Structured population models

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2014-02-03

Introduction

- Up until now we've tracked populations by density or size
- What are some organisms for which this seems like a good approximation?

What is a population for which unstructured models won't work well?

Structured populations

- If we think age or size are important to understanding a population, we might model it as a **structured** population
- What would this involve for a model?
- Instead of just keeping track of the total number of individuals in our population …

Regulation (not)

- Structured population models with regulation can have insanely complicated dynamics
- Here we will focus on understanding structured population models **without regulation**
- Individuals behave independently
- Average *per capita* rates do not depend on population size
- What is a practical situation where unstructured population models could be useful?

Age-structured models

- Simplest structured models keep track of **age**
- Model individuals per *age class*
- Typically use age classes of one year

- **Example**: Salmon live in the ocean for roughly a fixed number of years; if we know how old a salmon is, that strongly affects how likely it is to reproduce
- Age structured models are simple because we know how individuals move from one class to another

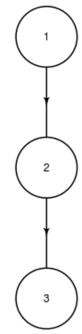


Figure 1: plot of chunk agepic

Stage-structured models

- In stage-structured models, we model how many individuals there are in different **stages**
- i.e., newborns, juveniles, adults
- more flexible than an age-structured model
- **Example**: forest trees may survive on very little light for a long time before they have the opportunity to **recruit** to the sapling stage

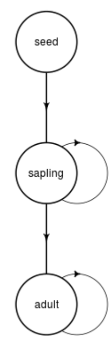


Figure 2: plot of chunk stagepic

Age structure and continuous time

- Age structured models are usually done in discrete time, for simplicity

- Since continuous-time models are generally simpler (and smoother), what makes them difficult for age-structured models?

- We will focus on age-structured, discrete-time, unregulated models – the simplest place to start

When to count

- We will choose a census time that is appropriate for our study
- Before reproduction, to have the fewest number of individuals
- After reproduction, to have the most information about the population processes
- Some other time, for convenience in counting

How to count

- What quantitities would we want to measure to understand an age-structured population?

- Should be related to the quantities we measure to understand simple populations

- These are the quantities that allow us to translate our ideas into an answer:

- If we have a given population structure this year, what do we expect to see next year? Or in 10 years?

Activity: counting and calculating

- Imagine a population of dandelions
- Adults produce 80 seeds each year
- 1% of seeds survive their first year to become adults
- 50% of first-year adults survive to reproduce again
- Second-year adults never survive
- **Will this population increase or decrease through time?**

Reproductive number

- Calculating the finite rate of increase λ for this population is surprisingly hard

- You need to know the proportion in each age class to calculate p; but it's not easy to find that proportion without knowing how the population is growing

- Calculating the reproductive number R is easier

- What does R tell us about λ?

Counting dandelions

- Easier to census before reproduction
- But we can do either: we just need to close the loop – count everything in the same units.
- What do you think R is for this population?

Measuring in age-structured models

Survivorship

- The first key to understanding how much each organism will contribute to the population is **survivorship**
- In the field, we estimate the probability of survival from age x to age $x + 1$: p_x

- Probability you will be *counted* at age $x+1$, given that you were *counted* at age x
- To understand how individuals contribute to the population, we are also interested in the **cumulative survival**: overall probability that individuals survive to age x: ℓ_x.

Patterns of survivorship

- nWhat sort of patterns do you expect to see in p_x?

- What about ℓ_x?

When do we start counting?

- Is the first age class called 0, or 1?
- In this course, we will start from age class 1
- If we count right *after* reproduction, this means we are calling newborns age class 1. Don't get confused.

