Rev Fish Biol Fisheries (2020) 30:121–135
https://doi.org/10.1007/s11160-020-09594-z

REVIEWS

One century away from home: how the red swamp crayfish took over the world

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Received: 22 May 2019 / Accepted: 14 January 2020 / Published online: 23 January 2020

Abstract The red swamp crayfish (*Procambarus clarkii*) (hereafter RSC), native to the southern United States and north-eastern Mexico, is currently the most widely distributed crayfish globally as well as one of the invasive species with most devastating impacts on freshwater ecosystems. Reconstructing the introduction routes of invasive species and identifying the motivations that have led to those movements is necessary to accurately reduce the likelihood of further introductions. In this study, we: (i) review the temporal evolution of the scientific literature on the RSC; (ii) compile georeferenced, time-explicit records of the species to provide a comprehensive understanding of its global expansion process; and (iii) evaluate the potential role of biological supply companies in the translocations of the RSC. The interest of the RSC in scientific research increased steadily since the beginning of the twentieth century until stabilization in the late 1960s. The number of studies related to the use of the RSC in aquaculture showed two peaking periods: the years elapsed between 1970s to mid-1980s, and a continuous increase since the mid-1980s. Research on the RSC as an invasive species has only been numerically relevant in recent times, with the number of studies increasing since the 2000s to represent currently around 25% of the scientific production dealing with this species. Although the first introductions of the RSC took place in the 1920s, our synthesis highlights the rapid expansion of the species since the 1960s, arguably promoted by the emergence of crayfish industry, but other introduction pathways such as the mitigation of schistosomiasis, potential releases from research experiments, school science programs or pet trade cannot be ruled out. Currently, the RSC is present in 40 countries of four continents and there is still potential for further expansion. Commercial suppliers from native (Louisiana) and non-native (California or North Carolina)

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s11160-020-09594-z) contains supplementary material, which is available to authorized users.

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areas in the United States have provided live-specimens of the RSC for scientific research around the world for decades, suggesting that the invasion process of the RSC could be more complex than generally assumed. Tracing the introduction routes of invasive species and understanding the motivations that have led to those movements of species is key to reduce their spread and the likelihood of future introductions.

Keywords Alien species · GBIF · Global translocations · Historical distributions · iNaturalist · Invasive species · Pathways of introduction · *Procambarus clarkii*

Background

Humans have transported plants and animals across biogeographical barriers for millennia, for cultural, leisure or commercial purposes (Forcina et al. 2015), albeit this movement of organisms has steeply accelerated since the mid-twentieth century (Capinha et al. 2015). When released into new areas, some of those transported species are able to survive, reproduce and establish self-sustaining populations, becoming invasive (Blackburn et al. 2011). Invasive species are now a widespread conservation issue and their impacts are considered one of the biggest threats to global biodiversity (Bellard et al. 2016). Identifying the invasion routes through which species are either transported from the native areas to non-native ones or moved among non-native areas is crucial to prevent further spread and to manage future emerging invaders (Estoup and Guillemaud 2010; Bertelsmeier et al. 2018).

Freshwater ecosystems are amongst the most severely threated in the world, due to the combination of habitat degradation, hydrological alteration, global warming, overexploitation, water pollution and invasive species (Reid et al. 2019). As a consequence of all these pressures, freshwater biodiversity is currently declining at a much faster rate than in terrestrial or marine environments (WWF 2016; Reid et al. 2019). Freshwater ecosystems are among the most invaded ecosystems in the world and particularly susceptible to the impact of invasive species (Ricciardi and MacIsaac 2011; Gallardo et al. 2016). At least sixteen freshwater crayfish species have been introduced into non-native areas worldwide (Logde et al. 2000), some of them being amongst the most impacting invasive species (Twardochleb et al. 2013 and references therein). The magnitude of the impact of invasive crayfish is often related to their frequent role as keystone species in freshwater ecosystems (i.e., due to their high abundances, large size, wide range of trophic interactions and their role as ecosystem engineers), affecting to both lower and upper trophic levels (Geiger et al. 2005; Reynolds et al. 2013).

Freshwater crayfish are relatively well-known species and exploited by humans in many regions around the globe (Gherardi 2011). Their accessibility and nutritional value (Tricarico et al. 2008) have contributed to make crayfish a relevant food item for many societies (Holdich 1993; Swahn 2004; Gherardi 2011; Patoka et al. 2016) and a source of economic development (Comeaux 1978; Gutiérrez-Yurrita et al. 1999). The use of crayfish as food is in the roots of several cultural traditions, such as the Swedish crayfish summer festivals, in which families and friends gather to eat crayfish (Edsman 2004; Swahn 2004). Being appreciated and easily transported organisms (crayfish can survive prolonged periods out of water, Gherardi and Barbaresi 2000), crayfish species have been introduced into new areas for a long time (Machino and Holdich 2006; Hobbs and Lodge 2010). In Europe, crayfish introductions have occurred at least since the Middle Ages (e.g., Gouin et al. 2003; Swahn 2004; Gherardi 2011). For example, Carl Linnaeus reported the introduction of the noble crayfish (*Astacus astacus*) to Sweden, which was promoted by King John III in the second half of the sixteenth century (Hobbs et al. 1989). This fact coincided in time with the importation of the Italian crayfish (*Austrapotamobius italicus*) from Tuscany to Spain, a personal initiative of King Philip II to imitate the costumes of the Tuscan court (Clavero et al. 2016).

North America possesses the largest diversity of freshwater crayfish in the world (382 species, Crandall and Buhay 2007), but little is known of crayfish uses by aboriginal North American inhabitants (Huner 2002). First European settlers noticed the presence of crayfish (e.g., they were already cited by Aldrovandi [1606]) and some crayfish species could be found in North American markets since the early nineteenth century (Penn 1943; Comeaux 1978). By the early twentieth century, three main crayfish industries had been developed in North America, targeting three different genera, namely *Faxonius* (formerly *Orconectes*) (in the Midwest), *Pacifastacus* (in Pacific Northwest) and *Procambarus* (in Louisiana) (Comeaux 1978). These are nowadays the most widely introduced genera worldwide and the ones producing the highest biodiversity impacts (Twardochleb et al. 2013). The first introduction of North American crayfish into other continents took place at least since the late nineteenth century, when the spiny-cheek (*Faxonius limosus*) and the virile (*F. virilis*) crayfish were introduced in Europe (Hobbs et al. 1989). But the most striking invasion process is that of the RSC, currently the most cosmopolitan freshwater crayfish, distributed across all continents except Australia and Antarctica (Loureiro et al. 2015).

