



In a Pinch: Mechanisms Behind Potential Biotic Resistance Toward Two Invasive Crayfish by Native African Freshwater Crabs

Josie South^{1,2,3*†}, Takudzwa C. Madzivanzira^{1,2,3}, Ntombizanele Tshali^{1,2}, John Measey^{4†} and Olaf L. F. Weyl^{1,2,3†}

¹ Department of Science and Innovation (DSI)/National Research Foundation (NRF) Research Chair in Inland Fisheries and Freshwater Ecology, South African Institute for Aquatic Biodiversity (SAIAB), Makhanda, South Africa, ² Centre for Invasion Biology, South African Institute for Aquatic Biodiversity, Makhanda, South Africa, ³ Department of Ichthyology and Fisheries Science, Rhodes University, Makhanda, South Africa, ⁴ Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Stellenbosch, South Africa

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*Correspondence:

Josie South
josiesouth93@gmail.com

†ORCID:

Josie South
orcid.org/0000-0002-6339-4225
John Measey
orcid.org/0000-0001-9939-7615
Olaf LF Weyl
orcid.org/0000-0002-8935-3296

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It is essential to incorporate mechanisms of biotic resistance into predictions of ecological impact conferred by invasive species. Trophically and functionally analogous native species have high potential to confer biotic resistance or to be susceptible to competitive exclusion by the invading species. In species with dominance hierarchies and high aggression the role of weapons, such as chelae, is emphasised and selected for. Differences in traits such as crushing capacity can indicate prey handling capabilities, while correlations between closing force and morphology can be used to understand the role of signaling in agonistic contests. Closing force strength can be used to infer the outcomes of both direct (predation) and indirect (competition) trophic interactions. Southern Africa has been invaded by two freshwater crayfish species (*Cherax quadricarinatus* and *Procambarus clarkii*). Biotic resistance of freshwater crabs toward crayfish invasions varies between geographic location and co-evolutionary history, thus comparing invasion histories without incorporating geographic context can produce unequivocal conclusions. We compared the closing force and chelae morphology of both crayfish species with a native trophically analogous freshwater crab, *Potamonautes perlatus*. Closing force increased significantly with mass for all species. There was significant interaction between sex and species on closing force. *Potamonautes perlatus* females showed significantly stronger maximum chela closing force than male *P. perlatus*, both sexes of *P. clarkii* and female *C. quadricarinatus*. Contrastingly, male *C. quadricarinatus* had significantly higher closing forces than both sexes of *P. clarkii* and female *C. quadricarinatus*, however, there was no difference between female *P. perlatus*. Native *P. perlatus* has the capacity to hold a competitive mechanical advantage over both invaders, but this varies with sex. Chelae length was not a significant predictor for closing strength in any of the species, which may be related to dishonest signaling in decapod species. This makes it imperative to assess whether

factors such as closing force actually translate to resource holding potential in a contest scenario. We thus provide evidence that African freshwater crabs may exhibit biotic resistance toward invasion and the first measurements for *C. quadricarinatus* closing force strength.

Keywords: *Procambarus clarkii*, *Cherax quadricarinatus*, *Potamonautes perlatus*, invasive species, competition, strength

INTRODUCTION

Non-native species introductions and subsequent establishment continues to threaten global biodiversity (Seebens et al., 2017; Meyerson et al., 2019). The likelihood of a particular species successfully establishing and persisting in a novel environment is influenced by both abiotic and biotic factors (Byers, 2002; Pearson et al., 2018; Kinney et al., 2019). For example, evidence toward the environmental matching hypothesis suggests that when the climate of the incumbent ecosystem matches the climate of the native range, the invader has a higher potential to both persist and perform better than when the climate does not (Capinha et al., 2013; Iacarella et al., 2015). The community assemblage of the invaded system can also facilitate or impede establishment via biotic resistance (deRivera et al., 2005; Alofs and Jackson, 2014). Theoretically, areas with high species richness are more likely to have species that are strong competitors or, indeed, predators, which make the system less invadable than those with low species richness (Elton, 1958; Tilman, 1999). Although, in areas where species are functionally similar there is a likelihood that the analogous native species are outcompeted or niche excluded by the invader (Dick et al., 2017; Zeng et al., 2019).

Species interactions shape community dynamics through consumptive effects, but also in non-consumptive manners such as intraspecific and interspecific competition for resources such as food, shelter, and reproduction (Sih et al., 2010; Lopez et al., 2019; Mofu et al., 2019; Zeng et al., 2019). Biotic resistance can thus be exhibited in both consumptive and competitive manners, however, in freshwater systems biotic resistance is driven overwhelmingly by consumption (Alofs and Jackson, 2014). Aquatic environments exhibit a higher occurrence of generalist feeding and omnivory leading to a lack of intraspecific and interspecific competition (Alofs and Jackson, 2014). Moreover, dietary plasticity and frequency dependent predation (i.e., prey switching) are common traits of successful invaders as it allows persistence of species via trophic niche separation and capacity to consume new resources when one is over-exploited (Snyder and Evans, 2006; Olsson and Nyström, 2009; Havel et al., 2015). Often, successful invasive species also outcompete and competitively exclude native species for resources through agonistic interactions, though, aggressiveness does not always equate to resource holding potential (Camerlink et al., 2015; Lopez et al., 2019).

