Population Modeling of *maculata* Apple Snails: One Model Does Not Fit All

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- *Pomacea maculata*, is recently renamed from the island applesnail, *Pomacea insularum*.
- Native to the Amazon basin.
- Introduced into United States through aquarium trade.

- Major agricultural pest in the Phillippines, China, Laos.
- Feeding on rice crops and causing great economic damage.
- Overgrazing can greatly alter natural balance of local ecosystem. **[Carlsson et al. 2004]**
- Invasive species, once established, very difficult to remove.
- Documented in Alabama, Florida, Georgia, Hawaii, Louisiana, and Texas.
- Known to be a carrier of the rat lungworm parasite in New Orleans and Mandeville, Louisiana populations.
- Historically confused with the channeled applesnail, *Pomacea canaliculata* **[Hayes et al. 2012]**.
- Snails in this experiment (collected from field, raised in lab) have been DNA tested.

- Rapid and profuse reproduction.
- Unknown predator community.
- Potential of population explosion.
- Potentially a vector for snail borne diseases.
- Little has been quantified re: life cycle
  - Eggs in clutches **[Colin et al. 2013]**
  - Clutches contain ≥ 1000 eggs **[Colin et al. 2013]**
  - Non-native range, even more **[Colin et al. 2013]**
  - Eggs begin hatching out, presumably in layers.

Goal:

- Build a mathematical model.
- Calibrate it to make accurate population projections.
- Quantify impact – environmental and economic.
- Aid field workers with control scenarios, cost efficiency.

How can the size of a population change?

- Birth.
- Death.
- Usually nonconstant.

$\Rightarrow$ Need to know the rate of population growth.

To measure the growth of snails at various stages of development, we conducted several growth experiments.

Juvenile to adult snails: weight and sex

- Measurements taken roughly weekly, for 13 weeks.
- Snails were individually marked
  - opaque florescent alpha numeric tags: originally attached to outside of the shell, later glued to operculum instead.
  - PIT tags: originally injected, later glued to the shell instead.
  - marking procedures in development: most individuals < 13 weeks
- Recorded: weight, operculum length, shell length, sex (if possible), identification, date.
- Egg masses removed from tank (no birth).
- Fed leafy plants, vegetables from grocery store.
- Snails used in this study were raised from eggs collected from the field.
- Closed population. No outside field snails introduced (no collection bias).

Sex ratio and weight differences

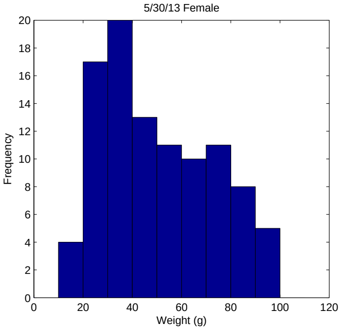
- Number of snails sexed: 99 females and 44 males
- Sex ratio is NOT 1:1.
  - Assuming 1:1 sex ratio may result in underestimation/overestimation in long-term simulations
- Females generally larger than males.
  - The maximal weight observed: 105.1 g for female and 77.2 g for male

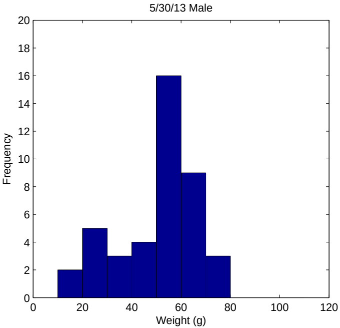
Female			
Top	Mean	Standard Deviation	Number of Observations
25 %	86.7	9.1	25
10 %	94.9	5.4	10

Male			
Top	Mean	Standard Deviation	Number of Observations
25 %	72.0	3.6	11
10 %	76.0	1.6	4

Weight differences (con't)

The weight distribution for females and males are different.