The origins of exploitation of the RSC is linked to the Cajuns, descendants of the French colonists in Acadia, north-eastern North America, who later settled in the Gulf Coast state of Louisiana in the late eighteenth century (Gutiérrez 1998). The Cajuns' customs, including the French taste for crayfish, gradually become established in Louisiana and the commercial exploitation of the RSC started growing since the late nineteenth century (Gutiérrez 1998; see in Brady 2013). The first fishermen harvested crayfish from wild stocks in swamps and marshes in south Louisiana, but water bodies were soon modified or constructed to store catches and allow longer harvesting periods, developing the aquaculture-based crayfish industry (Comeaux 1978). Crayfish production steeply increased in the 1960s, due to the transformation of several lands to that aim, often in combination with rice cropping (i.e., rice-crayfish fields) (Huner 2002). Land devoted to crayfish production increased from 400 ha in 1959 to 10,000 ha in 1970 (Clark and Avault 1975) and up to 49,000 ha in 1990 (LSU AgCenter 2016). The Louisiana crayfish industry became the most successful producer and seller of crayfish in North America (Comeaux 1978) reaching a farm-gate value of more than \$200 million (aquaculture plus wild harvested) in 2016 (LSU AgCenter 2016).

The high profitability of RSC industry led several entrepreneurs to try to replicate its aquaculture-based production in other areas (Hobbs et al. 1989; Huner 2002; Cheung 2010; Brady 2013). Transcontinental movements of the RSC to Africa and Europe gave rise to incipient crayfish industries in countries such as Kenya or Spain (Harper et al. 2002, for Kenya; Gutiérrez-Yurrita et al. 1999, for Spain). However, the most striking growth of crayfish production has taken place in China, which has recently overtaken the native production of Louisiana crayfish industry. Chinese production has increased from 6700 tonnes in the early 1990s (Xia 2007) up to more than one million tonnes in 2017, with a current commercial value of \$42 billion (China's Ministry of Agriculture and Rural Affairs 2018).

Here, we review the century-lasting invasion history of the RSC in order to describe its expansion, update the knowledge on its global distribution, report the main introduction routes and discuss the main pathways driving the translocations of this species. Based on a review of scientific and grey literature, as well as a collection of records worldwide, we (1) describe the historic variation in the research scope of the RSC from the early twentieth century to the present as well as the patterns of knowledge production in the RSC, (2) make a thorough description of introduction and expansion events along the last one century, and (3) explore the role of commercial companies in the expansion of this species. Commercial companies that ship live specimens for different purposes (e.g., aquarium hobby, education or research) may represent a relevant, though overlooked, introduction vector of the RSC worldwide (Chucholl 2013). Information related to aquarium species and pet trade is scarce and often inaccessible (see Chucholl 2013), but researchers usually report the provenance of model organisms in their scientific studies. This information could be a useful proxy for the potential role of commercial companies in the translocation of the RSC, and other organisms, around the world.

Historical variation in the research scope

A literature search on the RSC (see Appendix I in Supplementary Material), showed that out of 19,342,413 studies published over the last 95 years (from 1924 to 2019) on zoology, ecology, toxicology, biology, neurology, invasion science, and pet trade, only 5442 (< 0.03%) dealt with the RSC. While the total production of studies has constantly increased since the 1950s, the interest in the RSC intensified during the 1960s. Before the early 1960s, the ratio of publication was 1.5 studies on the RSC for each

10,000, but this ratio doubled by the late 1960s, having remained relatively constant since then (Fig. 1a).

In the beginnings of the global invasion process by the RSC (since 1924–1960), there were hardly any scientific studies on the species and very few of them dealt with either aquaculture/fisheries or invasions (Fig. 1b). In that time, studies on the RSC were mainly related to physiology, and the functioning of nervous and motor systems, using crayfish as a model with potential applications to increase knowledge of human

