Answers to Exercise 29

Harvest Models

Fixed-Quota versus Fixed-Effort: First Questions

QUESTIONS

1. What are the effects of different values of *R* and *K* on catches and population sizes in the two harvest models?
2. What are the effects of different values of *Q* on catches and population size in the population harvested under a fixed quota scheme?
3. What are the effects of different values of *E* on catches and population size in the population harvested under a fixed quota scheme?
4. How does the maximum sustainable yield (MSY) relate to *R* and/or *K*?
5. Is there any difference between fixed-quota and fixed-effort harvesting in terms of risk of driving the harvested population to extinction?

ANSWERS

1. Change *R* by entering different values into cell B6. Change ***K*** by entering different values into cell B7. Your changes will be automatically echoed in the models. After each change, examine your spreadsheet, your graph of population size and harvest, and your graphs of recruitment curve and quota or effort line.

   Try changing *K* from 2000 to 4000, leaving *R* at 0.50. You should see that the catch remains unchanged at 250 individuals per time period in the fixed quota scheme. This is hardly surprising, because that's the nature of a fixed quota—it does not change. The catch in the fixed effort scheme starts at 1000 and declines to an equilibrium of 500, which is twice the catch in the fixed effort harvest with the original carrying capacity of 2000.

   Your graph of the recruitment curve and fixed quota now shows the quota line (horizontal line) crossing the recruitment curve at two points, in contrast to just touching the recruitment curve at its peak with the original value of *K*. If you drop a vertical line from the right-hand crossing point to the X-axis, you should see that this is the equilibrium population size.

   Your graph of the recruitment curve and fixed effort line still shows the effort line crossing the recruitment curve at its peak, although that peak has shifted to a higher value of *N*.

   Reducing *K* to 1000 has more drastic effects. The population harvested by a fixed quota goes extinct, and the harvest goes to zero. The fixed effort population declines to an equilibrium at 250 individuals, and catch declines from 250 individuals per time period to 125.

   Your graph of the recruitment curve and fixed quota now shows the quota line (horizontal line) lying entirely above the recruitment curve. This means that the quota is larger than recruitment regardless of population size, and harvesters will remove more individuals from the population than are added to it. So it is not surprising that the population goes extinct.

   Your graph of the recruitment curve and fixed effort line still shows the effort line crossing the recruitment curve at its peak, although that peak has shifted to a lower value of ***N***.

   Restore *K* to 2000, and change *R* to 1.00. The population harvest according to a fixed quota now stabilizes at about 1707 individuals, a larger value than when ***R*** was 0.50. The harvest, of course, does not change. The fixed-effort population stabilizes at 1500 individuals, and the harvest stabilizes at 375 individuals per time period, more than with the original value of ***R*** = 0.50.

Your graph of the recruitment curve and fixed quota now shows the quota line (horizontal line) crossing the recruitment curve at two points again. As before, if you drop a vertical line from the right-hand crossing point to the X-axis, you should see that this is the equilibrium population size.

Your graph of the recruitment curve and fixed effort line now shows the effort line crossing the recruitment curve to the right of its peak.

Now change *R* to 0.40. The fixed-quota population goes extinct, and its harvest goes to zero. The fixed-effort population stabilizes at 500 individuals, and its harvest stabilizes at about 187 individuals per time period.

Your graph of the recruitment curve and fixed quota again shows the quota line (horizontal line) lying entirely above the recruitment curve. This means that the quota is larger than recruitment regardless of population size, and harvesters will remove more individuals from the population than are added to it. So it is not surprising that the population goes extinct.

Your graph of the recruitment curve and fixed effort line now shows the effort line crossing the recruitment curve to the left of its peak.

Finally, change *R* to 0.20. Again, the fixed-quota population goes extinct. The fixed effort population is still declining at the end of 50 time units, and seems headed for extinction also. Its harvest is likewise declining toward zero.

