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# Is gynogenetic reproduction in gibel carp (*Carassius gibelio*) a major trait responsible for invasiveness?

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**Abstract.** The invasion success of gibel carp (*Carassius gibelio*) depends on demographic and competitive traits. The major biological trait responsible for the invasiveness of *C. gibelio* is the mode of reproduction. Apart from sexual reproduction, which is typical in fish, *C. gibelio* is a unique cyprinid species able to reproduce through asexual gynogenesis, which is also known as sperm-dependent parthenogenesis, observed in all-female populations. Though the sexual and asexual forms of *C. gibelio* co-exist widely in natural habitats, the gynogenetic form has the capacity to modulate the range of effective ecological niches, which may facilitate the process of invasion. In this paper, we reviewed current knowledge of the sexual and gynogenetic forms of gibel carp along with their physiological advantages, immunological traits, and ability to withstand different environmental conditions. As parasitic infection may directly alter the immunology of hosts, and also indirectly alter their investment in reproduction, we provide some insights into the role of parasites as one of the potential drivers facilitating the coexistence of asexual and sexual forms. We highlight evidence that gibel carp have been identified as a serious threat to native species; hence, its impact on the ecosystem is also discussed.

**Key words:** fish, gynogenesis, invasive species, coexistence, immunity, environmental tolerance, parasites

## Introduction

Invasive species are non-native to a given ecosystem; they usually negatively affect biodiversity in natural habitats and may even cause economic losses (Xu et al. 2006, Beck et al. 2008, Xia et al. 2019). They are also identified as one of the main reasons for species extinction in nature (Roberts et al. 2013). The success of invasive species (or invaders) may depend on how ecologically distant they are from native species. The ecological and demographic differences between native and invasive species may enable invasives to exploit free nutritional resources to

avoid competition or make them less vulnerable to predators and parasites (Alcaraz et al. 2005). Factors related to species (biotic) or habitat (abiotic) determine whether a given species will be an invader (Ross 1991). The invasion process model proposed by Kolar & Lodge (2001) suggested transitional stages that an alien species has to pass through to become a successful invader. According to this model, these stages are the following: transportation, release, establishment and spread. A similar invasion model was proposed by Heger (2001), demonstrating several stages and steps in chronological order from the immigration of the species to the colonization of new localities (Fig. 1).

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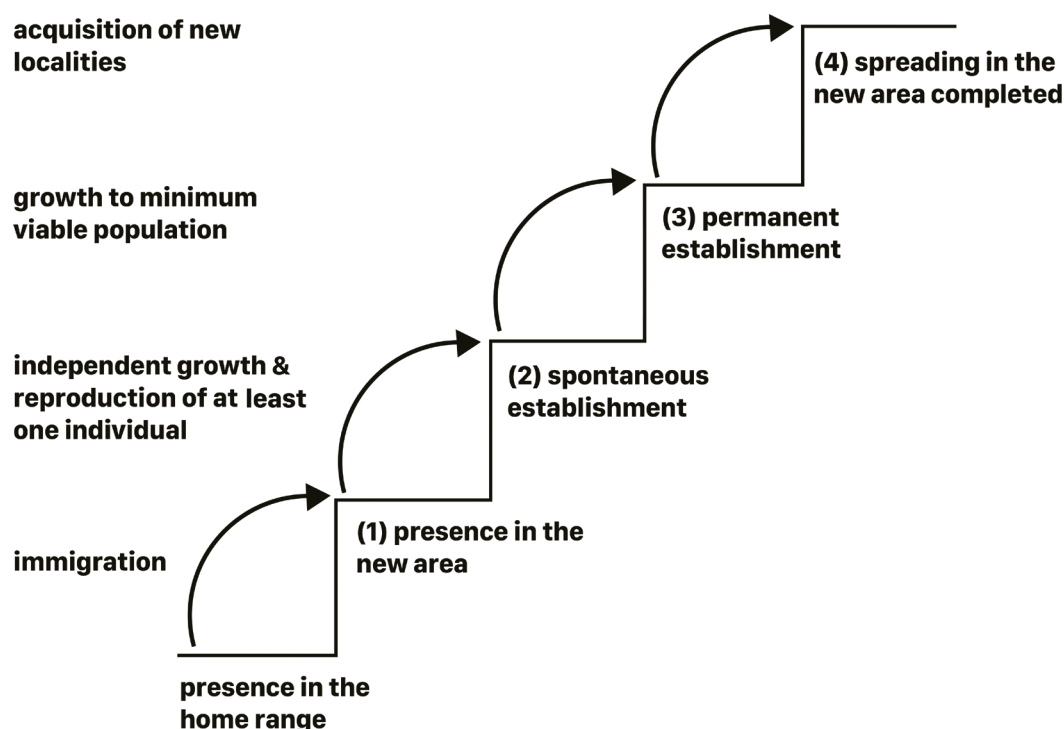


Fig. 1. Invasion model proposed by Heger (2001).

Gibel carp (*Carassius gibelio*) is considered an alien fish species in the hydrographic system of the Czech Republic (Lusková et al. 2010). It is also a widely distributed invasive fish among other European countries (Verreycken et al. 2007, Perdikaris et al. 2012, Ribeiro et al. 2015). This omnivorous species, occupying both lentic and lotic habitats, is an unwelcome competitor in the natural habitats of native fish species (Halačka et al. 2003). Gibel carp have been considered responsible for reducing population densities of crucian carp (*Carassius carassius*) and other native cyprinid species by altering the habitat structure (Savini et al. 2010, Wouters et al. 2012) and exerting reproductive pressure on other cyprinids (utilizing male cyprinids, especially *C. carassius* and *Cyprinus carpio*, for the induction of gynogenesis (Papoušek et al. 2008). It has also been reported to effect rapid changes in biodiversity and the food chain complex (Ruppert et al. 2017).

The gibel carp is considered to be a native species from central Europe to Siberia (Kalous et al. 2012), or alternatively to have been introduced to European waters from eastern Asia (Perdikaris et al. 2012). It invaded the Czech Republic from the River Danube through natural migration via the Slovakian section of the River Morava. The first record of this species comes from the lower reaches of the River Dyje. Consequently, it invaded the adjacent alluvial waters of the two rivers (the River

Dyje and the River Morava). Gibel carp rapidly dispersed through these river drainages. Around 1980 it appeared in the drainage of the River Labe (Halačka et al. 2003). In subsequent years, gibel carp populations rapidly increased in the drainage area of the lower and middle reaches of the River Labe and in the lower reaches of the River Vltava and their alluvial waters. At present, *C. gibelio* occurs in all suitable aquatic habitats in the Czech Republic (Halačka et al. 2003).