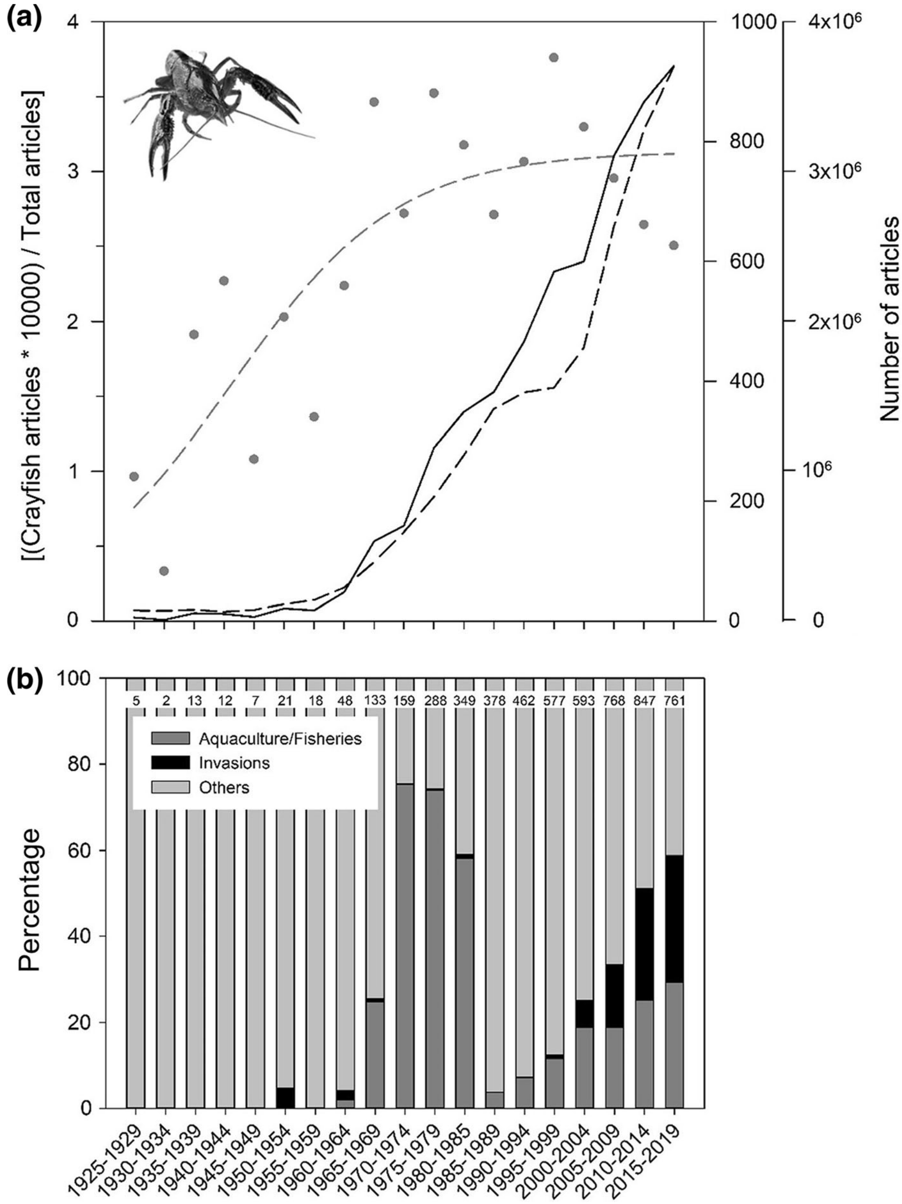


Fig. 1 Dynamic of articles published on the red swamp crayfish over the last ten lustrums (5-year periods) from 1925 to 2019. **a** Black line depicts the number of scientific manuscripts according to the categories (zoolog* OR *ecolog* OR *toxicol* OR *biolog* OR *neurolog* OR *invasi* OR 'pet trade'). For a better interpretation, number of articles published on the red swamp crayfish were multiplied by 10,000 and grey dashed line represents the curve fit on the ratio (*ratio = n*10,000/N)* as the number of articles on the red swamp crayfish divided by the total number of scientific articles. The scientific search was based on title, abstract or keywords. **b** Percentage of published articles on the red swamp crayfish according to two main thematic categories. Total number of articles based on the red swamp crayfish for each lustrum is indicated on top of the graph

locomotion and nervous system (Stark 1968). Physiology studies are still a relevant component of the scientific research focused on the RSC (Fig. 1b). Studies that focussed on the RSC as aquaculture species or its potential in fisheries increased in numbers in two periods: (i) between the mid-1960s and the early 1980s, arguably in relation to the growing commercial use of the RSC, reaching up to a 75% out of total number of studies on the RSC in the decade of 1970s; and (ii) a current peak after a continuous increase of the scientific production in this area since the mid-1980s. The number of studies dealing with the role of the RSC as an invasive species has notably increased since the 2000s, reaching around 25% of total studies in the decade of 2010s. Overall, our analysis of the scientific literature shows that the RSC has long been a model species in experimental biology, that later was studied due to the growing interest as commercial species for food industries and that only in last decades there have been a relevant production of scientific works dealing with the RSC as an invasive species.

The invasion history

We made an exhaustive search of RSC records both spatially and temporally, by reviewing scientific and grey literature as well as global biodiversity databases (e.g., the Global Biodiversity Information Facility (GBIF); iNaturalist) (see Appendix I in Supplementary Material). After discarding records with duplicate coordinates within the same year, our final dataset included a total of 6924 RSC records. In order to describe the expansion process of the RSC, we classified records in one of four historical periods: before 1950, 1951–1975, 1976–2000 and 2001–2019, which had 48, 271, 923, and 5682 records, respectively (Figs. 2 and 3). The number of records grew progressively since the beginning of the expansion in the 1920s but there was a striking increase in number of records since the 1990s (Fig. 2a), mainly associated to an increase in the available information in Europe as well as both native and non-native areas in North America (Fig. 2b). For example, for the 1951–1975 period there were three RSC records in Europe, a figure that increased to 307 records in the 1976–2000 period and to 2710 records after 2000 (Fig. 2b). This increase in the number of records is linked to the rapid expansion of the RSC across Europe, but also to a generalized increase on the amount of available information on biodiversity (e.g., Boakes et al. 2010). However, the low number of RSC records in Africa (< 1% of total records) and Asia (< 5% of total records) (Fig. 2) could be due to spatial biases in the collection of species occurrence data, which are

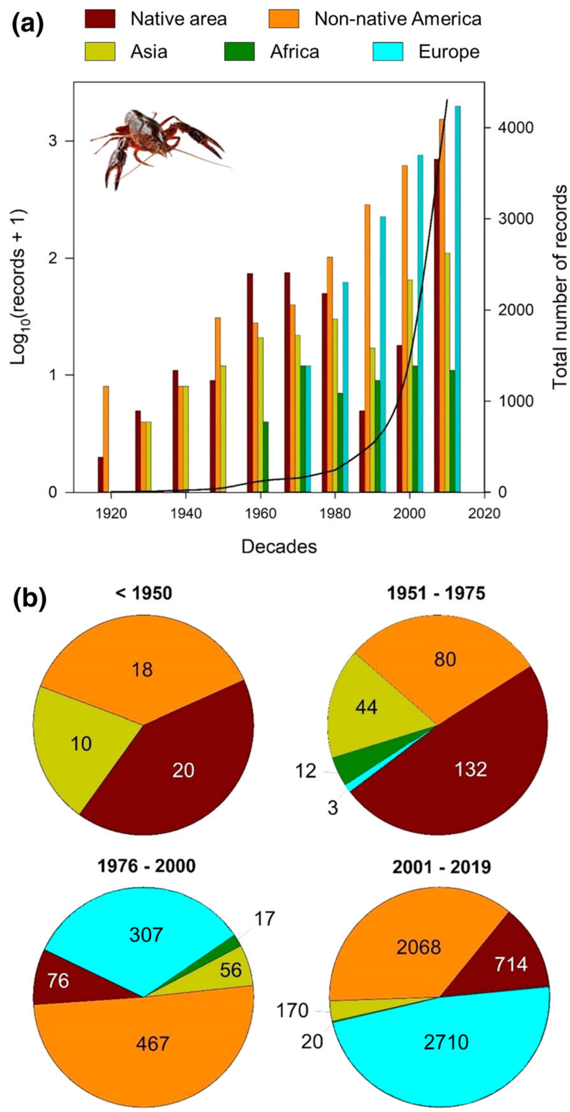


Fig. 2 Red swamp crayfish records along last century. **a** Decadal evolution in the total number of records (black line) and number of records for different biogeographical areas (note logarithmic scale of Y axis). **b** Proportion of total number of records for the four time-periods used in the presentation of our results, showing total numbers for each biogeographical area: native area, non-native area in America, Asia, Africa and Europe