Freshwater crayfishes are highly successful invaders, having established widespread invasive populations. While the impacts, both positive and negative, have been reported for various

crayfish species (see review by Lodge et al., 2012), the mechanisms that drive species persistence and increased impact are still somewhat unclear. The African continent is devoid of native crayfish species. This is potentially due to evolutionary competition with freshwater crabs (Ortmann, 1902; Lodge et al., 2012; Nunes et al., 2017a). Freshwater crabs of the genus *Potamonautes* are, however, present in almost all African freshwater habitats where they are trophically analogous to freshwater crayfish and provide essential nutrient cycling services (Hill and O’Keeffe, 1992; Dobson, 2004; Cumberlidge and Daniels, 2009; Peer et al., 2015). Potamonautid species typically exhibit high degrees of endemism and range restriction. These traits make them vulnerable to the impacts of habitat destruction and invasive species introductions (Cumberlidge and Daniels, 2009; Zeng and Yeo, 2018). Crabs and crayfish are polytrophic benthic omnivores that are both opportunistic scavengers and direct predators (Hill and O’Keeffe, 1992; Grey and Jackson, 2012). Due to the trophic similarities between crayfish and freshwater crabs it is likely that they will either provide an important component of biotic resistance or be competitively excluded by crayfish invasions (Lodge et al., 2012; Dick et al., 2017). Indeed, in Tanzania the red swamp crayfish, *Procambarus clarkii* (Girard, 1852) has replaced a native freshwater crab *Potamonautes neumannii* in many systems (Ogada, 2007), and has replaced *Potamonautes loveni* as the primary food source in African clawless otter diets in Lake Naivasha (Ogada et al., 2009). Similar trends are reported in Singapore where Australian redclaw crayfish *Cherax quadricarinatus* competitively excludes smaller native freshwater crabs from shelter resources (Zeng et al., 2019). In Cyprus the invasive *P. clarkii* shows shelter holding dominance over native freshwater crab *Potamonautes potamios* despite both species being equally aggressive (Savvides et al., 2015). Contrastingly, the European river crab *Potamonautes fluviatile* shows dominance in aggression and resource holding capacity toward the invasive *P. clarkii* but this may be driven by co-evolutionary history with the native *Astropotamobius italicus* crayfish (Cioni and Gherardi, 2004; Mazza et al., 2017). Again, there are similar reports that populations of native pseudoscorpionid crabs persisting despite the *C. quadricarinatus* invasion in Mexico, likely due to the co-evolutionary history with native crayfish (Bortolini et al., 2007). Predicting the impacts of invasive crayfish species on native biota via consumptive and non-consumptive effects by way of comparing invasion histories can thus produce unequivocal conclusions due to geographical context.

Southern Africa is suffering from an over-invasion scenario by functionally similar crayfish species which have been introduced

primarily through aquaculture ventures and the pet trade (Lodge et al., 2012; Russell et al., 2014; Nunes et al., 2017a,b; Weyl et al., 2020). *Cherax quadricarinatus*, the Australian redclaw crayfish and *P. clarkii* both have established invasive populations in South Africa (Nunes et al., 2017a,b). *Cherax quadricarinatus* is also present in Zambia (Nakayama et al., 2010; Nunes et al., 2016), Swaziland (Nunes et al., 2017a) and Zimbabwe (Marufu et al., 2018) while *P. clarkii* is invasive in Zambia, Uganda, Kenya, Egypt, Sudan, and Rwanda (Hobbs et al., 1989; Mikkola, 1996; Cumberlidge, 2009). Both species are likely to spread into ecologically and economically integral streams and wetlands, which will potentially threaten the stability of aquatic systems that provide refuge habitat for imperilled species such as Potamonautid crabs (Ahyong and Yeo, 2007; Belle et al., 2011; Nunes et al., 2017a,b; Zeng et al., 2019). To test whether there could be some degree of biotic resistance exhibited by African freshwater crabs, we measure and compare the maximum closing force of native *Potamonautes perlatus* to the invasive crayfish *C. quadricarinatus* and *P. clarkii*. Weapon performance can usually be assumed to be an honest signal and is correlated with aggression (Lappin and Husak, 2005; Wilson et al., 2007; Bywater and Wilson, 2012). We hypothesized that the invasive crayfish species would have a higher maximum closing force than *P. perlatus*. Closing force can indicate prey handling capacity (Meers, 2002; Miranda et al., 2016), but also, if closing force is related to morphology it can contribute to important signaling in agonistic contests (Wilson et al., 2007; Bywater et al., 2008; Bywater and Wilson, 2012). Thus, we also determined whether morphological and biological factors can be used to predict closing force.

METHODS

Animal Collection and Maintenance

Cherax quadricarinatus is native to Northern Australia and southeastern New Guinea. Populations have established in southern African freshwater systems where they were introduced and are spreading (Nunes et al., 2016, 2017a; Douthwaite et al., 2018). *Cherax quadricarinatus* tolerates a wide variety of habitats and environmental conditions (Masser and Rouse, 1997). One hundred and fifty live *C. quadricarinatus* samples (mean \pm sd carapace length: 63.20 ± 4.93 mm, mass: 67.34 ± 11.26 g) were collected from sugarcane irrigation ponds in Nkomazi, Komatipoort (Mpumalanga Province) supplied by the Komati River (S 25.55°, E 31.90°). Komatipoort has been invaded by *C. quadricarinatus* since 2002 and represents an invasion core for the species in South Africa (de Moor, 2002; De Villiers, 2015). A standard gear for trapping the redclaw crayfish was used, this consists of Promar collapsible traps baited with dry dog food. Traps were deployed at 1,600 h and retrieved at 800 h. Permits to transport and keep *C. quadricarinatus* were issued by the DEA (Permit Numbers: 50869181001115242, 50869181001120608). The crayfish caught were transported to a biosecure facility at the South African Institute for Aquatic Biodiversity (SAIAB) in insulated cooler boxes with source water from the dam and constantly aerated with battery pumps.

