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REVIEW

A Review of Freshwater Crayfish Introductions in Africa

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ABSTRACT

This review summarizes and analyses information on freshwater crayfish introductions in Africa. A total of 136 research papers and reports were found to be relevant. Forty-eight percent reported presence; 21% described negative impacts; 11% referred to potential socio-economic benefits; 9% evaluated control measures; 6% documented co-introduced parasites. Out of nine introduced crayfish species, five species *Astacus astacus*, *Cherax quadricarinatus*, *Faxonius limosus*, *Procambarus clarkii*, and *Procambarus virginalis* have established populations in the wild. *Astacus astacus* and *F. limosus* are present only in Morocco and *P. virginalis* is limited to Madagascar. *Cherax quadricarinatus* and *P. clarkii* have established populations in five and six countries, respectively. The main driver of crayfish introductions was to provide socio-economic benefits through aquaculture and fisheries development but there is limited evidence of success. Prevailing negative socio-economic impacts are linked to damage to agricultural water infrastructure, damage to fishing gear and declining fisheries performance. Ecological impacts pertain to direct and multi-trophic consumptive effects as well as indirect competitive effects primarily upon macro-invertebrates and potential spillover of parasites to other decapods. Research priorities are determining abundance, distribution and spread of crayfishes and assessing ecological impact to inform management decisions.

KEYWORDS
Freshwater; impacts; invasive crayfish; native biodiversity; spread; invasion management

Introduction

Freshwater crayfishes include more than 640 described species that are naturally distributed in all continents except mainland Africa and Antarctica (Crandall and Buhay 2008). Freshwater crayfish have been introduced into all continents except Antarctica (Lodge et al. 2012). Intentional introductions have been for fisheries enhancement (Audenaerde 1994; Foster and Harper 2007; Nunes, Zengeya, Measey et al. 2017), aquaculture (Lodge et al. 2012; Souty-Grosset and Fetzner 2016), and the pet trade (Lodge et al. 2012; Twardochleb et al. 2013; Souty-Grosset and Fetzner 2016). Unintentional introductions have occurred as stowaway propagules or via spread through interconnected waterways (Lodge et al. 2012).

Generally, freshwater crayfish species exhibit broad tolerances to a wide range of environmental conditions (Lodge et al. 2012), which, together with their large individual adult size, high fecundity and omnivorous trophic position (Hobbs and Lodge 2010), has facilitated their establishment and spread in a wide variety of freshwater habitats globally (Hobbs et al. 1989; Lodge et al. 2012; Twardochleb et al. 2013). Where present, freshwater crayfish tend to dominate invertebrate biomass (de Moor 2002; Geiger et al. 2005; Gherardi 2007) and, in their invasive range, they tend to exert an overall negative ecological impact on native biodiversity evidenced by reductions in the abundance of macrophytes, aquatic invertebrates, amphibians, and fishes (Twardochleb et al. 2013).

Mainland Africa is naturally devoid of freshwater crayfish species (Crandall and Buhay 2008; Lodge et al. 2012), in this region decapods in freshwater ecosystems are largely represented by potamonautid crabs (Wood et al. 2019). It is hypothesized that the absence

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of native crayfish in mainland Africa is either a result of evolutionary competition with freshwater crabs (Ortmann 1902; Lodge et al. 2012; Souty-Grosset and Fetzner 2016) or that they never evolved there to begin with (Souty-Grosset and Fetzner 2016). In contrast, Madagascar has seven endemic crayfish species of the genus *Astacoides* which are phylogenetically distinct from all other currently described crayfish species (Boyko et al. 2005; Ganzhorn et al. 2013) and are endemic to an inland area of about 60,000 km^2 in the southeast highlands of Madagascar (Boyko et al. 2005). The presence of crayfish on Madagascar is likely due to the unique evolutionary dynamics and paleogeography of the island which has been separated from mainland Africa since the breakup of Gondwana in the Toarcian period around 160 million years ago (Biswas 2008).

There is evidence that nine crayfish species have been introduced into Africa: the noble crayfish *Astacus astacus* (Linnaeus 1758), smooth marron *Cherax cainii* Austin and Ryan 2002, yabby *Cherax destructor* Clark 1936, Australian redclaw crayfish *Cherax quadricarinatus* (von Martens 1868), spiny cheek crayfish *Faxonius limosus* (Rafinesque 1817), American signal crayfish *Pacifastacus leniusculus* (Dana 1852), Louisiana red swamp crayfish *Procambarus clarkii* (Girard 1852), marbled crayfish *Procambarus virginalis* (Lyko 2017), and White River crayfish *Procambarus zonangulus* Hobbs and Hobbs 1990 (see https://www.cabi.org/isc/ and https://www.gbif.org/). Information on the introductions of these species, their status and distribution in different African countries, is scattered. In addition, given the evidence of ecological impacts on recipient ecosystems elsewhere (Lodge et al. 2012; Twardochleb et al. 2013), it is important that the consequences of these introductions are evaluated to assess the extent of their impacts and inform their management (Lodge et al. 2012).

This review summarizes and analyses information on all crayfish introductions in Africa (including Madagascar and the island states), their pathways of introduction into each country and spread into the wild, as well as their current status, distribution, and reported impacts. This study compiles current information to better understand the reasons and pathways that have driven these introductions, improve the understanding of the nature and magnitude of the environmental impacts they have generated, and identify knowledge gaps to better prioritize their management and, ultimately, avoid further introductions.

This systematic review was conducted following the guidelines for Preferred Reporting Items for Systematic reviews and Meta-Analyses (PRISMA) (see Moher et al. 2009), which include the establishment of a search protocol, data inclusion, data extraction, and analysis. The search protocol was undertaken using both the Institute of Scientific Information (ISI; Thomson Reuters) Web of Science online database and the SCOPUS database. These databases were used to search for English literature containing relevant information on crayfish species and introductions in Africa, published through to the end of 2019. For this, the search terms included the keyword combinations "crayfish"* AND "Africa."* With the aim of potentially retrieving additional relevant publications on this topic, given the number of lusophone and francophone countries in the region, the scope of the search protocol was enlarged to include articles published in Portuguese and French. In a similar manner to the English literature procedure, in March 2020 a search was carried out using the same terms, but in the two different languages ("lagostim" AND "Africa" in Portuguese, and "écrevisse" AND "Afrique" in French), in both ISI Web of Science and SCOPUS. Due to the extremely limited (or non-existent) number of results obtained for the searches in the two languages in these databases (see *Results* below), an additional search was undertaken in Google Scholar using the same search terms. As Madagascar is the only country in Africa with native crayfishes, the literature considered in the analysis was for introduced crayfish species only.

The potential of each publication to contribute relevant information to this systematic review was subsequently examined. Publications that were clearly not related to the topic under study were excluded based on their title, abstract or after a careful reading of the entire text, if necessary (Pereira et al. 2019). Studies that were not possible to fully access online were requested from authors by e-mail. After examining all the articles selected by the inclusion criteria, the reference lists of all publications were checked for additional relevant articles and gray literature (Pereira et al. 2019). Those which were not found in previous searches were then included in the analysis. Grey literature is reported as "unpublished data" and compiled as supplemental data (Supplemental data 1).

After article examination, the countries where crayfishes were reported, the year reported, the crayfish species reported, the pathway of introduction/spread and the distribution in the country, where available, were recorded. The articles were further categorized

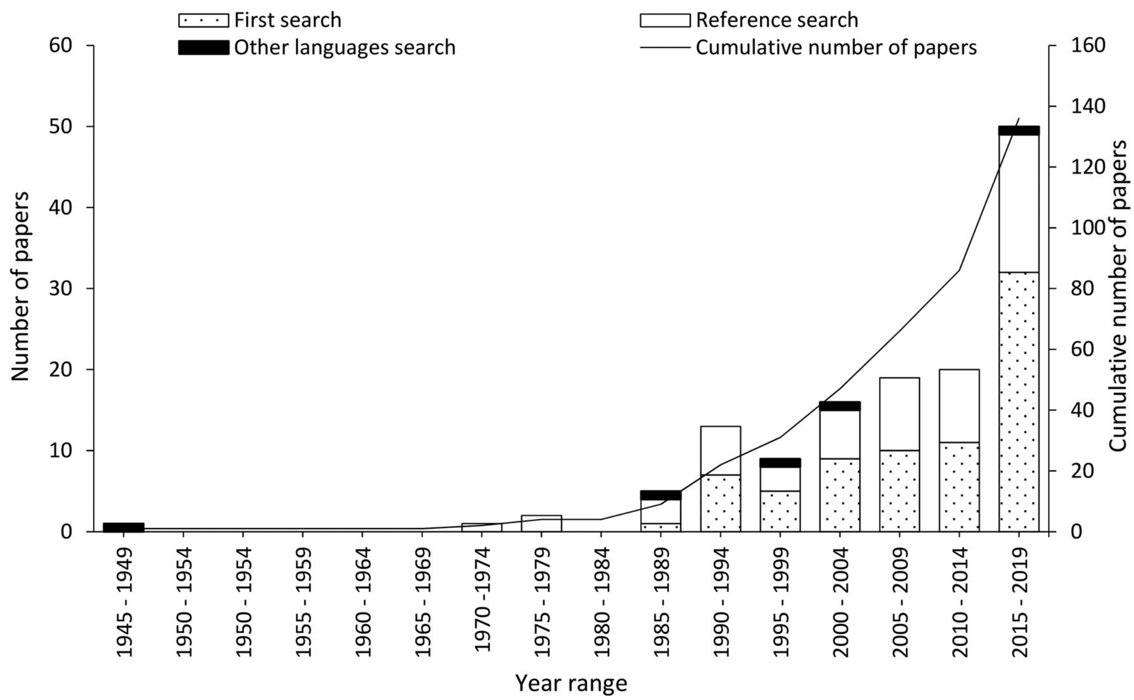

Figure 1. Number of papers (and cumulative number of papers) found in the English (first and references search) and other languages search (French and Portuguese) referring to crayfish introductions in continental Africa from 1948 to 2019.

according to the information generated by each study under the following headings: (1) introduction, distribution and spread; (2) co-introduced parasites; (3) impacts; (4) socio-economic benefits; (5) control. As many of the publications reviewed address several of these topics, a single article could be categorized under various headings.

