Life History Relationships

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References

Life history traits include growth rate; age and size at sexual maturity; the temporal pattern or schedule of reproduction; the number, size, and sex ratio of offspring; the distribution of intrinsic or extrinsic mortality rates (e.g., patterns of senescence); and patterns of dormancy and dispersal. These traits contribute directly to age-specific survival and reproductive functions.[1] The **FLife** package has a variety of methods for modelling life history traits and functional forms for processes for use in fish stock assessment and for conducting Management Strategy Evaluation (MSE).

These relationships have many uses, for example in age-structured population models, functional relationships for these processes allow the calculation of the population growth rate and have been used to to develop priors in stock assesments and to parameterise ecological models.

The **FLife** package has methods for modelling functional forms, for simulating equilibrium `FLBRP` and dynamic stock objects `FLStock`.

Packages

`FLife`, as with all FLR packages, is designed to use and augment a variety of other packages, e.g. `ggplot2` for plotting

```
library(ggplot2)
library(GGally)
```

`reshape` and `plyr` for data manipulation

```
library(reshape)
library(plyr)
```

as well as the other FLR packages

```
library(FLCore)
library(ggplotFL)

library(FLBRP)
library(FLasher)

#library(FLAssess)
```

and those such as `popbio` for analysing age or stage based population matrix models.

[1] http://www.oxfordbibliographies.com/view/document/obo-9780199830060/obo-9780199830060-0016.xml

```r
library(popbio)
```

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Quick Start

This section provide a quick way to get running and overview of what functions are available, their potential use, and where to seek help. More details are given in later sections.

The simplest way to obtain **FLife** is to install it from the `FLR` repository via the R console:

```r
install.packages("FLife", repos = "http://flr-project.org/R")
```

See help(install.packages) for more details.

After installing the **FLife** package, you need to load it

```r
library(FLife)
```

There is an example teleost dataset used for illustration and as a test dataset, alternatively you can load your own data.

```r
data(teleost)
```

The dataset contains life history parameters for a range of bony fish species and families, i.e. von Bertalanffy growth parameters (L_{∞}, k, t_0), length at 50% mature (L_{50}), and the length weight relationship (a, b).

When loading a new dataset it is always a good idea to run a sanity check e.g.

```r
is(teleost)
```

```
[1] "FLPar"     "array"     "structure" "vector"
```

The `teleost` object can be used to create vectors or other objects with values by age using **FLife** methods, e.g. to construct a growth curve for hutchen (*Hucho hucho*)

```r
vonB(1:10,teleost[,"Hucho hucho"])
```

```
 [1]  29.0  40.8  51.5  61.1  69.9  77.8  84.9  91.4  97.3 102.6
```

Plotting

Plotting is done using **ggplot2** which provides a powerful alternative paradigm for creating both simple and complex plots in R using the *Grammar of Graphics*[2] The idea of the grammar is to specify the individual building blocks of a plot and then to combine them to create the desired graphic[3].

The **ggplot** methods expects a `data.frame` for its first argument, `data` (this has been overloaded by **ggplotFL** to also accept FLR objects); then a geometric object `geom` that specifies the actual marks put on to a plot and an aesthetic that is "something you can see" have to be provided. Examples of geometric Objects (geom) include points (geom_point, for scatter plots, dot plots, etc), lines (geom_line, for time series, trend lines, etc) and boxplot (geom_boxplot, for, well, boxplots!). Aesthetic mappings are set with the aes() function and, examples include, position (i.e., on the x and y axes), color ("outside" color), fill ("inside" color), shape (of points), linetype and size.

[2] Wilkinson, L. 1999. *The Grammar of Graphics*, Springer. doi 10.1007/978-3-642-21551-3_13.
[3] http://tutorials.iq.harvard.edu/R/Rgraphics/Rgraphics.html

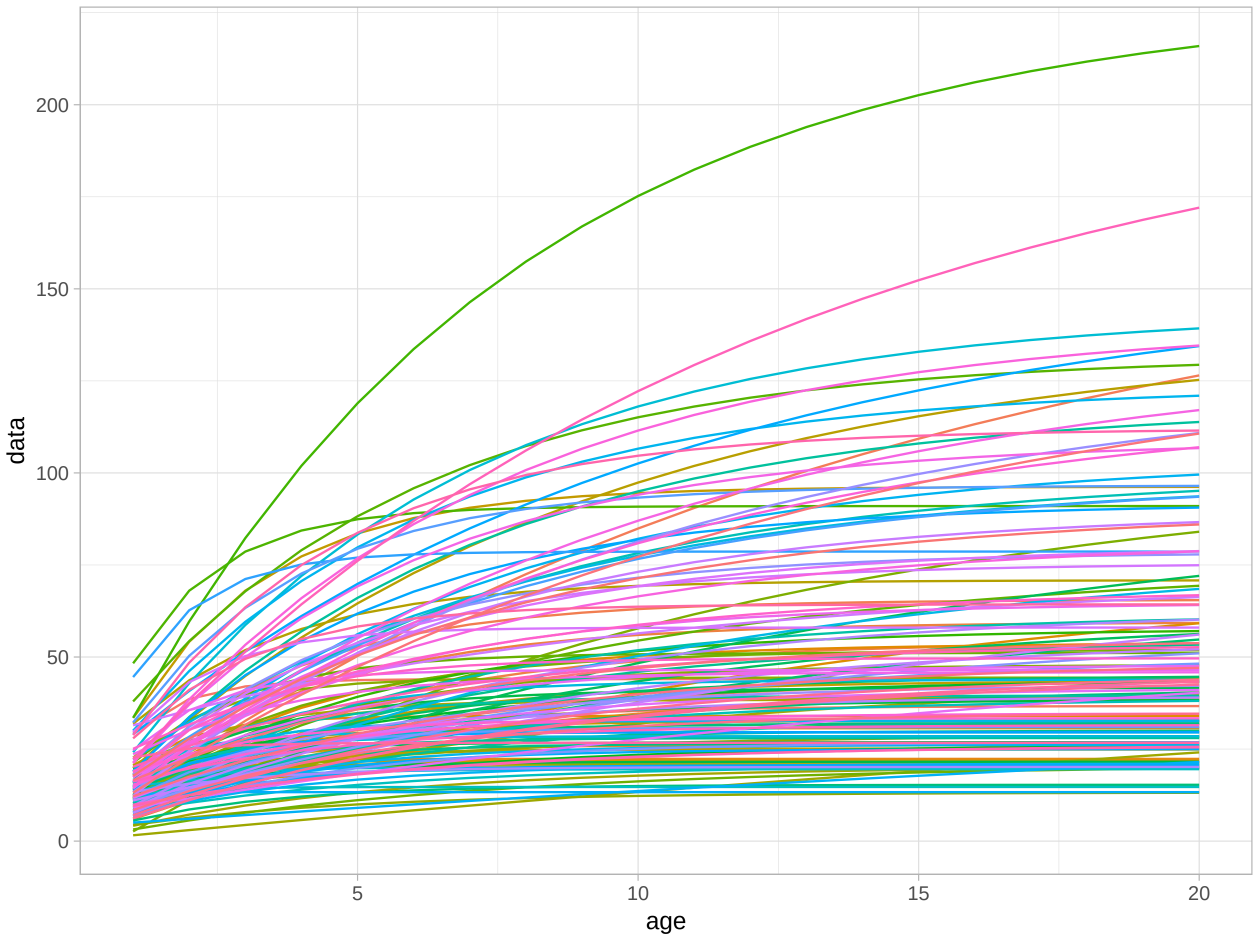

Figure 1: Von Bertalanffy growth curves.

```
age=FLQuant(1:20,dimnames=list(age=1:20))
len=vonB(age,teleost)

ggplot(as.data.frame(len))+
  geom_line(aes(age,data,col=iter))+
  theme(legend.position="none")
```

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Methods

Life History Parameters

Growth

Consider the von Bertalanffy growth equation

$$L_t = L_\infty(1 - e^{(-kt - t_0)})$$

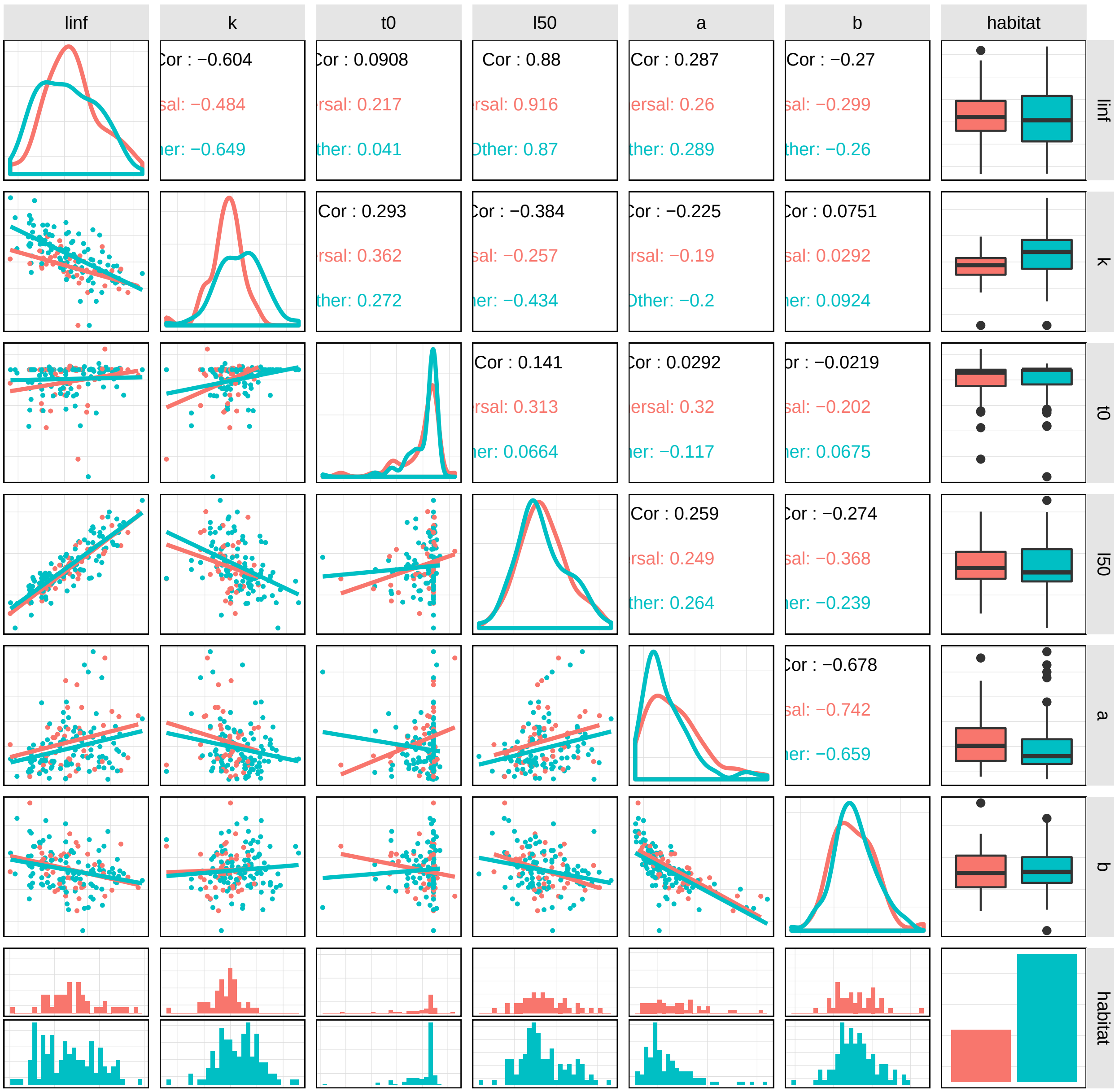


Figure 2: Relationship between life history parameters in the teleost dataset.

