Complex dynamics

Key concepts

- Cycles

- Overcompensation

- Bifurcation

- Aperiodic dynamics

Density dependence in seasonally reproducing populations

In the first chapter we investigated the dynamics of density-independent populations. We recognized that some species reproduce continually and other species synchronize reproduction seasonally. Interestingly, the long term dynamics that result from these two scenarios are very similar. Indeed, as we showed, geometric (discrete time) growth or decline can be interpreted as a sample from an exponential (continuous time) trajectory. In this sense, they are equivalent models. Then, in the second chapter we introduced density dependence. Are the discrete and continuous time situations equivalent in the case of density dependence as well? The short answer to this question is "no". The range of *complex dynamics* that result from the combination of density dependence and discrete time is the subject of this chapter.

Stock recruitment relationship

The dynamics of fish populations is a good starting place for studying complex dynamics. Pink salmon (*Oncorhynchus gorbuscha*) are one of many anadromous fish species that spawn in freshwater streams, migrate to the sea for growth and development, and return to their natal habitat on maturity to spawn. In the case of pink salmon, maturity is reached at two years of age. Adult animals "run" (enter spawning streams) between late late June and October. Females dig a nest called a "redd" and deposit their eggs, which are fertilized externally

Figure 1: Pink salmon (*Oncorhynchus gorbuscha*).

by one or more males, guarding them until she dies some days later. Eggs hatch in winter with juveniles emerging in the spring, migrating downstream to the ocean, and not returning for another year to year and a half at which point they are full grown. One consequence of this two year life cycle is that every spawning ground is used by two different populations – one that breeds in odd years and one that breeds in even years.

In fisheries science, it is customary to separate population counts into two categories. *Stocks*, designated S_t, refer to the breeding individuals in a population. *Recruits*, designated R_t, are the individuals returning to breed at some time later. In the case of pink salmon, this interval is two years. The *stock-recruitment relationship* relates the number of recruits in a given year to the stock two years prior. The observed stock recruitment relationship for even year pink salmon in Area 9, Central British Columbia is shown in Figure 2.

Plotting per capita recruitment, $Y_{t+2} = R_{t+2}/S_t$, shows that this is a density dependent relationship (Figure 3). Inspection of a number of other stocks shows that this density dependence is in fact a reliable feature of pink salmon populations. A theoretical idealization of this relationship is the *stock-recruitment curve*, $Y_{t+2} = e^{r-bS_t}$, introduced by fisheries scientist Bill Ricker (Figure 4). Transforming this equation using logarithms, we arrive at the linear equation $\ln Y_{t+2} = r - bS_t$. The parameters r and b may then be estimated from data using linear regression (Figure 5).

To develop a model for pink salmon population dynamics, we simply multiply this stock-recruitment curve by the size of the spawning population, yielding the *Ricker model* (Figure 6):

$$R_{t+2} = S_t e^{r-bS_t}. \tag{1}$$

If all recruits are included in the subsequent generation of spawners then this is a model for the biannual dynamics of the population, *i.e.*,

$$S_{t+2} = R_{t+2} = S_t e^{r-bS_t}. \tag{2}$$

However, if some proportion h are either harvested or die of natural causes prior to spawning then we must multiple R_{t+2} by $(1-h)$ to obtain the number of spawners at S_t, yielding

$$S_{t+2} = R_{t+2}(1-h) = (1-h)S_t e^{r-bS_t}. \tag{3}$$

If one thinks of the term e^{r-bS_t} as analogous to the reproductive multiplier λ, then this model may be interpreted as a density-dependent
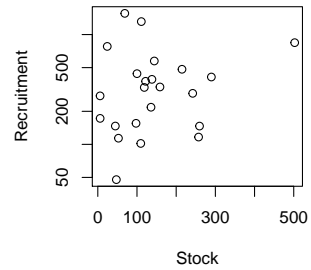

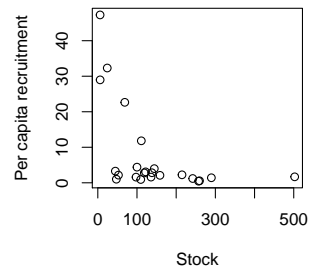Figure 2: Stock-recruitment relationship in pink salmon.

