3 Applied population dynamics: managing Pacific salmon

By the end of this chapter you should be able to:

- *Estimate population size from simple mark-recapture data*
- *Construct stock-recruit graphs that relate the number of individuals at time t+1 to the number in the previous generation.*
- *Interpret the stock-recruit graph to estimate the maximum sustainable harvest.*
- *Evaluate the stability of equilibria under different harvest scenarios.*

Pacific salmon are famous for their migration from the ocean to the tributaries and streams where they spawn. Some of the most impressive migrations occur in the Chinook and Sockeye salmon from Washington and Idaho. They swim more than 1500 km against the current of the Columbia and Snake rivers, jumping over waterfalls and climbing almost 2500 m in elevation as they return from the Pacific Ocean to their spawning sites. Similarly some populations of Chinook salmon in the Yukon must journey over 3000 km up the Yukon River to spawn.

Courtesy American Rivers

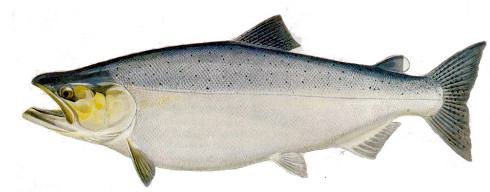
Historically, the Columbia River basin once supported an estimated 7 to 15 million salmon Heavy commercial fishing started a decline in the population of Columbia River salmon in the 1870s, a trend that has been exacerbated by land use changes, dams along the river system, changes in the ocean environment, and continued harvest. The population of spring Chinook salmon in Columbia river is currently less than 3% of the population size compared to when Europeans first arrived in the area. That story is alarmingly similar to the overexploitation and collapse of other economically important fisheries such as the Atlantic cod, mackerel, anchovies and whales.

In contrast, other populations of salmon, notably in Alaska and British Columbia, are currently thriving. Is it possible to design a program of sustainable management of those salmon stocks?

For long-distance migratory species such as salmon, it is common for individuals that originate in one management unit to pass through another management unit during part of their migration. In particular, many fisheries in Canada are dependent on fish that pass through the US and which are subject to harvest by US fisheries as they move upstream. The two countries signed the Pacific Salmon Treaty in 1985 (later updated in 1999) to try to conserve the salmon stocks and equitably apportion the harvest. In particular, the agreement assigns a harvest percentage in proportion to the fish that originate in each country, and sets harvest rates as a function of yearly estimates of abundance.

In order to set those goals, we need to be able to 1) estimate the total number of salmon and 2) determine the number that can be sustainably harvested.

All pacific salmon are *anadromous*, spending part of their life in fresh water and part of their life cycle in the ocean. The Chinook or king salmon is the largest of the five species and is one of the most important species economically. When eggs hatch, the young fish, or "fry", spend a few weeks to a few years in fresh water, depending upon the species. As they migrate downriver toward the ocean, numerous physiological changes occur that allow them to make the transition from fresh water to salt water. At that time the young salmon are called "smolts". Immature salmon may spend 2-5 years in the ocean. They feed on other fish as they make a slow, counter-clockwise circuit of the north Pacific following the prevailing currents. They make one complete circuit of the Pacific each year, from North America to Asia and back. Mortality among the young is quite high. Each female Chinook salmon will lay approximately 5000 eggs, of which only about 50 will survive to become smolts and enter the ocean. Of those 50, only approximately 2 will return to breed.



When adults return to spawn, they may travel hundreds of miles upstream to return to the precise tributary where they were born. It is thought that they follow faint chemical cues to locate their natal stream. The journey may take 1-2 months. As they travel upriver they do not feed at all, and change from the silver color of ocean fish to their mating colors of red, green, or brown.

After spawning, all of the adults die.

3.1 **How many salmon are there?**

If the stream is small enough, biologists can use weirs to temporarily trap the fish so all of the fish migrating upstream can be counted. Or, if the stream is also shallow and clear, biologists can simply count the salmon as they pass by. But in larger river systems some kind of sampling scheme must be used. One common method is the capture-mark-recapture method of estimating the population size.

