

# The occurrence, bionomics and potential impacts of the invasive freshwater snail *Tarebia granifera* (Lamarck, 1822) (Gastropoda: Thiaridae) in South Africa

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The Asian prosobranch snail *Tarebia granifera* was reported from South Africa (and Africa) for the first time in 1999 in northern KwaZulu-Natal though it was probably introduced sometime prior to 1996. In the 10 years since its discovery it has spread rapidly, particularly northwards, into Mpumalanga province, the Kruger National Park and Swaziland. The snail has colonized different types of habitat, from rivers, lakes and irrigation canals to concrete lined reservoirs and ornamental ponds. It reaches very high densities, up to 21 000 m<sup>-2</sup>, and is likely to impact on the entire indigenous benthos of the natural waterbodies of the region – more so than any other invasive freshwater invertebrate known from the country. The indigenous thiarids *Thiara amarula*, *Melanooides tuberculata*, and *Cleopatra ferruginea* are considered particularly vulnerable. Preliminary accounts of the reproductive biology and population fluctuations of *T. granifera* in KwaZulu-Natal are also presented.

## Introduction

The snail *Tarebia granifera* (Lamarck, 1822), called the ‘Quilted Melania’ in the aquarium industry, is a south-east Asian member of the freshwater prosobranch family Thiaridae (fig. 1). A detailed account of the anatomy of *T. granifera* was given by Tucker Abbott (1952) together with notes on its biology and bionomics while a dissection guide was provided by Malek (1962).

*Tarebia granifera* serves as the first intermediate host for a variety of trematodes in its native south east Asia. Amongst these are several species of the family Heterophyidae some of which have been reported as opportunistic infections in people (Watson, 1960), and another, *Centrocestus formosanus* (Nishigori, 1924), is an important gill parasite of fish. None has been reported from Africa. *T. granifera* also serves as intermediate host for the philopthalmid eyefluke *Philopthalmus gralli* Mathis & Ledger, 1910 which has recently been reported affecting ostriches on farms in Zimbabwe (Mukaratirwa et al., 2005). The snail host implicated in this outbreak was *Melanooides tuberculata* (Müller, 1774) but the rapid spread and high population densities achieved by *T. granifera*, which appears to be replacing *M. tuberculata* in South Africa, may exacerbate the problem in the future. For many years *T. granifera* was believed to be an intermediate host for the Asian lungfluke *Paragonimus westermani* (Kerbert, 1878), but Michelson showed in 1992

that this was erroneous. This has meant that the major interest in *T. granifera* outside Asia today is its invasive ability and its impact on indigenous benthic communities in colonized waterbodies.

*Tarebia granifera* has become invasive on at least three continents, North and South America and Africa. It occurs in several southern states of the U.S.A., Hawaii, many Caribbean Islands as well as Mexico, Venezuela, South Africa and Israel (Tucker Abbott, 1952; Prentice, 1983; Pointier et al., 2003; Appleton & Nadasan, 2002; Pointier et al., 2005, Pointier, 2008; Naranjo-Garcia et al., 2005; Ben-Ami, 2006). Initial introductions were presumably via the aquarium trade.

#### Distribution of *T. granifera* in southern Africa

The first report of *T. granifera* in South Africa, and indeed in Africa, was in 1999 when it was found in a concrete lined reservoir at Mandeni, northern KwaZulu-Natal (Appleton & Nadasan, 2002) but the actual date of introduction was 1996 or earlier. Since 1999 it has become widespread in the eastern half of South Africa, particularly the provinces of KwaZulu-Natal and Mpumalanga, over approximately five degrees of latitude (25°S-30°S). This spread has been rapid, taking less than 10 years, and was perhaps aided by the fact that the first report of *T. granifera* was close to the suspected point of introduction (Amatikulu. GPS 29°04'15.5"S, 31°38'52.5"E), and lay well within the sub-tropical lowlands that are suitable for colonization. To date *T. granifera* has been collected in 13 rivers and 5 lakes (four freshwater and one estuarine) and two dams. It has also been collected in the southern parts of the Kruger National Park in the lowveld of Mpumalanga province (A. Gerber, pers. comm.; Wolmarans & de Kock, 2006) and in Swaziland (fig. 2). This spread will doubtless continue into northern South Africa, Mozambique, Zimbabwe and beyond. It has not been possible to calculate the rate of dispersal.

