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FLife: An R Package for Modelling Life History Relationships and Dynamic Processes.

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SUMMARY

FLife is an R package for modelling life history traits, biological processes, density dependence and simulation of time series. Life history traits have many uses in stock assessment. They are used to provide advice for data poor stocks and to derive priors or fixed values for difficult to estimate population parameters in data rich stock assessments. While to ensure that advice is robust scenarios based on life history traits are used to condition Operating Models when conducting Management Strategy Evaluation.

KEYWORDS: Life History; FLR; Density Dependence; Stochasticity; Reference Points; Growth; Fecundity; Maturity; Natural Mortality;

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1. Introduction

Life history traits have many uses in stock assessment. For example indicators based on life history traits are used for data poor stocks and data rich stock assessments often require priors or fixed values for difficult to estimate biological parameters. FLife is an R package that models relationships between life history parameters, provides methods to simulates processes such as growth, fecundity and mortality. It also includes methods for modelling density dependence in recruitment, growth, fecundity and mortality. The package can be used to simulate time series for a variety of stochastic processes and includes methods for estimating life history parameters using empirical data and for conducting meta-analyses.

In data poor situations life history parameters, such as maximum size and size at first maturity have been used as proxies for productivity (Roff, 1984; Jensen, 1996; Caddy, 1998; Reynolds et al., 2001; Denney et al., 2002). For example in Ecological Risk Assessment (ERA) where the risk of a stock to becoming overfished is evaluated using indices of productivity and susceptibility to fishing (Hobday et al., 2011). Life history attributes are combined and used to rank stocks, populations or species in order of productivity (e.g. Corts et al., 2010; Arrizabalaga et al., 2011). Where attributes are not available for all species, life history relationships have been used to predict missing values, e.g. to derive maturity from size.

Stock assessment and the outcomes of Management Strategy Evaluations are highly sensitive to the assumptions about processes such as natural mortality-at-age and recruitment processes (Jiao et al., 2012; Simon et al., 2012). Therefore often scenarios are developed to conduct sensitivity analyses to evaluate the robustness of results and advice based upon them.

2. Data

An example dataset, teleost, is provided as part of the package; values are the Von Bertalanffy (1957) growth equation parameters k the rate at which the rate of growth in length declines and the asymptotic length L_∞, L_{50} the length at which 50% of individuals attain gonadal maturity for the first time and b the exponent of the length weight relationship.

The values and the relationship between them are plotted in **Figure** 1. The data are then summarised using principle components analysis (PCA) in **Figure** 2; the ellipses are the 95% normal probability densities, blue points are scrombidae and the black point is albacore. The first principal axis maximizes the variance, as reflected by its eigenvalue. The second component is orthogonal to the first and maximizes the remaining variance. The first two component account for over 70% of the variance and therefore yield a good approximation of the original variables. They therefore correspond to the interesting dynamics and lower ones to noise.The main features of the data as given by the first component are a contrast between large fish (L_∞), which mature at larger relative size ($L_{50} : L_\infty$) and small fish that mature at relatively small sizes. The second component contrasts thin streamlined species with more sedentary types (i.e. b the exponent of the length weight relationship).

3. Examples

A set of examples are provided to illustrate the use of the package, code is in the package vignette. First an population based on albacore was simulated for a Beverton and Holt stock recruitment relationship (steepness=0.75) and a fishery that selects mature fish.

3.1 Equilibrium

The assumed stock recruitment relationship has a big impact of the dynamics, although there is seldom sufficient information in fish stock data sets to determine either the function form or the parameters of the relationship. Five alternative forms, all with steepness of 0.75 and virgin biomass of 1000, are plotted in **Figure** 3. The corresponding production functions, i.e. equilibrium yield as a function of spawning stock biomss (SSB), are shown in **Figure** 4. The production function can be used to derive reference points such as those based on MSY or population growth rate.

Four population parameters were derived for use as reference points, i.e. i) population growth rate at low population size (r); ii) population growth rate at SSB_{MSY} ($r_{B_{MSY}}$), where SSB_{MSY} is the expected SSB at a level of fishing mortality that would provide the maximum long-term sustainable yield (MSY); iii) the ratio of SSB_{MSY} to virgin biomass (SSB_{MSY}/K); and iv) the size at which a year-class achieves its maximum biomass (L_{opt}).

r is equivalent to level of exploitation that would drive a population to extinction since a population can not replenish itself if the harvest rate is greater than r. In fisheries terminology r corresponds to a limit harvest rate reference point and $r_{B_{MSY}}$ corresponds to a target exploitation level. Limit reference points are also required to indicated when economic, recruitment and growth overfishing is occurring. Therefore F_{MSY} is now regarded as a limit. If SSB_{MSY}/K is much less than 1.0 then productivity will be maintained at low population levels; while L_{opt} is a measure of resilience to growth overfishing.

Production functions, were then calculated for density dependence natural mortality and fecundity and contrasted with assuming density dependence only acts in recruitment **Figure** 6. Assuming density dependence in M or fecundity results in an increase in MSY, B_{MSY} and F_{MSY}

3.2 Deterimistic Projections

To evaluate sustainability requires determining the productivity of a population and its response to perturbation. The stability of a population is strongly influenced by its life history characteristics and the form of density dependence. Therefore the response of a population to overfishing is evaluated in **Figure** 7 and for rebuilding in **Figure** 8, for density dependence in stock recruitment, natural mortality and fecundity. The response to overfishing is similar across processes, however, rebuilding trajectories depend on the form of density dependence. Predicting recovery trajectories based on time series obtained from a period of increasing exploitation is likely to be problematic.

3.3 Stochasticity

Stochasticity has important impacts on population dynamics and can be of various forms, e.g. it varies by year depending on the environment or by cohort since if conditions at an earlier age have an effect on later age classes. Examples of stochastic age effects are shown in **Figure** 9 and stochastic cohort effects in **Figure** 10.

Next populations were simulated for three levels of fishing mortality (0, 1 3 times F_{MSY}) and two selection patterns (corresponding to juvenile or mature age classes) for cohort effects in M and fecundity and autocorrelation in recruitment. The time series of SSB are shown in **Figure** 11. The spectral analysis performed for these time series **Figure** 12 shows that all time series are dominated by low frequencies (i.e. long-term variations) that result from cohort resonant effects, i.e. the propagation of stochastic recruitment into the age-classes and that led to a smoothing of the SSB (see Bjoernstad et al., 2004).

3.4 Model misspecification

One of the main uncertainties in stock assessment is the difference between models and reality. Therefore we include a model misspecification example, where in the simulated population natural mortality is a random variable, but is assumed to be constant at age in the virtual population analysis used to estimate numbers-at-age **Figure** 13. The effect is to assume that recruitment is more variable than it actually is.

3.5 Management Strategy Evaluation

An empirical Harvest Control Rule (HCR) has been adopted for southern bluefin tuna (SBT) to set Total Allowable Catches (TACs). The HCR is based on year-to-year changes in indices of relative stock abundance. Before the HCR was implemented the HCR parameters had to be tuned to meet management objectives using management strategy evaluation (MSE). **Figure** 14 shows an example MSE using an empirical HCR and an Operating Model generated using FLife.

