MATRIX MODELS OF POPULATIONS OF POWELLIPHANTA AUGUSTA IN CAPTIVITY AND IN THE WILD

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Abstract: The main population of a recently discovered species of landsnail, *Poweliphanta Augusta,* has been taken entirely into captivity. Using data from a sample population we model their growth with von Bertalanffy, logistic and Gompertz functions. We model their fecundity and mortality using data both from their distribution of sizes at capture and dynamics in captivity. We construct population matrix models for their population dynamics both in the wild and captivity. Using these matrix models we asses their ability to survive in these two environments, and calculate their stable size distribution in captivity. Additionally we evaluate the elasticity of these matrices to see the relative importance of their entries to their eigenvalues. Using these we evaluate the effects of small changes, and make recommendations about what changes to their dynamics would cause them to increase or decrease in number.

Key words: Poweliphanta Augusta; *Gompertz; von Bertalanffy; logistic; landsnails; population matrix model; elasticity analysis;*

INTRODUCTION

Poweliphanta Augusta is a recently discovered species of carnivorous land snail of the *Poweliphanta* genus, native only to the Stockton coal plateau of Mount Augustus in New Zealand (Walker, Trewick, & Barker, 2008; Walker K. 2006;) . Due to coal mining of their habitat by a New Zealand resource company, Solid Energy, most of the native population of snails has been removed. These snails are now held in captivity by the New Zealand Department of Conservation (DoC) or have been released outside their original habitat.

Before the mining, the Stockton plateau had highly acidic and infertile soil, low drainage and was exposed to heavy wind and rain. Despite these harsh characteristics it had become home to highly complex ecosystem, including many animals and plants that had been uniquely adapted to survive there. On the basis of this it was recommended for government protection on the basis of its complex ecology and biodiversity. (Overmars, Kilvington, Newell, & Rhodes, 1998).

The *Poweliphanta* genus are exclusively found in New Zealand, and like *P.Augusta*, most have extremely small habitats and generally suffer from declining populations due to predation (Walker K. , 2003). As a result the species and subspecies of this genus have been given a high conservation status.

One of the characteristics that differentiates *P.Augusta* from the majority of snails in their genus is their ability to survive in the harsh terrain of the Stockton plateau. Large land snails require both calcium for shell and egg formation, and plentiful earthworms for prey. As a result genera other than *P.Augusta* generally live in the areas where these prey are plentiful, areas with alkaline and well drained soil. (Walker, Trewick, & Barker, 2008)

On the basis of the work done on their mitochondrial DNA by (Trewick, 2008) they are believed to have a sister taxon relationship with the lowland species *P.Lingaria*, but are also believed to have been isolated for thousands of years during which they became a part of the unique Stockton ecosystem. (Walker K. , 2006;)

Like all of New Zealand, the Stockton plateau was protected by the 1991 Resource Management Act (Ministry for the Environment, 1991). Under this act, a project detrimental to the environment as the open cast mining of an area so ecologically valuable would not be allowed. However Solid Energy had a license to mine the area pre-dating it, and were allowed to expand their mining operation to encompass 94% of the natural habitat of *P.Augusta* (Save Happy Valley Coalition, 2009). Whilst this mine extension was legal it was described as *"noxious"* by the Environmental court who also went on to say *"we think there is little doubt that from the scientific and environmental point of view, the snails should not be moved"* and *"We record our disappointment at what has occurred".* (Kenderdine, 2006)

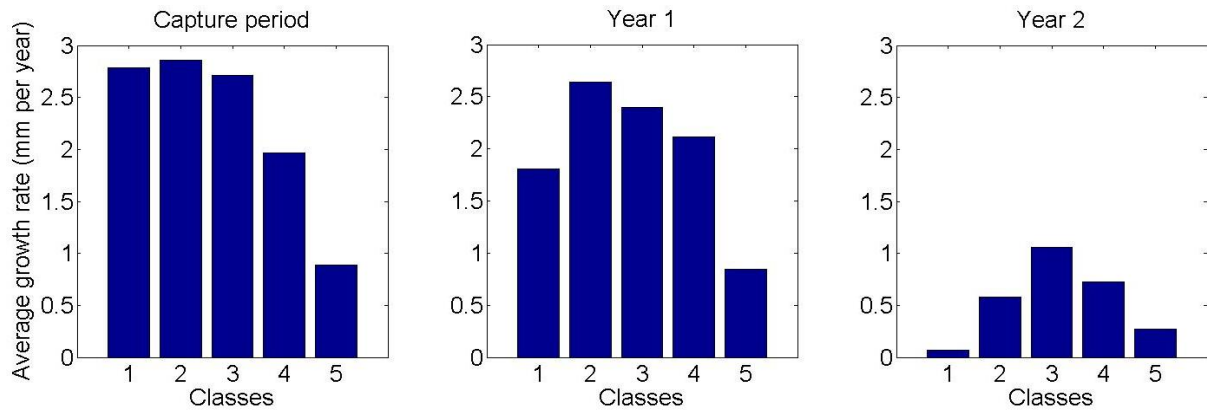A contributing factor to the courts negative view of the decision to let this area be mined was likely an