Most localities in South Africa (93%) lie below an altitude of 300 m above sea level where an estimated area of 39 500 km<sup>2</sup> has been colonized. The only known localities outside this area are the Umsinduzi River in Pietermaritzburg and its confluence with the Umgeni River which lie closer to 500 m. Tucker Abbott (1952) noted that on Guam Island, *T. granifera* occurred in streams and rivers at 983 m altitude but that these water-courses were consistently above 24°C indicating that temperature may be an important determinant of distribution.

*Tarebia granifera* also occurs in several estuaries along the KwaZulu-Natal coast. Prominent among these is the dense population ( $\pm 6038 \text{ m}^{-2}$ ) found at a salinity of 9.98‰



Fig. 1. Adult *Tarebia granifera* from Lake St Lucia, KwaZulu-Natal, South Africa (shell height 22.0 mm).

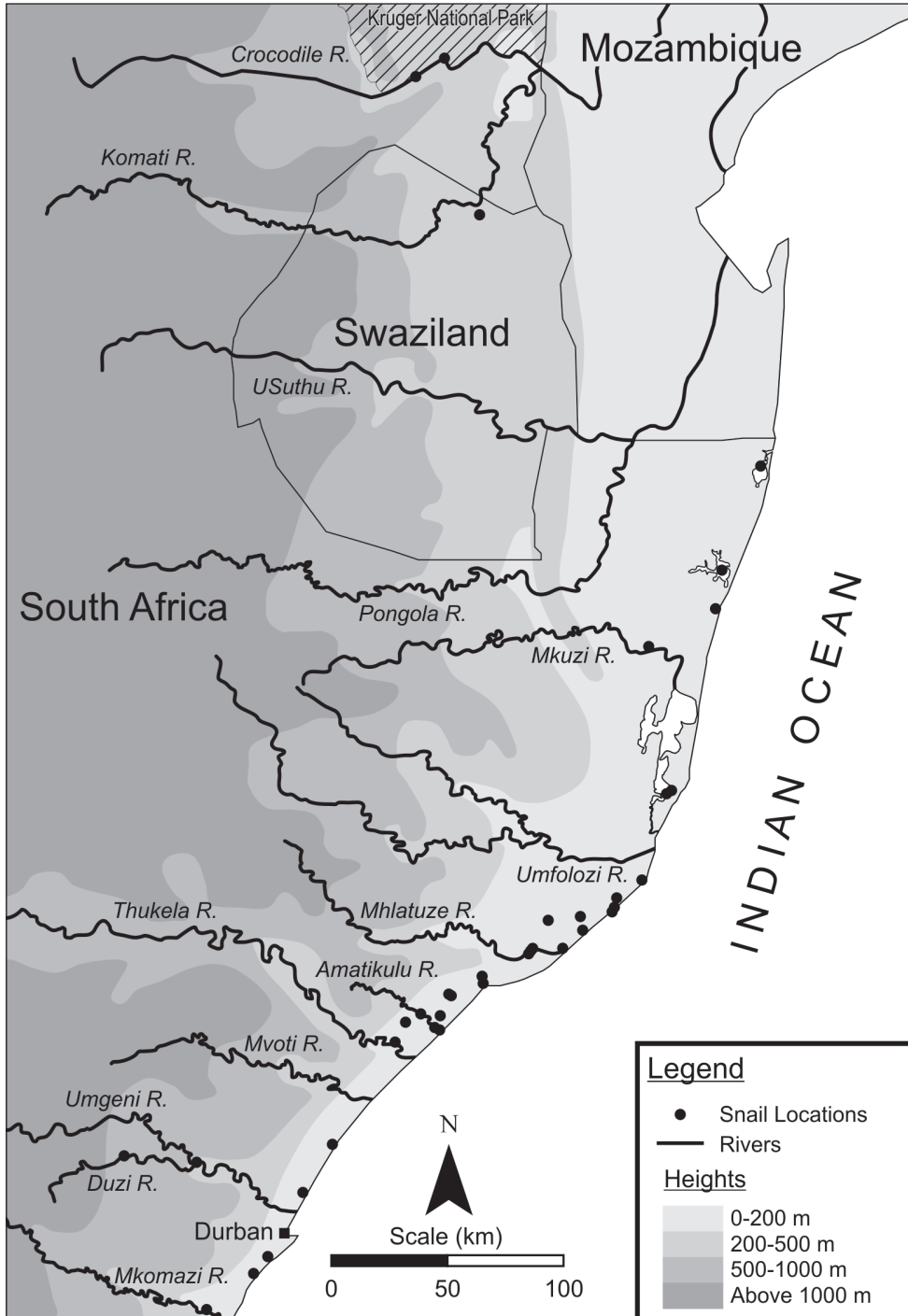


Fig. 2. Map showing the known distribution of *Tarebia granifera* in South Africa.

(28.5% sea water) in Catalina Bay, Lake St Lucia, KwaZulu-Natal (28°13'49.94"S, 32°29'7.37'E), a RAMSAR Wetland of International Importance and a World Heritage Site (Pillay & Perissinotto, 2008). These records show that *T. granifera* is able to colonize brack and moderately saline habitats and reach high densities though for how long is not known. Chaniotis et al. (1980a) suggested from observations in Puerto Rico that snails could survive temporarily saline conditions for several weeks by burying themselves in the substratum, emerging when fresh water returned.

In common with other Thiariidae, *T. granifera* is primarily a benthic species and in South Africa has been collected on a variety of substrata in both natural and artificial waterbodies, e.g. sand, mud, rock, concrete bridge foundations and the concrete walls and bottoms of reservoirs, irrigation canals and ornamental ponds. Many of these habitats were vegetated and the associated vegetation included many types of emergent monocotyledons (e.g. *Cyperus papyrus* L., *Scirpus* sp., *Typha* sp., *Phragmites* sp.) and dicotyledons (e.g. *Ceratophyllum demersum* L., *Potamogeton crispus* L., *Nymphaea nouchali* Burm.f.). Where densities are high, *T. granifera* may also occur on marginal, trailing vegetation and the floating *Eichhornia crassipes* (Mart.) Solms as well. It favours turbulent water and tolerates current speeds up to 1.2m.s<sup>-1</sup> and possibly greater. This habitat range is similar to that recorded for *T. granifera* in Puerto Rico by Chaniotis et al. (1980a).

### Dispersal

It is probable that dispersal of *T. granifera* from one waterbody or river catchment to another occurs passively via birds, notably waterfowl, which eat them and void them later, perhaps in another habitat. Evidence for this comes from the finding of many small *T. granifera* 5-7 mm in height and still containing the soft parts in unidentified bird droppings from the bank of the Mhlali River. Even though the shell of *T. granifera* is thick, most of these juveniles had been partially crushed with only a few still intact. Both the intact and damaged specimens could have been alive when passed and perhaps survived had they been deposited in water. None was large enough to have been reproductively mature (see below) and would have needed to survive in any new habitat for several months before reproducing.

Hockey et al. (2005) recorded the indigenous thiarid *Melanoides tuberculata* in the diet of the Whitefaced Duck, *Dendrocygna viduata* (Linnaeus, 1766). Since the food retention time in waterfowl is between 2 and 6 hours (Halse, 1984), such bird-aided dispersal in eastern South Africa with its numerous rivers and other wetlands, is likely to occur in short jumps from one system to the next.

Passive dispersal may also occur via weed on boats and boat trailers and via water pumped from one waterbody to another for industrial and irrigation purposes. In the Nseleni River juvenile *T. granifera* were commonly found with another invasive snail, *Lymnaea columella* Say, 1817, on floating clumps of water hyacinth *Eichhornia crassipes* which provide a vehicle for rapid downstream dispersal.

