Role of invasive and non-native fish species in the Balaton-catchment

PhD thesis

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IDEGENHONOS HALAK HELYE ÉS SZEREPE A BALATON-VÍZGYŰJTŐ ÖKOSZISZTÉMÁJÁBAN

Írta:
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Témavezető 1.: Dr. Kováts Nóra

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……
Az EDHT elnöke

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Abbreviations

ANI: Assemblage Naturalness Index

Arcsin-sqrt: arcus sinus-square root

AUC: Area Under the (ROC) Curve

CART: Classification and Decision Trees

DC: Direct current

DDT: Dichlore Diphenyl Trichlore-ethane

ERA: Ecological Risk Assessment

FISK I.: the version 1.19 of FISK

FISK II.: the version 2.03 of FISK

FISK: Fish Invasiveness Scoring Kit

GIS: Geographical Information System

H: Hypothesis

KBWPS: Kis-Balaton Waterquality Protection System

log: logarithm (10 based)

OLS: Ordinary Least Squares

PA: Presence/Absence

PCA: Principal Components Analysis

RA: Relative abundance

RDA: Redundancy Analysis

ROC: Recievers Opearating Curve

S: Number of Species

YOY: Young of the year

PEC: Predicted Environmental Concentration

PNEC: Predicted No Effect Concentration

Abstract

The fish assemblage of major lentic habitats of the Balaton catchment were analysed in the first study of this theses, including local environmental parameters and land use variables in order, to find relationships between these variables and the distribution and abundance of non-indigenous fish species. The studies have led to the conclusion that although at least one non-indigenous fish species was present in every examined site, the abundance of non-natives and also the deviation of the fish fauna from the natural state is the highest in the wetlands and the fish ponds under operation. Periodical dry-outs could be highlighted from the explanatory variables, which seemed to have positive relationships with the abundance of non-natives, especially with gibel carp (*Carassius gibelio*).

The long-term (1992-2011) changes of fish assemblage in the Lake Fenéki (Kis-Balaton Waterquality Protection System) were analysed in the second study, in order to assess the effects of the gibel carp invasion, which occurred after the impoundment. Although the invasion affected negatively the native assemblage, especially crucian carp (*Carassius carassius*) - which was completely outcompeted - the increase in the number of species and in diversity was not influenced in the examined period. Successive change in the fish assemblage was detected, however it showed a completely different pattern than former literature had indicated was from reservoirs of Central-Europe. Three phases were identified in the fauna development: a (1.) marsh phase, a (2.) invasion phase and a (3.) stabilization phase, instead of the formerly described 5 stages.

An Ecological Risk Assessment of non-indigenous species was conducted in the third study of this thesis, using the Fish Invasiveness Scoring Kit (FISK). Four of the 12 recently occurring non-native species were highlighted as of ‘high risk’ or invasive species, after the calibration of the method to the local conditions, from which gibel carp is considered to be the most dangerous, characterized by the highest score. Validation of the methodology was also carried out using the cumulative relative abundance and frequency of occurrence data, but no significant relationships have been found.

Kivonat

Az értekezés első vizsgálatában a Balaton-vízgyűjtő jelentősebb állóvízi élőhely-típusait elemezte a szerző a halállomány össztétele, a helyi szinten ható környezeti tényezők, és a terület használatát jellemző változók bevonásával, legfőképpen arra keresve a választ, hogy mely tényezők befolyásolják leginkább az idegenhonos halfajok elterjedését. A szerző megállapította, hogy bár minden vizsgált élőhelyen előfordult legalább egy idegenhonos faj, a fauna természetessége a működő halastavakban és a vizsgált berekterületeken a legkisebb, az idegenhonos fajok relatív abundanciája ugyanitt a legnagyobb. A vizsgált magyarázó változók közül kiemelendő, szignifikáns ható tényező az élőhely kiszáradása, amellyel úgy tűnik az idegenhonos fajok, de különösen az ezüstkárász (*Carassius gibelio*) tömegessége pozitív kapcsolatban van.

Az értekezésben bemutatott második vizsgálat a Kis-Balaton Vízminőség-védelmi Rendszer Fenéki-taván hosszú-távú (1992-2011) halállomány-összetétel dinamikai elemzésével foglalkozik, vizsgálja az ott lezajlott ezüstkárász-invázió hatásait. Ez a kutatás rávilágított arra, hogy bár az ezüstkárász invázió negatívan hatott a területen korábban előforduló őshonos faunaelemekre, teljesen kiszorította a széles kárászt (*Carassius carassius*), a frissen elárasztott víztározóban nem gátolta a fajszám és diverzitás növekedését a vizsgált időszakban. Megállapításra került, hogy a tározóban a halfauna szukcesszíven változott, de a folyamat nem volt megfeleltethető a közép-európai víztározók esetére korábban leírt modellnek. A korábban meghatározott öt fázis helyett csak hármat lehetett elkülöníteni: (1.) a lápi fázist; (2.) az inváziós fázist és (3.) a stabilizációs fázist.

A harmadik vizsgálatban a Fish Invasiveness Scoring Kit (FISK) segítségével került értékelésre a Balaton-vízgyűjtőn recensen megtalálható idegenhonos halfajok ökológiai kockázata. A módszer helyi viszonyokra való kalibrálása után megállapítható volt, hogy a 12 előforduló idegenhonos faj közül 4 sorolandó a magas kockázatú, invazív kategóriába, ezek közül is kiemelendő az ezüstkárász, amely a legmagasabb pontszámot kapta. A módszer validálásra is került: az első vizsgálatból származó kumulatív relatív abundancia és előfordulási gyakoriság adatok korrelációvizsgálata a FISK elemzésekből származó pontszámokkal megtörtént, de szignifikáns összefüggés nem mutatkozott.

Auszug

In der vorlegenden Dissertation analysieren wir die signifikanten Lebensraum-type von stehendes Gewässer von dem Einzugsgebiet des Plattensees mit die Verwendung variablen der Fischvorräte, der lokalen Umgebungsfaktoren und der Landnutzung, hauptsächlich um eine Antwort zu finden, welche Variablen die Verbreitung von nicht-heimische Fischarten meist beeinflussen. Unsere Erkennungen zeigten darauf zu, dass obwohl in Fall jeder geprüften Lebensraum mindestens eine die nicht-heimische Fischarte vorkommt, die Natürlichkeit der Fauna ist bei aktive Fischteichen und Haingebiete die Minderwertigste, die relative Abundanz der nicht-heimischen Fischarte hier jedoch die größte ist. Von die geprüften Erklärungsvariablen scheint die Austrocknung des Lebensraumes eine signifikante positive Verbindung mit der Masse die nicht-heimischen Arte, insbesondere mit der Masse des Giebels (*Carassius gibelio*) zu zeigen.

In unserer zweiten Untersuchung führten wir die langfristige Analyse der Dynamik der Fischbesatz-Zusammensetzung an Fenéki-teich des Kis-Balaton Wasserschutzsystems durch, untersuchten die Effekte der dort abgegangenen Giebel-Invasion. Diese Untersuchung zeigte, dass zwar die Giebel-Invasion ein negativer Einfluss auf die an diesem Gebiet früher vorkommenden Fauna Elemente hatte, völlig verdrängte den Bauernkarpfen (*Carassius carassius*), in fall der kürzlich überfluteten Reservoir inhibierte es nicht die Zunahme der Artenanzahl und Diversität in der Betrachtungszeitraum. Unsere Ermittlungen zeigten, dass die Fischfauna zeigte sukzessive Änderungen in Fall der Wasserspeicher, jedoch, der Ablauf des Prozesses passte in die früher für Mittel-Europäische Wasserspeicher vorgelegte Modelle nicht ein. Wir könnten nur 3 der früher definierte 5 Phasen trennen: (1.) Sumpf Phase; (2.) Invasionsphase; (3.) Stabilisationsphase.

In unserer dritten Untersuchung analysierten wir den Risikofaktor die im Plattensee Einzugsgebiet befindliche nicht-heimische Fischarten mit der Hilfe des Fish Invasiveness Scoring Kit (FISK). Nach der Kalibration der Methode zur Lokalverhältnisse haben wir festgestellt, dass 4 von 12 hervorkommende Fischrassen bedeuten ein großes Risiko, können als Invasiv klassifiziert werden. Unter diesen ist der Giebel ausprägend, mit der höchsten Punktzahl. Wir führten auch die Validierung der Methode durch: die kumulative Relativabundanz-, und Häufigkeitsdaten von unsere erste Untersuchung wurden mit Punktzahle des FISK-analyse vergleicht, jedoch eine signifikante Korrelation war nicht feststellbar.

1. Introduction

The problem of non-indigenous species and biological invasion has been widely discussed since the book entitled „*The Ecology of Invasions by Animals and Plants"* by Elton (1958) was published. In recent times, biodiversity of freshwaters has been decreasing at an alarming rate, faster than in terrestrial ecosystems (Dudgeon et al. 2006). In this process, exotic and invasive species were the second leading cause after habitat destruction and fragmentation (Rainbow 1998, Williamson 1999, Erős 2007). Freshwaters are considered as the most invaded habitats by alien species in the world (Cohen 2002). Biological invasions may cause not only ecological cataclysms, but also heavy economical costs (Pimentel et al. 2000, Perrings et al. 2002). These species can disturb native communities in many ways, e.g. by hybridization, competition, predation or parasitic interactions, either directly or indirectly (e.g.: Carmona-Catot et al. 2013, Kreps et al. 2012, Emde et al. 2012, Wouters et al. 2012, Preston et al. 2012). These effects are generally difficult to measure in economical terms, however the cost of defense against invasive species or the loss in the yields of agricultural product is increasing (Oreska and Aldridge 2011, Scalera 2010).

The introduction of fish species is a common phenomenon worldwide since the ancient Roman times, due to numerous reasons, such as aquaculture utilization or aquarium rearing (Balon 1995, Strecker et al. 2011). Although the generally negative effect of such introductions have been recognised, the number of intentional introductions (and the additional accidental ones) most probably will not show decreasing tendency, due to the increasing protein-need of the human population (Casal 2006).

In Hungary, exotic species have reached 25% ratio in the ichtyofauna (Harka and Sallai 2004), which is one of the highest ratios in Europe (Economidis et al 2000, Copp et al. 2006, Lusk et al 2010, Leunda 2010) but there is only scarce usable ecological or even up to date distribution information about the species. The need for and the significance of such studies is growing in parallel with the developing EU regulation on the prevention and management of the introduction and spread of invasive alien species (European Commision 2013).

In my opinion, the chance of controlling such an invasion, given the recent level of general knowledge, is limited. Hence, studies on the role of non-indigenous fish species in our waters and revealing the factors limiting or affecting their distribution patterns are needed.

Lake Balaton with its catchment is one of the most important and prominent regions of Hungary. Not only in the view of its natural heritage and beautiful landscapes, but also in its economical role. As the economic consequences of the spread of non-native species have been growing, he most detailed understanding of their present status is of high priority.

1.1 Aims

1. In the first part of my thesis, the status of non-indigenous species in the Balaton catchment was analyzed to:

1.1: describe the distribution patterns of non-indigenous species in the typical lentic habitats of the catchment.

1.2: reveal whether there are any spatial patterns in the distribution of non-native species in species composition or at assemblage structure level.

1.3: reveal the role of environmental and land use parameters in affecting the patterns of non-indigenous fish abundances.

2. The second main objective was an invasion scenario analysis of gibel carp (*Carassius gibelio*) in the Kis-Balaton Waterquality Protection System (KBWPS), regarding:

2.1 the temporal patterns in the change of fish assemblage structure between 1992 and 2011.

2.2 the effect of gibel carp invasion on the qualitative (species) composition of the native fish assemblage.

2.3. the effect of gibel carp invasion on the successive processes of the fish assemblage.

3. In the third study, the asymmetric adverse effect of non-natives was quantified using an Ecological Risk Assessment Protocol, based on recent information on the distribution and assemblage level role of non-natives. In this analysis:

3.1 the risk posed by non-indigenous fish species was quantified using the FISK (Fish Invasiveness Scoring Kit) algorithm.

3.2. the FISK was calibrated for the Balaton-catchment.

3.3 the FISK was validated for the catchment using relative abundance and frequency of occurrence data.

3.4 the results of the original (FISK v1.19) and revised (FISK v2.03) versions of FISK were compared.

4. In the fourth study, numerous sites were surveyed in the Balaton-catchment between 2011 and 2013. Five of these sites are wetlands ("berek") being situated by the southern shoreline of the lake and are under the Ramsar convention and members of Natura2000 network. Prior to our studies, the fish fauna of these habitats was almost unknown, hence my objective was to provide the first ichtyofaunistic data from these areas.

1.2 Definitions

The most important definitions of terms, which are used in the thesis are described and explained here:

Biological invasion: Successful establishment and spread of species outside their native range (Facon et al. 2006).

Invasive species: This definition is considered the most complicated and diverse one, thus here we present three formulations: (1) species with strictly monotonously expanding population (abundance) size at a given locality (Botta-Dukát et al. 2004). (2) A non-indigenous species that spreads from the point of introduction and becomes abundant (Richardson et al. 2000, Kolar and Lodge 2001). (3) Indigenous or non-indigenous species which spreads with or without the aid of humans, in natural or semi-natural habitats, producing a significant change in composition, structure or ecosystem processes or causing severe economic loss to human activity (Copp et al. 2005a). In my opinion spreading of a species without any kind of human help (for example building a canal between two river basins) is area expansion, not invasion.

Established species: a species with self-sustaining population, outside of its native range (Richardson et al. 2000, Kolar and Lodge 2001)

Indigenous species: a species found within its native range (Richardson et al. 2000, Kolar and Lodge 2001)

Non-indigenous species (=alien species, non-native species): a species introduced to areas beyond its native range by human activity (Richardson et al. 2000, Kolar and Lodge 2001)

Non-invasive species: a non-indigenous species that remains localized within its new environment (Richardson et al. 2000, Kolar and Lodge 2001)

Transition: One step in the invasion process (Richardson et al. 2000, Kolar and Lodge 2001)

Casual species: a species, which is introduced, but unable to sustain its presence without human intervention (Copp et al. 2005a), despite the ability to reproduce in the novel environment (Richardson et al. 2000).

Decision tree: Type of tree diagram used in determining the optimal strategy of action, in situations having several possible alternatives with uncertain outcomes. The resulting chart or diagram (which looks like a cluster of tree branches) displays the structure of a particular

decision, and the interrelationships and interplays between different alternatives, decisions, and possible outcomes (Snyder et al. 2012)

Ecological Risk Assessment (ERA): Estimates the likelihood of negative impact of a given stressor (here: non-indigenous species) on a recipient (here: ecosystem).

Introduction: is the deliberate (intentional) or unintentional (accidental) transfer and/or release, by direct or indirect human agency, of an organism into the wild, or into locations not completely isolated from the surrounding environment, by humans in geographical areas where the given taxon is not native. This applies to translocations within and between political states (countries) (Copp et al. 2005a).

2. Literature review

2.1 The biological invasion as a process

Biological invasion is a complex process. There are some more or less distinguishable phases or stages in the scenario (Kolar and Lodge 2001, Sakai et al. 2001, Heger and Trepl 2003). The stages are not rigid; they could also be described as a continuum (Williamson 2006). No real consensus in the literature can be found about the names and principally the definitions of the phases, hence, here we introduce one sequence of stages based on a review of fish invasions (Garcia-Berthou 2007):

1. Transport to a new geographical region
2. Escape or release to the wild
3. Establishment
4. Dispersal or spread
5. Interaction or integration (becoming a problem)

The probability of a transition between stages is low. It is generally argued that only 1% of the incoming species are able to become invasive. This phenomenon is named “The Rule of Tens” (or the Tens Rule) (Williamson and Brown 1986, Williamson and Fitter 1996). The rule was first realized by the study of plant invasion in Great-Britain, but the adaptability to other cases was revealed (Richardson and Pysek 2006). Recent papers, however, suggest that the vulnerability of freshwater ecosystem is considered higher, therefore introduction risk estimates from the Tens Rule are not reliable (Lapointe et al. 2012, Jaric and Cvijanovic 2012)

There is no recipe or general rule for a species to make each transition. A characteristic feature which enables or helps a successful transition can be a disadvantage, or even defeat for another (Kolar and Lodge 2001).

2.2 Possible mechanisms of an invasion

As cited above, the general characteristics of invasive species could not yet been identified, but some mechanism of an invasion could be characterized (Kolar and Lodge 2001). Two major sorts of goals could be identified in research papers searching for the general causes of invasions: (1) What enables a species to became an invader or a community to be invaded? (2) Comparison of successful and failed introductions in order to find a definitive list of characters that define a good invasion strategy or a vulnerable community (Facon et al. 2006). In spite of dozens of studies, carried out by the leading invasion biologists, these approaches failed (or only partly worked), because they focused separately either on the properties of the invaders or the communities (Alcaraz et al. 2005, Olden et al. 2006). Invasions mean matches or interactions between the species and ecosystems (Shea and Chesson 2002). A non-indigenous species is able to displace a native one due to two kinds of reasons: (1) It has 'a priori' natural pre-adaptations to exploit particular environments. In such cases, invasion is only limited by migration abilities (Allendorf and Lundquist 2003). (2) If there are no 'a priori' adaptations, some eco-evolutionary changes are needed (Lee 2002, Lambrinos 2004). With the combinations of these mechanism types, Facon et al. (2006) described a migration-based conceptual framework which could be useful to understand the invasion processes. They described three theoretical invasion scenarios:

(1) Migration change. According to this scenario, the pre-existing match between the invading organism and environment is essential. After a rapid change in the migration regime (eg. human help), the introduced species becomes capable of spreading in the new environment. Species with low natural migration abilities belong to this scenario. In the new environment, the invasive species performs better than natives, due to the reasons which are collectively discussed in the "enemy release hypothesis". Shortly, it means that invading species benefit from the lack of specific native or natural enemies (Elton 1958, Keane and Crawley 2002).

(2.) Environmental change. This scenario becomes possible, when there are no migration limits and a new match between the environment and the organism occurs due to environmental change. In such situations, it is difficult to separate whether the event is invasion or range expansion. There are three potential types of environmental changes: (1) climate change (subtypes: natural and human induced), (2) human induced local scale

disturbances, and (3) the case when an already running invasion process opens the door for another alien species (invasion meltdown) (Simberloff and Von Holle 1999).

(3.) Evolutionary change. The invasion starts with an internal change in the genom of the presumptive invader. It can be a simple mutation or even evoked by different evolutionary forces. This scenario occurs with high likelihood, if the founder population of the introduced species is small. In this case, genetic variation is low, which enables genetic drift and sometimes the population can gain evolutionary potential from this. In another situation, genetic variation can be increased by multiple introductions from spatially distant source populations. Higher genetic diversity sometimes results in a new invasive lineage (Facon et al. 2006).

2.3 Human modified aquatic habitats: seedbeds of invasions

2.3.1 Biological invasions in disturbed watersheds

Successful biological invasions involve complex interactions between the invading species and the recipient habitats (Hayes and Berry 2008). Biologists noticed a long time ago that certain regions and habitats appear to be particularly susceptible to invasions and several hypotheses have been constructed in order to find general rules (Marchetti et al. 2006). Site characteristics suggested to favor successful invasion include (1) similar environment to the native range of invader, (2) low to moderate environmental variability, (3) high degree of disturbance, especially by human activity, and (4) low native species richness (Elton 1958, Lodge 1993).

However, many species may get established in one habitat but fail to invade adjoining areas despite continous opportunity. By examining such an invasion on landscape or even catchment scale, we may be able to determine the reasons of their success or failure in given habitats, and afterwards, implement management efforts and make predictions regarding similar systems (Light 2003). According to the traditional view, the increasing intensity or frequency of disturbance facilitate invasions (Elton 1958, Moyle and Light 1996, Hierro et al. 2006, Johnson et al. 2008). However, some recent regional-scale studies indicated the inverse effect of disturbances. For example, Light (2003) found negative correlation between the occurrence of wet years and the abundance of the invasive signal crayfish (*Pacifastacus lenisculus)* in the Tucknee River basin (USA, California), and concluded that unpredictable

flow regime and occurrence of heavy floods affect negatively the abundance of the crayfish. Similarly negative effect of hydrological disturbance on invasion success of brown trout *(Salmo trutta* L.) was found in the Manuherikia catchment (New-Zealand) (Leprieur et al. 2006). These and similar results imply that disruption of natural disturbance regimes will increase the likelihood of successful invasions (Moret et al. 2006).

The effect of local and landscape variables on the distribution and assembly of native and non-indigenous fish species and assemblages in the streams of the Balaton-catchment were examined by Sály et al. (2011) and Sály (2013). These studies, in contrary to the former results of Wang et al. (2003) concluded that local variables have a higher role in predicting assemblage patterns than landscape variables. The pattern explaining power of local environmental variables have been negatively affected by the non-indigenous species, however on the other hand, they concluded that the effect of landscape variables on fish assemblages depended strongly on the level of disturbance, even though the types and level of disturbances were not exactly assessed.

2.3.2 Long-term fish fauna development and invasion scenario analysis in reservoirs

The importance of long-term (>10 years) research in fish ecology is unquestionable, but only relatively few such papers are available (Smokorowski and Kelso 2002). The importance of reservoirs is growing all over the world, in parallel with the expansion of the human population and increasing demand for energy or drinking water. (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 and Kubecka 1997), the relevance of reservoir studies is not 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 their deep and oligotrophic representatives (Gido et al. 2000, Riha et al. 2009). Their assemblage structure changes are 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) riverine species phase; (2) pike (*Esox lucius* L.) phase; (3) perch (*Perca fluviatilis* L.) phase; (4) transient perch-cyprinid phase; and (5) cyprinid-dominated phase. These studies

(e.g.: Hladík et al. 2008, Riha et al. 2009), even though some of them are quite recent, do not deal with the role of invasive species in such processes. Although numerous studies demonstrate the connection between the disturbance and invasibility even in the case of reservoirs (Havel et al. 2005, Johnson et al. 2008, Tarkan et al. 2012a), limited amount of data is available on the assemblage structuring function of an invasive species throughout longer periods.

2.4 Ecological Risk Assessment of non-indigenous species

Risk analysis has originally been used for the assessment of human health risk and typically restricted to hazard identification and dose-response measurements (Stohlgren and Schnase 2006). Risk assessment has also been used to quantify the consequences of (mainly chemical) contaminants, for example the effect of DDT on different bird species was assessed (Ratcliff 1967). In the 1990s, the basic concepts of risk analysis were used more frequently in the assessments of ecological risks (Stohlgren and Schnase 2006). Non-indigenous species can be considered as such ecological hazards, since their occurrence might cause damage or extinction of native communities or species. In risk assessment protocols designed for chemicals, the risk is defined as the ratio of the predicted environmental concentration (PEC) to the predicted no effect concentration (PNEC). In case of biological stressors, this ratio is incalculable, while the exposure might increase (or even fluctuate) in time and/or in space for example by migration and reproduction. These special features require special algorithms, protocols designed for the screening and assessment the role of non-indigenous species.

In many cases, the risk associated with already established non-indigenous species should also be assessed (retrospective assessment). On local scale, risk of dispersion from one habitat to another can be an issue of key importance, especially when there is any risk management option available to control within-country dispersal. The negative effect of non-indigenous species (also within the invasive category) is strongly asymmetric. Retrospective ecological risk assessment (ERA) might be able to make such differentiations between the species introduced formerly.

2.4.1 Protocol types

There are five commonly used types of risk assessment protocols, dealing with non-indigeous species: scoring systems, decision-tree models, combination of scoring-decision-tree systems, probabilistic models and niche modelling.

2.4.1.1 Scoring systems

Scoring systems prioritize the risk or threat posed by non-indigeous species. Scores are assigned based on the answers to a series of questions about the species, such as: species biology and ecology; potential to arrive, establishment and spread in an area; and potential impact on the invaded environment. Scores assigned to individual questions are combined in some manner, typically by addition or multiplication, by taking the mean or an extremum of sub-scores or by a combination of these to come up with an overall score for the species. An uncertainty rank is often assigned to the score for each question. These scores can then generate a prioritized list of high to low priority species and indicate the certainty associated with each score.

