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HABILITATION THESIS

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Marbled crayfish, an emerging invasive species

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Study II – Vodovsky, N., Patoka, J. and **Kouba, A.**, 2017. Ecosystem of Caspian Sea threatened by pet-traded non-indigenous crayfish. *Biological Invasions 19*, 2207-2217.

Study III – Lipták, B., Mrugała, A., Pekárik, L., Mutkovič, A., Gruľa, D., Petrusek, A. and **Kouba, A.**, 2016. Expansion of the marbled crayfish in Slovakia: beginning of an invasion in the Danube catchment? *Journal of Limnology 75*, 305-312.

Study IV – Veselý, L., Buřič, M. and **Kouba, A.**, 2015. Hardy exotics species in temperate zone: can “warm water” crayfish invaders establish regardless of low temperatures? *Scientific Reports 5*, 16340.

Study V – **Kouba, A.**, Tíkal, J., Císař, P., Veselý, L., Fořt, M., Příborský, J., Patoka, J. and Buřič, M., 2016. The significance of droughts for hyporheic dwellers: evidence from freshwater crayfish. *Scientific Reports 6*, 26569.

Study VI – Guo, W., Kubec, J., Veselý, L., Hossain, M.S., Buřič, M., McClain, R. and **Kouba, A.**, 2019. High air humidity is sufficient for successful egg incubation and early post-embryonic development in the marbled crayfish (*Procambarus virginalis*). *Freshwater Biology 64*, 1603-1612.

– PREFACE –

I first encountered crayfish in my childhood in the early nineties. At that time, my father was employed by a company, Astacus a.s. that, among other endeavours, conducted crayfish culture primarily for restocking. This activity was largely driven by Bohumil Nový, an enthusiastic nature conservationist from Maleč, Bohemian Forest. The business was unsuccessful, and crayfish culture was discontinued. Looking at proactive measures for conservation of native crayfish species in Europe almost three decades later, it seems that the concept was ahead of its time.

I was reintroduced to crayfish when studying fishery at the Faculty of Agriculture, University of South Bohemia in České Budějovice (USB). Crayfish research was interestingly novel among the topics offered for MSc research. My studies of crayfish began with conducting a comparison of early postembryonic development in native and non-native crayfish. I continued with research into intensification of juvenile crayfish culture during my Ph.D. study at the Research Institute of Fish Culture and Hydrobiology in Vodňany (later part of the Faculty of Fisheries and Protection of Waters, USB), all under the supervision of Prof. Pavel Kozák. Eventually, crayfish-related research became the core of my scientific interests. In recent years, this has chiefly consisted of study of non-native crayfish species in general, and marbled crayfish in particular.

– ACKNOWLEDGEMENTS –

It is a challenge to mention all the people who have assisted me in my scientific career, and this is far from an exhaustive list. I would like to express my sincere thanks to at least some of them, since the achievements mentioned below were, for the most part, feasible only thanks to the diverse collaboration. First, I would like to thank my former supervisor Pavel Kozák for advice and overall support during early stages of my scientific career. I thank all colleagues from our laboratory (at present the Laboratory of Freshwater Ecosystems) for keeping the team active and congenial. Among others, these include Miloš Buřič, Martin Bláha, Hamid Niksirat Hashjin, Lukáš Veselý, and Jan Kubec. Jitka Hamáčková is greatly appreciated for always maintaining our crayfish culture in extraordinarily good condition, a necessary prerequisite for reliable experimentation.

Additional appreciated collaborations include diverse crayfish-related topics. I would like to thank Adam Petrusek and his students, in particular Eva Kozubíková-Balcarová, Jiří Svoboda, and Agata Mrugała, for continuing progress in crayfish plague research. I am pleased to collaborate with Jiří Patoka on aspects related primarily to the freshwater decapod pet trade and research on New Guinean endemic *Cherax* spp. My thanks also go to Josef Velíšek and Alžběta Stará for collaboration in using marbled crayfish as a model species in ecotoxicology. I am honoured to mention Julian Reynolds for his kind advice, support, and help whenever needed.

