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Influence of environmental factors and individual traits on the diet of non-native hybrid bigheaded carp (*Hypophthalmichthys molitrix* × *H. nobilis*) in Lake Balaton, Hungary

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Abstract Planktivorous silver carp and bighead carp (collectively, the bigheaded carps) have been stocked worldwide and their invasion has caused severe impacts on many freshwater ecosystems. Exploiting the chance provided by the specific hybrid bigheaded carp stock in Lake Balaton (Hungary) covering the entire morphological range between the two species (including gill raker morphology), we implemented a comprehensive study (1) to reveal the feeding habits of hybrid bigheaded carps living in a mesotrophic, lacustrine habitat; and (2) to assess how biotic and abiotic environmental factors and gill raker morphology affect diet composition. We found that all bigheaded carps utilized primarily zooplankton and neglected the scarce and inefficiently digestible phytoplankton, irrespective of gill raker morphology. Moreover, we observed strikingly high levels of inorganic debris consumption, but the proportion of inorganic matter in the guts was not associated directly with the concentration of suspended inorganic particles. Variance in the diet composition of bigheaded carps was related mostly to environmental factors, including the wind-induced resuspension of inorganic particles and seasonally variable availability of food resources. In conclusion, the effects of abiotic environmental factors and available food resources could overwhelm the effect of gill raker morphology in shaping the feeding habits of bigheaded carps.

Keywords: Asian carp, filter-feeding, hybrid fishes, introduced fish species, planktivory, zooplankton

Introduction

Silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*H. nobilis*), collectively known as bigheaded carps, are cyprinid fishes native to the large rivers and lakes of eastern Asia (Kolar et al., 2007). From the early 1950s these filter-feeding fish species have been introduced worldwide to improve the water quality (because bigheaded carps were considered as effective biological control agents for algal blooms; Cremer & Smitherman, 1980; Xie & Liu, 2001), and to increase fishery yields (Kolar et al., 2007). However, recent studies demonstrated that bigheaded carps can adversely affect water quality, both by accelerating nutrient turnover and by consuming zooplankton which decreases the top-down control on phytoplankton (Yang et al., 1999; Borics et al., 2000). Moreover, bigheaded carps can cause a decline in fitness and condition factor in native fish populations (Irons et al., 2007; Sampson et al., 2009) and exert strong effects on community structure (Solomon et al., 2016). Therefore, the presence of bigheaded carps outside their native range is now considered a serious ecological threat (Cooke et al., 2009) and their stocking to natural waters has been prohibited or regulated in several countries (e.g., USA, Hungary; Kolar et al., 2007; Boros et al., 2014). In spite of the strict regulations, the spread of these invasive species is ongoing and their biomass is still high in many invaded habitats (Hayer et al., 2014 a,b).

Several previous studies dealing with the ecological impacts of non-native fish species emphasized that the detrimental effects of invaders are exerted mostly via food-web alterations or direct resource competition with the native fishes (e.g., Kleef et al., 2008; Khan & Panikkar, 2009; Britton et al., 2010; Sass et al., 2014). Bigheaded carps consume predominantly planktonic organisms (both phyto- and zooplankton) and thus they may compete for food with nearly all fish species at early life stages (Sass et al., 2014). Occupying a key trophic position in aquatic ecosystems, bigheaded carps can unfavourably affect the whole native fish community (Calkins et al., 2012). Accordingly, reliable assessment of the ecological effects of bigheaded carps requires a better understanding of their feeding habits and their interspecific, interindividual and habitat-related variability.

Bigheaded carps use their filtering apparatus (gill rakers) to harvest plankton or any other suspended particles that overlap in size with potential food resources. The general notion is that, in filter-feeding fishes, the filtering efficiency (i.e., size range of consumed food items) is primarily determined by the morphology of gill rakers (Lieberman, 1996; Kolar et al., 2007), which shows substantial differences between bighead carp and silver carp. Bighead carp have long, thin gill rakers which form a comb-like structure, while the gill rakers of silver carp have a spongy appearance due to the fusion of gill filaments (Kolar et al., 2007). The mesh-size of this fused, sponge-like apparatus ranges between 12 and 26 μm (Hampl et al., 1983; Lu et al., 2002), while the comb-like gill raker is characterised with larger mesh-sizes and is specialised to harvest particles larger than 50 μm (Kolar et al., 2007). Thus, silver carp is able to retain smaller particles more effectively than bighead carp. Consequently, silver carp is considered to be primarily a phytoplankton-feeder species (Smith, 1989; Vörös et al., 1997), while bighead carp is thought to be primarily zooplankton-feeder (Dong & Li, 1994; Kolar et al., 2007). However, recent investigations on Lake Balaton's (Hungary) bigheaded carp stock suggested that under certain environmental conditions the influence of gill raker morphology on the size distribution of the consumed food items may be less important than it was assumed earlier, presumably it is overwhelmed by the resource availability (Battonyai et al., 2015). Some studies also have argued that food selectivity of bigheaded carps may also be influenced by the mucus produced by the epibranchial organ, enabling fish to capture particles smaller than the mesh size of their gill rakers (Kolar et al., 2007 and references therein).

The relationship between the feeding habits of bigheaded carps and the characteristics of invaded habitat has been widely studied in the past, but the vast majority of these studies have focused only on how the feeding habit-related effects can induce alterations in the plankton community (Fukushima et al., 1999; Domaizon & Dévaux, 1999; Lu et al., 2002) and change the trophic state of ambient water (Lin et al., 2014). Although the influence of several environmental factors (e.g., transparency, temperature) on the diet composition of bigheaded carps is supposable, our knowledge on the effects of habitat attributes (i.e., environmental factors) is limited.

According to the regulation of the Hungarian governmental authorities, bigheaded carps had been stocked into Lake Balaton until the early 1980s. However, these fish still form a massive stock in the lake and exhibit high individual growth rates and condition factor, despite the low planktonic productivity (Boros et al., 2014). For a better understanding of factors influencing feeding habits, gut contents of hybrid bigheaded carps from Lake Balaton were examined and their compositions were evaluated in this study to reveal the relationship between consumed food and available food resources, abiotic environmental factors and individual traits of fish. Among the various individual traits (body size, gender, gill raker morphology), we paid special attention to the gill raker morphology. Lake Balaton's bigheaded carp stock consists mainly of hybrid (bighead carp × silver carp) individuals (Tátrai et al., 2009; Kovács et al., 2016), and gill rakers of these fish cover the entire morphological and functional range between the comb-like and sponge-like filtering apparatus types. The specific objectives of this study were: (i) to provide detailed data on the diet composition of introduced hybrid bigheaded carps living in a mesotrophic lake; and (ii) to assess how biotic and abiotic environmental factors and gill raker morphology affect diet composition in bigheaded carps.

Material and methods

Study area

Lake Balaton is the largest natural, shallow lake (surface area: 593 km^2; mean depth: 3.2 m) in Central Europe, situated at 46^{o} 42' - 47^{o} 04' N, 17^{o} 15' - 18^{o} 10' E (Hungary) and 104.8 m above sea level. The lake is mesotrophic with mean annual chlorophyll-*a* concentrations of 3.6-18.7 mg m^{-3} (Istvánovics et al., 2007). Due to strong sediment resuspension, the lake is generally turbid with a Secchi depth varying between 0.2 m and 0.8 m (Specziár et al., 2013). Oxygen deficiency has never been recorded in the lake, and concentrations of pollutants are low or insignificant. Forty-seven percent of the lake shore is covered by native reed grass *Phragmites australis* (Cav.) Trin. ex Steud., while the remaining part of the lake shore was stabilized with stones and concrete. Submerged macrophytes occur sparsely in the littoral zone. The most abundant fishes in the lake are bleak *Alburnus alburnus* (Linnaeus, 1758), common bream *Abramis brama* (Linnaeus, 1758), razor fish *Pelecus cultratus* (Linnaeus, 1758) and the hybrid bigheaded carps. Detailed information on the limnology and fish fauna of the lake can be found in studies of Herodek et al. (1988), Istvánovics et al. (2007) and Specziár et al. (2009, 2013).