The basic idea is that the ratio of marked to unmarked fish should be the same in two successive samples from the population. A number of fish are caught at time 1 and are marked. They are then released back into the population. At time 2, a second sample of fish are caught and we record the total number of fish that were marked and the total number of fish that were examined at time 2. If we assume that there is no effect of marking, the ratio of marked to total fish in the initial sample should equal the ratio of marked to total fish in the second sample:

$$\frac{m_1}{N} = \frac{m_2}{n_2}$$

N is the total population size, m_1 is the number of marked individuals at the first sample time, n_2 is the number of individuals examined at the second sample and m_2 is the number of marked individuals that are subsequently re-sighted in the second sample. All of those numbers are known except N. This can easily be rearranged to find an estimator of the total population size:

$$N = \frac{m_1 \cdot n_2}{m_2} \qquad \text{eq. 3.1}$$

This is called the Petersen method, after the Danish fisheries biologist C.G.J. Peterson who first used it in the late 1800s. Versions of this equation have a long history of use in ecology.

In its simple form, the Petersen equation has a couple of slight problems. For example, what happens if $m_2=0$? If few fish are marked, it is possible that no marked fish will be recovered in the second sample. Division by zero is undefined so it gives no estimate of abundance. Also, the simple estimator is biased: it tends to overestimate the population size, especially when few individuals are marked. A better estimator of abundance, although not as obvious, is:

$$\hat{N} = \frac{m_1(n_2+1)}{(m_2+1)} \qquad \text{eq. 3.2}$$

Many other methods have been devised to estimate population size from mark-recapture data (some can be substantially more complex) but all are built on the same basic foundation. Understanding this one will give you a good idea of how they all work.[1]

Assumptions of the Petersen mark recapture technique:

1 Closed population: there is no immigration, emigration, birth, or death in the interval between the two samples.
2 Marking does not affect the fate of the fish: marked and unmarked fish are equally likely to survive and travel upstream, and to be subsequently caught.
3 All fish have equal probability of being caught.
4 Marks are not lost or overlooked.
5 Marked and unmarked fish are well mixed.

As an example, let's consider the salmon that travel up the Yukon River to spawn in Alaska and Northern Canada. In one study, 419 Chinook salmon were captured and marked on the lower Yukon River. Later, 69 marked fish were recovered upstream out of a sample of 20,875 fish examined.

Using equation 3.2, what was the total population size of Chinook salmon traveling up the Yukon River? ___________

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[1] How reliable is this estimate of population size? Because the recaptured fish are only a sample of the marked fish, there will be some variation in the estimates. Any given sample may have slightly more or fewer marked fish than expected, which will lead to estimates of population size that are too high or too low. The standard error of our estimate of population size is: $SE(\hat{N})=\sqrt{\frac{m_1(n_2+1)m_2^2(n_2-m_2)}{(m_2+1)m_2^2(m_2+2)}}$. Adding and subtracting two standard errors to our estimate gives the approximate 95% confidence interval.

Of course this estimate of N is only valid if the assumptions are met. 1) For these salmon, there was a relatively short time between marking and recapture so it is reasonable to consider it a closed population. Furthermore the salmon were all traveling upstream past the marking station, so there could be no immigration from other areas. 2) A few marked fish apparently did not survive to pass an upstream checkpoint, so those marked fish were removed from the counts before analysis. 3) The average sizes of marked and unmarked fish were similar, which suggested that there was no strong bias in which fish were marked and caught. 4) They used two different kinds of marks, fin tags and radio transmitters. Some fin tags were lost, but the second mark provided a backup to identify the marked fish. 5) Fish arriving at different times may travel to different tributaries and thus may not mix completely. To counteract that problem, they marked a random subsample of fish on each day of the run, which ensured that marked fish were equally likely to be present in each part of the run.

So for salmon at least, the assumptions of this mark recapture technique are relatively easy to meet. For other animal species where population boundaries are not so clearly defined (for example many birds and mammals), it is important to allow for movement between populations. In that case, other mark recapture techniques are available that use two or more recapture dates to estimate survival and or population size in open populations.

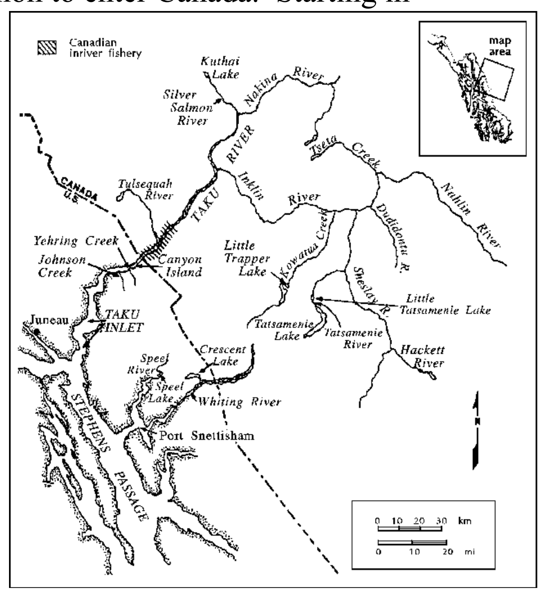
What will happen to your estimate of population size if some fraction of individuals leave (through death or emigration) in the interval between marking and recapture? Does eq. 3.2 still estimate N? ___________

