

Red swamp crayfish: biology, ecology and invasion - an overview

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ABSTRACT - Alien species have been transported and traded by humans for many centuries. However, with the era of globalization, biological invasions have reached notable magnitudes. Currently, introduction of alien species is one of the major threats to biodiversity and ecosystem functioning. The North American crayfish *Procambarus clarkii* is one of the most widely introduced freshwater species in the world, especially due to its high economic importance. It is responsible for great modifications in invaded environments causing irreparable ecological and economic damages. Its impressive ability to successfully colonize a wide range of environments is a consequence of its behavioural and biological characteristics that can adapt to features of the invaded location, conferring to this species a notable ecological plasticity. This review summarizes the available information regarding *P. clarkii*'s biology and invasive dynamics around the world in order to contribute to the understanding of the threats posed by its establishment, as well as to support management and impact mitigation efforts.

Key words: Alien biology, Exotic crayfish, Red swamp crayfish, Invasive features, Impact, Invasion management

INTRODUCTION

Human activities such as agriculture, aquaculture, recreation and transportation promote the spread of species across their natural dispersal barriers, a process which has been accelerated due to globalization. Species translocation may be intentional or accidental although most organisms die during the transport or soon after their release. Species that became invasive are those that persist, become established and cause negative effects on human health, economy, native biodiversity and ecosystem function (Kolar and Lodge, 2001).

Indeed, alien species introduction is one of the major threats to biodiversity and ecosystem functioning (Carlton, 1996; Lodge *et al.*, 2000). Some of the best known invasive freshwater alien species are the zebra mussel, *Dreissena polymorpha* (Pallas, 1771), the Asian clam, *Corbicula fluminea*

(Müller, 1774), the Nile perch *Lates niloticus* (Linnaeus, 1758) and the red swamp crayfish, *Procambarus clarkii* all of which have greatly affected rivers and lakes worldwide (Nalepa and Schloesser, 1993; D'Itri, 1997).

Procambarus clarkii, also known as red swamp crayfish or Louisiana crawfish, is native to northeastern Mexico and the southern USA; it has been introduced in all continents except Antarctica and Oceania, being now considered the most cosmopolitan freshwater crayfish species in the world (Hobbs, 1988; Gutiérrez-Yurrita *et al.*, 1999; Lindqvist and Huner, 1999; Gherardi, 2006; Chucholl, 2011). In a general way, this species shows good tolerance to a wide range of environmental conditions, elevated adaptive capacity, high growth rate and flexible feeding strategy (Hobbs *et al.*, 1989; Gutiérrez-Yurrita *et al.*, 1999; Alcorlo *et al.*,

2004; Souty-Grosset *et al.*, 2006; Gherardi, 2007), features that favour its establishment in new available habitats.

One of the biggest challenges to understand and predict biological invasions lies in understanding which biological and ecological characteristics might favour the colonization and establishment of exotic species in new areas as well as post-establishment patterns of spread, and how invasive species can outcompete native species. Thus, the present review aims to summarize and update existing information about the ecology, biology and invasive dynamics of *P. clarkii* around the world. Understanding of the invasion process in different countries and habitats as well as comprehending the characteristics of the species that might favour its successful invasions can help managers to recognize the potential threats that this species poses to newly invaded ecosystems and to support management and impact mitigation efforts.

This paper is divided into eleven sections that cover various aspects of *P. clarkii*'s systematics, life history, physiology, and ecology, as well as impacts observed in invaded areas. The review encompasses the traditional peer-reviewed literature, but also includes information available on reports and on the World Wide Web.

MORPHOLOGICAL ASPECTS

Procambarus clarkii's body, as a typical decapod crustacean, is divided into cephalothorax and abdomen, both parts having appendages following the decapod pattern (Hobbs, 1974). The abdominal appendages called pleopods are not always present in decapod males, but in this species, they are present in both males and females (Hobbs, 1974). The thoracic appendages (pereiopods) are five in number, as usual, but the first 3 pairs are chelate, which is a characteristic of the infraorder Astacidea (Taylor, 2002; Crandall and Buhay, 2008; Gherardi *et al.*, 2010). The carapace color is dark red, orange or reddish brown, although blue, yellow, white and black varieties are known (Gherardi, 2011); chelae are typically red on both surfaces. Juveniles are usually light green with a narrow dark band on either side of the abdomen and a broader lighter band along the dorsal surface. Adult specimens can measure up to 15 centimeters of total length, although most individuals are up to 12 centimeters (Henttonen and Huner, 1999).

This species presents external sexual dimorphism and sex can be distinguished by the position of the genital pores. The genital openings are located on the coxopodite of the third pair of pereiopods in females and on the fifth pair of pereiopods in males (Holdich and Lowery, 1988). Moreover, males have a copulatory organ formed by a modification of the first and second pair of pleopods (Fig. 1A) whereas in females the first pair of abdominal appendages is vestigial and the second has no modification (Fig. 1C) (Sukô, 1953; Huner, 1981).

Likewise most crayfish species, *P. clarkii* has sexual reproduction. Sexual maturity is reached in approximately three months and, depending on climate, it may produce two or three generations per year (Dörr *et al.*, 2006). In adult males, two different morphotypes that alternate between each other can be observed: the reproductive form or type I male, with hooks on the ischia of the 3rd and 4th pereiopods and more calcified copulatory organs (Fig. 1A), and the non-reproductive form or type II male, in which hooks are lacking (Fig. 1B) (Taketomi *et al.*, 1990; Henttonen and Huner, 1999). This morphotype alternation in males is a characteristic of the family Cambaridae (Hobbs and Jass, 1989). An adult male might remain as type I for up to 9 months in a year. *Procambarus clarkii* females, on the other hand, have no morphological alteration during reproductive phase and the only different characteristic is an increase in its receptivity to males, which might happen more than once a year depending on environmental characteristics (Sukô, 1953).