Assessment of abiotic environmental parameters and food resources

We measured a number of environmental variables that are believed to influence feeding efficiency and diet composition of bigheaded carps. At each field sampling occasion, we recorded water temperature (^{o}C), conductivity (μS cm^{-1}) and Secchi depth (cm). We took water column samples with a tube sampler to determine total suspended matter concentration (TSM, mg L^{-1}), inorganic suspended matter concentration (IOSM, mg L^{-1}), chlorophyll-a concentration (μg L^{-1}), phytoplankton percentage taxonomic composition by biovolume, zooplankton total dry biomass (g L^{-1}) and percentage taxonomic composition by dry biomass. Samples and data were collected around fishing nets, at times when fish samplings were conducted.

TSM was assessed by filtrating lake water samples through 1.2 µm Whatman GF/C glass fiber filters and filters were subsequently dried to constant weight at 60°C (ca. for 72 hours), whereas IOSM was estimated from the ash content of samples obtained by ignition at 550°C for 1 hour. Chlorophyll-*a* was extracted by acetone method (Aminot & Rey, 2000) and measured spectrophotometrically (Shimadzu UV-1601 spectrophotometer). Lake water subsamples for phytoplankton and zooplankton assemblage analysis were processed similarly as described in the gut content analysis (see below).

Gill raker morphology evaluation

Five morphotypes of gill rakers were assigned subjectively including comb-like type (type 1 gill raker; GR1), sponge-like type (type 5 gill raker; GR5) and intermediate (hybrid) structures (Fig. 1). The three intermediate gill raker morphotype classes represented transition between comb-like and sponge-like structures but to a different degree. GR3 category represented the completely intermediate type between the comb- and sponge-like structures, while hybrid gill raker areas closer to comb-like structure were classified into GR2 and those closer to sponge-like structure into GR4 (Fig. 1). The filtering apparatus of each bigheaded carp (N = 60) was then characterized based on the proportional area of GR1 to GR5 segments on the first left and right gill arches. Further, the filtering-to-respiratory part ratios (the relative width of gill raker to the width of gill filaments; RGRA) were also measured on the first left and right gill arches, because this is an important species-specific attribute in silver carps and bighead carps, and gill rakers of hybrids are generally intermediate in their development between the two species (Kolar et al., 2007).

Fish sampling and gut content analysis

Bigheaded carps were captured from the eastern basin of Lake Balaton by professional fishermen (Balaton Fish Management Non-Profit Ltd.) using 12 cm knot-to-knot mesh-size gillnets. Sampling was conducted in 2011 and 2013 at monthly intervals between March and October, except July and August when fishing was banned in the lake by local regulations.

Diet composition was assessed using gut contents collected from the anterior segment of the intestines, close to the pharynx. Although Vitál et al. (2015) recently argued that the analysis of the filtrate samples collected from the inner surface of the gill-rakers would likely provide more reliable picture of the food composition of bigheaded carps, we still decided to use gut content samples because we wanted to compare our results explicitly with preceding studies on bigheaded carp feeding, and the results of most of these studies are based on gut content analyses. We found a useful amount of freshly ingested food in the gut of altogether 60 adult specimens, ranging between 78-118 cm in standard body length (SL) and 10.7-35.0 kg in body mass (M). Each gut content sample was divided into three identical portions for phytoplankton, zooplankton and inorganic matter content analyses. Samples for phytoplankton analyses were preserved in Lugol's solution and were stored at 4°C until processing, while samples for zooplankton analyses were preserved in 70% ethanol. For phytoplankton counting and identification, we used a Zeiss Axiovert-40 CFL inverted microscope (400-fold magnification) and followed the method of Utermöhl (1958). Biovolumes of algae were assessed using taxon-specific measurements and relationships (Hillebrand et al., 1999). Identified phytoplankton organisms were classified as: Cyanobacteria, Centrales, Pennales, Chlorococcales, Desmidales, Cryptophyta, Dinophyta, Euglenophyta, Chrysophyceae, and Xanthophyceae. Zooplankton items and their fragments were identified and counted under binocular microscope at 40-fold magnification and their dry biomasses were assessed according to relevant length-mass relationships (Dumont et al., 1975). Zooplankton organisms were classified into the following categories: *Dreissena* larvae, rotifers, nauplius larvae of copepods, *Eudiapthomus* spp., *Cyclops* spp., harpacticoid copepods, *Bosmina* spp., *Daphnia* spp., *Diaphanosoma* spp., *Leptodora kindtii* and ostracods. Gut content subsamples for inorganic matter determination were measured for wet weight, then dried to constant weight at 60°C (ca. for 72 hours) and finally ignited at 550°C for 1 hour to assess their ash contents.

Stable isotope analysis

Samples for stable isotope analysis (SIA) were collected to complement the microscopic gut content analysis and reveal the relative contribution of different food resources (i.e., phytoplankton and zooplankton) in the diet of bigheaded carps. For this aim, seston (phytoplankton), zooplankton and fish muscle samples from each sampling month were analysed using a SERCON Integra 2 Stable Isotope Analyser to determine their stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotope signatures.

For phytoplankton SIA, water samples were first filtered through a 60 μm mesh-size plankton net to remove zooplankton (Baranyai & G.-Tóth, 2010; G.-Tóth et al., 2011) and then the filtrate samples were filtered onto pre-combusted GF/C glass fiber filters (1.2 μm pore-size). We assumed that the seston samples collected on the filters consisted mainly of algae. However, it must be noted that samples might contain a certain amount of resuspended sediment particles in addition to algae, because wind-driven turbulence in Lake Balaton results in a high concentration of resuspended inorganic sediment (rich in carbonates minerals) in the water column. Thus, evaluation of $\delta^{13}C$ measurements should be done with caution, because seston samples for SIA might contain some carbonate-derived inorganic carbon.

The suspensions (planktonic masses) retained by the 60 μm mesh-size net were collected separately and were treated as zooplankton samples. Moreover, dorsal muscle samples were excised and collected from bigheaded carps. All samples were dried to a constant weight at 60 °C and were homogenised prior to SIA.

During the calculations, we focused on estimating the contribution of zooplankton as a food resource for bigheaded carps, as the microscopic analyses showed the apparent dominance of this food item in the gut contents. The following mixing model was used to assess the relative contribution of zooplankton to the nutrition of bigheaded carp:

$$\% \text{ contribution of zooplankton} = 100 \times (\delta^{15}N_{BC} - F - \delta^{15}N_{S})/(\delta^{15}N_{Z} - \delta^{15}N_{S})$$

where the $\delta^{15}N_{BC}$ is δ N value of bigheaded carp, the $\delta^{15}N_{S}$ is δ value of seston and $\delta^{15}N_{Z}$ is δ of zooplankton, while F is the fractionation factor between successive trophic levels. Preceding studies reported fractionation factor values of 3‰ to 5‰ (Peterson & Fry, 1987) for N between tropic levels. In our calculations, we used an average 4‰ enrichment value for N.

Due to the extremely wide range of $\delta^{13}C$ signatures (see Results section) in seston samples (most probably arising from the presence of inorganic carbonates), it was assumed that $\delta^{13}C$ values were not appropriate for the assessment of carbon fluxes and to trace dietary contributions. Hence, here we rely on $\delta^{15}N$ values to evaluate the contribution of potential food resource to the diet of bigheaded carps.

Data analysis

Diet composition and feeding strategy of bigheaded carps were inspected with the graphical method proposed by Costello (1990) and modified by Amundsen et al. (1996). In this analysis, the prey-specific percentage abundance (PSA) of each food component was plotted in relation to its percentage frequency of occurrence (FO) in all fish studied. The PSA of a prey taxon is defined as its percentage of all prey items in only those predators (i.e., bigheaded carps) in which the taxon occurs as prey. The product of PSA and the corresponding FO value equals the mean percentage abundance of the given prey taxa in the diet of predators or their specified subset under study. Terms of individual and stock level specialization and generalization in respect to different prey taxa were used according to Amundsen et al. (1996) to describe the origin of the diet diversity.