$\Rightarrow$ **Female and male may have different growth dynamics.**

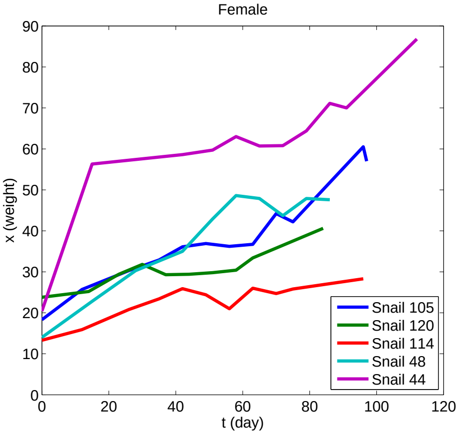
- Females and males may have different growth rates, or growth rate functions (depending on size).
- For our analysis, we consider females and males as different populations with distinct growth dynamics.

Growth rates: Direct calculation at individual level

- Growth rates from direct calculation not statistically supported.
  - Large amount of individual variation observed.
  - Smaller sample size in each weight range.
  - Individual data incomplete.
  - We didn't know how many growth phases were needed, what weight ranges the shifts occurred.
- However,
  - initial calculations of growth rates did confirm the notable differences between small and large snails we had previously suspected – smaller snails generally appear to grow faster than larger ones.
  - one constant growth rate is not appropriate for the whole population.

Individual variation

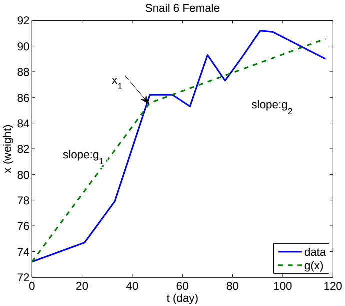
Even F/M snails with the same initial weight range show large amount of individual variation in growth rates.



Individual variation (con't)

- However, some trends were observed – small snails tend to grow faster than big snails, suggests growth is not constant.
- Determined "best fit" growth rates (change in size over a time interval) for weight ranges

$$g(x) = \begin{cases} g_1, & \text{if } x_{\min} \leq x \leq x_1 \\ g_2, & \text{if } x_1 < x \leq x_{\max} \end{cases}$$



Growth rates: Direct calculation at individual level

Table: Growth rates via direct calculation from individual records

Females; 99 total					
Stages	$\leq 23g$	$23.1 - 40g$	$40.1 - 53g$	$53.1 - 71g$	$> 71g$
Mean	0.3531553	0.2316956	0.2332250	0.0626806	0.0935414
std.	0.1199893	0.1525451	0.2550575	0.6382982	0.1362457
N	38	45	40	36	29

Males; 44 total				
Stages	$\leq 24g$	$24.1 - 40g$	$40.1 - 55g$	$> 55g$
Mean	0.302	0.1255556	0.2083333	0.05481481
std.	0.1031504	0.1399206	0.2375723	0.137795
N	10	9	24	27

Growth rates: Estimation at population level

We sought an approach that would take full advantage of the magnitude of the data set, and turned to a population-level approach.

- Determine growth rates in a population-level mathematical model of the female and male subpopulations.
- Quantifying their growth within such a framework is a matter of determining the form (and values of any associated parameters) of a growth rate function.

Population growth model

Since birth/death/predation/growth rates depend on size, we proposed a size-structured model governing the dynamics of the snail population density $p(t,x)$:

$$\frac{\partial p(t,x)}{\partial t} + \frac{\partial (g(x)p(t,x))}{\partial x} = -\mu p(t,x), \quad p(0,x) = p_0(x)$$

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 applesnail, respectively.

- More dynamics (not fluctuations) observed in weight than operculum width.
- growth rate $g(x)$ (perhaps $g(t,x,p)$)
- death (and predation) rate μ (perhaps $\mu(t,x,p)$)
- BC: $(g(x)p(t,x))|_{x_{\min}} = \int_{x_{\min}}^{x_{\max}} \beta_F(t,x)p(t,x)dx$ (zero birth rate under lab setting)

Statistical model of observation process:

$$Y_{j,n} = N_j(t_n;\theta) + \epsilon_{j,n}$$

- θ_0: the "true" value of θ which we assume to exist
- $\epsilon_{j,n}$: error process (i.i.d. random variables)
- $N_j(t_n;\theta) = \int_{x_{j-1}}^{x_j} p(x, t_n; \theta)\,\mathrm{d}x$: number of snails in group j at time t_n
- $\theta = \{\theta_i\}_{i=1}^{n_p}$: parameters in $g(x)$(female), or $h(x)$(male).