3.6 Empirical Methods

Beverton and Holt (1956) developed a method to estimate life history and population parameters length data. Based on which Powell (1979) developed a method, extended by Wetherall et al. (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.

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** 15).

4. Discussion and Conclusions

FLife has many potential uses e.g. for conducting Ecological Risk Assessments, estimating life history parameters from data, development of priors for use in stock assessment, building simulation model based on population and ecological processes and generating Operating Models for use in Management Strategy Evaluation.

The form of density dependence can affect overfishing and rebuilding trajectories. It is, however, difficult to determine whether density dependence is occurring and on what processes it acts using fisheries dataset (Sinclair et al., 2002). The main form of density dependence considered in stock assessment models, is the stock recruitment relationship, primarily as it is required to complete the life cycle. Other forms of density dependence may operate and it is necessary to use caution in selecting the type of density dependence, and specifying its parameters (Ginzburg et al., 1990).

Trends and fluctuations in populations are determined by complex interactions between extrinsic and intrinsic dynamics, While the dynamics of many marine fish are characterised by age-structured dynamics forced by stochastic recruitment i.e Cohort resonance. The resulting low-frequency fluctuations can potentially mimic or cloak critical variation in abundance linked to environmental change or over-exploitation (Bjoernstad et al., 2004).

The tools available in FLife can help to develop robust management control rules by building OMs that can be used to evaluate the robustness to uncertainty about ecological processes.

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5. Equations

The maximum theoretical rate of increase of a population in the absence of density-dependent regulation is given by

$$r = \frac{dN}{dt}\frac{1}{N} \tag{1}$$

where the intrinsic population growth rate (r) is a function of population size (N) and $\frac{dN}{dt}$ the instantaneous rate of increase of the population.

In ecology Leslie matrices (Leslie, 1945) are widely used to estimate r (Picard et al., 2009) and have been used in fisheries to develop Bayesian priors for r for use in stock assessment (see McAllister et al., 2001). The Leslie Matrix (A) is a transition matrix that models age dynamics. Each age-class is described by a vector (B_t) of length p equal to the terminal age. Entries in the matrix are fecundity (f_i) (the quantity of age zero females produced per unit of mature biomass by each age-class) and the survival (and growth if biomass) of an age-class (s_i) in each time step i, i.e.

$$\begin{aligned} n_1 &= f_2 n_2 + ... + f_3 n_p \\ n_2 &= s_1 n_1 \\ &... \\ n_p &= s_{p-1} n_{p-1} + s_p n_p \end{aligned} \tag{2}$$

The matrix of this linear system is

$$\mathbf{A} = \begin{pmatrix} 0 & f_2 & ... & f_p \\ s_1 & 0 & ... & 0 \\ & ... & & \\ 0 & ... & s_{p-1} & s_p \end{pmatrix} \tag{3}$$

If the initial population is

$$\mathbf{B}^0 = \begin{pmatrix} n_1 \\ n_2 \\ ... \\ n_p \end{pmatrix} \tag{4}$$

then after time step i=1 the population is given by

$$\mathbf{B}^i = \mathbf{A}^i \mathbf{B}^0 \tag{5}$$

As i tends to infinity the system reaches equilibrium and the contribution of each age group in the population becomes stable. The population growth rate r is then derived from λ the dominant eigenvalue of A (Caswell, 1989).

To construct the Leslie matrix requires estimates of f_i and p_i. In this study these were derived by combining a stock recruitment relationship with a spawner-per-recruit (S/R) and yield-per-recruit (Y/R) analyses. The life history parameters were used to derive mass (W), proportion mature (Q), natural mortality (M) and fishing mortality (F) at age.

$$S/R = \sum_{i=0}^{p-1} e^{\sum\limits_{j=0}^{i-1} -F_j - M_j} W_i Q_i + e^{\sum\limits_{i=0}^{p-1} -F_i - M_i} \frac{W_p Q_p}{1 - e^{-F_p - M_p}} \tag{6}$$

$$Y/R = \sum_{a=r}^{n-1} e^{\sum\limits_{i=r}^{a-1} -F_i - M_i} W_a \frac{F_a}{F_a + M_a} \left(1 - e^{-F_i - M_i}\right) + e^{\sum\limits_{i=r}^{n-1} -F_n - M_n} W_n \frac{F_n}{F_n + M_n} \tag{7}$$

The second term is the plus-group, i.e. the summation of all ages from the last age to infinity.

Growth in length is modelled by the Von Bertalanffy growth equation **?**

$$L = L_\infty (1 - exp(-k(t - t_0)) \tag{8}$$

where k is the rate at which the rate of growth in length declines as length approaches the asymptotic length L_∞ and t_0 is the hypothetical time at which an individual is of zero length.

Length is converted to mass using the length-weight relationship

$$W = aL_t^b \tag{9}$$

where a is the condition factor and b is the allometric growth coefficient.

Gislason et al. (2010) showed that M is significantly related to body length, asymptotic length and k. Temperature is non-significant when k is included, since k itself is correlated with temperature. We therefore model M as

$$M = 0.55L^{1.61}L_{\infty}^{1.44}k \tag{10}$$

Selection pattern of the fishery was represented by a double normal (see **?**)) with three parameters that describe the age at maximum selection ($a1$), the rate at which the left-hand limb increases (sl) and the right-hand limb decreases (sr) which allows flat topped or domed shaped selection patterns to be chosen.

$$f(x) = \begin{cases} 0 & \text{if } (a_{50} - x)/a_{95} > 5 \\ a_{\infty} & \text{if } (a_{50} - x)/a_{95} < -5 \\ \frac{m_{\infty}}{1.0+19.0^{(a_{50}-x)/95)}} & \text{otherwise} \end{cases} \tag{11}$$

The relationship between stock and recruitment was modelled by a Beverton and Holt stock-recruitment relationship (Beverton and Holt, 1993) reformulated in terms of steepness (h), virgin biomass (v) and $S/R_{F=0}$

$$R = \frac{0.8R_0h}{0.2S/R_{F=0}R_0(1-h) + (h-0.2)S} \tag{12}$$

where steepness is the ratio of recruitment at 20% of virgin biomass to virgin recruitment (R_0) and $S/R_{F=0}$ is the spawner per recruit at virgin biomass, i.e. when fishing mortality is zero. Steepness is difficult to estimate from stock assessment data sets as there is often insufficient contrast in biomass levels required for its estimation Pepin (2015).

S is spawning stock biomass, the sum of the products of the numbers of females, N, proportion mature-at-age, Q and their mean fecundity-at-age, F, i.e.

$$S = \sum_{i=0}^{p} N_iQ_iF_i \tag{13}$$

where fecundity-at-age is assumed proportional to biomass and the sex ratio to be 1:1. Proportion mature is 50% at the age that attains a length of $l50$, 0% below this age and 100% above.