We performed partial direct gradient analysis followed by a variance partitioning approach (Cushman & McGarigal, 2002; Peres-Neto et al., 2006) to evaluate the role of food resources (i.e., chlorophyll-a concentration, total zooplankton dry biomass, phyto- and zooplankton percentage taxonomic composition by biovolume and biomass, respectively), other environmental factors (i.e., water temperature, conductivity, Secchi depth, TSM, IOSM), seasonality (i.e., sampling months) and individual features of fish (i.e., gender, SL, RGRA and percentage area of different GR morphotypes) in gut content variability of hybrid bigheaded carps. Because of their extremely low representation in the gut content (<0.05% in abundance for all fish), four algae groups – Chrysophyceae, Cryptophyta, Desmidales and Xanthophyceae – were excluded from response variables to reduce their disproportionate effect in multivariate analyses (Legendre & Legendre, 2012). For analyses, percentage gut content data were arcsin√x transformed to improve their normality. Of the potential explanatory variables, phyto- and zooplankton percentage taxonomic composition and percentage GR morphotype data were arcsin√x transformed, and temperature, conductivity, Secchi depth, TSM, IOSM, SL, chlorophyll-a concentration, total zooplankton dry biomass and RGRA were lnx transformed prior to analysis. Month of sampling and gender were re-coded into binary dummy variables. A detrended correspondence analysis (DCA) with down weighting rare taxa indicated relatively long gradient length (3.27 in standard deviation units) in our data, therefore we chose canonical correspondence analysis (CCA) for further analysis (Lepš & Šmilauer, 2003). Potential explanatory variables were filtered for collinearity at r>0.7 (i.e., Pearson correlation analysis in Statistica 8.0 software package; www.statsoft.com) and subjected to a forward stepwise selection procedure (at $P<0.05$) based on Monte Carlo randomization test with 9,999 unrestricted permutations under the full model. This selection resulted in six effective explanatory variables for the final overall CCA model. Beside these variables, to improve readability of the graphical output of the analysis, we included some passive supplementary factors during this final analysis as well, such as males, total zooplankton abundance, chlorophyll-a concentration, GR1 and GR5. Supplementary factors were not used during the construction of the model, but based on the ordination results, their positions can be projected into the ordination space, and their meaning can be interpreted. Then, a series of CCA and partial CCAs were conducted to partition the effects of significant explanatory variables on gut content of hybrid bigheaded carps (Cushman & McGarigal, 2002). DCA and CCA analyses were performed using CANOCO version 4.5 software (ter Braak & Šmilauer, 2002).

Results

Abiotic environmental parameters and food resource

Measured values of abiotic environmental parameters such as water temperature, conductivity, Secchi depth, TSM and IOSM are summarized in the Table 1.

Chlorophyll-a concentration ranged between 1.5 and 7.3 μg L^{-1} (Fig. 2a) indicating quite low total phytoplankton biomass. The phytoplankton assemblage was dominated by pennate and centric diatoms (Fig. 2a). Other abundant algae were Chlorococcales and larger abundance of Dinophyta was occasionally observed.

The total zooplankton biomass varied considerably between sampling dates and ranged from 0.107 to 0.659 mg L^{-1} (Fig. 2b). In most sampling dates, copepods (i.e., *Eudiaptomus gracilis* and *Cyclops* spp.) represented the highest bulk of the zooplankton biomass, except in the warmest months, when *Diaphanosoma mongolianum*, a large-bodied cladoceran predominated.

Gill raker variability

In Lake Balaton, almost all bigheaded carps have gill rakers intermediate in morphology between those typical for bighead carp (GR1) and silver carp (GR5), but the proportion of different morphotype segments in the gill rakers varied considerably among individuals (Fig. 3). The most abundant gill raker morphotype segment was the GR3 (i.e., the intermediate type between bighead carp and silver carp), represented in 93% of the bigheaded carps with a median area of 58%. GR1 and GR5 morphotype segments occurred in 5% and 37% of individuals, respectively, and GR5 generally occurred only in minor proportions (median: 15%) of the total area of gill rakers. In most bigheaded carps, segments of two or three gill raker morphotypes occurred on the same gill arch, indicating complex gill raker morphology and various filtering capacity (i.e., complex food-size selectivity) even at the individual level.

Diet composition and feeding strategy

Zooplankton dominated over phytoplankton in the ingested food of bigheaded carps; the mean proportion of zooplankton ranged from 12.4% to 74.6%, whereas phytoplankton amounted between 0.0% and 42.8% (Fig. 4). Among zooplankters, rotifers, *Cyclops* spp. and *Bosmina* spp. were consumed in the largest quantity. However, beside planktonic crustaceans the occurrence of ostracods and some harpacticoid copepods in the gut contents indicated occasional role of benthic food resources in the diet of bigheaded carps as well. The most abundant phytoplankton taxa in the gut contents were diatoms, mainly taxa of Pennales. Moreover, 25.4-56.6% of the monthly mean gut content samples, proved to be inorganic matter, suggesting a significant amount of ballast feeding.

Graphical analysis of feeding strategy revealed that the most consistent component of the gut contents was the inorganic matter, which comprised a substantial proportion of the filtered matter in all bigheaded carps (Fig. 5). Both the frequency of occurrence and the prey-specific abundance of zooplankton taxa varied among seasons, but also indicated some taxon-specific tendencies. Namely, the consumption of rotifers was generally frequent at a moderate to low significance. On the other hand, *Bosmina* cladocerans, predacious cladoceran *Leptodora kindtii,* and harpacticoid copepods and ostracods were less frequently preyed by bigheaded carps but sometimes at substantial individual specialization. Diatoms were stable components of the gut contents in some periods but their prey-specific abundance never exceeded 24.2% and 8.6% regarding Pennales and Centrales taxa, respectively. Chlorococcales, cyanobacteria, Dynophyta and Eugleonophyta occurred also frequently in the gut content but their prey-specific abundances were negligible.

Influence of environment, season and individual traits on the diet composition

The CCA model explained 26.5% of the variance in the diet of bigheaded carps and indicated statistically significant, but moderate roles of IOSM, food resource (i.e. relative abundance by biomass of *Cyclops* spp. and Chlorococcales), gender, water temperature and individual variability in morphology of the filtering apparatus (Table 2; Fig. 6). Variance partitioning revealed that influences of the six explanatory variables retained for the final CCA model were mostly independent (i.e., majority of their explanatory power came from pure effects).

The first CCA axis accounted for the 12.7% of the variance in the diet data and positively correlated with *Cyclops* spp. relative abundance in the lake and negatively correlated with IOSM and water temperature (Fig. 6). All algae taxa found in the gut content received negative scores along this axis, while zooplankton taxa dispersed more in the ordination range and generally positioned in the positive range. The second CCA axis captured 5.8% of the total variance and positively correlated with females and negatively correlated with Chlorococcales abundance in the lake water and the percentage area of silver carp-like (GR4) hybrid gill raker morphotype. Inorganic matter content of the gut content seemed to be highly independent from the considered explanatory variables and positioned in the centre of the ordination space. Although with no identified significant effect in the CCA model, positioning of the supplementary variables indicated some positive tendencies between the consumption of algae and the chlorophyll-a concentration (i.e., total phytoplankton density) in the lake and the proportion of silver carp gill raker (GR5) morphotype, as well as between the consumption of zooplankton and the proportion of bighead carp gill raker (GR1) morphotype.

Stable isotope analysis

The average (±SD) $\delta^{13}C$ value of seston was –12.7 (±4.6)‰, while the average $\delta^{13}C$ values of zooplankton and bigheaded carp muscle samples were substantially lower than of seston, with average values of –26.4 (±1.34)‰ and –25.5 (±0.6)‰, respectively (Fig. 7). The difference between average $\delta^{13}C$ value of zooplankton and bigheaded carps (1.1‰) were close to the value of enrichment between successive trophic levels, suggesting direct carbon flow from zooplankton to bigheaded carps. The average (±SD) $\delta^{15}N$ values of seston, zooplankton and bigheaded carps were 2.3 (±1.4)‰, 4.7 (±1.5)‰ and 8.9 (±0.4)‰, respectively (Fig. 7). The differences between average $\delta^{15}N$ values of the three sample type indicated predator-prey interactions between bigheaded carps and zooplankton, and did not show direct trophic interaction between seston and bigheaded carps. Calculations based on the mixed model revealed that the average contribution of zooplankton to the diet of bigheaded carps was 104.2 (±22.4)%.

