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FLIFE: AN R PACKAGE FOR MODELLING LIFE HISTORY RELATIONSHIPS AND POPULATION DYNAMICS

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SUMMARY

FLife is an R package for modelling life history traits, biological processes such as density dependence and for simulating 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 for 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.

RÉSUMÉ

FLife est un package R servant à modéliser les caractéristiques du cycle vital, les processus biologiques, la dépendance de la densité et la simulation des séries temporelles. Les caractéristiques du cycle vital présentent de nombreux emplois dans l'évaluation des stocks. Elles sont utilisées afin de formuler un avis pour les stocks pauvres en données et afin de calculer des priors ou des valeurs fixes si des difficultés se posent pour estimer les paramètres de population des évaluations des stocks riches en données. Afin de garantir que l'avis est solide, des scénarios fondés sur les caractéristiques du cycle vital sont utilisés pour conditionner les modèles opérationnels lors de la réalisation de l'évaluation de la stratégie de gestion.

RESUMEN

FLife es un paquete R para la modelación de los rasgos del ciclo vital, los procesos biológicos, la dependencia de densidad y para la simulación de series temporales. Los rasgos del ciclo vital tienen muchos usos en las evaluaciones de stock. Se utilizan para proporcionar asesoramiento para stocks pobres en datos y para derivar distribuciones previas para valores fijos para parámetros de población difíciles de estimar en evaluaciones de stocks ricas en datos. Para garantizar que el asesoramiento es robusto, se utilizan escenarios basados en rasgos del ciclo vital para condicionar modelos operativos al realizar la evaluación de estrategias de ordenación.

KEYWORDS

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

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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. FLife is part of the FLR collection of tools for quantitative fisheries science, developed in the R language, that facilitates the construction of bio-economic simulation models of fisheries systems (Kell *et al.*, 2007), see http://www.flr-project.org/

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. Cortes *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.

Material and Methods

Data

An example dataset, teleost, is provided as part of the package; this includes values for 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_∞) 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).

Examples

The examples here are provided to illustrate the use of the package. The code full documentation can be found in the package documentation.

Equilibrium Dynamics

The first example simulates the equilibrium, i.e. the expected, dynamics for a population based on albacore and a fishery that selects mature fish. The equilibrium dynamics were derived by combining spawner-per-recruit and stock recruitment relationship.

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**.

Maximum sustainable Yield

Reference points such as MSY and B_{MSY} are found at found at the maxima of the production curves i.e. plots of the equilibrium yield against spawning stock biomass (SSB). These are shown in **Figure 4**

Population Growth Rate

The population growth rate at small population size (*r*) is equivalent to level of exploitation that would drive a population to extinction. Since a population cannot replenish itself if the harvest rate is greater than r. In fisheries terminology r corresponds to a limit harvest rate reference point and can be calculated from the Leslie Matrix (Leslie, 1945).

Global MSY

The maximum potential yield of a cohort is taken at a size (or age) where the gains due to growth are equal to the losses due to natural mortality. Although seldom possible to achieve in practice, calculating the length at which this would occurs (L_{opt}) provide a reference point for growth overfishing.

Density Dependence

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.

Production functions, were therefore calculated for density dependence natural mortality and fecundity and contrasted with the usual assumption made in stock assessment that density dependence only acts in recruitment **Figure 5**. Assuming density dependence in M or fecundity results in an increase in MSY, B_{MSY} and F_{MSY}

Next the response of a population to overfishing is evaluated in **Figure 6** and for rebuilding in **Figure 7**, 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.

Stochasticity

Stochasticity has important impacts on population dynamics and can be of various forms, e.g. depending on whether it varies due to annual changes in the environment or by cohort where conditions at an earlier age have an effect on later age classes. Examples of stochastic age effects are shown in **Figure 8** and cohort effects in **Figure 9**.

Next populations were simulated for three levels of fishing mortality (0, 1 and 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 10**. The spectral analysis performed for these time series **Figure 11** 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).

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 12**. The effect is to assume that recruitment is more variable than it actually is.

Management Strategy Evaluation

FLife can be used to conduct Management Stratagy Evaluation where a simulation model, i.e. operating model, is used to test for example a Harvest Control Rule (HCR). An empiriacl 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 13** shows an example MSE using an empirical HCR and an Operating Model generated using FLife.

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 14**).

