

Research Article

First record of giant freshwater prawn *Macrobrachium rosenbergii* (de Man, 1879) from small-scale fisheries in East Africa, confirmed with DNA barcodingBaraka Kuguru¹, Johan Groeneveld^{2,3,*}, Sohana Singh² and Boniventure Mchomvu¹¹Tanzania Fisheries Research Institute, PO Box 9750, Dar es Salaam, Tanzania²Oceanographic Research Institute, PO Box 10712, Marine Parade, 4056 Durban, South Africa³School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, KwaZulu-Natal, South AfricaAuthor e-mails: barakakuguru@gmail.com (BK), jgroeneveld@ori.org.za (JG), ssingh@ori.org.za (SS), b775r83@gmail.com (BM)

*Corresponding author

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Abstract

We report, for the first time in the wild, giant freshwater prawn *Macrobrachium rosenbergii* populations in East Africa. Specimens caught by fishermen in the lower reaches of the Ruvu River and Rufiji Delta in coastal Tanzania were identified based on their morphology, with confirmation through DNA barcode analysis. The East African specimens clustered with the western *M. rosenbergii dacqueti* subspecies in a phylogenetic analysis based on new and published mitochondrial 16S rRNA and cytochrome *C* oxidase subunit I (COI) sequences. Captured specimens spanned a size range of 110–310 mm total length and > 35% of females carried external eggs, implying that populations were established and self-sustaining. No active culture facilities or ponds with *M. rosenbergii* were found within the catchment. Nevertheless, the invasive populations supported a small-scale fishery that used bottom-set seine nets. The demonstrated presence of *M. rosenbergii* in at least two river systems, combined with the existence of favourable brackish water habitats for completing their life cycle, may indicate that river systems in East Africa are at a high risk of invasion by this species. Key information gaps for the region are highlighted.

Key words: bioinvasion, exotic species, reproductive viability, river prawn, Tanzania**Introduction**

The giant freshwater (or river) prawn *Macrobrachium rosenbergii* (de Man, 1879) is native to the tropical and subtropical Indo-West Pacific region, extending eastwards from India to Southeast Asia and Papua New Guinea (De Grave et al. 2013a). It is one of the most cultured freshwater prawns in the world, and the FAO Database on Introductions of Aquatic Species (FAO-DIAS 2009) lists at least 40 countries where it has been introduced for aquaculture. Escapees from aquaculture facilities have established exotic populations in Brazil (Silva-Oliveira et al. 2011; Iketani et al. 2016), Venezuela (Pereira et al. 1996), Panama (FAO-DIAS 2009), Martinique Island (Lim et al. 2002), Madagascar (Hanamura et al. 2008), the United States of America (Woodley et al. 2002), Taiwan and Russia (FAO-DIAS 2009).

Macrobrachium rosenbergii has not previously been reported from the wild in East Africa, apart from records from Uganda and Kenya in the early 1960s (FAO-DIAS 2009), which were subsequently dismissed as mistaken identification (Bailey and Crichton 1971). At least eight other *Macrobrachium* species are widespread in East African rivers and lakes (Bailey and Crichton 1971). Records from mainland Tanzania (Rufiji, Ruvu, Wami and Pangani rivers) and Kenya (Athi-Sabaki and Tana rivers) include *M. idella* (Hilgendorf, 1898), *M. rude* (Heller, 1862), *M. equidens* (Dana, 1852), *M. lepidactylus* (Hilgendorf, 1879), *M. scabriculum* (Heller, 1862) and *M. patsa* (Coutière, 1899) (cited in De Grave 2013a–f; De Grave et al. 2013b–d). *Macrobrachium moorei* (Calman, 1899) is endemic to Lake Tanganyika, and *M. niloticum* (J. Roux, 1833) is known from the Nile River, including Lake Turkana in Kenya.

There is no evidence as yet for serious ecological consequences following introductions of *M. rosenbergii* to new environments (Anger 2013), as observed for various crayfish species world-wide (Gherardi et al. 2011). Continued spread of *M. rosenbergii* to new environments nevertheless enhances the likelihood of competitive displacement of native species, shifts in species diversity through ecosystems effects (Hobbs et al. 1989; Lodge et al. 2000) and introduction of viral and bacterial disease (New et al. 2009). In contrast, the establishment of exotics has increased fishery yields without apparent detriment to native biodiversity in some situations (Dudgeon and Smith 2006).