Constant survivorship

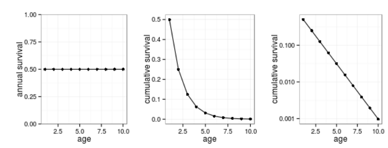


Figure 3: plot of chunk csurv1

Survivorship types

- There is a history of different types of survivorship depending on whether it increases, stays constant or decreases with age
- Real populations tend to be more complicated
- Most common pattern is: high mortality at high and low ages, with less mortality between ("bathtub-shaped hazard")
- increased mortality at high ages is **senescence**: interesting for many reasons but hard to measure

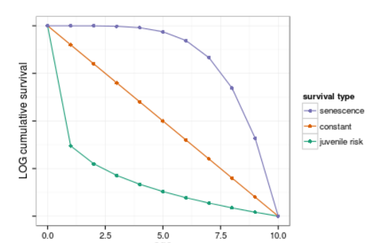


Figure 4: plot of chunk unnamed-chunk-1

Changing survivorship

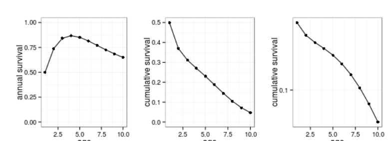


Figure 5: plot of chunk changing_surv

Fecundity

- Just as in our simple population growth models, we define fecundity as the expected number of offspring at the next census produced by an individual observed at this census
- Parent must survive from counting to reproduction
- Parent must give birth
- Offspring must survive from birth to counting
- Remember to think clearly about gender when necessary: are we tracking females, or everyone?

Fecundity patterns

- f_x is the average number of new individuals *counted* next census per individual in age class x *counted* this census
- Fecundity often goes up early in life and then remains constant
- It may also go up and then come down
- What is an organism in which fecundity would keep increasing indefinitely?

Life tables

- To analyze an age-structured model, we organize information about fecundity and mortality into **life tables**
- A life table is made from the perspective of a particular census time, and provides the information needed to project from one census to the next
- This is one *cycle* of the reproductive process being studied, and usually corresponds to one year
- How many survivors do we expect at the next census for each individual we see at this census?
- How many offspring do we expect at the next census for each individual we see at this census?

Mathematical model

- A life table gives us all the information we need to figure out how to go from the age distribution this year to the age distribution next year
- The first age group has all the surviving offspring
- Add up contributions from everyone
- Each other age group has the survivors from the previous age group

Dandelion example

- Adults produce 80 seeds each
- 1% of seeds survive to become adults
- 50% of first-year adults survive to reproduce again
- Second-year adults never survive
- What does the life table look like?

Dandelion life table

x	f_x	p_x
1	0.8	0.5
2	0.8	0

Dandelion dynamics (by age class)

Dandelion dynamics (total)

Dandelion dynamics (log scale)

Dandelion dynamics (total, log scale)

Dandelion dynamics (proportions)

Calculating R

- We calculate R by figuring out the estimated contribution at each age group, *per individual who was ever counted*
- We figure out expected contribution given you were ever counted by multiplying:

Dandelion life table (again)

x	f_x	p_x	ℓ_x	$\ell_x f_x$
1	0.8	0.5	1	0.8
2	0.8	0	0.5	0.4
R				1.2

Squirrel life table

x	f_x	p_x
1	0	0.25
2	1.28	0.46
3	2.28	0.77

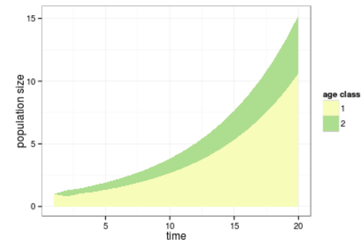


Figure 6: plot of chunk unnamed-chunk-2

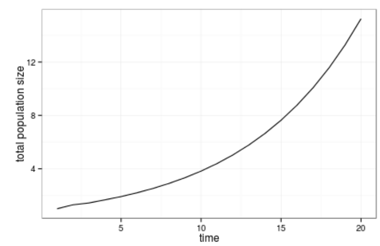
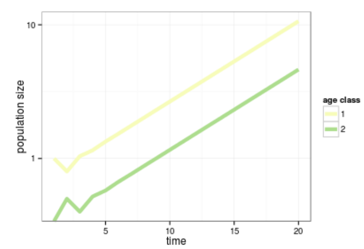


Figure 7: plot of chunk unnamed-chunk-3



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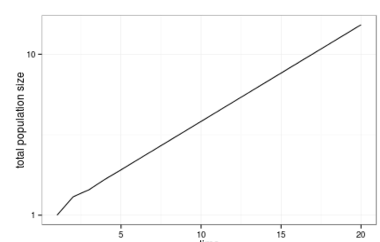

