

This manuscript is contextually identical with the following published paper:
Vital Z, Specziár A, Mozsár A, Takács P, Borics G, Görgényi J, G.-Tóth L, Nagy SA, Boros G (2015) Applicability of gill raker filtrates and foregut contents in the diet assessment of filter-feeding Asian carps. FUNDAMENTAL AND APPLIED LIMNOLOGY, 187: (1) pp. 79-86.

DOI: <http://dx.doi.org/10.1127/fal/2015/0698>

The original published pdf available in this website:

http://www.ingentaconnect.com/content/schweiz/fal/pre-prints/content-fal_000_0_0000_0000_vital_0698_prepub

Applicability of gill raker filtrates and foregut contents in the diet assessment of filter-feeding Asian carps

Zoltán Vital^{1*}, András Specziár¹, Attila Mozsár¹, Péter Takács¹, Gábor Borics², Judit Görgényi², László G.-Tóth¹, Sándor Alex Nagy³, Gergely Boros¹

¹ MTA Centre for Ecological Research, Balaton Limnological Institute, Klebelsberg Kuno str. 3., H-8237 Tihany, Hungary;

² MTA Centre for Ecological Research, Danube Research Institute, Department of Tisza Research, Bem sq. 18/C, H-4026 Debrecen, Hungary;

³ Department of Hydrobiology, University of Debrecen, Egyetem sq. 1., H-4032 Debrecen, Hungary

* Corresponding author: vital.zoltan@okologia.mta.hu

Abstract

Reliable estimation of the diet composition of filter-feeding Asian carps is essential to evaluate their effects on ecosystem functioning. In previous studies, the diet composition of these fishes was primarily determined based on the analysis of foregut contents. To assess the reliability of foregut content analysis in diet assessments, these were compared with gill raker filtrate analyses. Gill raker filtrates were found to be more reliable than foregut contents for determining food composition due to higher amounts of sample, significantly higher numbers of identifiable taxa (including both phytoplankton and zooplankton), and considerably higher numbers of intact planktonic individuals. The present findings indicate that diet composition analyses based on foregut samples alone are likely to underestimate the number of individuals and the biomass of planktonic species which are less resistant to digestive processes.

Keywords: bighead carp, diet assessment, digestion, phytoplankton, silver carp, zooplankton

Introduction

Filter-feeding silver carp (*Hypophthalmichthys molitrix*, Valenciennes 1844) and bighead carp (*H. nobilis*, Richardson 1845), collectively known as Asian carps, are native to the large rivers of eastern Asia, including Russian, Chinese and Korean territories. These planktivorous fishes have been introduced throughout the world since the early 1950s to increase fishery yields and to improve water quality in eutrophic lakes and rivers (Jennings 1988, Kolar et al. 2007). However, over the past two decades the general attitude regarding Asian carp stocking has changed considerably. This is because a number of studies have demonstrated that the presence of these fishes outside their native range may result in several forms of ecological degradation (Lin et al. 2014). Among these, one of the most important is food competition with native planktivorous fish (e.g., the larval fishes that forage on planktonic organisms) (Spataru and Gophen 1985, Chick & Pegg 2001, Sampson et al. 2009), thereby leading to interspecific competition and ultimately reduced fitness in native fish populations (Sampson et al. 2009). Moreover, Asian carps can cause the deterioration of water quality, both by accelerating nutrient turnover and by consuming significant amounts of zooplankton which decreases top-down control on phytoplankton (Lieberman 1996, Yang et al. 1999, Borics et al. 2000). In the light of these findings, the presence of filter-feeding Asian carps is now considered to be an ecological threat and a problem to be solved in many countries (Chick & Pegg 2001, Cooke et al. 2009).

Filter-feeding Asian carps use their gill rakers (filtering apparatus) to harvest phytoplankton, zooplankton, detritus or any other particles larger than 4–5 μm . For example, a study by Boros et al. (2014) reported that hybrid Asian carps (i.e., silver carp \times bighead carp) in Lake Balaton consume large amounts of inorganic particles that overlap in size with potential food resources and whose relative proportion can be up to 80% (in dry mass) of the total ingested matter. During feeding, Asian carps suck in water, which is pushed through the

gill rakers after closing the mouth. The filtered particles (including plankton) are trapped within the filtering apparatus (Figure 1), and the compressed filtrate is ingested subsequently. As the comb-like gill rakers of bighead carp are specialized to filter particles larger than 50 μm , this species is considered to be mainly a zooplankton feeder (Kolar et al. 2007). However, Xie (2001) pointed out that gill rakers of bighead carps are able to retain much smaller (i.e., 5–6 μm diameter) particles in some cases and phytoplankton consumption also could be an important component of this species' diet. Further, Jennings (1988) reported that if plankton biomass is high ($> 5 \text{ mg L}^{-1}$) and a size differential exists within the plankton community, bighead carp tends to selectively filter larger food items, such as zooplankton. However, when plankton biomass is sufficient, but without a size differential, food selectivity of bighead carp diminishes or ceases altogether. In general, bighead carp are effective at influencing the composition and size structure of the planktonic community by reducing the density of zooplankton and larger phytoplankters (Stone et al. 2000, Kolar et al. 2007).