Procambarus clarkii is native to southern and south-eastern USA and northern Mexico. In Africa, *P. clarkii* was introduced to South Africa, Zambia, Uganda, Kenya, Egypt, Sudan, and Rwanda (Hobbs et al., 1989; Mikkola, 1996; Cumberlidge, 2009). *Procambarus clarkii* lives in a variety of freshwater habitats, including lakes, ponds, rivers, canals, streams, seasonally flooded swamps and marshes, and ditches with mud or sand substrata and plenty of organic debris (Huner and Barr, 1991). Fifty-six live *P. clarkii* crayfish samples (carapace length: 58.62 ± 6.86 mm, mass: 59.54 ± 7.05 g) were collected from Mimosa Dam (S 27.88°, E 26.69°) in Free State Province South Africa, where there has been a recent invasion ((DEA), 2018) using traps baited with fish heads and dry dog food. Traps were deployed at 1,600 h and retrieved at 800 h. Mimosa Dam represents an invasion core population of *P. clarkii*. The crayfish caught were transported from Mimosa Dam to the biosecure facility at SAIAB in insulated cooler boxes with source water from the dam and constantly aerated with battery pumps. Permits to transport and keep *P. clarkii* were issued by the Department of Environmental Affairs (DEA) (Permit Numbers: 50869181001113030, 50869181002121045).

The same gear was also used to trap *P. perlatus* samples from Eastern Cape Dams (S 33.32°, E 26.52°; S 33.32°, E 26.52°; S 33.29°, E 26.51°; S 33.41°, E 26.50°). Traps were deployed at 1,600 h and retrieved at 800 h. Permits to sample crabs were issued by the Eastern Cape Department of Economic Development, Environmental Affairs and Tourism (CRO 19/18CR and CRO 21/18CR). Larger crabs were selected to most closely match the mass of the crayfishes, however, there were few females caught in the traps. Twenty crabs (carapace length: 53.27 ± 4.55 mm, mass: 96.29 ± 22.15 g) were caught and placed in 60 L cooler boxes with fresh dam water with battery powered air pumps and transported to the biosecure facility at SAIAB.

Not all collected animals were used in this experiment as they were in use for other research purposes at the time, therefore the animals used were a random subsample of the total collected animals (Table 1). Animals were maintained in species specific and sex specific holding tanks (60 L) with constantly filtered and aerated aged tap water which was replaced twice a week to maintain good water quality. Water temperature was maintained at $23 \pm 1^\circ\text{C}$ by a computer controlled recirculating heating: cooling air conditioner unit. The laboratory was held under a 12:12 light:dark regime. All animals were maintained on cabbage leaves, broad leaved pondweed *Potamogeton nodosus* and fennel-leaved pond weed *Stockenia pectinatus* and cultured *Eisenia* sp. worms.

Experimental Setup

Individual animals were selected from the holding tank haphazardly and patted dry before measurements were taken. Animals were weighed (to the nearest g), the chelae length (propodus) of both left and right chela, and cephalothorax length were measured with Vernier calipers (to the nearest mm), and sexed (Table 1). Animals with regenerated claws and females with eggs were excluded due to differences in energy conservation.

TABLE 1 | Median and range of morphometric values and closing force (*N*) values for *P. perlatus*, *C. quadricarinatus* and *P. clarkii* females and males.

Species	Sex (n)	Mass (g) (median and range)	Carapace length (mm) (median and range)	Left chela length (mm) (median and range)	Right chela length (mm) (median and range)	Left closing force (N) (median and range)	Right closing force (N) (median and range)
<i>Potamonautes perlatus</i>	F (n = 8)	95.1, 54.6–123.5	75, 59–87	33, 25–39	37, 27–45	11.0, 6.7–42.7	49.8, 10–153.4
<i>Cherax quadricarinatus</i>	F (n = 27)	76.2, 22.0–132.0	69, 45–86	31, 24–41	33, 24–44	6.0, 2.0–26.0	4, 2.0–30.0
<i>Procambarus clarkii</i>	F (n = 18)	50.4, 28.7–64.5	61, 47–66	36, 28–49	35, 31–45	3.3, 2.0–10.0	3.3, 2.0–5.3
<i>Potamonautes perlatus</i>	M (n = 6)	70.7, 46.3–117.2	65, 58–76	28, 21–35	32.5, 26–41	6.0, 2.7–10.0	14.67, 3.3–25.3
<i>Cherax quadricarinatus</i>	M (n = 25)	98.9, 38.1–144.6	71, 51–81	32, 25–41	34, 26–41	18.7, 3.3–136.7	19.43, 2.6–116.7
<i>Procambarus clarkii</i>	M (n = 21)	52.1, 25.7–76.8	60, 48–65	41, 30–52	40, 25–50	2.6, 2.0–37.4	3.1, 2.0–9.3

Chelae closing force measurements were completed *in vivo* in the laboratory using the Kistler system and the protocol outlined in Herrel et al. (1999), Singh et al. (2000), and Lailvaux et al. (2009). Animals were allowed to grip from the proximal region of the chela onto plates set at a gap of 6 mm, to allow comparison with Miranda et al. (2016). Closing force (*N*) was measured five times per individual, per chela, resulting in 10 measurements taken for each individual. Animals were given a rest period of 5 min between measurements. The laboratory, and holding tank water, were both held at (23 ± 1°C) throughout the entire acclimation and experimentation time.