Discussion

In Lake Balaton's hybrid-dominated bigheaded carp stock we found various types of gill rakers, including comb-like (typical for bighead carp and effective in filtering zooplankton), sponge-like (typical for silver carp and effective in harvesting phytoplankton) structures, and various types of complex, intermediate (hybrid) gill rakers. It is likely that major differences in gill raker morphology among individuals may be accompanied by a high inter-individual variability in food composition and trophic role (Spataru et al., 1983; Jayasinghe et al., 2015), because mesh size of the rakers determines the smallest size of consumable food items (Dong & Li, 1994; Vörös et al., 1997). Nevertheless, food composition of individuals with various types of gill rakers was quite similar, and zooplankton predominated in the gut contents of all examined bigheaded carps. It turned out that gill raker morphology exerts only minor influence on the consumed food, but the effects of environmental factors (inorganic suspended matter, resource availability) have a decisive role in shaping the food composition of bigheaded carps in Lake Balaton (see also Battonyai et al., 2015).

Most bigheaded carps possess hybrid-type (intermediate in development between comb-like and sponge-like structures) filtering apparatus in Lake Balaton. The different gill raker morphotypes are often represented on the same gill arch of a single individual. Sponge-like structures (i.e., GR5) were observed on the gill arches of most individuals, providing a theoretical chance for the vast majority of the stock to capture phytoplankton effectively. However, it appears that phytoplankton has only a negligible contribution to the diet of bigheaded carps in Lake Balaton, which could be explained at least in part by the low biomass of algae in Lake Balaton (monitored via the chlorophyll-a concentration in the water column). Previous laboratory experiments on the feeding habits of silver carp revealed that the intensity of grazing on phytoplankton was primarily determined by the density of algae in the ambient water (Herodek et al., 1989). Thus, in oligotrophic and mesotrophic habitats (such as Lake Balaton), the relative importance of phytoplankton in the food is supposed to be lower compared to that in highly productive, eutrophic or hypertrophic ecosystems. However, our knowledge on the importance of phytoplankton consumption by silver carp and more generally by bigheaded carps in habitats of low productivity is limited. Feeding habits of bigheaded carps were mainly studied in eutrophic water bodies and in fertilized aquaculture operations, particularly in relation with their use as tools of biomanipulation (Zhang et al., 2008; Xie & Liu, 2001) and to boost aquaculture yields by implementing polyculture technologies based on a more direct utilization of primary production (Kolar et al., 2007).

The wide range and extremely high $\delta^{13}C$ values of seston did not facilitate the traditional, stable carbon-isotope-based evaluation of dietary interactions. Such high $\delta^{13}C$ values (e.g., –10 to –15) for phytoplankton have been reported from shallow, eutrophic lakes (Gu & Schelske, 1996). Thus, in productive ecosystems the phytoplankton can be enriched in ^{13}C due to the high assimilation rate for ^{13}C-rich dissolved inorganic carbon (Gu & Schelske, 1996). However, in the case of Lake Balaton the observed high $\delta^{13}C$ values very likely were consequence of the presence of carbonate- derived inorganic carbon in seston samples, i.e., the $\delta^{13}C$ values did not represent reliably the phytoplankton. However, using $\delta^{15}N$ signatures, the complementary stable isotope analysis supported the findings of gut content analysis and suggested that ingested phytoplankton does not contribute substantially to the nutrition of bigheaded carps in Lake Balaton.

Beside the low abundance of algae in the water, the low contribution of phytoplankton in the nutrition of bigheaded carps might also be a consequence of restrained capability of bigheaded carps to digest and utilize most algae found in the lake. Görgényi et al. (2016) studied the consumption and digestion of algae by bigheaded carps in Lake Balaton and showed that cells or colonies of several phytoplankton species can survive the passage through the alimentary canal and can be found in viable form in the hindguts (i.e., in the faeces). Bitterlich (1985) and Gerking (1994) explained the low efficiency of bigheaded carps in utilizing some phytoplankton taxa with the lack of cellulase enzyme in the gut fluids and the relatively high pH in their digestive tract. Accordingly, the stable isotope analyses in this study confirmed that the vast majority of the metabolised nutrients was zooplankton-derived in bigheaded carps.

In the light of these findings, it seems that the fundamental benefit provided by the diverged gill raker morphologies of bigheaded carps (i.e., comb-like and sponge-like rakers) to escape interspecific diet overlap can diminish under certain environmental conditions, for instance in phytoplankton-poor environments like Lake Balaton is. According to Ke et al. (2008), this phenomenon is the matter of abundance and quality of available food resources. The same authors found that both silver and bighead carp showed preference for zooplankton and shared this higher quality food resource when it was abundant. However, substantial diet overlap was also observed when alternative food resources were depleted (Ke et al., 2008; Chen et al., 2011). Thus, in the mesotrophic Lake Balaton where the availability of digestible phytoplankton is low, bigheaded carps have no alternatives to feeding on zooplankton regardless of the differences of their individual gill raker morphology and the likewise moderate zooplankton abundance (G.-Tóth et al., 2011). On the other hand, under eutrophic conditions, which is actually the typical environment of bigheaded carps (Kolar et al., 2007), food resources are more abundant and diverse, and therefore, species-specific differences in the filtration capacity (i.e., utilizable food size spectra) may be more important in grazing on the most profitable food resource and avoiding interspecific competition.

Recent hydroacoustic surveys revealed that non-native bigheaded carps constitute about 20 – 30 % of the total fish biomass in the Lake Balaton (Tátrai et al., 2009; Boros, 2015). Because this massive bigheaded carp stock primarily feeds on zooplankton, it certainly can thereby exert a considerable ecological effect on the whole ecosystem of Lake Balaton (e.g., through top-down control). Through their intense grazing, bigheaded carps can alter the abundance and assemblage composition of zooplankton and consequentially indirectly the phytoplankton community as well (Lu et al., 2002; Zhou et al., 2011). Mass consumption of zooplankton especially limits the availability of food for several native species (e.g., bleak, razor fish and common bream) and the earliest, zooplanktivorous life stages of almost all fish species (Specziár & Rezsu, 2009). Moreover, bigheaded carps may affect the whole nutrient cycle of the lake through trophic cascades (Lieberman, 1996). For instance, by altering the structure of plankton community, these fish species affect the utilization patterns and the turnover time of nutrients in water column (Domaizon & Devaux, 1999; Mátyás et al., 2003).

The unintentional ingestion of inorganic particles is common in the case of filter-feeding animals, like herbivorous zooplankton (e.g., G.-Tóth et al., 1986; Rellstab & Spaak, 2007); however, this phenomenon is still poorly documented in filter-feeding fishes. The sampled hybrid bigheaded carps exhibited an unusually high level of inorganic debris consumption. It is also surprising that the proportion of the ingested inorganic debris in the gut content was highly independent of the environmental circumstances (considering both abiotic and food resource-related variables), and it did not correlate with gill raker morphology. Because neither the bighead carp-type, nor the silver carp-type gill rakers proved to be effective in avoiding inorganic debris consumption, it is likely that the entrapment of these small-sized suspended inorganic particles was facilitated by the mucus coating on the gill rakers (Sanderson, 1996; Gophen, 2014). The hydro-morphological attributes of Lake Balaton probably contributed to the high inorganic debris consumption of bigheaded carps. This large but relatively shallow lake is highly exposed to wind-generated turbulence, resulting in very high suspended sediment concentrations. Nevertheless, the statistical analysis failed to find any association between the amount of inorganic suspended material (IOSM) in the lake water and proportional contribution of inorganic matter in the gut. Normally fishes tend to avoid the ingestion of inorganic particles. However, because bigheaded carps seem not to be able to separate food from inorganic particles during their filtering activity, they presumably decrease the rate of filtration under unfavourable turbid conditions to set a limit for inorganic debris feeding. In contrast to other filter feeders such as herbivorous zooplankters (Rellstab & Spaak, 2007), bigheaded carps' inorganic debris consumption did not result in poor somatic conditions in Lake Balaton. The observed condition factor (expresses the "plumpness" of fish) and growth rates of fish were high in Lake Balaton compared to other bigheaded carp populations (Boros et al., 2014). Solving the contradiction between the seemingly poor food resources and the ideal condition factor and growth rate of bigheaded carps remains the task of future researches.