Silver carp can filter and consume smaller particles than bighead carp, owing to the different morphology of their epibranchial organs. This species has sponge-like gill rakers coated with mucus, which enhances filtering efficiency and enables them to harvest smaller particles (Spataru 1977, Kolar et al. 2007). In this respect, Vörös et al. (1997) found that silver carp were effective in filtering algae larger than 10 μm , even though other studies reported lower values (i.e., 4–5 μm) for the minimum size of filtered particles (Omarov 1970, Kucklantz 1985, Xie 1999). Silver carp is considered to be primarily a phytoplankton feeder (Kolar et al. 2007, and references therein), although Bitterlich (1985) suggested that it may not be able to meet its energy requirements by consuming phytoplankton alone. This is probably due to the low digestibility of some phytoplankton taxa (Dong et al. 1992) and to the gut fluids of silver carps lacking the cellulase enzyme needed to break down algal cell walls (Kolar et al. 2007). In fact, there is evidence for zooplankton consumption by silver carp,

especially when phytoplankton abundance is low (Spataru & Gophen 1985, Burke et al. 1986). Spataru & Gophen (1985) revealed that the proportion of zooplankton in the diet of silver carps can be up to 50% in some cases, while several other studies have demonstrated that the presence of silver carps results in a zooplankton community dominated by smaller individuals (e.g., Fukushima et al. 1999, Lu et al. 2002).

Field studies have shown that the combined stocking of bighead and silver carp could lead to decreased cladoceran, copepod and rotifer biomass in lakes where these fishes are not native (Liebermann 1996, Yang et al. 1999). To avoid reproduction, mainly hybrid Asian carps were introduced into natural waters in several countries, including Hungary, however later studies discovered that hybrids are in fact able to reproduce (Brummett et al. 1988). Hybrid Asian carps usually resemble one of the two parental species, but their morphological features (including the structure of gill rakers) are typically intermediate between bighead and silver carp (Kolar et al. 2007). Thus, it can be deduced that the feeding habits of hybrids differ from those of the parental species. Also, while the diet composition of both bighead and silver carp have been described in several studies, there is still limited knowledge of the filtering efficiency and feeding habits of their hybrids.

In previous studies aimed at exploring the feeding habits of filter-feeding Asian carps, the identification and measurement of consumed food items have been primarily based on foregut content analysis (e.g., Cremer & Smitherman 1980, Sampson et al. 2009, Cooke et al. 2009, Calkins et al. 2012). However, it is argued that the results obtained from foregut content samples may not reflect the actual feeding habits in several cases. This is because digestion of the food bolus starts immediately following ingestion and alters both the qualitative and quantitative food proportions as it reaches the foregut. Specifically, in the first phase of digestion Asian carps use their pharyngeal teeth to crush food particles, which reduces the

possibility of identifying the more fragile organisms that are less able to resist mechanical destruction (Xie 1999, 2001). Subsequently, enzymatic digestion of the food bolus occurs in the foregut, resulting in the disintegration of some important food items such as non-mucilaginous algae (Vörös et al. 1997). These physical and chemical processes may alter and bias sample composition, favouring the dominance of more resistant phytoplankton and zooplankton species. As a result, the analysis of foregut samples incurs the risk of overestimating the importance of some taxa (i.e., the more resistant ones) and underestimating or even completely overlooking the occurrence of some nutritionally very important but less resistant taxa in the fishes' food.

To elucidate the above issue, samples in the form of compressed filtrate were collected from the gill rakers prior to ingestion and from the foreguts of Asian carps, and their phytoplankton and zooplankton composition were compared in this study. The aim was to reveal any potential differences in the planktonic assemblages of gill raker filtrates and foregut content samples and to assess their respective applicability in determining the feeding habits of Asian carps.

