

Overlooked keystone species in conservation plans of fluvial ecosystems in Southeast Europe: a review of native freshwater crayfish species

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Abstract – Although a large number of rivers stretches in Southeast Europe (SEE) have a pristine status compared to the rest of Europe, these ecosystems and their freshwater biodiversity are perceptibly threatened. Since crayfish species are known to cover a wide spectrum of ecological functions they are considered as keystone species and ecosystem engineers. Therefore, their decline may substantially impair local biodiversity and ecosystem services. In this manuscript we present a brief overview of the status of the native freshwater crayfish and their habitats in SEE. Different forms of physical habitat degradation as well as invasive alien crayfish species and their pathogens (*e.g.*, *Aphanomyces astaci*) are simultaneously threatening endangered populations all over SEE. Even though all native crayfish species are listed in the IUCN Red List, so far none of the 33 LIFE rehabilitation projects performed in SEE, has crayfish as target species in their agenda. Furthermore, SEE countries rarely designated Natura 2000 sites for native crayfish. We propose future studies to assess the distribution and functional role of crayfish species in SEE, as well as to develop habitat suitability models for these species during future conservation projects.

Keywords: Astacidae / Balkans / Natura 2000 / river restoration / Southeast Europe

1 Introduction

In most parts of the world, human activities have altered the landscape and disrupted fluvial processes to the extent that fluvial and riparian ecosystems are among the world's most threatened (Tockner and Stanford, 2002; Helfield *et al.*, 2012). These disturbed river dynamics have massive negative consequences for riverine communities (Palmer *et al.*, 2010), especially aquatic keystone species and their ecosystem services (Malmqvist and Rundle, 2002; Richter *et al.*, 2003).

In order to regain ecological integrity of riverine systems and mitigate the threats of biodiversity loss, national governments under the European Union have implemented diverse laws and directives. The most important are the Water Framework Directive (WFD) 2000/60/EC (EC, 2000), the Floods Directive 2007/60/EC (EC, 2007) and the Conservation-directive of Natural Habitats and of Wild Fauna and Flora, also known as Habitats Directive 92/43/EEC (EC, 1992; European Union, 2020). Considering conservation issues in

the European Union, a network of nature protection areas called Natura 2000 was established. In spite of the “umbrella effect” of the EU Natura 2000 protected areas network, 60% of freshwater habitats are failing to have a good ecological status (EEA, 2018) while 46% are still threatened (critically endangered, endangered, or vulnerable), and therefore far from having a favourable conservation status (Grzybowski and Glińska-Lewczuk, 2019).

Here, we aimed to highlight the main threats to fluvial ecosystems in the SEE region through presenting an overall summary of the status of freshwater crayfish in the region. In order to do so, we have included existing studies originating from different countries in SEE. Finally, we suggest measures that can be additionally applied for successful conservation programs and emphasize obstacles that should be overcome.

2 Study area & Sources of information

In this study we put a focus on SEE countries bordering the Danube River basin and Adriatic drainages according to the Freshwater Ecoregions of the World (FEOW) map (FEOW, 2008). The main area of SEE includes the Mediterranean,