Formerly, the gibel carp was recognized as a subspecies of *Carassius auratus*, i.e. considered as *Carassius auratus gibelio* (Cherfas 1981, Jiang et al. 1983). Later, Rylková et al. (2013) designated *C. gibelio* a valid species, one of the members of the *C. auratus* complex (this complex includes *Carassius langsdorfii*, *Carassius cuvieri*, *C. auratus* and *C. gibelio*). Recent sampling in the River Dyje (Czech Republic) revealed four mitochondrial lineages of *C. auratus* complex, namely *C. gibelio*, *C. auratus*, *C. langsdorfi* and the so-called M-line, the three last lines were present at low frequency and mtDNA *C. gibelio* represented the most common line (96%) (Pakosta et al. 2018). Gibel carp has a specific mode of reproduction exhibiting both asexual and sexual reproduction, which is a rarity in nature and is documented only in a small number of freshwater fishes, including nine genera (Lamatsch & Stöck 2009). Some authors propose an even more complicated system of reproduction in

gibel carp, including unisexual gynogenesis, sexual reproduction, and a hybrid-like development mode or androgenesis (nucleo-cytoplasmic hybrid clone) in response to sperm from different species or gibel carp (Wang et al. 2011, Zhang et al. 2015, Gao et al. 2017).

As an invasive species gibel carp tend to aggressively occupy new habitats (Liasko et al. 2011); its rapid reproduction facilitated by gynogenesis (Paschos et al. 2004). For example, in the Czech Republic the early invasive population of gibel carp was composed of triploid females with gynogenetic reproduction, recognized in natural habitats of the River Dyje until 1995, when the first cases of males were detected. Subsequently, mixed populations of triploid gynogenetic females and sexual diploids have been documented (Lusková et al. 2004). Gibel carp spread rapidly by means of its own invasive strategy, assisted by human activity in tributaries of the Danube where it formed stable populations (Lusk et al. 2004). The rapid reproduction achieved by gynogenesis may facilitate the expansion of gibel carp, even when accidentally introduced into

the breeding ponds of common carp. In such cases, gibel carp may represent a threat to common carp production (traditionally undertaken in some East and Central European countries) due to competition for food and space (Šimková et al. 2015).

The aim of this study was to review the current knowledge of invasive gibel carp along with their physiological advantages, immunological traits, and ability to withstand different environmental conditions. We specifically focused on the potential advantages of this species related to multiple reproduction strategies potentially facilitating its invasion success.

### Genetic background of gynogenesis

In gynogenesis, embryos are formed from female genetic material only. The ovum is activated by sperm from male gibel carp or other cyprinid species. During activation, the sperm penetrates the ovum, but the sperm nucleus does not fuse with the ovum nucleus and there is no syngamy (Barbuti et al. 2012). As a consequence the offspring are clones of the gynogenetic female (Fig. 2).

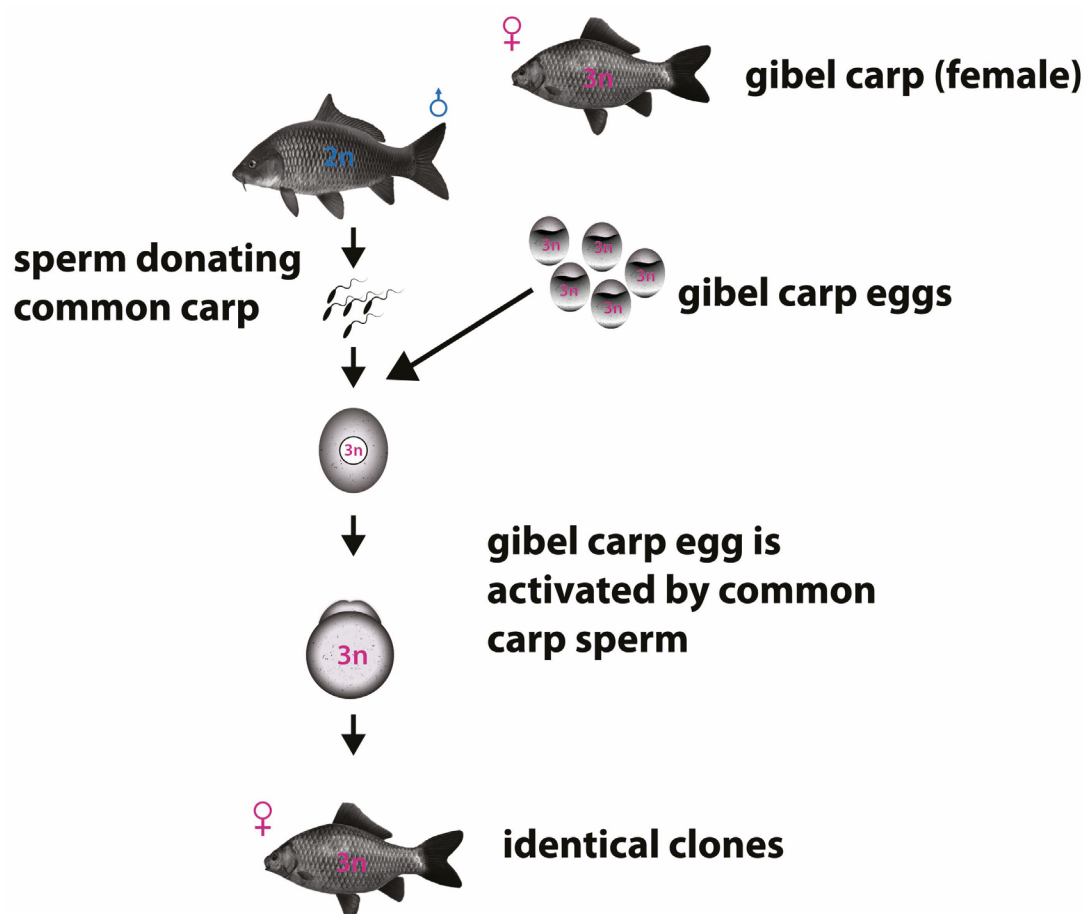
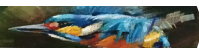


Fig. 2. Gynogenetic reproduction in gibel carp.





Li et al. (2014) hypothesized that the ancestor of gynogenetic hexaploid gibel carp is a tetraploid lineage of *C. auratus*, thus gibel carp may have originated via autotriploidy about 0.5 million years ago. First, *C. auratus* experienced polyploidization events and gained bisexual reproductive capacity through diploidization. Then, later, recurrent polyploidization events led to hexaploid gibel carp (Li et al. 2014). As a consequence of polyploidization there are different types of clonal reproduction documented in fish complexes, i.e. gynogenesis, parthenogenesis, hybridogenesis, and kleptogenesis (Lampert & Schartl 2010, Stöck et al. 2012, Choleva & Janko 2013, Li et al. 2016b). Due to its capacity to exhibit diverse ploidy within species, the gibel carp is a unique model for studying the transition of reproduction types (sexual *vs.* asexual) in relation to polyploidy (Lu et al. 2021).

Gynogenetic forms (functionally triploids and evolutionarily hexaploids,  $3n = 150$ ) and sexual forms (functionally diploids and evolutionarily tetraploids,  $2n = 100$ ) are morphologically indistinguishable in nature (Przybył et al. 2020). However, in studies of *C. gibelio*, it was shown that the chromosome number for hexaploids ranged between 156 and 162 (for East Asian form of *C. gibelio* shown Zhou & Gui 2002) and between 150 and 159 (for the European form of *C. gibelio* shown by Kalous & Knytl 2011), and was suggested that such hexaploids (at least the East Asian form) are able to reproduce by unisexual gynogenesis as well as by bisexual reproduction (Gui & Zhou 2010).