6. Figures

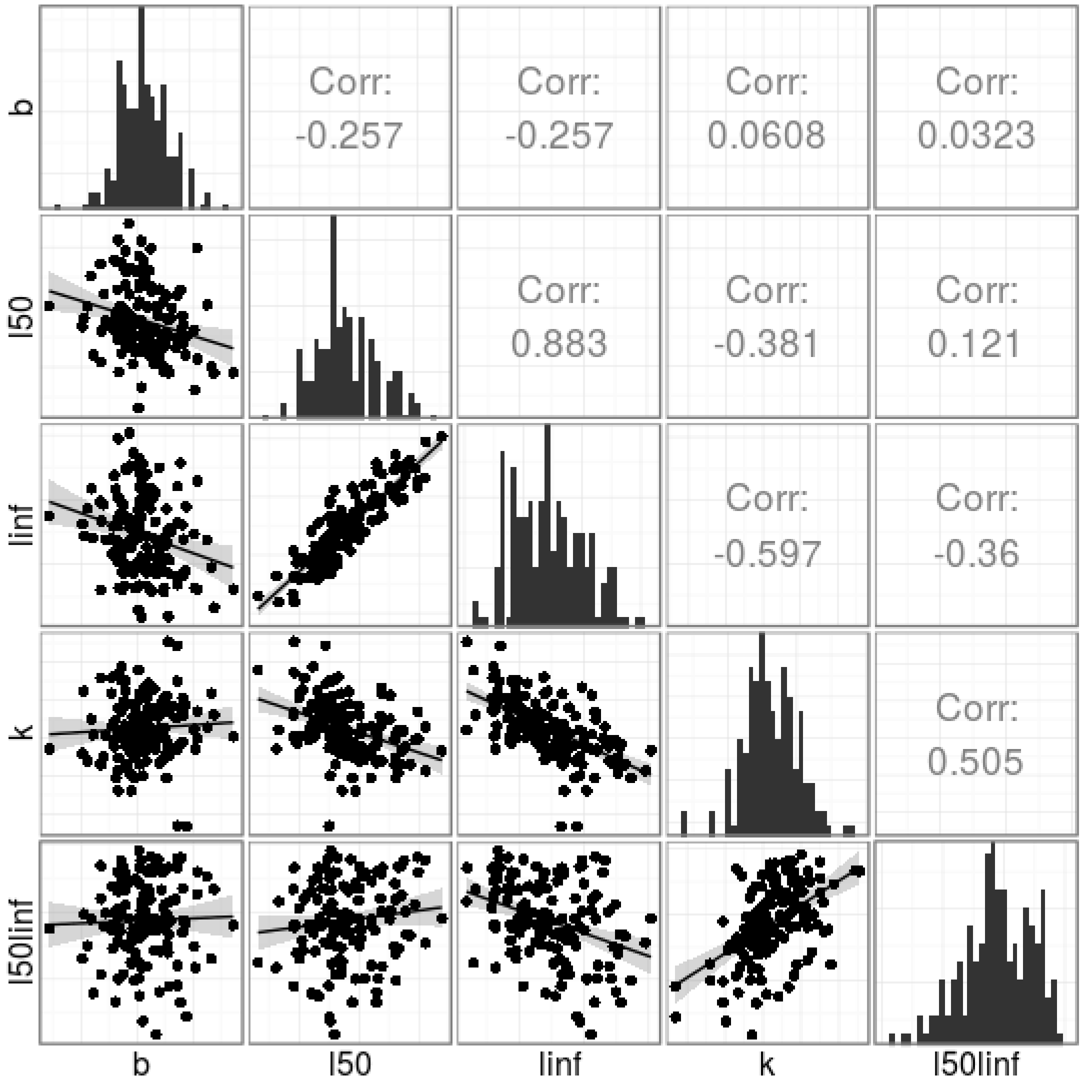

Figure 1: Life history parameter distribution and relationships between them for the teleost dataset on the log scale.

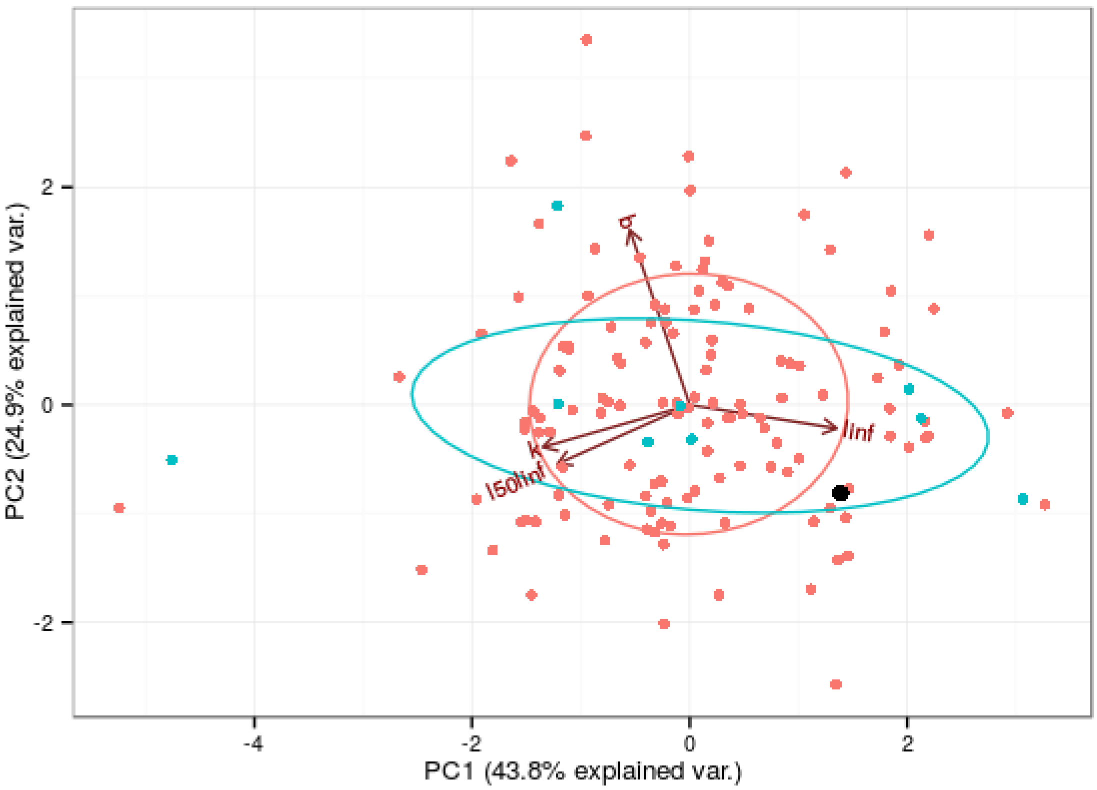

Figure 2: Principle components analysis of life history parameters for the teleost dataset; the ellipses are the 95% normal probability densities, blue are scrombidae and the black dot albacore.