Results

Literature search

Results presented herein are based on the total number of articles found in the ISI Web of Science and SCOPUS databases, and in Google Scholar for the Portuguese and French language searches, that matched the inclusion criteria (Pereira et al. 2019), as well as in the literature obtained from the reference lists of the selected publications.

The search of English literature on the Web of Science database resulted in 420 articles, of which only 75 matched the inclusion criteria. The same search on the SCOPUS database resulted in 52 articles, all of which had already been retrieved from the ISI Web of Science search, hence, only results from the ISI Web of Science were used in this study. An additional 56 articles of interest, which were initially not found in any of the databases but were, however, sourced from the initial searched articles reference lists, were included in the final results.

Regarding the searches of literature in Portuguese and French, no results were found in the ISI Web of Science database. The search performed in SCOPUS yielded 12 results in Portuguese and nine results in French, but none of those were relevant for this study. The search performed using Google Scholar produced 425 results in Portuguese, none of which were of relevance to this review. The same search in French showed 3210 results, although, Google Scholar only displays the first 1000 search records which, in this case, were actually limited to 850 results. Out of these 850 results, only five articles were relevant for this study, and their reference lists did not generate any additional relevant articles.

The earliest paper included in the present study was published in 1948 and described the introduction of crayfish species in Morocco. Since then, the number of papers studying invasive crayfish in continental Africa has been increasing, with a steady increase especially since 1988, and with most papers published in the period 2015–2019 (Figure 1). Forty-five percent of the papers reported on crayfish presence, distribution and spread; 6% reported on co-introduced parasites associated with their introductions; 11% of the articles assessed crayfish impacts; 31% referred to their socio-economic benefits; and 8% reported on crayfish control.

Introduction, establishment, and spread

From the literature search, there is evidence for the introduction of nine crayfish species into Africa.

Table 1. *Astacus*, *Faxonius*, and *Pacifastacus* species introduced to continental Africa, their native range, country of introduction, year, purpose, and location where they were introduced, date, and pathway of observations in the wild, location, and their current status in each country.

		Introductions into the country			Wild populations			
Species/native range	Country	Year	Purpose	Location	Date reported	Pathway	Location	Status
Astacus astacus Noble crayfish/Europe	Morocco	1914[a]	Fisheries	Jdida River	Failed	Release	Morocco	1914[a]
Faxonius limosus Spiny-cheek crayfish/ Eastern USA	Morocco	1937[b]	Fisheries	Lakes Roumi and Ifrah	Failed[b]			
		1940[c]	Fisheries	Lake Ifrah	1940s	Release	Lake Ifrah	Established in Lake Ifrah and several systems in the middle Atlas mountains[c]
		1948[d,e]	Fisheries	Lake Iffel	Late 1940s	Release	Lake Iffel	Established in Lake Iffel and several systems in the middle Atlas mountains[d,e]
Pacifastacus leniusculus American signal crayfish/ Northwestern USA	South Africa	1988[f]	Pet trade	Pet shops	No current records in captivity or wild[f]			

Sources:
[a]Benabid and Khodari (2000).
[b]Mouslih (1987).
[c]Vivier (1948).
[d]Melhaoui (Unpublished data).
[e]Tabib (Unpublished data).
[f]Nunes, Zengeya, Hoffman et al. 2017.

These are three Australasian Parastacidae species, *Cherax quadricarinatus*, *Cherax cainii*, and *Cherax destructor*; five North American Cambaridae species, *Procambarus clarkii*, *Procambarus virginalis*, *Procambarus zonangulus*, *Pacifastacus leniusculus*, and *Faxonius limosus*; and a European Astacidae species, the European noble crayfish *Astacus astacus*. Of the nine introduced species, there is evidence for establishment in the wild of five species: *A. astacus*, *C. quadricarinatus*, *F. limosus*, *P. clarkii*, and *P. virginalis*. Details of these crayfish introductions are reviewed by country (in chronological order) below and are summarized in Tables 1–3. Internal translocations between African countries of *C. quadricarinatus* and *P. clarkii* are shown in Figures 2 and 3. Geo-referenced locality data are provided as supplemental data to this manuscript (Supplemental data 2).

Morocco

Four freshwater crayfish species were introduced into Morocco for fisheries enhancement and for aquaculture (Tables 1–3). The first crayfish introduction into Morocco was *A. astacus* (Mouslih 1987; Benabid and Khodari 2000). This species was first introduced from France into the Ifrane province in 1914 as a personal initiative of Captain Belouin, Commander of the '21e Compagnie du '2e Étranger' and released into the Jdida River near Meknés (Mouslih 1987; Benabid and Khodari 2000). Although, this introduction appears to have failed, *A. astacus* were imported again in 1930 from the Paris region (France) and introduced into the Zerrouka and Tizguit rivers (Mouslih 1987). Establishment of *A. astacus* was successful in these rivers as well as in several associated impoundments (Mouslih 1987). Other subsequent introductions relate to the active production, stocking, and aquaculture of *A. astacus* by national agencies (Benabid and Khodari 2000). This includes the documented introduction of 2500 juveniles of the species from Germany in 1992 (Benabid and Khodari 2000). As a result, *A. astacus* is presently established in the Middle Atlas Mountains and parts of the Tizguit, Zerrouka, Sidi Mimoun, Ras-el-Ma, and Ben Smim River basins and associated impoundments (Chillasse et al. 2001; CABI 2020; Tabib Unpublished data).

In 2002, *C. quadricarinatus* was imported from Australia to a commercial fish farm in the Tangier region of Morocco (Fish Consulting Group Unpublished data). In 2014, this species was still in the experimental production phase and there is currently no evidence of Moroccan *C. quadricarinatus* being marketed, either nationally or internationally (Fish Consulting Group Unpublished data). No *C. quadricarinatus* have been reported in the wild in Morocco.

In 1937, *F. limosus* was introduced into lakes Roumi and Ifrah (Meknes region), but without success (Mouslih 1987). The first successful introduction was in 1940 into Lake Ifrah, where it soon established. In 1948, the Fishing Club of Fez introduced specimens from the

Table 2. *Cherax* species introduced to continental Africa, their native range, country of introduction, year, purpose, and location where they were introduced, date, and pathway of observations in the wild, location, and their current status in each country.

		Introductions into the country			Wild populations			
Species/native range	Country	Year	Purpose	Location	Date reported	Pathway	Location	Status
Cherax cainii Smooth marron/ Australia	South Africa	1976–19851[a]	Aquaculture	Several farms in Western Cape, Free State, Eastern Cape, Kwazulu Natal, and North West provinces	Only present in captivity at Smiling Valley Aquaculture farm[a]			
	Zambia	Early 1990s[b]	Aquaculture	Grubb Farm, Livingstone, upper Zambezi River	No current records in captivity or wild[b]			
Cherax destructor Yabby/ Australia	South Africa	1988[a]	Aquaculture	Kept at RAU, Randfontein farm in Gauteng Province and Gariep Dam Fisheries Station in Free State Province	No current records in captivity or wild[a]			
	Zambia	1992[b]	Aquaculture	Fish farm, Livingstone, upper Zambezi River	No current records in captivity or wild[c]			
Cherax quadricarinatus Australian redclaw crayfish/ Australia and Papua New Guinea	Morocco	2002[d]	Aquaculture	Fish farm in the Tangier region	Still in captivity for aquaculture[d]			
	Swaziland	Late 1990s[a,e]	Aquaculture	Farm next to Sand River Dam	2016	Escape	Sand River Dam	Established in the Sand River Dam and Mbuluzi River[a,e]
		Late 1990s[a,e]	Aquaculture	Farm near Manzini	2016	Escape	Usutu River	Established in the Usutu River[a,e]
	South Africa	[a]1988	Research	Zoology Department of the RAU	No records in captivity or wild establishments[a]			
		[a]1980s	Aquaculture	Farm in Western Cape	Farmer denied permits from South African Authorities to farm *C. quadricarinatus* and established farm in Swaziland[a]			
			Natural spread from Sand River Dam, Swaziland		2002	Unaided	Komati River	Established in the Inkomati Basin[a,e]
			Natural spread from Usutu River catchment, Swaziland		2016	Unaided	Usutu River	Present in Usutu River, Lake Nyamiti, and Pongola River[a,e]
	Zambia	1992[c]	Aquaculture	Miengwe Farm, Upper Kafue catchment	No current records in captivity or wild[c]			
		2001[c]	Aquaculture	Fish farm, Eastern end of the Kafue Flats	2001	Escape	Kafue River	Established in Kafue River and Lake Itezhi-tezhi[c]
		2001[c]	Aquaculture	Aquaculture cages at Siavonga, Lake Kariba	2002	Escape	Siavonga Lake Kariba	Established in Lake Kariba[c]
		2012[c]	Culture for consumption	Tank at Lealui in Mongu, Barotse flood plain	2014	Escape	Lealu Mongu	Established in the Barotse floodplain. Present in the Upper Zambezi River[c]

(Continued)

Table 2. Continued.

