

## Research Article

## Rapid population growth countered high mortality in a demographic study of the invasive snail, *Melanoides tuberculata* (Müller, 1774), in Florida

Kirsten Work\* and Cody Mills

Stetson University, DeLand, FL 32724, USA

E-mail: [kwork@stetson.edu](mailto:kwork@stetson.edu) (KW), [cmills@stetson.edu](mailto:cmills@stetson.edu) (CM)

\*Corresponding author

Received: 30 November 2012 / Accepted: 16 August 2013 / Published online: 17 September 2013

Handling editor: Sergey Mastitsky

### Abstract

*Melanoides tuberculata*, an exotic thiarid snail that originated in the Middle East, eastern Africa, and Southeast Asia, has invaded subtropical and tropical areas worldwide. This study provided a detailed picture of the characteristics of a population in central Florida. We collected 40 specimens of *Melanoides tuberculata* from a cool spring and cultured them and 54 of their offspring in the laboratory for 7 and 10 months, respectively. For both the adults and their F1 offspring, weekly or bimonthly measurements of individuals and counts of offspring produced estimates of growth, age at first reproduction, offspring production, and survival. From these measurements, we produced estimates of birth and death rates and a growth curve using a monomolecular model. We estimated predation rates on the snails with a three-day incubation of small (1–4 mm) *M. tuberculata* with crayfish in the laboratory. Finally, we produced a static life table from measurements of ~2,200 specimens of *M. tuberculata* collected from the spring. Growth and reproduction measurements from the laboratory indicated that the snails grew rapidly and were prolific. Only initial size significantly explained any variation in the growth of individuals and only first clutch size explained any variation in fecundity. Nonpredatory mortality in the laboratory was low, but crayfish-induced mortality was high. The life table analysis suggested that the spring population was stable and that mortality was extremely high on the smallest individuals, such as those used in the crayfish predation rate measurements, and on the largest individuals. Therefore, the potential of *M. tuberculata* to invade new habitats and quickly establish populations may be the result of its high population growth rate, but its population growth may be checked by local predators, such as crayfish and perhaps snail-eating turtles and raccoons.

**Key words:** *Melanoides tuberculata*; invasion; population demography

### Introduction

Florida, like subtropical areas worldwide, has an extensive exotic species problem. In the US, only California has been invaded by more fish species than Florida (121 vs. 262, Fuller et al. 1999). As of May 2012, the United States Geological Survey reported that Florida hosted 389 nonnative aquatic organisms, of which 189 were fish, 63 were plants, and 15 were snails (USGS 2012). In particular, Florida is threatened by the ornamental organism trade; the primary route of aquatic introductions to the US as a whole is through stocking and bait release, whereas the primary source of Florida aquatic introductions is through aquarium release (Padilla and Williams 2004). The aquatic plant and fish trade provides a likely route for the introduction of nonnative snails as well as for plants and fish,

as small snails can easily be overlooked on leaves or in transfer water for fish. In fact, 90% of the aquatic plants that Keller and Lodge (2007) sampled from vendors in the Great Lakes Basin carried secondary nonnative species and the vast majority of these hitchhikers were gastropods. Provided that abiotic conditions are adequate, the likelihood of snail introduction success is potentially high as many commonly traded snail species are parthenogenic, possess high reproductive and growth rates, and often have generalist feeding habits (Kolar and Lodge 2001; Sakai et al. 2001; McMahon 2002; Marchetti et al. 2004; Alonso and Castro-Díez 2008). Given that the aquarium trade is lightly regulated, with a wide array of tropical species for sale in most pet stores and easy access on the internet to even more species (Padilla and Williams 2004), it is likely that introductions occur, and will continue to occur, often.

Thiarid snails have invaded most continents (North America, South America, parts of Africa) and many islands with mild climates from their original distributions in tropical Africa, Asia, and Oceania (Clench 1969; Pointier et al. 1993a; Duggan 2002; Genner et al. 2004; etc.). Many of these thiarid invasions have been either *Melanoides tuberculata* (Müller, 1774) or *Tarebia granifera* (Lamarck, 1822), which have occurred as a result of aquarium releases or as intentional introductions for biocontrol (Pointier et al. 1993a; Cowie 2001; Karatayev et al. 2009). *Melanoides tuberculata* invasions have been well studied as this species may outcompete native snails, particularly hydrobes that may carry *Schistosoma* (Pointier 1993; Pointier et al. 1993a), and this species may serve as a host for numerous flukes itself (Dundee and Paine 1977; Pointier et al. 1993a; Pointier et al. 1994; Scholz and Salgado-Maldonado 2000; Guimarães et al. 2001; Ben-Ami and Heller 2005; Boguea et al. 2005; Derraik 2008), including species that infect humans and species that infect threatened fishes (Mitchell et al. 2000). In the Caribbean, *M. tuberculata* spread rapidly after repeated introductions in the 1970's and 80's and became the most prevalent aquatic snail on the island of Saint Lucia (Pointer 1993).

*Melanoides tuberculata* was first observed in the US in Texas and Florida in the 1960's (Murray 1964; Clench 1969, respectively). Although it has been established in Florida for decades, its range continues to expand. Recent discovery of the species in Biscayne National Park in South Florida (Murray et al. 2010) has reignited interest in this successful invader, given its potential to outcompete native snails and to host human and wildlife parasites. The purpose of this study was to measure reproductive and growth parameters that predict population growth of *M. tuberculata*, given the paucity of demographic data for *M. tuberculata* outside its native range, other than in the Caribbean. We predicted that *M. tuberculata* would exhibit high reproductive and growth rates and low mortality rates in the laboratory.