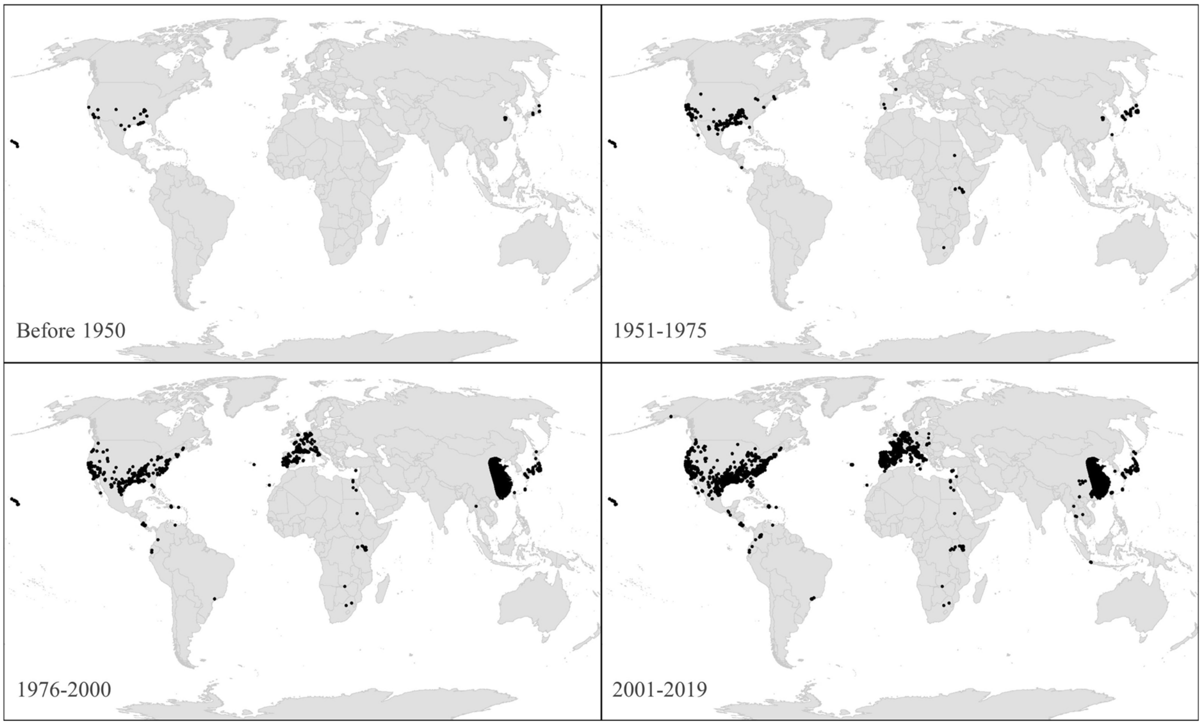


Fig. 3 Occurrence data (black dots) of the red swamp crayfish worldwide split in four periods: before 1950, 1951–1975, 1976–2000, and 2001–2019. Depicted area in China indicates the estimated distribution of the red swamp crayfish according to Xinya (1988)

common to historical and current datasets (e.g., Boakes et al. 2010). Such spatial biases may be even accentuated by the lack of repositories of biodiversity records, as not all countries provide their national biodiversity databases to GBIF. Therefore, the distribution of the RSC in Africa and Asia could be underestimated throughout the different periods considered here.

The beginnings (before 1950)

The RSC was cited for the first time outside of its native range in southern California in 1924 when probably several hundreds of individuals were introduced (Holmes 1924). From California the RSC was firstly translocated to Oahu Island, Hawaii, probably in 1927 (see Brock 1960) and subsequently in 1934, being expanded to other Hawaiian Islands afterwards (Penn 1954). Brasher et al. (2006) reported that live-specimens of the RSC were translocated from California to Hawaii in 1923, which would imply that either crayfish had been introduced into California earlier than 1924 (as reported by Holmes 1924) or the first introduction into Hawaii occurred later. Also, the RSC was introduced from Louisiana to Japan in either 1927 or 1930 (see references in Kawai 2017 and Penn 1954, respectively) and from there to China in 1930 (see Cheung 2010) (Table 1). As in the case of California and Hawaii, it is noteworthy that there is a lack of accuracy in the introduction dates of the RSC into Japan, even though this introduction event is well detailed in the literature. Although the RSC was translocated at large scale before 1950, the RSC did not arrive to Europe until the decade of 1970s.

There is a general consensus that the motivation to translocate live-specimens of the RSC in California, Hawaii and Japan, was to provide food for culturing the American bullfrog (*Lithobates catesbeianus*) (Hobbs et al. 1989). The RSC rapidly established viable populations and expanded across rice fields in California (Riegel 1959), various Hawaiian islands (Penn 1954) and the Honshu Island in Japan (Kawai 2017), being considered as a pest because of its burrowing activity (see Penn 1954). However there was a time-lag between its introduction (1924) and the action measures to ‘eradicate’ them by mid-twentieth

Table 1 First reports of red swamp crayfish, *Procambarus clarkii*, over the world

