

**Overfishing or environmental change: Establishing the frequency of changes
in productivity of marine fish stocks**

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Abstract

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The relative importance of environmental conditions and stock abundance in determining the productivity of fish stocks has been a subject of an on-going debate. The controversy can be formulated as four competing hypotheses: 1) productivity is driven by fishing pressure, which affects abundance, subsequent recruitment; 2) productivity is regime-driven, with periods of good and bad productivity unrelated to abundance; 3) productivity is random from year to year and unrelated to abundance and is temporally uncorrelated; and 4) both stock abundance and regimes of good and bad conditions interact to affect productivity. The goals of this study are (1) to evaluate the support for each of these hypotheses by examining the productivity of marine species using a large number of stocks, and (2) to evaluate the same hypotheses with respect to recruitment. This project uses historic data from about 230 assessments from the RAM Legacy Database. Each of the four hypotheses will be formulated as alternative models, and the support for the

hypotheses evaluated using model selection via AIC_c and AIC_c weights. The specific models are (1) a biomass-dynamic model relating surplus production to stock size, (2) a regime shift model accounting for temporal shifts in productivity; (3) a model that assumes productivity to be random and (4) a biomass-dynamics model that has regime changes in productivity parameters. Then a similar analysis was performed on recruitment. I found that when considering production the Abundance Hypothesis best explains 18.3% of stocks, the Regimes Hypothesis 38.6%, the Mixed Hypothesis 30.5%, and the Random Hypothesis 12.6%. When considering recruitment, the stock-recruitment Hypothesis best explains 17% of stocks, the Regimes Hypothesis 45%, the Mixed Hypothesis 21% and the Random Hypothesis 18%. If the production of a stock is determined by periodic regimes and the assessment of the stock does not recognize the shift in regimes, then the management system with respect to sustainable yield is incorrect. I do not suggest that we should abandon the goal of maintaining fish stocks at high abundance. Rather I simply show that it is unlikely that such policies will assure high and sustained recruitment. Thus, future work should identify and evaluate management strategies that would be robust to irregular jumps in average productivity.

KEYWORDS: Fish production, Productivity regime, Fishing, Environmental Change, Recruitment.

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Introduction

Many marine fish stocks exhibit pronounced fluctuations in abundance, potentially due to a combination of anthropogenic effects of fishing, bottom-up or top-down environmental controls, and interactive effects between the two. The productivity of fish stocks is shaped by birth, mortality, growth rates and migrations (Conover, 1992). Moreover, population productivity can shift from one stable state to another (Scheffer et al., 2009) and these regime shifts can range from short- to long-term, and are thought to be due to environmental shifts (Bakun, 2004). Fishing also impacts population abundance and potentially recruitment (Hsieh et al., 2006). The combined effect of fishing and environment can amplify population productivity (Hsieh et al., 2008).

The relative importance of natural environmental drivers and fishing on the dynamics of exploited stocks has long been debated. A well-known case is the Thompson-Burkenroad debate, where Thompson argued that the Pacific halibut population was largely driven by fishing (Thompson and Bell, 1934, Thompson, 1950) while Burkenroad (1948) emphasized the role of environment. There is a large body of literature relating fluctuations in abundance of exploited marine species to environmental variables (e.g., Cushing, 1982; Genner et al., 2004; Miller et al., 2011). Many studies have well established that population abundance may be driven by long-term environmental fluctuations (Fogarty et al., 1991; Walters and Parma, 1996; Letve et al., 2002; Hsieh et al., 2009). Environmental impacts are usually revealed post hoc through correlation analyses, which often reveal patterns of population variability on both inter-annual and

decadal time scales. These patterns can be caused by seasonal, climatic, inter-annual events such as the El Niño Southern Oscillation (ENSO) that last from 6 to 18 months, or multi-decadal climate regimes such as the Pacific Decadal Oscillation (PDO), lasting between 10 to 30 years (Mantua et al., 1997; Zhang et al., 1997). Baumgartner et al., (1992) found that anchovies and sardines vary over period of approximately 60 years. In the North Pacific, important ecosystem changes have been associated with PDO (Francis et al., 1998). Salmon productivity in Alaska was positively correlated with warm PDO phases, whereas salmon productivity in California, Oregon and Washington states was negatively correlated, with the opposite relationship observed during cold PDO phases (Hare, 1996; Hare et al., 1999). Some studies revealed that clupeid productivity was modulated by the PDO and inter-annual variations like ENSO (Chavez et al., 2003). Many other studies have identified that shifts in environmental factors are linked with fluctuations in fish abundance and population dynamics (Hare and Mantua, 2000; Mueter et al., 2007). These patterns reflect environmental impacts on gonadal development, maturity, egg viability, recruitment survival and growth (Drinkwater et al., 2010). Many studies (e.g. Megrey et al. 1996; Caley et al., 1996; Wilderbuer et al., 2002; Ciannelli et al., 2005) have focused on these large-scale variations at an ecosystem level as they need to be considered for the management of marine resources.

