LONG-TERM DEVELOPMENT OF FISH ASSEMBLAGE IN LAKE FENÉKI (KIS-BALATON WATER PROTECTION SYSTEM, HUNGARY): SUCCESSION, INVASION AND STABILIZATION

FERINCZ, Á.[1], STASZNY, Á.[2,3], ÁCS, A.[1], WEIPERTH, A.[4,5], TÁTRAI, I.[3]† and PAULOVITS, G.[3]

[1]*Department of Limnology, University of Pannonia, H-8200 Veszprém, Egyetem u. 10, Hungary*
[2]*Department of Aquaculture, Szent István University, H-2103 Gödöllő, Páter K. u. 1, Hungary*
[3]*Balaton Limnological Institute, Centre for Ecological Research*
Hungarian Academy of Sciences, H-8237 Tihany, Klebelsberg K. u. 3, Hungary
E-mail: paulovits.gabor@okologia.mta.hu
[4]*Department of Animal Taxonomy and Animal Ecology, Eötvös Loránd University*
H-1117 Budapest, Pázmány P. stny 1/c, Hungary
[5]*Danube Research Institute, Centre for Ecological Research, Hungarian Academy of Sciences*
H-2131 Göd, Jávorka Sándor u. 14, Hungary

This analysis of long-term (1992–2011) changes in the fish assemblage of the partially operating shallow, hypertrophic reservoir (Ingói-marsh, Lake Fenéki) was carried out on the occasion of the planned completion of the impoundment. Samplings were performed in standard localities with electrofishing. Three phases could be distinguished in fish fauna development. The first phase is characterized by two allochtonous marsh-species: the Mud-minnow (*Umbra krameri*) and the Crucian carp (*Carassius carassius*), and was fast replaced by the second invasion phase, characterized by the invasion of non-native gibel carp (*Carassius gibelio*),and the third phase by the dominance of roach (*Rutilus rutilus*) and bleak (*Alburnus alburnus*). The cumulative relative abundance of non-indigenous species reached a peak in the third year of the impoundment (1995; 56.4%), and remained high (>50%) until 2001. The number of species, Shannon-Weaver diversity, and relative abundance of piscivorous species correlated positively with the age of reservoir. The shift of the fish fauna between the two phases was dynamic and dramatic, since the all previously dominant species disappeared within 4 years. The impact of invasive gibel carp is considered as high, because it has completely replaced its native relative (*C. carassius*), but in the other hand it only was able to delay the natural successive process, not completely transform it.

Key words: gibel carp, diversity, assemblage structure, shallow reservoir

INTRODUCTION

The role of long-term (>10 years) research in fish ecology is unquestionable, but only relatively few papers have reported on this issue (SMOKOROWSKI & KELSO 2002). The importance of reservoirs is growing all over the world in parallel with the expansion of the human population and the increasing effects of climate change (ARNELL 1998, CHRISTENSEN *et al.* 2004, WILLIAMSON *et al.* 2009). Although these type of waterbodies are the target of most biomanipulation experiments (e.g., SCHARF 2008, SEDA & KUBECKA 1997), the relevance of reservoir

studies has not been restricted to application and management issues, and their role in recognition of community assembling rules is fundamental (GIDO *et al.* 2009).

Information on the fish fauna development of reservoirs is restricted mostly to the deep and oligotrophic lakes (GIDO *et al.* 2000, RIHA *et al.* 2009). Their assemblage structure changes have been characterized by successive processes with the participation of native species. These processes are well documented and usually well predictable. Based on several case studies, KUBECKA (1993) divided the assemblage development of Central European reservoirs into five phases, according to the change in dominant fish species during reservoir ageing: (1) a riverine species phase; (2) a pike, *Esox lucius* L., phase; (3) a perch, *Perca fluviatilis* L., phase; (4) a transient perch-cyprinid phase; and (5) a cyprinid-dominated phase. These studies (e.g., HLADÍK *et al.* 2008, RIHA *et al.* 2009), although some of them are considered recent, do not deal with the role of invasive species in such processes. Although numerous studies report the connection between the disturbance and invasibility even in case of reservoirs (HAVEL *et al.* 2005, JOHNSON *et al.* 2008, TARKAN *et al.* 2012a), little data could be found on the assemblage structuring function of an invasive species throughout longer periods.

This study evaluated the development of fish assemblage structure in a Pannonian Ecoregion impoundment, the Lake Fenéki (Kis-Balaton Waterquality Protection System, 2nd stage), over a 19-year period from its flooding, between 1992 and 2011. The following questions were examined: (1) Is there any temporal pattern in the change of fish assemblage structure during the 19-year period? (2) How does the gibel carp invasion affect the qualitative (species) composition of fish assemblage? (3) How does the gibel carp invasion affect the successive processes of the fish assemblage?

MATERIALS AND METHODS

Study area

The Ingó-marsh (46°38'46.68"N, 17°11'24.10"E) is the first inundated part of the shallow (1.1–1.2 m deep) hypertrophic (HATVANI *et al.* 2011, KOVÁCS *et al.* 2010) Lake Fenéki (also called Kis-Balaton Waterquality Protection System (KBWPS), 2nd stage) situated a few kilometres southwest from Lake Balaton (Fig. 1). Originally this area belonged to Lake Balaton as its most western basin. After 1863, the Sió-floodgate started to operate and the water level lowered by approx. 2 meters, then Kis-Balaton was disconnected. The complete drought of this area lasted for decades, but finally resulted in the complete disappearance of open water surfaces until the 1950's. The remains of native fish fauna could only survive in some draining channels and two small ponds (BÍRÓ & PAULOVITS 1994, KORPONAI *et al.* 2010). In the 1970's, after the recognition of the accelerating euthrophication of Lake Balaton, the reconstruction began on KBWPS (LOTZ 1988).

The system comprises two reservoirs: the first (Lake Hídvégi, 21 km²), which could characterized as open waterspace, gives ideal conditions for algae to reproduce and has been operating since

1985. The second (Lake Fenéki), which was our study area, was inundated partly (16 km² from the planned 54 km²) in 1992 (TÁTRAI *et al.* 2000). The main purpose of the KBWPS is to retain the nutrients carried by the River Zala (POMOGYI 1993).