Analyses

Differences in mass and cephalothorax length between species was determined using one way non-parametric Kruskal-Wallis tests and Dunn test *post-hoc*, with *p*-values adjusted for multiple comparisons using Holm-Bonferroni corrections. Handedness was assessed separately for each species, by comparing left and right chela closing force measurements using Friedmans test to account for repeated measures.

Closing force data were log-transformed and linear mixed-effects models were fitted, based on maximum likelihood. Initially the models were fitted separately to each left and right chelae. It was assumed that chela length would affect closing force, and to account for some individuals having asymmetrical chelae lengths between the left and right claws, we first ran a model to account for this rather than taking data from only one chela. Fixed factors were “species,” “mass,” “sex” and “chela length,” while “individual identity” was used as a random factor nested within “species.” A full model was fitted, containing “species,” “mass,” “sex” and “chela length,” and their interactions. Chela length was not a significant predictor of closing force so was removed from the model (see results) and only the maximum closing force obtained per individual was selected, regardless of left or right chelae. Cephalothorax length was significantly correlated with mass and thus not included in the analysis (Figure 1). If either the fixed factors, or the interaction did not have a significant effect, in subsequent steps the model was re-run

with non-significant terms removed, starting with the interaction term. The final model only contained significant terms to obtain the most parsimonious model. Differences were calculated *post-hoc* using χ^2 to communicate effect size. All analyses were performed in an R environment (R Core Team, 2018), using the package nlme (Pinheiro et al., 2018).

RESULTS

There were significant differences in mass of each species ($\chi^2 = 39.03$, *df* = 2, *p* < 0.001; Table 1, Figure 1), where *P. clarkii* weighed less than both *C. quadricarinatus* (*z* = 5.83, *p* < 0.001; Table 1, Figure 1) and *P. perlatus* (*z* = 4.11, *p* < 0.001; Table 1, Figure 1), however there was no difference between *P. perlatus* and *C. quadricarinatus* mass (*z* = 0.08, *p* = 0.93; Table 1, Figure 1).

Potamonautes perlatus had significantly stronger right chela closing force than left (Friedmans $\chi^2 = 15.05$, *df* = 1, *p* < 0.0001; Supplementary Figures S1, S2). Contrastingly, both *C. quadricarinatus* and *P. clarkii* had significantly stronger left chela closing force (respectively: Friedmans $\chi^2 = 5.68$, *df* = 1, *p* < 0.05, Friedmans $\chi^2 = 5.09$, *df* = 1, *p* < 0.05; Supplementary Figures S1, S2). Female *P. perlatus* had a higher left and right chela closing force than males (Table 1, Figure 2) whereas, male *C. quadricarinatus* had a higher left and right chela closing force than females (Table 1, Figure 2). There were no sex differences in left or right chela closing force in *P. clarkii* (Table 1, Figure 2). Chelae length did not affect closing force in any species on either left or right chelae (left: $\chi^2 = 0.19$, *df* = 1, *p* = 0.65; right: $\chi^2 = 0.83$, *df* = 1, *p* = 0.36).

There was a significant interaction between species and sex on maximum closing force (Table 2, Figure 3; Supplementary Figure S3). Species and sex both had significant main effects on closing force (Table 2, Figure 3; Supplementary Figure S3). Closing force increased significantly with mass for all species (Table 2, Figure 3; Supplementary Figure S3). Opposite trends in maximum closing force were seen between male and female *P. perlatus* and