The alteration between ploidy ratios in *C. gibelio* may also contribute to its invasion process. Przybył et al. (2020) compared ploidy and sex ratios for European and East Asian populations and revealed that incidence of diploid males and females (considered to reproduce sexually) is higher in Europe, whilst triploid females and males prevail in East Asian populations. Interestingly, higher genetic diversity and divergence were confirmed in triploids than in diploids in Asian populations, which facilitates their environmental adaptation (Jiang et al. 2013, Liu et al. 2017). Moreover, it was also shown that genotypic males play an important role in the creation of genetic diversity in gynogenetic gibel carp, this can be considered as a mechanism counteracting the Muller's ratchet process in gynogenetic gibel carp (Zhao et al. 2021). However, for the European form of the gibel carp, a weakened diversity of immune genes was

revealed for the triploid gynogenetic form (high proportion of triploid females expressed the same genotype) in the mixed population suggesting that the most common triploid form is a target of parasite adaptation (Šimková et al. 2013, see below). In some countries diploid populations of gibel carp have gradually displaced triploids (Liasko et al. 2011, Przybył et al. 2020). It was suggested that this trajectory could be linked with invasion, as this pattern was not evident in native populations of gibel carp (i.e. in East Asia) (Przybył et al. 2020). However, female triploids are still widely distributed throughout Europe. For example, from 2001 to 2007 in the Czech Republic the ploidy status of male and female gibel carp were investigated and an increasing trend in the proportion of diploid specimens in mixed populations was observed over time. However, a higher percentage of triploid females were also observed in the study areas, which indicates the important role of gynogenesis in maintaining local populations of *C. gibelio* (Halačka et al. 2003). Until 1990, European *C. gibelio* populations almost exclusively comprised triploid females, originating through gynogenesis and maintained as discrete clonal lineages. Such mixed diploid-polyploid populations consisting of diploids and triploids are not common in East Asia (the home range of *C. gibelio*) (Liu et al. 2017), which may indicate the potential link between the evolutionary trajectory of gibel carp populations and its invasiveness in European waters.

The reproductive mode of gynogenetic *vs.* sexual is indirectly revealed by sex and ploidy ratios (Przybył et al. 2020), even if the presence of triploid males may offer the possibility of bisexual reproduction even in triploid females (Gui & Zhou 2010, Zhang et al. 2015). Gynogenetic specimens of gibel carp are often determined using cytogenetic analyses, i.e. karyotypes (Liasko et al. 2010). Flow cytometry, erythrocyte measurement, nucleolar organizer region analysis, external morphology analysis and tissue measurement are also applied as ploidy determination techniques (Garcia-Abiado et al. 1999). Flow cytometry is an optical technique which determines particle fluorescence after treatment with a DNA-specific dye, such as propidium iodide (Harrell et al. 1998). High-throughput flow cytometry is commonly applied as a cost effective method in terms of reduced labour and consumables compared with more manually intensive methods (Cousin et al. 2009). As the cellular and nuclear dimensions of



erythrocytes have been shown experimentally to be proportional to ploidy level in teleost fishes (Beck & Biggers 1983), the size of erythrocytes offers an alternative to flow cytometry (Garcia-Abiado et al. 1999).

Polyploidy also plays a role in the sex determination system of gibel carp (Lu et al. 2021). It was predicted that two rounds of polyploidization and diploidization in gibel carp would lead to different sex determination mechanisms: genotypic sex determination (GSD) and environmental sex determination (ESD) (or temperature sex determination (TSD)) related to facultative reproductive strategies, i.e. unisexual and bisexual reproduction modes (Bachtrog et al. 2014, Mei & Gui 2015, Capel 2017, Zhu et al. 2018). GSD depends on genotypic elements during fertilization (Gamble & Zarkower 2012), whilst ESD is affected by several environmental factors, like temperature (Conover & Kynard 1981), photoperiod (Brown et al. 2014), social (Warner 1982), pH and dissolved oxygen (Baroiller et al. 2009). Genotypic and environmental sex determinations are not mutually exclusive in gibel carp (Li & Gui 2018).

To examine the effect of rearing temperature on sex determination of gibel carp, Li & Gui (2018) conducted an experiment with two artificial strains and one wild strain of gibel carp under a wide range of rearing temperatures. In the case of one artificial strain, all female offspring were generated when the temperature was less than 19 °C, while males were produced when the temperature was above 22 °C. Only male offspring were recorded at a temperature above 31 °C. In the case of the other artificial strain and the wild strain, all female offspring were generated at a temperature lower than 25 °C with males produced at temperatures higher than 28 °C.

Concerning the fertilization of eggs, there are differences between GSD and TSD males. Eggs fertilized by sperm from GSD males go through sexual reproduction events, such as swelling of the sperm nucleus. In contrast, when eggs are fertilized by sperm from TSD males, the sperm remain in a condensed state right through the first mitotic process (Zhu et al. 2018).

The presence of dual reproductive modes (gynogenetic and sexual) in gibel carp has been hypothesized as indicating an evolutionary

transition of reproduction from unisexual to sexual reproduction (Gui & Zhou 2010, Li et al. 2016a). Hence, it seems necessary to identify the specific genes related to reproduction and potentially also the genes involved in sex-determination in gynogenetic-sexual fish complexes. The gonadal transcriptomes of asexual *Poecilia formosa* and its parent sexual species *Poecilia mexicana* and *Poecilia latipinna* were analysed in a study by Schedina et al. (2018), in which the overall down-regulation of meiosis-related genes and the misregulation of many genes related to reproduction were revealed in asexual *P. formosa*, in contrast to sexual *P. mexicana* and *P. latipinna*.

### **Reproductive and physiological advantages facilitating the coexistence of gynogenetic and sexual forms of invasive gibel carp**

Gynogenetic gibel carp have the advantages of rapid growth and high fecundity (Perdikaris et al. 2012). From an evolutionary point of view, asexual reproduction has an advantage over sexual reproduction in that sexual reproduction suffers from the two-fold cost of producing males (Gibson et al. 2017); hence, gynogenesis ensures a faster rate of increase in the size of female gibel carp populations. Regarding demography, asexual individuals should exhibit lower fecundity when compared with sexual, according to the demographic advantage hypothesis (Leung & Angers 2017). However, on the basis of mathematical simulation, it was suggested that half of asexual individuals imitate the cost of sex by producing no offspring and that only the presence of non-reproductive individuals in asexual females can result in the long-term coexistence of sexual and asexual species (or forms) (Leung & Angers 2017).

