

Research Article

Shell crushing resistance of alien and native thiarid gastropods to predatory crabs in South Africa

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Received: 22 September 2015 / Accepted: 10 March 2016 / Published online: 11 April 2016

Handling editor: Kenneth Hayes

Abstract

The successful invasion of freshwater and coastal lakes of South Africa by the recently introduced thiarid snail *Tarebia granifera* may be due in part to release from predatory pressure. This study aimed to determine the comparative vulnerability of *T. granifera* and the widespread native aquatic thiarid *Melanooides tuberculata* to predation. These species also account for many thiarid invasions in the Americas, Europe and parts of Africa. We quantified the shell crushing resistance of these snails, as well as the maximal shell crushing capability of native freshwater crab predators, *Potamonautes sidneyi* and *P. perlatus*. Using an Instron isometric transducer, we showed that *Tarebia granifera* shells were significantly stronger than *Melanooides* shells, and exceeded the crushing strength we documented for both potential predatory crabs. The greater shell strength of *Tarebia granifera* was due to shape, sculpture and thickness characteristics. Shell strength of *Melanooides*, however, remained within the range of crushing strength of their potential predators. Assuming crushing to be the main form of crab predation on snails, we inferred *T. granifera* to be less vulnerable to durophagous attack and that their population growth is thus not limited by predation pressure.

Key words: performance, force, crab, snail, predation

Introduction

Interspecific interactions, such as predation, can affect the invasion success of alien species (see MacNeil et al. 2013). The enemy release hypothesis (i.e., escape from predators, parasites and pathogens) is one mechanism often proposed to explain why alien species exhibit higher competitive ability and therefore successfully invade certain habitats (Elton 1958; Tilman 1999). However, native predators can affect the success of invasions by feeding less on the alien species and more on the native competitors (Shinen et al. 2009; Lopez et al. 2010). The practical usefulness of the concept of biotic resistance to invasion has long been criticised and debated in invasion ecology because factors such as propagule pressure and repeated introductions from multiple source populations greatly increase the chance of

establishment (Alpert 2006; Heger et al. 2013; Ricciardi et al. 2013). To address how predation may affect the invasion process, the strength of interactions between native predators and alien species, as well as their native competitors and native prey, must be determined. This information will provide evidence for whether predator-prey interactions can control an alien invasive population (Grason and Miner 2012; Macneil et al. 2013).

As species are increasingly introduced to new habitats across the world through human activities, more opportunities arise to study the strength of novel interspecific interactions. Native predators may be able to easily feed on or even prefer alien species, quickly incorporating them into their diet and thus potentially increasing biotic resistance to invasion (Lopez et al. 2010; Barrios-O'Neill et al. 2014a). However, if alien prey are harder to handle, predators may ignore the

alien, and continue to focus on native species, which may also have to deal with additional new competition from the invasive (Lopez et al. 2010). For example, if the newly introduced alien species has previously developed defence mechanisms, such as an unusually hard shell, it will remain shielded from predation pressure. Shell crushing predation by crabs has been shown to affect shell morphology of prey gastropods (Brookes and Rochette 2007; Cox 2013; Weigand and Plath 2014) and is considered a driver of snail biodiversity and evolution (Vermeij 1987, 1994; West and Mitchel 2000; Harper 2006; Covich 2010 and references therein). The co-evolutionary relationship between crab predators and snail prey has been shown to vary in relation to heavier predation pressure leading to the formation of stronger shells (West and Cohen 1994, 1996).

The thiarid gastropod *Tarebia granifera* (Lamarck, 1822) is originally from South-East Asia but has successfully invaded rivers and lakes in North, Central, and South America, the Caribbean, and Africa (Appleton et al. 2009). In the 1990s, *T. granifera* was accidentally introduced to South Africa and has rapidly invaded eastern parts of the country, including the Kruger National Park and iSimangaliso Wetland Park (Appleton 2003). It has been suggested that *T. granifera* invasion success is attributed to release from predatory pressure due to its thick shell and operculum (Appleton et al. 2009). However, the predation release of *T. granifera* in South Africa may be only temporary and due to naïve responses of native crabs to this newly introduced alien species. Crabs may learn to use other methods to extract snails from their shells, such as peeling or hooking through the aperture. Over longer time periods, if the selection pressure is strong enough they might evolve stronger chelae to capitalise on the new resource presented by growing *T. granifera* populations.