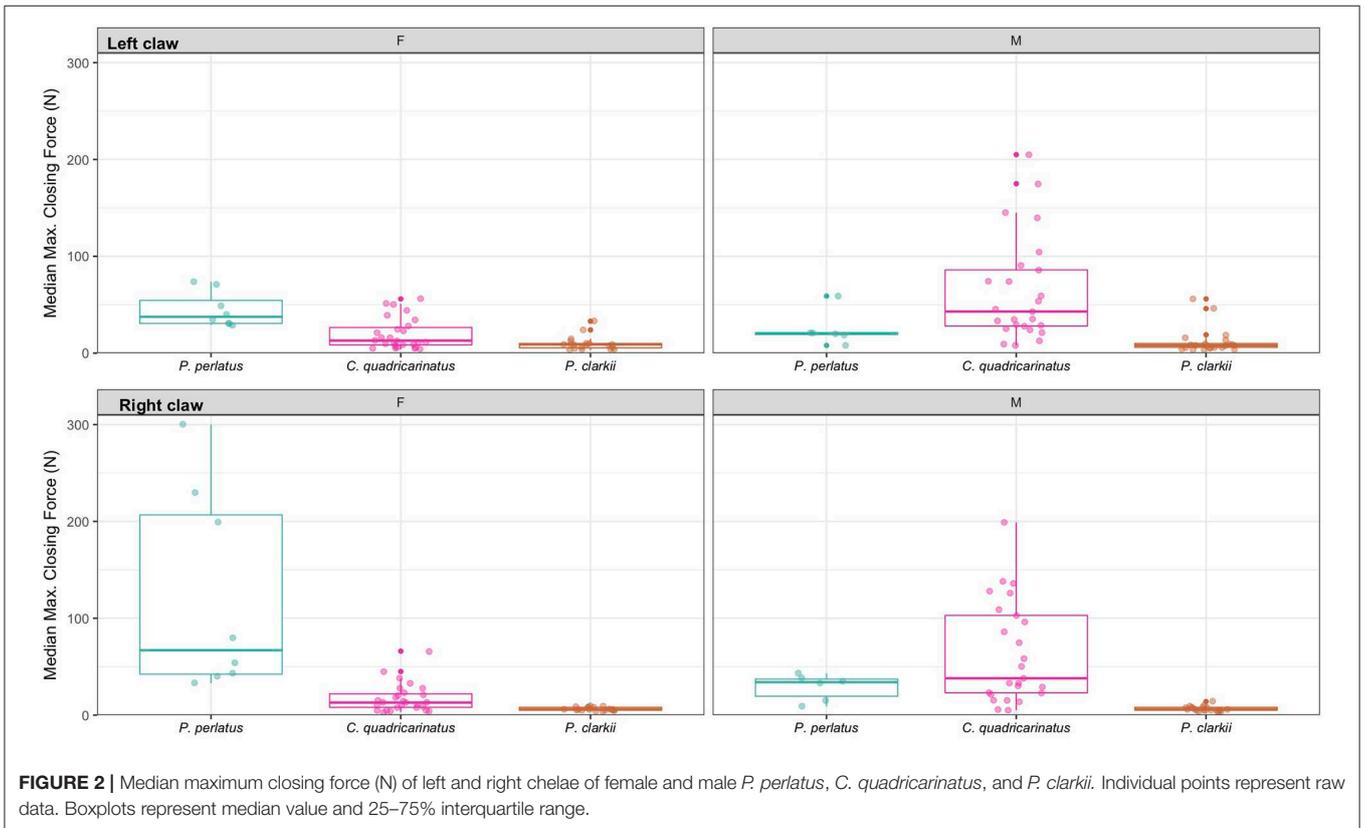
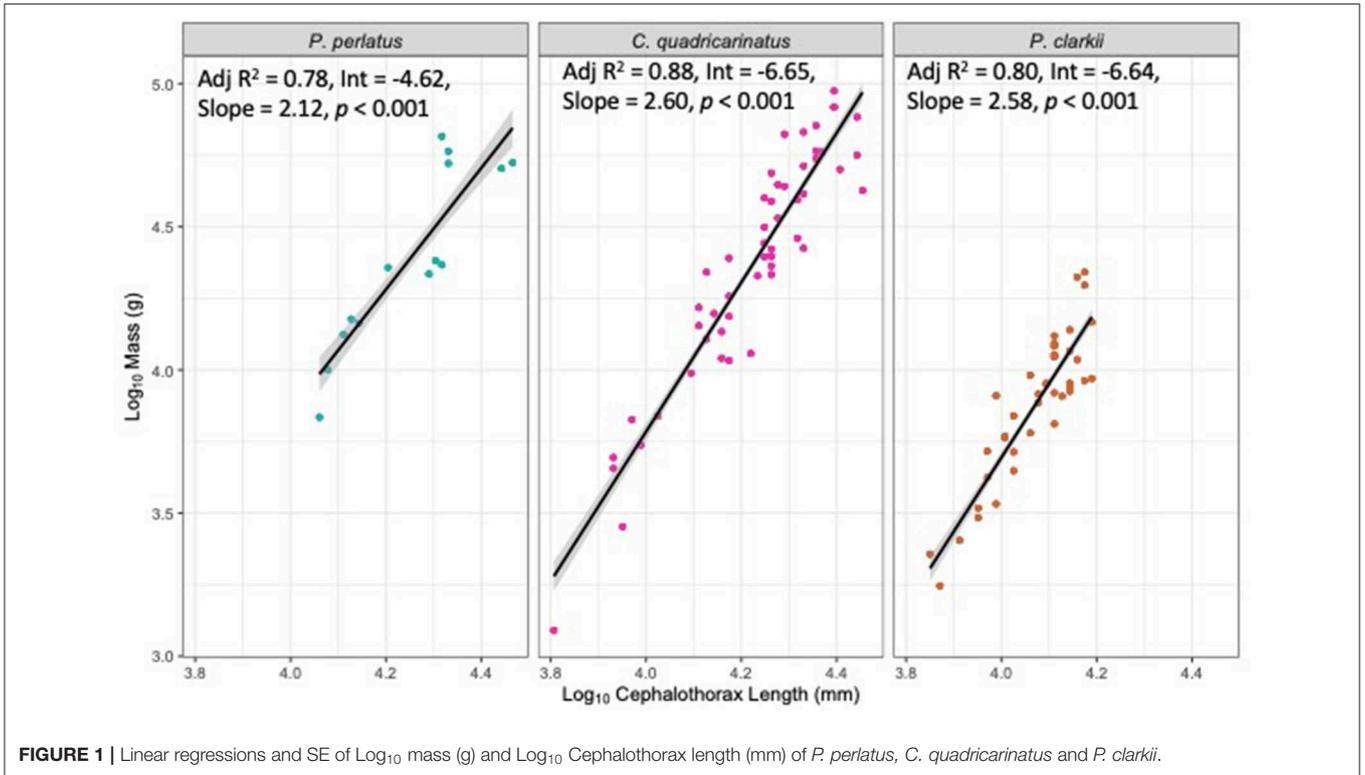


TABLE 2 | Model terms for all factors from a linear mixed effects model used to determine differences in maximum closing force (N) with regards to fixed factors “species,” “sex,” and “mass,” using a Type 3 Anova and χ^2 to report the effect size of a factor on the dependent variable.