Once established in a particular waterbody *T. granifera* is likely to disperse actively, both up and downstream in the case of flowing systems, as far as environmental factors like current speed and food availability will allow. The snail's tolerance of turbulent, flowing water was demonstrated by Prentice (1983) who reported it migrating upstream

on the Caribbean island of St. Lucia at a rate of 100 m month<sup>-1</sup> in streams discharging up to 50ℓ.s<sup>-1</sup>. In KwaZulu-Natal it has been collected in water flowing at up to 1.2 m.s<sup>-1</sup> which is likely to exceed the current speeds of at least the lower and middle reaches of many rivers and streams in South Africa making these watercourses open to colonization. Many rivers have already been colonized.

Its ability to actively migrate upstream in flowing systems has led to attempts to use *T. granifera* as a model for investigating dispersal by freshwater snails. Upstream movement was shown to depend on habitat heterogeneity and food distribution within the system and also on snail size (Snider & Gilliam, 2005). In food-rich environments, individuals of all sizes dispersed rapidly and widely whereas in food-poor environments only larger individuals did so. In standing waterbodies, e.g. lakes, dispersal was determined by turbulence and wave action (de la Vega et al., 2003) but the effectiveness of these limiting factors depended on the coefficient of snail weight/foot-area (sole) of migrating individuals. The sole of *T. granifera* is proportionally small when compared to other thiarids and smaller snails with their higher coefficients were less able to grip the substratum in the face of moving water and so not did disperse as effectively as larger ones. If so, the small size of the adults from Lake Msingazi needs an explanation.

### Population density

In Florida Tucker Abbott (1952) recorded an 'extraordinary' *T. granifera* density of 4444 m<sup>-2</sup> which falls within the range of densities measured with a Van Veen grab in a number of sites in northern KwaZulu-Natal (Table 1). The mean densities listed in this table varied between sites by a factor of 25 from 843.6 ± 320.2 m<sup>-2</sup> to 20764.4 ± 13828.1 m<sup>-2</sup>. Lowest densities were recorded at the northern end of Lake Msingazi where the water was ± 50 cm deep with sandy mud and sparse vegetation (*Scirpus* sp.) and exposed to wave action. Highest densities, apparently the highest yet measured anywhere, were recorded in the Nseleni River where the snails were on (and in) soft mud near the river's bank. This site was non-flowing, devoid of rooted vegetation but it was shaded by trees (*Barringtonia racemosa* (L.) Roxb.) and by floating *Eichhornia crassipes*. This between-site variability may be positively correlated to habitat heterogeneity and food availabil-

Table 1. Densities (D, no.m<sup>-2</sup>) and shell heights (H, in mm) of *T. granifera* at five sites in northern KwaZulu-Natal. Mandeni data were calculated from eight replicate quadrat samples on reservoir walls (Appleton & Nadasan, 2002), the other sites from three replicate benthic grab samples in ± 60 cm water (numbers m<sup>-2</sup>).

| Locality   | D (mean ±sd)      | D (range)    | H (mean ±sd) | H (range)  |
|--|-------------------|--------------|--------------|------------|
| Mandeni Reservoir (1999) (S29 15.806 E31 42.861) | 676.7 ± 444.8     | 120 - 1316   | 10.9 ± 2.5   | 0.8 - 22.0 |
| Sokhulu Reservoir (2006) (S28 32.307 E32 22.153) | 3418.8 ± 1269.1   | 2664 - 4884  | 13.4 ± 2.8   | 7.6 - 20.5 |
| Nseleni River (2006) (S28 41.591 E32 00.896)     | 20764.4 ± 13828.1 | 5905 - 33256 | 10.7 ± 2.8   | 4.4 - 18.5 |
| Mhlatuze River (2006) (S28 48.982 E31 56.089)    | 14.5 ± 10.0       | 4 - 33       | 9.6 ± 2.5    | 3.4 - 16.4 |
| Lake Msingazi (2006) (S28 43.663 E32 08.639)     | 843.6 ± 320.2     | 577 - 1199   | 9.5 ± 1.1    | 6.3 - 11.5 |
| Nhlabane estuary (2006) (S28 36.700 E32 17.090)  | 4440.0 ± 2198.1   | 2264 - 6660  | 7.1 ± 2.6    | 2.7 - 18.8 |
| Mhlali River (2008) (S28 93.012 E31 76.418)      | 1200.4 ± 1810.0   | 0 - 4056     | 6.8 ± 2.3    | 1.8 - 15.5 |

ity (de la Vega et al., 2003; Snider & Giliam, 2005). Table 1 also shows that there was considerable within-site variation, indicating that the distribution at individual sites was typically patchy.