It has been reported that *T. granifera* tends to outcompete or displace other widespread native gastropods in South Africa, such as *Melanoides tuberculata* (O. F. Müller, 1774) (Miranda and Perissinotto 2014a, b). However, *T. granifera* and *M. tuberculata* are sometimes sympatric and both are considered global invasive species (Pointier et al. 2003; Karatayev et al. 2009; López-López et al. 2009; Work and Mills 2013). Moreover, there is strong evidence that what is referred to as *M. tuberculata* is in fact a species complex (Genner et al. 2004, 2007), with some clades clearly polyphyletic.

This study assessed the comparative vulnerability to native crab predation of alien and a native aquatic snail species by: 1) determining if there are significant differences in shell morphology and crushing resistance between *T. granifera* and the native thiarid

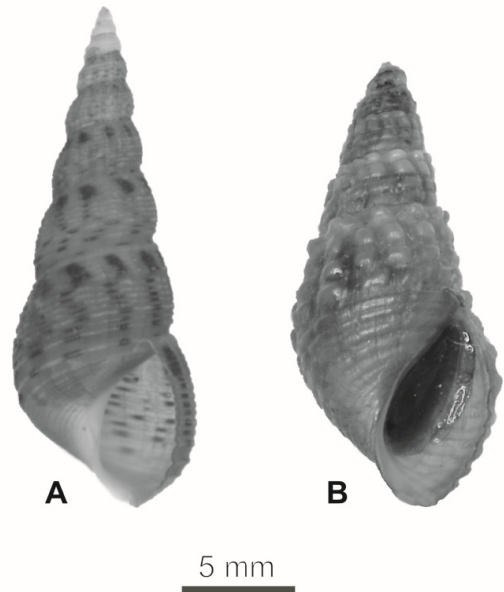


Figure 1. Shells of *Melanoides tuberculata* (A) and *Tarebia granifera* (B). See also Raw et al. 2016.

snail *M. tuberculata*; and 2) determining the maximal crushing capabilities of two native freshwater crabs: *Potamonautes sidneyi* (Rathbun, 1904) and *Potamonautes perlatus* (H. Milne Edwards, 1837).

Methods

Species selection and field collections

In 2014, *P. sidneyi* crabs, *M. tuberculata* and *T. granifera* snails were collected from Kosi Bay's Lake Nhlange (26°57'37"S 32°49'36"E), Lake Sibaya (27°22'11"S 32°42'56"E) and False Bay (27°57'7"S 32°22'37"E) in the St Lucia Estuary, KwaZulu-Natal. *Potamonautes perlatus* crabs were collected from the vicinity of Port Elizabeth, Eastern Cape (34°2'42"S 25°34'7"E). *Potamonautes sidneyi* occurs in Swaziland and Mozambique as well as in the Northern Cape, Eastern Cape, Mpumalanga, North-West, Gauteng, Free State, and KwaZulu-Natal provinces of South Africa. This species was also selected because of its common occurrence in freshwater bodies and observed crushing predation potential. The range of *P. perlatus* is restricted to the Western, Eastern and Northern Cape provinces of South Africa and possibly Namibia (Barnard 1935, 1950). *Potamonautes perlatus* is morphologically similar to *P. sidneyi* but attains greater sizes. *Melanoides tuberculata* was selected because it occurs within the combined range of both native