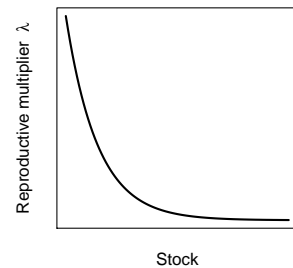Figure 3: Per capita stock-recruitment in pink salmon.

Figure 4: Shape of the density-dependent reproductive multipler λ in the Ricker model.
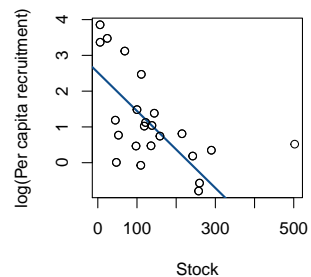

Figure 5: Per capita stock-recruitment in pink salmon on a logarithmic scale. Dropping one extreme observation (at $S = 502.4$), a linear regression model provides estimates of $\hat{r} = 2.52$ +/- 0.38 (s.e.) and $\hat{b} = -0.011$ +/- 0.003 (s.e.).

version of the discrete time model introduced in Chapter 1, which we might now write as $\lambda(S) = e^{r-bS_t}$. Indeed, as the size of the stock goes to zero, the reproductive multipler approaches the value e^r and the density independent model is recovered exactly. Thus, the quantity r plays exactly the same role in this equation that the intrinsic rate of increase plays in the density-independent models that result in geometric and exponential growth. That is, it is a measure of reproductive potential. The density dependence, by constrast, is brought in through the parameter b, which causes the reproductive multiplier to decline to zero as the stock size S_t gets large.

What is the carrying capacity of this model? By definition, carrying capacity is a positive equilibrium such that any population smaller than carrying capacity increases and any population larger than carrying capacity decreases. As an equilibrium, the carrying capacity is size of the population at which no fluctuations occur. Designating this particular population size by S^*, we rewrite equation 3 using S^* on both the left hand and right hand sides of the equation and solve, giving

$$S^* = \frac{r - \ln\left(\frac{1}{1-h}\right)}{b}. \tag{4}$$

In the abence of harvesting, this reduces to

$$S^* = \frac{r}{b}. \tag{5}$$

What do time series generated by the Ricker model look like? Figure 7 shows solutions of equation 2 obtained using $S_0 = 2$ for the initial condition and $r = 1$ for the intrinsic rate of increase. For comparison, the carrying capacity $S^* = r/b$ is plotted as a dashed line. Evidently, the Ricker model can exhibit the sigmoidal approach to carrying capacity reminiscent of the logistic model. This initial similarity masks a deep difference however. Recalling that $\lambda = e^r$ is a measure of the maximum reproductive potential of the species, we recognize that this model is for a species with $\lambda = e^1 \approx 2.72$. For pink salmon, which produce up to 2000, this value of of r seems too low. What happens as we increase r? Figure 8 shows solutions to the same model, except having set $r = 1.75$. In this case, we see two new phenomena. First, the population starting below carrying capacity does not smoothly approach equilibrium, but rather overshoots it – a phenomenon referred to as *overcompensation*. Second, this overcompensation leads to undershooting, which results in further overshooting, undershooting, *etc.* resulting in *damped oscillations* toward equilibrium.
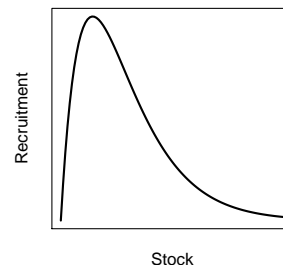

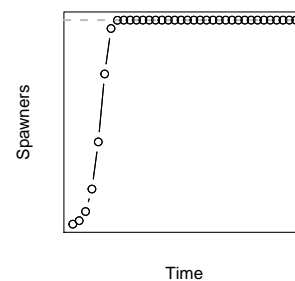Figure 6: Ricker stock-recruitment curve.
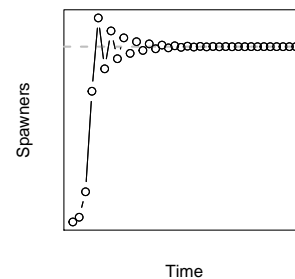

Figure 7: Solution of the Ricker model with $r = 1$.

