

A POSSIBLE NATURAL DISPERSAL MECHANISM AMONG JUVENILES OF THE BIOINVADER SNAIL *MELANOIDES TUBERCULATA* (THIARIDAE: GASTROPODA) BY FLOATATION

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Abstract Native to Africa through to SE Asia the invasive freshwater gastropod *Melanoides tuberculata* (Müller, 1774) has successfully spread to the American continent, and is a strong competitor of native gastropods. Deliberately introduced into the West Indies to combat schistosomiasis in the late 1970s, it is now widespread throughout the Caribbean. Its range has expanded to cover Brazil, where it was first observed in the 1960s, and throughout South America. Preying on eggs of local limnic molluscs, its impact has been devastating, with *M. tuberculata* replacing native populations (Ladd & Rogowski, 2012; Vogler et al., 2012). Furthermore, *M. tuberculata* exhibits parthenogenesis, is long-lived and is assumed to demonstrate an efficient dispersal mechanism; all of these factors are beneficial to a bioinvader that can reach high densities. With the addition of a high tolerance to variable environmental conditions such as salinity, eutrophication and pollution it is a voracious competitor with non-native species. Dispersal mechanisms of this bioinvader are key to learn about the spread of invasive species. The hypothesis of *Melanoides*' floating behaviour was studied in the laboratory for a better understanding of its dispersal techniques through major Brazilian hydrographic systems. During a period of six months, under controlled conditions, reproductive adults were observed, and juveniles were for the first time observed floating, and moving, below the water film using their foot as a surfboard, and the proboscis as a paddle. This data could be useful in future control methods.

Key words *Melanoides tuberculata*, floating, dispersal mechanism, juveniles

INTRODUCTION

Biological invasion processes can alter habitat properties, causing ecological imbalance and biodiversity decline (Enserink, 1999; Kolar & Lodge, 2001; Everett, 2000). Some exotic species have considerable capacity for invasion and colonization of new environments, due to a greater tolerance to limitrophe abiotic conditions, eventually being also adaptable to life in polluted and degraded areas (Machado & Oliveira, 2009). In addition, without specialised predators, they usually achieve remarkable reproductive success, reaching high population densities, which can drastically affect the ecological interactions and resource availability. In fact, harmful consequences related to the introduction of exotic organisms may be promptly detected in the structure and the trophic processes of the natural communities, these being the risks likely to extend to the economy, and, eventually, to public health as well (Machado & Oliveira, 2009).

Active and/or passive dispersion supports the presence and distribution of the organisms in

nature. The connection of a large set of biological and ecological characteristics usually defines the specificities and constraints in the occupation of a certain place by the organisms (Nava & Machado, 2013). In this context, molluscs are good examples for the 'at a snail's pace' paradox (*sensu* Kappes & Haase, 2012). Despite their restricted mobility, dispersion looks surprisingly unchallenging, being most of the species notorious r-strategists, relying on both, variable individual traits (e.g., size, sex, stage of reproductive maturation) and external factors (e.g., temperature, sediment, food availability).

Mostly attributed to anthropic activities, the introduction of exotic bivalves and gastropods have been continuously reported to Brazil (e.g., *Corbicula fluminea*, the Asian cockle, *Dreissena polymorpha*, the zebra mussel, *Limnoperma fortune*, the golden mussel), resulting in increasing depletion of benthic communities, and severe economic impacts (Beasley et al., 2003; Brugnoli et al., 2005; Karatayev et al., 2007; Alonso & Castro-Díez, 2008; Vianna & Avelar, 2010; Pestana et al., 2010; Kappes & Haase, 2012; Santos et al., 2012). *Melanoides tuberculata* (Müller, 1774) was first

observed in Santos City (23°S/46°W, São Paulo State) in the 1960s; it is a long-lived freshwater snail, a known bioinvasive and is monitored worldwide due to its accelerated dispersion (Vaz *et al.*, 1986; Boga *et al.*, 2005; Bolaji *et al.*, 2011). Supposedly introduced through the trade of ornamental algae and fish, the presence of this thiarid in the major river tributaries, and watersheds of Brazil has had a major ecological impact in this region.

Preying on, and out-competing for food with native gastropods, the ability of the species to tolerate highly variable environmental conditions is noteworthy (Farani *et al.*, 2015). Dispersed through pristine environments, as well eutrophic and polluted water bodies, it is a salt tolerant species observed in estuarine areas (Bolaji *et al.*, 2011). In all of these environments, it can overcome native thiarids, including unstable hypoxic environments with abundant floating aquatic macrophytes (Pointier *et al.*, 1991; Bedê, 1992). Additionally, offspring production is likely to rely on female parthenogenesis (Jesus *et al.*, 2007), which is also advantageous for rapid colonization. To add to its negative impact on the ecosystem, *M. tuberculata* has assumed an important role as vector of parasites, hosting several pathogens (particularly trematodes) that can affect animal and human health as well (Vaz *et al.*, 1986; Thiengo *et al.*, 1998).

