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Article *in* African Zoology · April 2018

DOI: 10.1080/15627020.2018.1448719

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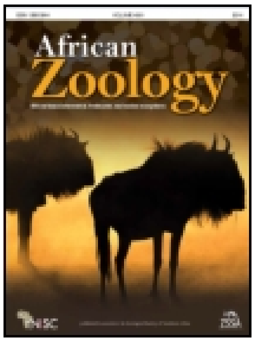

African Zoology

ISSN: 1562-7020 (Print) 2224-073X (Online) Journal homepage: http://www.tandfonline.com/loi/tafz20

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To cite this article: Lightone Marufu, Maxwel Barson, Portia Chifamba, Michael Tiki & Tamuka Nhiwatiwa (2018): The population dynamics of a recently introduced crayfish, Cherax quadricarinatus (von Martens, 1868), in the Sanyati Basin of Lake Kariba, Zimbabwe, African Zoology, DOI: 10.1080/15627020.2018.1448719

To link to this article: https://doi.org/10.1080/15627020.2018.1448719

Published online: 20 Apr 2018.

African Zoology 2018: 1–6
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This is the final version of the article that is
published ahead of the print and online issue

AFRICAN ZOOLOGY
ISSN 1562-7020 EISSN 2224-073X
https://doi.org/10.1080/15627020.2018.1448719

The population dynamics of a recently introduced crayfish, *Cherax quadricarinatus* (von Martens, 1868), in the Sanyati Basin of Lake Kariba, Zimbabwe

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The redclaw crayfish *Cherax quadricarinatus* is a recent introduction into Lake Kariba, Zimbabwe where it is rapidly spreading. There are, however, no studies that have investigated the population dynamics and possible ecological impacts of the crayfish in the lake. This study investigated aspects of the population biology of *C. quadricarinatus* in the lake. These included sex distribution, population growth and mortality parameters, probability of capture, recruitment and length at age of ge at maturity. Crayfish were captured monthly between January and December 2013 from 13 sites using opera house bait traps. Aspects of the species population biology were estimated using a fish stock assessment tool, FISAT II. A total of 3 205 crayfish were captured, of which 44% were male, 49% female and 7% intersex individuals. The asymptotic length (L_∞ = 112.88 mm), curvature parameter (k = 0.72), longevity (t_{max} = 4.17 years), growth performance index (ϕ = 3.96), total mortality (Z = 2.06 y^{-1}), fishing mortality (F = 1.07 y^{-1}), natural mortality (M = 0.99 y^{-1}), rate of exploitation (E = 0.52) and length-at-first capture (L_c = 44.48 mm) were estimated. Fecundity averaged 503 ± 229 eggs female^{-1} and increased with size (weight and carapace length). Gravid females were found throughout the year but the highest proportion of females with eggs (4–10%) were found in the first quarter, whereas recruitment peaked in May and June. The smallest crayfish with eggs (48.75 mm CL) was estimated to be 1.02 years and the largest (94.82 mm CL) 2.85 years. *Cherax quadricarinatus* exhibited an *r* strategy life-history pattern due to continuous reproduction and high fecundity. In Lake Kariba, *C. quadricarinatus* is now well into the establishment stage of the Introduction–naturalisation–invasion continuum and spreading in the lake. Management options should thus aim at preventing further spread and reducing the population size and the potential negative impacts of this species.

Keywords: fecundity, mortality, recruitment, reproduction, sex distribution

Introduction

Invasive aquatic species are among the most prominent threats to biodiversity in the world (Sala et al. 2000; Clavero and García-Berthou 2005; McGeoch et al. 2010). Freshwater crayfish are keystone species that are able to affect aquatic ecosystems at varying trophic levels (Momot 1995; Lodge et al. 2000; Kats and Ferrer 2003; Chucholl 2012). They are known to disturb ecosystem functions by competing with indigenous species, destroying habitats and ultimately changing the trophic structure of the invaded environment (Lockwood et al. 2007; Davis 2009; Chucholl 2012).

Classic examples include how *Procambarus clarkii* destroyed habitats in some Spanish lakes within a few years (Rodríguez et al. 2005), the crayfish plague (*Aphanomyces astaci*) epidemic in Europe that occurred after the introduction of invasive crayfish *Pacifastacus leniusculus*, *Procambarus clarkii* and *Orconectes limosus* (Parvulescu et al. 2012) and the displacement of native fishes by *P. leniusculus* in a British lowland river (Guan and Wiles 1997). These negative impacts are some of the reasons why the introduction of crayfish has been discouraged in some parts of Africa (de Moor 2002), despite being in demand as an aquaculture species.