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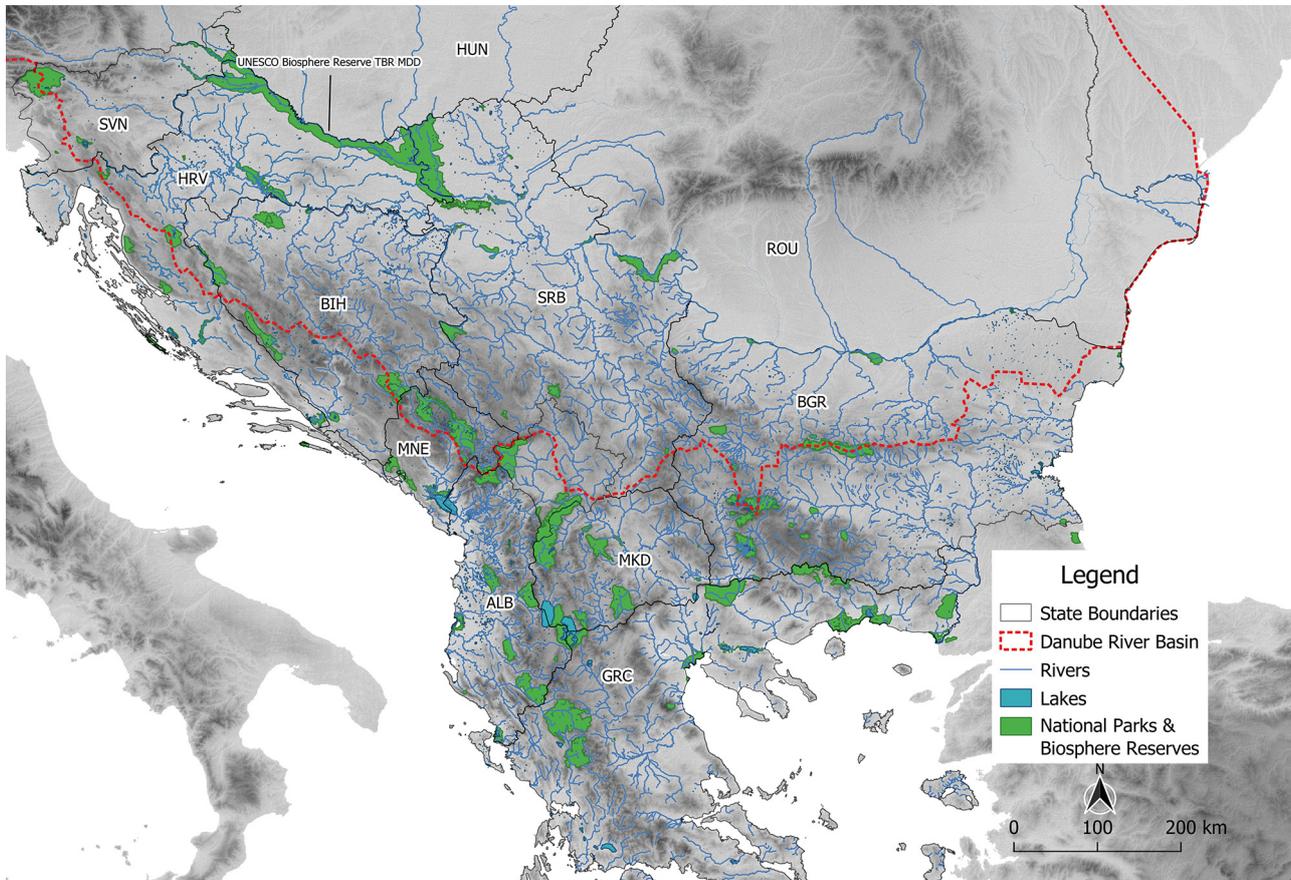


Fig. 1. Freshwaters in SEE with watershed of the Danube River basin marked with red line, produced in QGIS v. 3.16.10. Protected SEE areas (without Romania) with high category (National parks, World heritage, Biosphere reserves, Ramsar sites), highlighted in green, were taken from the Eco-masterplan for Balkan Rivers (Riverwatch and EuroNatur 2018) provided by Fluvius Vienna (<https://riverwatch.eu/en/balkanrivers/map>).

Alpine, Continental and Pannonian biogeographical regions (Eionet, 2021).

Literature included relevant publications, not restricted to any journals, and was searched by using the ISI Web of Science. For the chapters we discuss in this paper, we searched literature by crossing the following keywords: [Revitalization OR Rehabilitation OR Restoration] AND/OR [Macroinvertebrates OR Macrozoobenthos OR Crayfish] AND/OR [SIA OR Stable AND Isotope] AND [Southeast Europe OR Southeastern Europe OR Balkan OR Slovenia OR Croatia OR Serbia OR Bosnia and Herzegovina OR Montenegro OR Albania OR Macedonia OR Bulgaria OR Romania]. Number of ISI-publications found by crossed keywords search are listed in Table S1. Cited literature of every relevant paper was also consulted.

For the assessment of river restoration projects within the LIFE program the advanced search was used in the online tool of the LIFE Public Database (EC, 2021). Search criteria sorted by each country, included all projects with themes classified as “habitat – freshwater” or “water – river basin management” to get the wider possible spectrum.

For comparison within EU member states, Natura 2000 sites designated to each crayfish species listed in Annex

II of the Habitats Directive were taken from the Natura 2000 Public Database (EEA, 2021).