Despite the very high densities recorded in the Nseleni River, indigenous invertebrates were still present in the sediments. The bivalve *Chambardia wahlbergi* (Krauss, 1848) was present in the same area and a local fisherman was able to collect many large specimens for bait. Chironomids, oligochaetes (tubificids) and burrowing polychaetes were also found but in very low numbers. The low *T. granifera* densities reported for the Mhlatuze River may have been influenced by nearby sand-mining activities or, more likely, high flows and mobile sediments, but they nevertheless approach those recorded by Dudgeon (1980) for *T. granifera* in its native Hong Kong (18–193 m<sup>-2</sup>). Much higher densities have previously been observed elsewhere in the Mhlatuze River but were not measured.

Typically half or more of these snails were buried in the sediments and were not visible from the surface. This was also noticed in aquaria where they actively buried themselves in sand. This raises questions about the species' behaviour, viz. what proportion of a *T. granifera* population is buried at any time, how long can snails remain buried and is there some kind of alternation between periods of 'surface activity' and 'sub-surface quiescence'.

Two colour forms of *T. granifera* are found in KwaZulu-Natal, one has a pale brown basal whorl and a dark spire (e.g. Mandeni, Amatikulu, Nhlabane) and in the other the shell is entirely dark brown to almost black (e.g. Nseleni, Embokodweni, Umgababa, Msingazi). Intermediate forms exist. Two misshapen specimens were found in a sample from the Nseleni River, KwaZulu-Natal, in July 2006 (2/749, 0.3%). Both were medium sized, 10.9 and 15.4 mm in height, with the body whorl unusually inflated relative to the spire (fig. 3). In addition, the spires of many shells from several sites were severely eroded so that in some individuals little more than the basal whorl remained.

### Reproductive biology and population fluctuations

*Tarebia granifera* is both parthenogenetic and ovoviviparous, characteristics which are undoubtedly key to its success as an invader. Although no males have been found amongst hundreds dissected from KwaZulu-Natal, it is probable that a few are present. Males were found in most (6/7) populations examined in Puerto Rico by Chaniotis et al.



Fig. 3. One of two malformed *T. granifera* (15.4 mm) recovered from the Nseleni River, northern KwaZulu-Natal.

(1980b) but were generally uncommon at up to 22.7% of the population (mean 4.6%). Live sperm were present in the testes of these males but the genitalia were apparently non-functional. Tucker Abbott (1952) failed to find sperm in the gonads of male *T. granifera* from Florida. Most *T. granifera* are therefore clones of the female parent.

Embryos develop in a brood pouch. This pouch is a compartmentalized structure lying immediately above the oesophagus and develops only after the snail has reached maturity. Its size expands as the number of embryos increases (Tucker Abbott, 1952; Malek, 1962). Attainment of sexual maturity in *T. granifera* is generally indicated by the size of the smallest snail observed to give birth rather than a histological assessment of the development of the gonad and associated reproductive structures. Appleton & Nadasan (2002) estimated onset of maturity at 10-12 mm shell

height but unpublished data suggest a height closer to 8 mm in line with other published studies. Tucker Abbott (1952) estimated sexual maturity at between 5.5 and 8.0 mm at different stations over a short stretch of river in Florida. Chaniotis et al. (1980a) gave a similar estimate of 6.0-7.0 mm from a cohort of laboratory-bred snails in Puerto Rico. Young snails emerge through a birth pore on the right hand side of the head. When born the shell is <1-2 mm in height with between 1.5 and 4.8 whorls (fig. 4). Tucker Abbott (1952), Chaniotis et al. (1980a) and WHO (1981) cite the same frightening statistic that females can give birth to one juvenile every 12 hours! According to Chen (2003) these newborns have a high survival rate in the field.