Discussion

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 overexploitation (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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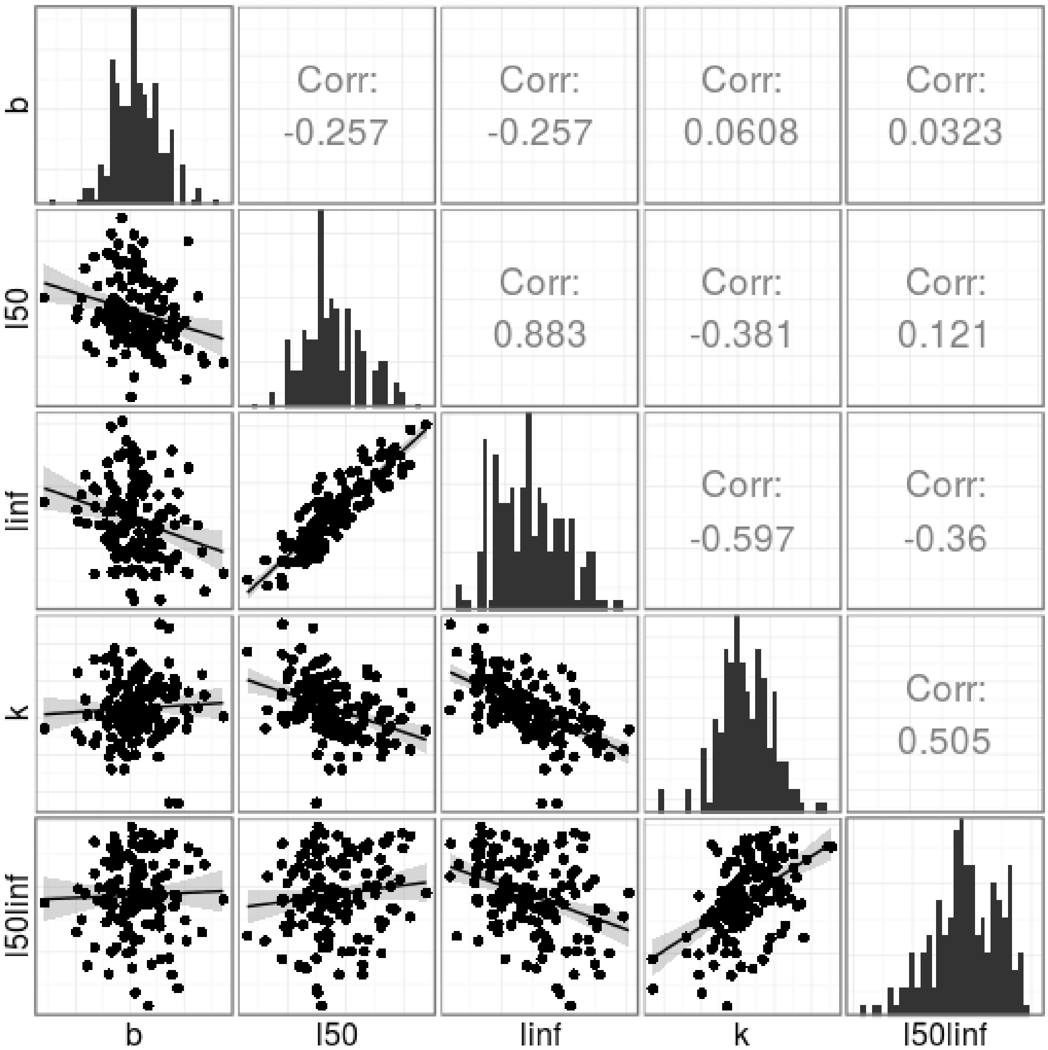

Figure 1. Life history parameters, distributions and relationships between them, all values are logged.

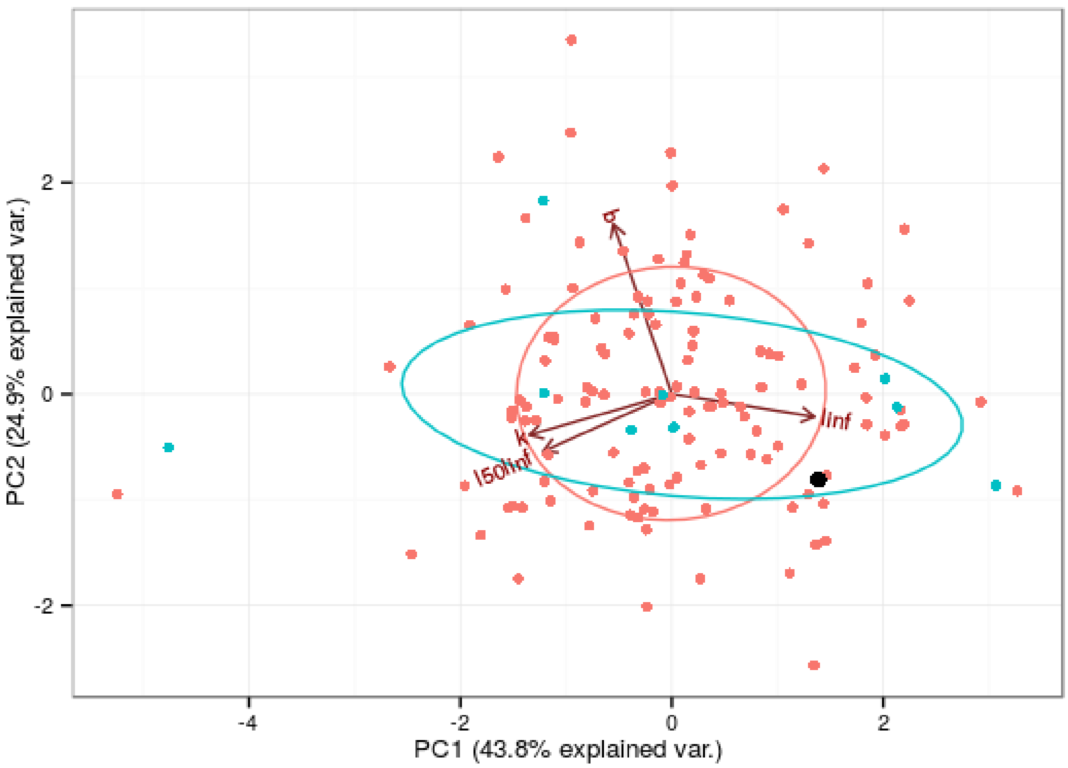

Figure 2. Life history data summarised using principle components analysis (PCA) the ellipses are the 95% normal probability densities, blue points are scrombidae and the black point is albacore. The first principal axis maximizes the variance, as reflected by its eigenvalue. The second component is orthogonal to the first and maximizes the remaining variance.