crab species and is morphologically similar and closely related to *T. granifera* (Figure 1). *Melanoides tuberculata* originates in subtropical and tropical Africa and southern Asia (Brown 1994; Genner et al. 2004, 2007). However, its invasion history is complex, as it has been repeatedly introduced across the world (Pointier et al. 2003; Facon et al. 2003, 2005; 2006, 2008; Genner 2004, 2007; De Kock and Wolmarans 2009; Oscoz et al. 2010; Strayer 2010; Van Bocxlaer et al. 2015). Although we are not in a position to resolve the nomenclatural and taxonomic issues for this group, we are confident that our work is addressing a single taxonomic unit, which is also considered a native morph in South Africa (see Raw et al. 2016; Figure 1). Here we use the name *M. tuberculata sensu lato*, with the recognition that this may be updated with future research (see also Raw et al. 2013, 2015, 2016; Appleton and Miranda 2015; Van Bocxlaer et al. 2015). *Tarebia granifera* has a wide native distribution in South-East Asia and has been introduced in North, Central and South America, as well as throughout the Caribbean islands, and most recently to Africa (Abbott 1958; Pointier et al. 2003; Ben-Ami 2006; Appleton et al. 2009; Karatayev et al. 2009).

Gastropod shell morphometrics

Snail shell height (SH) and width (SW) were measured with Vernier callipers (to the nearest 0.01 mm). The thickness of shells broken in the laboratory was measured at various locations along the height of the mid-dorsal region of the body whorl, using a Nikon SMZ25 microscope with NIS elements measuring software (to the nearest 0.01 mm). The presence-absence of shell sculpture which could influence shell breaking strength was also recorded. Analysis of covariance (ANCOVA) was used to compare size-standardized (covariate = shell width) differences in shell thickness between species. Untransformed data were used as model residuals conformed to assumptions of normality and equal variances. All statistical analyses were performed using the open source software R, version 2.14.1.

Gastropod shell breaking resistance

Forces were measured with an isometric transducer (type 9023, Kistler Inc., Winterthur, Switzerland) connected to a charge amplifier (type 5058a, Kistler Inc.) and set in a customised rig attached to a servo-hydraulic testing system (type 8801, Instron, Norwood, U.S.A.) in the laboratory. Live snails were positioned with the aperture down between two steel plates and subjected to increasing downward crushing forces at

a constant rate (20 N/sec). The maximum force in newtons (N) resulting in shell failure (i.e., breaking of the body whorl) was recorded (Edgell and Rochette, 2008). Fifty snails of each species, with a similar SH and collected from the same locality (i.e., Lake Nhlange) were used. ANCOVA was used to test for differences in shell breaking resistance between species (covariate = shell width). Data were log transformed to satisfy assumptions of normality and equal variances.

Crab morphometrics

Crab carapace widest width (CWW), and the propodus height (PH) of the crushing (or major) chela were measured with Vernier callipers (to the nearest 0.1 mm). Digital images of the crushing chela were analysed with ImageJ software to estimate relative percentage of occlusion type according to Brown et al. (1979) and also to measure the distance from the dactyl fulcrum to the insertion of the dactyl closer muscle apodeme (L1) and the distance from the fulcrum to the dactyl tip (L2), so that mechanical advantage (MA) could be calculated for each sex (Elner and Campbell 1981).

Crushing chela closing force

Measurements were done *in vivo* using the Kistler system and a protocol described in detail in other studies (Herrel et al. 1999; Singh et al. 2000; Lailvaux et al. 2009). Crabs were induced to pinch down with their crushing chela on plates set at a gape of 6 mm (based on the average SW of available gastropod prey) and positioned on the proximal region of the chelae. Closing force was measured five times per individual, with a resting period of 20 minutes between measures. Because the objective of this study was to estimate maximal capabilities of crabs, only the maximum closing force measurements (N) of the most cooperative individuals were considered (see Losos et al. 2002). Hence the data from 13 *P. sidneyi* crabs and 15 *P. perlatus* crabs are presented.

Prey handling time

To gain some insight into the behaviour and handling ability of crabs exhibiting the highest maximal shell crushing capabilities, a simple post hoc experiment was also conducted. Four large (60 – 80 mm CWW) male *P. perlatus* crabs were individually acclimated to 10 L buckets for a week, kept in a temperature controlled room ($25 \pm 1^\circ\text{C}$) with 12:12 photoperiod. Water was changed every 48 h and crabs were fed 20 g (wet weight) of fish muscle tissue daily. Crabs were then starved for 72 h before being presented

