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Money Kills Native Ecosystems: European Crayfish as an Example

Japo Jussila[1], Lennart Edsman[2], Ivana Maguire[3], Javier Diéguez-Uribeondo[4] and Kathrin Theissinger[5,6]*

[1] Department of Environmental and Biological Sciences, University of Eastern Finland, Kuopio, Finland, [2] Department of Aquatic Resources, Institute of Freshwater Research, Swedish University of Agricultural Sciences, Uppsala, Sweden, [3] Department of Biology, Faculty of Science, University of Zagreb, Zagreb, Croatia, [4] Department of Mycology, Real Jardín Botánico - CSIC, Madrid, Spain, [5] LOEWE Centre for Translational Biodiversity Genomics, Senckenberg Biodiversity and Climate Research Centre, Frankfurt, Germany, [6] Institute for Environmental Sciences, University of Koblenz-Landau, Landau, Germany

Native European crayfish conservation was triggered by invasion of crayfish plague disease agent, *Aphanomyces astaci*, starting 1860s in Northern Italy. Resulting crayfish plague epidemics quickly spread over Continental Europe, then to Finland, Sweden and finally, after running amok around Europe, *A. astaci* was discovered also in Iberian Peninsula, Norway, Ireland, and United Kingdom in 1970s and 1980s. By that time significant proportion of native crayfish stocks had been lost, and while crayfish plague epidemics were still recorded, also industrialization and waterways construction were causing damage to remaining native crayfish stocks. While alien crayfish introductions, at least *Faxonius limosus,* already gave rise to first wave of crayfish plague epidemics in late 19th century, later in 1960s it was decided that introductions of alien *Pacifastacus leniusculus* should be initiated to replace native European crayfish populations. Decisions were based on presumed advantages for fishery, suitable habitat requirements and supposed immunity against *A. astaci*. Furthermore, conservation of native European crayfish species was sidelined and focus shifted toward alien crayfish stocking routine and consumption. Alien crayfish species introductions resulted in repeated waves of crayfish plague epidemics among remaining native crayfish stocks. It was soon discovered that alien crayfish of North American origin were, as suspected, permanent reservoirs for *A. astaci*, that some of those alien species were losing their resistance against selected strains of *A. astaci* and struggled in European aquatic ecosystems. In this article, we introduce numerous motives behind grand mistake of introducing alien crayfish species to Europe and then promoting their stocks instead of focusing on conservation of native crayfish species. We outline how false economical, biological and ecologic assumptions were used to justify a hasty introduction of alien crayfish, which has further devastated native crayfish and also permanently changed European aquatic ecosystems, both with disastrous consequences. Lesson to be learnt is that science-based warnings about alien species damage to native ecosystems and native crayfish must be taken with utmost caution. Protection of native European crayfish should be core issue, not commercial activities.

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Antonín Kouba,
University of South Bohemia, Czechia

****Correspondence:***
Japo Jussila
japo.jussila@uef.fi

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Finally, we summarize main threats and actions needed to protect remaining native freshwater crayfish fauna in Europe.

Keywords: conservation, biased decision making, environmental economics, political ecology, fisheries administration, native and alien crayfish, shortsightedness

INTRODUCTION

The Role of Crayfish in Europe: Ecosystem vs. Economy

Of all ecosystems in the world, freshwaters are among the most diverse and vulnerable, while constituting only 0.8% of the Earth's surface (Strayer and Dudgeon, 2010). Inland waters exhibit a high degree of endemism and extinction rates (Dudgeon et al., 2006) due to their insular nature, frequently small size, and the limited dispersal ability of many freshwater species which commonly results in adaptation to narrow habitat conditions. These characteristics make freshwaters vulnerable to extensive and growing human pressures (Naiman and Turner, 2000; Jackson et al., 2001; Strayer and Dudgeon, 2010). In the past century, the rapid increase of human populations accompanied by economic development resulted in an equally rapid increase in the demand for freshwater provisioning services, such as water for consumptive use, irrigation, power generation or transport as indicated in the Millennium Ecosystem Assessment from 2005. Among many pressures to freshwaters and their rich biodiversity, land-use change, pollution, physical alteration and damming, water abstraction, climate change and introduction of alien species have caused the most severe degradations (Dudgeon et al., 2006; Domisch et al., 2011).

Freshwater biodiversity is significantly influenced by freshwater crayfish, which are keystone species and ecosystem engineers, important components of freshwater food webs, due their relatively large body size, long life span and omnivorous feeding habits (Holdich, 2002; Usio and Townsend, 2008; Weinländer and Füreder, 2016). Owing to these characteristics, crayfish can directly affect ecosystem processes, species abundance and diversity (Pyšek and Richardson, 2010). Thus, crayfish disappearance from an ecosystem can significantly alter freshwater ecosystem processes and services, species abundance and diversity, leading to changes in habitat structure and functioning as well as to watercourse succession and changes in the dynamics of sediment transport (Moorhouse and Macdonald, 2011). Since native freshwater crayfish have a key role in the ecosystem by ensuring its normal functioning, and frequently being economically important, they need to be conserved. In a modern approach to species conservation, apart from habitat conservation, the focus is also on the preservation of species genetic diversity. High genetic diversity enables survival of species through time due to higher adaptive potential and fast evolutionary response to environmental changes (Bickford et al., 2007; Eizaguirre and Baltazar-Soares, 2014).

On the other hand, crayfish are among the most widely translocated aquatic invertebrates, introduced both within and between continents mainly through extensive harvesting for food, aquaculture and aquarium trade (Kouba et al., 2014; Loureiro, 2020) (**Table 1**). Once brought into a new habitat some alien crayfish species frequently become established and invasive. Invasive crayfish species are characterized by advantageous life history traits such as fast growth rate, high fecundity and early maturation (Souty-Grosset et al., 2006), which contribute to their invasive success. Their aggressiveness, e.g., *Pacifastacus leniusculus* (Dana, 1852) (Söderbäck, 1991), *Procambarus clarkii* (Girard, 1852) (Souty-Grosset et al., 2006; Arce and Dieguez-Uribeondo, 2015), enable them to exclude native species in competition for space and food sources (e.g., Söderbäck, 1994a, 1995; Hudina et al., 2014; Pacioglu et al., 2020). Additionally, they may outcompete native species by reproductive interference (Söderbäck, 1994b). Further, their tolerance to a broad range of conditions including pollution or organic enrichment, e.g., *Faxonius limosus* (Rafinesque, 1817) (Souty-Grosset et al., 2006), and transmission of diseases such as crayfish plague, caused by pathogen *Aphanomyces astaci* Schikora (Persson and Söderhäll, 1983; Vey et al., 1983; Diéguez-Uribeondo and Söderhäll, 1993), enhances their potential to drastically affect native crayfish populations. Thus, invasive species are recognized as the second most important factor affecting biodiversity loss worldwide (Lodge et al., 2000; Fahrig, 2003) and determining the factors of their invasive success is a key issue in invasive species management (Capinha et al., 2013) in order to conserve native crayfish populations as well as local biodiversity and ecosystem functioning.

Commercial activity seems to have had a key role in the introduction of alien crayfish and their associated diseases to Europe, and thus to the devastation of the native European crayfish. Crayfish have been traded since the discovery of their worth as food item, either for nutritional purposes as a valuable source of proteins in remote and sometimes poor parts of Europe (Holdich, 2002; Maguire and Gottstein-Matočec, 2004; Gherardi, 2011) and other regions (Andriantsoa et al., 2019), or as a focal point of cultural events (Jussila, 1995; Edsman, 2004; Alonso et al., 2000). They have even been used as food during fasting within religious communities, in order to bypass regulations forbidding the consumption of animals during fasting (e.g., Swahn, 2004; Ackefors, 2005; Patoka et al., 2016b) and also as a source of additional income for people catching and marketing them to bourgeois and religious communities (e.g., Lehtonen, 1975; Bohman et al., 2006; Gherardi, 2011). Trading frequently included crayfish transport over long distances (Anon, 1899; Edsman and Schröder, 2009; Jussila et al., 2013b) resulting in a mix of the natural genetic composition of native species (e.g., Edsman et al., 2002; Makkonen et al., 2015). Moreover, by trading live alien crayfish species within Europe, the spreading of the crayfish plague pathogen *A. astaci* was facilitated around the continent, as crayfish were often placed in water bodies along the way to markets (e.g., Alderman, 1996).

TABLE 1 | Native and alien crayfish in Europe: distribution, introduction motivation and *A. astaci* relationship. Distribution indicates in which European countries species is present (two letter country codes; www.iban.com/country-codes); introduction indicates motivation with AQ, aquaculture; PT, pet trade; WS, wild stock creation; *A. astaci* status is V, vulnerable; C, carrier; n/a, no information on *A. astaci* relation available; background coloration indicative of native species = no color; early introduced aliens = dark gray; late introduced aliens = light gray. The data is based on Kouba et al. (2014) and unless otherwise indicated been updated using data from Invasive Species Compendium website (https://www.cabi.org/isc/search/index?q=crayfish).

