The estimation of growth dynamics for *Pomacea maculata* from hatchling to adult

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**Abstract.** *Pomacea maculata* is a relatively new invasive species to the Gulf Coast region and potentially threatens local agriculture (rice) and ecosystems (aquatic vegetation). The population dynamics of *P. maculata* have largely been unquantified, and therefore, scientists and field-workers are ill-equipped to accurately project population sizes and the resulting impact of this species. We studied the growth of *P. maculata* ranging in weights from 6 to 105 g, identifying the sex of the animals when possible. Our studied population had a 4:9 male:female sex ratio. We present the findings from initial analysis of the individual growth data of males and females, from which it was apparent that females were generally larger than males and that small snails grew faster than larger snails. Since efforts to characterize the male and female growth rates from individual data do not yield statistically supported estimates, we present the estimation of several parameterized growth rate functions within a population-level mathematical model. We provide a comparison of the results using these various growth functions and discuss which best characterizes the dynamics of our observed population. We conclude that both males and females exhibit biphasic growth rates, and thus, their growth is size-dependent. Further, our results suggest that there are notable differences between males and females that are important to take into consideration in order to accurately model this species’ population dynamics. Lastly, we include preliminary analyses of ongoing experiments to provide initial estimates of growth in the earliest life stages (hatchling to 6 g).

**Key words:** apple snails; growth dynamics; invasive species; mathematical modeling; population dynamics; sex ratio; statistical inference.

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**INTRODUCTION**

Invasive species are a main cause of biodiversity loss worldwide (Clavero and Garcia-Berthou 2005, Davis 2013). Invasive animals generally reproduce rapidly (Lodge 2001) and outcompete native species for food and habitat (Kolar and Lodge 2001), and once established, they are often very difficult to remove. Today, alien invasion as a cause for species endangerment and extinction is second only to habitat loss (Lowe et al. 2000).

Snails of the genus *Pomacea* are nicknamed “apple snails” as they are globular and reach the size of an apple (Cowie et al. 2006). They have attracted much attention due to their negative ecological impact (Dancel and Joshi 2000, Cowie 2002, Sin 2003, Joshi 2005, Cowie et al. 2006). For example, after *Pomacea* were first introduced into Taiwan between 1979 and 1981, 17,000 ha (1 ha = 100 acres, or 10,000 square meters) of rice and other crops had been infested by 1982. The area of infestation increased to 171,425 ha by 1986 (Mochida 1991). In 1982, the lost rice farming revenue was estimated as US $2.7 million, and increased to US $30.9 million in 1986 (Mochida 1991). Huge areas were treated with
pesticides (103,350 ha in 1986) at an additional cost. The spread of *Pomacea* in the Philippines (Adalla and Morallo-Rejesus 1989, Mochida 1991, Anderson 1993, Litsinger and Estano 1993, Naylor 1996) was much more rapid and resulted in more serious damage, with rice losses ranging from 5% to 100%, depending on locality and population density of the apple snails. In Japan, the cost of control in just 176 ha infested crops was US $64,385 (Mochida 1991).

Apple snails are also a concern due to their ecological impacts (Lach et al. 2000, Carlsson et al. 2004, Carlsson and Lacrousiere 2005, Carlsson and Bronmark 2006, Cowie et al. 2006, Boland et al. 2008). They feed on aquatic submerged plants, and overgrazing can greatly alter the natural balance of the local ecosystem (Carlsson et al. 2004). For example, in Thailand, the introduction of apple snails changed the habitat from a clear macrophyte-dominated system into a turbid plankton-dominated system (Carlsson et al. 2004). In the Philippines, native *Pila* are reported to have declined as a result of extensive application of pesticides against introduced *Pomacea* (Anderson 1993). In Hawaii, *Pomacea canaliculata* have rapidly spread to non-agricultural habitats (Lach and Cowie 1999). It has also been reported that *P. canaliculata* eat amphibian egg masses (Karraker and Dudgeon 2014). The available literature warns that apple snails are also a potential vector for disease transmission to humans and animals (Wallace and Rosen 1969, Keawjam 1986, Mochida 1991, Halwart 1994, Albrecht et al. 1996, Naylor 1996, Rawlings et al. 2007, Wang et al. 2007).

There are several unanswered questions regarding aspects of the life cycle of apple snails, an understanding of which is necessary to make accurate population projections and to anticipate the potential impact of control measures. Indeed, many researchers are currently working to characterize the processes affecting the population dynamics of various *Pomacea* species. Two such examples can be found in Coelho et al. (2012), in which the effects of food supply and temperature were studied on breeding in *Pomacea bridgesii*, and in Meyer-Willerer and Santos-Soto (2006), which is a study of the efficiency of *Pomacea patula* egg hatching and growth as a function of temperature and light intensity.

In this work, we focus on *Pomacea maculata*, which has been found in Louisiana and many other locations in the Gulf Coast region (USGS database n.d., https://nas.er.usgs.gov/queries/FactSheet.aspx?speciesID=2633). *Pomacea maculata* is currently on the 100 top invasive species list (Lowe et al. 2000). This species of apple snail has often been confused with *P. canaliculata* due to similar shell and egg mass morphology, and the group has recently undergone taxonomic revision (Rawlings et al. 2007, Hayes et al. 2012, Kyle et al. 2013). Snails used in this study have been DNA-tested and positively identified as *P. maculata*.

To the best of the authors’ knowledge, there are no studies of the growth rates or dynamics of *P. maculata*, or sex-dependent differences in these features. There have, however, been growth studies in the closely related *P. canaliculata* in which the authors established a temperature dependence on the feeding and growth rates of nine snails (Memon et al. 2011), and studies on the temperature effects on mortality rates in juveniles and adults (Seuffert and Martin 2016). Importantly, due to the temperature effects on the growth of apple snails, we report the growth rates in this study as specific to the temperatures at which the animals were kept during the period of observation.

In this paper, we discuss the insights gained into *P. maculata* population dynamics from observing the growth of closed populations raised in the laboratories and greenhouse of the Lafayet office of the USGS Wetland and Aquatic Research Center (WARC), which we describe in Methods: Growth experiments, along with ongoing efforts to measure smaller snails. We provide a brief description of a population-level mathematical model and inverse problem methodology in Methods: Mathematical model and methodology. We present our immediate findings and results from the direct analysis of the growth rates from individual records in Results: Sex ratio and weight difference between the sexes and Results: Growth rates: Direct calculation at individual level. In Results: Growth rate function estimation, we present the estimation of parameters in different models for growth rate functions and compare their suitability based on the implications of their biological interpretations as well as the minimized distance between the model and the data. Finally, we provide a rough initial estimate for the growth rates of snails in the earliest life stages in Results: Analysis of small snail data, based on preliminary data from ongoing efforts. In Conclusions and
Discussion, we conclude with a discussion of the results and suggestions for future studies within the broader context of developing a quantitative framework within which to study the population dynamics of *P. maculata*.

**METHODS**

In this section, we describe the methods by which the data were collected. All data discussed in this paper can be accessed at Sutton et al. (2017). We also present a succinct summary of the mathematical framework and related methodology used to make inferences about the characteristics of the apple snail growth dynamics.

**Growth experiments**

We describe the methods by which the snails’ growth was measured, and their sex identified. Our main data set spans a large range of sizes (6–105.1 g). These animals were measured over the span of several weeks and are our primary focus in the following analysis for the determination of growth dynamics. We also briefly describe ongoing efforts to study growth of apple snails in the earliest stages of life, which we use to provide a preliminary estimate of growth rates at weights below those in our main data set.

**Population 1: Juvenile and adult weights and sex**

To quantify *Pomacea maculata* growth dynamics, we recorded each snail’s weight, operculum length, and (when possible) sex, over a 13-week period (March–July 2013). The snails were kept in one large indoor tank and at a constant temperature of ≈ 21°C at WARC and fed leafy plants and vegetables from local grocery stores. This population came from individuals that were captured in the field 3 yr earlier, and thus, this study population was several generations removed from the original captured animals. Therefore, their size distributions and sex ratio are unaffected by capture bias. During this study, the population was closed—no outside snails were added, and no births were allowed (egg masses were removed). Thus, while fertility may be affected in a population kept in captivity, this particular factor does not affect the results presented in this work.

