Maximum Likelihood Lab 4: Population Dynamics

answer key

BIOHOPK 143H - Winter 2021

```
knitr::opts_chunk$set(fig.height = 4, fig.width = 6, message = FALSE, warning = FALSE)

### load the tidyverse packages
if (!require("tidyverse")) install.packages("tidyverse"); library(tidyverse)
```

```
## Loading required package: tidyverse
```

```
## -- Attaching packages --------------------------------------- tidyverse 1.3.0 --
```

```
## v ggplot2 3.3.3     v purrr   0.3.4
## v tibble  3.1.0     v dplyr   1.0.4
## v tidyr   1.1.3     v stringr 1.4.0
## v readr   1.4.0     v forcats 0.5.1
```

```
## -- Conflicts ------------------------------------------ tidyverse_conflicts() --
## x dplyr::filter() masks stats::filter()
## x dplyr::lag()    masks stats::lag()
```

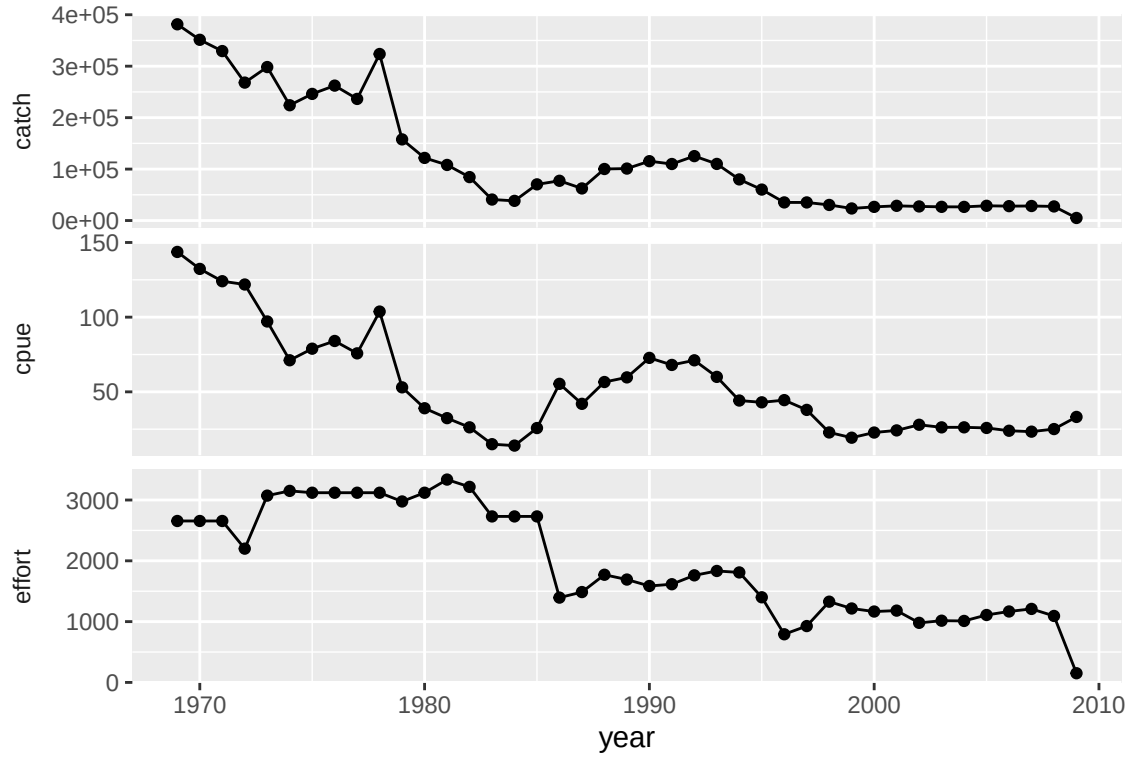
```
###  mvtnorm package for building autocorrelative model
if (!require("mvtnorm")) install.packages("mvtnorm"); library(mvtnorm)
```

```
## Loading required package: mvtnorm
```

Load and plot data

These data contain fisheries catch (in tonnes) and effort for pink and green abalone on Isla Natividad from 1969 to 2009 - catch data were not distinguished at the species level until 2002. The `cpue` column is just the catch divided by the effort. For the purposes of this exercise, we'll assume that pink and green abalone have the same demographic parameters - i.e., we'll be modeling this data as if it comes from a single population.

```
natividad <- read.csv("isla_natividad_abalone.csv")

natividad %>%
  pivot_longer(-year, names_to = "var") %>%
  ggplot(aes(year, value)) +
  geom_line() +
  geom_point() +
  facet_wrap(~var, scales = "free_y", strip.position = "left", nrow = 3) +
  theme(strip.placement = "outside",
        strip.background = element_blank(),
        axis.title.y = element_blank())
```



The Beverton-Holt model

In the Beverton-Holt model, which is discrete, n_{t+1} given n_t, the growth rate λ, and the density-dependent parameter α is:

$$n_{t+1} = \frac{\lambda n_t}{1 + \alpha n_t}$$

The carrying capacity for this model is given by:

$$K = \frac{\lambda - 1}{\alpha}$$

The model has the general solution for the population size n_t at time t:

$$n_t = \frac{K n_0}{n_0 + (K - n_0)\lambda^{-t}}$$

We don't have n at *any* time step, but we want to estimate it - to do so, we have to estimate λ, α, and n_0. But what data do we have to estimate these parameters with? Well, we can infer these parameters through the relationship between the observed catch and effort. In a continuous time model, the catch is simply the population size multiplied by the fisheries effort and catchability q (we have to estimate this) at a given time t:

$$\text{Catch}_t = n_t \times q \times \text{Effort}_t$$

In a discrete-time model, we have:

$$\text{Catch}_t = n_t \times \left(1 - e^{-q \times \text{Effort}_t}\right)$$

So, the three parameters we have to estimate for the deterministic part of our maximum-likelihood model are the growth rate λ, the density-dependent paramter α, and the catchability q, and we'll do so by comparing the observed catch (which we'll denote obs. Catch_t) to the estimated catch (which we'll denote with μCatch_t).

There's one thing we're missing here though - the initial population size n_0. We can estimate this as a separate parameter, or we can use our catchability estimate to derive one using the relationship between catch, effort, and the population size that we've defined above. Reorganizing the equation above, we have:

$$n_0 = \frac{\mu\text{Catch}_0}{1 - e^{-q \times \text{Effort}_0}}$$

The caveat here is that we need an estimate of n_0 to estimate the true catch at any given time μCatch_t, so for the first time step $t = 0$, we'll have to assume that the true and observed catch are the same:

$$n_0 = \frac{\text{obs. Catch}_0}{1 - e^{-q \times \text{Effort}_0}}$$

Maximum Likelihood Estimation

By now, we're pretty familiar with the process of creating a likelihood function for our model. Not much is different here, but since this model is a discrete dynamic model, we're going to loop through time to obtain our estimates.