Species	Distribution	Introduction[9]	*A. astaci*
Astacus astacus	AL, AD, AT, BY, BE, BA, BG, HR, CY, CZ, DK, GB, EE, FI, FR, DE, GR, HU, IT, LV, LI, LT, LU, MD, ME, NL, NO, PL, RO, RS, RU, SK, SI, SE, CH, UA		C V
Pontastacus leptodactylus	AT, BY, BE, BG, HR, CZ, DE, ES, FI, GB, GR, HU, IT, LV, LT, LU, MT[1], MD, NL, PL, RO, RS, RU, SK, CH, UA		C V
Astacus pachypus	RU, UA		n/a
Austropotamobius pallipes	AT, BA, HR, GB, FR, DE, IE, IT, LI, ME, SI, ES, CH		C V
Austropotamobius torrentium	AL, AT, BA, BG, HR, CZ, FR, DE, HU, IT, LU, MK, ME, RO, RS, SI, SK, ES, CH		V
Austropotamobius bihariensis	RO[16]		
Faxonius limosus	AT, BG[12], BY, BE, HR, CZ, GB, FR, DE, HU, IT, LV, LT, LU, NL, PL, RO, RS, RU, SK, SI[18], ES, CH	WS	C
Pacifastacus leniusculus	AT, BA[15], BE, HR, CY, CZ, DK, GB, EE, FI, FR, DE, GR, HU, IT, LV, LT, LU, MT[1], NL, NO, PL, PT, SK, SI, ES, SE, CH	AQ, WS	C V
Procambarus clarkii	AT, BE[11], CY, GB, FR, DE, HU[2], IT, MT[1], NL, PL[10], PT, ES, CH	AQ, PT, WS	C
Faxonius immunis	FR, DE	AQ, WS	C
Faxonius juvenilis	FR	WS	n/a
Faxonius cf. *virilis*	GB, ME, NL		C
Procambarus cf. *acutus*	BE[12], GB, NL		C
Procambarus virginalis	AT[13], BE[3], CZ[8], DE, EE[17], FR[19], HR[17], HU[2], IT[6], MT[1], NL[17], SE[4], SK, RO[7], UA[5]	PT	C
Procambarus alleni	HU[2]	PT	C
Cherax destructor	ES, IT	AQ, PT, WS	V
Cherax quadricarinatus	ES[14], GB, GR, HU[2], SI, MT[1]	PT, AQ	CV
Cherax holthuisi	HU[2]	PT	n/a
Cherax snowden	HU[2]	PT	n/a
Cherax sp. (2 different)	HU[2]	PT	n/a
Cambarellus patzcuarensis	HU[2]	PT	C

[1]Deidun et al., 2018; [2]Weiperth et al., 2020; [3]Scheers et al., 2021; [4]Bohman et al., 2013; [5]Novitsky and Son, 2016; [6]Vojkovská et al., 2014; [7]Pârvulescu et al., 2017; [8]Patoka et al., 2016a; [9]Chucholl, 2015; [10]Maciaszek et al., 2019; [11]Scheers et al., 2020; [12]Todorov et al., 2020; [13]Cab Direct UK, 2014; [14]Arias Rodríguez and Torralba Burrial, 2021; [15]Trožić-Borovac et al., 2019; [16]Pârvulescu et al., 2019; [17]Vogt, 2020; [18]Govedič, 2017; [19]Grandjean et al., 2021.

After struggling for around 100 years with *A. astaci* epidemics, some countries of Northern and Southern Europe, losing more native crayfish stocks and failing with previous introductions of *F. limosus* and *Faxonius virilis* (Hagen, 1870) decided, largely for commercial purposes, that mass introduction of other alien crayfish should start from North America, such as *P. leniusculus* in Sweden 1960s (Svärdson, 1965, 1995; Abrahamsson, 1973), *P. leniusculus* in Finland 1960s (e.g., Westman, 1973), *F. limosus* and *P. leniusculus* in Austria 1960s and 1970s (Spitzy, 1973) and *P. leniusculus* and *P. clarkii* in Spain 1970s (e.g., Diéguez-Uribeondo et al., 1997a). Previous attempts to also introduce other North American species had happened, but not on such a massive scale (Alonso et al., 2000; Souty-Grosset et al., 2006). As mentioned above, the introduction of the alien

P. leniusculus, together with organized hatchery and stockling production, resulted amongst other matters in further waves of *A. astaci* epidemics among native European crayfish stocks. The commercial value of the native crayfish such as *Astacus astacus* (Linnaeus, 1758), *Pontastacus leptodactylus* (Eschscholtz, 1823) and *Austropotamobius pallipes* (Lereboullet, 1858), has partially contributed to protecting their wild stocks via a possibility for their profitable exploitation. When facing extinction or severe decline in Continental Europe and Fennoscandia (*A. astacus*), the Mediterranean countries (*A. pallipes*), Eastern Europe and Turkey (*P. leptodactylus*), their commercial value could be seen as directed against these European native crayfish. This resulted in the potential income from crayfish being used several times, one could say every time, when introductions of alien crayfish were discussed and justified (e.g., Westman, 1973; Söderbäck and Edsman, 1998; Alonso et al., 2000; Sahlin et al., 2010).

Monetary benefits have played a crucial role in the alien crayfish introductions, as there have also been at least temporary economic gains from alien species through aquaculture (e.g., Bohman et al., 2006) and exploiting wild stocks (Jussila and Mannonen, 2004; Bohman et al., 2006). In Fennoscandia, the economic benefits may have initially been obvious (e.g., Kirjavainen and Sipponen, 2004), Spain appears to be the same (e.g., Gutiérrez-Yurrita et al., 2017), while in Central Europe and Balkans the economics gains have been considerably smaller (e.g., Maguire and Gottstein-Matočec, 2004; Souty-Grosset et al., 2006). Even when discussing the initial cumulative benefits, the long term direct and indirect economic gains have so far been negligible or even negative when the whole aquatic ecosystem and society is taken into account (e.g., Gren et al., 2009). In Spain, the Scientific Committee of Spanish Ministry has finally declared that alien *P. leniusculus* and alien *P. clarkii* are not naturalized but invasive and detrimental to local aquatic ecosystems (Díaz, 2021). The entire ecosystem should always be considered when alien species benefits are discussed, even though short-term thinking favors money and ignores intangible benefits.

One crucial issue in the native crayfish conservation has been, and also will be in the future, several contrasting interests promoting either native crayfish conservation or alien species introductions. This issue has been discussed in detail by Biasetti et al. (2021), highlighting the complex network of intangible ideas and values relevant to different interest groups with also strong economic interest involved. Conservation obstinacy has been mentioned as an example of wasting resources to fight lost causes, as conservation outcome could, in some cases, be hard or even impossible to predict (Lehmann et al., 2002; Gontier et al., 2006) while we argue that lost causes can only be species extinctions. Animal welfare issues can also be relevant, since native species might have to be raised under artificial conditions and alien species eradication could be cruel (e.g., Cowan and Warburton, 2011). Finally, social factors of conservation are important and actions would require community acceptance and support with intensive awareness raising campaigns taking place. Ecosystem health or biodiversity as such are complex entities and adding diverse individual attitudes and expectations to considerations when native species conservation acts are planned, the result can easily be counterproductive for native species. The conservation of native crayfish should thus be seen as an attempt to conserve native ecosystem health, as the native crayfish are true keystone species and ecosystem managers in the most positive sense of the phrase.

We have used cases from Fennoscandian policies and practices as an overwhelming example of official management strategies, based often on economical justifications rather than ecological, to highlight the detrimental effects of alien species to native species and ecosystems. In addition, *P. leniusculus* alone is the most widespread alien crayfish species in Europe and is present in at least 28 countries (Kouba et al., 2014; **Table 1**). The magnitude of alien crayfish promotion by governmental institutions has been of such fundamental proportions in Fennoscandia, that several cases have been discussed from a Fennoscandian view point, however, with cases from Continental Europe being introduced. The regions might differ, the species might differ, but the outcome seems to be repeated. Money talks and native European crayfish walks, this time, out. This review on policy and practice is about the dramatic chain of events affecting the fate of European freshwater crayfish.

On the Brink of Extinction: Crayfish Plague Is Wiping Out Native Crayfish Stocks

Over the past 150 years, freshwater crayfish in Europe have faced a severe challenge caused by the pathogen *A. astaci*, probably introduced with alien crayfish species of North American origin, with mass mortalities first reported by Cornalia (1860). Today, the European native crayfish populations are in decline nearing extinction both regionally and species-wise (e.g., Souty-Grosset et al., 2006). Due to its devastating effects on the native crayfish populations of Europe, *A. astaci* is today considered among the world's 100 worst invasive species (Lowe et al., 2004). *A. astaci* belongs to the class of Oomycetes a diverse group of fungus-like organisms, including not only a wide variety of plant and animal pathogens, but also saprophytic species (Diéguez-Uribeondo et al., 2009). *A. astaci* itself is originally a very specific parasite (Unestam, 1969a; Unestam, 1972; Diéguez-Uribeondo et al., 2009) of freshwater crayfish species from North America that have developed some tolerance and resistance whilst also alternative hosts have been reported and speculated (e.g., Unestam and Weiss, 1970; Svoboda et al., 2014; Martín-Torrijos et al., 2021b) (**Table 2**). However, in the European crayfish, the parasite causes a lethal disease known as crayfish plague. The pathogen spreads from host to host by producing free-swimming zoospores; should a suitable host be found, the zoospores then encyst, germinate, and start to grow hyphae into the host tissues, typically resulting in death of the host (Söderhäll and Cerenius, 1999; Cerenius et al., 2009; Rezinciuc et al., 2016). By contrast, in *A. astaci* infected North American crayfish species, there is a continual but low level of sporulation (Strand et al., 2012; Svoboda et al., 2013).

The presence of North American crayfish, and thus most likely the pathogen *A. astaci,* has caused high mortalities and numerous population collapses among all native European crayfish species

TABLE 2 | *Aphanomyces astaci* haplogroups (genotypes) and crayfish carrying these haplotypes as latent infections. Genotypes of *A. astaci* can only be distinguished on a molecular (genetic) level, as no morphological differences exist.