Does eq. 3.2 still give an estimate of N if some individuals enter the population (through births or immigration) between the two sample times? (Hint: will the new individuals be marked or unmarked?) _____________

What if marking the fish increases their mortality? How will that affect the estimate of N? ______________

3.2 **Your turn:**

The Taku river system in southeast Alaska and Canada is an almost pristine environment that supports large runs of several species of salmon. Crossed by no roads, the Taku river system is the largest intact salmon-bearing river in North America. The Chinook salmon on the Taku river enter the river in late spring near Juneau, Alaska, and spawn in Canadian tributaries in August. There has been a commercial salmon fishery in the Taku inlet since the late 1800s. However large harvests in the 1960s and 1970s severely depleted the stock. Canadian fishermen were concerned that the US fishery was not allowing sufficient salmon to enter Canada. Starting in 1975, catch was limited to try to rebuild the Taku River Chinook salmon population.

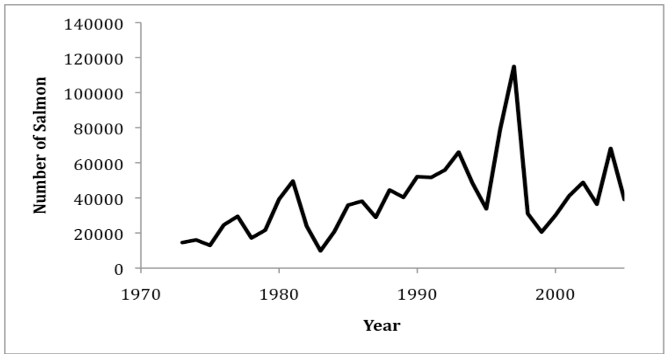


The average number of salmon in the Taku from 1973-1983 was averaged about 25000. The table below shows mark-recapture result from the 1990s, after the limits on the commercial fishery had been in place for several years. Was the program successful in allowing the population of Taku salmon to recover?

Table 1. Mark-recapture data from the Taku river:

Year	Marked (m1)	Recovered (m2)	Examined (n2)	Total number (N)
1989	328	42	5270	
1990	270	26	5194	
1996	1113	74	5319	
1997	915	47	6022	

Fig. 3.2. Taku River Chinook salmon, 1973 to 2005



3.3 How many fish can be caught without causing the population to collapse?

Regulatory agencies are charged with the often contradictory tasks of conserving the natural salmon populations while at the same time maintaining the economic health of the commercial and sport fishing industry. Thus they must manage the populations to maximize the sustainable harvest of fish. How should the fishing regulations be structured and what should be the maximum allowable catch in order to best meet those conflicting goals? Here is where a model can be useful. If we can capture the essential population dynamics in a simple model, then we can vary the parameters of that model to see how proposed changes will affect the population size. We can project population growth under different harvest scenarios and choose the most sustainable strategy.

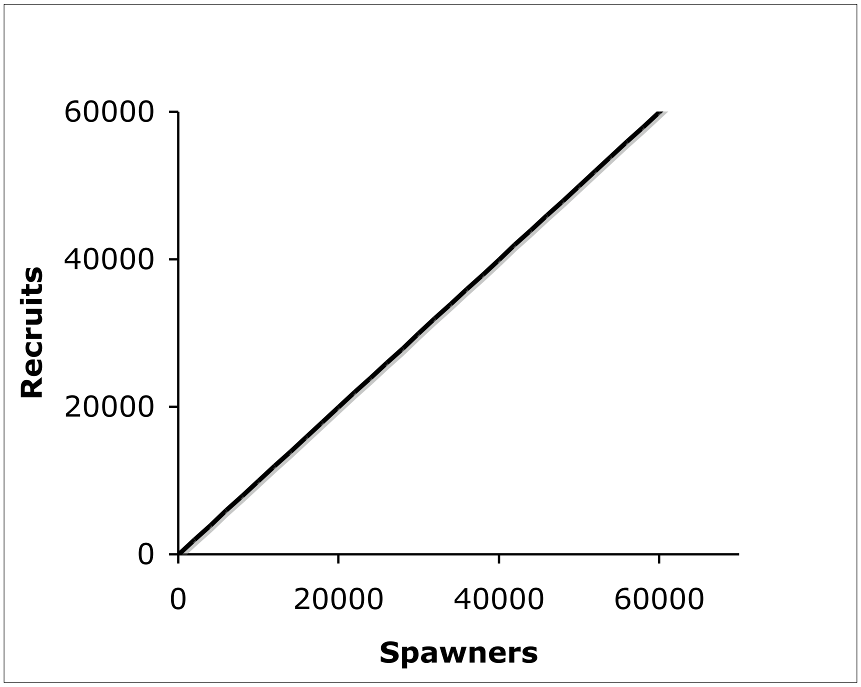
Pacific salmon are *semelparous*: they reproduce once and then die. Juveniles can spend varying amounts of time in the ocean before returning to spawn, but the majority of Chinook salmon return to spawn in their fourth or fifth year.