## Methods

### *Melanoides* collection and culture

In May 2011, we collected specimens of *Melanoides tuberculata* by hand from Volusia Blue Spring, a first magnitude spring in Central Florida. The

spring discharges  $4.6 \text{ m}^3 \text{ s}^{-1}$  (range =  $1.8\text{--}6.1 \text{ m}^3 \text{ s}^{-1}$ , Scott et al. 2004) and the substrate is limestone, sand, or silty sand. The run is comparatively wide (20–30 m) and short (620 m) and the tree canopy covers no more than half the width of the run. The water is cool ( $21^\circ\text{C}$ ), possesses moderate conductivity ( $1400 \mu\text{S cm}^{-1}$ , range =  $1060\text{--}2840 \mu\text{S cm}^{-1}$ ), and is oligotrophic to mesotrophic (Scott et al. 2004). In recent years, dense beds of *Oscillatoria* sp. and *Vaucheria* sp. have developed in areas with lower anthropogenic disturbance.

We collected the snails randomly from one location known to regularly possess *M. tuberculata* and immediately transported the snails back to the laboratory in a 5 gallon bucket of spring water. We measured these snails for total shell length with digital calipers to the nearest 0.1 mm and isolated 40 within a size range of 16–23.8 mm. We put each of these individuals into their own 1 L plastic jar and arranged the jars haphazardly. The jars contained 0.5 L of spring water and a limestone rock collected from Volusia Blue Spring. The snails were cultured first in natural light from laboratory windows (3 months) under continuous aeration and later under the fluorescent light of a second laboratory (5 months). We fed the snails fresh, boiled spinach ad libitum and changed their water every two weeks for the first three months. After the first three months, the containers had been colonized by abundant algae, upon which the snails fed, and we supplemented this food source with boiled spinach approximately once a month. Although this change in feeding regime may have affected growth, the regular production of copious feces after the reduction in spinach supplementation indicated that the snails were feeding on the periphyton growing in the jars. We measured the shell lengths of these individuals every other day for the first two weeks and then when the water was changed for the rest of the study. After these individuals began to reproduce in early June, we collected, counted, and measured their first clutches of offspring. We only counted, and did not measure or retain, successive clutches. From the first clutches produced by 18 of the original snails, we randomly selected and isolated three offspring from each individual, put them into plastic Solo® cups of 300 ml of spring water, and randomly arranged the cups. Although the cups were smaller than the adult containers, the snail size:water volume was comparable between the adults and the offspring (500 mL:22.8 mm vs.

300 mL:14.3 mm). We measured, fed, and changed the water of the offspring when we measured the adults. Therefore, the juvenile snails received bimonthly spinach ad libitum until the algae had colonized the containers (~5 months), after which spinach supplementation was reduced to approximately monthly. We followed the F1 generation for longer than the adults, until they began to reproduce after a total of 10 months.

We also estimated mortality of *M. tuberculata* juveniles resulting from crayfish predation in the laboratory. We collected three crayfish (*Procambarus* sp., all 6–8 cm in length) from a local retention pond and held them under continuous aeration within 3 L glass jars, half-filled with water from the retention pond from which they were collected. We added no substrata to the jars. To prepare a trial, we collected newly released *M. tuberculata* from the cultured population and measured and sorted them into total shell length size classes (1–2 mm, 2–3 mm, 3–4 mm). We added ten individuals from each size class to each of the three jars and allowed the crayfish to feed for 3 days. This crayfish:snail ratio was much higher than the ratio in the field, as there would have to be >175 crayfish m<sup>-2</sup> to achieve the same ratio with the density of ~5300 small (≤ 4 cm) snails m<sup>-2</sup> in the field. Therefore, the difference in density between the laboratory measurements and the field should have made the mortality estimates conservative, although the lack of substrate may have reduced crayfish search times. At the end of the incubation period, we collected, counted, and measured the shell lengths of the remaining snails. These mortality estimates were replicated twice with three crayfish in each trial.

Finally, we collected specimens of *Melanoidea tuberculata* from Volusia Blue Spring again in May 2012. These snails were collected using a net with 1 mm mesh to better capture the smallest individuals. Using the net, we collected all material on the substrate and the sand/silt down to a depth of approximately 5 cm (after which no more snails appeared to be collected) and within the area of a 1 m<sup>2</sup> quadrat. We dumped each net collection into a 1 mm sieve to filter out the sand and silt before immediate transport to the laboratory in a 5 gallon bucket of spring water. From this 1 m<sup>2</sup> sample, we sorted out and measured the total shell length of all the individuals with digital calipers to the nearest 0.1 mm.