I would like to thank my parents for giving me overall support and freedom. Last but not least, I offer my heartiest gratitude to my wife Anna, daughters Veronika and Terezie, and son Martin, for their love.

This thesis is dedicated to Francesca Gherardi, a brilliant Italian zoologist, ethologist, and ecologist who sadly passed away in 2013. I met her as a young student at the conference *European Crayfish: food, flagships and ecosystem services* in Poitiers, France in 2010. I have been always impressed by her scientific curiosity that extended to a broad range of topics.

– INTRODUCTION –

Freshwater ecosystems and biological invasions

Freshwater ecosystems occupy about 0.8 % of the earth's surface and make up 0.01% of its water, but support disproportionally high biodiversity. Although not fully inventoried, over 125,000 species of freshwater animals described so far represents almost 10% of all known animal species, as well as one third of all vertebrates (Balian et al., 2007; Dudgeon et al., 2006; Strayer and Dudgeon, 2010). Species include 17,800 known fishes (Fricke et al., 2020), an estimated 7,000 dragonflies (Kalkman et al., 2007), 1,200 described mussels (Lopes-Lima et al., 2018), 1,600 crabs (Cumberlidge, 2016), and almost 700 crayfish (Crandall and De Grave, 2017).

The status of freshwater systems is critically important to human populations, which form an integral part of the biosphere. Availability and quality of drinking water is obviously crucial to human existence. Insufficient quantity and unequal distribution of freshwater on the earth, accompanied by ever-increasing human demands and degradation in quality, has led to a crisis both from both human and biodiversity standpoints (Albert et al., 2020; Schwarzenbach et al., 2010; Vörösmarty et al., 2010). Conservation and sustainable utilization of natural resources in general, and freshwater ecosystems in particular, are critical to preserving the planet. Ongoing trends of fresh water degradation are unprecedented and alarming. Globally, wetlands are vanishing at three times the rate of forests, and the loss of freshwater vertebrate populations is more than double that of terrestrial and marine populations (Albert et al., 2020; Darwall et al., 2011; Tickner et al., 2019). The risk of extinction of freshwater species is consistently higher than for their terrestrial and marine counterparts (Clausnitzer et al., 2009; Collen et al., 2014; Ricciardi and Rasmussen, 1999), making freshwater conservation an urgent priority.

The accelerating rates of international trade, travel, and transport, particularly beginning in the second half of the 20th century, have led to a translocation of biota throughout the world. The number of species introduced into new locations is increasing (Hanafiah et al., 2013; Pyšek et al., 2010; Seebens et al., 2015) among taxa and regions (Cohen and Carlton, 1998; Ricciardi et al., 2017; Seebens et al., 2017) worldwide. Many introduced organisms have become established and spread into new environments with negative consequences (Allendorf and Lundquist, 2003; Jeschke and Pyšek, 2018). Biological invasions often result in irreversible changes, and costs are tremendous (Pimentel et al., 2000; Vilà et al., 2010). Thus, invasions are consistently considered one of the major threats to global biodiversity and ecosystem functioning, as evidenced by their effects on freshwater ecosystems (Catford et al., 2012; Simberloff et al., 2013; Strayer, 2010).

Crayfish and crayfish plague

Crayfish are the largest of freshwater invertebrates and among the longest-lived (Johnston and Robson, 2009; Souty-Grosset et al., 2006). They are often considered keystone species (Momot, 1995; Reynolds and Souty-Grosset, 2011) and ecosystem engineers (Creed and Reed, 2004; Statzner et al., 2000) due to their prominent role in biological as well as physical modification of the ecosystems they inhabit (Twardochleb et al., 2013). Based on their substantial individual size and high population abundance, feeding patterns, and dominance in interactions (Reynolds and Souty-Grosset, 2011), several crayfish species have been recognized as invasive (Gherardi and Acquistapace, 2007; Lodge et al., 2000; Twardochleb et al., 2013). Native crayfish species are directly and indirectly threatened by their non-native counterparts (Crandall and Buhay, 2008; Richman et al., 2015; Taylor et al., 2019). The proportion of non-native crayfish generating negative environmental consequences is high, affecting both biodiversity and ecosystem function (Gherardi, 2006; Olden et al., 2006; Scalici et al., 2010).