Cherax quadricarinatus is not indigenous to Africa (Adegboye 1983), but has been introduced for aquaculture and now occurs in South Africa (de Moor 2002; Nunes et al. 2017), Swaziland (Nunes et al. 2017), Mozambique (Nunes et al. 2017), Zambia (Thys van der Audenaerde 1994) and, more recently, in Zimbabwe (Marufu et al. 2014). *Cherax quadricarinatus* originates from northern Australia and Papua New Guinea (Austin 1996). Its introduction into Lake Kariba, which is shared between Zimbabwe and Zambia, is an example of an accidental introduction. It was initially introduced into fish farms in Livingstone, Zambia, for aquaculture purposes in 1992 (Thys van der Audenaerde 1994). The species is also believed to have escaped from another fish farm in Siavonga, Zambia from where it directly escaped into Lake Kariba (Kafue River Trust 2017). A study

African Zoology is co-published by NISC (Pty) Ltd and Informa UK Limited (trading as Taylor & Francis Group)

Published online 20 Apr 2018

by Nakayama et al. (2010) was one of the first to observe *C. quadricarinatus* in catches from the lake. The species is rapidly spreading in the lake (Marufu et al. 2014), and there is a need for management of the species.

Studies of the population biology of invasive species have been shown to be important for effective management purposes (Grandjean et al. 2000; Sakai et al. 2001; Alhassan and Armah 2011). For example, Freeman et al. (2010) recommended the use of biological control and integrated pest management options after undertaking research to better understand the population biology of the invasive signal crayfish *Pacifastacus leniusculus*. However, studies on the population dynamics of alien populations of *C. quadricarinatus* in the wild are rare (Ahyong and Yeo 2007; Vega-Villasante et al. 2015). This is in contrast to the numerous studies on its growth under aquaculture and experimental conditions (Romero 2002; Thompson et al. 2005; Barki et al. 2006). Such studies of captive crayfish populations are not easily translated to conditions in the wild (Archard and Braithwaite 2010) and give little insight into possible life-history strategies employed in the wild.

Cherax quadricarinatus is a recent introduction into Lake Kariba and there have been no comprehensive studies that assess basic biological aspects of the species, such as reproduction and growth. Only one previous study (Marufu et al. 2014) has reported on some elements of the reproductive and growth biology of *C. quadricarinatus* in the lake. That study, however, was limited to one sampling event and the results were preliminary. The aim of the present study was, therefore, to undertake a more comprehensive assessment of the reproductive and growth biology of *C. quadricarinatus* in Lake Kariba by assessing aspects of its reproductive biology and population dynamics. This information will be used to determine the stage of the introduction–naturalisation–invasion continuum of *C. quadricarinatus* in the lake (*sensu* Blackburn et al. 2011) and subsequently advise on possible management approaches to minimise its spread and impact.

Materials and methods

Study site

The study was done in the Sanyati Basin of Lake Kariba (Figure 1). Lake Kariba is a man-made reservoir that was constructed in 1960. The lake is shared between Zimbabwe and Zambia and was constructed mainly for hydroelectric power generation. The dam height is 128 m and the lake has a maximum length of 280 km and a width of 32 km. The lake has a total surface area of 5 580 km^2 and an estimated volume of carrying capacity of 185 km^3. The Sanyati Basin is one of the five basins of Lake Kariba. It is located in the north-eastern end of the lake. The length of the basin is 46 km with a mean width of 27km and a total surface area of 1 223 km^2. The mean depth is 33 m and the total volume is 40×10^6 m^3.

Crayfish capture

A total of 13 sites along the north-eastern shoreline of the Sanyati Basin were sampled monthly between January and December 2013 (Figure 1). Crayfish were trapped using the method described by Marufu et al. (2014). Six opera house activity traps (with a base length of 1 m and width of 0.5 m) were placed at each site and removed the following morning. Cooked maize meal paste was used as bait. The number of crayfish caught in each trap, as well as their carapace length (mm), mass (g) and sex were recorded. Crayfish were sexed by examining the location and type of genital pores as described by Vazquez and Lopez-Greco (2007). Individuals that could not be sex differentiated, due to possession of both male and female genital pores, were recorded as intersex individuals. Chi square analysis was used to assess if the sex ratios departed from the expected ratio (1:1) for females and males.