The water in KBWPS is slightly alkaline (pH = 7.5–8.5); characterized with 600–700µS/cm conductivity (see more: HATVANI *et al.* 2011, KOVÁCS *et al.* 2010).

Sample collection

Samplings have been carried out seasonally from 1992 to 2011 (3 samplings yearly: April/May, June/July and October). Altogether the data of 12 years were included in the analysis; data were lacking or not standard in other years (1998; 2002; 2004–2008 and 2010). A standard locality, near the vegetated (reed and reed-mace) shoreline and inundated willow-bushes was electrofished from a boat, using a 12V battery powered device (used at Pulse DC 300–500 V; 50–70 Hz). Based on the results of SPECZIÁR *et al.* (2012) this method is powerful enough to get reliable information regarding the assemblage structure. This sampling site represents all of the typical habitats of the Ingó-marsh. The duration of each sampling occasion was 60 minutes, which is equal to 1606±210 m transects. Each individual caught was identified at species level, and then released.

Statistical analysis

Ordinary Least Square (OLS) regression has been used for trend detection in case of a cumulative number of specimens. Logarithmic regression has been used for trend detection by species num-
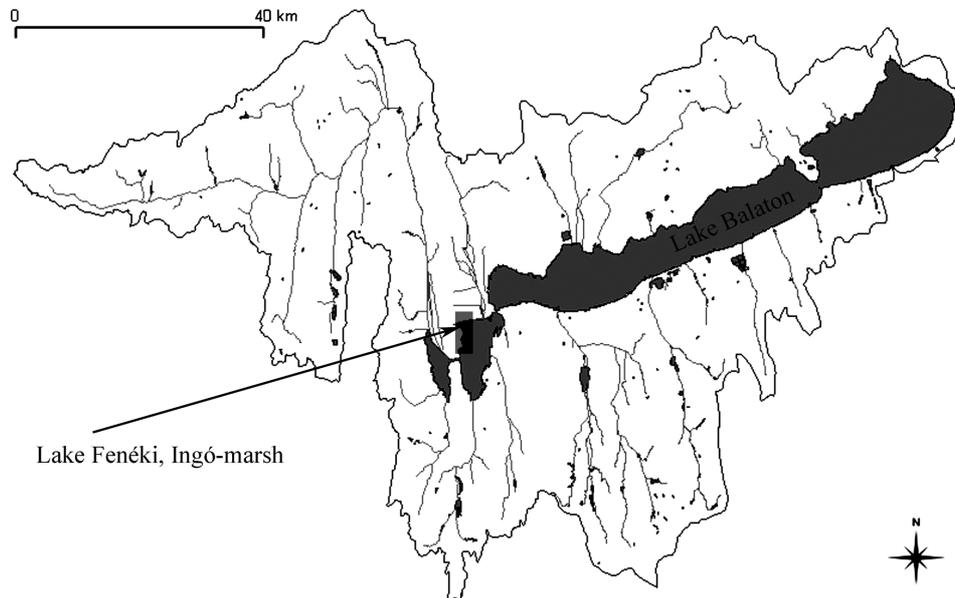
Fig. 1. Overlooking map of the Balaton-catchment, with the sampling site (Dark rectangle marked by the arrow indicates the flooded area of Lake Fenéki)

ber and Shannon diversity. Individual based rarefaction analysis was used to examine the changes in the estimated number of species over the years and to assess how the sampling efforts affected our estimates (ERŐS *et al.* 2008). The rarefaction analysis was carried out with PAST v. 1.91 software (HAMMER *et al.* 2008).

Relative abundances were calculated as ratio of number of individuals of a given species to the total number of individuals in the catch. A species considered to be dominant if its relative abundance reached 5% at least in one year). Cumulative abundances of species groups (eg. non-indigenous species; natives) were calculated as summarized relative abundances of species belonging each group. Relative abundance data were arcsin-square root transformed. Centered Principal Components Analysis (PCA) was carried out on the relative abundance data matrix to explore the patterns of assemblage level changes. Analyses were performed with SYN-TAX2000 software (PODANI 2000).

The functional composition (i.e. 'trophic guild') of fish assemblages was determined based on the work of ERŐS *et al.* (2009). Species which were lacking from this study were categorized using the system of BALON (1981). In order to assess changes in the relative abundance of trophic guilds in the sampling period, the OLS method was used.

RESULTS

2149 specimens of 23 species (Table 1) were caught in the sampling period, between 1992 and 2011. The cumulative number of individuals caught varied year to year and showed a significant increasing trend ($R^2 = 0.654$; P = 0.001) during this period (Fig. 2). Significant logarithmic increasing trend could be discovered by the number of fish species ($R^2 = 0.759$; P < 0.0001), which was increased from 3 to 18 (Fig. 3).

The same increasing trend could be observed by the Shannon-Weaver indices ($R^2 = 0.772$; P < 0.0001) (Fig. 4). Rarefaction curves (Fig. 5) supported the in-
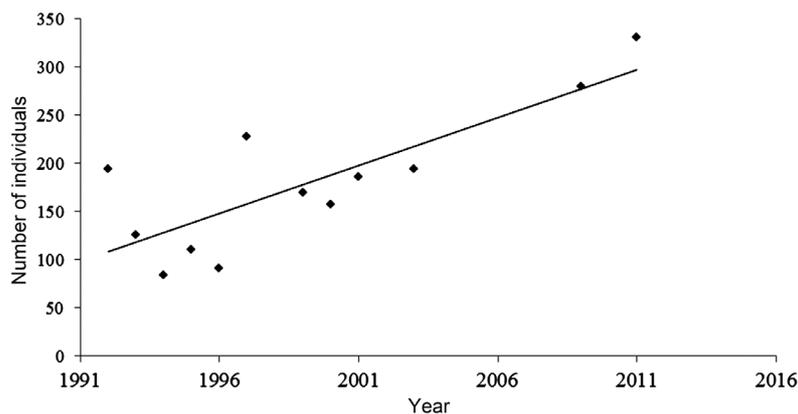
Fig. 2. Relationships between the age of Lake Fenéki and cumulative number of specimens caught in a sampling year (y = 107.7 + 9.63x; $R^2 = 0.654$, P = 0.001)
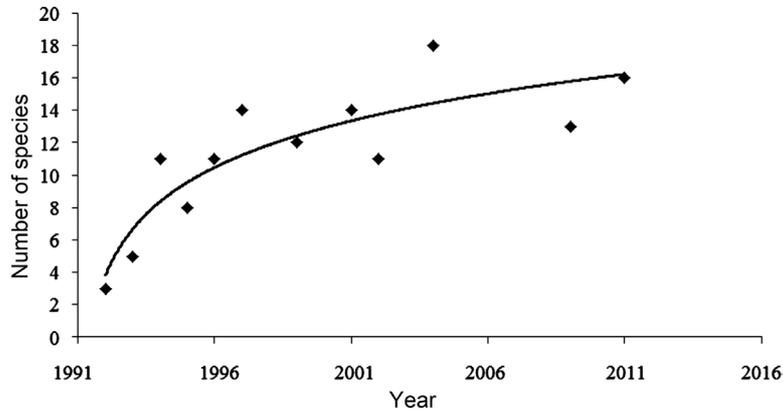
Fig. 3. Relationships between the age of Lake Fenéki and the number of fish species ($y = 4.141\ln(x) + 3.807$; $R^2 = 0.759$; $P < 0.0001$)