Fig. 1 Average growth rates for size classes, based on the linear interpolation of sizes of individuals.

affidavit by Kathleen Walker (Walker K. , 2006) in it she notes that *P.Augusta* had neither been successfully bred in captivity, nor successfully transplanted to another area and that in the past other genera of Powelliphanta had usually faired poorly when relocated outside of their natural range.

We have modelled the growth of an individual snail using the Gompertz, logistic and Von Bertalanffy functions as discussed in (Hernandez-Llamas & Ratkowsky, 2004; Turner Jr., Bradley Jr., Kirk, & Pruitt, 1976). Due to changing growth rates, we create separate models for their growth at capture and their growth in the first and second year of captivity.

These models of individual growth were used to develop matrix models of the dynamics of populations in the wild and in captivity, similar to those discussed in (Caswell, 2001; Lefkovich, 1965). We calculate the elasticity of these matrices to find the sensitivity of their parameters to proportional perturbations, and discuss the effect that this should have on the priorities of people working with the captive snails or looking for a new habitat.

Conditions in captivity

In their statistics, the Department of Conservation divided snails into five size classes, based on the maximum diameters of their shells: hatchlings (<13mm), juveniles (13-20mm), sub adults 1 (20-27mm) , sub adults 2 (27-32mm) and adults (>32mm) (DoC, 2009). We number these classes 1-5 respectively. Table 1 shows the numbers of snails found in each of these classes.

Not all snails were captured at the same time. We define the period that they were found in, from 25/07/2006 to 30/05/2007 as the capture period. In this period a total of 6044 snails were found. In addition to

this 7 snails were taken into captivity four months later, on the date 09/09/2007. In this body of work we define 30/05/2007, the end of the capture period, as day zero, taking all dates after and before as relative to it. Labelling the periods form 31/05/2007-30/05/2008 and 31/05/2008-30/05/2009 as year 1 and year 2 respectively

The maximum diameter and weight of all the snails when they were captured was recorded, as well as the maximum diameter of the parent of each egg that has been found. Additionally we have the size class of every snail on its death, although in the data provided by the Department of Conservation there is no distinction made between members of the classes sub adults 1 and 2. (DoC, 2010) Measurements of maximum diameter are thought to be accurate to within 1mm, with errors being caused by the angle the snail is held at (Gerraty, 2010).

Whilst we do not have more than one measurement for the majority of snails in the population, we have multiple measurements of the snails in a small sample. It contains 240 snails from the wild, picked to represent so that for each size class there were 10 snails each from the 10 sub areas their habitat was divided into. (DoC, 2009) In addition to the snails that were captured from the wild put in this sample, it also contains 146 snails that were born in captivity.

These snails were measured at intervals of roughly once a year initially, although in the second year of captivity some snails begin to be measured more often, in intervals as small as 100 days. As a result the number of measurements for each snail varies.

Because we do not have data for all snails after the second year of captivity, we create our models exclusively from data obtained in those years and have three to five measurements for the majority of our

snails. The rates at which these snails have grown in different years are shown in Fig. 1.

Due to the fact that we have comparatively few measurements we use linear interpolation to estimate each snail's size on a given date. As each snail may enter or leave a size class between measurements we also use linear interpolation to estimate the length of time each snail spends in each class. During the capture period, year 1 and year 2, we average the interpolated amount grown by each snail on each day to find the average growth rate.