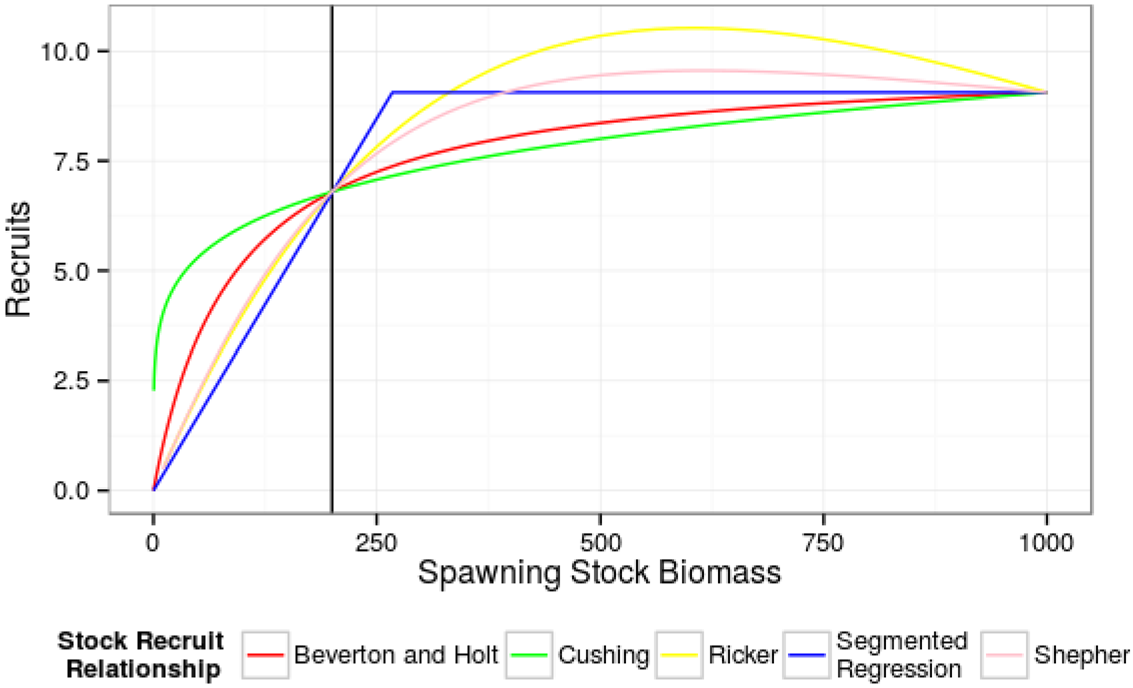

Figure 3: Comparison of stock recruitment relationships with steepness of 0.75 and virgin biomass of 1000.

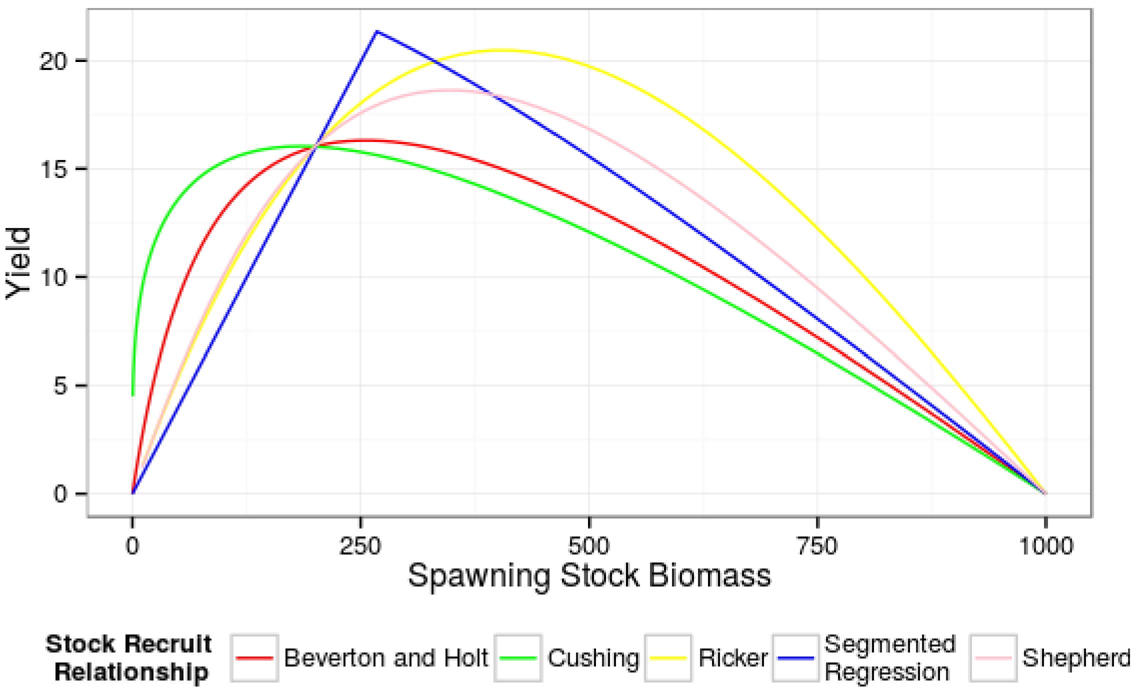

Figure 4: Production functions, for stock recruitment relationships with steepness of 0.75 and virgin biomass of 1000 stones

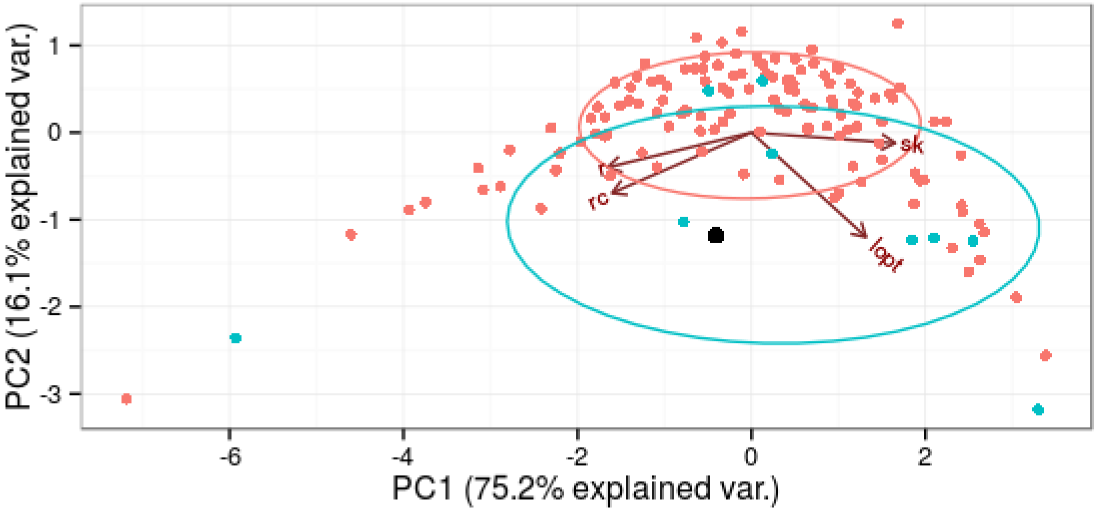

Figure 5: Principle components analysis of population parameters and reference points;, the ellipses are the 95% normal probability densities, blue are scrombidae and the black dot albacore.

