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Review Paper

Freshwater crayfish invasions in South Africa: past, present and potential future

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Freshwater crayfish invasions have been studied around the world, but less so in Africa, a continent devoid of native freshwater crayfish. The present study reviews historical and current information on alien freshwater crayfish species introduced into South Africa and aims to indicate which areas are at risk from invasion. As is the case elsewhere, South Africans have shown a keen interest in both farming and keeping freshwater crayfish as pets, which has resulted in *Cherax cainii*, *Cherax destructor*, *Cherax quadricarinatus* and *Procambarus clarkii* being introduced to the country. There is evidence of successful establishment in the wild for *C. quadricarinatus* and *P. clarkii* in different parts of the country. Species distribution models suggest that the eastern part of the country and parts of the Eastern and Western Cape are at higher risk of invasion. At present, illegal translocations represent the most likely pathway of crayfish spread in South Africa. A continued risk of invasion by freshwater crayfish species in South Africa is highlighted, which reinforces the need for more research, as well as for strong mitigation measures, such as stronger policing of existing regulations, management or eradication where feasible and public education.

Keywords: Africa, alien species, aquaculture, *Cambaridae*, management, modelling, pathways, *Parastacidae*

Introduction

Freshwater crayfish (infraorder Astacidae) are a diverse decapod group with more than 600 species naturally distributed on all continents, except continental Africa and Antarctica (Crandall and De Grave 2017). Crayfish have been introduced globally (Lodge et al. 2012) and, with at least ten introduced species, Europe has been one of the most affected areas (Kouba et al. 2014). Crayfish have been introduced mainly for aquaculture and aquarium trade purposes, both of which have resulted in deliberate and accidental releases into the wild (Lodge et al. 2012; Kouba et al. 2014). In invaded habitats, freshwater crayfish can act as novel predators, competitors, vectors of pathogens and, where native crayfish occur, can hybridise with indigenous species (Gherardi 2007; Lodge et al. 2012). They are considered keystone species, which often cause strong alterations in multiple trophic levels of invaded ecosystems (Momot 1995; Nyström et al. 2001; Dorn and Wojdak 2004).

Although freshwater crayfish invasions and their impacts have been extensively studied in Europe and North America, this is not the case in continental Africa, where four alien crayfish species are known to have been introduced (Boyko 2016). Three of these are native to Australasia, the smooth marron *Cherax cainii* Austin and Ryan 2002, the Australian redclaw crayfish *Cherax quadricarinatus*, von Martens 1868 and the common yabby *Cherax destructor* Clark 1936, whereas the red swamp crayfish *Procambarus clarkii* Girard 1852 is native to North America. It is important to note that, in the early literature, the widely distributed aquaculture species, *C. cainii,* was often erroneously called *C. tenuimanus* Smith 1912, a range-restricted species from the Margaret River system, Western Australia (Austin and Ryan 2002). Similarly, although *C. destructor* was originally referred to as *C. albidus* and was considered part of the *C. destructor* species-complex, *C. d. albidus* and *C. d. destructor* are currently considered separate subspecies of *C. destructor* (Austin et al. 2003; Munasinghe et al. 2004).

Available data indicate that *C. cainii* and *C. destructor* failed to establish populations in the wild, despite being introduced to South Africa and Zambia in the 1970s and 1980s (Mikkola 1996). *Procambarus clarkii* was introduced to Uganda, Rwanda, Kenya, Egypt, Sudan, Zambia and South Africa (Hobbs et al. 1989; Mikkola 1996; Cumberlidge 2009; Boyko 2016). It has successfully established in Lake Naivasha, Kenya and the Nile River, Egypt, where its impacts are fairly well documented (Lowery and Mendes 1977; Mikkola 1978; Loker et al. 1992; Emam and Khalil 1995; Ibrahim et al. 1995, 1997; Harper et al. 2002; Smart

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et al. 2002; Foster and Harper 2006a, 2006b; Gherardi et al. 2011b; Saad et al. 2015; Jackson et al. 2016). *Cherax quadricarinatus* occurs in the wild in Zimbabwe (Marufu et al. 2014), Zambia (Nakayama et al. 2010; Tyser and Douthwaite 2014; Nunes et al. 2016), Mozambique (Chivambo et al. 2013), Swaziland and South Africa (de Moor 2002; du Preez and Smit 2013; Tavakol et al. 2016; Nunes et al. 2017a; Petersen et al. 2017). Although studies have reported introductions of this species in Africa, and research interest is growing, detailed studies on the current status, distribution and impacts of *C. quadricarinatus* on the continent are still lacking.

Since de Moor's study on the potential impacts of alien freshwater crayfish in South Africa (de Moor 2002), published research on crayfish invasions in the country has been limited to only five articles (du Preez and Smit 2013; Tavakol et al. 2016; Nunes et al. 2017a, 2017b; Petersen et al. 2017).

Because there appears to be no systematic record keeping of the introduction history of crayfish species into South Africa, or of their current status in the country, the goal of this review was to compile historical and current information on crayfish introductions in South Africa. Information was gathered from old publications, scattered grey literature, experts and enthusiasts, as well as reports and anecdotal accounts. Secondary aims were: to determine which areas in the country are at higher risk from invasion, to generate new information to guide future management actions, and to identify priority areas for future research on crayfish invasions in South Africa.

Material and methods

Scientific and grey literature, media reports/articles and records gathered in fishing and aquarium forums were reviewed, and experts and Provincial conservation officials were interviewed. This was done to reveal the history of crayfish introductions in South Africa, identify historical and contemporary locations of crayfish farms and determine areas where former and present crayfish populations occur in the wild. Although five species of freshwater crayfish (*C. quadricarinatus*, *C. destructor*, *C. cainii*, *C. tenuimanus* and *Astacus leptodactylus* Eschscholtz, 1823) are listed in the Alien and Invasive Species regulations (RSA 2016) of the South African National Environmental Management Biodiversity Act (NEMBA, Act No. 10 of 2004) as occurring in the country, no records of *A. leptodactylus* having been introduced into the African continent have been found. Therefore, we focused on the other four alien crayfish species known to have been introduced in South Africa: *C. quadricarinatus*, *C. destructor*, *C. cainii* and *P. clarkii*.

For investigating the occurrence of crayfish populations in 2015–2017, the approach differed depending on the species. For *C. cainii*, sampling was undertaken in areas of potential species presence (see below), whereas information on current populations of *C. quadricarinatus* and *P. clarkii* in South Africa was obtained mostly from Nunes et al. (2017a, 2017b). For *C. destructor*, which was not detected during sampling for the three other crayfish species, no targeted searches were possible, given that there are no records of populations in the wild in South Africa. Finally, ecological niche modelling methods were used to assess which areas in South Africa are climatically suitable for the establishment of these four alien crayfish species.

Sampling surveys for smooth marron, C. cainii

Sampling was conducted during 2016 and 2017 at nine river and dam sites, mostly at or near localities of known old *C. cainii* farms (Table 1, Figures 1, 2). This included Rooikrans Dam, the Buffalo River and a tributary next to the old Pirie trout hatchery near King William's Town (Figures 1, 2b), two sites close to the old Amalinda Fish Station near East London (Figures 1, 2c), and four sampling sites close to Nieu-Bethesda (Table 1, Figure 1), an area of suspected crayfish presence. Each sampling site was surveyed once in 2016 and once in 2017 for crayfish presence/absence. This was done by visual observation surveys, consisting of walking for 5–10 minutes along the margins of the water body and looking for crayfish specimens or moults, and by direct sampling using six to ten ©Promar 61 × 46 × 20 cm collapsible crayfish/crab traps baited with approximately 100 g of dry dog food, set in the evening and left overnight for 14–16 h. The traps were checked the following morning for presence of crayfish and other bycatch, such as fish and crab specimens.