Scoring systems can be used for screening in both introduced/established and not yet introduced situations. Species that receive a score below a given threshold may be deemed to pose such a sufficiently low risk that no management actions, preventative measures or prohibitions on importation are necessary. Alternatively, a high score may indicate that preventative measures or prohibitions are necessary (Snyder et al. 2012).

2.4.1.2 Decision-tree models

A decision-tree is designed to screen species in or out of the class of invasive species in a systematic manner. In most cases, a dichotomous tree structure is used. A series of dichotomous questions must be answered leading the risk assessor to a decision: screen in; screen out; or assess further.

Decision-trees are not typically considered to be methods of prioritization or ranking. A screened out species is qualified as posing *no* risk and a screened in species poses *some* risk. Most decision-trees in the invasive species literature do not address prioritizing species.

Nonetheless, since decision-trees employ an iterative process, they could also be modified to prioritize screened in species based on the different decision-tree paths that led to the determination (Tucker and Richardson 1995, Snyder et al. 2012).

This family of methods assumes that (potentially) invading species differs from non-invasive species in some way. If a sort of differences between invasives and others could be found, the potential invaders could be identified (Kolar 2004). The differentiation might be based on species life history characteristics, such as: r-selected traits, high dispersal, parthenogenetic or vegetative reproduction, high genetic variability, phenotypic plasticity, large native range, eurytopy, polyphagy, human commensalism (Lodge 1993). (One could argue with the usefulness of these characters in special cases, when an invasive makes a transition in the cascade!)

The method involves multivariate statistical analyses (discriminant analysis (DA), CART analysis) based on every available data about life history characters, collected from literature sources. The major limitation of this method is that it can only predict those potential invaders, which already made a successful invasion elsewhere (Kolar 2004).

In practice, this approach was used in the case of the historical fish invasions in the Laurentian Great Lakes. Kolar and Lodge (2002) were able to differentiate fish species introduced successfully from those that failed. They used 26 variables (14 life history traits, 5 environmental factors, 6 aspects of invasions history and the degree of human use). The DA and classification and decision trees (CART) analyses identified 4 variables that discriminated a successful invader with 87 – 96% accuracy.

2.4.1.3 Scoring-Decision-Tree Systems

Occasionally , scoring and decision-tree approaches have been combined, typically with the scoring system embedded within a decision-tree framework where the score leads the assessor through a series of decisions and, ultimately, a certain screening decision (Snyder et al. 2012). Probably the widely used protocol of this type is the European Plant Protection Organization Prioritization Protocol (EPPO) (Brunel 2009).

2.4.1.4 Probabilistic modelling

Probabilistic systems use prior knowledge on species biology and invasion history elsewhere to form invasion probabilities for the assessment area in question, and incorporate quantitative uncertainty and variation (Diez et al. 2012). Probability thresholds related to risk are determined using known invasive and non-invasive species in the assessment area. For example, Keller et al. (2007) used a nuisance probability model within a decision-tree framework to assess the risk of freshwater molluscs.

2.4.1.5 Niche modelling

This methodology is based on a general machine learning algorithm, used to predict the distribution of species from geographical and ecological data (Stockwell and Peters 1999, Drake and Bossenbroek 2004). Input parameters consist of presence/absence (PA) information of species in discreet localities and spatially explicit niche parameters such as temperature, precipitation or elevation for example. During the modeling process, an iterative search for nonrandom correlations between the distribution data (PA datasets) and niche parameters is carried out. The outputs are identified areas where the investigated species may become established. The accuracy of the models could be tested using datasets from the native range of the species to be investigated. This tool is powerful enough to be used for any taxon and allows predictions about the potential distribution with fairly fine resolution. There are some disadvantages too: the result predicts only the potential ranges, and gives no information about impacts, nevertheless, it needs precise geospatial data distribution information (Stockwell and Peters 1999, Stockwell and Peterson 2002, Payne and Stockwell 2002, Kolar 2004).

Niche modelling was successfully used for predicting the potential range of zebra mussel *(Dreissena polymorpha*) in the USA (Drake and Bossenbroek 2004), distribution of 12 fish species in Kansas (McNyset 2005), and recently for modelling the potential holarctic distribution of amur sleeper (*Perccottus glenii*) (Reshetnikov and Ficetola 2011).

2.4.2 The Fish Invasiveness Scoring Kit (FISK)

For the Ecological Risk Assessment of non-native fish in the Balaton-catchment, the Fish Invasiveness Scoring Kit (FISK) was selected (Copp et al. 2005b, Copp e al. 2009). The reason for choosing this protocol was multiple: between the ERA tools reviewed, this was the most widely used (United Kingdom, Belarus, Japan, Australia, Florida (US), Iberian Peninsula, Finland, Turkey and Balkans), least complicated, but scientific-based one, with a well-understandable, "policy maker friendly" output (Copp et al. 2009, Mastitsky et al. 2010, Verreycken et al. 2009, Onikura et al. 2011, Vilizzi and Copp 2012, Almeida et al. 2013, Puntila et al. 2013., Lawson et al. 2013, Simonović et al. 2013, Tarkan et al. 2013). The baseline of FISK is the WRA (Weed Risk Assessment) system, developed by Pheloung et al. (1999) and according to Snyder et al. (2012) belongs to the Scoring system type ERA tools. The FISK is using 49 questions to assess the potential risk related to 8 topics, like: domestication/cultivation; climate and distribution; invasive elsewhere, undesirable traits, feeding guild; reproduction; dispersal mechanism and persistence attributes. These topics cover the whole sequence of invasion process.

2.5 Non-indigenous fish species in the Balaton catchment: a brief review

In this section, the introduction history of non-indigenous fish species, which are permanently and recently inhabiting the Balaton catchment was revieved. According to recent and comprehensive surveys, 12 non-native fish species can be found in the catchment (**Table 1**, Specziár 2009, Erős et al. 2009, Takács et al. 2011, Sály et al. 2011, Ferincz et al. 2012).

Table 1.: Introduction history, origin and occurrence of non-indigenous fish species currently inhabiting the Balaton catchment (*: not yet reported from the reservoir spaces, only from tributaries)

Taxon	Original area	Intro-duction	Way	Lake Balaton	KBWPS	Tribu-taries	Other (wetlands, marshes, fish ponds)
Proterorhinus semilunaris	Ponto-Caspian	mid-19th century	ballast water?	+	-	+	-
Oncorhynchus mykiss	North-America	1885	introduction	-	-	+	-
Anguilla anguilla	Europe	1890s	introduction to Balaton (1963-1991)	+	+	+	-
Lepomis gibbosus	North-America	1897/1905	introduction	+	+	+	+
Gambusia holbrooki	North-America	1939	introduction to Lake Héviz	-	-	+	-
Pseudorasbora parva	Far-East	1962	accidental introduction	+	+	+	+
Ctenopharyngodon idella	Far-East	1965	introduction to fish ponds	+	+	+	+
Neogobius fluviatilis	Ponto-Caspian	1970	ballast water	+	+	+	-
Carassius gibelio	Far-East	1970s	accidental	+	+	+	+
Hypophthalmichthys molitrx x H. nobilis	Far-East	1972	introduction (biomanipulation)	+	+	+	+
Ameiurus melas	North-America	1980s	introduction to fish ponds	+	+	+	+
Percottus glenii	Far-East	2008	accidental	-	-*	+	-

More information about failed introductions and non-natives which disappeared could be found in the works of e.g.: Entz and Sebestyén (1942), Bíró (1997), Bíró et al. (2003), Harka and Sallai (2004). The first standardized surveys of fish fauna were started only in the late 1980s by examining the lake (Paulovits et al. 1994), the KBWPS (Bíró and Paulovits 1994), and the tributaries (Szipola and Végh 1992). The fish fauna of such important and abundant habitats like marshlands, abandoned or even functioning fish ponds are still only partially known (Ferincz et al. 2014).

Traditionally the book of Herman (1887) has been handled as reference condition regarding the fish fauna. It has also mentioned the most probably first non-native species from the lake: the tubenosed goby (*Proterorhinus semilunaris*). Three other species, pumpkinseed (*Lepomis gibbosus*), rainbow trout (*Oncorhynchus mykiss*) and eel (*Anguilla anguilla*) were

introduced to the catchment until the end of the 19th century for aquaculture and ornamental purposes (Herman 1890, Gönczy and Tölg 1997, Vutskits 1897, Györe 1995). The introduction of mosquitofish (*Gambusia affinis*) into the thermal lake of Héviz remained local, as the species cannot overwinter outside the lake (Specziár 2004).

The next wave of introductions started in the 1960s and lasted for a decade: several species with Far-Eastern origin were stocked. Topmouth gudgeon (*Pseudorasbora parva*) was a typical free rider, which was introduced with an uncontrolled stock of common carp (*Cyprinus carpio*) (Pintér 1987). The first stock of grass carp (*Ctenophayngodon idella*) arrived in 1965 into a fish pond in the catchment. It needs to be mentioned that grass carp has never been stocked directly (and verifiably) to the lake (Harka and Sallai 2004). The taxonomical status of the stock silver and bighead carps (*Hypophthalmichthys molitrx; H. nobilis)* is unclarified in the lake. *H. molitrix* was introduced in order to maintain the euthrophication problem of Lake Balaton, but the origin of the recent population is unclarified. The hybridisation of the two species was indicated by recent studies (Takács et al. 2011, Boros et al. 2012), thus I refer them as hybrids in this theses. This large-scale biomanipulation experiment was a major mistake and caused more problems than benefits (Virág 1995, Boros et al. 2012, Boros et al. 2013).

The monkey goby (*Neogobius fluviatilis*) was found in the lake in 1970, but due the low intensity of ichtyological investigations in this period, the exact date of its establishment is not known (Bíró 1972). The species most probably arrived through the Sió canal, in a ballast tank of a ship. Our knowledge on the introduction of gibel carp (*Carassius gibelio*) into the Catchment is limited. The gynogenetic form of the species has occurred since the 1970s (Tóth 1975, Specziár 2009). The first specimen most probably came accidentally with the stock of other species.

As such, the last intentional introduction can be dated to the early 1980s, when black bullhead (*Ameiurus melas*) were stocked into a fish pond near Fonyód. The species escaped rapidly, then began to spread and outcompeted the formerly introduced congener brown bullhead (*Ameiurus nebulosus*) (Harka 1997). Last of the introduced species, amur sleeper (*Perccottus glenii*) appeared in 2008 in a tributary of the KBWPS. This small bodied Odontobutiid species is considered the main threat for the native, strictly protected mudminnow (*Umbra krameri*), spreading continously in the vegetated canal (Erős et al. 2008, Takács et al. 2012a).

The speed and stages of introductions are illustrated in **Figure 1**. The slope of the curve is slightly lower than it was found in the case of the Hungarian section of the Danube for the same period (Weiperth et al. 2013), but this could be explained with the accessibility of the watershed. The Balaton catchment is still considered as a quite closed system, which could be an advantage in the future. Conservation management can benefit from this isolation, if appropriate regulations allow. Two main periods of mostly intentional introductions can be distinguished on the graph. The first occurred in the late 19th century and meant two aquaculture utilized species (eel, rainbow trout) and the pumpkinseed which was stocked for ornamental purposes. The second wave of intentional introductions in the 1960s and ’70s is considered more problematic and resulted altogether in 4 new species.

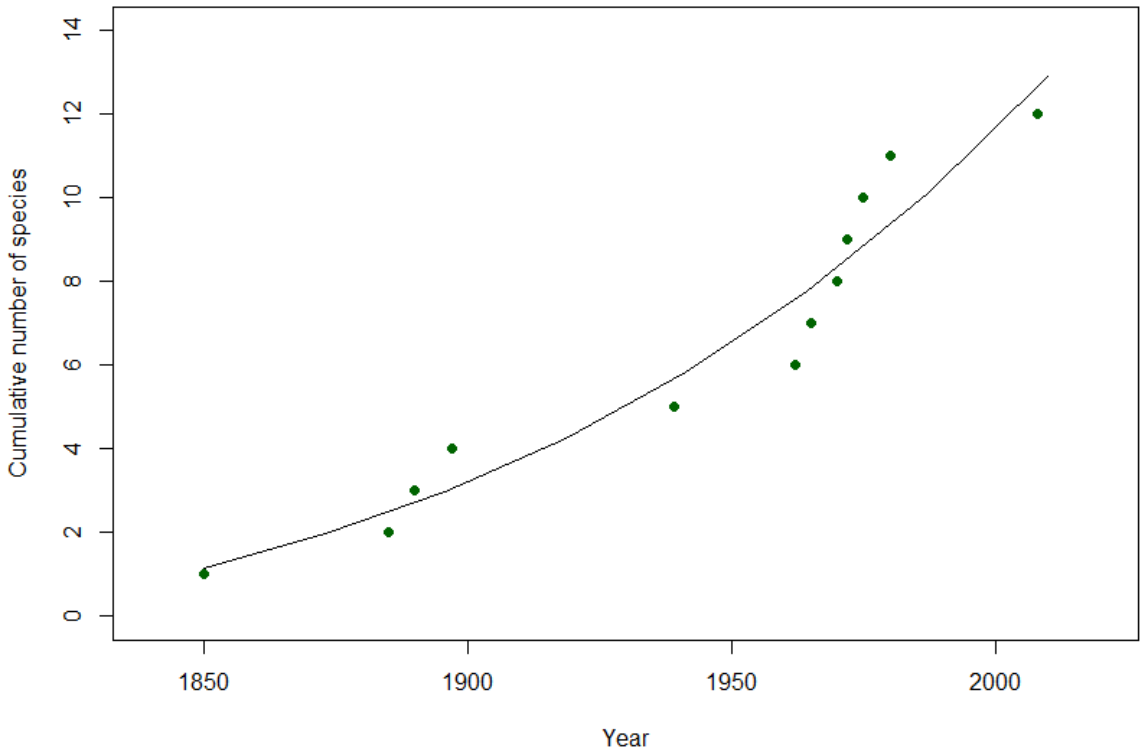

Figure 1: Cumulative number of established non-indigenous species between 1850 and 2010 (2nd degree polynomial regression, R^2=0.9314, F=61.07, p<0.00001)

2.6 The “berek” areas: Almost unknown marshlands in the neighborhood of Europe’s most well investigated lake

Before the water conditions of Lake Balaton were regulated, the wetland areas recently lying in the southern shoreline of Lake Balaton had belonged to the lake as shallow bays (these specific wetlands are called berek in Hungarian). After the opening of the Sió-floodgate in 1863/64, the water level was lowered by app. 2 m, these bays which were usually situated behind a sand bar got disconnected. The still water covered areas behind the bar have only been drained partially after further channalization and suction (Dövényi 2010, Zlinszky and Tímár 2013). The remained wetland areas and their huge canal system provided refugia for the flora and fauna to survive, at least partially. These marshland areas in general are considered to be almost unknown in the view of their ichtyofauna, which is surprising because ichtyological studies have been intensive in the catchment at least since 2006 (Sály et al. 2011, Takács et al. 2011). The review of Majer and Bíró (2001) mentioned these areas as potentially characterized by valuable ichtyofauna, however, no exact data have been provided. Only sporadic literatural data exist regarding the fish fauna of these areas. Faunistical datasets from some reports, based on non-standardized methods indicated the presence of 6 species in the Ordacsehi-berek (**Figure 3.**), including the protected sunbleak (*Leucaspius delineatus*) (Ferincz 2005, 2006). The presence of mudminnow (*Umbra krameri*) was also published by Harka and Sallai (2004) from the Ordacsehi-berek. The presence of 5 species was verified in the Nagyberek by Ferincz et al. (2010) and an additional species, weatherfish (*Misgurnus fossilis*) was noticed in 2013 (Ferincz et al. 2013).

Regarding their role in nature conservation and international conventions (Natura2000, Ramsar Convention), the description and monitoring of the ichtyofauna of these marshlands would be necessary.

3. Materials and methods

3.1 Survey of the non-indigenous fish species of the catchment: factors affecting the distribution of non-indigenous species

3.1.1 Study area and sampling campaign

Altogether 15 lentic sampling localities were chosen in different parts of the catchment (**Figure 2**). Fish samples were collected from April of 2011 to November of 2011.

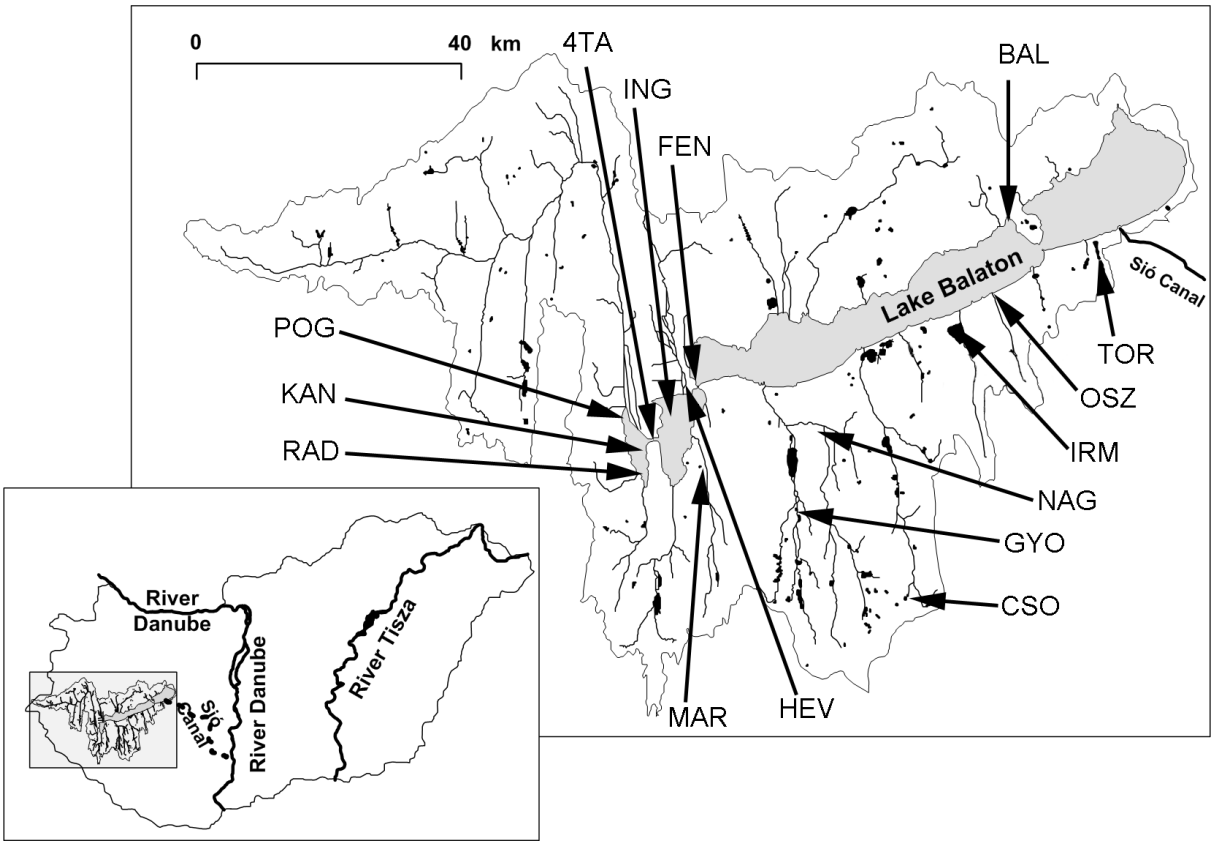

Figure 2.: Map of the Balaton catchment, with the sampling sites surveyed in 2011 (Abbreviations: HÉV: Hévíz-páhoki Canal, Fenékpuszta; FEN: Lake Balaton, Fenékpuszta; BAL: Lake Balaton, Sajkod; TOR: Pond 10., Siófok-Töreki Pond System; OSZ: Őszöd-marshland, Balatonőszöd; IRM: Pond 7., Balatonlelle-Irmapuszta Pond System; NAG: Nagyberek; GYO: Pond 2., Marcali-Gyótapuszta Pond System; CSO: Csombárdi – pond, Csombárd; MAR: Marótvölgyi-Canal, Főnyed; RAD: Inner Reservoir Space of KBWPS-I (Kis-Balaton Water Protected System).; KÁN: Inner Reservoir Space of KBWPS-I.; POG: Outer Reservoir Space KBWPS – I.; ING: KBWPS-II., 4TA: Interconnecting canal between KBWPS I.-II.)

The whole catchment area can be considered to be highly modified by human land use (e.g. Sály et al. 2011). As described in Section 2.5, the fish fauna of the small watercourses and the lake itself is quite well known. The sampling sites of this study were selected to represent mostly unexplored, but typical lentic wetlands of the catchment: intensively managed fish ponds (2 sites); extensively managed, nature reserve ponds (2 sites); marshes (or wetlands) (2 sites); canals (2 sites); the reservoirs of Kis-Balaton Waterquality Protection System (KBWPS) (5 sites); and the littoral zone of Lake Balaton (2 sites) Sampling sites were as follows:

Hévíz-páhoki Canal, Fenékpuszta (HÉV): This canal carries the outflowing water of the thermal lake of Héviz into River Zala. The estuary is situated close to the outflow of River Zala from the second stage of Kis-Balaton Water Protection System. Sampling area is located 1 km upstream from the estuary. The vegetation of the shorezone is mostly reed, and massive submerse vegetation.

Lake Balaton, Fenékpuszta (FEN): Detailed description of Lake Balaton can be found e.g. in Istvánovics et al. (2007). The sampling site was situated app. 1.5 km north of the Zala estuary and can be characterized by semi-natural, wide vegetation on the edge.

Lake Balaton, Sajkod (BAL): This site is located in the most protected and most natural bay of Lake Balaton. It can be characterized by high quality, wide reed and reed-mace belt and dense submerse vegetation in patches.

Siófok-Töreki Pond System (TOR), Pond 10: This relatively small (12.4 ha) valley-dam pond is a part of a fish pond system (altogether 11 ponds), recently used as a recreational (angling) pond. Native and non-native species (carp (*Cyprinus carpio*); pikeperch (*Sander lucioperca*); grass carp (*Ctenopharyngodon idella*)) are often stocked. The shoreline has a narrow vegetation line, with some fallen trees. The water supply originates from the Cinege-creek, flowing to Lake Balaton.

Őszöd-marshland, Balatonőszöd (OSZ): This area (app. 70 ha) formerly had belonged to Lake Balaton, but after the opening of the Sió-floodgate it became disconnected. A peat mine was operated until the 1970s and afterwards, the borrow pits were inundated. The water supply is provided mainly from precipitation and the level is regulated by suction to Lake Balaton. The open water surface is spotted by reed islands. Shoreline vegetation is developed.

Balatonlelle-Irmapuszta Pond System (IRM), Pond 7: This pond is a typical fish farming pond in this area. The 46 ha open water surface is surrounded by a developed reed belt. The

water supply is provided by the Tetves-creek which is connected to Lake Balaton, but sometimes inadequately.

Nagyberek (NAG): This area is the largest remain of a former bay of Lake Balaton. The sampling area is situated in the northern part of the app. 350 ha reconstructed wetland (mostly open water surface with reed islands and inundated willow bushes). Water supply mostly comes from precipitation, water level is controlled by a floodgate.

Marcali-Gyótapuszta Pond System (GYO), Pond 2: The oldest pond system in the watershed, with a dam. Area of the sampling pond is 36 ha, with reed in the littoral, dense submerged vegetation in the whole area of the pond. Its water supply comes from the Boronka-creek. Since 2002, only extensive fish management has been implemented, with the aim of nature conservation.

Csombárdi Pond (CSO): One of the most southern ponds in the watershed. It is connected to the Pogányvölgyi Stream system. Approximately 2/3 of its 7 ha area is covered by vegetation (mostly cattail, reed to less extent), the submerged vegetation is also dense. Since 2008, only extensive fish management has been implemented, with the aim of nature conservation.

Marótvölgyi-Canal, Főnyed (MAR): The canal is one of the most important tributaries of the 2nd phase of the Kis-Balaton Water Protection System, and has several intensely managed fish ponds in its watershed. Although its area is heavily modified, its vegetation has a natural character: the shorezone is covered by reed, the submerged vegetation is very dense. It is the first site of occurrence of the amur sleeper (*Perccottus glenii*) in the watershed (Erős et al. 2008).