Genotypes			Species dying on crayfish plague outbreaks	Latent infections with genotype characterization	
Haplogroup*	**Haplotype***	**RAPD-PCR based****		**European species**	**North American species**
A (lineage 1)	a	A (As)	*Astacus astacus*[1] *Austropotamobius pallipes*[1] *Austropotamobius torrentium*[1] *Pontastacus leptodactylus*[2]	*Astacus astacus*[5] *Pontastacus leptodactylus*[2] *Austropotamobius torrentium*[9]	*Faxonius rusticus*[6] *Faxonius obscurus*[7] *Faxonius etnieri*[8] *Procambarus hybus*[8] *Procambarus acutus*[8]
		C (PsII)	*Pacifastacus leniusculus*[2]	unknown	
B (lineage 1)	b	B (PsI)	*Pacifastacus leniusculus*[1] *Astacus astacus*[1] *Austropotamobius pallipes*[1] *Austropotamobius torrentium*[1] *Pontastacus leptodactylus*[2]	*Pontastacus leptodactylus*[2]	*Pacifastacus leniusculus*[1]
E (lineage 1)	e	E (Or)	*Astacus astacus*[1] *Austropotamobius torrentium*[4]	Not observed	*Faxonius immunis*[7] *Faxonius limosus*[7]
NEW1 (lineage 1)	Usa-1	Not tested	Not observed	Not observed	*Faxonius tricuspis*[8]
NEW2 (lineage 1)	Usa-2	Not tested	Not observed	Not observed	*Cambarus striatus*[8]
D (lineage 2)	d1	D (Pc)	*Austropotamobius pallipes*[1] *Austropotamobius torrentium*[1]	Not observed	*Cambarellus shufeldtii*[8] *Procambarus clarkii*[1]
	d2		*Austropotamobius pallipes*[1]	Not observed	*Procambarus abiusus*[8] *Procambarus clarkii*[1] *Procambarus fallax*[1]
	d3	Not tested	*Cambaroides japonicus*[3]	Not observed	*Procambarus clarkii*[3]
	Usa-3	Not tested	Not observed	Not observed	*Procambarus raneyi*[8]
	Usa-4	Not tested	Not observed	Not observed	*Faxonius* sp.[8]
	Usa-5	Not tested	Not observed	Not observed	*Procambarus raneyi*[8]
	Usa-6	Not tested	Not observed	Not observed	*Cambarellus shufeldtii*[8] *Procambarus clarkii*[8]

**Based on phylogenetic analyses of mitochondrial DNA regions; **alternative terminology of RAPD-PCR groups; [1]Makkonen et al. (2018); [2]Panteleit et al. (2018); [3]Martín-Torrijos et al. (2018); [4]Mojžišová et al. (2020); [5]Jussila et al. (2021a); [6]Panteleit et al. (2019); [7]Butler et al. (2020); [8]Martín-Torrijos et al. (2021b); [9]Jussila et al. (2017).*

(e.g., Souty-Grosset et al., 2006). The invasive North American crayfish species appears to tolerate and resist the crayfish plague infection across their original distribution in North America (e.g., Martín-Torrijos et al., 2021b). This seems to be the result of a balanced relationship arising from coevolution (Unestam, 1969b; Cerenius et al., 2009). Thus, the pathogen was usually unable to freely infect its North American host because their immune system can encase the pathogen within the cuticle (Söderhäll and Cerenius, 1999; Cerenius et al., 2009). However, susceptible crayfish and *A. astaci* seemed to have created a novel and complex relationship, with evidence for a rapid co-evolution of native crayfish and *A. astaci* (Jussila et al., 2015, 2021a). Moreover, the alien crayfish in their newly invaded biogeographic regions in Europe show increased susceptibility with even population collapses reported (e.g., Jussila et al., 2014a; Sandström et al., 2014; Thomas et al., 2020). As a result, among crayfish stocks in Europe, the resistance of both native European and alien crayfish against the crayfish plague has changed, as has the virulence of the disease agent *A. astaci* (e.g., Jussila et al., 2015).

Currently, four distinct haplogroups (i.e., group of strains evolutionarily related as judged by mitochondrial concatenated sequences, *sensu* Makkonen et al., 2018) of *A. astaci* are known to infect native and alien crayfish in Europe and Asia (**Table 2**), named as A, B, D, and E haplogroups (e.g., Kozubíková et al., 2011; Kozubíková-Balcarová et al., 2013; Makkonen et al., 2018; Martín-Torrijos et al., 2018), with haplogroup D consisting of d1, d2, and d3 haplotypes (Makkonen et al., 2018; Martín-Torrijos et al., 2018). These haplogroups and haplotypes can only be distinguished on a genetic level, as no morphological differences exist. Recent studies on *A. astaci* in the south-eastern United States indicate that this region seems to be a center of diversity of the pathogen. In this region, 19 additional North American crayfish species were found to carry *A. astaci* and six new haplotypes of the pathogen were identified

(Martín-Torrijos et al., 2021b). Laboratory infection trials have shown extensive variation in the virulence among different strains of some haplogroups (e.g., Makkonen et al., 2012, 2014; Francesconi et al., 2021). In general, strains of haplogroups B, D and E seem to possess higher virulence (e.g., Makkonen et al., 2012; Jussila et al., 2013a; Francesconi et al., 2021) than those of haplogroup A, which, on the other hand, appear to be more variable in their virulence (Makkonen et al., 2012, 2014). Furthermore, latent crayfish plague infections with *A. astaci* from the haplogroup A, and in some cases also haplogroup B, without mass mortalities have been reported in the native European *A. astacus* (Jussila et al., 2011; Viljamaa-Dirks et al., 2011; Maguire et al., 2016), *P. leptodactylus* (Kokko et al., 2012; Svoboda et al., 2012; Ungureanu et al., 2020), *A. torrentium* (Van Paula Schrank, 1803) (Kušar et al., 2013; Maguire et al., 2016; Jussila et al., 2017) and *A. pallipes* (Manfrin and Pretto, 2014; Maguire et al., 2016) (**Tables 1**, **2**).

Aphanomyces astaci has been under high selective pressure to adapt to the European crayfish hosts and its new environmental conditions since its original introduction to Europe 150 years ago (Jussila et al., 2015, 2016a). After its presumed arrival in Europe in the 1850s (Alderman, 1996), it had access to a variety of host habitats across the European native crayfish spectrum (Souty-Grosset et al., 2006) (**Table 1**). All European crayfish species were susceptible to *A. astaci* of haplogroup A, the first intruder, and the outcome of the crayfish plague epidemic during the first decades was massive mortality among European crayfish populations. If it had not had assistance from humans, the disease might have had a short history in Europe. But the spread of the disease agent was unintentionally aided by transferring it to new water bodies and populations through commercial marketing chains and through natural water ways also along with alien invasive crayfish species (Alderman, 1996). The rapid and efficient spread allowed for both the constant presence of epidemics and opportunities for *A. astaci* to jump from one European crayfish species host to the next and, apparently, to also jump back and forward among crayfish species in close proximity (e.g., Diéguez-Uribeondo, 2006; Jussila et al., 2015; James et al., 2017).

It has long been presumed that *A. astaci* strains of haplogroup A may have been naturally selected by lowered virulence toward a balanced host-pathogen relationship, which has been demonstrated experimentally only during the last decade (e.g., Makkonen et al., 2014; Jussila et al., 2014b; Francesconi et al., 2021). Some wild native European and Turkish crayfish stocks, which are viable and producing commercial catches, have been shown to be latent carriers of *A. astaci* (e.g., Svoboda et al., 2012; Kokko et al., 2018; Jussila et al., 2021a). Laboratory scale infection studies have revealed significant virulence differences among and within *A. astaci* haplogroups and even the existence of very low virulent strains (e.g., Makkonen et al., 2012; Jussila et al., 2017; Francesconi et al., 2021). The invasive crayfish, especially *P. leniusculus*, have lately been shown to be susceptible to *A. astaci*, which points to the high virulence of the infecting *A. astaci* haplogroup B and possibly a lowered resistance of *P. leniusculus* toward *A. astaci* (Aydin et al., 2014; Jussila et al., 2014a; Thomas et al., 2020). Laboratory experiments have demonstrated that the *A. astaci* of haplogroup B, although highly virulent, is also capable of exhibiting a significant but narrow range of virulence variation (Jussila et al., 2013a). This indicates that even *A. astaci* of haplogroup B could be adapting in Europe (Ungureanu et al., 2020), while the presence of a permanent host habitat for the *A. astaci* of haplogroup B allows for the maintenance of high virulence without the immediate threat of the parasite's evolutionary suicide due to the outbreak of a devastating crayfish plague epidemic (Jussila et al., 2015). A similar trend has been observed in *A. astaci* of haplogroup D currently infecting some *Procambarus* species (e.g., Martín-Torrijos et al., 2017; Makkonen et al., 2018). Furthermore, some strains of this haplogroup have shown adaptation to warmer temperatures than other strains from other haplogroups (Diéguez-Uribeondo et al., 1995; Rezinciuc et al., 2014) and tolerance to brackish waters (Martín-Torrijos et al., 2021b). These evolutionary adaptations might be regional between specific populations of crayfish and *A. astaci,* as a consequence of host-parasite co-evolution (e.g., Svoboda et al., 2012; Makkonen et al., 2014; Jussila et al., 2017). It has recently been shown that the *A. astaci* strain carried by *Faxonius rusticus* (Girard, 1852) is genetically different from all other *A. astaci* strains described to date (Panteleit et al., 2019), leading the authors to hypothesize that each North American crayfish species might carry its own *A. astaci* haplogroup, or haplotype, to which it evolved resistance against. In other words, there might be as many strains of *A. astaci* as there are different species of crayfish in North America; over 300 (Mathews et al., 2008). If the mode of action and virulence of *A. astaci* depends on the different host species or populations, this could have a high impact on the invasion success of the invasive species. However, recent studies in North America by Martín-Torrijos et al. (2021b) do not seem to support this hypothesis since no clear species-specific or distributional patterns of the haplotypes and crayfish species were found. Further investigations are needed to enhance our understanding on the phylogeography of *A. astaci*.

The introduction of different *A. astaci* haplogroups into Europe and the repeated introductions of its chronically infected hosts are a classic example of a man-made ecological disaster, stemming from the naive belief that the manipulation of an ecosystem would be straightforward. Currently, the native European crayfish species are on the brink of extinction (Richman et al., 2015). *A. astaci* itself has apparently adapted rather well to European conditions (Jussila et al., 2016a), and seems to be currently co-evolving while maintaining contact with its relatively resistant hosts as new crayfish stocks were imported from North American into Europe (e.g., Jussila et al., 2016a). One could predict that this will inevitably lead to possible total eradication of the remaining native European crayfish stocks. The original introduction of *A. astaci* to Europe, though it was most probably purely accidental, has not only seriously devastated native crayfish populations throughout Europe, but also resulted in further damage due to misguided management attempts such as further introductions of alien crayfish species from North America to rectify the situation (Souty-Grosset et al., 2006; Jussila et al., 2015, 2016a).