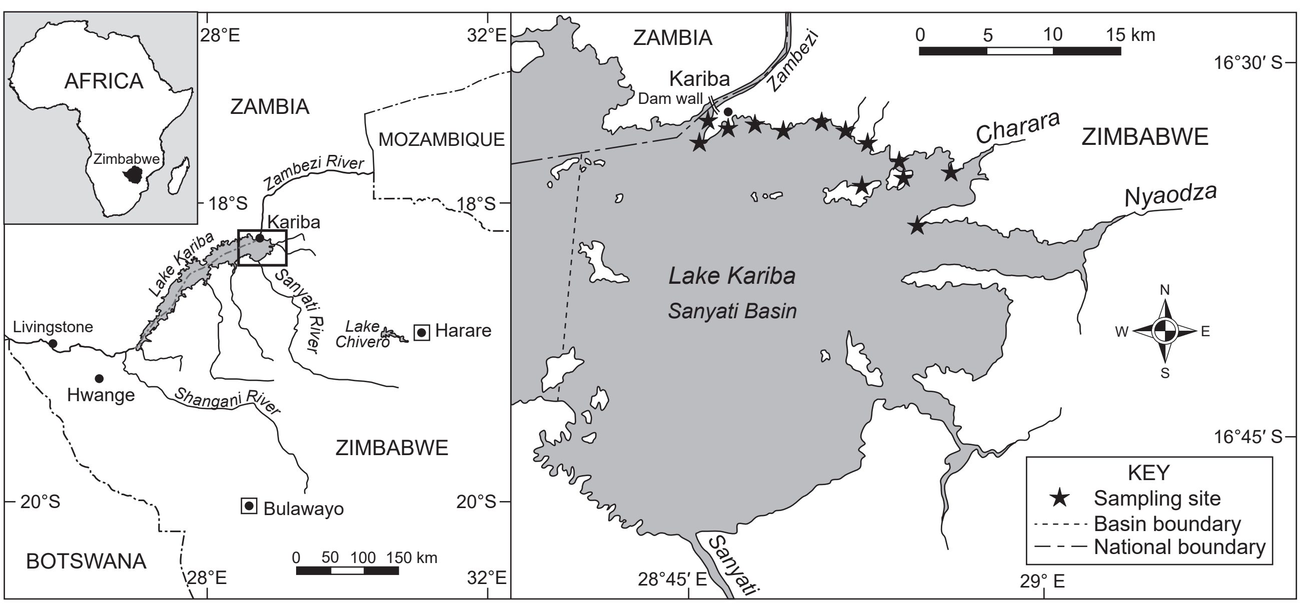

Figure 1: Map of the Sanyati Basin, Lake Kariba showing the sampling sites

Crayfish growth, longevity and mortality

Analysis of growth and mortality parameters were estimated using the FiSAT II (FAO–ICLARM Stock Assessment Tools) version 1.2.2 (2000–2005) software (Gayanilo et al. 2005). A length frequency graph was produced by classifying the carapace length frequency using 5 mm intervals and plotted using the appropriate mid-lengths.

First estimates of mortality, longevity and recruitment were also determined using FiSAT II. The instantaneous rate of annual mortality (Z) using the length-converted catch curve (Pauly 1990) and longevity (t_{max}) was estimated using the equation $t_{max} = (3/K) + t_0$, where K is the von Bertalanffy growth parameter and t_0 is the x-intercept from the fit of the von Bertalanffy growth function (Chucholl 2011, 2012).

Fecundity

A method described by Chucholl (2012) was used to determine the fecundity of *C. quadricarinatus*. All females with eggs were captured and transported to the laboratory for further analysis. All attached eggs were stripped off using forceps and counted using a counter. The weight (g) and carapace length (mm) of females with eggs were measured. In order to minimise bias due to excessive losses of eggs during transportation, only females with >300 eggs were used in further analysis. A linear model for the data was plotted and its goodness of fit value (R^2) assessed. The correlation (r) between fecundity and crayfish size (carapace length and weight) was also determined.