Your graph of the recruitment curve and fixed quota again shows the quota line (horizontal line) lying entirely above the recruitment curve, now by a wider margin. This means that the quota is larger than recruitment regardless of population size, and harvesters will remove more individuals from the population than are added to it. So it is not surprising that the population goes extinct.

Your graph of the recruitment curve and fixed effort line now shows the effort line lying entirely above the recruitment curve. As in the fixed quota model, the harvest is now greater than recruitment regardless of population size. And likewise, the population goes extinct.

2. Restore *R* to 0.50 and *K* to 2000. Change *Q* from 250 to 300. You should see that the quota line once again lies entirely above the recruitment curve, and the population goes extinct.

   Change *Q* to 200. Now the quota line crosses the recruitment curve at two points, and the population stabilizes at the right-hand crossing point.

   The original value of *Q* = 250 was the maximum sustainable yield, as you can confirm by setting *Q* to values closer and closer to 250, above and below. You should see that any value of *Q* greater than 250 will drive the population to extinction. Any value of ***Q*** less than 250 will result in a larger equilibrium population, but will of course result in a smaller harvest.

3. Change *E* from 0.25 to 0.20. The effort line now crosses the recruitment curve to the right of its peak, and the population stabilizes at the crossing point. This results in a larger equilibrium population and a smaller harvest.

   Change *E* to 0.30. The effort line now crosses the recruitment curve to the left of its peak, and the population stabilizes at the crossing point. This results in a smaller equilibrium population and a smaller harvest.

   Change *E* to 0.50. The effort line now touches the recruitment curve at N=0 and lies above it everywhere else. The population and harvest are both still declining at the end of 50 time units, heading for extinction.

   The original of *E* = 0.25 gave the maximum sustainable yield of 250 individuals per time period, as you can confirm by plugging in values of *E* above and below 0.25.

Note that the MSY is the same in both models. This must be the case, because the MSY is a property of the population, not of the harvesting scheme. The harvesting schemes are just two ways of attempting to harvest the MSY.

4. Examine your graphs of recruitment against population size (either model). You should see that recruitment is greatest when $N \sim K/2$. As we said earlier, a sustainable harvest cannot exceed recruitment. Therefore, the maximum sustainable harvest, or MSY, must equal the maximum recruitment. Changing values of *R* and *K* will have shown you that both of these parameters affect the recruitment curve, so MSY must be related to both ***R*** and ***K***. We will derive the exact relationship in the next section.

5. The two harvest schemes have rather different implications for the risk of driving the harvested population to extinction. You should have noticed as you were changing values of *R, K, Q*, and *E*, that any decrease of *R* or *K* from the original values, and any increase of *Q*, drove the fixed-quota population to extinction. However, the fixed-effort population persisted under most of the same values of *R* and *K*, and only the highest values of *E* drove it to extinction. So it would seem that a fixed effort harvest is less likely to drive the harvested population to extinction. We will investigate this in more detail in the last part of the exercise.

Fixed-Quota versus Fixed-Effort: More Questions

QUESTIONS

6. What happens to a population harvested at the MSY under a fixed quota, if it starts out at its carrying capacity?
7. What happens to a population harvested at the MSY under a fixed quota, if it starts out at less than half its carrying capacity?
8. What happens to a population harvested at the MSY under a fixed effort strategy, if it starts out at its carrying capacity?
9. What happens to a population harvested at the MSY under a fixed effort strategy, if it starts out at less than half its carrying capacity?
10. You can calculate exact values for the fixed quota and the fixed effort that produce the maximum sustainable yield because you **know** the exact values of *R* and *K* for the harvested populations. In the real world, however, managers must **estimate** these values, and estimates are always subject to error. What happens to each of the harvested populations if you overestimate *K*? In other words, what happens if *K* is actually smaller than you think it is?
11. What happens if you overestimate *R*?
12. What happens if you set the quota or the effort too high?
13. Do you see another reason why setting a fixed-quota at the maximum sustainable yield is a risky strategy?
14. Is the fixed-effort harvest less risky?
15. What happens if managers decide to build a safety margin into a fixed-quota harvest?
16. In answering Questions 6–15, you will have seen two ways in which a fixed-effort harvest is less risky than a fixed-quota harvest. A fixed-effort harvest is not completely without risk, however.