where L_t is length at time t, L_∞ the asymptotic maximum length, k the growth coefficient, and t_0 the time at which an individual would, if it possible, be of zero length.

As L_∞ increases k declines. in other words at a given length a large species will grow faster than a small species. for example Gislason, Pope, et al. (2008) proposed the relationship

$$k = 3.15L_\infty^{-0.64}$$

There also appears to be empirical relationship between t_0 and L_∞ and k i.e.

$$log(-t_0) = -0.3922 - 0.2752log(L_\infty) - 1.038log(k)$$

Therefore for a value of L_∞ or even L_{max} the maximum size observered as $L_\infty = 0.95L_{max}$ then all the growth parameters can be recovered.

Maturity

There is also a relationship between L_{50} the length at which 50% of individuals are mature

$$l_{50} = 0.72L_\infty^{0.93}$$

and even between the length weight relationship

$$W = aL^b$$

Natural Mortality

For larger species securing sufficient food to maintain a fast growth rate may entail exposure to a higher natural mortality Gislason, Daan, et al. (2008). While many small demersal species seem to be partly protected against predation by hiding, cryptic behaviour, being flat or by possessing spines have the lowest rates of natural mortality Griffiths and Harrod (2007). Hence, at a given length individuals belonging to species with a high L_∞ may generally be exposed to a higher M than individuals belonging to species with a low L_∞.

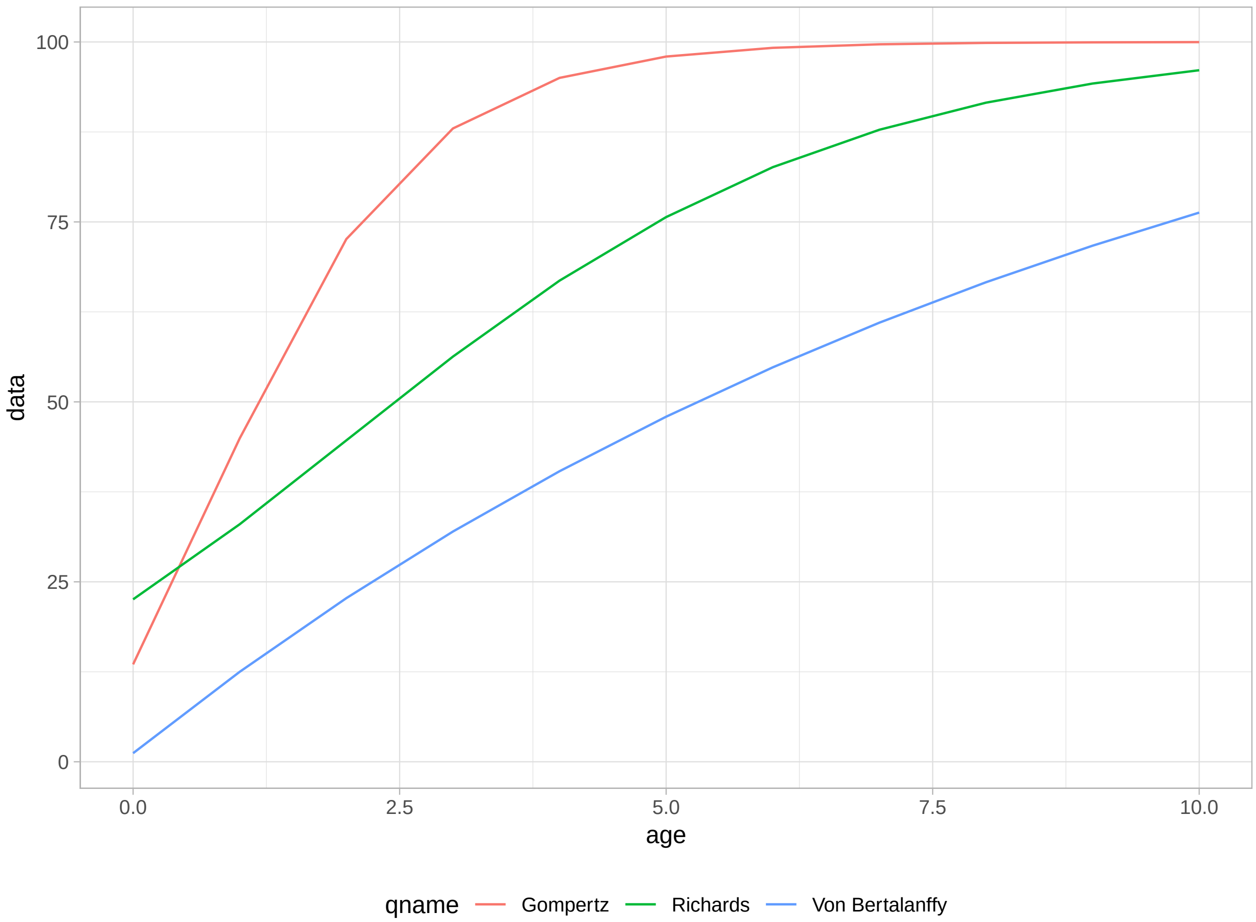
$$log(M) = 0.55 - 1.61log(L) + 1.44log(L_\infty) + log(k)$$

Functional forms

In **FLIfe** there are methods for creating growth curves, maturity ogives and natural mortality vectors, selection patterns, and other ogives. All these methods are used to create `FLQuant` objects.

Growth

gompertz, richards, vonB



Ogives

dnormal, knife, logistic, sigmoid

```
dnormal( age,FLPar(a1=4,sl=2,sr=5000))
```

```
An object of class "FLQuant"
, , unit = unique, season = all, area = unique

    year
age  1
  0  0.06250
  1  0.21022
  2  0.50000
  3  0.84090
  4  1.00000
  5  1.00000
  6  1.00000
  7  1.00000
  8  1.00000
  9  1.00000
  10 1.00000

units:
```

```r
knife(   age,FLPar(a1=4))
```

```
An object of class "FLQuant"
, , unit = unique, season = all, area = unique

    year
age  1
  0  0
  1  0
  2  0
  3  0
  4  1
  5  1
  6  1
  7  1
  8  1
  9  1
  10 1

units:
```

```r
logistic(age,FLPar(a50=4,ato95=1,asym=1.0))
```

```
An object of class "FLQuant"
, , unit = unique, season = all, area = unique

    year
age  1
  0  7.6733e-06
  1  1.4577e-04
  2  2.7624e-03
  3  5.0000e-02
  4  5.0000e-01
  5  9.5000e-01
  6  9.9724e-01
  7  9.9985e-01
  8  9.9999e-01
  9  1.0000e+00
  10 1.0000e+00

units:  proportion
```

```r
sigmoid( age,FLPar(a50=4,ato95=1))
```

```
An object of class "FLQuant"
, , unit = unique, season = all, area = unique

    year
age  1
  0  7.6733e-06
  1  1.4577e-04
  2  2.7624e-03
  3  5.0000e-02
  4  5.0000e-01
  5  9.5000e-01
```

```
  6  9.9724e-01
  7  9.9985e-01
  8  9.9999e-01
  9  1.0000e+00
  10 1.0000e+00
```

```
units:
```

Natural Mortality

Many estimators have been propose for M, based on growth and reproduction, see Kenchington (2014).

