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Review

The red swamp crayfish *Procambarus clarkii* in Europe: Impacts on aquatic ecosystems and human well-being

Catherine Souty-Grosset[a,*], Pedro Manuel Anastácio[b], Laura Aquiloni[c], Filipe Banha[b], Justine Choquer[a], Christoph Chucholl[d], Elena Tricarico[c]

[a] Université de Poitiers, Laboratoire Ecologie & Biologie des Interactions—UMR CNRS 7267, Equipe Ecologie Evolution Symbiose, 5, rue Albert Turpin, TSA 51106, 86073 Poitiers Cedex 9, France
[b] MARE —Centro de Ciências do Mar e do Ambiente, Departamento de Paisagem, Ambiente e Ordenamento, Escola de Ciências e Tecnologia, Universidade de Évora, Rua Romão Ramalho, 59, 7000-671 Évora, Portugal
[c] Dip. Biologia, Universita degli Studi di Firenze, via Romana 17 I-50125 Firenze, Italy
[d] Fischereiforschungsstelle BW (Fisheries Research Station, Lake Constance), Argenweg 50/1, D-88085 Langenargen, Germany

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ABSTRACT

Procambarus clarkii is currently recorded from 16 European territories. On top of being a vector of crayfish plague, which is responsible for large-scale disappearance of native crayfish species, it causes severe impacts on diverse aquatic ecosystems, due to its rapid life cycle, dispersal capacities, burrowing activities and high population densities. The species has even been recently discovered in caves. This invasive crayfish is a polytrophic keystone species that can exert multiple pressures on ecosystems. Most studies deal with the decline of macrophytes and predation on several species (amphibians, molluscs, and macroinvertebrates), highlighting how this biodiversity loss leads to unbalanced food chains. At a management level, the species is considered as (a) a devastating digger of the water drainage systems in southern and central Europe, (b) an agricultural pest in Mediterranean territories, consuming, for example, young rice plants, and (c) a threat to the restoration of water bodies in north-western Europe. Indeed, among the high-risk species, *P. clarkii* consistently attained the highest risk rating. Its negative impacts on ecosystem services were evaluated. These may include the loss of provisioning services such as reductions in valued edible native species of regulatory and supporting services, inducing wide changes in ecological communities and increased costs to agriculture and water management. Finally, cultural services may be lost. The species fulfils the criteria of the Article 4(3) of Regulation (EU) No 1143/2014 of the European Parliament (species widely spread in Europe and impossible to eradicate in a cost-effective manner) and has been included in the “Union List”. Particularly, awareness of the ornamental trade through the internet must be reinforced within the European Community and import and trade regulations should be imposed to reduce the availability of this high-risk species.

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* Corresponding author.
E-mail addresses: catherine.souty@univ-poitiers.fr (C. Souty-Grosset), anast@uevora.pt (P.M. Anastácio), laura.aquiloni@gmail.com (L. Aquiloni), filipebanha@hotmail.com (F. Banha), Cchucholl@aol.com (C. Chucholl), elena.tricarico@unifi.it (E. Tricarico).

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1. Introduction

In freshwater ecosystems, biotic exchange is the most important driver of biodiversity change (Sala et al., 2000; Dudgeon et al., 2006). Invasive species are amongst the most relevant causes of extinctions (Lodge, 2001), threatening biodiversity worldwide, particularly in aquatic ecosystems (Carpenter et al., 2011). In comparison with other worldwide geographic localities, threatened European crayfish face the greatest number of pressures, of which the most widespread is invasive crayfish species (Richman et al., 2015). This is the case with the red swamp crayfish *Procambarus clarkii*, a successful coloniser in Europe as also elsewhere (Gherardi, 2006, 2013) that may quickly become established in new environments. Loureiro et al. (2015) recently provided an overview of its occurrence worldwide, biology, ecology and invasion. This North American crayfish is considered as one of the most widely introduced freshwater species in the world, especially due to its high economic importance. Contrary to other invertebrates whose introductions were mainly accidental (García-Berthou et al., 2007), initially *P. clarkii* was intentionally introduced for its food value (Hobbs et al., 1989). In Europe, the first introductions of *P. clarkii* from North America occurred in Spain since 1973 for aquaculture (Habsburgo-Lorena, 1978). After escaping into freshwater bodies, this species has since steadily spread across Europe and is currently recorded from 16 European territories (Table 1). Populations are most prevalent in Italy, Portugal, Spain and France, but the species is also present in England, Netherlands, Belgium, Switzerland, Germany and Austria, as well as in a number of islands (*i.e.* São Miguel-Azores, Cyprus, Majorca, Sardinia, Sicily and Tenerife) (Boets et al., 2009; Holdich et al., 2009; Kouba et al., 2014; Souty-Grosset et al., 2006). Unlike in southern Europe, where the species was primarily introduced to support crayfish harvest or production (Souty-Grosset et al., 2006), most *P. clarkii* populations in Central Europe are apparently associated with releases from the aquarium and food trade that occurred later, *i.e.* from the mid-1980s onwards (Chucholl, 2013a; Dehus et al., 1999; Dümpelmann et al., 2009).

Consequently, in Europe the red swamp crayfish is a long-established non-indigenous crayfish species (NICS), listed among the 100 worst invasive species and considered as the most plastic ecologically invasive decapod (DAISIE, 2011). This crayfish tolerates warmer water and features a more *r*-selected life history than indigenous crayfish species (ICS) (Reynolds and Souty-Grosset, 2012), being able to modulate its life history. In North America, Huner and Barr (1991) reported that preferred temperatures are between 21 °C and 27 °C while Anastácio et al. (1999b) summarized literature values for optimum, maximum and minimum temperatures for *P. clarkii* showing that the species can be active in the range of 10–41 °C, that it prefers temperatures of 20–28 °C and that its embryonic development is stopped below 5 °C. However Chucholl (2011a) has recently shown that, within its north-eastern range limit in Europe (southern Germany), the crayfish is able to cope well with new cold habitats by modulating its life history. Even in Italy reproductive plasticity of the species is reported at a temperature below its thermal optimum (Peruzza et al., 2015). Thus *P. clarkii* is capable of spreading to northern and colder habitats, quite different from its native habitat, and, up to now, considered “safe” from its invasion. Thus, the red swamp crayfish may ultimately accelerate native crayfish declines through crayfish plague transmission and direct competition (Holdich et al., 2009).

The aim of this paper is to summarize and update knowledge about the impacts of *P. clarkii* in Europe on native biota and ecosystems, as well as on human economy and well-being and the implications for regulation of invasive alien species.

2. Impacts of *P. clarkii* on ecosystems

P. clarkii has invaded not only freshwaters (rivers/streams, lakes, ponds, irrigation channels reservoirs) but also estuaries due to its salinity tolerance. Casellato and Masiero (2011) showed its survival in levels up to 25 ppt and even observed moults and mating, indicating that the species could invade the estuarine and brackish environments of the Adriatic coast as already reported for some Tyrrhenian areas (Scalici et al., 2010), with all the implied consequences for the native fauna and for human livelihoods. The species also occupies terrestrial-natural or semi-natural swamps and terrestrial humid zones such as meadows or those managed as rice fields. Recently, this invasive crayfish was found for the first time in European caves, specifically in Portugal and Italy (Mazza et al., 2014). Indeed, the presence of *P. clarkii* in caves is noteworthy, representing a new threat for groundwater ecosystems through potential negative impacts on the native communities: it can prey on several cave endemic species, since it feeds on diverse items in proportion to their availability (Mazza et al., 2014). Most occurrences in Germany are localized and confined to summer-warm ponds and artificial lakes; it is currently undergoing active spread in areas characterized by gravel pit lakes, such as along the Rhine and Danube River plains (Chucholl, 2011b; Dümpelmann et al., 2009; Gross, 2013).

Among the top 27 animal alien species introduced into Europe for aquaculture and related activities, *P. clarkii* showed the largest range of impacts (eight types), from outcompeting native species to altering food web composition and habitat structure (Savini et al., 2010, Fig. 1). The literature mostly concerned predation, herbivory, habitat change, food prey, competition, community dominance, bioaccumulation, and food web alteration. Being omnivorous, *P.*

Table 1
Mode of arrival of *Procambarus clarkii* in Europe: year of introduction and/or year of first record from bibliographic analysis.