creasing trend in the number of species and showed that samplings were reliable in most years examined, as most of the curves reached an asymptote, although the sample sizes were relatively small.

Changes in the assemblage structure

The year by year changes of relative abundance ratios of dominant species determined three phases of assemblage development (Fig. 6). A dramatic and rapid change appeared after the second year of flooding: the original marshland fish fauna, which survived in draining channels and was characterized by Mudminnow (*Umbra krameri* WALBAUM, 1792) and Crucian carp (*Carassius carassius* L.,
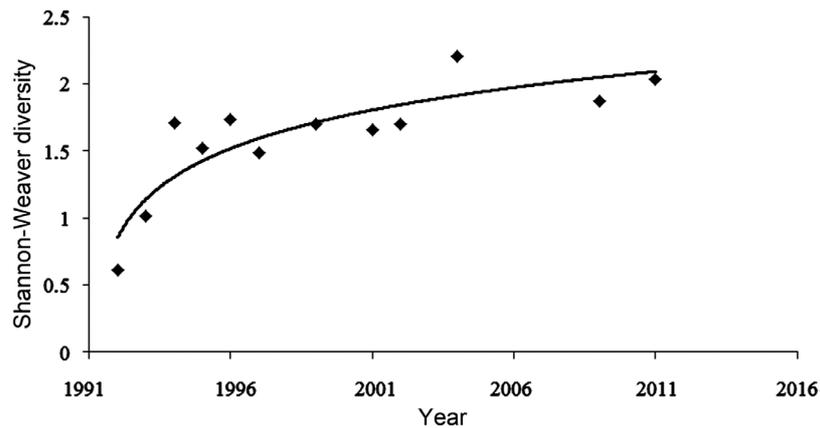
Fig. 4. Relationships between the age of Lake Fenéki and the Shannon–Weaver index ($y = 0.414\ln(x) + 0.852$; $R^2 = 0.772$; $P < 0.0001$)

Table 1. The species composition, relative abundance and trophic guilds (TG). Om = omnivore, Pi = piscivore, In = invertivore, Pl = planktivore, Na = native, Al = alien

| Species | | Year | | | | | | | | | | | | TG | Status |
Scientific name	Common name	1992	1993	1994	1995	1996	1997	1999	2000	2001	2003	2009	2011		
Esox lucius	Pike	0.00	0.00	0.00	0.00	0.00	0.00	0.59	0.64	1.61	0.52	1.07	0.91	Pi	Na
Umbra krameri	Mudminnow	80.93	65.60	1.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	In	Na
Rutilus rutilus	Roach	0.00	4.80	9.52	17.27	23.08	33.77	15.38	14.65	24.19	26.29	12.50	36.25	Om	Na
Scardinius erythrophthalmus	Rudd	0.00	0.00	0.00	1.82	1.10	0.88	7.10	0.00	4.30	11.86	2.86	0.60	Om	Na
Aspius aspius	Asp	0.00	0.00	2.38	0.91	2.20	1.32	4.73	1.27	2.69	2.06	1.07	0.60	Pi	Na
Alburnus alburnus	Bleak	0.00	0.00	5.95	0.00	5.49	3.07	2.96	17.20	0.00	11.34	27.50	3.93	Pl	Na
Ballerus ballerus	Zope	0.00	0.00	0.00	0.00	5.49	0.44	0.00	0.00	0.00	0.00	0.00	0.00	Om	Na
Blicca bjoerkna	White bream	0.00	0.00	0.00	0.91	0.00	0.44	1.18	0.64	1.08	1.55	0.00	3.02	Om	Na
Abramis brama	Bream	0.00	0.00	28.57	20.00	4.40	0.44	10.06	3.18	4.30	9.28	5.00	12.39	Om	Na
Carassius carassius	Crucan carp	11.34	12.80	1.19	0.00	1.10	0.00	0.00	0.00	0.00	0.52	0.00	0.00	Om	Na
Carassius gibelio	Gibel carp	0.00	16.00	39.29	42.73	42.86	46.05	49.70	48.41	44.62	21.13	31.07	18.73	Om	Al
Cyprinus carpio	Common carp	0.00	0.00	1.19	2.73	0.00	3.07	0.00	2.55	6.99	2.58	3.21	8.76	Om	Na
Tinca tinca	Tench	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.64	0.00	1.55	0.00	0.00	Om	Na
Pseudorasbora parva	Topmouth gudgeon	0.00	0.00	4.76	13.64	9.89	4.82	2.96	7.01	5.91	3.61	1.07	1.81	Pl	Al
Hypophthalmichthys molitrix	Silver carp	0.00	0.00	1.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	Pl	Al
Rhodeus sericeus	Bitterling	0.00	0.00	0.00	0.00	0.00	3.07	1.18	0.00	0.00	2.58	1.43	0.60	In	Na
Misgurnus fossilis	Weatherfish	7.73	0.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	Pl	Na
Silurus glanis	Wels	0.00	0.00	0.00	0.00	2.20	0.00	0.00	0.64	1.61	1.03	11.43	4.83	Pi	Na
Anguilla anguilla	Eel	0.00	0.00	4.76	0.00	2.20	0.00	0.00	0.00	0.00	0.52	0.00	0.00	In	Al
Lepomis gibbosus	Pumpkinseed	0.00	0.00	0.00	0.00	0.00	0.88	2.96	1.27	2.69	1.55	1.43	2.72	In	Al