Age at maturity a_{50}

Rikhter and Efanov

$$M = \frac{1.521}{a_{50}^{0.72}} - 0.155$$

Jensen

$$M = \frac{1.65}{a_{50}}$$

Growth

Jensen

$$M = 1.5k$$

Griffiths and Harrod

$$M = 1.406W_\infty^{-0.096}k^{0.78}$$

where $W_\infty = \alpha L_\infty^\beta$

Djabali

$$M = 1.0661L_\infty^{-0.1172}k^{0.5092}$$

Growth and length at maturity L_{50}

Roff

$$M = 3kL_\infty\frac{(1-\frac{L_{50}}{L_\infty})}{L_{50}}$$

Rikhter and Efanov

$$M = \frac{\beta k}{e^{k(a_{50}-t_0)}-1}$$

where $a_{50} = t_0 + \frac{log(1-\frac{L_{50}}{L_\infty})}{-k}$

Varing by length

Gislason

$$M_L = 1.73L^{-1.61}L_\infty^{1.44}k$$

Charnov

$$M_L = k\frac{L_\infty}{L}^{1.5}$$

Varying by weight

Peterson and Wroblewsk

$$M_W = 1.28W^{-0.25}$$

Lorenzen

$$M_W = 3W^{-0.288}$$

Senescence

Conversions

ages, len2wt, wt2len

```
, , unit = unique, season = all, area = unique

    year
age  1957 1958 1959 1960 1961
  1    1    1    1    1    1
  2    2    2    2    2    2
  3    3    3    3    3    3
  4    4    4    4    4    4
  5    5    5    5    5    5
  6    6    6    6    6    6
  7    7    7    7    7    7
  8    8    8    8    8    8
  9    9    9    9    9    9
  10  10   10   10   10   10

        [ ...  51 years]

    year
age  2013 2014 2015 2016 2017
  1    1    1    1    1    1
  2    2    2    2    2    2
  3    3    3    3    3    3
  4    4    4    4    4    4
  5    5    5    5    5    5
  6    6    6    6    6    6
```

```
  7   7    7    7    7    7
  8   8    8    8    8    8
  9   9    9    9    9    9
  10 10   10   10   10   10

, , unit = unique, season = all, area = unique

    year
age  1957    1958    1959    1960    1961
  1   7.2432  7.4290  7.6631  7.2432  7.1791
  2  10.0662  9.7610 10.1961 10.3540  9.9329
  3  11.6225 12.1644 12.0046 12.1869 12.2760
  4  13.4257 13.9591 13.8208 13.9591 14.5180
  5  14.8125 14.4704 14.8730 15.3827 14.9926
  6  16.9270 16.4112 16.7507 16.7388 16.9037
  7  19.3008 17.9360 18.6626 18.4984 17.9567
  8  18.9639 19.8150 19.0009 19.3633 19.0470
  9  20.3601 19.9415 20.8623 20.3682 19.8234
  10 20.9386 21.1419 20.7777 20.9386 20.8852

      [ ...  51 years]

    year
age  2013    2014    2015    2016    2017
  1   7.5478  7.8297  6.2145  6.6943  6.8399
  2  10.2281 10.1316  8.6624  8.7066  8.8366
  3  11.5230 11.6471 10.6266 10.5373 10.9696
  4  12.7650 12.6411 12.7445 12.5571 12.1869
  5  14.7361 14.6123 14.0778 13.7507 13.9248
  6  15.2406 15.6049 14.7820 14.8730 14.9330
  7  16.3116 16.3740 15.5912 15.6049 15.3120
  8  17.0196 16.9154 16.3241 16.3116 16.6069
  9  18.7767 16.6069 16.6911 16.8569 16.8217
  10 16.7269 18.3214 16.5948 17.2579 17.7263
```

Generation of missing life history relationships

```
par=lhPar(FLPar(linf=100))
par
```

```
An object of class "FLPar"
params
     linf         k        t0         a         b     ato95       a50
 100.0000    0.1653   -0.1138    0.0003    3.0000    1.0000    4.3462
     asym        bg        m1        m2        a1        sl        sr
   1.0000    3.0000  217.3564   -1.6100    5.3462    1.0000 5000.0000
        s         v
   0.9000 1000.0000
units:  cm
```

There are relationships between the life history parameters and size, growth, maturation, natural mortality and productivity, as seen in the following.

Simulation

lhPar, lhEql

Function Forms

Population dynamics

Ecological

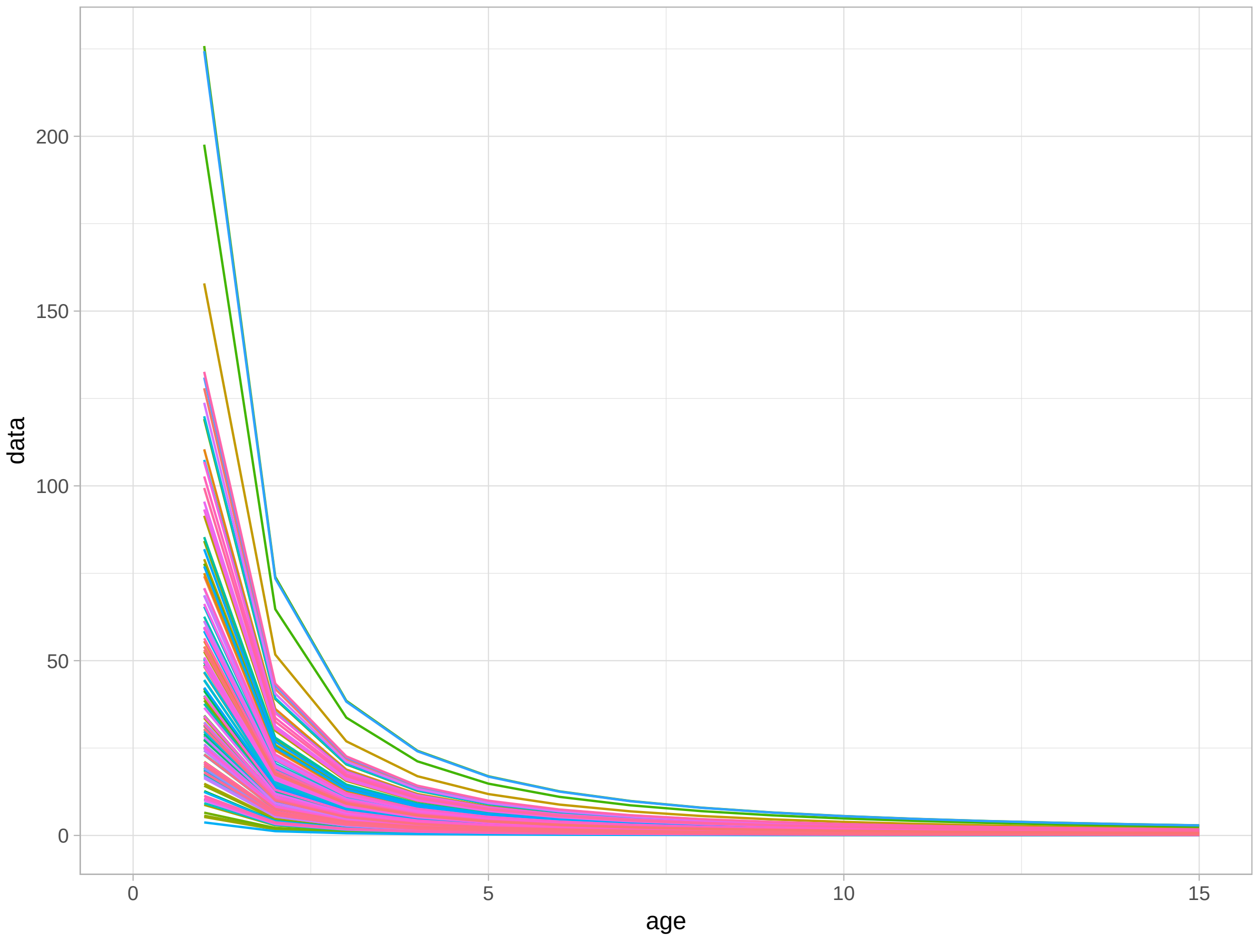
leslie, r

life history traits

```
An object of class "FLPar"
iters:  145

params
              linf                    k                   t0
45.100000(28.02114)  0.246667( 0.17297) -0.143333( 0.13590)
               l50                    a                    b
22.100000(11.71254)  0.011865( 0.00776)  3.010000( 0.15271)
units:  NA
```

Natural Mortality



Stock recruitment

Fishery

Reference points

lopt, loptAge

Density Dependence

matdd, mdd

Parameter estination

moment, powh

Stationarity

rod

Random variables

rnoise

Reference points

```
data(ple4)
rodFn=FLife:::rodFn
refs(ple4)
```

Simulation

Simulation of equilibrium values and reference points

```
eql=lhEql(par)

ggplot(FLQuants(eql,"m","catch.sel","mat","catch.wt"))+
  geom_line(aes(age,data))+
  facet_wrap(~qname,scale="free")+
  scale_x_continuous(limits=c(0,15))
```

```
An object of class "FLPar"
params
      r      rc     msy    lopt      sk    spr0  sprmsy
 0.3938  0.1385 58.5952 63.6029  0.1972  0.1518  0.0333
units:  NA NA NA NA NA NA NA
```

Creation of FLBRP objects

Stock recruitment relationships

bevholt $r = \frac{aS}{b+ssb}$

ricker $r = aSe^{-bS}$

cushing $r = aS^b$

Density Dependence

Modelling density dependence in natural mortality and fecundity.

```
data(teleost)
par=teleost[,"Hucho hucho"]
par=lhPar(par)
hutchen=lhEql(par)

scale=stock.n(hutchen)[,25]%*%stock.wt(hutchen)
scale=(stock.n(hutchen)%*%stock.wt(hutchen)%-%scale)%/%scale

m=mdd(stock.wt(hutchen),par=FLPar(m1=.2,m2=-0.288),scale,k=.5)
```