In this model, our independent variable is fishery effort, and our dependent variable is fishery catch. Because the variance in catch doesn't increase much as the catch increases in size, and because the catch never gets close to zero (the minimum possible value), a Normal distribution is probably adequate for this data. If it turns out that a Normal distribution isn't the best choice, that'll show in our **residuals plots** - just like we'd do for an ordinary linear regression.

So, our model is:

$$\begin{aligned}
\text{obs. Catch}_t &\sim \text{Normal}(\mu\text{Catch}_t, \sigma^2) \\
\mu\text{Catch}_t &= n_t \times \left(1 - e^{-q \times \text{Effort}_t}\right) \\
n_t &= \frac{\lambda n_{t-1} \times e^{-q \times \text{Effort}_{t-1}}}{1 + \alpha\left(n_{t-1} \times e^{-q \times \text{Effort}_{t-1}}\right)} \; ; \; t \in (1, 2, \ldots, t_{\max}) \\
n_0 &= \frac{\text{obs. Catch}_0}{1 - e^{-q \times \text{Effort}_0}}
\end{aligned}$$

Likelihood function

Here's a function that returns a negative log-likelihood given the parameters (`lambda`, `alpha`, `q`, and `sigma`) and some data (`t`, the time steps, `obs_catch`, the observed catch at time t, and `obs_effort`, the observed effort at time t).

Here, we've raised `alpha` and `q` to the power of 10 inside the function, and multiplied `sigma` by 10,000 - that way, the coefficients are all on similar scales to make things easier for the optimizer.

Take a minute to make sure you understand the code:

> **This function for the negative log-likelihood is pretty similar to the other ones we've seen, only here, we loop through time to obtain the expected catch values conditional on the parameter values.**

```r
beverton_holt_nll <- function(par, t, obs_catch, obs_effort) {

  lambda <- par[1]; alpha <- 10^par[2]; q <- 10^par[3]; sigma <- par[4]*1e4

  tmax <- length(t)

  ## empty vectors to store simulated catch
  mu_catch <- rep(0, tmax)
  mu_stock <- rep(0, tmax)

  ## estimate for stock size at time t = 1
  mu_stock[1] <- obs_catch[1]/(1 - exp(-q * obs_effort[1]))

  ## loop through time, store simulated catch and stock
  for (ti in 1:tmax) {
    if(ti < tmax) {
      mu_stock[ti + 1] <- (lambda * mu_stock[ti] * exp(-q * obs_effort[ti])) /
        (1 + alpha * (mu_stock[ti] * exp(-q * obs_effort[ti])))
    }
    mu_catch[ti] <- mu_stock[ti] * (1 - exp(-q * obs_effort[ti]))
  }

  if (sigma >= 0) {
    nll <- -sum(dnorm(obs_catch, mean = mu_catch, sd = sigma, log = TRUE))
    return(nll)
  }  else {
    return(5000)
  }

}
```

Maximum Likelihood Estimates

Not much is new here. I won't go through finding initial values for this model, since we'll do that next week when we fit a Bayesian Beverton-Holt model to a different dataset, but one thing that's new here is the `control` argument - we've increased the maximum number of iterations (`maxit`).

Here are the maximum likelihood estimates:

```r
bh_mle <- optim(
  par = c(lambda = 1.2, alpha = log(0.0025), q = log(0.049), sigma = 3.9),
  fn = beverton_holt_nll,
  t = natividad$year,
  obs_catch = natividad$catch,
  obs_effort = natividad$effort,
  control = list(maxit = 1000),
  hessian = TRUE
)

bh_mle
```

```
## $par
##    lambda     alpha         q     sigma
##  1.090678 -7.694453 -4.303808  3.900584
##
```

```
## $value
## [1] 491.6009
##
## $counts
## function gradient
##      615       NA
##
## $convergence
## [1] 0
##
## $message
## NULL
##
## $hessian
##               lambda         alpha             q         sigma
## lambda  2.884522e+04 -2.063770e+03 -7.016462e+03 -0.0442179768
## alpha  -2.063770e+03  1.615596e+02  5.105124e+02  0.0006655583
## q      -7.016462e+03  5.105124e+02  1.753809e+03 -0.0069437789
## sigma  -4.421798e-02  6.655583e-04 -6.943779e-03  5.3873423838
```

and their standard errors:

```
var_cov <- solve(bh_mle$hessian)
se <- sqrt(diag(var_cov))
se
```

```
##     lambda      alpha          q      sigma
## 0.03677964 0.28436654 0.15452469 0.43083699
```

Catch & CPUE Estimates

Now, we can plot the estimated stock and catch over time, using the parameters estimated from our model. First, though, we need to define a function to return our estimated stock and catch, given the parameter estimates:

```
beverton_holt <- function(lambda, alpha, q, n0, t, effort) {

  tmax <- length(t)
  stock <- rep(0, tmax); stock[1] <- n0
  catch <- rep(0, tmax)

  for (ti in 1:tmax) {
    if(ti < tmax) {
      stock[ti + 1] <- (lambda * stock[ti] * exp(-q * effort[ti])) /
        (1 + alpha * (stock[ti] * exp(-q * effort[ti])))
    }
    catch[ti] <- stock[ti] * (1 - exp(-q * effort[ti]))
  }

  data.frame(t = t, stock = stock, catch = catch)
}
```