Ecological niche modelling

Ecological niche models were developed to predict the potential of the four crayfish species to establish populations in uninvaded aquatic systems in South Africa. Environmental conditions, including precipitation and water temperature in the species' distribution area, in both the native and introduced ranges, were matched with environmental conditions in receiving systems in South Africa, in order to predict areas of climate congruence.

Environmental data sources

The dataset of environmental variables was composed of bioclimatic variables (Table 2) that have been widely used in species ecological niche modelling (Hijmans et al. 2005; http://www.worldclim.org). These variables represent annual trends (mean annual temperature and annual precipitation), seasonality (annual range in temperature and precipitation) and either extreme or limiting environmental factors (temperature of the coldest and warmest months and precipitation of the wet and dry quarters). The predictive ability of ecological niche models is sensitive to the selection of environmental variables used to train the models, hence various procedures have been suggested to preselect variables (e.g. Peterson and Nakazawa 2008; Zengeya et al. 2013; Lübcker et al. 2014). This study took advantage of the inbuilt method of regularisation in MaxEnt (Phillips et al. 2006) that deals with the selection of environmental variables, regularising some to zero, given that this application has been shown to perform well and is thought to outperform other preselection procedures (Elith et al. 2011).

Species data sources

Georeferenced occurrence data for the native and introduced ranges of the four crayfish species was obtained from published literature, as well as from biodiversity databases, such as the Atlas of Living Australia (http://bie.

Table 1: Coordinates, location and elevation (m) of sampling sites in the Eastern Cape province surveyed for presence of *Cherax cainii* in 2016 and 2017

Site No.	Coordinates		Location	Elevation (m)
EL01	32°57′ S	27°52′ E	East London	60
EL02	33°00′ S	27°49′ E	East London	30
KW01	32°45′ S	27°19′ E	King William's Town	491
KW02	32°44′ S	27°18′ E	King William's Town	520
KW03	32°45′ S	27°22′ E	King William's Town	456
NB01	31°50′ S	24°35′ E	Nieu-Bethesda	1 376
NB02	31°50′ S	24°33′ E	Nieu-Bethesda	1 412
NB03	31°53′ S	24°34′ E	Nieu-Bethesda	1 285
NB04	31°50′ S	24°28′ E	Nieu-Bethesda	1 401

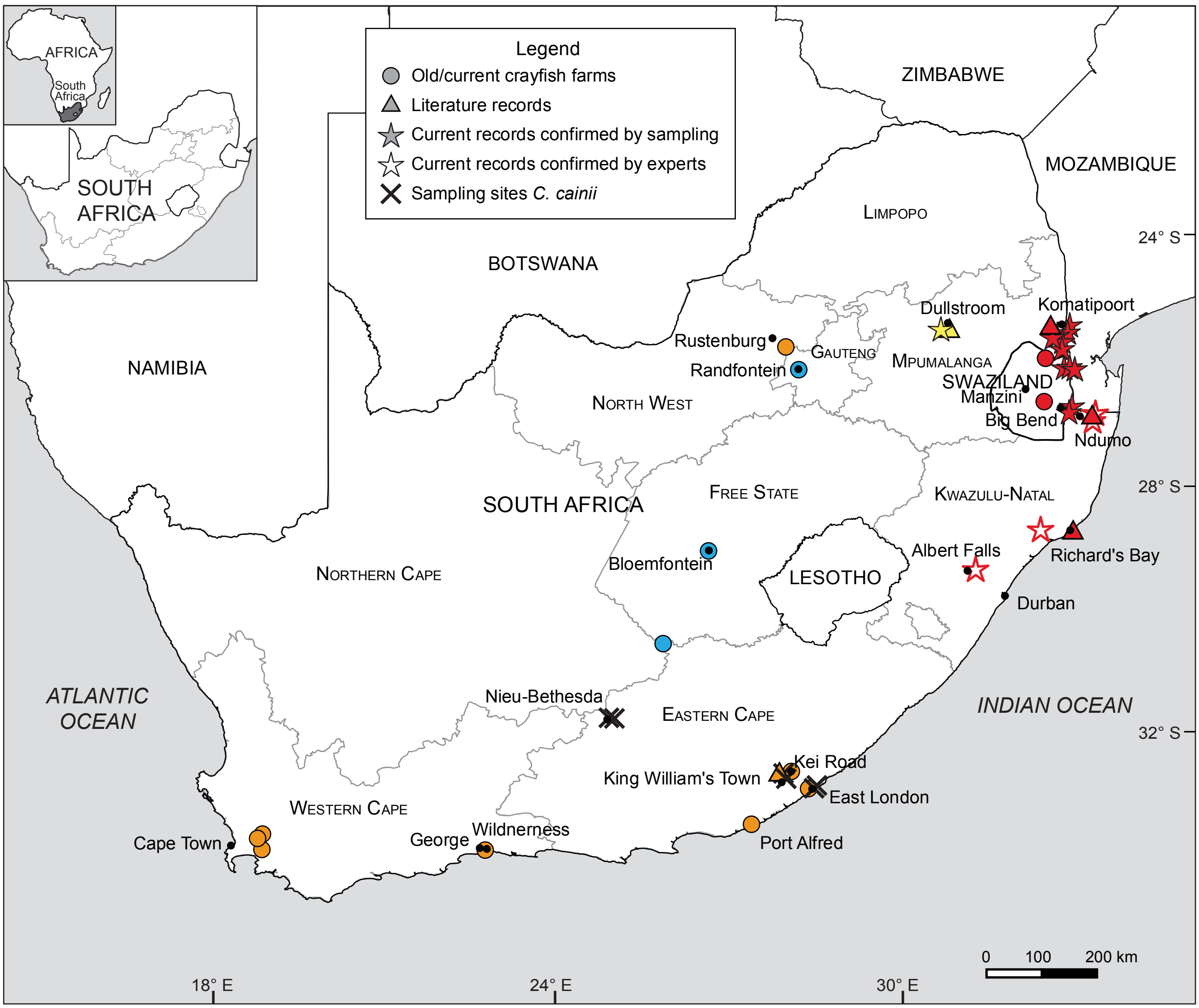

Figure 1: Locations of past and present crayfish farms and breeding grounds, records of crayfish presence reported in the literature, current records of crayfish presence confirmed either by sampling or by experts, and locations of nine sampling sites surveyed for the presence of *Cherax cainii*. *C. cainii:* orange, *C. quadricarinatus:* red, *C. destructor:* blue, *P. clarkii:* yellow