Territories	Mode of arrival	Pathway	Introduction (year)	First record (year)	References
Austria	intentional	release		2005	Petutschnig et al. (2008)
Azores (Pt)	intentional	release	1990/1991	1993	Correia and Costa (1994)
Belgium	intentional	release	1983–1985		Boets et al. (2009)
Cyprus	intentional	release	1984		Stephanou (1987)
England	intentional	escape		1991	Ellis et al. (2012)
France	intentional	release	1976		Laurent (1997)
Germany	non intentional	escape	mid-1980s		Troschel and Dehus (1993)
Italy	intentional	escape	1989		Delmastro (1999)
Majorca (Sp)	unknown	unknown	1985	1991	Mayol et al. (1991); Slater, (1992)
Netherlands	intentional	escape	1980s	1985	Soes and Koese (2010)
Portugal	non intentional	unaided	1979	1979	Ramos and Pereira (1981)
Sardinia (It)	intentional	unknown		2005	Orrù et al. (2009)
Sicily (It)	intentional	unknown		2003	D'Angelo and Lo Valvo (2003)
Spain	Intentional	release	1973		Habsburgo-Lorena (1986)
Switzerland	intentional	unknown	1997		Stucki (1997)
Tenerife (Sp)	intentional	unknown	1997	1997	Arteaga et al. (2006)

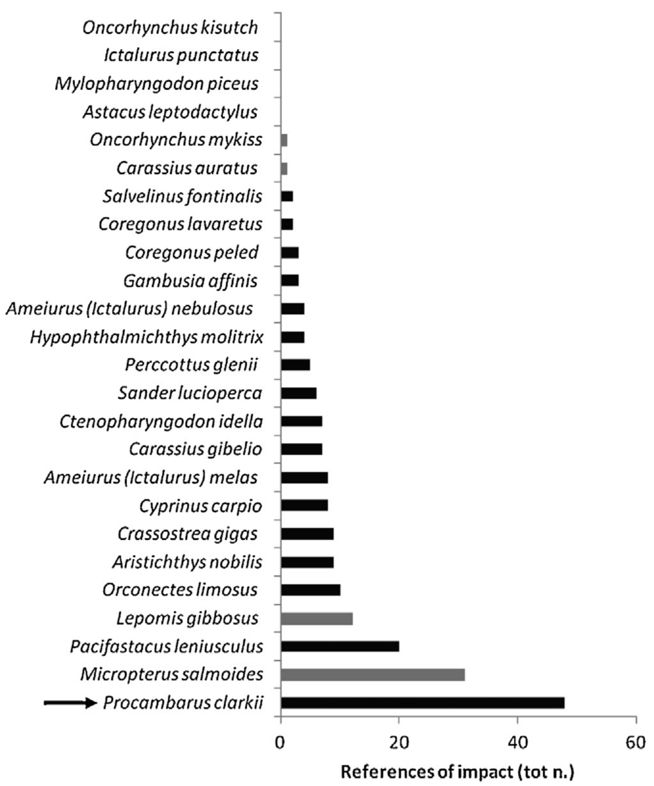

Fig. 1. Number of references concerning environmental impact of the top 27 alien aquatic cultured species in Europe. In black "very high confidence in referencing impact", in grey "high confidence". *Procambarus clarkii* has the largest number of types of impacts. Impact heterogeneity expressed as number of impact types per species. Impact types are: (1) food web alteration, (2) bioaccumulation of toxic substances in tissue, (3) community dominance in native ecosystem, (4) competition for food or space with native species, (5) introduction of new food item in the ecosystem, (6) modification of physical-chemical properties of habitats, (7) consumption of aquatic plants and algae, (8) hybridization with native species and loss of genetic integrity, (9) predatory activity on native species (modified from Savini et al., 2010 by *E. Tricarico*).

clarkii has a pivotal effect on trophic structure of invaded freshwaters and estuaries, interacting with different trophic levels and changing how the ecosystem functions (Angeler et al., 2001; Cruz et al., 2008; Dorn and Wojdak, 2004; Gherardi and Acquistapace, 2007).

2.1. Burrowing activity

The red swamp crayfish can be considered an ecosystem engineer, completely transforming the habitats it invades. The use of burrows allows this species to withstand environmental extremes (*e.g.* high temperatures and dehydration) and protects the crayfish from predators during sensitive phases of their life history (Gherardi, 2006). In Europe the species usually digs simple burrows in fine sediment, although more complex structures are possible (Barbaresi et al., 2004). Burrowing activity tends to occur when the ratio of fine particles over coarser particles is above 0.1–0.2 and the period of most intense burrowing in Portugal is from May-October (Correia and Ferreira, 1995). In the same study, mean tunnel depth across several types of habitats was 0.28–0.58 m but even reached 4.2 m. Burrows were mostly at water surface level in rice fields and above water level in marshland reservoirs. Souty-Grosset et al. (2014) showed that, in fishponds in Central France, the digging activity of *P. clarkii* is enhanced in cases of rapid water leakage and loss of moisture in the substrate. Arce and Diéguez-Uribeondo (2015) confirmed that rice-growing areas in Europe/Spain have been largely affected by crayfish habits, mainly due to their digging behaviour. For example, in the Ebro Delta Natural Park (NE Spain) – one of the main rice-producing areas within the Mediterranean region –they established links between the local densities of crayfish, the abundance of burrows they use to shelter, and the intensity of damage by crayfish digging activity. Additionally, burrowing behaviour may also cause river or channel bank erosion and increase water turbidity (Anastácio and Marques, 1997; Rodríguez et al., 2003). Barbaresi et al. (2004) showed its "consumerist" use of the burrows: the time of burrow occupation is short and crayfish are not faithful to the same burrow. At the end of their foraging excursions, they excavate new burrows. Burrowing by red swamp crayfish in European coastal wetlands (Scalici et al., 2010) could reduce coastal protection from severe storms and sea level rise. In northern Italy, crayfish burrowing damages 30% of the irrigation canals, costing 8% of the annual income of the management authority (M. Fantesini, pers. comm. in Lodge et al., 2012).

2.2. Modification of physico-chemical properties

Water quality, in particular dissolved oxygen and turbidity, can be heavily affected by burrowing activity of *P. clarkii*, and this was experimentally demonstrated in laboratory and outdoor studies (Anastácio and Marques, 1997; Anastácio et al., 2005a). In a Spanish floodplain wetland, water quality impoverishment was mainly due to the increase of dissolved inorganic nutrients (soluble reactive phosphorus and ammonia), and a significant increase of total suspended solids occurred, likely because of crayfish associated bioturbation (Angeler et al., 2001). Field observations in Spanish lagoons also suggest that crayfish affect turbidity (Rodríguez et al., 2003). Crayfish acting as ecosystem engineers affect not only the habitats used by fish for shelter or spawning but also the whole state of the aquatic ecosystem. The changes in water characteristics alter aquatic ecosystems and are believed to induce cyanobacteria blooms (Yamamoto, 2010).

2.3. Dispersal overland

Although its post-establishment spread could occur through several mechanisms of active and passive transport, involving both human and animal vectors, the desiccation resistance of *P. clarkii* strongly contributes to easy dispersal overland, being capable to survive out of water more than 10 h, in South Europe summer conditions (Banha and Anastacio, 2014). Regarding active dispersal, this species has indeed the ability to exit the water and moves overland to distances up to 1 km (Kerby et al., 2005; Cruz and Rebelo, 2007). In water it can rapidly spread across a watershed, covering distances, varying according to the environmental conditions, from 38 m day^{-1} (*e.g.* Aquiloni et al., 2005; Gherardi et al., 2002a) to 255 m in half a day (Anastácio et al., 2015). It has been recorded as covering up to 4000 m in rice field habitats within seven days (Gherardi and Barbaresi, 2000). Concerning the speed of spread, Bernardo et al. (2011) found rates of 7.7 km (annual downstream colonization rate) and 4.6 km (upstream colonization rate). The other known natural process of *P. clarkii* dispersal involves passive external transport (*i.e.* ectozoochory) of juveniles by waterbirds (Águas et al., 2014; Anastácio et al., 2014). Additionally, the juveniles of this species could also be accidentally transported between wetlands by human activity, on mud attached to off-road vehicles (Banha et al., 2014). The high order or magnitude of the transport distances involved in these processes requires their consideration in *P. clarkii* management. Finally, another dispersal process with human intervention is connected to the live bait use of *P. clarkii* by anglers and the consequent discarding of live individuals to water. The mechanism could be relevant to the spread of *P. clarkii* in the Iberian Peninsula, where this species is one of the most used baits (Banha and Anastácio, 2015).