		Introductions into the country			Wild populations			
Species/native range	Country	Year	Purpose	Location	Date reported	Pathway	Location	Status
	Zimbabwe		Unaided pathway from Siavonga Lake Kariba, Zambian side		2011	Unaided	Sanyati Basin, Lake Kariba	Established Lake Kariba, present in the Zambezi River downstream of Lake Kariba[f] Also present in Sebakwe Dam[g]
	Mozambique		Unaided pathway from Usutu River catchment, Swaziland		2009	Unaided	Mbuluzi River	Established in Pequenos Libombos reservoir[h]
			Unaided pathway from the middle Zambezi system		2013	Unaided	Garganta basin, Lake Cahora Bassa	Present in Lake Cahora Bassa[c]
	Namibia		Unaided pathway from Upper Zambezi		2016	Unaided	Zambezi River Katima Mulilo	Present in the Zambezi River in Katima Mulilo, Namibia[c]
	Mauritius	Late 1980s–1980s[i]	Aquaculture	Kept at a farm in Mauritius for aquaculture trials	No current records in captivity or wild[i]			

Sources:
[a]Nunes, Zengeya, Measey et al. (2017).
[b]Mikkola (1996).
[c]Douthwaite et al. (2018).
[d]Fish Consulting Group (Unpublished data).
[e]Nunes, Zengeya, Hoffman et al. (2017).
[f]Marufu et al. (2014).
[g]AT. Chakandinakira (Department of Fisheries, Zimbabwe pers. comm. 2019).
[h]Chivambo et al. (2019).
[i]New and Kutty (2010).

Table 3. *Procambarus* species introduced to continental Africa, their native range, country of introduction, year, purpose, and location where they were introduced, date, and pathway of observations in the wild, location, and their current status in each country.

		Introductions into the country			Wild populations			
Species/native range	Country	Year	Purpose	Location	Date reported	Pathway	Location	Status
Procambarus clarkii Louisiana red swamp crayfish/Northern Mexico, and Southern and Southeastern USA	Egypt	1980[a]	Aquaculture	Fish farm in Manial Sheeha	1980s	Escape	Nile River	Established in the Nile River[a]
	Kenya	1966[b]	Fisheries and disease control	Solai and Subukia dams	Late 1960s	Release	Solai and Subukia dams	Established in Solai and Subukia dams and Eldoret river system[b]
		1970[b]	Fisheries	Lake Naivasha	1973	Release	Lake Naivasha	Established in Lake Naivasha and its tributaries[b]
	Morocco	Late 90s–early 2000s[c]	Fisheries	Nador canal, Merja Zerga	2010	Release	Nador canal, Merja Zerga	Established in the Merja Zerga, Merja Fouwarate and Nador Canal[c,d]
	Rwanda	Unknown	Biocontrol	Mukungwa Valley	2014	Release	Mukungwa Valley	Present in Mukungwa Valley[e]
	South Africa	1962–19876	Pet trade	Pet shops in cities	No current records in captivity or wild[f]			
		1980s[f,g]	Fisheries	Driehoek Farm, Dullstroom Mpumalanga Province	1988	Release	Valleijspruit and Berry Dams	Present in Dullstroom farm ponds in the Crocodile River catchment[f,g]
		2016[h]	Sport and angling	Pet shops	2018	Release	Mimosa dam	Established in Mimosa Dam[h]
	Sudan	1975[i]	Unknown	Unknown systems in Sudan	No current records in captivity or wild[i]			
		Unaided pathway from Nile River, Egypt[j]			2019	Unaided	White Nile River	Present in the White Nile River[j]
	Tunisia	2014[k]	Sport and angling	Gombare Lake	2014	Release	Gombare Lake	Present in Gombare Lake, Lake Guitoune and Lebna dam[k]
	Uganda	1966[b]	Fisheries	Lake Bunyonyi	1966	Release	Lake Bunyonyi	Established in Lake Bunyonyi[b]
	Zambia	1979[l]	Aquaculture	Farm near Kitwe in Livingstone	No current records in captivity or wild[l,m]			
		1979[m]	Aquaculture	Farm in Livingstone	1995	Escape	Maramba River	Present in Maramba River[m]
Procambarus virginalis Marbled crayfish/ Marmorkrebs/No native range	Madagascar	2003[n]	Unknown	Ambohimangakely village	2003	Release	Ditches, fields, ponds in Ambohimangakely village	Present in several habitats from the central highlands to the east coast of Madagascar[n,o]
Procambarus zonangulus White River Crayfish/ South central USA	Egypt	1980[a]	Aquaculture	Fish farm in Manial Sheeha	1980s	Escape	Nile River	Got outcompeted by *P. clarkii*[a]

Sources:
[a]Ibrahim and Khalil (2009).
[b]Foster and Harper (2007).
[c]Yahkoub et al. (2019).
[d]Sara and El Moutaouaki (2019).
[e]Seburanga et al. (Unpublished data).
[f]Nunes, Zengeya, Measey et al. (2017).
[g]Nunes, Hoffman et al. (2017).
[h]Barkhuizen et al. (Unpublished data).
[i]National Research Council (Unpublished data).
[j]SEMA. Makawi (University of Khartoum pers. comm. 2019).
[k]Bouaoud et al. (2020).
[l]Mikkola (1996).
[m]Douthwaite et al. (2018).
[n]Jones et al. (2009).
[o]Andriantsoa et al. (2019).

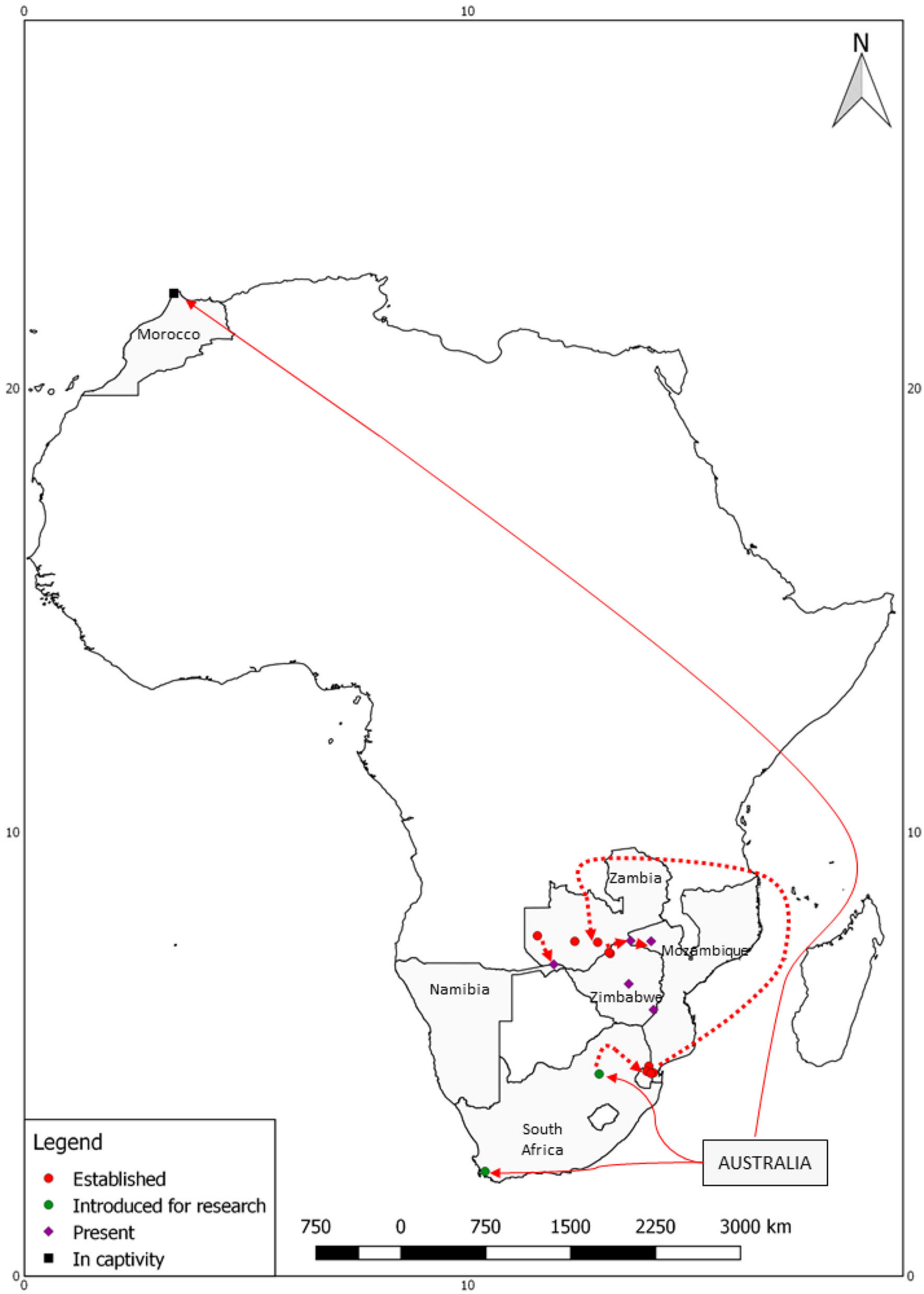

Figure 2. Introduction routes of *Cherax quadricarinatus* from Australia to Africa and introduction locations within the continent. Dashed red lines show translocations within the African continent whilst the continuous red line shows introductions from outside the continent.

Seine, in Paris, to Lake Iffel near the town of Fez (Vivier 1948). As a result of intentional introductions and natural spread, *F. limosus* is now widely established in Morocco, particularly at altitudes between 1000 and 2200 m, where it has successfully established in several natural lakes in the Middle Atlas region (Holdich and Black 2007; Melhaoui Unpublished data; Moroccan Farmer Unpublished data; Tabib Unpublished data).