Figure 8: Solution of the Ricker model with $r = 2$.

Given this surprise, we may wonder what happens if we increase r still further. At the value $r = 2.1$ we see that these damped oscillations have given way to diverging oscillations toward a stable sequence of values oscillating at a fixed distance from the equilibrium, a pattern referred to as a 2-cycle (Figure 9). At the value $r = 2.6$ the 2-cycle has given way to a 4-cycle (Figure 10) and at $r = 2.70005$ we observe an 8-cycle (Figure 11). Counting the periods of these cycles, 2, 4, 8, ... we observe that there is a pattern to the changes in the pattern. Specifically, each time there is a change in dynamics there is a doubling of the period of the cycle. At $r = 2.8$ an even stranger phenomenon appears: the dynamics become completely aperiodic (non-repeating). This phenomenon is known as *dynamical chaos* and the pattern we observed is called the *perdiod doubling route to chaos*.

We can investigate this period doubling route to chaos more comprehensively by constructing a *bifurcation diagram*. The bifurcation diagram collects the various values of the population's trajectory visited by the system, known as the *attractor*, for a particular value of some parameter (in our case r) and plots them against that parameter. Figure 13 shows the bifurcation diagram of the Ricker model. Inspecting this graph beginning at the origin we see that increasing r simply increases the value of the carrying capacity, which is stable. However, at the value $r \approx 2$ this stable branch "bifurcates" into a 2-cycle, which exists over a smaller interval of r, before bifurcating again at a slightly larger value of r. Indeed, the intervals over which each new period exists get smaller and smaller so that eventually the dynamics become aperiodic. Besides this regularity, two additional features also appear. First, even within the "aperiodic region" there exist windows in which the population becomes *period-locked* to some low dimensional cycle. Additionally, with every increase in r after the first bifurcation the minimum of the attracting set becomes smaller and smaller and the maximum of the attracting set becomes larger and larger so that the amplitude in fluctuations increases. These results predict that for populations exhibiting aperiodic population dynamics, the greater the reproductive potential the more variable the population dynamics will be.

These properties of this diagram – multi-generational cycles, period-doubling, increasing amplitude fluctuations, aperiodic dynamics and phase-locking – are not special to the Ricker model, but are common features of discrete time models, models with time delays, and sufficiently complex continuous time delay models. Two of these features, multi-generational cycles and aperiodic dynamics, have inspired much research in population ecology aimed at determining whether or not these phenomena occur in natural populations.
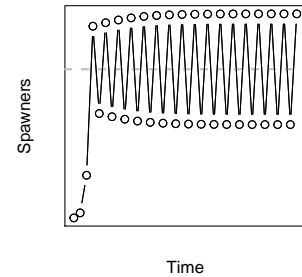

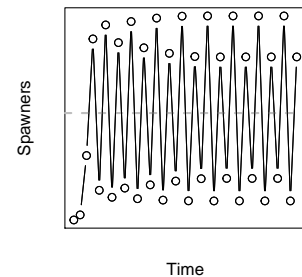Figure 9: Solution of the Ricker model with $r = 2.1$.

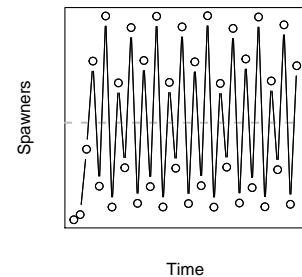Figure 10: Solution of the Ricker model with $r = 2.6$.

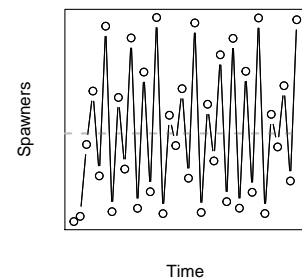Figure 11: Solution of the Ricker model with $r = 2.70005$.

Figure 12: Solution of the Ricker model with $r = 2.8$.
This sequence of smaller and smaller windows is called the *Feigenbaum cascade* after the mathematician who proved its convergence
Continuous time models must have at least two dimensions to produce cycles and three dimensions to produce chaos.