KBWPS – I, Lake Hídvégi (Kis-Balaton Water Protection System) (KAN; RAD; POG): For detailed descrition of KBWPS, see e.g. Pomogyi 1993; Tátrai et al. 2000; Korponai et al. 2010. Sampling was carried out in the moderately developed reed-cattail vegetation in the littoral of the reservoir which was inundated in 1985. Submerged vegetation is not typical, the bottom is normally muddy.

Interconnecting canal of KBWPS – I and II. (4TA): An approximately 20-30 m wide canal in the former bed of River Zala, with a dense macrophyte (willow bushes, reed) coverage in the shoreline.

KBWPS – II, Lake Fenéki (ING): See in details in section 3.2.1.

Unfortunately, due to the drought inducated waterlevel decrease in case of the Fenékpuszta site (FEN) and the complete drying out of Nagyberek (NAG), the dataset of these sampling sites included only 1 or 2 samplings. Hence, these places were excluded from the further analyses.

3.1.2 Sampling methods: Source of fish datasets

Electrofishing was carried out seasonally, 3 times in each site: in spring (April/May), summer (June/July) and autumn (October) in 2011. Sampling was conducted along the same transect in every season near the vegetated shoreline from a small, 12 V electric motor powered rubber boat using a SAMUS 725 MP, 12 V battery-powered device (used at Pulse DC 380-580 V; 50-70 Hz). Based on the methodological investigations of Erős et al. (2009) and Specziár et al. (2012), this method has adequate power to obtain reliable information regarding the assemblage structure. The duration of each sampling occasion was 60 minutes, which represented a transect length of 1606 ± 210 m, in average. Each captured fish was identified at species level and then released, except the non-natives. The data of 0+ (YOY) fish were excluded from the analyses.

3.1.3 Environmental Data

The sampling sites were charactized by 13 habitat and 6 land use characteristics (Table 2). For littoral macrovegetation cover (Reed, Rmace, LOther), percentage ratios were calculated based on visual estimation for every 50 m segment of the transects we electrofished. For the calculation of percentage ratios for bottom quality and means for water depth, they were measured at 10 randomly selected points close to the transects. These measurements were conducted during summer sampling. A HORIBA U-10 water quality checker was used to measure turbidity, conductivity and pH at each sampling occasion. Surface area and land use data were gathered from digitalized topographical maps using GIS software or from literature sources (Dövényi 2010, VKKI 2010). In some cases (mainly for the assessment of the occurrence of droughts), the managers of the watersheds (staff of the national park directorates) were interviewed.

Table 2: List of the environmental variables used in the RDA and variance partitioning (all habitat characteristic data were log(x+1) transformed)

	Name	Abbreviation	Measure	Mean±SD
Habitat characteristics (Local effects)	Reed (*Phragmites communis*)	Reed	Shoreline coverage (%)	58.46±27.69
	Reed-mace (*Typha* sp.)	Rmace	Shoreline coverage (%)	29.76±26.03
	Other macrophytes in the littoral zone (e.g.: *Carex* sp., *Juncus* sp.)	LOther	Shoreline coverage (%)	9.61±13.65
	Submerse macrophytes (*Potamogeton* sp., *Myriophillum* sp., *Ceratophyllum* sp.)	Smerse	Coverage (%)	27.07±28.85
	Area	Area	km^2	52.06±156.7
	Silt	Silt	Bottom coverage (%)	62.3±30.92
	Sand	Sand	Bottom coverage (%)	18.46±21.07
	Gravel	Gravel	Bottom coverage (%)	10.38±18.24
	Clay	Clay	Bottom coverage (%)	8.84±11.46
	Turbidity	Turbid	NTU	117±118.7
	Conductivity	Cond	µS/cm	703.38±136.3
	pH	pH		8.41±0.41
	Average depth	Depth	cm	105.38±44.99
Land use characteristics	Activity of commercial fisheries	Fishing	Binary data	
	Water level managed by suction	Suction		
	Water supply from inflow/tributary	Inflow		
	Watershed dried out at least once in the last 10 years	Drought		
	Human made habitat	Constructed		
	Protected habitat	Protected		

3.1.4 Statistical Analysis

Spearman rank correlation was applied to test the relationship between the total abundance (mean/cumulative number of specimen) and spatial frequency of occurrence data. The taxonomic diversity of each sampling site was assessed by using Shannon-index. The incrimination or stress of Shannon's H, caused by the non-indigenous species was assessed using the Assemblage Naturalness Index (ANI) (Sály 2007, 2009). The relationship between ANI and total relative abundance of non-native species was tested with Spearmann's rank correlations. These analyses were conducted in PAST software (Hammer et al. 2001).

The arcsin-sqrt transformed fish datasets based on relative abundance (RA) data, summarized for each site were used for the assemblage level analyses. The pattern of species composition (PA) was assessed in a PCA ordination. A Bray-Curtis dissimilarities based nearest neighbour cluster analysis was performed in paralel and its results were displayed on the ordination diagram. Another PCA was performed on the RA dataset. All environmental variables listed in **Table 2** were used in a forward selection procedure of redundancy analysis (RDA) to select variables that significantly explain the distribution of the non-indigenous species. Forward selection revealed significant effects both among habitat characteristics (reed coverage, clay bottom coverage, turbidity, area) and land use variables (drought occurrence), which were used in a variance partitioning model (Borcard et al. 1992). A similar model was built for the native species only, to investigate the potential effect of the investigated variables on the native fish assemblage. These analyses were made in R software (R Development Core Team 2013), with the package 'packfor' (Dray et al. 2013) and 'vegan' (Oksanen et al. 2013).

3.2 Invasion scenario analysis of gibel carp in Lake Fenéki (Kis-Balaton Waterquality Protection System)

3.2.1 Study Area

The Ingó-marsh (N: 46°38'46.68", E: 17°11'24.10") 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), being situated a few kilometres southwest from Lake Balaton (**Figure 2**, ING). 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, and Kis-Balaton became disconnected. The area continued to dry out, and the complete disappearance of open water surfaces happened only in the 1950s. The remains of the native fish fauna could only survive in some draining canals and two small ponds (Bíró and Paulovits 1994, Korponai et al. 2010). In the 1970s, after the recognition of the accelerating euthrophication of Lake Balaton, the reconstruction of KBWPS began (Lotz 1988).

The system is made of two reservoirs: the first (Lake Hídvégi, 21 km^2), which is characterized as open watersurface gives ideal conditions for algae to reproduce and has been operating since 1985. The second (Lake Fenéki), which was the study area, was inundated partly (16 km^2 from the planned 54 km^2) 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 by 600–700 µS/cm conductivity (see more: Kovács et al. 2010, Hatvani et al. 2011).

3.2.2 Sample collection

Seasonal samplings have been carried out from 1992 to 2011 (3 samplings annually: April/May, June/July and October). Altogether, data from 12 years were included in the analysis as data were lacking or not standard in some years (1998; 2002; 2004-2008 and 2010). I was involved to these surveys only in 2009 and 2011, other datasets was provided by my supervisor. A standard locality near the vegetated (reed and reed-mace) shoreline and inundated willow-bushes was electrofished from a boat, using a 12 V battery powered device (used at Pulse DC 300-500 V; 50-70 Hz). 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, in average. Each individual caught has been identified at species level, and then released.

3.2.3 Statistical analysis

Ordinary Least Square (OLS) regression has been used for temporal trend detection in the cumulative number of specimen. Logarithmic regression has been used for yearly total species number and Shannon-diversity, calculated for the whole sample for the year.

Relative abundances were calculated as the ratio of number of individuals of a given species to the total number of individuals in the catch. Cumulative relative 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, at first on the whole time-series. As huge contrast between the first two years (1992 and 1993) and latter years were recognized, another PCA on the datasets of years between 1994 and 2011 was performed. An Analysis of Similarities (ANOSIM) on the Morishita dissimilarity matrices was performed on the two most possible groups, revealed by the PCA, to test whether their assemblage structures differs significantly. Analyses were performed with vegan package in R statistical environment (Oksanen et al. 2013, R Development Core Team 2013).

The functional composition (i.e. ‘trophic guild’) of fish assemblages was determined based on the work of Erős et al. (2009). Species missing from this study were categorized by 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.

3.3 Ecological Risk Assessment of non-indigenous fish species of the Catchment using the FISK (Fish Invasiveness Screening Kit) algorithm

The FISK questionnaire has two versions. The orignal (FISK v1.19, FISK I, Appendix 1) was developed and first time used in the UK, by Copp et al. (2009), then successfully adopted in Belarus (Mastitsky et al. 2010), Belgium (Verreycken et al. 2009) and Japan (Onikura et al.

2011). Although the usability of the scoring system was excellent in the temperate zone, the reliability was proved to be not enough under mediterranean or sub-tropical climate. To solve this problem, the questionnaire was modified (FISK v2.03, FISK II, Appendix 2) and tested for the first time in the Penninsular Florida (Lawson et al. 2013).

The FISK I assessments were undertaken independently by three researchers (Ádám Staszny, András Weiperth and Árpád Ferincz). Each person calculated the total FISK scores for each species. Altogether 12 species (*Carassius gibelio; Perccottus glenii; Anguilla anguilla; Lepomis gibbosus; Neogobius fluviatilis; Gambusia holbrooki; Hypophthalmichtys molitrix x nobilis; Ameiurus melas; Pseudorasbora parva, Proterorhinus semilunaris, Ctenopharyngodon idella, Oncorhynchus mykiss*) have been assessed, as currently present non-indigenous species of the catchment according to Takács et al. (2011). The FISK II assesments were performed by only the author.

Receivers operating characteristic (ROC) curves were used to assess the predictive ability of the FISK test, with the final objective to determine a 'cut-off value' which is a threshold for discriminating invasive and noninvasive species. Since '*a priori*' categorization of the species is needed for this test, the database of Invasive Species Specialist Group (http://www.issg.org/) and FishBase (http://www.fishbase.org/home.htm) were used for this issue (Table 3). Independent ROC curves were constructed for the min. FISK I (lowest scores from the three assessments), the mean FISK I and II score, to determine the difference between the cut-off values. For statistical testing the difference of two ROC curves, the Venkatraman method was used (Venkatraman 2000). Statistically, a ROC curve is a graph of sensitivity versus 1 minus specificity (1 - specificity), and in the present context the sensitivity of the FISK test will be the proportion of invasive fish species that are correctly identified by the test, whereas specificity refers to the proportion of noninvasive fish species that are correctly identified as such. An important measure of the accuracy of the calibration analysis is the area under the ROC curve. If this area is equal to 1.0, then the ROC curve consists of two straight lines, one vertical from 0.0 to 0.1 and the next horizontal from 0.1 to 1.1. In such cases, the test is 100% accurate because both the sensitivity and specificity are 1.0, so there are no false positives or false negatives. On the other hand, a test is not accurate if the ROC curve is a diagonal line from 0.0 to 1.1. The ROC area for this line is 0.5, with ROC curve areas typically being between 0.5 and 1.0 (Copp et al. 2009). The best FISK threshold (cut-off) value that maximizes the true positive rate (true invasive classified as invasive) and minimizes the false positive rate (true non-invasive classified as invasive) was determined

using a combination of Youden's J statistic (Youden 1950) and the point closest to the top-left part of the plot with perfect sensitivity or specificity. For the global ROC curve, a smoothed mean ROC curve was also generated and bootstrapped confidence intervals of specificities computed along the entire range of sensitivity points (0 to 1, at 0.1 intervals).

Spearman rank correlations were used to find relationships between the log-transformed FISK scores and characteristic indicators of non-native distribution (frequency of occurrence, cumulative relative abundance). The mean of FISK I and FISK II scores was compared using paired t-tests.

Analyses were carried out with package pROC for R statistical environment (R Development Core Team 2013, Robin et al. 2011) and 2000 bootstrap replicates were used.

3.4 Faunistical surveys of five marshland (berek) areas in the southern shoreline of Lake Balaton

3.4.1 Study area

The situation of the five marshland areas in the Balaton-catchment is showed in **Figure 3**.

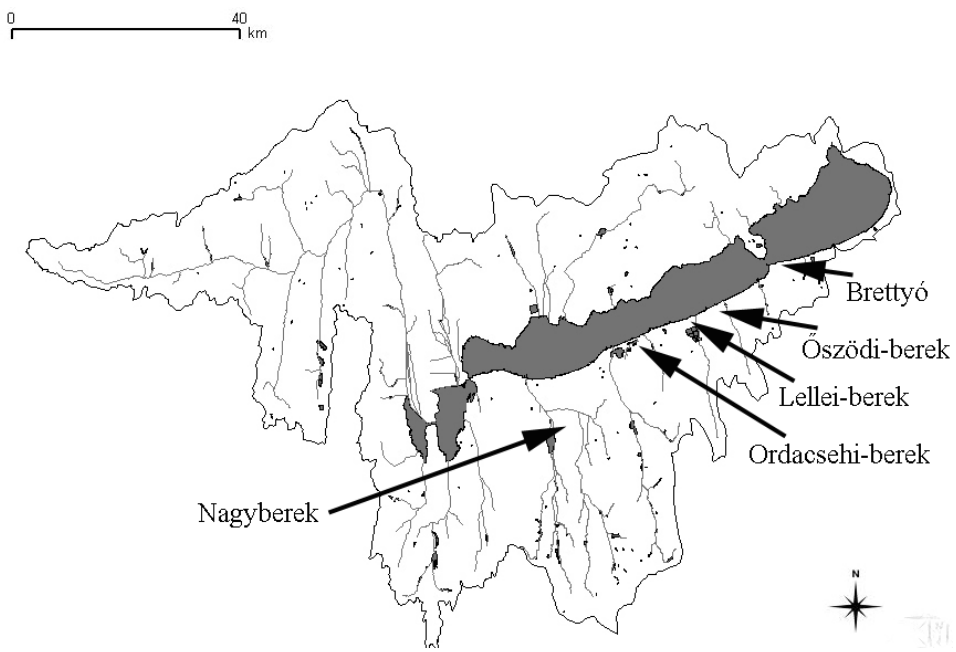

Figure 3: The marshland habitats in the Balaton catchment sampled between 2011 and 2013.

Nagyberek: The first sampling was in the spring of 2011, but as the area dried out (partially, fishes were still found in refugia in the deeper points) in the summer, the next fishing was in May of 2012, then July of 2012. Another drying out occurred in the autumn of 2012. Three samples (May, July, October) were taken during 2013. The sampling point is located near the main draining floodgate (Nekota-floodgate, (N46°39.313 E17°30.170)).

Ordacsehi-berek: Altogether 4 sampling points were laid in the Ordacsehi-berek. One of them, a peat borrow pit was sampled both in 2012 and 2013 (twice a year: in July and in October). Two samples in 2013 were taken from the other three points (N46°45.842 E17°37.258. 46°44.968 E17°35.980 and N46°45.784 E17°37.255): two peat borrow pits and a draining canal.

Lellei-berek: The main draining canal (N46°47.454 E17°43.977) of this marsh was sampled two times in 2013 (July and October).

Őszödi-berek: The sampling point is identical to the one described in 3.1.1. Samples were taken seasonally (May, July, October) between 2011 and 2013.

Brettyó (Zamárdi): The main draining canal crossing the marshland was sampled once in July 2011.

3.4.2 Sampling methods

Sampling was conducted along the same transect each time, close to the vegetated shoreline from a small, 12 V electric motor powered rubber boat using a SAMUS 725MP, 12 V battery-powered device (used at Pulse DC 380-580 V; 50-70 Hz) The duration of each sampling was 60 minutes, which represented a transect length of 1606 ± 210 m. Each captured fish was identified at species level and then released. Sampling point coordinates were registered using a Garmin GPSMAP 78HCx GPS receiver.

3.4.3 Statistical analysis

Data on the number of specimens were transformed to RA datasets. As the sampling effort was inequal, individual based rarefaction analyses was used to assess representativity (Brettyó was excluded due to N=1) (Gotelli and Colwell 2001). The ANI was used to assess the stress

of diversity caused by non-indigenous species (Sály 2007, 2009). A PCA on the arcsin-sqrt transformed RA data was used to compare the fish assemblages of the wetlands. Analyses were made with vegan package in R statistical environment and PAST software (Hammer et al. 2001, Oksanen et al. 2013., R Development Core Team 2013).

4. Results

4.1 Survey of the non-indigenous fish species of the catchment: factors affecting the non-indigenous fish distributions

4.1.1 Species composition, diversity and naturalness

The total number of specimens caught was N = 10739. Altogether 29 fish species were identified at the 14 sampling sites, of which 10 (34.5%) were non-indigenous (**Table 3)**. At least 1 non-native species was recorded at each sampling site (min.: 1 in Pogányvári-víz), with the highest number of 6 (Töreki) (**Figure 4**). Gibel carp (*Carassius gibelio*) was observed at every sampling site. The monkey goby (*Neogobius fluviatilis*) and mosquitofish (*Gambusia holbrooki*) were found only in one habitat. The latter species is capable of overwintering only in Lake Hévízi, due to its high temperature requirements (Specziár 2004).

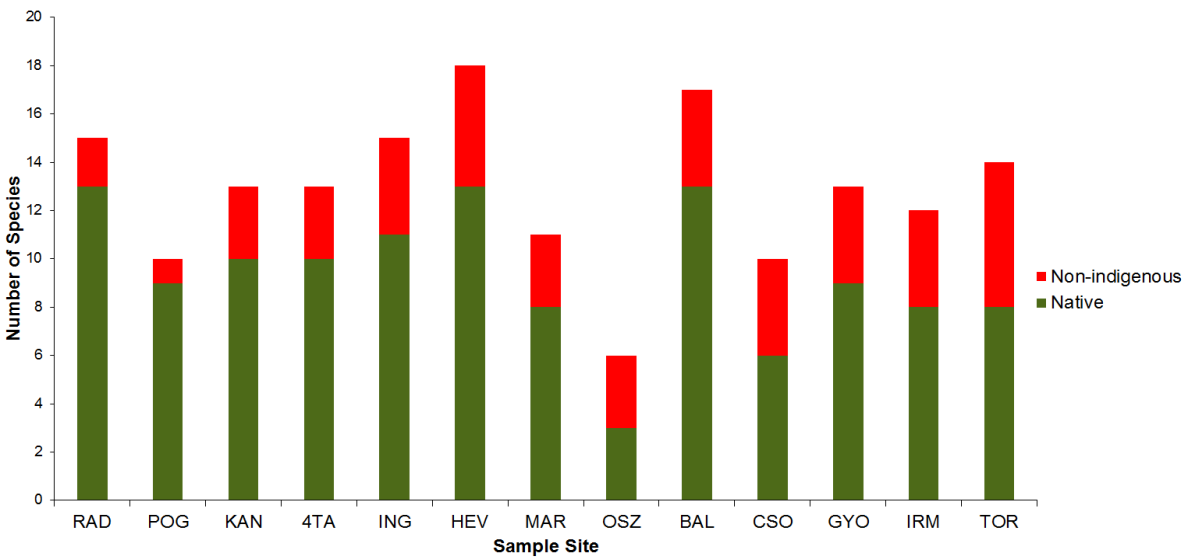

Figure 4: Total number of species in the sampling site

Table 3: Species composition, relative abundance, diversity and Assemblage Naturalness index of the examined habitats

Species			Sampling site													Status
Scientific name	Common name	Abbreviation	**RAD**	**POG**	**KAN**	**4TA**	**ING**	**HEV**	**MAR**	**OSZ**	**BAL**	**CSO**	**GYO**	**IRM**	**TOR**	
Rutilus rutilus	Roach	RUT_RUT	59.29	35.85	76.86	29.86	28.48	1.83	24.78	0.00	21.52	9.20	41.16	0.07	0.08	Native
Carassius gibelio	Gibel carp	CAR_GIB	18.18	8.96	8.42	28.98	21.69	82.93	5.16	93.14	0.66	26.71	0.47	47.30	64.06	Alien
Lepomis gibbosus	Pumpkinseed	LEP_GIB	0.26	0.00	1.82	0.00	2.32	0.00	0.00	0.29	0.22	29.38	3.95	0.87	0.59	Alien
Cyprinus carpio	Common carp	CYP_CAR	1.32	2.12	2.24	0.71	6.29	0.61	0.00	0.00	3.36	0.89	3.26	7.46	5.46	Native
Perca fluviatilis	Perch	PER_FLU	1.84	1.18	3.51	0.18	1.49	0.06	0.06	0.00	4.16	10.98	4.88	0.00	0.00	Native
Abramis brama	Bream	ABR_BRA	1.58	2.83	0.70	6.54	7.95	0.61	0.00	0.00	0.95	0.00	0.47	0.00	0.17	Native
Aspius aspius	Asp	ASP_ASP	3.56	7.55	0.56	1.24	1.66	0.00	0.00	0.00	0.36	0.00	0.00	0.00	0.00	Native
Silurus glanis	Wels	SIL_GLA	0.40	0.24	1.40	2.12	5.30	1.83	0.00	0.00	0.22	0.00	0.00	0.07	0.08	Native
Blicca bjoerkna	White bream	BLI_BJO	7.91	4.72	0.28	11.13	3.81	0.00	0.00	0.00	1.60	0.00	0.00	0.00	0.00	Native
Alburnus alburnus	Bleak	ALB_ALB	1.58	33.73	2.81	2.47	17.38	1.83	0.00	0.00	56.60	0.00	0.00	0.33	1.60	Native
Scardinius erythrophthalmus	Rudd	SCA_ERY	2.24	2.12	0.00	13.07	0.99	0.61	0.40	0.49	3.43	10.39	11.86	0.13	0.00	Native
Tinca tinca	Tench	TIN_TIN	0.26	0.00	0.00	0.00	0.00	0.61	0.18	1.49	0.22	0.00	1.86	0.00	0.17	Native
Sander lucioperca	Pikeperch	SAN_LUC	1.32	0.00	0.70	0.00	0.00	0.00	0.00	0.00	0.73	2.97	0.00	0.00	0.50	Native
Gymnocephalus cernuus	Ruffe	GYM_CER	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	Native
Esox lucius	Pike	ESO_LUC	0.13	0.00	0.00	1.24	0.50	1.22	1.32	2.43	0.44	0.00	2.33	0.67	0.00	Native
Pseudorasbora parva	Topmouth gudgeon	PSE_PAR	0.00	0.00	0.56	2.12	0.99	0.61	0.00	2.16	0.00	8.61	0.00	42.70	23.26	Alien
Rhodeus sericeus	Bitterling	RHO_SER	0.00	0.00	0.14	0.35	0.66	0.00	0.00	0.00	5.32	0.00	25.58	0.27	0.08	Protected
Neogobius fluviatilis	Monkey goby	NEO_FLU	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	Alien

Table 3 continued

Species			Sampling site													Status
Scientific name	Common name	Abbreviation	**RAD**	**POG**	**KAN**	**4TA**	**ING**	**HEV**	**MAR**	**OSZ**	**BAL**	**CSO**	**GYO**	**IRM**	**TOR**	
Perccottus glenii	Amur sleeper	PER_GLE	0.00	0.00	0.00	0.00	0.00	1.22	0.30	0.00	0.00	0.00	0.00	0,00	0,00	Alien
Anguilla anguilla	Eel	ANG_ANG	0.00	0.00	0.00	0.00	0.00	1.22	0.00	0.00	0.00	0.00	0.00	0,00	0,00	Alien
Gambusia holbrooki	Mosquitofish	GAM_HOL	0.00	0.00	0.00	0.00	0.00	3.05	0.00	0.00	0.00	0.00	0.00	0,00	0,00	Alien
Umbra krameri	Mudminnow	UMB_KRA	0.00	0.00	0.00	0.00	0.00	1.22	67.19	0.00	0.00	0.00	0.00	0,00	0,00	Protected
Misgurnus fossilis	Weatherfish	MIS_FOS	0.00	0.00	0.00	0.00	0.00	0.61	0.36	0.00	0.00	0.00	0.00	0,00	0,00	Protected
Ctenopharyngogon idella	Grass carp	CTE_IDE	0.00	0.00	0.00	0.00	0.00	0.42	0.42	0.00	0.15	0.59	0.70	0,00	0,76	Alien
Squalis cephalus	Chub	SQU_CEP	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0,00	0,00	Native
Cobitis elongatiodes	Spined loach	COB_ELO	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.00	0,00	0,00	Protected
Carassius carassius	Crucian carp	CAR_CAR	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.30	1.63	0,00	0,00	Native
Ameiurus melas	Black bullhead	AME_MEL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.86	0,07	0,42	Alien
Hypophthalmichthys molitrix	Silver carp	HYP_MOL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0,00	2,77	Alien
Number of species			15	10	13	13	15	18	11	6	17	10	13	12	14	
Shannon diversity			1.414	1.625	1.000	1.837	2.023	0.977	0.934	0.297	1.444	1.815	1.741	1.049	1.105	
Cumulative number of individuals			759	421	713	567	601	167	1673	1009	1370	337	430	1501	1191	
Assemblage Naturalness Index (ANI)			0.025	0.009	0.025	0.072	0.072	0.244	0.016	0.483	0.003	0.261	0.021	0.303	0.394	

The numerical interpretation of stress is the Assemblage Naturalness Index (**Figure 5**). Stress is correlated with the relative number of non-indigenous species (Spearman r=0.97; p<0.0001). The highest stress (ANI) values were found in IRM, TOR, OSZ, CSO and HEV.