Because all of the parents die each generation and cohorts are somewhat synchronized, should this population be modeled using a discrete or continuous model?_________

3.3.1 Stock-recruit graphs

A useful way to look at the dynamics of the salmon population is to graph the number of recruits vs the number of spawners in the previous generation. (N_{t+1} vs N_t). We will define “recruits” as the number of offspring that successfully survive and return to breed four years later. That is convenient because there are lots of data on the number of fish that return to the river to spawn, but very few data on the population size or mortality of juveniles in the streams and ocean. For simplicity, we will assume that all fish return in their 4^{th} year, so we can use the discrete population growth model.

Imagine we have a growing population of fish with K=40,000. Sketch an approximate graph of the number of returning fish (recruits, N_{t+1}) vs the number of spawners in the previous generation. (Nt)



(Hint: To determine the general shape of the curve, we can define some landmark positions. If there are no spawners, there can be no recruits so we know it starts at the origin. The 45 degree line shows when the number of recruits exactly equals the number of spawners (i.e. $N_{t+1}=N_t$). If the population is growing, what will be the relationship between the number of recruits and number of spawners? (equal? more? fewer?) At the carrying capacity, what will be the relationship between the number of recruits and number of spawners? If the population of spawners is above the carrying capacity, what will be the relationship between the number of recruits and the number of spawners?)

3.4 **Maximum sustainable harvests**

Now we are just about ready to calculate the maximum sustainable harvest rate. The stock-recruit graph shows that the population is growing when the stock-recruit curve is above the 1:1 line. When the number of recruits is equal to the number of spawners (intersects the replacement line), the population is stable.

From the logistic or Ricker curve, population growth is at its maximum at intermediate densities. That means the population can recover fastest when densities are intermediate.

We can define a sustainable harvest, as that which will prevent the population from declining. That means that the number of recruits minus the number of fish caught should be at least equal to the number of spawners the previous generation. (For salmon, almost all of the fishing is done as the salmon swim upriver. Since the time between fishing and and spawning is short, we can ignore other sources of mortality in that interval between fishing and spawning). On the stock-recruit graph, the number of fish that can be caught (H, for "harvest") is the vertical distance between the stock-recruit curve and the 1:1 line. One way to think about this is that we can sustainably harvest only the "excess" recruits above the replacement value. We want to find the population size of spawners (S*) that maximizes the distance of the recruitment curve above the 1:1 line. This is called the **maximum sustainable yield or MSY**. The maximum sustainable harvest of salmon will occur at some intermediate density of spawners, where the population size of spawners is large enough to produce a large number of potential recruits while at the same time density-dependent mortality is not too great. The maximum sustainable harvest can be found graphically from the stock-recruit curve by calculating H for various spawner densities.

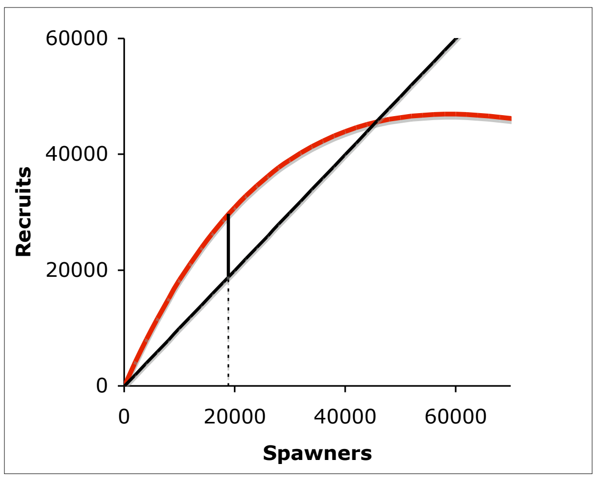


Figure 3.3. Stock-recruit curve for λ=2.17, K=45,000. For these parameters, the MSY is approximately H=10,800, which occurs when S=S=19,000.*

The idea that there is a harvestable "excess" depends on density dependent or compensatory mortality. Without density dependence, there would be a direct relationship between harvest and recruitment. Many studies have shown that the survival of fry is strongly density dependent.