The snails were kept in a large cylindrical fiberglass tank (78 cm radius × 76 cm height) and filled with between 340 and 435 L of municipal water. The bottom of the tank was bare except for a screen across the drain hole in the center of the floor of the tank. This screen was held in place with bricks. A large metal screen was placed across the top of the tank to prevent snails from climbing out. A circulation pump, housed in a metal mesh to keep snails from being caught in the pump, was placed at the bottom of the tank near the center. The hose from the pump ran from the bottom of the tank and out of the water and was suspended above a concrete block that stood above the water surface. Thus, as a means of aeration, water was pumped from the bottom of the tank, over the block, and then back into the tank. At a minimum of once a week, the tank was completely drained and refilled with fresh water. Occasionally, as needed, algae was scrubbed from the side and bottom of the tank and other surfaces during the weekly water exchanges.

For data collection, we drained the tank and removed the snails. The size of the operculum and length of the snail for each individual were recorded (±0.01 mm). All live snails were weighed to within two-tenths of a gram using an electronic scale (±0.02 g).

During the period of observation, several identification techniques were tried. Eventually all snails were individually marked with a unique alphanumeric tag glued to either just below the apex of the shell or on the operculum. Later in the study, the alphanumeric tags were supplemented with radio frequency identification tags epoxied near the shell apex on snails larger than 20 g. Because of the size of the tank and other factors, it was difficult to collect and identify every single snail for every measurement day. That is, while nearly every snail was collected each time, inevitably a few were not. Furthermore, mortality and tag loss occurred throughout the study. As a result, the weight, length, and sex records do not span the entire observation period for all individuals.

Once an individual reached sexual maturity, their sex was determined by noting the location of their reproductive organs, which in both sexes are a salmon or orangish color and can be easily distinguished (with practice) from other parts of their anatomy. In males, the penal sac can be seen near the top and center on the front of the mantle. In females, the oviduct is toward the back and to the left side of the mantle. Over the course
of the study, we were able to determine the sex of most individuals on at least three occasions. If a snail was observed inserting its penis into another snail, it was classified as a male and its mate as a female. If a snail was observed laying an egg mass, we classified it as a female.

Population 2: Juvenile weights
In January 2015, to make room for renovations, the snail tank was moved from the laboratory to the greenhouse. At the beginning of July 2015, unusually warm weather and overcrowding led to a massive die-off of all adult and juvenile apple snails in our snail tank. We removed the dead snails, changed the water, cleaned the bottom of the tank, and allowed egg masses laid a few days before the die-off to hatch out in the tank. The egg masses hatched out over the course of ten days between 15 and 25 July 2015. On 25 September 2015, we drained the tank and collected all the snails (1287 in total). They were individually weighed to within 0.001 g, and their shell length was measured to within 0.1 mm. Then, 150 snails were randomly selected and returned to the tank for continued monitoring. The rest were euthanized.

Population 3: Hatchling weights and hatch-out rate
In October 2015, snails in Population 2 became sexually mature and began to lay egg masses on the side of the tank. We lined the sidewall of the tank with aluminum foil and collected the egg masses by cutting out the sections of the foil they were laid on. These sections of foil with egg masses were affixed to the side of 10-L buckets, with water at the bottom, and allowed to hatch out. We collected nine egg masses in this fashion from November to December 2015 to more closely observe the hatch-out process and measure hatchling weights. The hatchling buckets were placed in the larger snail tank in order to keep it at the same temperature as the tank. We checked the hatchling buckets every 2–8 d, and new hatchlings in each hatchling bucket were weighed to within 0.001 g.

Mathematical model and methodology
We briefly present a size-structured mathematical model for the population dynamics of apple snails. This is an appropriate framework since our initial data analysis (discussed in Results: Growth rates: Direct calculation at individual level) suggests that their growth rates are dependent on size, and it is widely believed that their vital processes are also size-dependent. We remind the reader that the size measurement used here is weight, and indeed, size refers specifically to weight throughout this work.

Due to the differences observed between female and male apple snails described in Results: Sex ratio and weight difference between the sexes, we model them as separate populations with (potentially) different growth dynamics. The dynamics of the female and male population densities, \(u(t, x)\) and \(v(t, x)\), respectively, are given by the partial differential equations (PDEs):

\[
\begin{align*}
\frac{\partial u(t, x)}{\partial t} + \frac{\partial (g(x)u(t, x))}{\partial x} &= -\mu u(t, x) \quad u(0, x) = u_0(x), \\
\frac{\partial v(t, x)}{\partial t} + \frac{\partial (h(x)v(t, x))}{\partial x} &= -\nu v(t, x) \quad v(0, x) = v_0(x),
\end{align*}
\]

for \(t \geq 0\), and \(x_{\min} \leq x \leq x_{\max}\), where \(x_{\min}\) and \(x_{\max}\) represent the minimal and maximal weight achievable by an apple snail, respectively. The function \(g(x)\) is the per capita growth rate of female apple snails of weight \(x\), and \(h(x)\) is the growth rate of male apple snails of weight \(x\). The death rate \(\mu\) is likely to be a function of \(x\), that is, \(\mu(x)\), but we assume that it is constant for these initial efforts, and can refine this quantification in future efforts, if need be. In this model, the death rate should be interpreted as accounting for death by all causes, including predation. In taking a constant death rate \(\mu\), the reciprocal \(1/\mu\) is the lifespan, which was given as approximately 29 months in Yusa et al. (2006) for the similar species Pomacea canaliculata.

The boundary conditions for both subpopulations are given by

\[
\begin{align*}
(g(x)u(t, x))|_{x=x_{\min}} &= \int_{x_{\min}}^{x_{\max}} \beta_f(t, x)u(t, x)dx, \\
(h(x)v(t, x))|_{x=x_{\min}} &= \int_{x_{\min}}^{x_{\max}} \beta_m(t, x)v(t, x)dx.
\end{align*}
\]  

(2)

Here, \(\beta_f\) and \(\beta_m\) are the rates at which female apple snails beget female and male apple snails, respectively. For the data considered in this work, the birth rate is zero since all egg masses were removed once laid, so we can safely neglect this modeling issue for the present study. We remark...
that the female and male subpopulations are then decoupled, since the birth rate is zero, and all rates are assumed to be independent of population size.

We briefly describe the estimation of parameters \( \theta \) of the female growth rate function \( g(x; \theta) \) in model (1) and note that the methodology is the same to estimate parameters in the male growth rate function \( h(x; \theta) \). For a more rigorous discussion, see Appendix S3 and references therein. The data used for estimation of the growth rate parameters are the numbers of individuals within a weight range, denoted by

\[
N_l(t_i; \theta) = \int_{x_{l-1}}^{x_l} u(t_i, x) dx, \tag{3}
\]

for \( l = 1, 2, \ldots, L \) (with \( x_0 = x_{\text{min}}, x_L = x_{\text{max}} \)), and at observation times \( t_i \) with \( i = 1, \ldots, n_d \). The initial observation time \( t_0 \) corresponds to the initial observation date (10 April 2013), and \( t_1, \ldots, t_{n_d} \) are the number of days after that. For the computations in this work, we approximate the integral above using the trapezoidal rule.

Estimates for the values \( \hat{\theta} \) of the parameters are those that minimize the distance between the data and the corresponding model quantities (Eq. 3), where

\[
\hat{\theta} = \arg \min_{\theta \in \Theta} J(y; \theta) = \arg \min_{\theta \in \Theta} \sum_{i=1}^{n_d} \sum_{l=1}^{L} (N_l(t_i; \theta) - y_{il})^2, \tag{4}
\]

using the data set \( \{y_1, \ldots, y_{n_d}\} \). The objective functional in Eq. 4 is minimized over a set of feasible real values of the parameters \( \Theta \subset \mathbb{R}^{n_p} \), where \( n_p \) is the number of parameters appearing in the function \( g(x; \theta) \).