REPRODUCTION

The knowledge of the reproductive strategy of invasive species is central to the understanding of its invasion ecology as it determines the potential for population increase and range expansion. In *Procambarus clarkii*, mating period, as well as recruitment and sexual maturation, vary according to hydrographic period and environmental conditions (Sommer, 1984; Alcorlo *et al.*, 2008) and therefore, due to the combined effects of these factors, reproduction may change after the species is introduced into different regions.

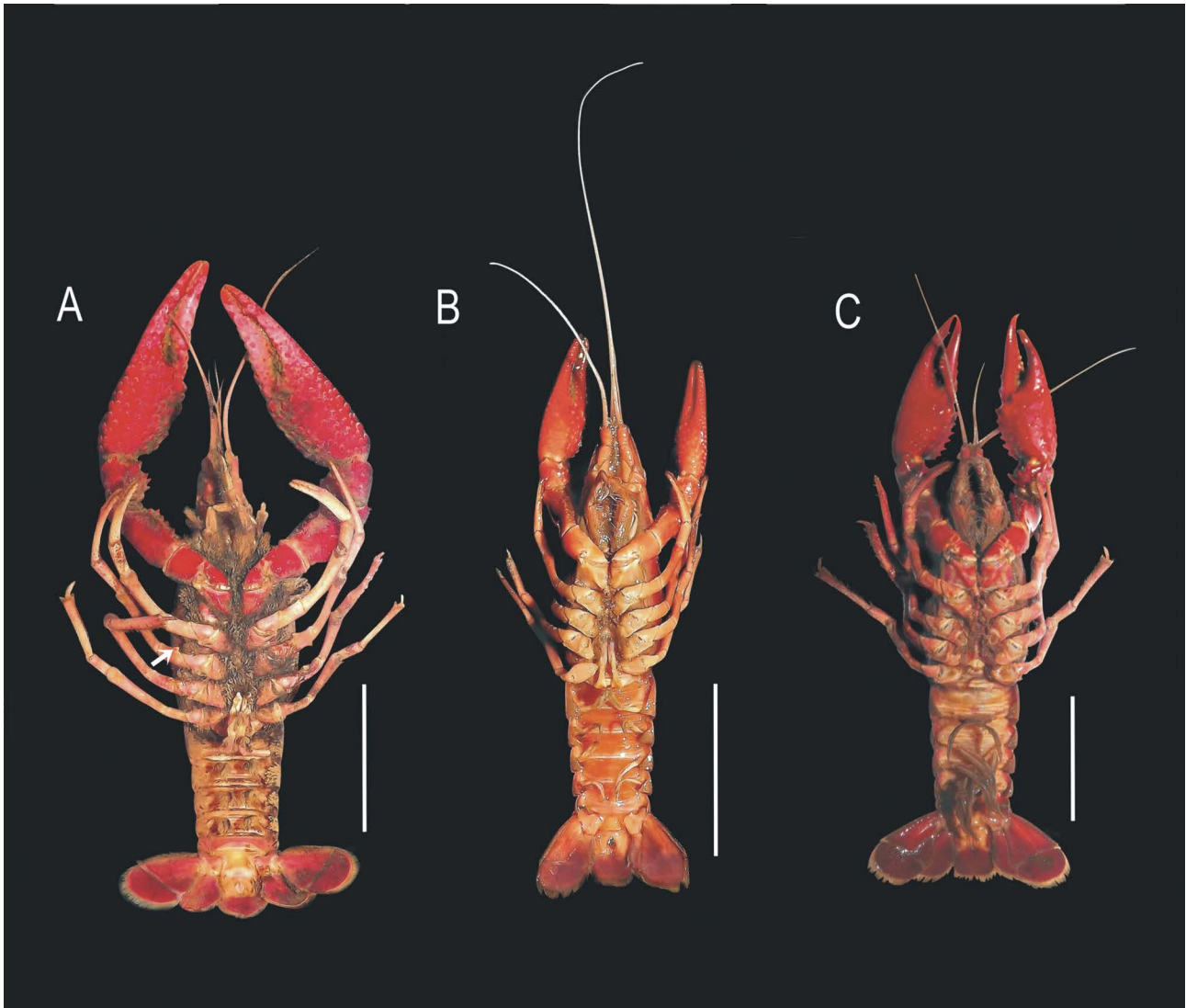


Figure 1. Ventral view of *Procambarus clarkii* individuals. A: Morphotype I male (reproductive form) showing the more calcified copulatory organ and the copulatory hooks on the 3rd and 4th pereopods' ischia. B: Morphotype II male (non-reproductive form) without the copulatory hooks and softener copulatory organ. C: Female showing the first pair of abdominal appendages which is vestigial and the *annulus ventralis*. Scale bars = 2 cm.

Reproduction is regulated by pheromones perceived by receptors located on the antennae which are responsible for interspecific and intraspecific recognition and behavioural modulation (Ameyaw-Akumfi and Hazlet, 1975). After sex recognition, male courts female through a specific sequence of movements followed by copulation, when the male turns the female with her dorsal surface against the substrate, holding her chelipeds and both ventral regions remain in contact. Thereafter, male deposits the spermatophore in the *annulus ventralis* (not in the genital pore) (Fig. 1C), which is the female's sexual receptacle, located between the bases of the posterior walking legs (Ameyaw-Akumfi, 1981; Gherardi *et al.*, 2010).

Days, weeks or months after mating, depending on environmental conditions, the female safeguards herself in a burrow and starts oviposition; this process may occur in open water but this is very uncommon (Holdich and Lowery, 1988). The number of eggs per brood may reach up to 700 (Penn, 1943; Noblitt *et al.*, 1995) although it depends on female size and is also related to water temperature, population density and the length of the hydroperiod (Alcorlo *et al.*, 2008). The embryonic development time depends on atmospheric temperature and may be inhibited under 10 °C (Sukô, 1953). After hatching, juveniles are kept under the female's abdomen for three weeks (Holdich and Lowery, 1988).