Table 1 (continued)

Species			Year													TG	Status
Scientific name	Common name		1992	1993	1994	1995	1996	1997	1999	2000	2001	2003	2009	2011		
Sander lucioperca	Pikeperch		0.00	0.00	0.00	0.00	0.00	0.88	1.18	0.64	0.00	0.52	0.00	2.11	Pi	Na
Perca fluviatilis	Perch		0.00	0.00	0.00	0.00	0.00	0.88	0.00	1.27	0.00	1.55	0.36	2.11	In	Na
Neogobius fluviatilis	Monkey goby		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.60	In	Al
Number of species			3	5	11	8	11	14	12	14	11	18	13	16		
Shannon diversity			0.62	1.02	1.71	1.52	1.74	1.49	1.7	1.65	1.7	2.2	1.88	2.03		
Number of individuals			194	125	84	110	91	228	169	157	186	194	280	331		

1758) disappeared rapidly in parallel with the beginning of the gibel carp (*Carassius gibelio* BLOCH, 1782) invasion (Fig. 7). The second phase could be characterized by the strong dominance of non-native species, mainly gibel carp. The transition between the the second and third phase was not so fast and easily determinable, but it can be discerned in Figure 8. The years of the invasion phase are located in the 1:1 quarter, while the years of the stabilization phase mostly in the 2:2 quarter of the biplot. The position of the year 1997 is a little confusing, however, it could be explained by the high abundance of gibel carp and the co-dominance of roach (Fig. 6), then it was to be grouped into the invasion phase. After 2001, in parallel with the collapse of gibel carp invasion a stabilization phase began. This phase could be characterized by the dominance of roach (*Rutilus rutilus* L., 1758) and bleak (*Alburnus alburnus* L., 1758).

The amplitude of transition between the first and second phase is illustrated well in Figure 7, as the PCA of the arcsin-square-root transformed relative abundances of the first two years (1992–1993) showed positive correlation with PC1, which explained most (70%) of the total variation. The segregation of these variables could be clearly caused by the high relative abundance of Mudminnow and Crucian carp. Considering the assemblage structure of the other years examined, the discrimination of these variables by PC1 is almost impossible. Regarding PC2, a, trend-like pattern could be recognized between years.

On the biplot of this second ordination (Fig. 8), the transition after the invasion phase could be recognized, although not so intensively as in case of the first one. Based on this PCA, the second phase, characterized by the dominance of Gibel
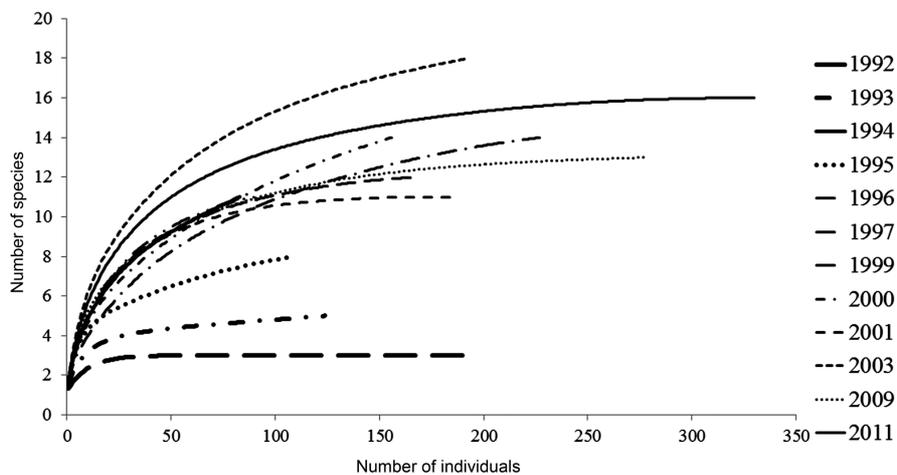
Fig. 5. Estimated number of species (SD's ignored in order to improve visibility) as a function of number of individuals collected in each sampling year

carp and co-dominance of roach and bleak lasted until 2000–2001 and after these two intermediate years, the third phase began, characterized by the dominance of native bleak and roach.

The role of non-indigenous species in fish fauna development

As Figure 6 indicates, the cumulative abundance of non-indigenous species increased from 0% rapidly and peaked at 56.7% in 2000, the 8th year after the
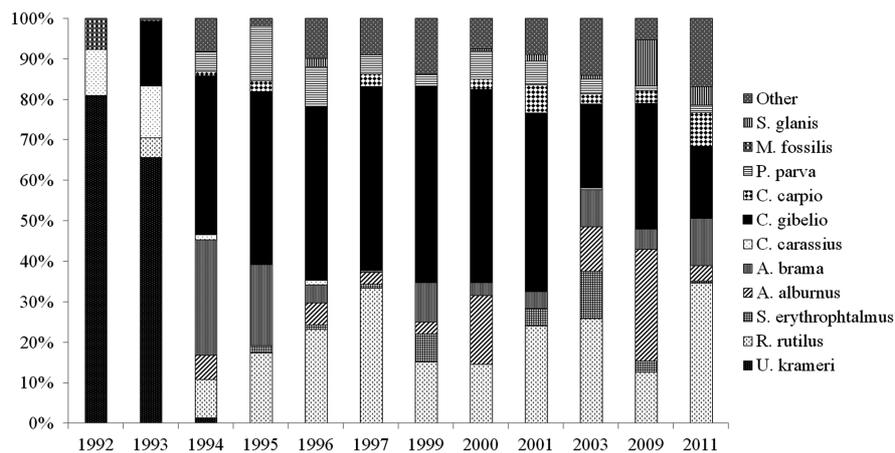
Fig. 6. Relative abundance of the fish species in Lake Fenéki in the sampling years

flooding. Out of the 6 non-natives, gibel carp was the most abundant throughout the years studied (Fig. 9), and only topmouth gudgeon (*Pseudorasbora parva* TEMMINCK et SCHLEGEL, 1842) could become dominant species (relative abundance reached 5%) at least in one year. After 2001, the cumulative ratio of non-natives decreased in parallel with the collapse of the gibel carp invasion (Figs 6 & 9).