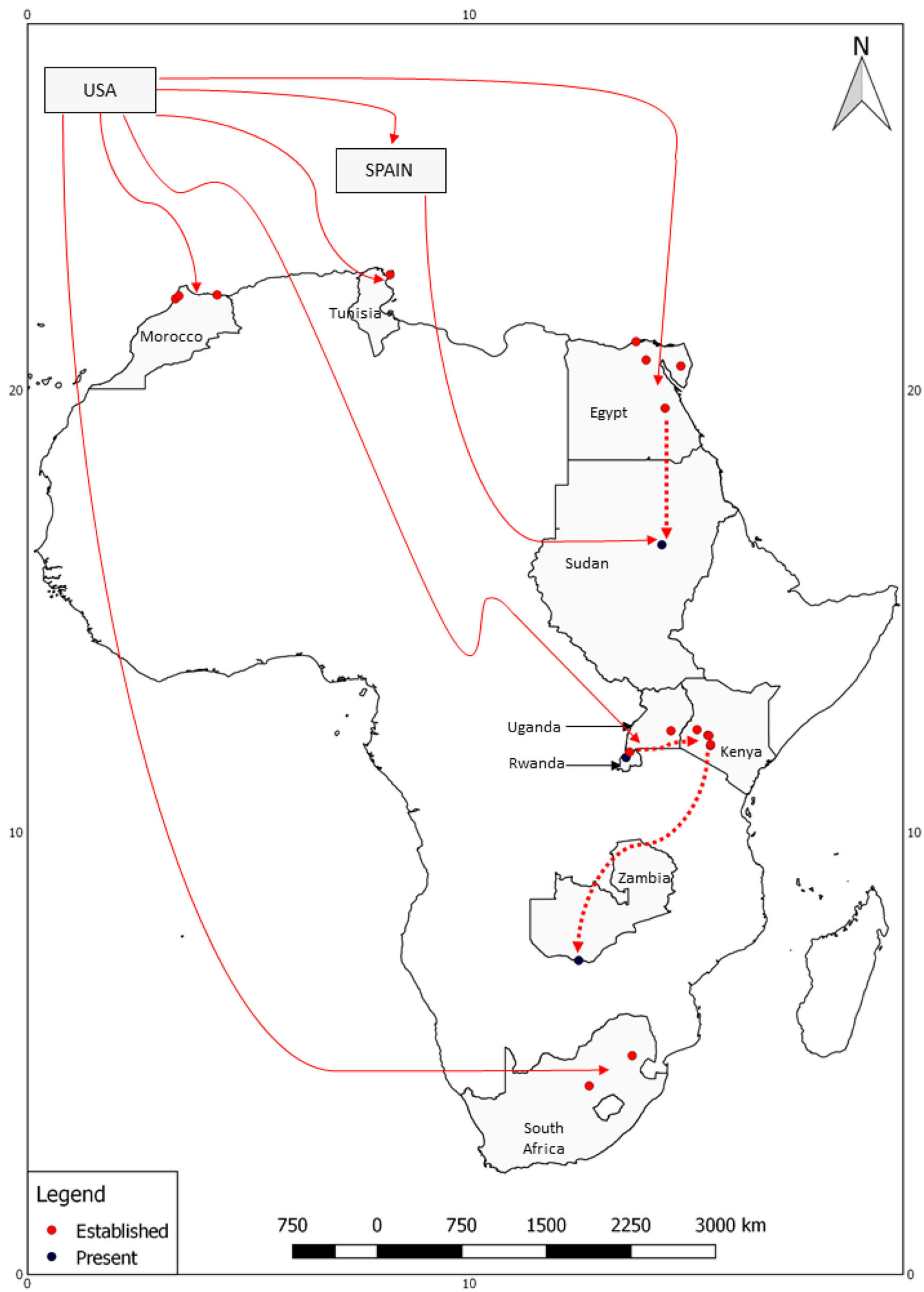

Figure 3. Introduction route of *Procambarus clarkia* from North America to Africa and introduction locations within the continent. Dashed red lines show translocations within the African continent whilst the continuous red line shows introductions from outside the continent.

Juvenile *P. clarkii* specimens were illegally introduced into the Nador Canal (Gharb region) and the Low Loukkos Marshes (Larache region) in the late 1990s or early 2000s by an owner of an eel farm in Kenitra (Yahkoub et al. 2019). Local fishermen first observed the species in the Nador Canal in early 2010

(Yahkoub et al. 2019). Populations of *P. clarkii* established in both localities and the species is now widespread and abundant in the Gharb region where it has invaded tidal lagoons (e.g., Merja Zerga, Merja Fouwarate) and marshes (El Qoraychy et al. 2015; Sara and El Moutaouakil 2019; Yahkoub et al. 2019). Wetland sites on the Rmel plateau and Bas Loukous in the north-western coast of Morocco are also invaded by *P. clarkii* (Sara and El Moutaouakil 2019).

Egypt

Two crayfish species, *P. clarkii* and *P. zonangulus*, have been introduced into Egypt for aquaculture in the 1980s (Ibrahim and Khalil 2009) (Table 3).

Specimens of *P. clarkii* were introduced from the United States of America (USA) to a private fish farm at Giza governorate in Manial Sheeha, from here they accidentally escaped into the adjacent Nile River (Ibrahim et al. 1995). The species has been spreading rapidly throughout all aquatic ecosystems in Egypt since the 1980s. It is now established in aquatic systems from Giza to the whole Delta region in the north, and to Qena governorate in the south (Ibrahim et al. 1995; Hamdi 2011). In addition, *P. clarkii* has established populations in ditches in the Sinai desert due to connectivity facilitated by irrigation systems (Ibrahim and Khalil 2009; Khalil and Sleem 2011).

In the Nile River, *P. clarkii* accidentally escaped together with *P. zonangulus* (Ibrahim and Khalil 2009). For some time both species coexisted in mixed populations within many localities along the Nile River, although, *P. clarkii* was more abundant than *P. zonangulus* (Ibrahim and Khalil 2009). More recent surveys, however, suggest that *P. zonangulus* has disappeared completely from the Egyptian water bodies (Ibrahim and Khalil 2009).

Sudan

In 1975, *P. clarkii* was introduced to Sudan from Spain (National Research Council Unpublished data). This species also spread from the Nile River and is said to be present in the White Nile River close to Jebel Aulia Dam (SEMA. Makawi, University of Khartoum, Sudan pers. comm. 2019).

Uganda

The only crayfish species present in Uganda is *P. clarkii* (see Foster and Harper 2007). In 1966, *P. clarkii* imported from the USA was cultured at Fisheries Resources Research Institute/National Agricultural Research Organisation's ponds at Kajjansi near Entebbe and Lake Victoria (Lowery and Mendes 1977), where it was still present in 2006 (Foster and Harper 2007). The species is established in Lake Bunyonyi (Southwest Uganda), where it is exploited for the local restaurant trade (Foster and Harper 2007). This species could be quite widespread in Ugandan freshwater systems, but under-recorded, and may even have colonized the periphery of Lake Victoria (Foster and Harper 2007). Furthermore, anecdotal records suggest that *P. clarkii* may have established in the Kagera River, which enters Lake Victoria on the Uganda–Tanzania border (Foster and Harper 2007). Presently, *P. clarkii* is abundant in Lake Bunyonyi and around its catchment (Kabiza Wilderness Safaris pers. comm. 2019).

Kenya

The Kenyan Fisheries Department first introduced *P. clarkii* in 1966 from Uganda Fisheries Department Ponds at Kajansi near Entebbe, Uganda, with the intention to enhance commercial fisheries in dams and lakes in the area (Lowery and Mendes 1977; Oluoch 1990; Mikkola 1996). The secondary reason for introduction in Kenya was as a biocontrol agent for gastropod vectors of schistosomiasis (Hofkin et al. 1991). An unspecified number of *P. clarkii* were introduced to two dams located at Solai and Subukia, within the Rift Valley (Oluoch 1990). This species was also further introduced to various farm dams and ditches, as well as the streams and rivers draining these dams across Kenya, including the catchment area of the Nzoia River draining to Lake Victoria (Lowery and Mendes 1977). Since 1991, *P. clarkii* has also been recorded in abundance at Eldoret, on the Eldoret river system (Foster and Harper 2007).

Around 1970, approximately 300 *P. clarkii* were introduced into Lake Naivasha, near Marina Bay, from Subukia Dam (Oluoch 1990), to provide food for the introduced largemouth bass *Micropterus salmoides* (Foster and Harper 2007). In the immediate eastern basin of the lake, as well as in Marina Bay, *P. clarkii* established and thrived, reaching a density of three adult individuals per m^2 within three years (Lowery and Mendes 1977). In 1975, a commercial fishery was opened for *P. clarkii* in Lake Naivasha (Mikkola 1996) and by 1977, *P. clarkii* was prevalent throughout the lake (Oluoch 1990). Presently, *P. clarkii* is widely distributed throughout Lake Naivasha and its tributaries (Jackson et al. 2016).

Rwanda

The only recorded report of *P. clarkii* in Rwanda was in the Mukungwa Valley where it was introduced to control the invasive water hyacinth (Seburanga et al Unpublished data). There are no further details on its establishment and spread in Rwandan freshwater systems.

Swaziland

There are anecdotal reports that two *C. quadricarinatus* batches were introduced from Australia to Swaziland, one at a farm located near the Sand River Dam, close to the Komati River and the other to a farm near Manzini or Big Bend, in the Usutu River catchment (Nunes, Zengeya, Hoffman et al. 2017). The farm located near the Sand River Dam was granted a permit in the late 1990s and successfully established. Crayfish subsequently escaped from captivity into the Sand River Dam and later spread via the Sand River into the Komati River, a transboundary river that flows through Swaziland and South Africa (de Moor 2002; de Moor 2004; Nunes, Zengeya, Hoffman et al. 2017). The further detection of *C. quadricarinatus* in an outlet of Lake Nyamiti, in the Ndumo Game Reserve (South Africa) in 2012, and the fact that in 2015 the species was established in the Usutu River close to Big Bend, implies that crayfish also escaped from the other aquaculture farm close to Manzini (in the Usutu River catchment) (Nunes, Zengeya, Hoffman et al. 2017; Nunes, Zengeya, Measey et al. 2017). This species has also colonized a large area of the Mbuluzi River and its tributary Mlawula (Nunes, Zengeya, Hoffman et al. 2017).