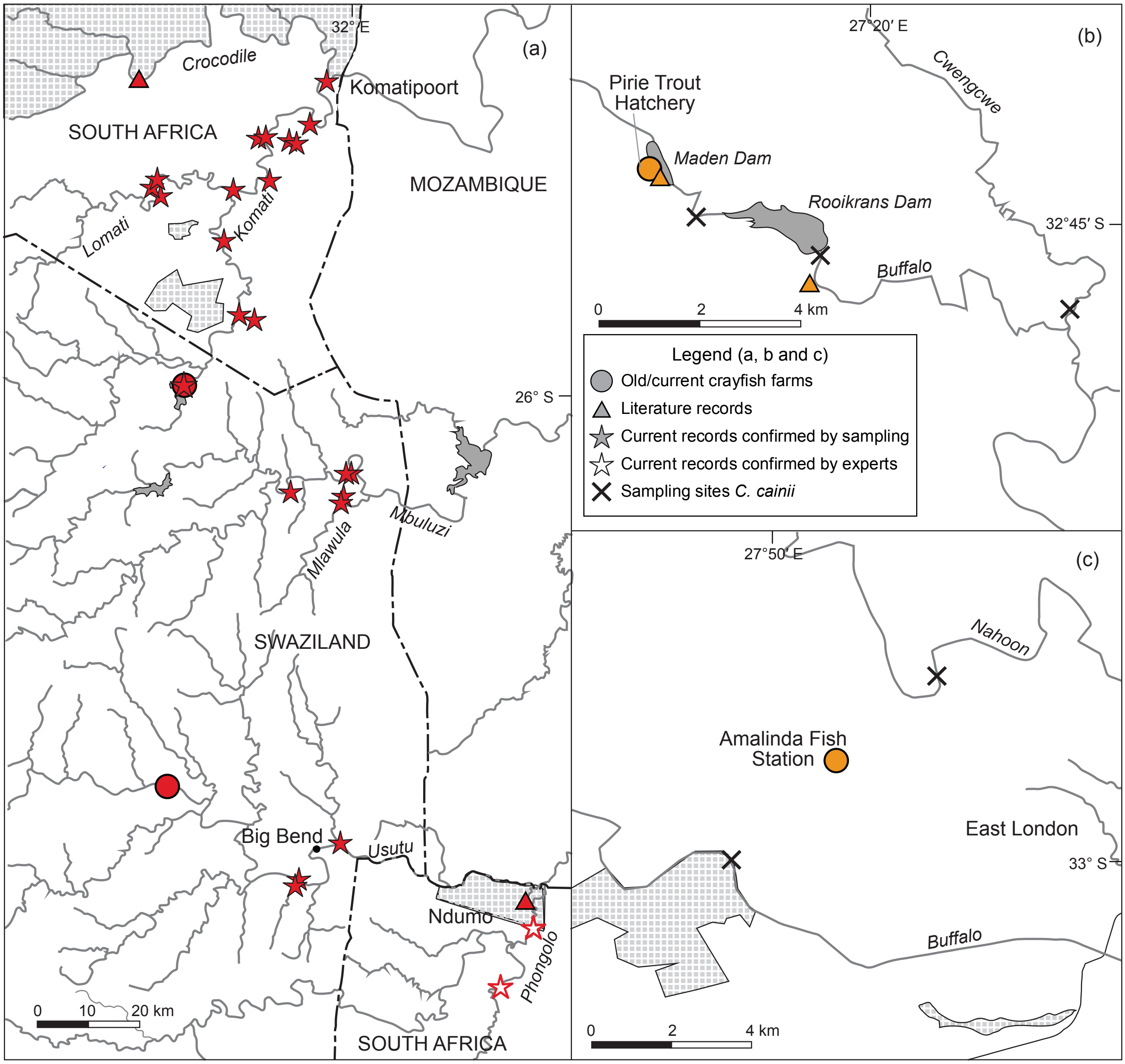

Figure 2: (a) Locations of distribution records of *Cherax quadricarinatus* in South Africa and Swaziland, and areas where presence of *C. cainii* was suspected near b) Maden Dam and c) East London. Light grey areas represent nature conservation areas. *C. cainii*: orange, *C. quadricarinatus*: red

ala.org.au/) and the Global Biodiversity Information Facility (GBIF) (http://www.gbif.org/). These biodiversity databases are a collection of occurrence records from various sources, including museum specimen records, other biodiversity databases and citizen science.

Model building

Model building was performed using a maximum entropy method implemented in the MaxEnt modelling package (MaxEnt v3.2.19; Phillips et al. 2006), by combining bioclimatic variables and species occurrence records to construct a model of climatic similarity between crayfish species' known range and potential receiving river systems in South Africa. MaxEnt makes use of presence and pseudo-absences, or background localities, to project potential species distribution models. In the present study, georeferenced records for both the native and introduced ranges of all species were used for background delimitation. Background was restricted to climatic zones with known occurrence records of each species, by overlaying the Köppen-Geiger climate classification system (Kottek et al. 2006) with the known distribution of each crayfish species, following Thompson et al. (2011). The model was then calibrated with 10 000 pseudo-absence points

Table 2: List of environmental variables used in ecological niche modelling of *Cherax quadricarinatus*, *C. destructor*, *C. cainii* and *Procambarus clarkii* in South Africa

BIO1 = Annual mean temperature
BIO2 = Mean diurnal range (mean of monthly (maximum temperature–minimum temperature))
BIO3 = Isothermality (P2/P7) (*100)
BIO4 = Temperature seasonality (standard deviation *100)
BIO5 = Maximum temperature of warmest month
BIO6 = Minimum temperature of coldest month
BIO7 = Temperature annual range (P5–P6)
BIO8 = Mean temperature of wettest quarter
BIO9 = Mean temperature of driest quarter
BIO10 = Mean temperature of warmest quarter
BIO11 = Mean temperature of coldest quarter
BIO12 = Annual precipitation
BIO13 = Precipitation of wettest month
BIO14 = Precipitation of driest month
BIO15 = Precipitation seasonality (coefficient of variation)
BIO16 = Precipitation of wettest quarter
BIO17 = Precipitation of driest quarter
BIO18 = Precipitation of warmest quarter
BIO19 = Precipitation of coldest quarter

drawn at random from the defined background. Ten niche models were then constructed using the inbuilt method of replicates in MaxEnt. In each model, all occurrence records were partitioned into two equal sets for calibration (training set) and validation (testing set) and a consensus map was created as an average of the ten projection maps.

For all models, the algorithm's parameters were set to a maximum number of 500 iterations, a regularisation multiplier of 1, convergence threshold of 0.00001, test percentage of 0 and only hinge features were selected. Hinge features allow for simpler and more concise approximations of the true species response to environmental variables (Phillips and Dudik 2008), preventing overfitting of the model without increasing complexity and hence improving model performance (Phillips et al. 2006). In addition, clamping was selected to minimise predictions to regions of environmental space outside the limits encountered during training, because extrapolation may overinflate areas of climatic suitability (Elith et al. 2010). The logistic output format indicates climatic suitability, not establishment probability (Elith et al. 2011), with values ranging from 0 (unsuitable habitat) to 1.0 (greatest relative species suitability). The predictions of potential crayfish distribution ranges in non-invaded river systems in South Africa were first projected individually for each of the four crayfish species. The four models were then combined into an additive map, using a weighted sum approach (with equal weighting of 0.25 for each model), to produce a risk map highlighting areas that are highly climatically susceptible to freshwater crayfish establishment in South Africa.

Model evaluation

The performance of the niche model for each crayfish species was evaluated using the maximum possible test AUC, which defines the discrimination ability between presence and background of the models. Values range from 0 (indicating random distribution) to 1.0 (indicating perfect prediction), with values >0.5 being considered to indicate that the model discriminates better than a random model (Manel et al. 2001). All AUC model performance measures were calculated in MaxEnt and predictions with an AUC value greater than 0.9 were considered to be acceptable (Swets 1988; Fielding and Bell 1997).

Results

Cherax cainii (smooth marron)

Introduction history

Cherax cainii was first imported and introduced into South Africa in 1976 by a private fish farmer in Natal (now KwaZulu-Natal) for aquaculture purposes (Table 3), but this venture was short-lived (de Moor and Bruton 1988; van den Berg and Schoonbee 1991). In 1982, the first authorised and successful *C. cainii* farm was established at George, Western Cape (Walmsley 1987). Safriel and Bruton (1984) identified *C. cainii* as a candidate with high potential for aquaculture in South Africa and, from then onwards, several aquaculturists started exploring the possibility of farming this species (Walmsley 1987). As a result, several consignments of *C. cainii* were imported from Western Australia into South Africa (Mitchell and Kock 1988; van den Berg et al. 1990; van den Berg and Schoonbee 1989, 1991). Depending on the destination province, permits were issued for either research or aquaculture activities. In 1987, a workshop organised by the Foundation for Research Development and the Council for Scientific and Industrial Research was held in Stellenbosch, with the aim of establishing criteria and regulations for the introduction and farming of *C. cainii* for the guidance of entrepreneurs, farmers and regulating agencies (Walmsley 1987). By this time, permits for *C. cainii* farming had already been issued in the Western and Eastern Cape, Free State and Mpumalanga Provinces (Walmsley 1987).