Predictor	Maximum closing force (N)		
	χ^2	df	p-value
Species	39.25	2	<0.001
Sex	32.94	1	<0.001
Mass	23.02	1	<0.001
Species*Sex	29.86	2	<0.001

C. quadricarinatus, however there was no difference between male and female closing force in *P. clarkii* ($p = 0.46$). Female *P. perlatus* had a significantly stronger closing force than male *P. perlatus*, female *C. quadricarinatus*, and both sexes of *P. clarkii* (all $p < 0.01$). There was no difference between female *P. perlatus* closing strength and male *C. quadricarinatus* or between male *P. perlatus* and female *C. quadricarinatus* (both $p > 0.05$). However, male *C. quadricarinatus* had significantly higher maximum closing forces than male *P. perlatus* ($p < 0.01$). Male *P. perlatus* had significantly stronger maximum closing forces than both sexes of *P. clarkii* (all $p < 0.01$). There was no difference between maximum closing force of *P. clarkii* females and *C. quadricarinatus* females ($p = 0.58$).

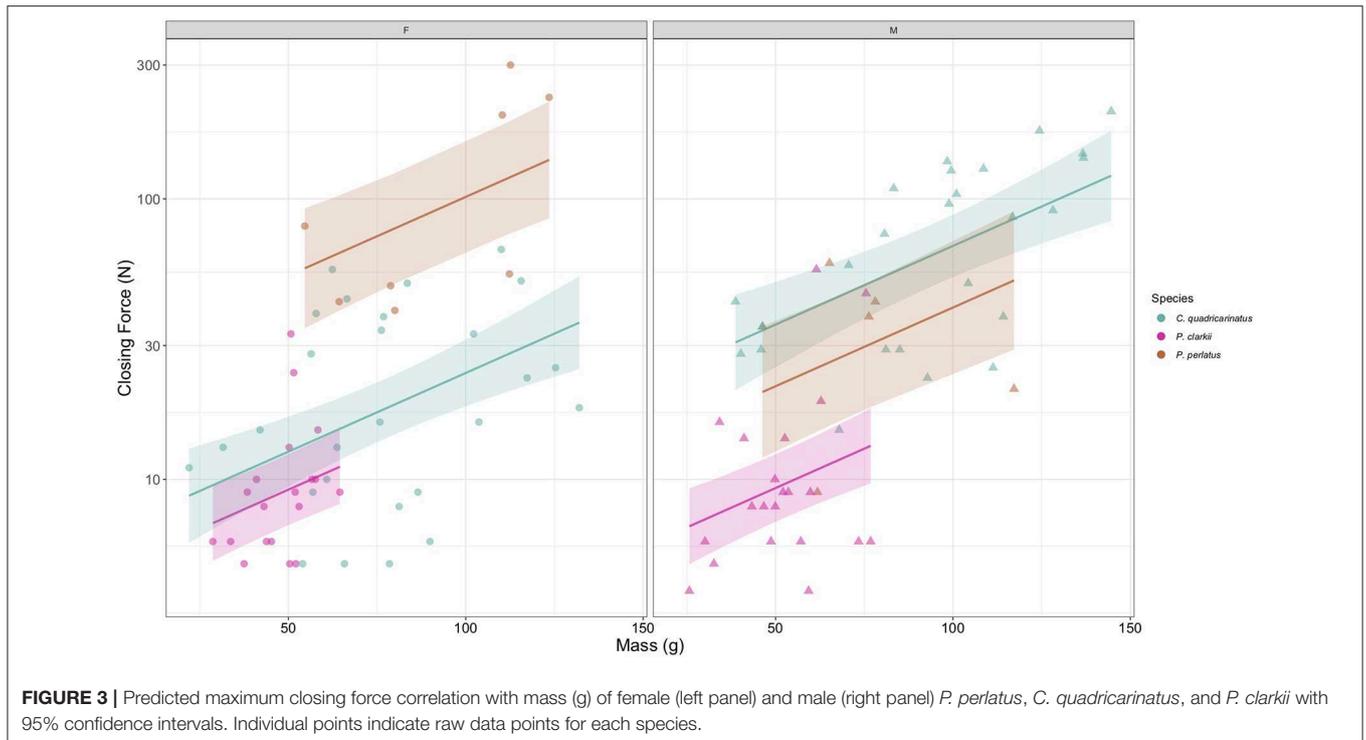
DISCUSSION

Determining what makes systems resilient to biological invasion is a many faceted challenge (Holling, 1973; Havel et al., 2015). Nonetheless, by understanding basic differences in physical capacity it is possible to infer how performance can relate to species interaction outcomes within an invasion scenario (Griffen and Mosblack, 2011). We predicted that the invasive crayfish species would have a higher maximum closing force than native crabs, however, this proved to be unequivocal at least when considering animals of the same size. Given that there have been reports of invasive crayfish reducing abundance of trophically analogous decapods (Ogata, 2007; Ogata et al., 2009; Zeng et al., 2019), these results suggest that *P. perlatus* has the capacity to hold a competitive mechanical advantage over both invaders, but that this varies with sex. Unfortunately, our results are based on a small sample size of native *P. perlatus* which may confound results with regards to sex based differences. Nonetheless, there was a more even amount of males and females amongst smaller *P. perlatus* individuals (50–80 g) whereas the heavier individuals (>100 g) were predominantly female. Our results indicate that there are other mechanisms at play that may cause freshwater crabs to be competitively excluded by invasive crayfish species, rather than brute strength. Although, population size structure, growth rates, and maximum attainable mass of each species will affect competitive exclusion. For example, larger individuals will have a higher resource holding potential over smaller individuals of any species. Resultingly, it is possible to determine maximum