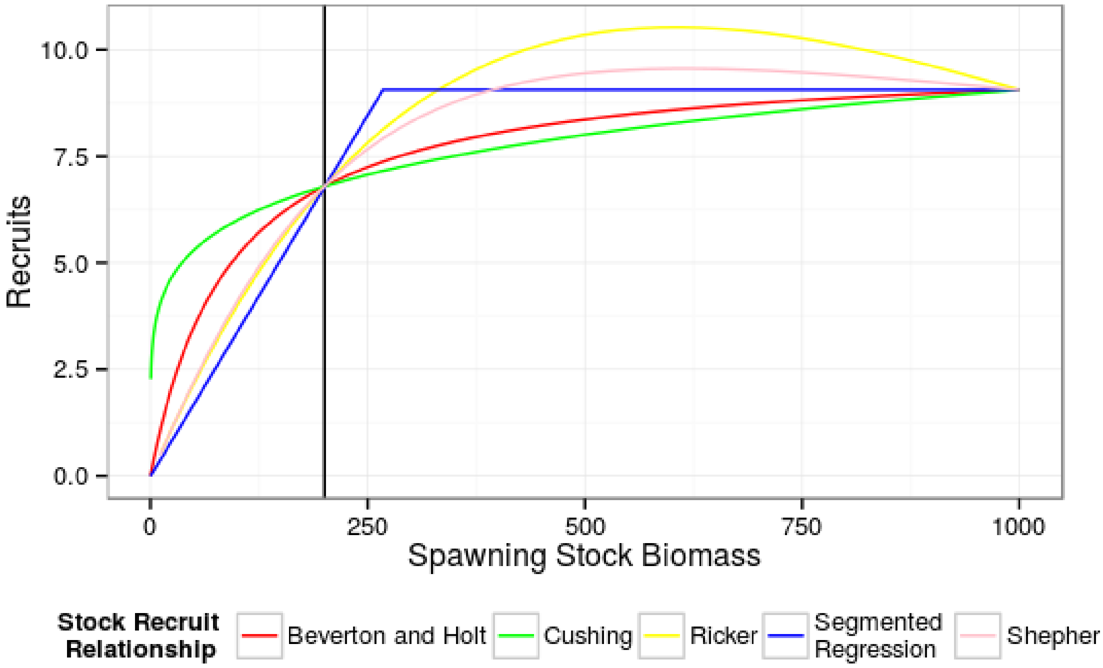

Figure 3. Stock recruitment relationships for a steepness of 0.75 and vigin biomass of 1000.

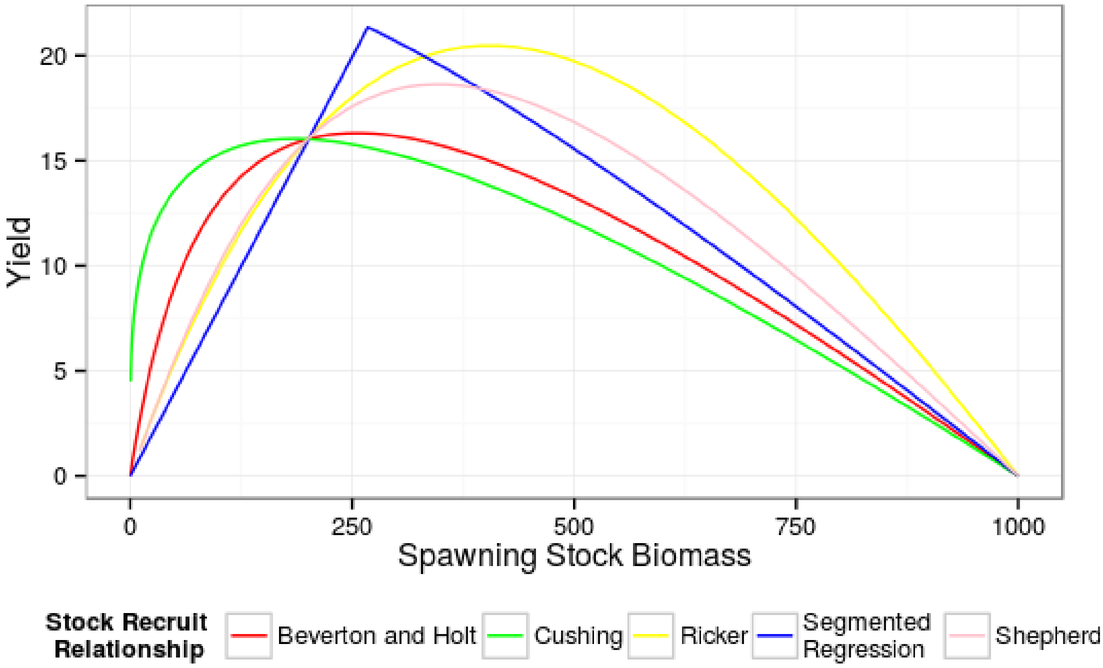

Figure 4. Production curves, Yield v SSB, for a steepness of 0.75 and vigin biomass of 1000.