The alternative perspective is that fishing pressure primarily drives fish abundance and that fish abundance determines recruitment and productivity. Previous studies show that abundance is correlated with fishing pressure and not with environmental variables (Jonzén et al., 2001; Hsieh et al., 2006). Thus, these authors argued that variability present in fish stocks does not result from direct environmental tracking, but mainly from

fishing pressure (Anderson et al., 2008). Fluctuations in population abundance can increase or dampen depending on life history traits and harvest strategies, depending on age-structure dynamics (Wikstrom et al., 2011). Moreover, fishing may impact population abundance and recruitment through recruitment overfishing or through the stock-recruit relationship by selecting older individuals with higher fecundity. In some cases, fishing can make a population more sensitive to environmental shifts. For example, when fishing truncates the age-structure of a population it can increase temporal variability (Botsford et al., 2011).

The quantitative analysis of the importance of abundance and environment in determining productivity can be traced to competing analysis in the 1990s. Myers and Barrowman (1996) investigated the relationship between recruitment and spawning stock biomass. Using 364 times series, they found that when there is a sufficient range in spawner abundance, the highest recruitments occur when spawner abundance is high; the lowest recruitments occur when spawner abundance is low; and the mean recruitment is higher if spawner abundance is above the median rather than below it. In response to this paper, Gilbert (1997) claimed that recruitment followed different mean values during successive periods. Favorable environmental conditions for a species will induce a good recruitment regime and this will, in turn, lead to high abundance. Unfavorable environmental conditions will induce a bad recruitment regime and this will lead to low abundance. The overall data would show periods of high abundance and high recruitment and periods of low abundance and low recruitment. Gilbert (1997) argued that these data would be mistaken for an impact of abundance on recruitment, when it was in fact the impact of recruitment on abundance. A central component of Gilbert's hypothesis is that

periods of good and weak recruitment must persist for a sufficient period of time to create the appearance of a stock-recruit relationship via the adjustment of spawning stock to shifting recruitment levels.

To date it has been a major challenge to disentangle the relative importance of each driver on population dynamics and there has been no quantitative evaluation of the frequency with which fish stock productivity is abundance-driven or environmentally-driven. I address these issues through a meta-analysis using worldwide stock assessment datasets. For the surplus production index I pose four competing hypotheses (1) production comes in alternating regimes of high and low production, (2) production is related to population abundance, (3) production is related to population abundance with the maximum sustainable yield changing between regimes and (4) production is random and not explained either by regime changes or population abundance. Our fundamental question is how frequently does each hypothesis provide the best explanation for the changes in observed production. To answer that question I use the Akaike Information Criteria corrected (AICc) in two ways, either a “winner takes all” approach in which I determine for each stock which hypothesis had the highest support from the data, or a “relative support” approach in which I calculate the relative support for each hypothesis for each stock. For the recruitment index, I identify a range of similar hypotheses regarding the relationship between spawning biomass, regime changes, and recruitment, and then evaluate the support for each hypothesis using AICc. Then I tested the model selection for both methods using simulated data.