### Statistics

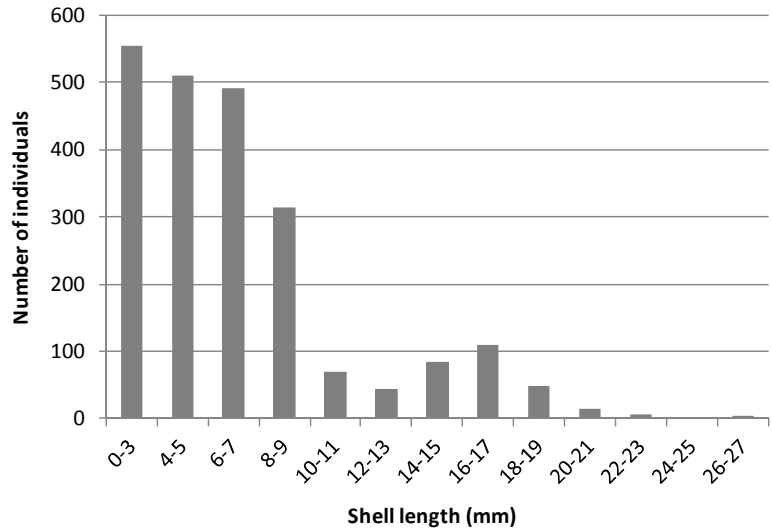
Measures of growth and reproduction were normally distributed, so we analyzed these parameters with correlation and linear regression. We also used multiple regression to predict offspring growth, with maternal size, maternal growth, and maternal reproductive output as predictive variables. To determine whether crayfish snail consumption was size-specific, the number of snails remaining in each of the three size classes after the three day incubation period was compared with a Kruskal-Wallis test and the size of the remaining snails was compared with the initial mean size with a t-test. Finally, we used a monomolecular model to describe *M. tuberculata* growth in the laboratory after Pointier et al. (1992). All statistics were run with SPSS 19.0 (SPSS, Inc. 2010).

We used the census data from the May 2012 sample and the demographic parameters calculated from the laboratory cultures to create a static life table. The age of the census snails was estimated from the monomolecular growth curve calculated in the laboratory from measurements of adults and F1 offspring. The number of females in each age class was adjusted to represent 92.6% of the total census (the proportion of the 40 snails cultured in the laboratory that were female). Given that birth rate was unrelated to maternal size in the laboratory and that we had cultured a range of sizes, we used the average birth rate of all individuals for all mature snails to estimate offspring production in the life table. From the life table, we estimated generation time (G), instantaneous growth rate (r), net reproductive rate (R<sub>0</sub>), finite rate of increase (λ), and total reproductive output (R<sub>0</sub>) of the Volusia Blue Spring *M. tuberculata* population. Finally, we used the estimate of the total number of offspring produced to estimate the mortality rate of newly released offspring as a proportion of the number of age-0 individuals collected.

### Results

The May 2012 Volusia Blue Spring *M. tuberculata* sample indicated that the population was dense (~2,200 individuals m<sup>-2</sup>) and only 13% of the snails were mature (Figure 1). Of the 40 individuals that we brought into the laboratory for culture in May 2011, 7.5% were male and all were mature based on their size (Table 1). Within two weeks, all of the females had released their first clutch, which was the largest clutch observed

**Figure 1.** Size frequency distribution for *Melanoides tuberculata* collected from Volusia Blue Spring in May 2012. Size was represented as total shell length (mm).



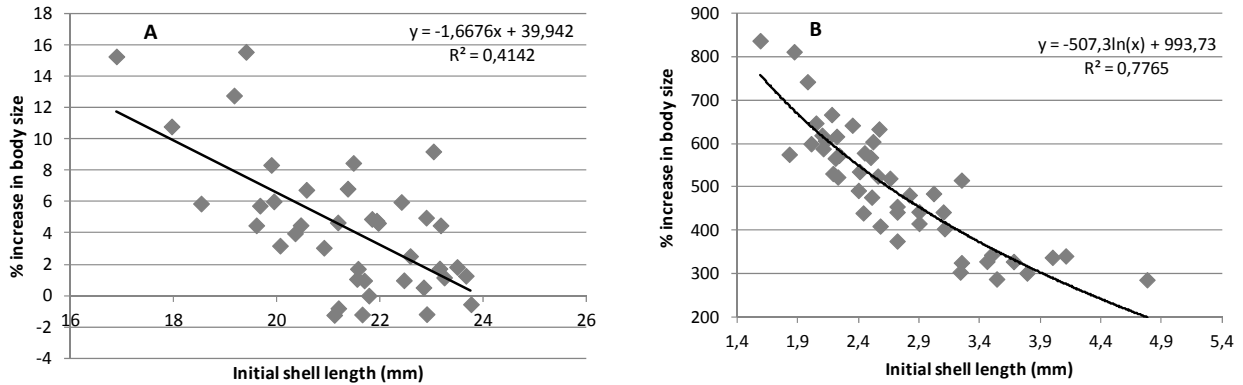
**Table 1.** Demographic parameters of Volusia Blue Spring and of West Indies *Melanoides tuberculata* grown in the laboratory. Values indicate mean, standard deviation, and range. West Indies *M. tuberculata* demographic parameters were taken from Facon et al. (2005).

Parameter	Volusia Blue Spring	West Indies
Size of field collected snails	10.2 ± 5.2 (2.1–36.0) mm n = 2,230	
Initial size of adults raised in the laboratory	21.3 ± 1.6 (16.9–23.8) mm n = 40	
Growth rate of adults	0.0050 ± 0.0043 (0–0.017) mm day <sup>-1</sup> n = 40	
Birth rate	0.45 ± 0.20 (0.15–0.97) offspring day <sup>-1</sup> n = 37	0.87 (0.30–1.5) offspring day <sup>-1</sup>
Size of F1 individuals when released	2.47 ± 0.060 (1.6–3.6) mm n = 54	2.31 (1.7–3.2) mm
Maximum growth rate of F1 individuals	0.12 (0.022–0.12) mm day <sup>-1</sup> n = 54	0.20 (0.17–0.25) mm day <sup>-1</sup>
Size at first reproduction	14.8 ± 0.8 (13.2–16.1) mm n = 52	16.4 (13–18) mm
Age at first reproduction for F1 individuals	217 days n = 52	116 (110–120) days
Size of first clutch of F1	2.37 ± 1.54 (1–6) individuals n = 37	

for each snail during the study. Despite the uncharacteristically large size of the first clutch, the size of this clutch predicted the future fecundity of individuals, as the initial clutch was correlated significantly with total reproductive output ( $r^2 = 0.25$ ,  $F = 11.83$ ,  $df = 36$ ,  $p = 0.002$ ). The birth rate of *M. tuberculata* was high and these reproducing snails grew slowly (Table 1). Maternal growth rate was positively correlated with the adult's body size at the start of the study ( $r^2 = 0.23$ ,  $F = 11.38$ ,  $df = 39$ ,  $p = 0.002$ , Figure 2A), but not with total reproductive output ( $F =$