chela strength for these species through correlation with mass and sex but it is unclear as to whether chela strength can actually be a predictor for resource holding potential or success in agonistic contests.

Closing force relates to ability of an individual to pinch down onto a subject. Whether this is for direct predation, during agonistic contests, reproductive purposes, or even to withstand abiotic disturbances such as high flow rates (Gherardi, 2002; Ion et al., 2019). It can be assumed that the larger the closing force the more damage may be conferred to the recipient despite high force conferring a high energy cost to the individual (Herrel et al., 1999; Wilson et al., 2007). Our results of chela closing force fall well within the range reported for *P. perlatus* (18–598 N) (Miranda et al., 2016), and for *P. clarkii* (males: 1.35 ± 0.41 N/g; females: 2.22 ± 0.89 N/g; see **Supplementary Figure 3** for N/g results) (Claussen et al., 2007; Malavé et al., 2018). Similar to our results (Claussen et al., 2007) and Malavé et al. (2018) found sexual dimorphism in chela length where male *P. clarkii* had longer chela than females but this did not relate to closing force. This is likely related to reproductive activities and the cost of signaling during male-male contests (Stein, 1976). Contrastingly, *P. perlatus* females were stronger than males indicating a difference in resource holding potential between sexes and species. These differences may also be exacerbated in a natural setting when individuals are in or out of reproductive status. For example, female *P. clarkii* are more aggressive and more successful when they are maternal compared to non-maternal females and males (Peeke et al., 1995; Figler et al., 2005). Another native African crab species (*Potamonautes sidneyi*) had a significantly weaker closing force than *P. perlatus* (8–43 N) (Miranda et al., 2016). There is no prior published data on the closing force of *C. quadricarinatus*, but for comparative purposes the closing force of the largest terrestrial arthropod, the coconut crab (*Birgus latro*), is 29.4–1765.2 N (Oka et al., 2016), of which the lower ranges all overlap with the three species in the present study. In a first attempt to incorporate *C. quadricarinatus* into impact assessments, Zeng et al. (2019), show that larger bodied *C. quadricarinatus* have a competitive advantage over a native freshwater crab (*Parathelphusa maculata*) when competing for shelter space.

The presence of heterochely or “cutter vs. crusher” is well-established in marine decapods but it is less evident in freshwater crayfish species (Govind, 1989; Schenk and Wainwright, 2001; Lele and Pârvulescu, 2019). In essence it describes potential handedness between left and right chelae. *Potamonautes perlatus* had stronger right chela, whereas *C. quadricarinatus* and *P. clarkii* had stronger left chela. As claw length was not an effective predictor of strength it suggests a degree of ambidexterity between left and right chelae in all of these species as a response to likelihood of losing chelae during agonistic bouts (Kouba et al., 2011; Lele and Pârvulescu, 2019). The lack of strong morphometric predictors reinforces the concept of dishonest signaling in crayfish species (Wilson et al., 2007; Malavé et al., 2018). This combination of potential dishonest signaling and opposite trends in dominant chelae could be



a factor in competition between crab and crayfish species despite *P. perlatius* females dominating mechanically. Potential for biotic resistance, either consumptive or competitive, is likely to be species specific and still further regulated by other biotic and abiotic parameters (deRivera et al., 2005). In this case, size mis-matches, differential spatial ecology, abundance, and type of resources present in a system are all possible factors that could be driving the likelihood of biotic resistance.

Freshwater crabs and crayfish are polytrophic keystone consumers that occupy an unusually large dietary niche breadth as a result of generalist feeding strategies (Jackson et al., 2014, 2016). Chelae are regularly used in decapod feeding to assist in subduing, capturing, holding, and manipulating resource items (Loya-Javellana et al., 1993; Mariappan et al., 2000). This is particularly important when considering durophagous feeding, as crushing predators are thus limited by their strength to process prey items such as snails, but also limited by the shell resistance and predator induced phenotype changes (DeWitt et al., 2000; Evers et al., 2011; Miranda et al., 2016). There is limited information on crush resistance of African gastropod species, but the invasive snail *Tarebia granifera* has a resistance of 100 ± 6 (mean \pm se) N, while native *Melanoides tuberculata* has a resistance of 31 ± 4 N (Miranda et al., 2016). However, in its invasive range in Lake Malawi *M. tuberculata* has a crush resistance range of 18.63–94.73 N (Evers et al., 2011). *Bulinus globosus* and *Bulinus nyassanus* are native gastropods of Lake Malawi, which have crush resistance ranges of 2.29–4.79 N and 8.33–117.82 N, respectively (Evers et al., 2011). All three of the species represented in this study, besides female *P. clarkii*, have the capacity to handle all of these