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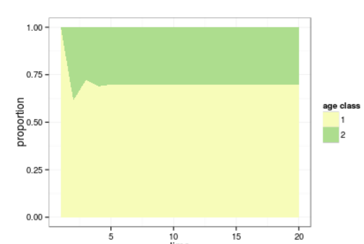


Figure 10: plot of chunk unnamed-chunk-6

x	f_x	p_x
4	2.28	0.65
5	2.28	0.67
6	2.28	0.64
7	2.28	0.88
8	2.28	0

Squirrel dynamics (by age class)

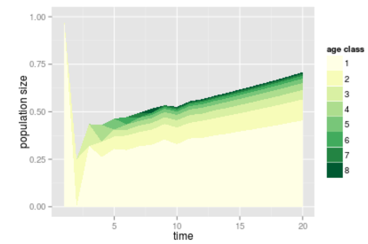


Figure 11: plot of chunk sdyn1

Squirrel dynamics (total)

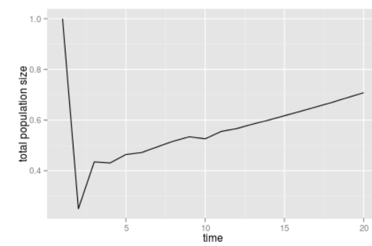


Figure 12: plot of chunk unnamed-chunk-7

Squirrel dynamics (log scale)

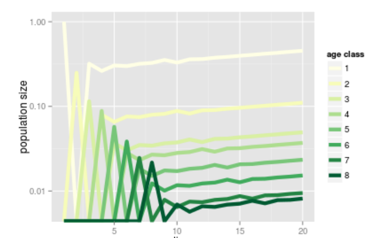


Figure 13: plot of chunk unnamed-chunk-8

Squirrel dynamics (total, log scale)

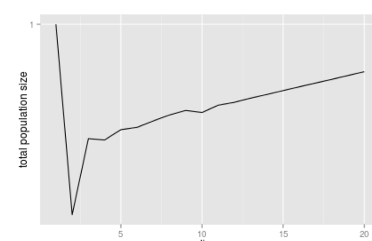


Figure 14: plot of chunk unnamed-chunk-9

Squirrel dynamics (proportions)

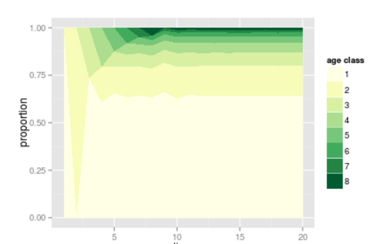


Figure 15: plot of chunk unnamed-chunk-10

Squirrel life table (again)

x	f_x	p_x	ℓ_x	$\ell_x f_x$
1	0	0.25	1	0
2	1.28	0.46	0.25	0.32
3	2.28	0.77	0.115	0.2622
4	2.28	0.65	0.08855	0.2019
5	2.28	0.67	0.05756	0.1312
6	2.28	0.64	0.03856	0.08792
7	2.28	0.88	0.02468	0.05627
8	2.28	0	0.02172	0.04952
R				1.109

Squirrel observations

- What observation would you make about this life table?

Calculation details

f_x vs. m_x

- Here we focus on f_x – the number of offspring seen at the next census (next year) per organism of age x seen at this census
- An alternative perspective is m_x: the total number of offspring per reproducing individual of age x
- What is the relationship?

Calculating R

- The reproductive number R gives the average lifetime reproduction of an individual, and is a valuable summary of the information in the life table
- $R = \sum_x \ell_x f_x$
- If $R > 1$ in the long (or medium) term, the population will increase
- If R is persistently < 1, the population is in trouble
- We can ask (for example):
- Which years have a large contribution to R?
- Which values of p_x and f_x is R sensitive to?

The effect of old individuals

- Estimating the effects of old individuals on a population can be difficult, because both f and ℓ can be extreme

- The contribution of an age class to R is $\ell_x f_x$

- Reproductive potential of old individuals may or may not be important

Sea turtles

- Charismatic macrofauna (i.e., people care about them)
- Juvenile mortality: nesting habitat destruction, light pollution
- Adult mortality: fishing bycatch
- Which is more important?
- Despite the obviousness of juvenile mortality, adult mortality matters more (Crouse, Crowder, and Caswell 1987)

Dynamics

- In an *unregulated* population, what sort of behaviour do we expect initially?