We compute standard errors \( \text{SE}(\hat{\theta}_p) \) for each parameter estimate \( \hat{\theta}_p \) (\( p \in \{1, \ldots, n_p\} \)) by

\[
\text{SE}(\hat{\theta}_p) = \sqrt{\Sigma_{pp}},
\]

the square root of the diagonal values of the \( n_p \times n_p \) estimated covariance matrix

\[
\Sigma \approx \hat{\Sigma} = \hat{\sigma}^2 \left( \chi^T(\hat{\theta}) \chi(\hat{\theta}) \right)^{-1}.
\]

The estimated variance \( \hat{\sigma}^2 \) of the observational errors in the covariance matrix is given by

\[
\hat{\sigma}^2 = \frac{1}{n_d - n_p} \sum_{i=1}^{n_d} \sum_{l=1}^{L} (N_l(t_i; \hat{\theta}) - y_{il})^2.
\]

The sensitivity matrix \( \chi(\theta) \) of size \( (L \cdot n_d) \times n_p \) is made up of elements \( ((\partial N_i/\partial \theta_p)(t_i; \theta)) \), which are approximated via a forward difference

\[
\frac{\partial N_i}{\partial \theta_p}(t_i; \theta) \approx \frac{1}{\Delta \theta_p}(N_i(t_i; \theta_1, \ldots, \theta_p + \Delta \theta_p, \ldots, \theta_{n_p}) - N_i(t_i; \theta_1, \ldots, \theta_p, \ldots, \theta_{n_p})).
\]

The increment \( \Delta \theta_p = 0.01 \cdot \theta_p \) for each \( p \in \{1, \ldots, n_p\} \) is used for the computation of standard errors in this paper.

Before turning to the data, it is prudent to first estimate known parameters with generated data. That is, we compute a forward solution of model (1) with known growth functions \( g(x) \) and \( h(x) \), and generate data with varying levels of noise. With the generated data, we can then estimate the parameters \( \theta \) (which parameterize \( g(x) \) for the female subpopulation and \( h(x) \) for the male subpopulation).

This allows us to anticipate our ability to estimate parameters from data, and the reliability of those estimates when a known level of noise has been introduced into the simulated data. Specifically, this allows us to avoid the situation in which we are attempting to estimate parameters from data that are simply not sensitive to, or affected by, changes in those parameters. Even if our data on hand are sensitive to the unknown parameters, it very well may be that the standard errors grow excessively large as the variance in the observations is increased. Therefore, this practice informs us as to whether or not we should expect an acceptable level of reliability in the resulting estimates. Additionally, it is a good exercise to ensure that the computations performed are correct. Although the results are not shown here for the sake of brevity, we report that several estimation studies from generated data were conducted with various initial guesses for the growth rate estimates using a piecewise constant growth function. The results suggested that we could expect to estimate these growth rates with a reasonable level of reliability.

In Results: Growth rate function estimation: Piecewise constant growth, we use a model comparison statistic to determine the form of the piecewise constant growth function. It is used to tell whether a special, simpler case of a more general model provides a better fit to a given set of data. This statistic is only valid in the case of "nested
models” and is therefore an appropriate tool to help in determining how many growth stages there are (using a model in which it is assumed that growth is constant within each stage).

When fitting the data with the more general model, there are more degrees of freedom (df), which necessarily results in at least as good of a fit (the same or lower minimized objective functional in Eq. 4), as when fitting the data with the simpler model. That is, the more general model will do as well, if not better, in providing a fit to the data. The statistic $U$ is used to determine whether or not this improvement in fit is statistically significant. Specifically, the value of the computed statistic $U$ indicates the confidence level $(1 - \alpha) \times 100\%$ at which to reject the null hypothesis $H_0$, where $H_0$ is essentially the hypothesis that the simpler model is sufficient for that data set. A more complete description of this statistic is given in Appendix S3.

All solutions of the model and fits to data were performed using Matlab R2014a. Any statistical analyses were run using R-2.15.0.

RESULTS

We present here our results from studying these three populations of apple snails via direct measurement of individual weights and also via inference within the population. As diet, temperature, and stocking capacity play a role in apple snail growth and reproductive capacity, we note that all specific growth rates and parameter values of growth rate functions reported are specific to the environment(s) described in Methods: Growth experiments only. However, the features of apple snail growth that is characterized here very likely apply to the species, as we discuss further in Conclusions and Discussion.

Sex ratio and weight difference between the sexes

For Population 1, we identified 99 snails as female and 44 as male. The population had a non-Fisherian sex ratio of 4:9 (male:female).

Females in Population 1 were larger on average than males, as is evident by comparison of the weights of the largest 25th and 10th percentile, and the maximum recorded weights of each sex presented in Table 1 for Population 1. The maximum weight observed was 105.1 g for females and 77.2 g for males. The distributions of the female and male subpopulations as a function of weight were also different, as shown in Fig. 1. These differences suggest that females and males have different growth rates, or growth rate functions (depending on size).

These results suggested size dimorphism of *Pomacea maculata*. Other studies have also documented similar features in two other closely related species. Sexual dimorphism in weight, shell length, and shape of *Pomacea canaliculata* (Estebenet and Cazzaniga 1998, Estoy et al. 2002, Martin and Estebenet 2002, Wu et al. 2011) and *Pomacea scalaris* (Martin 1993, Wu et al. 2011) was observed. Thus, we were further motivated to study the growth dynamics of males and females of this species separately. All weight records for an individual, even those recorded before it was classified as male or female, were considered as part of the data set for that sex’s subpopulation.

Growth rates: Direct calculation at individual level

There was a great deal of variation in the time courses of weight measurements between each individual in Population 1. However, some trends within subpopulations (small females, small males, etc.) were apparent. Generally, growth appeared to be size-dependent, with faster growth seen in smaller animals, and slower growth in larger animals. However, direct measurements of growth rates of snails, as calculated by the change in weight during the length of the time interval between measurements, within small subpopulations of the same sex (small, medium, or large) varied considerably. Examples are given in Appendix S1: Fig. S1 for selected individual snails that were initially of small, medium, and large weight, relative to this data set.

This approach did not yield statistically supported estimates for the growth rates within

| Sex   | Top wt % | Mean (g) | Standard deviation (g) | Number of individuals |
|-------|----------|----------|------------------------|----------------------|
| Female | 25       | 86.7     | 9.1                    | 25                   |
|       | 10       | 94.9     | 5.4                    | 10                   |
| Male  | 25       | 72.0     | 3.6                    | 11                   |
|       | 10       | 76.0     | 1.6                    | 4                    |

Note: The maximum weight was 105.1 g and 77.2 g for females and males, respectively.
these weight intervals, due to the large amount of variation observed, likely due to incomplete individual records. Therefore, we used a population-level-based approach, to estimate growth rates in a mathematical model of female and male (sub)population dynamics. Since the initial calculated growth rates do generally appear to be different between small and large snails (with smaller snails generally appearing to grow faster than larger ones), we consider growth rate functions that depend on size.

**Growth rate function estimation**

In developing a model for the population dynamics of a species whose life and death processes as well as growth rates depend heavily on size, it is important to understand how individuals grow in time. We reiterate that we have used weight as a measure of size in this work. There are several reasonable candidates for a model of the average individual’s growth throughout their life-span, and there may be important differences in the biological implications of each and in the resulting population projections. Since our goal is to develop a quantitative tool for making accurate population projections, and to make projections under various management scenarios, care should be taken in determining an appropriate model for the growth rate function. We discuss the estimation of parameters in different growth rate models from the main data set, and a comparison of the appropriateness of each, as judged by these analyses.

**Piecewise constant growth.**—As a simple means of modeling the dependence of the growth rates on the size of the animals, we first use a piecewise constant growth rate function, given by

\[
g(x) = \begin{cases} 
g_1(x) & x_{\min} \leq x < x_1 \\
g_2(x) & x_1 \leq x < x_2 \\
\vdots & \\
g_M(x) & x_{M-1} \leq x \leq x_M = x_{\max} 
\end{cases},
\]

for the female growth rate \(g(x)\), and a similar for the male growth rate \(h(x)\). Such a model is appropriate if there are constant rates within the weight range of each growth stage. We estimate the rates \(\{g_i\}_{i=1}^M, \{h_i\}_{i=1}^M\) (using the parameter estimation framework described briefly in Results: Growth rate function estimation: Piecewise constant growth, and in more detail in Appendix S2: Figs. S1, S2), for the female and male subpopulations, respectively, using the endpoints of the weight ranges in Results: Growth rates: Direct calculation at individual level as candidates for the endpoints of the weight ranges, based on the individuals in Population 1, considered here.