2.4. Vector of diseases

P. clarkii is one of the vectors of the crayfish plague, which is mostly asymptomatic in North American crayfish species but lethal to crayfish from other regions (Longshaw, 2011; Souty-Grosset et al., 2006). This disease, caused by the parasitic Oomycete *Aphanomyces astaci*, constitutes a remarkable threat to indigenous crayfish species, thus being one of the leading causes of native crayfish population decline in Europe (Gutiérrez-Yurrita and Montes, 1999; Holdich et al., 2009; Souty-Grosset et al., 2006). In southern Germany, illegal introductions of *P. clarkii* into lakes have been linked to losses of native noble crayfish (*Astacus astacus*) stocks, most likely due to crayfish plague transmission (Chucholl, 2011b). Most recently, a rapid crash of an abundant narrow-clawed crayfish population (*Astacus leptodactylus* species complex) was followed by detection of *P. clarkii* (C. Chucholl, unpubl. data). Red swamp crayfish also host a rich microfungal flora in their stomachs (Garzoli et al., 2014). Besides *A. astaci*, *P. clarkii* may carry many other pathogens, parasites, epibionts and diseases that can affect other species. In particular, the overall pathogen risk of the red swamp crayfish is very high, not only due to the potential for dispersal and impact of the crayfish plague (Aquiloni et al., 2011) but also through carrying the fungal pathogen *Batrachochytrium dendrobatidis* that causes lethal skin infections (chytridiomycosis) in amphibian species worldwide (McMahon et al., 2013). Brannelly et al. (2015) argued that a 6% infection prevalence found in a species that is as widely traded as *P. clarkii* represents a significant risk and deserves to be considered in biosecurity measures. In humans, the species was found as a possible agent of transmission of the bacterium *Francisella tularensis* (Anda et al., 2001) and other parasites (cited in Longshaw, 2011 and Souty-Grosset et al., 2006).

2.5. Consumption of aquatic plants and algae, including phytoplankton

Rice fields: as when introduced in other regions of the world (California: Grigarick and Way, 1982; Kenya: Rosenthal et al., 2005; China: Yue et al., 2010), the red swamp crayfish affects rice production in Europe. This species causes water loss, damage to rice field banks and ditches (Arce and Dieguez-Uribeondo, 2015; Correia, 1993; Ocete and Lopez, 1983; Marques et al., 1992), direct consumption of rice seed and plants (Anastácio et al., 2005b), and clogging of pipes (F. Gherardi, pers. obs. in Lodge et al., 2012). Consumption is the most important cause of rice destruction (Anastácio et al., 2005b) and a consumption peak is observed during the second week of rice development (Anastácio et al., 2006). Although seedlings are more affected than seeds, at high crayfish densities the majority of both items are heavily affected (Anastácio et al., 2005c). Rice plants density can be reduced by 100% at densities of 3 and 5 crayfish m^{-2} but some infesting macrophytes survive at 3 crayfish m^{-2} and very few at 5 crayfish m^{-2}. Feeding trials show that crayfish clearly prefer rice seedlings to some common infesting plants in the rice fields (Barradas et al., 2004). In spite of this, crayfish may consume rice field algae and prefer them in relation to other rice field weeds (Barradas et al., 2004, 2006).

Freshwater/aquatic and semi-aquatic macrophytes: the red-swamp-crayfish can greatly affect macrophyte cover in European freshwater systems (*e.g.* Rodríguez et al., 2003). Plant material is extremely frequent in crayfish stomachs particularly in adult (*e.g.* Gutierrez-Yurrita et al., 1998; Ilhéu and Bernardo, 1993a). Grazing by *P. clarkii* on macrophytes and extensive burrowing activity can alter freshwater environments, modifying them from macrophyte-dominated areas with clear water to phytoplankton dominated turbid areas (Geiger et al., 2005; Matsuzaki et al., 2009; Rodríguez et al., 2003). Moreover, by consuming directly leaf litter, the red swamp crayfish increased rates of leaf litter breakdown, whereas virile and Turkish crayfish reduced breakdown by consuming other invertebrates that usually fed on the leaf litter (Jackson et al., 2014). Consumption and non-consumptive destruction by red swamp crayfish were implicated in declines of native macrophytes in Germany. This may be to such an extent that the macrophyte community in a gravel pit lake in North-Rhine Westphalia has been almost entirely depleted five years after the first detection of *P. clarkii* (Gross, 2013). A strong, density-dependent link between biomass and species composition of macrophytes and *P. clarkii* was also evidenced by in situ enclosure experiments (Chucholl, 2013b; Gherardi and Acquistapace, 2007). In the first study (Chucholl, 2013b), *P. clarkii* led to a depletion of native *Myriophyllum spicatum* (mostly resulting from uprooting) and *Chara* sp. (mostly resulting from consumption), but had no significant effect on the alien *Elodea nuttallii*. Thus, it induced a marked shift in the relative abundance of these macrophyte species in favour of the alien *Elodea*, which is consistent with an invasional meltdown scenario. In the second study (Gherardi and Acquistapace, 2007), the red swamp crayfish strongly inhibited the biomass of the hydrophytes *Nymphoides peltata* and *Potamogeton* spp. by grazing, coupled with their non-consumptive plant clipping and uprooting, while, in contrast, *Utricularia australis* was avoided by *P. clarkii*, even when other resources were restored. Van der Wal et al. (2013) showed that *P. clarkii* strongly inhibit macrophyte development once favourable abiotic conditions for macrophyte growth are restored in a Dutch peat lake. Finally, Carreira et al. (2014) studied the impact of *P. clarkii* on the macrophyte community of Mediterranean temporary ponds, testing in laboratory if consumption and fragmentation of five macrophyte species were correlated in palatability tests and in a preference test. *P. clarkii* consumed preferably *Juncus heterophyllus* and avoided *Carex divisa* and *Ranunculus peltatus* during preference test. Consequently, as in the presence of preferred species, consumption and fragmentation of the non-preferred species were heavily reduced, *P. clarkii* may remove macrophyte species from the community sequentially, from the most to the least preferred species.

2.6. Predation of macroinvertebrates

P. clarkii can have strong consumptive and trait effects (e.g. antipredator behaviour) on aquatic macroinvertebrate prey, resulting in differential impacts on different species (Correia et al., 2005). As an example, the extinction of two gastropods, *Lymnaea peregra* and *L. stagnalis*, in the Doñana National Park (south-western Spain) is coincident with its introduction (Montes et al., 1993). Overall, macroinvertebrate diversity is negatively affected by crayfish, but the effect is inversely proportional to crayfish size (Correia and Anastácio, 2007). In fact, red swamp crayfish juveniles tend to have a larger proportion of animal material in their diet than adults which rely mostly on vegetable material (Correia, 2003; Gutierrez-Yurrita et al., 1998; Ilhéu and Bernardo, 1993a). However, when given the choice between animal prey and plants, *P. clarkii* in general prefers animal prey according to the food available, such as macroinvertebrates with slow escape reactions (Ilhéu and Bernardo, 1993b) with low turbidity visual cues are indeed sufficient to mediate their detection by *P. clarkii* (Correia et al., 2007). Experimental results show that the presence of *P. clarkii* can affect the abundance of an insect, *Chironomus riparius*, and a gastropod, *Physella acuta*, but not of a bivalve, *Corbicula fluminea.* In the same study, *Physella acuta* was the only species that exhibited an antipredator behaviour to *P. clarkii* (Correia et al., 2005). A strong top down pressure of *P. clarkii* on aquatic snails was also experimentally shown for southern Germany, where the abundance of three snails (*Radix ovata*, *Lymnaea stagnalis* and *Planorbis corneus*) sharply decreased with increasing crayfish density (Chucholl, 2013b). Crayfish are also important predators of major rice macroinvertebrate pests such as Chironominae larvae (Correia and Anastácio, 2007). Adults are able to predate other decapod species such as *Atyaephyra desmarestii*. Both species prefer shallow pool microhabitats with abundant aquatic vegetation, and crayfish density and its cephalothorax length are negatively correlated with shrimp densities (Banha and Anastácio, 2011). Field studies in southern Spain have confirmed that *P. clarkii* prefers animal food sources, and that it reduces the amount of herbivory and diversifies its animal diet (mostly macroinvertebrates) in spring (Alcorlo et al., 2004). In southern Germany, the trophic diversity of *P. clarkii's* diet was highest in mid-summer and in smaller crayfish. Chironomidae larvae and *Dreissena polymorpha* were the most preferred prey, whereas sediment-dwelling taxa were rarely consumed. The number of consumed small and agile prey was negatively correlated with crayfish size, suggesting an ontogenetic shift in diet (Chucholl, 2013b). In addition to these direct effects, there have been reports of captures of large macroinvertebrates, mostly Dytiscidae, but also some freshwater shrimp and Odonata larvae by commercial crayfish traps in the south of Spain (Geiger et al., 2005). In Italy, the intense predatory behaviour of *P. clarkii* has driven to extinction a once locally abundant semiaquatic beetle (*Carabus clatratus*) (Casale and Busato, 2008). *P. clarkii* feeds on the diverse items present in a given invaded habitat in proportion to their availability so that its diet can change with habitats (Gherardi, 2006). It also quickly learns to feed on unknown prey: in laboratory naive individuals of this species required less than 12 h to learn to maximize capture rate of larvae (Diptera, *Chaoborus* sp.), evidencing its predation capabilities in newly invaded habitats (Ramalho and Anástacio, 2011).