with 10 live snails of 5 mm SW over a period of 60 minutes whilst being filmed with a small digital camera mounted on the edge of the bucket. Two of the crabs were presented with 10 *T. granifera* snails as prey and two were presented with 10 *M. tuberculata* snails (SW of all snails \approx 5 mm). The footage was analysed and handling times were recorded with a stopwatch. Handling time in a successful attack was recorded as the time from first clasp with the chela to the time the crab consumed the prey entirely. If the attack was unsuccessful (i.e. ending in the rejection of the prey which remained intact or suffered only minor damage to the shell lip or tip), handling time was recorded as the time from first clasp to the time the prey was dropped. The number of attempted attacks and percentage successful attacks was also recorded (Rheinallt and Hughes 1985; Yamada and Boulding 1998).

Results

Gastropod shell morphometrics and breaking resistance

The body whorl shell thickness of *M. tuberculata* snails used in the study was significantly different from that of *T. granifera* snails (ANCOVA: $F_{1,50} = 32.91$, $P < 0.001$; Figure 2a). *Tarebia granifera* snails had thicker shells, with an average body whorl shell thickness of $0.16 \text{ mm} \pm 0.01 \text{ SE}$, versus $0.11 \text{ mm} \pm 0.003 \text{ SE}$ in *M. tuberculata*.

In terms of shell sculpture, *T. granifera* shells have conspicuous knobs whereas *M. tuberculata* shells are smoother. In this study, *Melanoides tuberculata* shell height to shell width ratio (SH/SW) ranged from 2.17 to 4.71 mm, average $3.09 \text{ mm} \pm 0.05 \text{ SE}$, whereas the shells of *T. granifera* were comparatively less elongated with SH/SW range from 1.64 to 2.71 mm, average $2.14 \text{ mm} \pm 0.03 \text{ SE}$. The shell crushing resistance of *T. granifera* was significantly different from that of *M. tuberculata* (ANCOVA: $F_{1,50} = 269.53$, $P < 0.001$; Figure 2b). *Tarebia granifera* shells resisted an average crushing force of $100 \text{ N} \pm 6 \text{ SE}$, while *M. tuberculata* only resisted an average of $31 \text{ N} \pm 4 \text{ SE}$.

Crab morphometrics, crushing chela closing force and prey handling time

Potamonautes perlatus crabs (47.0 – 86.1 mm CWW, average $60.5 \text{ mm} \pm 3.4 \text{ SE}$) exhibited crushing chela maximum closing forces ranging from 18 to 598 N, average $130 \text{ N} \pm 39 \text{ SE}$ (Figure 3). Crushing chela maximum closing forces of smaller *P. sidneyi* crabs (26.8 – 49.2 mm CWW, average $37 \text{ mm} \pm 1.9 \text{ SE}$) ranged from 8 to 43 N, average $20 \text{ N} \pm 3 \text{ SE}$ (Figure 3).

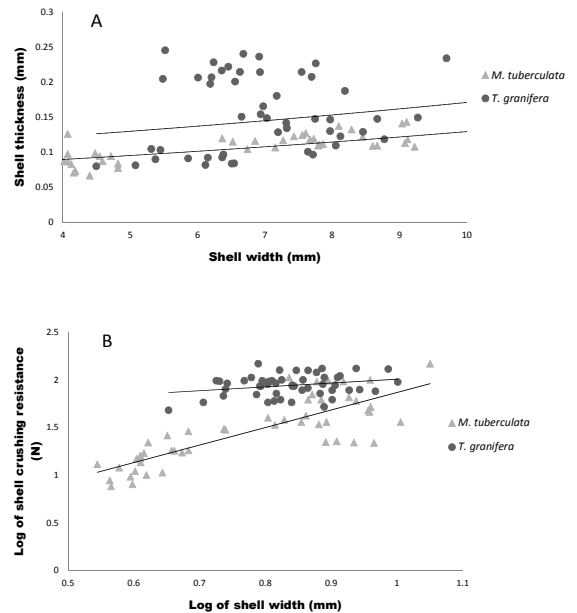


Figure 2. Comparison of a) shell width by body whorl shell thickness allometry, and b) log shell width by log shell crushing resistance, between sympatric populations of *M. tuberculata* and *T. granifera*.