TROPHIC ECOLOGY

Procambarus clarkii is a generalist omnivore species whose opportunistic diet favours its own successful establishment in different types of water bodies (Gutiérrez-Yurrita *et al.*, 1999). Despite the fact that its diet in natural habitats is not widely studied, much information has been collected in its invasive range (D'Abramo and Robinson, 1989; Feminella and Resh, 1989; Ilhéu and Bernardo, 1993; 1995; Gutiérrez-Yurrita *et al.*, 1998; Alcorlo *et al.*, 2004). They are reported to feed on plant and animal detritus, macrophytes and live animals such as molluscs, insects, annelids, nematodes, platyhelminthes, tadpoles and fingerlings (Fig. 2) (Huner and Barr, 1991; Ilhéu and Bernardo, 1993; 1995; Gutiérrez-Yurrita *et al.*, 1998; 1999; Parkyn *et al.*, 2001; Correia, 2002; Buck *et al.*, 2003; Cruz and Rebelo, 2005).

Regarding *P. clarkii*'s predators, the most widely cited in literature are fishes, birds and mammals like otters and capybaras (Delibes and Adrián, 1987; Holdich and Lowery, 1988); juveniles can also be eaten by odonate nymphs, coleopteran larvae and aquatic hemipterans (Fig. 2) (Gydemo *et al.*, 1990).

Invasive species might bring exotic diseases that can reach much higher severity than in its native distribution area (Fig. 2). By far, the most known and studied pathogen of *P. clarkii* is the parasitic Oomycete *Aphanomyces astaci*, the causative agent of crayfish plague, which is lethal to many species of crayfish (Alderman and Polglase, 1988; Holdich *et al.*, 2009). This pathogen initially infects the exocuticle and after the endocuticle; in more susceptible species or individuals, it penetrates the basal lamina, underneath the epidermis cell layer and spreads throughout the body, invading connective tissue and blood vessels (Cerenius *et al.*, 1988). *Aphanomyces astaci* does not produce sexual structures, with transmission occurring via zoospores released from infected animals and it is able to survive for several days in water and several weeks in mud (Alderman and Polglase, 1988; Diéguez-Uribeondo *et al.*, 1995; Edgerton *et al.*, 2002). Besides *A. astaci*, another parasitic fungus that can infests *P. clarkii* carapace and constitute a threat to other crustaceans is *Saprolegnia parasitica* (Diéguez-Uribeondo *et al.*, 1994).

The great threat posed by the introduction of *A. astaci*, was the trigger to initiate studies on freshwater crayfish pathology in the mid-1900s and this organism has become one of the most

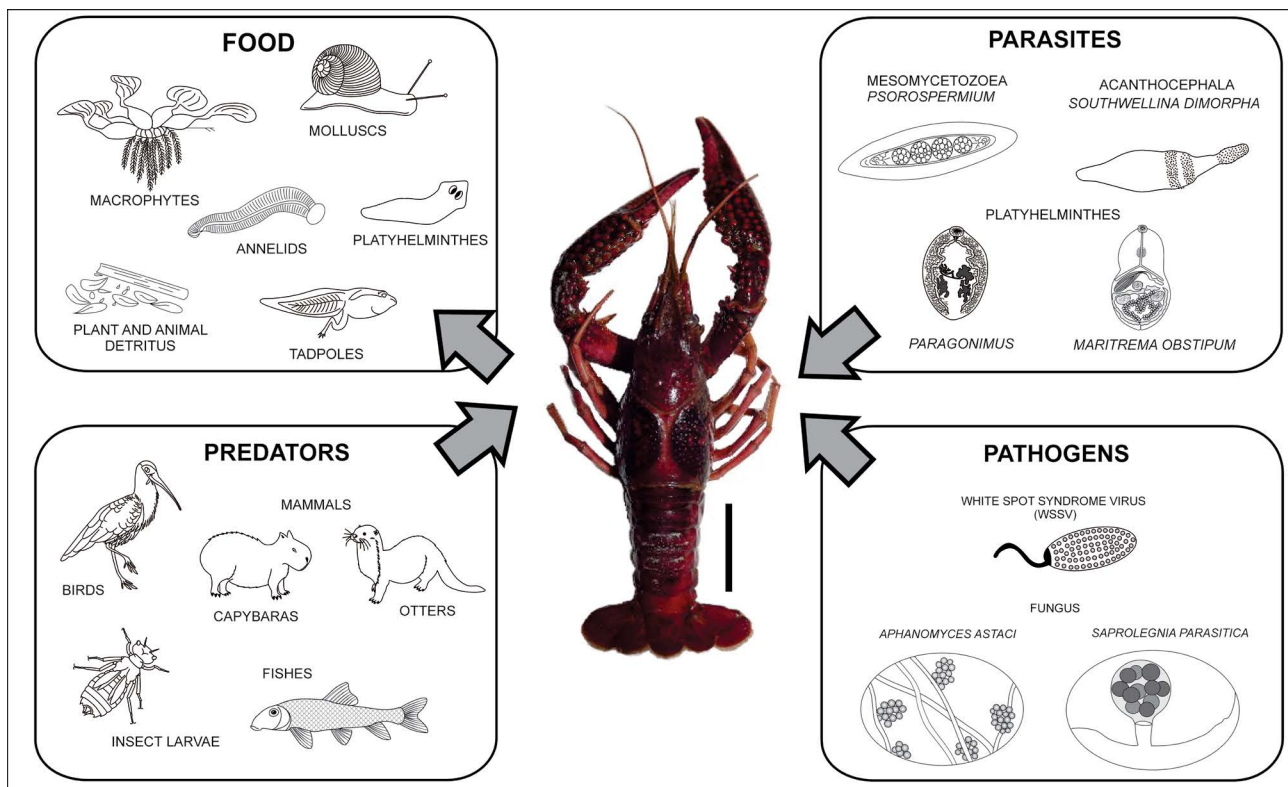


Figure 2. Trophic ecology and biotic relationships of *Procambarus clarkii* regarding food items, predators, pathogens and parasites.

intensively studied of all invertebrate infectious diseases (Alderman and Polglase 1988). However, *P. clarkii* may host many other parasites, pathogens and symbionts that are not as much studied as *A. astaci*, although some of them may affect human health.