0.21,  $df = 36$ ,  $p = 0.65$ ). Surprisingly, the birth rate was not related to the size of the adult ( $F = 1.69$ ,  $df = 39$ ,  $p = 0.20$ ) nor to the growth of the adult ( $F = 0.008$ ,  $df = 39$ ,  $p = 0.93$ ). Over the course of the study, the 37 females in culture produced 2816 offspring.

Most of the 54 offspring (96.3%) isolated for growth measurements survived to adulthood. The two offspring that perished both had shell deformities that reduced the size of the aperture and they died within a month of birth. Mean offspring shell length was  $2.47 \pm 0.060$  mm



**Figure 2.** The relationship of body size to growth for mature *Melanooides tuberculata* (A) and their offspring (B) grown in the laboratory. Size was represented as total shell length.

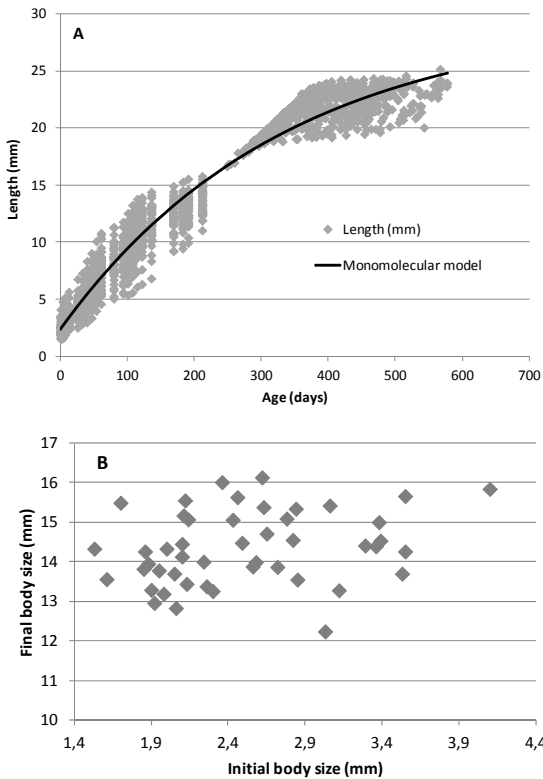
**Table 2.** Static life table calculated from the Volusia Blue Spring census of *Melanooides tuberculata* in 2012. Lengths at a given age were predicted from the monomolecular model calculated from laboratory data on growth rates. Census data at a particular age was used to determine demographic parameters:  $l_x$  (survivorship),  $b_x$  (birth rate),  $V_x$  (mean birth rate per individual), and  $x l_x b_x$  (age specific individual birth rate). To determine the survival of the individuals from their release to our collection, the number of age-0 individuals was predicted from the  $R_0$  (net reproductive rate).

Age (months)	Length (mm)	Census (individuals)	$l_x$	$b_x$	$V_x$	$x l_x b_x$
0	2.0	4198		0	0	0
1	4.6	1100	0.19	0	0	0
2	6.8	763	0.12	0	0	0
3	8.7	86	0.11	0	0	0
4	10.5	55	0.031	0	0	0
5	12.2	95	0.012	14.7	0.17	0.87
6	13.7	72	0.0071	14.7	0.10	0.63
7	15.0	26	0.0095	14.7	0.14	0.98
8	16.3	16	0.016	14.7	0.21	1.90
9	17.5	4	0.013	14.7	1.15	1.70
10	18.5	2	0.014	14.7	1.21	2.00
11	19.5	2	0.0048	14.7	0.42	0.77
12	20.3	2	0.0024	14.7	0.21	0.42
>12	21+	9	0.0036	14.7	0.32	0.68

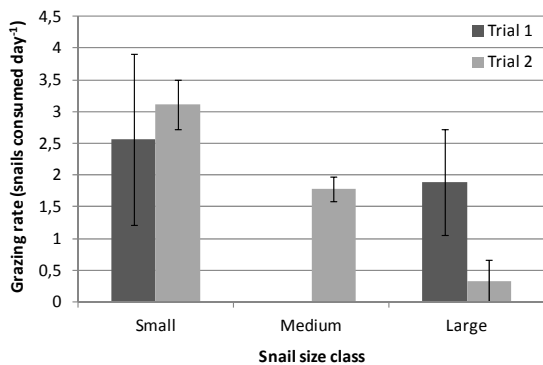
when released from the female (Table 1) and this initial size was unrelated to maternal body size ( $F = 0.244$ ,  $df = 46$ ,  $p = 0.62$ ), maternal growth ( $F = 1.65$ ,  $df = 46$ ,  $p = 0.21$ ), or to maternal reproductive output ( $F = 3.11$ ,  $df = 46$ ,  $p = 0.084$ ). The offspring grew quickly and their growth was negatively correlated with initial body size, both absolutely ( $r^2 = 0.15$ ,  $p = 0.008$ ) and as a percentage of initial size ( $r^2 = 0.87$ ,  $p < 0.001$ , Figure 2B). Like the initial size, the growth of the offspring was unrelated to maternal size ( $F = 0.62$ ,  $df = 46$ ,  $p = 0.44$ ), maternal growth ( $F = 0.79$ ,  $df = 46$ ,  $p = 0.38$ ), total maternal reproductive output ( $F = 0.29$ ,  $df = 46$ ,  $p = 0.60$ ), or to production of F2 offspring ( $F = 3.09$ ,  $df = 46$ ,  $p = 0.085$ ). Their growth