Changes in trophic guilds

The rapid assemblage composition changes of the first two years examined caused functional changes as well (Fig. 10). However, the OLS analysis resulted in significant positive correlation in case of reservoir age and relative abundance of piscivores ($R^2 = 0.757$; $P < 0.0001$) for the whole examined period, their relative
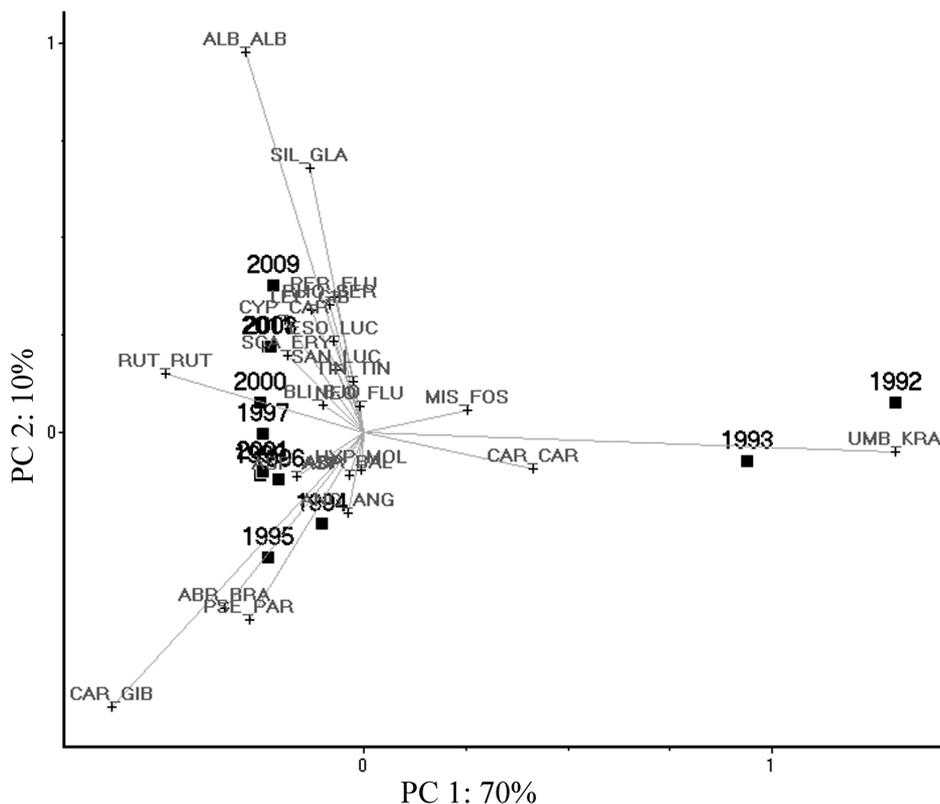
Fig. 7. PCA biplot of the arcsin-square root transformed relative abundance data of the whole sampling period (1992–2011) (Variables: Sampling years; Objects: Relative abundances) (abbreviations were constructed from the Latin names of the species, using the first 3 characters of genus and species names, like CAR_GIB= *Carassius gibelio*)

abundance was very low (<2%) throughout the years. Although no significant linear trends were observed by the other trophic guilds, the first transition in the assemblage structure resulted in notable decrease in relative abundance of invertivores (from 80% to 0.05%), due to the disappearance of Mud-minnow and increase of omnivores (from 19% to 79%), due to the expansion of cyprinids. This state became stable during the later periods.

DISCUSSION

The present fish fauna of Lake Fenéki is the result of mostly natural processes, as fishing is prohibited in the Nature Conservation area. The number of species and
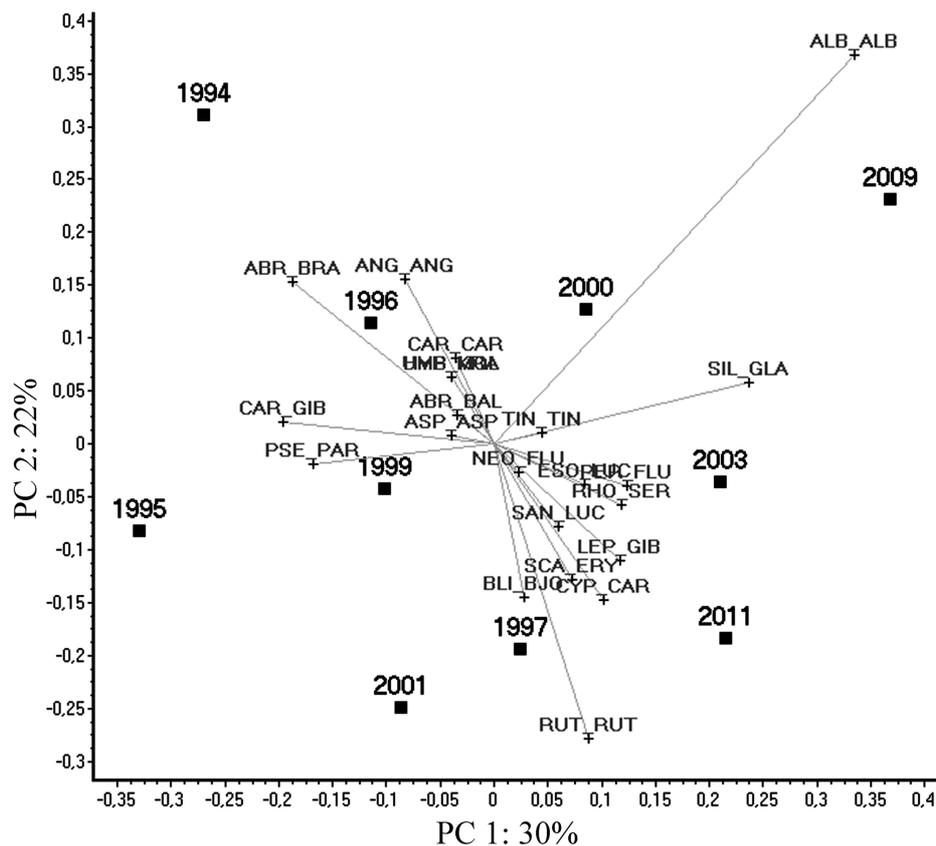
Fig. 8. PCA biplot of the arcsin-square root transformed relative abundance data of the period 1994–2011 (Variables: Sampling years; Objects: Relative abundances)
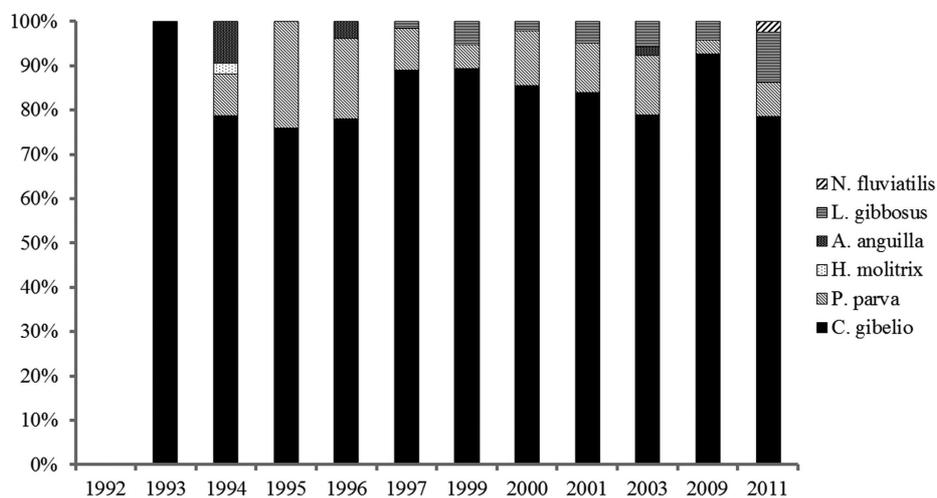
Fig. 9. Proportion of each species in the cumulative abundance of non-native fish species in Lake Fenéki