Country	Date	Site of introduction	Source	Purpose
Africa (8)				
Egypt	*1980s*	Giza/Cairo/Nile Delta	United States	Aquaculture
Kenya	1966	Solai/Subukia	Kajansi (Uganda)	*Aquaculture*/Disease
Morocco	2008	Merja Zerga	Seville (Spain)	*Aquaculture*
Rwanda	2019	Kigali	–	–
South Africa	1962	Potchefstroom	–	*Aquaculture*
Sudan	1975	Khartoum	Louisiana (US)	Aquaculture
Uganda	1963	Kajjansi	Louisiana (US)	Aquaculture/Disease
Zambia	< 1979	Livingstone	Naivasha (Kenya)	Aquaculture
America (11)				
Brazil	*< 1986*	São Paulo	United States	Pet trade
Canada	2017	Vancouver	–	–
Colombia	1985	Cauca Valley	–	Aquaculture
Costa Rica	1966	Alajuela City	–	–
Dominican Republic	1977	Santo Domingo	United States	Aquaculture
Ecuador	1986	Taura River	–	Aquaculture
Guatemala	*2019*	*Técpan*	–	–
Mexico	1955	Cananea	–	–
Puerto Rico	< 1978	–	–	*Aquaculture*
Venezuela	1978	–	Louisiana	Aquaculture
US (39)				
Alabama	1961	Auburn	–	Aquaculture
Alaska	2004	Kenai	–	–
Arizona	1969	Lower Colorado Basin	–	–
California	< 1924	Pasadena	Louisiana	–
Colorado	2018	Denver	–	–
Connecticut	2017	Near Norwich	–	–
Delaware	2018	Brandywine Creek	–	–
Dist. of Columbia	2016	Anacostia River	–	–
Florida	1951	Hudson	*Louisiana*	Aquaculture
Georgia	*1989*	Athens	–	–
Hawaii	1923	Oahu island	California	Food source
Idaho	1975	Nampa	Nevada/California	–
Illinois	2001	Chicago River	–	–
Indiana	*< 1986*	–	–	–
Kansas	2017	Kansas City	–	–
Kentucky	< 1944	–	–	–
Maine	1980	Kennebec River	–	–
Maryland	1963	Patuxent Area	Louisiana	Food source
Massachusetts	2010	Amherst	–	–
Michigan	2013	Holland	–	–
Minnesota	2016	Tilde Lake	–	–
Missouri	2009	Table Rock Reservoir	–	–
Nebraska	2014	Missouri River	–	–

Table 1 continued

Country	Date	Site of introduction	Source	Purpose
Nevada	1944	Las Vegas River	*California*	–
New Jersey	2016	Saxton Lake	–	–
New Mexico	1944	Grande River	–	–
New York State	2002	Long Island	–	–
North Carolina	1980s	–	–	–
Ohio	1967	Sandusky Bay	–	*Fishing*
Oklahoma	1969	McCurtain Co.	–	–
Oregon	1990s	Willamette Valley	–	–
Pennsylvania	1990	Schuylkill River	–	–
Rhode Island	1970	Arcadia	–	–
South Carolina	< 1978	–	Louisiana	Aquaculture
Tennessee	2018	Nashville	–	–
Utah	1978	Tooele Co.	–	–
Virginia	1972	York-Pamunkey	–	–
Washington State	2000	Pine Lake	–	–
Wisconsin	2009	Kenosha Co.	–	–
Asia (7)				
China	1930	Nanjing	Japan	Pets
Hong Kong	*< 1960s*	Hong Kong	–	*Pet trade*
Indonesia	2018	Java Island	–	Pet trade
Israel*	2008	Hadera	–	–
Japan	1927/1930	Ōfuna/Kamakura	New Orleans (US)	Food source
South Korea	< 2005	Incheon	–	*Pet trade*
Taiwan	1960s	–	–	Aquaculture/Pet trade
Thailand	1987	Chiang Mai province	United States	Aquaculture
Europe (14)				
Austria	< 2005	Salzburg	–	–
Belgium	1983-85	Vielsalm	–	*Human consumption*
Cyprus	< 1987	Athalassa dam	–	–
England	1991	Hampstead Heath Park	Kenya	*Human consumption*
France	1974	Charente-Maritime	Spain/Kenya	Aquaculture
Germany	1975-76	Lake Hechtsee	–	–
Hungary	2015	Budapest	–	Pet trade
Italy	1977	Banna Stream	*Spain*	Aquaculture
Malta	2016	Fiddien Valley	China	Pet trade/Aquaculture
Poland	2018	Żerań Canal (Warsaw)	–	Pet trade
Portugal	1979	Caia River	Badajoz	Natural dispersion
Spain	1973	Badajoz	Louisiana	Aquaculture
Switzerland	1989	Schübelweiher	–	Fishing
The Netherlands	1985	The Hague	–	*Human consumption*

Number in brackets indicates the total number of countries or states where the red swamp crayfish is established or probably established. (−) means unknown data. *Italics* indicate no confirmed information. *Indicates eradicated into the country (Israel). Full information on the spreading of the red swamp crayfish for each country is detailed in Appendix II and all references are included in Appendix III (Supplementary Material) century (Chang and Lange 1967). On the other hand, the RSC was introduced into China in 1930 short after its introduction to Japan (Table 1) by Japanese citizens who presumably used the species as pets (Cheung 2010). Cheung (2010) described that the apprehension of Chinese society to everything that came from Japan in the early twentieth century could have stopped the expansion of the RSC to other areas nearby, since Chinese people thought that the introduction of the RSC was a Japanese conspiracy to harm their rice fields. In fact, Chinese population neither appreciated the crayfish nor considered it edible by mid-twentieth century (Cheung 2010), a rejection that probably also limited the expansion of the RSC across China in the first decades after its introduction (Xinya 1988) (Fig. 3).

Expansion of red swamp crayfish industry (1951–1975)

While the Louisiana crayfish industry was blooming around 1960s (LaCaze 1970; Gary 1974), there were numerous attempts to emulate that production system through translocations of the RSC to different areas (see new wild introductions in Fig. 3), either from native area (Louisiana) or from other regions previously invaded (see Table 1). For that purpose, the species was also introduced in Africa (Sudan, Kenya) in the late 1960s and Europe (Spain) in the early 1970s. By 1975 the exploitation of the RSC had started to gain importance in different non-native areas, including states of U.S.A. (e.g., California, see in Huner 1977) and countries such as Kenya, Spain, France and Italy (see Appendix II in Supplementary Material). But introductions also involved other purposes such as mitigation of schistosomiasis (e.g., Uganda and Kenya, Hofkin et al. 1991) or supplying the pet market (e.g., Hong Kong, Taiwan or France, Hobbs et al. 1989). The motivation for other many introductions remains unclear (e.g., different States of U.S.A. and Mexico, South Africa or Costa Rica) (see Appendix II in Supplementary Material). Apart from the new introductions, the RSC continued expanding in the territories where it had been introduced before 1950, notably in western U.S.A. and Japan (Fig. 3).