The systematics of the *M. rosenbergii* species group has not yet been fully resolved, and some debate remains on whether it comprises a single wide-ranging species (Holthuis 1995), or two genetically and morphologically distinct subspecies (de Bruyn et al. 2004; Wowor and Ng 2007; Iketani et al. 2011): *M. rosenbergii dacqueti* (Sunier, 1925) from the Asian mainland and Malaysia, and *M. rosenbergii rosenbergii* (de Man, 1879) from east of Huxley's Line, in the Philippines and Papua New Guinea.

A fisheries survey of the lower Ruvu River and Rufiji Delta in mainland Tanzania identified occasional small-scale fisheries for freshwater prawns, which generated more income than fish catches. Fishermen reported that the fishery had been active for three to four years, and that prawns were more abundant after periods of flooding. Anecdotal information suggested that *M. rosenbergii* may also be present in the Pangani River, and the Tana River in Kenya. We report, for the first time, wild populations of the giant freshwater prawn *M. rosenbergii* in East Africa. *Macrobrachium rosenbergii* specimens were identified based on their morphology (Wowor and Ng 2007) and DNA barcoding. The size composition, body metrics and egg-bearing status of captured *M. rosenbergii* were used to evaluate whether populations are self-sustaining in the wild.

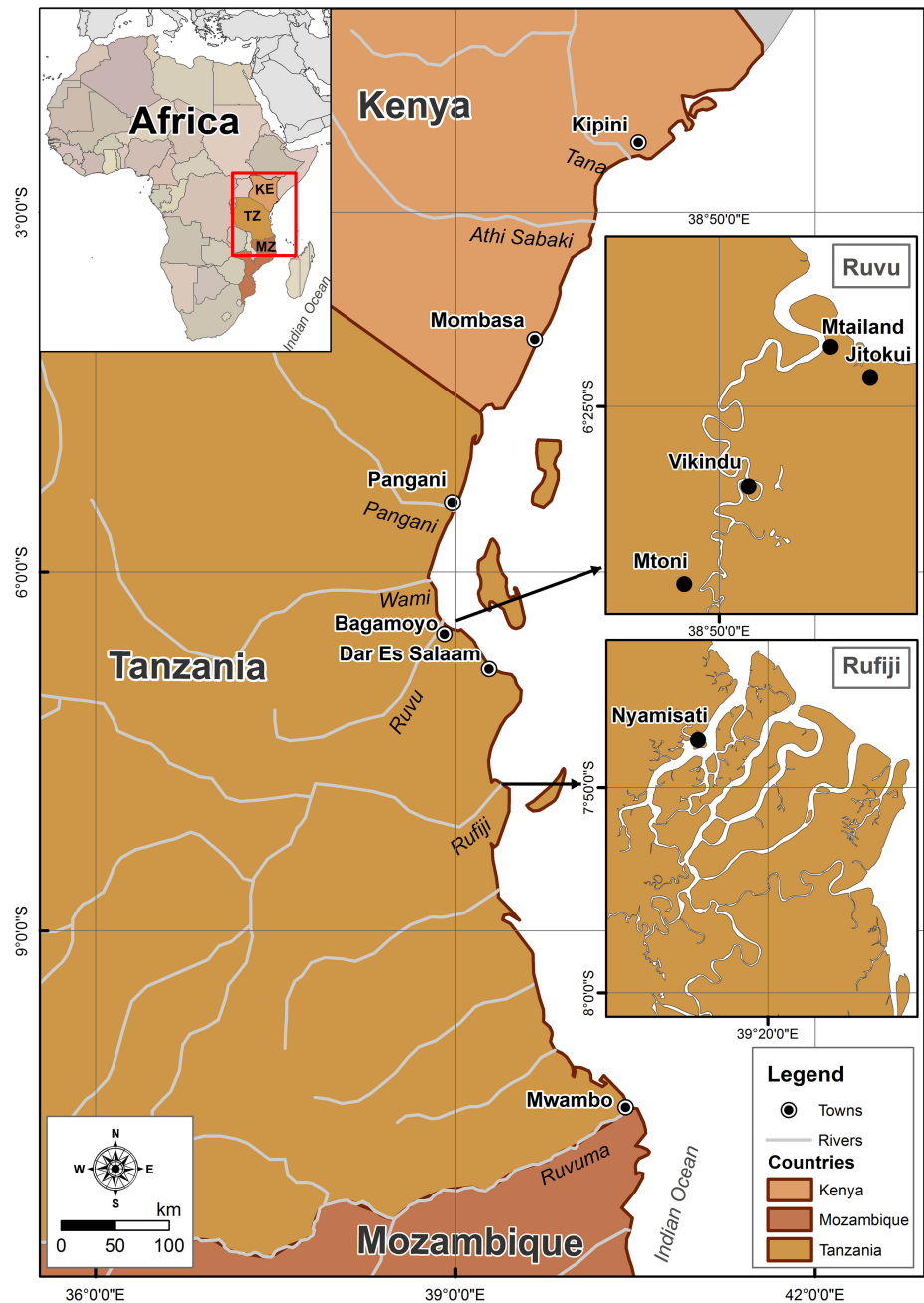


Figure 1. Sampling sites in the lower Ruvu River and the Rufiji Delta in Tanzania (black circles), and the location of other major estuaries in Kenya and Tanzania where *Macrobrachium rosenbergii* are likely to be found.