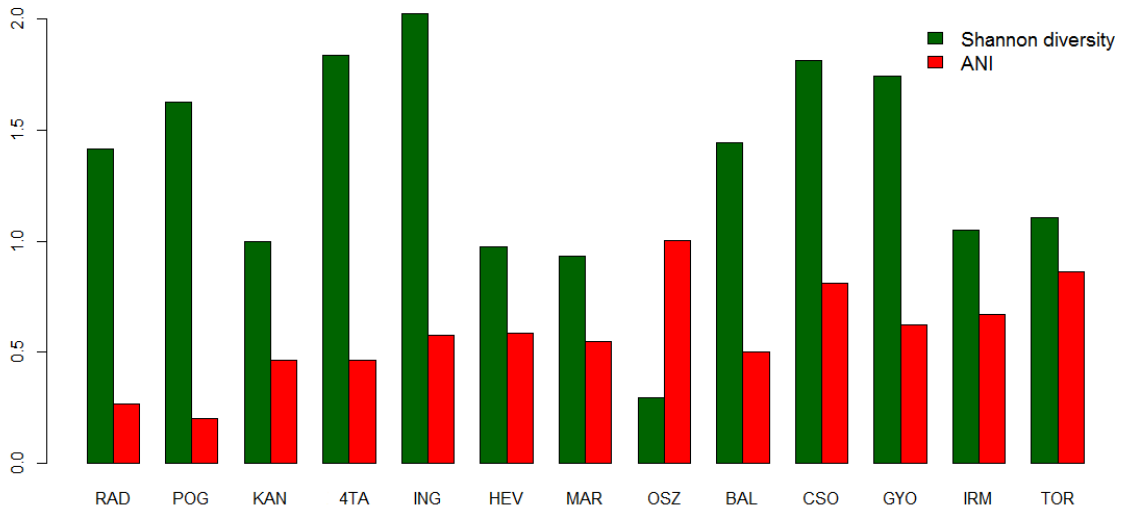

Figure 5: Shannon-diversity and its stress with non-indigenous species (ANI)

Positive relationship was found between the spatial frequency of occurrence and cumulative abundance (**Figure 6**.). The non-indigenous *Carassius gibelio* was the most abundant and at the same time, the most frequent member of the fish fauna. This species could be found at all (13) sampling sites and with 3278 specimens, it represented 30.52% of all the fish that were caught. The most frequent and either abundant native species was *Rutilus rutilus*, which was found at all but one sites. Regarding the other species, 15 occurred at at least 6 sampling sites, hence were considered to be frequent in the whole sample. Among non-indigenous fishes, six (60%) occurred at less than 3 sites (*Anguilla anguilla, Gambusia holbrooki, Ameiurus melas, Perccottus glenii, Neogobius fluviatilis and Hypophthalmichtys sp.*), while the others could be considered frequent members of fish assemblages in the investigated habitats. The number of protected species in the samples was 4. Among them, *Rhodeus sericeus* was the most frequent with 7 occurrences, while the most abundant was the strictly protected *Umbra krameri*.

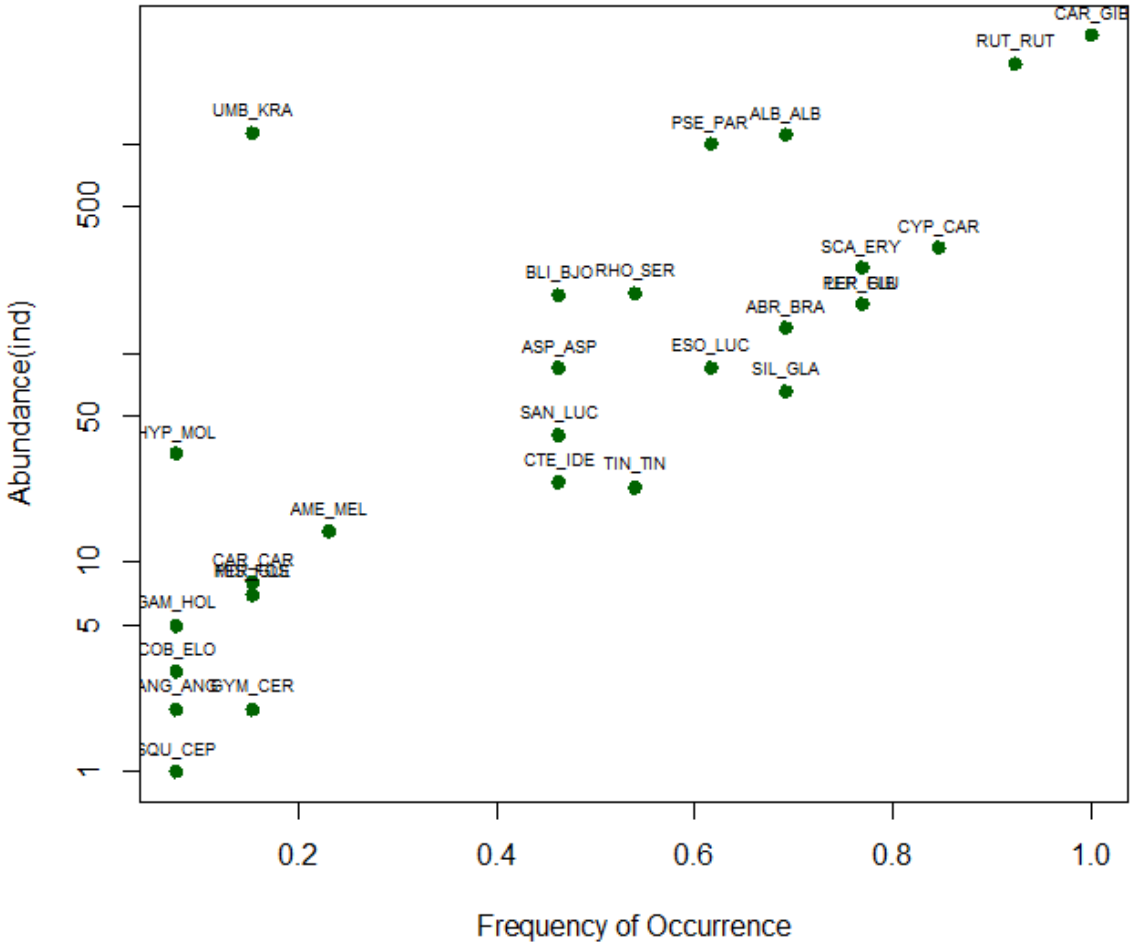

Figure 6: Compositional structure of fish fauna in the examined watersheds, based on the spatial frequency of occurrence and abundance (based on the summarized dataset; the abbreviations of fish species were constructed using the Latin name of the fish, see Table 3)

The PCA analysis of species compositions in the surveyed habitats revealed three main groups (**Figure 7**). Relatively high number of species, with relatively low number of non-natives characterized the first group. Habitats from the two reservoirs of KBWPS and Lake Balaton belonged here (KAN, RAD, POG, ING, 4TA, BAL). The sampling site of two canals (HEV and MAR) formed the second group with relatively high number of species and also relatively high number of non-indigenous fishes. The third group could be divided into two subgroups: the subgroup of fish ponds (CSO, GYO, IRM, TOR) and the subgroup of the marshland Őszödi-berek (OSZ). All of these could be characterized by low number of species

and relatively high number of aliens, but the most possible reason for the statistical division of OSZ was its extremely low species number (6), of which 50% was non-indigenous.

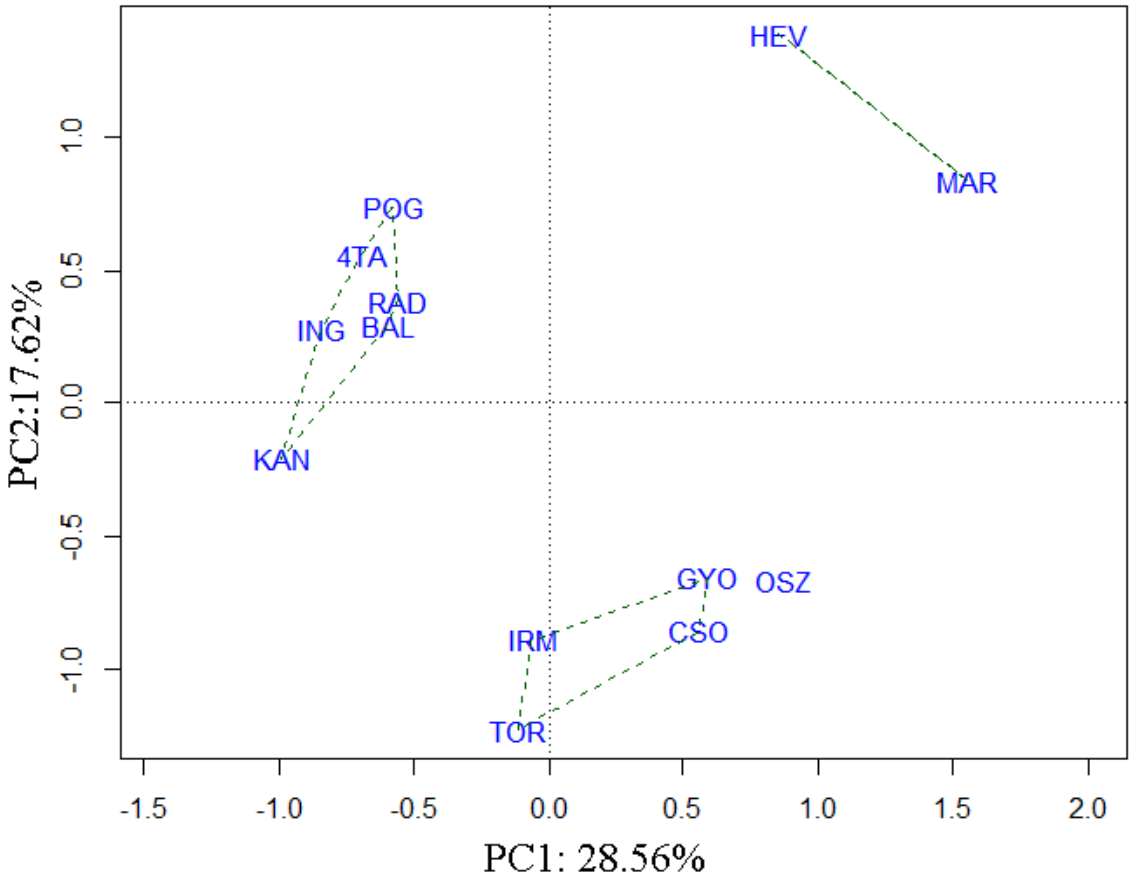

Figure 7: Patterns of species composition based on a PCA ordination (green scattered line indictes the fitted polygons based on the cluster analysis; see: 3.1.1 for abbreviations of sites)

4.1.2 Patterns in relative abundances

Carassius gibelio was dominant at every site, except for the fish pond of Csombárd (CSO), where *Lepomis gibbosus* was the most abundant species (**Table 3**, **Figure 8**). The relative abundance of this cyprinid exceeded 50% at 3 localities (OSZ, TOR, HEV). The second most important and abundant exotic species was *Pseudorasbora parva*, which reached high abundance in the two intensively managed fish ponds (TOR: 23.26%, IRM: 42.7%). The

cumulative relative abundance of non-indigenous species exceeded that of the natives in 5 sites of the total 13 (38.5%). It should be noted, that most of the non-indigenous species (7 of 10) could not become dominant at any sampling site.

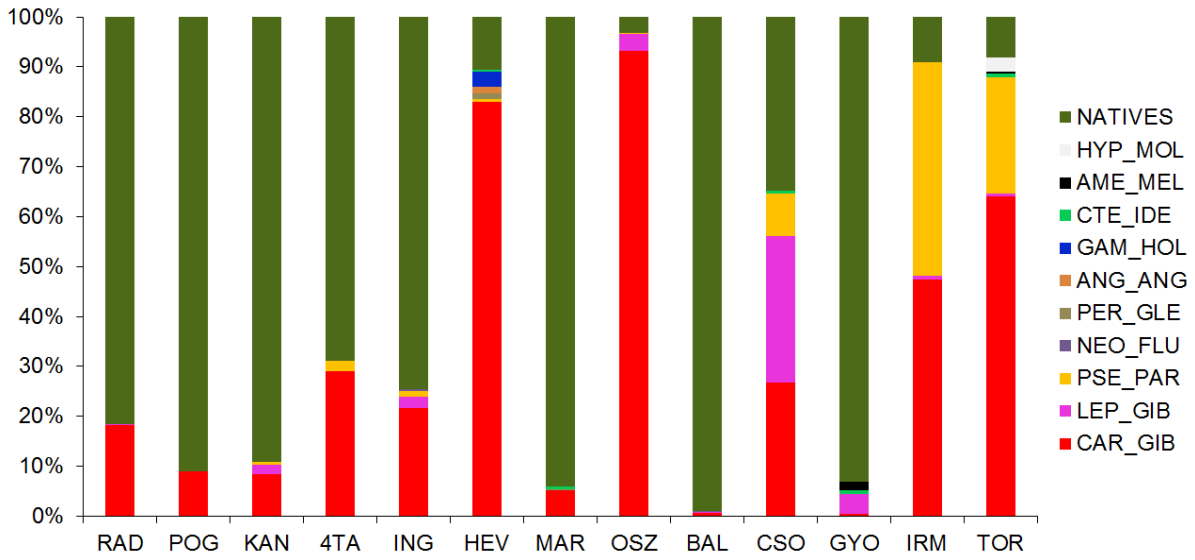

Figure 8: Relative abundances of non-indigenous species (see Table 3 for details)

Most of the species in the PCA ordination were associated with the centroid (**Figure 9**), and only *Rutilus rutilus*, *Alburnus alburnus*, *Umbra krameri* and *Carassius gibelio* were clearly separatable, hence these species can be regarded the discriminative agents between the sites. Five main groups of habitats could be discriminated according to the biplot. The *C. gibelio* (CAR_GIB) dominated group (1) consisted of four sites (TOR, IRM, HEV, OSZ): the two intensive fish ponds, the marshland and a canal. Sites belonging to the (2) group (KAN, RAD, GYO) could be characterized by semi-natural fish fauna with the dominance of *Rutilus rutilus* (RUT_RUT). Two of them are located in the KBWPS-I (KAN, RAD) and one is an extensive fish pond, managed by the Duna-Dráva National Park Directorate for more than 10 years. The next (3) group of habitats (BAL, POG, ING) was also characterized by natural-like fish fauna, but their dominant species was *Alburnus alburnus* (ALB_ALB). There was a transitionary group (4) of sites with two members (4TA, CSO), which were rather associated to the centroid then other groups. The last group (5) was a unique one (MAR), with the extreme dominance of the strictly protected *Umbra krameri*.

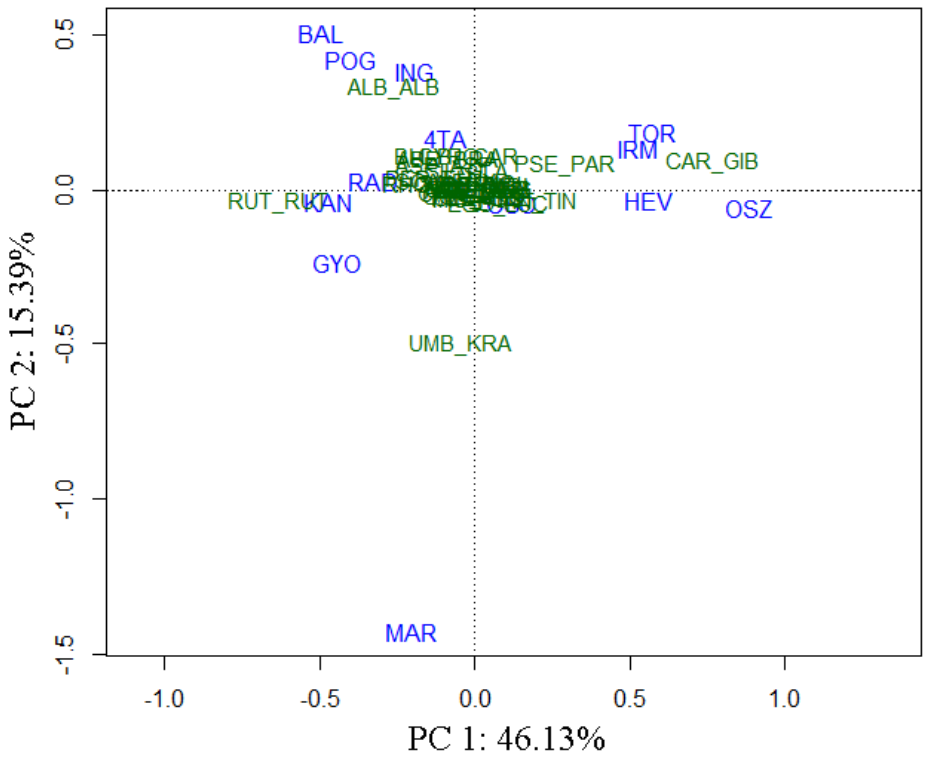

Figure 9: Differences in the assemblage structures of habitats, based on the arcsin-square-root transformed relative abundances (PCA; the full names of sites can be found in 3.1.1; the abbreviations of fish species were constructed using the Latin names of the fish, see Table 2.)

4.1.3 Effect of local environmental and land use pattens on the relative abundance of non-indigenous fish species

The first two axes of the RDA model based on the whole assemblage explained 61.5% of the total variance (**Figure 10**). The forward selection resulted in 5 significant environmental variables: 4 from the ’Habitat characteristics’ and 1 from the ‘Land use’ group (**Table 4**). From these variables ‘Drought’ (Occurrence of dry-out in the last decade), ‘Clay’ (Percentage ratio of clay bottom) and ‘Reed’ (Percentage ratio of reed in the littoral zone) correlated positively with the first canonical axis, while ‘Area’ and ‘Turbidity’ correlated negatively. The habitats of the (1) group (described in 4.1.2) seems to be discriminated by this main gradient. The assemblages of group (3) show difference between the gradient determined by ‘Area’ and ‘Turbidity’.

Table 4: The significant environmental variables resulted from the forward selection procedure. Dataset: whole assemblage

Variable group	Significant variables	R^2	F value	P value
Land use	Drought	0.301	4.743	0.004
Habitat characteristics	Clay	0.139	2.505	0.004
	Reed	0.109	2.206	0.023
	Area	0.1	2.314	0.034
	Turbidity	0.085	2.296	0.029

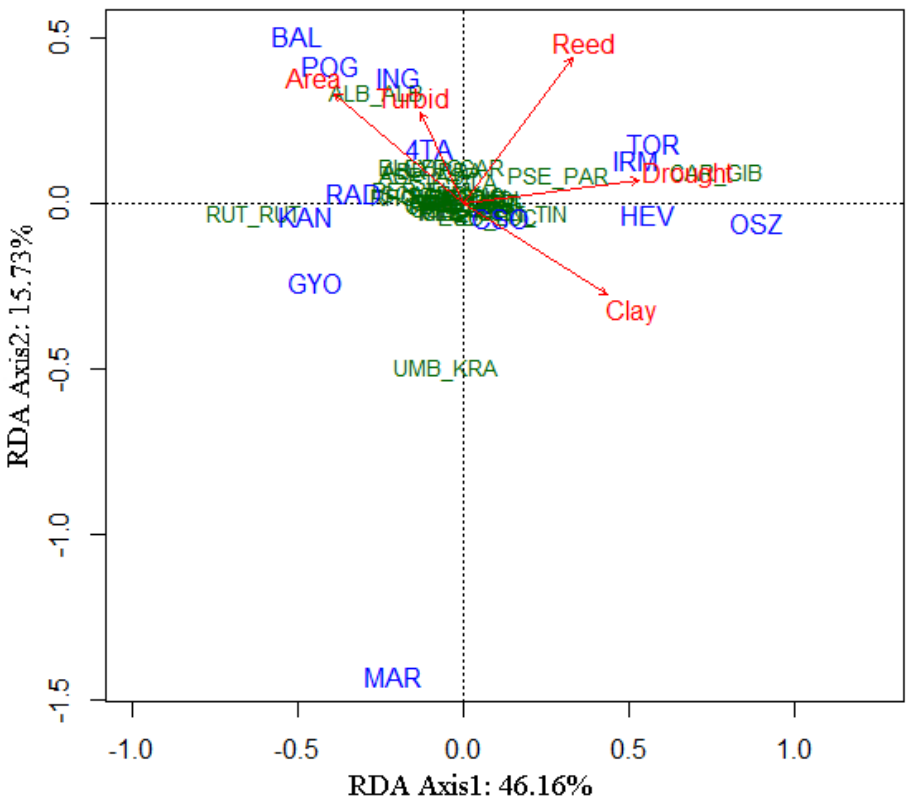

Figure 10: RDA ordination of the whole fish assemblage, based on the RA data. Red arrows represents the significant ones after the forward selection procedure. (The full names of sites can be found in 3.1.1; the abbreviations of fish species were constructed using the Latin names of the fish, see Table 2.)

The first two axes of RDA explained 56.19% of the total variance in the analysis of the native assemblage, which was still relatively high (**Figure 11**.). The forward selection resulted only

in 3 significant environmental parameters: ‘Turbidity’ from the ‘Habitat characteristics’ group and ‘Suction’ (Water level managed by suction) together with ‘Drought’ (Occurrence of dry-out in the last decade) (**Table 5**).

Table 5: The significant environmental variables resulted from the forward selection procedure. Dataset: native assemblage

Variable group	Significant variables	R^2	F value	P value
Habitat characteristics	Turbidity	0.107	4.134	0.003
Land use	Suction	0.191	3.562	0.001
	Drought	0.107	2.25	0.009

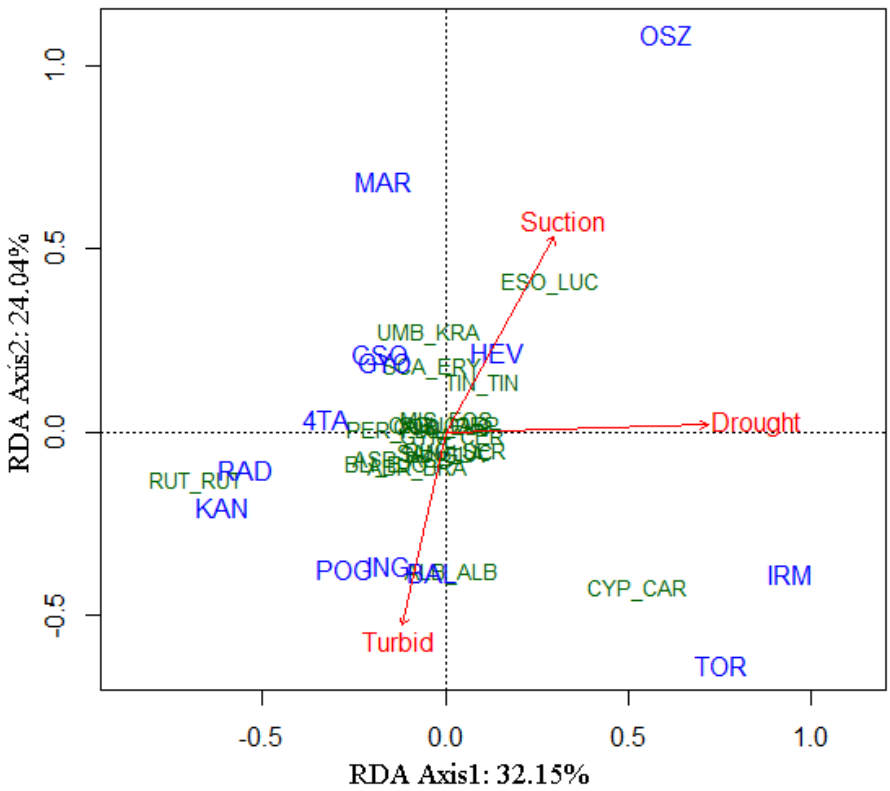

Figure 11: RDA ordination of the native fish assemblage, based on the RA dataset. Red arrows represents the significant ones after the forward selection procedure. (The full names of sites can be found in 3.1.1; the abbreviations of fish species were constructed using the Latin names of the fish, see Table 2.)