Among viruses, the White Spot Syndrome Virus (WSSV) is perhaps the most devastating of all crustacean viruses. WSSV has a very wide host range, including *P. clarkii* (Chang *et al.*, 1998; Baumgartner *et al.*, 2009). Bacterial infections are also very common and can be developed by a variety of Gram positive and Gram negative forms that can inhabit their external exoskeleton, gut and frequently the haemolymph (Thune, 1994). One of the most studied bacteria that affects *P. clarkii* is *Vibrio mimicus* (Thune, 1991) and it is recognized as a cause of gastroenteritis in humans when feeding on contaminated raw crayfish (Mac Eachern, 2010).

Regarding Platyhelminthes, digeneans are the most common parasites of *P. clarkii*. Within Paragonimidae, species from *Paragonimus*, highly evolved parasites with a complex life cycle that involves at least three different hosts, i.e., snails, crustaceans, and mammals, are known to use crayfish species, including *P. clarkii*, as intermediate hosts (Sogandares-Bernal, 1965); the adults of *Paragonimus* reside and mate in the lungs of a variety of mammalian hosts, wild and domestic animals, as well as humans, causing a disease named paragonimiasis (Lane *et al.*, 2009; Procop, 2009).

Some digeneans also may use *P. clarkii* as intermediate host, for example: some species of *Microphallus* (Microphallidae), whose adults parasitize bird and fish species, being larvae cercariae maybe found in the hepatopancreas of *P. clarkii* (Overstreet *et al.*, 1992); *Maritrema obstipum* (Van Cleave and Mueller, 1932) (Microphallidae), whose definitive host are birds and mammals and intermediate host maybe freshwater crustaceans and snails, being larvae cercariae found in the gills and hepatopancreas of *P. clarkii* (Etges, 1953; Longshaw, 2011); *Sogandaritrema progeneticum* (Sogandares-Bernal, 1962) (Microphallidae) that parasitizes some crayfishes, including *P. clarkii* (Sogandares-Bernal, 1965; Lotz and Corkum, 1983); *Gorgoderia amplicava* (Looss, 1899) (Gorgoderidae), whose definitive host are some anuran species, may use

freshwater bivalves from de family Sphaeriidae and crustaceans as intermediate host. The immature form of *G. amplicava* can be found in the stomach of *P. clarkii* (Longshaw, 2011). Another example is *Macroderoides typicus* (Winfield, 1929) (Macroderoididae) that uses the freshwater fish bowfin, *Amia calva* Linnaeus, 1766, as definitive hosts and freshwater gastropods and crayfishes as intermediate hosts. In *P. clarkii*, cysts have been observed in the cephalothorax and antennae (Longshaw, 2011).

Acanthocephalans are obligate parasites that require usually two hosts, an invertebrate and a vertebrate. Typically, the invertebrate host is an insect or a crustacean and the vertebrate hosts can include mammals, birds and fish. These helminths are not considered significant pathogens of freshwater crayfish. However, when there is a high prevalence of infection, crayfishes might become stressed and more susceptible to other diseases (Amin, 1998). *Southwellina dimorpha* (Schmidt, 1973) (Polymorphidae) is the most studied acanthocephalan observed in *P. clarkii* and its cysts are in the anterior portion of the crayfish abdomen, usually attached along the intestine (Lantz, 1974; Alderman and Polglase, 1988).

Procamburus clarkii is also vulnerable to microsporidians, intracellular parasites belonging to the Phylum Microspora (Alderman and Polglase 1988). One example is *Thelohania contejeani* (Henneg, 1892), that has caused mass mortalities of crayfish in Europe (Alderman and Polglase, 1988; Dunn *et al.*, 2009; Edgerton *et al.*, 2002). Another known disease is psorospermiasis, caused by *Psorospermium* (Mesomycetozoa) that colonizes gills, hepatopancreas, antennal gland, connective and neural tissues, ovary membranes and cardiac and skeletal muscle (Hennton *et al.* 1994; Ragan *et al.*, 1996; Longshaw, 2011).

Additionally, a range of ectocommensals or ectosymbionts from a number of different Phyla can infest the crayfish exoskeleton, including gills. Most of them are temnocephalans (Platyhelminthes, Temnocephalida) that usually are not pathogenic to crayfish, however, they may impair proper gill functioning if present in such high numbers as to impede water flow in the gill cavity (Edgerton *et al.*, 2002). No temnocephalans were reported on *P. clarkii* but considering their wide range of occurrence among crayfishes (Edgerton *et al.*, 2002; Longshaw, 2011), it is

believed that the Red Swamp Crayfish might also be infested by them. Branchiobdellidans (Annelida, Clitellata) may also be observed on crayfishes, including *P. clarkii*, but infestations usually take place only when individuals are already ill; infested healthy animals are rarely found (Gelder *et al.*, 1999). Temnocephalids are predominantly found in the southern hemisphere and no branchiobdellid species occur naturally in the southern hemisphere (Holt, 1975) although both groups have been found outside their native range, as well as many other crayfish diseases, due to anthropogenic movements of the crayfish host (Gelder, 1999; Volonterio, 2009).

BEHAVIOUR

Different behavioural characteristics may contribute to the invasive potential of species; aggressive behaviour, for example, may influence competitive displacement of native species (Dick *et al.*, 1995; Gamradt *et al.*, 1997; Usio *et al.*, 2000), locomotion and dispersal ability can influence rates of spread and spatial patterns of invasion (Johnson and Carlton, 1996; Lewis, 1998), burrowing behaviour might help coping with environmental stress (Gherardi, 2001) and parental care can improve reproductive fitness by increasing brood survival (Marchetti *et al.*, 2004).

Procambarus clarkii is a social animal with formation of social dominance hierarchies in adults and juveniles (Figler *et al.*, 1995; Issa *et al.*, 1999). Little is known about how the hierarchical relationship forms over time and is subsequently maintained, despite some evidences shown by Figler *et al.* (1995) where dominance seems to be size-based. High levels of aggressiveness, experience of winning and attacking or approaching first also may contribute to the formation and maintenance of a dominant hierarchy (Bovbjerg, 1956; Lowe, 1956; Copp, 1986; Issa *et al.*, 1999).