ASSESSMENT OF POLICY AND PRACTICE

Human Impact on the Struggle Between Native and Alien Crayfish

The high financial and cultural values of the freshwater crayfish in Europe, namely *A. pallipes*, *A. astacus,* and *P. leptodactylus*, and the devastation of the native crayfish stocks during 19th and 20th century (Alderman, 1996; Alonso et al., 2000; Jussila et al., 2016a) encouraged fisheries officers and researchers in several European countries to grasp the opportunity to introduce alien freshwater crayfish into Europe (Lodge et al., 2000; Holdich et al., 2009). During the first wave of the crayfish plague epidemics in Europe from the 1860s onward, the cause of mass mortalities among European crayfish populations was not known to the scientific community, not to mention administrators or the common public. It took until the 1930s to discover that *A. astaci* was the organism causing crayfish plague epidemics (Schikora, 1903, 1906; Schäperclaus, 1935; Nybelin, 1936), while it took much longer to fully understand how to halt its spread. Within 50 years from arrival, the crayfish plague epidemic's first wave had permanently changed European aquatic ecosystems by almost wiping out native crayfish from Continental Europe (Jussila et al., 2015) and collapsing native crayfish stocks in Fennoscandia (Jussila and Mannonen, 2004; Bohman et al., 2006; Jussila et al., 2015). Within one century, crayfish plague epidemics were even reported from the Iberian Peninsula to the United Kingdom and Ireland, which were all but the last safe havens for the native European crayfish (Reynolds, 1988; Holdich and Reeve, 1991; Diéguez-Uribeondo et al., 1997a, respectively). Even though in some parts of south-eastern Europe alien crayfish were introduced quite early, e.g., in Greece (Perdikaris et al., 2017), other parts of south-eastern Europe resisted alien crayfish introductions for a long time compared to the rest of Europe (Holdich, 2002). The first record of *F. limosus* in freshwaters of Croatia was in 2003 (Maguire and Gottstein-Matočec, 2004), while *P. leniusculus* was first recorded in 2008 (Maguire et al., 2008). In both cases, alien crayfish species spread naturally through big rivers (Danube and Mura, respectively) from neighboring countries (Hungary and Slovenia, respectively) and continued their expansion toward east (i.e., *F. limosus* to Serbia and Romania) causing irreversible negative impact onto the native astacofauna in the region, i.e., in the south-eastern Europe. It was only in 2011 that *P. leniusculus* was illegally introduced to the Korana River (Hudina et al., 2013) situated in the continental part of Croatia in the karstic region that is known as a hotspot of the *A. torrentium* and *A. astacus* diversity (Klobučar et al., 2013; Lovrenčić et al., 2020; Gross et al., 2021), inflicting great damage to the populations of these vulnerable species distributed in this area.

A common mistake made whenever a large-scale epidemic is happening is the open spreading of the disease agent and organisms that are carrying the disease (Alonso et al., 2000; Bohman et al., 2006; Diéguez-Uribeondo, 2006). In most cases, it can be claimed that due to the lack of prior knowledge, it was not possible to apply strategies or tactics that would have prevented the disease spreading and resulting wide epidemic. When the pandemic started in the late 19th century, the cause of the mass mortalities among native European crayfish populations was not known, while several alternative theories were discussed (Alderman, 1996). Some of those were based on the actual disease agent being responsible, but even then there did not seem to be rational strategies implemented to save the valuable natural resource of European freshwater crayfish (e.g., Fiskeriverket, 1993; Alderman, 1996; Jussila et al., 2016a). The Europeans were caught by surprise regarding *A. astaci,* and proper means of attempting to stop the spreading of *A. astaci* happened only after the whole Continental Europe and large parts Fennoscandia were hit by crayfish plague epidemics.

Repeated introductions of the disease agent carriers, i.e., alien crayfish of North American origin, but also pathogens spreading through natural waterways, made matters even more complicated, as eradication of the permanent disease carriers became impossible and prevention of spreading very hard (e.g., Alonso et al., 2000; Pârvulescu et al., 2012; Peay et al., 2019). Europeans have imported alien crayfish for various reasons from North America since the late 19th century (Henttonen and Huner, 1999; Alonso et al., 2000; Souty-Grosset et al., 2006), but the prime mistake was made during the mid-20th century when decisions to start mass introductions of alien *P. leniusculus* to fill the now mostly empty freshwater courses in Europe were made. The possibility of introducing novel diseases, e.g., *Psorospermium haeckeli*, *Saprolegnia* spp. (Diéguez-Uribeondo and Söderhäll, 1993; Diéguez-Uribeondo et al., 1994), even the possibility of introducing novel strains of *A. astaci,* were played down (e.g., Westman, 1973), while the Swedes had their concerns (e.g., Svärdson, 1995). The decision to introduce crayfish from the region where the crayfish plague disease originated, the disease that had already eradicated most European crayfish stocks, was made (e.g., Kilpinen, 2003). Several North America species have been introduced, but the main focus was on *P. leniusculus* (Abrahamsson, 1973; Souty-Grosset et al., 2006; Holdich et al., 2009). The deliberate large-scale introduction of *P. leniusculus* in Sweden starting in the 1960s resulted in a fivefold increase in the spread of crayfish plague epidemics in the country (Bohman et al., 2006; Bohman, 2020).

It is difficult to appreciate how this decision was made and justified from an ecologically perspective, mainly because it was obvious that the introduction of *P. leniusculus* would result in further spreading of *A. astaci* in Europe (e.g., Kilpinen, 2003). Field introductions during the period of 1960–1967, thus before the massive importation of *P. leniusculus* to Fennoscandia, indicated that *P. leniusculus* was a carrier of *A. astaci* and thus eradicated coexisting *A. astacus* populations (Unestam, 1969b). The import license application of *P. leniusculus* to Finland was first rejected in 1967 by the veterinary administration due to risks of introducing diseases, namely crayfish plague (Kilpinen, 2003). Later the same year, the veterinary administration was bypassed and an import license granted using political maneuvers and ignoring the risks. Unestam (1969a) already discussed *P. leniusculus* resistance against *A. astaci,* clearly indicating that the possibility of *P. leniusculus* acting as a permanent reservoir existed, yet permits were given to stock 58,100 adult *P. leniusculus* from Lake Tahoe, California, into 64 natural waters in Sweden in 1969 (Svärdson, 1968; Abrahamsson, 1973). Also, alien *P. leniusculus* was introduced as resistant to *A. astaci*, even immune, while the obvious outcome from this resistance, i.e., *P. leniusculus* as a spreading vector for *A. astaci*, was largely ignored.

Promotion of the Harmful Alien Species Is Not Conservation of the Native Species: Cases From Fennoscandia

Soon after the introduction of *P. leniusculus* to Fennoscandia, it was discovered that even the most sophisticated stockling production systems might produce *P. leniusculus* that were carriers of *A. astaci* (e.g., Makkonen et al., 2010), while some *P. leniusculus* stocks remained in disease-free status for a while once established from farm raised stocklings. This did not halt the stocking of the disease carrying *P. leniusculus* into numerous water bodies, even though there were strict national regulations banning introductions of diseased organisms into the wild (e.g., Fiskeriverket, 1993; Ruokonen et al., 2018; Jussila and Edsman, 2020): a case of fisheries administration favoring the distribution of an alien species even if it was suspected or known to carry and spread *A. astaci* (e.g., Kilpinen, 2003). The relaxed attitude among fisheries administrators, even an attitude that favors alien species over native ones (e.g., Ruokonen et al., 2018; Jussila and Edsman, 2020), is bound to cause devastation of the native crayfish, even when it is already claimed to be vulnerable and threatened, as has been the case in Sweden (Bohman and Edsman, 2011).

Initial optimistic assumptions, based sometimes on biased analyses and even wishful thinking, can be hard to correct when new scientific information surfaces. It was discovered some 20 years after the initiation of major alien crayfish stocking campaigns that the *P. leniusculus* wild stocks were declining, even collapsing in some cases (Jussila et al., 2014a, 2016b; Sandström et al., 2014). Sometimes this information was ignored and those managing the wild *P. leniusculus* stocks were kept in the dark, which was evident during meetings with stake holders in Finland and Sweden. The initial inflated information regarding the resistance of *P. leniusculus* against *A. astaci* infection was not corrected when the first stock collapses were observed and reported (e.g., Jussila et al., 2014a; Sandström et al., 2014) and local fisheries managers were wondering how the collapses were even possible. The original assumption of disease resistance was used to justify further spreading of the alien crayfish, even after it was discovered that it was spreading very virulent *A. astaci* of haplogroup B and it was quite obvious that it too was suffering from the infection itself (e.g., Aydin et al., 2014; Jussila et al., 2014a).

It is common to deprecate novel findings indicating that an alien harmful species could have developed new diseases under the new environmental conditions. In Fennoscandia, it was discovered some 20 years after the intensive *P. leniusculus* stocking program that established *P. leniusculus* stocks were showing gross symptoms that were then studied and described as eroded swimmeret syndrome, i.e., ESS (Sandström et al., 2014; Edsman et al., 2015). The suspected disease causes total or partial erosion of the female swimmerets and thus prevents the female from hatching eggs, resulting in reproductive failures. Later it was been discovered that male *P. leniusculus* also show similar gross symptoms including gonopod trauma (Jussila et al., 2016b, 2021b). It took a while before the existence of ESS was admitted to affect populations of *P. leniusculus* in Finland. Even then, the response was based on undermining the possible population level effects of ESS. This was motivated by trying to maintain the suspected good reputation of *P. leniusculus* in Fennoscandia (e.g., Jussila and Edsman, 2020). Despite struggling in some parts of Europe, alien *P. leniusculus* is still the second worst alien crayfish in Europe and still spreading (**Table 1**).