We use the model comparison statistic (described briefly in Methods: Mathematical model and
methodology, and in detail in Appendix S3) to determine whether allowing for different growth rates in different weight ranges provides a statistically significant improved fit to the data. That is, we compute the statistic to determine whether or not to reject the null hypothesis \( H_0 \), which is essentially that the simpler model is sufficient, with confidence level \((1 - \alpha) \times 100\%\).

The results from using the model comparison statistic to compare the different forms of the piecewise constant female growth rate function, and corresponding level of confidence (with which one would reject the null hypothesis) are given in Table 2. The inclusion of one particular endpoint, \( x_1 = 40 \, \text{g} \), provided a statistically significant improvement in the fit to the data; that is, we reject the null hypothesis with confidence level between 94% and 98% (emphasized in bold in Table 2).

Using the same approach with the data for the male subpopulation, we examine the possibilities (also summarized in Table 2) of including the endpoints from Results: Growth rates: Direct calculation at individual level to distinguish the weight ranges of distinct growth phases. Again, the inclusion of one endpoint, \( x_1 = 24 \, \text{g} \), provided a statistically improved fit (with confidence level 91–95% for the cases considered) to the data. The estimated growth rate parameters and corresponding statistics for this two-phase growth function are given in Table 3.

Since the endpoint \( x_1 \) for both male and female in the biphasic piecewise constant function (5) was based on initial observed trends discussed in Methods: Growth experiments, and therefore, arrived at somewhat heuristically, we attempted to estimate the endpoint in a least squares approach, both while fixing the growth rate parameters \((g_1, g_2)\) and \((h_1, h_2)\) and while estimating all parameters \( \theta = (g_1, g_2, x_1)^T \) and \( \theta = (h_1, h_2, x_1)^T \). Neither attempt led to an estimate that was substantially different from the initial guess for the estimated value, and the sensitivity of the quantities \( \text{N}_l(t) \) for \( l = 1, \ldots, L \) to that parameter was computed to be

Table 2. Model comparison statistic results to determine the form of the piecewise constant growth function (5) for female and male apple snails.

| Sex   | \( M \) | \( H_0 : \{x_i\}_{i=1}^{M-1} \) | \( M \) | \( H_0 : \{x_i\}_{i=1}^{M-1} \) | \( U \) | Conf. level (%) |
|-------|--------|-------------------------------|--------|-------------------------------|-------|----------------|
| Female| 1 \( \emptyset \) | \( \{23\} \) | 2 \( \{40\} \) | 1.240 | 73 |
|       | 1 \( \emptyset \) | \( \{23\} \) | 2 \( \{40\} \) | 5.866 | 94 |
|       | 1 \( \emptyset \) | \( \{23, 40\} \) | 3 \( \{23, 40\} \) | 9.000 | 8 |
|       | 2 \( \{23\} \) | \( \{23, 40\} \) | 3 \( \{23, 40\} \) | 5.866 | 97 |
|       | 2 \( \{40\} \) | \( \{23, 40\} \) | 3 \( \{40, 53\} \) | 0.116 | 26 |
|       | 2 \( \{53\} \) | \( \{40, 53\} \) | 3 \( \{40, 53\} \) | 4.265 | 96 |
|       | 3 \( \{23, 40\} \) | \( \{23, 40, 53, 71\} \) | 5 \( \{23, 40, 53, 71\} \) | 0.118 | 5 |
|       | 3 \( \{23, 40\} \) | \( \{23, 40, 53\} \) | 4 \( \{23, 40, 53\} \) | 0.115 | 26 |
|       | 3 \( \{23, 40\} \) | \( \{23, 40, 71\} \) | 4 \( \{23, 40, 71\} \) | 0.0400 | 5 |
|       | 3 \( \{40, 53\} \) | \( \{40, 53, 71\} \) | 4 \( \{40, 53, 71\} \) | 0.00037 | 4 |
|       | 4 \( \{23, 40, 53\} \) | \( \{23, 40, 53, 71\} \) | 5 \( \{23, 40, 53, 71\} \) | 0.00369 | 4 |
|       | 4 \( \{23, 40, 71\} \) | \( \{23, 40, 53, 71\} \) | 5 \( \{23, 40, 53, 71\} \) | 0.0780 | 21 |
|       | 4 \( \{40, 53, 71\} \) | \( \{23, 40, 53, 71\} \) | 5 \( \{23, 40, 53, 71\} \) | 0.00950 | 7 |
|       | 5 \( \{23, 40, 53, 71\} \) | \( \{23, 40, 53, 60, 71, 85\} \) | 7 \( \{23, 40, 53, 60, 71, 85\} \) | 0.525 | 23 |
|       | 7 \( \{23, 40, 53, 60, 71, 85\} \) | \( \{17, 23, 40, 53, 60, 71, 85\} \) | 8 \( \{17, 23, 40, 53, 60, 71, 85\} \) | 0.430 | 48 |
|       | 8 \( \{17, 23, 40, 53, 60, 71, 85\} \) | \( \{17, 23, 40, 53, 60, 71, 85\} \) | 9 \( \{17, 23, 40, 53, 60, 71, 85\} \) | 0.486 | 51 |
| Male  | 1 \( \emptyset \) | \( \{24, 55\} \) | 3 \( \{24, 55\} \) | 4.213 | 87 |
|       | 1 \( \emptyset \) | \( \{24, 55\} \) | 2 \( \{55\} \) | 0.919 | 66 |
|       | 1 \( \emptyset \) | \( \{24\} \) | 2 \( \{24\} \) | 4.056 | 95 |
|       | 2 \( \{55\} \) | \( \{24, 55\} \) | 3 \( \{24, 55\} \) | 3.017 | 91 |
|       | 2 \( \{24\} \) | \( \{24, 55\} \) | 3 \( \{24, 55\} \) | 0.112 | 26 |
|       | 3 \( \{24, 55\} \) | \( \{24, 40, 55\} \) | 4 \( \{24, 40, 55\} \) | 0.945 | 18 |
|       | 3 \( \{24, 55\} \) | \( \{14, 24, 40, 55, 64\} \) | 6 \( \{14, 24, 40, 55, 64\} \) | 0.641 | 57 |
|       | 4 \( \{24, 40, 55\} \) | \( \{14, 24, 40, 55, 64\} \) | 6 \( \{14, 24, 40, 55, 64\} \) | 0.287 | 13 |
Table 3. Estimated growth rates and corresponding statistics for the biphasic piecewise constant growth function with endpoints \(x_1 = 40\) for females and \(x_1 = 24\) for males) as determined in Results: Growth rates: Direct calculation at individual level and the “best fit” endpoints \(x_1 = 38\) for females and \(x_1 = 28\) for males.

| Sex     | \(x_1\) | \(g_1\) | \(g_2\) | \(\hat{\theta}_p\) | \(\hat{\theta}_p\) | \(SE(.05)\) | Sum of squared error | \(\sigma^2\) |
|---------|---------|---------|---------|----------------|----------------|-------------|---------------------|-------------|
| Female  | 40      | 0.268   | 0.072   | 0.03           | 0.05           | 1043        | 130                 |
|         | 38      | 0.272   | 0.0748  | 0.03           | 0.04           | 979         | 124                 |
| Male    | 24      | 0.208   | 0.0879  | 0.03           | 0.01           | 366         | 45.7                |
|         | 28      | 0.200   | 0.0806  | 0.02           | 0.007          | 336         | 16.3                |

approximately zero. This suggests that our data do not contain information on this parameter and its value should be fixed. Therefore, we simply estimate the growth rates \(\theta = (g_1, g_2)^T\) and \(\theta = (h_1, h_2)^T\) from female and male data, respectively, while holding \(x_1\) fixed, for each integer \(x_1 \in \{15.16, \ldots, 44\}\). The results from the best fit, as judged by the lowest sum of squared error (SSE), are given in Table 3.