**Chapter I: Frequency and intensity of productivity regime
shifts in marine fish stocks**

Abstract

Fish stocks fluctuate both in abundance and productivity (net population increase), and there are many examples demonstrating that productivity increased or decreased due to changes in abundance caused by fishing and alternatively where productivity shifted between low and high regimes, entirely unrelated to abundance. While shifts in productivity have been described, the frequency and intensity of these shifts in productivity regimes have not previously been assessed. I use a data base of trends in harvest and abundance of 230 fish stocks to evaluate, for the first time, the proportion of fish stocks whose productivity is primarily related to abundance vs. those who appear to manifest regimes of high or low productivity. I evaluated the statistical support for four hypotheses: (1) the Abundance Hypothesis, where production is always related to population abundance, (2) the Regime Hypothesis, where production shifts irregularly between regimes that are unrelated to abundance, (3) the Mixed Hypothesis, where, even though production is related to population abundance, there are irregular changes in this relationship, and (4) the Random Hypothesis, where production is random from year to year. This paper found that the Abundance Hypothesis best explains 18.3% of stocks, the Regime Hypothesis 38.6%, the Mixed Hypothesis 30.5%, and the Random Hypothesis 12.6%. Fisheries management agencies need to recognize that irregular changes in productivity are common and that harvest regulation and management targets may need to be adjusted whenever productivity changes.

Introduction

Modern fisheries management is predicated on there being a repeatable relationship between stock size and the long term yield of fish stocks (Beddington et al., 2007) and that population production (and thus, long term yield) will be maximized by holding stocks within a specific range of population sizes. In the U.S. and some other developed countries, stocks are classified as overfished if their abundance falls below this range of population sizes and fishing pressure is reduced to rebuild stocks to levels that are thought to produce long term maximum sustainable yield (Murawski, 2010). Many other national and international fishery management organizations have similar goals. However, some have argued that fish stock production is primarily or even totally determined by irregular changes in the environment rather than population size (Burkenroad, 1946; Burkenroad, 1953; Gilbert, 1997). Despite the rise of non-equilibrium or multiple-equilibrium perspectives in ecology (Wu and Louks, 1995), fisheries management is still based largely on a “Balance of Nature” worldview in which inter-annual fluctuations of vital rates are centered on a stationary mean and populations vary around long-term equilibrium under a controlled harvest rate policy.

This debate has significant consequences for fisheries management. If the production of fish stocks depends upon population abundance, then rebuilding stocks currently at low abundance will result in higher sustainable harvests. If however, production is environmentally-driven, then the harvest foregone to rebuild stocks is lost. There are

often other reasons that larger stock sizes and low fishing pressure provide economic or ecological benefits(Hilborn, 2007), but a major argument for rebuilding depleted stocks has been the promise of higher sustained yield in the future.

From 1950 to the early 1990s there was considerable debate about the relationship between population size and resulting recruitment of young fish. Many argued that there was little relationship between the two, and fishing stocks down to low abundance did not decrease the number of new fish subsequently entering the population (Gulland, 1983). In the 1990s, Myers used several hundred data sets of stock size and recruitment to show there was a statistical relationship between the two – when abundance was very low, lower recruitment was found (Myers et al., 1994). Gilbert (1997) challenged Myers conclusions and argued that the apparent relationship between stock size and recruitment was often spurious. Recruitment shifting between high and low regimes would result in high stock size during the periods of high recruitment, and low stock size during periods of low recruitment. Gilbert noted that, recruitment dropped to low levels while stock sizes were high in many of Myers data sets, and the decline in stock size resulted from the recruitment declines rather than recruitment declining after stock size declined.

The production of sustainable yield depends not only upon recruitment, but also somatic growth and survival from natural mortality. To understand the comparative importance of population size and environment in determining production I need to look at all three processes. Surplus production, the net change in biomass from one year to the next in the absence of fishing, incorporates all three processes and can easily be calculated from available fish stock assessments (Hilborn, 2001). These data are model outputs not

observed data, they come from stock assessments and are the results of population model fitting. Thus, results from this analysis need to be interpreted with caution.

Worm et al. (2009) assembled a data base with the history of abundance and catch from published assessments that now includes 355 stocks (Ricard et al., 2011). Specific information on each stock and criteria for exclusion of some stocks from this analysis is contained in the materials and methods section. From these data, there is sufficient information for 230 stocks to calculate the history of surplus production in each year, defined as the change in total biomass plus the catch for the year. I pose four competing hypotheses (1) production comes in alternating regimes of high and low production, (2) production is related to population abundance, (3) production is related to population abundance with the maximum sustainable yield changing between regimes and (4) production is random and not explained either by regime changes or population abundance. Our fundamental question is how frequently does each hypothesis provide the best explanation for the changes in observed production.