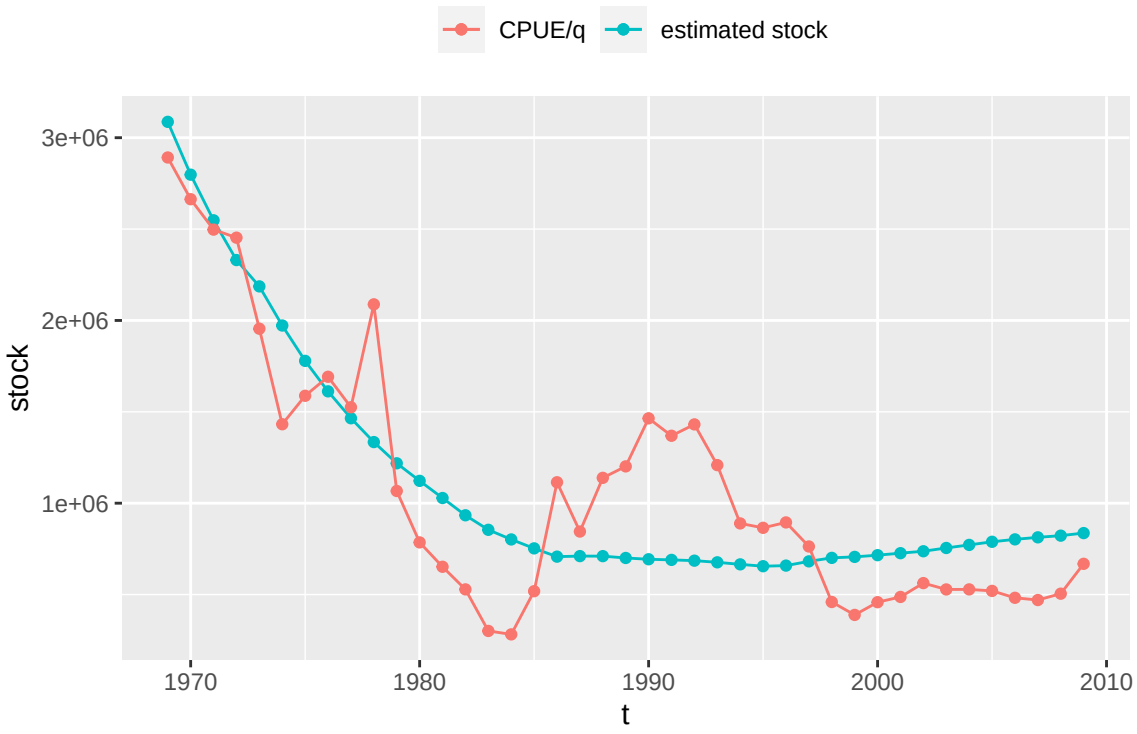
Applying this function to our data and parameter estimates:

```
n0 <- as.numeric(natividad$catch[1]/(1 - exp(-10^bh_mle$par[["q"]] * natividad$effort[1])))

bh_fit <- beverton_holt(
```

```
  lambda = bh_mle$par[["lambda"]],
  alpha = 10^bh_mle$par[["alpha"]],
  q = 10^bh_mle$par[["q"]],
  n0 = n0,
  t = natividad$year,
  effort = natividad$effort
)
```

Plotting the estimated stock, as well as the catch-per-unit-effort divided by the catchability:

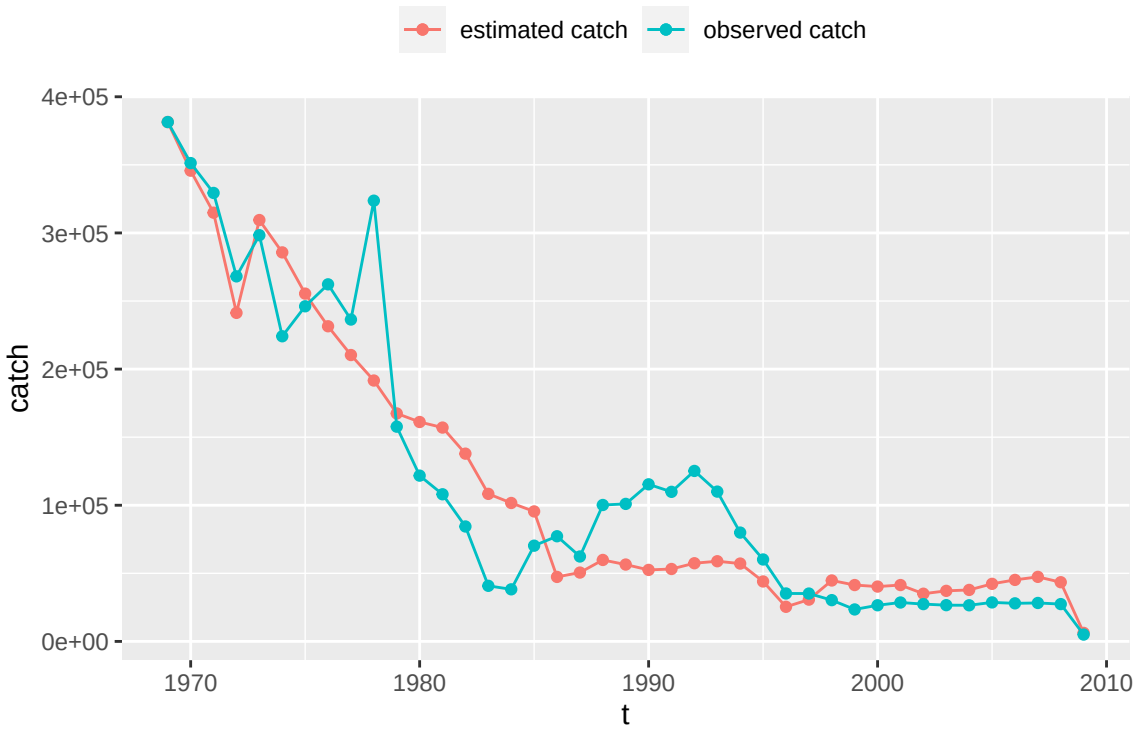
```
bh_fit %>%
  ggplot(aes(t, stock)) +
  geom_line(aes(color = "estimated stock")) +
  geom_point(aes(color = "estimated stock")) +
  geom_line(aes(x = year, y = cpue/(10^bh_mle$par[["q"]]), color = "CPUE/q"),
            data = natividad) +
  geom_point(aes(x = year, y = cpue/(10^bh_mle$par[["q"]]), color = "CPUE/q"),
             data = natividad) +
  theme(legend.position = "top",
        legend.title = element_blank())
```



And now plotting the estimated catch against our observed catch. Looks like a pretty good fit!

```
bh_fit %>%
  ggplot(aes(t, catch)) +
  geom_line(aes(color = "estimated catch")) +
  geom_point(aes(color = "estimated catch")) +
  geom_line(aes(x = year, y = catch, color = "observed catch"),
            data = natividad) +
  geom_point(aes(x = year, y = catch, color = "observed catch"),
```

```
            data = natividad) +
theme(legend.position = "top",
      legend.title = element_blank())
```



Model Assumptions

We've assumed that our data are:

$$\text{obs. Catch}_t \sim \text{i.i.d. Normal}(\mu\text{Catch}_t, \sigma^2)$$

This implies a few things:

- The residuals are approximately normal (of course).
- The variance of the residuals is constant - σ^2 does not depend on the value of the response or the predictors.
- Once we know our estimated catch (μCatch_t), the observations are **independent** - in other words, knowing which part of Isla Natividad the data came from, or which year the data were collected in, would not provide us with any **additional** information that the model hasn't already.