Methods

Study site

Fish were sampled from Lake Balaton (Hungary), which is the largest shallow lake in Central Europe with a surface area of 596 km² and a mean water depth of approximately 3.3 m. Although the lake has been subject to serious eutrophication in the past decades, water quality has improved significantly since restoration efforts (Istvánovics et al. 2007). Accordingly, oligotrophic conditions were found between April and November 2013 in the Siófok and Szemes basins (mean chlorophyll *a*: $4.8 \pm 2.2 \mu\text{g L}^{-1}$; min: $2.5 \mu\text{g L}^{-1}$; max: $7.3 \mu\text{g L}^{-1}$), where fish sampling was conducted.

The most abundant fish species in the lake are bleak (*Alburnus alburnus*, L.), bream (*Abramis brama*, L.), roach (*Rutilus rutilus*, L.) and razor fish (*Pelecus cultratus*, L.) (Specziár et al. 2009). Filter-feeding Asian carps (i.e., silver carps, bighead carps and most of their hybrids) were introduced to Lake Balaton in the early 1970s to increase fishery yields and to improve water quality. However, as this intervention did not result in any notable improvements, Asian carp stocking has been stopped and banned since 1984 (Boros et al. 2014). Since then, the biomass of Asian carps has increased in the lake due to low fishing pressure and constant recruitment from poorly-defined sources (likely fish escapes from nearby ponds and natural reproduction, but the importance of these factors has not yet been quantitatively assessed). Based on the latest extensive fish survey (Tátrai et al. 2009), the total biomass of Asian carps (with 95 % dominance of hybrids) totalled 4000–5000 tonnes in Lake Balaton, equal to one-third of the total fish biomass in the lake.

Sampling and processing

In total, 47 hybrid Asian carps were collected from the eastern and central basins of Lake Balaton between June and November 2013 using 12 cm mesh-size gill nets. The total body length of the sampled fish ranged from 91 to 127 cm and their body mass varied between 10 and 31 kg. Foregut content samples were obtained from the initial section of the alimentary tract, where sufficient amounts of food bolus were found. Gill raker filtrates 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 (Figure 1).

Samples for phytoplankton analysis were preserved in Lugol's solution and stored at 4 °C until processing, whereas samples for zooplankton analysis were preserved in 70% ethanol. Wet masses of samples for microscopic analyses were recorded before preservation, and sub-samples were dried to constant weight at 60 °C to assess the moisture content of each sample.

In order to achieve comparable results, data were expressed as the number of individuals per unit of sample dry mass ($n \times g^{-1}$).

Phytoplankton counting and identification were carried out using a Zeiss Axiovert-40 CFL inverted microscope (400-fold magnification) and followed the method of Utermöhl (1958). Identified phytoplankton organisms were classified as: Cyanobacteria, Chrysophyta (Chrysophyceae, Xanthophyceae and Bacillariophyceae Centrales and Pennales), and Chlorophyta (Chlorococcales and Desmidiaceae, Dinophyta, Cryptophyta, Euglenophyta). Different zooplankton species and zooplankton fragments were counted and identified with a binocular microscope at 40-fold magnification. Zooplankton organisms were classified according to the following categories: *Cyclops* spp., *Eudiapthomus* spp., harpacticoid copepods, *Bosmina* spp., *Daphnia* spp., *Diaphanosoma* spp., ostracods, *Dreissena* larvae, rotifers, and nauplius larvae of copepods.

Statistical methods

Non-parametric Mann-Whitney *U* tests were applied to reveal the differences in taxon richness and total number of food items between gill raker filtrates and foregut samples. Subsequently, similarity percentage (SIMPER) tests (Clarke 1993) were used to assess the importance of different taxa in explaining potential variances between gill raker and gut content samples. Statistical analyses were performed using PAST 2.17 (PAleontological STatistics, Norway) (Hammer et al. 2001), and the statistical significance of all tests was set at the $p = 0.05$ level.

Results

Filtrate was found in the gill rakers of 32 individuals (68.1 % of the examined fish), while a sufficient amount of foregut content was found in 28 individuals (59.6 %). In total, 19 fish had both sample types present and were chosen for comparative analysis. However, although

the quantity of sample material was sufficient for analysing phytoplankton in all of these 19 individuals, zooplankton analysis was possible only in 11.