In the late 1980s, as a result of difficulties experienced in *C. cainii* farming at Pirie trout hatchery (see *Farming activities*, below), the Zoology Department of the Rand Afrikaans University (RAU, now University of Johannesburg) conducted research on the factors affecting *C. cainii* aquaculture. This was because it was believed that farming this species was very likely to become a viable and profitable industry (van den Berg et al. 1990; van den Berg and Schoonbee 1989, 1991). The research concluded that, although *C. cainii* was successfully bred and maintained in the laboratory, its slow growth and late sexual maturity would constrain profitability from its culture. It was consequently recommended to redirect efforts to farming other *Cherax* species (van den Berg and Schoonbee 1991).

Several parasites were co-introduced with *C. cainii*. In 1987/1988, *Temnocephala chaeropsis* was identified on *C. cainii* imported from Australia. This turbellarian, a common symbiont of Australian freshwater crayfish, was initially thought to pose a threat to crayfish aquaculture (Mitchell and Kock 1988). However, in 1992/1993, further experiments showed that *T. chaeropsis* did not cause *C. cainii* mortality, but that observed mortalities were a result of *Aeromonas hydrophila*, a bacterial disease that can spread to humans (Avenant-Oldewage 1993). As a result,

Table 3: Date and pathway of first introduction and first naturalisation, and area and province of first naturalisation of four alien crayfish species introduced into South Africa

Species	Date of first introduction	Pathway of first introduction	Date of first record of naturalisation	Pathway of first naturalisation	Area of first naturalisation
Cherax cainii	1976	Aquaculture	1983 or 1986*	Unintentional escape from aquaculture facility	Buffalo River, next to Pirie Trout Hatchery (Eastern Cape)
Cherax quadricarinatus	1988	Research purposes	2002	Unaided dispersal (Unintentional introduction through natural dispersal, after escape from aquaculture facility in Swaziland)	Komati River, next to Swaziland border (Mpumalanga)
Cherax destructor	1988	Research purposes	-	-	-
Procambarus clarkii	1962 (unconfirmed) 1982 (confirmed)	Ornamental/ aquarium trade	1980 (unconfirmed) 1988 (confirmed)	Intentional release by aquarist	Dams and Crocodile River on Driehoek Farm, Dullstroom (Mpumalanga)

* potential inconsistency between supposed first date of escape into the wild (see *Populations in the wild* for *C. cainii*)

de Moor (2002) concluded that, because of the potential negative impacts of parasites introduced with *C. cainii* and its disappointing results in terms of aquaculture, the environmental damage caused by this species was likely to outweigh its economic benefits.

Farming activities

Cherax cainii was first imported into KwaZulu-Natal for farming purposes in 1976. Around this time, it also appears to have been introduced into the Western Cape for aquaculture, albeit without a permit. The first recognised experimental *C. cainii* farm in South Africa was established in the Western Cape in 1982 (Walmsley 1987; de Moor and Bruton 1988) just outside George, later being moved to the hills near Wilderness, where it was called Amanzi Marron Farm (Figure 1). Although in 1986 it was selling live *C. cainii* to other farmers, its operations ceased around 1987/1988 (Walmsley 1987; de Moor and Bruton 1988).

Cherax cainii was also kept at Jonkershoek hatchery, near Stellenbosch (Figure 1), in 1983 and 1984, with the aim of investigating the conditions required for it to survive in outdoor ponds and its possible survival and impacts if released into natural waters (Ashton et al. 1986; Bok 1987; de Moor and Bruton 1988). The species was also farmed in earthen ponds at Amalinda Fish Station near East London, probably for experimental purposes (Bok 1987) (Figure 1). In 1985, the President of the Republic of Ciskei, now in the Eastern Cape province, decided to introduce *C. cainii* from George with the aim of farming and selling it as a means of income for local people (Walmsley 1987). Farming took place at the Pirie trout hatchery, near the Maden and Rooikrans dams close to King William's Town (Figures 1, 2b). In 1986, these *C. cainii* specimens became part of a research programme administered by the Department of Agriculture and Rural Development of the Republic of Ciskei (Walmsley 1987). From these hatcheries, *C. cainii* later escaped into the Buffalo River (Figure 2b).

There is a record of a different batch of *C. cainii* having been imported from Australia into a farm near Rustenburg in 1986 (van den Berg and Schoonbee 1989) (Figure 1). This occurred despite the old Transvaal Provincial Administration stating that it would issue permits for the rearing of *C. cainii* only for research activities (Walmsley 1987). By 1987, 31 farmers in the Cape Province, now the Western and Eastern Cape provinces, had applied for permits to establish *C. cainii* farms, and seven of them had already been approved by the Cape Directorate of Nature and Environmental Conservation, had obtained stock and started operations (Walmsley 1987). At this time, two permits to start *C. cainii* farms in the Free State province were also granted (Walmsley 1987; Mitchell and Kock 1988). In 2006, five *C. cainii* farms were reported operating in South Africa, two in the Western Cape, two in the Eastern Cape and one in the Free State. The farm in the Free State utilised *C. cainii* plus *C. destructor* and *C. quadricarinatus* (Botes et al. 2006). Other crayfish farms were located at Klapmuts, Western Cape (P Britz and T Hecht, Rhodes University, pers. comm.), and at Kei Road (Burgess 2007) and Port Alfred (T Hecht, Rhodes University, and E Truter, Amatola Fly Fishing Club, pers. comm.), in the Eastern Cape (Figure 1).

This species never became properly established in the aquaculture industry. Van den Berg and Schoonbee (1991) reported that, in 1991, some farms were active, but no crayfish were regularly marketed. However, from 1993 to 1997, 1–2 tonnes year^{-1} of *C. cainii* were being produced in South Africa, which increased to 4 tonnes in 1998 (Hoffman et al. 2000). An optimistic production of 8 tonnes in 2003 was reported by Shipton and Britz (2007), whereafter production decreased to 2 tonnes in 2005 (Britz et al. 2009) and to below 1 tonne year^{-1} from 2006 to 2011 (Britz et al. 2009; DAFF 2012a, 2012b). Subsequently, *C. cainii* aquaculture in South Africa seems to be limited to Smilling Valley Aquaculture, a farm located at Kei Road, Eastern Cape Province that was founded in 2000 (Burgess 2007) and which produced 5 tonnes in 2013 (DAFF 2015).

Populations in the wild

As has often happened at aquaculture facilities, some specimens of *C. cainii* escaped from the Pirie trout hatchery into the Buffalo River (de Moor and Bruton 1988) (Figures 1, 2b). De Moor and Bruton (1988) indicated that this first accidental escape took place in 1983/1984, and that in 1986 the remains of a *C. cainii* carapace were found close to Maden Dam (Table 3). However, according to Walmsley (1987), *C. cainii* was introduced into this area only in 1985, suggesting that one of these initial records must have been erroneous. In 1988, *C. cainii* specimens were again observed in the Buffalo River, this time approximately 500 m downstream from Rooikrans Dam (de Moor and Bruton 1988) (Figure 2b). Although no directed surveys have been undertaken since 1988, there have been no further reports of *C. cainii*, and thus the species is assumed to have failed to establish in the wild (de Moor and Bruton 1996). There were also anecdotal reports of *C. cainii* being found in small streams at Nieu-Bethesda, near Graaff-Reinet, during the mid-1990s (Anchor Environmental Consulting 2012).