The great spreading worldwide (1976–2000)

In the late twentieth century, there was an acceleration of the expansion of the RSC in several non-native areas, including Europe (Gutiérrez-Yurrita et al. 1999; Changeux 2003), China (Xinya 1988), non-native areas in the U.S.A. (Hobbs et al. 1989) and Kenya (Harper et al. 2002). In the last quarter of the twentieth century, the RSC also arrived to different countries in South America (Colombia, Ecuador, Venezuela), the Caribbean (Dominican Republic, Puerto Rico), and Africa (Zambia, Egypt) (Fig. 3). In Europe, multiple secondary introductions led to a rapid expansion of the RSC over Spain, Portugal, Italy and France (see Oficialdegui et al. 2019), as well as its arrival to Germany, Belgium, the Netherlands, Switzerland, United Kingdom and several European islands (e.g., Cyprus, Balearic and Canary Islands in Spain, and Azores in Portugal) (see Appendix II in Supplementary Material). Besides, numerous importations of live-specimens took place from Spain and Kenya to French and Italian farms as well as English restaurants since late 1970s to early 1980s (Holdich 1993; Laurent 1990), which could have generated escapes or releases into the wild (Oficialdegui et al. 2020). By the late 1990s, the RSC was the most important farmed freshwater crayfish species in Europe (54.6% of the total European production), being mainly farmed in Spain (Ackefors 1998) but also in Italy (D'Agaro et al. 1999). Moreover, the RSC was highly exploited for recreational fishing (Changeux 2003) and human consumption in France (Holdich 1993).

Interestingly, although the RSC was present in China since 1930, only since the early 1980s Chinese scientists initiated aquaculture experiments aimed at setting up crayfish industry (Xinya 1988). The rapid development of these initiatives, together with the growth of commercial sales in pet shops, caused the spread of the RSC across eastern China (Cheung 2010). Thus, the expansion of the RSC in China had a delay of more than 50 years since its introduction and establishment. Time-lags among different stages of the invasion process (e.g., between establishment and spread) are a common feature of several invasion processes (Crooks and Soulé 1999; Clavero and Villero 2013). In Africa, the main crayfish fishing areas were Lake Naivasha and several watercourses in Kenya (Harper et al. 2002) and the Nile Delta in Egypt (Hamdi 1994). Simultaneously, many other countries (e.g., Puerto Rico, Dominican Republic, Ecuador, Zambia, among others) attempted to culture the RSC by carrying out experiments on its adaptability and suitability indoor or directly in semi-natural areas, often leading to accidental escapes or releases into the wild (see Appendix II in Supplementary Material).

Current status (2001–2019)

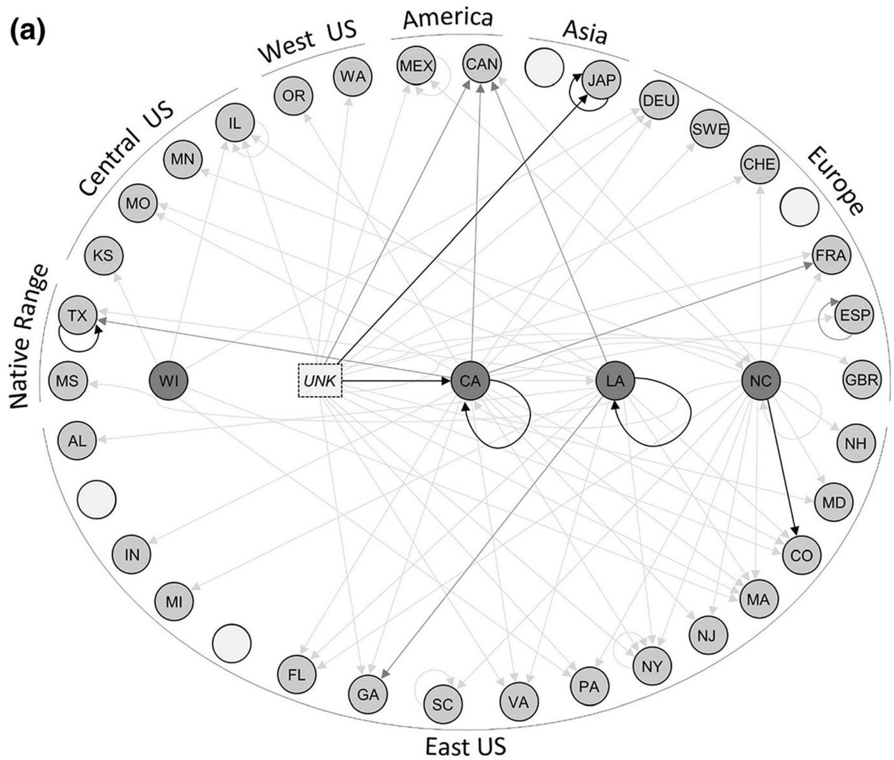
The RSC has recently expanded over areas, where it had been previously introduced, of western and eastern U.S.A., north-eastern Mexico, European countries, China and, to a lesser extent, other territories (Table 1; Fig. 3). Secondary human-deliberated introductions are key in the invasion process, where established populations in invaded areas act as source of new introductions at long- and short-distance (see Oficialdegui et al. 2019). It has also been registered in new areas of Europe (Austria, Hungary, Poland and several Mediterranean islands: Corsica, Sardinia, Sicily and Malta), Africa (Morocco) and Asia (South Korea, Israel and Indonesia) (Fig. 3). The RSC is now present in 40 countries of four continents (Table 1), but there are potential areas for further expansion, as for example, the islands of Indonesia (see in Putra et al. 2018), as well as in territories of southern South America, the Mediterranean Basin, and large parts of Africa and Australia (Larson and Olden 2012). Once the RSC is introduced and established, populations seem to be viable in the long-term (Fig. 3 and Appendix II in Supplementary Material). In fact, most of previously established populations around the world remain at present (except Alaska in U.S.A., Israel and Tenerife Island in Spain, as far as we know). This is an indication that eradication has thus far proven difficult (Gherardi et al. 2011) and calls for an effort to prevent any possible future introduction to new areas.