Abiotic environmental factors, namely IOSM and water temperature accounted for a remarkable proportion of the explained variance in the diet of bigheaded carps. In our opinion, the effect of these factors is mainly indirect and they may designate certain patterns of food availability. Specifically, IOSM indicates the strength of wind-generated turbulence of the water which can alter the distribution, abundance and assemblage structure of planktonic organisms (Baranyai & G.-Tóth, 2010; Baranyai et al., 2011). For instance, some zooplankton taxa are sensitive to turbulence and respond to windy weather with decreased abundance either due to increased mortality (O'Brien et al., 2004) or because of they migrate into the benthic zone (Baranyai & G.-Tóth, 2010). On the other hand, turbulence can displace benthic taxa into the water column (Goździejewska et al., 2006) creating a food resource for planktivores such as bigheaded carps. The occasional occurrence of benthic crustaceans (e.g., *Ostracoda* and *Harpacticoida* species) in the gut contents of bigheaded carps supports this hypothesis. Moreover, because fishes are able to effectively discern the inorganic contaminants in food (e.g., Callan & Sanderson, 2002; Finger, 2008), the high amount of suspended inorganic material may alter taste-sensitive foraging performance of bigheaded carps, resulting in decreased feeding intensity and altered food selection. Water temperature correlated strongly with the binary dummy variables describing seasonality of samples (i.e., name of months) and also represented seasonal patterns of food resources. Therefore, considering all the direct and indirect effects signified by the explanatory factors retained for the final CCA model to describe the background of dietary variability of bigheaded carps in Lake Balaton, we can submit that variability of the food resource availability and water turbidity are the factors which influence the feeding of these fish principally, whereas individual gill raker morphology has little importance in this particular environment.

Conclusions

Our findings emphasize the importance of environmental factors (especially turbidity and seasonally dissimilar availability of food resources) in shaping the feeding habits of bigheaded carps. However, results of this study also reveal some uncommon patterns in the feeding behavior of these filter-feeding fishes in this particular mesotrophic environment, where the ingested and especially the utilized food was mainly zooplankton, irrespective of the gill raker morphology and hybrid status of individuals. This study contradicts the general assumption that silver carp with its sponge-like gill raker consume mainly phytoplankton and shows that in certain habitats the nutritional role of this food resource could be negligible. Consequently, bigheaded carps can be considered direct food competitors of the zooplanktivorous native fishes and early, zooplanktivorous life stages of nearly all fish species in Lake Balaton. Further research is needed to explore what circumstances can cause the diminishing dietary and functional differences among fish species with markedly different filtering organs and to investigate the impact of invasive bigheaded carps on the native biota and nutrient cycling in low productivity ecosystems.

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Figure captions

Fig. 1 Morphological variability of gill rakers of hybrid bigheaded carps in Lake Balaton, Hungary. Five morphotypes of gill raker structures were defined ranging from the comb like, bighead carp type (type GR1; a) through transitional forms (type GR2-4; b-d) to the sponge like, silver carp type (type GR5; e).

Fig. 2 Mean chlorophyll-a concentration (μg L^{-1}) and percentage taxonomic composition of phytoplankton by biovolume (b) as well as mean total dry biomass (mg L^{-1}) and percentage taxonomic composition of zooplankton by dry biomass (b) in Lake Balaton, Hungary by sampling dates. Time series of chlorophyll-a concentration is indicated by continuous line for monthly samples and by dotted line for loose sampling periods.

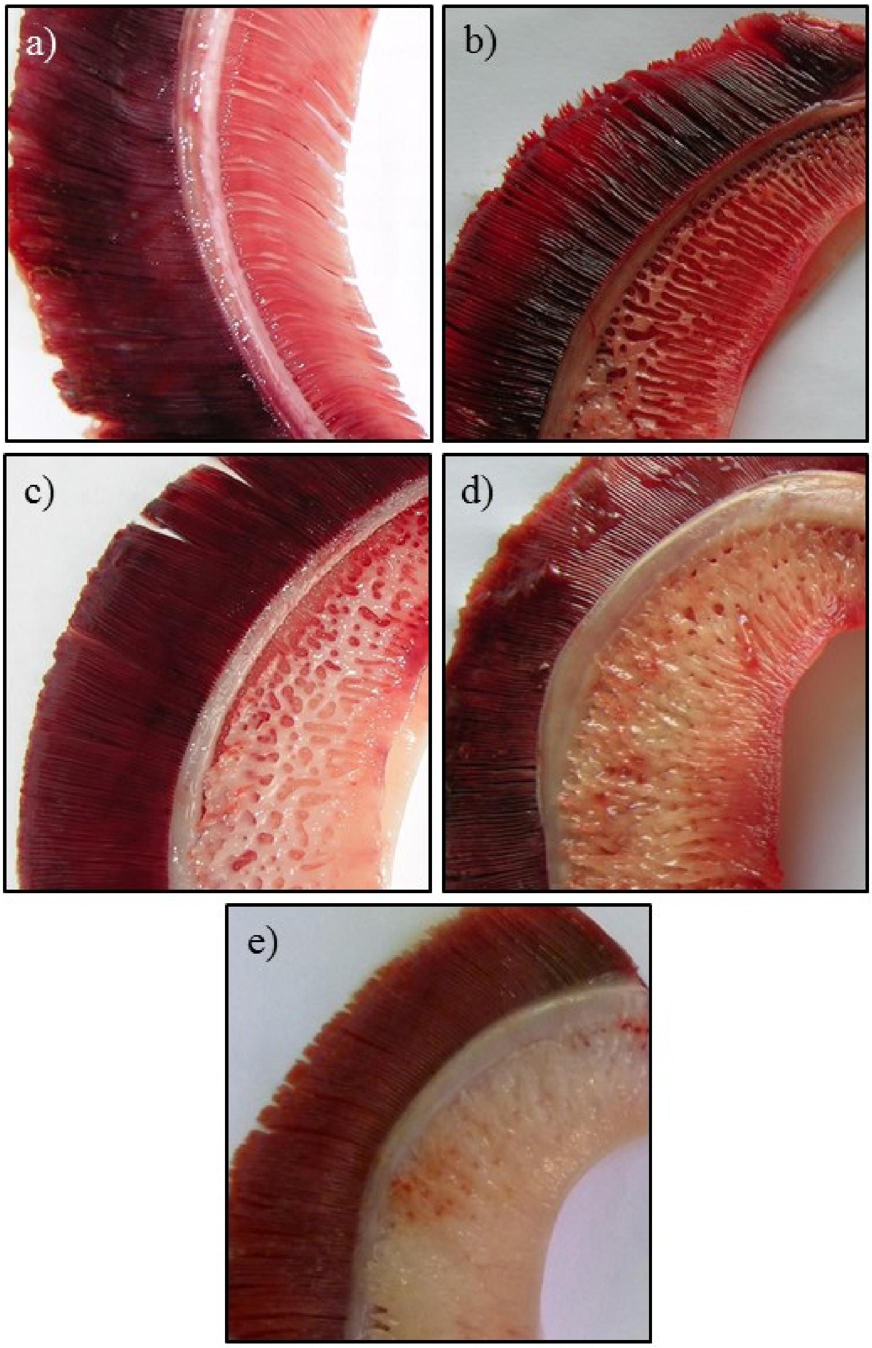
Fig. 3 Gill raker structure demonstrated by the relative area of different morphotype segments of each bigheaded carp analysed for food composition in Lake Balaton, Hungary. Each column represents a fish in the sample. GR1 to GR5 gill raker morphotypes are specified in Fig. 1.