Thus, this analysis suggests that there are two distinct growth phases for both males and females, and a constant growth rate is inappropriate for these animals. The best growth function assuming a piecewise constant form for females is then

\[
g(x) = \begin{cases} 
0.272 & x_{\text{min}} \leq x < 38 \\
0.0748 & 38 \leq x \leq x_{\text{max}} 
\end{cases}, \tag{6}
\]

where the growth rate \(g(x)\) has units of g/d. The best piecewise constant growth function for males is

\[
h(x) = \begin{cases} 
0.200 & x_{\text{min}} \leq x < 28 \\
0.0806 & 28 \leq x \leq x_{\text{max}} 
\end{cases}, \tag{7}
\]

and the related statistics are summarized in Table 3. The fit of the model to the data for selected dates with these growth functions is shown in Figs. 3, 4. The same best fit model solution and data are shown for all observation dates in Appendix S2: Figs. S1, S2. The graphs in Fig. 2 show growth for an average individual snail as represented by the two functions (6) and (7). That is, according to this piecewise constant growth model, the female and male apple snails grow at a higher constant rate for an initial weight range and then transition to a slower constant growth rate for its larger sizes. Interestingly, the females and males appear to grow at similar rates in the larger weight ranges and the differences occur in the early stages. We note that the variance is much higher for the growth rate of the larger females, which can be reasonably attributed to the energy and resources required to reproduce. That is, females “grow” in weight prior to laying an egg mass, and then quickly drop in weight immediately once they lay the egg mass.

Differences in growth rates in early stages would have a larger impact on the projection of future population sizes, as it affects the number and rate at which males and females reach larger (reproductive) sizes, which are also thought to be associated with lower predation rates. Additionally, if this size at which the animals shift from a faster to a slower growth rate is indicative of a maturation point, it would be important to know whether or not the time to maturation differed between males and females. However, this would correspond to 118 and 110 d for females and males, respectively, as indicated in the lower panels of Fig. 2. Since these time points are not very different, and the level of uncertainty in these values depends on the variance in the observations, as well as the associated model and its interpretation, we do not suggest that there is a difference in time to reproduction as based on these analyses.

This piecewise constant function is admittedly a simplistic view of what is likely a more complicated growth process. Indeed, it does not reflect many of the growth trajectories seen in the data, even if the fluctuations were smoothed out. We considered that the apple snails’ growth rate may depend on size in a different manner, and investigated other forms for the growth functions \(g(x)\) and \(h(x)\), which were derived based on hypothesized biological relationships.

**von Bertalanffy growth.**—A common model for individual growth rates as a function of size is the von Bertalanffy growth function (Von Bertalanffy 1938), given by
Like the piecewise constant growth function estimated in Results: Growth rate function estimation: Piecewise constant growth, the von Bertalanffy growth model decreases with increasing size. In order to use the same data set and therefore to be able to directly compare results with those when using other growth models, we use a change of variables (from length to weight) in Eq. 8. Necessarly, we first determine an appropriate relationship between length \( y \) and weight \( x \), with results summarized in Table 4.

Based on the results shown in Table 4, we conclude that there is not a remarkable difference in the length–weight relationship between the female and male \( P. \) maculata and that it is reasonable to use \( y = 0.0007x^3 \) for both. This agrees with the work done by Wu et al. (2011) that also suggests a cubic relationship between the operculum length and weight in both \( P. \) canaliculata and \( P. \) scalaris of smaller sizes (between 20 and 52 mm in operculum length and 0 and 0.028 g in weight).

Combining the length–weight relationship \( y = ax^\beta \) with Eq. 8 results in the von Bertalanffy growth function

\[
\frac{dx}{dt} = \beta r x^{1/\beta} x^{(\beta - 1)/\beta} - \beta rx,
\]

that now depends on size \( x \), where \( x \) is weight. We note that \( a \) does not appear in the growth function and \( \beta = 3 \) from the analysis in Table 4.

We estimate values for \( \theta = (r_f, x_f, \infty) \) that parameterize the female growth function \( g(x) \)
from the female data and $\theta = (r_m, x_{m, \infty})$ in the male growth function $h(x)$ from the male data, where the subscripts indicate whether the parameters are for the female or male growth rate functions. The results and corresponding standard errors are given in Table 5.

The standard errors suggest that the parameters estimated with lower bound set at zero are reliable, since the values are small in comparison with the value of the parameter estimate itself. However, the initial estimated maximum weight (92.9 g) for the female snails is lower than that observed (which was around 105 g) and certainly lower than the maximum size $x_{max}$ used for computing solutions of the population dynamics model. If we repeat this process and set the lower bound for $x_{f, \infty}$ to $x_{max} = 109$, the resulting estimate is the value of the lower bound. We interpret this to mean that the “true value” for this data set is below this lower bound. We note that the standard error for this value is larger as in the previous estimation attempt, as is the SSE, which indicates that not only does this result in not as good of a fit to the data, but there is less reliability in the resulting estimated parameter value. Again, the values of the parameters for females and males are different, which supports the notion that there are sex-dependent differences in growth dynamics for this population. We interpret these results to mean that the average largest size that a female snail in this population may achieve is approximately 92.9 g.

Therefore, the issue with using this as the growth model is that if the estimated parameter value $x_{f, \infty} = 92.9$ g is used, the growth function $dx/dt = g(x)$ is negative above $x_{f, \infty}$ and the characteristics of the hyperbolic PDEs in (I) will
The solutions of the population models are then not unique. Therefore, we do not consider this a good candidate for the growth dynamics within this population-level model. Additionally, while this model is consistent with the decreasing nature of the growth function, the two phases of growth suggested by the analysis in Results: Growth rate function estimation: Piecewise constant growth are not consistent with this model. For these reasons, we conclude that this model is not a good candidate for the growth dynamics of this population.

Sigmoid growth.—In selecting another growth model, we seek one that also is appropriate for the features captured in the piecewise constant function—namely a function that is appropriate for biphasic growth (faster growth for smaller sizes, and slower growth for larger sizes), and that approaches zero for large $x$, but remains non-negative for all $x$. We investigate an adaptation of a sigmoid growth function, like the common logistic, or Verhulst model, which was named in 1845 by Pierre Francois Verhulst (1845). While the logistic function is commonly

Table 4. Regression analysis for the relationship between snail operculum length $y$ and weight $x$.

| Sex   | $y = a(x)$                          | $R^2$ |
|-------|-------------------------------------|-------|
| Female| $y = -84.6 + 3.36x$                 | 0.854 |
|       | $y = \exp(0.411 + 0.0840x)$        | 0.879 |
|       | $y = 0.000716x^3$                  | 0.965 |
|       | $y = 0.000450x^{3.12}$             | 0.875 |
| Male  | $y = -60.5 + 2.71x$                | 0.808 |
|       | $y = \exp(0.663 + 0.0775x)$       | 0.839 |
|       | $y = 0.000684x^3$                  | 0.968 |
|       | $y = 0.000993x^{2.92}$             | 0.870 |

Note: The boldface lines emphasize the best fit length-weight relationships.

intersect in the weight domain. The solutions of the population models are then not unique. Therefore, we do not consider this a good candidate for the growth dynamics within this population-level model. Additionally, while this model

Fig. 4. Male apple snails ($N_t(t_i; \hat{\theta})$ in $L$ weight ranges ($l = 1, \ldots, L$)) at fixed times $t_i$ with $i = 1, 4, 7, 10$ with the two-phase piecewise constant growth rate function (7), where the parameter values have been estimated from the male apple snail data.
used to model the size of a population, we consider it to model the individual growth rate of the apple snails as it preserves some of the observed features of this species’ growth. A logistic function or logistic curve is a common “S” shape, or sigmoid curve, which we shift and reflect so that it agrees qualitatively with the growth dynamics observed in our population. The forms of the growth functions used here are

\[ g(x) = \frac{a_f}{1 + e^{b_f(x-c_f)}} \quad \text{and} \quad h(x) = \frac{a_m}{1 + e^{b_m(x-c_m)}}, \]

for female and male apple snails, respectively. With these growth functions, the initial stage of growth is exponential. Then, as the individual matures, growth slows (asymptotically) to zero.