The fitness-related traits of sexual and asexual forms are important for their coexistence in nature and some of them may potentially contribute to the invasiveness of gibel carp. Spatial data on the growth and development of the gynogenetic and sexual forms of gibel carp in the Czech Republic indicate that gynogenetic triploid females have significantly higher growth rates than sexual diploids (Vetešník et al. 2004). Fitness and condition-related traits were examined in gynogenetic and sexual forms of gibel carp in order to reveal whether there are some physiological advantages exhibited by the gynogenetic form, which initially invaded the hydrological systems of the Czech Republic. However, it was shown that gynogenetic and sexual females expressed the



same gonado-somatic index, which is considered a measure of reproductive performance or fitness, and that both female forms exhibited a similar level of oestradiol in blood plasma (Šimková et al. 2015). In contrast, a weak fitness advantage measured by fecundity, egg viability, and hatchling growth rate was found for the sperm-dependent asexual species *Phoxinus eos-neogaeus* when compared to its sexually reproducing parental species, *Phoxinus eos* and *Phoxinus neogaeus* (Mee et al. 2013a).

Concerning other physiological traits, the hepatosomatic index (a measure of fish condition) of gynogenetic gibel carp was shown to be higher when compared to the sexual counterpart, which indicates a better physiological condition (energy/metabolic reserves) for the gynogenetic form (Šimková et al. 2015). However, Šimková et al. (2015) also showed a physiological disadvantage for gynogenetic females, i.e. lower aerobic performance when compared to sexual males. This disadvantage in gynogenetic females seems to be compensated by higher oxygen-carrying capacity per erythrocyte when compared to the sexual form. Finally, the authors proposed that a potential trade-off between the high number of erythrocytes with lower oxygen-carrying capacity per erythrocyte in sexual males and the low number of erythrocytes with high oxygen-carrying capacity per erythrocyte in gynogenetic females may represent a potential mechanism contributing to the coexistence of gynogenetic and sexual gibel carp.

Differences in the effectiveness of the immune systems and contrasting susceptibility to parasite infection may represent another potential mechanism facilitating the coexistence of asexual and sexual forms of gibel carp, thereby contributing to its invasive ability. Hakoyama et al. (2001) reported lower nonspecific immunity and higher parasite loads of generalist trematode parasite species (*Metagonimus* sp.) in the gynogenetic form of the *C. auratus* complex. In contrast, Šimková et al. (2015) showed no difference in nonspecific immunity between the gynogenetic and sexual forms of *C. gibelio*, but revealed higher specific immunity (measured by IgM level) in gynogenetic females. In accordance with the Red Queen hypothesis, which postulates antagonistic co-evolution between hosts and parasites, parasites are under selection to infect the most common host genotypes in the local population (Seger & Hamilton 1988, Hamilton et

al. 1990). Thus, in a species (or species complex) with coexisting asexual and sexual forms, due to reduced genetic diversity asexual hosts or the most common asexual phenotypes/genotypes are the targets of parasite adaptation, whilst sexual hosts escape from parasite infection because of high genetic variability generated by recombination (Lively et al. 1990). The high level of parasite infection in common asexual clones could then favour genetically diverse sexual individuals and promote the short-term coexistence of sexual and asexual forms in the same habitat. This response was shown for the sexual top minnow *Poeciliopsis monacha* coexisting with two gynogenetic triploid clones of *Poeciliopsis 2monacha-lucida* (Lively et al. 1990). A study of gibel carp focused on the variability of major histocompatibility complex (MHC) genes (representing functional immune genes in vertebrates) and parasite load showed that if gynogenetic and sexual forms coexist in a slightly biased ratio (gynogenetic females comprising 60% of a population and sexuals comprising 40%), the most common MHC clones of the gynogenetic form suffer from high parasite richness or high intensities of infection by metazoan parasites (mostly by host-specific gill monogeneans of *Dactylogyrus*) (Šimková et al. 2013). However, the temporal dynamics of parasite infection in gynogenetic and sexual forms of gibel carp coexisting in the same habitat (with gynogens comprising an estimated 37% of the population and sexuals comprising 63%) was not consistent with the prediction of the Red Queen hypothesis in a 4-year study (Pakosta et al. 2018), indicating the effects of multiple abiotic and biotic factors on parasite load in both forms. The sexual form was even more strongly infected by monogenean ectoparasites in the first and last years, whilst the gynogenetic form was more strongly parasitized by nematodes in the two final years.

Considering other asexual-sexual complexes in fish, no consistent pattern of parasite load between asexual *P. formosa* and sexual *P. latipinna* was observed on the spatial scale, i.e. among different populations (Tobler & Schlupp 2005). Similarly, the mechanisms predicted by the Red Queen hypothesis did not explain the coexistence of sexual and asexual forms in the *Cobitis taenia* hybrid complex (Kotusz et al. 2014).

### Modulation of the ecological niche after invasion

Ecological communities with low species richness are vulnerable to invasions (Milardi et al. 2019).





Fish invasion is generally more plausible in areas with native endemic species with a restricted distribution and/or in areas influenced by human activities. Concerning invasive gibel carp, a negative effect on native fish species was documented in the Ömerli Reservoir, Turkey (Gaygusuz et al. 2007). A significant decrease in the abundance of white sucker (*Catostomus commersonii*) in North America in response to an increase in gibel carp abundance was also reported (Ruppert et al. 2017). Gibel carp has also been reported as a serious threat to commercially important fish species such as European eel (*Anguilla anguilla*) and tench (*Tinca tinca*), as well as to other native fish species (Perdikaris et al. 2012). An alternative hypothesis suggests that an invading species may frequently occur in species-rich communities (Stachowicz & Byrnes 2006). A study carried out by Stohlgren et al. (2006) showed a positive relationship between the densities of native and non-indigenous fish species; however, native fish species richness was not significantly correlated with invasive fish richness. In many cases, the competition for resources between native species and invaders actually helps the invasion by altering the food web architecture. Successful invasion by non-native forms in fish can vary widely between geographic regions, ranging from 38 to 77% (Ross 1991). Successful establishment by an invading fish species is expedited by a broad dietary and habitat niche (García-Berthou 2007, Courant et al. 2017). It has been observed that in some systems niche differentiation can also play a role in the co-existence of sexual and asexual forms of fishes (Weeks et al. 1992, Doeringsfeld et al. 2004). For example, the co-existence of sperm-dependent asexual *Chrosomus* spp. and its sexual hosts can be maintained by a combination of niche separation and conspecific mate preference (Mee et al. 2013b). However, no information on the potential niche preferences or mating preferences of gynogenetic and sexual forms of invasive gibel carp is currently available.

The trophic niche width of gibel carp is broader than that of native species in all invaded areas (Özdilek & Jones 2014). This ecological characteristic along with gynogenetic reproduction, dietary plasticity, and environmental stress tolerance make gibel carp a successful invasive species (Lusková et al. 2010). Further, the gibel carp is benthopelagic (Erdoğan et al. 2014), readily taking a dominant position in lentic and slow-running waters (Aydin et al. 2011). It may impact the populations of a

variety of native freshwater fish species by directly competing for food, i.e. pelagic zooplankton and benthic invertebrates (Lusk et al. 2010), or alter the top-down control of zooplankton (Bondarev et al. 2019). Specifically, due to competition for food and space, gibel carp are responsible for the disappearance of some native cyprinoid species in some areas, i.e. *C. carassius*, *T. tinca*, *Leucaspis delineatus* and *Scardinius erythrophthalmus* and for the reduction of their population densities in others (Lusk et al. 2010). Gibel carp have wider niches than any other co-existing species and can occupy any vacant niche by slightly altering its dietary pattern (Özdilek et al. 2019).