Results

Sex distribution

A total of 3 205 crayfish were caught between January and December 2013. Overall, females were the most abundant (49% of the total catch), whereas intersex crayfish were the least frequent (7%) (Table 1). Sex ratio was significantly different from the expected sex ratio of 1:1 ($\chi^2 = 8.77$, df = 1, $p < 0.05$), with proportions of the different sexes varying throughout the year (Figure 2). Between January and March, males were more active, but from April females constituted a higher proportion of the catch compared with males. The proportion of intersex individuals remained below 10% of the catch throughout the sampling period, except for the month of June in which it was 25% (Figure 2).

Growth parameters

The length frequency histograms for *C. quadricarinatus* in Lake Kariba derived from the FiSAT II analysis and the resultant von Bertalanffy growth model are shown in Figure 3. The observed maximum carapace length (L_{max}) was estimated to be 107.5 mm, whereas the predicted extreme carapace length (L1) was 109.14 mm (95% confidence interval 104.48–113.80 mm). The curvature parameter ($K = 0.72$), asymptotic length ($L_\infty = 112.88$ mm) and $t_0 = -0.09$ were also derived. From the estimation of L_∞, K and t_0, longevity ($t_{max} = 4.17$), growth performance index ($\phi = 3.96$) and total mortality ($Z = 2.06$) were estimated.

Table 1: Distribution of sexes in *Cherax quadricarinatus* from Lake Kariba between January 2013 and December 2013

	Males	Females	Intersex	Total
Total caught	1401	1582	222	3205
Mean catch ± SD	215.53 ± 44.47	243.38 ± 62.09	34.15 ± 31.12	477.69 ± 107.07
Ratio (%)	44	49	7	100

Fecundity

A total of 25 females with eggs were caught during the study. Length at age data were used to estimate the age of the smallest (1.02 years) and largest (2.85 years) crayfish that were caught with eggs by using the growth curve derived in Figure 3. The mean weight and carapace length of females with eggs was 71.20 ± 27.87 g and 67.08 ± 11.20 mm, respectively, with the mean number of eggs being 502.71 ± 228.78 eggs female^{-1} (Table 2). *Cherax quadricarinatus* was generally found to be gravid throughout the year, with the highest proportion of females with eggs found in the early months of January to March and then decreasing to less than 2% from April to December (Figure 4). Fecundity increased with size (Figure 5) with regression analysis indicating a strong correlation between both length and weight with number of eggs ($R^2 = 0.62$ and $R^2 = 0.73$, respectively).

Discussion

Population dynamics studies can help to reveal important biological aspects of an alien species invasion and its progress along the introduction–naturalisation–invasion continuum (Davis 2009; Blackburn et al. 2011). The current study has provided evidence that *C. quadricarinatus* is now well into the 'establishment stage' on the introduction–naturalisation–invasion continuum because it has been able to survive and reproduce multiple generations since its introduction into the lake. This, in conjunction with the wide extent of occurrence of *C. quadricarinatus* in the Zambezi River Basin (see Nunes et al. 2016), shows that the species can be considered fully invasive (*sensu* Blackburn et al. 2011).

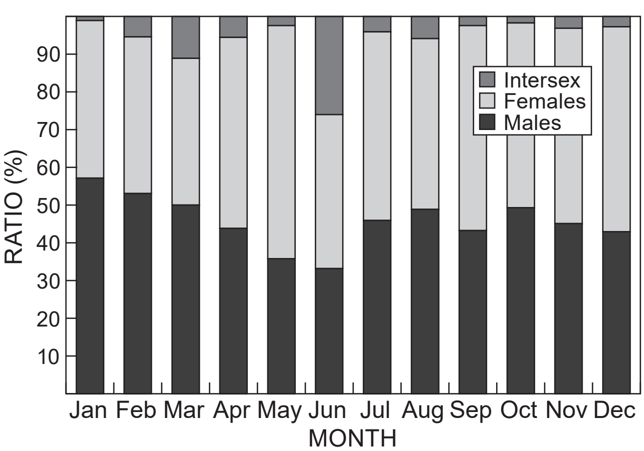

Figure 2: Changes in the sex distribution of *Cherax quadricarinatus* in the Sanyati Basin of Lake Kariba