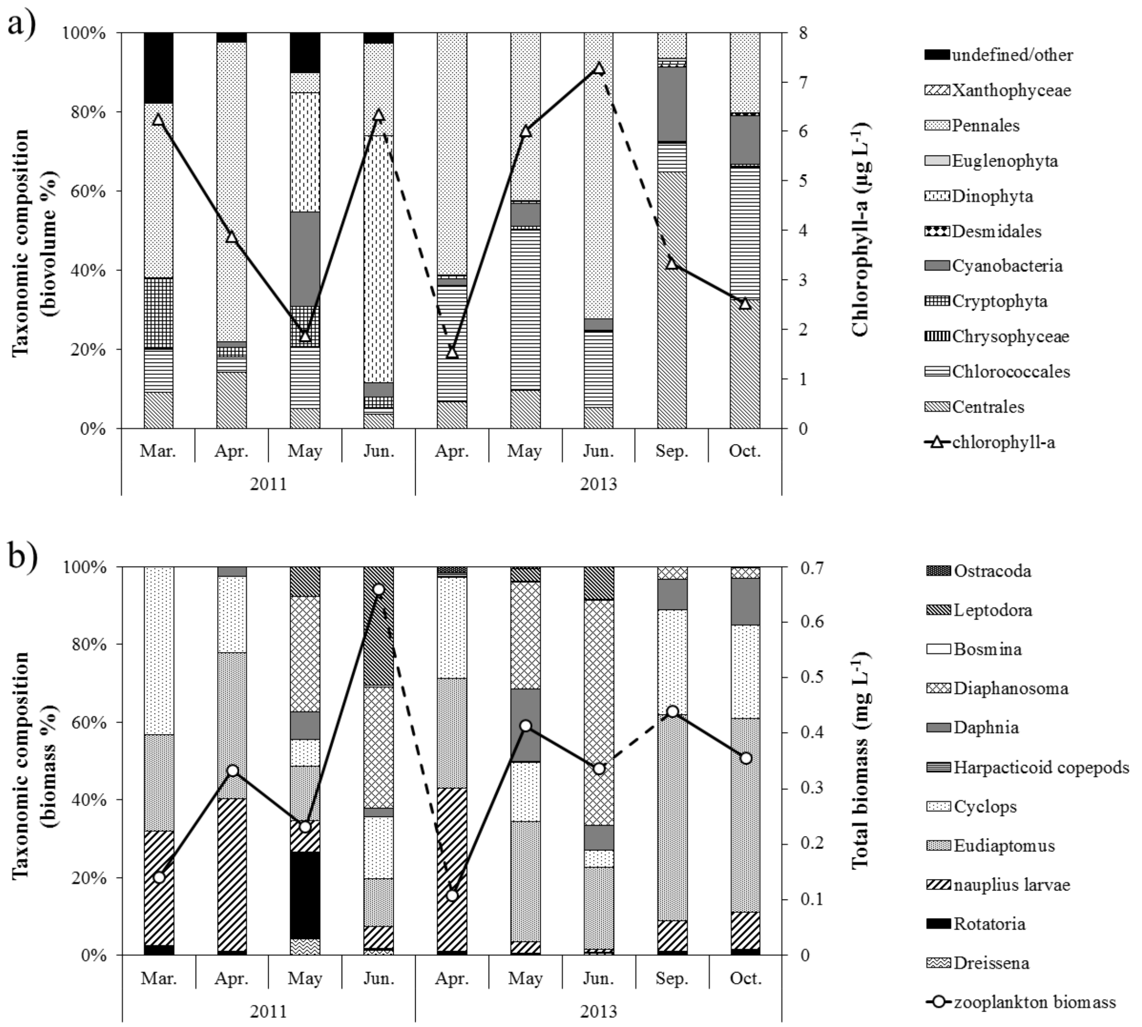
Fig. 4 Percentage contribution of zooplankton, phytoplankton and inorganic matter by sampling occasions to the gut content of bigheaded carps in Lake Balaton, Hungary.

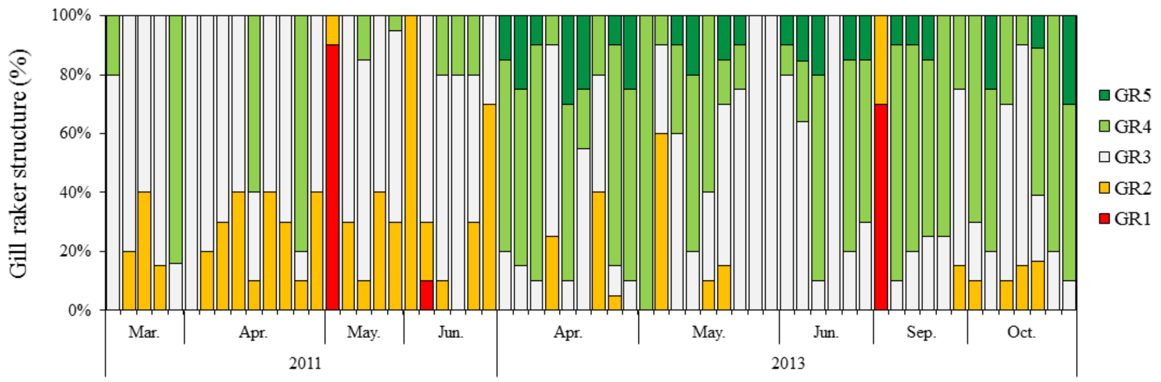
Fig. 5 Feeding strategy of bigheaded carps by sampling occasions plotted according to Amundsen et al. (1996). The horizontal axis represents the relative role of individual to stock level utilization of particular food components (o, zooplankton groups written in italic letters; Δ, algae groups written in normal letters; ■, inorganic matter written in underlined letters). Whereas, the vertical axis represents the rate of specialization with low scores indicating generalization and scores close to 100% indicating strong specialization. Thus, the overall importance of a food component increases from the lower left to the upper right corner of the plot and the sum of products of x and y axis scores for all food components equals one. Centr., Centrales; Penn., Pennales; Dreis., *Dreissena* larvae; Rota., Rotatoria; naupl., nauplius larvae of copepods; Eudia., *Eudiapthomus* spp.; Cycl., *Cyclops* spp.; Harp., Harpacticoid copepods; Bosm., *Bosmina* spp.; Daph., *Daphnia* spp.; Lept., *Leptodora kindtii*; Ostr., Ostracoda; inorg., inorganic matter.