Members of the classes 1,2 and 3 growing at a rate of almost 3 mm per year on average (2.8, 2.9 and 2.7 mm per year respectively), members of classes 4 and 5 grow slower at rates of 2.0 and 0.9 mm per year respectively. In the first year of captivity classes 1 2 and 3 reduce their average growth rates to 1.8, 2.6 and 2.4 per year. Class 4 shows a small increase to 2.1mm per year and class 5 reduces to 0.8 mm per year. In the second year we see even greater reductions in growth rate with the five classes reaching 0.1, 0.5, 1.0, 0.7 and 0.3 mm per year respectively.
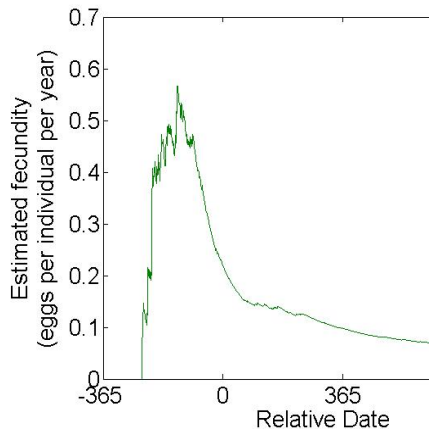

Fig. 2 Rolling estimate of fecundity

In Fig. 2 we see an estimate of the rate that eggs had been laid. Notably within the capture period we see just over half of all eggs being laid, despite the fact that on average during this time there were fewer adult snails in captivity, even for an adult snail captured on the first day of this period it would represent less than a third of its total time in captivity.

Because after the capture period we see rapid declines in fecundity, we needed a method to calculate
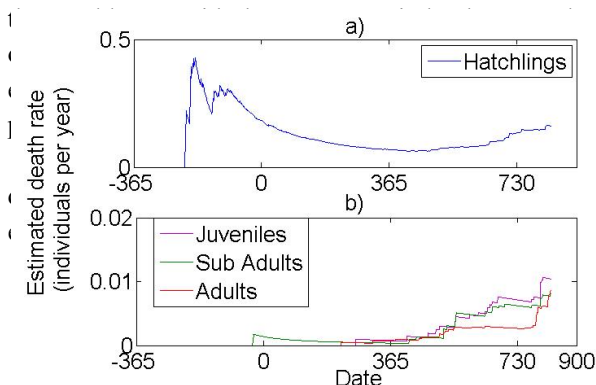

Fig. 3 Rolling death rate estimates for a) hatchlings b) other

any day. We label this chance day As not all snails have been in captivity for the same length of time we use $( )$ to represent the total number of days in captivity spent by snails before day . Correspondingly we use $( )$ to represent the number of eggs produced before day . We then find the mean number of eggs produced per adult snail per day and per year before the day , with the formulas:

$$\text{day}( )=$$
$$\text{year}( )=365 \ \text{day}( )$$

(1)

In Fig. 2 we see our rolling estimate of fecundity. Our estimate of adult fecundity year reaches a maximum of 0.57 during the capture period, and rapidly declines afterward to less than 0.2 eggs per adult per year for almost all of year 1 and year 2.

Additionally we run these models through year 1 and year 2 separately to get the fecundity and mortalities we shall use for our models of the population in captivity. These results are shown in Table 2

The Hatchlings produced in captivity, initially had maximum diameters were closely grouped (standard deviation of 0.6mm) around a mean of 8.15mm.

We develop a similar estimate of mortality. If class has $( )$ deaths before day the per individual per day mortality rate day is calculated as

$$\text{day} \ ( )= \ ( ) \ ( )$$

(2)

Because each snail may only die once but have multiple eggs the method of calculating the annual mortality form the daily one is more complicated than calculating annual fecundity from daily fecundity (1).

$$\text{year} \ ( )=1-1- \ \text{day} \ ( )365$$

(3)

In Fig. 3 we see the estimated rate of deaths in the classes snails are divided into. Notably graphs of data for the hatchlings are on different axes to the same data for the other size classes. The death rates of the larger size classes (Fig. 3b) have been almost zero throughout the capture period and the first year, and began to rise in the second year. The hatchling death rate saw sharp spikes in the capture period, reaching 0.43, remained low in the first year, and increased slowly throughout the third year.

During the time the snails have been in captivity they have seen dramatic change in birth rates, death rates and growth rates (Fig. 1-3). As a result it is hard to determine which of these dynamics is consistent with those of a population living in the wild.

METHODS

Overview

We attempt to model the population living both in captivity and in the wild. Because we do not have accurate growth data for individuals living in the wild, and the growth rates of individuals in captivity is declining, we fit our models to the initial growth rates and sizes of individuals in captivity. As a result we determine the lengths of time that individuals spend in the five size classes.