Occurrence of drying out showed strong association with the first axis of the RDA, and two groups of habitats could be discriminated along this gradient. Ponds and marshes (TOR, IRM, OSZ) seemed to be positively correlating. All other habitats showed no or a negative relationship with this parameter. The two other significant environmental variables ('Suction' and 'Turbidity') correlated negatively. This gradient had much less discriminative power.

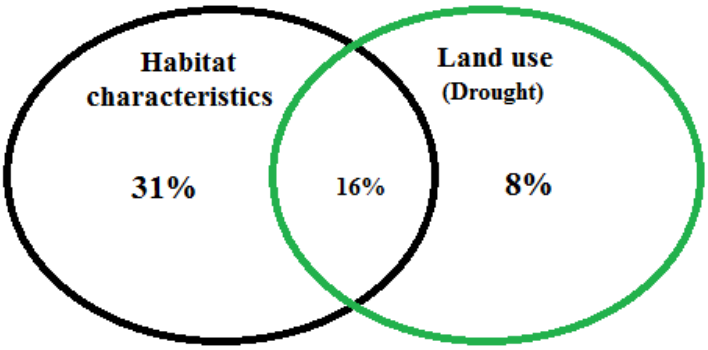

Figure 12: Variance partitioning of the RDA model (Figure 7) constructed for the whole fish assemblage and the significant environmental variables (listed in Table 4). Unexplained variance: 45%

According to the variance partitioning of the RDA model of the whole fish assemblage, significant environmental variables explained 55% of the total variance (**Figure 12**). Altough the pure variance explained by the 'Habitat characteristics' variable group was much higher (31%, see also in **Table 4**), the explanatory value of the only significant 'Land use' variable 'Drought' was also high (8%). The shared effect of the two groups was 16%.

Completely different results have been observed by partitioning the variance based on the RDA model of the native fish assemblage (**Figure 13**). The only significant "Habitat characteristics" variable was 'Turbidity', which explained 7% of the total variation. Significant 'Land use' variables (see in **Table 5**) explained 36% of variation. No significant shared effect could be observed in this case and the total expalined variation was a bit less than in the case of the whole assemblage (43%).

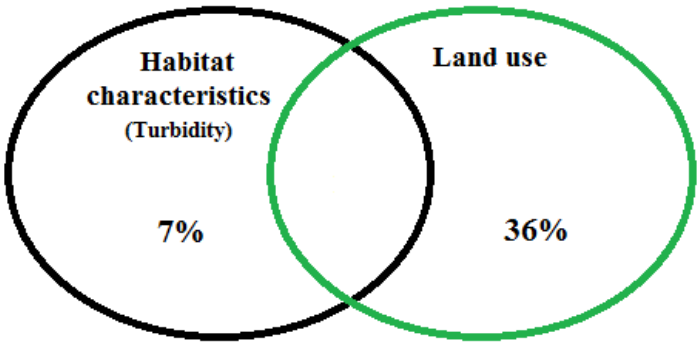

Figure 13: Variance partitioning of the RDA model (Figure 7) constructed for the native fish assemblage and the significant environmental variables (listed in Table 5). Unexplained variance: 57%

4.2 Invasion scenario analysis of Gibel carp (*Carassius gibelio*) in the KBWPS-II (Lake Fenéki)

4.2.1 Species number, diversity

2149 specimen of 23 species (**Table 6**) were caught in the sampling period between 1992 and 2011. The cumulative number of individuals caught varied annually and showed a significantly increasing trend (R^2=0.654; P=0.001) during the period (**Figure 14**).

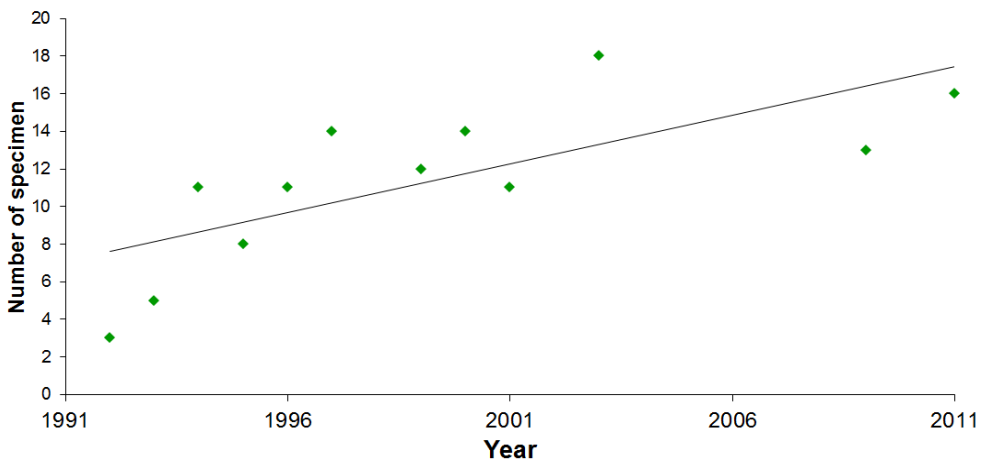

Figure 14: Relationship between the age of Lake Fenéki and cumulative number of specimen caught in a sampling year (y=107.7+9.63x; R^2=0.654, P=0.001)

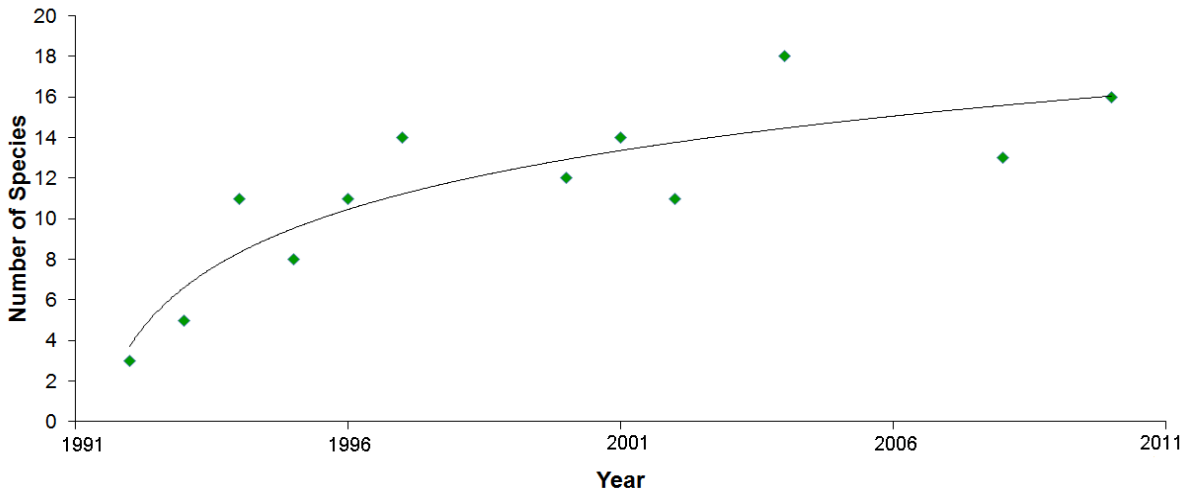

Figure 15: Relationship between the age of Lake Fenéki and cumulative number of species caught in a sampling year (y=107.7+9.63x; R^2=0.654, P=0.001)

Significantly increasing logarithmic trend could be observed in the number of fish species (R^2=0.759; P<0.0001), which increased from 3 to 18 (**Figure 15**). The same increasing trend could be observed in case of the Shannon indices (R^2=0.772; P<0.0001) (**Figure 16**).

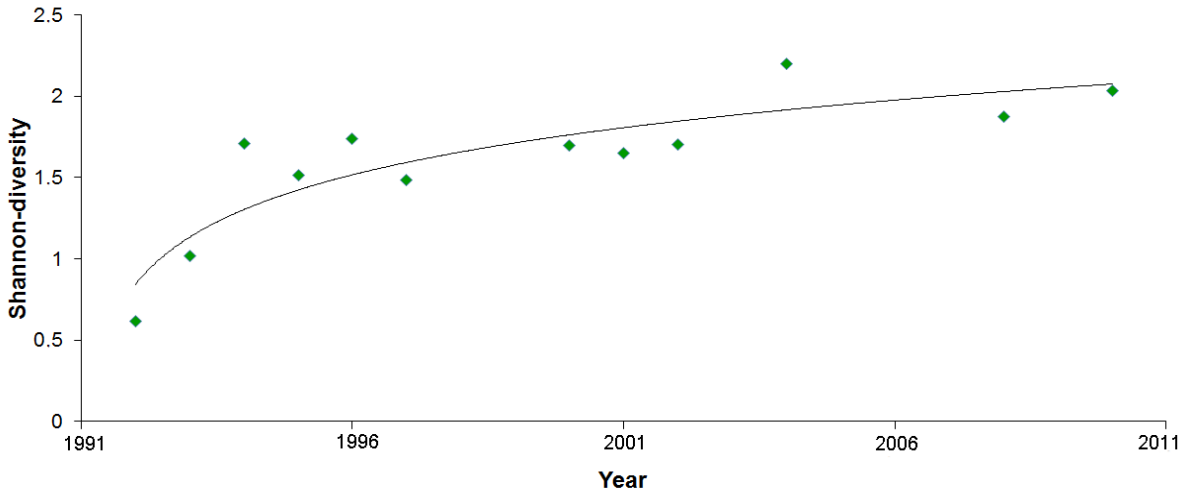

Figure 16: Relationship between the age of Lake Fenéki and the Shannon index (y=0.414ln(x)+0.852; R^2=0.772; P<0.0001)

Table 6: The species composition, relative abundance and trophic guilds in KBWPS-II Lake Fenéki between 1992 and 2011

Species							**Year**							**Trophic guild**
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	Piscivore
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	Invertivore
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	Omnivore
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	Omnivore
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	Piscivore
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	Planktivore
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	Omnivore
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	Omnivore
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	Omnivore
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	Omnivore
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	Omnivore
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	Omnivore
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	Omnivore
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	Planktivore
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	Planktivore
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	Invertivore
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	Omnivore
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	Piscivore
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	Invertivore
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	Invertivore
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	Piscivore
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	Invertivore
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	Invertivore
Number of species		3	5	11	8	11	14	12	14	11	18	13	16	
Shannon diversity		0.616	1.017	1.707	1.517	1.737	1.485	1.699	1.653	1.704	2.202	1.875	2.033	
Number of Individuals		194	125	84	110	91	228	169	157	186	194	280	331	

4.2.2 Changes in the assemblage structure

The annual changes in the relative abundance of dominant species determined three phases of assemblage development (**Figure 17**). A dramatic and rapid change appeared after the second year of flooding: the original marshland fish fauna, which survived in draining canals and was characterized by mudminnow (*Umbra krameri*) and crucian carp (*Carassius carassius*), disappeared rapidly in parallel with the beginning of the gibel carp (*Carassius gibelio*) invasion (**Figure 18**).

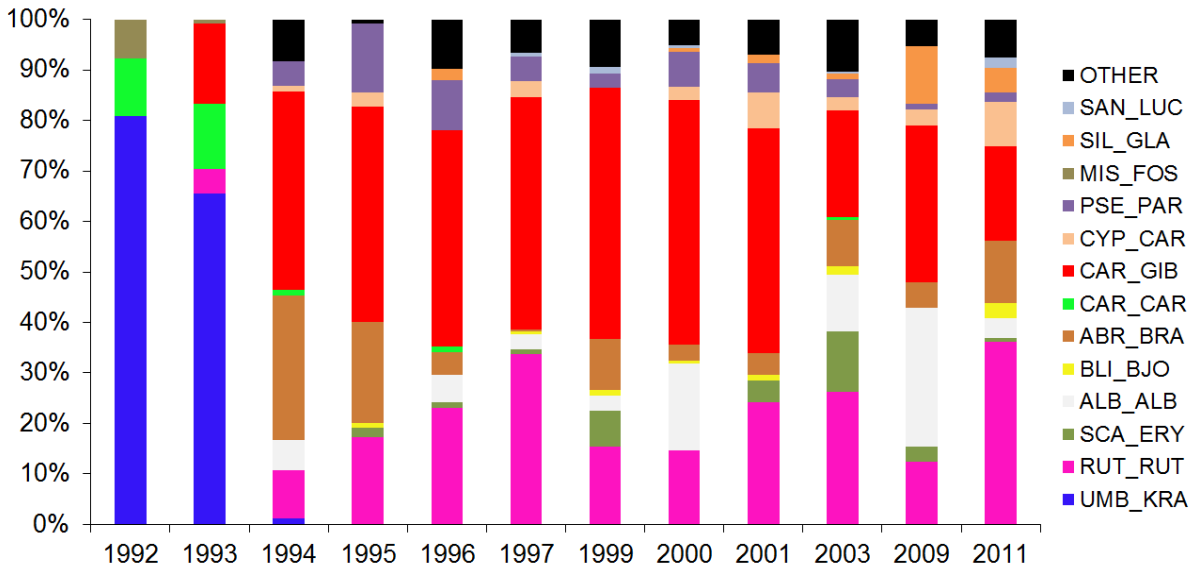

Figure 17: Relative abundance of dominant fish species in the investigated years (see Table 6 for details)

The second phase could be characterized by the strong dominance of non-native species, mainly gibel carp. The transition between the the second (invasion) and third phase (stabilization) was not so fast and easily determinable, but it can be observed in **Figure 19**. The years of the invasion phase are located in the 1:1 quarter, while the years of the stabilization phase located mostly 2:2 quarter of the biplot. The position of the year 1997 is somewhat confusing, however, it can be explained by the high abundance of gibel carp and the co-dominance of roach, therefore, it can 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*) and bleak (*Alburnus alburnus*).

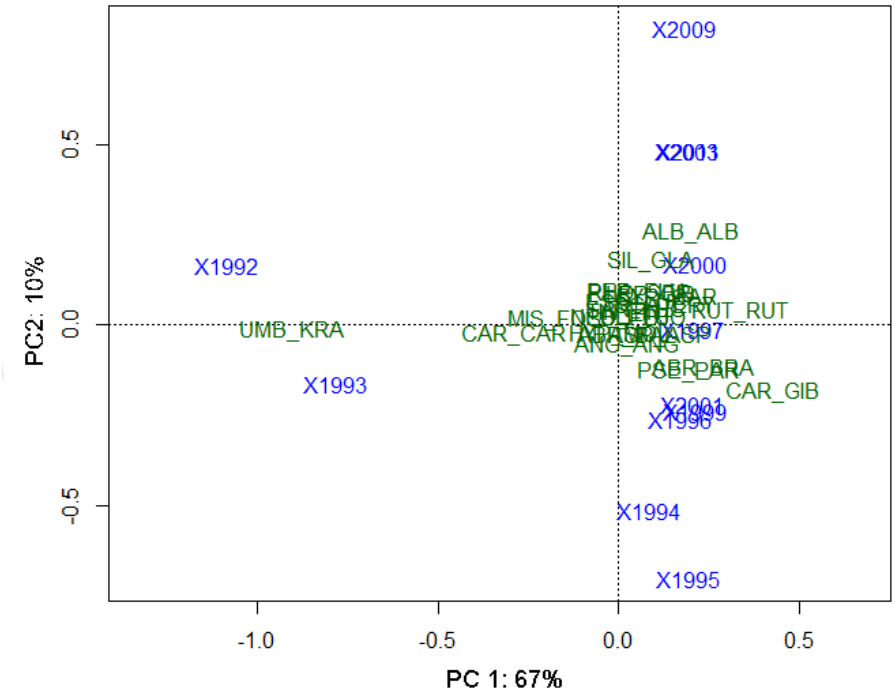

Figure 18.: PCA biplot of the arcsin-square root transformed relative abundance data of the whole sampling period (1992-2011) (Variables: Sampling years; Objects: Relative abundances)

The speed of transition between the first and second phase is visible in **Figure 18**, as the position of the first two years (1992-1993) was strongly positively associated with PC1, which explained most of the total variation (70%). The separation of these samples was caused by the high relative abundance of mudminnow and crucian carp. Considering the assemblage structure of the other years, the discrimination of these samples with PC1 is almost impossible. Regarding PC2, a trend-like pattern could be recognized.

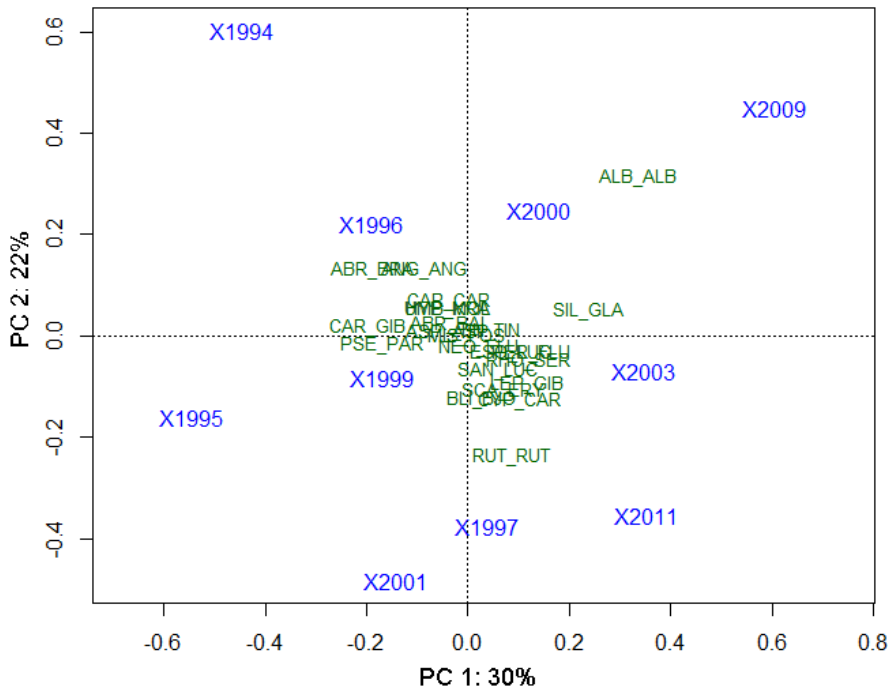

Figure 19: PCA biplot of the arcsin-square root transformed relative abundance data from the period of 1994-2011 (Variables: Sampling years; Objects: Relative abundances)

On the biplot of this second ordination (**Figure 19**), the transition after the invasion phase is illustrated, although it is not that clear as it was in the case of the first phase. Based on this PCA, the second phase, characterized by the dominance of gibel 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 (ANOSIM: R=0.821, p=0.0082).

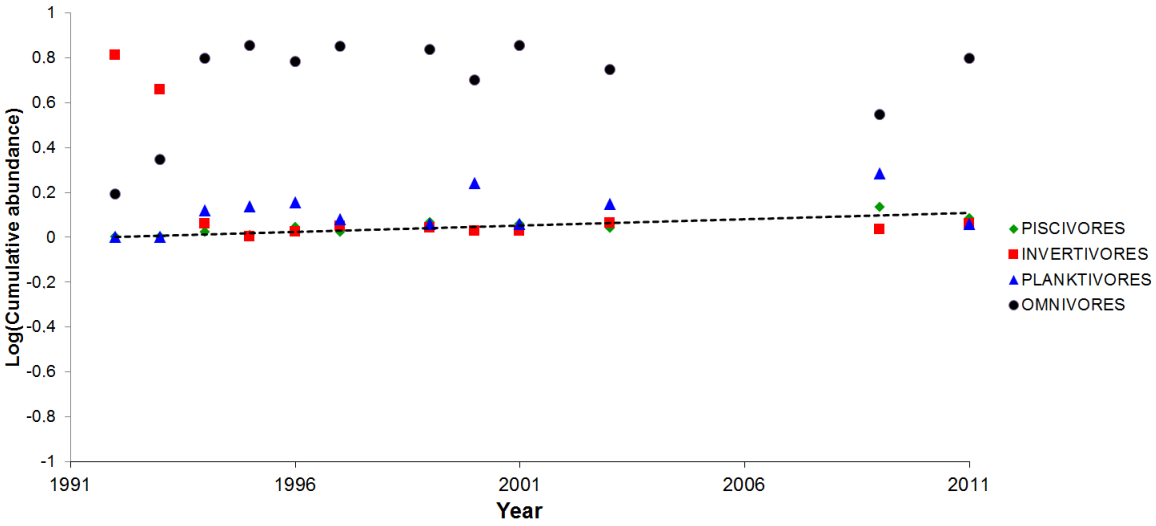

Figure 20: ***Trends in the relative abundance of trophic guilds in Lake Fenéki (Piscivores:*** **y=0.06+0.003x; R^2=0.757; P>0.00001)**

The rapid assemblage composition changes of the first two years caused functional changes as well (**Figure 20**). The OLS analysis resulted in significant positive correlation in the case of reservoir age and relative abundance of piscivores (R^2=0.757; P<0.0001) for the whole examined period, even though their relative abundance was very low (<2%). Although no significant linear trends were observed in the other trophic guilds, the first transition in the assemblage structure resulted in a considerable decrease in the relative abundance of invertivores (from 80% to 0.05%), due to the disappearance of mudminnow and an increase of omnivores (from 19% to 79%), as a consequence of the expansion of cyprinids. This situation was stable during the later periods.

4.3 Ecological Risk Assessment of Non-indigenous Species

The Area Under the Curve (AUC) for the Recievers Operating Characteristics (ROC) curves examined is presented in **Table 7**. Since the values of the AUC varied between 0.8571 and 0.9714 (**Figure 21 and 22**), this indicated that FISK was generally able to discriminate reliably between invasive and non-invasive species.