Short-term monetary benefits are sometimes regarded as more valuable than long-term ecological sustainability, and thus the promotion of the alien species could be justified by economic reasons. The designated area for the introductions of the alien *P. leniusculus* in Sweden was originally limited to the south-eastern part of the country (Bohman et al., 2006). The designated area in Finland was originally only the great lakes in southern Finland, too (Ruokonen et al., 2018). Due to intensive promotion of *P. leniusculus* as a commercially lucrative species and initial good development of the introduced stocks (e.g., Ackefors, 1999; Kirjavainen and Sipponen, 2004), the illegal introductions of *P. leniusculus* northwards were commonplace (Bohman et al., 2006; Bohman and Edsman, 2011; Ruokonen et al., 2018). In Finland, fisheries administration, instead of taking a firm stand against illegal introductions, drafted several crayfishery strategies, which all included the regions of illegal introductions within the newly designated region for *P. leniusculus* (Ruokonen et al., 2018). This only encouraged the spread of the alien crayfish and *A. astaci* it is carrying, resulting in further devastation of the remaining native *A. astacus* stocks.

Emphasizing the alien species' economic benefits could sideline conservation attempts of the native species. The start of the crayfish season is one of the widely publicized events in Fennoscandian late summer (Taugbøl et al., 2004; Jussila et al., 2015; Jussila and Edsman, 2020). The premium price for the crayfish is paid during the first few days of the crayfishing season due to high demand, while the prices stay considerably high throughout the season (Jussila, 1995). To boost the start of the crayfish season trade, the ministry in charge of fisheries arranged an importation of alien *P. leniusculus* from England to Finland, an exception to the EU Alien Species Regulation 1143/2014, using an economic justification. This is again an example of trying to boost the economic reputation of the alien species and thus undermine the fundamentals of the EU Alien Species Regulation 1143/2014.

The strategy for alien species eradication can be deliberately and erroneously implemented to actually give an upper hand to the alien harmful species over the native species. Eradication of the harmful alien *P. leniusculus* is one of the EU Alien Species Regulation No 1143/2014 aims and there have been national strategies drafted and also implemented to test different strategies and techniques (Edsman and Schröder, 2009;

Bohman and Edsman, 2013; Huusela-Veistola et al., 2019). In Finland, the National Research Institute for Natural Resources, LUKE, has been asked by Ministry of Agriculture and Forestry to assess the possible gains on relaxing *P. leniusculus* trapping regulations, such as open or early season, no bag limits, no specific trapping licenses, encouragement to removal trapping, etc. (Anon, 2019). The official justification is that the relaxed trapping regulations would encourage recreational trappers to increase their trapping pressure, which would then result in halting the spread, or even cause eradication, of the wild *P. leniusculus* stocks. While in theory this might seem achievable, the reality is different. Anyone understanding motivational aspects of the crayfish trapping would claim that recreational trappers would stop trapping when the catch per unit effort (CPUE) falls below a certain limit, for example 0.5, which is well above any rational CPUE that would result in eradication of the population. The planned relaxation of *P. leniusculus* trapping regulations would make the alien harmful *P. leniusculus* a more tempting target than *A. astacus* for a recreational crayfish trapper as the alien species' stocks would then be easier to access. This would only encourage the general public to spread the alien harmful species even more and it would also give a hidden message of the alien harmful species actually being more desirable than the native species. At four international freshwater crayfish scientific conferences, conclusions and resolutions have been issued: IAA17 in Kuopio, Finland (2008), Crayfish conservation meeting in Olot, Spain (2015), IAA21 in Madrid, Spain (2016) and IAA Gotland, Sweden (2019). At all four meetings it was clearly stated that "*the control of invasive crayfish species by intensive recreational and commercial fisheries does not represent a feasible method for this purpose. Instead, it favors the further spread and increase of these alien populations*" (Furse, 2008; Edsman et al., 2019).

Pet Trade Causing Problems as Means to Spread Alien Crayfish Species and Their Diseases

The ornamental aquatic pet trade is another important but frequently overlooked pathway for the introduction of alien crayfish species and their diseases into Europe (Hänfling et al., 2011; Chucholl and Wendler, 2017). While there are numerous parasitic organisms and viral diseases in crustaceans worldwide (Bojko et al., 2020), some of which might become a serious threat for crayfish in the future, the main disease threatening crayfish in Europe to date is the crayfish plague. Crayfish imported from North America to be sold as pets or kept in private aquaria are often vectors of the crayfish plague pathogen *A. astaci*. In a study by Mrugała et al. (2014) six crayfish species were identified as vectors for the first time, with horizontal transmission of *A. astaci,* i.e., the transmission of the pathogen between crayfish individuals kept in close proximity. These results were confirmed in a study by Panteleit et al. (2017), where a further nine crayfish species were identified as vectors for *A. astaci* for the first time. One of the most problematic crayfish in the pet trade is probably the marbled crayfish, *P. virginalis* Lyko, 2017, due to its parthenogenetic reproduction and its high popularity as a pet (Patoka et al., 2014). It probably evolved from *Procambarus fallax* Hagen, 1870, an American species native to Florida and South Georgia, after triploidization in the German pet trade in the mid 1990s (Vogt et al., 2018). The species was first recorded in the wild in Germany in 2003 (Marten et al., 2004) and has since established numerous populations in at least 17 countries worldwide, mainly in Europe[1] (Vogt, 2020; Scheers et al., 2021) (**Table 1**). However, European mean water temperatures are widely below the optimum for reproduction of *P. virginalis* (Seitz et al., 2005). Consequently it has been suggested that when new *P. virginalis* populations become established, it is to some extent due to the invasive potential of this species, but the location of the occurrences is rather dependent on human-mediated releases (Martin et al., 2010). The pet trade presumably led to the introduction of *P. virginalis* into Sweden, Romania, Ukraine, and many other countries (Marten et al., 2004; Chucholl and Pfeiffer, 2010; Bohman et al., 2013; Novitsky and Son, 2016; Weiperth et al., 2020), and the number of different alien crayfish species could be expected to increase as the pet trade through different channels, e.g., on-line trade, will develop (Kotovska et al., 2016; Vodovsky et al., 2017; Weiperth et al., 2020).

Some countries in Europe have stricter rules for pet trade. Examples are Ireland and Scotland, where keeping alien crayfish is illegal and the crayfish pet trade is strictly regulated (Peay, 2009), yet *P. virginalis* is still for sale on the pet market in Ireland (Faulkes, 2015a). Another example is Sweden where all importation, transport and keeping of any live crayfish species from abroad is banned (Edsman, 2004). Laws and regulations can only be effective if they are also enforced (Faulkes, 2015b). When this is not possible, other methods (e.g., education of pet traders and pet owners) to reduce the negative effects of the pet trade need to be implemented. Recognizing threats that alien species and pet trade pose to native European biodiversity, the EU recently adopted regulations dealing with alien invasive species in Europe, including crayfish (EU Pet Trade Regulation No 2016/1141). However, the list of species of Union concern includes only five alien crayfish species which already have established viable populations in Europe, namely *F. limosus*, *F. virilis*, *P. leniusculus*, and *P. virginalis*. This list does not include species that are imported through international pet trade, but are not yet invasive or established in the European aquatic ecosystems. It is very important, that species which are known to have a high invasive potential or species which are known carriers of *A. astaci*, are added to the invasive species list or, alternatively, to prepare a white list of crayfish that would not present concern to European freshwaters and native astacofauna, supported by scientific evidence.

Twisting the Definitions and Creating New Language to Cause Confusion

One common way to cause confusion among the general public and thus also those pondering conservation issues, is a deliberate erroneous usage of alien species arguments when discussing native species (e.g., Courtine and Willett, 1986; Clavero et al., 2016). The concept of an alien species, in the case of Finland,

[1] https://faculty.utrgv.edu/zen.faulkes/marmorkrebs/

is that the species has spread to Finland later than 1850 and the spreading has been assisted by man (Niemivuo-Lahti, 2012). If arrived later than 1850 by natural spreading to Finland, the species is considered a newcomer, but not an alien species. In the EU Alien Species Regulation No 1143/2014, for matters to be simpler and easier to define, whole nations or geographical regions, such as peninsulas, are considered one entity with regard to alien species spreading. Thus, *A. astacus* in Finland, even though originally considered as a southern species in its spreading (Lehtonen, 1975), is regarded a native species in all regions within Finland. Regardless, to improve the status of alien *P. leniusculus* and to weaken the status of native *A. astacus*, there have been claims that native *A. astacus* is actually an alien species above Jyväskylä (latitude 62°14′), according to information regarding its distribution during early days (e.g., Lehtonen, 1975). In the same way, claims have been made that *A. astacus* was introduced into Sweden during the 1500s by the kings. Later genetic studies have shown that *A. astacus* has inhabited Swedish aquatic ecosystems since the last ice age, thus being native to Sweden (Edsman et al., 2002; Gross et al., 2013; Dannewitz et al., 2021). Similarly, *A. pallipes* has been claimed to have been introduced to Spain from Italy only in the 1500s (Clavero et al., 2016), despite genetic evidence dating the species origin on the Iberian Peninsula from the last glaciation (Matallanas et al., 2011, 2016; Jelić et al., 2016; Martín-Torrijos et al., 2021a). Such scenarios, of course, create confusion and employ everyone to waste resources in order to correct the deliberate misinterpretation in any given case.

Another twisted argument in favor of alien invasive species is the claim that introduced North American crayfish species *P. leniusculus, P. clarkii*, or *F. limosus* are immune against *A. astaci* infection, a definition that is commonly used when justifying the introduction and spreading for example alien *P. leniusculus* in Europe (e.g., Bohman et al., 2006; Jussila et al., 2015). However, it has been shown directly in laboratory tests (Unestam and Weiss, 1970; Persson and Söderhäll, 1983; Vey et al., 1983) and indirectly from wild stock observations, that these alien species, particularly *P. leniusculus,* can be quite often susceptible to *A. astaci* infection and stock collapses due the crayfish plague epidemics have been reported (Jussila et al., 2014a; Sandström et al., 2014; Martín-Torrijos et al., 2019; Thomas et al., 2020). This, again, is one example on how decision makers aim to justify their considerations of the first alien species introductions, and how difficult it is to get the novel message of state of the art facts recognized, even though being supported by reliable data. The debates regarding alien *P. leniusculus* spreading *A. astaci* and thus devastating native crayfish populations, quite often bring up claims that not all alien signal stocks or individuals are chronically infected with *A. astaci,* which also neglects the long term competitive displacement of native species by alien *P. leniusculus*. This argument of exceptions to the rule, i.e., alien *P. leniusculus* being most often infected with *A. astaci*, should bring up the magnitude of the risks when attempting to spread alien *P. leniusculus*, but in most cases a principle of cautious approach is ignored, leading to actions detrimental to native crayfish. The possibility of a favored outcome, a false positive expectation, seems to be a strong motivator sidelining serious ecological considerations and cautious approach.