Known to compete with the planorbid *Biomphalaria glabrata* and *B. straminea* (intermediate hosts of the trematode *Schistosoma mansoni*), *M. tuberculata* has been intentionally introduced in the West Indies as biological control agent, a management strategy recognised to have positive effects to prevent schistosomiasis (Pointier, 2001). Ironically, *M. tuberculata* demands regular monitoring and control strategies, because it has become an important parasite vector and presents a hazardous risk to public health. For instance, it can host the liver fluke *Clonorchis sinensis*, and the lung fluke *Paragonimus westermani*, which are responsible for human clonorchiasis and paragonimiasis respectively (Malek & Cheng, 1974).

In general, gastropods demonstrate very creative strategies of dispersal and to escape from predators, including:

(1) jumping, using the operculum or the muscular foot positioned as a lever (e.g., *Nassarius vibex*, *Strombus maculatus*),

(2) floating upside down at the surface with the aid of egg mass or producing bubbles with the mucus (e.g., *Janthina* spp., 'the bubble-rafting violet snails'),

(3) sailing with the foot usually extended like a 'sail', taking advantage of the wave movements in the surf zone (e.g., *Hastula inconstans*), or

(4) crawling underneath the water surface – a complex action usually involving the pallial cavity (filled with air, providing buoyancy), ciliary pedal locomotion and/or mucus trails and muscular waves (e.g., *Sorbeoconcha physidae*) (Gore, 1966; Field, 1977; Miller, 1979; Lee *et al.* 2008; Churchill *et al.*, 2011).

In the latter the water's surface tension supports the gastropod's weight (mostly juvenile stages), so they can even graze algae during crawling, alternatively they continue floating, taking advantage of the tension of the water film as strategy to drift away (Little & Nix, 1976; Argonies & Hartke, 1995; Nava & Machado, 2014). Assuming a passive displacement, following the paths defined by the marine currents and winds, rafting (*sensu* Thiel & Gutow, 2005) has been commonly reported among freshwater gastropods of the family Hydrobiidae (e.g., *Hydrobia*, *Pyrgophorus*, *Potamopyrgus*) (Alonso & Castro-Diez, 2008). However, the literature does not describe any similar behaviour for the family Thiaridae.

Despite the remarkably wide geographic distribution and rapid recent spread of *M. tuberculata*, biological and ecological data on this bioinvader are scarce and lack information on mechanisms adopted by the thiarid for dispersion. Taking advantage of the water film, floating has been conspicuously observed among several gastropod species. Thus, intending to discern how *M. tuberculata* has dispersed through major Brazilian hydrographic systems and freshwater reservoirs, juveniles (n=60) and adults (n=90) of the thiarid were collected and monitored in laboratory for analysis of the biological cycle. During a period of six months, under controlled conditions, reproductive adults were observed, and juveniles were for the first time observed floating, and moving, below the water film using their foot as a surfboard, and the proboscis as a paddle. So far, passive dispersion by floating vegetation has been suggested as a vehicle for *M. tuberculata* rapid downstream dispersal (Peso *et al.*, 2011). Indeed, smaller lighter, juvenile shells may have an advantage for surfing (as a 'dispersive stage'),

while heavier adults would remain buried in the substrate. This hypothesis is supported by the embryonic part of the shell in adults often being eroded, due to the burrowing nature of *M. tuberculata* adults in nature.

MATERIAL AND METHODS

Study Areas

Dique do Tororó (12°59'4" S, 38°30'21" W)

Sampling was carried out on 23rd October/2015. The artificial water reservoir of the Dique do Tororó is approximately 2,000 meters in length, and with the aspect of a large lake with dark waters. Historically, it was the place where local populations used the waters for their domestic routine (Neto, 2014). Although transformed into an important tourist and recreational point of Salvador City, the discharge of domestic sewage has made the Dique do Tororó a hotspot for contaminated water and a source of schistosomiasis and so not recommended for human use (Amorim *et al.*, 1975).