Estimate for the values $\hat{\theta}$ of the parameters are those that minimize the distance between data and the corresponding model quantities

$$\hat{\theta} = \arg\min_{\theta\in\Theta} J(y;\theta) = \arg\min_{\theta\in\Theta} \sum_j \sum_n (N_j(t_n;\hat{\theta}) - y_{j,n})^2$$

using the data set $\{y_1, ..., y_{n_d}\}$.

Compute standard errors $SE(\hat{\theta}_p)$ for each parameter estimate $\hat{\theta}_p$ ($p \in \{1, ..., n_p\}$) by $SE(\hat{\theta}_p) = \sqrt{\hat{\Sigma}_{p,p}}$, the square root of the diagonal values of the $n_p \times n_p$ estimated covariance matrix

$$\hat{\Sigma} = \hat{\sigma}^2 \{\kappa^T(\hat{\theta})\kappa(\hat{\theta})\}^{-1}.$$

Estimated variance $\hat{\sigma}^2$ of the observational errors is given by

$$\hat{\sigma}^2 = \frac{1}{n_t - n_p} \sum_j \sum_n (N_j(t_n; \hat{\theta}) - y_{j,n})^2.$$

Piecewise constant growth function

- Initially we take a *m*-stage piecewise constant growth function

$$g(x) = \begin{cases} g_1, & \text{if } x_{\min} \le x \le x_1 \\ g_i, & \text{if } x_{i-1} < x \le x_i; i = 2, ..., m-1 \\ g_m, & \text{if } x_{m-1} < x \le x_{\max} \end{cases}$$

- Female: $g(x)$; Male: $h(x)$
- Determine possible endpoints ($\{17, 23, 40, 47, 53, 60, 71, 85\}$ for females and $\{14, 24, 40, 55, 64\}$ for males) and growth rates for each stage

Approach

- Estimate the rates $\{g_i\}_{i=1}^{m}$, $\{h_i\}_{i=1}^{m}$ with certain values of m
- Use model comparison statistic to determine whether the inclusion of an increase in the number of growth phases and the inclusion of which x_i's provided a statistically significant improved fit to the data.

Model comparison statistic results

Table: Model comparison statistic – female

H_0		H_a		U	Confidence Level
M	$\{x_i\}_{i=1}^{M-1}$	M	$\{x_i\}_{i=1}^{M-1}$		
1	$\emptyset$	2	$\{23\}$	1.240	73 %
1	$\boldsymbol{\emptyset}$	**2**	$\boldsymbol{\{40\}}$	**5.850**	**98 %**
1	$\boldsymbol{\emptyset}$	**3**	$\boldsymbol{\{23, 40\}}$	**5.866**	**94 %**
2	$\boldsymbol{\{23\}}$	**3**	$\boldsymbol{\{23, 40\}}$	**5.866**	**97 %**
2	$\{ 40 \}$	3	$\{ 23, 40 \}$	0.0103	8 %

- **Single-stage growth function is not suitable for female.**
- **More than 2 stages are not necessary.**
- **40 should be included as an end point.**

Model comparison statistic results (con't)

Table: Model comparison statistic - male

H_0		H_a		U	Confidence Level
1	$\emptyset$	3	{ 24, 55 }	4.213	87 %
1	$\emptyset$	2	{ 55 }	0.919	66 %
1	$\boldsymbol{\emptyset}$	**2**	**{ 24 }**	**4.056**	**95 %**
2	**{ 55 }**	**3**	**{ 24, 55 }**	**3.017**	**91 %**
2	{ 24 }	3	{ 24, 55 }	0.112	26 %

- **Single-stage growth function is not suitable for male.**
- **More than 2 stages are not necessary.**
- **24 should be included as an end point.**