During recent surveys, no *C. cainii* specimens or moults were detected, either during visual observations or in any of the crayfish traps set at potential introduction sites (Figures 1, 2).

Potential spread and further colonisation

Given that *C. cainii* does not currently seem to occur in the wild in South Africa, there is no risk of spread from wild populations. However, if the species manages to escape from aquaculture facilities, as has occurred before, the areas projected to be most at risk are located mainly in the eastern part of the country and at some isolated areas in the Eastern and Western Cape Provinces (Figure 3). Climatic suitability to *C. cainii* in South Africa was mostly restricted to upland areas in the Greater Berg, Kromme,

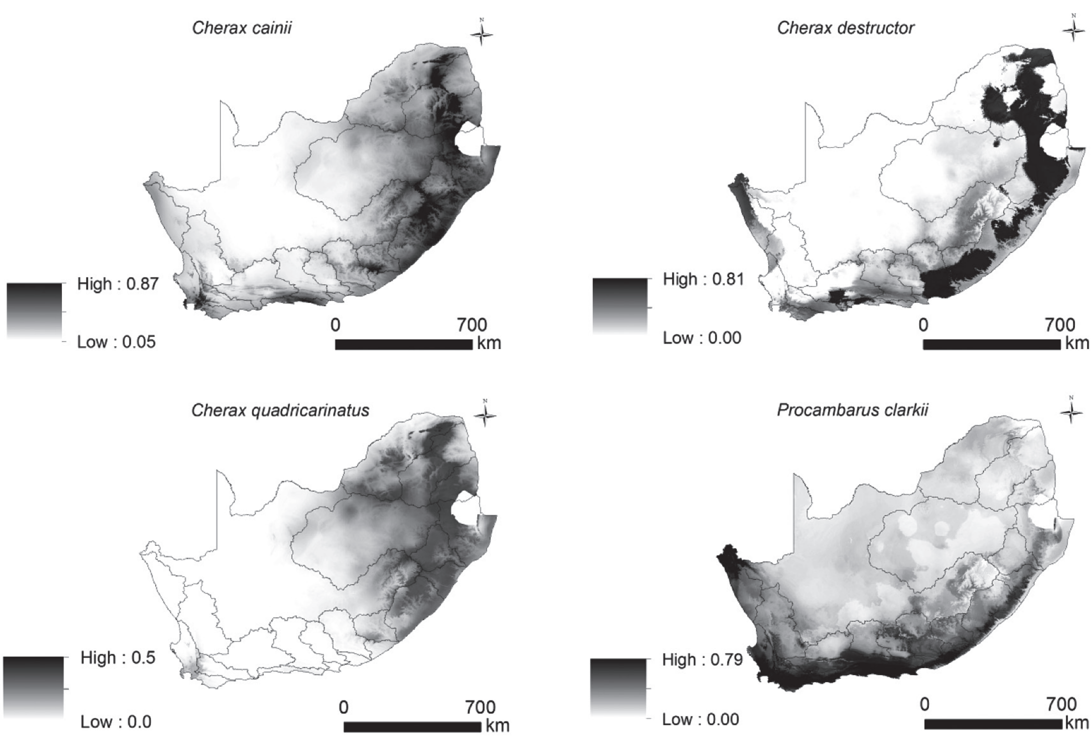

Figure 3: Potential distribution ranges of *Cherax cainii*, *C. destructor*, *C. quadricarinatus* and *Procambarus clarkii* in South Africa, based on ecological niche models constructed using occurrence records from species' native and introduced ranges. Potential distribution indicated by shading, dark = high, light = low probability of suitable climatic conditions. Primary river catchment areas as defined by Department of Water and Sanitation, Republic of South of Africa (http://www.dwa.gov.za/iwqs/gis_data/)

Great Kei, Mzimvubu, uMngeni, Phongolo, Crocodile and Limpopo catchment areas (Figure 3). As predicted, these areas include the region in the Buffalo River, where the species was once present, but appears to have failed to establish in the long term.

Cherax quadricarinatus (Australian redclaw crayfish)

Introduction history

The earliest record of *C. quadricarinatus* introduction into South Africa was mentioned by van den Berg and Schoonbee (1991), who stated that some specimens were imported from Australia in 1988 (Table 3). This is mentioned in the context of the start of experimental research on the aquaculture potential of this and other *Cherax* species by the Zoology Department of the RAU. The research concluded that *C. quadricarinatus* could be maintained at limited expense in the Johannesburg area, suggesting high aquaculture potential (van den Berg and Schoonbee 1991).

Farming activities

Despite restrictions on imports of *C. quadricarinatus* into South Africa, this species, together with *C. destructor,* was imported into the Free State Province in the early 1990s, from where larvae were sold for aquaculture purposes (Mikkola 1996). From 1997 onwards, the frequency of requests for permits to import *C. quadricarinatus* increased (de Moor 2004). However, following the conclusions of a consultancy report commissioned by the Department of Agriculture on the potential impact of alien crayfish species in South Africa (de Moor and Holden 1997), most provincial nature conservation departments decided to prohibit the importation and use of *C. quadricarinatus* (de Moor 2004). Subsequently, *C. quadricarinatus* has not been mentioned in any aquaculture report from the Department of Agriculture, Forestry and Fisheries, although there are anecdotal accounts of illegal *C. quadricarinatus* farming operations occurring in the country (K Halley, Department of Agriculture, Forestry and Fisheries, pers. comm.).

However, a permit for its use was granted in the late 1990s by Swaziland authorities to a prospective farmer who had had his permit application denied in South Africa (de Moor 2004). A *C. quadricarinatus* facility was established next to the Sand River Dam (Figures 1, 2a), from where the species later escaped into natural waters and spread into South Africa. There are also anecdotal records of another *C. quadricarinatus* farm near Manzini or Big Bend, Swaziland (A Howland, Inyoni Yami Swaziland Irrigation Scheme, pers. comm.) (Figures 1, 2a), from where crayfish probably also escaped and spread into South Africa.

Populations in the wild

Cherax quadricarinatus was first detected in the wild in South Africa in 2002, in the Komati River, Mpumalanga Province, close to the Swaziland border (de Villiers 2015) (Table 3). This was most likely the result of the Sand River Dam facility being abandoned by its owner because the activity stopped being profitable (Nunes et al. 2017a). This may have allowed crayfish to escape into the Sand River Dam and, probably during floods in the year 2000, spread through the Sand River into the Komati River, a transboundary river that flows through the two countries (de Moor 2002, 2004; A Howland, Inyoni Yami Swaziland Irrigation Scheme, pers. comm.). In 2013, the species was reported to be widespread in the Komati River (van Rooyen 2013), and in 2014 another study pointed out its presence at two specific localities in the area (Tavakol et al. 2016). The latter study highlighted the presence of three temnocephalan species, *Craspedella pedum*, *Diceratocephala boschmai* and *Didymorchis* sp., on crayfish body surfaces and in their branchial chambers.

In a recent study on the distribution of *C. quadricarinatus* in South Africa and Swaziland, Nunes et al. (2017a) report the species' presence in the Komati and Lomati Rivers in South Africa, but not in the upper reaches of these rivers in Swaziland (Figure 2a). As such, the species does not seem to be spreading upstream of the point of first introduction in the Komati River in Swaziland, but only downstream into South Africa. The authors could not sample the section of the Komati River that flows into Mozambique, but it is likely that the species has spread there too. The species has also colonised several irrigation dams on farms in the Komatipoort area, supposedly through water abstraction from the Komati River, but more probably by human translocation. In Swaziland, *C. quadricarinatus* has colonised a large area of the Mbuluzi River, as well as its tributary the Mlawula. It is also present in the Usutu River close to Big Bend (Nunes et al. 2017a) (Figure 2a).