3 Status of SEE rivers with a focus on the Danube River basin

In contrast to situation in the rest of Europe, an assessment of a total of 34,468 km of rivers in 2012 showed that around 30% of rivers on the Balkan Peninsula still have a near-natural (referred as pristine) status, and therefore a very high conservation value (Schwarz, 2012). Additionally, SEE is considered a unique hotspot for freshwater fauna (Griffiths *et al.*, 2004). Of all European threatened species, 52% of molluscs (151 species) and 28% of freshwater fishes (52 species) occur in the Balkan region (Huđek *et al.*, 2020; Schwarz, 2012). The river network of SEE with its protected areas (National parks, World heritage, Biosphere reserves, Ramsar sites) as well as the watershed of the Danube River basin are shown in Figure 1. However, the amount of natural river stretches is drastically declining due to anthropogenic impacts. Beside designation of conservation sites, active river restoration is also implemented in order to mitigate

anthropogenic impacts, restore previous natural states and create conditions for the return of natural processes, native species and watercourse functions (Palmer *et al.*, 2010; Blagus and Tadić, 2018). As described in the WFD, member states should aim to achieve at least a *good status* for freshwater systems by defining and implementing necessary measures within integrated programs. Yet, not every country in SEE is a member of the European Union and the WFD is not applied there. All SEE countries are however members of the Energy Community, which obligates them under the legal framework to implement several EU directives. These include directives to prevent or remedy environmental damage on the environment (Energy Community, 2018).

One of the biggest recent conservation projects within SEE is the nomination for a Transboundary UNESCO Biosphere Reserve “Mura-Drava-Danube” (TBR MDD) which stretches over five countries (SEE sections shown in Fig. 1), where, according to the WWF Europe, most of the ecologically important riverine habitats can be found. However, anthropogenic impacts already led to a loss of up to 80 % of the former floodplain areas and altered about 1100 km of natural river banks and stretches (WWF Austria, 2013). River sections within Croatia and Hungary have been designated as a Biosphere Reserve by UNESCO since July 2012 (UNESCO, 2012) and the whole area in its present dimension was established in September 2021 (WWF Adria, 2021). In the mentioned area several sites were already assigned as Natura 2000 sites and a few restoration measures were executed (e.g. LIFE Programme, 2014, 2015). Within the framework of these restorations, some preliminary ecological baseline studies were carried out, e.g. on Avi-, Entomo-, Ichthyo- and Herpetofauna in the Old-Drava oxbows (BioRes Bt., 2015).

The planning and construction of Hydropower plants (HPPs) in SEE is currently booming, due to greenhouse gas reduction goals (Schwarz, 2012; EC, 2018; Huđek *et al.*, 2020). Unfortunately, in most SEE countries EU Natura 2000 sites or regional parks are not an obstacle for the construction of HPPs that are known to have negative impacts on river ecosystems (Schwarz, 2012; Neubarth, 2018). Beside the existing ca. 1500 HPPs, 108 are in construction and 3431 more are planned over the whole SEE region (Schwarz, 2020). Taking the high number of planned HPPs into account, it is not surprising that 45% of them are planned or built in protected areas (Schwarz, 2020). Weiss *et al.* (2018) predicted that eleven of the 69 endemic fish species inhabiting the region will potentially suffer extinction, if most or all planned hydropower projects are carried out. Additionally, a review by Huđek *et al.* (2020) showed that the monitoring stations at HPP in the Balkans, insufficiently assess the impact on macroinvertebrates communities, if at all. These mentioned studies show that strategies for the development of renewable energy are still often in contrast with fluvial habitat preservation as previously addressed by Schwaiger *et al.* (2013).

4 Freshwater crayfish - diversity and threats

European freshwater crayfish play a significant role for freshwater ecosystems. Considered as keystone species

(Nystrom *et al.*, 1999; Dorn and Wojdak, 2004; Kouba *et al.*, 2014), crayfish provide top-down and bottom-up control through their omnivorous diet. From grazing macrophytes to active predation on macroinvertebrates and even small vertebrates, crayfish are known to control freshwater community composition (Usio, 2000; Füreder *et al.*, 2006; Mathers *et al.*, 2020). Through burrowing activities for food search and dwelling for shelter they also contribute to sedimentation processes in the benthic zone and are therefore considered as ecosystem engineers (Creed Jr., 1994; Statzner *et al.*, 2000; Weinländer and Füreder, 2016). Aside from being active predators, they also form an important part of food webs as prey species (Reynolds *et al.*, 2013). Since crayfish cover a specific ecological niche, their decline may thus substantially impair local biodiversity and ecosystem services.