Pratinha River (12°24'00" S, 41°33'13" W)

Sampling was carried from 27th to 30th November/2015. Located in the domain of a karst plateau (with a predominance of limestone rocks), within the limits of the Marimbus/Iraquara Protected Area (Decree No. 2,216 of June 14, 1993), the transparent waters of the Pratinha River flows into the Santo Antônio River, a tributary of the Paraguaçu River. With a total area of approximately 125,000 ha, it flows through land with diverse environmental problems (e.g., burnings, deforestation, garbage and sewage, unsanctioned tourism, occupation of permanent preservation areas and mining activities). Among other attributions, the water from Pratinha River is destined for human use ('Instituto de Meio Ambiente e Recursos Hídricos', INEMA, Bahia State).

Collections

For collection of the individuals, a manual net (23×17cm) with a 1.0mm mesh was used. In the laboratory, the specimens were placed in transparent plastic containers (200 ml) with perforated lids. The thiarids were fed with fragments of almond leaves (*Terminalia catappa* Linn) (Farani *et al.*, 2015). Water replacement was performed every 48 hours (using water from the collection site). During the experiment, samples were kept inside a germination chamber with photoperiod and temperature control (constant at 22 °C). Daily monitoring and observations extended for 18 days (time interval during which biological analyses were developed). For long-term behaviour analyses, the snails remained in the chambers for a six-month period. Data were collected with support of a stereomicroscope (model NIKON SMZ1000), and photographic documentation was obtained with a digital camera (model NIKON COOLPIX995) coupled to the optical equipment.

Age classes

Based on the Sturges rule (Sturges, 1926), individuals of *M. tuberculata* were separated into six size classes, and two major categories defined: juvenile and adults (Table 1). According to Okumura (2006), *M. tuberculata* reaches sexual maturity between 9.97mm and 10.28mm. Thus, 'juvenile' snails had a shell length of less than 10mm, while 'adults' were larger than 10mm. Three replicates per size class were adopted, with five individuals from each class used per sampling site (Table 1). Shell morphometry was performed using a Mitutoyo® digital caliper.

RESULTS

A total of 150 individuals (juveniles=60, adults=90) were observed throughout the

Table 1 Size class distribution, being two categories

Class	Size (mm)	Category	Dique (n)	Pratinha (n)
1	0–5.0	J	15	15
2	5.0–10.0	J	15	15
3	10.0–15.0	A	15	15
4	15.0–20.0	A	15	15
5	20.0–25.0	A	-	15
6	25.0–30.0	A	-	15

experiment period. The two largest class sizes (5 and 6) were not found in the Dique do Tororó population. In the containers with adult snails (classes 3 to 6) new recruits were recorded daily. 203 newborn snails were added to the samples of the Dique do Tororó, and 312 to the Pratinha River, and of these juveniles (24 hours after hatching), the recorded average shell size varied between 1.0–2.0mm, with 3 (eventually 4) turns of teleoconch. The large ones (collected in the field), already fully striated, varied between 3.0–6.0mm, with 5 turns of teleoconch.

The flotation behaviour was strictly documented for classes 1 and 2 from both collection sites and the new recruits (added to class 1) followed a rather conspicuous pattern: inverted position (the shell hanging beneath), opercular opening facing upward, oval foot anteriorly extended (just below the proboscis), and held in contact with the water film (Fig. 1). Moving slowly and systematically in small groups of two to ten individuals all class 1 juveniles ($n=30$) were observed exploring the water film for up to 1 hr. No air bubbles were produced. Movements relied strictly on the foot, and the proboscis was used as an oar and alternated between passive drift and active food-seeking behaviour. In fact, the foot in a juvenile snail (1.0mm) may represent up to 50% of the shell length, however, it does not grow proportionally. For an adult snail of 2.0cm, the foot is equivalent to $\frac{1}{4}$ of the shell length. In relation to the movements, these often alternated between swimming (a series of straight-line displacement), and smooth, rotating movements, both occurring in synchrony with the extension and retraction of the proboscis, which clearly assumes the role of 'rowing'. Conspicuous throughout the process the radula is continuously and strongly projected through the oral opening, promoting a current, seemingly advantageous in promoting the sliding of the shell under the water film.