This species was first reported from KwaZulu-Natal in June 2009 in a small wetland behind a residential area close to Richards Bay (R Jones, Ezemvelo KZN Wildlife, pers. comm.) (Figure 1). However, given that this was an isolated record, and was from a site far distant from the initial introduction source, it is believed that it was the result of a release by an aquarist. Furthermore, two surveys in 2016 did not find any specimens in the area (Nunes et al. 2017a).

Later, in 2012, *C. quadricarinatus* was recorded elsewhere in KwaZulu-Natal, also carrying the temnocephalan *D. boschmai* (du Preez and Smit 2013). Four individuals (one with eggs) were detected in an outlet of Lake Nyamiti in the Ndumo Game Reserve, a water body that connects to the Usutu River, which also flows through Swaziland (Figures 1, 2a). The source of this population is thought to be the aquaculture farm close to Manzini or Big Bend, Swaziland, located in the Usutu River catchment. Crayfish might have escaped or have been intentionally introduced into the Usutu River, making their way into the Ndumo Game Reserve (Nunes et al. 2017a). A 2013 study on the status of artisanal fisheries in the villages bordering the Ndumo Game Reserve found that local people were actively catching, selling and consuming *C. quadricarinatus*, suggesting that the species was present in sufficient numbers to constitute an economic resource, as well as to provide a form of sustenance (Coetzee et al. 2015). Although in 2016 Nunes et al. (2017a) did not detect *C. quadricarinatus* in either the Ndumo Game Reserve or in the Phongolo River close to Pongolapoort Dam, the species is reported to be present in the Phongolo River close to Ndumo Game Reserve (C Penning, Ndumu River Lodge, and R Kyle, Ezemvelo KZN Wildlife, pers. comm.) (Figure 2a).

Even though, in the same study, no specimens were found in the Crocodile River, Mpumalanga, (Nunes et al. 2017a), there has been a recent record of the species in this river upstream of the authors' sampling points (Petersen et al. 2017). These specimens are thought to have been illegally stocked in the river, having been translocated from an invaded nearby irrigation dam (Petersen et al. 2017) (Figure 2a).

There are anecdotal records of the species having been introduced by fishermen as prey for largemouth bass in several South African impoundments, including Hartbeespoort, Kwena, Loskop and Pongolapoort dams (L Coetzer, Department of Agriculture and Rural Development and Land Administration, pers. comm.), but most records are from Goedertrouw and Albert Falls dams (R Kyle, Ezemvelo KZN Wildlife, pers. comm.). However, no crayfish were detected during surveys in Pongolapoort, Goedertrouw and Albert Falls dams in 2016 (Nunes et al. 2017a). Nevertheless, the large sizes (>1 000 ha) of these dams makes it hard to be certain of the species' absence without dedicated comprehensive and long-term monitoring. Finally, there are anecdotal reports of *C. quadricarinatus* being present in Gauteng and Limpopo provinces (L Coetzer, Department of Agriculture and Rural Development and Land Administration, pers comm.) but, once again, targeted and comprehensive surveys are needed to validate these reports.

Potential spread and further colonisation

Cherax quadricarinatus is confirmed as established in various areas of South Africa, with reproducing and spreading populations in the Komati/Lomati area and in the Ndumo Game Reserve. As such, the imminent risk of spread threatens mainly the upstream parts of the Lomati and Crocodile rivers, where the species is already present, as well as their tributaries. Wetlands and pans of the Ndumo Game Reserve and upstream sections of the Phongolo River are also at high risk.

Primary catchment areas that were modelled to be climatically suitable for *C. quadricarinatus* were largely restricted to the east of the country and include the Crocodile, Phongolo, uMngeni, Mzimvubu, Orange, Thukela, Olifants (west) and Limpopo catchment areas (Figure 3). The projected distribution of *C. quadricarinatus* in South Africa correctly predicted all areas with known and suspected established populations (see Figure 2) as climatically suitable.

Cherax destructor (common yabby)

Introduction history

Together with *C. quadricarinatus*, *C. destructor* was introduced from Australia into South Africa in 1988, for experimental research by the RAU (Table 3). This research determined that *C. destructor* was easy to produce and that it had aquaculture potential (van den Berg and Schoonbee 1991).

Farming activities

In 1990 and 1991, a farm in the Randfontein/Tarlton area, Gauteng Province (Figure 1), obtained stock from RAU to host some experimental indoor trials on *C. destructor*. This farm had no outdoor 'commercial-scale' operation (P Cowley, South African Institute for Aquatic Biodiversity, pers. comm.). During the 1990s, this species was imported, together with *C. quadricarinatus*, into the Free State province where it was farmed and bred (Mikkola 1996). Du Preez and Smit (2013) reported that in 1999 *C. destructor* was present at the Gariep Dam Fisheries Station, Free State (Figure 1). A visit to, and key-informant interviews with, employees of this Fisheries Station in August 2016 found no indication of crayfish farming activities taking place at this facility (A Nunes, pers. obs.). In 2003, an individual from Bloemfontein was the only South African to hold a permit from a conservation authority to breed and trade *C. destructor* (Smith 2003). This is, perhaps, the same Free State producer who was reported to be growing *C. destructor*, as well as *C. cainii* and *C. quadricarinatus*, in 2006 (Botes et al. 2006).

Populations in the wild

As for *C. quadricarinatus*, there are anecdotal records of *C. destructor* introductions by fishermen into several South African dams. However, these records, gathered by fishing and aquarium enthusiasts, should be interpreted with caution, as there are no confirmed past or present records of *C. destructor* in the wild in South Africa.

Potential spread and further colonisation

Although *C. destructor* has not been reported in South Africa for several years, either in the wild or in aquaculture facilities, large parts of the country seem to be climatically suitable for the species, especially those in the east and south of the country. Primary catchments projected to be suitable include the Limpopo, Crocodile, Phongolo, uMngeni, Mzimvubu, Great Kei, Great Fish, Keiskamma, Bushmans and Gourits catchment areas (Figure 3).

Procambarus clarkii (red swamp crayfish)

Introduction history

The first potential record of *P. clarkii* in South Africa dates from 1962 (Table 3). However, this record remains unconfirmed, as it refers to the observation of two moribund animals caught in a freshwater habitat close to Potchefstroom, with no specimens or pictures being available to confirm their identification (van Eeden et al. 1983). Nevertheless, it is plausible that this species was *P. clarkii*, taking into account that, in 1982, a South African aquarist from the Free State was reported to be rearing *P. clarkii* illegally, and that *P. clarkii* specimens had been offered for sale in some pet shops for some time (van Eeden et al. 1983; Ashton et al. 1986). In 1987, the Cape Department of Nature and Environmental Conservation confiscated *P. clarkii* specimens from pet shops in East London, George, Cape Town and Kimberley (Anonymous 1987). *Procambarus clarkii* seems to have been illegally imported into South Africa through the aquarium trade, rather than through aquaculture. At the time, other freshwater crayfish species (e.g. *Astacus* sp. and *Pacifastacus leniusculus*) seem to have also been available for purchase through the aquarium trade in South Africa (de Moor and Bruton 1988).

Farming activities

There are no documented records of farming activities of *P. clarkii* in South Africa. In the proceedings of a 1987 workshop on *C. cainii* farming in South Africa (Walmsley

1987), the Department of Development Aid reported their interest in using *P. clarkii* for aquaculture in paddy rice systems that were being developed in Kangwane, now Mpumalanga province, and on the Makatini flats, KwaZulu-Natal. To our knowledge, no introduction ever took place.

Populations in the wild

The only population of *P. clarkii* recorded in the wild in South Africa was reported in 1988 from Driehoek Farm, a put-and-take trout-angling farm close to Dullstroom, Mpumalanga (Figure 1), (Schoonbee 1993). Schulz (1993) stated that *P. clarkii* had been present at that farm from as early as 1980 (Table 3).