We estimate the parameters in (10), \( \theta = (a_f, b_f, c_f)^T \) and \( \theta = (a_m, b_m, c_m)^T \), via the least squares approach described briefly in Methods: Mathematical model and methodology. The results are summarized in Table 6, and the growth functions with the estimated parameter values are shown in Fig. 5. Again, we notice a difference in parameter values between the male and female growth functions, but most standard errors do not suggest a reasonable level of reliability in the parameter estimates. In fact, the result for the parameter value for the estimate \( \hat{c}_m \) was consistently the fixed lower bound used in the minimization routine for that parameter. This suggests that a minimum for the objective functional \( J(y; \theta) \) in (4) has not been successfully found. Further, the sensitivity with respect to that parameter was near machine zero, which indicates that these data are not sensitive, that is, do not contain information on this parameter, and therefore, it should not be estimated. Thus, we do not report a standard error for that parameter, and we did not include this parameter in the sensitivity matrix (which would have been very ill-conditioned) to compute standard errors for the other parameters. The lack of information on this parameter in this particular data set should only be interpreted as that, and not that this value is zero for the male population.

| Sex | Lower bound | \( \theta_0 \) | \( \theta_1 \) | \( \theta_2 \) | SE(\( \theta_0 \)) | SE(\( \theta_1 \)) | SE(\( \theta_2 \)) | \( \sigma^2 \) | Sum of squared error |
|-----|-------------|--------------|--------------|--------------|----------------|----------------|----------------|--------------|------------------|
| Female | \( r_f \) | 0.00663 | 0.00150 | 183.353 | 1466.825 |
| | \( x_f \infty \) | 92.907 | 0.00165 | 191.343 | 1530.740 |
| Female | \( r_f \) | 0.00577 | 0.00145 | 50.427 | 403.418 |
| | \( x_f \infty \) | 109 | 26.409 | |
| Male | \( r_m \) | 0.00454 | 0.00114 | 1195.3 | 170.8 |
| | \( x_m \infty \) | 82 | 3.075 | |

Table 5. Parameter estimates for \( \theta = (r, x_f, \infty)^T \) and \( \theta = (r, x_m, \infty)^T \) in the von Bertalanffy growth model for the female growth rate \( g(x) \) and male growth rate \( h(x) \), respectively, along with the corresponding statistics.

Table 6. Estimation of parameters \( \theta = (a_f, b_f, c_f)^T \) and \( \theta = (a_m, b_m, c_m)^T \) in growth functions (10) for female growth rate \( g(x) \) and male growth rate \( h(x) \), respectively.

Fig. 5. Sigmoid growth function (Eq. 10) with estimated parameter values in Table 6 for females \( g(x) \) and males \( h(x) \).
value of this parameter determines the biphasic nature of the sigmoid function, and the weight at which the beginning phase ends and the later phase begins, which occurs around 24 g as per results in Results: Growth rate function estimation: Piecewise constant growth. There is a notable lack of males around that weight range on many observation dates, which may explain the lack of sensitivity to this parameter. With \( c_m = 0 \), the sigmoid function reduces to an exponential, which is not consistent with a two-phase growth function, which was statistically supported from model comparison test results using the piecewise constant growth function. In addition, the SSEs from fitting both the female and male data using the sigmoid growth function were greater than when the piecewise constant function is used, indicating that the agreement between the model and data is inferior when the sigmoid growth function is used. Thus, we do not judge this model to be appropriate for the growth dynamics of this species based on the information in this data set.

Biphasic power function growth.—A common choice for biphasic growth is based on power functions in two stages. A simple power function for the growth rate

\[
\frac{dx}{dt} = rx^\phi
\]  

(11)

has been used in several examples (such as in Roff 1983, Kozlowski and Wiegert 1986, Roff 1986, Kozlowski and Uchmanski 1987, Kozlowski and Wiegert 1987, Kozlowski 1992), with the value of \( \phi = 2/3 \) being a common choice. The parameter \( r \) is a growth rate or habitat quality parameter; a large \( r \) corresponds to a productive habitat as it results in a large growth rate. This simple power function is often an accurate representation of pre-reproductive growth, but its use for more general growth dynamics is not typically appropriate since growth is assumed to approach a constant rate after maturity. Day and Taylor (1997) extended it to model more general growth dynamics by using a power function during pre-maturity, but then employed a declining exponential function, such as

\[
\frac{dx}{dt} = e^{-(x-x^*)n}rx^{2/3},
\]  

(12)

to model growth after maturity. This models a shift in energy allocation to reproduction, an approach that was taken in other studies (Kozlowski and Wiegert 1986, Kozlowski 1992) as well. Here, the factor \( e^{-(x-x^*)n} \) is simply the proportion of resources devoted to growth, which is only <1 after an optimal maturity age \( x^* \), and an exponential rate \( \eta \) of decline.

For the weight range (both pre- and post-maturity) of our main data set, we use the growth function

\[
\frac{dx}{dt} = \begin{cases} \begin{aligned} rx^{2/3} & \quad x \in [x_{\text{min}}, x^*], \\ \exp(- (x-x^*) \eta) rx^{2/3} & \quad x \in (x^*, x_{\text{max}}]. \end{aligned} \end{cases}
\]

(13)

To estimate parameters \( \theta = (r_f, \eta_f)^T \) in the female growth function \( dx/dt = g(x; \theta) \), we initially fix \( x^*_f = 40 \). Similarly, we fix \( x^*_m = 24 \) to estimate parameters \( \theta = (r_m, \eta_m)^T \) in the male growth function \( dx/dt = h(x; \theta) \), based on the values for analogous parameters in the piecewise constant growth function (Results: Growth rate function estimation: Piecewise constant growth). Those results are summarized in Table 7. However, the values \( x^*_f \) and \( x^*_m \) were not successfully estimated in Results: Growth rate function estimation: Piecewise constant growth. Those results are also summarized in Table 7. The biphasic power functions with the estimated parameter values \( \hat{\theta} = (r_f, \eta_f, x^*_f)^T \) and \( \theta = (r_m, \eta_m, x^*_m)^T \) for females and males, respectively, are shown in Fig. 6.

The results from estimating the parameters in the biphasic power function, including the maturation weight \( x^*_f \), suggest that the values obtained are reasonable, as the standard errors for the estimated parameters are small in comparison with their respective parameter values. Further, the improvement in the agreement between the model and data (as judged by the lower SSE) is considerable. However, the same cannot be said when considering the inclusion of \( x^*_m \) in the estimated parameters in the male growth function. The fit is only slightly improved and the standard errors are considerably larger for parameters \( r_m \) and \( \eta_m \) whereas their standard errors are small enough to suggest reliable estimated parameter values when \( x^*_m \) is fixed. Again, this is likely due to the small
number of males in the weight range of the shift from juvenile to adult. Since the results for the female population did allow for reliable estimation of all parameter values, it is reasonable to expect that the male parameter estimates and statistics would also be improved if there were simply more males with weights in range nearby. We expect that the male parameter estimates and statistics might be improved if there were simply more males with weights in range nearby. The use of the biphasic power growth function resulted in the best fit, with the weight at which the growth shift occurs, $x^*$, fixed. The fit to the male data did not yield statistically reasonable estimated parameter values, likely due to the scarcity of males in the weight range in which the growth shift likely occurs. We note that the estimated values are different for $x^*$ in the piecewise constant and biphasic growth functions. However, this can be explained by recognizing that compared to a constant growth rate. However, a piecewise constant growth function is likely an oversimplification of the growth within each phase. So we investigated other candidates for growth functions with features that were consistent with our observations. The minimized SSE for these growth functions are shown in Table 8, for direct comparison.