Figure 13: Bifurcation diagram of the Ricker model with $b = 0.005$.
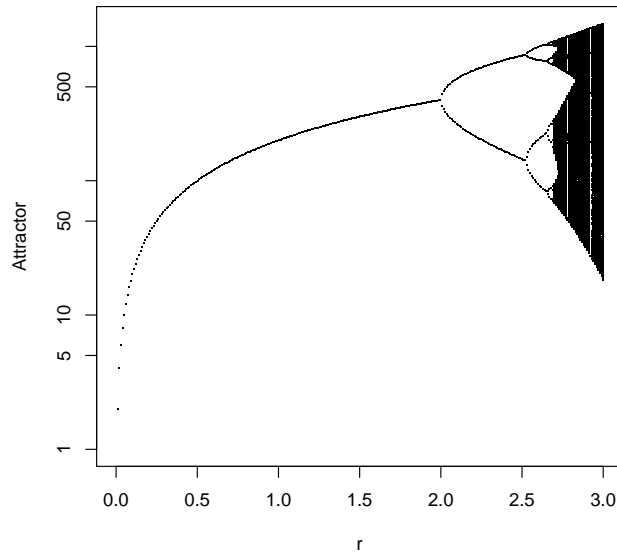
First, in fisheries research, it is well known that many populations cycle. For instance, Figure 14 shows the number of spawning fish in Area 9 in each year from 1950 to 1996. We can investigate the presence of cycles by computing the autocorrelation function, which consists of the coefficient of correlation for each value of the series with itself at a lag of τ. That is the autocorrelation at lag $\tau = 1$ is the correlation coefficient between the series R_t and R_{t+1}. The autocorrelation at lag $\tau = 2$ is the correlation coefficient between the series R_t and R_{t+2}. The autocorrelation function up to lag 16 is plotted in Figure 15). The statistically significant, negative autocorrelation coefficient at lag 2 indicates that this population does cycle between large and small values. (Correlation coefficients were calculated after taking logarithms. Autocorrelation coefficients larger than the blue line are significantly different than zero at the $\alpha = 0.05\%$ level.) Indeed, the alternating tapering coeffients of correlation are precisely what we would expect for a slightly noisy autoregressive process such as would be obtained by a population following the Ricker model.
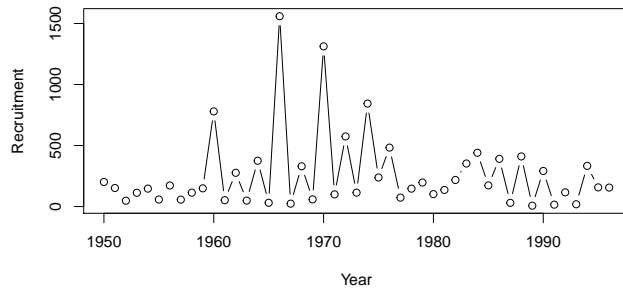
Figure 14: Recruitment of pink salmon in Area 9, Central British Columbia, Canada.

We recall, however, that pink salmon have a two-year generation time. So, these are actually two different spawning populations, *i.e.*, the "even year" population and the "odd year" population, with their dynamics superimposed. If we separate out just the even year population or just the odd year population (16), and compute the autocorrelation functions for these time series we fail to find any evidence for the two-generation cycle predicted by the Ricker model (17). In fact, a meta-analysis of the Myers stock-recruitment database fails to find evidence of multi-generational (overcompensatory) cycles in all of 306 unique stock return time series.
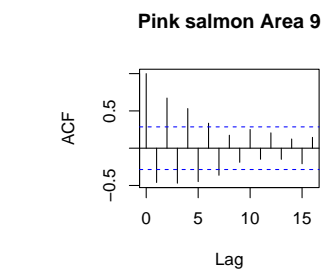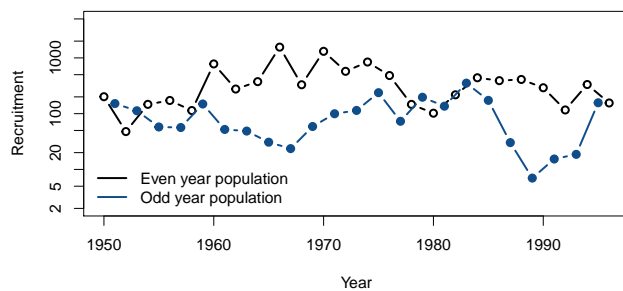
Pink salmon Area 9

Figure 15: Autocorrelation of the recruitment of pink salmon in Area 9, Central British Columbia, Canada.