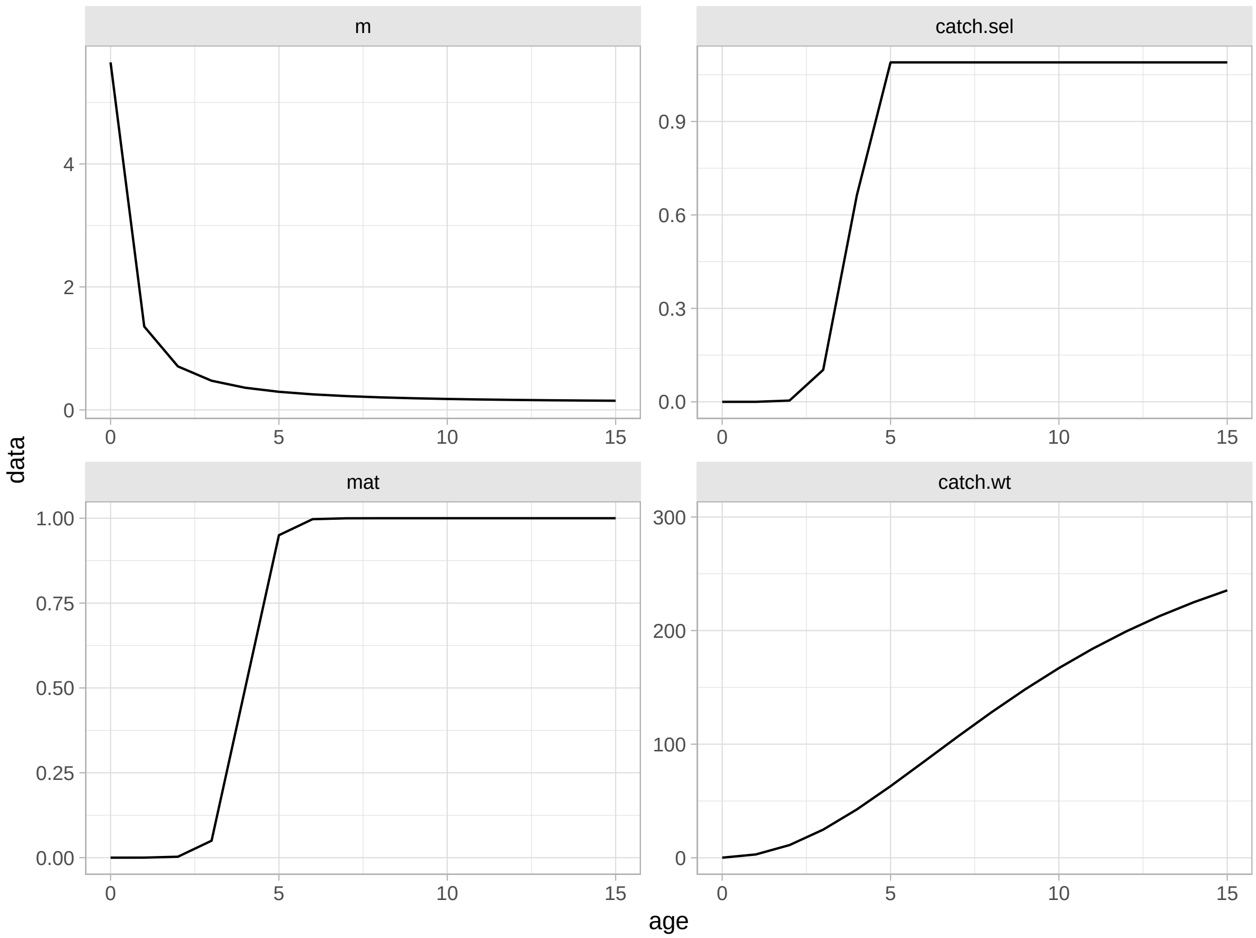


Figure 3: Age-vectors of growthm natural mortality, maturity and selection pattern

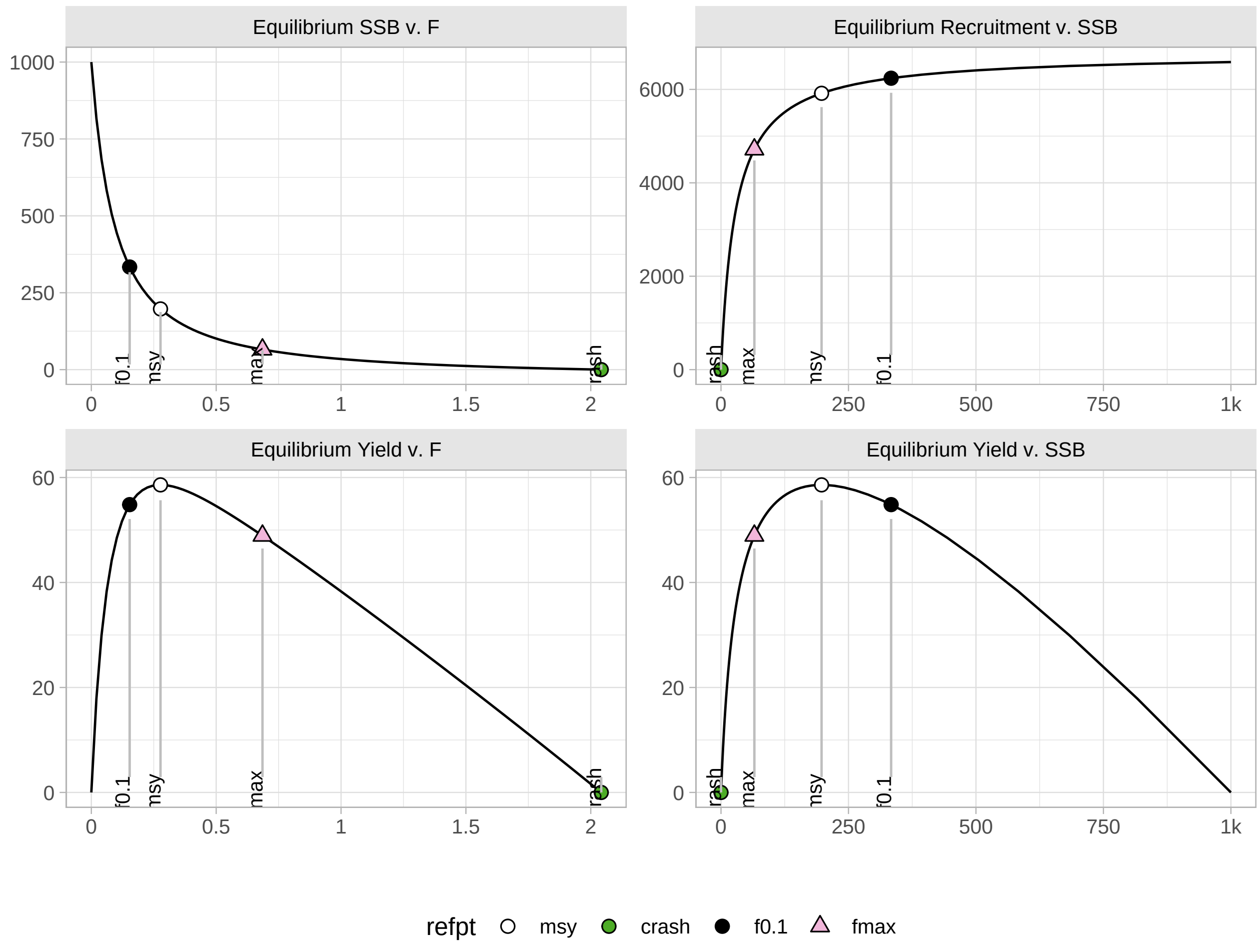


Figure 4: Equilibrium curves and reference points.

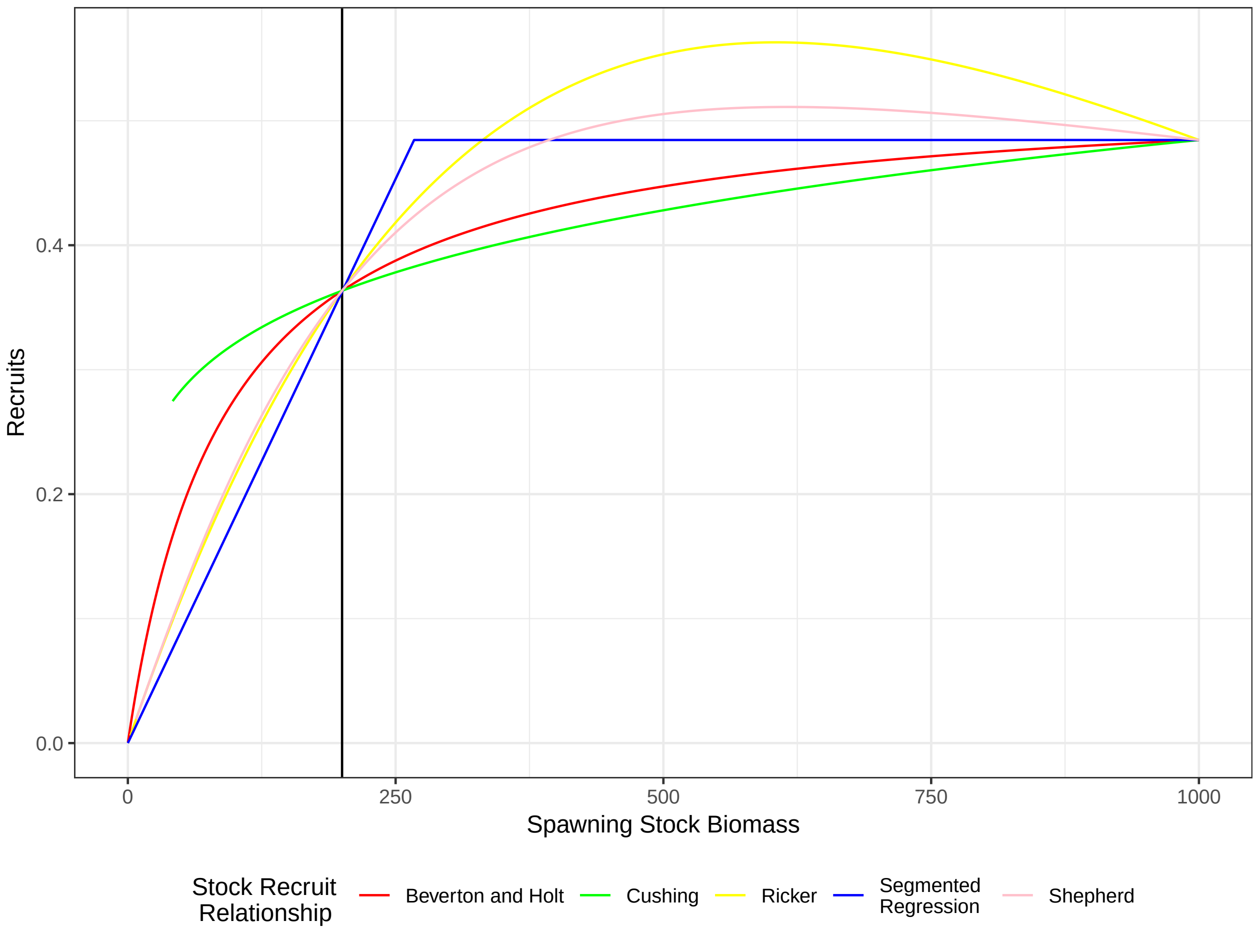


Figure 5: Stock recruitment relationships for a steepness of 0.75 and vigin biomass of 1000