slowed with increasing age and size ( $F = 7288$ ,  $df = 1836$ ,  $p < 0.001$ , Figure 3A). However, because the smaller individuals grew more rapidly, all individuals approached the same mean size by maturity, such that the relationship between initial body size and later body size disappeared by the end of the study ( $F = 3.12$ ,  $df = 46$ ,  $p = 0.084$ , Figure 3B). These offspring reached maturity, as indicated by release of the first clutch, by  $14.8 \pm 0.81$  mm, although the smallest snail to release offspring was 13.2 mm in length (Table 1).

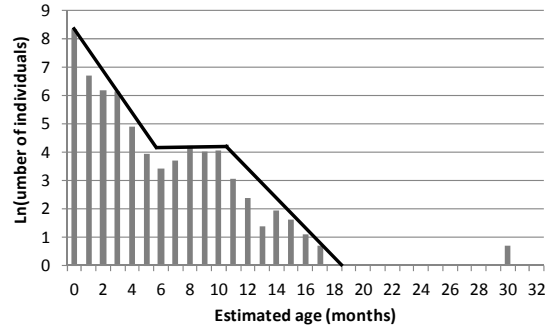
When presented with juvenile *M. tuberculata*, all three crayfish rapidly attacked them. However, most attacks were unsuccessful, as suggested by the regular sounds of snails dropping to the bottom



**Figure 3.** Size dependent growth of *Melanoides tuberculata* in the laboratory. The growth curve indicates a reduction in growth with age (A) and all individuals grew to approximately the same size by maturity, regardless of initial body size (B). Size was represented as total shell length.



**Figure 4.** Size selective consumption of snails by *Procambarus* sp. The bars represent the grazing rate on the two (trial 1) to three (trial 2) size classes of *M. tuberculata*. Error bars represent standard deviations. Small snails were represented by 1–2 mm individuals; medium snails by 2–3 mm individuals; and large snails by 3–4 mm individuals. Size was represented as total shell length.



**Figure 5.** The distribution of individuals with respect to age as estimated from the monomolecular model calculated in the laboratory. The black lines represent differences in the estimated mortality rates at different ages.

of the jars and observation of intact dropped snails. Despite the apparently low success rate of attacks, the crayfish consumed  $4.9 \pm 0.96$  to  $5.1 \pm 0.50$  snails  $\text{day}^{-1}$  and they preyed upon the smallest snails preferentially ( $H = 7.2$ ,  $k = 3$ ,  $p = 0.026$ , Figure 4). Although the first trial yielded no significant difference between grazing rates of crayfish on large and small snails, the average size of the snails was significantly larger after the three day incubation period in the second trial ( $t = -6.30$ ,  $df = 10$ ,  $p < 0.0002$ ).

The static life table calculated from the census data indicated that mortality rates on juvenile individuals likely was high (Table 2). The majority of the snails were immature and, if the population that produced those offspring was approximately the same size as the census, the census data suggested that roughly 75% of the offspring produced would not survive a month (1100 age-1 month individuals/4198 age-0 individuals = 26% survival, Table 2, Figure 5). The data also suggested that, of those that survive the first month, only approximately 10% would survive to maturity. Survival of snails larger than 23 mm also appeared to be extremely low, suggesting high mortality rates for the largest snails as well (Figure 5).

## Discussion

As expected, *M. tuberculata* was abundant in Volusia Blue Spring, most of the individuals collected in the field were immature, and this species' growth and reproductive rates in the laboratory were high. These characteristics, in combination with its proclivity to move with the aquarium trade and its broad tolerances and

feeding preferences (Madsen 1992; Rader et al. 2003; Coat et al. 2009), may help to explain its ability to colonize and, in some cases, dominate the snail assemblages of systems all over the subtropical and tropical world (Pointier 1993; Pointier et al. 1993a; Pointier et al. 1994; El-Kady et al. 2000; Guimarães et al. 2001; Karatayev et al. 2009). Future research should determine how natural variation affects the birth, growth, and death rates of this species in the wild. Furthermore, the species' success also may be the result of repeated introductions; even established populations may be regularly re-inoculated (G. Warren, pers. comm.), particularly considering that even a casual internet search provides a wealth of aquarium sources on culture, sale, and trade of *M. tuberculata* and that Florida clearly has an influx of aquarium escapees (Padilla and Williams 2004).

In this study, the population density of *M. tuberculata* (~2,200 individuals m<sup>-2</sup>) was moderate relative to population density estimates made in South Florida in the 1960's (133 - 37,000 individuals m<sup>-2</sup>, Roessler et al. 1977) and to other parts of the world (100 - 13,400 individuals m<sup>-2</sup> in Lake Chad and Martinique, respectively, Lévêque 1971; Pointier et al. 1989). Specimens of *M. tuberculata* from Volusia Blue Spring grew at a similar or slower rate than laboratory-reared morphs from the West Indies (Table 1, Pointier et al. 1993b, Facon et al. 2005) and from Israel (shell length at 300 days, or  $S_{300} = \sim 17$  mm, Livshits and Fishelson 1983). As a result of the relatively slow growth rate, the Florida snails reproduced later, but at a smaller size than the West Indies snails (Table 1). Furthermore, the mean size of liberated offspring was slightly larger than those from the West Indies, but the smallest snails liberated in our study were considerably smaller than the mean for those from the West Indies (1.61 mm). It is likely that in our cultures, the larger offspring were overlooked at the time of release and therefore, their liberation size was overestimated.