Means to Make Things Right, Only Too Little and Too Late

Eradication of the Alien Species: Another Disaster Waiting Due to no Proper Eradication Means

Alien species eradication is a very complex task, especially for aquatic species, and thus bound to cause problematic situations. Risks are often unknown both because little data is available on the magnitude of the introduction of alien species and also uncertainty about positive and negative effects of potential measures and actions to be undertaken. Under severe uncertainty about knowledge and value ambiguity in management objectives, the best initial step would be to perform a robust decision analyses (Sahlin et al., 2021).

The eradication of *P. leniusculus* from limited water bodies, such as golf courses or irrigation ponds, has been tried and shown to be successful (Peay et al., 2006; Sandodden, 2019). Successful attempts have also been reported for the eradication of *P. clarkii* and Australian *Cherax destructor* (Clark, 1936) in Spain (Alcorlo and Diéguez Uribeondo, 2014). Biocides, even though discussed controversially, have been used efficiently in the United Kingdom, Sweden, Norway, and Spain to tackle alien crayfish introductions (Peay et al., 2006, 2019; our personal observation). In the Italian project RARITY different approaches (e.g., removal by trapping, pheromones, sterilization of males) have been applied simultaneously, resulting in temporary significant reduction in the *P. clarkii* population size in Italy (RARITY, 2020). Other methods that were applied with more or less success include electrofishing, manual removal of crayfish and introduction of predators or specific diseases into the system, building physical barriers, water body drainage and shock liming (Gherardi et al., 2011; Stebbing et al., 2014; Bohman and Edsman, 2013). A recent study (Krieg et al., 2020) showed that implementation of different drastic measures, e.g., drainage of water body in combination with chemicals or barriers, could reduce alien crayfish population size or even eradicate a whole population. On the other hand, controlling invasive crayfish in big rivers (e.g., Danube and Drava) is almost impossible, and mechanical removal from the water body could only slow down their dispersal (Hudina et al., 2017; Krieg and Zenker, 2020). Still, achievable strategies for alien crayfish management in such systems include a combination of methods that would increase ecosystem resilience and continuous crayfish trapping (both fishermen and authorities) as well as involvement of well-informed citizens, as shown in the study of Lemmers et al. (2021). Also, the application of biological and ecological data on invasive crayfish to develop new tailored approaches to the management of specific invasive populations may improve invasive crayfish control (Hudina et al., 2016).

When eradication attempts are planned in habitats common especially in Fennoscandia, but also elsewhere in Europe, where lakes are interconnected by rivers to form watercourses stretching hundreds of kilometers, it is soon realized that effective eradication is impossible, or the vanishing of the alien harmful *P. leniusculus* could be an indication of drastic changes in the aquatic ecosystem. In this case, the alien species could be of least concern. Even though roughly 10% of Finnish surface area is freshwater (MMM, 2020), there have been plans for eradication or limiting the spreading of the harmful alien species (Erkamo et al., 2019). However, once *P. leniusculus* is released into the aquatic ecosystem there are very limited possibilities for its practical and effective eradication. In addition to the large size of the watercourses in Finland, most of them are shallow, lacelike structures, allowing basically their whole benthic area for crayfish settling.

The release of diseases targeting alien species has been widely suggested and even used in some cases (e.g., McColl et al., 2018; Wells et al., 2018). They have been shown to function as planned initially in some cases (e.g., Saunders et al., 2010), while some have faced problems right from the start (e.g., Holden, 1995). Pathogens are known to have evolved into diseases targeting different species, as is the case with *A. astaci* (e.g., Jussila et al., 2015; Simmonds et al., 2019). In Finland, the authority responsible of veterinary issues was planning to eradicate a sparse *A. astacus* population, a protected species, suspected to be carriers of *A. astaci,* by using another virulent haplogroup B strain of *A. astaci.* Once the suspected remaining *A. astacus* would have been eradicated, it would have allowed reintroduction of healthy stock into those water bodies. The scheme was introduced in a research proposal and later discussed in a conference in Olot (Girona, Spain, 2015), with a lively interaction between audience and presenter. Luckily, the project was not funded. The idea of fixing an obvious mistake, in this case the introduction of *A. astaci* to Europe several times, by making another, known to be a potential mistake from experience and reports, is a strange human urge.

Exploitation of the Alien Species: Another Form of Alien Species Promotion?

One of the main driving forces behind the spreading of the alien crayfish species and devastation of the native European species has been ongoing exploitation of those alien species stocks that have been illegally introduced to regions which have specifically been allocated for the native species. This has been a common phenomenon in Finland, Sweden, and Spain (Alonso et al., 2000; Sahlin et al., 2017; Ruokonen et al., 2018). Thus, even though there have been attempts to halt the spreading of the alien crayfish species, the actions of the fisheries administrations in all three countries have actually encouraged the spreading of the alien crayfish (e.g., Alonso et al., 2000; Bohman et al., 2006; Ruokonen et al., 2018), despite national laws banning these introductions for various reasons, mostly motivated by conservation (e.g., Edsman and Schröder, 2009; Caffrey et al., 2014; Erkamo et al., 2019) and legislation (e.g., Jussila and Edsman, 2020). In Finland, a partial motivation must have been the alien *P. leniusculus* population crashes (e.g., Jussila et al., 2014a), resulting in the urge to push up the alien *P. leniusculus* catch figures, all in promotion of the alien *P. leniusculus* and at the cost of native *A. astacus*. It should clearly be mentioned here that although population density can be thinned and their spreading slowed down through intense trapping (e.g., Hein et al., 2007), there are no examples of successful eradication of crayfish populations by strong trapping pressure. Intensive fishing with baited traps as well as hand searching and removal is highly unsuccessful since only a minimal fraction of the total population is removed (Chadwick et al., 2020; Krieg et al., 2020). On the contrary, intensive trapping as a control measure may rather be a potential damaging activity by limiting cannibalistic predation pressure on the remaining population (Houghton et al., 2017), increasing fitness in remaining individuals (Moorhouse and Macdonald, 2011), inducing early onset of sexual maturity (Holdich et al., 2014), increasing intentional anthropogenic spread (Edsman, 2004) and by increasing bycatch of non-target species (De Palma-Dow et al., 2020).

The promotion of the alien *P. leniusculus* in Finland has been taken to the level of selecting a Crayfish King annually, namely a person who has done the most to promote alien *P. leniusculus* in Pirkanmaa county in southern Finland and thus causing the most damage to native *A. astacus* in that region, the latter normally not mentioned in this context. The nomination gets wide media coverage, not least because quite often the award is handed over by a minister in charge of fisheries and thus also crayfisheries. This minister should also be in charge of protecting native aquatic resources, such as fish and crayfish, but quite ironically does not see any conflict here.

The Conservation of the Native Species Is a Challenging Task

Timescale Creates Problems: Humans Short-Term Planning

Our attempts to solve ecological problems tend to be based on short-term thinking. While timeframes of decades or even centuries are required to remedy some matters, the lack of immediate personal or corporate benefit (e.g., Wu et al., 2017) and higher levels of uncertainty are seen as difficult to justify. Looking for the quick fix might be practical when trying to show benefits to the general public, but from the natural ecosystem's viewpoint this time frame is negligible. The idea to compensate for the declining native natural resources by introducing alien species while there are still native specimens left is bizarre. On the other hand, it is quite understandable that the time scale of human thinking is rather short and quite often does not stretch over generations, not to mention over decades or millennia. From nature's viewpoint, thousand years is not a long time frame and is in many cases not even long enough for any kind of drastic evolutionary changes. Animal species are normally spreading with variable pace (e.g., Messager and Olden, 2018; Melotto et al., 2020), while introductions of alien crayfish species have happened via quick and violent moments, in the false belief that human actions do not result in negative changes within ecosystems.

How does the obvious human selfishness affect decision making? Are we bound to only look for solutions which allow us to reap the glory for ourselves? Are the decisions actually based on selfish gains (like, e.g., political votes) instead of trying to actually solve the problems in the long run and maintain rational balance for the foreseeable future? Quite often the best solution would have been to do nothing and let solutions be based on natural progression of matters, even though, in the case of European crayfish, that would have taken a very long time for them to possibly bounce back. At least in Finland and Spain, there are now obvious indications that the native crayfish could be recovering in some water bodies previously considered void of native species (personal observation from Finland and Spain; Diéguez-Uribeondo et al., 1997a; Jussila et al., 2016b; Martín-Torrijos et al., 2017). This often happened in Sweden before the introduction of *P. leniusculus*, and later more frequently, as a result of liming in acidified waters (Bohman, 2020). It is also rather common that after alien *P. leniusculus* introductions, there is a short period when also *A. astacus* turns up in trap catches (e.g., Jussila et al., 2016b; Bohman, 2020), even for several years (e.g., Westman and Savolainen, 2001; Westman et al., 2002), while even in these reported Finnish cases of co-existence *A. astacus* have since disappeared (Erkamo, 2020). Thus, *A. astacus* has been in these water bodies, though at such low densities that trapping them has not been worth the effort. However, *A. astacus* must have been waiting for the moment to bounce back and take a stronger position in the aquatic ecosystem. After the hasty introduction of the alien *P. leniusculus*, *A. astacus* faces little or no chance to recover in the long run. It would have been wiser to wait.