Aphanomyces astaci (Oomycetes, Saprolegniales) is a crayfish parasite native to North America (Unestam, 1969; Unestam, 1972). North American crayfish species show substantial resistance to *A. astaci* and are typically present as chronic non-symptomatic carriers (Cerenius et al., 2003; Söderhäll and Cerenius, 1999). The introduction of *A. astaci* into Europe has led to the spread of the so-called ‘crayfish plague’, a name referring to the rapid mass mortality observed amongEuropean crayfish populations. The first outbreaks in Europe occurred in 1859 in the Po River basin of Italy and led to the extirpation of several Italian white-clawed crayfish *Austropotamobius pallipes* populations (Cornalia, 1860). It has since spread across most of the continent and into Turkey (Alderman, 1996). Occurrence of chronic infections in native European crayfish populations is a newly discovered phenomenon.

However, such infections thus far seem to be rare, and factors behind their establishment remain poorly understood (Kokko et al., 2012; Kušar et al., 2013; Pârvulescu et al., 2012; Schrimpf et al., 2012; Svoboda et al., 2012). The pathogen is currently confirmed in other locations harbouring similarly susceptible native crayfish: South America (Peiró et al., 2016), Indonesia (Putra et al., 2018), and Japan (Martin-Torrijos et al., 2018; Mrugała et al., 2017), posing a threat to remaining populations. Recently, the role of freshwater crabs (Schrimpf et al., 2014; Svoboda et al., 2014b; Tilmans et al., 2014) and shrimp (Mrugała et al., 2019; Putra et al., 2018; Svoboda et al., 2014a) as alternative hosts of this pathogen is being investigated. The mass mortality seen in crayfish has not been observed yet, but non-lethal effects cannot be ruled out. Following decades of research, *A. astaci* is considered one of the best-studied of invertebrate pathogens (Svoboda et al., 2017). Because of its devastating effect on the crayfish species not native to North America, *A. astaci* was classified among the world´s 100 most invasive species (Lowe et al., 2000).

Native and 'Old' non-native crayfish in Europe

The number of crayfish species native to Europe is low (Kouba et al., 2014; Souty-Grosset et al., 2006), and newly discovered species are rare (Pârvulescu, 2019). The level of species diversity in Eastern Europe is largely undefined and may consist primarily of the genus *Pontastacus*. However, this field of study remains largely unexplored, and clear evidence for previously suggested species diversity (Crandall and De Grave, 2017; Starobogatov, 1995) remains insufficient (Bláha et al., 2017; Maguire et al., 2014). Population decline of native crayfish stocks in Europe caused by crayfish plague outbreaks, combined with poor results of restocking of native species, contributed to the interest in supplementation with alternative resistant species (Laurent, 1997). Although some attempts at introduction have not been successful (Abrahamsson, 1973; Kossakowski, 1966), a range of non-native crayfish species are currently established, and their numbers steadily increase.

The spiny-cheek crayfish *Faxonius limosus* is the first non-native species to be successfully established in Europe. Its native range is the lower reaches of the Delaware River (Rhoades, 1962) on the east coast of the USA in the Chesapeake Bay area of the states of Pennsylvania, Maryland, and possibly in other rivers of the region

(Filipová et al., 2011). It has been introduced into numerous US states and Canada (Hobbs Jr, 1974; Taylor et al., 2007). It was first brought to Europe in 1890, when 90 specimens (McDonald, 1893) were released into a fishpond near Barnówko in Pomerania, a part of present-day western Poland (Kossakowski, 1966). This introduction is presumed the be the exclusive source of the species in Europe (Filipová et al., 2011). Thanks to its active dispersal and human assistance, the spiny-cheek crayfish is widely distributed and established in 25 European regions (Holdich et al., 2009; Kouba et al., 2014) with recent reports of its occurrence in Slovenia (Govedič, 2017), Bulgaria (Trichkova et al., 2015), and Estonia (Kaldre et al., 2020). Spiny-cheek crayfish entered the Czech Republic, most likely via upstream migration through the River Elbe from Germany (Petrusek et al., 2006). It is the most widespread non-native crayfish in the Czech Republic, primarily inhabiting the rivers Elbe and Vltava and downstream stretches of their tributaries. Species occurrence in standing waters as well as apparently isolated localities is also reported (Petrusek et al., 2006), confirming human-mediated translocations. The spiny-cheek crayfish is the main reservoir of the crayfish plague pathogen in the Czech Republic (Kozubíková et al., 2009).