diversity showed an increasing trend throughout the whole period examined, seemingly not affected by the gibel carp invasion. The same trends were described for other Central European reservoirs (PENCZAK *et al.* 1998, RIHA *et al.* 2009). The
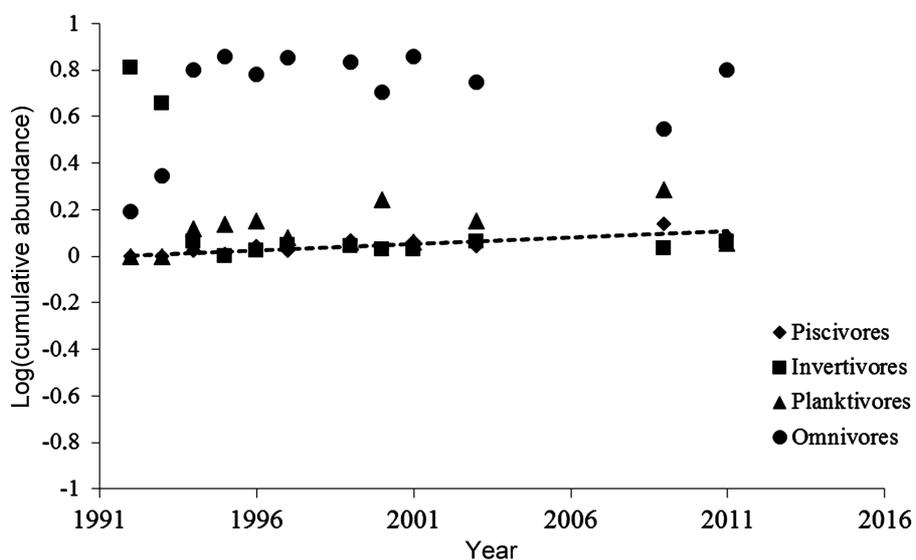
Fig. 10. Trends in the relative abundance of trophic guilds in Lake Fenéki (Piscivores: y = 0.06 + 0.003x; R^2 = 0.757; P > 0.00001)

trends in diversity estimates suggest that the gibel carp invasion did not influence the colonization of native fish species extremely.

The development of fish assemblage structure can be divided to three stages. The first stage (marsh phase; 1992–1993) could be characterized by bog-dwelling species (Mud-minnow and Crucian carp), which survived in draining channels formerly located in the study area. The transition between the first and second stage was fast and dramatic, but this could be considered usual in such modified, disturbed and artificial waterbodies (SEDA & KUBECKA 1997, WOLTER 2001).

The second phase (invasion phase), characterized by the constant high relative abundance of gibel carp, lasted from 1994–2001. The fast expansion of this species has often been reported not only from artificial and disturbed waters (GAYGUSUZ et al. 2007, MARKOVIC et al. 2007, PAULOVITS et al. 1998), but from natural waters, as well (TARKAN et al. 2012b, VETEMAA et al. 2005). Numerous hypotheses were described as the reason for this fast invasion, for example a special oxygen-deficit tolerance mechanism (LUTZ & NILSSON 1994), omnivorous feeding (BALIK et al. 2003, SPECZIÁR et al. 1997), effective predator avoidance (GERE & ANDRIKOVICS 1991), and an alternative gynogenetic spawning strategy (BEUKEBOOM & VRIJENHOEK 1998; KALOUS et al. 2004). Few comparative datasets are available regarding the magnitude and duration of such gibel invasions. MARKOVIC et al. (2007) investigated the fish assemblage changes in the Gruza Reservoir (Serbia), and still found high (>40%) gibel carp relative abundance after 20 years. A constantly increasing gibel population has been examined in the Ömerli Reservoir (Turkey), between 2002 and 2007 (TARKAN et al. 2012b).

After the year 2001, a notable decrease in gibel carp abundance and in parallel an increase of native roach and bleak populations have occurred. The reason of the collapse of the gibel carp invasion has not been clarified yet, since the selective fishing of the species for nature conservation purposes started only in 2004, three years after the decrease (MAGYARI 2009). The fish assemblage structure after the second transition (stabilization phase) corresponds well with the last stage of successive process described by KUBECKA (1993). This phase is usually characterized by the dominance of cyprinids, mostly roach (RIHA et al. 2009, SCHARF 2008, SEDA & KUBECKA 1997).