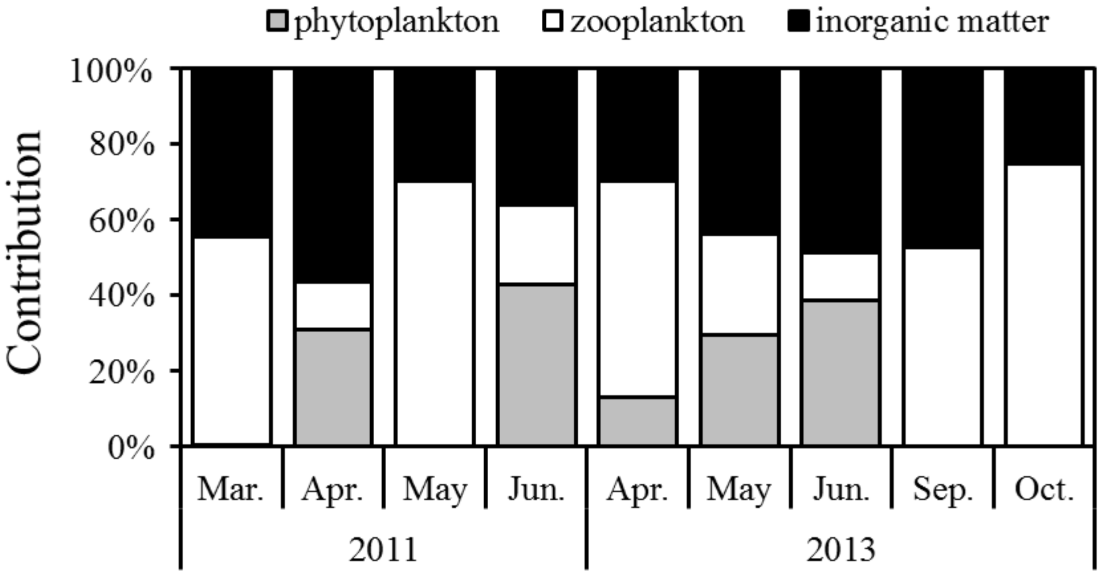
Fig. 6 Canonical correspondence analysis plot describing the relationship between the percentage gut content composition (o, zooplankton groups written in small italic letters; Δ, algae groups written in small normal letters; ■, inorganic matter written in small underlined letters) of hybrid bigheaded carps and forward selected, significant (at $P<0.05$) environmental factors, seasonality and certain individual traits of fish (→, continuous explanatory variables; and ●, binary dummy explanatory variables written in large letters) in Lake Balaton, Hungary. Some passive, supplementary variables are also plotted in grey. Percentage variance represented by axes are indicated in brackets (of diet data; of diet-explanatory variables relation) after the axis name (for a more detailed statistics see Table 2). Scale factor for plotting is 4.9.

Fig. 7 Stable isotope values (‰) of bigheaded carps (♦) and their potential preys (●, zooplankton; ▲, seston/phytoplankton). Each symbol shows average value of one sampling month. The empty symbols and whiskers represent the mean and the SD of a given sample type.

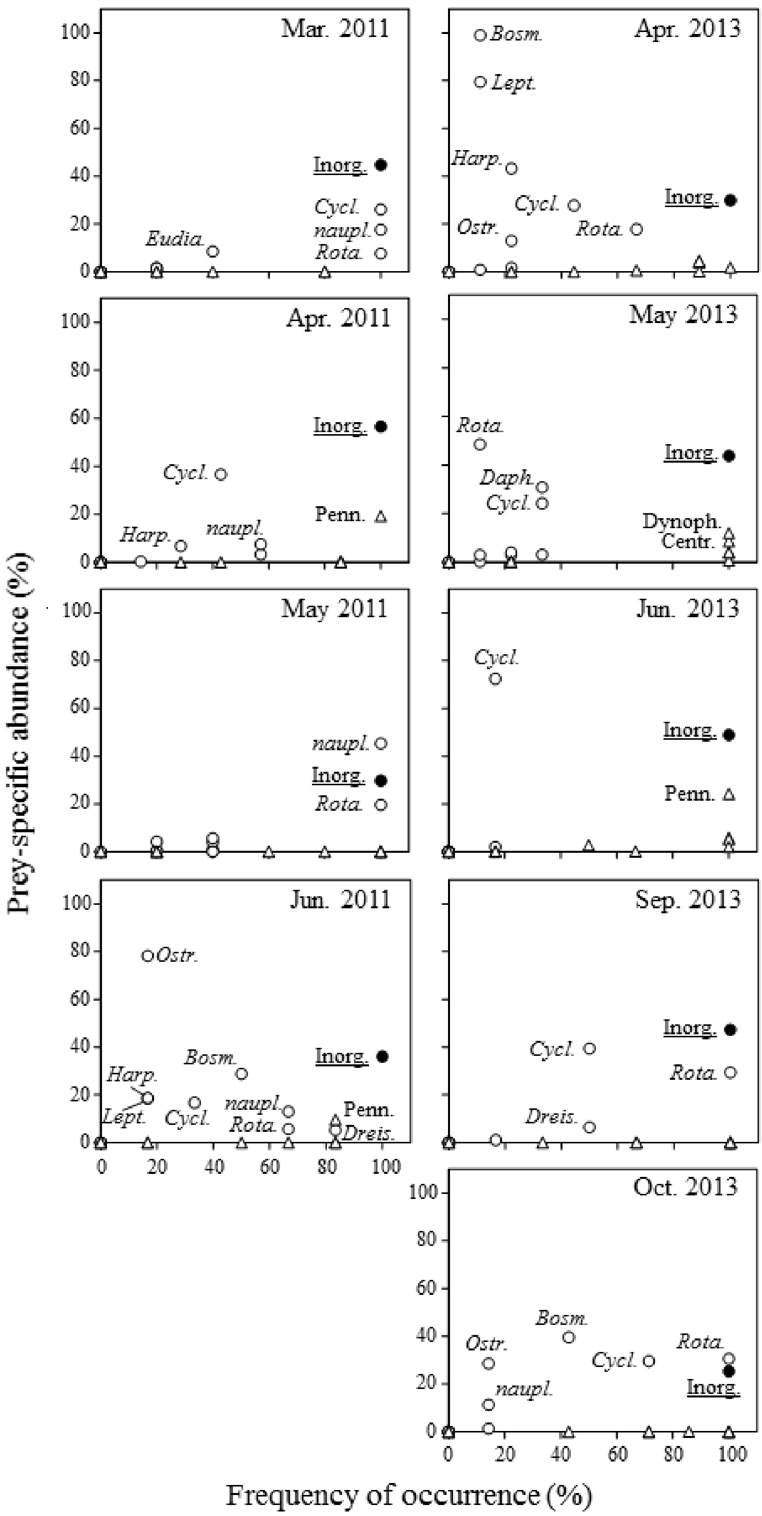

a)
b)
c)
d)
e)


a)
Taxonomic composition (biovolume %)
Chlorophyll-a (µg L-1)
undefined/other
Xanthophyceae
Pennales
Euglenophyta
Dinophyta
Desmidales
Cyanobacteria
Cryptophyta
Chrysophyceae
Chlorococcales
Centrales
chlorophyll-a
b)
Taxonomic composition (biomass %)
Total biomass (mg L-1)
Ostracoda
Leptodora
Bosmina
Diaphanosoma
Daphnia
Harpacticoid copepods
Cyclops
Eudiaptomus
nauplius larvae
Rotatoria
Dreissena
zooplankton biomass
Mar.
Apr.
May
Jun.
Sep.
Oct.
2011
2013