### Environmental tolerance

Declines in native cyprinoid fish populations have been initially attributed to habitat degradation but the invasion of gibel carp has also been identified as an additional negative factor affecting native species (Özdilek & Jones 2014). Gibel carp were shown to alter the flow of nutrients in ecosystems or cause a change in turbidity (Crivelli 1995). A decrease in water quality may even increase the abundance of this species. For example, an increase in the population density of gibel carp and positive changes to reproductive parameters, i.e. spawning period, gonad size, and reproductive effort, were shown in comparison with native fish species over a period of years in a system with low water quality measured by total phosphorus and chlorophyll-a (Tarkan et al. 2012).

There are multiple factors contributing to the increase in gibel carp population size in aquatic ecosystems. The most important is the unique capacity of gibel carp to rapidly reproduce by gynogenesis (see above). Other factors include a capacity to tolerate environmental degradation, tolerance of predation and resistance to food competition from other species (Holčík & Žitňan 1978, Paschos et al. 2004). Gibel carp can also withstand extremely adverse environmental conditions. For example, gibel carp juveniles resulting from gynogenesis (more specifically, from the activation of gibel carp eggs by sperm from *Rutilus ylikiensis*) exhibited specific growth rates of 3.14% and 0.91% at  $\text{NH}_3$  concentrations of 0.51 mg/l and 8 mg/l, respectively (Paschos et al. 2004). Gibel carp have the largest somatic glycogen stores among the vertebrates (25-30% of their liver being glycogen) (Hochachka & Somero 1984, Hyvärinen et al. 1985), which allows them to survive anoxia for prolonged periods (De Boeck et



al. 2010). The effect on gibel carp of a predefined level of exposure to copper ( $LC_{50}$  330  $\mu\text{g}/10$  days) was evaluated in a study by De Boeck et al. (2010), in which the level of response of the stress hormone cortisol increased. As a consequence, not only was there a change in ion regulation, but also an alteration in energy metabolism resulting from the promotion of glycogenolysis and increasing glucose levels in the blood. In a similar study, extra glycogen was found to be used by fish exposed to copper in both lethal and sub-lethal doses (Eyckmans et al. 2011). Gibel carp can also tolerate hypoxia and low temperatures (Liasko et al. 2011); with acclimation it can also survive in saline water (Elger & Hentschel 1981). It has the capacity to colonize inland waters with high levels of eutrophication, which otherwise negatively affects the overall diversity of ichthyofauna and the body weights of other fish species (Paulovits et al. 2014).

### Impact of gibel carp on ecosystems

Invasive species can have a significant impact on ecosystems by affecting community composition, the distributions of populations, and food webs (Gurevitch & Padilla 2004, David et al. 2017). In some areas of the Baltic ecosystem, high abundance and slow growth suggest that gibel carp may already exert an influence on the coastal food web (Navodaru et al. 2002, Vetemaa et al. 2005). The potential impact of gibel carp on ecosystems is evidenced in several European countries, where the decline of native crucian carp and degradation of its habitat have been reported to be linked to the invasion of gibel carp (Navodaru et al. 2002, Gaygusuz et al. 2007 Paulovits et al. 2014). Gibel carp not only change the composition of native fish populations but also affects native benthic invertebrate communities (Ruppert et al. 2017). Its impact on invertebrate communities is as a “bio-turbator” (a species that reworks soils and sediments) (Richardson et al. 1995). It is able to occupy turbid water, which is often unsuitable for invertebrate communities (Bilotta & Brazier 2008). In addition to causing turbidity, gibel carp can

also cause damage by feeding on and uprooting aquatic plants (Richardson et al. 1995), and thus may affect entire aquatic ecosystems (Van der Veer & Nentwig 2015). This species is also capable of preying on amphibians, molluscs, annelids, crustaceans, and insects (Meyer et al. 1998). Vertebrates in higher trophic levels are typically vulnerable to anthropogenic threats. Özdilek & Jones (2014), using estimates to express the trophic positions of fish species, identified a lower trophic position and slightly lower vulnerability to anthropogenic threats for gibel carp when compared to other members of fish communities, this likely contributing to its invasion success.

### Conclusions

Alien species are continually introduced into many regions of the world, though not all survive and coexist with the resident native species. Many introduced species, however, have dramatic impacts on native biodiversity and ecosystem functions (Gallien & Carboni 2017). The biggest risks are posed by species with wide ecological tolerance and that exhibit traits linked to invasiveness (Allendorf 1991). The specific biological traits of gibel carp; the coexistence of sexual and asexual forms in the same habitats, the capacity to rapidly reproduce by gynogenesis, the potential for environmental sex determination, as well as its ecological tolerance (including its resistance to anoxia and its capacity to expand its niche width and occupying new areas) have made this species one of the most successful non-native invasive fish species in the waters of the Czech Republic, as well as in Central and eastern Europe.