Materials and methods

Coastal Tanzania (Figure 1) has a humid tropical climate and high seasonal rainfall between October and May. Rivers drain into the Western Indian Ocean (WIO), often forming deltas dominated by dense mangrove forests (Bosire et al. 2016). The Ruvu River ($\approx 12,000 \text{ km}^2$ catchment basin) terminates in a meandering medium-sized estuary surrounded by rice farms, scattered rural settlements, and dense mangrove forests (Saha et al. 2014). In contrast, the Rufiji Delta drains most of southwestern Tanzania ($\approx 179,000 \text{ km}^2$ catchment basin, Shagude 2016), terminating in a major mangrove-covered delta system (Wagner and Sallema-Mtui 2016).



Figure 2. Male *Macrobrachium rosenbergii dacqueti* (total length 225 mm; 13 teeth on dorsal rostrum margin; 10 on ventral margin) caught in lower Ruvu River, near Bagamoyo. Photograph by Johan Groeneveld.

Field sampling and laboratory work

River prawns were sampled during fisheries surveys of the lower Ruvu River (Nov–Dec 2017) and the Rufiji Delta (Jan–Feb 2018). Fishing gear used by fishers were bottom-set seine nets (50–75 mm mesh), deployed for 1 to 16 h (overnight) before hauling. The nets were operated from dugout canoes, departing for fishing grounds between 05h30 and 10h00, and returning to landing sites between 09h00 and 14h00. The average time spent fishing per day was 4.1 ± 0.4 h ($n = 151$). The nets caught mainly prawns and several fish species.

Prawns were collected at landing sites (see Figure 1) from fishermen returning from fishing grounds. *Macrobrachium rosenbergii* (Figure 2) was identified based on the numbers of teeth on the ventral and dorsal margins of the rostrum, presence of elongated chelipeds with equal length in large males, and large (giant) size of individual prawns (Bailey and Crichton 1971; Holthuis 1980; Wowor and Ng 2007). Specimens were weighed (W) to the nearest gram (g) and measured with Vernier callipers to the nearest millimetre (mm). The total length (TL) was measured from the tip of the rostrum to the end of the telson, and the carapace length (CL) from the eye socket to the postero-dorsal carapace edge. The endopodite morphology of the second pleopod pair, and larger chelipeds in mature males, were used to determine gender. The presence of eggs in females was recorded.

Physio-chemical information at sampling locations in the lower Ruvu River, measured with a conductivity probe (YSI EC 300A, YSI, USA), was obtained from Saha et al. (2014), and water temperature and salinity readings were taken with a SBE 19plus V2 SeaCAT Profiler in May 2018.

No comparable information could be obtained for the sampling locations in the Rufiji Delta.

Genomic DNA was isolated from leg tissue using the Qiagen DNeasy Blood and Tissue DNA purification kit (Qiagen, CA-USA), following the manufacturers protocol. The cytochrome oxidase subunit I (COI) was amplified using the standard, universal primers LCO1490 and HCO2190 (Folmer et al. 1994) and 16S rDNA was amplified using universal 16S primers 16Sar and 16Sbr (Kessing et al. 2004). The PCR's were carried out in 25 μ L reaction volumes, containing 12.5 μ L of OneTaq Quick-Load 2X Mastermix (New England BioLabs Inc.), 0.2 μ M of each 10 μ M primer, 2 μ L of 2–10 ng genomic DNA and 9.5 μ L of PCR-grade H₂O. Thermal cycling comprised denaturation at 95 °C for 10 minutes, 35 cycles of 95 °C for 30 seconds, and annealing temperatures of 50 °C for 30 seconds for COI and 72 °C for 45 seconds for 16S. Final extension was carried out at 72 °C for 10 minutes. The PCR reactions were run with a negative and positive control.