Our results suggest that among non-natives, only gibel carp reached as much relative abundance, which probably could affect fish fauna development significantly. The most serious qualitative impact of the gibel carp invasion has been the displacement of the native congener, Crucian carp. This process has long been hypothesized (LELEK 1980, TARKAN et al. 2009), and the possible mechanisms described, such as hybridization (HAENFLING et al. 2005, TÓTH et al. 2005) and re-

productive/interference competition. As mentioned above, gibel carp is known to exhibit gynogenetic reproductive strategy, exploiting the males of other species to activate egg development (BEUKEBOOM & VRIJENHOEK 1998, KALOUS *et al.* 2004, TARKAN *et al.* 2012*a,b*).

Regarding the process of fish fauna succession, although the dominance of gibel carp lasted for a decade, the recent assemblage structure of Lake Fenéki is considered to have become more and more similar to the fauna of the reed habitats of Lake Balaton (ERŐS *et al.* 2009), which could be used as a natural reference point.

In conclusion, the most significant impact of the gibel carp invasion was the displacement of native Crucian carp. Although the magnitude of invasion was high, it only was able to delay the natural successive process, not completely transform it.

*

REFERENCES

ARNELL, N. W. (1998) Climate change and water resources in Britain. *Climatic Change* **39**: 83–110.

BALIK, I., KARASAHIN, B., ÖZKÖK, R., CUBUK, H. & UYSAL, R. (2003) Diet of silver crucian carp (Carassius gibelio) in Lake Egirdir, Turkey. *Turkish Journal of Fisheries and Aquatic Sciences* **3**: 87–91.

BALON, E. K. (1981) Additions and amendments to the classification of reproductive styles in fishes. *Environmental Biology of Fishes* **6**: 377–389.

BEUKEBOOM, L. W . & VRIJENHOEK, R. C. (1998) Evolutionary genetics and ecology of sperm-dependent parthenogenesis. *Journal of Evolutionary Biology* **11**: 755–782.

BÍRÓ, P. & PAULOVITS, G. (1994) Evolution of the fish fauna in Little Balaton Water Reservoir. *Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie* **25**: 2164–2168.

CHRISTENSEN, N. S., WOOD, A. W., VOISIN, N., LETTENMAIER, D. P. & PALMER, R. N. (2004) The effects of climate change on the hydrology and water resources of the Colorado river basin. *Climatic Change* **62**: 337–363.

ERŐS, T., TÓTH, B., SEVCSIK, A. & SCHMERA, D. (2008) Comparison of fish assemblage diversity in natural and artificial rip-rap habitats in the littoral zone of a large river (River Danube, Hungary). *International Review of Hydrobiology* **93**(1): 88–105.

ERŐS, T., SPECZIÁR, A. & BÍRÓ, P. (2009) Assessing fish assemblages in reed habitats of a large shallow lake – A comparison between gillnetting and electric fishing. *Fisheries Research* **96**: 70–76.

GAYGUSUZ, Ö , TARKAN, A. S. & GÜRSOY GAYGUSUZ, C. (2007) Changes in the fish community of the Ömerli Reservoir (Turkey) following to introduction of non-native gibel carp Carassius gibelio (Bloch, 1782) and other human impacts. *Aquatic Invasions* **2**: 117–120.

GERE, G. & ANDRIKOVICS, S. (1991) Untersuchungen über den Ernährungsbiologie des Kormorans (Phalacrocorax carbo sinensis) sowie deren Wirkung auf den trophishen Zustand des Kisbalaton. *Opuscula Zoologica, Budapest* **24**: 115–127.

GIDO, K. B., MATTHEWS, W. J. & WOLFINBARGER, W. C. (2000) Long-term change in a reservoir fish assemblage: Stability in an unpredictable environment. *Ecological Applications* **10**(5): 1517–1529.

GIDO, K. B., SCHAEFER, J. F. & FALKE, J. A. (2009) Convergence of fish communities from the littoral zone of reservoirs. *Freshwater Biology* **54**: 1163–1177.

HAENFLING, B., BOLTON, P., HARLEY, M. & CARVALHO, G. R. (2005) A molecular approach to detect hybridisation between crucian carp (Carassius carassius) and non-indigenous carp species (Carassius spp. and Cyprinus carpio). *Freshwater Biology* **50**: 403–417.

HAMMER, O., HARPER, D. A. T. & RYAN, P. D. (2008) PAST – Palaeontological Statistics. Version 1. 81, Available at: http://folk.uio.no/ohammer/past (last accessed 15.04.2012).

HATVANI, I. G., KOVÁCS, J., KOVÁCSNÉ, SZ, I., JAKUSCH, P. & KORPONAI, J. (2011) Analysis of long-term water quality changes in the Kis-Balaton Water Protection System with time series-, cluster analysis and Wilks' lambda distribution. *Ecological Engineering* **37**: 629–635.

HAVEL, J. E., LEE, C. E. & VANDER ZANDEN, M. J. (2005) Do reservoirs facilitate invasions into landscapes? *BioScience* **55**(6): 518–525.

HLADIK, M., KUBEČKA, J., MRKVIČKA, T., ČECH, M., DRAŠTIK, V., FROUZOVA, J., HOHAUSOVA, E., MATĚNA, J., MATĚNOVA, V., KRATOCHVIL, M., PETERKA, J., PRCHALOVA, M. & VAŠEK, M. (2008) Effects of the construction of a reservoir on the fish assemblage in an inflow river. *Czech Journal of Animal Sciences* **53**(12): 537–547.

JOHNSON, P. T. J., OLDEN, J. C. & VANDER ZANDEN, M. J. (2008) Dam invaders: impoundments facilitate biological invasions into freshwaters. *Frontiers in Ecology* **6**(7): 357–363.

KALOUS, L., DEVRIN, M. & BOHLEN, J. (2004) Finding of triploid Carassius gibelio (Bloch, 1780) (Cypriniformes, Cyprinidae) in Turkey. *Cybium* **28**: 77–79.

KORPONAI, J., BRAUN, M., BUCZKÓ, K., GYULAI, I., FORRÓ, L., NÉDLI, J. & PAPP, I. (2010) Transition from shallow lake to a wetland: a multi-proxy case study in Zalavári Pond, Lake Balaton, Hungary. *Hydrobiologia* **641**: 225–244.

KOVÁCS, J., HATVANI, I. G., KORPONAI, J. & KOVÁCSNÉ, SZ. I. (2010) Morlet wavelet and auto-correlation analysis of long term data series of the Kis-Balaton Water Protection System (KBWPS). *Ecological Engineering* **36**: 1469–1477.