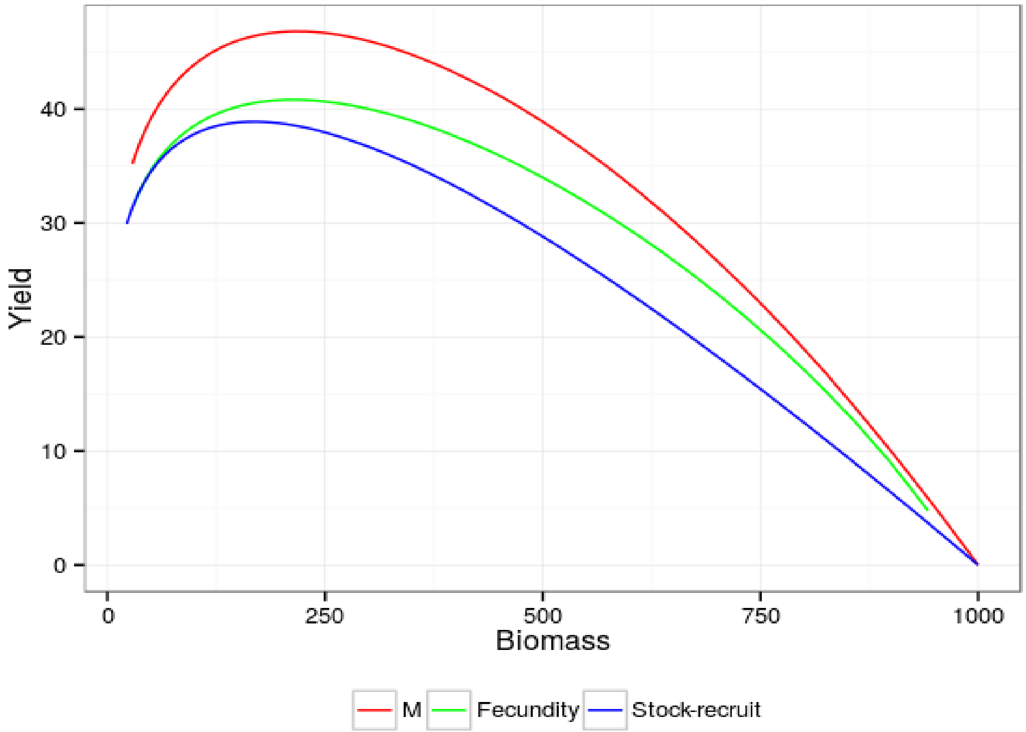

Figure 5. Production functions for density dependence in natural mortality, fecundity and stock recruitment.

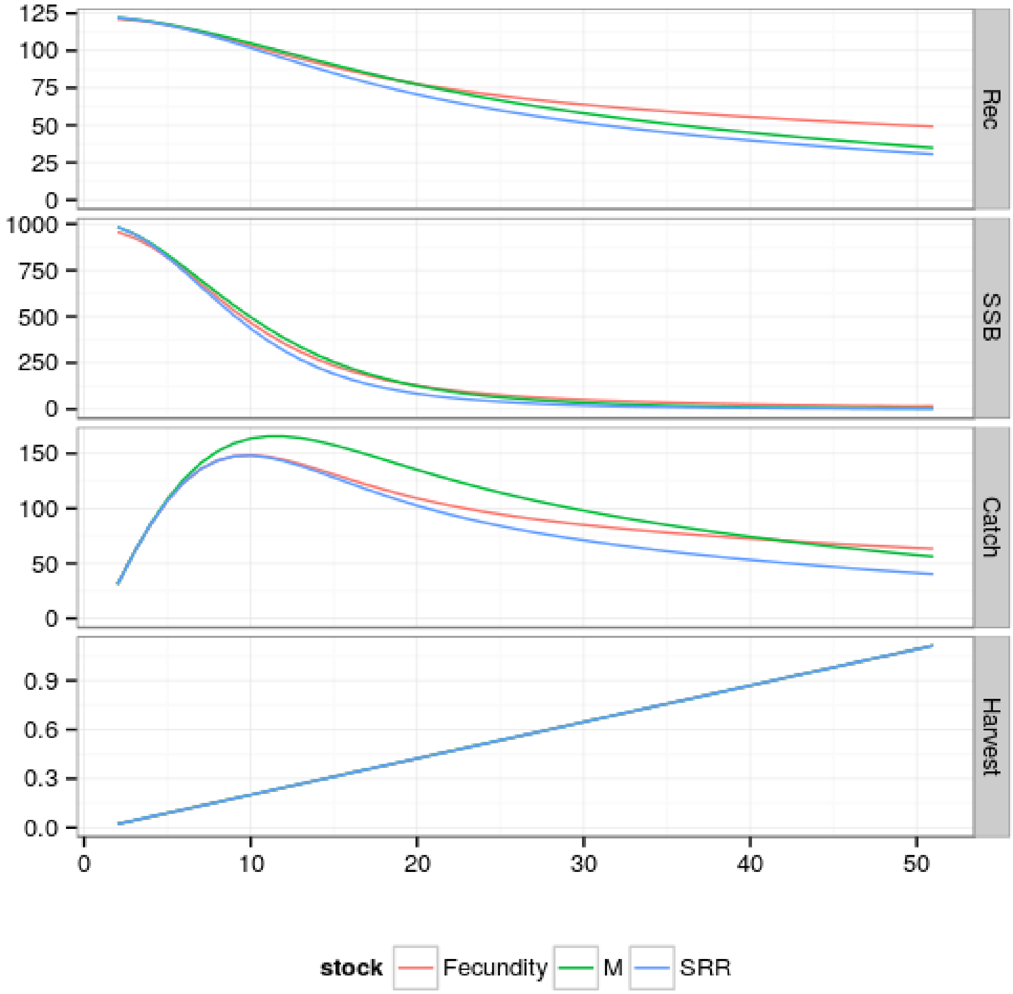

Figure 6. The response of a population to overfishing for density dependence in stock recruitment, natural mortality and fecundity.