Sequencing was performed at the Central Analytical Facilities at Stellenbosch University. Chromatograms were inspected manually using FinchTV v. 1.4.0 (www.geospiza.com), and species identity verified using the Barcode of Life Data Systems web platform (BOLD; www.boldsystems.org) for COI and GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) for COI and 16S. Sequences were aligned using Clustal X implemented in BioEdit v. 7.2.5 (Hall 1999), optimised manually, and deposited at GenBank (accession numbers in Table 1).

Data analysis

For samples from the Ruvu River, linear regression was fitted for TL and CL, and a non-linear regression for TL and W, using a least-squares algorithm in Microsoft Excel. Accurate weight measurements were not available for Rufiji Delta, and no regressions were therefore attempted. A two-sample Student's *t*-test for unequal variance was used to compare mean TL of prawns caught in the Ruvu River with those caught in the Rufiji Delta.

Neighbour-joining phylogenetic trees (Saitou and Nei 1987) were constructed for COI and 16S sequences. Analyses were performed in MEGA X (Kumar et al. 2018) using the Kimura 2-parameter (K2P, Kimura 1980) measure with 1000 bootstrap replicates to determine the mean K2P genetic distances and standard errors. *Macrobrachium idae* (Heller, 1862), *M. lamarrei* (H. Milne Edwards, 1837), and *M. nipponense* (De Haan, 1849) were used as outgroups in the COI alignment, and *M. australiense* Holthuis, 1950, and *M. lar* (Fabricius, 1798) were used in the 16S alignment.

Results

Of 151 *M. rosenbergii* collected at the Ruvu River, 57 were females, 26 males (a sex ratio of 1:0.46) and 68 specimens were not sexed. The TL of specimens

Table 1. GenBank accession numbers and locality of origin of *Macrobrachium* specimens used in the neighbour-joining trees based on COI and 16S rRNA sequences. New records are indicated with an *.

Species / Subspecies	GenBank Accession	Locality	Reference	
COI				
<i>Macrobrachium rosenbergii dacqueti</i>	MK113934–38	Rufiji, Tanzania *	This study	
	MK113940–43	Ruvu, Tanzania *		
	GQ995505–10 and GQ995517	Brazil	Iketani et al. 2011	
	JF792432–39	India		
<i>Macrobrachium rosenbergii</i>	GQ995511–16 and GQ995518	Brazil	Iketani et al. 2011	
<i>Macrobrachium idae</i>	FM958070	–	Wowor et al. 2009	
<i>Macrobrachium nipponense</i>	KF547935	–		
<i>Macrobrachium lamarrei</i>	KX214618	–		
16S rRNA				
<i>Macrobrachium rosenbergii dacqueti</i>	MK113944	Rufiji, Tanzania *	This study	
	MK113945–48	Ruvu, Tanzania *		
	AY203904	NE Malaysia	De Bruyn et al. 2004	
	AY203905	Malaysia		
	AY203907	S Vietnam		
	AY203908	SW Thailand		
	AY203911	SE Thailand		
	AY203913	Java, Indonesia		
	AY203914	Vietnam		
	AY203915	SW Malaysia		
	GQ985381–88	Northern Brazil		Iketani et al. 2011
	JF792428–31	India		
	<i>Macrobrachium rosenbergii</i>	AY203906	Papua New Guinea	De Bruyn et al. 2004
AY203909		Indonesia		
AY203910		Philippines		
AY203916–22		Australia		
<i>Macrobrachium australiense</i>	AY203923	–		
<i>Macrobrachium lar</i>	AY203922	–		

ranged from 145–310 mm (mean TL = 217 ± 36 (SD) mm; Figure 3). Males (246 ± 25 mm) were larger than females (196 ± 21 mm), and 38% of males were larger than the largest female measured (251 mm). A bimodal size frequency histogram peaked at 175–200 mm and 250–275 mm TL, consistent with a hypothesis of sexual dimorphism. Some 37% of females bore eggs, which ranged in colour from bright orange to grey. The smallest egg-bearing female had a TL of 151 mm and weighed 40 g.

Of 88 specimens collected at the Rufiji Delta, 66 were females and 22 were males (1:0.33). The TL ranged from 110–273 mm (mean TL = 202 ± 43 mm; Figure 3). Males (226 ± 49 mm) were larger than females (194 ± 38 mm), and the size frequency histogram also peaked at 175–200 mm, with a preponderance of individuals larger than 200 mm TL. Nevertheless, the mean TL of *M. rosenbergii* measured at Rufiji Delta was smaller than at the Ruvu River ($p = 0.004$). Of 66 females at Rufiji Delta, 27 (41%) bore eggs. The smallest egg-bearing female measured 161 mm TL.