European freshwaters are inhabited by indigenous crayfish species (ICS) belonging to the genera *Pontastacus*, *Astacus* and *Austropotamobius* (Souty-Grosset *et al.*, 2006; Crandall and De Grave, 2017). Due to their historical usage as a food source and frequent translocation by humans, distribution patterns of some species have changed throughout history (Maguire *et al.*, 2018). The ICS appearing in SEE freshwaters are as follows:

- 1 *Astacus astacus* (Linnaeus, 1758) (Noble crayfish) is mainly distributed in the tributaries of the Danube River and other water bodies belonging to the Black Sea basin (Pârulescu and Zaharia, 2013). There are also few recorded populations in the Adriatic Sea drainage, e.g. Croatia and Albania, where they were probably introduced (Maguire and Gottstein, 2004; Mrugała *et al.*, 2017) and the Prespa Lake and its adjacent tributaries, shared by North Macedonia, Albania and Greece (Krstić, 2012). Outside the Black Sea basin, the widest distribution can be found in the northern and central Greece (Perdikaris *et al.*, 2017).
- 2 *Pontastacus leptodactylus* (Eschscholtz, 1823) (Narrow-clawed crayfish or Turkish crayfish) is a widely distributed taxon across Europe, including the Danube River basin in SEE (Trichkova *et al.*, 2013). Mainly introduced in western Europe by anthropogenic translocation, its native range is restricted to the Ponto-Caspian and Asia Minor basins (Kouba *et al.*, 2014). However, this species is not distributed in all of the southwestern Balkans (Trožić-Borovac, 2011) but is spreading into new areas previously inhabited by *A. astacus* (Maguire *et al.*, 2011; 2018).
- 3 *Austropotamobius torrentium* (Schrank, 1803) (Stone crayfish) has a wide distribution in SEE (Kouba *et al.*, 2014). However, results showed that this species is the most sensible to anthropogenic pressure on their habitats (e.g., canalization, influx of pesticides from surrounding cultivated fields) (Machino and Füreder, 2005; Füreder *et al.*, 2006) and prefers intact natural water courses with high habitat heterogeneity (Weinländer and Füreder, 2010; Trichkova *et al.*, 2013).
- 4 *Austropotamobius pallipes* (Lereboullet, 1858) (White-clawed crayfish), in SEE countries mainly lives in freshwaters of the Adriatic basin (Kouba *et al.*, 2014) with a few recorded exceptions like the Una River (Trožić-Borovac, 2011), which belongs to the Black Sea drainage.

The first molecular phylogenetic study of the genus *Austropotamobius* by Trontelj *et al.*, (2005) indicated that the centre of genetic diversity for *A. torrentium* lies in the southern Balkan peninsula, while the primary centre of radiation of *A. pallipes* was probably in Istra, both regions in SEE. High genetic diversity within this genus was also confirmed for *A. pallipes* by Jelić *et al.* (2016), and studies on *A. torrentium* by Klobučar *et al.* (2013) and Lovrenčić *et al.* (2020a) showed that the hotspot of this species diversity is located in the Dinaric karst of Croatia. High genetic diversity in the Black Sea basin for *A. astacus* was shown by Schrimpf *et al.* (2014), especially in the western Balkans. Lovrenčić *et al.* (2022) confirmed these findings by showing, that Croatian populations harbour an important part of species genetic diversity and represent significant genetic reservoir at the European level. For *P. leptodactylus* Maguire *et al.* (2014) found two distinct evolutionary lineages, one Asian and one European.

The distribution of crayfish has been assessed at the continental scale in the very detailed publication “Atlas of Crayfish in Europe” by Souty-Grosset *et al.* (2006). However, there are still gaps that need to be filled for the Balkan Peninsula and SEE in general.

Native crayfish species, face simultaneously multiple threats such as:

- 1 *water pollution*. Even if some crayfish species can withstand moderate water pollution (Simić *et al.*, 2008), it is an important factor causing the disappearance of freshwater crayfish in the whole of Europe (Füreder *et al.*, 2002; Schulz and Schulz, 2004). Various toxicants such as fertilizers, insecticides, polychlorinated biphenyls (PCBs) or heavy metals can negatively affect crayfish distributed in contaminated waterbodies (Füreder *et al.*, 2006). Related to the latter, inundated areas of the Drava River have shown to accumulate excessive amounts of heavy metals (*e.g.* As, Cu, Cd and Hg) originating from developing industry, agriculture as well as urbanization (Tošić *et al.* 2019). These substances accumulate in crayfish through the food chain and may cause toxic or teratogenic effects (Kouba, *et al.*, 2010).
- 2 *habitat loss*. Hydro-morphological degradation and fragmentation (Holdich *et al.*, 2009) of the habitat by dams or other watercourse changes, decreases local populations gene flow, resulting in genetic diversity reduction. The following bottleneck may eventually end up in population extinction (Keller and Waller, 2002; Fitzpatrick *et al.*, 2012). Furthermore, due to habitats reductions, intraspecific competition occurs more often. This may results in age and sex ratio changes as the number of sexually mature females decreases because of direct competition with males over food and space (Abrahamson, 1966). Reduction in water levels, due to excessive water abstraction for agriculture or to climatic droughts have also major negative effects (Füreder *et al.*, 2006; Simić *et al.*, 2008; Holdich *et al.*, 2009). Maguire *et al.* (2011), for example, established that 68% of the disappearance of *A. pallipes* populations from the Adriatic Sea waterbodies can be linked to habitat loss through water abstraction and water body engineering.
- 3 *competition with non-indigenous crayfish species (NICS)* for habitat and food sources (Schulz and Schulz, 2004; Souty-Grosset *et al.*, 2006; Simić *et al.*, 2008; Weinländer

and Füreder, 2009; Twardochleb *et al.*, 2013). In SEE, as in Europe in general, the most abundant and widespread invasive species are *Pacifastacus leniusculus* (Dana, 1852) (Signal crayfish), *Faxonius limosus* (Rafinesque, 1817) (Spiny-cheek crayfish), both introduced before the 1980s in Europe (Spitzzy, 1973; Holdich *et al.*, 2009), and the parthenogenetic *Procambarus virginalis* Lyko, 2017 (Marbled crayfish). These NICS are widely distributed in water bodies of SEE and are continuously invading new freshwaters (Twardochleb *et al.*, 2013; Maguire *et al.*, 2018; Dragičević *et al.*, 2020; Weiperth *et al.*, 2020). With a more aggressive behaviour and higher female fecundity, NICS are often superior competitors and long-term coexistence results not only in displacing habitat (Füreder *et al.*, 2006; Hudina *et al.*, 2016) and creating trophic endpoints for native crayfish (Nystrom *et al.*, 1999; Vander Zanden *et al.*, 1999; Weinländer and Füreder, 2016; Pacioglu *et al.*, 2020), but also in changes in their morphology, growth rate and physiology (Hudina *et al.*, 2012; Pârvulescu *et al.*, 2015). A common ground for the implementation of legislation between the EU and its neighbouring countries has been proposed but has not yet been applied (Piria *et al.*, 2017). Only Montenegro aligned its legislative framework with the EU Alien Regulation 1143/2014 on non-native species (Piria *et al.*, 2021).

Pacifastacus leniusculus appears in the Mura River as well as in the Drava River, from where it spread naturally over Austria and Slovenia further down the Danube River basin. This invasive species was also illegally introduced into the Korana River, a tributary of the Sava River, in Croatia and into the Una River in Bosnia and Herzegovina (Simić *et al.*, 2008; Maguire *et al.*, 2011). *Faxonius limosus* spread as well into south through the Danube River from Hungary (Maguire and Klobučar, 2003; Maguire and Gottstein, 2004) and further downstream into Serbian (Pavlović *et al.*, 2006; Zorić *et al.*, 2020), Bulgarian (Todorov *et al.*, 2020) and Romanian (Pârvulescu *et al.*, 2009) freshwaters. This species has also been recorded in the Slovenian part of the Drava River (Govedič, 2017).

Procambarus virginalis was found in the waterbodies of the Balaton region in Hungary (Ludányi *et al.*, 2016) as well as in a lake near the Drava River in Croatia (Dobrović *et al.*, 2021; Samardžić *et al.*, 2014). Given the fact, that this invasive species is known to reproduce by parthenogenesis, this makes the marbled crayfish even a bigger concern, because only one female might be enough to establish a new population (Scholtz *et al.*, 2003).

Procambarus clarkii (Girard, 1852) (Red swamp crayfish), which is considered as a high-risk species for European freshwaters (Kouba *et al.*, 2014), has not yet been found in countries of SEE. However, as this species is already established in 16 European territories, *P. clarkii* is still a species of future concern (Souty-Grosset *et al.*, 2016).