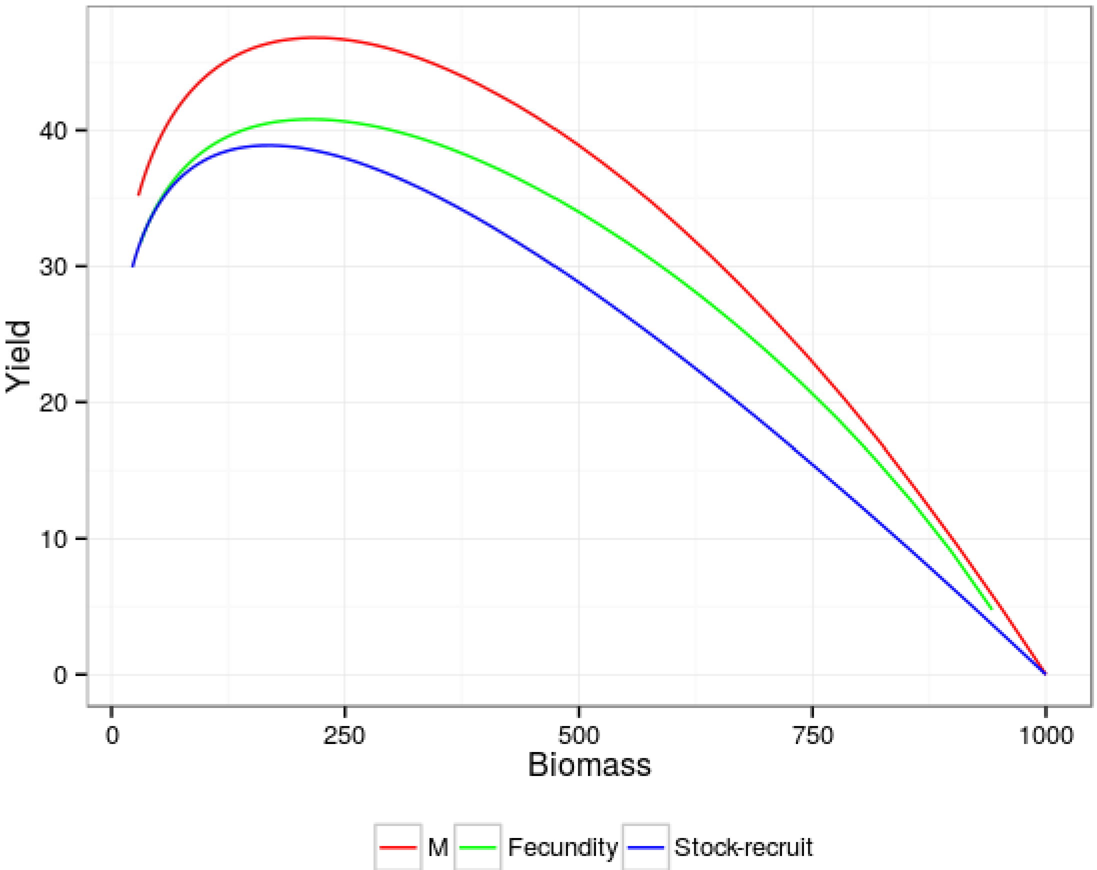

Figure 6: Production functions, based on yield and SSB, for density dependence in stock recruitment, natural mortality and fecundity.

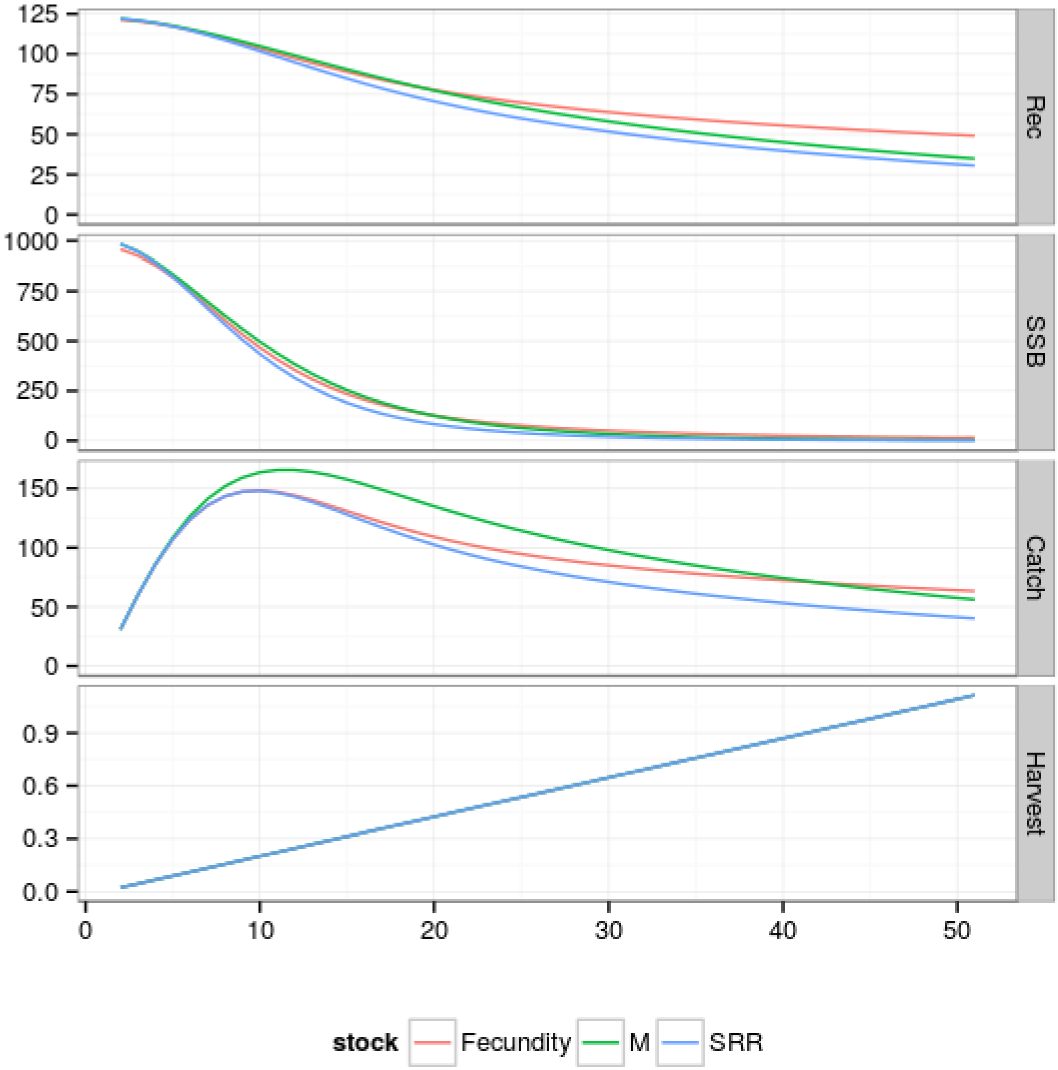

Figure 7: Overfishing trajectories for examples with density dependence in stock recruitment, natural mortality and fecundity