- In the long term?

approach a **stable age distribution** (SAD: proportion in each class)

Mathematical results

- It can be shown (by linear algebra) that an unregulated population following a constant life table will:
- Reach a stable age distribution: the proportion of individuals in each age group approaches a constant
- Eventually grow exponentially: increase by the same factor λ each time step
- There is one unusual exception to this rule:
- Populations with *independent cohorts* can keep changing λ and their distribution every year

Regulation again

- There is a lot of mathematical study of unregulated, age-structured populations, but it should be taken with a grain of salt

- Understanding this behaviour is helpful:

- interpreting age structures in real populations

- beginning to understand more complicated systems

Measuring growth rates

- In a constant population, each age class replaces itself: $R = \sum_x \ell_x f_x = 1$
- In an exponentially changing population, each year's **cohort** is a factor of λ bigger (or smaller) than the previous one
- A cohort is a group that enters the population at the same time
- λ is the finite rate of increase, like before
- Looking back in time, the cohort x years ago is λ^{-x} as large as the current one
- The existing cohorts need to make the next one: $\sum_x \ell_x f_x \lambda^{-x} = 1$

The Euler equation

- If the life table doesn't change, then λ is given by $\sum_x \ell_x f_x \lambda^{-x} = 1$
- We basically ask, if the population has the structure we would expect from growing at rate λ, would it continue to grow at rate λ?
- On the left-side cohort started as λ times smaller than the one after it
- Then got multiplied by ℓ_x.
- Under this assumption, is the next generation λ times bigger again?

λ and R

- If the life table doesn't change, then λ is given by $\sum_x \ell_x f_x \lambda^{-x} = 1$
- What's the relationship between λ and R?
- When $\lambda = 1$, the left hand side is just R.
- If $R > 1$, the population more than replaces itself when $\lambda = 1$. We must make $\lambda > 1$ to decrease LHS and balance.
- If $R < 1$, the population fails to replace itself when $\lambda = 1$. We must make $\lambda < 1$ to increase LHS and balance.
- So R and λ tell the same story about whether the population is increasing

Time scales

- λ gives the number of individuals per individual *every year*
- R gives the number of individuals per individual *over a lifetime*
- What relationship between R and λ do we expect for an annual population (individuals die every year)?
- For a long-lived population

Studying population growth

- λ and R give similar information about your population
- R is easier to calculate, and more generally useful
- But λ gives the actual rate of growth
- More useful in cases where we expect the life table to be constant with exponential growth or decline for a long time

Growth and decline

- If we think a particular period of growth or decline is important, we might want to study how factors affect λ
- Complicated, but well-developed, theory
- In a growing population, what happens *early in life* is more important to λ than to R.
- In a declining population, what happens *late in life* is more important to λ than to R.
- A common error is to assume that periods of exponential growth are more important to ecology and evolution the periods of exponential decline. In the long term, these should balance. Why?

Age distributions

- If a population has constant size (ie., the same number of individuals are born every year), what determines the proportion of individuals in each age class?

- What if the population is growing?

Stable age distribution

- If a population has reached a SAD, and is increasing at rate λ (given by the Euler equation):
- the x year old cohort, born x years ago originally had a size λ^{-x} relative to the current one
- a proportion ℓ_x of this cohort has survived
- thus, the relative size of cohort x is $\lambda^{-x}\ell_x$
- SAD depends only on survival distribution ℓ_x and λ.

Patterns

- Populations tend to be bottom-heavy (more individuals at lower age classes)
- Many individuals born, few survive to older age classes
- If population is growing, this increases the lower classes further
- More individuals born more recently
- If population is *declining*, this shifts the age distribution in the opposite direction
- Results can be complicated
- Declining populations may be bottom-heavy, top-heavy or just jumbled

- Population pyramids from Romania, Canada, Estonia, China

University cohorts

- McMaster accepts only first-year students. For any given stage (e.g., end of third year) the same proportion drop out each year
- What can you say about the relative size of the classes if:
- The same number of students is admitted each year?
- More students are admitted each year
- Fewer students are admitted each year