We then construct matrix models of the population as a whole, using these lengths of time to calculate the probability an individual will move out of a size class.

Due to the variability of our estimates of birth rate and death rate in captivity, we derive the relationship between these unknown parameters and the stable size distribution of our population in the wild which is also the right eigenvector of our population matrix.

After calculating the components of this matrix we consider its elasticity to determine the effects of changing individual parameters on long term population growth.

We develop models of the captive population using the growth, death and birth data from each individual year. Using these we consider the long term stability of the captive population.

Finally we calculate the elasticises of the matrix representing the population in the second year of captivity, and examine the importance of its components

Creating and comparing models of growth

We chose to test growth models of three different kinds, Von Bertalanffy, Logistic and Gompertz (Turner, Bradley Jr., Kirk, & Pruitt, 1976) all of which have two parameters to be estimated. The first of these parameters is ∞, measured in millimetres, which is

These models, assume that the creature at a given size, , will always grow at a given rate, , however we have seen that snails of a given size grow less in later years of captivity than snail of that size when first captured (Fig. 1). As a result, rather than fitting a growth function that relates to for an individual (Ricklefs, 1967) (Hernandez-Llamas & Ratkowsky, 2004) we fit to for the entire sample populatino between their first two size measurements.

We estimate the parameters and ∞, by dividing our models into and a non linear term and use a method of least squares to estimate their coeficients, with data from the snails measurements at capture, and their first measurement in captivity. We choose these first two measurements to minimize the effect of the snails slowing growth.

We find with the formula, and pair it with which is defined in terms of the first two measurements 1 and 2:

$$= \ 2 - \ 1 \quad 2 - \ 1 \ = \ 2 + \ 12$$

$$(7)$$

Fig. 4 shows the curves in eq. 4-6 being fitted to the data. Each blue datapoint represents a pairing *(,)*. Curves were also fit ro pairings of the form *(1,)* and *(2,)* but it made little differerance to the parameter values of the models.

Data points that had values in excess of two standard deviations, away from the mean value for the group were removed, alongside data points with negative values.

In Table 4 we see that the logistic model has a considerably beter R-squared value (0.44) than either of the other two models (0.28 and 0.38). Because this data represents growth between the first and second measurements made on different snails, and these measurements were not made a constant interval of time apart, we have several sources of error. In addition to measurement error, we have potential for error due to varying growth rates between snails and varying growth rates caused by different lengths of time in captivity. Bearing this in mind the data is quite well fitted by the logistic model.
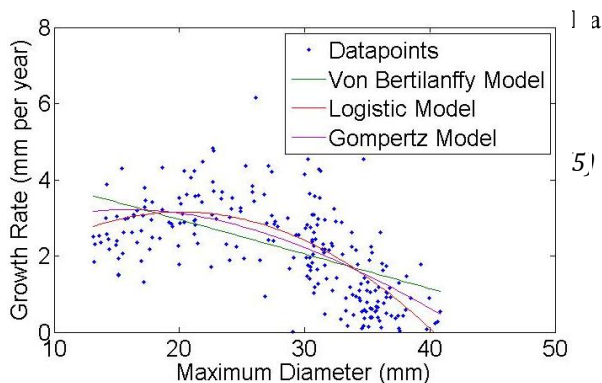
To model the growth of each individual during years 1 and 2 of captivity we use the same process, but rather than using the size of each individual on its first measurements we use a linear interpolation on each individuals maximum diameter, to find it at the beggining and end of year 1 and year 2. The parameter values of these models and their R-squared terms are also shown in Table 4.

Due to the dramatically better fit atchieved with the logistic model in each case, we assume logistic growth throught the rest of this paper.

Estimating time spent in each life stage

Before we can develop population models we need to know how long it will take for a hatchling to become ready to breed.

We solve the eq. 4-6 to find the length of time it would take for an individual of a given size to reach another given size.

From this we can estimate the time taken spent in each life stage, for a hatchling to reach adult, using the parameters we established by fitting the curves.

Because in our models growth is dependant on size, we also need a starting size for hatchlings. In our data 8.15mm has been the mean initial maximum diameter.

The predicted length of time spent in each class, according to the model we made for initial growth and growth in year 1 and year 2 are shown in Table 3.