2.7. Impact on amphibians

Crayfish presence is negatively related to the breeding probability for several salamander, frog, and toad species (Cruz et al., 2006; Ficetola et al., 2011, 2012). Under laboratory conditions, *P. clarkii* was shown to consume amphibian larvae more efficiently than the native crayfish *Austropotamobius pallipes* (Gherardi et al., 2001; Renai and Gherardi, 2004). Apparently, the poisons contained in several amphibians are not an effective deterrent for *P. clarkii*.

Naive Iberian waterfrog (*Pelophylax perezi*) populations respond behaviourally to *P. clarkii* and its predation pressure seems to induce the evolution of diverse antipredator defences in *P. perezi* populations with longer coexistence time with *P. clarkii* (Nunes et al., 2013a). Another study highlighted that five out of nine anuran species alter their behaviour due to crayfish in a mechanism mediated by chemical cues from consumed conspecifics (Nunes et al., 2013b). In spite of this, Almeida et al. (2011) found that only anuran tadpoles of permanent habitats altered their behaviour and life-history traits in the presence of *P. clarkii* but also confirmed a mediation process by chemical cues from consumed conspecifics. Arribas et al. (2014) quantified the effects of *P. clarkii* on amphibian larvae: the western spadefoot toad *Pelobates cultripes* experienced the highest survival, whereas crayfish reduced survival in the Mediterranean treefrog *Hyla meridionalis* by 32% and by 50% in *P. perezi*.

Non-lethal injuries caused by crayfish on amphibian larvae are common. The presence of *P. clarkii* was the strongest predictor of tail injury frequency in Iberian spadefoot toad (*Pelobates cultripes*) tadpoles in pond habitats. Tadpole tail loss decreased survivorship; injured tadpoles developed deeper tail muscles and shallower tail fins and injuries may induce delayed fitness costs (Nunes et al., 2010). Four of nine anuran larvae species altered their morphology or life history when reared with fed crayfish, indicating among-species variation in the ability to respond to a novel predator (Nunes et al., 2014). This last study suggests a high risk of local extinction and reduced diversity of the invaded amphibian communities.

Antipredator responses towards *P. clarkii* can differ among amphibians. For example, *Bufo bufo* responded similarly to *P. clarkii* as towards a native predator (dragonfly larvae), while *Discoglossus galganoi* responded to the native predator but not to *P. clarkii* (Almeida et al., 2011). These authors hypothesized that anuran species breeding in permanent habitats may be relatively protected against *P. clarkii*.

2.8. Interaction with fish and other crustaceans

In comparison with indigenous crayfish species, *P. clarkii* tends to be more active and aggressive, to occur in greater densities and to show more interactions with fish (Reynolds, 2011): red swamp crayfish feed on *Micropterus salmoides* eggs in their nests, probably also on *Esox lucius* eggs, which are large and adhere to vegetation. Invasive *P. clarkii* are also important predators of fish in temporary Mediterranean streams (Ilhéu et al., 2007). There are bidirectional trophic interactions, which change depending on species relative size, between another invader, the mosquitofish (*Gambusia holbrooki*), and *P. clarkii* (Anastácio et al., 2011). Adult crayfish predate on mosquitofish and mosquitofish can predate on recently hatched crayfish. There may in fact be a facilitation of *P. clarkii's* invasion since it can profit from the presence of *G. holbrooki*. On the other hand, the largemouth black bass (*M. salmoides*), natural predator of crayfish in America, switches from mosquitofish to *P. clarkii* when crayfish become more abundant and needs a four days learning period to optimize crayfish capture rates (Ramalho, 2012). Ilhéu et al. (2007) investigated the effects on vertebrates in dry-season stream pools in Southern Portugal. Fish was the third most consumed item, present in 24% of crayfish stomach contents, this type of food being dominant in 24% of the pools. In Portugal, high vulnerability of fish makes them the ideal prey only during the low water conditions associated with the temporary character of some streams. As the surface water disappears, in the extreme confinement of the very shallow pools, fish are totally predated. In addition to these direct effects, bycatch of fish by commercial crayfish traps have been reported in the south of Spain and in Portugal (Banha and Anastácio, 2015; Geiger et al., 2005; Gutierrez-Yurrita et al., 1997).

Concerning the other crustaceans present in the invaded habitats, from laboratory studies, *P. clarkii* outcompetes the other species, except the native European river crab *Potamon fluviatile*. The red swamp crayfish showed to have greater chelae strength than the indigenous European crayfish *A. pallipes* and to dominate it (Gherardi and Cioni, 2004).

2.9. Bioaccumulation of toxic substances

Toxic materials in water may have catastrophic effects on crayfish (Reynolds and Souty-Grosset, 2012). Inorganic or organic materials accumulated within the aquatic food web may also directly affect freshwater crayfish, causing mortalities or damage at cellular and organism level (Füreder et al., 2006). Susceptibility is now known to differ between cambarid, parastacid and astacid crayfish, and even within a single genus. Laboratory assays showed that copper concentrations in the water up to 500 $\mu g\, l^{-1}$ during 96 h would not suffice to change concentrations in crayfish soft tissues (Maranhão et al., 1995). In spite of this, in a study on the relative concentrations of heavy metals in freshwater macrodecapods from Italy, Gherardi et al. (2002b) found that *P. clarkii* showed significantly higher accumulation for most of the metals analysed, including the non-essential cadmium, nickel and lead, than did the indigenous white-clawed crayfish, *Austropotamobius pallipes*, and the river crab, *Potamon fluviatile*. It was also discovered that *P. clarkii,* collected in Massaciuccoli Lake (Italy), accumulated cyanotoxins in all the analysed organs. The highest concentration of microcystins was found in intestine, followed by hepatopancreas/stomach and abdominal muscle (Tricarico et al., 2008). In some areas the red swamp crayfish has become the major food item for otters (*Lutra lutra*) and several other vertebrates (Delibes and Adrian, 1987; Geiger et al., 2005) that can accumulate heavy metals and toxins eating this species. Alcorlo and Baltanás (2013) indeed found a significant correlation between five heavy metal elements (As, Cd, Zn, Cu, Pb) measured in *P. clarkii* and predator nitrogen isotope, possibly indicating that the transfer of pollutants to higher order food web levels (humans included) is mediated by this crayfish.

3. Socioeconomic impacts following the establishment of the red swamp crayfish

In developed countries a range of ecological, cultural and economic aspects of freshwater crayfish are important. Freshwater crayfish species provide a wide variety of services, including direct economic benefits, for humankind. Crayfish catching provides a useful income to local fishermen. Marketing, processing, transportation and other activities benefit from crayfish and provide increased income to the inland fisheries sector. In Europe, crayfish consumption increased in the 19th century, leading to the introduction of species coming from outside Europe. Lodge et al. (2012) have evaluated the negative impacts of invasive crayfish introductions on ecosystem services. These may include the loss of provisioning services- such as reductions in valued edible native species, of regulatory and supporting services, inducing wide changes in ecological communities and increased costs to agriculture and water management (Table 2). Finally, cultural services may be lost, such as the disappearance of festivals celebrating native crayfish (Reynolds and Souty-Grosset, 2012).