Figure 16: Recruitment of even year pink salmon in Area 9, Central British Columbia, Canada.

These results lead us to two further questions.

- What prevents the generation of cycles, dynamical chaos, or other high amplitude fluctuations in fish populations?

- Why are the two populations of such dramatically different sizes? (If odd and even year salmon runs are just two populations identical in all respects expect that they spawn in alternate years, one would expect the two populations to be of similar size.)

The two most probable answers to the first question are:
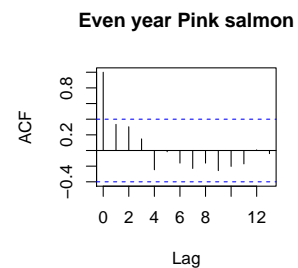
Even year Pink salmon

Figure 17: Autocorrelation of the recruitment of even year pink salmon in Area 9, Central British Columbia, Canada. These data fail to provide any evidence for multi-generational cycles.

- *Harvest indeuced stability.* Harvesting reduces the realized growth rate of the population sufficiently to force the population to remain in the stable zone.

- *Strong density regulation.* The density dependence exhibited by the Ricker model is too severe. To build a more accurate model we require a stock recruitment curve with more severe curvature.

Although both answers could plausibly explain why we fail to see cycles or high amplitude fluctuations in fisheries data, they differ with respect to the hypothesized mechanism as well as the empirical consequences of changing fishing practice. If the first answer is correct, a release from fishing pressure (or a comparison with unharvested species) is predicted to result in cycles. However, if the second answer is correct, then we are left to inquire what the density dependence actually looks like. Depending on the form this density dependence takes, release from fishing may or may not result in cycles or other high amplitude fluctuations.

Harvest induced stability

To examine the hypothesis of harvest induced stability, it will help to define $a = e^r$. Then equation 2 may be rewritten as

$$S_{t+2} = (1 - h)aS_te^{-bS_t}. \tag{6}$$

Since $a = e^r$ then we can also write $r = \ln(a)$ and interpret the bifurcation diagram in Figure 13 as a bifurcation diagram of a where the x-axis is plotted on a logarithmic scale. Alternatively, we can replot by exponentiating r arriving at the bifurcation diagram in Figure 18.

To be effective at stabilizing the pink salmon population, harvesting must reduce per capita reproductive output to $e^r_{crit} \approx 7.4$ offspring per spawner, where r_{crit} is the value of r at which the stable equilibrium in Figure 13 bifurcates into a 2-cycle. From Figure 5, we estimate the maximum pre-harvest recruitment to be $e^{\hat{r}} \approx = e^2.52 \approx 12.4$. Thus, harvesting would need to remove uproughly $(12.4 - 7.4)/12.4 \approx$ 40% of the returning recruits annually to achieve stability. Given recent annual harvests of more than ten million individuals it seems that the hypothesis of harvest induced stability is indeed a plausible explanation for the failure to observe cycles in pink salmon.

Strong regulation and the Beverton-Holt model

Alternatively, the hypothesis of strong regulation suggests that the Ricker curve in Figure 6 does not sufficiently capture severe density
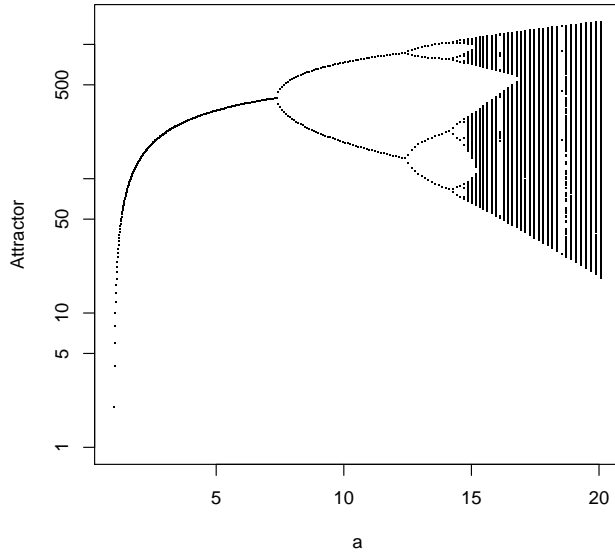
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Figure 18: Bifurcation diagram of the "a version" Ricker model with $b = 0.005$.