- 4 *the crayfish plague* caused by the pathogen *Aphanomyces astaci* Schikora, 1906. All of the introduced NICS in Europe are potential vectors of this pathogenic oomycete that causes the crayfish plague (Souty-Grosset *et al.*, 2006; Weinländer and Füreder, 2009), a disease which is known since the 19th century (Edgerton *et al.*, 2004). While NICS are mostly immune or less susceptible, this disease is able to lead to a quick death of native crayfish (Oidtmann *et al.*,

2002). With this advantage NICS can replace native species even faster. However, recent studies showed that native crayfish, which managed to survive over decades in habitats infested with the crayfish plague, can gain a partial resistance to this disease (Kušar *et al.*, 2013; Maguire *et al.*, 2016; Pacioglu *et al.*, 2020).

5 *climate change*. As most other native organisms, indigenous crayfish currently suffer from this major pressure (Edsman, *et al.* 2010; Pecl, *et al.* 2017). Changes in precipitation patterns and the frequency of extreme weather conditions, which result in water temperature increase and changes in the water flow regimes, negatively impact ICS (Moss *et al.*, 2009). Additionally, climate change may increase future spread of NICS and their pathogens (Hulme, 2017). Future climate change will probably have further negative impacts onto ICS population, through contracting number of suitable habitats for their survival as shown in a recent study by Lovrenčić *et al.* (2022).

Considering all these threats, indigenous crayfish are listed in the IUCN Red List of endangered species (IUCN, 2011) with a “Vulnerable” (VU) or higher status, except for *A. torrentium*, and are protected by national and European laws (Weinländer and Füreder, 2010). In some of the SEE countries in which evaluation according to IUCN Red List criteria were used, certain ICS have a higher threatened status than at the global scale; *e.g.* *A. torrentium* has a VU status in Croatia, whereas on international level its status *dada* is deficient (DD), or *A. astacus* is evaluated as “Endangered” (EN) in Serbia in contrast to VU at the global level (Simić *et al.*, 2008; Maguire *et al.*, 2018).

However, only a few studies put a focus on crayfish populations within the frame of broad-scale conservation projects, like Natura 2000 and compare the effectiveness of designated sites to the actual species distribution (Lovrenčić *et al.*, 2020b). Additionally, only Slovenia, Croatia, Bulgaria and Romania contribute to the Natura 2000 network and assess the local crayfish status in protected areas as members of the European Union (Trichkova *et al.*, 2013; Todorov *et al.*, 2014).

We investigated Natura 2000 sites for each protected crayfish species listed in Annex II of the Habitats Directive (Fig. 2). Except Romania no other SEE member state designated Natura 2000 sites for *A. astacus* (AstAst). In total 135 Natura 2000 sites have *A. astacus* listed in Annex II (Fig. 2A), with the most designated sites per country located in Germany (42) and Latvia (22). In contrast, 389 of all Natura 2000 sites were designated for *A. torrentium* (AusTor), among them 224 in SEE countries (Fig. 2B). Compared to the country size, Slovenia has almost five times more sites (120) than Croatia (25). Germany and Bulgaria designated 119 and 67 sites for *A. torrentium*, respectively. The highest number of all Natura 2000 sites concerned *A. pallipes* (AusPal), with 812 sites, Slovenia and Croatia contributing with only 11 and 26 sites for this species, respectively (Fig. 2C). In comparison countries outside SEE like Italy (312), France (251) and Spain (186) contributing most Natura 2000 sites. List of Natura 2000 sites designated for *A. astacus*, *A. pallipes* and *A. torrentium* can be found in Tables S2, S3 and S4, respectively.