The smallest SSE overall, and presumably the “best fit,” was achieved when the piecewise constant growth function was used. The use of the biphasic power growth function resulted in the second best fit (with the weight at which the growth shift occurs, $x^*$, fixed). The fit to the male data did not yield statistically reasonable estimated parameter values, likely due to the scarcity of males in the weight range in which the growth shift likely occurs. We note that the estimated values are different for $x^*$ in the piecewise constant and biphasic growth functions. However, this can be explained by recognizing that

Comparison of growth functions.—The growth dynamics for the apple snails in this data set (with weights spanning 6–105 g) are best described as exhibiting two distinct growth phases, an observation that is supported by a residual-based statistical test that was used to determine that a two-phase piecewise constant growth function resulted in a statistically significant improvement in the fit to data as compared to a single growth function. However, a piecewise constant growth function is likely an oversimplification of the growth within each phase. So we investigated other candidates for growth functions with features that were consistent with our observations. The minimized SSE for these growth functions are shown in Table 8, for direct comparison.

The smallest SSE overall, and presumably the “best fit,” was achieved when the piecewise constant growth function was used. The use of the biphasic power growth function resulted in the second best fit (with the weight at which the growth shift occurs, $x^*$, fixed). The fit to the male data did not yield statistically reasonable estimated parameter values, likely due to the scarcity of males in the weight range in which the growth shift likely occurs. We note that the estimated values are different for $x^*$ in the piecewise constant and biphasic growth functions. However, this can be explained by recognizing that

**Table 7. Estimated parameter values $\theta$ in both the biphasic power female growth rate $g(x; \theta)$ and male growth rate $h(x; \theta)$ (with weights spanning 6–105 g) are best described as exhibiting two distinct growth phases, an observation that is supported by a residual-based statistical test that was used to determine that a two-phase piecewise constant growth function resulted in a statistically significant improvement in the fit to data as compared to a constant growth rate. However, a piecewise constant growth function is likely an oversimplification of the growth within each phase. So we investigated other candidates for growth functions with features that were consistent with our observations. The minimized SSE for these growth functions are shown in Table 8, for direct comparison.**

| Sex   | $\theta^*_f$ | $\theta^*_m$ | SE($\hat{\theta}_f$) | SE($\hat{\theta}_m$) | $\sigma^2$ | Sum of squared error |
|-------|--------------|--------------|----------------------|----------------------|----------|---------------------|
| Female | 0.034 (0.006) | 26.7 (N/A)   | 185 (1481)           | 1041 (N/A)           |          |                     |
| Male   | 0.026 (0.008) | 15.2 (N/A)   | 47 (377)             | 359 (N/A)            |          |                     |

**Fig. 6. The biphasic power function (Eq. 12) growth rates with estimated values for parameters $\theta = (r_f, h_f, x^*_f)^T$ and $\bar{\theta} = (r_m, h_m, x^*_m)^T$ shown in Table 7 for females $g(x)$ and males $h(x)$.”

**Table 8. Comparison of the sum of squared errors for the best fit of the model to the female and male data with all growth functions.**

| Sex   | Piecewise constant | von Bertalanffy | Sigmoid | Biphasic power |
|-------|--------------------|-----------------|---------|---------------|
| Female | 979                | 1466.8          | 1195.3  | 1041          |
| Male   | 336                | 403.4           | 355.4   | 359           |
the first phase and the beginning of the second phase in the biphasic growth function are faster growth rates overall and correspond to the first phase of the piecewise constant growth rate function for both the females and males.

Since the parameter estimates were reliable for the female subpopulation (and there is not a similar lack of individuals in a weight range), it is reasonable to expect that there would be an improvement for the fitting of the male growth data using a data set with more males in this weight range. There were other issues in using both the von Bertalanffy and the sigmoid functions for this data set, specifically outlined in Results: Growth rate function estimation: von Bertalanffy growth and Results: Growth rate function estimation: Sigmoid growth. We conclude that the piecewise constant and biphasic power functions are the best candidates for the growth rates for this population, and should be considered for future studies, although of course the parameter values in each case should be revisited. We reiterate that the parameter values may very well be different when describing the growth of apple snails at different temperatures, consuming different food, and at perhaps different population densities. However, the qualitative nature of their growth is likely driven by the natural history of the animal’s lifespan, and therefore, they are likely conserved.

**Sex dependence of growth dynamics**

Growth dynamics, particularly if they differ between the sexes, are important to accurately project future population sizes as they strongly affect the number of, and rate at which, females and males reach a sexually reproductive stage. This is important especially since predation and survival rates are thought to be size-dependent. Thus, the differences in the male and female populations warrant particular attention. To briefly summarize, in this data set, notable differences are the observed uneven sex ratio (4.9 male:female), the overall larger sizes of females as compared to males, and the differences in estimated growth rate parameter values in all growth rate functions in Results: Growth rate function estimation.

We examine whether there is a statistically supported difference in the growth dynamics between the sexes in this data set. We use the model comparison statistic, described briefly in Methods: Mathematical model and methodology, and in further detail in Appendix S3, to determine whether allowing for any differences in male and female growth dynamics provides a statistically significant improvement in fit to the data of the entire population. The statistic is used to determine whether the null hypothesis (which is that there are no differences in parameters between male and female subpopulations) should be rejected as compared to allowing for differences in the parameters in the male and female growth rate functions. The model (both PDEs in Eq. 1) is fit to the data of the entire population (both male and female), as it is necessary that the same data set is used in both cases being compared. For example, for the piecewise constant growth function, the restriction on the parameter space is that \( g_1 = h_1, g_2 = h_2 \) and \( x_1^* = x_m^* \). This is a difference of 3 df. We consider this question in the context of the piecewise constant growth rate function and the biphasic power function as the two best candidates for the growth model (Results: Growth rate function estimation: Comparison of growth functions).

In considering the piecewise constant growth function (Results: Growth rate function estimation: Piecewise constant growth), we compare the “best fit” case with \( x_1 = 38 \) for females and \( x_1 = 28 \) for males (Eqs. 6 and 7), with the estimation of \( g_1 = h_1, g_2 = h_2, \) and \( x_1 \) the same value for the models being used to fit both the male and female data. We estimate these parameters with \( x_1 \) fixed at each of the integers \( x_1 \in \{15, 16, \ldots, 44\} \). For the average of the best fit \( x_1 \) for females and males, i.e., \( x_1 = \frac{1}{2}(38 + 28) = 33 \), we would reject the null hypothesis with 72% confidence. While this does not provide strong support for the differences in the growth dynamics between the sexes being important, we remark that it would be reasonable to expect stronger results if there were more males in the data set, and also if the data used to estimate the parameters were more sensitive to one \( x_1 \) of the three parameters in the growth function.

In using the biphasic power function (Results: Growth rate function estimation: Biphasic power function growth), we are able to estimate \( x_1^* \) and \( x_m^* \) but the standard errors for the parameters in the male growth function \( (r_m, \eta_m, \text{ and } x_m^*) \) are high if \( x_m^* \) is estimated. However, the standard
errors are reasonable for $r_f$, $\eta_f$, and $x_f^*$, when $x_f^*$ is estimated, and we conclude that the standard errors for male parameters would likely be improved by an increase in the number of males in the likely weight range of $x_m^n$. Therefore, we use these “best fit” values and minimized objective functions in computing the model comparison statistic. Again, we assume $x' = x_f^* = x_m^n$, $r_f = r_m$, and $\eta_f = \eta_m$ and compute the model comparison statistic for the entire population (both female and male snails), with the result that we should reject the null hypothesis with 63% confidence. While this also does not strongly suggest a difference in growth dynamics between the sexes, it is not negligible. Again, it is likely that this somewhat weak statistical result is due to the lack of information in the data (no male individuals) in the weight range in which the maturity shift occurs. Since there is not a difference in the data fit for several values of this parameter, the fit will not substantially improve or worsen due to a restriction on this parameter. We would anticipate that the confidence level would increase with more male individuals in this weight range as the identifiability of that parameter increases.

Overall, there are several data features that are suggestive of differences in the growth dynamics between female and male subpopulations. Females generally reach larger sizes than males, and the growth rate parameters in each function investigated are different. The results of the model comparison test in this section do not provide strong statistical support, but it is reasonable to expect a stronger result with a different data set. Namely, if there were more males observed in the weight range in which the shift from one growth phase to another occurs, a more marked difference in data fits would result, and thus, a higher value for the model comparison statistic. This absence of males in that key weight range may also explain why the data are not more sensitive to one of the three parameters estimated in the piecewise constant function. In addition, since the females outnumber the males in this population, the effects of growth differences between the sexes may be somewhat masked with the application of this test. Considering all of these aspects, we argue that the differences between males and females are notable and likely important.