Piecewise constant growth function

Thus, a 2-stage piecewise constant growth function

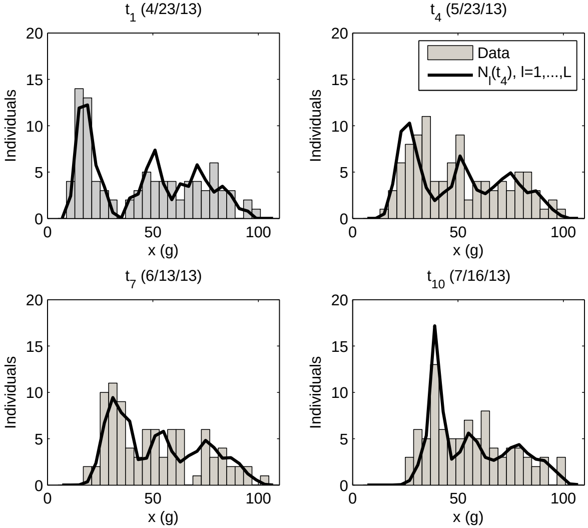
$$g(x) = \begin{cases} g_1, & x \in [x_{\min}, x^*] \\ g_2, & x \in (x^*, x_{\max}] \end{cases}$$

is more appropriate for both males and females, than constant growth rate for these animals.

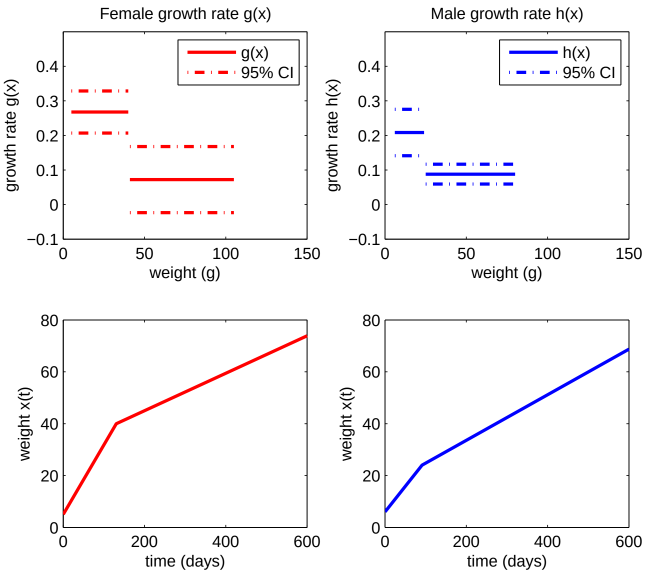
Table: Piecewise constant function

	θ	$\hat{\theta}$	$SE(\hat{\theta})$	SSE
Female	g_1	0.2688	0.0310	979
	g_2	0.0722	0.0487	
Male	h_1	0.208	0.0342	336
	h_2	0.0879	0.0146	

Female data vs model solution



Piecewise constant growth function



- Piecewise constant growth function likely too simplistic.
- We tried other growth functions widely used to quantify growth dynamics of a biological population:
  - von Bertalanffy growth function, sigmoid function, etc.
  - But some of them didn't provide a good fit for this data set for various reasons.

Biphasic power function

Using a power function for prematurity but then scaling that by employing a decline in energy allocation to growth after maturity:

$$g(x; r, \eta, x^*) = \begin{cases} rx^{2/3} & : x \in [x_{min}, x^*] \\ exp(-(x - x^*)\eta)rx^{2/3} & : x \in (x^*, x_{max}] \end{cases}$$

- r: a habitat quality parameter
- η: scales the rate of exponential decline
- x^*: the optimal weight at maturity
  - Initially, we set $x_F^* = 40$ and $x_M^* = 24$.

	$\hat{r}$	$SE(\hat{r})$	$\hat{\eta}$	$SE(\hat{\eta})$	SSE
Female	0.034	0.006	0.174	0.050	1481
Male	0.026	0.008	0.045	0.014	377

Biphasic power function (con't)