The number of identified phytoplankton individuals (cells) did not differ significantly between gill raker filtrates and foregut contents, whereas there was a significant difference in zooplankton content between the two sample types ($p < 0.01$). On average, 24 times more zooplankton individuals were counted in the gill raker filtrates than in the foreguts (Table 1), and a significantly higher number of both phytoplankton ($p < 0.01$) and zooplankton taxa ($p < 0.001$) were found in the gill rakers than in the foreguts (Table 1). The lower number of phytoplankton taxa in the foreguts were mainly Dinophyta, Cryptophyta, Euglenophyta algae and pennate diatoms, which were found in most gill raker filtrates but were scarce in foreguts. In the case of zooplankton, *Eudiaptomus* spp., *Diaphanosoma* spp. and *Daphnia* spp. were found in most of the gill raker filtrates, although these taxa were rare in gut contents and therefore responsible for the significant statistical differences. Finally, the SIMPER test (which takes into consideration the relative abundances of different taxonomical groups) revealed that the significant differences between sample types could be attributed mainly to two phytoplankton groups, namely Centrales and Cyanobacteria (Table 2) and to three zooplankton taxa (i.e., *Eudiaptomus* spp., *Daphnia* spp. and *Rotatoria* spp.) (Table 2).

To explore the ability of each phytoplankton and zooplankton taxon to resist digestive processes, the number of estimated individuals (per unit of dry sample mass) was compared in both sample types. Accordingly, the number of algal cells of Centrales was on average 74% higher in foreguts than in gill raker filtrates. The number of Chrysophyceae was found to be four orders of magnitude higher in gill raker filtrates than in the foreguts (Table 2). Also, the number of zooplankton individuals was consistently higher in gill raker filtrates in the case of all identified taxa. The lowest difference was observed in case of rotifers (2.5 times higher

numbers in gill raker filtrates), whereas the highest difference was found in the numbers of *Eudiaphthomus* spp., which were four orders of magnitude higher in number of individuals in the foreguts relative to the filtrates (Table 2). Based on gut content analysis, the majority (> 60%) of the phytoplankton consumed by Asian carps consisted of centric diatoms (Figure 2a) and the majority (> 60%) of zooplankton consisted of rotifers (Figure 2b). The relative proportion of both centric diatoms and rotifers was less than 20% in the gill raker filtrates, indicating that these taxa were not dominant based solely on gill raker filtrates (Figure 2a,b).

The proportion of phytoplankton debris was two orders of magnitude higher in the foreguts than in the gill raker filtrates (significant difference, $p < 0.001$; Table 1). However, because of their extremely high amounts, the number of zooplankton fragments could not be counted in the foregut contents, preventing the quantitative comparison of sample types. Regardless, gut contents clearly contained more zooplankton-derived debris, suggesting differences between sample types.

Discussion

This study aimed to elucidate whether foregut contents can be reliably used to determine the actual feeding habits of filter-feeding Asian carps, or whether filtrates collected from gill rakers more reliably reflect the composition of the food originally consumed. The present results clearly indicate that gill raker filtrates provide more realistic estimates, as significantly more planktonic (i.e., both phytoplankton and zooplankton) taxa were identified in these samples, which were not exposed to digestive processes. The number of intact (i.e., identifiable) zooplankton individuals was also remarkably higher in gill raker filtrates than in foregut contents. The latter contained zooplankton (but also phytoplankton) fragments, inappropriate for species determination, in high quantities. Moreover, there was a higher probability of sample occurrence in gill rakers ($n = 32$ compared with foregut sample $n = 28$), rendering this kind of sampling more suitable for diet composition analysis of Asian carps.

The observed differences in composition between the two sample types (i.e., foregut contents vs. gill raker filtrates) might be attributed to the different ability of potential food items to resist physical and chemical digestive processes. In this respect, Vörös et al. (1997) reported that non-mucilaginous cyanobacteria, *Cryptomonas* spp. and diatoms are easily digestible by Asian carps, whereas other taxa, such as *Chlorococcalean* green algae, mucilaginous cyanobacteria (*Chroococcales*) and *Euglenophyta*, are more resistant. Xie (1999, 2001) also pointed out that some phytoplankton taxa can cope with the different digesting processes and survive passage through the entire alimentary tract. These findings imply that the relative proportion of more resistant taxa is expected to increase in the food bolus as it passes through the alimentary tract. The results of the present study, highlighting differences between gill raker filtrate and foregut samples, support this assumption. The number of counted individuals of *Chlorococcales* and *Euglenophyta* was at least 50% of the filtrate-derived sample, whereas the proportion of *Chrysophyceae*, *Dinophyta*, Desmidiaceae and *Cryptophyta* was lower than 25%. These results are in accordance with the findings of Vörös et al. (1997), who reported that cells of *Cryptophyceae* degraded significantly only 30 minutes after ingestion. On the other hand, Vörös et al. (1997) noted that centric diatoms were abundant in foregut contents, which contradicts the findings of the present study.