Stable population

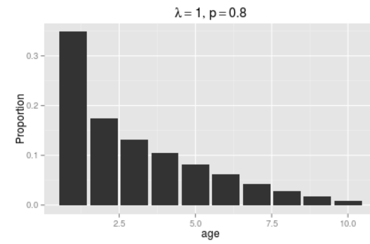


Figure 16: plot of chunk unnamed-chunk-12

Shrinking population

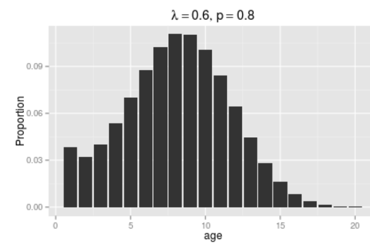


Figure 17: plot of chunk unnamed-chunk-13

Growing population

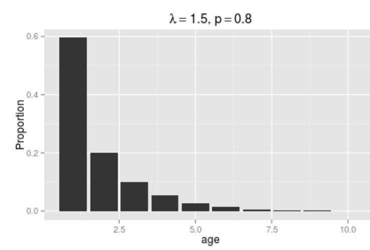


Figure 18: plot of chunk unnamed-chunk-14

Populations that don't converge

- There is an exception to the rule that populations converge to a stable distribution, and grow at a stable rate: populations with **independent cohorts**
- Suppose all salmon reproduce **exactly** when they're four years old.

Salmon: proportions

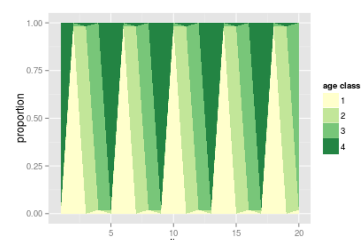
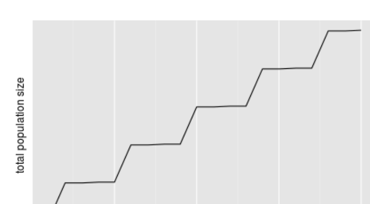


Figure 19: plot of chunk unnamed-chunk-16

Salmon: total dynamics (log scale)



Independent cohorts

- Some populations really follow strict time schedules
- I don't know of any cases with strictly independent cohorts
- Either cohorts are not strict, or all but one cohort goes extinct.
- What will happen if you add a bunch of salmon to an unregulated population that follows a realistic time schedule (*almost* independent cohorts)?

Forest example

- When we go to an apparently stable forest ecosystem, it seems to be dominated by large trees, not small ones. Why?
- Large trees are larger

Density dependence

- We can also ask, what happens when we have an age-structured population regulated by density dependence?
- Mostly beyond the scope of this course
- Some principles:
- We expect smooth dynamics when delays are small and compensation is weak
- Oscillations otherwise
- We expect the age distribution to reflect the shape of ℓ_x, and also whether the population has been growing or declining recently

Stage structure

- Stage structure works just like age structure, except that what stage you are in is not strictly predicted by how old you are
- Age-structured models need fecundity, and survival probability
- In stage-structured models survival is typically broken into:
- More complicated models are also possible

Unregulated growth

- What happens if you have a constant stage table (no regulation)?
- Fecundity, and survival and recruitment probabilities are constant
- Similar to constant life table
- Can calculate R and λ (will be consistent with each other)
- Can calculate a stable stage distribution
- Unregulated growth cannot persist

Summary

- If the life table remains constant (no regulation or stochasticity):
- Reach a stable age (or stage) distribution
- Grow or decline with a constant λ

- Factors behind age distribution can be understood
- Real situations are more complicated, but these calculations provide useful guidance
- See (Caswell 2000; Morris and Doak 2002) for all the gory details
- Lamppost theory

References

Caswell, Hal. 2000. *Matrix Population Models: Construction, Analysis and Interpretation.* Sunderland, MA: Sinauer.

Crouse, Deborah T., Larry B. Crowder, and Hal Caswell. 1987. "A Stage-Based Population Model for Loggerhead Sea Turtles and Implications for Conservation." *Ecology* 68 (5) (October): 1412–1423. doi:10.2307/1939225. http://www.esajournals.org/doi/abs/10.2307/1939225.

Morris, William F., and Daniel F. Doak. 2002. *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis.* Sinauer.