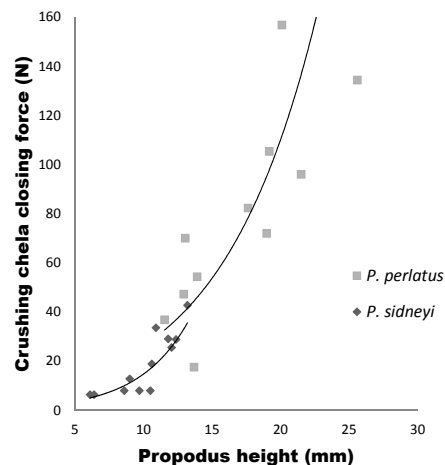


Figure 3. Crushing chela propodus height by maximum closing force, of *P. perlatus* and *P. sidneyi* crabs measured *in vivo*.

The crushing chelae of *P. perlatus* and *P. sidneyi* exhibited similar occlusive geometry (Figure 4), consisting of 32 to 36 % rounded or molariform area, 59 to 62 % asymmetrical occlusive area and ending in a pointed tip. The average mechanical

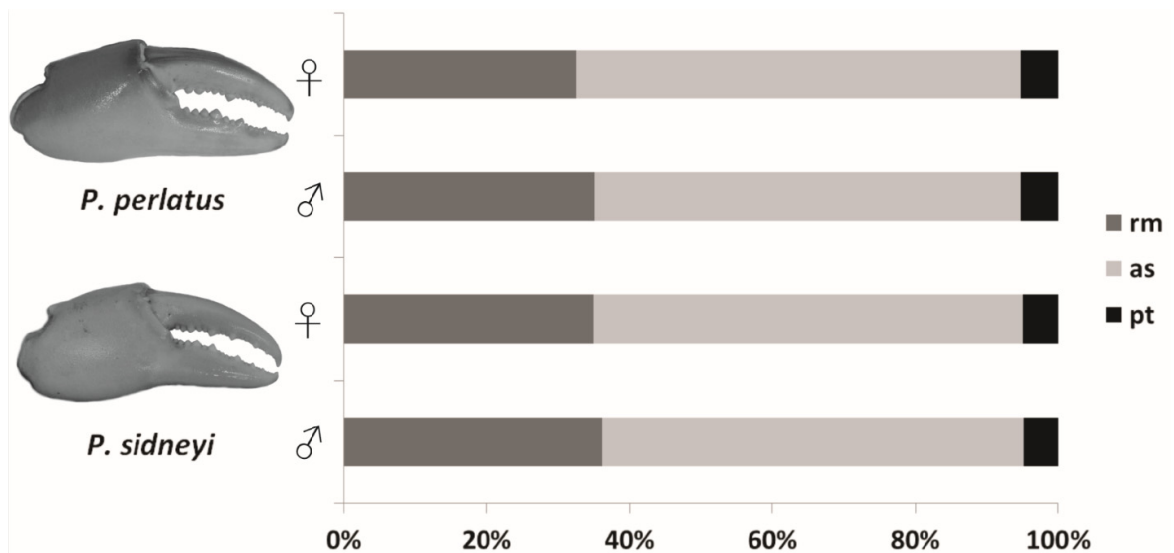


Figure 4. Occlusive geometry of the crushing chela of female and male *P. perlatus* and *P. sidneyi* (total $n = 40$, $n = 10$ for each sex) presented as average percentage rounded or molariform area (rm), asymmetrical occlusive area (as) and pointed tip (pt).

Table 1. Prey handling time, attack rate and % successful attacks by male *P. perlatus* crabs (60–80 mm CWW) under controlled conditions.