Let's examine whether the assumptions are realistic. For some of these assumptions, it can be hard to tell with only 41 observations, but we should still give it a shot - if something is super off, it'll probably show up even in small samples.

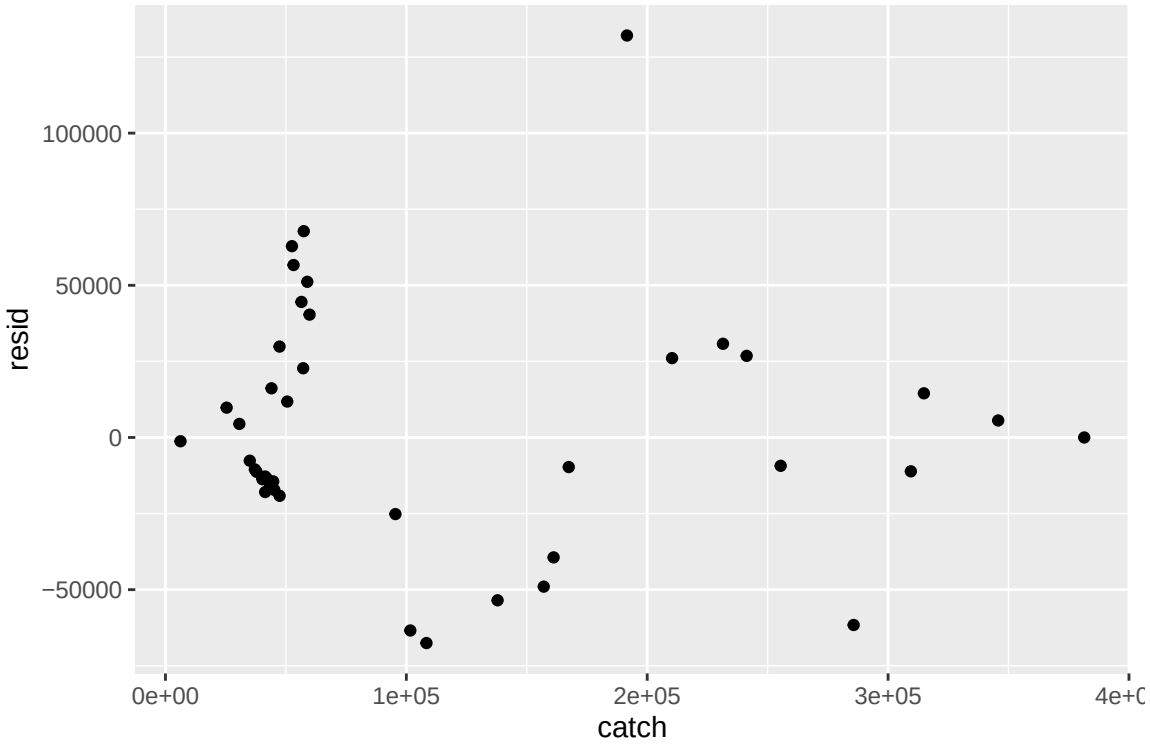
Heteroskedasticity

Let's plot the residuals (the observed catch minus the estimated catch) against the fitted values (the estimated catch). What we're looking for here is evidence of **heteroskedasticity** - whether the variance in the residuals is constant over the range of the fitted values.

How do you feel about these residuals? As your eyes move across the x-axis, does the dispersion along the y axis seem to change much?

> **Your answer may differ because this is somewhat subjective, but to me the spread of the residuals looks pretty alright as we move across the range of catch values. There's no obvious "fanning" of the residuals from being tightly clustered at small values of the catch to being more dispersed for larger values.**

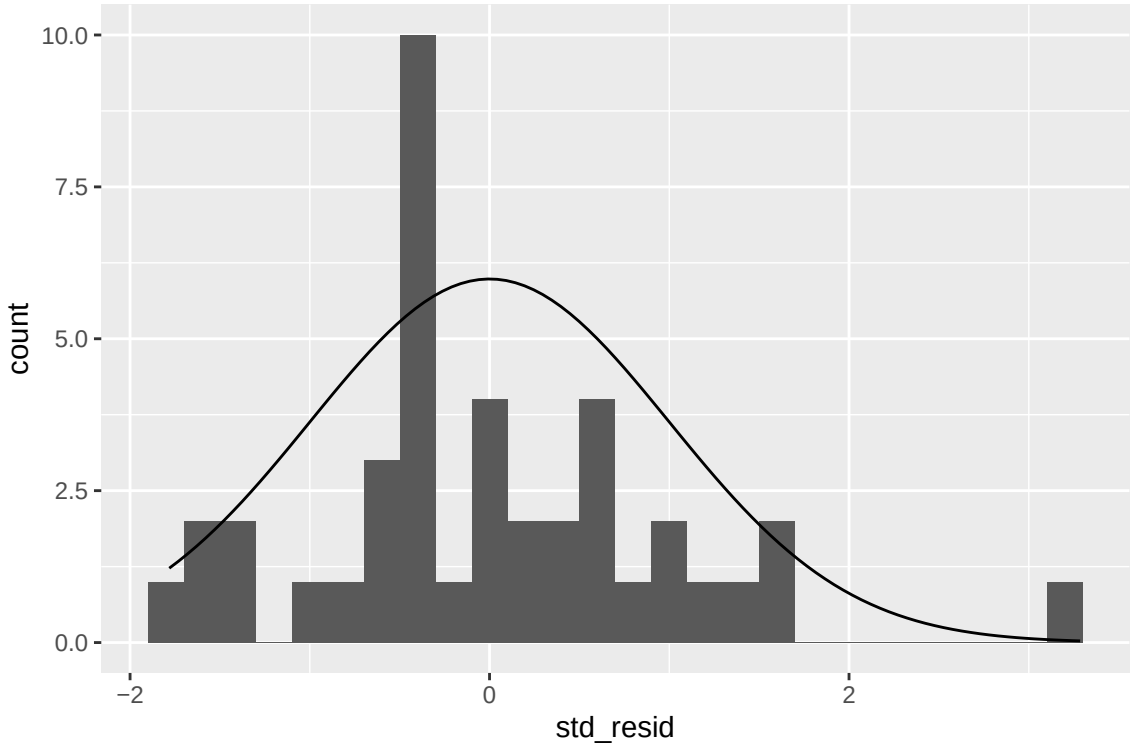
```
bh_fit$resid <- natividad$catch - bh_fit$catch

bh_fit %>% ggplot(aes(catch, resid)) + geom_point()
```



Normality of the Residuals

Now let's plot a histogram of the standardized residuals (I've superimposed a normal distribution for good measure).