The slower growth of our Florida spring *M. tuberculata* specimens relative to snails isolated from the West Indies may have been due to a combination of lower culture temperature, the reduction in spinach supplementation in the latter part of the experiment, and differences in life history characteristics of the morph in question. The temperature of the West Indies cultures was not reported by Pointier et al. (1992) or by Facon et al. (2005), but their surface water temperatures were undoubtedly higher than the year-round 21°C of Volusia Blue Spring and our

**Table 3.** Life table parameters for Volusia Blue Spring and West Indies *Melanooides tuberculata*. For Volusia Blue Spring, daily rates of  $G$  = generation time,  $r$  = instantaneous rate of increase,  $\lambda$  = finite growth rate are presented with  $R_0$  = net reproductive rate. Pointier et al. (1992) presented data in fortnights; therefore, data presented in parentheses for Volusia Blue Spring represent a conversion of the daily values to values in fortnights.

Parameter	Volusia Blue Spring	West Indies
$G$	8.27 (16.54)	23.1–33.6
$R_0$	1.20	
$r$	0.0098 (0.094)	0.14–0.24
$\lambda$	1.01 (1.10)	1.15–1.28

laboratory. Second, our snail containers were colonized by many species, including abundant algae upon which the snails apparently fed and we reduced spinach supplementation. Interestingly, one species of algae, *Vaucheria* sp., became superabundant in the containers, perhaps due to a lack of snail foraging on this species. This species is a nuisance alga that produces extensive algal mats in Volusia Blue Spring. Finally, it is possible that the Volusia Blue Spring morph used in this study is not one of the morphs that invaded the West Indies, which varied in life history characteristics themselves (Facon et al. 2005). Facon et al. (2003) identified morphs from all over the world and the morphs that they analyzed from Florida matched morphs from Indonesia and Brunei, although certainly it is possible that their subsample only picked up one of several morphs that has invaded Florida.

The life table estimates of population growth rates were extremely rough. It is likely that birth rates calculated in the laboratory overestimated field birth rates, even given the reduction in spinach supplementation in the latter five months of the study. Furthermore, the monomolecular growth curve adequately described the growth of snails in the laboratory; however, the asymptote for this curve was much smaller than the largest snail observed in the field (29 mm vs. 39 mm) and the laboratory growth curve would predict that the largest snail in the field would be infinitely old. Therefore, it is likely that we underestimated growth rates. However, the life table parameters that we calculated from our field census/laboratory growth and birth rates were comparable to those calculated for West Indies snails by Pointier et al. (1992, Table 3). Given its broad ecological tolerances (Mitchell and Brandt 2005; Coat et al. 2009; Murray et al. 2010) and its extreme fecundity, it would appear

that *M. tuberculata* has the potential to rapidly expand its population in new suitable habitats. Although it is likely that the mortality rates calculated from the cultures (3.7%) and from the crayfish predation study underestimate mortality, two crayfish feeding within 1 m<sup>2</sup> could consume enough age-0 snails to account for the loss of snails between birth and one month. It also is likely that other invertebrates and fish consume juvenile snails and undoubtedly contribute to the loss of larger immature individuals. Predation by musk turtles, which have been shown to prey heavily on snails (Berry 1975), and raccoons, for which widespread incidence of trematode infection indicates snail predation (Hamir et al. 1993), may account for the high mortality in the larger size classes.

Regardless of the relatively slow growth and low fecundity that we observed in this study compared to the growth of West Indies morphs, our Volusia Blue Spring population was extremely fecund and matured quickly in the larger context of proliferation in Florida springs. Even if our rough life table overestimates the population growth rate, due to underestimates in mortality and overestimates in growth and fecundity, the species clearly has the potential to dominate new habitats, as has been evident from its displacement of native hydrobes in the West Indies (Pointier 1993; Pointier et al. 1993a) and in South America (Pointier et al. 1994; Guimarães et al. 2001; Giovanelli et al. 2005; Karatayev et al. 2009) and rapid spread in the Great Basin in the western US (Rader et al. 2003). This study, and others like it, highlight the need for greater control over the aquarium trade.

## Acknowledgements

We would like to thank Blue Spring State Park for their cooperation in obtaining snails and water. We also would like to thank Dr. Terry Farrell for his helpful comments on the manuscript, and the anonymous reviewers who greatly improved the manuscript through their contributions.