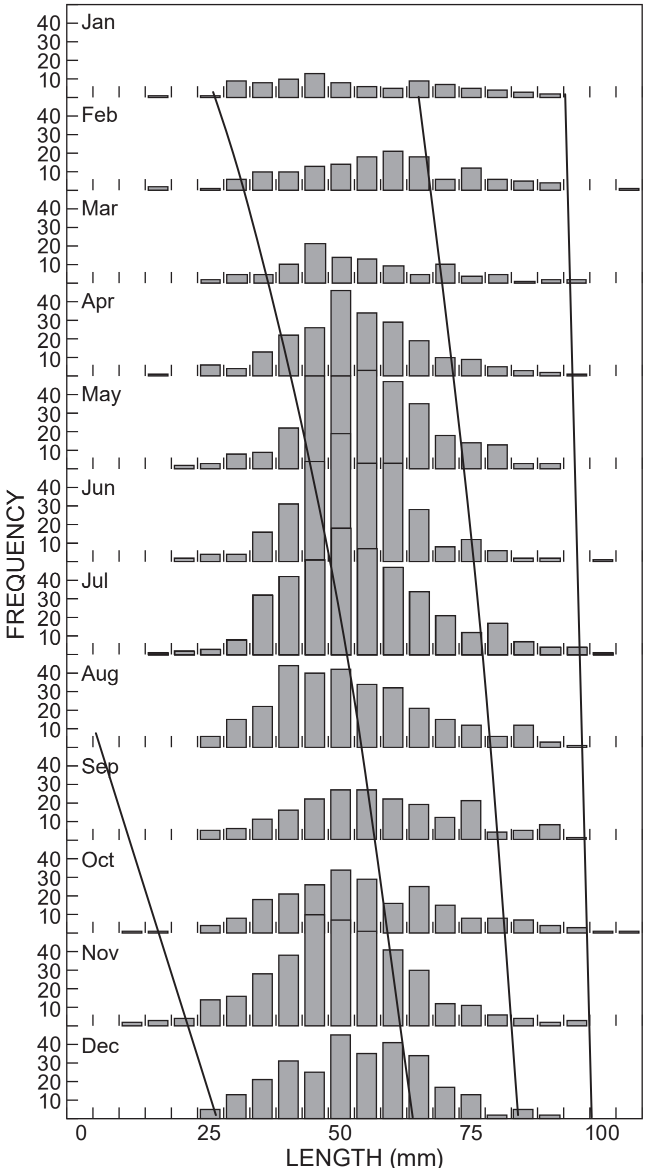

Figure 3: Estimated VBGF growth model of *Cherax quadricarinatus* caught in Lake Kariba after analysis with FiSAT II. Histograms represent the distribution of the size classes at 5 mm intervals

Table 2: Fecundity of *Cherax quadricarinatus* caught from the wild in Lake Kariba, Zimbabwe

	Mean ± SD	Minimum	Maximum
Eggs	502.71 ± 228.78	305	1 084
Weight (g)	71.20 ± 27.87	34.26	93.02
Carapace length (mm)	67.08 ±11.20	54.09	94.82

The current study indicated that, at the onset of the year, more males were caught compared with females. The likely explanation is that most females during January–March were ovigerous, and consequently less active and therefore less likely to be caught by activity traps. Similar conclusions were made in other studies on different crayfish species also studied in the wild (Frutiger et al. 1999; Grandjean et al. 2000; Dorr et al. 2006). The results also showed the occurrence of intersex individuals (with both male and female genital pores) in the population, which was not reported in previous studies on crayfish in Lake Kariba (Marufu et al. 2014; Nakayama et al. 2014). The proportion of intersex individuals in Lake Kariba (7%) was higher than the 2–4% reported by Brummet and Alon (1994) under culture conditions. Other studies (also under culture conditions) have found the proportion to be even lower at 1.2% (Sagi et al. 1996), whereas proportions as high as 17% have been reported (Medley and Rouse 1993). Intersex individuals are known to predominantly occur when culture conditions are stressful (Vazquez and Lopez Greco 2007). In addition, the occurrence of endocrine disrupting pollutants (EDPs) in crustaceans has been shown to increase the number of intersex individuals (Barki et al. 2006; Moore and Stevenson 1991). A study by Nakayama et al. (2010) found that *C. quadricarinatus* in Lake Kariba tissues contained EDPs. The EDPs present in high concentration (mg kg^{-1} dry weight) in muscle tissue included zinc (78 ± 10), copper (33 ± 8) and chromium (1.86 ± 0.98), while lead, nickel and chromium were also found in lower