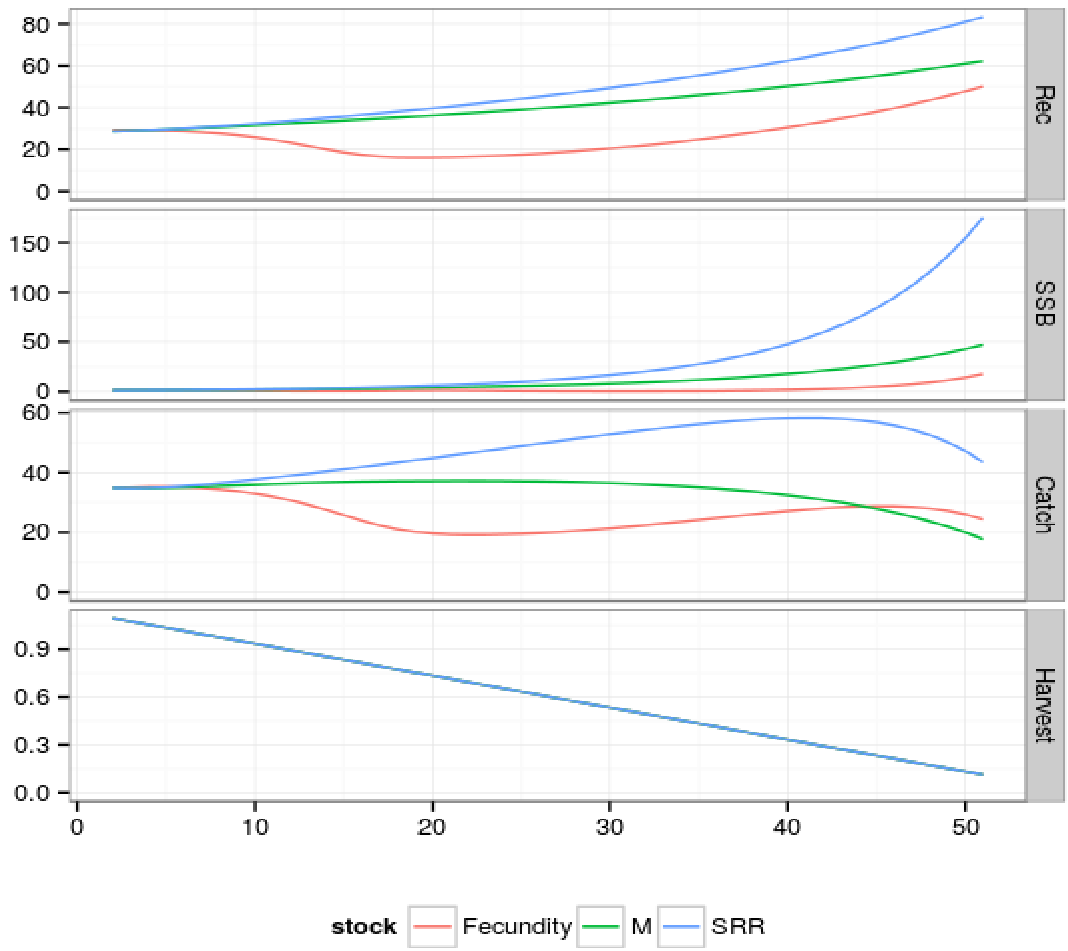

Figure 7. The response of a population to a reduction in fishing for density dependence in stock recruitment, natural mortality and fecundity.

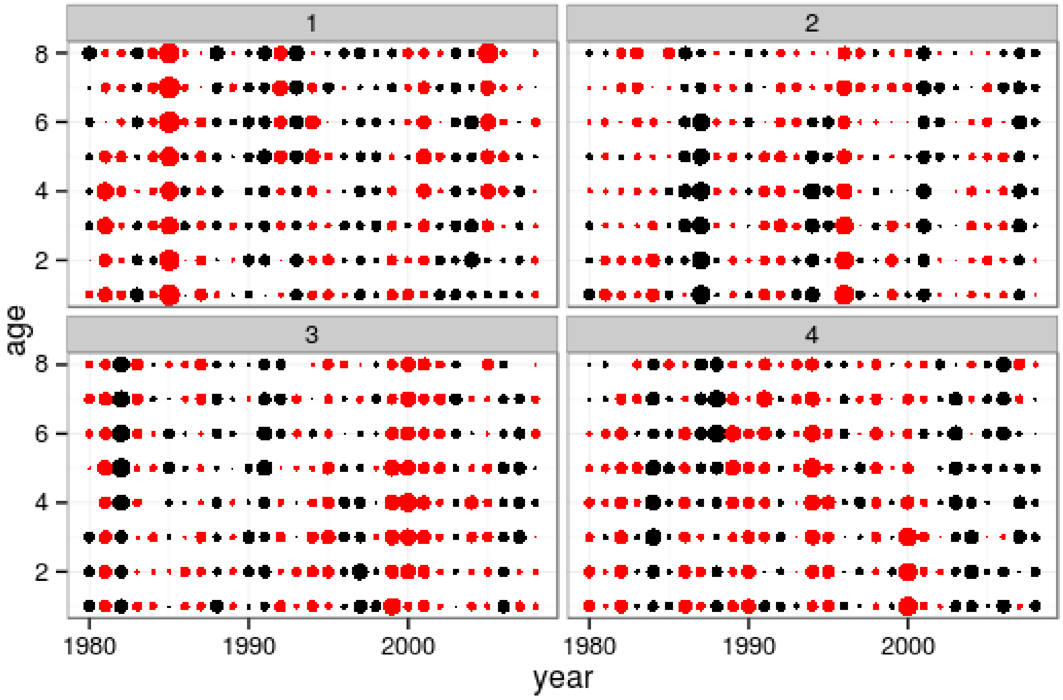

Figure 8. Stochastic age effects.