The second species to be established in Europe was the signal crayfish *Pacifastacus leniusculus*. Its native range is from the Pacific Ocean to the Rocky Mountains in the US states of Idaho, Oregon, and Washington and the Canadian province of British Columbia. It has been introduced into California, Nevada, and Utah (Taylor et al., 2007). From 1926 through 1930, signal crayfish were introduced into Japan for commercial purposes, outcompeting the endemic *Cambaroides japonicus* in the wild (Kawai et al., 2002; Usio et al., 2007). Signal crayfish were first imported into Europe in 1959, when ~60 specimens from California were brought to Sweden (around 60; Svärdson, 1995). Since the species was found to be comparable in ecological and gastronomic characteristics to the noble crayfish, the population of which had been devastated by crayfish plague outbreaks since 1907, signal crayfish were released into open waters. After the success of this pilot attempt, massive introductions from multiple sources followed, accompanied by secondary introductions in Sweden as well as into other European countries (Brinck, 1977; Holdich et al., 2009; Petrusek et al., 2017). This eventually resulted in 30 invaded European regions (Kouba et al., 2014), with recent reports of occurrence in Malta (Deidun et al., 2018). The signal crayfish is currently the most widespread non-native crayfish species in Europe. In 1980, onethousand juvenile signal crayfish were imported from Sweden into what was then Czechoslovakia for commercial production, which was ultimately unsuccessful. These introductions were concentrated in the Vysočina Region, which remains the core area of its occurrence, but the crayfish have dispersed through migration and human intervention, including to distant locations throughout the country (Jurek, 2014).

At the time of the primary introductions into Europe, signal crayfish were believed to be immune to crayfish plague, and the close relationship between the causative agent and North American crayfish was not well understood. Eventually research revealed its status as a chronic carrier, in common with many North American species (Filipová et al., 2013; James et al., 2017).

The third non-native crayfish with widespread establishment in the European wild also originates from the North American continent. The red swamp crayfish *Procambarus clarkii* is native to north-eastern Mexico and several states in the southeast US. Its first documented introductions took place in the early 20th century, when it was taken to the Hawaiian Islands (1923), the Pacific basin areas of the USA (1924), Japan (1927), and China (1929) for purposes including aquaculture, fishing bait, human consumption, and feed for cultured American bullfrogs *Lithobates catesbeianus* (Brasher et al., 2006; Holmes, 1924; Penn, 1954). Since the 1960s, red swamp crayfish have been introduced into numerous African countries, as well as Central and South America (Hobbs et al., 1989; Holdich, 1988; Hunner, 1977). In Europe, it was legally introduced into Spain (Badajoz 1973; Seville 1974) from Louisiana, USA. Based on the initial success of these introductions, further large-scale stocking followed. Chiefly through human intervention, but also thanks to its own high dispersion capability (Carral et al., 1993; Habsburgo-Lorena, 1986; Habsburgo-Lorena, 1979), the red swamp crayfish has spread into 18 European regions (Kouba et al., 2014), most recently to Poland (Maciaszek et al., 2019), Hungary (Gál et al., 2018; Weiperth et al., 2015), and Malta (Deidun et al., 2018). The pet trade has gradually become recognized as a significant red swamp crayfish introduction pathway (Faulkes, 2015; Patoka et al., 2018). The species has not been documented in the wild in the Czech Republic. However, despite the ban in the European Union (EU, 2014, 2016), it remains available among aquarists. The red swamp crayfish is now the most widespread of crayfish species, occurring in all continents except Australia and

Antarctica (Hobbs et al., 1989). Its introduction history has recently been reviewed by Oficialdegui (2019).