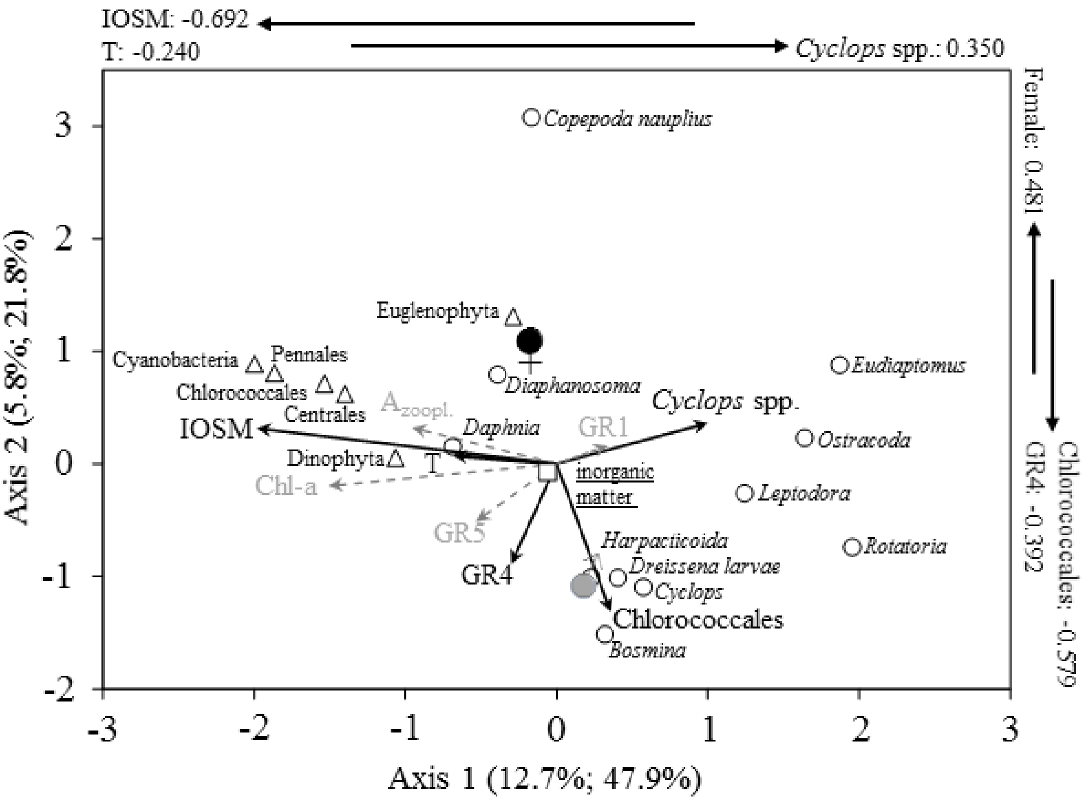

Gill raker structure (%)
GR5
GR4
GR3
GR2
GR1
Mar.
Apr.
May.
Jun.
Sep.
Oct.
2011
2013


phytoplankton
zooplankton
inorganic matter
Contribution
100%
80%
60%
40%
20%
0%
Mar.
Apr.
May
Jun.
Apr.
May
Jun.
Sep.
Oct.
2011
2013

783



Mar. 2011
Inorg.
Cycl.
naupl.
Rota.
Eudia.
Apr. 2013
Bosm.
Lept.
Harp.
Cycl.
Inorg.
Ostr.
Rota.
Apr. 2011
Inorg.
Cycl.
Penn.
Harp.
naupl.
May 2013
Rota.
Inorg.
Daph.
Cycl.
Dynoph.
Centr.
May 2011
naupl.
Inorg.
Rota.
Jun. 2013
Cycl.
Inorg.
Penn.
Jun. 2011
Ostr.
Bosm.
Inorg.
Harp.
Lept.
Cycl.
naupl.
Rota.
Penn.
Dreis.
Sep. 2013
Inorg.
Cycl.
Rota.
Dreis.
Oct. 2013
Bosm.
Ostr.
Rota.
Cycl.
naupl.
Inorg.
Prey-specific abundance (%)
Frequency of occurrence (%)


IOSM: -0.692
T: -0.240
Cyclops spp.: 0.350
Female: 0.481
Chlorococcales: -0.579
GR4: -0.392
Copepoda nauplius
Euglenophyta
Cyanobacteria
Pennales
Chlorococcales
Centrales
Diaphanosoma
Azoopl.
Cyclops spp.
Eudiaptomus
IOSM
Daphnia
GR1
Ostracoda
Dinophyta
T
inorganic matter
Chl-a
Leptodora
GR5
Harpacticoida
Rotatoria
Dreissena larvae
GR4
Cyclops
Chlorococcales
Bosmina
Axis 2 (5.8%; 21.8%)
Axis 1 (12.7%; 47.9%)

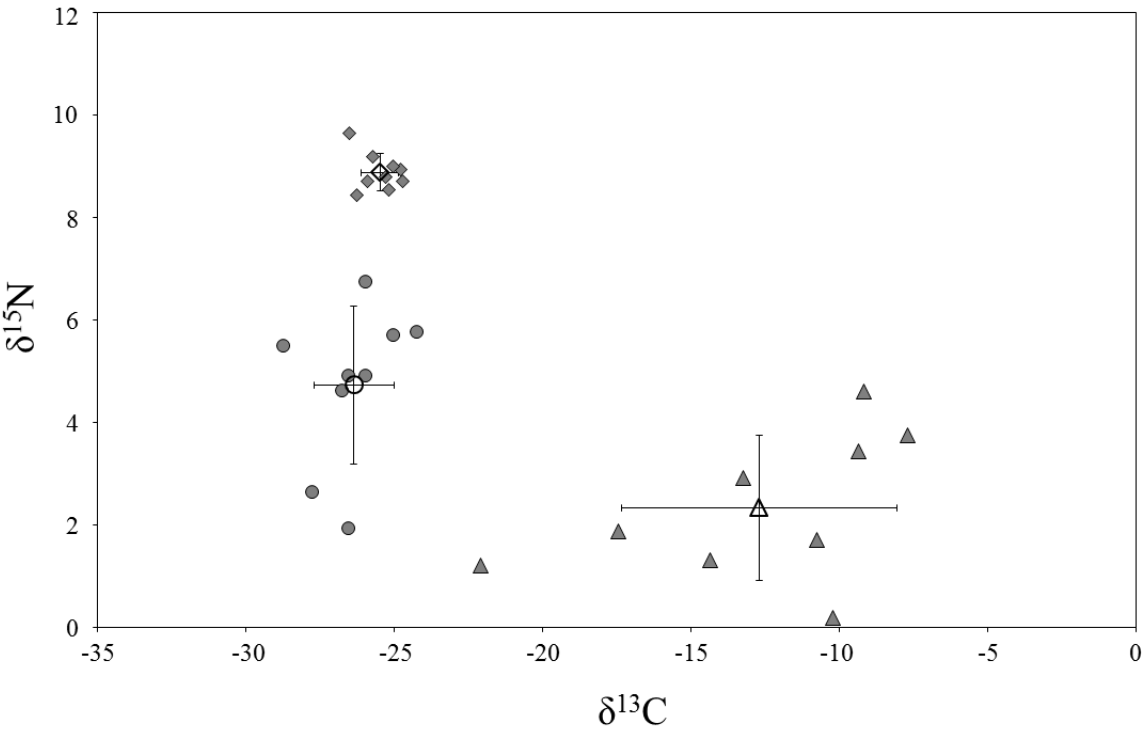

δ15N
δ13C

Table 1. Means and ranges of water temperature (T, °C), conductivity (Cond., μS cm^{-1}), Secchi depth (cm), total suspended matter concentration (TSM, mg L^{-1}) and inorganic suspended matter concentration (IOSM, mg L^{-1}) at bigheaded carp sampling sites in Lake Balaton, Hungary.

		Temperature		Conductivity		Secchi depth		TSM		IOSM	
		mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
2011	Mar.	8.9	0.4	0.677	0.002	79	5.5	9.49	0.40	9.23	0.51
	Apr.	14.2	0.3	0.688	0.003	51	3.2	16.27	0.50	12.87	0.45
	May	21.3	1.9	0.725	0.087	157	2.9	3.06	0.28	2.20	1.18
	Jun.	20.4	0.1	0.920	0.000	36	1.2	33.17	1.26	22.33	0.60
2013	Apr.	18.2	0.2	0.711	0.002	61	5.9	11.30	0.10	8.03	0.23
	May	15.1	0.1	0.695	0.002	34	3.0	16.57	7.13	12.20	6.41
	Jun.	20.3	0.2	0.696	0.004	31	2.1	39.40	0.69	18.40	4.16
	Sep.	12.7	0.3	0.762	0.003	92	2.5	7.33	0.96	3.87	0.68
	Oct.	14.9	0.4	0.758	0.003	81	1.2	12.89	1.42	6.47	0.74

Table 2. Forward selected significant (F and P are indicated) explanatory variables and their percentage explanatory power in total and from pure effect in the canonical correspondence analysis of the percentage gut content data of hybrid bigheaded carps in Lake Balaton, Hungary.

Explanatory variables in the final model	F	P	Total explained variance (%)	Explained variance as pure effect (%)
Inorganic suspended matter	6.82	<0.001	10.51	8.33
Share of Chlorococcales in the phytoplankton	3.04	0.002	4.84	3.32
Female	2.42	0.011	4.14	2.92
Share of *Cyclops* spp. in the zooplankton	1.97	0.038	4.32	3.71
Water temperature	2.10	0.028	3.49	3.45
Area of gill rake type 4	1.90	0.054	2.62	2.18
Full model (all axes)	3.18	<0.001	26.48	-