    What happens to a population harvested under a fixed-effort strategy, if the effort is set too high? How does a high effort increase the risk of extinction in a fixed-effort harvest?

ANSWERS

6. Return R to 0.50, K to 2000, Q to 250, and E to 0.25. Examine your graph of N_t and harvest versus time for the fixed-quota population.

   You should see the population decline from K to $K/2$, and stay there.

   Thus, taking the maximum sustainable yield from a population by fixed quota means reducing it to half its carrying capacity.

7. Set N_0 for the fixed quota population to a value slightly less than $K/2$. Overwrite the formula in cell D12 with the value of your choice.

   You should see the population decline to zero. This happens because the harvest line is above the recruitment curve for all values of $N < K/2$. In other words, if the population falls to less than half its carrying capacity, the fixed quota harvest will remove more individuals from the population than are recruited into it, and the population will shrink.

   Thus, if for any reason (e.g., bad weather or poor food supply), the population declines below $K/2$, a fixed quota harvest will drive it to extinction. If the population has already been reduced to $K/2$ by harvesting at the MSY, falling below $K/2$ is very likely to occur sooner or later, given the normal annual variability in most populations.

   Incidentally, this also answers a question posed in the Introduction, about whether the equilibrium at $N=K/2$ under a fixed quota harvest is a stable equilibrium or an unstable one. The answer is: neither - it is a metastable equilibrium. If N departs from $K/2$ to a higher value, it will return to $K/2$, as it would for a stable equilibrium. However, if N departs from $K/2$ to a lower value, it will continue to move away from $K/2$, as it would for an unstable equilibrium. N will continue to shrink until it reaches zero (which is a stable equilibrium, although undesirable in most cases.) This is a mathematical way of expressing the riskiness of fixed-quota harvesting.

8. Examine your graph of N_t and harvest versus time for the fixed-effort population.

   You should see the population decline from K to $K/2$, and stay there.

   Thus, taking the maximum sustainable yield from a population by fixed effort also means reducing it to half its carrying capacity.

9. Set N_0 for the fixed quota population to values between $K/2$ and zero. Overwrite the formula in cell G12 with the value of your choice.

   As long as $N_0 > 0$, you should see the population increase to $K/2$, and stay there. This happens because the harvest line is below the recruitment curve for all values of $N < K/2$. In other words, if the population falls to less than half its carrying capacity, the fixed effort harvest will remove fewer individuals from the population than are recruited into it, and the population will grow.

   This is one way in which a fixed effort harvest is less risky than a fixed quota harvest. If the population has already been reduced to $K/2$ by harvesting at the MSY, falling below $K/2$ will result in a harvest that is not only smaller than the MSY but, more importantly, smaller than recruitment, which allows the population to recover (at least to $K/2$).

   Incidentally, this demonstrates that the MSY is a stable equilibrium under fixed-effort harvesting. If N departs from $K/2$ in either direction, it will return to $K/2$. Again, this is a mathematical expression of the lower risk associated with fixed-effort harvesting.

10. Restore the formula =B7 to cells D12 and G12. Leave Q and E unchanged, and adjust K in cell B7 downward. Do you see the logic of this? Try several values of K, changing it slightly each time. Examine all your graphs after each change.

    You should see that any overestimate of K results in extinction of the fixed quota population.

    The fixed effort population declines, but eventually stabilizes without going extinct.

11. Restore the value of *K* in cell B7 to 2000. Leave *Q* and *E* unchanged, and reduce *R* in small increments, as you did with *K* above. Examine all your graphs after each change.

    You should see the same results as when you overestimated *K*.

12. Return R and K to their original values (0.50 and 2000), and increase Q and E slightly. You should see that the fixed quota population goes extinct, but the fixed effort population persists, albeit at a smaller equilibrium size.