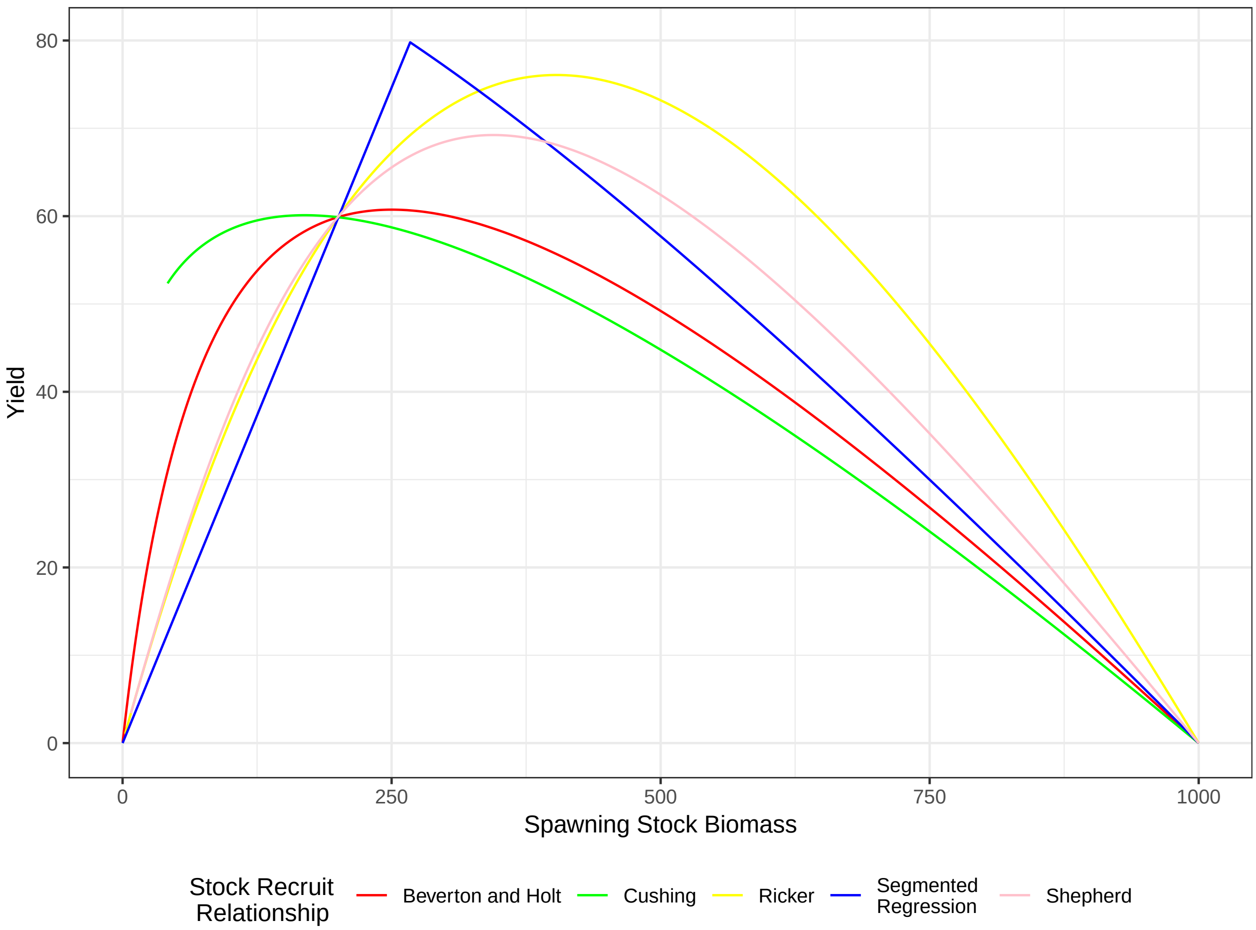


Figure 6: Production curves, Yield v SSB, for a steepness of 0.75 and vigin biomass of 1000.

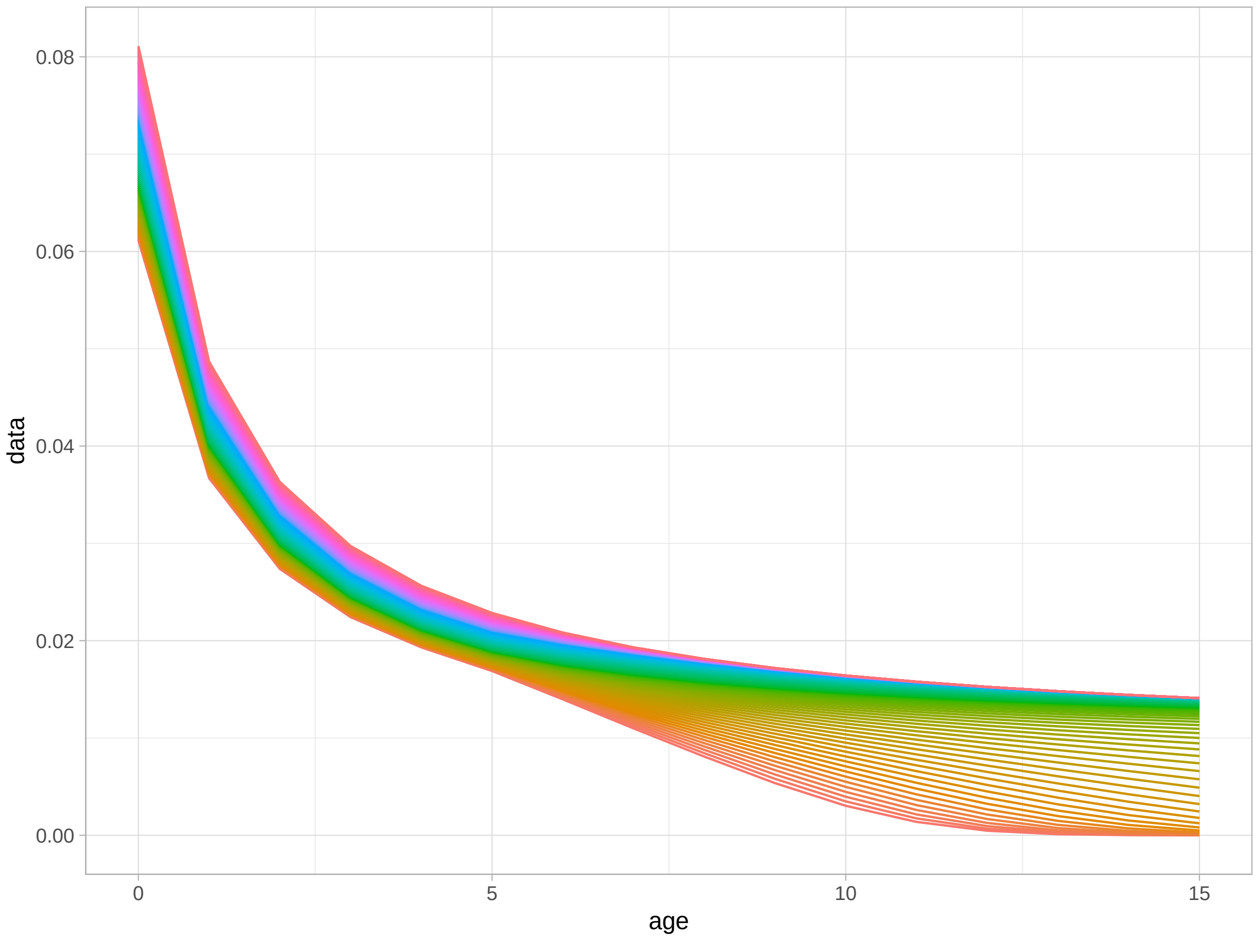


Figure 7: Density Dependence in M

```
ggplot(as.data.frame(m))+
   geom_line(aes(age,data,col=factor(year)))+
   theme(legend.position="none")+
    scale_x_continuous(limits=c(0,15))
```

```
scale=stock.n(hutchen)[,25]%*%stock.wt(hutchen)
scale=(stock.n(hutchen)%*%stock.wt(hutchen)%-%scale)%/%scale

mat=matdd(ages(scale),par,scale,k=.5)

ggplot(as.data.frame(mat))+
    geom_line(aes(age,data,col=factor(year)))+
    theme(legend.position="none")+
    scale_x_continuous(limits=c(0,15))
```