Zooplankton composition of the gill raker filtrates was taxonomically more diverse compared to that of the foregut contents, revealing that only a few, less fragile species are able to resist the physical and chemical effects of digestion and reach the foregut intact. Sutela and Huusko (2000) studied the digestibility of different zooplankton species and found that hard-bodied taxa (e.g., *Bosmina* sp. and *Daphnia* sp.) could be found in the entire alimentary tract of vendace (*Coregonus albula*, L.) and whitefish (*Coregonus lavaretus*, L.) larvae, whereas soft-bodied zooplankton species were more abundant in the first quarter of their alimentary tract. Moreover, Creeco and Blake (1983) found that blueback herrings (*Alosa*

aestivalis, Mitchill 1815) can utilize rotifers with high efficiency. The results of the present study suggest that the most digestion-resistant zooplankton taxa were rotifers and ostracods, whereas *Eudiaptomus* spp., *Daphnia* spp. and *Diaphanosoma* spp. almost completely disappeared from the food bolus by the time it reached the foregut. Although the range of food of the former three fish species may not overlap completely with that of Asian carps, there are zooplankton taxa (e.g., *Daphnia* spp.) that can be found in the diet of all of these species. In contrast to the results of Sutela and Huusko (2000), the present study showed that the ability of *Daphnia* spp. to resist digestion is low, as their total number decreased by two orders of magnitude in the alimentary tract of Asian carps by the time the food reached the foregut. It can be inferred that these interspecific differences in zooplankton digesting capacity could result from the different anatomical features of the alimentary tract of fish species (e.g., presence of pharyngeal teeth in Asian carps or different enzymes).

The proportion of planktonic debris was considerably higher in the foreguts than in the gill raker filtrates, and the difference between sample types was even more notable (albeit unquantifiable) in case of zooplankton, due to the uncountable amounts of zooplankton fragments in the foreguts. This finding draws attention to the role of pharyngeal teeth in crushing food particles, a process described in previous studies (e.g., Xie 1999, 2001). However, the mechanical destruction caused by pharyngeal teeth of Asian carps rendered it impossible to identify or count several organisms that might have been present in the food.

Conclusions

Based on foregut content analysis, the importance of some species seems to be negligible or undefinable in the diet of Asian carps, while other species seem to represent a major component of the ingested food. However, direct comparison of foregut contents with gill raker filtrates in this study revealed that the contribution of the different plankton taxa to fish nutrition can be underestimated if evaluation is based solely on the former method,

highlighting the importance and more reliable applicability of gill raker filtrate analysis. Also, it is very likely that the diet composition determined microscopically from gut content samples is biased towards barely digestible components, and thus these analyses may result in improper estimates of the assimilated food resources of Asian carps, with consequent bias in understanding the role of these fish in aquatic ecosystems. Overall, further studies involving other filter-feeding fish species, such as paddlefish (*Polyodon spathula*, Walbaum 1792), gizzard shad (*Dorosoma cepedianum*, Lesueur 1818) or Atlantic menhaden (*Brevoortia tyrannus*, Latrobe 1802), are encouraged to test whether the same differences between gill raker filtrates and gut contents would be found or whether differences between sample types observed in this study are unique to Asian carps. With more comprehensive analyses including a wide range of species, researchers could provide a new, generally applicable and more reliable method for the food assessment of filter feeding fishes, which are important members of several fish communities around the world.

Acknowledgements

We thank Izabella Battonyai, Ildikó Starkné Mecsnóbel, Géza Dobos and Zoltán Poller for their assistance with the sample processing and Stephanie Palmer for assistance in manuscript preparation. The study was supported by OTKA (K 83893).

TÁMOP-4.2.2.A-11/1/KONV-2012-0038, Balaton Fish Management Non-Profit Ltd and The Lake Balaton Development Council also contributed to this study.

References

Bitterlich, G., 1985: The nutrition of stomachless phytoplanktivorous fish in comparison with tilapia. – *Hydrobiologia* **121**: 173–179.

Borics, G., Grigorszky, I., Szabó, S. & Padisák, J., 2000: Phytoplankton associations under changing pattern of bottom-up vs. top-down control in a small hypertrophic fishpond in East Hungary. – *Hydrobiologia* **424**: 79–90.

Boros, G., Mozsár, A., Vitál, Z., Nagy, A. S. & Specziár, A., 2014: Growth and condition factor of hybrid (Bighead *Hypophthalmichthys nobilis* Richardson, 1845 × silver carp *H. molitrix* Valenciennes, 1844) Asian carps in the shallow, oligo-mesotrophic Lake Balaton. – *J. Appl. Ichthyol.* **30**: 546–548.

Brummett, R. E., Smithermann, R. O. & Dunham, R. A., 1988: Isozyme expression in bighead carp, silver carp and their reciprocal hybrids. – *Aquaculture* **70**: 21–28.