South Africa

The literature on crayfish invasions in South Africa, from the first introductions up to 2017, are well summarized in Nunes, Zengeya, Measey et al. (2017). Six crayfish species have been imported into South Africa: *P. clarkii*, *C. quadricarinatus*, *C. cainii*, *C. destructor*, *P. leniusculus*, and *Astacus* sp. (Tables 1–3). Pet trade in the 1980s resulted in the illegal importation of *P. clarkii*, *P. leniusculus* and *Astacus* sp. into South Africa (de Moor and Bruton 1988). Legal introductions brought *Cherax cainii* into South Africa for aquaculture initiatives, while *C. destructor* and *C. quadricarinatus* were imported for research purposes in 1988 (see Nunes, Zengeya, Measey et al. 2017). There is evidence for the establishment of two species in the wild, *P. clarkii* and *C. quadricarinatus*.

In 1976, *C. cainii* was imported and introduced into South Africa by a private fish farmer in KwaZulu-Natal for aquaculture purposes, although, this venture was short-lived (de Moor and Bruton 1988). Several farmers developed an interest to venture into *C. cainii* farming and applied for permits, and several consignments of *C. cainii* were imported from Western Australia into South Africa (Mitchell and Kock 1988; van den Berg et al. 1990). Farming of *C. cainii* was somewhat unsuccessful and currently, only two farms are operational and located in the Eastern Cape Province (Nunes, Zengeya, Measey et al. 2017). There are currently no reports of *C. cainii* in the wild (Nunes, Zengeya, Measey et al. 2017), despite *C. cainii* individuals being detected in the Buffalo River in the 1980s as a result of aquaculture escape (de Moor and Bruton 1988). *Cherax destructor* was introduced in 1988, together with *C. quadricarinatus*, from Australia into South Africa for experimental research (see Nunes, Zengeya, Measey et al. 2017). While there are anecdotal records of *C. destructor* introductions by fishermen into several South African dams, there are no records of *C. destructor* in the wild in South Africa (Nunes, Zengeya, Measey et al. 2017).

In 1988, *C. quadricarinatus* was imported into South Africa for research on its aquaculture potential at the Rand Afrikaans University (RAU, now University of Johannesburg) (see Nunes, Zengeya, Measey et al. 2017). South Africa imposed biosecurity restrictions on importation and culturing of *C. quadricarinatus*, so instead a farmer established a *C. quadricarinatus* farm next to the Sand River Dam in neighboring Swaziland, from where specimens later escaped and spread into South Africa (Nunes, Zengeya, Hoffman et al. 2017; Nunes, Zengeya, Measey et al. 2017). The first record of *C. quadricarinatus* in South African freshwater systems was in 2002, in the Komati River, Mpumalanga Province, close to the Swaziland border (see Nunes, Zengeya, Hoffman et al. 2017). Recently, Nunes, Zengeya, Hoffman et al. (2017) confirmed the widespread presence of *C. quadricarinatus* in the Komati River, and its presence in one of its tributaries, the Lomati River. This species was also confirmed to be present in the Crocodile River, although, the densities were low (Petersen et al. 2017). In 2012, *C. quadricarinatus* was detected in an outlet of Lake Nyamiti in the Ndumo Game Reserve (Du Preez and Smit 2013), probably as a result of its spread from the Usutu River in Swaziland (Nunes, Zengeya, Measey et al. 2017). In 2013 the species was caught and sold in the villages next to the Ndumo Game Reserve (Coetzee et al. 2015), which suggests high abundances in the area (Nunes, Zengeya, Measey et al. 2017).

Unconfirmed records of *P. clarkii* in South Africa are reported from 1962 and in the 1980s the species was illegally sold in pet shops (van Eeden et al. 1983).

The first *P. clarkii* populations in the wild were recorded in 1991 from two dams on a trout farm close to Dullstroom, in Mpumalanga (Schoonbee 1993). The attempt to eradicate these populations by reducing water level and physically removing specimens by hand and dipnets proved unsuccessful, as Nunes, Hoffman et al. (2017) sampled a *P. clarkii* specimen 22 years later. In 2018, a second record of a wild established population of *P. clarkii* was discovered in Mimosa Dam, a small municipal dam in Odendaalsrus, Goldfields, Free State Province (Barkhuizen et al Unpublished data). This population is believed to have been introduced to provide stock for the pet trade (Barkhuizen et al. Unpublished data). Live *P. clarkii* specimens are also being illegally bred and sold as pets by aquarists and enterprising individuals in Port Alfred and Port Elizabeth in the Eastern Cape Province (J. South pers. obs. 2019).

Zambia

Four crayfish species were imported into Zambia for aquaculture: *P. clarkii*; *C. cainii*; *C. destructor;* and *C. quadricarinatus* (Audenaerde 1994). The first to be introduced was *P. clarkii* to a farm located in Livingstone in 1979 from Lake Naivasha, Kenya (Audenaerde 1994). Although, the farmer claimed that there were no *P. clarkii* escapees from his farm (see Douthwaite et al. 2018), a population of *P. clarkii* has been reported from the Maramba River, adjacent to the farm in Livingstone (Douthwaite et al. 2018). This species has been present in the river since 1995, although, never caught in large numbers (Douthwaite et al. 2018). Between 1979 and 1981, a batch of *P. clarkii* was also translocated from the farm in Livingstone to ponds near Kitwe, where cultivation failed, but there are reports that they escaped into the Kafue River (Audenaerde 1994). No established populations have however been reported from the Kafue catchment (Douthwaite et al. 2018). Another separate *P. clarkii* introduction was made to Siavonga on Lake Kariba, in 1979, but cultivation efforts there also failed (Mikkola 1996) and there have been no reports of this species from Lake Kariba (Douthwaite et al. 2018; AT Chakandinakira, Department of Fisheries, Zimbabwe pers. comm. 2019).

The three *Cherax* species were translocated from South Africa to Zambia in the early 1990s (Mikkola 1996), but only *C. quadricarinatus* has successfully established in the wild (see Douthwaite et al. 2018). Although, *C. quadricarinatus* individuals were initially taken to other sites, at unspecified times (see Douthwaite et al. 2018), the only record of establishment in the wild from these translocations is from Miengwe Farm on the upper Kafue catchment (Douthwaite et al. 2018). Additionally, in 2001, *C. quadricarinatus* was imported from a farm that was closing down in Swaziland to a fish farm at the eastern end of the Kafue Flats, from where specimens escaped (Douthwaite et al. 2018). The species has now spread to most parts of the Kafue catchment (Douthwaite et al. 2018).

Another batch of *C. quadricarinatus* imported from Swaziland were also transferred to aquaculture cages at Siavonga in Lake Kariba, from where they escaped into the lake in 2002 (Nakayama et al. 2010; Douthwaite et al. 2018). Besides this accidental escape into Lake Kariba, there are also anecdotal reports that *C. quadricarinatus* was intentionally introduced (Welz Unpublished data). Nakayama et al. (2010) showed that by 2008 *C. quadricarinatus* had established in the wild at Siavonga on the Zambian shore of the Sanyati Basin of Lake Kariba, a basin where the species is now present in high abundance (T.C. Madzivanzira pers. obs. 2018).

In the upper Zambezi River, a new population was reported to be spreading on the Barotse floodplains after their introduction near Mongu (Nunes et al. 2016). This population arose from informal aquaculture escapes, as road construction workers had been culturing *C. quadricarinatus* for their own consumption, which then escaped during the annual inundation of the floodplain (G. Chisule, Department of Fisheries, Zambia pers. comm. 2019; M. Muomba, WWF, Zambia pers. comm. 2019). Individual *C. quadricarinatus* have subsequently been reported from sites 95 km upstream (Lukulu) of the introduction point in Lealui, Mongu and 100 km downstream (Senanga) from the introduction point. In addition, *C. quadricarinatus* was also reported from a major tributary, the Luanginga River 40 km from the introduction point (TC Madzivanzira pers. obs.).

Zimbabwe

Accidental and intentional introductions of *C. quadricarinatus* in Zambia led to spread of the species into Zimbabwe and consequently establishing in Zimbabwean side of Lake Kariba and the Zambezi River downstream of the dam wall. In 2011, the species was first reported on the Zimbabwean side of the Sanyati Basin of Lake Kariba (Marufu et al. 2014), an area where it is now established and abundant (Marufu, Barson et al. 2018). This species has also been reported in the Nyaodza, Sanyati and Gache-Gache rivers, which feed into the Sanyati Basin of

Lake Kariba (AT Chakandinakira, Department of Fisheries, Zimbabwe pers. comm. 2019). This species is also present in Kanyemba on the Zambezi River below the Kariba Dam (AT Chakandinakira, Department of Fisheries, Zimbabwe pers. comm. 2019). Populations of *C. quadricarinatus* have also been reported from Mazvikadei and Claw Dams in the middle Zambezi catchment (Douthwaite et al. 2018), Sebakwe Dam in the Midlands province of Zimbabwe, as well as the Save catchment in Gonarezhou National Park, Southwest of Zimbabwe (C. Mungenge, Department of Fisheries, Zimbabwe pers. comm. 2019).

Namibia

In 2016, specimens of *C. quadricarinatus* were first observed in the Zambezi River, Katima Mulilo (Douthwaite et al. 2018). It is possible that this is a result of dispersal from the *C. quadricarinatus* invasion in Mongu, Zambia.