If the harvest rate is adjusted to maintain the population of spawners at S* the population could, in principle, be maintained indefinitely while at the same time producing the maximum long-term yield of fish. One of the problems of fisheries management is determining what that level is and how to ensure that harvests are maintained at a sustainable level. Imagine that you are the manager: how should you structure the fishery to maximize the harvest of fish without endangering the population? We can imagine a couple of very simple rules for regulating harvests.

3.4.1 Harvest rule 1: constant number of fish caught per year

Such a rule could be implemented by issuing permits to catch a particular number of fish each year.

Salmon are typically harvested as they return to the rivers, right before spawning. So the number of successful recruits that survive to breed is the number of recruits minus the number that are harvested, R'=R-H. At equilibrium the number of successful recruits must equal the number of spawners the previous generation, so R-H=S. We can rewrite that equation as R=H+S. That is the equation of a straight line on the stock-recruit graph with slope=1 and intercept =H. On the stock-recruit graph, the effect is to move the 1:1 line up H units (Fig 3.4). The modified line is higher that the 1:1 line because not all of the incoming recruits are allowed to spawn.

As before, there will be an equilibrium where the number of recruits exactly equals the (modified) replacement line. For small numbers of fish harvested, there are two equilibrium population sizes (Fig 3.4). The upper equilibrium is stable which we can see by imagining small perturbations in the number of spawners. If the number of spawners is slightly to the right of the equilibrium (i.e. the return of spawners is slightly greater than expected), the recruitment curve is below the modified replacement line and the population will decline back towards the equilibrium. If the number of spawners is to the left of the equilibrium, the number of recruits is greater than the replacement value and the population will increase.

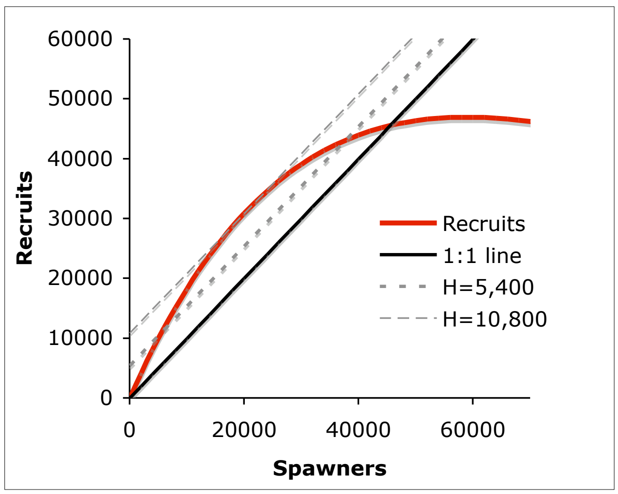


Figure 3.4. Harvest rule 1: constant number of fish; λ=2.17, K=45,000. The maximum sustainable harvest for this river is approximately H=10,800. Source: Reisenbichler 1990 NMFS F/NWC-187

In contrast, the lower equilibrium is unstable. If the number of spawners is to the left of the equilibrium, the recruitment curve is below the modified replacement line. That means there are insufficient recruits to replace the current spawners so the population will decline. That will move the number of spawners even farther to the left, where recruitment is even lower, and eventually the population will decline to extinction. If we perturb the number of spawners to the right of the equilibrium, the recruitment curve is above the replacement line. There will be even more spawners the next generation, moving the population even farther to the right of the equilibrium. The population will continue to grow until it reaches the upper equilibrium value.

If we increase the number of fish harvested, the effect is to move the modified replacement line higher on the stock recruit graph. The two equilibria get closer and closer together until you reach a maximum harvest where there is a single equilibrium.

Is that equilibrium stable? ________________

(Hint: What will happen after a particularly good year, when more fish survive and return to spawn than expected? What happens after a bad year? can the population recover?)

(For that reason, few managers would use the constant harvest rule.)