This species is defined as nocturnal (Gherardi, 2001) although some individuals were observed performing long displacements both by day and by night (Gherardi and Barbaresi, 2000; Barbaresi *et al.*, 2004). Regarding its locomotion, home-range faithfulness and dispersal abilities, some findings have been controversial, which might indicate that behaviour varies according to environmental characteristics. According to Gherardi and Barbaresi (2000), *P. clarkii*

specimens are capable of major usage of space, moving up to 4 km·day⁻¹. Gherardi *et al.* (2002b) found that locomotory speed is significantly correlated with crayfish size and the extent of locomotion is variable, ranging from 1 to 11 m·day⁻¹; in this study, neither speed nor distance walked were related to gender. Barbaresi *et al.* (2004), on the other side, showed that both sexes disperse although males and females use space differently, females being more nomadic than males.

The movement pattern seems to be complex, with one or more short peaks of intense locomotion (“wandering” phases) alternated with periods of scarce mobility, with slow speeds or no movement (“stationary” phases) (Gherardi and Barbaresi, 2000; Gherardi *et al.*, 2000; Gherardi *et al.*, 2002a; Barbaresi *et al.*, 2004; Aquiloni *et al.*, 2005).

Like many crayfish species, *P. clarkii* is an efficient digger which uses a combination of tactile and visual information, together with environmental use of cues (i.e. humidity cues) to orientate its burrowing behaviour; burrows are used as refuge to avoid predation, dehydration and environmental stress as well as to nest (Huner and Barr, 1991; Barbaresi and Gherardi, 2006). However, despite the great importance of these shelters, individuals seem not to return to previously occupied burrows at the end of their foraging excursions despite the time and energy expended to excavate them (Barbaresi and Gherardi, 2006).

This species, like most freshwater crayfishes, shows relatively complex parental care (Figler *et al.*, 1995; 1997; Vogt and Tolley, 2004). Mothers often remain in their burrow for many weeks as they execute few cleaning and feeding acts; hatchlings and young remain attached to mother’s abdomen for 3 to 4 months (Huner and Barr, 1991; Huner, 1994). This behaviour, despite being costly, increases reproductive fitness by augmenting brood survivorship and therefore improving the colonization capability of the species.

GENETICS

Genetic analyses of *Procambarus clarkii* populations are being carried out around the world, using different molecular markers

Table 1. Studies regarding *Procambarus clarkii* genetics evidencing the locality investigated, number of populations, whereas this populations are native or invasive, genetic marker used and authors.

Locality	n° populations	Status	Genetic marker	Author
Italy	4	invasive	RAPD (DNA)	(Barbaresi <i>et al.</i> , 2003)
Portugal	1	invasive		
USA	1	native		
Mexico	1	native	mtDNA (CO1), microsatellites (PcLG-07, PcLG-15, PcLG-26, PcLG-28, and PcLG-37)	(Barbaresi <i>et al.</i> , 2007)
Spain	1	invasive		
France	1	invasive		
Portugal	1	invasive		
Italy	6	invasive		
Switzerland	1	invasive		
China	6	invasive	microsatellites (PCL02, PCL06, PCL11, PCL17, PCLG03, PCLG07, PCLG09, PCLG13 and PCLG17)	(Yue <i>et al.</i> , 2010)
USA	1	native	mtDNA (CO1), 16S (rRNA), microsatellites (PcLG-03, PcLG-04, PcLG-07, PcLG-09, PcLG-10, PcLG-13, PcLG-15, PcLG-17, PcLG-29, PcLG-32, PcLG-48 and PcL24)	(Li <i>et al.</i> , 2012)
Japan	1	invasive		
China	35	invasive		
USA	2	native	mtDNA (CO1)	(Torres and Álvarez, 2012)
Mexico	1	native		
Mexico	5	invasive		
Costa Rica	1	invasive		
China	11	invasive		
Taiwan	1	invasive	ITS1 (rRNA)	(Liu <i>et al.</i> , 2013)
USA	1	invasive	mtDNA (CO1), microsatellites (PcLG-04, PcLG-07, PcLG-15, PcLG-16, PcLG-17, PcLG-27, PcLG-28, PcLG-29, and PcL-48)	(Paulson and Martin, 2013)

(Barbaresi *et al.*, 2007; Yue *et al.*, 2010; Li *et al.*, 2012; Paulson and Martin, 2013) (Table 1). Genetic information can give helpful insights about connection between populations, and might help to infer the invasion history of exotic populations by identifying the location of origin, colonization events and dispersal routes and thus contribute to the understanding of invasion dynamics and to direct management efforts (Wilson *et al.*, 1999; Kreiser *et al.*, 2000; Lee, 2002; Reynolds and Souty-Grosset, 2012; Paulson and Martin, 2013).

In Europe, the genetic variability of *P. clarkii* invasive populations was first studied by Barbaresi *et al.* (2003); five populations were analyzed and showed high genetic variation within and among populations. After that, Barbaresi *et al.* (2007) investigated 12 populations from France, Italy, Mexico, Portugal, Spain, Switzerland and USA; their results revealed a pronounced level of genetic variation in this species that could be the result of multiple introduction events with individuals from different sources and/or a single introduction

of a large number of individuals from a genetically diverse source population. These authors also found a high inter-population differentiation, indicating an absence of gene flow among studied populations.