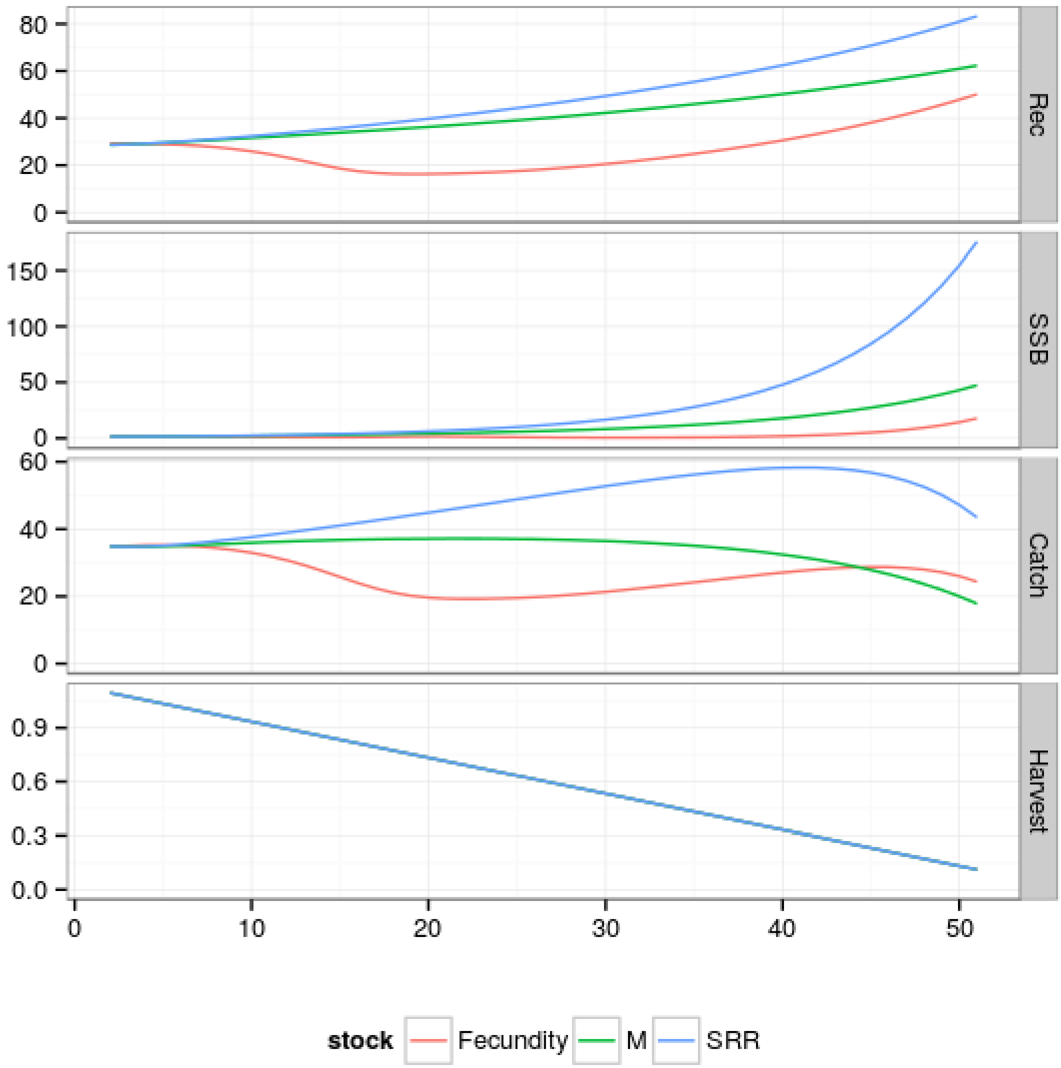

Figure 8: Rebuilding trajectories for examples with density dependence in stock recruitment, natural mortality and fecundity