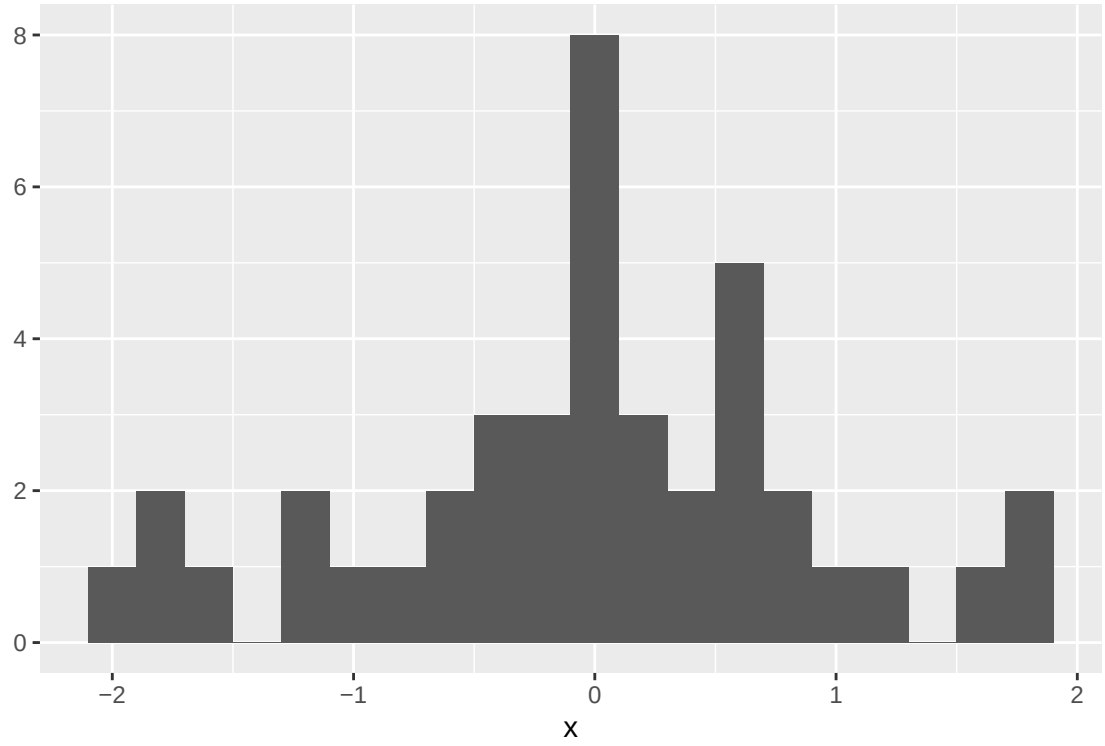
```
## standardized residuals
bh_fit$std_resid <- scale(bh_fit$resid)

bh_fit %>%
  ggplot(aes(std_resid)) +
  geom_histogram(binwidth = 0.2) +
  stat_function(fun = function(x, ...) dnorm(x, ...)*15,
                args = list(mean = 0, sd = 1))
```



Do these residuals look approximately normal to you? One good way to get a sense for what normal residuals should look like with 41 data points is to plot histograms of 41 random samples from a normal distribution and compare them. Do this three or four times by re-running the R chunk below. Do you think the residuals seem normal or not?

> **To me, these data look approximately normal, or at least as normal as we can expect given that there's 40 samples, so the normal distribution seems like a fine approximation here. The residuals are more clustered around the mean, and are not very skewed.**

```
n <- nrow(natividad)
x <- rnorm(n, mean = 0, sd = 1)
qplot(x, binwidth = 0.2)
```



Residual Autocorrelation

Take a look at the above plot of the estimated catch vs. the observed catch - for any given year which we've over-estimated catch, it seems like we've also over-estimated catch for the adjacent years. Same goes for the years we under-estimate catch. Which of the assumptions that we outlined above does this violate? Why?

> **The observations adjacent to each other tend to be similar, even after adjusting for the model - years with positive residuals tend to be adjacent to other years with positive residuals. Therefore, for any data point Catch_t, the data adjacent in time to Catch_t contain *additional* information about Catch_t that our model does not - this implies a lack of *independence* of the residuals across time, a violation of the third assumption outlined above.**

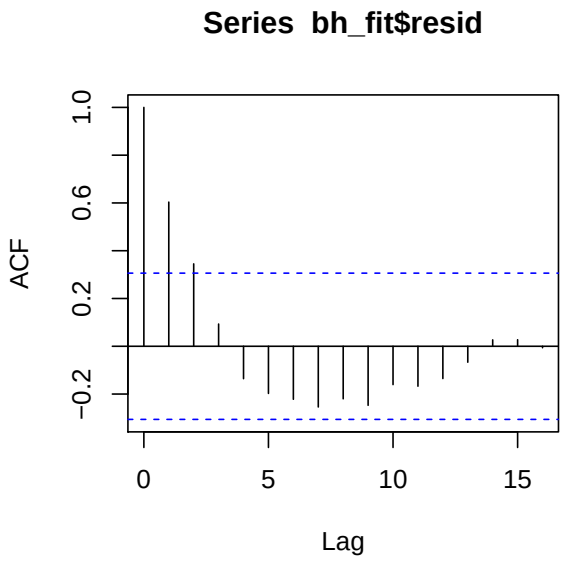
One way to check this is to plot the **autocorrelation function** (ACF) - the correlation of the residuals at time t with the residuals at time $t-1$. The fist plot below displays the ACF, starting with lag 0 (i.e., the correlation of the data at time t with that at time t, which is always equal to 1), and increasing in lag. The lag 1 autocorrelation is about 0.6 here, and the lag 2 autocorrelation is about 0.36.

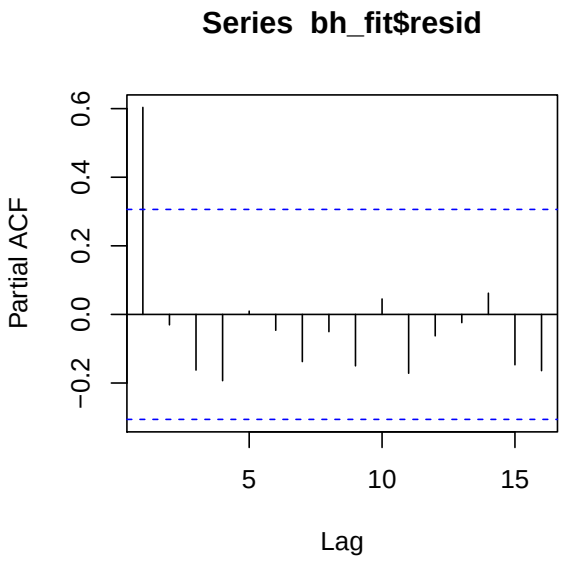
We can also plot the **partial autocorrelation function** - which, for each lag, is the ACF at that lage, *adjusted for the lower-order lags* - notice that the x-axis on this plot starts at lag 1, not lag 0.