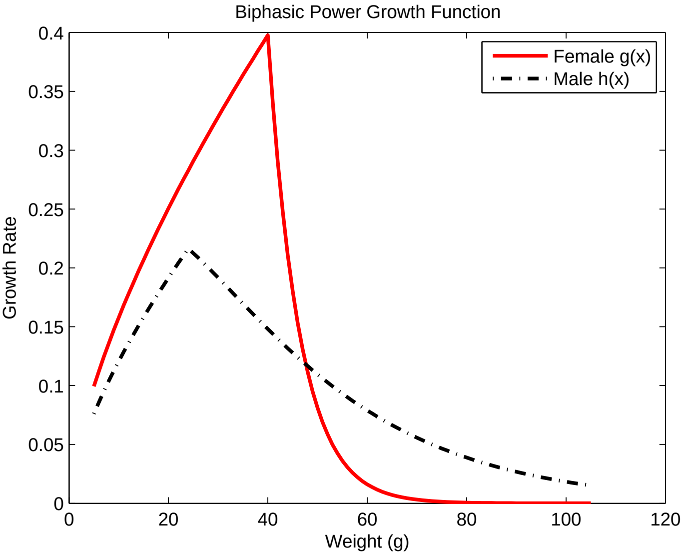


Table: Estimated values of best two candidates for growth functions

Female					Male				
θ_p	$\hat{\theta}_p$	$SE(\hat{\theta}_p)$	$\hat{\sigma}^2$	SSE	θ_p	$\hat{\theta}_p$	$SE(\hat{\theta}_p)$	$\hat{\sigma}^2$	SSE
Piecewise constant growth function									
g_1	0.272	0.0300	124	979	h_1	0.200	0.0175	16	336
g_2	0.0748	0.0434			h_2	0.0806	0.00712		
x_f^*	38				x_m^*	28			
Biphasic power growth function									
r_f	0.039	0.007	149	1041	r_m	0.031	0.027	51	359
η_f	0.084	0.037			η_m	0.040	0.013		
x_f^*	26.727	6.413			x_m^*	15.240	25.145		

Comparison of growth functions

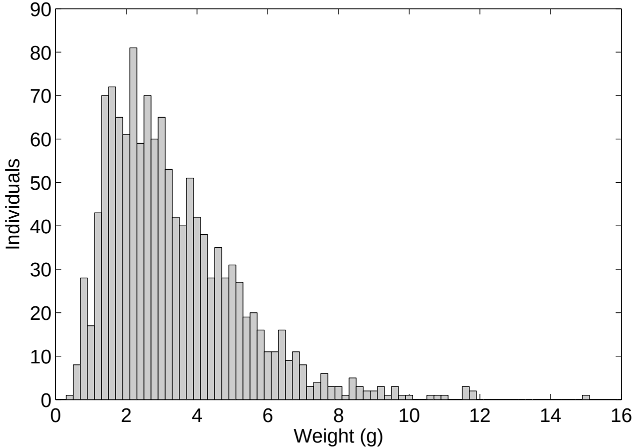
Table: Comparison of the sum of squared errors (SSE) for the best fit of the model to the female and male data with all growth functions.

	Sum of Squared Errors (SSE)			
	piecewise constant	von Bertalanffy	sigmoid	biphasic power
Female	979	1466.8	1195.3	1041
Male	336	403.4	355.4	359

Juvenile weights

- Massive die-off in our snail tank at the beginning of August 2015.
- Several egg clutches were laid on the side of the tank just days before that die-off.
- Hatched out between July 15 and 25, 2015.
- On September 25, 2015, we drained the tank and collected all the snails (1352 in total, 1287 with intact shell).
- Individually weighed and measured shell length.
- 150 snails were randomly selected and returned to the tank for continued monitoring. The rest were euthanized.

Figure: Weight distribution of snails measured on September 25, 2015.



Variability in growth rate strongly suggested!

Time to reach reproductive maturity

On October 6, 2015, first egg clutch was found in tank.

- **this population of *P. maculata* reached reproductive maturity in 73-83 days**
- much earlier than other researchers observed
  - Arfan et al: becoming reproductively matured in the 32nd week after hatchling
  - Ostrom et al: juvenile to adult maturity in 180 days
- important piece of information for long term population projection
- has impact on the prediction of different control strategies
- might has impact on how big snails can grow into and how long snails can live

Hatchling weights

- Collected egg clutches from the side of the snail tank and allowed them to hatch out in individual buckets
  $\rightarrow$ follow snails from single egg clutch.
- Every 5-8 days, snails in each hatchling bucket were weightd in groups of 5-20 until the hatchlings were large enough to be measured individually.
- Followed 7 cohorts of snails (from 7 egg masses) using this method.