### Analysis of small snail data

To address the growth of the snails smaller ($x<6$ g) than those in our main data set (Population 1), we provide here an initial analysis of preliminary results of ongoing data collection efforts. With knowledge of the weights of hatchlings (Population 3), and a large group of snails (Population 2) that hatched out over a ten-day period, with weights that overlap those of our main data set, we provide rough estimates of the growth of snails in the earliest stages of their life cycle.

The weights of hatchlings (Population 3) are shown in Table 9. Since the hatchling weights are close to the measurement error ($\pm 0.001$ g) of the scales, they were weighed in small groups to get a measurement that was sufficiently above the sensitivity of the scale, and hopefully then, not substantially affected by measurement error. These average weights were then divided by the number of individuals in the measurement, giving the individual weight. The standard deviation reported is then likely an underestimate for the standard deviation of these weights if they were truly done individually. In an attempt to get a more accurate estimate for the standard deviation, we also weighed 91 hatchling snails individually to more accurately estimate the standard deviation, with the knowledge that the weights would then potentially be more affected by the sensitivity of the scale.

The individually weighed snails were taken from two egg masses, and indeed, the standard deviation is larger than that of snails weighed in groups, but was still on roughly the same scale and would lead to a similar interpretation of the variance in the measurements. There were notable differences in the average weights of hatchlings from different egg masses, which could be due to variation among individuals or the differences in the number of days in which the snails began hatching out (which is unknown for these data on a finer timescale of 2–7 d). This will be investigated in current and future studies, as

| Weight measurement | Mean    | Standard deviation | Total number |
|--------------------|---------|--------------------|--------------|
| Individuals        | 0.00180 | 0.0007             | 91           |
| All in groups      | 0.00162 | 0.0006             | 2041         |
more egg masses are laid in our resident sexually mature (adult) populations. We use the average for the individual hatchling weights as found from the snails measured in groups (due to the substantially larger sample size) to calculate a rough estimate of the growth rate for this small weight range.

The data from the snails in Population 2 that were weighed on 25 September 2015 are shown in Fig. 7 and clearly overlap the weights of the snails in our main data set. This group of snails began hatching no earlier than 15 July, and they finished hatching by 25 July. Our estimates of hatchling size (Table 9) can then be used to estimate an approximate lower and upper bound for the mean growth rate for this lowest weight range, under the assumption that all snails hatched out on the earliest possible day (15 July) and the last possible day (25 July), respectively. We note that the weight distribution of the snails on 25 September suggests that there may be considerable variability in these growth rates, which would agree with the fluctuations of the individual data records (examples in Appendix S1: Fig. S1) and poor statistical support of the growth rates calculated directly from individual data records in Results: Growth rates: Direct calculation at individual level. It is not immediately possible to deduce whether, or to what extent, this variability is important without better knowledge of the hatch-out process during the ≈10 d. This will be investigated in further studies, but here we restrict our attention to providing an initial estimate in this paper. The lower bound for the growth rate is 0.0463 g/d and the upper bound is 0.0537 g/d.

**Conclusions and Discussion**

We studied the sex-specific growth dynamics of an invasive species, *Pomacea maculata*, the maculata apple snail, as part of the larger goal of building a quantitative framework within which to accurately project population sizes, and predict the impacts and cost-effectiveness of potential control scenarios. The population sizes and impacts thereof on the local ecosystems, and rice crops of south Louisiana, are unknown. The vital processes, which are thought to be size-dependent, as well as the growth processes of this species have largely been unquantified, making it difficult to address pertinent questions associated with the recent arrival and spread of an invasive species.

Our analysis was primarily focused on the data collected on snails with weights 6–105 g,
but preliminary information allowed us to provide estimates for apple snail growth rates throughout its lifespan. We note that it is important to interpret the growth rates reported as being temperature- and perhaps food-specific as we, along with others, have observed a dependence of growth rates on temperature and diet. Not surprisingly, we initially noted a dependence of the growth rates on size, but the variance observed between and among individuals, as well as the incompleteness of the individual records, hindered our ability to determine the nature of this size dependence and statistically supported corresponding rates. Estimating growth rate parameters in a population-level model via a least squares approach resulted in statistically supported estimates. Further, the use of a model comparison statistic allowed us to conclude that a two-stage or biphasic (piecewise constant) growth rate function provided a statistically significant improvement in the fit to data as compared to a simple constant growth rate.

The maximum size of snails grown in our laboratory was similar to the maximum size of snails collected in swamp ecosystems in south Louisiana. However, they were smaller than the maximum size seen in more open systems in the same region such as marsh edges and ponds by about 10 mm in shell length, or an estimated 60 g difference in weight. While we followed precedent in providing the snails with a mostly lettuce, and strictly vegetarian diet, we have since come to the conclusion that these snails may be more omnivorous than previously suspected. Most recently, it was reported that their sister species, Pomacea canaliculata, will feed on amphibian egg masses when given the chance (Karraker and Dudgeon 2014), and there have also been reports of egg cannibalism (Horn et al. 2008). Therefore, we expect that the growth parameters might be different under different nutritional circumstances.

We analyzed and compared results from the use of three other growth rate functions with two stages. Two models, a piecewise constant and biphasic power function, were found to be the best for our observed population in this weight range. As projections of population sizes, particularly under various proposed management scenarios, would be highly dependent on the growth functions, particularly in a size-structured model, it is important to consider many growth models. That is, one should keep in mind any shortcomings of a growth model, as we have noted throughout these efforts, and adopt any suitable modifications, should they become apparent. Future work will certainly involve revisiting these growth models as more data become available, particularly in the earlier life stages.

There were notable differences between the male and female apple snails that are important for accurately projecting population sizes, namely the 4:9 male:female ratio, which has several implications when studying a species’ population-level dynamics. It is intuitive that population projections from an inaccurately predicted pairing rate will be affected, but inaccuracies in projected population sizes would be further compounded if there are other sex-dependent differences on vitality or growth. There were also observed differences in the weight distributions and in overall sizes (with females generally being larger) as clear indicators that the growth processes are different between these subpopulations. Additionally, the parameter values in all growth functions used to fit the population-level model to the data were different between males and females. The results from using the model comparison statistic to explore whether or not the differences resulted in statistically significant improvements in the data fits were not strong, but that is likely due to the low number of male individuals in the weight ranges in which it appears that the shift from one growth phase to the other occurs. That shift is one of three unknown parameters in both growth functions that provided a reasonable fit to the data. As a whole, these observations and results do appear to suggest key differences between the sexes, which should be taken into consideration in future quantitative studies of this species. Indeed, the extent to which these sex-dependent differences affect population projections, if at all, will be examined in future simulation studies as more growth and vital data are collected in the earlier stages of the apple snails’ life cycle.

It is interesting that it is during the earlier growth phases that the parameter values are the most different between the sexes. While it has not been directly studied, the sex of these and other similar animals is thought to be determined by environmental factors, and not genetically. Therefore, one would think that individuals would be the same pre-maturation and no differences in
growth rates would be evident. This raises the question of whether or not the sex is determined by environmental factors or by a combination of environmental and genetic or purely genetically. It is also possible that there is another growth phase that signifies a developmental stage for sizes below those in our main data set, or overlapping with our main data set, but animals in those weight ranges were not present in high enough numbers for this to have been determined via the inference approach taken here. A better and more quantitative understanding of the development of the snails from hatching to adulthood would help in the interpretation of these results, and vice versa.

While we were able to glean several insights related to the growth of *P. maculata*, and related sex-dependent differences, there is still much to learn to construct a quantitative description of their population dynamics. Namely, some insight into the laying rates of females, the hatching-out processes from egg masses, and the growth dynamics of hatchlings to juvenile and adult snail life stages would be helpful. Further, it may be important to explicitly address the variability seen in the growth rates of individuals. Of course, there are several other pertinent issues that would require field study of this species, such as spread/migration rates and predation. The knowledge gained from this work, however, is presented as a groundwork upon which to build to answer these larger questions relating to the growth, spread, and possible control of this invasive species.

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