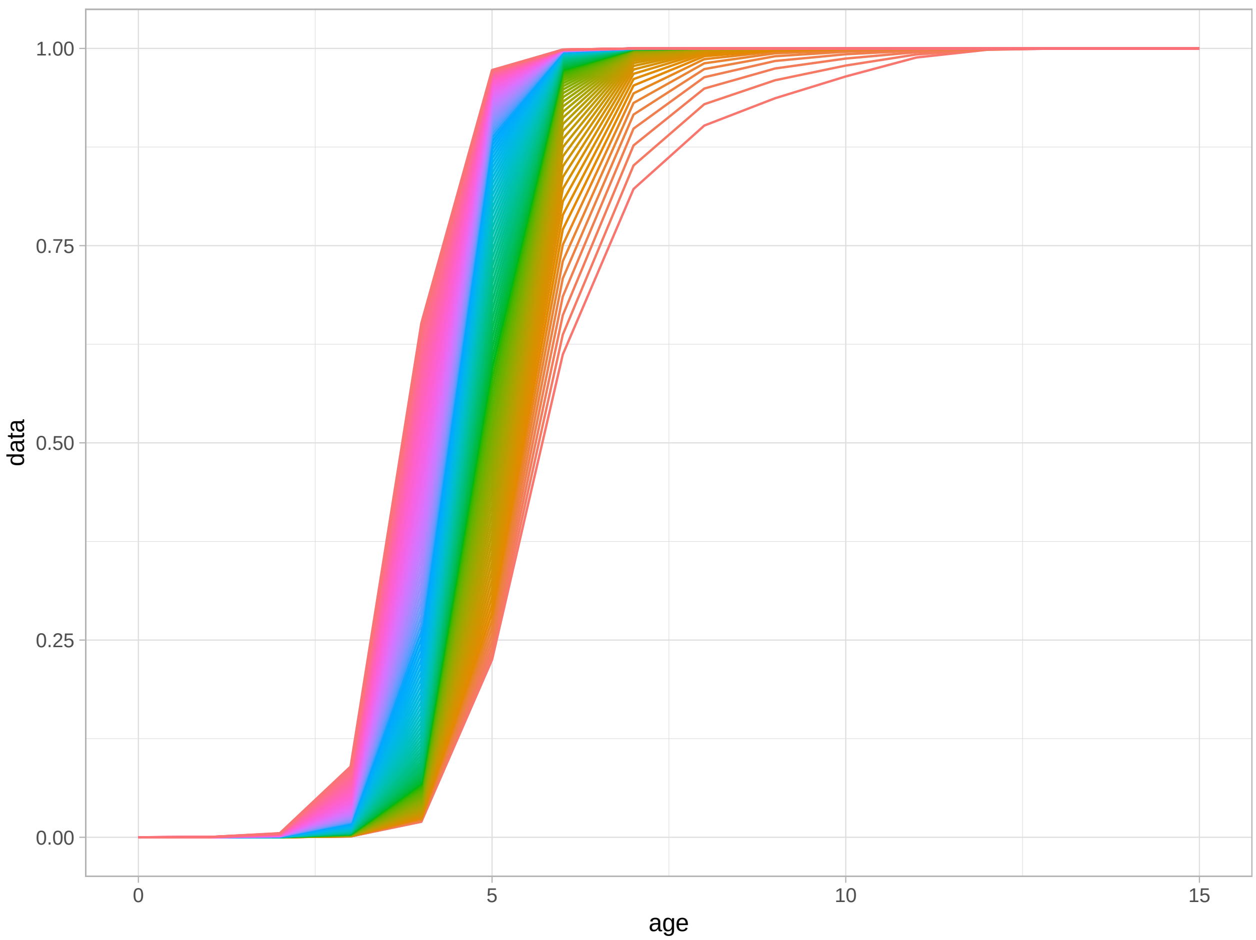
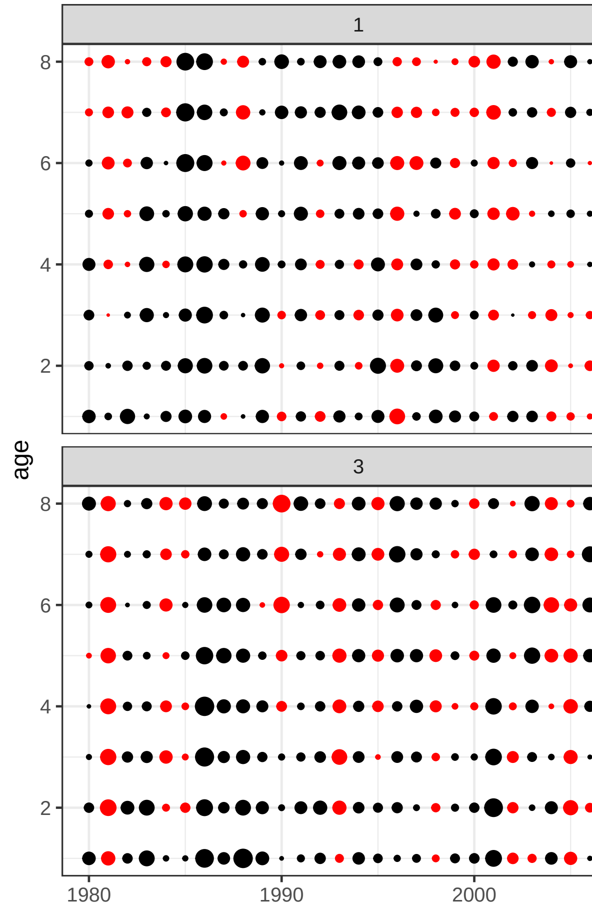
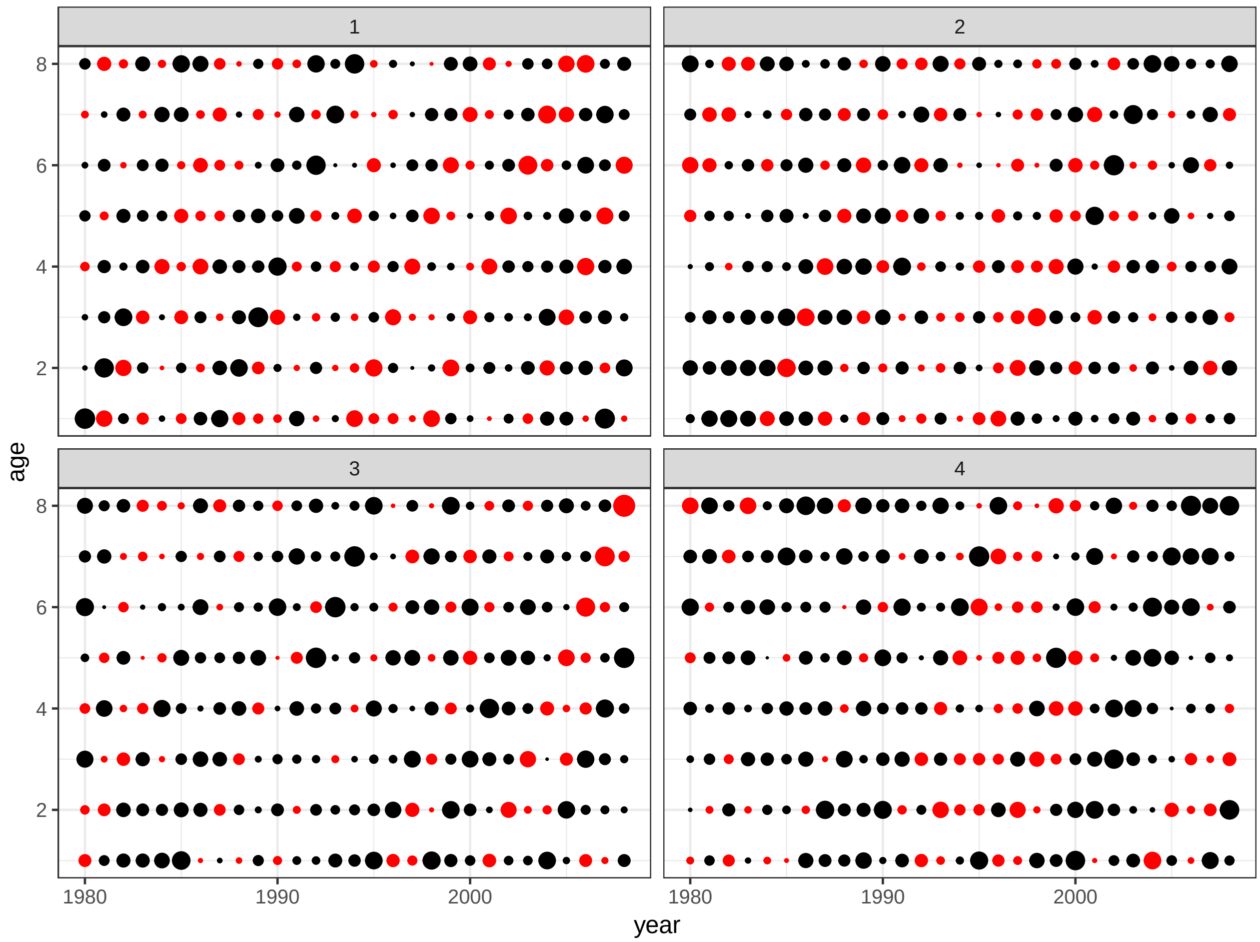


Figure 8: Density Dependence in M

Noise



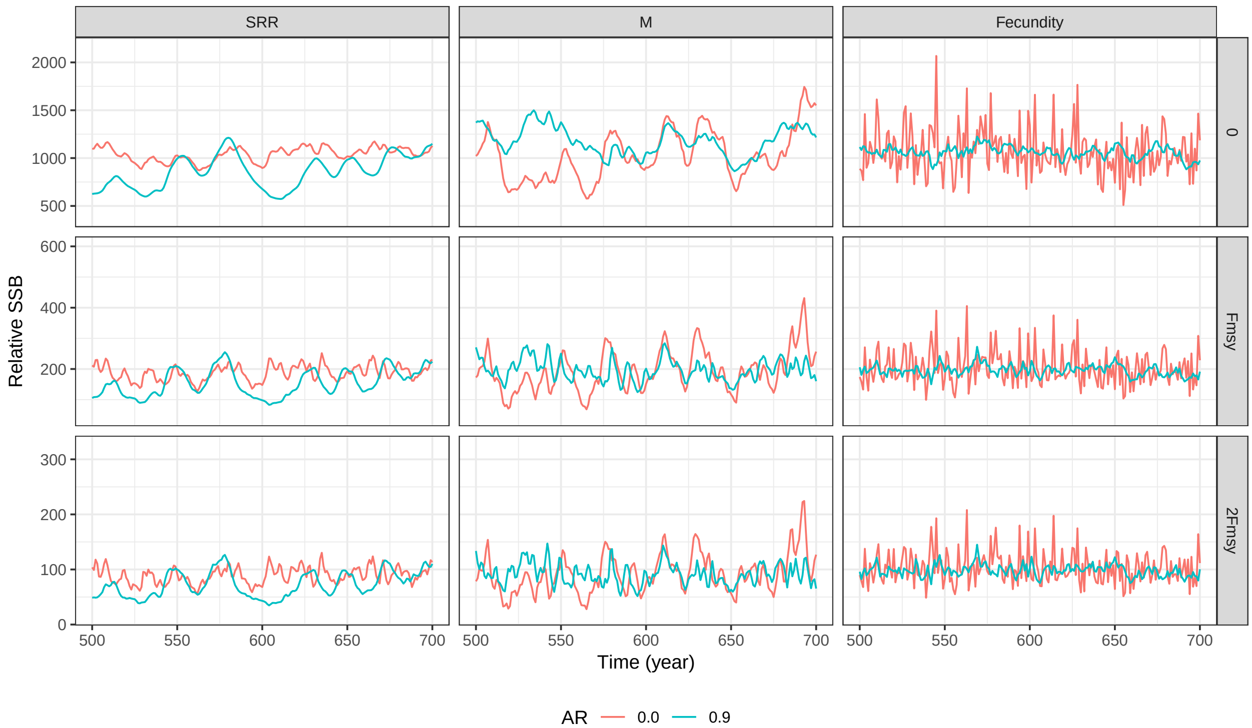
Methods to simulate random noise with autocorrelation, e.g. by age or cohort