Modelling a population in the wild

We compose the population vector $(\ )$ from entries of the form $(\ )$, representing the number of individuals in the h class at the time

$$+1=\quad (\ ) \tag{8}$$

Whilst the snails have been previously divided into 5 stages, the data we have suggests that there is little difference between classes 2-4, juveniles, sub adults 1, sub adults 2 respectively. In this model we merge these classes into one larger class of sub adult with a maximum diameter between 13 and 32 mm. As a result we now have three classes: juveniles, sub adults and adults.

We also assume that the lengths of time spent in each class shown in Table 3 based on the logistic model are an accurate portrayal of what will happen in the wild. We create the probabilities and representing the probability that a snail remains in, or grows out of the th class in a year given that it survives for that year. If the expected time a snail will remain in the h class is then we set $=1$ and $=-1$ respectively.

We define the value as the probability an individual survives 1 year in the h class, and to be the number of hatchlings produced per adults per year, because data relating to these values has varied so much (Fig. 2 and Fig. 3) we will be unable to estimate them from year$(\ )$ and year .

Using these components we can construct a population matrix to be used in eq.8 of the form

$$= 1 \ 10 \quad 1 \ 1 \ 2 \ 200 \ 2 \ 2 \ 3 \tag{9}$$

This population will have a stable size distribution , which will also be the right eigenvector corresponding to the matrixes largest eigenvalue, .

$$= \tag{10}$$

We have additional information about the structure of their population in the wild shown in Table 1. Because hatchlings are comparatively small (<13mm) we shall assume that this table represents the correct numbers for the other classes of snails (2 and 3), but that the full number of hatchlings in the wild 1 was not collected.

Solving this to obtain components of the eigenvector in terms of our parameters we obtain a system of equations:

$$1= \ 3 \ 1 \ 1+ \quad 2= 1 \ 1 \ 1 \ 2 \ 2+ \quad 11(12)(\\ 3= 2 \ 2 \ 2 \ - \ 3 \qquad\qquad 13)$$

Initially we have 6 unknowns (1, , , 1, 2, 3) however we can simplify this with a small number of assumptions. The population of *P.Augusta* on the Stockton plateau has remained there for thousands of years (Trewick, 2008) over this time it has neither disappeared, nor expanded to any great size, as a result we assume it had reached a stable size, and as a result had ≈1 as its eigenvalue.

Having seen the death rates of the larger size classes remain very close to each other in captivity in Fig. 3 we assume that they will have similar death rates from natural causes in the wild. Additionally as snails in these classes are much larger than the hatchlings, we also assume that they will have similar death rates form predation. As a result we give snails in the adults class the same annual survival probability as snails in the sub adult class and set 3= 2.

In eq.13 2 is related exclusively to known parameters. From this equation we can derive its value 0.83. Our remaining unknown parameters are related to each other in eq. 12 and 13. We solve these for 1 and

and substitute the value of our known parameters to obtain

$$=-0.41+0.00047 \quad 1 \quad 1=1731 \quad 1 \qquad (14)(15)$$

These dependencies are graphed together in Fig. 5.
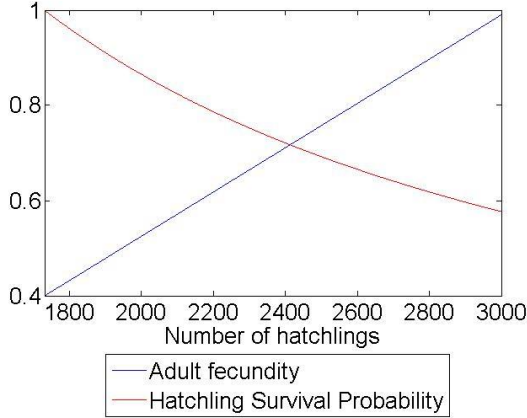

Fig. 5 Dependence of   and   on

We can constrain 1 so it corresponds with the range of values for 1 and   seen in captivity. In Fig. 2 we see estimated fecundity,   year , ranging from 0-0.71 If these values are representative of a population in the wild we can get an upper bound on the value of 1 of 2097.

The region where 1<2097 corresponds to 1>0.82. Comparing this with Fig. 3a we can see that estimated mortality has been consistent with this after the capture period (year1<0.18). Assuming that hatchling deaths in the wild remain in this range would give us a new lower bound for 1 of 1845

As a result the range of values for 1 supported by our data on 1 and   , (1845-2097) is very narrow.