In China, Yue *et al.* (2010) first studied 6 populations from East China and found evidences of a recent bottleneck and significant heterozygote deficit in all of them, suggesting founder effects and non-random mating; all populations also presented high genetic differentiation between each other. Later, Li *et al.* (2012) used genetic information of 35 invasive populations from central and east China to investigate initial entry point(s), dispersal patterns, genetic diversity and genetic structure. The authors confirmed that the city of Nanjing was the first introduction point in China and found a relatively high genetic diversity in Chinese populations which they attributed as a result of adaptive variation or perhaps signaling human-mediated dispersion. More recently, Liu *et al.* (2013) analyzed

the population genetic structure among 11 populations from east continental China and one population from Taiwan using different genetic markers. They found an intrapopulation genetic variation of 95.26%, much higher than interpopulation variation (4.74%) and also observed that the genetic differentiation between Taiwan and continental China populations was moderate, although Chinese populations (Taiwan and continental combined) were highly differentiated from studied North American populations.

In the Ash Meadows, Nevada (USA), investigations regarding the genetic diversity and gene flow between *P. clarkii* populations revealed the colonization process in the area. It was shown that drainages were utilized to move from central to peripheral springs and isolated springs were colonized by few individuals with rare subsequent emigration (Paulson and Martin, 2013).

Torres and Álvarez (2012) investigated the genetic variation among nine populations of the red swamp crayfish, being three populations from its native range (Illinois and Louisiana, United States and northern Coahuila, Mexico) and six from invaded areas (central Coahuila, southern Nuevo León, Durango, Chihuahua and Chiapas, Mexico, and Cartago, Costa Rica); these authors ascertained that populations from the native range remain very similar to each other and that some introduced populations can be directly associated to some of the native populations. Additionally, they found low genetic variation in both native and introduced populations; these results are divergent from almost all studied invasive populations of *P. clarkii*.

The high level of genetic diversity found by different researchers in distinct invasive populations around the world indicates that the high genetic variability of *P. clarkii* might facilitate its success of establishment and adaptation to new environments (Barbaresi et al., 2007). On the other hand, the studies that found low genetic diversity (Torres and Álvarez, 2012) argue that despite this fact, populations are still successful in establish and flourish due to a phenomenon named “general-purpose genotype” proposed by Baker (1965), in which different phenotypes would be produce through plasticity and thus, the population would be able to cope with different environmental conditions.

High genetic diversity in invasive populations is usually related to multiple introductions or the existence of gene flow among established populations while low genetic diversity is associated with isolated introductions, founder effect and genetic bottlenecks. Both genetic scenarios were observed in invasive populations of *P. clarkii* and it seems that this species may cope with both situations by different strategies and succeed.

CAUSES OF INTRODUCTION

Shipping and aquacultural activities are the main agents of introduction of invasive alien crustaceans around the world (Hänfling et al., 2011). Regarding alien freshwater crayfishes, shipping and ballast water are not important pathways but aquaculture and activities associated with the aquarium and bait industry are (Cohen and Carlton, 1995; Ruiz et al., 1997). Indeed, the aquaculture of *Procambarus clarkii* is the most important vector of introduction, this species being one of the most important freshwater decapods farmed for consumption (Huner, 1988; Hobbs and Lodge, 2010). Furthermore, this species has also been introduced as food for fishes and for other edible species like bullfrogs (Gherardi et al., 2011; Lodge et al., 2012).

In Africa, *P. clarkii* has also been introduced as a biological control agent to reduce snail populations, which are intermediate hosts of schistosomiasis (Bilharzia) (Lodge et al., 2005). Besides, escapes from garden ponds and the pet trade are also important introduction pathways (Dehus et al., 1999; Soes and Van Eekelen, 2006; Dümpelmann et al., 2009). Furthermore, especially in Europe, the red swamp crayfish has also been introduced to replace indigenous species, like *Austropotamobius pallipes* Lereboullet, 1858 for example, which was nearly extinct (Anastácio and Marques, 1995; Holdich, 1999).

INVASION RANGE AND HISTORY

Despite being native to the central southern United States and northeastern Mexico (Fig. 3), *Procambarus clarkii* has been cultured extensively through the USA and was introduced by humans into different parts of the northern region, currently being found in Arizona, California, Georgia, Hawaii, Idaho, Indiana, Maryland, Nevada, New Mexico, New York, North Carolina, Ohio,

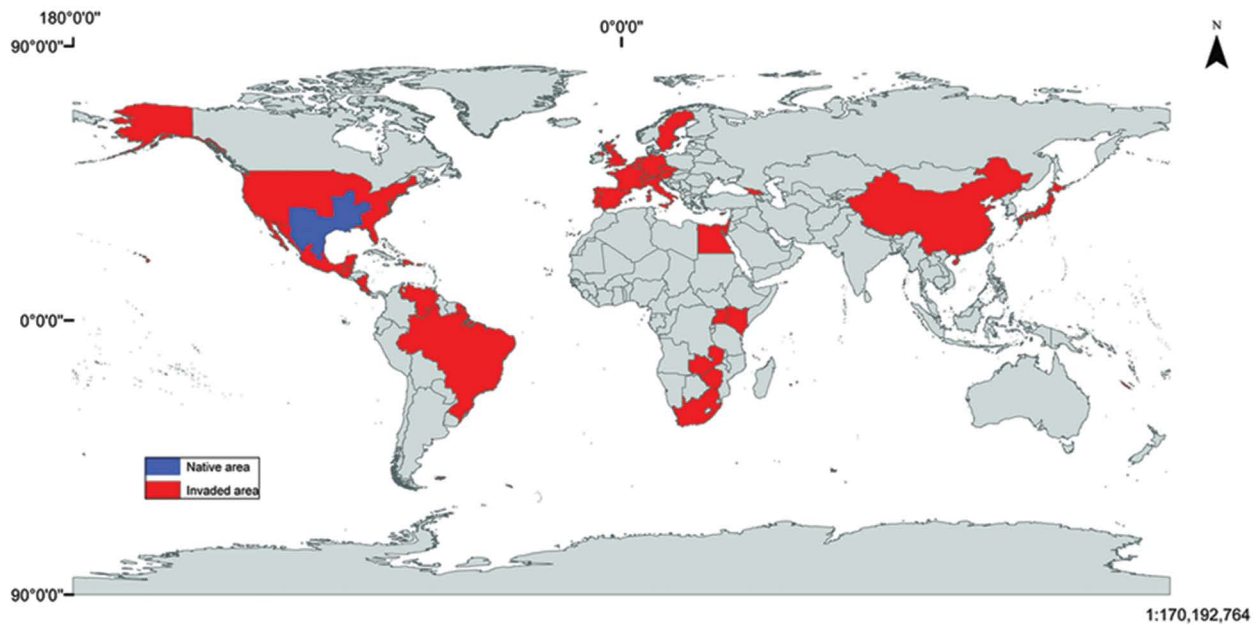


Figure 3. *Procambarus clarkii* native and invasive distribution in the world.