What the combination of these plots tell us is that the correlation between the observed catch at any given time t and the observed catch at time $t-1$, after taking into account our model estimates for the catch, is *still* about 0.6!

That's a huge issue if we want standard errors and confidence intervals, because the model, in effect, thinks we have a lot more independent observations than we do.

```
par(mfrow = c(1, 2))
acf(bh_fit$resid)
acf(bh_fit$resid, type = "partial")
```






```
par(mfrow = c(1, 1))
```

We can fit an AR1 (auto-regressive order 1) model to the residuals to get an estimate of our residual autocorrelation (we'll call this the "AR1 coefficient").

```
resid_AR1 <- arima(bh_fit$resid, order = c(1, 0, 0))
phi <- as.numeric(coef(resid_AR1)[1])
phi
```

```
## [1] 0.5898104
```

Autoregressive Model

Residual covariance matrix

To address this issue, we're going to model the observations as arising from a **multivariate normal distribution**, where the expected covariance between the residuals of two observations is going to be a function of how far apart those observations are in time.

This means that, instead of a single value σ for the standard deviation of our normal distribution, we're going to have a **matrix** of variances (on the diagonal) and covariances (off the diagonal), which we derive from only two parameters: σ (our residual standard deviation) and ϕ, the correlation between adjacent observations.

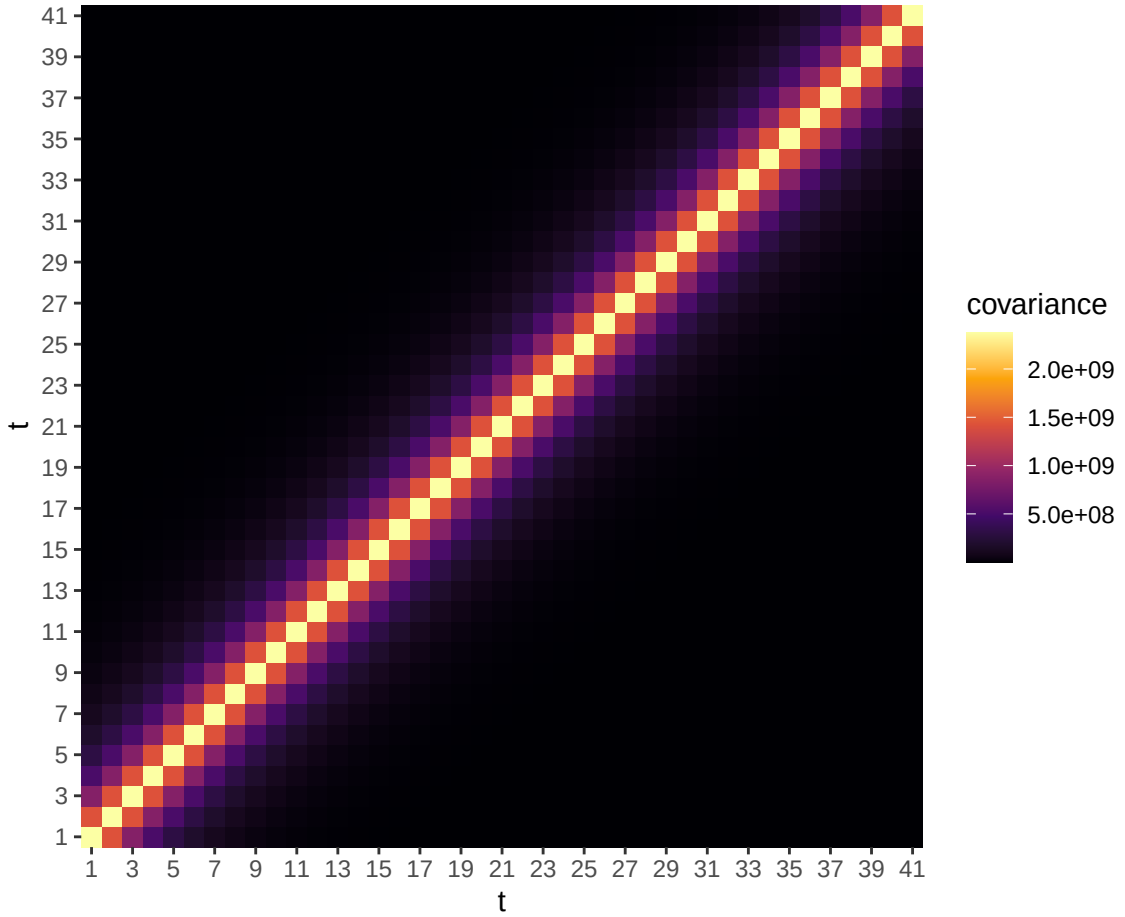
Let's visualize the variance-covariance matrix by plotting it for different values of ϕ between 0 and 1. As you change the value of ϕ, what do you notice? Interpret this in the context of the model.

> **As we increase the value of ϕ, the covariance between distant data points increases, as indicated by the color of the cells further off of the diagonal becoming warmer. At $\phi = 0$, the observations off of the diagonal do not covary. Using a non-zero value of ϕ in this model would indicate that observations are no-longer assumed to be independent in time, and are instead expected to covary to an extent that is determined by (a) the overall variance, and (b) the distance (in time) between each data point. In this way, we can think of the version of the model we've fit above as a special case of the model that we fit below, which incorporates a covariance matrix with autocorrelation.**

Given ϕ and σ, what is the covariance between a data point at time t and at time $t-1$? What about time t and $t-2$? Can you figure out a general expression for the covariance between data at time t and $t-\delta$?

> **The covariance at time lag δ, as a function of the variance σ^2 and the lag-1 autocorrelation ϕ, is $\left(\sigma^2/\left(1-\phi^2\right)\right)\phi^\delta$. The correlation at time lag δ is just ϕ^δ**

```
plot_var_cov <- function(phi, sigma = bh_mle$par[["sigma"]]*1e4, tmax = nrow(natividad)) {

  var_cov <- sigma^2/(1-phi^2)*phi^(abs(outer(1:tmax, 1:tmax, "-")))

  reshape2::melt(var_cov) %>% ggplot(aes(Var1, Var2, fill = value)) +
    geom_raster() + scale_fill_viridis_c(option = "inferno") +
    scale_x_continuous(breaks = seq(1, tmax, 2)) +
    scale_y_continuous(breaks = seq(1, tmax, 2)) +
    coord_fixed(expand = FALSE) +
    labs(x = "t", y = "t", fill = "covariance")
}

plot_var_cov(phi = 0.6)
```



Likelihood Function

Now, let's modify the likelihood function we defined above to allow for autocorrelated observations. There's only a few changes here compared to the first version. What are they and what do they do?