In 1991, a field survey demonstrated that the species was present in a section of the Crocodile River crossing that farm, as well as in two out of the seven dams on the farm that were used for trout fishing (Schoonbee 1993). However, in 1993, Schulz (1993) found *P. clarkii* to be present in only one of the dams, and investigated the feasibility of its eradication. Toxicity experiments examining the effects of various types and amounts of poison on mortality levels of fish (*Tilapia sparmanii*), crabs (*Potamonautes perlatus*) and *P. clarkii* were run, but it was concluded that the use of any type of poison would also kill most native aquatic species, which was not desirable (Schulz 1993). It was consequently recommended that *P. clarkii* should be eradicated through the reduction of the water level in the dam, inspection of all rock crevices where crayfish could hide and by physical removal by hand or with dipnets of any crayfish found (Schulz 1993). The Transvaal Nature and Environmental Conservation Directorate did put an eradication plan into practice (A Hoffman, Mpumalanga Tourism and Parks Agency, pers. comm.), but no report is available of which actions were taken, how many individuals were removed, or whether subsequent monitoring occurred.

In 2015 and 2016, all seven dams on Driehoek Farm, as well as the section of the Crocodile River that crosses the farm, were sampled in repeated surveys using several sampling techniques (Nunes et al. 2017b). The authors found that *P. clarkii* was still present in the area (Figure 1), but detected only one individual, indicating low species abundance (Nunes et al. 2017b).

Potential spread and further colonisation

Although only one individual was found in a dam at Driehoek Farm, *P. clarkii* must be established there, given that it has persisted in the area over the past 28 years. The species appears to not have spread beyond the farm, but in case translocations do occur, other areas of the country might be at risk, because they are climatically suitable for the species. These are located mainly in the Western and Eastern Cape provinces and include the Greater Berg, Bree, Gourits, Kromme, Swartkops, Bushmans, Keiskamma, Great Kei, Mzimvubu, uMngeni and Phongolo catchment areas (Figure 3).

Discussion

The present review shows that the history of freshwater crayfish introductions in South Africa is complex. Nevertheless, it is similar to the situation in many other countries around the world, in that South Africa has shown an interest in both farming freshwater crayfish and keeping them as aquarium pets. Although in the beginning the interest was largely focused on importing and farming *C. cainii*, it progressively changed towards other species, such as *C. destructor* and *C. quadricarinatus*. This was probably the result of a combination of the former species' slow growth and the poor understanding of its aquaculture requirements and technologies, which ended in several failed trials. In recent times, probably because of strict legal requirements for acquiring permits, interest in crayfish farming activities seems to have gradually decreased. Consequently, both the illegal pet trade, especially for *P. clarkii*, and deliberate translocations by fishermen or individuals interested in farming crayfish, are now the most dangerous active pathways of crayfish spread.

There is evidence that *C. quadricarinatus* and *P. clarkii* have established wild populations in South Africa (Nunes et al. 2017a, 2017b). *Cherax quadricarinatus* has been shown to spread rapidly both upstream and downstream in South Africa (see Nunes et al. 2017a), whereas *P. clarkii* appears restricted to a single locality (Nunes et al. 2017b). The other species are either restricted to isolated aquaculture facilities (*C. cainii*) or have not been reported for several years (*C. destructor*). Notably, the present study shows a geographical pattern related to both crayfish commercial activities and their invasions in South Africa, depending on the species being investigated. Whereas *C. cainii* has been farmed and documented mainly in the Western and Eastern Cape provinces, *C. quadricarinatus* is found in Mpumalanga and KwaZulu-Natal, *C. destructor* activities were centred in Free State and Gauteng and the sole location of *P. clarkii* is a farm in Mpumalanga.

Overall, the areas in South Africa apparently at most risk from crayfish species invasions, because of environmentally suitable conditions, include most of the eastern part of the country (Mpumalanga and KwaZulu-Natal) and specific parts of the Eastern and Western Cape (Figure 4). This indicates that provincial environment authorities in these areas should be especially alert for this problem. For the Eastern and Western Cape, in particular, given that currently no crayfish occur in the wild in these provinces, the authorities should implement early warning and rapid response systems, to be put into practice immediately in case a crayfish specimen is detected.

Invasion pathways and future spread

Aquarium trade

In the early 1980s, van Eeden et al. (1983) were already calling for the destruction of all specimens of *P. clarkii* offered for sale or in private possession. Although a successful operation confiscating *P. clarkii* specimens from several pet shops was conducted in 1987 by the Cape Department of Nature and Environmental Conservation (Anonymous 1987), today, more than 30 years later, this and other crayfish species (e.g. *C. quadricarinatus*) are still available for sale via online advertisement websites and in some pet shops around the country (A Nunes, pers. obs.). This indicates that the aquarium trade still represents a relevant pathway of secondary introductions of alien

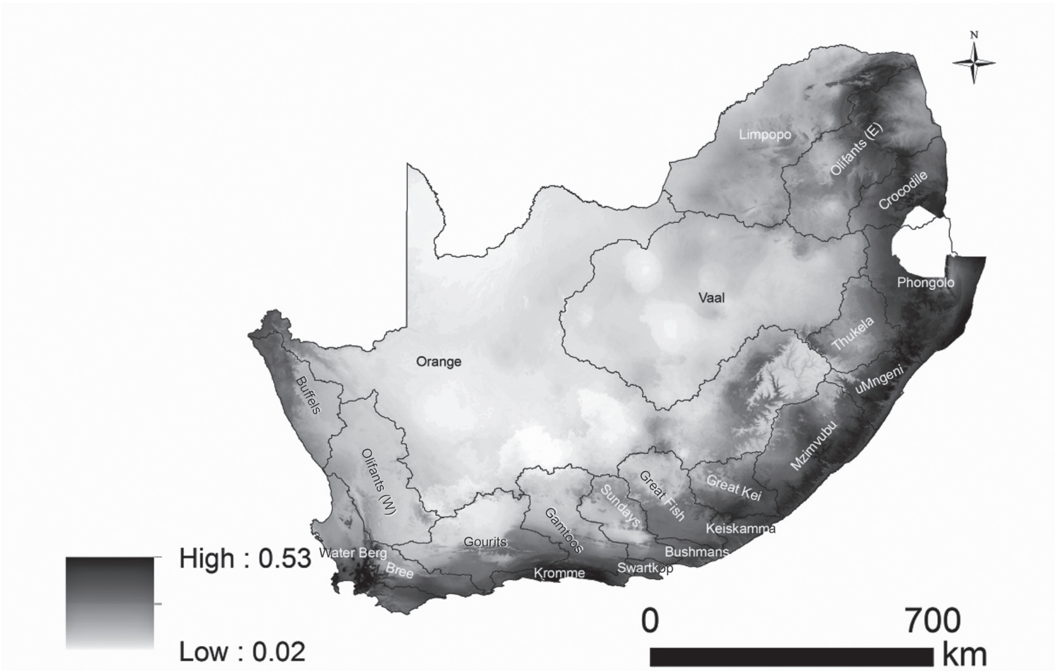

Figure 4: Combined potential distribution ranges of *Cherax cainii*, *C. destructor*, *C. quadricarinatus* and *Procambarus clarkii* in South Africa, based on weighted sum of ecological niche models constructed using occurrence records from species' native and introduced ranges. Potential distribution indicated by shading; dark = high, light = low probability of suitable climatic conditions. Primary river catchment areas as defined by the Department of Water and Sanitation, Republic of South of Africa (http://www.dwa.gov.za/iwqs/gis_data/)

crayfish in South Africa. Given the importance of pet trade as a pathway of crayfish introductions around the world, and its increase in recent decades (Chucholl 2013, Faulkes 2015), we suggest immediate increased enforcement to halt the illegal aquarium and online trade of freshwater crayfishes in South Africa.