The number of dorsal rostral teeth on 11 male specimens (145–265 mm TL) collected at the Ruvu River ranged from 11–15 (mode of 14), with the apical tooth included (Figure 2). Counts of ventral rostral teeth ranged from 9–13, with a mode of 12. Chelipeds of males with a TL > 200 mm were

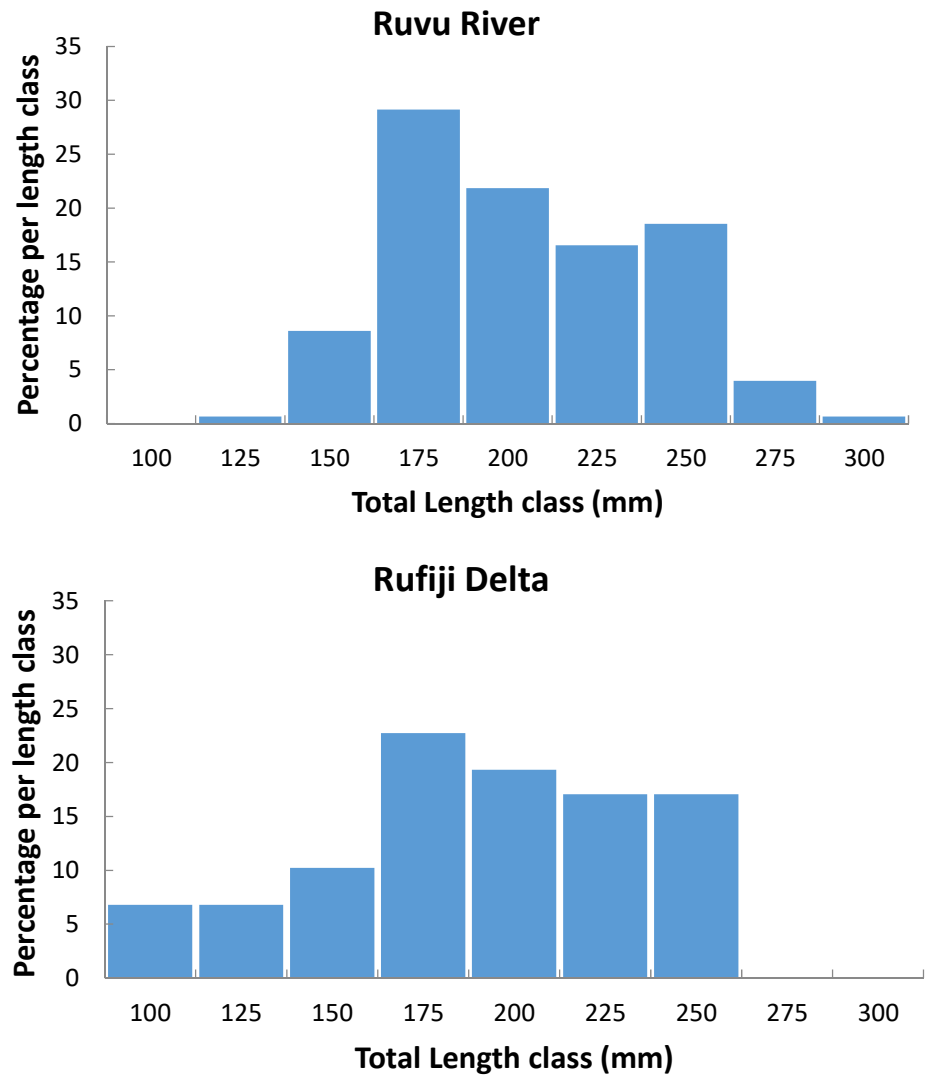


Figure 3. Length-frequency distribution (TL, mm) of *Macrobrachium rosenbergii* caught by fishers in the Ruvu River (n = 151) and Rufiji Delta (n = 88), respectively.

elongated, of equal length, and coloured orange and blue. The basal crest in all specimens was relatively high - comparable to the image of *M. r. dacqueti*, rather than that of *M. r. rosenbergii* in Figures 3 and 4 of Wowor and Ng (2007). Based on the morphological characters observed, all specimens were identified as *M. rosenbergii*, and possibly *M. r. dacqueti*.

Individual body weight of specimens collected at the Ruvu River ranged from 25–317 g, with males (mean 153 ± 40 g) weighing twice as much as females (mean 76 ± 26 g). The linear regression of CL and TL (sexes pooled) had a high coefficient of variation ($r^2 = 0.86$, Figure 4). The non-linear W and TL regression also fitted the pooled data well ($r^2 = 0.95$, Figure 4), and the exponent (3.07) was close to 3.0 (all data combined), indicating isometric growth (Froese 2006). Sex-wise W and TL regressions also showed isometric growth in females ($W = 0.00003 \times TL^{2.96}$, $r^2 = 0.79$, n = 57) and males ($W = 0.08 \times TL^{2.6}$, $r^2 = 0.89$, n = 26).