Burke, J. S., Bayne, D. R. & Rea, H., 1986: Impact of silver and bighead carps on plankton communities of channel catfish ponds. – *Aquaculture* **55**: 59–68.

Calkins, H. A., Tripp, S. J. & Garvey, J. E., 2012: Linking silver carp habitat selection to flow and phytoplankton in the Mississippi River. – *Biol. Invasions* **14**: 949–958.

Chick, J. H. & Pegg, M. A., 2001: Invasive carp in the Mississippi River Basin. – *Science* **292**: 2250–2251.

Clarke, A., 1993: Seasonal acclimatization and latitudinal compensation in metabolism: do they exist? – *Funct. Ecol.* **7**: 139–149.

Cooke, S. L., Hill, W. R. & Meyer K. P., 2009: Feeding at different plankton densities alters invasive bighead carp (*Hypophthalmichthys nobilis*) growth and zooplankton species composition. – *Hydrobiologia* **625**: 185–193.

Crecco, V. A. & Blake M. M., 1983: Feeding ecology of coexisting larvae of American shad and blueback herring in the Connecticut River. – *T. Am. Fish. Soc.* **112**: 498–507.

Cremer, M. C. & Smitherman, R. O., 1980: Food habits and growth of silver and bighead carp in cages and ponds. – *Aquaculture* **20**: 57–64.

Dong, S., Li, D., Bing, X., Shi, Q. & Wang, F., 1992: Suction volume and filtering efficiency of silver carp (*Hypophthalmichthys molitrix* Val.) and bighead carp (*Hypophthalmichthys nobilis* Rich.). – *J. Fish. Biol.* **41**: 833–840.

Fukushima, M., Takamura, N., Sun, L., Nakagawa, M., Matsushige, K. & Xie, P., 1999: Changes in the plankton community following introduction of filter-feeding planktivorous fish. – *Freshwater Biol.* **42**: 719–735.

Hammer, O., Harper, D. A. T. & Ryan, P. D., 2001: PAST: Paleontological Statistics software package for education and data analysis. – *Palaeontologica Electronica* **4**: 9 pp.

Istvánovics, V., Clement, A., Somlyódy, L., Specziár, A., G-Tóth, L. & Padisák, J., 2007: Updating water quality targets for shallow Lake Balaton (Hungary), recovering from eutrophication. – *Hydrobiologia* **581**: 305–318.

Jennings, D. P., 1988: Bighead carp (*Hypophthalmichthys nobilis*): a biological synopsis. Fish and Wildlife Service Biological Report No. 88., pp. 1–47.

Kolar, C. S., Chapman, D. C., Courtenay, W. R. Jr., Housel, C. M., Williams, J. D. & Jennings, D. P., 2007: Bigheaded carps – a biological synopsis and environmental risk assessment. Am. Fish. Soc, Bethesda: pp. 1–204.

Kucklantz, V., 1985: Restoration of a small lake by combined mechanical and biological methods. – *Verh. Internat. Verein. Theor. Angew. Limnol.* **22**: 2314–2317.

Lieberman, D. M., 1996: Use of silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*Aristichthys nobilis*) for algae control in a small pond: Changes in water quality. – J. Freshwater Ecol. **11**: 391–397.

Lin, Q., Jiang, X., Han, B. P. & Jeppesen, E., 2014: Does stocking of filter-feeding fish for production have a cascading effect on zooplankton and ecological state? A study of fourteen (sub)tropical Chinese reservoirs with contrasting nutrient concentrations. – Hydrobiologia **736**: 115–125.

Lu, M., Xie, P., Tang, H., Shao, Z. & Xie, L., 2002: Experimental study of trophic cascade effect of silver carp (*Hypophthalmichthys molitrix*) in a subtropical lake, Lake Donghu: On plankton community and underlying mechanisms of changes of crustacean community. – Hydrobiologia **487**: 19–31.

Omarov, M. O., 1970: The daily food consumption of the silver carp *Hypophthalmichthys molitrix* (Val.). – Journal of Ichthyology **10**: 425–426.

Sampson, S. J., Chick, J. H. & Pegg, M. A., 2009: Diet overlap among two Asian carp and three native fishes in backwater lakes on the Illinois and Mississippi rivers. – Biol. Invasions **11**: 483–496.

Spataru, P., 1977: Gut contents of silver carp–*Hypophthalmichthys molitrix* (Val.)–and some trophic relations to other fish species in a polyculture system. – Aquaculture **11**: 137–146.