3.4.2 Harvest rule 2: constant percentage of fish caught per year

A second strategy would be to issue licenses for a particular number of fishing boats, or opening the season for a particular number of days per year, regardless of the success and number of fish that are caught. An advantage of the constant percentage rule is that fewer fish are caught when population size is low.

At S*, some fraction h=H/R can be caught without reducing the population size. If a fraction h of the returning salmon are caught, then 1-h of the recruits return to spawn successfully. For exact replacement the surviving recruits must equal the number of spawners, so R(1-h) = S or R=1/(1-h) S. This will be a straight line on the stock-recruit graph with intercept=0 and slope=1/(1-h). The modified replacement line is higher that the 1:1 line because only a fraction of the incoming recruits escape harvest and are allowed to spawn. For any given harvest percentage, we can find the equilibrium where the recruitment curve intersects the modified replacement line.

Again the goal is to set the harvest rate so that the number of fish harvested (H) will be a maximum.

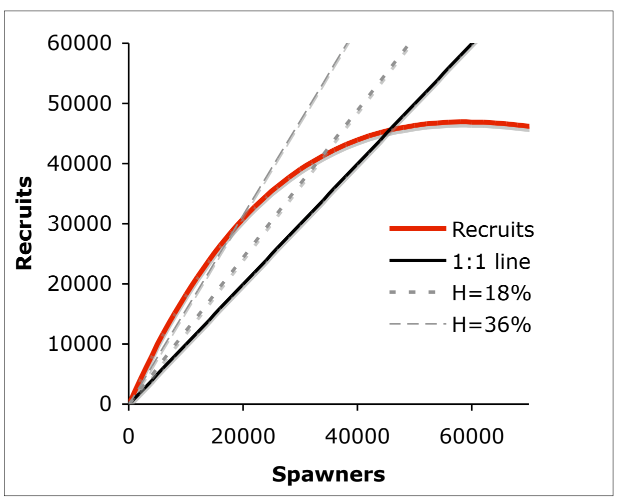


Figure 3.5 Harvest rule 2: constant fishing effort; λ=2.17, K=45,000. The maximum sustainable harvest for this river is approximately H=10,800 (36% at MSY). Source: Reisenbichler 1990 NMFS F/NWC-187

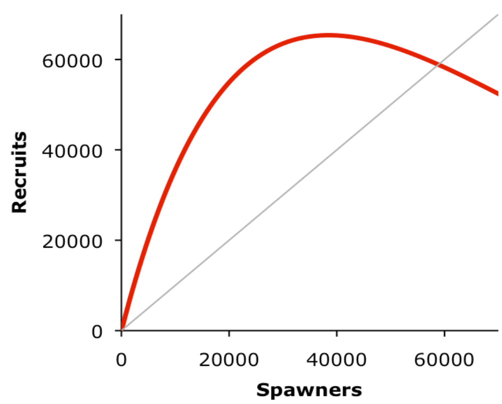
Harvest rule 2 has only a single non-zero equilibrium, as can be seen from the curves in fig 3.5

Is this equilibrium stable? ___________

If for some reason the number of spawners drops below S*, the recruitment curve in rule 2 is above the modified replacement line and the population will grow until it returns to S*. Similarly, if S>S*, the recruitment curve will be below the modified replacement line and the population size will decrease.

What happens if managers set the harvest rate is slightly too high? how does that change the stock-recruit graph? Will the population recover?

Returning to the case of the Taku River salmon, what is the maximum sustainable harvest for those fish? The actual stock-recruit graph for chinook in the Taku Rivers system is shown below.



Approximately what population size of spawners (S*) produces the maximum sustainable harvest? _________

What is the approximate catch at the maximum sustainable harvest?___________

The current escapement goal for Chinook salmon in the Taku River is 30,000 to 55,000 spawners. How does that match your estimate of the required number of spawners for sustainability?_________

3.5 Gaps between theory and reality

The idea of a maximum sustainable yield is appealing in theory, and for a long time it formed the basis of fisheries management. However there are many problems with MSY as a practical management approach. Ricker's definition of MSY was based on their being an average catch of fish, continuously taken, under existing environmental conditions. In practice, there will be good and bad years that will affect the productivity of the fish stocks and thus cause the MSY to vary from year to year. These equations also assume that we know the population size and harvest effort without error. In fact, those parameters are very hard to measure precisely. [look at fig 3.6, below] In addition it is difficult to specify the harvest effort in advance because fishermen will always try to increase their efficiency. As efficiency increases the actual harvest rate than expected.