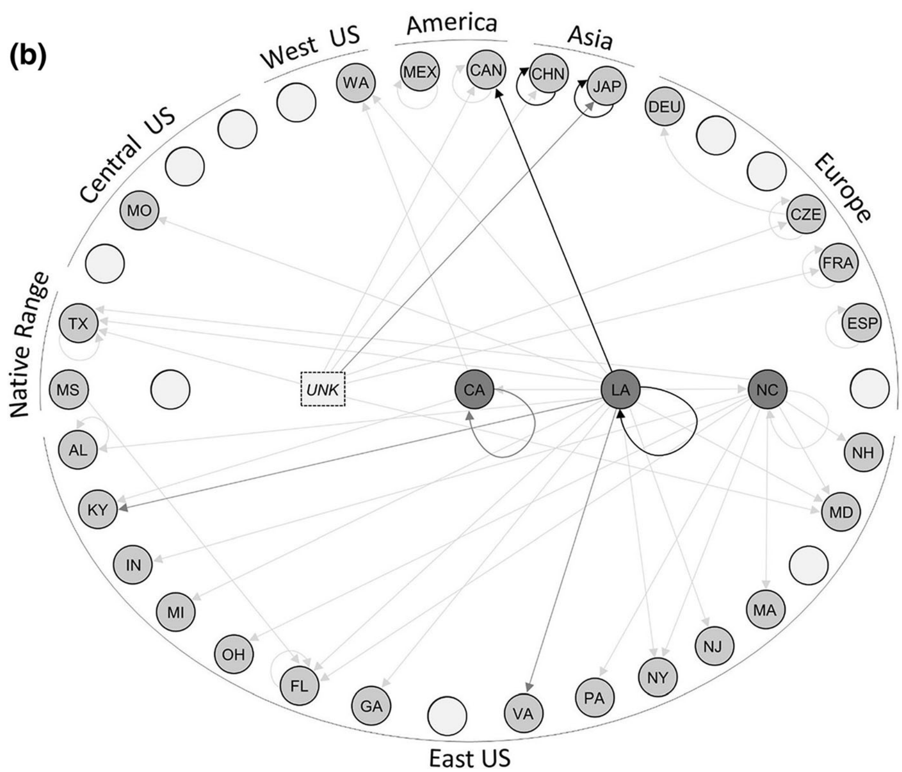
Commercial supply companies as potential source

The use of RSC as model species in scientific studies could give further information on how and where specimens have been obtained from. As such, we identified the origin of RSC in 729 out of 2053 scientific studies in the selected years (see Appendix I in Supplementary Material for details). Overall, the 67% studies obtained RSC commercially and 33% from the wild. The percentage of crayfish obtained from commercial supply companies seems to have declined over time, with a 73% of the 456 studies analysed before 1990 and 56% of the 273 studies analysed after that date (see Appendix I in Supplementary Material). The recent decrease in commercially-obtained RSC in scientific research is arguably related to the increased availability of wild populations nearby due to the continuous expansion of the species since the mid-twentieth century (Fig. 3).

Fig. 4 Network of the main commercial translocations of the ▶ red swamp crayfish (**a**) since 1961–1990; and **b** in 1995, 2000, 2005, 2010 and 2015 based on 334 and 158 scientific studies, respectively. The States with main commercial companies are depicted in the middle of the ellipse and recipient States (abbreviates) or countries (ISO codes) around. Empty circles indicate the absence of connexions with that particular State or country in the period. *UNK* shows unknown commercial suppliers. Black, light grey and dark grey arrows depict the direction and frequency of movements of crayfish: casual (< 5), semi-frequent (5–9) and very frequent (> 10), respectively. ISO country codes: MEX, Mexico; CAN, Canada; CHN, China; JAP, Japan; DEU, Germany; SWE, Sweden; CHE, Switzerland; CZE, Czech Republic; FRA, France; ESP, Spain; GBR, United Kingdom. Abbreviate United States codes: WI, Wisconsin; CA, California; LA, Louisiana; NC, North Carolina; NH, New Hampshire; MD, Maryland; CO, Colorado; MA, Massachusetts; NJ, New Jersey; NY, New York; PA, Pennsylvania; VA, Virginia; SC, South Carolina; GA, Georgia; FL, Florida; OH, Ohio; MI, Michigan; IN, Indiana; KY, Kentucky; AL, Alabama; MS, Mississippi; TX, Texas; KS, Kansas; MO, Missouri; MN, Minnesota; IL, Illinois; OR, Oregon; WA, Washington

Most of studies based on commercially-obtained crayfish also detailed the commercial company or area from where crayfish were bought. The main suppliers of the RSC worldwide were based in U.S.A. (in the States of Louisiana, California, North Carolina and Wisconsin), which supplied crayfish up to 292 studies (Fig. 4a and b). Until 1990, these four source-states of U.S.A. provided crayfish to eight countries, and 24 states of U.S.A., including themselves (Fig. 4a), with an exportation rate of 100% for Wisconsin (n = 6), 92% for North Carolina (n = 39), 48% for Louisiana (n = 64) and 46% for California (n = 72). From 1991 onwards, the state of Wisconsin lost its role of main supplier of the RSC. The States of Louisiana, California and North Carolina provided crayfish to two countries (Canada and U.S.A.) exclusively, and to 20 states of U.S.A. (Fig. 4b), with an exportation rate of 79% for North Carolina (n = 14), 74% for


(a)
West US
America
Asia
Central US
Europe
Native Range
East US
OR
WA
MEX
CAN
JAP
DEU
SWE
CHE
FRA
ESP
GBR
NH
MD
CO
MA
NJ
NY
PA
VA
SC
GA
FL
MI
IN
AL
MS
TX
KS
MO
MN
IL
WI
UNK
CA
LA
NC


(b)
West US
America
Asia
Central US
Europe
Native Range
East US
WA
MEX
CAN
CHN
JAP
DEU
CZE
FRA
ESP
NH
MD
MA
NJ
NY
PA
VA
GA
FL
OH
MI
IN
KY
AL
MS
TX
MO
UNK
CA
LA
NC

Louisiana (n = 62) and 40% for California (n = 5). Importantly, Japan and China have also become important suppliers of the RSC but their exportation rate was very low, mostly supplying themselves (Fig. 4a and b).