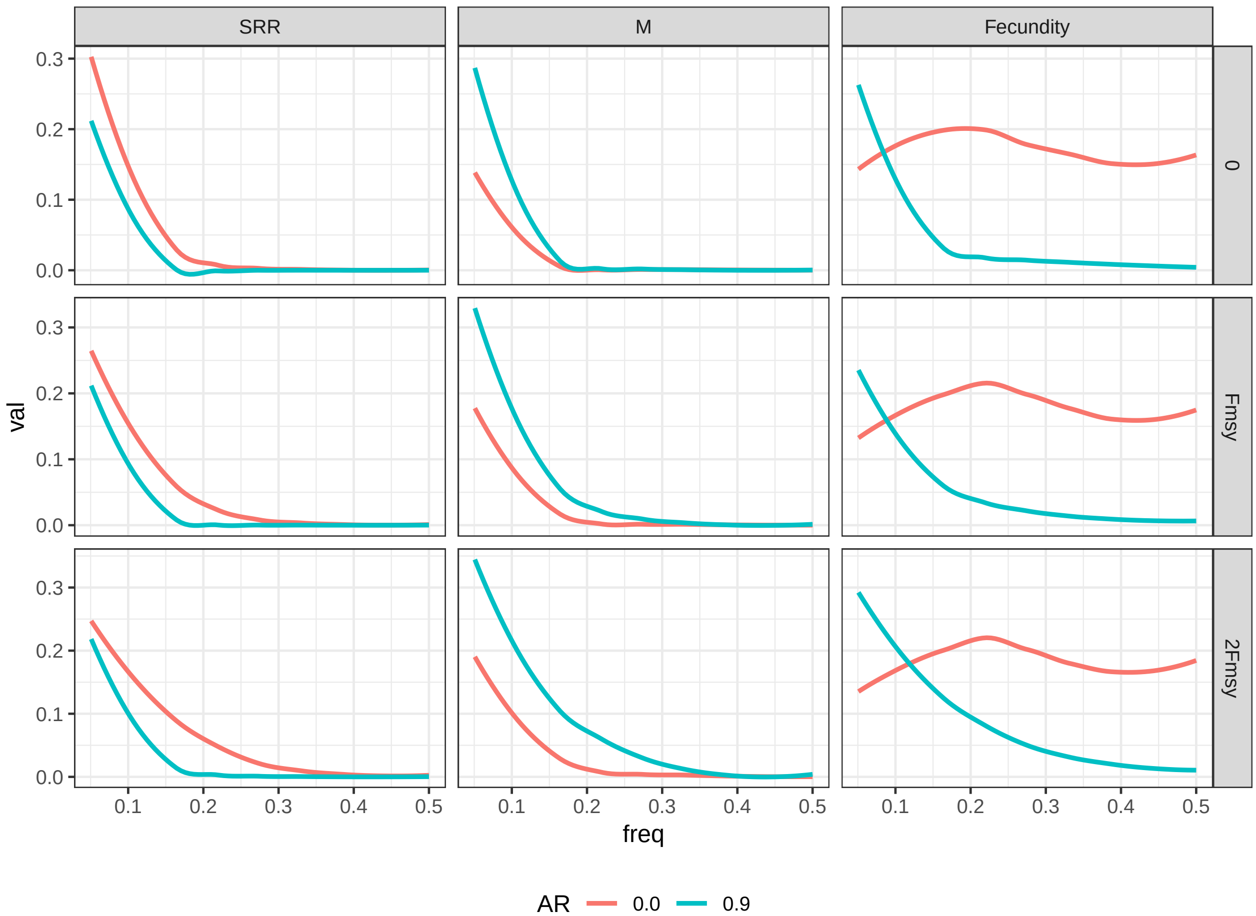


1
2
3
4
age
8
6
4
2
1980
1990
2000
year

Random Noise in R, M and Mat

AR Noise in R, M and Mat





MSE using empirical HCR

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Estimation

Life history parameters can also be used to estimate quantities of use in stock assessment

Beverton and Holt (1956) developed a method to estimate life history and population parameters length data. e.g.

$$Z = K\frac{L_{\infty} - \overline{L}}{\overline{L} - L'} \tag{1}$$

Based on which Powell (1979) developed a method, extended by Wetherall, Polovina, and Ralston (1987), to estimate growth and mortality parameters. This assumes that the right hand tail of a length frequency distribution was determined by the asymptotic length L_{∞} and the ratio between Z and the growth rate k.

The Beverton and Holt methods assumes good estimates for K and L_{∞}, while the Powell-Wetherall method only requires an estimate of K, since L_{∞} is estimated by the method as well as Z/K.These method therefore provide estimates for each distribution of Z/K, if K is unknown and Z if K is known.
%As well as assuming that growth follows the von Bertalanffy growth function, it is also assumed that the population is in a steady state with constant exponential mortality, no changes in selection pattern of the

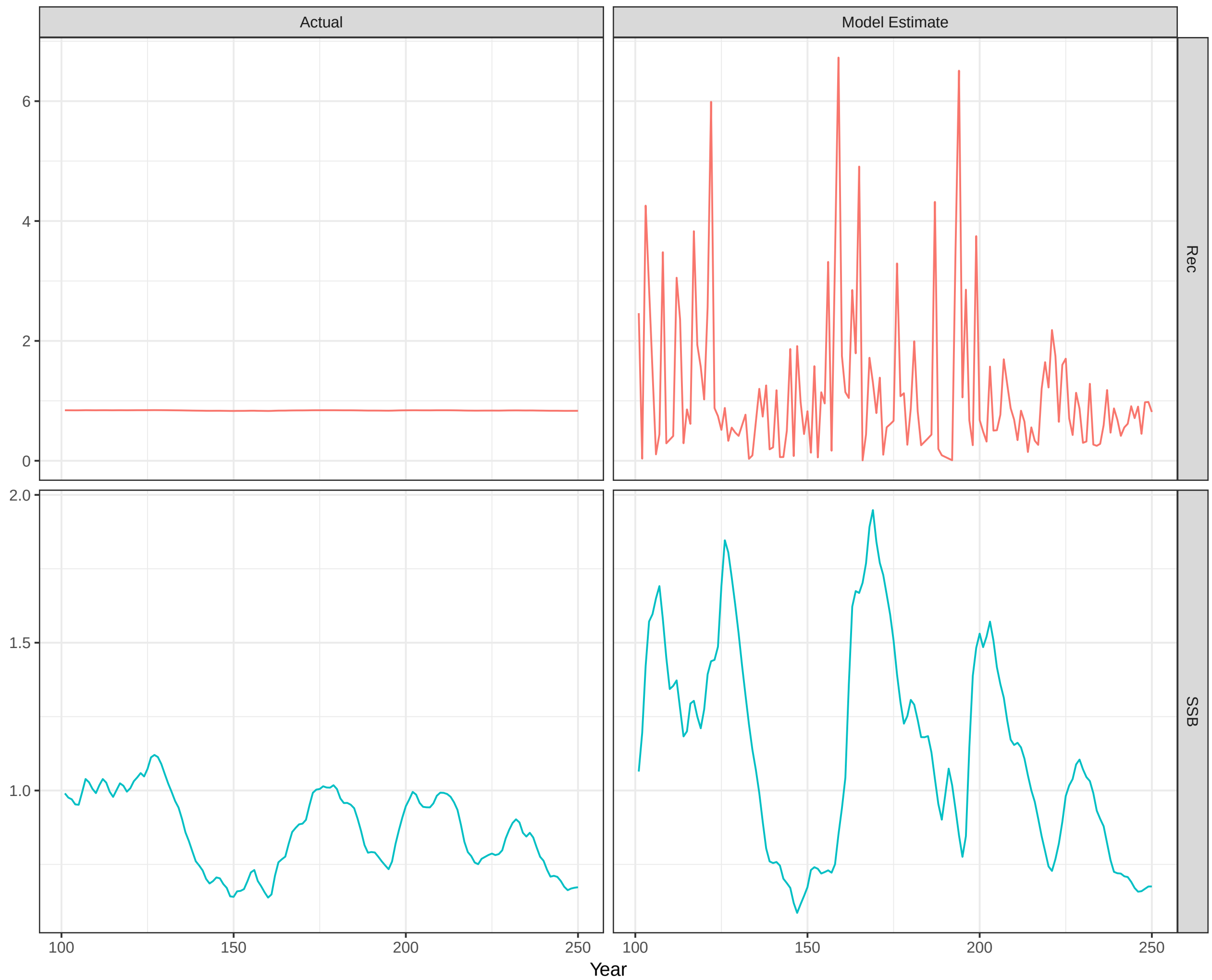


Figure 9: Cohort Effects

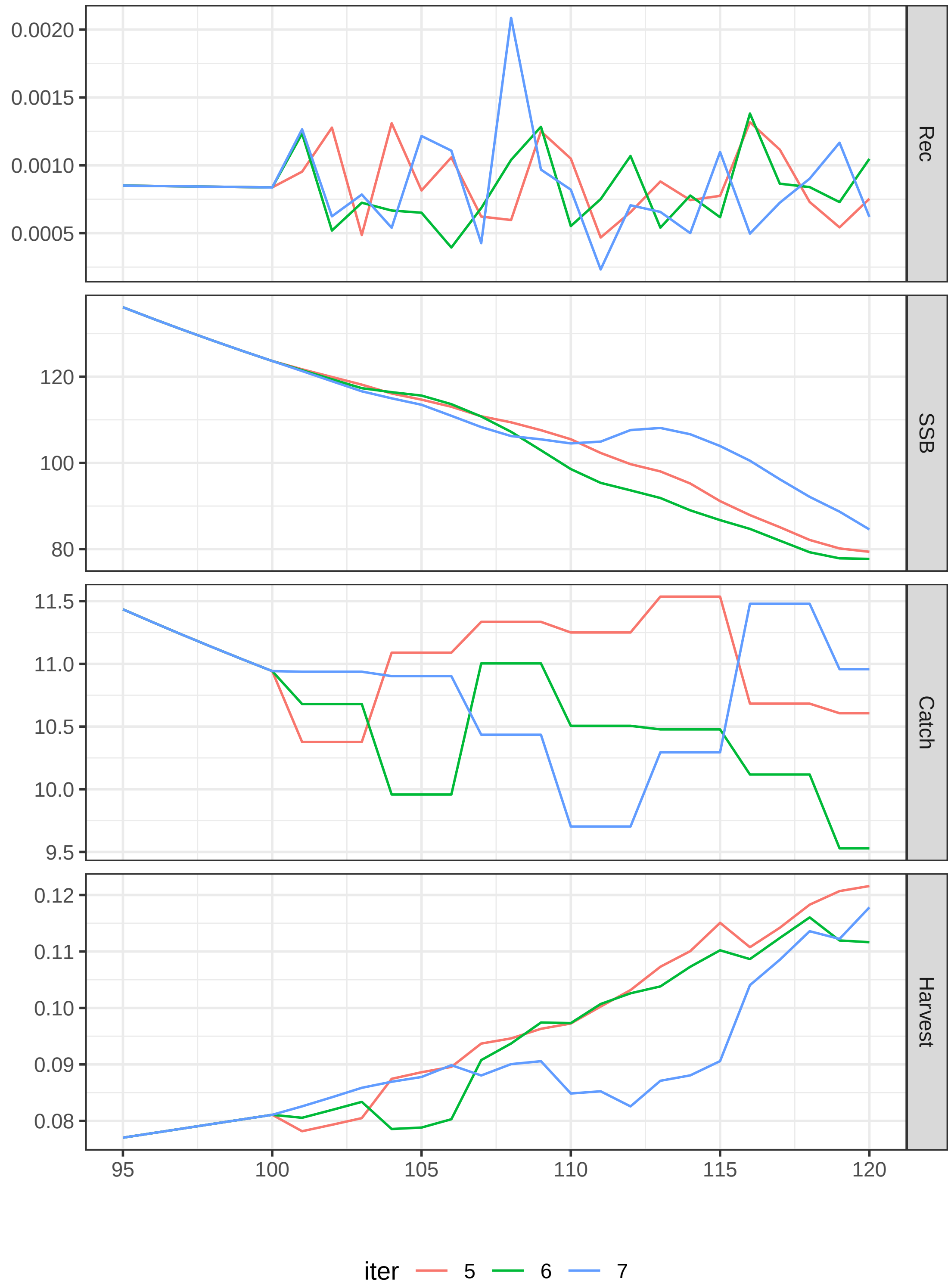


Figure 10: MSE using empirical HCR

fishery and constant recruitment. In the Powell-Wetherall method L' can take any value between the smallest and largest sizes. Equation 1 then provides a series of estimates of Z and since