Mozambique

The first observation of *C. quadricarinatus* was in the Pequenos Libombos reservoir, Maputo Province, southern Mozambique during late 2009, early 2010 (Chivambo et al. 2019). Assuming this was not the result of an exceptional translocation event, the species probably spread naturally from the Inkomati Basin in Swaziland through the Mbuluzi River until the Pequenos Libombos Dam (Nunes, Zengeya, Hoffman et al. 2017; Chivambo et al. 2019). Another population of *C. quadricarinatus* was confirmed in the Garganta basin of Lake Cahora Bassa in 2015 (Douthwaite et al. 2018). The source of this population is most likely from upstream sources, which include Lake Kariba on the Zambezi River and the Kafue River in Zambia.

Tunisia

Between 2014 and 2015, *P. clarkii* was illegally introduced in the Gombare Lake catchment by aquarists (M.W. Bouaoud, University of Tunis El Manar, Tunisia pers. comm. 2020). At present, there is evidence of the establishment of the species in Gombare Lake (Bouaoud et al. 2020). Dead specimens and burrows were also observed in Lake Guitoune and Lebna reservoir, which provides evidence of their presence in these localities (Bouaoud et al. 2020) (Table 3).

Madagascar

In 2003, *P. virginalis* was introduced to Madagascar in Ambohimangakely, a village 15 km from the capital city, Antananarivo by foreign contractors working on a road building project (Jones et al. 2009). Genetic sequencing indicates that the Malagasy *P. virginalis* population originated from a German stock (Gutekunst et al. 2018). The motivation for the introduction into Madagascar freshwater systems remains unknown (Jones et al. 2009). In 2003 vendors, fishermen and farmers in Ambohimangakely confirmed observing *P. virginalis* in drainage ditches, rice fields, brick pits, and fish ponds. In 2005, *P. virginalis* was observed being sold in markets close to Antananarivo (Jones et al. 2009). In 2017, this species had colonized lakes and rice fields in the central highlands, as well as swamps close to the east coastline covering a total area of about 1,00,000 km^2 (Gutekunst et al. 2018). The invasive ranges of *P. virginalis* in Madagascar includes overlap with the natural habitats of the native *Astacoides betsileoensis* (in Andragnaroa River, central Madagascar) and *Astacoides granulimanus* (in a channel connected to a rice field in Sahavondronina, North East of Madagascar) but not yet with that of the other five native *Astacoides* species with narrow distribution ranges (Andriantsoa et al. 2019).

Mauritius

Aquaculture trials to farm *C. quadricarinatus* were carried out in the late 1990s in Mauritius (Bhikajee Unpublished data). Due to production challenges, the aquaculture ventures failed despite heavy investment by both the government and the private sectors (de Lestang Unpublished data) and culture of *C. quadricarinatus* was discontinued (New and Kutty 2010). There are no reports of freshwater crayfish in the wild.

Co-introduced parasites and diseases

Invasive alien species (IAS) have the capacity to be a vector for the introduction of other invasive species, as they often transport invasive parasites and diseases (Hulme 2014).

In South Africa, Mitchell and Kock (1988) reported the turbellarian *Temnosewellia chaeropsis* on *C. cainii* imported from Australia to commercial farms of South Africa. Avenant-Oldewage (1993) showed the potential for infection of native freshwater crabs (*Potamonautes warreni*) by non-native *T. chaeropsis* via vector *C. cainii*. In Lake Nyamiti South Africa, *C. quadricarinatus* sampled were infested with the non-native *Diceratocephala boschmai* (Du Preez and Smit 2013). Tavakol et al. (2016) reported three temnocephalans, *Craspedella pedum*, *D. boschmai*, and

Table 4. Summary of documented impacts of crayfish species in Africa.

Impact mechanism	*Cherax quadricarinatus*	*Procambarus clarkii*	*Procambarus virginalis*
Negative environmental effects			
Competition		●[a]	
Predation		●[a]	●[b]
Herbivory		●[c]	
Introduction of pathogens	●[d,e,f]	●[a]	
Environmental modification		●[g,h,i]	●[b]
Negative socio-economic effects			
Destruction of dams, canals and levees		●[j]	
Destruction of fishing gear	●[k,l]	●[m,n]	
Predation on fish catches	●[k,l]	●[a]	
Impacts on agriculture		●[i]	●[b]
Positive socio-economic effects			
Establishment of fisheries	●[o,p]	●[a]	●[b,q]
Aquaculture	●[l]	●[b]	

● effect documented on African continent.
Sources:
[a]Foster and Harper (2006).
[b]Andriantsoa et al. (2019).
[c]Hickley and Harper (2001).
[d]Du Preez and Smitt (2013).
[e]Douthwaite et al. (2018).
[f]Tavakol et al. (2016).
[g]Harper et al. (1990).
[h]Gherardi et al. (2011).
[i]Sara and El Moutaouaki (2019).
[j]El-Gendy (Unpublished data)
[k]Weyl et al. (2017).
[l]Nunes et al. (2016).
[m]Lowery and Mendes (1977).
[n]Ibrahim and Khalil (2009).
[o]Coetzee et al. (2015).
[p]T.C. Madzivanzira pers. obs. (2019).
[q]Andriantsoa et al. (2020).

Didymorchis sp. on *C. quadricarinatus* from Laagwaterbrug and Masibekela dams in the Komati system, South Africa. In the Kafue flats in Zambia, Douthwaite et al. (2018) reported the presence of non-native temnocephalans, commonly found on *C. quadricarinatus*, on the crab *Potamonautes unispinus*. During recent surveys, temnocephalans were observed on crayfish individuals in the Barotse floodplain, Zambia and in Lake Kariba, Zimbabwe (T.C. Madzivanzira pers. obs. 2019).

In the Nile River and its tributaries in Egypt, *P. clarkii* is a vector for the fungus *Trichosporon jirovecii*, which could potentially spread to other aquatic organisms (Abdallah et al. 2018). It is important to note that crayfish plague, caused by the fungus *Aphanomyces astaci* (Holdich 2003; Longshaw 2016) has not been reported from Africa, although, Foster and Harper (2006) hypothesized that this could have contributed to the disappearance of *Potamonautes loveni* stocks in Lake Naivasha, Kenya.

Ecological impacts

The impacts arising from crayfish introductions in Africa are summarized in Table 4. Of the five established crayfish species, there is only evidence for documented impacts of *C. quadricarinatus* and *P. clarkii*.

Impacts on macrophytes

In Lake Naivasha and its tributaries, the population expansion of *P. clarkii* in the 1970s coincided with the decline in the blue water lily *Nymphaea caerulea* and other floating-leaved and submerged macrophytes, as a result of direct consumption by crayfish (Hickley and Harper 2001; Harper and Mavuti 2004).

Impacts on other decapods

On mainland Africa, freshwater crabs are trophically analogous to crayfish and therefore are candidates to either offer biotic resistance or be highly susceptible to competition (Alofs and Jackson 2014). In the Malewa River in Kenya, for example, *Potamonautes loveni* was only recorded from sites where *P. clarkii* was absent, upstream of a weir, which likely acted as a migration barrier for *P. clarkii* (Foster and Harper 2006). In a separate study in Malewa River, Jackson et al. (2016) used a combination of field surveys and field experiments to examine the impacts of *P. clarkii* on native freshwater crabs. Growth rates of both species were reduced significantly in the presence of one another. Over a three year period, crab abundance declined at sites invaded by *P. clarkii*, with the species becoming extirpated at one locality (Jackson et al. 2016). In Lake Bunyonyi, Uganda, *P. clarkii* also appears to have negatively impacted abundances of the freshwater crab *Potamonautes mutandensis*, although, the specifics of this have not been studied (Cumberlidge 2018).

In an attempt to deduce mechanisms behind potential biotic resistance of freshwater crabs toward the two dominant invasive crayfish in southern Africa, South et al. (2020) compared the closing force and chelae morphology of the Cape river crab *Potamonautes perlatus* and the crayfish species *P. clarkii* and *C. quadricarinatus*. These traits can be used as proxies for prey handling capabilities and agonistic contests outcomes. Female *P. perlatus* showed a significantly stronger maximum chela closing force than female *C. quadricarinatus* and both sexes of *P. clarkii*, and did not differ significantly from male *C. quadricarinatus*. While this shows some capacity for native African freshwater crab species to offer biotic resistance, closing force was significantly correlated with body mass in all species. Therefore, if the crayfish attain a higher mass than the crabs, they are likely to retain a competitive advantage, which may explain abundance patterns seen in the field (South et al. 2020).

Impacts on invertebrates

Crayfishes have been assessed experimentally for biocontrol efficacy on disease vectors, the results of these can be considered as inferred ecological impacts on taxa in the wild. In Kenya and Egypt, *P. clarkii* effectively preys upon bulinid snails (Hofkin et al. 1991; Mkoji, Hofkin et al. 1999), biomphalarid, bulinid, lymnaeid, melanoid, and helicid snails (Khalil and Sleem 2011). Similarly, *C. quadricarinatus* preys upon bulinid snails in Zambia (Monde et al. 2017). In Madagascar, freshwater biomphalarid snails were absent at locations colonized by *P. virginalis*, suggesting possible predation, which was confirmed in a laboratory experiment (Andriantsoa et al. 2019). In addition, under experimental conditions, *P. clarkii* has been shown to impact on abundance of anopheles mosquitoes in Kenya (Mkoji, Boyce et al. 1999) and the southern house mosquito in Egypt (Heikal et al. 2018). These examples infer that there is potential for both *P. clarkii* and *C. quadricarinatus* to exert pressure on freshwater invertebrate communities.