dependence exhibited by fish populations at even modest population sizes. To investigate this hypothesis we need to try a different equation to represent the stock-recruitment relation. The *Beverton-Holt* model is one such candidate. This model suggests the stronger form of density dependence given by

$$\lambda(S_t) = \frac{e^r}{1 + aS_t}. \tag{7}$$

Whereas the Ricker equation is exponential (and therefore linear after transforming to a logarithmic scale), the Beverton-Holt model is hyperbolic. Accordingly, density dependence in this model is initially quite severe (the slope is steeper at small population sizes than for the Ricker model), tapering off to become more gradual at larger population sizes.

For comparison with the Ricker model we rearrange equation 7 to give $\ln Y_{t+2} = r - \ln(1 + aS_t)$. Fitting this model with *nonlinear regression* yields the result in Figure 20. Just as the Ricker model from above, this model does appear to provide a reasonable fit to the data. Moreover, unlike the Ricker model, the extreme observation at $S = 502.4$ is also reasonably well fit.

The equation for the population dynamics is

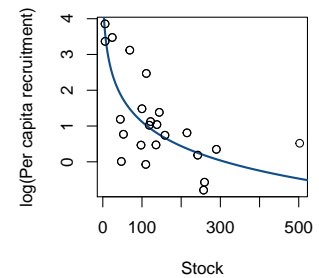$$S_{t+2} = S_t \frac{e^r}{1 + aS_t}. \tag{8}$$

Figure 19: Per capita stock-recruitment in pink salmon on a logarithmic scale. A nonlinear regression fit provides least squares estimates of $\hat{r} = 4.74$ +/- 2.1 (s.e.) and $\hat{a} = 0.37$ +/- 0.79 (s.e.).

The dynamics exhibited by this model are considerably less dramatic than those of the Ricker model. Indeed, at relatively small values of S the two may be nearly equivalent (Figure 20). However, as the family of curves in Figure 21 shows, the only change that occurs as r increases in the Beverton-Holt model is that the approach to equilibrium is faster. This is a key difference between the two models. Further, it means that strong regulation may be the cause of our failure to see cycles in fish population dynammics.

Does overcompensation happen in nature?

The outcome of our study of pink salmon is a little unsettling. Clearly, salmon populations fluctuate considerably. But, the magnitude of these fluctuations is neither periodic nor do extremes run close to zero as they would if they were aperiodic. Instead, pink salmon populations appear to be fluctuating around an equilibrium. Further, it appears that the two possible explanations for the lack of overcompensation (harvest-induced stability and strong density dependence) cannot be distinguished without taking further, improbable actions such as a moratorium on pink salmon fishing. Perhaps, however, overcompensation occurs elsewhere in nature.

An initially plausible place to find overcompensatory dynamics is insect populations. Insect species often exhibit density dependence and many, especially phytophagous insects, reproduce once per year in a life cycle referred to as univoltinism. Is overcompensation possibly common in univoltine insect species? This question was taken up in a classic paper from 1976.[1] The authors fit a simple dynamical model to data on 24 different laboratory and field populations of insects. From the estimated parameters of the model, the authors determined that only one species (a beetle, *Leptinotarsa decemlineata*) should exhibit sustained oscillations with an additional three species exhibiting damped oscillations toward an equilibrium. Parameter estimates for the other 20 species were all in the range corresponding to a monotonic approach to equilibrium. These results were surprising since a well known experiment by A.J. Nicholson using the Australian sheep blowfly (*Lucilia cuprina*)[2] had exhibited extremely erratic overcompensatory oscillations. Indeed, we now know that this experiment was the biological manifestation of dynamical chaos.[3]