3.1. *P. clarkii* consumption and market

Today, currently catching for home consumption is modest and does not tap potential production. The importance of *P. clarkii* as a human food item has been growing worldwide. According to FAO (2010), the global mean production has increased almost 200% per year, and in 2008 reached 41,704 Tons and 1,862,938 USD. More recently *P. clarkii* livestock production represents 99% of the worldwide crayfish market (Seaweb, 2014). Although *P. clarkii* was introduced in several countries, it is industrially exploited mostly in USA, China and Spain, this European country being the third world producer with 4.1% of total biomass, corresponding to a mean of 3700 t/year (MBC, 2001). In Europe, only the Spanish region of the Guadalquivir marshes has a transformation industry capable to export to other Spanish regions (central and north Spain, Madrid and Valladolid provinces), countries of central and north Europe (such as France, Sweden, Belgium and Denmark) (Gutiérrez-Yurrita and Montes, 1999) and in recent years even to China and USA (El Mundo, 2014; MBC, 2001). In 2007, the Spanish region had four factories producing packed live crayfish, boiled crayfish (fresh or frozen peel off abdomens or whole crayfish) and crayfish flour (Junta de Andalucía, 2007). The introduction of this crayfish generated professional fishing activity (Gutiérrez-Yurrita and Montes, 1999), with a peak in 1986, of approximately 500 fishermen. In other Spanish regions (e.g. Extremadura, Valencia and Ebro delta) and Portugal (Vouga, Tagus and Mondego lowlands), professional crayfish capture was also developed, mostly supporting the Guadalquivir factories (Gutiérrez-Yurrita and Montes, 1999; MBC, 2001; Rodrigo et al., 2006). In 2000, 116 Portuguese anglers dedicated to these species reported in total more than 106 t, being the most captured freshwater species in Portugal by total biomass (Rodrigo et al., 2006). In other invaded European countries, such as France (in more than 13 departments especially in the south; Agence de L'Eau (2002) and Italy (in Umbria and especially in Tuscany; Simoni et al., 2004), there are still fishing activities on this species, but mainly for local markets.

Similar to other items, the commercial value of *P. clarkii* depends on supply and demand. However, factors such as crayfish size, quality or abundance are the main rulers, with prices increasing with individual size and quality and decreasing along with its abundance (Gutiérrez-Yurrita and Montes, 1999; MBC, 2001). In Spain, values near 3 Euros/kg were registered during the 1980′s, at the beginning of production, stabilizing at 1.4 Euros/kg in the 1990′s, but reaching on some occasions almost 10 Euros/kg (Gutiérrez-Yurrita and Montes, 1999). Today the value has decreased approximately to 0.40 Euros/kg (comparing MBC, 2001 and El Mundo, 2014). However, in France and Italy, with much fewer captures, because the demand exceeded supply, the prices in some cases reached 15 Euros/kg (Agence de L'Eau, 2002; Simoni et al., 2004). In conclusion, European data on *P. clarkii* captures, value and economic impacts are scarce and different sources provide different values for the same regions and period (Table 3). Thus, the economic relevance of *P. clarkii* in Europe is under-estimated, being the production and income probably much higher than reported.

Table 2
Impact of Procambarus clarkii on ecosystem services (modified from Lodge et al., 2012; Gherardi, 2013)

Affected service	Description of impact of *P. clarkii*
Provisioning: Food, ornamental	It is consumed as food instead of native species, today protected. It reduces the provisioning of other food by spoiling valuable fish and damaging fish nets. Responsible of lower production of rice fields. Risk of release as blue, orange, white and mixed color varieties bred specifically for the ornamental market
Regulating: Water	It increases suspended solids and induces turbidity of aquatic habitats, sometimes dominated by toxic cyanobacteria
Regulating: Diseases	It accumulates cyanobacteria toxins and heavy metals that can be transferred to its consumers, above all birds but also humans included. It is a possible agent of transmission of the bacterium *Francisella tularensis* (Anda et al., 2001)
Regulating: Pests	It is a vector of parasites and pathogens, including crayfish plague. Other parasites cited in Souty-Grosset et al. (2006) and Longshaw (2011)
Regulating: Hazards	Its intense burrowing in coastal wetlands reduces protection from storms and sea level rise
Supporting: Erosion	Its activity (foraging, burrowing and locomotion) causes erosion of littoral zones. 'Honeycombing' increases bank erosion and inflicts costs in areas with canal irrigation systems and water control structures
Supporting: Nutrients	It reduces organic matter and increases phosphorus and nitrogen in sediments
Supporting: Refuge	It reduces the abundance of macrophytes via herbivory and stalk-cutting, thus decreasing refuge availability for many species
Supporting: Community, foodweb	It increases abundance of aquatic birds and otters but causes problems for heavy metals transmission; it causes decline of many invertebrate taxa, larval amphibians, and aquatic plants
Supporting: Production	The loss of macrophytes reduces the surface for the growth of attached algae but often enhances phytoplankton
Cultural: Recreation, tourism	The decreased abundance of the native European crayfishes *Austropotamobius pallipes* leads to the loss of local activities focused on crayfish. The higher abundance of aquatic birds can lead to an increase of birdwatchers in the area; on the contrary, if the invaded water body is too much altered by the species, the ecotourism can decrease
Cultural: Heritage value	The reduction of native crayfish stocks affects their heritage value as well other native species predated by this species
Cultural: Aesthetics enjoyment, inspiration	The loss and destruction of habitats and the homogenization of landscapes affect aesthetic enjoyment

3.2. *Cost of damage caused by* P. clarkii

The economic impact of invasive species can be enormous. Species such as the zebra mussel (*Dreissena polymorpha*), the American red swamp crayfish (*P. clarkii*), and the American mink (*Mustela vison*) cause hundreds of millions of Euros of damages every year with costs mainly related to ecological impacts and control measures (Kettunen et al., 2009). Costs mostly occur in the agricultural, forestry, and fishery sectors. Regarding agricultural economic impacts specifically, crayfish infestation has seriously damaged drainage systems because of its feeding and burrowing activities, causing important losses of rice yield (Anastácio et al., 2000, 2005c). Infestations at experimental densities of 1 crayfish m^{-2} can decrease rice grain production by 41.61% (Anastácio et al., 2000). In Portugal, in 2004 rice farmer associations estimated a mean direct monetary loss of approximately 43€ per ha (Cooperativa_Agricola_de_Soure, 2004). Considering a nationwide rice production area of 25,000 ha, this would represent over one million euros of damage per year. However, these calculations do not account for indirect losses due, for example, to reconstruction of levees or leakage of water from flooded fields.

A recent economic analysis on alien invasive species in France (Wittmann, 2015) shows that, among 600 invasive species (fauna and flora), *P. clarkii* is the fifth invasive species classified according to the level of presence and impacts in the whole country. Moreover, the red swamp crayfish is the ninth invasive species in terms of cost, considering both management and impact: it caused 707 k€ in five years (2009–2013) e.g. 141 k€ per year, more than of the American signal crayfish *Pacifastacus leniusculus* (189 k€ in five years, 38 k€/year).

Some years ago in Northern Italy, Gherardi (pers. comm.) reported a 6% decrease in production of rice due to *P. clarkii.* As the invasive crayfish clogs irrigation pipes in Italy (F. Gherardi, pers. obs.), the annual estimated cost due to *P. clarkii*'s invasion in Latium (Central Italy) varies between 139,179 euros and 1,167,680 euros including damages to angling, fisheries, aquaculture, and irrigation ditches (Gherardi et al., 2009). As the red swamp crayfish is a carrier of the crayfish plague that is wiping out entire populations of European crayfish, the disease alone is estimated to have an economic cost of over €53 million/year (European Union, 2014).

4. Management of *P. clarkii*

Several control methods are already known and applied to *P. clarkii*, including trapping, construction of physical barriers, biocontrol by indigenous fish predators, male sterilization, the use of pheromones as bait for traps and use of biocides (see Gherardi et al., 2011 for a review). An integrated pest management (IPM) approach, using a range of control and containment techniques to suit different habitats and population status is advocated to obtain positive results. A cost-benefit analysis should be performed in order to find the most appropriate and efficient method for each situation, and to evaluate whether intervention strategies can be designed to produce greater economic benefits than the costs required to implement them (Keller et al., 2008). As pinpointed by Lodge et al. (2012), it would be necessary to quantify the impacts caused by alien crayfish such as *P. clarkii* on ecosystem services, including monetized ones, to better inform management decisions in order to have a reliable cost-benefit analysis.