13. A fixed-quota MSY harvest is risky because even slightly overestimating *K* or *R*, or setting *Q* even a little too high, drives the harvested population to extinction.

14. A fixed-effort MSY harvest is less risky because overestimating *R* or *K*, or setting *E* too high (within limits), does not drive the population to extinction, although it may result in a smaller surviving population and a smaller harvest. To drive the population to extinction, you must set $E = R$.

15. To simulate a safety margin, set a fixed quota less than the MSY value.

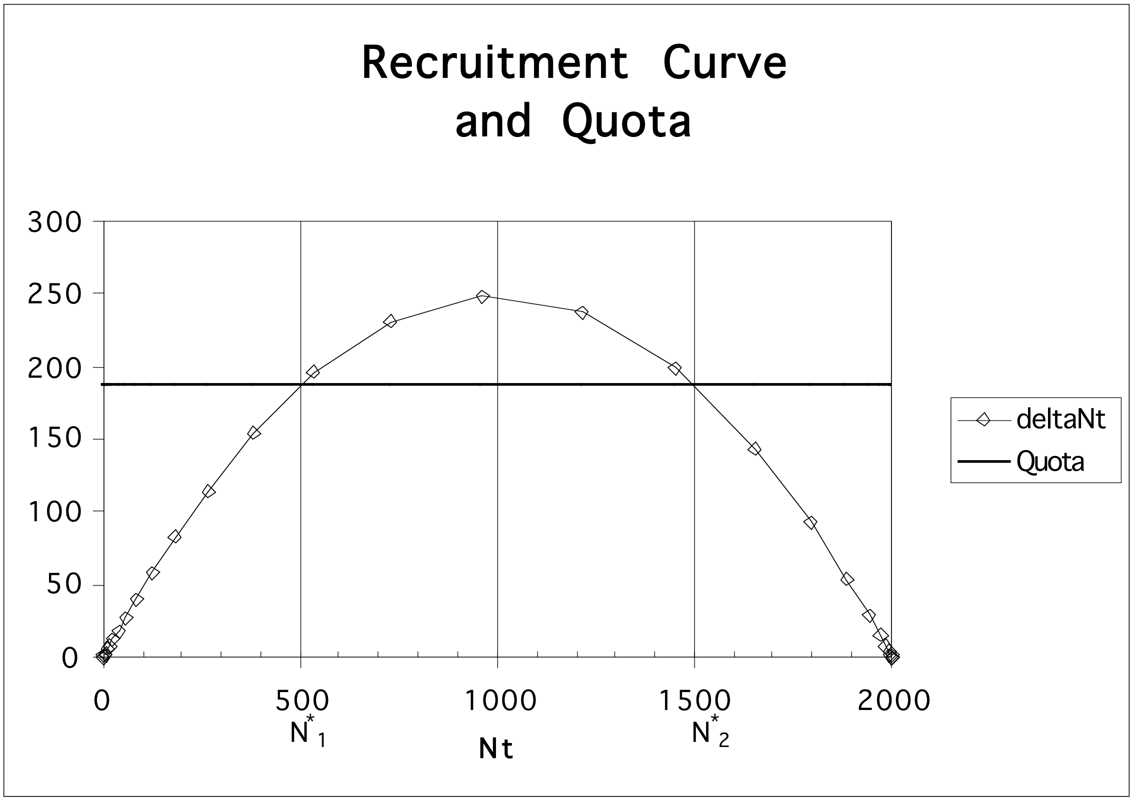
    Examine your graph of the recruitment curve with the fixed-quota line superimposed. Notice that the fixed-quota line now crosses the recruitment curve at two points ($N = N^*_1$ and $N = N^*_2$, see graph below). Both points are equilibria, where harvest equals recruitment, and are therefore sustainable yields. Both points represent lower harvests than the MSY, so they are not **maximum** sustainable yields.

    Set the initial population size of the fixed-quota population to values greater than $\boldsymbol{N^*_2}$, between N^*_2 and N^*_1, and less than N^*_1. What happens to the population size in each case?