Extrapolation of these data to the population fluctuations reported from Cuba (Yong et al., 1987; Ferrer López et al., 1989; Fernández et al., 1992) suggest that sexual maturity is reached at an age of about five months. This is in rough agreement with Chaniotis et al. (1980a) who reported variation in maturation period from 97-143 days (3.2-4.8 months) in laboratory cultures. Tucker Abbott (1952) and WHO (1981) give a longer maturation period of 6-12 months, also from laboratory data. It is difficult to relate shell size at the onset of maturity to age since the size structure of populations vary over time and from one locality to another. This is also the case in KwaZulu-Natal where shell sizes in some habitats, e.g. Lake Msingazi, were smaller than in others (table 1).

Dissection of *T. granifera* from Amatikulu, KwaZulu-Natal, showed blastula stage embryos in the brood pouches of snails as small as 8 mm shell height (C.C. Appleton, unpublished data). Small numbers of shelled embryos, including veligers, were found in snails of 10-14 mm but became more plentiful in snails >14 mm and especially those >20 mm. Importantly, unshelled embryos (blastula, gastrula and trochophore stages) were



Fig. 4. Scanning Electron Micrograph of a newborn *T. granifera*.

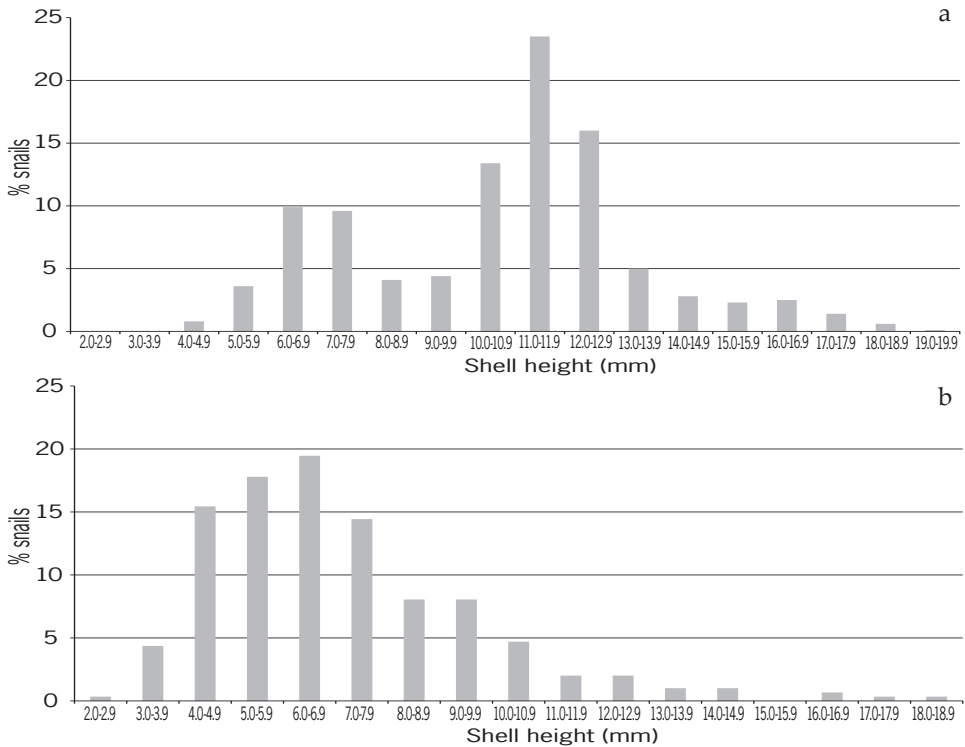


Fig. 5. Size distributions of *T. granifera* sampled in (a) the Nseleni River and (b) Lake Msingazi in northern KwaZulu-Natal.

not found in snails >16 mm and the numbers of shelled embryos themselves decreased in the largest snails, >24 mm. This suggests that differentiation of germinal cells in the ovary and their subsequent arrival in the brood pouch as blastulae is not a continuous process over a breeding season but occurs as one or more 'cohorts' or 'pulses' which stop before the birth rate of young snails reaches its maximum. Based on these observations, it seems that while the first birth may occur in snails as small as 8 mm, these are few and most juveniles are born to snails >14 mm. It is probable therefore that cohorts of smaller snails (see below) are too young to contribute much to recruitment.