4.1. *Control methods*

While *P. clarkii* is cultured and harvested from inundated rice fields in much of its native range, particularly in southern USA (FAO, 2007–2016), the species causes damage to crops in Europe that has often outweighed benefits of harvest (Anastácio et al.,

Table 3
Procambarus clarkii production, prices and fishermen number in Europe.

Country	Region	Date	Biomass captured (tonnes per year)	Price (Euros/kg)	Number of fishermen per year	Note	Source
France	Brière/Camargue	2002/2015		10–12		Maximum value	Agence de L'Eau (2002); Souty-Grosset, pers. comm.
Italy	Fimon lake	2007–2012	2				La Piana et al. (2012)
	Fucecchio marshes	2014	0.8	10		Estimated using maximum capture value per week	Scovacricchi (2010)
	Massaciuccoli lake	2004		8–15			Simoni et al. (2004)
	Massaciuccoli lake	2014	20.8	6–15		Estimated using maximum capture value per week	Scovacricchi (2010)
	Trasimeno lake	2014	26	6–15		Estimated using maximum capture value per week	La Piana et al. (2012); Scovacricchi (2010)
Portugal		1995	700			Exported to Spain	Gutiérrez-Yurrita et al. (1999)
		~1999		1–2			
		~1999		4		Maximum value	
	Mondego river	2000	3.7		25		Rodrigo et al. (2006)
	Vouga river	2000	14.8		27		
	Tagus river	2000	88.3		64		
Spain		1976–1980		2.8			Gutiérrez-Yurrita et al. (1999)
		~1999		0.17–9		Minimum-Maximum values	
		1980–2000		1.4		Mean value	
		1986	5000			Maximum value	
		1974–1976	0				FAO, 2015
		1982–2000	2151			Mean value	
		2003–2012	1500				
		1994	274			Minimum value	
		1985–1986	3350			Maximum value	
		2000–2001	0			From aquaculture	INE (2008)
		2002	87.1			From aquaculture	
		2003–2005	0			From aquaculture	
	Canary islands	~1999		4		Maximum value	
	Castilla y Léon	2005–2006	6				POSPE (2014)
	Extremadura	2006	42	~40		Maximum value for largest individuals	Junta de Extremadura (2008)
	Guadalquivir marshes	1976–1981			50–100		Gutiérrez-Yurrita et al. (1999)
	Guadalquivir marshes	1982–1991			More than 150		
	Guadalquivir marshes	2007	3000				Junta de Andalucía (2007)
	Guadalquivir marshes	2014		0.4			El Mundo (2014)
	Madrid	~1999		4		Maximum value	Gutiérrez-Yurrita et al. (1999)
	Valencia	~1999		3			

2005c). Control methods are continuously being investigated and improved. For example, the use of a surfactant was proposed to control crayfish activity during the initial rice growth period but was not effective in field trials (Anastácio et al., 2000). Integrated production of crayfish and rice has been proposed as an alternative to mitigate crayfish socioeconomic impact and to control crayfish populations in rice field areas (Anastácio et al., 1995, 1999a,b). Promising results are coming from sexual pheromones: the use of water conditioned by receptive females (Stebbing et al., 2004 with *P. leniusculus*, in UK) or live crayfish (Aquiloni and Gherardi, 2010 with *P. clarkii*, in Italy) proved to be a highly selective bait in attracting sexually mature males into the traps. Problems are the isolation of the decapod pheromones and their chemical characterization to artificially produce them. Recent advances in this direction have been obtained in *P. clarkii* (Piazza et al., 2014). Another available technique is the Sterile Male Release Technique (SMRT, Aquiloni et al., 2009), *i.e.* the release of large numbers of sterile, but sexually active, males into the wild to mate females, who will then produce non-viable eggs. This technique meets all the requirements indicated in literature for an optimum control technique (Holdich et al., 1999; Lodge et al., 2006) and, unlike traditional intensive trapping, the effectiveness of SMRT increases when the population density is low (*e.g.* early stages of invasion). An integrated approach using SMRT and intensive trapping is preferable because of its synergic effect: the trapping immediately reduces the population, enabling selection of the animals for the sterilization by X-rays and, at the same time, increases the probability of sterile males mating with the few remaining females. Recently, the combined use of SMRT and intensive trapping in a small lake in the north-eastern Italy led to a collapse of the *P. clarkii* population of 87% in only two years of activity (Aquiloni and Zanetti, 2014).

While some authors believe that fish predators have no possibility of eradicating an established alien crayfish population and little chance of reducing it, eels introduced into the Rumensee, a small artificial impoundment in Switzerland, substantially reduced an expanding *P. clarkii* population to less than 10% within three years, whereas pike, introduced at the same time, had no obvious effect (Frütiger and Müller, 2002). These authors concluded that the effect of predatory fish is highest if shelter is sparse. Recently, laboratory and field experiments with European eels as potential controllers for invasive crayfish *P. clarkii* in Italy found that eels ambushed small and soft-shell crayfish from behind, and the presence of eels indirectly reduced crayfish trophic activity (Aquiloni et al., 2010). In a closed system in south-eastern France (Camargue)—in which eel population dynamics were assessed by means of a multistate capture–recapture model, and their diet analysed using stable isotope analysis- the invasive crayfish resulted to be their most important prey, and every size-class of crayfish was consumed (Musseau et al., 2014).

4.2. *Aquarium trade with* P. clarkii *as the most sold crayfish: a new threat*

The increasing European and internet trade enhances the risks of transporting live crayfish, indigenous or non-indigenous, from one country to another. Fairs across Europe sell aquarium fish and invertebrates, and there are no cross-border controls. Particularly, the "invertebrates boom" among German aquarium hobbyists since the early 2000s is eliciting great concern, leading to the import of more than 120 NICS, of which approximately 20 are commonly available, including *P. clarkii* (Chucholl, 2013a). Similarly, in Italy Mazza et al. (2015) found a booming internet trade for aquatic species, and the red swamp crayfish is one of the most sold species. Using the Freshwater Invertebrate Invasiveness Scoring Kit (FI-ISK) (Tricarico et al., 2010), four of the common ornamental NICS were rated as high-risk (Fig. 2), *i.e.* they are likely to become invasive once released and to inflict ecological or economic damages; among these high-risk species, *P. clarkii* consistently attained the highest risk rating (Chucholl, 2013a; Papavlasopoulou et al., 2014; Tricarico et al., 2010). Moreover, most of the imported NICS originate from North or Central America and are therefore potential carriers of crayfish plague. Indeed, 27% of screened batches from the Central European aquarium trade included crayfish individuals infected with crayfish plague (Mrugała et al., 2014) including *P. clarkii*.

The popularity of NICS, as assessed by availability in the trade, as well as size were identified as the major determinants of the likelihood of release, with large species that are widely available through the aquarium trade being most likely to be introduced into nature (Chucholl, 2013b). The red swamp crayfish fits both criteria and releases from aquaria and escapes from garden ponds have become a new, ongoing introduction pathway for this invasive species in Germany and Austria (Chucholl, 2013a; Dehus et al., 1999; Dümpelmann et al., 2009). This invasion risk also applies to other European countries, because *P. clarkii* is one of the most common and widespread crayfish species in the European aquarium trade (Chucholl, 2013a; Mazza et al., 2015; Papavlasopoulou et al., 2014; Patoka et al., 2014; Peay et al., 2010). The situation is different in the North American pet trade: *P. clarkii* is prevalent and often auctioned, but less often sold than three other species, perhaps because it is more expensive (Faulkes, 2015). This popularity is mostly driven by the species' appealing coloration (including blue, orange, white and mixed color varieties bred specifically for the ornamental market), undemanding nature and prolific breeding habits. The latter traits, however, also imply that *P. clarkii* can easily overpopulate aquaria, which promotes discard of unwanted crayfish or excess stock into nature.

Since the risk of introduction into nature is directly related to species' availability (Chucholl, 2013b), a drastic reduction of the availability of high-risk species, including those carrying crayfish plague, has been repeatedly suggested (Chucholl, 2013b; Mrugała et al., 2014; Patoka et al., 2014).