Table 7: The AUC and treshold values of different ROC curves constructed based on the FISK scores

	AUC	95% CI	Treshold ("Cut off vale")
FISK I (Mean)	0.9714	0.089	19.5
FISK I (Min.)	0.8571	0.057	19.75
FISK I(Max.)	0.9714	0.089	26.75
FISK II	0.9571	0.086	18.5

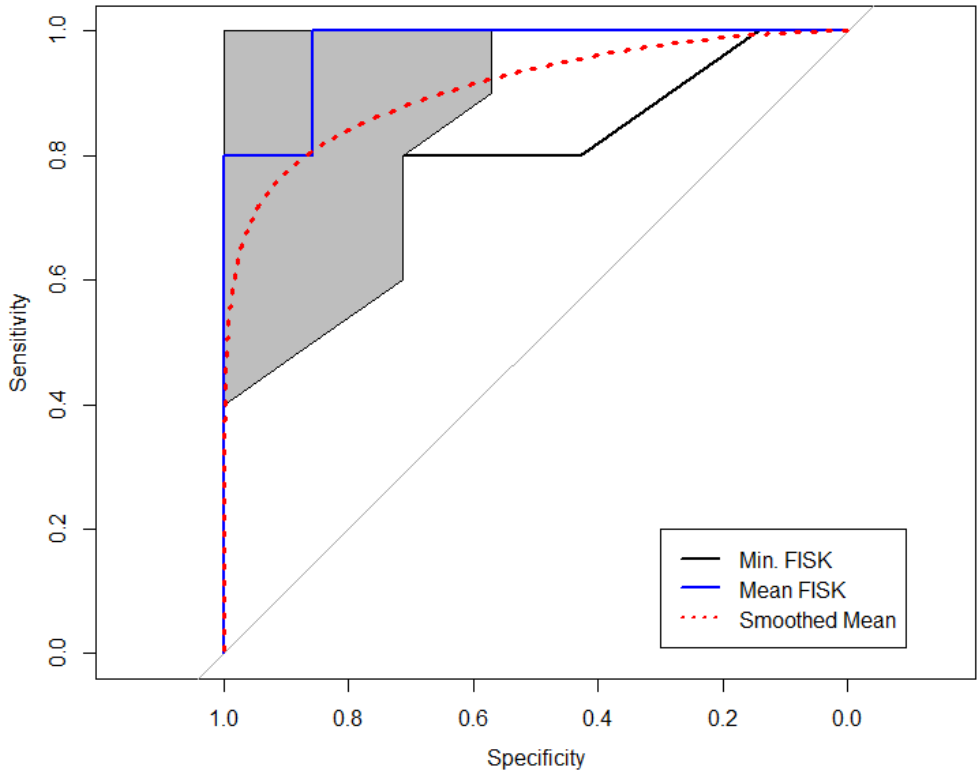

Figure 21: Receiver operating characteristic (ROC) curves for 12 freshwater fish species assessed with the FISK v1 tool for the Balaton catchment, with smoothing line and confidence intervals of specificities for the mean scores („Min FISK" represents the minimum outcome scores of three independent researchers; Mean FISK represents the mean scores of the three assessors)

The Venkatraman permutation test used to compare the ROC curves constructed for each FISK score dataset found no statistically significant difference between the curves (see **Table 8**). Based on that the mean FISK I and FISK II scores were included in further analysis. Paired t-test found differences between the mean of FISK I and FISK II scores, with the latter being significantly lower **(**Students paired t-test: t=3.947, df=9, p=0.00337, **Figure 23**). Youden's and closest point statistics provided similar best threshold of 19.5 for the mean FISK I and 18.5 for FISK II, which were therefore chosen as the calibration thresholds of FISK risk outcomes for the Balaton catchment, and thus to distinguish between medium risk

and high risk species. (Species with score below the threshold are considered ‘medium risk’, and above the treshold ‘high risk’ species.)

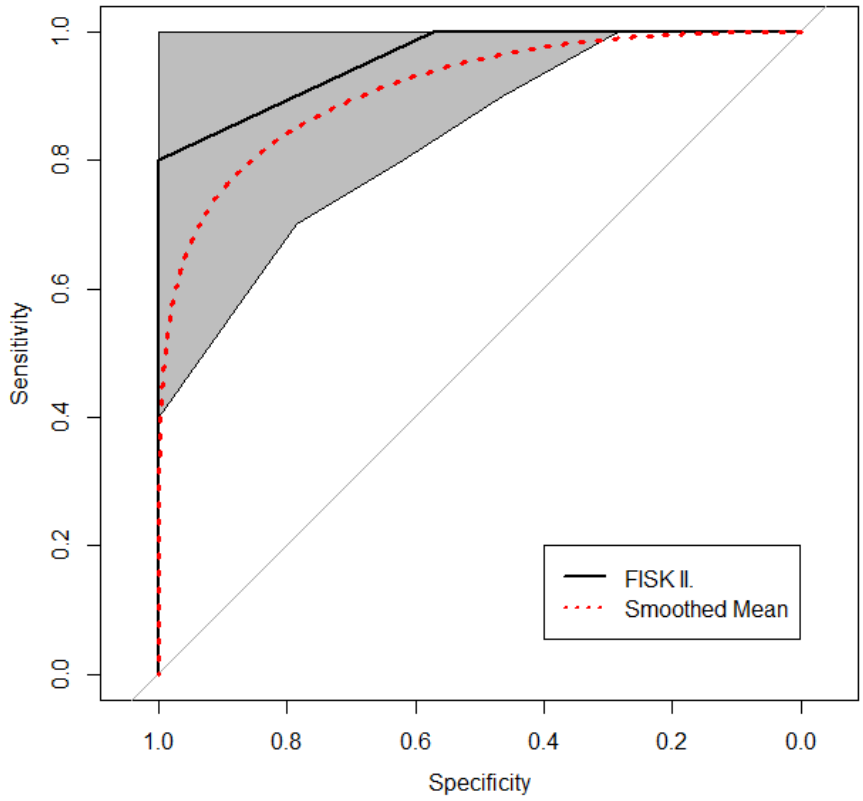

Figure 22: Receiver operating characteristic (ROC) curves for 12 freshwater fish species assessed with the FISK v2 tool for the Balaton catchment, with smoothing line and confidence intervals of specificities

Table 8: Results of Venkatraman permutation tests to determine the difference between the ROC curves

	FISK I Min	FISK I Max	FISK I Mean	FISK II
FISK I. Min	-			
FISK I. Max	E=8 p=0.755	-		
FISK I. Mean	E=8 p=0.496	E=0 p=1	-	
FISK II.	E=8 p=0.75	E=2 p=0.6895	E=2 p=0.742	-

First, the categorization was processed independently in the case of FISK I and FISK II results, then the two categorizations were paired. When consensus was found between the two

results, the species was grouped into the appropriate risk category. For those species where no consensus was found, the new intermediate ‘Medium/High’ category was introduced.

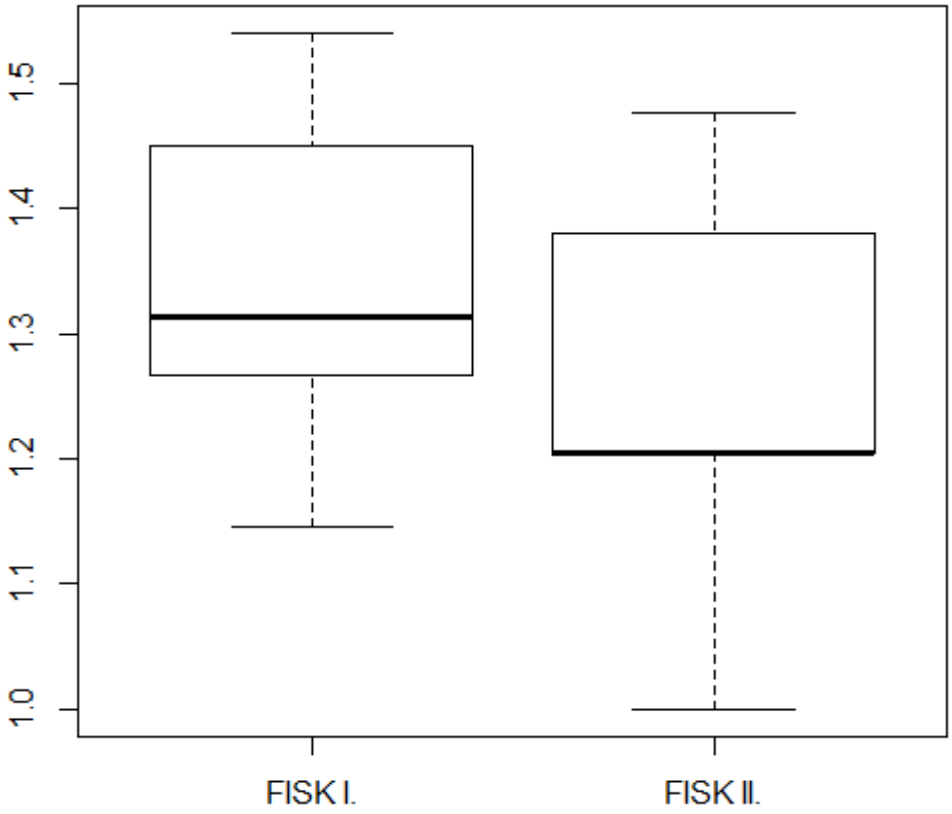

Figure 23: Difference between the mean scores of two FISK assessments (Students paired t-test: t=3.947, df=9, p= 0.00337)

The final result of the risk assessment is presented in **Table 9**. Six of the twelve (50%) species were rated as posing medium risk (*Proterorhinus marmoratus, Onchorhynchus mykiss, Neogobius fluviatilis, Gambusia holbrooki, Hyphophthalmichtys molitrix x nobilis, C. idella*). The number of species in the intermediate ‘medium/high’ category was 2 (16.67%) and altogether 4 species (33.33%; *Lepomis gibbosus; Angiulla anguilla*) were characterized as of high risk (*Ameiurus melas, Carassius gibelio, Perccottus glenii, Pseudorasbora parva*).

Table 9: Fish species assessed with FISK for the Balaton catchment. For each species, *a priori* invasiveness (as per http://www.issg.org and www.fishbase.org) and protection status (as per www.iucnredlist.org); the result of the assessment (Risk category, see the text for details), and reference scores from: UK: United Kingdom (Copp et al. 2009), FL: Flanders (Verreycken et al. 2009); BY: Belarus (Mastitsky et al. 2010.); TR: Turkey (Tarkan et al. 2013); FIN: Finland (Puntila et al. 2013); ESP: Iberian Peninsula (Almeida et al. 2013); Balkans: four counties of the Balkan Penninsula (Simonović et al. 2013.)

	„A priori" categoy	Risk Category	FISK I Mean	FISK II	UK	FL	BY	TR	FIN	ESP	Balkans
Ameiurus melas	Invasive/ Not evaluated	High	32.17	25	28.8	25		27	18	32.7	24.5
Anguilla Anguilla	Non-Invasive/ Critically Endangered	Medium/High	21.50	16	-	-	-	-	-	20	-
Carassius gibelio	Invasive/ Not evaluated	High	34.67	30	36.5	34	34	38	34	37.8	30.5
Ctenopharyngodon idella	Non-Invasive/ Not evaluated	Medium	18.50	16	24	16	14	29	21	31.3	17.5
Gambusia holbrooki	Invasive/ Not evaluated	Medium	14.00	13.5	-	-	-	30	-	24.7	19
Hypophthalmichthys molitrx x H. nobilis	Invasive/ Near threatened	Medium	17.50	16	23	11	15	29.3	-	-	16.4
Lepomis gibbosus	Non-Invasive/ Not evaluated	Medium/High	19.67	16	27.5	25	-	26.3	13	28.7	21.3
Neogobius fluviatilis	Non-Invasive/ Not evaluated	Medium	19.33	10	19	10	15.5	-	24	-	18
Oncorhynchus mykiss	Invasive/ Not evaluated	Medium	14.33	8	-	-	21	13.5	15.5	20.7	15.3
Percottus glenii	Non-Invasive/ Vulnerable	High	26.33	24	28	27	38	16	27	-	18.8
Proterorhinus marmoratus	Non-Invasive/ Least concern	Medium	18.00	10	18.5	13	20	-	12	-	13
Pseudorasbora parva	Invasive/ Not evaluated	High	28.17	21	35	26	37	29	28	31.3	18.3

To validate the FISK results, the recent (2011) datasets of frequency of occurrences and cumulative relative abundances (see 3.1 and 4.1 for details) were used. Spearman rank correlations indicated no relationship between the FISK scores and these attributes of non-indigenous species (**Figure 23, Table 10**).

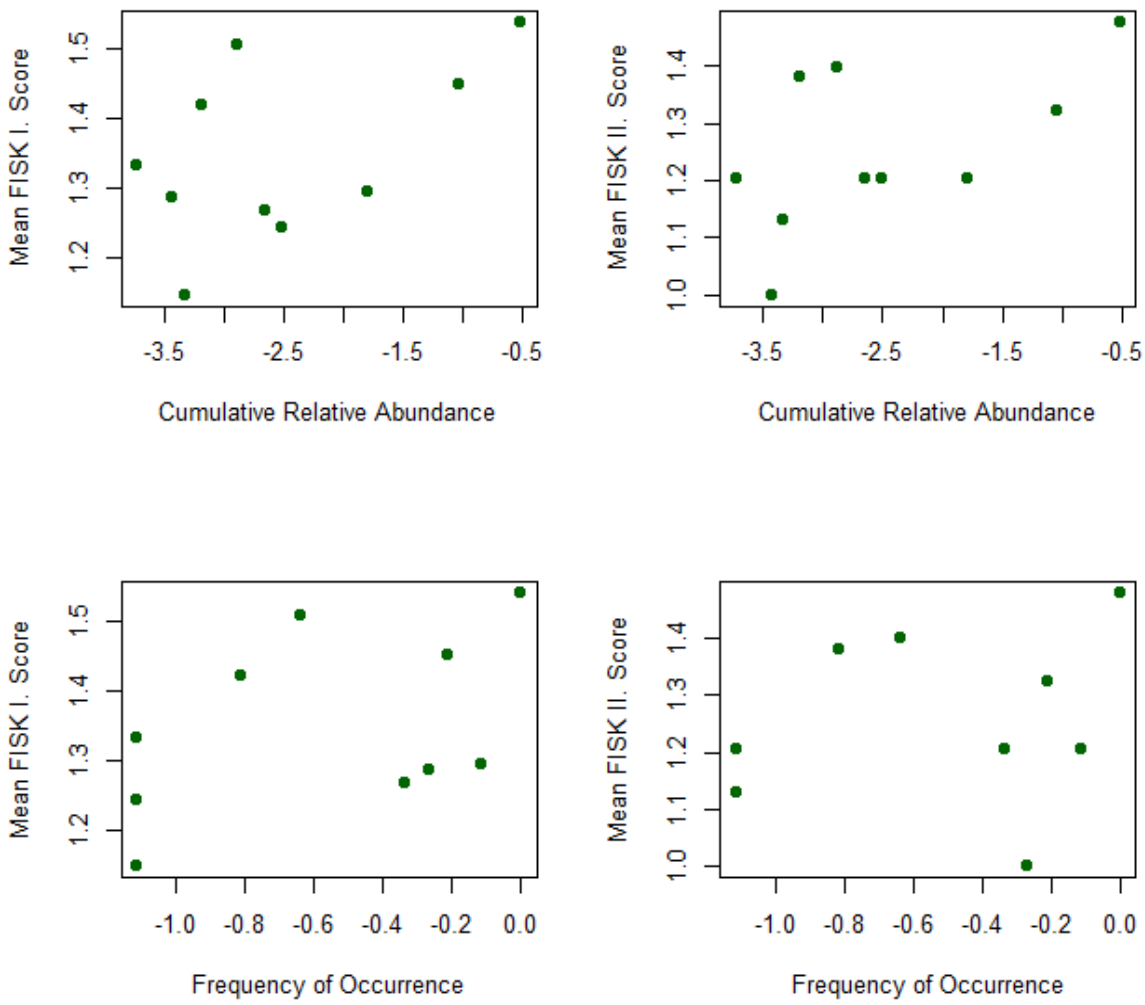

Figure 23: Corelation between FISK scores and distribution indicators (frequency of occurrence, cumulative reative abundance) of non-indigenous fish species

Table 10: Results of Spearman correlation tests between FISK scores and distribution indicators (frequency of occurrence, cumulative reative abundance) of non-indigenous fish species.

	Cumulative relative abundance	Frequency of occurrence
FISK I	r=0.382 p=0.279	r=0.534 p=0.112
FISK II	r=0.557 p=.094	r=0.342 p=0.334

4.4 Faunistical examination of five marshland (berek) areas in the southern shoreline of Lake Balaton

Altogether 3790 specimens of fifteen species were caught during the samplings, of which mudminnow (*Umbra krameri*) was strictly protected and two other species were protected (**Table 11**). The number of non-natives was four, of which gibel carp was the most abundant.

Table 11: Fish fauna of the 5 marshland areas (Lellei-berek, Őszödi-berek, Ordacsehi-berek, Nagyberek and Brettyó) investigated between 2011 and 2013 (relative abundances)

Species	Protection	Origin	Lellei-berek	Őszödi-berek	Nagyberek	Ordacsehi-berek	Brettyó
Carassius gibelio		non-native	49.00	92.99	94.17	17.36	100.00
Pseudorasbora parva		non-native	29.61	0.67	2.58	5.79	0.00
Ameiurus melas		non-native	0.27	0.00	0.00	0.00	0.00
Alburnus alburnus		Native	0.27	0.00	0.68	0.00	0.00
Lepomis gibbous		non-native	11.42	2.76	0.00	0.83	0.00
Perca fluviatilis		Native	0.13	0.00	0.00	0.00	0.00
Rutilus rutilus		Native	1.46	0.00	1.56	0.00	0.00
Rhodeus sericeus	+	Native	6.51	0.00	0.00	0.00	0.00
Cyprinus carpio		Native	0.13	0.00	0.27	0.00	0.00
Scardinius erythrophthalmus		Native	1.06	1.19	0.20	0.00	0.00
Esox lucius		Native	0.13	1.94	0.00	0.00	0.00
Misgurnus fossilis	+	Native	0.00	0.22	0.54	0.83	0.00
Tinca tinca		Native	0.00	0.22	0.00	0.00	0.00
Umbra krameri	+	Native	0.00	0.00	0.00	58.68	0.00
Carassius carassius		Native	0.00	0.00	0.00	16.53	0.00

The ANI and Shannon-diversity values are presented in **Table 12**. Lellei-berek is characterized by the highest Shannon-diversity, but the naturalness is the highest in Ordacsehi-berek.

Table 12: Number of species, diversity and naturalness of the fish fauna of the investigated wetlands

	Lellei-berek	Őszödi-berek	Nagyberek	Ordacsehi-berek	Brettyó
Number of species	11	7	7	6	1
Number of non-natives	4	3	2	3	1
Number of specimen	753	1340	1474	121	102
Shannon-diversity	1.303	0.357	0.3067	1.158	0
ANI	0.329	0.415	0.276	0.119	*+inf*

The representativity of our sampling was very high in Őszödi-berek and Nagyberek, based on the rarefaction analysis (**Figure 25**). In the other habitats, more effort could have resulted in finding some new species.

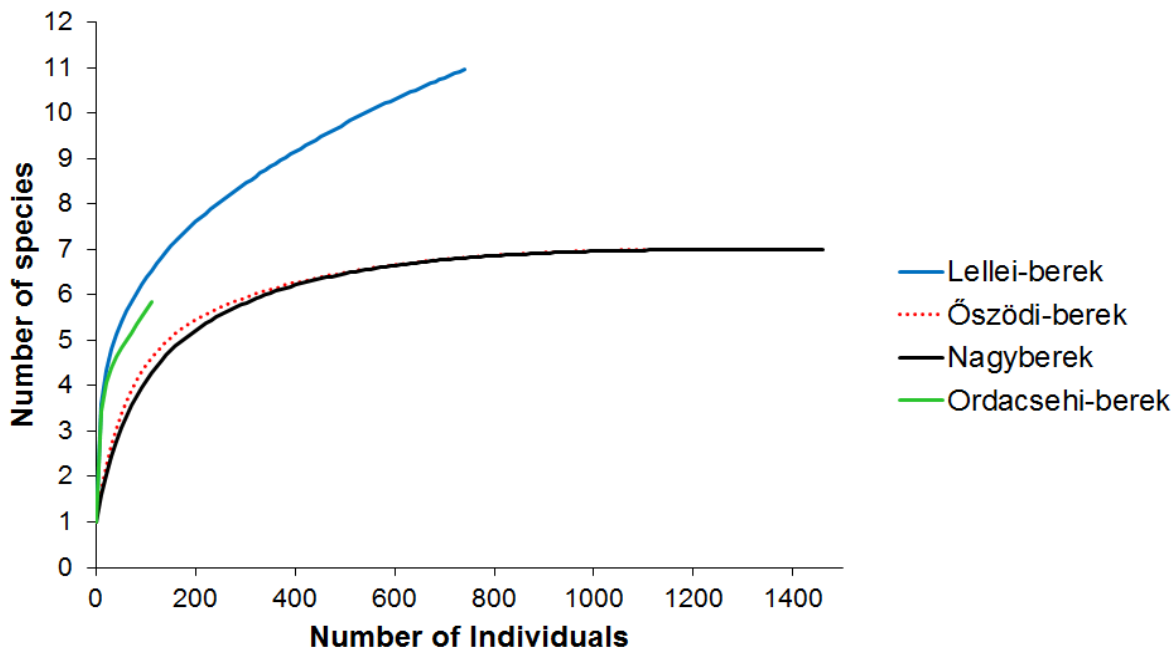

Figure 26: Individual based rarefaction curves of 4 wetland habitats surveyed between 2011 and 2013 (Brettyó is excluded from this analysis)

The five habitats could be divided into 3 groups based on the PCA. The three habitats belonging to the first group were characterized by low number of species and the strong dominance of gibel carp. In the second group (Lellei-berek) the gibel carp was still dominant, but the group was characterized by relative high number of species. In the third group, the Ordacsehi-berek was a unique habitat, with the dominance of mudminnow.

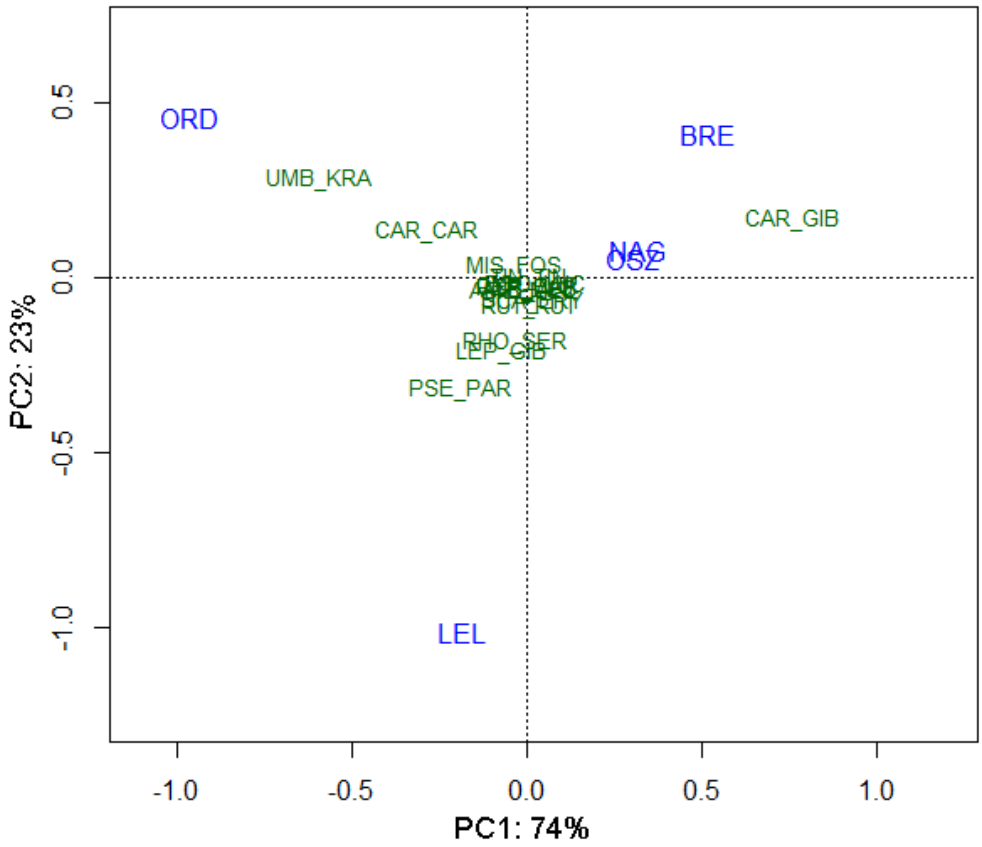

Figure 26: PCA ordination of the 5 wetland habitats surveyed between 2011 and 2013 (abbreviations are constructed using the first 3 characters of the name of the habitat)

5. Discussion

5.1 Occurrence and distribution patterns of non-indigenous species

5.1.1 Species composition, diversity, naturalness and assemblage structure

Approximately 70% (29 species) of all fish species currently inhabiting of the Balaton catchment were found during the surveys (Takács et al. 2011). This number could be considered moderate, but after taking into consideration the fact that stream systems, with their characteristic species (eg. *Phoxinus phoxinus*, *Barbatula barbatula*, *Onchorhynchus mykiss*), were missing from the survey, compared to previous researches the representativeness of this survey was good (Takács et al. 2011, Sály 2013). The effectiveness of catching non-natives was good: 10 from the formerly reported 12 species (83%) were found, which is a high figure. The methodological investigations conducted in Lake Balaton reported 20 species, of which 3 (15%) were non-native inshore and 15 species including 3 (20%) non-indigenous species offshore (Erős et al. 2009, Specziár et al. 2009)

Patterns in the ichtyocoenological structure (**Figure 6**) and the positions of non-natives in the frequency-abundance plot in the lentic habitats of the catchment were similar to those in the small watercourses investigated by Sály (2013). The positions of rare non-indigenous species, which have no self-sustaining populations (*Anguilla anguilla, Hypophthalmichtys* sp.) or need special habitat conditions (*Gambusia holbrooki*) is similar to those natives which are generally not characteristic for lentic habitats (*Cobitis elongatoides, Squalius cephalus*). These species have no real effect on the structure of the fish assemblages. The major difference from the results of Sály (2013) is the position of *Ctenopharyngodon idella*. This species, together with *Ameiurus melas, Neogobius fluviatilis* and *Lepomis gibbousus*, is in a more or less central position in the graph. The latter species have self-sustaining populations in the catchment, while *Ctenpharyngodon idella* have not. The most probable reason is that fish ponds and abandoned fish ponds were included in this survey, where these species had been stocked intentionally. *Carassius gibelio* and *Pseudorasbora parva* were the most abundant and, at the same time, the most frequent non-native fish species of the lentic systems of the catchment, with influential role in the structure of assemblages.