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## Literature

- Alcaraz C., Vila-Gispert A. & García-Berthou E. 2005: Profiling invasive fish species: the importance of phylogeny and human use. *Divers. Distrib.* 11: 289–298.
- Allendorf F.W. 1991: Ecological and genetic effects of fish introductions: synthesis and recommendations. *Can. J. Fish. Aquat. Sci.* 48: 178–181.
- Aydin H., Gaygusuz Ö., Tarkan A. et al. 2011: Invasion of freshwater bodies in the Marmara region (northwestern Turkey) by nonnative gibel carp, *Carassius gibelio* (Bloch, 1782). *Turk. J. Zool.* 35: 829–836.
- Bachtrog D., Mank J.E., Peichel C.L. et al. 2014: Sex determination: why so many ways of doing it? *PLOS Biol.* 12: e1001899.
- Barbuti R., Mautner S., Carnevale G. et al. 2012: Population dynamics with a mixed type of sexual and asexual reproduction in a fluctuating environment. *BMC Evol. Biol.* 12: 49.
- Baroiller J.F., D'Cotta H. & Saillant E. 2009: Environmental effects on fish sex determination and differentiation. *Sex. Dev.* 3: 118–135.
- Beck M.L. & Biggers C.J. 1983: Erythrocyte measurements of diploid and triploid *Ctenopharyngodon idella* × *Hypophthalmichthys nobilis* hybrids. *J. Fish Biol.* 22: 497–502.
- Beck K., Zimmerman K., Schardt J. et al. 2008: Invasive species defined in a policy context: recommendations from the federal invasive species advisory committee. *Invasive Plant Sci. Manag.* 1: 414–421.
- Bilotta G.S. & Brazier R.E. 2008: Understanding the influence of suspended solids on water quality and aquatic biota. *Water Res.* 42: 2849–2861.
- Bondarev D.L., Kunah O.M., Fedushko M.P. & Hubanova N. 2019: The impact of temporal patterns of temperature and precipitation on silver Prussian carp (*Carassius gibelio*) spawning events. *Biosyst. Divers.* 27: 106–117.
- Brown E.E., Baumann H. & Conover D.O. 2014: Temperature and photoperiod effects on sex determination in a fish. *J. Exp. Mar. Biol. Ecol.* 461: 39–43.
- Capel B. 2017: Vertebrate sex determination: evolutionary plasticity of a fundamental switch. *Nat. Rev. Genet.* 18: 675–689.
- Cherfas N.B. 1981: Gynogenesis in fishes. In: Kirpichnikov V.S. (ed.), *Genetic bases of fish selection*. Springer-Verlag, Berlin, Germany: 255–273.
- Choleva L. & Janko K. 2013: Rise and persistence of animal polyploidy: evolutionary constraints and potential. *Cytogenet. Genome Res.* 140: 151–170.
- Conover D.O. & Kynard B.E. 1981: Environmental sex determination: interaction of temperature and genotype in a fish. *Science* 213: 577–579.
- Courant J., Vogt S., Marques R. et al. 2017: Are invasive populations characterized by a broader diet than native populations? *PeerJ* 5: e3250.
- Cousin A., Heel K., Cowling W.A. & Nelson M.N. 2009: An efficient high-throughput flow cytometric method for estimating DNA ploidy level in plants. *Cytometry A* 75: 1015–1019.
- Crivelli A.J. 1995: Are fish introductions a threat to endemic fresh water fishes in the northern Mediterranean region? *Biol. Conserv.* 72: 311–319.
- David P., Thébault E., Anneville O. et al. 2017: Impacts of invasive species on food webs: a review of empirical data. In: Bohan D.A., Dumbrell A.J. & Massol F. (eds.), *Networks of invasion: a synthesis of concepts*. Academic Press, London, UK: 1–60.
- De Boeck G., Smolders R. & Blust R. 2010: Copper toxicity in gibel carp *Carassius auratus gibelio*: importance of sodium and glycogen. *Comp. Biochem. Physiol. Part C Toxicol. Pharmacol.* 152: 332–337.
- Doeringsfeld M.R., Schlosser I.J., Elder J.F. & Evenson D.P. 2004: Phenotypic consequences of genetic variation in a gynogenetic complex of *Phoxinus eos-neogaeus* clonal fish (Pisces: Cyprinidae) inhabiting a heterogeneous environment. *Evolution* 58: 1261–1273.
- Elger M. & Hentschel H. 1981: The glomerulus of a stenohaline fresh-water teleost, *Carassius auratus gibelio*, adapted to saline water. *Cell Tissue Res.* 220: 73–85.
- Erdoğan Z., TorcuKoç H., Serkan K.G. & Ulunehir G. 2014: Age, growth and reproductive properties of an invasive species *Carassius gibelio* (Bloch, 1782) (Cyprinidae) in the İkizcetepeler Dam Lake (Balıkesir), Turkey. *Period. Biol.* 116: 285–291.
- Eyckmans M., Celis N. & Horemans N. et al. 2011: Exposure to waterborne copper reveals differences in oxidative stress response in three freshwater fish species. *Aquat. Toxicol.* 103: 112–120.
- Gallien L. & Carboni M. 2017: The community ecology of invasive species: where are we and what's next? *Ecography* 40: 335–352.



- Gamble T. & Zarkower D. 2012: Sex determination. *Curr. Biol.* 22: R257–262.
- Gao F.X., Wang Y., Zhang Q.Y. et al. 2017: Distinct herpesvirus resistances and immune responses of three gynogenetic clones of gibel carp revealed by comprehensive transcriptomes. *BMC Genomics* 18: 561.
- García-Abiado M.A.R., Dabrowski K., Christensen J.E. et al. 1999: Use of erythrocyte measurements to identify triploid saugeyes. *N. Am. J. Aquac.* 61: 319–325.
- García-Berthou E. 2007: The characteristics of invasive fishes: what has been learned so far? *J. Fish Biol.* 71 (Suppl. D): 33–55.
- Gaygusuz Ö., Tarkan A. & Gaygusuz G. 2007: Changes in the fish community of the Ömerli Reservoir (Turkey) following the introduction of non-native gibel carp *Carassius gibelio* (Bloch, 1782) and other human impacts. *Aquat. Invasions* 2: 117–120.
- Gibson A.K., Delph L.F. & Lively C.M. 2017: The two-fold cost of sex: experimental evidence from a natural system. *Evol. Lett.* 1: 6–15.
- Gui J.F. & Zhou L. 2010: Genetic basis and breeding application of clonal diversity and dual reproduction modes in polyploidy *Carassius auratus gibelio*. *Sci. China Life Sci.* 53: 409–415.
- Gurevitch J. & Padilla D.K. 2004: Are invasive species a major cause of extinctions? *Trends Ecol. Evol.* 19: 470–474.
- Hakoyama H., Nishimura T., Matsubara N. & Iguchi K. 2001: Difference in parasite load and nonspecific immune reaction between sexual and gynogenetic forms of *Carassius auratus*. *Biol. J. Linn. Soc.* 72: 401–407.
- Halačka K., Lusková V. & Lusk S. 2003: *Carassius "gibelio"* in fish communities of the Czech Republic. *Ecohydrol. Hydrobiol.* 3: 133–138.
- Hamilton W.D., Axelrod R. & Tanese R. 1990: Sexual reproduction as an adaptation to resist parasites (a review). *Proc. Natl. Acad. Sci. U. S. A.* 87: 3566–3573.
- Harrell R.M., Heukelem W.V. & Kerby J.H. 1998: A comparison of triploid induction validation techniques. *Prog. Fish-Cult.* 60: 221–226.
- Heger T. 2001: A model for interpreting the process of invasion: crucial situations favouring special characteristics of invasive species. In: Brundu G., Brock J.H., Camarda I. et al. (eds.), *Plant invasions: species ecology and ecosystem management*. Backhuys Publishers, Leiden, the Netherlands: 3–10.
- Hochachka P.W. & Somero G.N. 1984: Biochemical adaptations. *Princeton University Press, Princeton, USA*.
- Holčík J. & Žitňan R. 1978: On the expansion and origin of *Carassius auratus gibelio* in Czechoslovakia. *Folia Zool.* 7: 239–250.
- Hyvärinen H., Holopainen I.J. & Piironen J. 1985: Anaerobic wintering of crucian carp (*Carassius carassius* L.). I. Annual dynamics of glycogen reserves in nature. *Comp. Biochem. Physiol. Part A Physiol.* 82: 797–803.
- Jiang F.F., Wang Z.W., Zhou L. et al. 2013: High male incidence and evolutionary implications of triploid form in northeast Asia *Carassius auratus* complex. *Mol. Phylogenet. Evol.* 66: 350–359.
- Jiang Y.G., Yu H.X., Chen B.D. & Liang S.C. 1983: Biological effect of heterologous sperm on gynogenetic offspring in *Carassius auratus gibelio*. *Acta Hydrobiol. Sin.* 8: 1–13. (in Chinese with English summary)
- Kalous L., Bohlen J., Rylková K. & Petrtýl M. 2012: Hidden diversity within the Prussian carp and designation of a neotype for *Carassius gibelio* (Teleostei: Cyprinidae). *Ichthyol. Explor. Freshw.* 23: 11.
- Kalous L. & Knytl M. 2011: Karyotype diversity of the offspring resulting from reproduction experiment between diploid male and triploid female of silver Prussian carp, *Carassius gibelio* (Cyprinidae, Actinopterygii). *Folia Zool.* 60: 115–121.
- Kolar C.S. & Lodge D.M. 2001: Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.* 16: 199–204.
- Kotusz J., Popiołek M., Drozd P. et al. 2014: Role of parasite load and differential habitat preferences in maintaining the coexistence of sexual and asexual competitors in fish of the *Cobitis taenia* hybrid complex. *Biol. J. Linn. Soc.* 113: 220–235.
- Lamatsch D.K. & Stöck M. 2009: Sperm-dependent parthenogenesis and hybridogenesis in teleost fishes. In: Schön I., Martens K. & Dijk P. (eds.), *Lost sex*. Springer, Dordrecht, Netherlands: 399–432.
- Lampert K.P. & Scharl M. 2010: A little bit is better than nothing: the incomplete parthenogenesis of salamanders, frogs and fish. *BMC Biol.* 8: 78.
- Leung C. & Angers B. 2017: Imitating the cost of males: a hypothesis for coexistence of all-female sperm-dependent species and their sexual host. *Ecol. Evol.* 8: 266–272.