Here, we've added an additional parameter phi, and we've changed the likelihood function to a multivariate normal distribution with a covariance matrix as defined above, so that data which are adjacent in time are no longer assumed to be independent.

```
beverton_holt_nll_AR1 <- function(par, t, obs_catch, obs_effort) {

  lambda <- par[1]; alpha <- 10^par[2]; q <- 10^par[3]; sigma <- par[4]*1e4; phi <- par[5]

  tmax <- length(t)

  mu_catch <- rep(0, tmax)
  mu_stock <- rep(0, tmax)

  mu_stock[1] <- obs_catch[1]/(1 - exp(-q * obs_effort[1]))

  for (ti in 1:tmax) {
    if(ti < tmax) {
      mu_stock[ti + 1] <- (lambda * mu_stock[ti] * exp(-q * obs_effort[ti])) /
        (1 + alpha * (mu_stock[ti] * exp(-q * obs_effort[ti])))
    }
    mu_catch[ti] <- mu_stock[ti] * (1 - exp(-q * obs_effort[ti]))
  }

  if (sigma >= 0) {
    var_cov <- sigma^2/(1-phi^2)*phi^(abs(outer(1:tmax, 1:tmax, "-")))
    nll <- -sum(dmvnorm(obs_catch, mean = mu_catch, sigma = var_cov, log = TRUE))
    return(nll)
  }  else {
    return(5000)
  }

}
```

Maximum Likelihood Estimates

Let's obtain maximum likelihood estimates for this model. How do these estimates compare to the previous ones? How do the standard errors compare? Why do you think the standard errors from this model differ from those from the model that does not include an autocorrelation term?

The estimates are pretty similar to the estimates we obtained without accounting for residual autocorrelation. It's usually the case that when we model the *covariance* of our data points (as opposed to adding terms to the model to change the trend - for example, if we had modified our mathematical model) that the fitted parameters are nearly identical. However, the standard errors from this model are about twice as wide as in the other model. As we accumulate more data, we become increasingly certain in our maximum likelihood estimates, which results in narrower standard errors. But if these data are correlated, each new data point doesn't contribute as much information about the parameters of interest as if these data were independently distributed. So, in a way, the standard errors in the model accounting for autocorrelation are wider because the model recognizes that the data do not contain as much information about the parameters as the model previously assumed it did.

```
bh_mle_AR1 <- optim(
  par = c(lambda = 1.2, alpha = log(0.0025), q = log(0.049), sigma = 3.9, phi = phi),
```

```
  fn = beverton_holt_nll_AR1,
  t = natividad$year,
  obs_catch = natividad$catch,
  obs_effort = natividad$effort,
  control = list(maxit = 1000),
  hessian = TRUE
)

bh_mle_AR1
```

```
## $par
##     lambda      alpha          q      sigma        phi
##  1.0856174 -7.7196868 -4.3024733  3.0982155  0.5975134
##
## $value
## [1] 482.3976
##
## $counts
## function gradient
##      393       NA
##
## $convergence
## [1] 0
##
## $message
## NULL
##
## $hessian
##               lambda         alpha             q        sigma        phi
## lambda  8166.1650032 -5.378026e+02 -2.012410e+03 -0.195950534 169.450334
## alpha   -537.8026019  3.944884e+01  1.347246e+02  0.008666866 -10.834200
## q      -2012.4098090  1.347246e+02  5.115753e+02  0.038746307 -42.094332
## sigma     -0.1959505  8.666866e-03  3.874631e-02  8.550417746   0.611628
## phi      169.4503344 -1.083420e+01 -4.209433e+01  0.611628025  68.847602
```

```
var_cov_AR1 <- solve(bh_mle_AR1$hessian)
se_AR1 <- sqrt(diag(var_cov_AR1))
se_AR1
```

```
##     lambda      alpha          q      sigma        phi
## 0.06535688 0.51838632 0.26302083 0.34210089 0.12380389
```

Demographic Parameters

Density-dependence

Let's back-transform the estimate of α to obtain an estimate for the density-dependent parameter on the correct scale:

```
alpha <- 10^bh_mle_AR1$par[["alpha"]]
alpha
```

```
## [1] 1.906835e-08
```

Finite Growth Rate

We can obtain an asymptotic 95% confidence interval for λ with:

```
lambda <- bh_mle_AR1$par[["lambda"]]
lambda_CI <- qnorm(c(0.025, 0.975), lambda, sd = se_AR1[["lambda"]])
lambda_CI
```

```
## [1] 0.9575203 1.2137145
```

Do you think this is a realistic confidence interval? Based on the confidence interval, what do you think the likelihood profile for λ looks like?

> **The majority of the values contained in this range strike me as realistic, but personally, I think that it's unrealistic for this confidence interval to include values of λ below 1. The population appears to recover slightly after a downturn in 1990's, despite continued exploitation, which suggests to me that the intrinsic growth rate of this population *must* be positive - I expect that, if we were to plot a likelihood profile for the λ parameter, it would not be symmetric around the maximum likelihood estimate - instead, I expect that the likelihood would drop off sharply (or, equivalently, the negative log likelihood would climb sharply) as λ approached 1 from above.**

Carrying Capacity

We can obtain an estimate of the carrying capacity K using the estimates of λ and α:

$$\hat{K} = \frac{\hat{\lambda} - 1}{\hat{\alpha}}$$

The AR1 model gives an estimate of about 4,490,000 abalone:

```
K = (lambda - 1)/alpha
K
```

```
## [1] 4490026
```

The ordinary model agrees pretty closely:

```
as.numeric((bh_mle$par[["lambda"]] - 1)/(10^bh_mle$par["alpha"]))
```

```
## [1] 4486972
```

Maximum Sustainable Yield

For the Beverton-Holt model, the population size at MSY is given by:

$$N_{\text{msy}} = \frac{\lambda - \sqrt{\lambda}}{\alpha}$$

For our AR1 model, this gives:

```
N_msy = (lambda - sqrt(lambda))/alpha
N_msy
```

```
## [1] 2291113
```

MSY is given by:

$$Y_{\text{msy}} = N_{\text{msy}} - \frac{N_{\text{msy}}}{\lambda - \alpha \times N_{\text{msy}}}$$

Which, for our AR1 model, gives:

```
MSY = N_msy - N_msy/(lambda - alpha * N_msy)
MSY
```

```
## [1] 92199.68
```

Exercises

Read sections 11.1 - 11.4 of *Ecological Models and Data in R*, and answer the following questions based on the reading.