    For N_0 values between *K* and N^*_2, and for values between N^*_2 and N^*_1, *N* returns to N^*_2. For N_0 values less than N^*_1, *N* goes to zero.

    Thus, reducing the quota below the MSY reduces the risk of extinction associated with a fixed-quota harvest. Under normal circumstances, *N* will remain stable at N^*_2. If chance variability reduces ***N*** below $\boldsymbol{N^*_2}$, the population will recover to $\boldsymbol{N^*_2}$, unless the reduction is so severe that ***N*** falls below $\boldsymbol{N^*_1}$. By setting a low quota, managers can increase the spread between $\boldsymbol{N^*_1}$ and $\boldsymbol{N^*_2}$, and reduce the risk of extinction. But doing so also reduces the allowed harvest, and it may be politically difficult to set quota low enough to ensure the harvested population's survival.

Figure 1. Fixed quota harvest with a safety margin.



16. Incrementally increase *E*, leaving other parameters unchanged. Examine your graphs of harvest and population size, and of effort and recruitment.

    As you increase *E*, you should see the effort line become steeper and steeper, and thus closer and closer to the recruitment curve on the left hand side.

    As you increase *E*, you should also see the equilibrium population size get smaller and smaller.

    Both factors increase the risk of extinction. Because the effort line is close to the recruitment line, anything that reduces recruitment may cause recruitment to fall below harvest, and lead to population decline, perhaps to zero.

    Likewise, a small population is at greater risk of extinction from random variation in ***N***.

Annual Variation

QUESTIONS

17. Does the addition of stochastic variation to the model increase the risk of extinction for a population harvested at the MSY under a fixed quota?
18. Does the addition of stochastic variation to the model increase the risk of extinction for a population harvested at the MSY by fixed effort?
19. Does reducing a fixed quota below the MSY (i.e., building in a safety margin) prevent extinction of a stochastically-varying population?

20. Does the addition of stochastic variation to the model increase the risk of extinction for a population harvested above the optimal effort (i.e. the effort that yields the MSY)?

ANSWERS

17. Examine your graph of population size and harvest for the fixed-quota population.

    Press the recalculation key. You should see all the population values and graphs change, as the spreadsheet recalculates the random values and resulting population sizes.

    Repeat this recalculation many times, while watching your graph of population size and harvest.

    You should see that with the quota set at the MSY, and *R* varying by 0.5, the population often goes extinct within the 50 time-units shown.

    Recall that the MSY was a sustainable harvest in the deterministic model. Plainly, variation increases the risk of extinction.

    You can quantify this increased risk, if you wish, by keeping a tally of the total number of trials (recalculations) and the proportion of trials in which the population goes extinct.

18. Repeat the recalculation experiment described above for the fixed effort population.

    You should see that the fixed-effort population rarely, if ever, goes extinct with these parameter values.

19. Simulate a safety margin by changing the quota from 250 to 200 in cell F9.

    Repeat the recalculation experiment, while observing your graph of population size and harvest.

    You should see that, although the risk of extinction is reduced compared to harvesting at the MSY, the population still goes extinct fairly often.

    Even a quota as low as 100 produces occasional extinctions.

20. Simulate harvesting at greater than optimal effort by changing the effort from 0.25 to 0.40 in cell I9.

    Repeat the recalculation experiment, while observing your graph of population size and harvest.

    You should see that the fixed-effort population often becomes quite small and may be still declining after 50 time units. Whether or not the population goes extinct in the model, a very small population is plainly at greater risk of extinction than a large one.

    This scenario represents a serious overestimate of the MSY. Overestimating the optimal effort to this degree in the deterministic model of fixed effort did not produce extinction, but with stochastic variation, it can. Thus, stochastic variation also increases the risk of extinction under a fixed-effort harvest, but to a lesser degree than under a fixed quota harvest..

    Try smaller values of ***E***, representing better estimates of the MSY. You should see the risk of extinction decrease with smaller efforts.

The Bonus Analysis (Allee effect) is left for the reader to work out.