## References

- Alonso A, Castro-Diez P (2008) What explains the invading success of the aquatic mud snail *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca)? *Hydrobiologia* 614: 107–116, <http://dx.doi.org/10.1007/s10750-008-9529-3>
- Ben-Ami F, Heller J (2005) Spatial and temporal patterns of parthenogenesis and parasitism in the freshwater snail *Melanooides tuberculata*. *Journal of Evolutionary Biology* 18: 138–146, <http://dx.doi.org/10.1111/j.1420-9101.2004.00791.x>
- Berry JF (1975) The population effects of ecological sympatry on musk turtles in Northern Florida. *Copeia* 1975(4): 692–701, <http://dx.doi.org/10.2307/1443321>
- Bogea T, Cordeiro F, Silva de Gouveia J (2005) *Melanooides tuberculatus* (Gastropoda: Thiaridae) as intermediate host of Heterophyidae (Trematoda: Digenea) in Rio de Janeiro metropolitan area, Brazil. *Revista do Instituto de Medicina Tropical de São Paulo* 47(2): 87–90, <http://dx.doi.org/10.1590/S0036-46652005000200005>
- Clench W (1969) *Melanooides tuberculata* (Muller) in Florida. *Nautilus* 83: 72
- Coat S, Monti D, Bouchon C, Lepoint G (2009) Trophic relationships in a tropical stream food web assessed by stable isotope analysis. *Freshwater Biology* 54(5): 1028–1041, <http://dx.doi.org/10.1111/j.1365-2427.2008.02149.x>
- Cowie R (2001) Invertebrate invasions on Pacific Islands and the replacement of unique native faunas: a synthesis of the land and freshwater snails. *Biological Invasions* 3: 119–136, <http://dx.doi.org/10.1023/A:1014529019000>
- Derraik J (2008) The potential significance to human health associated with the establishment of the snail *Melanooides tuberculata* in New Zealand. *Journal of the New Zealand Medical Association* 121(1280): 25–32
- Duggan I (2002) First record of a wild population of the tropical snail *Melanooides tuberculata* in New Zealand natural waters. *New Zealand Journal of Marine and Freshwater Research* 36: 825–829, <http://dx.doi.org/10.1080/00288330.2002.9517135>
- Dundee D, Paine A (1977) Ecology of the snail, *Melanooides tuberculata* (Muller) intermediate host of the human liver fluke (*Opisthorchis sinensis*) in New Orleans, Louisiana. *The Nautilus* 91: 17–20
- El-Kady G, Shoukry A, Reda L, El-Badri Y (2000) Survey and population dynamics of freshwater snails in newly settled areas of the Sinai Peninsula. *Egyptian Journal of Biology* 2: 42–48
- Facon B, Pointier J, Glaubrecht M, Poux C, Jarne P, David P (2003) A molecular phylogeography approach to biological invasions of the New World by parthenogenic Thiarid snails. *Molecular Ecology* 12: 3027–3039, <http://dx.doi.org/10.1046/j.1365-294X.2003.01972.x>
- Facon B, Jarne P, Pointier J, David P (2005) Hybridization and invasiveness in the freshwater snail *Melanooides tuberculata*: hybrid vigour is more important than increase in genetic variance. *Journal of Evolutionary Biology* 18: 524–535, <http://dx.doi.org/10.1111/j.1420-9101.2005.00887.x>
- Fuller P, Nico L, Williams, J (1999) Nonindigenous Fishes Introduced into Inland Waters of the United States. Special Publication 27. American Fisheries Society, Bethesda, MD, 613 pp
- Genner M, Michel E, Erpenbeck D, De Voogd N, Witte F, Pointier J (2004) Camouflaged invasion of Lake Malawi by an Oriental gastropod. *Molecular Ecology* 13: 2135–2141, <http://dx.doi.org/10.1111/j.1365-294X.2004.02222.x>
- Giovanelli A, Vieira M, Coelho da Silva C (2005) Interaction between the intermediate host of schistosomiasis in Brazil, *Biomphalaria glabrata* (Say, 1818) and a possible competitor, *Melanooides tuberculata* (Muller, 1774): A field study. *Journal of Molluscan Studies* 71: 7–13, <http://dx.doi.org/10.1093/mollus/eyi004>
- Guimarães C, de Souza C, Soares D (2001) Possible competitive displacement of planorbids by *Melanooides tuberculata* in Minas Gerais, Brazil. *Memórias do Instituto Oswaldo Cruz* 96: 173–176, <http://dx.doi.org/10.1590/S0074-02762001000900027>
- Hamir AN, Snyder DE, Hanlon CA, Rupprecht CE (1993) Trematode (*Phagicola* sp.)-induced mesenteric lymphadenitis and enteritis in raccoons (*Procyon lotor*). *Veterinary Pathology* 30: 373–376
- Karatayev A, Burlakova L, Karatayev V, Padilla D (2009) Introduction, distribution, spread, and impacts of exotic freshwater gastropods in Texas. *Hydrobiologia* 619(1): 181–194, <http://dx.doi.org/10.1007/s10750-008-9639-y>