Another possible location for natural overcompensation is populations with age structure, which gives rise to *population inertia*. As we have seen here, one of the key ingredients for overcompensation is a time lag that allows the population to "overshoot" its equilibrium. Long-lived species with late age at first reproduction exhibit a life cycle that can give rise to this kind of time lag. In this case, more ex-
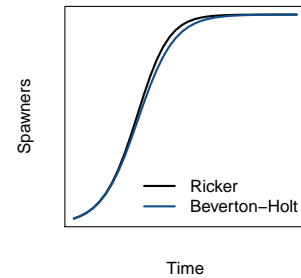

Figure 20: At a small value of r ($r = 0.35$) the Ricker model and Beverton-Holt model give very similar solutions.
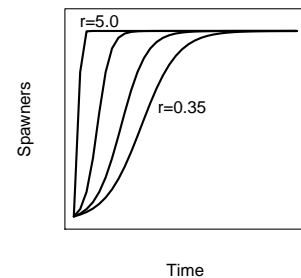

Figure 21: Solutions of the Beverton-Holt model at values of $r = 0.35$, $r = 0.5$, $r = 1$, and $r = 5$.

[1] M P Hassel, Lawton J.H., and May R.M. Patterns of dynamical behaviour in single species populations. *Journal of Animal Ecology*, ??:471–486, 1976

[2] Aj Nicholson. An outline of the dynamics of animal populations. *Australian Journal of Zoology*, 2(1): 9, 1954. ISSN 0004-959X. DOI: 10.1071/ZO9540009; and a. J. Nicholson. The Self-Adjustment of Populations to Change. *Cold Spring Harbor Symposia on Quantitative Biology*, 22 (0):153–173, 1957. ISSN 0091-7451. DOI: 10.1101/SQB.1957.022.01.017

[3] Simon N Wood. Statistical inference for noisy nonlinear ecological dynamic systems. *Nature*, 466(7310):1102–1104, 2010. ISSN 0028-0836. DOI: 10.1038/nature09319

amples of overcompensation are known. For instance, Higgins *et al.* showed that large fluctuations in Dungeness crab (*Cancer magister*) are best explained as the results of damped oscillations, induced by age-structured density-dependence in vital rates, excited by environmental fluctuations.[4] In another interesting example, a wild population descended from feral individuals of a primitive breed of domestic sheep (*Ovis aries*) lives on the islands of Soay and Hirta in the St. Kilda archipelago off the western coast of Scotland. This population has been the subject of intense ecological and evolutionary study since 1959. In 1992, it was shown that the population fluctuations of the Soay sheep are due to overcompensatory mortality interacting with age-specific responses to winter severity, a result that was later seen to interact with weather, implying that both density dependence and the magnitude of climate variation are key to understanding the dramatic fluctuations exhibited by this population.[5]

Test yourself

- When are recruitment and spawning stock equal in size?

- What is overcompensation?

- How does overcompensation result in cycles?

- What are aperiodic dynamics?

- What features of a species' life history predispose it to overcompensatory dynamics?

Homework

1. Find the equilibrium of Beverton-Holt model.

2. Consider a population with density dependent growth given by the Beverton-Holt model with parameters $r = 0.96$ and $a = 0.0044$, and initial population size $S = 147$. What will be the population size after five generations?

3. What is the carrying capacity of the population in the previous question? Is it stable?

4. The version of the Beverton-Holt model introduced in this chapter does not consider harvesting. Modify equation 8 to represent the dynamics of a harvested fish population.

5. Another discrete time density-dependent model is the *logistic map*, $x_{t+1} = r x_t (1 - x_t/k)$, which is named for its similarity to the continuous time logistic equation. Find the equilibria of this model.

Iterate the model for a range of values of r. Plot the bifurcation diagram. How is the logistic map like the Ricker model? How is it different?

6. Sometimes, for instance to prepare data for time series analysis, it is useful to think about the dynamics of the logarithm of population size. Consider the change of variable $x = \ln(S)$. What is the difference equation for the logarithm of population size according to the Ricker model, *i.e.*, find the expression for f in the difference equation $x_{t+1} = f(x_t)$. Recall that on the ordinary scale and with annual generations rather than biannual generations, Ricker model dynamics are give by $S_{t+1} = S_t e^{r-bS_t}$.

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