A naturalness gradient could be recognized in the separation of the three main groups regarding their species composition, where the sub-group of the third group (Őszödi-berek)

could be characterized as having the most heavily-modified species composition and the third group (habitats of KBWPS and Lake Balaton) with the most natural fauna. The second group of the two canal habitats, (in their examined section) is considered to stagnating waters. However, in wetter periods or at the time of the autumn timed fish harvesting drought of fish ponds, they might be characterized by slowly running or sometimes with running water, as they are the recipients of these waters. With the high amount of water, valueless 'junk-fishes' (mostly non-natives) also arrive. The intermediate position of the second group may be explained by this phenomenon.

Fish ponds of the Balaton catchment were assumed to be major sources of non-native species by Sály et al. (2011) and Erős et al. (2012, 2014). They found high abundance of non-indigenous species, especially *C. gibelio* and *P. parva* in the neighbouring, connected sections of small watercourses in the examined area. Area covered by fish ponds in the catchment of the investigated stream segments was the most important human disturbance variable, being positively associated with the abundance of non-native species in the surveyed streams (Erős et al. 2012). This observation has not been studied adequately regarding the communities of fish ponds. More evidence on the high persistence of *C. gibelio* and *P. parva* in aquaculture systems and especially in their water supporting canals were provided from South Moravia region of Chech Republic (Musil et al. 2007).

The analyses of RA datasets provided indirect evidence for this 'polluting ponds' hypothesis (sensu Erős et al. 2012). The association between the most abundant non-native species (*Carassius gibelio*) and the fish ponds (Töreki, Irmapuszta) on the PCA biplot (**Figure 9.**) supports the theory that masses of non-native species might escape from the fish ponds and contribute to the degradation of natural waters of the catchment. Two other habitats are associated with *Carassius gibelio* on the PCA: the Hévíz-Páhoki-canal and the Őszödi-berek. The position of the former habitat could be explained with the same effect of fish ponds, but the latter one is not connected to any pond, therefore, its position might be explained by environmental or land use characteristics. The position of the other sites was associated mostly with native species (*Rutilus rutilus* or *Alburnus alburnus*) on the PCA, or they were in transient position, as Csombárdi-pond, which had been functioning as a fish pond years before our survey.

The relationship of fish ponds and non-native species has a long history. One of the most typical reasons for introduction and therefore, a pathway for a non-native fish is aquaculture or fish farming (Hickley and Chare 2004, Copp et al. 2005a, Gozlan et al. 2010).

C. gibelio was e.g. originally imported to Hungary for fish farming purposes (Szalay 1954), and numerous similar examples from all over the world could be mentioned (e.g.: Naylor et al. 2005, Casal 2006).

The invasion facilitating role of reservoirs has been demonstrated worldwide (e.g. Moyle and Light 1996, Clavero and Hermoso 2011, Tarkan et al. 2012a). Results discussed here, however, were contrary to this theory: the surveyed reservoir (ING, POG, RAD, KAN) and shallow lake (BAL) habitats were dominated by native species. Management history of these sites may provide explanation for this finding. The surveyed reservoirs are parts of the KBWPS which were inundated more than 20 years ago (22 and 29), and no notable human disturbance (e.g. fish stocking, heavy water level fluctuations) have happened since then. The decline and stabilization of *C. gibelio* abundance after its invasion are described in a long-term study in the second reservoir of Kis-Balaton (Ingó-marsh, ING) (Ferincz et al. 2012). The invasion of the species peaked 8 years after the impoundment, with the relative abundance of 56.4%. Afterwards, a quite fast decreasing tendency could be observed from the 10th year of the impoundment resulting in a relative abundance of 18% by 2011. It should be noted, however, that although the abundance of non-natives was low, they were present in all reservoirs during our study, meaning potential source populations.

The difference of fish community between the intensively (productive; TOR, IRM) and the extensively (non-productive; CSO, GYO) managed fish ponds was also visible. The latter ponds were characterized by near natural (GYO) or transitional (CSO) fish fauna, in line with the time since they had been abandoned (see 3.1.1).

5.1.2 Effect of local environmental and land use patterns on the relative abundance of non-indigenous fish species

High RA of *C. gibelio* in the Őszödi-berek (and in other wetlands, see 4.4 and 5.4) could not be explained by the effect of fish ponds. Additionally, the reason for the high abundance of non-indigenous fish species is still unknown. The RDA model constructed for the whole fish assemblage revealed the occurrence of drying outs (within the ‘land use’ variable group) as a significant factor, which additionally showed a positive linkage with the *C. gibelio* abundance. Although the variance partitioning of this RDA model (Figure 10.) revealed only 8% of explained variance for this variable, there was no other significant local environmental variable that would have showed a similar relationship with the RA of this species in the

RDA. Hence, it can be suggested that this variable plays an important role in the abundance patterns of *C. gibelio*. A series of local invasion events were assumed, mediated by the periodical dry-outs. In case of wetland areas it is a semi-natural process, potentially facilitated by the climate change. The drying out of a waterbody does not necessarily mean the complete extinction of the local fish fauna. There are usually some refugia, for example, a deeper hole in the bottom, where a small portion of fish might survive. As *C. gibelio* have an effective oxygen deficiency tolerance mechanism (Lutz and Nilsson 1994), it can tide over unfavourable periods. After the re-flooding of the habitat, re-colonization starts, and the alternative gynogenetic reproduction mechanism of the species can become advantageous (Kalous et al. 2004, Tarkan et al. 2012b) and results in large monodominant populations until the next drying out. From the habitat point of view, these desiccations can be interpreted as disturbances. And since the wetland areas of the Balaton catchment are not adapted to such events, this process is an alteration in their natural disturbance regime, which could facilitate invasions (Moret et al. 2006, Clarck and Johnston 2011). This scenario is similar in fish ponds, where desiccation occurs in 1-5 year periods, associated with fish harvesting, depending on the type of the pond. Small-bodied fish might find refugia in the fish bed, until the pond is refilled.

When another RDA model was constructed without the data of non-natives, the 'drought' variable was still significant, as along with 'suction'. These two land use variables were accounting for 36% of the total variance, while among local variables, only 'Turbidity' was significant (accounting for 7%). The occurrence of drying outs is only related to the two examined fish ponds. The native fish fauna of these ponds is strongly dominated by *Cyprinus carpio*, which is a strong discriminating factor from other habitats in the RDA (**Figure 11**). This species is stocked intentionally, being considered the most important species for fish farming. The variance explained by land use variables is therefore mostly probably attributable to this species.

5.1.3 The role of local invasions on catchment level and management opportunities

The local invasions of gibel carp are probably the main drivers of the source-sink dynamics of non-native species on the catchment level (Erős et al. 2012). Fish ponds, angling ponds and wetlands are source populations of non-natives (mainly *C. gibelio* and *P. parva*), providing continuous pressure for the streams and other semi-natural habitats of the system.

Such dynamics were also reported not only in human-modified and non-native-stressed habitats (Woodford and McIntosh 2010, Glowaczki and Penczak 2013), but also in case of a beaver-influenced natural landscape (Schlosser 1998).

The management possibilities on non-native fish invasions are reviewed by Britton et al. (2010a). The limited possibilities of complete eradication (by piscicides or removal) are obvious, as the methods impose substantial collateral damage on native species and need huge effort (Simberloff 2002, Koehn 2004). As this study revealed the role of a management related disturbance factor (occurrence of drying-out), this implies the opportunity to control individual invasion events simply by providing continuous water cover in wetlands, and by alternative management of fish ponds. The potential decline of *C. gibelio* in the studied habitats might result in a simultaneous decrease of its abundance in adjoining streams.

5.2 Invasion scenario analyisis of *Carassius gibelio* in Lake Fenéki (KBWPS-II)

The present fish assemblage of Lake Fenéki is the result of mostly natural processes, as fishing is prohibited in the Nature Conservation area. The number of species and diversity showed an increasing trend throughout the whole study period, seemingly not affected by the gibel carp invasion. The same trend was described in other Central European reservoirs (Penczak et al. 1998, Riha et al. 2009). The trend in diversity suggests that gibel carp invasion did not strongly influence the colonization of native fish species.

The development of fish assemblage structure can be divided into three stages. The first stage (marsh phase; 1992-1993) could be characterized by bog-dwelling species (mudminnow and crucian carp), which survived in draining canals formerly presented in the study area. The transition from the first to the second stage was fast and dramatic, but this can be considered usual in such modified, disturbed and artificial waterbodies (Seda and Kubecka 1997, Wolter 2001).

The second phase (invasion phase), characterized by the constantly high relative abundance of gibel carp, lasted from 1994 to 2001. The fast expansion of this species is often reported not only from artificial and disturbed waters (Gaygusuz et al. 2007, Markovic et al. 2007, Paulovits et al. 1998), but also from natural waters (Tarkan et al. 2012b, Vetemaa et al. 2005). Numerous hypotheses were formulated for the reason for this fast invasion, for example, a special tolerance mechanism for oxygen deficiency (Lutz and Nilsson 1994),

omnivorous feeding (Balik et al. 2003, Specziár et al. 1997), effective predator avoidance (Gere and Andrikovics 1991), and an alternative gynogenetic spawning strategy (Beukeboom and Vrijenhoek 1998, Kalous et al. 2004). Only a few comparative datasets are available regarding the magnitude and duration of such gibel carp 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 described 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 has occurred. The reason for the collapse of the gibel carp population 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 and Kubecka 1997).

The results suggest that among non-natives, only gibel carp reached such a high relative abundance that may have considerably affected fish fauna development. The most serious qualitative impact of the gibel carp invasion was the displacement of the native congener, crucian carp. This process has long been known (Lelek 1980, Tarkan et al. 2009), and the possible underlying mechanisms may be hybridization (Haenfling et al. 2005, Tóth et al. 2005) and reproductive/interference competition (Kalous et al. 2004, Tarkan et al. 2012b). gibel carp is known to exhibit gynogenetic reproductive strategy, exploiting the males of other species to activate egg development (Beukeboom and Vrijenhoek 1998, Kalous et al. 2004, Tarkan et al. 2012a,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 became more and more similar to the fauna of the reed habitats of Lake Balaton (Erős et al. 2009), which latter could be used as a natural reference.

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 was only able to delay the natural successive process, and could not completely alter it.

5.3 Ecological Risk Assesment using the FISK algorithm

5.3.1 Calibration of FISK and Risk Assessment of non-indigenous fish species in the catchment

The scores obtained here (18.5 and 19.5) were consistent with most of the cut-off values across the globe (17 in southern Australia – 23 in Turkey) (Copp et al. 2009, Mastitsky et al. 2010, Verreycken et al. 2009, Onikura et al. 2011, Vilizzi and Copp 2012, Almeida et al. 2013, Puntila et al. 2013, Tarkan et al. 2013). The only exception is the Balkans region, where a cut-off value of 9.5 was determined (Simonović et al. 2013). In the Balkans, where the number of local endemic species is high, many species have become invasive and caused adverse effects on the native fish assemblage as a result of within region, between catchment translocations. These species have no real invasive profile in general, that is why low output scores have been gained from the FISK, which influenced the cut-off value negatively (Simonović et al. 2013).

Taxonomic patterns of the highest score species show similarity to the former studies. Cyprinids and ictalurid catfishes fell also in this category (Mastitisky et al. 2010, Almeida et al. 2013, Puntila et al. 2013, Tarkan et al. 2013).

Carassius gibelio received the highest score (both in FISK I and FISK II), similarly to all other examined areas in Europe and Asia Minor (Copp et al. 2009, Mastitsky et al. 2010, Verreycken et al. 2009, Almeida et al. 2013, Puntila et al. 2013, Tarkan et al. 2013). The species has a long history of invasiveness and according to results presented in 4.1 and 5.1, it was the most common non-native species in the lacustrine ecosystems of the Balaton catchment. It has been reckoned as native to Far-East (Banarescu 1990). Establishment of the species in the Danube - water system could have occurred in two ways. The first is natural area expansion over Romania (Holcik 1980), the second is anthropogenic and well documented. For aquaculture utilization, the species was imported from Bulgaria to HAKI (Halgazdálkodási és Öntözési Kutatóintézet, Szarvas) in 1954 (Szalay 1954). Subsequently, a fast invasion began. The first report from the Hungarian section of the Danube is from 1975 (Tóth 1975), but no similar data is available on the first observation in Lake Balaton. Bíró (1997) dated the introduction of *Carassius gibelio* to the mid 1970s.

Ameiurus melas is characterized by the second highest scores both in FISK I and FISK II assessments. The species is categorized into the 'high risk' category in all European and Asia Minor studies where it was assessed, except for Finland (Copp et al. 2009, Mastitsky et al. 2010, Verreycken et al. 2009, Almeida et al. 2013, Puntila et al. 2013, Tarkan et al. 2013). The black bullhead occurred (imported for aquaculture) in Europe first in France in 1871 (Coucherousset et al. 2006). The species expanded relatively slowly; however, nowadays this is the most widespread North American ictalurid catfish in Europe (Pedicillo et al. 2008). The expansion was human-mediated in some cases, for example, it was imported to Hungary from Italy in 1980 (Harka 1997). In other situations, a slow, self-managed spreading was observed: e.g. in Spain (first recorded in 1984 (Elvira 1984)) and Portugal (first recorded in 2002 (Gante and Santos 2002)). The black bullhead is tolerant of harsh water conditions (e.g. water pollution, low dissolved oxygen levels), is omnivorous, aggressive, and has parental care and prolonged reproduction period (Braig and Johnson 2003, Novomenská and Kovác 2009, Scott and Crossman 1973). Although characterized by a high score, its abundance and frequency of occurrence is generally low in the examined waters of the Catchment.

The third 'top' species is *Perccottus glenii*. The reputation of the species is confusing: while it is classified as "Vulnerable" in the IUCN red list, it is also rated as of 'medium risk' in Turkey (Tarkan et al. 2013). The invasion of amur sleeper (or rotan, from Russian) is a hotspot in freshwater fish biology. The expansion of this small odontobutid (*Perciformes: Odontobutidae*) species is well documentated in Eastern and Central Europe (Nalbant et al. 2004, Kosco et al. 2003, Simonović et al. 2006, Reshetnikov 2004, Nowak et al. 2008, Terlecki and Palka 1999, Harka and Sallai 1999, Erős et al. 2008, Jurajda et al. 2006), probably because of the lesson gained from the former gibel carp invasion. The native range of the species is situated in the Russian Far East and in the northern part of Korean Penninsula. The Eurasian expansion started with two introduction events (St. Petersburg, 1912 and Moscow 1948, released from aquaria) (Kosco et al. 2003). The first Hungarian specimen of the amur sleeper was collected in 1997, in the Tiszafüred section of River Tisza (Harka 1998). After that date, the spread of the species was a continous natural-like (non-human mediated) process. The amur sleeper invaded the highly vegetated canals, oxbows and other lentic habitats along the Tisza valley (Harka and Sallai 1999, 2004, Takács 2007). In this period, ichtyologists expected, that the species needs decades to reach the Transdanubian region (Erős et al. 2008). On the 22th April 2008, one specimen of amur sleeper was caught in the Kisvid section of the Marótvölgyi canal (N46 30.556 E17 17.314 (see **Figure 27**), flowing

into the Kis-Balaton section of River Zala, which is the main inflow of Lake Balaton (Erős et al. 2008).

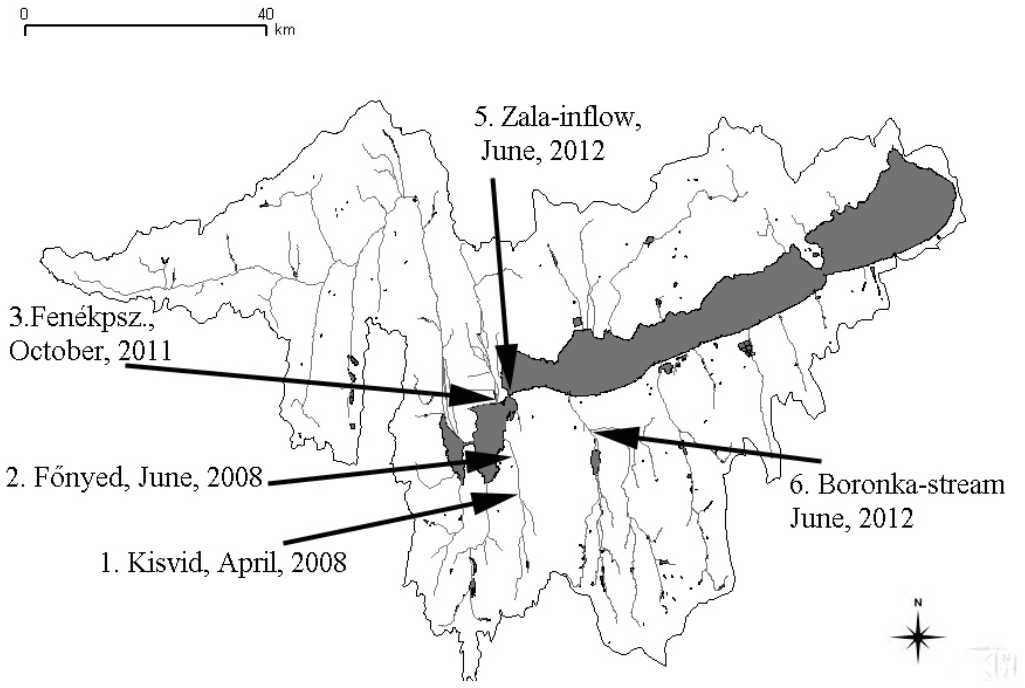

Figure 27: Distribution map of the amur sleeper (*Perccottus glenii*) in the Balaton catchment

An other specimen of the species was identified in the Marótvölgyi canal nearby Főnyed (N46 38.024 E17 15.756, ca. 15 km lower section) on 25th June 2008 (Harka et al. 2008). The next finding of the species from the system was from the Főnyed-site, mentioned above (Antal et al. 2009). On 11th October 2011, our working group sampled the Hévíz-Páhoki (N46 42.051 E17 14.252) canal nearby Fenékpuszta and caught two specimen of the species (Ferincz et al. 2012). This occurrence is interesting, because the amur sleeper spreads typically downhill within river basins. The species reached the inflow of the River Zala (N46 42.109 E17 15.494) in 2012 and in paralel, it was caught in another inflow, in the Boronka-stream (N46 39.467 E17 25.979) (Takács et al. 2012a). The last occurrence is quite unexpected. Two hypotheses were built for its explaination: (1) the possibility of multiple introductions and (2) the possibility of spontaneous spreading (Takács et al. 2012a). The amur sleeper was introduced to the catchment most possibly via an uncontrolled fish transport from the Tisza Valley and similar invasion pathways are often described worldwide (Cohen 2002, Garcia-Berthou 2007). In the case of the first hypothesis, a second, accidental introduction

was assumed. In the second case, the process is natural area expansion. In my opinion, the first hypothesis is more realistic, because the inflow of River Zala (N46 42.365 E17 15.888) and Boronka-stream (N46 42.470 E17 22.922) are quite far from each other (approx. 10 km) and the metaphytic amur sleeper could not be able to bridge this distance. The diet of the amur sleeper includes wide range of animal species from all trophic levels and quite similar to that of the native endangered *Umbra krameri* (Reshetnikov 2003, Kosco et al. 2008, Kati et al. 2013). Moreover, the habitats of these species are the same, and hence interference through larval predation can occur (Kosco et al. 2008, Kati et al. 2013).

Pseudorasbora parva is also ranked in the 'high risk' category, similarly to all European and Asia Minor countries (Copp et al. 2009, Verreycken et al. 2009, Almeida et al. 2013, Puntila et al. 2013, Tarkan et al. 2013). This small mainly planktivorous fish species (also called: stone moroko) is described as the most invasive fish species of Europe (Gozlan et al. 2005). It is native in the Far East: China, Korea and even in the western regions of Japan (Pinder et al. 2005). The introduction to Europe (and Middle Asia) happened accidentally in 1960-1962 (same time in Hungary), when larvae of large herbivorous cyprinids (*Hyphophthalmichtys sp.* and *Ctenopharyngodon idella*) were imported from China (Boltachev et al. 2006, Perdices and Doadrio 1992). The continental-scale invasion happened in the 1970-80's (Anhelt 1989, Pintér 1987, Bianco 1988), and currently, the species is widespread throughout Europe and locally abundant in every suitable habitat (Pollux and Korosi 2006). Extremely high abundances often occur in small angling ponds, nursing ponds and canals of pond aquaculture facilities (Britton et al. 2010b, Adamek and Siddiqui 1997, Rosecchi et al. 2001). There is little available information about its effect on native fish assemblages, but competition for spawning with the endangered *Pseudorasbora pumila* was observed in Japan (Konishi and Takata 2004), and trophic overlaps with *Rutilus rutilus* and *Scardinius erythrophthalmus* was described, which resulted in trophic level shifts (Britton et al. 2010c).

The status of *Hypophthalmichtys molitrix x Hypophthalmichtys nobilis* is special in Lake Balaton. In the current assessment, it was classified into the 'medium risk' category, as in Flanders and Belarus (*H. molitrix* was used for reference; Mastitsky et al. 2010, Verreycken et al. 2009). The species was introduced in 1973, and until 1983, 889 metric tons of silver carp were released in the water. The recapture was not efficient enough, and therefore, one third of the total fish biomass of the Lake is "Asian carp" (Virág 1995, Tátrai et al. 2005, Boros et al. 2012). There are several proofs, which confirm that the 'Asian carps' recently inhabiting Lake

Balaton have escaped from aquacultures and fish ponds located in the southern region of the Catchment. (1) The length distributions of the samples collected by the commercial fisheries suggest that most of the fish have an age of maximum 10+. (2) Juvenile specimen were only caught in the upstream of the southern inflows, where the aquacultures are located. (3.) The analyses of the ovaries of female fish found only crude eggs in the spawning period and athretising eggs in autumn (Boros et al. 2012). Assessments in this study were strongly based on these findings, and the FISK scores are in coherence with it.

There is a seemingly incosistent pattern in the results at species level in international context. *Gambusia holbrooki* is usually rated as 'high risk' species (Almeida et al. 2013, Simonović et al. 2013, Tarkan et al. 2013), but it was only a 'medium risk' species for the Balaton catchment. This means that even though its invasive potential is high, the climatic conditions of the Catchment are now able to control the spread of this species. This species is able to reach the Lake during one average summer, because of its effective ovoviviparous spawning strategy (Specziár 2004) and this small and feline-looking fish usually has serious negative impact to the recipient environment mainly through the fish, macroinvertebrate and amphibian fauna (Vidal et al. 2010, Smith et al. 2008, Englund 1999). With the increasing frequency of warmer winters (as a consequence of climate change), the limitation of mosquitofish might decrease.