5. Climate change and predicting the impact of *P. clarkii*

Climate change and invasive alien species (the so called "double trouble"; Mainka and Howard, 2010) can act synergistically on imperilling native species and ecosystems. In particular, climate change can facilitate species introduction, colonization and successful reproduction, allowing their persistence and spread (Walther et al., 2009), particularly for warmer alien species as *P. clarkii*. In addition to being vectors of crayfish plague (Diéguez-Uribeondo and Söderhäll, 1993), it can adversely impact on the aquatic environments due to rapid growth, feeding habits, burrowing activities (Souty-Grosset et al., 2014) and dense populations, and will be further favoured by climate change (Capinha et al., 2013; Gherardi et al., 2013). Climate warming can also increase its competitiveness. Gherardi et al. (2013) analysed the agonistic behaviour of pairs composed by similarly sized males of the combinations of three alien species: *O. limosus*, *P. leniusculus*, *P. clarkii*, at two different temperatures (20° and 27° C). While the first two species reduced their agonistic behaviour at the higher temperature (*O. limosus* spent more time motionless and *P. leniusculus* was more often the subordinate), *P. clarkii* still showed the same aggressiveness, outcompeting both species, and confirming that the red swamp crayfish will dominate the ecology of future European water basins.

The red swamp crayfish is highly adapted to oscillating water levels and hydrological intermittence. It has strong burrowing capabilities (Correia and Ferreira, 1995) that allow for survival during periods of drought – facilitating its invasion into harsh environments – and it is very tolerant to desiccation during exposure to air (Banha and Anastacio, 2014). The predictable future scenarios of increasing frequency and intensity of extreme events causing hydrological intermittence (IPCC, 2013) may in fact promote the frequency of overland dispersal events of *P. clarkii*. This species exits the water searching for new areas during the first rains after strong decreases of water level (Ramalho and Anastácio, 2015). Capinha et al. (2012) demonstrated that climate change might have large effects on the distribution of native European crayfish species, by causing range contractions and promoting greater sympatry with crayfish-plague-transmitting North American crayfishes. Only *P. clarkii* was predicted to increase its European distribution in the future, thus possibly enhancing its impacts if no management measures are promoted and confirming the scenario forecast by Liu et al. (2011). On the contrary, in the Iberian Peninsula, the first area of introduction in Europe, projections for future suitable areas for *P. clarkii* under climate change scenarios show moderate modifications, with a decrease in 2080, mostly in the interior of the Iberian Peninsula (Capinha et al., 2012).

6. The urgency of a unified, strengthened legislation in europe for controlling the red swamp crayfish

Across Europe the overwhelming vector for invasive crayfish is humans, who may translocate crayfish to establish a new fishery

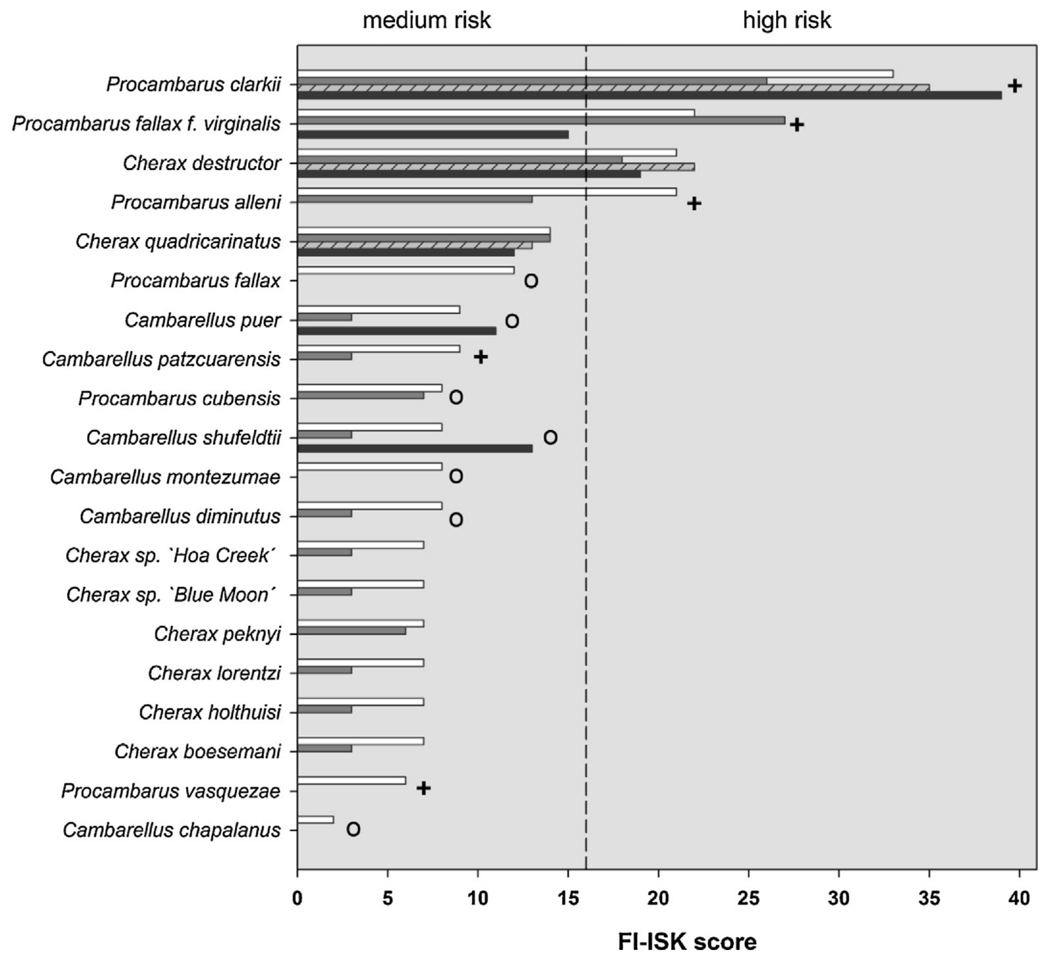

Fig. 2. Potential invasiveness of 20 commonly available Non Indigenous Crayfish Species (NICS) in the European aquarium trade, as assessed by an invasiveness screening tool (FI-ISK), per reference country. White: Germany (Chucholl 2013b), grey: Czech Republic (Patoka et al., 2014), grey hatched: Greece (Papavlasopoulou et al., 2014), and black: Italy (Tricarico et al., 2010). The vertical dashed line represents the threshold, above which species are considered as high-risk (Tricarico et al., 2010). ' + 'denotes known carriers of crayfish plague (Mrugała et al., 2014) and 'oí denotes potential carriers due to North or Central American origin (Chucholl, 2013b).

(Britain, Sweden) and/or buy crayfish on the web for home aquaria, and then dump surplus unwanted crayfish into the nearest pond or stream (Germany and adjacent countries). In Europe, several laws protect indigenous crayfish by banning imports of NICS and/or regulating their use (Holdich and Pöckl, 2005). The commercial value of the red swamp crayfish varies across Europe, and harvesting may be encouraged or prohibited depending on its perceived impact.

In Spain, sale of live red swamp crayfish is allowed (Vedia and Miranda, 2013). In Portugal, this is forbidden by law (Decreto-lei 565/99): in this law, *P. clarkii* is considered an invasive species with well-known impacts. Annual restocking, an essential step in crayfish production, is currently forbidden. Additionally, the species should be subjected to a national control program although this has never been implemented. Although it is not allowed to trade or transport live individuals of this species, this is very frequent, mainly with exports of live individuals to Spain. Unfortunately, a control or eradication program in Portugal would always be unsuccessful on a long term, since the species would spread from Spain where the legislation is much less restrictive and there is a legal trade of the species.

In Italy, the law forbids the release of invasive species into natural water bodies (D.P.R. 120/2003) but no control and/or penalty are foreseen. About fishery, each region (20) has its own fishery laws and each province (110) its regulation. Overall, fishing alien crayfish is allowed, while releasing the caught crayfish in the wild is forbidden. Transport of alive alien crayfish is forbidden only in very few provinces.

In France, the red swamp crayfish is considered as a species capable of causing biological disequilibrium (Article R-232-3 of the Environmental Code). The law therefore prohibits the importation, transportation and marketing of live crayfish (decree of 21 July 1983).

In the U.K, there are differences, not necessarily well understood by the public, in the regulation and policy regarding crayfish in the four constituent countries. Live crayfish could be taken from areas where they can be legally caught or sold for food, to Ireland or Scotland, where keeping or sale is completely banned, or to areas of England and Wales currently free from non-native crayfish. In Northern Ireland, where *A. pallipes* is protected, alien crayfish are banned from sale, and there are no known wild populations of alien crayfish. It is an offence to introduce any non-native crayfish into the wild, although the ban does not concern introductions for food or private collections. According to the Wildlife and Countryside Act 1981 in England, Wales and Scotland "it is an offence to release or to allow the escape of the alien crayfish into the wild".