Prey species (SW \approx 5 mm)	Handling time (seconds)		No. attempted attacks in 60 mins	Overall % successful attacks
	Successful attack (average \pm SE)	Unsuccessful attack (average \pm SE)		
<i>Melanoides tuberculata</i>	167 \pm 40	87 \pm 19	6 – 9	67
<i>Tarebia granifera</i>	117 \pm 10	159 \pm 168	8 – 12	8

advantage (MA) of the crushing chela for both species was also similar: 0.26 for females ($n = 10$) and 0.25 for males ($n = 10$) in *P. perlatus*, 0.25 for both females ($n = 10$) and males ($n = 10$) in *P. sidneyi*. Large male *P. perlatus* crabs were able to completely crush the shells of *M. tuberculata* and *T. granifera* in successful attacks. However, *P. perlatus* had more difficulty in handling *T. granifera*, often dropping these snails or spending time trying to crack the shell of certain individuals with no success (Table 1). Evidence of crab attack included damage to the shell lip and tip which were often broken off. The overall attack success of large crabs on *T. granifera* was low despite a slightly elevated attack rate when compared with *M. tuberculata* (Table 1).

Discussion

Tarebia granifera snails exhibit thick rotund shells with knobs which are significantly more crush-resistant than shells of *M. tuberculata* (Figures 1 and 2). Thick shells can deter crab crushing predation (Trussell 1996; West and Cohen 1996). Furthermore,

knobs may spread crushing force over an increased surface area or reduce the muscular leverage of the predator (West et al. 1991; Sälgeback and Savazzi 2009). Similarly, more rotund shells, with a lower SH/SW ratio, may be more crush-resistant (DeWitt et al. 2000). The crushing force resistance estimates in the current study are within the range of those reported by West et al. (1991) for *M. tuberculata*. *Tarebia granifera* has been estimated to have diverged from the *Melanoides* clade around 8.6 Ma in Asia (Genner et al. 2007) where the diversity of freshwater crabs is the largest in the world (Yeo et al. 2008; Shih and Ng 2011). *Tarebia granifera* has developed thicker shells compared to African *M. tuberculata* populations. However, thicker shells require additional calcium which may be limiting or difficult to sequester in certain habitats, thus making snails more vulnerable to shell crushing predators. Consistent with this, unusually small or eroded shells have been reported by Miranda et al. (2011) in the St Lucia Estuary and Lake Sibaya. Further studies may address intraspecific differences in crushing resistance in different habitats.

Shell damage, particularly scars, can represent failed crushing or peeling attacks by predators, so their frequency in a population can be used to assess predation pressure (see Edgell and Rochette 2008). No noticeable damage of this kind has been observed in *T. granifera* shells from natural environments in South Africa (Miranda et al. 2011). Indeed, West et al. (1991) commented that regeneration scars are only rarely found in African thiarids, with the exception of specimens from Lake Tanganyika which are also thought to have been involved in a co-evolutionary arms race with native crabs, resulting in unusually strong shells and armament (West and Cohen 1994). However, scars on shells are likely to be size-specific. Smaller shells are more likely crushed, whereas intermediate sizes may escape if dropped during attempted predation, and the largest individuals may only be vulnerable to attacks from the largest crabs. Furthermore, it is expected that predation pressure from shell-breaking predators such as crabs will be most intense on smaller individuals.

Although they overlap in general distribution and can be found in the same habitat, the two native freshwater crabs used in this study can be inferred as not having a significant impact on *T. granifera* populations. The current study demonstrates that native crabs have difficulty in overcoming the stronger shell defences of *T. granifera*. The strength estimates in the current study are in line with those reported by Marijnissen (2007) for *P. platynotus* (Cunnington, 1907) and the strongest *P. perlatus* crabs exhibit a crushing chela maximum closing force similar to that of mud crabs (genus *Scylla*) and lobsters (Elnor and Campbell 1981; Yap et al. 2013). Large *P. sidneyi* crabs are able to crush the weaker shelled *M. tuberculata*, but they are unlikely to successfully prey on *T. granifera*. However, even some of the largest and strongest *P. perlatus* have a much lower attack success rate on *T. granifera* than on *M. tuberculata* (Table 1). Strength, chela gape and time limitations may cause hungry crabs to reject prey (Yamada and Boulding 1998). In accordance with optimal foraging theory, even if peeling is employed as an alternative handling technique to overcome stronger shell defence, it may be more cost effective to spend that handling time consuming other prey or food items (Hughes and Seed 1995; Yamada and Boulding 1998). Further noteworthy preliminary observations were made during the current study. After the prey handling experiment, the large *P. perlatus* crabs were presented with both *T. granifera* and *M. tuberculata* in the lab. Interestingly, crabs seemed to attack the closest snail and move on to the next if unsuccessful. No preference or selection for either species was apparent despite