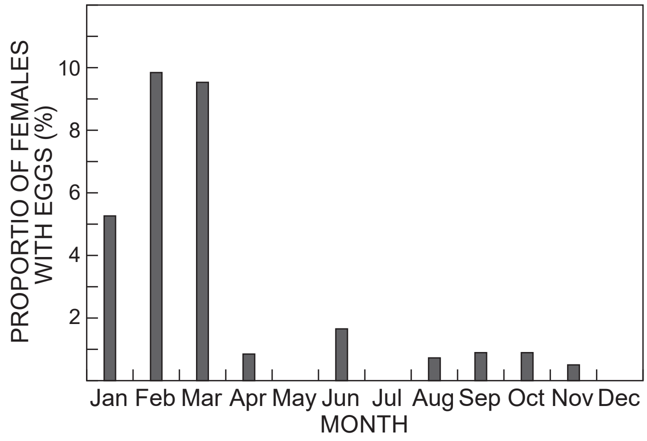

Figure 4: Proportion of *Cherax quadricarinatus* females with eggs out of total number of females caught

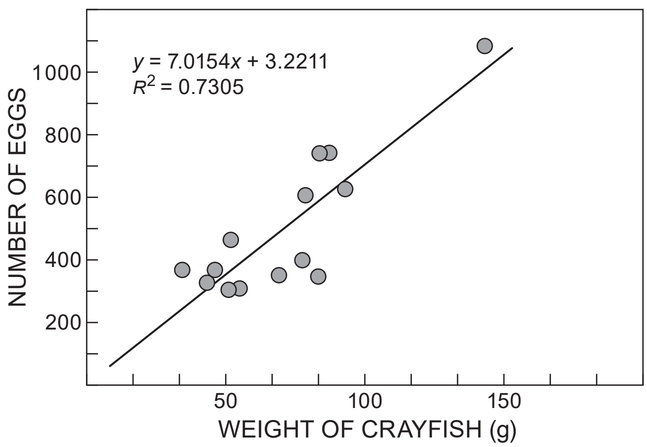

Figure 5: Linear fit between weight (g) and number of eggs of *Cherax quadricarinatus* caught in the wild of Lake Kariba, Zimbabwe

amounts (Nakayama et al. 2010). This warrants further investigation.

There is some indication that *C. quadricarinatus* in Lake Kariba is following a more '*r*' selected life-history strategy than in its native range. Length-at-age data revealed that *C. quadricarinatus* in Lake Kariba had a higher growth rate than for crayfish reared under controlled (aquaculture) conditions reported by Leland et al. (2015). The minimum length at maturity (estimated during the current study; 1.02 years) was similar to that reported by Rouse et al. (1991) for the same species but relatively younger when compared with a related species such as *Cherax cainii* (2–3 years) (Beatty et al. 2004) and another species *Austropotamobius torrentium* (3–4 years) (Streissl and Hodl 2002). *Cherax quadricarinatus* in Lake Kariba is producing eggs at much smaller sizes (Masser and Rouse 1997) but at higher fecundity than in its native range or under culture conditions (Sagi et al. 1997). The average number of eggs per female recorded in Lake Kariba (502) was much greater than that reported for *C. quadricarinatus* under culture conditions (321; King 1993; Sagi et al. 1997; Tropea et al. 2012). These *r* strategist characteristics are typical of an invader in a new environment. The fast growth rate, short life span, high fecundity and continuous reproduction are all indicative of an *r* strategist to ensure successful establishment in a new environment.

In conclusion, *Cherax quadricarinatus* can now be considered an established invasive species in the Zambezi basin and elsewhere (see Nunes et al. 2016, 2017). As recommended by Blackburn et al. (2011), management options at this stage of invasion should aim at containment strategies and preventing further spread. An important aspect of this will be developing monitoring programs to determine the status of this species throughout the river basin.

Acknowledgements — This study was funded by the Research Council of Zimbabwe and the University of Zimbabwe Vice Chancellor's Data Collection Fund as part of a DPhil study by Lightone T Marufu. We thank the University of Zimbabwe Lake Kariba Research Station (ULKRS) staff for their support during the study. We also appreciate the assistance received from the Zimbabwe National Parks and Wildlife Management Authority during the study.

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Received 5 January 2017, revised 26 February 2018, accepted 2 March 2018
Associate Editor: Olaf Weyl