'New' non-native crayfish in Europe

Introductions of spiny-cheek crayfish, signal crayfish, and red swamp crayfish have caused severe reductions in biodiversity and ecosystem damage. In addition to the spread of crayfish plague, these invasive species have outcompeted native crayfish in multiple respects, including higher aggression and dominance in mutual interactions, greater competitiveness for critical resources such as food and shelter, more rapid growth and maturation, shorter egg incubation time, and higher fecundity as well as showing broader environmental tolerance. They have spread widely across Europe causing, not only extirpation of native crayfish populations but, in several cases, having devastating impact on the newly occupied ecosystems. These three non-native species are recognized as invasive (Gherardi and Acquistapace, 2007; Lodge et al., 2000; Souty-Grosset et al., 2006) and are listed as European Union invasive species of concern (EU, 2014, 2016). They are often referred to as 'Old NICS' (old non-indigenous crayfish species). The primary motivation for their introductions was re-stocking after the collapse of native crayfish populations, often combined with fishery and aquaculture aspirations (Holdich et al., 2009).

Since 1980, additional non-native crayfish species have been introduced into Europe (New NICS), often through escape or intentional release of aquarium-bred specimens. The breeding of crayfish for ornamental purposes and the ready availability of alien species in pet shops and through the internet represents a major threat, as these trade activities are difficult to control. Breeders are known to release their surplus stock into open waters (Chucholl, 2013; Patoka et al., 2014a), especially when the market is saturated with such stock. Similarly, they may release animals when faced with an originally well-meant regulation forbidding keeping certain species. Such releases may be seen as a possible solution if the reasons for such a ban are not communicated properly (Patoka et al., 2018). Stocking of crayfish into garden ponds from which they can easily disperse overland (Herrmann et al., 2018; Chucholl et al., 2012) is another problematic activity (Patoka et al., 2017; Patoka et al., 2014b; Peay, 2009).

The European distribution of New NICS is currently low, but rapid expansion can be expected for at least some species. Reports of new releases are increasing. These recently-arrived non-native species include the North American calico crayfish *Faxonius immunis*, Kentucky River crayfish *Faxonius juvenilis*, virile crayfish *Faxonius* cf. *virilis*, white river crayfish *Procambarus* cf. *acutus*, marbled crayfish *Procambarus virginalis*, and Mexican dwarf crayfish *Cambarellus patzcuarensis*. The Australian species are represented by the yabby *Cherax destructor*, and redclaw *Cherax quadricarinatus* (Gál et al., 2017; Kouba et al., 2014).

Each mentioned species represents a unique entity with its own well-known or presumed European introduction history and biology. For example, the calico crayfish was first reported in Europe in two locations in the Upper Rhine system of southern Germany in the mid-1990s (Dehus et al., 1999; Gelmar et al., 2006). Its introduction pathway is not entirely clear; introduction from aquaria and as fishing bait have been suggested (Dehus et al., 1999; Lodge et al., 2012). The species was not known in the pet trade prior to its confirmed presence in the wild (Gelmar et al., 2006), making an introduction as fishing bait, possibly by Canadian soldiers stationed at an airbase near the locations in which the species were first reported, more likely (Chucholl, 2013). The calico is spreading upstream and downstream, primarily in the Rhine. It is more successful in direct interactions and in competition for shelter with the spiny-cheek crayfish, displacing the latter's previously well-established populations (Chucholl, 2009; Chucholl, 2012). In turn, ongoing research suggests that similar factors might lead to displacement of the calico crayfish by the marbled crayfish (Hossain et al., 2020), which has been consistently reported in the area in recent years (Herrmann et al., 2018; Chucholl et al., 2012; Marten et al., 2004). This implies that New NICS may also represent a severe environmental risk and, under certain circumstances, contribute to species displacement, including of Old NICS.