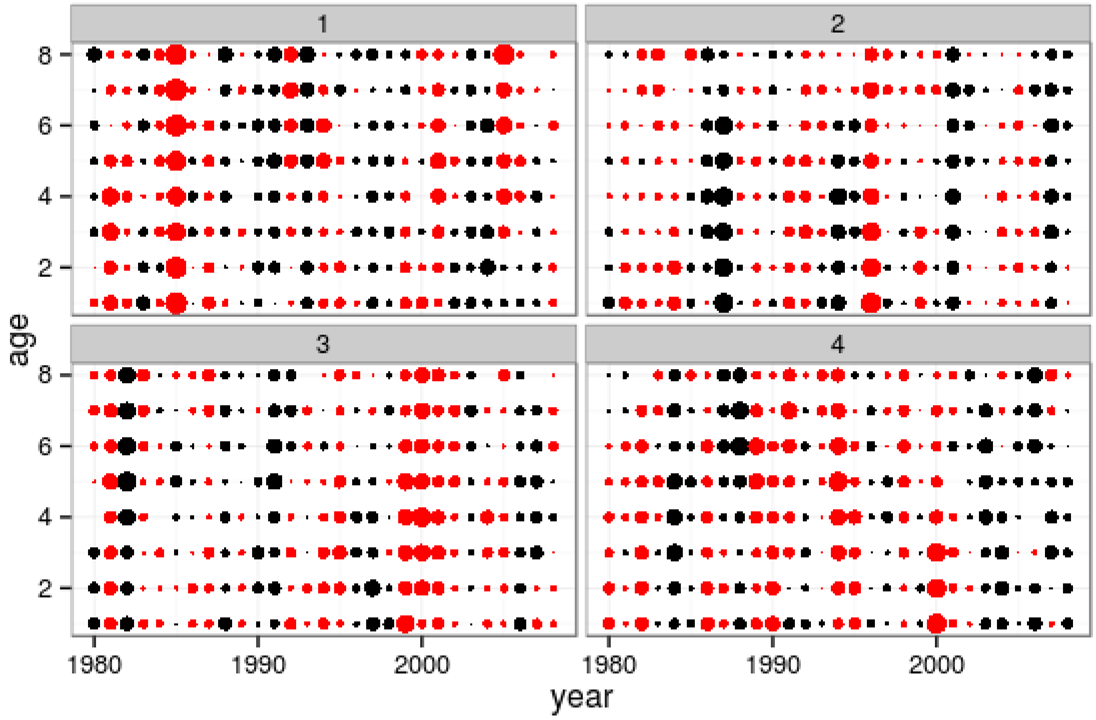

Figure 9: Stochastic age effects

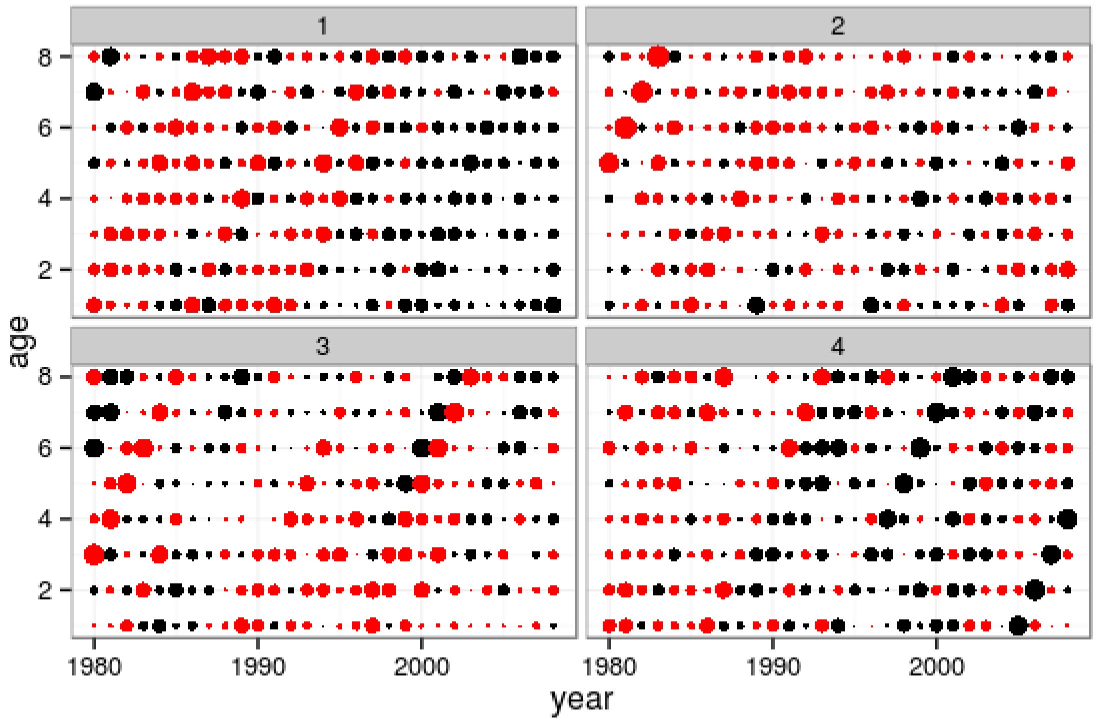

Figure 10: Stochastic cohort effect.

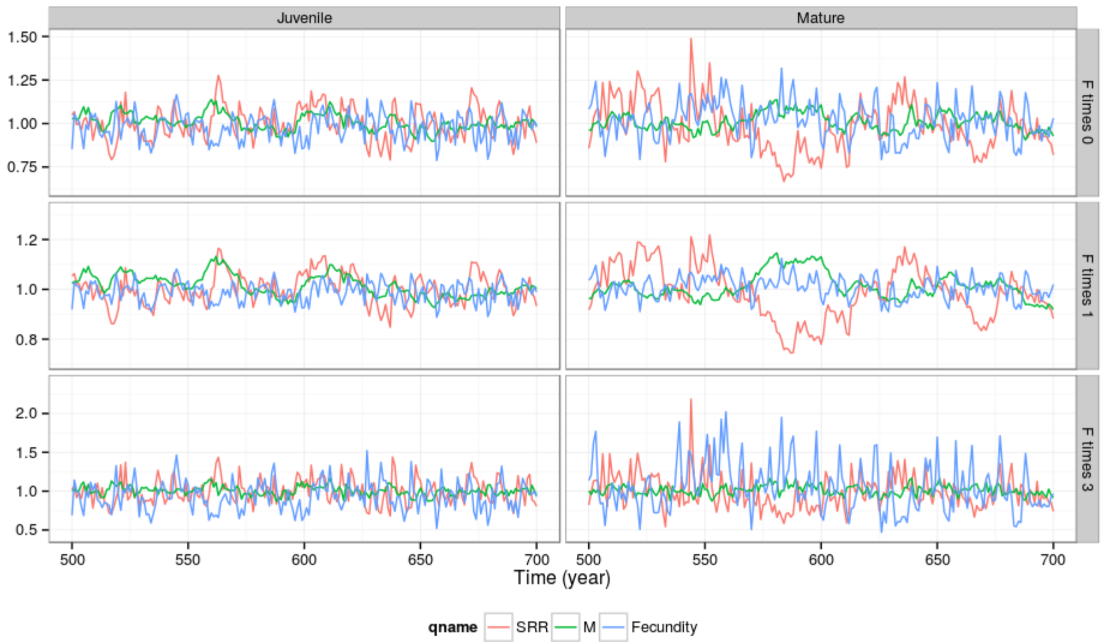

Figure 11: Time series of SSB for three levels of exploitation and two selection patterns.