Predicting the outcome of an alien species introduction is quite often made too soon, before it has taken its niche properly, leading to false promotion of the alien species role in the aquatic ecosystem (e.g., Kirjavainen and Westman, 1999; Kirjavainen and Sipponen, 2004; Jussila et al., 2016b). In Fennoscandia and Spain, the promotion of the alien *P. leniusculus* (and also *P. clarkii* in Spain) was based on the period when it was only settling down to aquatic ecosystem and was not properly established yet: populations were growing, there was a lot of free habitat, plenty of resources and as a result stress levels were low. This resulted in rapid spreading of these alien crayfish and the virulent *A. astaci* strains they have been carrying (Diéguez-Uribeondo et al., 1997b; Bohman et al., 2006; Ruokonen et al., 2018; Martín-Torrijos et al., 2019). In Fennoscandia and Spain, only 20 years after introduction, the alien *P. leniusculus* stocks were showing signs of maladaptation (Jussila et al., 2014a, 2016b; Sandström et al., 2014; Larumbe, 2020) and warning signs of not being quite suitable to conditions in their novel habitat. From the native European crayfish perspective this was too late, while this still was only early stages when the spreading of the alien *P. leniusculus* is considered. It is hard to change the positive message later, even though it is obvious that alien *P. leniusculus* stocks are not performing as originally told, especially since the alien *P. leniusculus* promoters do not change their story but largely ignore the bad news.

Money Creates Problems: Human Monetary Thinking

The urge to plan and introduce alien species to new regions has long been a temptation. The fundamental question is why alien species introductions are more tempting than conservation of native species. The already known to be flawed justifications are repeated in order to hide the quite obvious indications of introduction failures and severe negative impact on native species (e.g., Lodge et al., 2000; Westman, 2002; Jussila and Edsman, 2020). In Finland, the catch of the *P. leniusculus* was predicted to double every year due to an increasing number of introduced alien *P. leniusculus* populations being established and starting to produce commercial size crayfish after the early 1990s (e.g., Kirjavainen and Sipponen, 2004; Jussila and Edsman, 2020). This prediction was made early into the introduction scheme, mainly to encourage those managing wild crayfish stocks to introduce alien *P. leniusculus* instead of native *A. astacus*. An annual doubling of catches would have easily resulted in some 30,000,000,000 alien *P. leniusculus* been caught by 2010, which is not exactly what happened, since annual *P. leniusculus* catch briefly peaked at 7 million in mid 2010s and then leveled at around 3 million (Erkamo, 2019). Instead, alien *P. leniusculus* was discovered to be suffering similar population collapses during 1990s and 2000s as *A. astacus* in the past (Jussila et al., 2014a; Sandström et al., 2014) and being affected by *A. astaci* and novel diseases (Jussila et al., 2013b; Edsman et al., 2015). Both consequences were largely ignored and vigorously debated against in public. It took the government research institute LUKE until the mid-2010s to admit that their statistics showed the introductions of the alien *P. leniusculus* actually having only a small, even negligible, impact on the total catch of crayfish in Finland (Erkamo, 2019).

One of the unexpected dangers *A. astacus* is facing is possible restrictions on trapping wild *A. astacus* stocks, as has been suggested in Sweden, due to a fundamentalist view on conservation practices (Edsman, 2020a). Crayfish have been traditionally trapped because of their market value, the beach price for *A. astacus*, a minimum 10 cm long, being between one and two euro each (Jussila, 1995; Jussila and Mannonen, 2004). The income for a crayfish trapper could easily be several thousand euros during the crayfish season, which amongst other matters is a valuable lesson to a young crayfish trapper of the value of the natural resource (Jussila, 1995). If trapping of the *A. astacus* is restricted, one can always illegally introduce *P. leniusculus* in the water body, because trapping of *P. leniusculus* will not be restricted in the foreseeable future and it would thus enable trapping incomes. Even though the beach price of *P. leniusculus* is less than half compared to *A. astacus*, this scheme would work against conservation of the native *A. astacus*. Sometimes it would definitely be worth catching and eating a few endangered crayfish, for the benefit of the rest of the population. Even without the economic argument a carefully managed fishery by many local fishing right owners will be favorable for conservation by increasing the will for local people to protect the native crayfish (Edsman and Śmietana, 2004).

The fast buck ideology might have something to do with the alien species introduction and bluntly ignoring the necessity to conserve native species. It might be easy to predict a bright future in the case of unknown factors affecting the outcome of the alien species introduction. The North American crayfish species considered for introduction to Europe were thriving in their original distribution area despite *A. astaci* being present there in its most virulent haplotypes (e.g., Makkonen et al., 2019). It must have been tempting to claim that these species would be doing similarly in Europe, despite the fact that only the general climate features would be the same, while there are differences between North American and European aquatic ecosystems in terms of potential pathogens and parasites (e.g., Martiny et al., 2006; Litchman, 2010). Most of the aquatic and geological features would be different from, for example, conditions in Lake Tahoe, which was one of the main sources of *P. leniusculus* being introduced to Europe (Westman, 1973; Henttonen and Huner, 1999). Ignoring the fact that Lake Tahoe is very deep and rather constant in water temperature compared to rather shallow and low volume water courses in Europe is a grave mistake, which was verified by a Swedish research group (e.g., Sandström et al., 2014), showing that one of the main variables explaining alien *P. leniusculus* population crashes was warmer water temperature. In this case, climate change would make matters even worse for alien *P. leniusculus*, while it might not help native *A. astacus* either (e.g., Capinha et al., 2013; Préau et al., 2020).

One cannot ignore recent political changes across Europe and at the national level, with the more populist and nationalistic tendencies gaining support (Aalberg et al., 2016; Scoones et al., 2018; Borras, 2020). Quite often these populist movements tend toward conservative and rightwing policies, which tend to ignore the importance of conservation values (Cortes-Vazquez, 2020). There has been an increase in ideologies and movements characterizing nature conservation and an ecologically sound lifestyle as being detrimental to the well-being of individuals, and even a threat to the western life style as such (Apostolopoulou and Adams, 2015). In this political atmosphere, short-term economic benefits tend to gain the upper hand and indirect or intangible long-term benefits, such as ecosystems with biodiversity and strength, are not considered valid priorities (e.g., McCarthy, 2019). These political tendencies, of course, threaten the existence of vulnerable native species and whole native ecosystems, including native European crayfish struggling with detrimental diseases, such as *A. astaci* infections, and pollutants from industrial activities. The well-being of society, in this context, does not include the well-being of natural, native resources (Cortes-Vazquez, 2020) but rather short-term economic benefits.

Lively and productive native ecosystems, as they can be taken when considering native European crayfish stocks in their prime, offer both intangible benefits in the form of recreation and economic benefits in the form of trapping income and sales of trapping related gear and licenses (Jussila, 1995; Jussila and Mannonen, 2004; Bohman and Edsman, 2011). In Fennoscandia, productive native crayfish stocks have been used in the tourism industry as sites for trapping crayfish and then having crayfish parties on the lakesides (e.g., Jussila et al., 2016a), as have lately also the alien *P. leniusculus* stocks been utilized. In the context of conservation, the general public could be educated during the recreational trapping and the following crayfish parties on the importance of native crayfish stocks from both recreational and economic viewpoints. As most, if not all, of the native *A. astacus* populations are not open access, the hospitality enterprises are important in terms of widening possibilities for positive experiences been offered by the productive native crayfish stocks.

DISCUSSION

The Future for the Native European Crayfish Is Bright, if We Just Try, Right?

We would like to summarize the threats and necessary actions to ensure the maximum conservation outcome for the native European crayfish, with several aspects presented in the **Table 3** and outlined in the following paragraphs (cf. Caffrey et al., 2014).

First of all, if ever again attempting to introduce alien species to substitute declining native species, one should be aware that such actions will cause more damage than benefit to the ecosystem or society (Kouba et al., 2021). In Sweden, from a purely national economic perspective, disregarding the disastrous effects on biodiversity, the massive introduction of *P. leniusculus* resulted in a cost rather than a benefit in the end (Gren et al., 2009). The loss of local native species populations, especially if it is limited to a certain region as opposed to a species extinction, even though a serious issue as such, is not a reason to correct the mistake by making another one. The spreading of alien crayfish in Europe is a classic and sad example of how matters can easily be made worse for the native species by introducing alien species to compensate local or regional losses of native species stocks (Gherardi and Holdich, 1999). The causes for their decline have multiple origins, and some of those must be corrected, such as pollution of water, acid rain and waterways construction (Edsman and Schröder, 2009), which the EU has taken a firm stand against (e.g., Paloniitty, 2016). Then, when habitats and environment have been restored to an ecologically maintainable level, one has to wait and see how ecosystem resilience will do its job. Sometimes less is more. If alien species have been introduced, on purpose or by accident, conclusions regarding the establishment and success of these populations should be reached only after a considerable time period, in the case of *P. leniusculus* in Finland more than 20 years after its introductions. In most cases this is too late and the progress of matters cannot be reversed. Maybe being more cautious and suspicious in the first place and eschewing the introduction of alien crayfish into Europe would have been best.

Alien crayfish should at least be restricted to limited designated regions, as is the general aim of the all European national crayfisheries strategies, and those alien crayfish populations which have been stocked, without permission and in most cases illegally, should be banned from all exploitation (e.g., Edsman et al., 2019). It thus would be strictly pointless to spread alien crayfish, which so far has been common practice and partially encouraged by the fisheries administration at least in Spain, Finland and Sweden (e.g., Alonso et al., 2000; Ruokonen et al., 2018; Jussila and Edsman, 2020). If broadly adopted, by banning introductions and trapping of the illegally established populations of alien crayfish at least some social pressure would be created, potentially resulting in hesitation when planning the

TABLE 3 | Means to secure the conservation of native European crayfish.

Threat	Action
Alien crayfish species	✓ No more stockings to novel water bodies. ✓ No commercialization of live crayfish. ✓ Halt the alien species pet trade. ✓ Early detection and rapid eradication of newly emerging alien crayfish populations. ✓ Full economical responsibility for illegal spreading.
Aphanomyces astaci	✓Halt the spread of alien crayfish. ✓ Awareness that North American crayfish are chronic reservoirs and the source of the crayfish plague. ✓ Increased awareness of fishing gear disinfection. ✓ Fish stockings only if verified disease free. ✓ Understanding of molecular mechanisms for crayfish plague resistance for selective breeding.
Lack of EU level interest	✓Impose EU regulations on halting pet trade of crayfish. ✓ qPCR test for *A. astaci* of imported ballast water. ✓ Funding of native crayfish related management and research.
Impaired communication with national governments	✓Awareness of the validity of science. ✓ Participating in national planning. ✓ Relevant applications of academic output. ✓ Demand for transparent crayfisheries policies. ✓ Stronger law enforcement.
People having wrong, old, and false information	✓Awareness-raising campaigns. ✓ Media releases.
People disconnected from nature	✓Awareness raising campaigns. ✓ Boosting motivation for conservation. ✓ Targeting kids as means to educate general public. ✓ Citizen Sciences programs (e.g., https://alien-csi.eu/).
Interest group inactivity	✓Awareness-raising of the material and intangible benefits of conservation for society.

next illegal introduction. The role of information campaigns should be more focused in this context, as it has been clear in the past that one of the main reasons for the irresponsible spreading of alien crayfish species has been messages which do not clearly state the risks related to alien species. One of the main reasons for this misleading information has been the reluctance of those in charge to admit that expectations have not been met and thus the instructions should be revised in order to avoid repeating mistakes.