Spataru, P. & Gophen, M., 1985: Feeding behaviour of silver carp *Hypophthalmichthys molitrix* Val. and its impact on the food web in Lake Kinneret, Israel. – Hydrobiologia **120**: 53–61.

Specziár, A., Erős, T., György, Á. I., Tátrai, I. & Bíró, P., 2009: A comparison between the Nordic gillnet and whole water column gillnet for characterizing fish assemblages in the shallow Lake Balaton. – *Ann. Limnol.–Int. J. Lim.* **45**: 171–180.

Sutela, T. & Huusko, A., 2000: Varying resistance of zooplankton prey to digestion: Implications for quantifying larval fish diets. – *T. Am. Fish. Soc.* **129**: 545–551.

Stone, N., Engle, C., Heikes, D. & Freeman, D., 2000: Bighead carp. Stoneville: Southern Regional Aquaculture Center Publication No. 438.

Tátrai, I., Paulovits, G., Józsa, V., Boros, G., György, Á. I. & Héri, J., 2009: Distribution and standing stocks of introduced fish species in Lake Balaton (*Halállományok eloszlása és a betelepített halfajok állománya a Balatonban*) In: Bíró, P., Banczerowski, J. (eds) *A Balaton kutatások fontosabb eredményei 1999-2009.* – MTA, Budapest, pp. 129–141. (in Hungarian)

Utermöhl, H., 1958: Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. – *Mitteilungen der internationale Vereinigung für theoretische und angewandte Limnologie* **9**: 1–38.

Vörös, L., Oldal, I., Présing, M. & V.-Balogh, K., 1997: Size-selective filtration and taxon-specific digestion of plankton algae by silver carp (*Hypophthalmichthys molitrix* Val.). – *Hydrobiologia* **342/343**: 223–228.

Xie, P., 1999: Gut contents of silver carp, *Hypophthalmichthys molitrix*, and the disruption of a centric diatom, *Cyclotella*, on passage through the esophagus and intestine. – *Aquaculture* **180**: 295–305.

Xie, P., 2001: Gut contents of bighead carp (*Aristichthys nobilis*) and the processing and digestion of algal cells in the alimentary canal. – *Aquaculture* **195**: 149–161.

Yang, Y., Huang, X. & Liu, J., 1999: Long-term changes in crustacean zooplankton and water quality in a shallow eutrophic Chinese lake densely stocked with fish. – *Hydrobiologia* **391**: 195–203.

Figure 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).



Figure 2

(a) Phytoplankton composition of gill raker filtrates (estimated $n = 1.02 \times 10^7$ individuals per column) and foregut contents (estimated $n = 1.26 \times 10^7$ individuals per column) of Asian carps in Lake Balaton, Hungary. ‘Other’ includes phytoplankton taxa representing less than 3% of the samples (i.e., Chrysophyceae, Xanthophyceae, Dinophyta, Cryptophyta, Euglenophyta,). (b) Zooplankton composition of gill raker filtrates (estimated $n = 5.48 \times 10^5$ individuals per column) and foregut contents (estimated $n = 2.31 \times 10^4$ individuals per column) of Asian carps in Lake Balaton, Hungary. ‘Other’ includes zooplankton taxa representing less than 3% of the samples (i.e., harpacticoid copepods, *Bosmina* spp., ostracods).