Impacts on food webs

Freshwater crayfish are among the most common omnivores in freshwater systems and are associated with substantial effects across multiple levels of freshwater food webs (Olsen et al. 1991; Dorn and Wojdak 2004; Nilsson et al. 2012; Twardochleb et al. 2013). Stable isotope analysis (SIA) has been used to document IAS conferred disruption to food webs and community structure, through comparing niche width of invaders relative to native species as well as nutrient transfer pathways across trophic levels (Bodey et al. 2011). In Africa, only three studies have investigated the diet of invasive crayfish using SIA: *P. clarkii* in Lake Naivasha (Grey and Jackson 2012), *P. clarkii* in Lake Naivasha tributaries (Jackson et al. 2016) and *C. quadricarinatus* in Lake Kariba (Marufu, Dalu et al. 2018). In Lake Naivasha, *P. clarkii* individuals exhibited considerable intraspecific isotopic variability, indicating a broad choice in diet, ranging from submerged macrophytes, terrestrial plants, hippo dung matter, mixed detritus, chironomids, and oligochaetes (Grey and Jackson 2012). In Lake Naivasha tributaries, Jackson et al. (2016) used SIA to determine the trophic niche width of *P. clarkii* and native crabs. Contrary to what was hypothesized, competition between the invasive *P. clarkii* and native crabs resulted in the reduction in the diet breadth of both species. In spite of this, performance in the native crabs was reduced in the presence of *P. clarkii*, as revealed by field experiments (Jackson et al. 2016). Marufu, Dalu et al. (2018) found that all *C. quadricarinatus* sizes were in the same trophic level. In Lake Kariba *C. quadricarinatus* diet comprised mostly macrophytes, followed by macroinvertebrates, detritus, and finally fish and crayfish (Marufu, Dalu et al. 2018). Generally both small and large *C. quadricarinatus* consumed mainly macroinvertebrates and macrophytes, respectively, although, larger individuals consumed more fish (Marufu, Dalu et al. 2018).

Where introduced, crayfish have been incorporated into the diets of a variety of non-native and native predators. In Lake Naivasha, *P. clarkii* became incorporated into the diet of the introduced largemouth bass *Micropterus salmoides* (Hickley et al. 1994), common carp *Cyprinus carpio*, birds including herons, African fish eagle *Haliaeetus vocifer* and cormorants; and African clawless otter *Aonyx capensis* (Smart et al. 2002; Ogada et al. 2009). Local residents at Kantunta, Zambia reported seeing otters, reed cormorant *Phalacrocorax africanus*, hadada ibis *Bostrychia hagedash*, *H. vocifer*, marabou stork *Leptoptilos crumeniferus* eating *C. quadricarinatus* and finding them in the gut contents of the fish *Clarias gariepinus* and *Serranochromis* sp. in the area (Douthwaite et al. 2018). Remains of *C. quadricarinatus* have also been observed in the gut contents of *C. gariepinus*, *Oreochromis andersonii*, *Serranochromis macrocephalus*, *Synodontis macrostigma*, and *Mormyrus lacerda* from the Kafue flats, Zambia (Tyser and Douthwaite 2014). The pied kingfisher *Ceryle rudis* has been seen eating juvenile crayfish on the middle Zambezi River (Douthwaite et al. 2018) and crayfish have been found inside the guts of largemouth bass caught at the Claw and Mazvikadei dams in Zimbabwe (Douthwaite et al. 2018). In Lake Kariba, Zimbabwe, results of stable isotope analyses highlighted that *C. quadricarinatus* was now becoming an important food source across all tigerfish size classes (Marufu et al. 2017). In Lake Kariba *C. quadricarinatus* was also found to be present in gut contents of *C. gariepinus* and *Heterobranchus longifilis* (AT Chakandinakira, Department of Fisheries, Zimbabwe pers. comm. 2019).

These SIA studies indicate the wide ecological niche that is occupied by crayfish in African environments and their increasing inclusion in the diets of higher level organisms. Actual assessments of impact on recipient communities have, however, not been investigated.

Socio-economic impacts

Positive socio-economic impacts

Crayfish introductions have almost always been intentional; hence, most introductions produce a potential positive impact on at least one ecosystem service (Lodge et al. 2012). With the exception of South Africa, where wild caught *P. clarkii* were illegally sold to the aquarium trade (L Barkhuizen, Free State DESTEA pers. comm. 2018) the intended use for the introduced crayfishes was for food. Kenya exported several hundred tonnes of live *P. clarkii* to Europe between 1975 and 1981 (Oficialdegui et al. 2019) when the industry collapsed as a result of a European Union imposed import ban due to a cholera outbreak in East Africa (Foster and Harper 2007). A resistance to consuming crayfish is reported from several countries. Foster and Harper (2007) reported that people residing near Lake Naivasha in Kenya did not eat crayfish and referred to them as "insects" or "red scorpions." In Uganda, local people around Lake Bunyonyi do not eat crayfish because of its appearance (Foster and Harper 2007; Kabiza Wilderness Safaris pers. comm. 2019) and in Egypt *P. clarkii* is called "the cockroach of the Nile" and is not widely consumed (Ibrahim and Khalil 2009). Despite this documented resistance to consuming freshwater crayfish at the local level, they are often on offer in restaurants which cater for a more cosmopolitan clientele in Kenya (Foster and Harper 2007), and Zambia and Mozambique (OLF Weyl pers. obs.). In Madagascar, where there is a culture of eating native crayfishes, *P. virginalis* is generally accepted as a source of dietary protein and it contributes positively to household economy and food security (Andriantsoa et al. 2019; 2020).

There is little literature available on successful aquaculture for freshwater crayfish in Africa. Mikkola (1996) stated that few crayfish aquaculture projects that can be regarded as "successful" in the African continent (Mikkola 1996) and examples of failed crayfish farms are documented for Swaziland, South Africa (Nunes, Zengeya, Hoffman et al. 2017; Nunes, Zengeya, Measey et al. 2017), and Zambia (Nakayama et al. 2010; Douthwaite et al. 2018)

Negative socio-economic impacts

Crayfish have negatively impacted the livelihoods of people who rely on the fishing industry for subsistence and income in Africa. Crayfish impact directly upon fisheries by scavenging on and partially consuming fish caught in gillnets (Lowery and Mendes 1977; Weyl et al. 2017). In Lake Naivasha, Kenya, fishermen reported on how *P. clarkii* were spoiling their catches resulting from partial consumption of fish caught in gillnets (Lowery and Mendes 1977). Fishermen have also reported substantial damage to gill nets by *P. clarkii* in Lake Naivasha (Lowery and Mendes 1977) and in the Nile River, Egypt (Ibrahim and Khalil 2009). In the Kafue River, Zambia, Zambia, Weyl et al. (2017) reported observations that *C. quadricarinatus* predation on fish entangled in gill nets could result in losses of up to 30% of the catch, as well as considerable damage to the fishing gear. In Mozambique, predation by and competition with *C. quadricarinatus* is hypothesized to have contributed to a decline in tilapia fisheries in Pequenos Libombos Reservoir (Chivambo et al. 2019). Many fishermen in Madagascar expressed that *P. virginalis* was destroying their fish catches as they perceive that crayfish can prey upon juvenile fishes (Andriantsoa et al. 2019).

In Egypt, *P. clarkii* damaged earth dams and irrigation canals (Ibrahim and Khalil 2009), as well as rice fields, through their burrowing activities (Abdel-Kader 2016). In the Gharb region of Morocco, *P. clarkii* excavated burrows that caused the loss of irrigation water beyond the reach of rice plant roots through accelerated infiltration (Sara and El Moutaouaki

2019). This caused an increase in the frequency of irrigation in rice fields close to the water source upstream, which then had knock on effects for other rice farmers downstream as a result of reduced water availability. In this region, burrowing activities by *P. clarkii* has caused a reduction in arable land area and an overall decline in rice yields (Sara and El Moutaouaki 2019). Around the catchment of Lake Bunyonyi in Uganda, farmers complained about *P. clarkii* making burrows in the fields, eating plant roots, spreading a fungus which destroys young crops and boring through earthen fish ponds causing leaks (Blanc Unpublished data). In Madagascar, *P. virginalis* populations have been shown to negatively impact rice farming due to burrowing activities, which dry up the rice fields and require farmers to regularly repair their banks and irrigation canal (Andriantsoa et al. 2020). Burrows made by *P. clarkii* have also been observed on the shores of Mimosa Dam in Free State Province, South Africa (Barkhuizen et al. Unpublished data).

Control

Compared to Europe and North America, little research has been done to address the collective impacts of crayfish introductions in the African continent, but based on their potential impacts, invasion history, and lack of evolutionary history in the region (other than in Madagascar), researchers advocate strongly against allowing for further introductions and spread of crayfish in freshwater systems (Mikkola 1996; de Moor 2002; Appleton et al. 2004; Lodge et al. 2005; Nunes et al. 2016; Nunes, Zengeya, Measey et al. 2017; Weyl et al. 2017; Marshall 2019; South et al. 2020). Examples in this review have shown how difficult it has been to prevent crayfish introductions. Once crayfish establish, eradication is almost impossible and management is extremely difficult (Hobbs et al. 1989; Gherardi et al. 2011) and control measures include biological control, chemical application, and mechanical or physical removal (Gherardi et al. 2011; Manfrin et al. 2019).

In Africa, rice farmers in Egypt use the chemical Furadan 10G to control the expanding populations of *P. clarkii* as well as other pests, which are damaging their rice fields (Abdel-Kader 2016). Little information is however, available about the toxicity of Furadan 10G on other aquatic organisms (Alves et al. 2002; Abdel-Kader 2016). In an attempt to eradicate *P. clarkii* from the trout farm in South Africa, the water level in the dam where the species was present was reduced and crayfish were physically removed by hand or using dipnets (see Nunes, Zengeya, Measey et al. 2017). This eradication program was unsuccessful, as 22 years later *P. clarkii* were still present in the dam (Nunes, Hoffman et al. 2017). Burrowing species such as *P. clarkii* are unlikely to be controlled by such measures as draining of impoundments (de Moor 2002). Another eradication attempt, using a combination of methods which included intensive trapping and scoop netting, only reduced crayfish densities but did not result in eradication in Mimosa dam, a small reservoir in the Free State province of South Africa (Barkhuizen et al. Unpublished data).