Another interesting case it the Australian yabby. This species was first introduced into Spain in 1983. The crayfish originated from a breeding facility in California, USA and were stocked into a site close to Girona in Catalonia. In the subsequent two years, further introductions were conducted close to Zaragoza in Aragon, and the species occurrence was later confirmed in the province of Navarra. In 2005, two Navara populations were eradicated by crayfish plague (Bolea, 1996; Souty-Grosset et al., 2006), which also eliminated other known Spanish yabby populations

(J. Dieguéz-Uribeondo, pers. comm., 2012). However, at least one population likely persists (Kouba et al., 2014). Beginning in the early 1990s, experiments to culture yabby in closed intensive breeding facilities for commercial purposes were conducted in Italy, mainly in central and northern parts of the country (D'Agaro et al., 1999). Later, the species successfully established in the Natural Preserve of Laghi di Ninfa of central Italy (Scalici et al., 2009). This population recently disappeared, most likely as a result of expansion of the crayfish-plague-carrying red swamp crayfish into the area (Mazza et al., 2018). Yabby is less vulnerable to crayfish plague than are the European native crayfish species (Mrugała et al., 2019; Mrugała et al., 2016), but its long-term co-occurrence with more virulent *A. astaci* strains (Svoboda et al., 2017) remains to be determined. Yabby has recently been detected in Sicily (Deidun et al., 2018), France (C. Souty-Grosset, pers. comm., 2019), and Ireland (J. Reynolds, pers. comm., 2019).

Marbled crayfish

Among the non-native crayfish species introduced into Europe, one is extraordinary. The marbled crayfish (marmorkrebs) *Procambarus virginalis* is known for its parthenogenetic mode of reproduction, unique among decapods. The marbled crayfish is a novel species closely related to the slough crayfish *Procambarus fallax* (Martin et al., 2010), an abundant, sexually reproducing freshwater crayfish species native to Florida and southern Georgia in the US (Taylor et al., 2007). Marbled crayfish may have originated from the slough crayfish through a macromutation that resulted in its reproductive isolation (Vogt et al., 2015). All known animals can be traced back to an initial population (Lyko, 2017). Early reproductive studies, in combination with microsatellite analyses, suggest that marbled crayfish utilize apomictic parthenogenesis, resulting in genetically identical offspring (Martin et al., 2007; Vogt et al., 2008). A *de novo* draft assembly of the marbled crayfish genome has been recently generated and shows a triploid AA'B genotype with a high level of heterozygosity (Gutekunst et al., 2018). Comparative whole-genome sequencing of animals from various aquarium lineages and wild populations confirm that the marbled crayfish meta-population represents a single, genetically homogeneous clone. Genetic variants may be generated by an ongoing accumulation of natural mutations, but their numbers are greatly limited by the extremely young evolutionary age of the species (Gutekunst et al., 2018).

The marbled crayfish was first reported in the German aquarium trade in 1995 (Lukhaup, 2001; Werner, 1998), from where it dispersed (Scholtz et al., 2003). It is usually readily available from pet markets (e.g. Faulkes, 2015; Chucholl, 2013; Kotovska et al., 2016; Patoka et al., 2014a). In 2003, the first single marbled crayfish was observed in the European wild (Marten et al., 2004), with further records following (Chucholl et al., 2012; Kovács et al., 2015; Nonnis Marzano et al., 2009). The situation accelerated in 2010, when established populations were found in Germany (Chucholl and Pfeiffer, 2010) and Slovakia (Janský and Mutkovič, 2010). Since then, the marbled crayfish has spread considerably, primarily in Europe (Hossain et al., 2018; Vogt, 2020) but has also been documented in Japan (Kawai and Takahata, 2010), and, especially, in Madagascar (Jones et al., 2009), which harbours what is probably the largest population of the species globally. For the local people, marbled crayfish represents inexpensive protein and an attractive source of income (Andriantsoa et al., 2019).

Marbled crayfish can be a carrier of crayfish plague both within the pet trade (Mrugała et al., 2015) and in the wild (Keller et al., 2014). Natural populations seem to often be crayfish plague-free, most likely as a result of a bottleneck effect (Lipták et al., 2017; Lipták et al., 2016). This may quickly change if transmission from previously infected crayfish occurs (James et al., 2017a; Lipták et al., 2016; Mrugała et al., 2015). This is especially the case with respect to contact with already widespread Old NICS crayfish, the populations of which are often infected (Svoboda et al., 2017 for review). Introduction of this disease may be a significant advantage to marbled crayfish in competition with susceptible native crayfish.