Oklahoma, Oregon, South Carolina and Utah (Clark and Wroten, 1978; Huner, 1986; Johnson, 1986; Ruiz *et al.*, 1997). In northwestern Mexico, it has been successfully introduced in the states of Baja California and Sonora (Clark and Ralston, 1976; Campos and Rodríguez-Almaraz, 1992).

In Europe, *P. clarkii* was first introduced into the Iberian Peninsula, legally imported from Louisiana for commercial purposes in 1973, at two aquaculture installations in Seville and Badajoz (Habsburgo-Lorena, 1979). The commercial success led to illegal introductions throughout Portugal, Spain, France and Italy. Thereafter, it dispersed rapidly throughout the Mediterranean region and central Europe, either actively in rivers or passively by human translocations (Anastácio and Marques, 1995; Barbaresi and Gherardi, 2000). Today, the red swamp crayfish is widespread and abundant in Europe, including central and northern European countries, where climatic features were initially considered a potential barrier to its spread (Huner, 2002; Souty-Grosset *et al.*, 2006; Ilhéu *et al.*, 2007; Holdich *et al.*, 2009). In fact, as observed by Chucholl (2011), populations at higher latitudes tend to be sparse and isolated from each other, while at lower latitudes populations are dense and widespread.

In Asia, this crayfish species is widely established in China and Japan. It was initially introduced to Japan in 1927 from New Orleans, USA, as food for bullfrog aquaculture and the pet trade, and now

it can be found in the whole country, including Okinawa Islands (Mito and Uesugi, 2004; Kawai and Kobayashi, 2005). From Japan, *P. clarkii* was introduced to Nanjing, China in 1929 (Yan *et al.*, 2001; Li *et al.*, 2007) and has rapidly spread to most provinces of China, having established dense populations (Li *et al.*, 2005). Furthermore, a reproducing population of *P. clarkii* was also found in Israel by Wizen *et al.* (2008), but just this first record exists for this country so far.

The red swamp crayfish is also established in Africa, with records from Egypt, Kenya, South Africa, Sudan, Uganda, Zambia and Zimbabwe (Huner, 1988; Hobbs *et al.*, 1989; Arrignon *et al.*, 1990; Mikkola, 1996; Holdich, 1999; Smart *et al.*, 2002; El Zein, 2005; Foster and Harper, 2007). It was originally introduced to Kenya in 1966, from Uganda; after that, active dispersal ability and human mediated translocation resulted in its range expansion through the country (Oluoch, 1990). In Egypt, the first established population was found in the early 1980s, probably derived from a commercial aquaculture facility in Giza (El Zein, 2005; Fishar, 2006) and within the last few years, it has successfully established in various sites of the river Nile and its branches (Fishar, 2006). Regarding *P. clarkii* invasion in South Africa, Sudan, Uganda, Zambia and Zimbabwe, no historical information about introduction is available, just present occurrence data of established populations.

Some Central and South American countries were colonized as well, but no information about introduction pathways and dates of establishment are available for most of them. In Costa Rica, invasive populations are known in the provinces of Cartago, Heredia, Alajuela, Guanacaste and Limón (Peña, 1994). *Procambarus clarkii* occurrence is also registered for Belize, Dominican Republic, Guatemala, Nicaragua, Puerto Rico and Venezuela (Huner and Avault, 1979; Huner, 1986; Hobbs et al., 1989; Williams et al., 2001). In Brazil, *P. clarkii* has 17 established populations, all of them in Southeast Brazil, having been introduced for the aquarium trade and later released into nature accidentally or deliberately (Magalhães et al., 2005; Banci et al., 2013; Loureiro, 2015).

IMPACTS

Procambarus clarkii occupies an important position in the trophic structure of invaded environments, interacting with different trophic levels and changing the whole ecosystem functioning (Angeler et al., 2001; Dorn and Wojdak, 2004; Gherardi and Acquistapace, 2007; Cruz et al., 2008). Its flexible feeding strategy affects both lower and higher trophic levels by grazing on macrophytes and algae and preying on macroinvertebrates, fish fingerlings and tadpoles (Rodríguez et al., 2003; Rodríguez et al., 2005; Gherardi, 2006; Gherardi and Acquistapace, 2007).

Its efficiency on grazing macrophytes and extensive burrowing activity can alter freshwater environments, modifying them from macrophyte-dominated areas with clear water to phytoplankton dominated turbid areas (Rodríguez et al., 2003; Geiger et al., 2005; Matsuzaki et al., 2009). Macrophytes are particularly important to aquatic environments because they function as service providers and ecosystem engineers (Jones et al., 1994; 1997; Duarte, 2000) avoiding erosion, facilitating nutrient cycling and providing habitat to associated faunal communities (Duarte, 2000; de Groot et al., 2002; Gurnell et al., 2006), and serious changes may occur in aquatic environments if submersed plant species are overgrazed. Additionally, the burrowing behaviour might also cause river or channel bank erosion and increase water turbidity (Anastácio and Marques, 1997; Rodríguez et al., 2003). These changes in water characteristics alter aquatic ecosystems and

are believed to induce cyanobacterial blooms (Yamamoto, 2010).