	Mean	Standard Deviation	Total Number
Individuals	0.00180	0.0007	91
All in Groups	0.00162	0.0006	2041

$\Rightarrow$ Rough estimates of growth rate for snails weighed on September 25, 2015: 0.0463 - 0.0537 g/day.

Temperature dependent growth

- During March 26, 2016 and June 3, 2016, we set up inside and outside trials to study the seasonal effect on hatchling growth rates.
- Inside trials were kept in saltwater lab, where the temperature is around 21 °C (weekly average temperature during this period was 20.461-21.331 °C).
- Outside trials were kept in greenhouse, where temperature fluctuate.

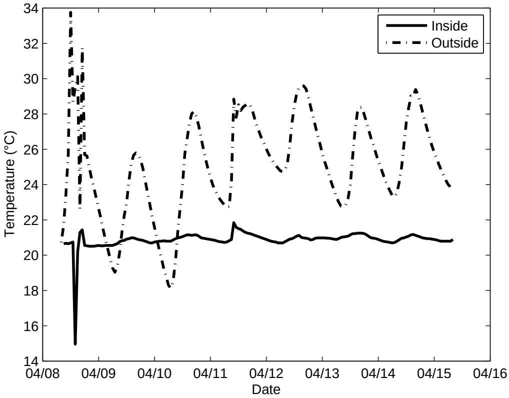
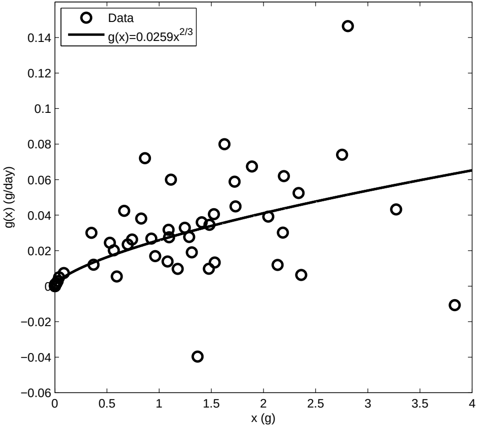


Figure: Hourly temperature in the saltwater lab (inside) and greenhouse (outside) from 4/8/2016 8:00 to 4/15/2016 7:00 (CST) measured by temperature loggers.

Early growth dynamics under steady temperature

Using the cohort average growth rates and mean weights of inside hatchling data sets, we were able to obtain estimates for early stage growth rates. Clearly power growth function provided a better fit for the weight range $x \in [x_{min}, 4]$.



Temperature dependent growth

Table: Estimated parameter values in $g(x) = \theta x^{2/3}$ under different temperature.

	Temperature($^\circ$C)	$\hat{\theta}$	x	$\frac{g(T)-g(T_{base})}{g(T_{base})}$
Outside	[5.5,10.5)	0.0062	$[x_{min}, 0.2]$	-0.7606
	[10.5,15.5)	0.0153	$[x_{min}, 0.2]$	-0.4093
	[15.5,20.5)	0.0345	$[x_{min}, 0.7]$	0.3320
	[21.5,26.5)	0.1183	$[x_{min}, 7]$	3.5676
	[26.5,31.5)	0.0802	$[x_{min}, 27]$	2.0965
Inside	[20.5,21.5)	0.0259	$[x_{min}, 4]$	0

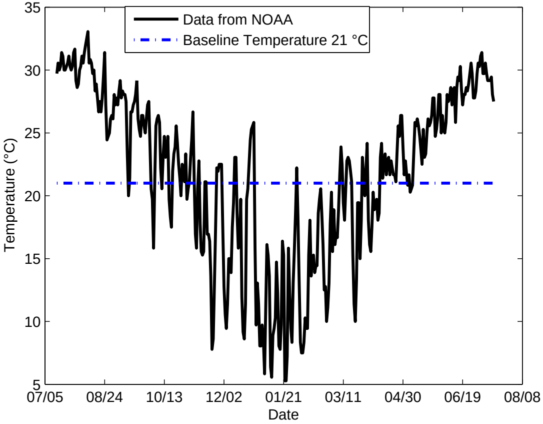


Figure: Daily average temperature data from 7/15/2015 to 7/15/2016 obtained from NOAA.