Multiple life history traits make the marbled crayfish highly successful compared to other crayfish, including those not native to Europe. The mode of reproduction is foremost. The marbled crayfish also shows rapid growth, early maturation, and frequent reproduction with short incubation time and high fecundity (Hossain et al., 2019; Lipták et al., 2017; Seitz et al., 2005; Vogt, 2015). It can exist on a wide variety of feeds (Lipták et al., 2019), and is highly tolerant to a range of environmental factors (Guo et al., 2019; Kouba et al., 2016; Veselý et al., 2015). The marbled crayfish is listed among European Union invasive alien species of concern (EU, 2014, 2016).

Its characteristics make marbled crayfish a perfect candidate for aquaculture (Jurmalietis et al., 2019; Toenges et al., 2020), but, given the potential environmental risks, such activity should be strictly avoided. Exploitation of existing Malagasy stock seems justifiable, as it can reduce the population (Andriantsoa et al., 2019), but concerns related to secondary introduction into adjacent territories remain.

Genetic uniformity, favourable biological traits, and ease of culture (Jimenez and Faulkes, 2010) make marbled crayfish a promising model organism in several research disciplines (Hossain et al., 2018; Vogt, 2008; Vogt, 2011). Available genome (Gutekunst et al., 2018), methylome, and transcriptome of the species (Gatzmann et al., 2018) support advanced applications.

The marbled crayfish is a unique and fascinating animal from several standpoints. Its sudden appearance and accompanying gaps in our knowledge about its biology have presented an excellent opportunity for studying this enigmatic species. A series of selected articles focusing on a variety of aspects of marbled crayfish ecology and biology comprise the core of this habilitation thesis.

– SUMMARY OF PUBLICATIONS –

This habilitation thesis comprises six selected publications, most related exclusively to the marbled crayfish. I am the first author of two articles. Three first authors are my former (Lukáš Veselý and Boris Lipták) and present (Guo Wei) Ph.D. students, while one contribution is an international collaboration. The selected research begins with a study of the distribution of marbled crayfish in Europe, followed by a report of its availability in the pet trade and a survey of its established populations in Slovakia. The marbled crayfish ability to overwinter in the temperate zone of central Europe was confirmed experimentally. When it became obvious that the marbled crayfish is capable of forming an integral part of our astacofauna, we investigated the species in the context of apparent stressors, testing its burrowing and reproduction capacities under simulated conditions of severe drought.

Study I

When preparing our Czech monograph 'Biologie a chov raků' later published in a second edition and translated into English (Kozák et al., 2015), we were faced with a need for European crayfish distribution maps. The most relevant available maps were from the Atlas of Crayfish in Europe (Souty-Grosset et al., 2006), as used in a comprehensive review by Holdich et al. (2009). In Study I (Kouba et al., 2014), to better illustrate the actual situation, we re-plotted data from the atlas onto a new colour map suitable for presentation purposes, which also shows topography of the European landscape. We conducted an extensive literature review, accompanied by comment from over 70 authorities from 32 countries. Native ranges of European crayfish were occasionally modified according to available information on distribution and phylogeographic reports and on the recommendations of contributors from the respective countries. We also prepared maps illustrating data of non-indigenous crayfish species with limited distribution in Europe, including the marbled crayfish. The resulting maps were published in an open access article, which is frequently cited.

The situation with the marbled crayfish remains in a state of flux. In addition to increasing numbers of their populations in already invaded countries, the species has appeared in Austria, Croatia, Czech Republic, Denmark, Estonia, Hungary, Malta, Romania, and Ukraine (Vogt, 2020), with impending reports of occurrence in more areas.

Study II

The number of countries invaded by the marbled crayfish is evidently increasing rapidly. It is one of the most popular pet-traded crayfish species worldwide despite its ban in certain areas (EU, 2014, 2016, Faulkes, 2015), and the pet trade is the primary pathway of its introductions, both intentional and non-intentional. Given the rapid reproduction of the species, hobby keepers are soon faced with an issue of overpopulated aquaria. Once their list of friends and customers interested in crayfish-keeping is exhausted, release into the wild may be seem a viable option. Due to the susceptibility of diverse crayfish species to crayfish plague and negative effects on local biota and ecosystems in general, marbled crayfish presence in the pet trade is concerning. Eastern Europe is rich in species susceptible to the crayfish plague. A pet trade survey, along with assessment of risk posed by traded species, including marbled crayfish, was conducted in Study II (Vodovsky et al., 2017).