Grab sampling in two different types of habitat, the Nseleni River and Lake Nhlabane, on successive days in winter (26 and 27 July 2006), revealed different population structures. In the Nseleni River population the size class distribution was bimodal with cohorts of juveniles in the 6.0-7.9 mm and 11.0-12.9 mm classes (fig. 5a) while in Lake Nhlabane there was only a single peak, in the 5.0-6.9 mm class (fig. 5b). In both populations the younger cohort (5.0-7.9 mm) was present while in the Nseleni population there was an older cohort (11.0-12.9 mm) as well. Although the size ranges of both populations were similar (table 1), the mean size and density of the Nhlabane population were smaller, partly because of the absence of the older cohort there. Small numbers of mature individuals (up to 18 mm) were present in both populations. Using the growth rate of Chaniotis (1980a) of  $0.87 \pm 0.16$  mm/month, the younger cohort of juveniles was esti-



mated to have been born the previous summer and would have been 5-7 months old while the older juvenile cohort was probably born in spring and about 10 months old. The absence of the older cohort in the Nhlabane samples may point to a recent colonization event. Maximum shell heights of sampled *T. granifera* varied from 18.5 mm in the Nseleni River to 25.1 mm in the Embokodweni River (table 1).

Little is known of the long term population fluctuations of *T. granifera* and findings seem to be contradictory. Studies in Cuba (Yong et al., 1987; Ferrer López et al., 1989; Fernández et al., 1992) indicate that the snail lives for more than a year though maximum densities were recorded at different times of the year in different habitats. Using a catch per unit effort netting technique, Yong et al. (1987) and Ferrer López et al. (1989) found highest densities in summer when temperatures reached their maximum whereas Fernández et al. (1992) found highest densities in November (late autumn) when temperatures reached their minimum. Fernández et al. (1992) also suggested that *T. granifera* density was positively correlated with  $\text{Ca}^{++}$  concentrations and negatively with  $\text{NH}_4$  concentrations.

Data from several KwaZulu-Natal localities have provided evidence that population 'crashes' occur from time to time, perhaps as often as every few years (C. Appleton, unpublished observations). In such situations densities have been noted to drop by as much as 95%, i.e. from  $\pm 1000 \text{ m}^{-2}$  to  $\pm 50 \text{ m}^{-2}$ . This may indicate intermittent failure of the spring/summer breeding effort but that after a period of months, numbers build up again. The reproductive biology of *T. granifera* needs to be investigated in detail before its population dynamics can be properly interpreted from quantitative sampling.

### Ecological impact

No studies have been done on the impact of *T. granifera* on the benthic fauna of invaded habitats in South Africa. However invasive *T. granifera* have been associated with the disappearance of two indigenous benthic gastropod species from rivers in Puerto Rico and have displaced the vegetation-associated pulmonate *Biomphalaria glabrata* (Say, 1818) from streams and ponds on several Caribbean islands (Prentice, 1983; Samadi et al., 1997). Although the responsible mechanism is not understood, this has led to suggestions that it could be useful as a biocontrol agent in snail control operations within integrated schistosomiasis control programmes. In the light of these examples therefore, it would be naïve to think that it does not compete for space and resources (e.g. food) with indigenous infaunal and epifaunal invertebrates in South Africa, especially where its densities are high. Under such conditions it is likely to alter the structure and diversity of the entire benthic communities of invaded habitats and perhaps the vegetation-associated communities as well.