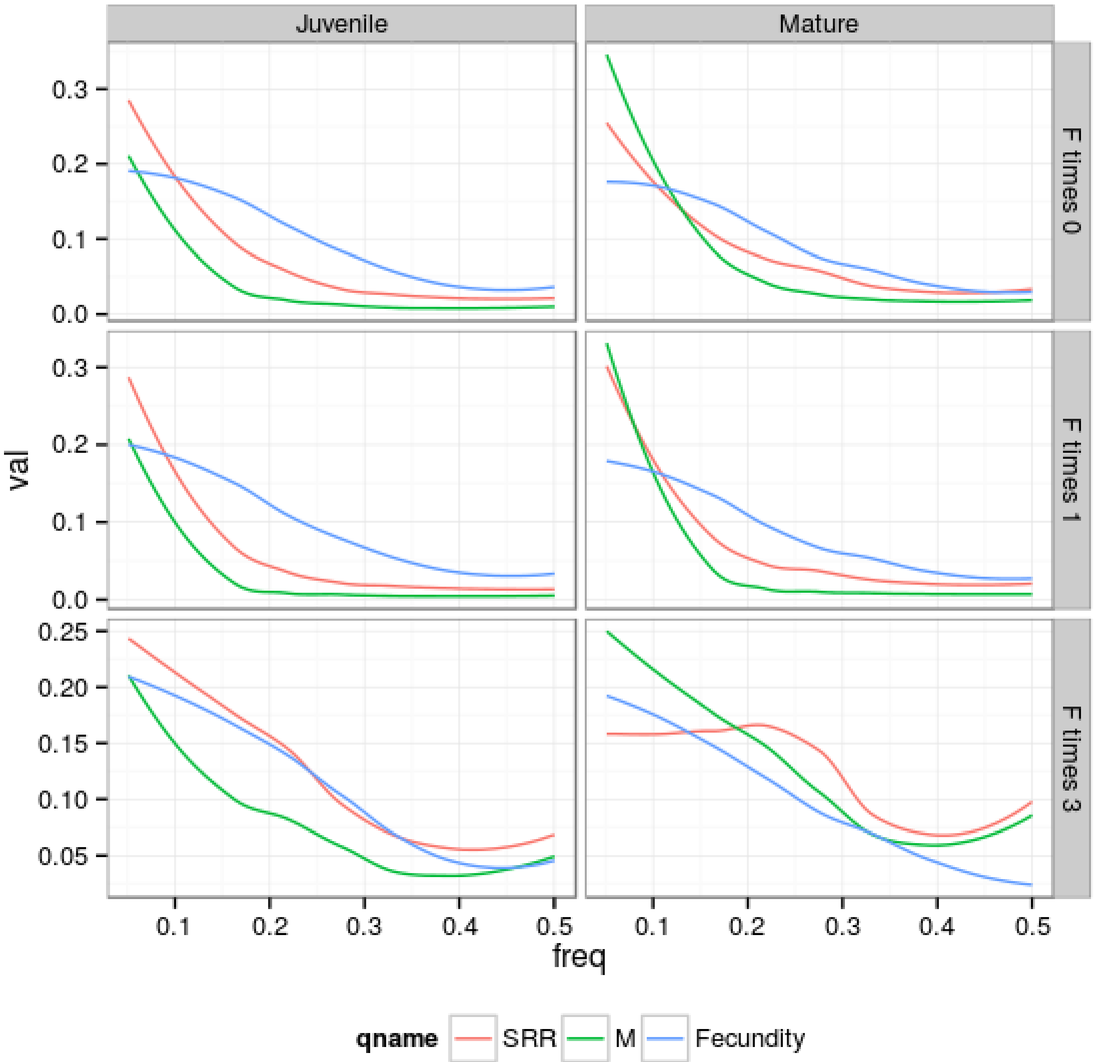

Figure 12: Spectra of SSB for three levels of exploitation and two selection patterns..

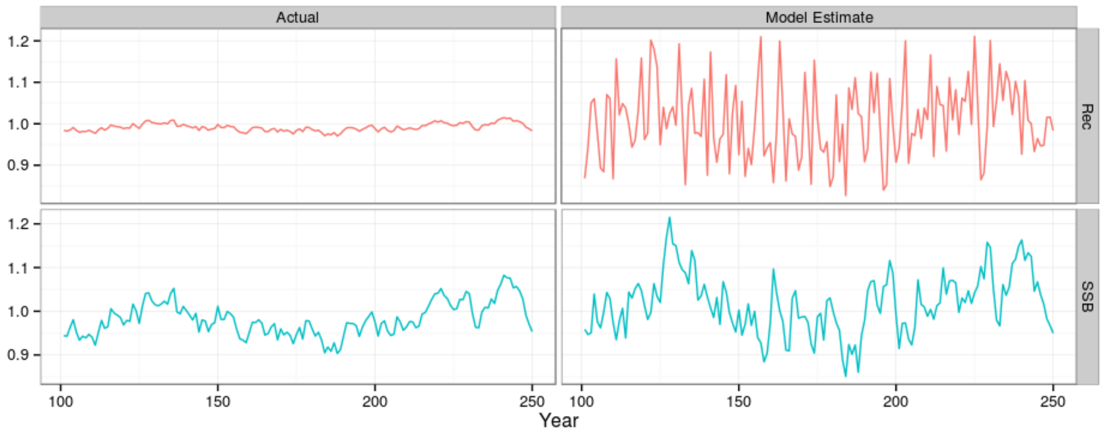

Figure 13: Model misspecification example, where in the simulated population natural mortality is a random variable, but is assumed to be constant at age in the virtual population analhysis used to estimate numbers-at-age.

Figure 14: An example of an MSE conducted using FLIfe to construct an Operating Model.

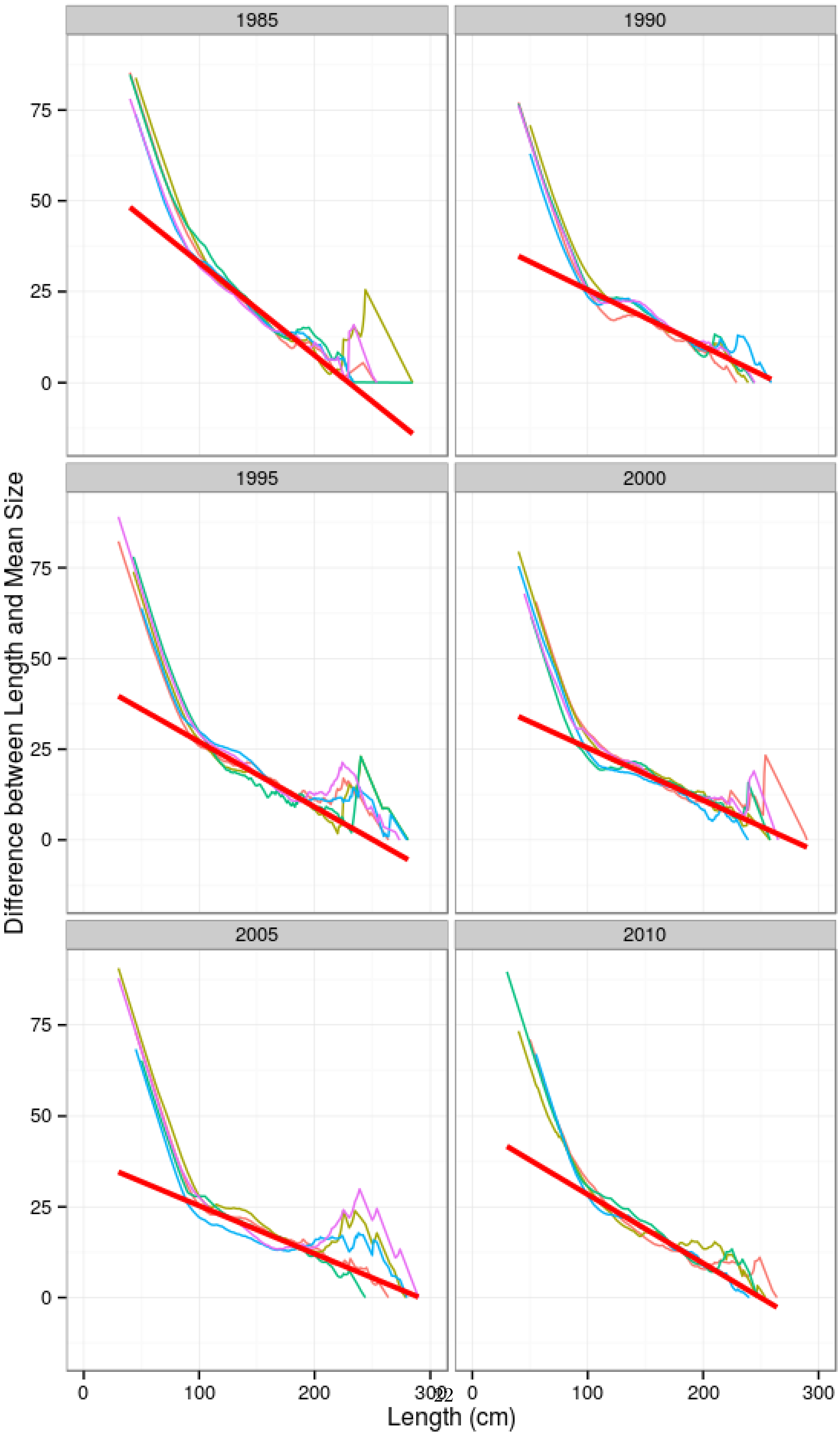

Figure 15: Powell-Wheatherall plots