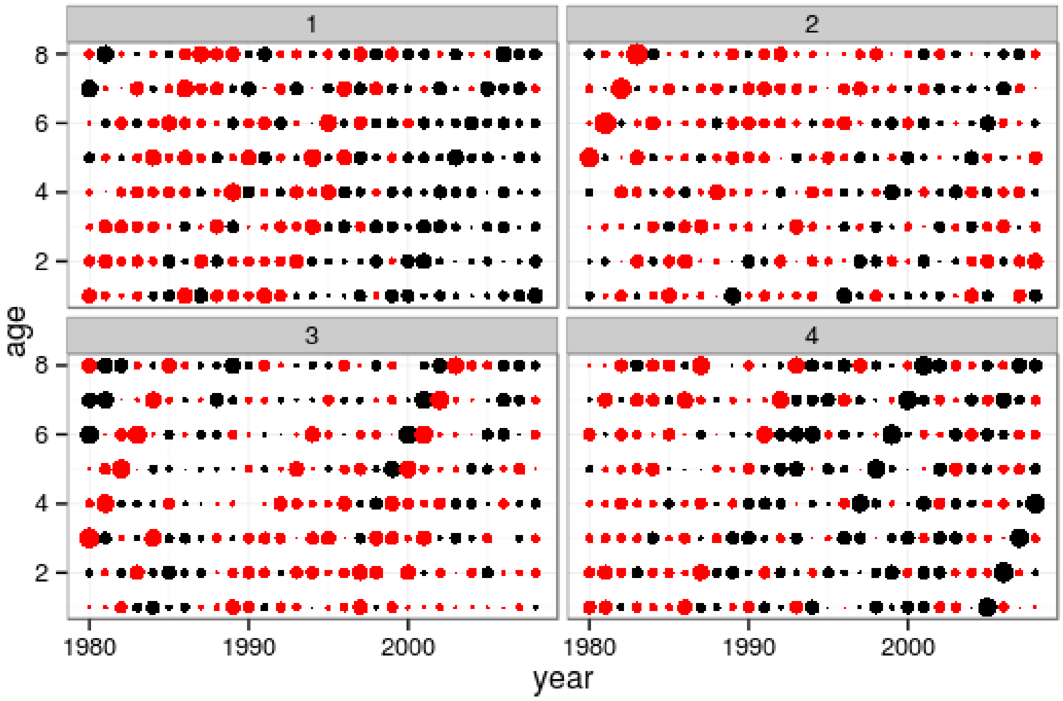

Figure 9. Stochastic cohort effects.