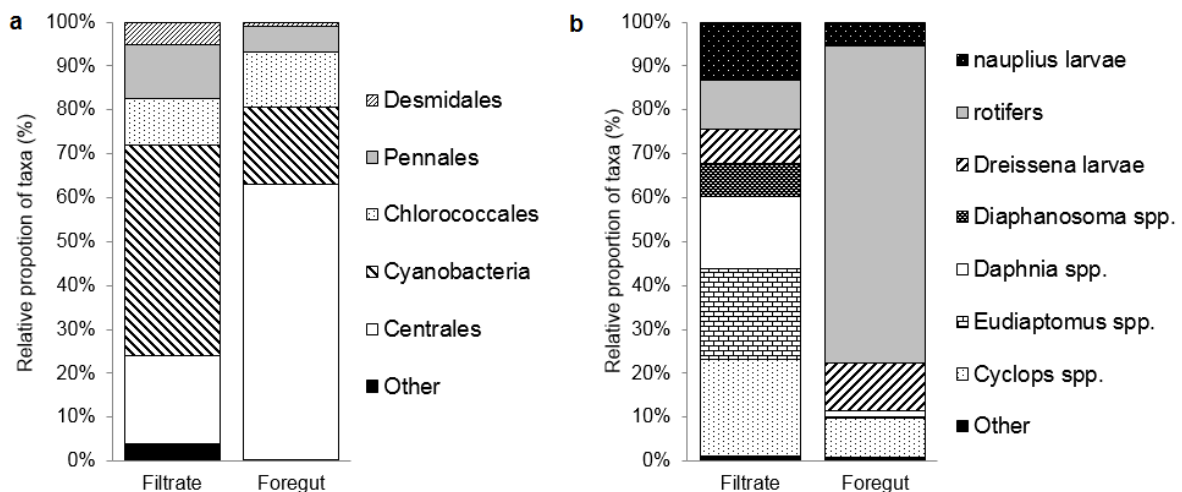


Table 1

Mean number of identified plankton taxa and individuals and estimated plankton debris (per g dry sample mass) in the gill raker filtrate and foregut content of Asian carps in Lake Balaton (Hungary).

		Filtrate		Foregut content	
		Mean	SD	Mean	SD
Phytoplankton	Taxa	6.3	0.87	5.3	0.82
	Individuals	5.35×10^5	8.31×10^5	6.65×10^5	7.41×10^5
	Debris	4.8	7.97	2.60×10^2	4.22×10^2
Zooplankton	Taxa	5.9	1.45	2.8	1.60
	Individuals	4.98×10^4	5.04×10^4	2.10×10^3	2.44×10^3

Table 2

Mean number of estimated phytoplankton and zooplankton individuals in filtrate and foregut contents (per g dry sample mass), with corresponding foregut to filtrate abundance ratio and overall contribution.

Taxon	Filtrate		Foregut content		Ratio (%) ¹	Contribution % ⁽²⁾
	Estimated n (mean)	SD	Estimated n (mean)	SD		
Phytoplankton						
Centrales	1.07×10 ⁵	1.10×10 ⁵	4.17×10 ⁵	4.43×10 ⁵	390.3	43.2
Cyanobacteria	2.57×10 ⁵	5.23×10 ⁵	1.16×10 ⁵	2.01×10 ⁵	45.1	26.6
Chlorococcales	5.69×10 ⁴	8.21×10 ⁴	8.42×10 ⁴	1.23×10 ⁵	147.9	11.7
Pennales	6.57×10 ⁴	9.11×10 ⁴	3.88×10 ⁴	3.59×10 ⁴	59.0	10.9
Chrysophyceae	8.19×10 ³	2.44×10 ⁴	2.00×10 ⁰	8.00×10 ⁰	0.0	3.3
Desmidiales	2.76×10 ⁴	6.86×10 ⁴	6.53×10 ³	1.20×10 ⁴	23.7	2.3
Dinophyta	1.08×10 ⁴	3.65×10 ⁴	3.10×10 ¹	1.31×10 ²	0.3	1.2
Euglenophyta	2.84×10 ³	3.38×10 ³	1.42×10 ³	2.67×10 ³	50.1	0.5
Xanthophyceae	0	0	1.37×10 ³	5.39×10 ³	-	0.2
Cryptophyta	2.86×10 ²	4.96×10 ²	2.90×10 ¹	9.20×10 ¹	10.2	0.1
Zooplankton						
<i>Eudiaptomus</i> spp.	1.03×10 ⁴	1.33×10 ⁴	2.00×10 ⁰	7.00×10 ⁰	0.0	27.5
<i>Cyclops</i> spp.	1.10×10 ⁴	1.14×10 ⁴	1.86×10 ²	2.46×10 ²	1.7	21.7
rotifers	5.50×10 ³	5.91×10 ³	1.52×10 ³	1.84×10 ³	27.6	16.5
<i>Daphnia</i> spp.	8.22×10 ³	1.50×10 ⁴	3.10×10 ¹	6.90×10 ¹	0.4	11.9
nauplius larvae	6.66×10 ³	8.38×10 ³	1.11×10 ²	3.38×10 ²	1.7	8.8
<i>Dreissena</i> larvae	3.94×10 ³	1.05×10 ⁴	2.31×10 ²	4.57×10 ²	5.9	6.2
<i>Diaphanosoma</i> spp.	3.64×10 ³	5.71×10 ³	2.00×10 ⁰	6.00×10 ⁰	0.1	5.7
ostracods	1.23×10 ²	2.38×10 ²	1.20×10 ¹	3.80×10 ¹	9.7	1.0
harpacticoid copepods	1.71×10 ²	2.91×10 ²	2.00×10 ⁰	7.00×10 ⁰	1.4	0.3
<i>Bosmina</i> spp.	2.37×10 ²	7.13×10 ²	5.00×10 ⁰	1.10×10 ¹	2.0	0.3

¹: Foregut to filtrate abundance ratio

²: Taxa are sorted in descending order of contribution to group difference