$$\overline{L} - L' = a + bL' \tag{2}$$

a and b can be estimated by a regression analysis where

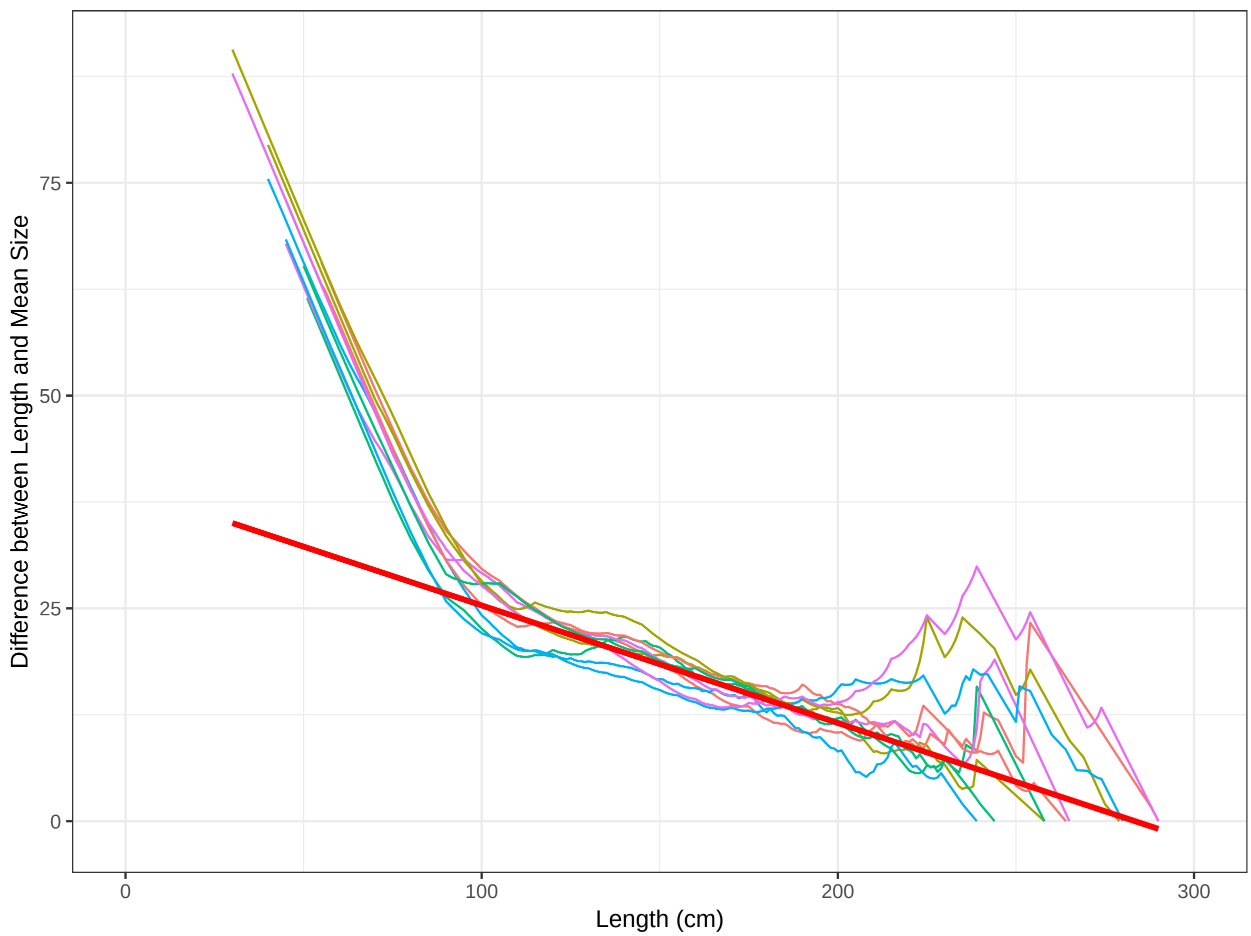
$$b = \frac{-K}{Z+K} \tag{3}$$

$$a = -bL_\infty \tag{4}$$

Therefore plotting $\overline{L} - L'$ against L' therefore provides an estimate of L_∞ and Z/K

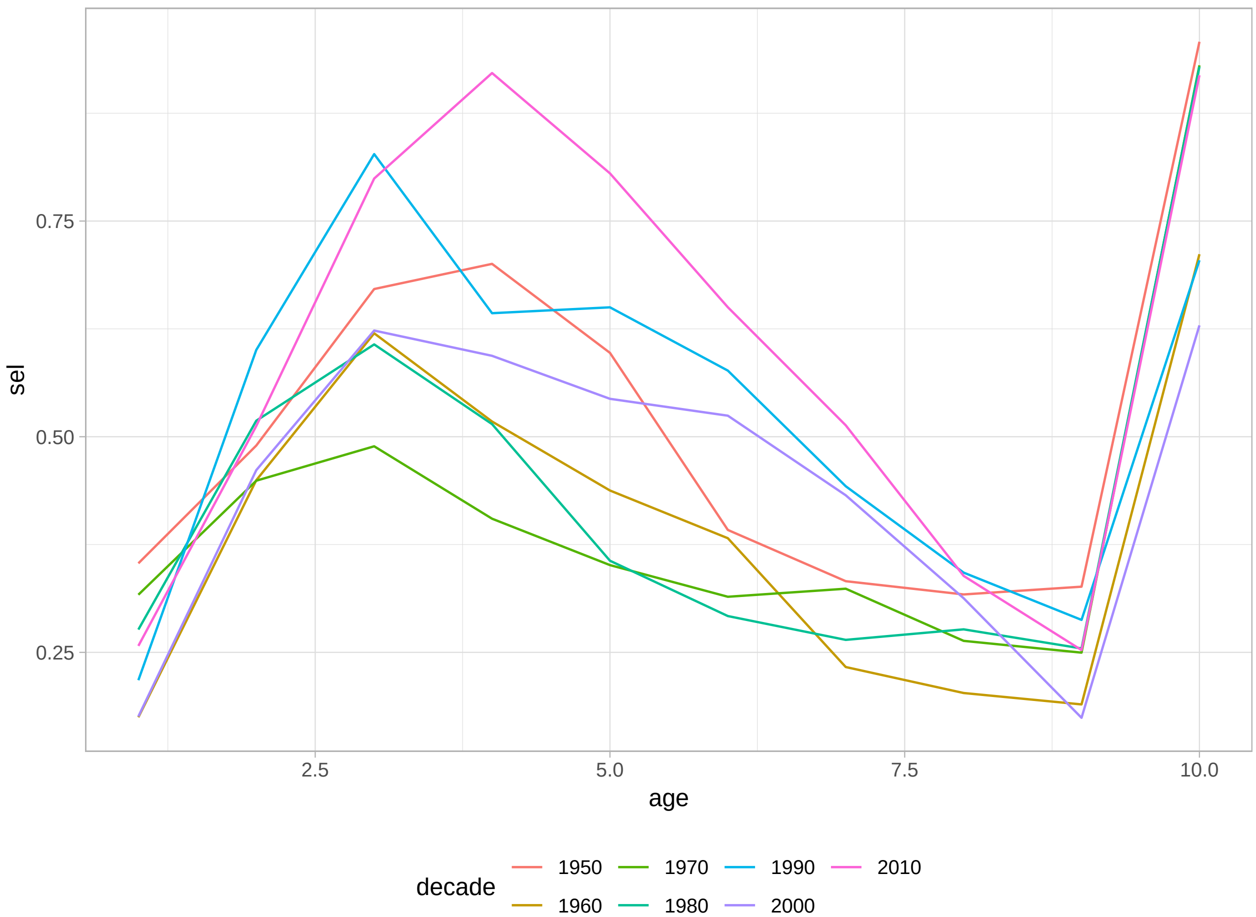
Plotting $\overline{L} - L'$ against L' provides an estimate of L_∞ and Z/k, since $L_\infty = -a/b$ and $Z/k = \frac{-1-b}{b}$. If k is known then it also provides an estimate of Z (**Figure ??**).

```
  age   obs    hat    sel
1   1 42703 263252 0.0194
2   2 40141 161176 0.0298
3   3 79353  98680 0.0962
4   4 56560  60416 0.1119
5   5 31888  36990 0.1031
6   6 10988  22647 0.0580
```



Catch curve analysis

```r
data(ple4)
ctc=as.data.frame(catch.n(ple4))
ctc=ddply(ctc,.(year), with, cc(age=age,n=data))
ctc=ddply(transform(ctc,decade=factor(10*(year%/%10))),.(decade,age),with,data.frame(sel=mean(sel)))
ggplot(ctc)+
  geom_line(aes(age,sel,colour=decade))
```



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More Information

- You can submit bug reports, questions or suggestions on `FLife` at the `FLife` issue page,[4] or on the *FLR* mailing list.
- Or send a pull request to https://github.com/lauriekell/FLife/
- For more information on the FLR Project for Quantitative Fisheries Science in R, visit the FLR webpage.[5]
- The latest version of `FLife` can always be installed using the `devtools` package, by calling

[4] https://github.com/lauriekell/FLife/issues
[5] http://flr-project.org

```r
library(devtools)
install_github("lauriekell/FLife")
```

‘

Software Versions

- R version 3.5.1 (2018-07-02)
- FLCore: 2.6.10
- FLPKG:
- **Compiled**: Wed Dec 5 05:50:44 2018
- **Git Hash**: 29d05db

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