Furthermore, *P. clarkii* is one of the vectors of the crayfish plague, which is mostly asymptomatic in North American crayfish species such as *P. clarkii*, *Orconectes limosus* (Rafinesque, 1817) and *Pacifastacus leniusculus* (Dana, 1852), but lethal to crayfish from other regions (Souty-Grosset et al., 2006; Aquiloni et al., 2010; Longshaw, 2011). This disease, caused by *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 et al., 1999; Souty-Grosset et al., 2006; Holdich et al., 2009). Besides *A. astaci*, *P. clarkii* may carry many other pathogens, parasites, epibionts and diseases (see “Trophic ecology”) that can affect other species, man included.

In addition to its influence on biodiversity, *P. clarkii* can also have a considerable economic impact. Primarily, costs of ecological damage and control measures can be highlighted (Kettunen et al., 2008). Costs of damage mainly occur in the agricultural, forestry, and fishery sectors. Regarding agricultural economic impacts specifically, crayfish infestation has caused serious damage to drainage systems as a consequence of its burrowing activities, causing important losses of rice yield (Sommer, 1984; Gaudé, 1986; Correia and Ferreira, 1995; Anastácio et al., 2000; 2005).

The red swamp crayfish is also a problem for fisheries once it spoils valuable fish caught in gill-nets, damages fish nets and is considered a pest in many fish ponds (de Moor, 2002; Maezono and Miyashita, 2004).

MANAGEMENT AND CONTROL

Procambarus clarkii invasion management options include the elimination or reduction of populations employing physical, chemical or biological methods and the use of legislation to prohibit the transport and release of specimens.

Removal campaigns using traps, fyke or seine nets and electro-fishing are commonly utilized as physical control, although they are often biased by crayfish size and sex (Westman et al., 1978; 1979). These methods are effective for population reduction but eradication is unlikely if populations are not restricted in range and size (Gherardi et al., 2011). Nevertheless, when physical control

is to be used, it is better to invest in continued trapping than short-term intensive trapping, which can cause a feedback response in the population by stimulating faster maturation of juveniles and larger offspring per brood (Skurdal and Qvenild, 1986; Holdich *et al.*, 1999). Drainage of ponds is also extensively used, especially in water bodies with dense populations, as well as diversion of rivers and construction of barriers; nonetheless, the efficiency of these methods is not yet confirmed, especially for pond drainage, since *P. clarkii* is resistant to drought due to its burrowing capacity (Kerby *et al.*, 2005; Gherardi *et al.*, 2011).

Another common practice to eradicate or control crayfish populations is with biocide, the most used being the application of xenobiotics, organophosphate, organochlorine, and pyrethroid insecticides (Cecchinelli *et al.*, 2012). Chemical methods, however, were found to be ineffective because of their selective efficiency, with individual crayfish being differentially affected depending on size. In Italy, a laboratory test using the synthetic pyrethroid ciflutrin was found to be relatively effective (Quaglio *et al.*, 2002). Chemical control of crayfish activity, aiming to induce temporary inactivity, was also tested without success in rice field ecosystems (Anastácio *et al.*, 2000).

Besides being expensive, especially when applied to large areas, chemical control methods may have devastating impacts on native species and affect a wide range of organisms (Velez, 1980; Roqueplo and Hureauux, 1989). In fact, there are no selective biocides for crayfish or even crustaceans and development of resistance is frequent. Furthermore, the possibility of bioaccumulation and biomagnification cannot be discounted.

Biological control methods were also employed worldwide, including the use of fish predators, disease-causing organisms and microbes that produce toxins (Holdich *et al.*, 1999; Frutiger and Müller, 2002) but the only method that has been successful so far is the use of predaceous fish like eels, burbot, perch and pikes (Westman, 1991; Aquiloni *et al.*, 2010; Freeman *et al.*, 2010). Nevertheless, biocontrol might be risky since it may lead to new species introductions and it is not specific to the target organism, possibly also affecting native organisms as well.

All methods mentioned above present environmental costs that can overcome their benefits. In fact, no single method for eradication

is apparently successful. Thus, a combination of methods should be considered, such as trapping and the introduction of predatory fish species (Gherardi *et al.*, 2011).

FINAL REMARKS

Species moved beyond the limits of their normal geographic ranges by human actions usually have strong ecological impacts (Witte *et al.*, 1992; Parker, *et al.*, 1999; Hall and Mills, 2000; Latini and Petrere, 2004) and the effects of biological invasion in freshwater habitats seem to be greater than in terrestrial ecosystems, especially because freshwater invasive species have a greater tendency to disperse (Sala *et al.*, 2000; Beisel, 2001). Additionally, the importance of freshwater environments to humankind is enormous and modifications on its services will have a strong impact on human welfare.

Crayfish species have social, economic and ecological significance in several regions around the world, favouring their introduction into allochthonous areas (Reynolds and Souty-Grosset, 2012). *Procambarus clarkii* is among these successfully and widely translocated species, and its importance is mainly associated with aquaculture and the aquarium trade, being the most harvested crayfish species in the world and thus, the most intentionally introduced (Hobs and Lodge, 2010; Lodge *et al.*, 2012).

The great concern regarding this species intensive introduction is that *P. clarkii* is a successful colonizer which has specific features that increase its invasive ability and favours its colonization success across the world, in different climatic and geographic areas; these features are its ecological plasticity, resistant gene pool to population changes, adaptation of its biology and life cycle to changing environmental conditions, high tolerance to salinity, oxygen and temperature variations, high somatic growth and reproductive output, short development time and flexible feeding strategy (Alcorlo *et al.*, 2004; Gherardi, 2006; Jones *et al.*, 2009). Therefore, after establishment, this species may quickly become a keystone species and cause serious changes in native plant and animal communities, altering water quality and sediment characteristics (Gherardi, 2007).

In many countries, legislation designed to prevent crayfish spread is unsuccessful and causes conflicts due to the strong relationship between humans and crayfish that results from its recreational or commercial importance. However, once introduced into favorable habitats, *P. clarkii* is difficult to eliminate (Holdich, 1988). Different management and control methods were cited before although their applicability and efficiency is site-specific. Unsuccessful population control is frequent and apparently solutions cannot be standardized. Therefore, the most economically and environmentally effective technique is prevention of introduction and range expansion.

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