Seasonal component

Assume the growth rate of snails weighing x g at time t to be

$$g(x,t) = g_{base}(x,t)(1 + \Delta g(x,t))$$

where $g_{base}(x,t)$ is the baseline growth rate for snails weighing x g at time t, which is the growth rates at 21 °C, and the seasonal component is given by

$$\Delta g(x,t) = Asin[\frac{2\pi}{C}(t+\lambda)] + D$$

where the parameter A is the amplitude of the sine wave representing the seasonal variation in growth rate, λ is the time lag between mean temperature and growth oscillation, and $C = 365$ since the growth rate is per day.

Seasonal component(cont'd.)

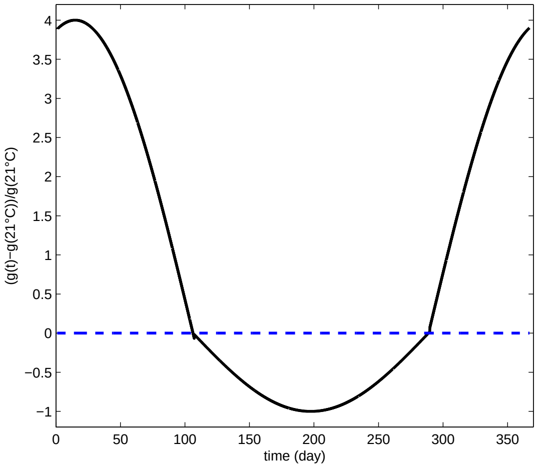


Figure: Seasonal component assuming t_0 is 7/15/2015.

Size-dependent mortality function

Assume

$$\mu(x) = a_1 e^{-b_1 x} + a_2 + a_3 e^{b_3 x},$$

where x is the weight of applesnail, a_1, a_2, a_3, b_1 and b_3 are constants.

- This approach incorporates three adjustment hazard patterns:
  - hazard for immature animals,
  - hazard for mature animals,
  - hazard for senescence.
- These three risks are assumed to be competing, but noninteracting [Siler 1979].

Size-dependent mortality function(cont'd.)

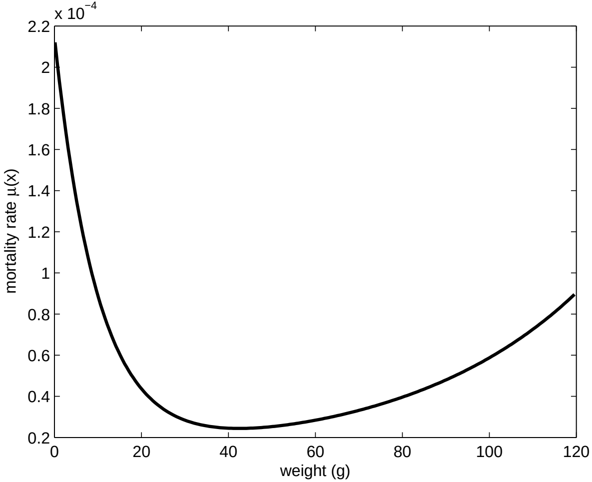


Figure: Mortality function $\mu(x) = a_1 e^{-b_1 x} + a_2 + a_3 e^{b_3 x}$ with $a_1 = 0.0002$, $a_2 = 0.00001$, $a_3 = 0.000004$, $b_1 = 0.1$ and $b_3 = 0.025$.

Current/Future Work

- Does variability in growth rates provide improvement?
- Characterization of hatching out process.
- Birth rate $\beta(x, t, p)$ may involve (distributed) time delay.
- Death rate $\mu(x, t, p)$.
- Growth rate $g(x, t, p)$.
- Modify field data collecting strategy.
- Quantify the local populations.
- Predict long-term population dynamics and impacts.
- Recommendation re: population control.

Thank You

Questions?