eliminate a considerable ecological risk because the presence of these exotic species could result in the decline of native fish populations, as previous studies have demonstrated (Spataru and Gophen, 1985; Chick and Pegg, 2001; Sampson *et al.*, 2009).

ACKNOWLEDGEMENTS

We thank I. Mecsnóbel and Z. Poller for their skilful assistance. Bigheaded carps for this study were provided by the Balaton Fish Management Non-Profit Ltd. This study was supported by an OTKA grant (K 83893).

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Cite this article as: I. Battonyai, A. Specziár , Z. Vitál, A. Mozsár, J. Görgényi, G. Borics, L.G. Tóth and G. Boros, 2015. Relationship between gill raker morphology and feeding habits of hybrid bigheaded carps (*Hypophthalmichthys* spp.). *Knowl. Manag. Aquat. Ecosyst.*, 416, 36.