- Liasko R., Koulis A., Pogrebniak A. et al. 2011: Influence of environmental parameters on growth pattern and population structure of *Carassius auratus gibelio* in Eastern Ukraine. *Hydrobiologia* 658: 317–328.
- Liasko R., Liousia V., Vrazeli P. et al. 2010: Biological traits of rare males in the population of *Carassius gibelio* (Actinopterygii: Cyprinidae) from Lake Pamvotis (north-west Greece). *J. Fish Biol.* 77: 570–584.
- Li X.Y. & Gui J.F. 2018: Diverse and variable sex determination mechanisms in vertebrates. *Sci. China Life Sci.* 61: 1503–1514.
- Li Z., Liang H.W., Wang Z.W. et al. 2016b: A novel allotetraploid gibel carp strain with maternal body type and growth superiority. *Aquaculture* 458: 55–63.
- Li X.Y., Zhang X.J., Li Z. et al. 2014: Evolutionary history of two divergent *Dmrt1* genes reveals two rounds of polyploidy origins in gibel carp. *Mol. Phylogenet. Evol.* 78: 96–104.
- Li X.Y., Zhang Q.Y., Zhang J. et al. 2016a: Extra micro chromosomes play male determination role in polyploid gibel carp. *Genetics* 203: 1415–1424.
- Liu X.L., Jiang F.F., Wang Z.W. et al. 2017: Wider geographic distribution and higher diversity of hexaploids than tetraploids in *Carassius* species complex reveal recurrent polyploidy effects on adaptive evolution. *Sci. Rep.* 7: 5395.
- Lively C.M., Craddock C. & Vrijenhoek R.C. 1990: Red Queen hypothesis supported by parasitism in sexual and clonal fish. *Nature* 344: 864–867.
- Lu M., Li X.Y., Li Z. et al. 2021: Regain of sex determination system and sexual reproduction ability in a synthetic octoploid male fish. *Sci. China Life Sci.* 64: 77–87.
- Lusk S., Lusková V. & Hanel L. 2010: Alien fish species in Czech Republic and their impact on the native fish fauna. *Folia Zool.* 59: 57–72.
- Lusk S., Koščo J., Lusková V. et al. 2004: Alien fish species in the floodplains of the Dyje and the Bodrog rivers. *Ecohydrol. Hydrobiol.* 4: 199–205.
- Lusková V., Halačka K., Vetešník L. & Lusk S. 2004: Changes of ploidy and sexuality status of “*Carassius auratus*” populations in the drainage area of the River Dyje (Czech Republic). *Ecohydrol. Hydrobiol.* 4: 165–171.
- Lusková V., Lusk S., Halačka K. & Vetešník L. 2010: *Carassius auratus gibelio* – the most successful invasive fish in waters of the Czech Republic. *Russ. J. Biol. Invasions* 1: 176–180.
- Mee J.A., Chan C. & Taylor E.B. 2013a: Coexistence of sperm-dependent asexuals and their sexual hosts: the role of differences in fitness-related traits. *Environ. Biol. Fishes* 96: 1111–1121.
- Mee J.A., Fred N., Hanisch J.R. et al. 2013b: Diets of sexual and sperm-dependent asexual dace (*Chrosomus* spp.): relevance to niche differentiation and mate choice hypotheses for coexistence. *Oikos* 122: 998–1008.
- Mei J. & Gui J.-F. 2015: Genetic basis and biotechnological manipulation of sexual dimorphism and sex determination in fish. *Sci. China Life Sci.* 58: 124–136.
- Meyer A.H., Schmidt B.R. & Grossenbacher K. 1998: Analysis of three amphibian populations with quarter-century long time-series. *Proc. R. Soc. Biol. Sci. Ser. B* 265: 523–528.
- Milardi M., Gavioli A., Soininen J. & Castaldelli G. 2019: Exotic species invasions undermine regional functional diversity of freshwater fish. *Sci. Rep.* 9: 17921.
- Navodaru I., Buijse A.D. & Staras M. 2002: Effects of hydrology and water quality on the fish community in Danube delta lakes. *Int. Rev. Hydrobiol.* 87: 329–348.
- Özdilek Ş.Y. & Jones R.I. 2014: The diet composition and trophic position of introduced Prussian carp *Carassius gibelio* (Bloch, 1782) and native fish species in a Turkish river. *Turk. J. Fish Aquat. Sci.* 14: 769–776.
- Özdilek Ş.Y., Partal N. & Jones R.I. 2019: An invasive species, *Carassius gibelio*, alters the native fish community through trophic niche competition. *Aquat. Sci.* 81: 29.
- Pakosta T., Vetešník L. & Šimková A. 2018: A long temporal study of parasitism in asexual-sexual populations of *Carassius gibelio*: does the parasite infection support coevolutionary Red Queen dynamics? *BioMed Res. Int.* 2018: 6983740.
- Papoušek I., Vetešník L., Halačka K. et al. 2008: Identification of natural hybrids of gibel carp *Carassius auratus gibelio* (Bloch) and crucian carp *Carassius carassius* (L.) from lower Dyje River floodplain (Czech Republic). *J. Fish Biol.* 72: 1230–1235.
- Paschos I., Nathanailides C., Tsoumani M. et al. 2004: Intra and inter-specific mating options for gynogenetic reproduction of *Carassius gibelio* (Bloch, 1783) in Lake Pamvotis (NW Greece). *Belg. J. Zool.* 134: 55–60.
- Paulovits G., Ferincz Á., Staszny Á. et al. 2014: Long-term changes in the fish assemblage