5.3.2 Validation of FISK for the Catchment

No significant correlations were observed between the average relative abundances of the assessed species and the FISK I or FISK II scores. Two alternative explanations can be possible: (E1) the assessed species had – in some cases – not enough time to invade the catchment yet, and this masked the statistics, or (E2) the integrity and biotic resistance of the ecosystem is high, and not easily invadeable.

E1 is seemingly supported by the case of *Perccottus glenii* and maybe the *Ameiurus melas*. *P. glenii* was described from the catchment only 5 years ago (Erős et al. 2008). Such a short time probably was not enough to perform a real invasion, however, it is spreading fast (see 5.3.1 for details). *A. melas* has been present in the catchment for a much longer period (Wilhelm 2013). The spread of the species was not well documented and its case is more confusing due to the other ictalurid catfish *Ameiurus nebulosus*, which was introduced in the

early 20th century, but was completely displaced by *A. melas* lately (Harka and Sallai 2004, Wilhelm 2013). The reason for the displacement is mostly unknown, but competition between the two congeners can be assumed, which might have caused a lag-phase in the expansion of *A. melas*. This assumption is supported by numerous recent observations of anglers throughout the catchment, while the occurrence of *A. melas* has increased in their catch in the last 1-2 years.

The question of the catchment-scale invadeability is complex, as habitats of the catchment are diverse. The results described in 4.1 and 5.1 indicated that 'invadedness' of the examined habitats are strongly asymmetric. High abundance of invasive non-indigenous species is characteristic only in habitats in which disturbance occurs with high frequency. Non-natives could be found in other places with much less abundance. These findings might support the second theory, while the biological resistance of less disturbed habitats is enough to resist the propagule pressure of non-natives from the other invaded habitats. E2 could be invalidated by the examples of invasive mussels. Rapid and prominent invasion of of the zebra mussel (*Dreissena polymorpha*), then quagga mussel (*Dreissena bugensis*) in Lake Balaton indicates no such biotic resistance, as before the establishment of *D. bugensis*, *D polymorpha* became the most abundant bivalve (both in abundance and biomass) in the lake (Balogh et al. 2008, Balogh and Purgel 2012). The situation with chinese pond mussel (*Sinanodonta woodiana*) is similar. It was described from the lake in 2006 (Majoros 2006) and until 2011, it became the dominant species and displaced the native *Anodonta* species, especially in the Keszthely Basin (Benkő-Kiss et al. 2013)

5.3.3 Comparison of FISK I and FISK II systems

Although no significant difference was found between the ROC curves of FISK I and FISK II assessments, at the species level, the mean of scores were significantly lower in the case of FISK II. This difference is most possibly due to the slight methodological changes between the two versions, more precisely in the 'Feeding guild' related questions and by the 'Ultimate body size' (for example, *L. gibbosus* and *P. glenii* reach 10 cm, but not 15 cm) (Lawson et al. 2013). In my opinion, the usability of FISK I under temperate climate is still appropriate, but FISK II is more user friendly and gives more comparable results.

5.4 Faunistical examination of five marshland (berek) areas in the southern shoreline of Lake Balaton

The fish assemblage of each habitat is species-poor, compared to the other studied lacustrine habitats in the catchment (4.1). Most of these wetlands are connected to streams flowing into Lake Balaton at least periodically. There is no evidence for the mixing of their fish fauna, but the species numbers characterizing these waterflows are much higher (Sály et al 2011, Takács et al. 2011). This species-poorness could be explained by the special features of these habitats: the fishes of such a wetland are affected by both environmental stress (habitat conditions: high temperature, low amount dissolved oxygen) and frequent disturbances (periodical drying-outs). (Terminology has been used after: Borics et al. 2013). These two factors decrease species number and increase the dominance of opportunistic species (Gray 1989).

Within these generally low species numbers, the number of non-indigenous species was high. The most abundant one was gibel carp, as it was reported from the whole catchment (see 4.1). This species is dominant in all investigated wetlands, and its RA is above 90% at 3 out of 5 sites. The reason for this extreme dominance is probably the same what we described in 5.1.2.

I have to point out that although protected species could be found in 4 habitats, in Lellei-berek this species was bitterling (*Rhodeus sericeus*), which is not a typical bog-dwelling species (Harka and Sallai 2004). Based on the species composition and the high density characterizing this habitat, the effect of the nearby Irmapuszta fish pond system can be assumed, similarly to the ‘polluting ponds’ hypothesis discussed above (5.1.1), originally described by Takács et al. (2007) and Sály et al. (2011).

The fish fauna of the Ordacsehi-berek was separated clearly based on the PCA. The strictly protected mudminnow was its dominant species (58.7%), which makes it a valuable, although not unique habitat of this species (see 4.1, Takács et al. 2012b). The RA of crucian carp was also high. The gibel carp was only the third on the dominance list, and its abundance was low compared to the other wetlands. In the current situation, this habitat is the most valuable and probably refers best to the disappeared, historical fish assemblage of the wetlands described by Herman (1887).

6. Summary

The negative effect of non-native, invasive species on their recipient ecosystem is a widely discussed, commonly recognised fact nowadays. The size of this effect is largely asymmetric, either between the species, or the habitats being invaded. The reckonassiance of these effects is considered a hard and complex work. At first, the distribution pattern of non-native fish species and the effect of 19 explanatory variables were examined in the Balaton catchment. The second work included in this dissertation is a case study, which addressed to assess the effect of the *Carassius gibelio* invasion on the fish assemblage of a given habitat. In the third part, non-indigenous species were ranked based on an ecological risk assessment protocol.

The fish fauna of lentic habitats of the catchment were studied directly on the field. Multivariate statistical analyses were used to display the rules in the distribution patterns. RDA ordination and variance partitioning have been used to determine the relationship between the most abundant and most frequent fish species (*C. gibelio*) and the occurrence of desiccations. This species is able to perform a series of local invasions, mediated by the desiccation events, due to its stress tolerance and colonization ability.

Mostly basic ordination tools were used in the second examination to analyze a long-term (19 years) dataset of the KBWPS II. This study aimed to reveal the effect of the *C. gibelio* invasion on the assemblage development of the newly impounded reservoir. The increase in the number of species and diversity was continous despite the invasion. Successive dynamics of colonization was detected, which could be characterized by three stages: 1. marsh phase, 2. invasion phase, 3. stabilization phase. The fish fauna was restructured completely during the examined period, and the displacement of *C. carassius* by *C. gibelio* was confirmed for the first time in natural water.

Ecological Risk Assessment of non-indigenous species was preformed using the Fish Invasiveness Scoring Kit (FISK). After the calibration of the method to the local conditions, 4 of the 12 recently occurring species were highlighted as of ‘high risk’ or invasive species, of which gibel carp was considered to be the most dangerous, characterized by the highest score. Validation of the methodology was also carried out using the cumulative relative abundance and frequency of occurrence data, but no significant relationships were found.

The study of the fish fauna of five wetlands (berek), lying in the southern shore of the lake revealed that these habitats were mostly characterized by degraded fish fauna and the dominance of non-native species.

The most problematic non-native fish species of the Balaton catchment was *C. gibelio*, while each analysis concluded that independently. The best protection and management tool of a non-native species is prevention, but the results of this thesis might provide further help to the handling of this problem.

7. Összefoglalás

Az idegenhonos, invazív fajok negatív hatása az őket befogadó ökoszisztémákra, natív élőlény közösségekre mára közismert tény. A hatás nagysága azonban korántsem egyforma, sem a fajok közötti összevetésben, sem például a benépesített élőhelyet tekintve. Ezen aszimmetriának felderítése viszont nem könnyű feladat, komplex vizsgálatokat igényel. A disszertáció négy, a Balaton-vízgyűjtőn végzett vizsgálat eredményein keresztül értékeli a megtalálható idegenhonos fajok elterjedési mintázatát, az ezt magyarázó változókat, majd egy esettanulmányon keresztül mutatja be az ezüstkárász (*Carassius gibelio*) hatását a halállomány összetételére, ennek szerveződésére, végezetül pedig ökológiai kockázatbecslő módszert alkalmazva kategorizálja az idegenhonos halfajokat.

Első vizsgálatomban közvetlen terepi felméréseket alkalmazva megismertem a vízgyűjtő állóvizi ökoszisztémáiban előforduló idegenhonos fajokat, majd többváltozós mintázatelemző módszereket alkalmazva képet kaptam az egyes élőhely-típusok halállományaiban előforduló szabályszerűségekről. Kötött kanonikus ordinációt és variancia-partícionálást alkalmazva megállapítotam, hogy a leggyakoribb és legabundánsabb ezüstkárász tömegességi mintázatát jól magyarázza az élőhely esetenkénti (periodikus) kiszáradása, mivel a faj stressztoleranciája és kolonizációs képessége kiemelkedő.

Második vizsgálatomban főként egyszerű ordinációs technikát alkalmazva egy hosszútávú, 19 évet átfogó adatsort elemeztem, hogy kiderítsem, milyen hatással van az ezüstkárász inváziója egy újonnan elárasztott víztározó benépesülési dinamikájára. Megállapítottam, hogy az invázió lezajlása ellenére a fajszám és a diverzitás növekedése nem volt gátolt. A népesülés szukcesszív dinamikával jellemezhető, amely 3 szakaszra osztható: 1. lápi fázis, 2. inváziós fázis, 3. stabilizációs fázis. A halállomány a vizsgált időszak alatt teljesen átstrukturálódott, a legfigyelemreméltóbb, hogy az eddig feltételezett folyamatot, mely szerint az ezüstkárász kiszorítja a széles kárászt, természetes vízi körülmények között a Hídvégi-tavon igazoltam.

Harmadik vizsgálatomban a Fish Invasiveness Scoring Kit (FISK) segítségével elemeztem a Balaton-vízgyűjtőn recensen megtalálható idegenhonos halfajok ökológiai kockázatát. A módszer helyi viszonyokra való kalibrálása után megállapítottam, hogy a 12 előforduló idegenhonos faj közül 4 sorolandó a magas kockázatú, invazív kategóriába, ezek közül is kiemelendő az ezüstkárász, amely a legmagasabb pontszámot kapta. Elvégeztük a módszer

validálását is: az első vizsgálatunkból származó kumulatív relatív abundancia és előfordulási gyakoriság adatokat korreláltattam a FISK elemzésekből származó pontszámokkal, de szignifikáns összefüggést nem kaptam.

A negyedik vizsgálat során a Dél-Balatoni-berkek Natura2000-es és Ramsari területek halállományát vizsgálva rávilágítottam, hogy ezen területek – halállományukat tekintve – erősen degradáltak, de megfelelő természetvédelmi beavatkozással ez az állapot javítható lenne.

Összegzésként elmondható, hogy minden elemzésem külön-külön is rávilágított arra, hogy a Balaton-környéki állóvizi élőhelyek leginkább problematikus halfaja az ezüstkárász. Véleményem szerint a dolgozatban közzétett eredmények hatékonyan hozzájárulhatnak a faj károkozása elleni gyakorlati védekezéshez is.

8. Thesis points

1. The first faunistical data from the southern-shore marshy Natura2000 sites (Őszödi-berek, Brettyó, Lellei-berek, Nagyberek) were provided. The fish fauna of these sites was generally species-poor and dominated by non-indigenous species.

2. Standardized fish sampling protocol was used to assess the fish assemblage of fish ponds under operation, hence the formerly hypothesized source-habitat role of these waters has finally been proved indirectly. High abundance of non-indigenous species was observed in all examined fish ponds.

3. Significant correlation between the relative abundance of non-indigenous species (especially the Gibel carp (*Carassius gibelio*)) and the utilization of the waterbody was revealed: the occurrence of drying-outs was correlated with the abundance.

4. The analysis of long-term datasets revealed successive-like process in the fish fauna development in Lake Fenéki between 1992 and 2011. This was proceeded off different way as it had been published previously, mainly due to the Gibel carp invasion, which occurred in the early years.

5. The gibel carp invasion that occurred in the first part of the study period did not inhibit the colonization of new species. The number of species and Shannon-diversity could be characterized by saturation-curve.

6. The long time hypothesized phenomenon, that non-native gibel carp (*Carassius gibelio*) is able to outcompete the native congener crucian carp (*Carassius carassius*) has been proved first time under natural water conditions, in Lake Fenéki between 1992 and 2011.

7. Of available Ecological Risk Assesment algorithms, Fish Invasiveness Scoring Kit (FISK) was used in Hungary for the first time to assess the 12 non-indigenous species, recently reported from the catchment. The method was calibrated to the local conditions, and a species was considered to be ‘high risk’ if its FISK score was above 19.5.

8. The efficiency of the FISK algorithm was tested using the recent relative abundance and frequency of occurrence datasets. No correlations have been found between the FISK scores and these characteristics.

9. Tézispontok

1. Első alkalommal közöltem halfaunisztikai adatokat az Őszödi-berek, a Brettyó, a Lelleiberek és a Nagyberek Natura 2000-es és Ramsari-területekről. Megállapítottuk, hogy ezen élőhelyek halfaunája általában meglehetősen fajszegény és idegenhonos elemekben gazdag.

2. A vízgyűjtőt tekintve első alkalommal végeztem munkatársaimmal standardizált halmintavételeket működő halastavakon, aminek segítségével igazoltuk a korábbi feltételezést, mely szerint a vízgyűjtőn az idegenhonos fajok elterjedésében forrás-élőhelyeknek tekinthetők, mivel bennük az idegenhonos fajok relatív abundanciája magas.

3. Igazoltam, hogy a Balaton vízgyűjtőn az idegenhonos halfajok elterjedési mintázata kapcsolatba hozható az adott víztest hasznosításával, különösen pedig a kiszáradások gyakoriságával. Az idegenhonos fajoknak, ezeken belül leginkább az ezüstkárásznak (*Carassius gibelio*) kedvez, ha az élőhely időnként kiszárad (kiszárítják).

4. Hosszú távú adatsort elemezve megállapítottam, hogy a KBVR-II. (Fenéki-tó) Ingóiberekben a halállomány szukcesszív jellegű folyamatban alakult át 1992 és 2011 között. Ez a folyamat azonban a szakirodalomban korábban közöltektől eltérően zajlott. Az eltérés egyik oka a frissen elérasztott területen lezajlott ezüstkárász-invázió volt.

5. Megállapítottam, hogy a Fenéki-tavon a vizsgált időszak elején, az elárasztást követően tapasztalt ezüstkárász-invázió nem gátolta meg az új fajok betelepülését. A teljes vizsgálati időszakra vonatkoztatva mind a fajszám, mind a diverzitás telítési görbével volt jellemezhető.

6. A Fenéki-tó példáján, természetes vízi körülmények között igazoltam azt a szakirodalomból régóta ismert nézetet, mely szerint az invazív ezüstkárász kiszorítja az őshonos széles kárászt.

7. Magyarországon elsőként alkalmaztam ökológiai kockázatbecslő eljárást az idegenhonos fajok negatív hatásának értékelésére. A Fish Invasiveness Scoring Kit (FISK) segítségével 12, a vízgyűjtőn recensen megtalálható idegenhonos fajt vizsgáltunk. A módszert a vízgyűjtőre kalibráltam, így egy adott halfaj akkor tekintendő magas kockázatúnak, ha FISK pontszáma nagyobb mint 19,5.

8. A FISK hatékonyságát saját, a Balaton-vízgyűjtő állóvizi rendszereire vonatkozó relatív abundancia és relatív gyakoriság adatokkal tesztelve nem kaptam összefüggést a FISK pontszám és ezen két változó köszött.

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12. Data of Scientific activities

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13. Appendices

Appendix 1: The FISK I (v.1.19) Questionnaire

ID		**Risk query:**
		Biogeography/historical
	1	Domestication/cultivation
1	1.01	Is the species highly domesticated or cultivated for commercial, angling or ornamental purposes?
2	1.02	Has the species become naturalised where introduced?
3	1.03	Does the species have invasive races/varieties/sub-species?
	2	*Climate and Distribution*
4	2.01	Is species reproductive tolerance suited to climates in the risk assessment area (1-low, 2-intermediate, 3-high)?
5	2.02	What is the quality of the climate match data (1-low; 2-intermediate; 3-high)?
6	2.03	Does the species have broad climate suitability (environmental versatility)?
7	2.04	Is the species native to, or naturalised in, regions with equable climates to the risk assessment area?
8	2.05	Does the species have a history of introductions outside its natural range?
	3	*Invasive Elsewhere*
9	3.01	Has the species naturalised (established viable populations) beyond its native range?
10	3.02	In the species' naturalised range, are there impacts to wild stocks of angling or commercial species?
11	3.03	In the species' naturalised range, are there impacts to aquacultural, aquarium or ornamental species?
12	3.04	In the species' naturalised range, are there impacts to rivers, lakes or amenity values?
13	3.05	Does the species have invasive congeners?
		B. Biology/Ecology
	4	*Undesirable (or persistence) traits*
14	4.01	Is the species poisonous, or poses other risks to human health?
15	4.02	Does the species out-compete with native species?
16	4.03	Is the species parasitic of other species?
17	4.04	Is the species unpalatable to, or lacking, natural predators?
18	4.05	Does species prey on a native species (e.g. previously subjected to low (or no) predation)?
19	4.06	Does the species host, and/or is it a vector, for recognised pests and pathogens, especially non-native?
20	4.07	Does the species achieve a large ultimate body size (i.e. > 10 cm FL) (more likely to be abandoned)?
21	4.08	Does the species have a wide salinity tolerance or is euryhaline at some stage of its life cycle?
22	4.09	Is the species desiccation tolerant at some stage of its life cycle?
23	4.10	Is the species tolerant of a range of water velocity conditions (e.g. versatile in habitat use)
24	4.11	Does feeding or other behaviours of the species reduce habitat quality for native species?
25	4.12	Does the species require minimum population size to maintain a viable population?
	5	*Feeding guild*
26	5.01	Is the species a piscivorous or voracious predator (e.g. of native species not adapted to a top predator)?
27	5.02	Is the species omnivorous?
28	5.03	Is the species planktivorous?

29	5.04	Is the species benthivorous?
	6	*Reproduction*
30	6.01	Does it exhibit parental care and/or is it known to reduce age-at-maturity in response to environment?
31	6.02	Does the species produce viable gametes?
32	6.03	Does the species hybridize naturally with native species (or uses males of native species to activate eggs)?
33	6.04	Is the species hermaphroditic?
34	6.05	Is the species dependent on presence of another species (or specific habitat features) to complete its life cycle?
35	6.06	Is the species highly fecund (>10,000 eggs/kg), iteropatric or have an extended spawning season?
36	6.07	What is the species' known minimum generation time (in years)?
	7	*Dispersal mechanisms*
37	7.01	Are life stages likely to be dispersed unintentionally?
38	7.02	Are life stages likely to be dispersed intentionally by humans (and suitable habitats abundant nearby)?
39	7.03	Are life stages likely to be dispersed as a contaminant of commodities?
40	7.04	Does natural dispersal occur as a function of egg dispersal?
41	7.05	Does natural dispersal occur as a function of dispersal of larvae (along linear and/or 'stepping stone' habitats)?
42	7.06	Are juveniles or adults of the species known to migrate (spawning, smolting, feeding)?
43	7.07	Are eggs of the species known to be dispersed by other animals (externally)?
44	7.08	Is dispersal of the species density dependent?
	8	*Tolerance attributes*
45	8.01	Any life stages likely to survive out of water transport?
46	8.02	Does the species tolerate a wide range of water quality conditions, especially oxygen depletion & high temperature?
47	8.03	Is the species susceptible to piscicides?
48	8.04	Does the species tolerate or benefit from environmental disturbance?
49	8.05	Are there effective natural enemies of the species present in the risk assessment area?

Appendix 2: The FISK II (v.2.03) questionnaire

ID		Question
A. Biogeography/Historical		
1. Domestication/Cultivation		
1	1.01	Is the species highly domesticated or widely cultivated for commercial, angling or ornamental purposes?
2	1.02	Has the species established self-sustaining populations where introduced?
3	1.03	Does the species have invasive races/varieties/sub-species?
2. Climate and Distribution		
4	2.01	What is the level of matching between the species' reproductive tolerances and the climate of the RA area?
5	2.02	What is the quality of the climate match data?
6	2.03	Does the species have self-sustaining populations in three or more (Köppen-Geiger) climate zones?
7	2.04	Is the species native to, or has established self-sustaining populations in, regions with similar climates to the RA area?
8	2.05	Does the species have a history of being introduced outside its natural range?
3. Invasive elsewhere		
9	3.01	Has the species established one or more self-sustaining populations beyond its native range?
10	3.02	In the species' introduced range, are there impacts to wild stocks of angling or commercial species?
11	3.03	In the species' introduced range, are there impacts to aquacultural, aquarium or ornamental species?
12	3.04	In the species' introduced range, are there impacts to rivers, lakes or amenity values?
13	3.05	Does the species have invasive congeners?
B. Biology/Ecology		
4. Undesirable traits		
14	4.01	Is the species poisonous/venomous, or poses other risks to human health?
15	4.02	Does the species out-compete with native species?
16	4.03	Is the species parasitic of other species?
17	4.04	Is the species unpalatable to, or lacking, natural predators?
18	4.05	Does the species prey on a native species previously subjected to low (or no) predation?
19	4.06	Does the species host, and/or is it a vector, for one or more recognised non-native infectious agents?
20	4.07	Does the species achieve a large ultimate body size (i.e. >15 cm total length) (more likely to be abandoned)?
21	4.08	Does the species have a wide salinity tolerance or is euryhaline at some stage of its life cycle?
22	4.09	Is the species able to withstand being out of water for extended periods (e.g. minimum of one or more hours)?
23	4.10	Is the species tolerant of a range of water velocity conditions (e.g. versatile in habitat use)
24	4.11	Does feeding or other behaviours of the species reduce habitat quality for native species?
25	4.12	Does the species require minimum population size to maintain a viable population?
5. Feeding guild		
26	5.01	If the species is mainly herbivorous or piscivorous/carnivorous (e.g. amphibia), then is its foraging likely to have an adverse impact in the RA

		area?
27	5.02	If the species is an omnivore (or a generalist predator), then is its foraging likely to have an adverse impact in the RA area
28	5.03	If the species is mainly planktivorous or detritivorous or algivorous, then is its foraging likely to have an adverse impact in the RA area?
29	5.04	If the species is mainly benthivorous, then is its foraging likely to have an adverse impact in the RA area?
6. Reproduction		
30	6.01	Does the species exhibit parental care and/or is it known to reduce age-at-maturity in response to environment?
31	6.02	Does the species produce viable gametes?
32	6.03	Is the species likely to hybridize with native species (or use males of native species to activate eggs) in the RA area?
33	6.04	Is the species hermaphroditic?
34	6.05	Is the species dependent on the presence of another species (or specific habitat features) to complete its life cycle?
35	6.06	Is the species highly fecund (>10,000 eggs/kg), iteropatric or has an extended spawning season relative to native species?
36	6.07	What is the species' known minimum generation time (in years)?
7. Dispersal mechanisms		
37	7.01	Are life stages likely to be dispersed unintentionally?
38	7.02	Are life stages likely to be dispersed intentionally by humans (and suitable habitats abundant nearby)?
39	7.03	Are life stages likely to be dispersed as a contaminant of commodities?
40	7.04	Does natural dispersal occur as a function of egg dispersal?
41	7.05	Does natural dispersal occur as a function of dispersal of larvae (along linear and/or 'stepping stone' habitats)?
42	7.06	Are juveniles or adults of the species known to migrate (spawning, smolting, feeding)?
43	7.07	Are eggs of the species known to be dispersed by other animals (externally)?
44	7.08	Is dispersal of the species density dependent?
8. Persistence attributes		
45	8.01	Are any life stages likely to survive out of water transport?
46	8.02	Does the species tolerate a wide range of water quality conditions, especially oxygen depletion and temperature extremes?
47	8.03	Is the species readily susceptible to piscicides at the doses legally permitted for use in the risk assessment area?
48	8.04	Does the species tolerate or benefit from environmental disturbance?
49	8.05	Are there effective natural enemies of the species present in the risk assessment area?