KUBECKA, J. (1993) Succession of fish communities in reservoirs of Central and Eastern Europe. Pp. 153–168. *In:* STRASKRABA, M., TUNDISI, J. G. & DUNCAN, A. (eds): *Comparative reservoir limnology and water quality management.* Kluwer Academic Publishers Group, Amsterdam.

LELEK, A. (1980) *Threatened freshwater fishes of Europe. Nature and Environment Series No. 18.* Council of Europe, Strasbourg, 269 pp.

LOTZ, G. (1988) A Kis-Balaton Vízvédelmi Rendszer. (The Kis-Balaton Water Protection System.] *Hidrologiai Tájékoztató* **10**: 20–22. [in Hungarian]

LUTZ, P. L. & NILSSON, G. E. (1994) *The brain without oxigen, causes of failure and mechanisms for survival.* R. G. Landes Company, Austin, pp. 49–63.

MAGYARI, M. (2009) A természetmegőrzési célú természetesvízi halgazdálkodás lehetőségei a Kis-Balatonon – Possibilities of nature conservation aimed fishery in Kis-Balaton Waterquality Protection System, MSc Thesis, University of Kaposvár, 77 pp.

MARKOVIC, G., LENHARDT, M. & GACIC, Z. (2007) Successions of the ichtyofauna in an eutrophic Serbian reservoir. *Acta Ichtyologica Romanica* **2**: 151–160.

PAULOVITS, G., TÁTRAI, I., KÁLMÁN, M., KORPONAI, J. & KOVÁTS, N. (1998) Role of Prussian carp (Carassius auratus gibelio Bloch) in the nutrient cycle of the Kis-Balaton Reservoir. *International Review of Hydrobiology* **83**: 467–470.

PENCZAK, T., Głowacki, L., Galicka, W. & KOSZALINSKI, H. (1998) A long-term study (1985–1995) of fish populations in the impounded Warta River, Poland. *Hydrobiologia* **368**: 157–173.

PODANI, J. (2000) *Introduction to the exploration of multivariate biological data*. Backhuys, Leiden, 407 pp.

POMOGYI, P. (1993) Nutrient retention by the Kis-Balaton Water Protection System. *Hydrobiologia* **251**: 309–320.

RIHA, M., KUBECKA, J., VASEK, M., SEDA, J., MRKVICKA, T., PRCHALOVA, M., MATENA, J., HLADIK, M., M. CECH, M., DRASTIK, V., FROUZOVA, J., HOHAUSOVA, E, JAROL, O., JUZA, T., KRATOCHVIL, M., PETERKA, J. & TUSER, M. (2009) Long-term development of fish populations in the Rimov Reservoir. *Fisheries Management and Ecology* **16**: 121–129.

SCHARF, W. (2008) Development of the fish stock and its manageability in the deep, stratifying Wupper Reservoir. *Limnologica* **38**: 248–257.

SEDA, J. & KUBECKA, J. (1997) Long-term biomanipulation of Rimov Reservoir (Czech Republic). *Hydrobiologia* **345**(2–3): 95–108.

SMOKOROWKSI, K. E. & KELSO, J. R. M. (2002) Trends in fish community structure, biomass, and production in three Algoma, Ontario, lakes. *Water, Air, and Soil Pollution: Focus* **2**: 129–150.

SPECZIÁR, A., TAKÁCS, P., CZEGLÉDI, I. & ERŐS, T. (2012) The role of the electrofishing equipment type and the operator in assessing fish assemblages in a non-wadeable lowland river, *Fisheries Research* **125–126**: 99– 107.

SPECZIÁR, A., TÖLG, L. & BÍRÓ, P. (1997) Feeding strategy and growth of cyprinids in the littoral zone of Lake Balaton. *Journal of Fish Biology* **51**: 1109–1124.

TARKAN, A. S., COPP, G. H., ZIEBA, G., GODARD, M. J. & CUCHEROUSSET, J. (2009) Growth and reproduction of threatened native crucian carp Carassius carassius in small ponds of Epping Forest, south-east England. *Aquatic Conservation: Marine and Freshwater Ecosystems* **19**: 797–805.

TARKAN, A. S., COPP, G. H., TOP, N., ÖZDEMIR, N., ÖNSOY, B., BILGE, G., FILIZ, H., YAPICI, EKMEKCI, F. G., KIRANKAYA, S. G., EMIROGLU, Ö., GAYGUSUZ, Ö., GÜRSOY GALGUSUZ, C., OYMAK, A., ÖZCAN, G. & SAC, G. (2012*a*) Are introduced gibel carp Carassius gibelio in Turkey more invasive in artificial than in natural waters? *Fisheries Management and Ecology* **19**(2): 178–187.

TARKAN, A. S., GAYGUSUZ, Ö., GÜRSOY GAYGUSUZ, C., SAC, G. & COPP, G. H. (2012*b*) Circumstantial evidence of gibel carp Carassius gibelio reproductive competition exerted on native fish species in a mesotrophic reservoir. *Fisheries Management and Ecology 19(2): 167–177.*

TÁTRAI, I., KÁLMÁN, M., KORPONAI, J., PAULOVITS, G. & POMOGYI, P. (2000) The role of the Kis-Balaton water protection system in the control of water quality of Lake Balaton. *Ecological Engineering* **16**: 73–78.

TÓTH, B., VÁRKONYI, E., HIDAS, A., EDVINÉ MELEG, E. & VÁRADI, L. (2005) Genetic analysis of offspring from intra- and interspecific crosses of Carassius auratus gibelio by chromosome and RAPD analysis. *Journal of Fish Biology* **66**: 784–797.

VETEMAA, M., ESCHBAUM, R., ALBERT, A. & SAAT, T. (2005) Distribution, sex ratio and growth of Carassius gibelio (Bloch) in coastal and inland waters of Estonia (north-eastern Baltic Sea). *Journal of Applied Ichthyology* **21**: 287–291.

WILLIAMSON, C. E., SAROS, J. E., VINCENT, V. F. & SMOL, J. P (2009) Lakes and reservoirs as senti-
    nels, integrators, and regulators of climate change. *Limnology and Oceanography* **54**(6):
    2273–2282.
WOLTER, C. (2001) Rapid changes of fish assemblages in artificial lowland waterways. *Limnologica*
    31: 27–35.