Monitoring

Given the difficulty of controlling crayfish populations once they are established, early detection and rapid response programs become a critical element, especially if eradication is the management goal (Tobin 2018; Faulkner et al. 2020). Key to this is the development of appropriate monitoring methods.

Trapping

Globally, baited traps are the most commonly applied method, although they are biased toward large adults and males over other members of the population (Brown and Brewis 1978; Capelli and Magnuson 1983). A variety of traps and baits have been used in crayfish research in Africa. These include collapsible traps baited with dry dog food, fish or chicken in South Africa (Nunes, Zengeya, Hoffman et al. 2017), Swaziland (Nunes, Zengeya, Hoffman et al. 2017) and Tunisia (Bouaoud et al. 2020); opera traps baited with cooked maize meal in Lake Kariba Zimbabwe (Marufu et al. 2014, Marufu, Barson et al. 2018); rectangular traps baited with fish in South Africa (Barkhuizen et al. Unpublished data) and Morocco (Yahkoub et al. 2019); and cylindrical traps baited with fish in Egypt (Ibrahim and Khalil 2009). As disparate gears and sampling methods can result in unequivocal results in estimates of population abundance and distribution of crayfish, developing a standard sampling method is critical to determining cohesive knowledge bases regarding crayfish distributions in Africa (Larson and Olden 2016). Therefore, research into developing feasible standardized field sampling approaches is an urgent requirement for further invasion assessments.

Citizen science

Citizen science can be a powerful tool in conservation as it encourages stakeholder engagement and understanding of the natural environment (Brossard et al. 2005; Seymour et al. 2020). Citizen science initiatives present an emerging opportunity for the collection of datasets on IAS, particularly in understudied regions such as Africa, where sampling effort and baseline information is often lacking. Numerous citizen science projects focused on IAS reflect its potential for data gathering on IAS while ensuring effective and high-quality societal engagement (Novoa et al. 2018; Shackleton et al. 2019). Involving local people in collecting data or even in conservation plans offers a good route to integrate public views and values concerning conservation actions that should be taken (Devictor et al. 2010; Seymour et al. 2020). It is, however, important to note that in the African context, poverty and a concomitant lack of access to equipment and network services is likely to be a considerable barrier to citizen science projects in rural areas. As a result, initiatives encouraging the public to report the presence of crayfish to local environmental authorities are more likely to gain traction. An example is an initiative that has been started between the South African Institute for Aquatic Biodiversity (SAIAB) and CABI to distribute posters and information to hotels and lodges across Namibia and Zambia to kickstart an early warning system for invasive freshwater crayfish.

eDNA

The application and advancement of molecular techniques are increasingly being recognized as emerging priorities for invasion science (Darling et al. 2017; Dehnen-Schmutz et al. 2018), presenting novel opportunities for crayfish monitoring. In particular, the environmental DNA (eDNA) approach is likely to become an important method for early detection of IAS introductions, understanding trends in distribution, impacts on native biodiversity and ecosystems, and monitoring the effectiveness of management efforts, such as eradication attempts (Darling et al. 2017). Elsewhere, eDNA based methods have also been used to detect the presence of potential pathogens carried by invasive crayfish (Robinson et al. 2018; Wittwer et al. 2018). The relative merit of the application of species specific, compared to community based, eDNA methods will likely vary according to the management goal. Studies applying eDNA methods to the detection of crayfish currently remain fairly rare and largely focus on species specific detection methods (Geerts et al. 2018). Some successes in the detection of several species (*P. clarkii*, Geerts et al. 2018; *F. rusticus*, Dougherty et al. 2016; *P. leniusculus*, Harper et al. 2018; *P. virginalis*, Mauvisseau et al. 2019), suggest that eDNA analysis has the potential to become an efficient and reliable method for crayfish surveillance and management. To date, eDNA techniques have not been applied to crayfish detection in Africa. Further, it should be recognized that, although, much progress has been made toward standardization and validation of eDNA methods, there are potential pitfalls linked to false positives and false negatives when assays are not fully validated, just as they can for many other ecological monitoring approaches (Ficetola et al. 2015). Consequently, the detection of crayfish in African freshwater systems using eDNA will require considerable field validation using traditional monitoring approaches such as trapping.

Conclusion

The most effective strategy in managing IAS is to prevent their arrival in the first place, and recent work involving risk analyses helps to refine estimates of the likely invasion pathways and the time at which the pathway is most likely to result in the successful establishment of an IAS (Tobin 2018; Faulkner et al. 2020). Nonetheless, countries which share land borders are only as secure as their neighboring countries biosecurity legislation and implementation, which is particularly concerning in the African context with regards to budget restrictions and large scale population flow throughout the region (Faulkner et al. 2020).

Examples in this review have shown how difficult it is to prevent crayfish introductions. In the event of a failure to prevent IAS from arriving, early detection and rapid response programs become a critical element, especially if eradication is the management goal (Robertson et al. 2020). Eradication becomes a less economically and biologically feasible option as the IAS occupies a larger area, the size of the invaded system increases, as well as reliability of methods used (Tobin et al. 2014). Although, crayfish eradication is notoriously difficult, if not impossible, improvements in traditional crayfish control methods and the emergence of novel control techniques also present a potential opportunity to increase the success of management attempts (see Manfrin et al. 2019 for a full review). Integrated approaches to control IAS are likely the most effective way forward (Stebbing et al. 2014), although, there have been few attempts at using an integrated approach to crayfish management in Africa, likely not only due to high costs and resource limitations but also lack of impact assessments.

Human attitudes and behaviors toward IAS are highly dependent on the socio-economic context, and this may result in management conflicts (Woodford et al. 2016; Zengeya et al. 2017). In Africa, positive socio-economic contributions of crayfish species are only documented for Kenya (Foster and Harper 2007) and Madagascar (Andriantsoa et al. 2019, 2020), however, local context will influence whether conflict over management interventions is likely to occur. For example, community resistance to management will likely be more pronounced in Madagascar than Kenya, since the invasive *P. virginalis* has been accepted as a key staple to local livelihoods in Madagascar, probably due to the occurrence of native crayfish species in the country. Resistance from managing invasive crayfish is likely to be less pronounced in Southern African countries where there are few socio-economic benefits. There is a suspected relationship between greater levels of exposure to crayfish and the likelihood of acceptance into local people's livelihoods. Therein, if crayfish species become naturalized and utilized for economic gains then the possibility of management conflict is high as this will promote intentional propagation throughout freshwater systems. For progress to be made in addressing these potential conflicts, there is a need to establish a formal dialogue between regulators, crayfish users and conservationists as suggested by Ellender et al. (2014), so that policies for established non-native fisheries are supported by all stakeholders before they become a "wicked problem" (Woodford et al. 2016).

The lack of data on establishment, spread, and ecological impacts of crayfishes are important knowledge gaps as there is insufficient evidence to compel policymakers to implement legislation or management actions to minimize further introductions or spread. Future research is required on generating cross border, contextually appropriate, and robust abundance and distribution data for invasive crayfish and functionally similar native species to form baseline assessments as invasions progress. Such data can inform ecological niche models to predict presence/absence and prioritize monitoring sites (Nunes, Zengeya, Measey et al. 2017). As current research efforts are geographically, temporally, and methodologically disjunct, this will require the development of a regular monitoring scheme employing standardized sampling protocols to detect new invasions and robustly compare density estimates and population structure across regions. Once a cohesive method has been established the data should be incorporated into a database of locality records of formal and informal presence/absence data for crayfish and freshwater crab species at a national scale. In more contained invasions, such as within dam environments, a focus should be on evaluating the efficacy and potential biases of intensive manual depletion on crayfish populations. With regards to invasion impacts the specifics of trophic interactions with native species should be assessed, especially along an invasion gradient as this can give insights on the effect of crayfish abundance on nutrient pathways as well as acting as a forecasting system as the invasion progresses. Prediction of impact in situ is troublesome, especially considering the large scales of the invaded systems, therefore contextually relevant experimental approaches should be combined with comparable field data to ground truth predictions. This should involve competitive and consumptive resistance as well as species specific impact assessments via contest experiments, functional response analysis, and mesocosm experiments. Researchers should maintain a focus on native freshwater crab co-occurrence and population dynamics over a long term and whole systems scale to assess changes in community composition as basic ecology of the continents closest functional analogue is lacking.

Understanding crayfish impacts on specific ecosystem services is necessary not only for their regulation and management, but also to guard against detriment to human wellbeing in a continent where food security and water resources are already precarious (Egoh et al. 2020). This is particularly relevant as some of the crayfish species were introduced for aquaculture and there are ongoing requests for the use of crayfishes, and indeed other species, in both inland fisheries and for aquaculture (Nunes, Zengeya, Measey et al. 2017; Moshobane et al. 2020). As economic information on fisheries and aquaculture development based on invasive crayfish is lacking, research into the factors driving the success, or failure, of such enterprises could provide important information for decision makers needing to consider economic and environmental factors in decision making. As crayfish invasions contribute to economic losses through consumption of catches and destruction of fishing gear, nonetheless the actual realized economic impact of such scavenging behavior has not yet been quantified and therefore may be potentially over or under-estimated. Quantitative surveys should address contextually different socio-economic impacts of different crayfish species and address this with regards to whether the communities affected can also derive positive benefits from the invasion.

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