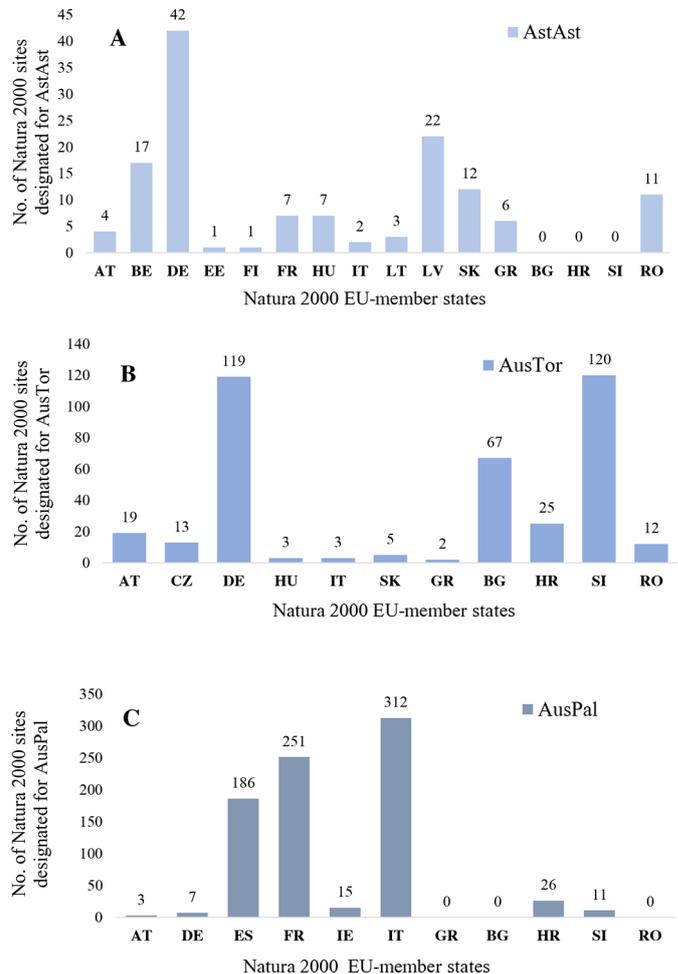


Fig. 2. Designated numbers of Natura 2000 sites per member states which have (A) *Astacus astacus* (AstAst), (B) *Austropotamobius torrentium* (AusTor) and (C) *Austropotamobius pallipes* (AusPal) listed in Annex II of the Habitats Directive. EU-member states are shown in two-letter country codes according to the EU (Eurostat, 2021) (https://ec.europa.eu/eurostat/statistics-explained/index.php?title=Glossary:Country_codes). Member states from SEE were put together on the right side for easier comparison.

Concerning conservation projects including river restoration or rehabilitation efforts, crayfish are rarely listed in the policies. Analysing the database of LIFE programmes for crayfish species as target species, we found 477 LIFE projects from 1992 - 2020 classified as “habitat – freshwater” or “river basin management” in EU and non-EU countries. Among these, 33 LIFE projects were performed in SEE countries (48 LIFE projects, if Greece is included) (Fig. 3), none of them mentioning crayfish in their project description. In contrast, 48 LIFE projects in other European countries had crayfish species in their agenda or at least mentioned them in some way in their project description. Out of these projects around half of them were conducted in Italy (Fig. 3). In total 20 LIFE projects with crayfish in their agenda executed restoration measures, most of them in Italy (12) and Austria (3) (Fig. 4). Detailed

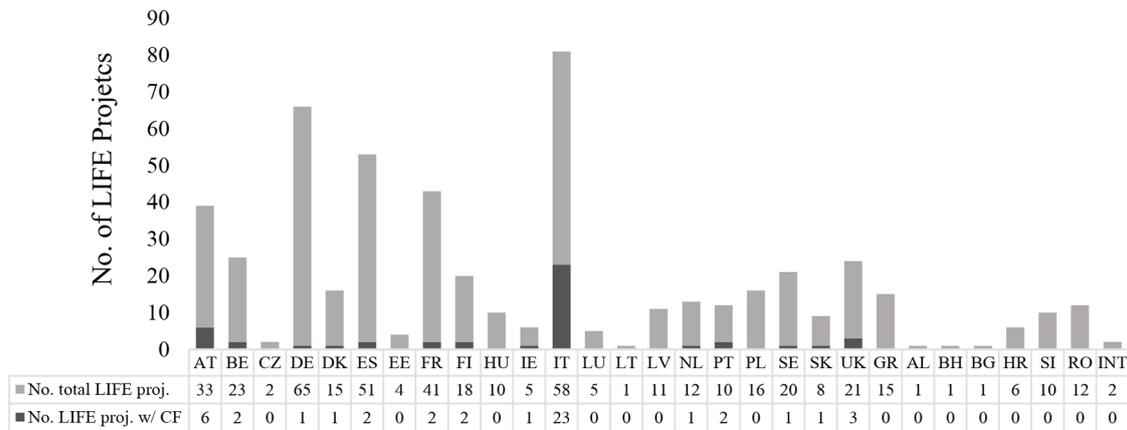


Fig. 3. Number of LIFE projects in each EU and non-EU member state from 1992 – 2020 classified as “habitat – freshwater” or “river basin management”. Black fractions of the columns show the number of projects containing crayfish in the agenda (No. LIFE proj. w/ CF). INT = International transboundary programs including non-EU SEE countries.