While competitive exclusion by alien over native crayfish is a major risk to the long-term persistence of native crayfish in Europe, the hitchhiking disease pathogen that comes along with the alien crayfish possesses a much more immediate threat (e.g., Unestam, 1969a; Jussila et al., 2014b). Now that various *A. astaci* strains from different genotypes are present in various European water bodies (**Table 2**), its spread not only via alien crayfish, but also via fish (Oidtmann et al., 2002) or other species transporting *A. astaci* zoospores, i.e., birds and mammals preying on crayfish (Anastácio et al., 2014) appears inexorable, and we might have to start to think about how to make co-existence of the pathogen and native crayfish possible. It has been suggested that the main mechanism underlying the increased resistance of the North American crayfish species against the crayfish plague is the constant overexpression of prophenoloxidase-related genes, inhibiting pathogen growth and hence infection development. In European crayfish species, the enzymatic activation of the prophenoloxidase-cascade is often too inefficient and slow to successfully combat the disease (Cerenius et al., 2003). Therefore, in European native crayfish the infection leads to death usually within a few days or weeks, depending on the pathogen strain and virulence (Makkonen et al., 2014; Becking et al., 2015). However, recent reports indicate that European native crayfish wild populations exposed to *A. astaci* of haplogroup A, in some cases even haplogroup B and D, can sometimes resist the deadly acute crayfish plague infection (Svoboda et al., 2012; Jussila et al., 2017; Martín-Torrijos et al., 2017). Significant differences in disease resistance have also been observed in controlled infection experiments (Makkonen et al., 2012; Martín-Torrijos et al., 2017; Francesconi et al., 2021). It is thus a major future challenge to identify target genes and molecular pathways, which underlie the defense mechanisms of the crayfish immune system under an *A. astaci* challenge that might be responsible for an increased resistance toward crayfish plague infection. In perspective, such results might become the basis of selective breeding programs focusing on resistance-genes. Subsequently, reintroduction programs could make use of crayfish plague resistant crayfish to be released into their original habitats. That being said, there would then be a risk of promoting yet another reservoir for *A. astaci* among native crayfish populations. Thus, speeding up the positive selection process by genetic enhancement of resistance against pathogens has to be carefully considered in the context of the conservation of the native crayfish species.

International pet trade polices like EU Pet Trade Regulation 2016/1141 need to be extended to cover more species which have high invasive potential and are known *A. astaci* vectors. More conservatively, instead of a blacklist of forbidden species, which takes too much time on EU level to be extended by additional species, it could be suggested to have a white list of species allowed for trade within the EU. Such a list seems to be more in line with a precautionary principle regarding the prevention of introducing invasive species unintentionally. Additionally, a frequent eDNA test of ballast water and the water used during animal cargo for presence of *A. astaci* spores and other emerging diseases using molecular methods would be highly advisable and definitely compulsory in cases where animal cargo could be entering the EU market (Brunner, 2020). Without effective implementation of national and international biosecurity measures, the occurrence, transboundary spread and serious economic and ecological impact of aquatic animal diseases will continue. In this regard, globally agreed standards for sanitary measures to apply to international trade in live aquatic animals are laid out in the OIE Aquatic Animal Health Code[2] and in the OIE Manual of Diagnostic Tests for Aquatic Animals[3]. Finally, public education is probably the key factor to reduce the risk of alien crayfish to be released into the wild. Education of retailers and pet crayfish owners is an important aspect to alleviate the threat posed by the pet trade.

People's awareness can contribute to public engagement benefiting nature conservation, which would be initiated by environmental education as part of the school curriculum. Recent successful conservation campaigns in Finland and Sweden (e.g., LIFE+ CrayMate and other regional campaigns; Jussila, 2016) have resulted in the common public being more aware of the possible benefits of native *A. astacus* stocks and the dangers of the alien *P. leniusculus* (Jussila, 2016). During the 3-year LIFE+ CrayMate awareness campaign, 2013 – 2016, the targeted fishing rights owners, mostly private persons responsible of the management wild fish and crayfish stock, initiated *A. astacus* restocking programs within carefully selected waters and at least in Southern Karelia region the success rate of the introductions was above 50% (Tiitinen, 2020) similarly to what has been observed in Northern Savo during the 2020s (Kosunen, 2020). At the same time, people became more aware of the role of alien *P. leniusculus* as the main reason for the spreading of *A. astaci* and the devastation of the native *A. astacus* stocks. This came as a surprise since the Finns have a strong tradition of trapping and eating crayfish, while the knowledge regarding the basics of crayfish biology and ecology seemed thin. In Fennoscandia an information campaign called "The Crayfish Myth Buster"[4] (in Swedish, Finnish, and English) was launched on the web in 2006 and people were directed to the website by advertisements in commercial radio jingles, TV, newspapers, flyers, special hats, and information on milk cartons. The campaign dealt with the 21 most common myths, exaggerations and misunderstandings of freshwater crayfish. In a very recent project ("MaNaKa," 2017–2020) German authorities funded an awareness campaign to encourage and instruct fishing clubs, water leaseholders and nature conservation authorities to safely stock suitable water bodies with the endangered native *A. astacus*. The colonization of waters previously free from crayfish plague, if carefully selected, should make an important contribution to the preservation of *A. astacus* in Germany. As an example from the south-east Europe, there have been campaigns in Croatia dedicated to raise awareness of the problems that invasive crayfish cause to freshwater diversity (Pavić et al., 2021). Unfortunately, those activities rarely attained the expected result. Even though there were workshops organized for local inhabitants focusing on the problems that *P. leniusculus* could cause to karstic habitats, *P. leniusculus* was illegally introduced into another karstic river (Una River) bordering Croatia and Bosnia and Herzegovina (Trožić-Borovac et al., 2019). Local education campaigns and workshops are needed in the regions where alien crayfish are present and also where they are not yet present but highly likely to spread. Currently, an action plan for alien crayfish in Croatia is being developed, involving local stake holders (fisherpersons, policy makers, protected areas employees, local inhabitants, school teachers, NGOs, etc.) as well as astacologists and the wider scientific community (Faller, 2020). In Croatia, a mobile application for invasive species alert has recently been developed and is now available for citizens (MGOR, 2020).

Finally, natural resources, such as reproductive native crayfish populations, can be taken as exploitable resources, while this approach should not be applied to all native crayfish populations or their distribution regions. The exploitation, and thus the commercial value of the wild crayfish stock, might be a means to protect and conserve native crayfish populations or even a whole species (e.g., Taugbøl, 2004), providing that exploitation is sustainable and spreading of diseases is prevented. When exploitation is discussed, one should introduce ecology into the debate and bear in mind that exploitation should not result in biodiversity decline or drastic ecosystem changes. Exploitation should thus be based on wide ecosystem sustainability, which would then allow both ecosystem health and thriving variety of species, in this case aquatic species, while also ensuring income and benefits to those attempting to exploit natural resources. Discussions regarding exploitation of natural resources quite often, if not always, focus on maximum economical gain, ignoring the long-term health of the exploited natural resource or the ecosystem where this resource belongs to. It never ceases to surprise how those interested in economic gain tend to forget that conservation is actually a rather selfish activity, in most cases, if successful, allowing the existence of human beings and the cultural frame that we rely on. Thus, conserving native European

[2]https://www.oie.int/standardsetting/aquatic-code/

[3]https://www.oie.int/standard-setting/aquatic-manual/

[4]www.krafta.nu

crayfish, protecting them against alien species and their diseases, works for us, too, allowing us to enjoy natural resources and, in the case of the Swedes and maybe the Finns, also crayfish parties, while having nicely prepared *A. astacus* (e.g., Fürst and Törngren, 2003; Edsman, 2004; Jussila et al., 2016a), but not in excess.

Quite a few of the suggested management and conservations actions have been implemented at least partially and with some success, for example LIFE+ CrayMate awareness campaign in Finland. As more radical actions we suggest that a fundamental principle of *polluter pays* should be enforced in the cases where the alien species are spreading and resulting in damage to the native ecosystems (e.g., Gaines, 1991). In Finland, and many other European countries, spreading of alien species is illegal, while so far the legal system fails to find culprits or ignores the cases as meaningless in their impacts (our observation). If an alien species cannot be eradicated, a *functional eradication* could be limiting or even eliminating ecological damage, as has been observed in the case of *P. rusticus* in North America (Green and Grosholz, 2021). Recent advances in bioengineering would also allow *genetic biocontrol*, which is based on modifications of the organism's genome in a heritable way that would for example disrupt the reproduction of the alien species (e.g., Teem et al., 2020). However, such methods are to date only applicable for some insect and vertebrate model species. In the case of freshwater crayfish, the most basic genomic knowledge required for genetic bioengineering, i.e., a fully annotated reference genome, is still lacking.

In this paper we clearly articulate and showcase that human perception and knowledge, or rather the lack of them, together with plain greed, are the most crucial components of the sad predicament of native freshwater crayfish species in Europe. The alien species threat has to be dealt with resolutely. However, to solve the problem of the invasive freshwater crayfish spread today, the most important thing is to manage people rather than the crayfish themselves (e.g., Robbins, 2011; Edsman, 2020b).

AUTHOR CONTRIBUTIONS

JJ, LE, IM, JD-U, and KT contributed equally in fact finding and writing process. All authors contributed to the article and approved the submitted version.

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