Aquaculture activities

As *C. cainii* is the only species legally permitted for aquaculture in South Africa, and a permit imposing strict protocols is required for undertaking this activity, it is unlikely that commercial aquaculture will contribute significantly to secondary introductions and the spread of alien crayfish species in South Africa. However, it is important to emphasise that there are illegal crayfish farming activities occurring in the country (K Halley, Department of Agriculture, Forestry and Fisheries, and L Coetzer, Department of Agriculture and Rural Development and Land Administration, pers. comm.), which substantially increase the likelihood of escapes into the wild, because of poor biosecurity measures. It is also important to point out that specimens of both *C. cainii* and *C. quadricarinatus* have previously escaped from legal aquaculture facilities, in both South Africa (de Moor and Bruton 1988) and Swaziland (de Moor 2002, 2004), which highlights the risk of these activities. Moreover, given the history of the failure of attempts to develop crayfish aquaculture in southern Africa, it is unlikely that this industry will succeed in the future. Furthermore, as these failed ventures often resulted in the release of propagules into the environment, both accidentally and via sales to third parties, we suggest that the use of crayfish in aquaculture be treated with caution.

Deliberate translocations

Informal spread and deliberate stocking by fishermen, farmers with dams, or citizens in general for recreation purposes, poses a very high risk. Stocking crayfish in farm dams for personal use or in public dams for fish bait is not permitted in South Africa (RSA 2016), but it has happened in the past and is probably still taking place. This represents one of the most dangerous pathways of alien crayfish spread in South Africa.

Natural spread

Cherax quadricarinatus has been continuously spreading both upstream and downstream from its points of introduction in natural waterways in South Africa and Swaziland at a rate that might reach 14.6 km year^{-1} (Nunes et al. 2017a). Moreover, this spread can be substantially enhanced by extreme rainfall/floods, which frequently occur in both Mpumalanga and KwaZulu-Natal, and which can unexpectedly greatly extend the species' invaded range. For *P. clarkii* populations, even though they do not seem to have spread from the area of introduction in the past 22 years, a summer period with abnormally high temperatures (perhaps instigated by climate change) could potentially cause densities to increase drastically. The population could then explode, colonise, and spread in the Crocodile River. Finally, due to their ability to disperse overland, crayfish can potentially colonise isolated freshwater bodies.

Management considerations

Management and eradication of alien crayfish species around the world has proven to be very challenging (see review in Gherardi et al. 2011a). In South Africa, the two species that are established in the wild, *P. clarkii* and *C. quadricarinatus*, would require very different management strategies. Given that the only *P. clarkii* population in the country is localised in a dam on a trout farm, where its density seems to be extremely low, this presents the perfect opportunity to attempt eradication, especially considering that crayfish eradication seems possible only for populations in small and enclosed water bodies (Gherardi et al. 2011a). Furthermore, given that *P. clarkii* is listed as a prohibited species in the NEMBA regulations (RSA 2016), its eradication is a legal requirement. Nunes et al. (2017b) suggest that, although chemical poisoning seems to be the only effective technique for eradicating crayfish populations, the high concentrations required and non-specificity of these toxic products, make the use of this technique undesirable. Alternative options include the use of mechanical techniques (intensive trapping, electrofishing and removal by hand), coupled with total dewatering of the dam. Importantly, the fact that *P. clarkii* exhibits burrowing habits that allow it to withstand extreme environmental conditions, such as drought (Kouba et al. 2016, Souty-Grosset et al. 2016), has to be taken into account, given that it can hinder the success of any attempted physical, mechanical or chemical eradication.

The case of *C. quadricarinatus* is much more complex, given that the species is widespread in the country and numerous illegal activities, such as translocations, farming and commercial sales seem to be taking place. *Cherax quadricarinatus* provides a classic example of an alien conflict-generating species, i.e. a species that is likely to cause negative impacts to the environment, but which simultaneously has the potential to provide socio-economic benefits (see Zengeya et al. 2017). This conflict is evident in South Africa, and has been occurring for several years, with environmental conservation agencies (and often scientists) advocating for management or eradication actions, whereas aquaculturists and production-oriented organisations (e.g. Department of Agriculture) aim to exploit the species commercially through harvesting and aquaculture activities. For example, a media article published in 2013 stated that the population of *C. quadricarinatus* in the Nkomazi region of Mpumalanga was underutilised and could be exploited to provide food and a lucrative income for the locals (van Rooyen 2013). Recently, an article published in the local media also stated that farming freshwater crayfish species, such as *C. quadricarinatus*, might alleviate the extensive poaching crisis of marine lobsters in South Africa (de Villiers 2017). Such articles, biased towards commercial exploitation of crayfish, might actually promote further translocations by humans and increase the species' distribution range.

The decision on whether or not to allow farming of *C. quadricarinatus* in South Africa does not have a simple answer and should not be lightly considered. If the utilisation of *C. quadricarinatus* for aquaculture production is allowed, even if restricted to those provinces where wild populations currently occur, there is likely to be an increase in crayfish escapes and translocations into uninvaded waterways (see Nuñez et al. 2012). Even if they are prevented from escaping, there are always unforeseen risks, such as theft. For example, a breeder in Bloemfontein had 400 specimens of *C. destructor* stolen from his facility, despite the crayfish being kept behind locked doors and an electric fence (Smith 2003). Furthermore, at the Amalinda Fish Station, East London, staff was reportedly selling *C. cainii* to fishermen for use as bait (D Churches, Amalinda Fish Farm, pers. comm.).

The successful management of *C. quadricarinatus* populations, as well as the control of illegal activities involving the species, would require a large and concerted effort by national and provincial environment authorities in South Africa, Mozambique and Swaziland, as well as by scientists, recreational fishermen, farmers/landholders, aquarists and the general public. Because many of these entities are likely to have different views on the actions that should be taken, the use of a recently proposed framework for engaging stakeholders in the management of alien species (Novoa et al. 2018) could help to tackle this issue.

It is doubtful that management actions could have a significant impact on *C. quadricarinatus* populations that are already established, indicating that conservation efforts should focus instead on containing further spread or translocations into uninvaded catchments. This should be done by implementing intensive and continued trapping effort, aiming at a decrease in species density at the invasion fronts. Educating the general public on the potential risks of introducing crayfish into the highly diverse freshwater ecosystems of South Africa, as well as establishing early warning systems to report new introductions, is also fundamental. The use of autocidal methods, such as the sterile male release technique, through which a large number of males are sterilised and then released into the wild, could be worth investigating for *C. quadricarinatus* populations in South Africa. However, not much research has been done on the topic, albeit that by Aquiloni and co-workers (2009).

Future directions

Although introductions of freshwater crayfish species in South Africa and subsequent escapes into the wild have occurred for more than 50 years, there is still a need for scientific research on these invasions. The most urgent necessity is to investigate the potential adverse ecological impacts of crayfish introductions in South Africa, focusing mainly on *C. quadricarinatus*. This is not only because this is the most widespread species in the country, but also because no research has been done on its impacts on invaded ecosystems anywhere else in the world. Potential impacts, such as competition with and parasite and disease transfer to native decapod species (freshwater crabs or prawns), disturbance of reproductive activity and nesting success of substrate-spawning fish, and the general influence of crayfish on food web structure and functioning, should be investigated. Furthermore, it would be important to understand which biotic and abiotic parameters influence crayfish spread and establishment the most, as a tool that might help develop effective control and management measures for this species. Finally, a continuous monitoring program should be implemented, to provide up-to-date knowledge of *C. quadricarinatus* distribution and abundance in South Africa. This information would be the foundation for any control or management program to be implemented successfully.

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