We can now calculate possible population matrices based on these bounds. Assuming 1 is at its minimum bound 1845 we obtain:
Conversely, assuming 1 is at its maximum bound 2097 we obtain:

$$=0.4100.570.410.70000.130.82 \qquad (17)$$

We can use the method to find elasticity set out in (Caswell, 2001) this will show us the population response to proportional perturbations. For   , an element of   , the corresponding value of the elasticity matrix   , is defined as $=\partial \quad \partial \quad .$

For $1=1845$ we obtain
$$=0.0800.200.120.21000.030.44 \qquad (18)$$

For $2=2097$ we have

$$=0.0600.300.090.22000.030.44 \qquad (19)$$

The element 33 in either case exceeds all other elements. As a result the population would be by far most sensitive to changes in the survival probability of the breeding population, 33.

In captivity we have seen extremely low mortality rates amongst adult snails Fig. 3. These correspond to much higher survival probabilities than those predicted in the wild $2= 3=0.82.$ this discrepancy could be explained by the predation of *Poweliphanta* snails by other species as noted in (Walker K. J., 2003).

Because of the large value of 33 even small increases in predation over that of their original habitat could destabilise an otherwise stable population, once they are returned to the wild. Conversely a small decrease would allow them to thrive.

Modelling a population in captivity

The captive population has different dynamics to those predicted for the wild. Whilst there is no predation, so much lower death rates for the larger size classes, fecundity and growth rates are gradually dropping as shown in Fig. 1 and Fig. 2.

Because key characteristics of the population are changing whilst they are in captivity, our aim here is to create two separate matrix models for the dynamics observed in the first and second years of captivity. As a result our model is of the form:

$$+1= ( ) ( ) \qquad (20)$$

Where $( )$ is a matrix of the form shown in eq.9, but with all of the parameters in its entries also being functions of time. These entries can be calculated from Table 2, and Table 3.

In Table 3 we see the effect of the changed values of our models. Snails spend longer in all classes. The

$$=0.4700.450.470.70000.130.82 \qquad (16)$$

time required for snails to reach adult hood is also dangerously long. Whilst *Poweliphanta* lifespans have been estimated to be as long as 20 years (DoC, 2010) it would be potentially very dangerous for a population for it to take 18 years for hatchlings to reach breeding age.

We choose not to create models for the capture period, due to the additional complexity caused by each snail being in captivity for a different period of

time, and the fact that most snails spend considerably less than half of a year in captivity during this period

MATRIX MODELS OF CAPTIVITY

We can create matrices in the form of (eq. 10) to model the population whilst it remains in captivity. For the data from year 1

$$A_1 = \begin{matrix} 0.74 & 0.13 & 0.22 \\ 0.92 & 0 & 0 \\ 0 & 0.07 & 0.999 \end{matrix}$$

This has a dominant eigenvalue of $\lambda = 1.053$ corresponding to the stable size distribution (eigenvector) of 1.57 adults and 1.03 sub adults for every hatchling.

For the data from year 2

$$A_2 = \begin{matrix} 0.77 & 0.13 & 0.32 \\ 0.97 & 0 & 0 \\ 0 & 0.01 & 0.995 \end{matrix}$$

This has a dominant eigenvalue of $\lambda = 1.003$ corresponding to the stable size distribution (eigenvector) of 2.38 adults and 1.81 sub adults for every hatchling.

It may be noted that the dominant eigenvalues for the matrix model of the population both in Year 1 and Year 2 are greater than 1. These suggest that the population of the snails in captivity will increase in the long term.

However, it seems unlikely that adult snail death rates will remain as low as they are in Table 2. The year 2 death rate in this table is 5.5×10^{-3}, if a population were to have this as their death rate we would expect snails to live for an average of 181 years after becoming adults, which is unrealistic.

In Fig. 6 we see estimates of the sizes of the three classes of snails in captivity for the next 20 years. The estimate for 0 years in captivity corresponds to the number of snails in each class after they were captured minus the deaths in this period. The estimate for year 1 corresponds to the product of A_1 with the class sizes in the zero years. Estimates for year two and beyond are from the product of A_1 with the previous year's class sizes.

Due to the very low death rates of the adult class it continues to increase in number for the period of time show in this graph. This increase in number corresponds with increasing numbers of hatchlings, despite the low fecundity. However as hatchling growth is slow, the number of sub adults decreases.