Harvest Rule 3: (minimum escapement)

For all of those reasons, it may be better to have targets for the number of fish, as long as you modify those targets each year, depending on the current population of spawners. The approach that is currently used for managing pacific salmon is to set a minimum escapement goal, to try to ensure that there are *at least* S* spawners that escape harvest and are allowed to reproduce.

3.6 **Your turn: Changes in productivity of Columbia and Snake River Chinook**

Numerous habitat changes have affected the productivity of Chinook salmon populations in the Columbia River basin. One of the largest changes was the completion of a series of hydroelectric dams on the Snake River in the early 1970s. Schaller et al. collected stock-recruit data for different time periods. Below are their data for recruitment during the periods 1930-1974 and 1975-1990.

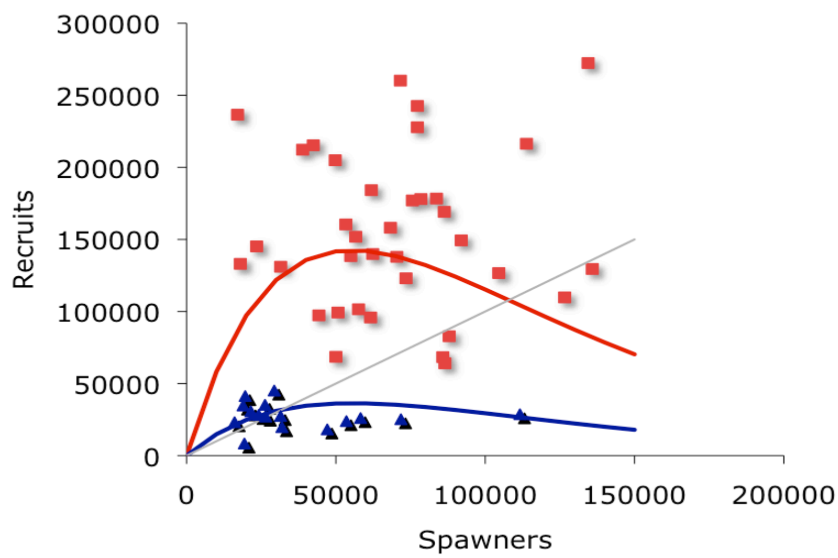


Figure 3.6. Stock-recruit curves for the Columbia River chinook salmon at two time periods: 1930- 1974 (red squares) and 1975-1990 (blue triangles).

What was the approximate maximum sustainable harvest (MSY) for salmon in the first part of the century (1930-1974)? ________________

What is the approximate MSY for salmon since then (1975-1990)? ________________

Answers.

p. 3 $\hat{N} = \frac{419 \cdot 20{,}876}{70} = 124{,}958$ $SE(\hat{N}) = \sqrt{\frac{420 \cdot 20{,}876 \cdot 350 \cdot 20{,}806)}{70 \cdot 70 \cdot 71}} = 13{,}547$ Adding and subtracting two standard errors to our estimate gives the approximate 95% confidence interval. The population size is somewhere between 98,000 to 152,000, with the best estimate being approximately 125,000.

p 4

- if individuals leave then eq. 3.2 will still work, so long as marked and unmarked inviduals leave at the same rate.
- if some individuals enter the population they will necessarily be unmarked. That will change the underlying ratio of marked and unmarked fish and therefore make it impossible to know the value of N.
- If marking increases the mortality of the fish, then eq. 3.2 will no longer estimate N (because it will change the underlying ratio of marked to unmarked fish).

Your turn, p. 5:

1989, 40207
1990, 51950
1996, 78949
1997, 114813

p 6. discrete
p 7. Because we said the population is growing, R>S and the recruit curve will be above the line when population sizes are small. At carrying capacity, R=S so the recruit curve will cross the 1:1 line. The result should look like figure 3.3.

p 10 rule 1 (constant harvest): single equilibrium at MSY is unstable.
p 11 rule 2 (constant effort): equilibrium is stable.

p. 11. Taku stock-recruit curve
S* is approximately 24,000
H=35,000
The current escapement goal of 30,000-50,000 is larger than S*, so it should be sustainable.

Your turn, p 12
For the early years, the MSY occurs with about S*=45,000 spawners and allows a harvest of roughly 120,000 fish.
After 1980, the recruitemt curve is only barely above the replacement line. S* is about15,000 with a harvest of only a couple of thousand salmon.