Study III

Our knowledge of distribution and biology of marbled crayfish remains limited. It is highly likely that the species actual range is far greater than is currently known and that numerous populations await discovery. The known biology largely relies on data observed in laboratory cultures, while the situation in the wild is poorly understood. Study III (Lipták et al., 2016) provides data on newly reported populations of marbled crayfish in Slovakia and basic information of its biology in the wild. This initial report can stimulate consistent targeted research on marbled crayfish in the wild, which is thus far limited (Vogt, 2018).

Study IV

Low winter temperatures were previously presumed sufficient to limit the establishment of marbled crayfish in temperate zones. The appearance of populations in the wild in Germany and Slovakia (Chucholl and Pfeiffer, 2010; Janský and Mutkovič, 2010), together with reports of overwintering in areas that freeze during winter (Chucholl et al., 2012; Kaldre et al., 2015), have proven this assumption wrong. Due to the lack of data of the precise temperatures in the studied sites and of access to the marbled crayfish locations, we conducted an experiment under temperature-controlled conditions. Study IV (Veselý et al., 2015) assessed the overwintering capability of four warm-water non-native crayfish species, including the marbled crayfish. Specimens were acclimatized and maintained for 6.5 months at temperatures simulating the winter temperature regime of European temperate zone lentic ecosystems, including at ~2.5 °C for three months. Despite high mortality, marbled crayfish successfully overwintered. Given the recent mild winters, these temperatures do not represent a barrier to establishment under our climatic conditions.

Study V

Long-term severe drought can be devastating to freshwater biota. In order to remain in contact with water or stay in a sufficiently humid environments to avoid desiccation, the ability to retreat to the hyporheic zone is crucial. Study V (Kouba et al., 2016) compared the ability of three European native and five non-native crayfish, including the marbled crayfish, to survive and construct vertical burrows during a seven day simulated drought. In contrast to native crayfish, marbled crayfish proved to be both successful burrowers and tolerant of desiccation.

Study VI

Through our investigations of burrowing and reproduction, we obtained indirect evidence that the red swamp crayfish might successfully reproduce in burrows without free standing water. To investigate this possibility in crayfish, we conducted a series of experiments using artificial burrows with high air humidity and marbled crayfish as a model species. Study VI (Guo et al., 2019) demonstrated the ability of marbled crayfish to undergo terminal phases of embryogenesis, including hatching, as well as early post-embryonic development under high air humidity conditions only, which is not a trait of European native crayfish. Post-embryonic development was interrupted in the absence of water and successfully resumed when re-immersed. This highlights the importance of drought-oriented adaptations of freshwater organisms as well as the potential of marbled crayfish as an invasive species

– FUTURE PERSPECTIVES –

While our ongoing research on the marbled crayfish has yielded much valuable information, it seems that the number of unanswered questions increases with each investigation, stimulating further research. A wide range of previous studies has focused on pairwise comparisons of crayfish species traits in a native vs. one or two NICS, usually under single temperature conditions. However, populations of NICS are appearing in unexpected combinations, with the role of temperature as a key environmental factor being almost always overlooked. Since marbled crayfish disperse into regions with different temperature regimes, studies of its interactions with already widespread Old NICS as affected by temperature are needed. Further, these species co-occurrences provide an opportunity for studying transmission of the crayfish plague pathogen, given the unique relationships between NICS and specific *A. astaci* genotypes. Assessment of trophic roles of co-occurring NICS is another important direction of future research.

Ongoing investigation of marbled crayfish will provide critical information applicable to multiple fields. The marbled crayfish is increasingly recognized as a valuable model species. We use it in our research, primarily in ecotoxicology and behaviour, and integrate its study into the education of our bachelor and master's degree students. Publications in popular magazines are essential targets to publicise the expansion of activities focused on protection of freshwater ecosystems in general, and crayfish conservation in particular.

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Study I

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