gastropod species. The relatively high crush resistance of the invaders suggests that this may facilitate their persistence in a system, however it should also be considered that if the southern African crayfish invasion persists there could be an invasion meltdown scenario where predation is concentrated on the native gastropods and facilitates population expansion of the invasive gastropods (Ricciardi, 2001; Simberloff, 2006). An invasion meltdown scenario may also be facilitated in the wild by *Potamonautes* sp. via differences in biotic resistance. Although, the cost-benefit of undertaking crushing activities for food, rather than reproductive efforts, should be investigated as it is likely that predators select for forage with low handling demands (Murdoch, 1969; Behrens Yamada and Boulding, 1998). The present study focuses on the relative differences in closing force with respect to resource utilisation and non-consumptive competition but direct predation by either crabs or crayfish upon heterospecific juveniles is also likely. Therefore, addressing actual contest outcomes and consumption rates between different sized individuals of each species would further our understanding of competitive interactions.

Handling vegetation and crushing prey items require differences in closing force and dentition patterns (Sibbing, 1991; Herrel et al., 1999). Thus, differences in closing force could also relate to niche separation between the species when they occur in sympatry, which could in turn facilitate species persistence of both natives and invaders. *Procambarus clarkii* exhibit this pattern of niche breadth reduction when found in sympatry with *P. loveni*, where they affect leaf litter breakdown due to direct consumption (Jackson et al., 2016; Nishijima et al., 2017), possibly related to differences in chela morphology (Sibbing, 1991). Further, *P. clarkii* is

capable of exerting predatory pressure on planktonic prey items which do not need strong crushing capacity to handle (South et al., 2019). Little work has been completed on the diet and trophic niche of *C. quadricarinatus* in either its invasive or native range. Nonetheless, Marufu et al. (2018) found the main diet components of the Lake Kariba *C. quadricarinatus* population to be predominantly macrophytes, detritus and macroinvertebrates. In Lake Kariba the trophic niche of crayfish differed with size class, wherein macroinvertebrate consumption increased with size, which could potentially be due to the positive relationship between mass and closing force (Marufu et al., 2018). Comparative functional morphology of decapod chelae and feeding apparatus should thus be incorporated into invasion risk assessments as ecomorphology can help to predict impact (Nagelkerke et al., 2018).

Due to the complex nature of trophic interactions and food web structuring, particularly within a stochastic aquatic environment, it is difficult to determine mechanisms of biotic resistance *in situ* (Havel et al., 2015). Comparing species traits is a first step in assessing whether native species will exhibit some degree of either competitive or consumptive resistance toward invaders (Funk et al., 2008; Kumschick and Richardson, 2013; Zeng et al., 2015). The results presented here indicate that chelae closing force can be predicted by body mass and sex of the individual for all three decapod species but in order to correctly predict biotic resistance these must be validated further by assessing actual resource holding potential. Consequently, when trait based analysis should be complemented with other predictive assessments such as the comparative functional response and relative impact potential metrics (Dick et al., 2017; Dickey et al., 2018; South et al., 2019; but see Vonesh et al., 2017), but also with contest based experiments (Lopez et al., 2019; Zeng et al., 2019). Unfortunately, there is a severe paucity of data on the ecological impact of *C. quadricarinatus* but also on the basic ecology of Potamonautid crabs in southern Africa. Further, the specific dynamics of invasion and the recipient system can mediate trait expression in populations across the invasion gradient, whereupon crayfish at the invasion front can be more aggressive (Pintor et al., 2009), or they have smaller and less heavy chela as a response to reduced competition (Messenger and Olden, 2019). Therefore, a considerable amount of baseline assessment (i.e., abundance, size structure, fecundity, distribution, and diet) is needed to be completed in order to effectively assess the risk that both invasive crayfish species pose toward functionally similar and ecologically important species such as freshwater crabs. Further, assessing actual interaction frequency and habitat or resource use overlap between different sized native and invasive decapod species would determine the potential degree of biotic resistance in the environment.

DATA AVAILABILITY STATEMENT

The raw data generated and used in the analysis are publicly available at <https://doi.org/10.6084/m9.figshare.11993961>.

ETHICS STATEMENT

This research was given ethics clearance by the Animal Ethics Subcommittee, Rhodes University (Ethics No. DIFS2718) and SAIAB Ethics Committee (#25/4/1/7/5_2018_06).

AUTHOR CONTRIBUTIONS

JS, TM, JM, and OW conceived the study. JM provided the equipment. OW provided the funding. JS, NT, and TM conducted the experiments. JS analysed the data and wrote the first draft. JS, TM, NT, JM, and OW all contributed toward manuscript editing and final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2020.00072/full#supplementary-material>

Supplementary Figure 1 | Median maximum closing force (N) per mm of chelae right chelae for *P. perlatus*, *C. quadricarinatus*, and *P. clarkii*. Individual points represent raw data. Boxplots represent median value and 25–75% interquartile range.

Supplementary Figure 2 | Median maximum closing force (N) per mm of chelae left chelae for *P. perlatus*, *C. quadricarinatus*, and *P. clarkii*. Individual points represent raw data. Boxplots represent median value and 25–75% interquartile range.

Supplementary Figure 3 | Median maximum closing force (N) per g of animal for *P. perlatus*, *C. quadricarinatus*, and *P. clarkii*. Individual points represent raw data. Boxplots represent median value and 25–75% interquartile range.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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