3.7 **OPTIONAL The Ricker model**

In chapter 2 we used the logistic model to describe the dynamics of populations that have density-dependent growth. The logistic model captures many aspects of real populations (slow initial growth, maximum growth at intermediate densities, then slow growth as the population approaches the carrying capacity). But it is only one possible model. It was derived starting with the simple assumption that there was linear density dependence: each additional individual in the population reduces the pool of available resources by a constant amount.

However the *discrete* version of the logistic model can give unrealistic results at extremely high densities. Under some extreme conditions it can even predict that the population will become negative, which is of course impossible. Because of that problem, fisheries biologists have used alternative models of density dependent growth. One is the **Ricker model** (Ricker, 1954).

The logistic and Ricker models are very similar at low density, but they differ in the way density dependence is modeled. In the Ricker model, density dependence is not linear.

The Ricker model can be written:

$$N_{t+1} = N_t \lambda^{(1-\frac{N_t}{K})} \qquad \text{eq 3.3}$$

For comparison, the *discrete* version of the logistic model is

$$N_{t+1} = N_t + r_d N_t (1 - \frac{N_t}{K}) \qquad \text{eq 3.4}$$

where r_d=1- λ. Although he formulas look very different, both models predict a similar S-shaped growth curve. Both predict a similar initial growth rate at low density and both stabilize at the same carrying capacity, but the Ricker equation has a slightly slower approach to K (Fig. 3.7).

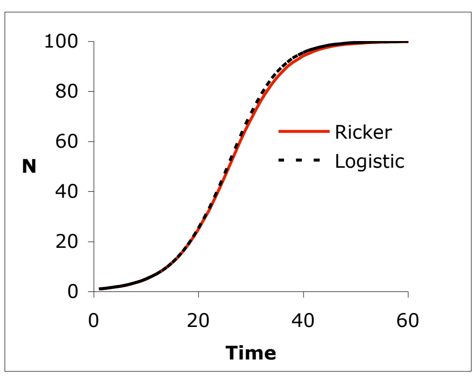


Figure 3.7. The logistic and Ricker population growth models predict a similar approach to the carrying capacity. For both curves λ=1.2 and K=100.

However, at very high densities, well above carrying capacity, the two models differ. The difference is particularly pronounced when r is large (i.e. for organisms that have high fecundity). Notice that at the highest population densities, the logistic model predicts a negative number of offspring!

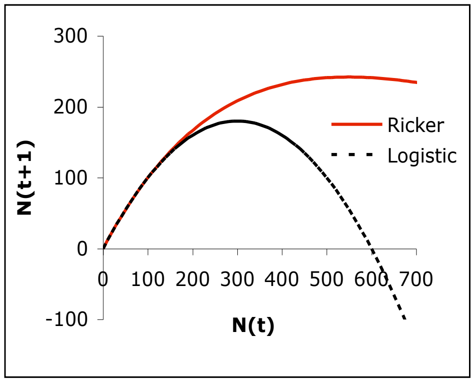


Figure 3.8. The Ricker and logistic models differ at extremely high densities.

Which model is correct? In a very real sense they both are correct. We want a simple description that captures the most important aspects of the biological system. Here the idea we are focusing on is density-dependent population growth and both clearly capture the way population growth declines at high density and eventually stabilizes at some final carrying capacity. We also want a model that is easy to understand and that is analytically tractable. The logistic is slightly more convenient in that respect.

The Ricker model has a long history in fisheries biology. Moreover, for our populations of salmon the shape of the density dependent recruitment (Fig 3.9) is clearly non-linear. So most fisheries biologists use the Ricker model to develop harvest strategies for salmon.

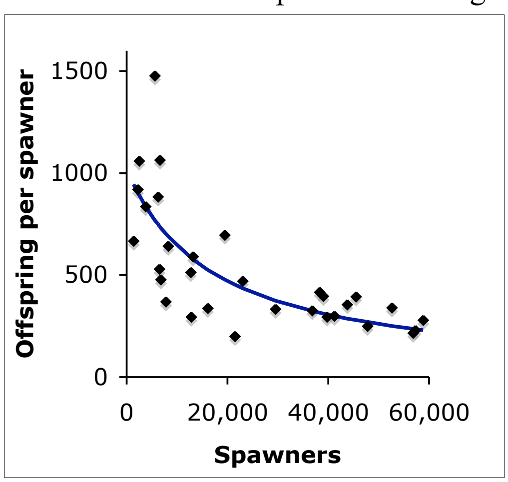


Figure 3.9. Density dependent reproduction in Snake River spring Chinook salmon. The per capita birth rate is a non-linear function of adult density. Data from Zabel et al. 2005.