Young snails initially congregate at the surface in small groups but are later joined by additional small groups to form larger aggregations of up to 10 individuals. In these small clusters they seem more agitated, constantly exploring and touching adjacent individuals with the proboscis, while the radula remained 'scraping' the water surface. Eventually, they simply float together, keeping the proboscis retracted and the large foot close to the mouth (similar to a 'collar'). In this case, the

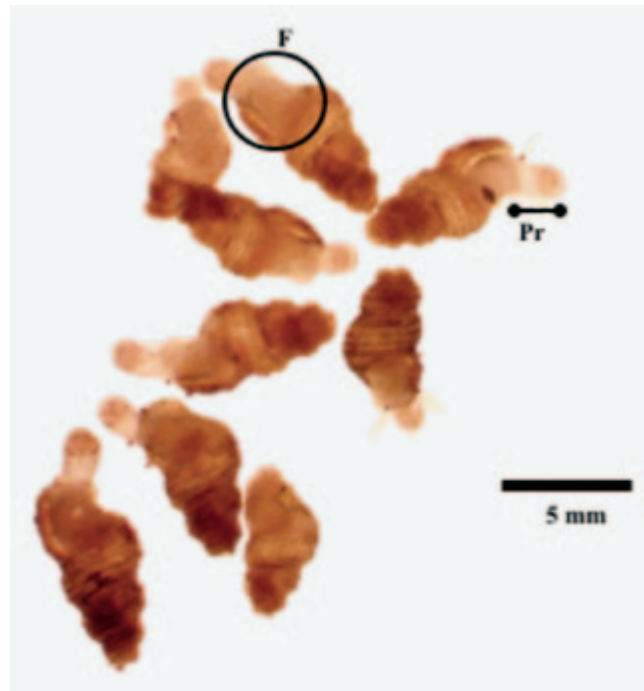


Figure 1 A bundle of juveniles of *Melanoides tuberculata* floating upside down. Pr=proboscis, F=foot.

tension of the surface maintains both the contact of the shells and the cohesion of the group.

It is important to note that bubble production was not observed for either category. Floating ability has not been diagnosed among adult snails, although they are skillful in climbing vertical surfaces.

DISCUSSION

For the first time floating behaviour was observed and described in the bioinvader gastropod *M. tuberculata*. Apparently restricted to juveniles, floating is likely to be biased by shell size and weight, although environmental stresses (e.g., resource depletion) may also play an important role as a trigger. However, even under controlled experimental conditions, the chance of the behaviour having been induced due to 'artifacts' can not be ignored. The pressure of a restricted space may have led to the exploration of the biofilm formed on the water surface — as suggested by Orvain & Sauriau (2002), a common trend among gastropods kept in a 'microcosm'. On the other hand, juveniles are also highly tolerant to salt variation, being able to survive under harsh environmental conditions (Oliveira *et al.*, unpublished data). Thus, as a more efficient

dispersal stage, juveniles could take advantage of the currents in lotic environments, floating to areas closer to the estuaries, resulting in dispersion, and the establishment of new populations.

M. tuberculata has been characterised as an organism adapted to estuarine environments and brackish waters — a suggestive scenario that corroborates dispersion through a salt gradient (Roesler *et al.*, 2007; Wingard *et al.*, 2008). Although the hypothesis of a ‘buoyant-dispersant-juvenile’ is lacking empirical support to be fully assumed, some divergent aspects on the fluctuation capacity between juveniles and adults can be pointed out. For instance, individuals over 1.0cm often have a reduced foot, compared to shell size, which could make surfing unfeasible for this size category.

The practice of surfing is not unprecedented, being frequently observed in *Hastula* species — these snails use waves and the well-developed foot to actively move along the spray zone (Miller, 1979). Furthermore, fluctuation and/or ‘rafting’ has been reported for several other marine invertebrate taxa, including crustaceans and cnidarians (Highsmith, 1995). Among the gastropods, the most typical pattern has been observed to some mimetic sea slugs that live associated with filamentous green algae (Jensen, 1993). But in contrast, data on mechanisms and strategies for dispersal of freshwater molluscs are relatively unexplored. Brown (2007) emphasises the resistance and survival of bivalves and gastropods to the ingestion and passage through the fish digestive tract — an important dispersional adaptive process. Live individuals could be also transported adhered externally to bird feet or feathers, or even through the faeces (Malone, 1965; Green & Figuerola, 2005). Finally, considering the darker colouration of the adult shells of *M. tuberculata*, it could be assumed that they would be more vulnerable to predation, or even exposure to UV radiation. This may warrant a preference for being buried (or semi-buried) in the substrate, avoiding exposure. Or, as mentioned by Olson & Barbieri (2013), besides behavioural strategies, the survival of these organisms increases as a function of body size and shell thickness (the shell being an important element for photoprotection). Certainly, beyond its natural distribution and floating ability, the rapid adaptation and establishment of the bioinvader gastropod *M. tuberculata* are likely to be

linked to a series of biological, behavioural, morphological and physiological aspects. How these aspects operate together by enhancing its survival at distinct life stages, for now, remains largely unclear.

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