It is noteworthy that most of the main suppliers of the RSC worldwide are based in non-native areas within the U.S.A. (e.g., California, North Carolina and Wisconsin), though crayfish production in the native area (Louisiana) could have been reduced as crayfish industry was partly damaged by hurricanes in the 2000s. Moreover, our synthesis showed that there have been more translocations than generally assumed (Fig. 4). For example, even though the RSC is native from Texas or northern Mexico, several translocations took place from other invaded areas (e.g., California or North Carolina), even scientific studies carried out in Louisiana obtained crayfish from Louisianan and Californian commercial supply companies. Recently, a genetic study by Oficialdegui et al. (2019) showed that two main routes for the RSC invasion seemed to occur in U.S.A. (i.e. westwards and eastwards from the native range) suggesting the role of commercial companies (located in North Carolina and California) in the spread of the RSC within both areas. RSC movements within the United States (Fig. 4) show that while commercial supply companies in California sent crayfish to everywhere, commercial supply companies in North Carolina mainly supplied crayfish to the east of U.S.A., which could explain the results on genetic variability found in western and eastern U.S.A. wild populations, respectively (Oficialdegui et al. 2019). However, it is remarkable that some states in the north-eastern U.S.A. (e.g., New York, Massachusetts, Connecticut and Maryland) have received numerous shipments of crayfish from diverse areas (Fig. 4). Also, Canada has long received many shipments of crayfish (Fig. 4) but wild-populations have only been detected recently (iNaturalist 2019). We found an unexpectedly large number of unreported transoceanic RSC translocations to Europe, where the invasion history of the RSC was supposedly well-known (see Appendix II in Supplementary Material). Moreover, while commercial supply companies in U.S.A. showed high exportation rates of crayfish, most of the shipments of crayfish in Asia took place within the countries (see Japan and China in Fig. 4). However, there was a series of shipments whose suppliers are unknown and hence their invasion routes could not be reconstructed. Although most of specimens used in scientific studies are often sacrificed after the experiments, escapes from research centres have been described in literature (e.g., the exotic mummichog in Spain, Gisbert and López 2007). Beside of research, other pathways of introductions could remain hidden in the translocation of alien species because the uptake of live-crayfish commercially can be extrapolated to schools and universities (Larson and Olden 2008), general citizens, fishermen or farmers who may obtain live-specimens (Lodge et al. 2000). Therefore, our review highlights the risk of shipping highly invasive species out of their native area by showing the amount of translocations that have occurred for a long time. In this context, scientific studies focusing on highly invasive species should always indicate where live-specimens come from. Hence, particular attention should be paid to introduction routes of highly invasive species out of their native range.

Management implications

Understanding the introduction routes of invasive species and disentangling the motivations that have led to movements of species is crucial to reduce the likelihood of future introductions. Recently, Lockwood et al. (2019) showed that the pet trade of exotic species contributed to the introduction of non-native species worldwide by analysing information across taxa and research disciplines. Linking wild occurrences of invasive species with the introduction pathways such as escapes from aquaculture (Olenin et al. 2008), the releases from pet trade (Chucholl 2013; Patoka et al. 2015; Faulkes 2015) or through educational material (Larson and Olden 2008) is crucial to prevent new emerging alien species in wild. This review shows how multitude long- and short-distance translocations, many of them unreported, have shaped the current distribution of the RSC, the largest for any freshwater crayfish worldwide. The history of this global-scale invasion can be used as a world benchmark for future invasions involving commercially exploited species by helping managers and policy makers to design and implement efficient management strategies such as the implementation of control measures on commercial activities which involve translocations of live specimens. Furthermore, invasive species policies are generally applied at national or smaller scales, often being inconsistent across countries (Peters and Lodge 2009), when movements of alien species are a global issue (Hulme 2009). More efforts should be put in the use of high-impact freshwater species in aquaculture, ornamental and academic purposes, reducing drastically their availability for trade. Additionally, commercial supply companies could play a determining role in raising awareness to potential keepers of invasive species which may end up being released into the wild or escaped.

Synthesis and future perspectives

We have described the global-scale, century-lasting invasion process of one of the most harmful invasive species worldwide. Our review combined literature search and hundreds of records from biodiversity databases to show how and why the RSC has expanded its range over the world during the last 95 years, including an exhaustive description on the invasion process in all countries where the RSC is, or is suspected to be, established (see full details in Supplementary Material). Finally, we also pointed out some of the potential pathways of introduction for the RSC and discussed the relevant role of commercial suppliers in the translocation of live-specimens worldwide. Our conclusions are also useful for any other freshwater alien species commercially exploited by humans.

Although we conducted an exhaustive literature search (scientific and grey literature) on the RSC, issues associated to old literature (e.g., local language or regional reports are hard to find) could have caused information gaps in some invaded areas resulting in biased or underestimated crayfish distribution. Specifically, we were unable to find literature or introduction reports in the first 50 years of the RSC presence in China, albeit the species was allegedly restricted to the first introduction area (Xinya 1988). Information on RSC distribution in Africa seemed to be spatially-biased, because many studies focused on Kenya but introduction reports for other African countries were scarce and sometimes unclear (e.g., South Africa, Sudan or Zambia; see Appendix II in Supplementary Material). Therefore, further studies on less represented regions (e.g., Asia or Africa) may acquire information of species distribution data from additional sources such as museum collections which provide an important coverage of species' ranges mainly for the past species' distributions (see Boakes et al. 2010). Another alternative would be to work with local experts who can supply accurate data on past species distribution. While a lot of information is available in public databases, occurrence or introduction reports are sometimes incomplete or inaccurate (e.g., imprecise geographical coordinates or lack of verification by experts). Even so, we wish to encourage administrations to develop citizen science projects that involve people in the early detection and spread of invasive species (e.g., iNaturalist). Early detection and rapid action response is a cost-effective way of preventing establishment of alien species and avoid devastating impacts in the future.

Acknowledgements We are grateful to Biblioteca Campus Cartuja for providing us old literature which was not available online. We also thank David Aragonés from Laboratorio de SIG y Teledetección (LAST-EBD) at Estación Biológica de Doñana (CSIC) and three anonymous reviewers for their valuable comments on the first draft of the manuscript. F.J.O. was supported by a grant associated to the project (RNM-936) funded by the Andalusian Government.

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