Fig. 6 Estimates of class sizes for 20 years of captivity

Whilst this model predicts that the number of snails shall increase it is very sensitive to changes in adult mortality. The elasticity matrix corresponding to A_2 is

$$E_2 = \begin{matrix} 0.02 & 0.07 & 0.00 \\ 0.20 & 0 & 0 \\ 0 & 0.00 & 0.75 \end{matrix}$$

The value corresponding to a_{33} is vastly in excess of all other elements of this matrix.

If we solve the equation $A_2 = \lambda$ for an unknown value of a_{33}, adult survival, we get that $a_{33} < 0.985$ corresponds to $\lambda < 1$, and a decreasing population. As a result it is imperative to keep adult mortality as low as possible.

DISCUSSION

One problem encountered by our models was the difference in growth rates between individual snails. Because we fit our curves to information that described the majority of snails and excluded outliers it is possible that there are a still group of snails growing faster than the majority of the population, who will reach breeding size much earlier. Whilst this is possible, it is also possible that the apparent faster growth of some snails is due to measurement error. As we have only a small number of measurements per snail it is hard to determine which.

If a small number of snails were growing faster they could contribute to sustaining the breeding population of adults, despite increasing death rates.

As a result a good extension could be to model the snails growth individually, although as growth rates are declining such a model may have to they include functions of the length of time these snails have spent in captivity.

Our models of the population in captivity suggest that the population is stable for the immediate future. However as the observed death rates within the adults class have been increasing since the beginning of their

time in captivity, it is very possible that population dynamics will become stable in the near future.

However it is clear that with individuals having such dangerously low growth rates, it is clear that biological reasons for these effects have to be found, so that we can increase these growth rates again.

The difference between the growth rates observed in the second year of captivity, when compared to the third year illustrate that these snails growth rates can change extremely quickly. If a biological explanation is found it is possible that current growth rates could be improved greatly.

Our models of the population in the wild illustrate the importance of adults remaining from year to year. As a result it is important to put them in an area of low predation.

Further modelling of the population in the wild could include density dependence. Due to the nature of the data we have we were unable to include it. As we do not have the details of which snails are kept together, or the numbers of snails in each container, we do not have the data necessary to assess the effects of varying densities on their reproduction.

A second addition that could be made to the models developed here is time delay. In captivity eggs have taken 12-15 months to hatch (although this may be much shorter in the wild) It is possible that the number of eggs that hatch in any year depends both on the number of adults in that year, and the last.

ACKNOWLEDGEMENTS

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Class number	Classification	Range of maximum diameters (mm)	Number captured	Number of eggs produced during captivity
1	Hatchlings	0< ≤13	848	0
2	Juvenile	13< ≤20	954	0
3	Sub adult 1	20< ≤27	902	0
4	Sub adult 2	27< ≤32	1046	17
5	adult	32≤	2150	546

Table 1 initial class sizes and egg production

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Year	Birth rate	Death rates		
		Hatchlings	Sub adults	Adults
1	0.13	0.30×10^{-1}	0.50×10^{-2}	0.90×10^{-3}
2	0.15	0.20	0.15×10^{-2}	0.55×10^{-2}

Table 2 Table of Birth rates and death rates in year 1 and year 2

Stage	Predicted length of time at each stage(in years)		
	First two measurements	Year 1	Year 2
Hatchlings	2.01	4.2	24.6
Juvenile	2.32	4.8	27.6
Sub adult 1	2.31	4.9	25.9
Sub adult 2	2.05	4.2	20.6
Total time to adulthood	8.69	18.2	98.8

Table 3 Estimates of time spent in each stage of growth

Values used for 1	Values used for 2	Model type		∞	R squared
Measurement on capture	First Measurement in captivity	Von Bertalanffy	0.09	52.59	0.28
		Logistic	0.31	40.31	0.44
		Gompertz	0.20	43.20	0.38
Interpolated size at the beginning of year1	Interpolated size at the end of year1	Von Bertalanffy	0.04	53.2	0.28
		logistic	0.15	40.6	0.41
		Gompertz	0.09	43.5	0.37
Interpolated size at the beginning of year2	Interpolated size at the end of year2	Von Bertalanffy	0.03	103.1	0.023
		Logistic	0.02	44.1	0.15
		Gompertz	0.01	51.3	0.10

Table 4 The R-squared values and parameters for growth models