1. Process and Observation Error

What is observation error? What is process error? What problems can arise when we try to estimate parameters for systems with both process and observation error? For the Beverton-Holt model that we fit to the Isla Natividad abalone catches, which of these types of error did we use? Explain your answer.

> **In Chapter 11 of *Ecological Models and Data in R*, Ben Bolker distinguishes process and observation error as:**
>
> Dynamic models contain both *process error*, which feeds back on future states of the population, and *observation error*, which affects only the current observation.
>
> **The model we've estimated above, and all the models we've estimated with maximum likelihood, assumes observation error only - in this case, the observed catch is normally distributed around some true catch, and the error at each time step does not affect our estimate of the true catch at the next time step.**
>
> **If there is process error in the system, than there is random (or, at least, apparently random) variation in the number of individuals added to the population at each time step. There are many reasons for why this might occur, but when it does occur for a population at any given time t, than the population at time $t + 1$, and all other times steps after, is also affected. By contrast, if a population is growing according to simple and deterministic dynamics, and the variation in the data arises entirely from our sampling methodology (for example, camera traps or transect counts), than the error in our observed population size at time t does *not* impact the population at time $t + 1$, or any time steps after that**
>
> **In reality, both of these types of error are probably in play for any natural population that we'd actually be interested in studying, which can make estimating demographic parameters for natural populations growing over time extremely challenging. A wide class of models, called *state-space* models, which include both process and observation error, are increasingly used to fit data from natural populations, but they can be quite challenging to use and develop. As the amount of error (either observation or process error) increases, methods that assume only process error or only observation error will give us increasingly different answers.**

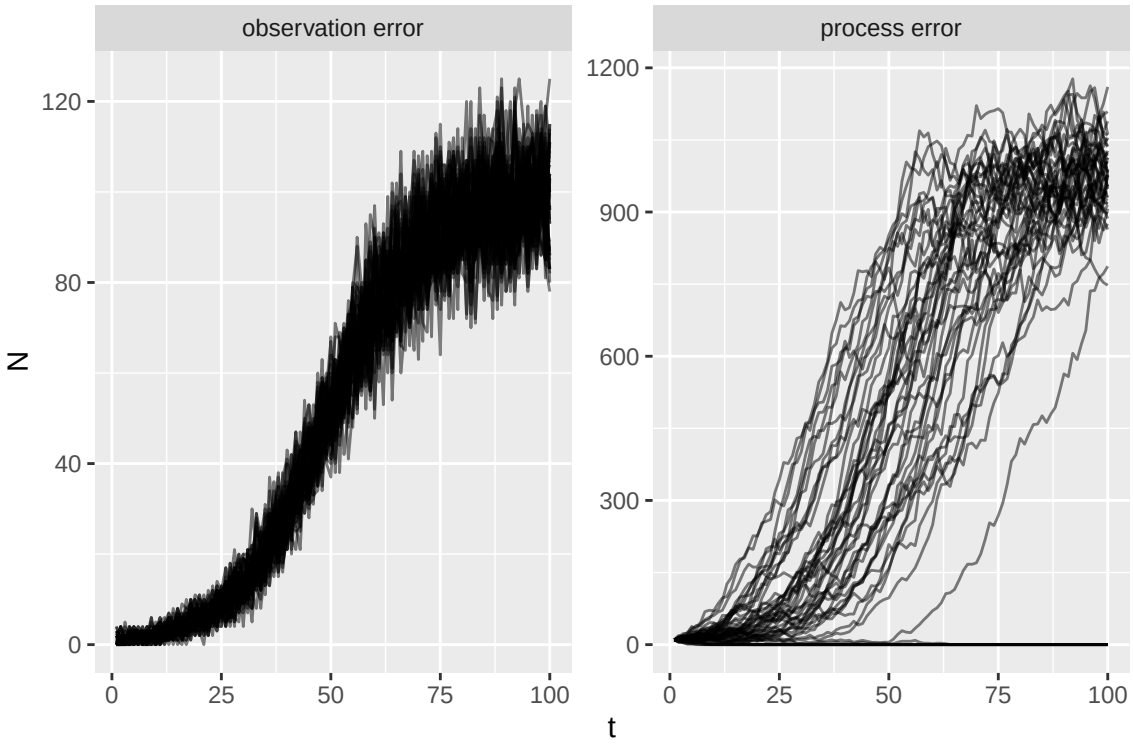
2. Stochastic Simulation

Using the code provided below, run 15 simulations of (1) the observation-error-only Beverton-Holt model, and (2) the process-error-only Beverton-Holt model. The code for the observation error model is in the first chunk, and the code for the process error model is in the second chunk (all you need to do is re-run the code in each of these chunks at least 15 times each). How do the outcomes of these sets of simulations differ?

I've plotted 50 runs with (1) observation error only and (2) process error only. As you can see, models with observation error look how you might expect - each of the population trends is *different*, but plotted together it's clear that the populations are fluctuating around the same trend. The process error model, however, results in populations which diverge over time - some grow to the carrying capacity much more quickly than others, and some populations, just by random chance, collapse to zero.

```
### parameter values - same between observation and process models
N0 <- 10 # initial population size
lambda <- 1.1 ## finite growth rate
alpha <- 1e-04 ## density dependence
p <- 0.1 ## probability of observation

### empty population vectors
tmax <- 100 ## number of time steps
N <- rep(NA, tmax) ## true population size
Nobs <- rep(NA, tmax) ## observed population size
N[1] <- N0 ## initialize population

### loop over time, store true population
for (t in 1:(tmax - 1)) {
  N[t + 1] = (lambda * N[t])/(1 + alpha*N[t])
}
t <- 1:tmax

### observed population size
Nobs = rbinom(tmax, size = round(N), prob = p)

plot(Nobs ~ t, type = "l")
```

```
### empty population vectors
tmax <- 100 ## number of time steps
Nproc <- rep(NA, tmax) ## true population size
Nproc[1] <- N0 ## initialize population

### loop over time, store true population
for (t in 1:(tmax - 1)) {
  Nproc[t + 1] = rpois(1, lambda * Nproc[t])/(1 + alpha*Nproc[t])
}
t <- 1:tmax

plot(Nproc ~ t, type = "l")
```


observation error
process error
N
t
120
80
40
0
1200
900
600
300
0
0
25
50
75
100