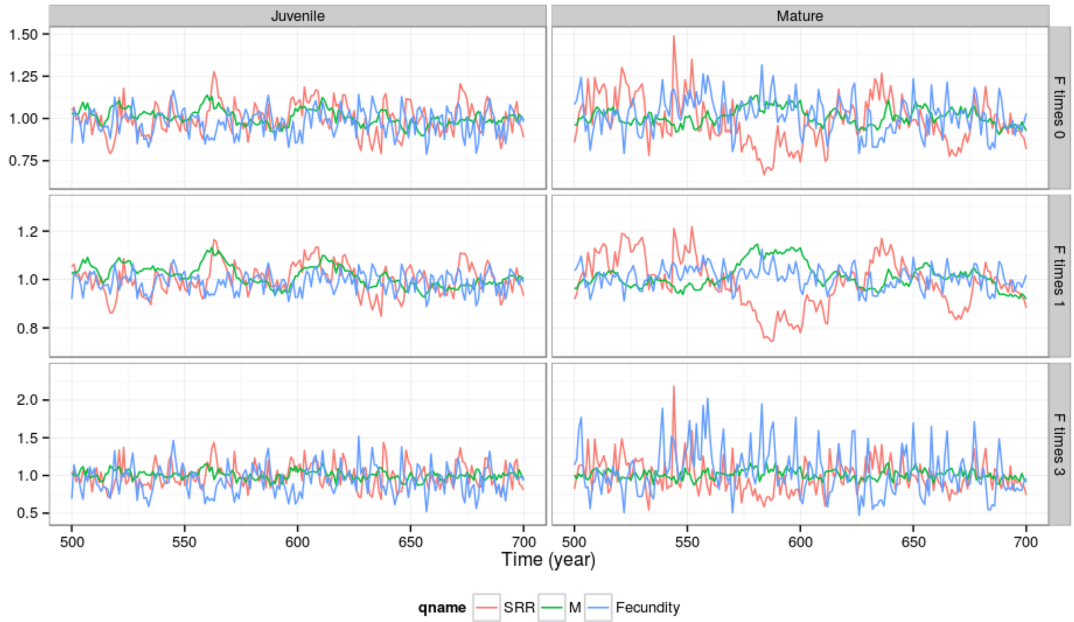

Figure 10. Time series of SSB

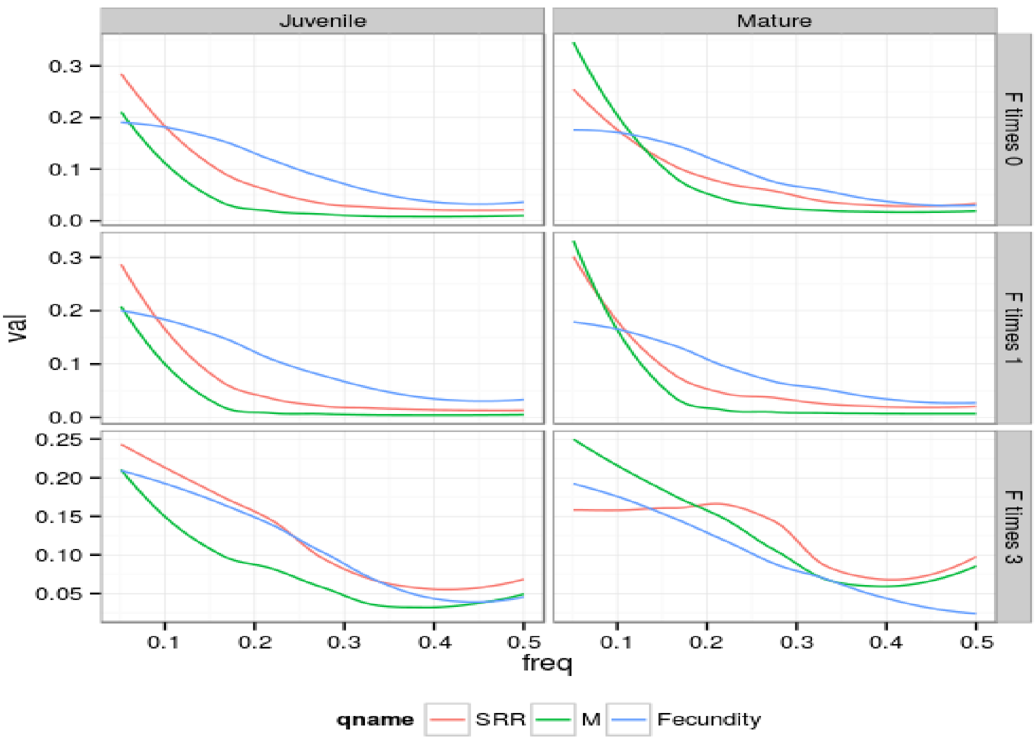

Figure 11. Spectral analysis.

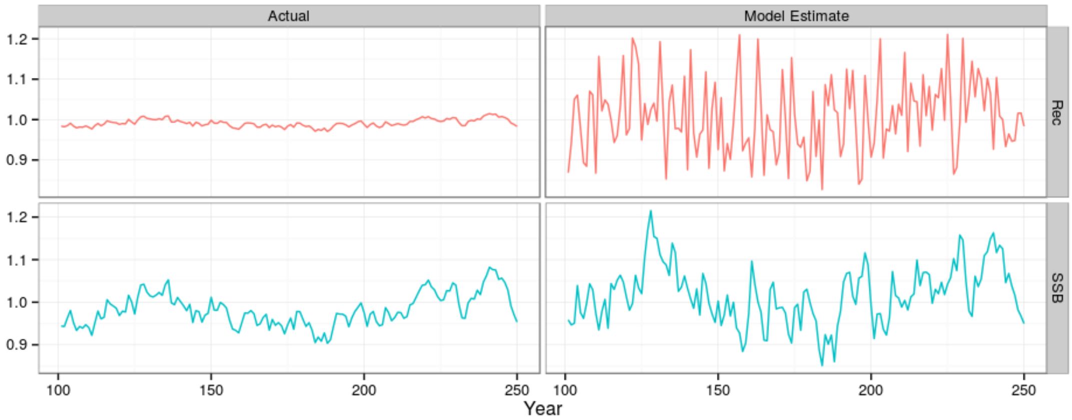

Figure 12. Time series from model misspecification example.