- structure of a shallow eutrophic reservoir (Lake Hídvégi, Hungary), with special reference to the exotic *Carassius gibelio*. *Int. Rev. Hydrobiol.* 99: 373–381.
- Perdikaris C., Ergolavou A., Gouva E. et al. 2012: *Carassius gibelio* in Greece: the dominant naturalised invader of freshwaters. *Rev. Fish Biol. Fish.* 22: 17–27.
- Przybył A., Przybylski M., Spóz A. et al. 2020: Sex, size and ploidy ratios of *Carassius gibelio* from Poland. *Aquat. Invasions* 15: 335–354.
- Ribeiro F., Rylková K., Moreno-Valcárcel R. et al. 2015: Prussian carp *Carassius gibelio*: a silent invader arriving to the Iberian Peninsula. *Aquat. Ecol.* 49: 99–104.
- Richardson M.J., Whoriskey F.G. & Roy L.H. 1995: Turbidity generation and biological impacts of an exotic fish *Carassius auratus*, introduced into shallow seasonality anoxic ponds. *J. Fish Biol.* 47: 576–585.
- Roberts P.D., Diaz-Soltero H., Hemming D.J. et al. 2013: What is the evidence that invasive species are a significant contributor to the decline or loss of threatened species? A systematic review map. *Environ. Evid.* 2: 5.
- Ross S.T. 1991: Mechanisms structuring stream fish assemblages: are there lessons from introduced species? *Environ. Biol. Fishes* 30: 359–368.
- Ruppert J. L.W., Docherty C., Neufeld K. et al. 2017: Native freshwater species get out of the way: Prussian carp (*Carassius gibelio*) impacts both fish and benthic invertebrate communities in North America. *R. Soc. Open Sci.* 4: 170400.
- Rylková K., Kalous L., Bohlen J. et al. 2013: Phylogeny and biogeographic history of the cyprinid fish genus *Carassius* (Teleostei: Cyprinidae) with focus on natural and anthropogenic arrivals in Europe. *Aquaculture* 380–383: 13–20.
- Savini D., Occhipinti-Ambrogi A., Marchini A. et al. 2010: The top 27 animal alien species introduced into Europe for aqua-culture and related activities. *J. Appl. Ichthyol.* 26: 1–7.
- Schedina I.M., Groth D., Schlupp I. & Tiedemann R. 2018: The gonadal transcriptome of the unisexual Amazon molly *Poecilia formosa* in comparison to its sexual ancestors, *Poecilia mexicana* and *Poecilia latipinna*. *BMC Genomics* 19: 12.
- Seger J. & Hamilton W.D. 1988: Parasites and sex. In: Michod R.E. & Levin B.R. (eds.), *The evolution of sex*. Sinauer Associates Inc., Sunderland, USA: 176–193.
- Stachowicz J. & Byrnes J. 2006: Species diversity, invasion success, and ecosystem functioning: disentangling the influence of resource competition, facilitation, and extrinsic factors. *Mar. Ecol. Prog. Ser.* 311: 251–262.
- Stohlgren T.J., Barnett D., Flather C. et al. 2006: Species richness and patterns of invasion in plants, birds, and fishes in the United States. *Biol. Invasions* 8: 427–447.
- Stöck M., Ustinova J., Betto-Colliard C. et al. 2012: Simultaneous Mendelian and clonal genome transmission in a sexually reproducing, all-triploid vertebrate. *Proc. R. Soc. Biol. Sci. Ser. B* 279: 1293–1299.
- Šimková A., Hyršl P., Halačka K. & Vetešník L. 2015: Physiological and condition-related traits in the gynogenetic-sexual *Carassius auratus* complex: different investments promoting the coexistence of two reproductive forms? *BMC Evol. Biol.* 15: 154.
- Šimková A., Košář M., Vetešník L. & Vyskočilová M. 2013: MHC genes and parasitism in *Carassius gibelio*, a diploid-triploid fish species with dual reproduction strategies. *BMC Evol. Biol.* 13: 122.
- Tarkan A.S., Gaygusuz Ö., Gürsoy Gaygusuz Ç. et al. 2012: Circumstantial evidence of gibel carp, *Carassius gibelio*, reproductive competition exerted on native fish species in a mesotrophic reservoir. *Fish. Manag. Ecol.* 19: 167–177.
- Tobler M. & Schlupp I. 2005: Parasites in sexual and asexual mollies (*Poecilia*, Poeciliidae, Teleostei): a case for the Red Queen? *Biol. Lett.* 1: 166–168.
- Van der Veer G. & Nentwig W. 2015: Environmental and economic impact assessment of alien and invasive fish species in Europe using the generic impact scoring system. *Ecol. Freshw. Fish* 24: 646–656.
- Verreycken H., Anseeuw D., Van Thuyne G. et al. 2007: The non-indigenous freshwater fishes of Flanders (Belgium): review, status and trends over the last decade. *J. Fish Biol.* 71: 160–172.
- Vetemaa M., Eschbaum R., Albert A. & Saat T. 2005: Distribution, sex ratio and growth of *Carassius gibelio* (Bloch) in coastal and inland waters of Estonia (north-eastern Baltic Sea). *J. Appl. Ichthyol.* 21: 287–291.
- Vetešník L., Lusk S., Halačka K. & Spurný P. 2004: Morphometric characteristics and growth of *Carassius auratus* in the lower part of the River Dyje (Czech Republic). *Ecohydrol. Hydrobiol.* 4: 215–221.
- Wang Z.-W., Zhu H.-P., Wang D. et al. 2011: A novel nucleo-cytoplasmic hybrid clone formed via

- androgenesis in polyploid gibel carp. *BMC Res. Notes* 4: 82.
- Warner R. 1982: Mating systems, sex change and sexual demography in the rainbow wrasse, *Thalassoma lucasanum*. *Copeia* 3: 653–661.
- Weeks S.C., Gaggiotti O.E., Schenck R.A. et al. 1992: Feeding behavior in sexual and clonal strains of *Poeciliopsis*. *Behav. Ecol. Sociobiol.* 30: 1–6.
- Wouters J., Janson S., Lusková V. & Olsén K.H. 2012: Molecular identification of hybrids of the invasive gibel carp *Carassius auratus gibelio* and crucian carp *Carassius carassius* in Swedish waters. *J. Fish Biol.* 80: 2595–2604.
- Xia Y., Zhao W., Xie Y. et al. 2019: Ecological and economic impacts of exotic fish species on fisheries in the Pearl River basin. *Manag. Biol. Invasions* 10: 127–138.
- Xu H., Ding H., Li M. et al. 2006: The distribution and economic losses of alien species invasion to China. *Biol. Invasions* 8: 1495–1500.
- Zhang J., Sun M., Zhou L. et al. 2015: Meiosis completion and various sperm responses lead to unisexual and sexual reproduction modes in one clone of polyploidy *Carassius gibelio*. *Sci. Rep.* 5: 10898.
- Zhao X., Li Z., Ding M. et al. 2021: Genotypic males play an important role in the creation of genetic diversity in gynogenetic gibel carp. *Front. Genet.* 12: 875.
- Zhou L. & Gui J.F. 2002: Karyotypic diversity in polyploid gibel carp, *Carassius auratus gibelio* Bloch. *Genetica* 115: 223–232.
- Zhu Y.-J., Li X.-Y., Zhang J. et al. 2018: Distinct sperm nucleus behaviors between genotypic and temperature-dependent sex determination males are associated with replication and expression-related pathways in a gynogenetic fish. *BMC Genomics* 19: 437.