The benthic invertebrate communities of rivers and lakes in northern KwaZulu-Natal have been documented (Schoonbee, 1964; Hart, 1979; Walley, 1979; Hart & Appleton, 1997) so that it is possible to predict infaunal taxa that are likely to be impacted. In sandy/muddy-bottomed rivers, e.g. Amatikulu, Umhlatuze and Nseleni, these include the bivalves *Chambardia wahlbergi* and *Corbicula fluminalis* (Krauss, 1848), gomphid dragonfly nymphs and polychaete worms. In lakes, e.g. Nhlabane and Umsingazi, *C. fluminalis* and burrowing crustaceans (isopods and amphipods) would be affected. Susceptible epifaunal invertebrates include indigenous prosobranch snails, e.g. *Lanistes*

*ovum* Troschel, 1845 (Ampullariidae), *Thiara amarula* (Linnaeus, 1758), *Melanoides tuberculata* and *Cleopatra ferruginea* (Lea, 1850) (Thiaridae), decapod shrimps (*Caridina* and *Macrobrachium* spp.) and crabs (*Potamonautes* and *Varuna* spp.) as well as odonatan nymphs, notably Libellulidae. On rocky substrata, a different range of invertebrates is likely to be affected, viz. ephemeropteran nymphs (Baetidae, Caenidae, Heptageniidae), trichopteran larvae (notably Hydropsychidae), simuliid larvae, pulmonate limpets *Burnupia* and *Ferrissia* spp. (Ancyliidae), bryozoans, sponges as well as algal and periphyton growth on colonized surfaces.

### Competition with indigenous Mollusca

Anecdotal reports and observations suggest that in KwaZulu-Natal the indigenous thiarid *M. tuberculata* is becoming less common and pressure from the spread of *T. granifera*, particularly at high densities, is a possible explanation. Like *T. granifera*, *M. tuberculata* is parthenogenetic and ovoviviparous and grows to a similar size. A comparison between our observations on *T. granifera* and *M. tuberculata* in terms of selected reproductive statistics (table 2) suggests that the two are similar in size at first birth and juvenile output. Although the geographic ranges of the two species coincide, *T. granifera* frequently occurs alone. Data from several habitats where the species occur sympatrically show however that in all such situations *T. granifera* becomes numerically dominant.

In view of its spread into the saline St Lucia estuary system (see above) and other estuaries and lagoons along the KwaZulu-Natal coast, *T. granifera* is likely to impact on another indigenous thiarid, the poorly known *Thiara amarula*. This species has been recorded from the brackish reaches of several estuaries along the coast of KwaZulu-Natal and Mozambique. Both *T. amarula* and *T. granifera* occur in the Nhlabane estuary and in July 2006, the latter was present at between 2000 and 6000 m<sup>2</sup> (table 1) while only two specimens of the former were found. Previous collections at the same site showed *T. amarula* to be fairly common.

It is important to note too that three of the mollusc species mentioned above, viz. *C. ferruginea*, *L. ovum* and *C. wahlbergi*, reach the southern limits of their African distributions in north-eastern KwaZulu-Natal (Appleton, 1977) – the area now colonized by *T. granifera*. Being at the limits of their ranges, these species may be particularly vulnerable to interference from dense populations of *T. granifera*. Studies on the ecological impact of *T. granifera* are urgently needed.

Table 2. Selected reproductive characteristics of *T. granifera* and *M. tuberculata*.

| Characteristic   | <i>Tarebia granifera</i> | <i>Melanoides tuberculata</i> |
|--|--------------------------|-------------------------------|
| No. embryos (all stages) in brood pouch                | 1-77                     | 1-64                          |
| Size of parent at 1 <sup>st</sup> release of juveniles | 8.0 mm                   | 5.0 mm                        |
| Size of parent at peak release of juveniles            | 24.0 mm                  | 20.0 mm                       |
| Size of juveniles at birth                             | 0.7-2.1 mm               | 1.2-2.2 mm                    |

### Economic importance of *Tarebia granifera*

In addition to its role as intermediate host for several economically important trematode species, *T. granifera* has colonized reservoirs, dams and ponds on the premises of three large industrial plants in northern KwaZulu-Natal and been pumped out of at least one of them, blocking pipes and damaging equipment. This generally happens when snail densities are high and the damage is due to individuals being crushed so that pieces of shell and soft tissue are carried into machinery. Details of the nature and extent of this damage and the costs incurred are not available. It is not possible to say how the snails reached these reservoirs but there is no doubt that *T. granifera* is able to pass unharmed through pumps, probably as juveniles. The snail has also interfered with the circulation of water through the ponds at a fish hatchery in the region by blocking pipes and pumps.

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