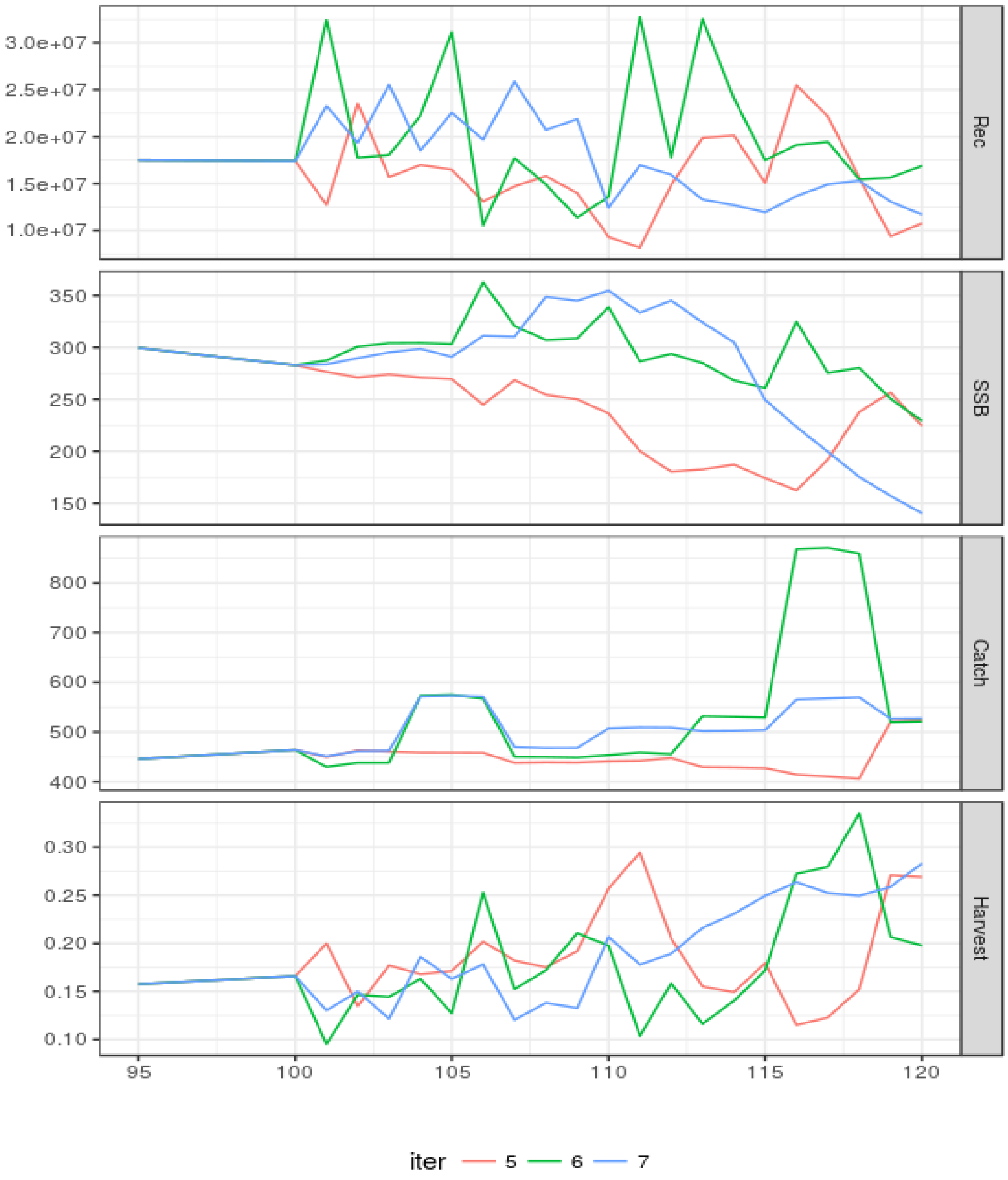

Figure 13. Results from an example MSE using an empirical HCR and an Operating Model.

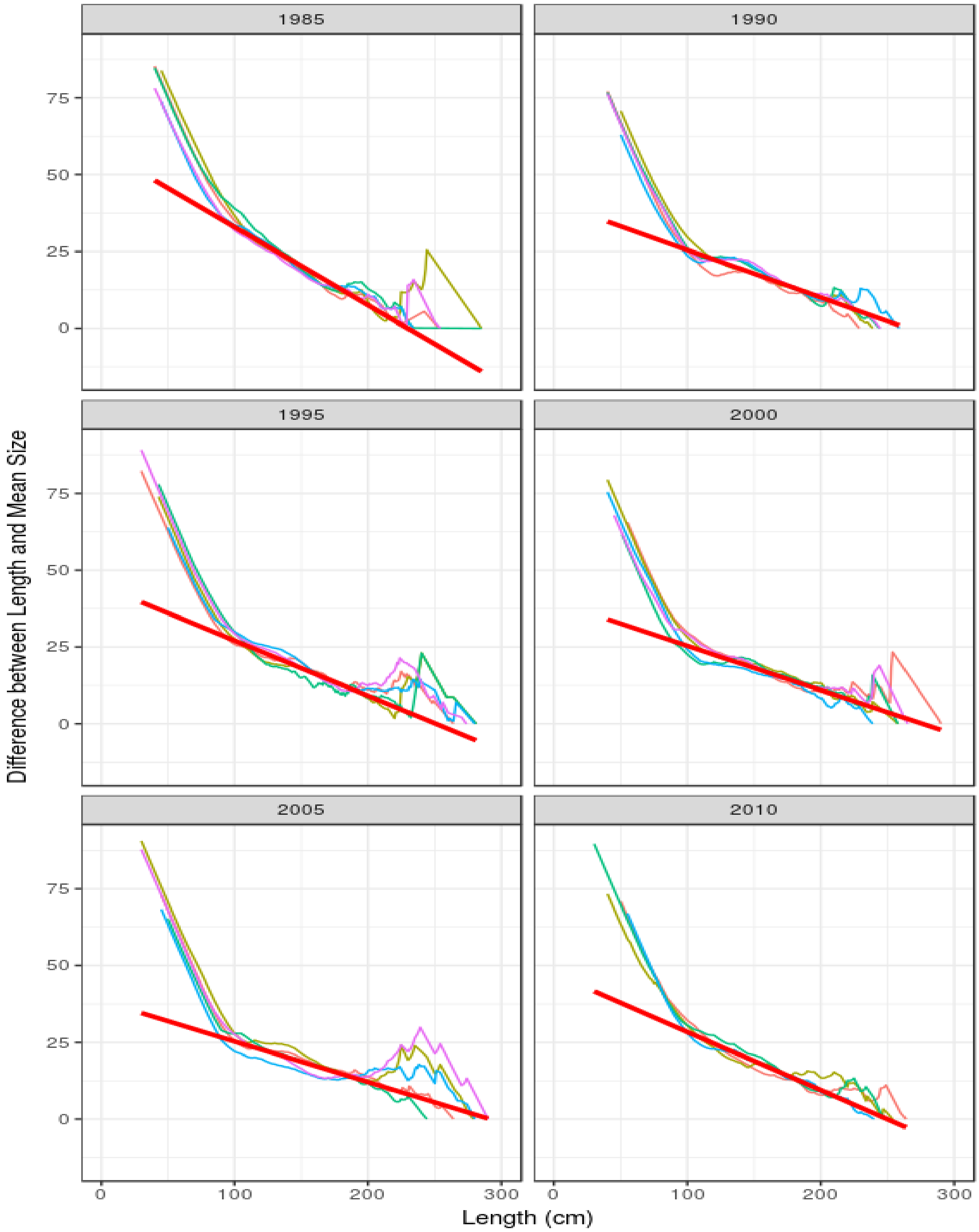

Figure 14. Powell-Wetherall plots