The 16S and COI sequences of five specimens collected from Ruvu River and five from Rufiji Delta were verified against references on GenBank.

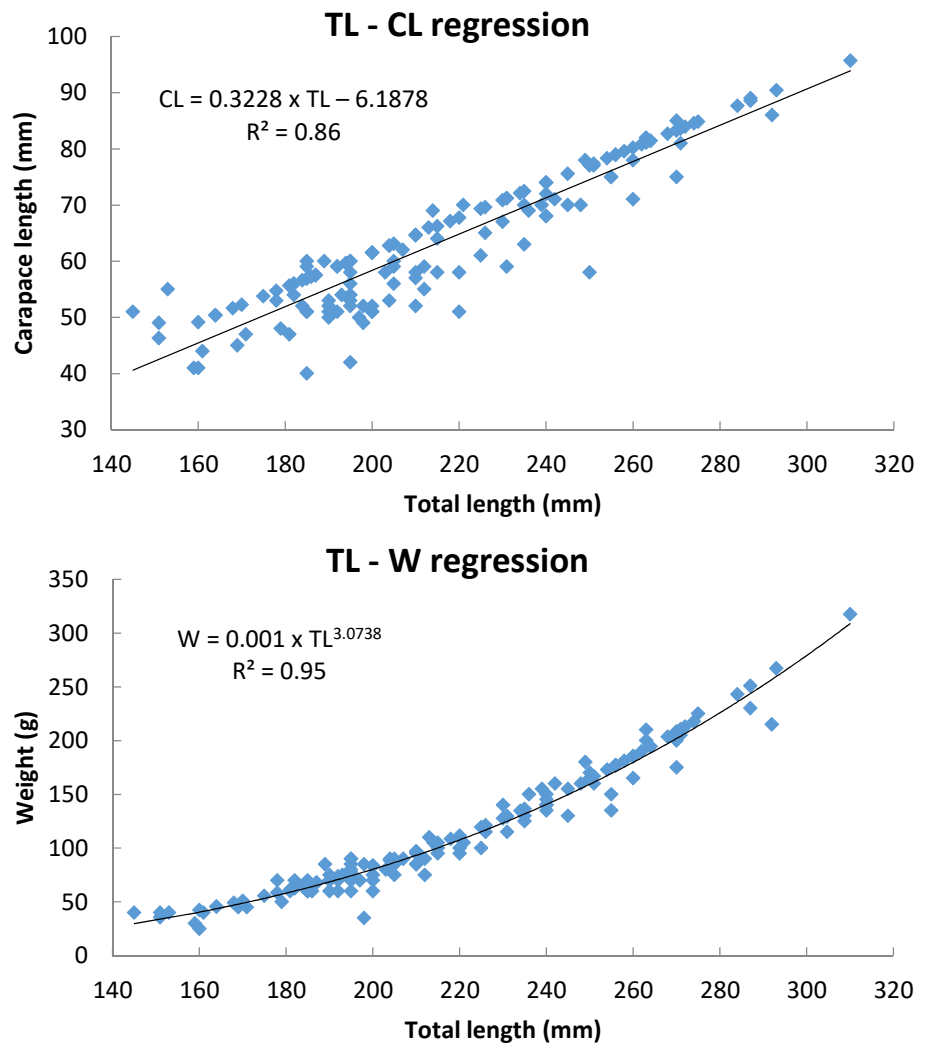


Figure 4. Regressions of total length versus carapace length, and total length versus body weight of 151 *Macrobrachium rosenbergii* specimens caught by fishers in the Ruvu River.

The COI alignment consisted of 567 base-pairs with 548 conserved sites, 17 variable sites and 11 parsimony informative sites, and had a 100% identity to *M. rosenbergii* (MF563572) from India. The 16S alignment consisted of 473 base-pairs, with 432 conserved sites, 40 variable sites and 21 parsimony informative sites, and had a 99% identity to *M. rosenbergii* (KM610154), also from India.

The neighbour-joining tree for COI and 16S indicated that there were two distinct clades, supported by high bootstrap values (Figure 5). One clade corresponded to *M. r. rosenbergii*, while the other corresponded to *M. r. dacqueti*. The sequences from East Africa clustered with the *M. r. dacqueti* form. Genetic divergence between *M. r. rosenbergii* and *M. r. dacqueti* was 1.9% using COI, and 5.8% using 16S, comparable to genetic divergence values obtained by Iketani et al. (2011).