the continued high attack success on *M. tuberculata*. Like *P. lirrangensis* (Rathbun, 1904) of Lake Malawi (Weigand and Plath 2014), *P. sidneyi* and *P. perlatus* could be considered opportunistically carnivorous scavengers. Their occlusive geometry, indicative of a serrate rather than molariform dentition, as well as low mechanical advantage, suggest that they are adapted to an omnivorous diet (Yamada and Boulding 1998). However, there is evidence that *T. granifera* is part of *P. sidneyi* diet in Lake Sibaya (Peer et al. 2015). It is likely that *M. tuberculata* was predated upon by *P. sidneyi* in the past, but the native snail appears to have either disappeared from that area or its population is currently below detection threshold (Miranda and Perissinotto 2012). Further studies on the ecological interactions that occur in the field between predators and thiarids are needed. Population-level predator impacts should be addressed, as well as local adaptations in different habitats, such as the development of different armament and handling strategies.

The spread of *T. granifera*, like that of other alien invasive gastropods (Alonso and Castro-Díez 2008), is undoubtedly driven by a combination of factors such as changes in its migration regime as a result of human activity (Facon et al. 2006; Appleton and Miranda 2015), high rate of parthenogenetic reproduction (Facon et al. 2008; Miranda and Perissinotto 2012), ability to dominate benthic invertebrate assemblages in various habitats (Dussart and Pointier 1999; Miranda and Perissinotto 2014a, b), the production of chemical cues which deter other potential competitive snails (Raw et al. 2013, 2015) and escape from native predators. According to Appleton et al. (2009), the strong shell defences of *T. granifera* may even facilitate endozoochorous dispersal by waterfowl. Although *M. tuberculata* is native to South Africa, it has a complex global invasion history and alien morphs may be present in South Africa (Genner et al. 2004; Van Bocxlaer et al. 2015). Although they can be found in the same habitat, the interactions between *T. granifera* and *M. tuberculata* seem to result in mutual exclusion, where one displaces the other (Pointier et al. 1998; Contreras-Arquieta and Contreras-Balderas 1999; Karatayev et al. 2009; López-López et al. 2009).

Some aspects of the potential for biotic resistance to alien invasion can be quantified in terms of the mechanisms involved in interspecific interactions, e.g., the crushing strength of predators and crushing resistance of prey. This information could be incorporated into a functional response approach addressing the strength of predator-prey interactions involving native and alien species (MacNeil et al. 2013; Barrios-O'Neill et al. 2014b). Further insight

into the invasion success and ecological effects of alien invasive species can be gained by continuing to monitor these interactions in different habitats, whilst also taking evolutionary trajectories and relationships into consideration (Sakai et al. 2001; Smith 2004; Shine 2012).

Acknowledgements

Mr Etienne Phillips and the staff and students of eNtsa (Nelson Mandela Metropolitan University, Port Elizabeth) are thanked for their invaluable assistance with the engineering and technical aspects of this work. We are also grateful to all Reviewers, including Dr Ellinor Michel and Dr Alan Covich, for their constructive input which strengthened the paper. This work is based on research supported by the South African Research Chairs Initiative of the Department of Science and Technology (DST) and National Research Foundation (NRF) of South Africa. Any opinion, finding and conclusion or recommendation expressed in this material is that of the author(s) and the NRF does not accept any liability in this regard. Permission for this study was granted under a Research Agreement with the iSimangaliso Wetland Park Authority for the project titled "Climate Change and the Management of KZN estuaries: St Lucia Estuary".

Specimens were collected under an integrated environmental and fisheries research and development permit for the purposes of scientific investigation or practical experiment in terms of section 83 of the South African Marine Living Resources Act, 1998 (Act n. 18 of 1998), ref. RES2014/06. Ethical clearance was approved by the Nelson Mandela Metropolitan University Research Ethics Committee (Animal), ref. A14-SCI-ZOO-009 and A13-SCI-ZOO-006.

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