- Keller RP, Lodge DM (2007) Species invasions from commerce in live aquatic organisms: problems and possible solutions. *BioScience* 57: 428–436, <http://dx.doi.org/10.1641/B570509>
- Kolar C, Lodge D (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution* 16(4): 199–204, [http://dx.doi.org/10.1016/S0169-5347\(01\)02101-2](http://dx.doi.org/10.1016/S0169-5347(01)02101-2)
- Lévêque C (1971) Equation de Von Bertalanffy et croissance des mollusques benthiques du lac Tchad. *Cahiers de l'O.R.S.T.O.M., serie Hydrobiologie* 5: 263–283
- Livshits G, Fishelson L (1983) Biology and reproduction of the freshwater snail *Melanooides tuberculata* (Gastropoda: Prosobranchia) in Israel. *Israel Journal of Zoology* 32: 21–35
- Marchetti M, Moyle P, Levine R (2004) Invasive species profiling? Exploring the characteristics of non-native fishes across invasion stages in California. *Freshwater Biology* 49: 646–661, <http://dx.doi.org/10.1111/j.1365-2427.2004.01202.x>
- Madsen H (1992) Food selection by freshwater snails in the Gezira irrigation canals, Sudan. *Hydrobiologia* 228: 203–217, <http://dx.doi.org/10.1007/BF00006587>
- McMahon RF (2002). Evolutionary and physiological adaptation of aquatic invasive animals: r selection versus resistance. *Canadian Journal of Fisheries and Aquatic Science* 59: 1235–1244, <http://dx.doi.org/10.1139/f02-105>
- Mitchell A, Salmon M, Huffman D, Goodwin A, Brandt T (2000) Prevalence and pathogenicity of a heterophyid trematode infecting the gills of an endangered fish, the fountain darter, in two central Texas spring-fed rivers. *Journal of Aquatic Animal Health* 12: 283–289, [http://dx.doi.org/10.1577/1548-8667\(2000\)012<0283:PAPOAH>2.0.CO;2](http://dx.doi.org/10.1577/1548-8667(2000)012<0283:PAPOAH>2.0.CO;2)
- Mitchell AJ, Brandt TM (2005) Temperature tolerance of red-rim Melania, *Melanooides tuberculatus*, an exotic aquatic snail established in the United States. *Transactions of the American Fisheries Society* 134: 126–131, <http://dx.doi.org/10.1577/FT03-178.1>
- Murray H (1964) *Tarebia granifera* and *Melanooides tuberculatus* in Texas. *Bulletin of the American Malacological Union* 1964: 15–16
- Murray JB, Wingard GL, Phillips EC (2010) Distribution of the non-native gastropod *Melanooides tuberculatus* in Biscayne National Park, Florida. US Geological Survey Open File Report 2010–1126
- Padilla D, Williams S (2004) Beyond ballast water: aquarium and ornamental trades as sources of invasive species in aquatic ecosystems. *Frontiers in Ecology and the Environment* 2(3): 131–138, [http://dx.doi.org/10.1890/1540-9295\(2004\)002\[0131:BBWAAO\]2.0.CO;2](http://dx.doi.org/10.1890/1540-9295(2004)002[0131:BBWAAO]2.0.CO;2)
- Pointier J, Delay B, Toffart J, Lefevre M, Romero-Alvarez, R (1992) Life history traits of three morphs of *Melanooides tuberculata* (Gastropoda: Thiaridae), an invading snail in the French West Indies. *Journal of Molluscan Studies* 58: 415–423, <http://dx.doi.org/10.1093/mollus/58.4.415>
- Pointier JP (1993) The introduction of *Melanooides tuberculata* (Mollusca: Thiaridae) to the island of Saint Lucia (West Indies) and its role in the decline of *Biomphalaria glabrata*, the snail intermediate host of *Schistosoma mansoni*. *Acta Tropica* 54(1): 13–18, [http://dx.doi.org/10.1016/0001-706X\(93\)90064-I](http://dx.doi.org/10.1016/0001-706X(93)90064-I)
- Pointier JP, Guyar A, Mosser A (1989) Biological control of *Biomphalaria glabrata* and *B. straminea* by the competitor snail *Thiara tuberculata* in a transmission site of schistosomiasis in Martinique, French West Indies. *Annals of Tropical Medicine and Parasitology* 83: 263–269
- Pointier J, Therón A, Borel G (1993a) Ecology of the introduced snail *Melanooides tuberculata* (Gastropoda: Thiaridae) in relation to *Biomphalaria glabrata* in the marshy forest zone of Guadeloupe, French West Indies. *Journal of Molluscan Studies* 59:421–428, <http://dx.doi.org/10.1093/mollus/59.4.421>
- Pointier J, Thaler L, Pernot A, Delay B (1993b) Invasion of the Martinique island by the parthenogenetic snail *Melanooides tuberculata* and the succession of morphs. *Acta Oecologica* 14(1): 33–42
- Pointier J, Incani R, Balzan C, Chrosiecchowski P, Prypchan S (1994) Invasion of the rivers of the littoral central region of Venezuela by *Thiara granifera* and *Melanooides tuberculata* (Mollusca: Prosobranchia: Thiaridae) and the absence of *Biomphalaria glabrata*, snail host of *Schistosoma mansoni*. *The Nautilus* 107(4): 124–128
- Rader R, Belk M, Keleher M (2003) The introduction of an invasive snail (*Melanooides tuberculata*) to spring ecosystems of the Bonneville Basin, Utah. *Journal of Freshwater Ecology* 18(4): 647–657, <http://dx.doi.org/10.1080/02705060.2003.9664007>
- Roessler MA, Beardsley GL, Tabb DC (1977) New records of the introduced snail, *Melanooides tuberculata* (Mollusca: Thiaridae) in south Florida. *Florida Scientist* 40: 87–94
- Sakai A, Allendorf F, Holt J, Lodge D, Molofsky J, With K, Baughman S, Cabin R, Cohen J, Ellstrand N, McCauley D, O'Neill P, Parker I, Thompson J, Weller S (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics* 32: 305–332, <http://dx.doi.org/10.1146/annurev.ecolsys.32.081501.114037>
- Scholz T, Salgado-Maldonado G (2000) The introduction and dispersal of *Centrocestus formosanus* (Nishigori, 1924) (Digenea: Heterophyidae) in Mexico: a review. *American Midland Naturalist* 43(1): 185–200, [http://dx.doi.org/10.1674/0003-0031\(2000\)143\[0185:TIADOC\]2.0.CO;2](http://dx.doi.org/10.1674/0003-0031(2000)143[0185:TIADOC]2.0.CO;2)
- Scott TM, Means GH, Meegan RP, Means RC, Upchurch SB, Copeland RE, Jones J, Roberts T, Willet A (2004) Springs of Florida. Florida Geological Survey, Bulletin No. 66
- SPSS, Inc. (2010) SPSS Statistics, Version 19. IBM, Armonk, New York, USA
- USGS (2012) United States Geological Survey Nonindigenous Aquatic Species Program. <http://nas.er.usgs.gov> (Accessed 15 July 2012)