Discussion

Based on phenotypic and genotypic analyses, we provide the first records of *M. rosenbergii* populations in the wild in East Africa. Mitochondrial DNA

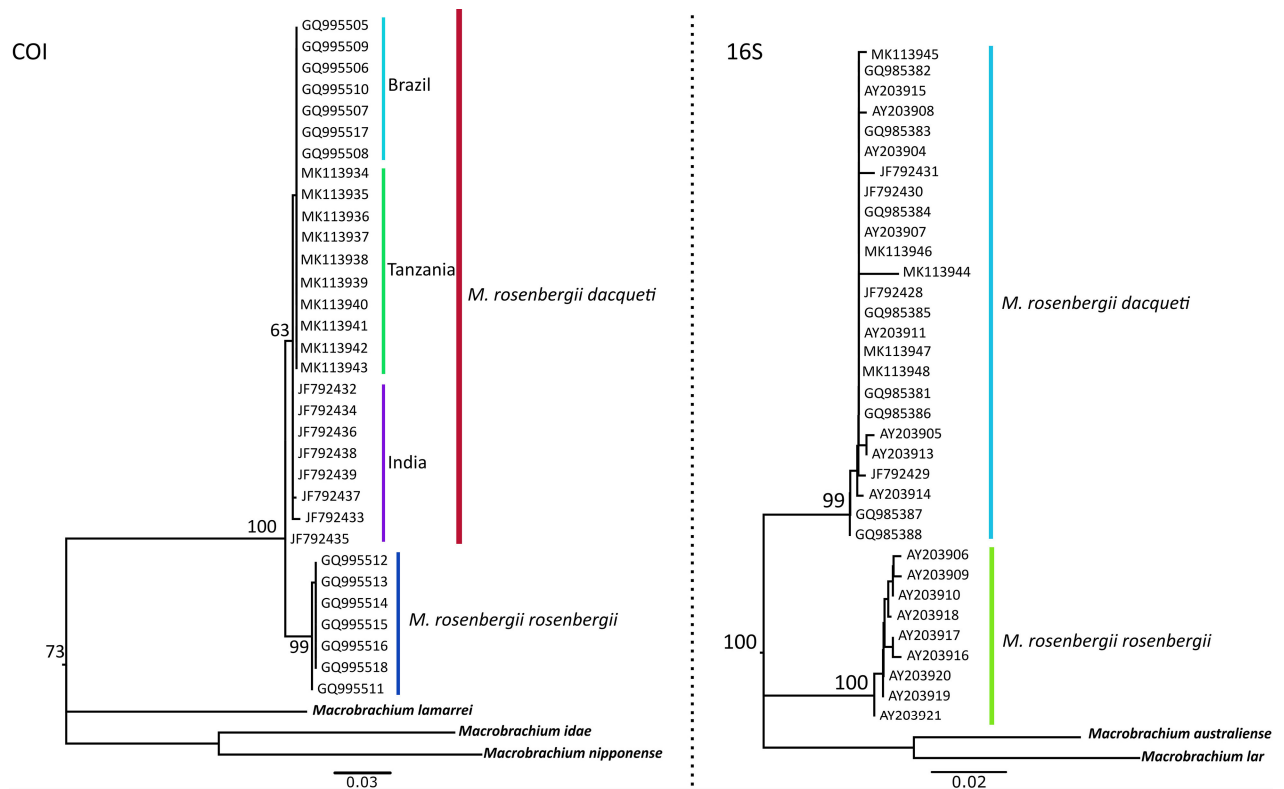


Figure 5. Neighbour-joining trees based on COI and 16S rDNA showing the relationships between *Macrobrachium rosenbergii dacqueti* and *M. rosenbergii rosenbergii*. Bootstrap support from 1000 replicates is indicated on the nodes.

sequences (COI and 16S) confirmed that sampled specimens belonged to the western subspecies *M. r. dacqueti*. The vast majority of cultured *Macrobrachium* worldwide, and most invasions where they are not native, comprise of *M. r. dacqueti*, traced to brood-stock imported to Hawaii from Malaysia (Wowor and Ng 2007).