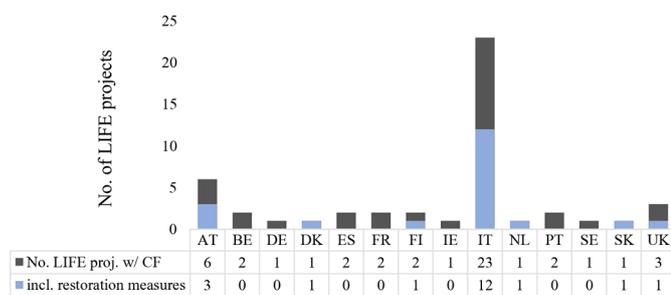


Fig. 4. Total number of LIFE projects in each EU member state from 1992 - 2020 classified as “habitat – freshwater” or “river basin management” containing crayfish in the agenda. Blue fractions of the columns show the number of projects with restoration measures.

projects description can be found in Table S5 for LIFE projects including crayfish and Table S6 for all LIFE projects in SEE countries.

5 Obstacles and need for action

As highlighted in this review, native crayfish face various threats that jeopardize their conservation (Weinländer *et al.*, 2014; Pacioglu *et al.*, 2020). It is therefore essential to provide protected recovery zones and refugia for freshwater crayfish as well as to include crayfish in restoration measures of SEE freshwaters.

However, previous studies have reported that success rates of stocking and reintroduction of once present freshwater invertebrates remain quite low, even after restoration activities (Palmer *et al.*, 2010; Geist and Hawkins, 2016; Leps *et al.*, 2016; dos Reis Oliveira *et al.*, 2020). We assume that in the latter cases, habitat is still not suitable for reintroduced species after river restoration. However, it is difficult to support or refute this assumption as no studies describing restoration effects on crayfish populations are available to date for SEE.

Hence, habitat suitability modelling may be a helpful tool to indicate which restoration measures are helpful for ICS

recovery zones in future projects (Ghia *et al.*, 2013; Weinländer *et al.*, 2014). In addition to keep the population status of native and invasive species in protected areas further updated, long term monitoring is essential (Trožić-Borovac, 2011; Kouba *et al.*, 2014).

Furthermore, the roles played by freshwater crayfish in SEE freshwater ecosystems, is not sufficiently known. Various studies performed food web analyses through gut content or food choice analyses (Nyström *et al.*, 1999; Correia, 2002; Weinländer and Füreder, 2016). Complementary to this classical method, trophic position and trophic niche width of crayfish in Europe was also assessed using stable isotope analyses (SIA). Most of SIAs focused on the differences between ICS and NICS (Olsson *et al.*, 2009; Ercoli and Ruokonen, 2014; Veselý *et al.*, 2021), whereas scarce researches compared the dietary change of those species during different stages of invasion (Pacioglu *et al.*, 2020). The latter study showed a gradual contraction of the trophic niche of native crayfish and a decrease in trophic overlap with invasive species over time and was the only study we found to date, focusing on SEE countries. Assessing the food web structure and trophic position of various crayfish communities in their habitats by trophic niche modelling should be thus a priority in SEE countries.

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Supplementary Material

The Supplementary Material is available at <https://www.kmae.org/10.1051/kmae/2022016/olm>.

Table S1: Number of ISI-publications found by crossed keywords search in the ISI Web of Science.

Table S2: Natura 2000 Sites with *Astacus astacus* listed in Annex II of the Habitats Directive.

Table S3: Natura 2000 Sites with *Austropotamobius pallipes* listed in Annex II Habitats Directive.

Table S4: Natura 2000 Sites with *Austropotamobius torrentium* listed in Annex II Habitats Directive.

Table S5: LIFE projects in European countries from 1992 - 2020 including crayfish in their agenda and classified as “habitat – freshwater” or “river basin management”. Grey labelled projects carried out restoration measures.

Table S6: LIFE projects in SEE countries from 1994 - 2017 classified as “habitat – freshwater” or “river basin management”. None of them have crayfish in their agenda. Grey labelled projects carried out restoration measures.

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