In Germany, according to the Federal Nature Conservation Act, *P. clarkii* is considered invasive. Fishery laws of the federal states prohibit its introduction into the wild (however, the situation is unclear for private water bodies, such as garden ponds); harvest is not restricted (no minimum legal size or closing season) but requires a fishing licence. Import and trade are not regulated.

In the Netherlands, Soes and Koese (2010) reviewed the most relevant Dutch legislation concerning invasive crayfish. Fisheries law 1963 [Visserijwet 1963] regulates which fish as well as some molluscs and crustaceans can be harvested and released. No crayfish are included in the fisheries law list, which came into force on January 1, 1983. It is not allowed to release into the wild crayfish for commercial exploitation, but it is not forbidden to harvest crayfish. However, because fishing gear is needed to harvest crayfish, it is still not allowed to harvest crayfish without a licence for using gear. For exotic species, Article 14 of the Flora and Fauna law states that it is prohibited to release animals or eggs of animals into the wild. However, this article states also that the prohibition does not apply to those fish included in the list of the Fisheries law 1963.

In Belgium (Delsinne et al., 2013), despite the prohibition of importation, trade and holding alien crayfish, the species is already spreading in the country (especially in the Flemish Region), and natural spreading from neighbouring countries is expected since dense populations are now close to the Belgian border. Nevertheless, such measures can certainly limit secondary releases in the environment, slow down its current spread and prevent colonization of some natural districts of the country.

Most EU countries now ban importation of live crayfish. However, a unified, strengthened legislation should be established in Europe to ensure a total ban on import, trade and holding of live *P. clarkii*. At the European level, in 2015, each Member State has adopted the recent aforementioned EU Regulation 1143/2014 on invasive alien species. This new regulation follows the hierarchical approach (prevention; early detection and rapid response; control/eradication and mitigation) recommended by the Convention on Biological Diversity in 2002 for invasive alien species. Prevention includes risk assessment protocols, control of pathways, regulations and increase of public awareness. The risk analysis aims at identifying potentially invasive species and assessing risks associated with those species. The outcomes of this process are intended to inform decision-makers of potential risks, leading either to a prohibition of use (and thus to draft a list of forbidden species) or to a management program to mitigate species impacts. Using the Freshwater Invertebrate Invasiveness Scoring Kit (FI-ISK), Tricarico et al. (2010) screened several crayfish species and found that *P. clarkii* reached the highest risk score together with *Pacifastacus leniusculus*, confirming thus its great invasiveness. Recently, Copp et al. (2014a, 2014b), developing the ENSARS (European Non-native Species in Aquaculture Risk Analysis Scheme) which contains protocols for evaluating all the risks associated with the cultivation of alien species (species biology, pathway, infectious agents, impacts), scored the red swamp crayfish among the moderately high risk species. Whatever the protocol of risk assessment used (*e.g.* GABLIS, HARMONIA, GISD, GISS IUCN, ISEIA, Blackburn et al., 2014; Vanderhoeven et al., 2015), the species ranks as highly invasive for Europe, as demonstrated by high scores of risks, or by the suggestion to insert it in the black list at the end of the protocols (E. Tricarico, pers. comm.).

The risk assessment protocols are part of EU Council Regulation 708/07 "concerning use of alien and locally absent species in aquaculture" (implemented with the Commission Regulation No 535/08), in force since 2009 (European Parliament 2007, 2008). In this regulation, the novelty is the "white list" approach, in that only importation of species that have been appropriately screened after a thorough risk assessment analysis can be approved for cultivation. A white list is indeed attached to the regulation but no alien crayfish is included. Risk assessment analysis is also considered in EU regulation 1143/2014 as a tool to draft a black list of invasive alien species of Union/Member State concern for which management actions are required. Recently, the first draft of the species of Union concern has been developed (and it is expected to enter in force for the beginning of 2016), and *P. clarkii* is included, following completely the criteria listed in the article 4 of this EU regulation. This means that each member state is obliged to conduct control activities on this species to accomplish the Regulation or penalties are expected. The regulation also foresees the identification of pathways of introduction as well as the draft of action plans to control them (article 13). For *P. clarkii*, the main identified pathways are aquaculture (already controlled by EU regulation 708/2007) and aquarium trade: Such legal action should be accompanied by other, in part already ongoing, risk mitigation efforts, such as customer education, self-regulation of the aquarium trade, and raising risk awareness of the public.

The need for trade regulation of NICS at the EU level is also evident in the case of the related Marmorkrebs (*Procambarus fallax* f. *virginalis*), whose establishment success in five EU member states is entirely driven by ongoing propagule pressure from the aquarium trade (Chucholl, 2014; Samardžić et al., 2014; Vojkovská et al., 2014). For aquarium trade, no regulatory framework is in force, but only a recommendation on a Code of Conduct on Pets and Invasive Alien Species (Recommendation n. 154/2011). The main problem today is that trade of alien crayfish occurs mainly through the Internet which cannot be easily controlled and managed. According to the EU regulation 1143/2014 (articles 14, 19), in 2016 each Member State should establish a surveillance system for early detection and rapid response, and have in place effective management measures for the invasive alien species of Union concern.

7. Conclusions

The direct impacts of the red swamp crayfish on fauna and flora cause indirect effects on the ecosystem through trophic cascades. *P. clarkii* alters benthic invertebrate community structure with differing functional effects, often mediated via trophic cascades: for example, the introduction of *P. clarkii* to Lake Chozas (Spain) caused a reduction of macrophyte plant coverage by 99% which in turn caused 71% loss in macroinvertebrate genera, 83% reduction in amphibian species, 75% loss in duck species, and 52% reduction in waterfowl (Rodríguez et al., 2005). Recently, Jackson et al. (2014) observed that red swamp crayfish predation upon snails evidently promoted benthic algal standing stock via reduction in grazing pressure. However, a trophic cascade whereby the crayfish consumed native invertebrate shredders, causing a reduction in net leaf litter decomposition, was decoupled by red swamp since crayfish consumed leaf litter directly.

From all the studies analysed at a management level, *P. clarkii* is considered as (i) a burrower in the water drainage systems in southern and central Europe (ii) an agricultural pest in Mediterranean territories, consuming, for example, young rice plants, and (iii) above all a threat to the restoration of water bodies in northwestern Europe.

Concerning the problem of well-established populations of the red swamp crayfish, Condé and Domínguez (2015) suggest compromise measures in order to reconcile its economic exploitation and environmental concerns in Iberian Peninsula, selling live males from monosex cultures and processed females (boiled, canned or packed) in order to stop further invasions. The transformation of *P. clarkii* into an economic resource with minimum environmental hazard seems feasible, but only in certain areas, such as Portugal, where it is already present in every river basin (while native crayfish are no longer present). However, in territories where indigenous crayfish species (ICS) are still present, such as Spain, Italy, and France, *P. clarkii* can carry the crayfish plague to native specimens, as it seems difficult to ensure they are completely free from any pathogens. Consequently, decisions are urgently needed to control the spread of both *P. clarkii* and *A. astaci* for the conservation of indigenous crayfish biodiversity.

A constant update of the species status is also essential, and new communication tools, like smart phones, and the role of internet social networks provide good and effective means for this. The priority is to (i) reduce the new introductions in the field (ii) increase the general awareness on alien crayfish, including their role in aquatic environments (iii) promote the conservation and social values of native species and their threats. Attitudes towards introduction and eradication can depend on a combination of several factors, such as stakeholder interest, personal socio-demographic characteristics, environmental behaviour and personal experience (García-Llorente et al., 2008). For example, in Doñana national park (Spain) people are aware of the red swamp crayfish and its impacts, but fishermen are less willing to contribute to eradication because of the economic benefits coming from its sale.

Finally, since recent years, the red swamp crayfish is widely available through the aquarium trade and on the internet and is a popular pet in many countries in Western and Eastern Europe. Indeed the new difficult challenge is to reinforce the awareness of this internet based trade within the European Community while import and trade regulations should be imposed to reduce the availability of this high-risk species throughout Europe. For better management of such an invasive species, the EU Regulation 1143/2014, Article 19, specifies that the commercial use of invasive alien species already present can be temporarily allowed under management measures for eradicating them, regulating their population or their confinement, but only if it is strictly justified and that all controls suitable are in place to prevent their further spread.

Notwithstanding the complexity of the problem to face and the strong limitation of the means to do it, we are confident that the solution will only arise through a constant and constructive exchange of information and practice between policy makers, managers and scientific researchers.

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