We found no official information on imports or culture of *M. rosenbergii* in Tanzania, and a visit to aquaculture ponds at Kilosa agriculture research centre in the Ruvu catchment basin provided no evidence of past or present *M. rosenbergii* culture. Native *M. idella* was common in rivers and dams near Kilosa, supported by DNA barcoding of specimens collected there, and are used for local consumption (B. Mchomvu, *pers. obs.*). We could therefore not confirm that *M. r. dacqueti* caught by fishermen in the Ruvu River were escapees from upstream dams or aquaculture ponds.

The presence of ovigerous females suggests that *M. rosenbergii* reproduces in the Ruvu and Rufiji systems. Females can carry between 5000 and 100 000 eggs per batch, depending on their size, and may spawn several times per year (Cavallo et al. 2001; New 2002). Samples covered a wide size range of 110–310 mm TL, implying the presence of several age-classes. In combination, these factors suggest the existence of self-sustaining *M. rosenbergii* populations in the Ruvu River and Rufiji Delta, particularly in view of the apparent absence of recent culture facilities in upstream catchments (B. Mchomvu, *pers. obs.*). *Macrobrachium rosenbergii* in East

Africa therefore corresponds to category D2: “Self-sustaining population in the wild, with individuals surviving and reproducing a significant distance from the original point of introduction” in a unified framework for biological invasions (Blackburn et al. 2011). Whether *M. rosenbergii* can disperse between estuaries, as a fully invasive species across multiple sites (category E; Blackburn et al. 2011) remains unclear, and is a key knowledge gap. Based on larval rearing in artificial seawater, Mather and de Bruyn (2003) suggested that *M. rosenbergii* may be capable of at least limited marine dispersal, potentially facilitating invasions to adjacent estuaries.

An ecological niche model constructed by Silva-Oliveira et al. (2011) to assess potential areas at risk of invasion by *M. rosenbergii* predicted a low probability (< 0.36) of suitable habitat in East Africa. The most important contributors to the model were mean annual temperature, downstream distance (proximity to saline waters), and precipitation in July. Our finding of *M. rosenbergii* in the Ruvu and Rufiji systems contradicts the model’s prediction, begging the question of which other factors, not considered in the model, are likely to facilitate habitats suitable for *M. rosenbergii* in East Africa.

Most rivers in East Africa are relatively short, often with deltaic estuaries (Duvail et al. 2017) surrounded by large wetlands, thus shortening the downstream distance that egg-bearing females need to migrate to reach estuarine conditions to release their larvae and complete their life cycle. The lower Ruvu River and Rufiji Delta are fringed by dense mangrove forests (Mangora et al. 2016), providing shelter or nurseries for fish and crustaceans, potentially including *M. rosenbergii*, before they migrate upstream to freshwater habitats (Bowles et al. 2000). Seasonal rainfall and a strong tidal influence can facilitate either downstream or upstream migrations of drifting or benthic phases. The lower Ruvu River is ≈ 7 m deep at high tide, well-mixed, with water temperature ranging from 25–29 °C in June 2013 (Saha et al. 2014) and May 2018. At the upstream Vikundu landing site (Figure 1), salinity ranged from 0–3 ppt, and at the downstream Mtailand site, from 3–15 ppt on an outgoing tide in May 2018. These conditions do not coincide with the season during which biological samples were collected (Nov–Jan), but are indicative of habitats available to *M. rosenbergii* in East Africa.

From a fisheries perspective, landings of *M. rosenbergii* can increase fishery yields where fish markets are easily accessible; for example, it is a short trip from Ruvu River landing sites to the Dar-es-Salaam fish market. The bulk of *M. rosenbergii* landed at sampled sites (see Figure 3) were larger than the size at maturation (105–137 mm TL in males and 81 mm in females; Nagamine and Knight 1980; Ra’Anan et al. 1991), suggesting that East African populations are lightly fished. The absence of juveniles < 110 mm TL in landings further suggests that they are not selected by seine nets (50–75 mm mesh), or that juveniles inhabit different habitats than larger conspecifics

(Raman 1967). Nevertheless, whether small-scale fisheries targeting *M. rosenbergii* in East African rivers will control or reduce established populations remains a key knowledge gap, with implications for biodiversity conservation as well as livelihood opportunities for fisher communities.

In conclusion, we demonstrate the presence of self-sustaining *M. rosenbergii* populations in at least two river systems in East Africa, based on morphological characters and DNA barcoding. The populations support small-scale fisheries using bottom-set seine nets. The potential impact of *M. rosenbergii* in East African river systems now needs to be appraised, including their present distribution range throughout the region, impacts on native biota, mode of invasion and spread into new systems, and mitigation measures to reduce further spread of the species. The practicality of existing small-scale fisheries, as a mitigation measure to control established *M. rosenbergii* populations in East Africa, should be investigated.

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