For each hypothesis I calculated the likelihood of the observed data given the associated model (see materials and methods). The most widely used method for evaluating the support data provide for multiple competing hypotheses is the Akaike Information Criterion for small samples (AICc) (Burnham and Anderson, 2002; Hobbs and Hilborn, 2006). I used the AICc in two ways, either a “winner takes all” approach in which I determine for each stock which hypothesis had the highest support from the data, or a “relative support” approach in which I calculated the relative support for each hypothesis for each stock. I also tested our methods by simulating data where the true underlying

determinant of production was productivity regimes, population abundance, a mixed effect, or was random.

Materials and Methods

Data and choice of stocks

Time series of biomass, catch and fishing rate were extracted from the RAM Legacy Stock Assessment Database (Ricard et al., 2011) for 355 stocks on December 10th 2010. Only 279 stocks had no missing data points within the time series, thus were initially selected for analysis. A total of 49 of the 279 data sets were excluded from the analysis for the following reasons; the units of biomass and catch were not comparable for 8 stocks, 24 stocks had a time series of less than 20 years and for 17 stocks the estimated stock total biomass was the result of a deterministic model and was by definition a function of stock biomass. The analysis was thus conducted with 230 stocks.

Alternative models considered

Surplus production is defined as the net change in biomass, plus harvest (Hilborn, 2001).

$$1) S_t = B_{t+1} - B_t + C_t$$

where S_t is the surplus production during year t ; B_t is the stock total biomass at time t ; and C_t is the catch removed between times t and $t+1$.

To test if surplus production is related to biomass, a Fox surplus production model (Fox, 1975) was fitted to the data. For the purpose of this study, I assumed that most stocks reach maximum yield at lower than half carrying capacity (e.g. Yoshimoto and Clarke,

1993). Using the Fox model also simplifies the estimation process. The Fox model (Quinn and Deriso, 1999) can be written as.

$$2) \quad \hat{S}_t = -em \left(\frac{B_t}{B_\infty} \right) \ln \left(\frac{B_t}{B_\infty} \right)$$

where \hat{S}_t is the predicted surplus production during year t ; B_∞ is the carrying capacity; m is the maximum sustainable yield and e is the Euler's number.

Productivity regimes are defined here as the change in surplus production from one state to another. For the productivity regime model, the challenge is to estimate the years when the productivity regime shifted (called break-points). I used the sequential t-test analysis of regime shifts (STARS) (Rodionov, 2004; Rodionov and Overland, 2005), which has been widely used in similar applications (A'mar, 2009). The STARS method estimates a series of break points that mark the first year of each regime. The predicted surplus production for each year within regime i is simply the average surplus production during that regime.

$$3) \quad \bar{S}_i = \frac{\sum_{j=f_i}^{f_{i+1}-1} S_j}{f_{i+1} - f_i}$$

where f_i is the first year of regime i ; \bar{S}_i is the predicted average surplus production during regime i ; S_j is the surplus production in year j .

The mixed model combines the effect of the biomass on the stock and productivity regime. For the mixed model, the estimated years at which break-points happened were

determined as for the Productivity regime model. To test if surplus production is related to biomass and productivity regimes, two alternative regime-varying surplus production models were fitted to the data. The first model assumes that carrying capacity is regime-independent, but maximum sustainable yield is regime-dependent thus the exploitation rate that produces maximum sustainable yield changes between regimes (Equation 4). The second model assumes that both carrying capacity and maximum sustainable yield are regime dependent (Equation 5).

$$4) \hat{S}_t = -em_i \left(\frac{B_t}{B_\infty} \right) \ln \left(\frac{B_t}{B_\infty} \right)$$

m_i is the maximum sustainable yield during regime i ;

$$5) \hat{S}_t = -em_i \left(\frac{B_t}{B_{\infty,i}} \right) \ln \left(\frac{B_t}{B_{\infty,i}} \right)$$

$B_{\infty,i}$ is the carrying capacity during regime i ;

The random production model assumes that the variability in the data is neither explained by fishing nor by changes in productivity regimes so the predicted surplus production in any year is simply the average surplus production over all years.

$$6) \hat{S}_t = \frac{\sum_{t=1}^y S_t}{y}$$

Parameter estimation

For all models, the set of parameters that maximizes the likelihood was found by ignoring observation error in measuring biomass and catch, and assuming process error.

$$7) \quad L(S | \hat{\theta}) = L = \prod_t \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(S_t - \hat{S}_t)^2}{2\sigma^2}}$$

where \hat{S}_t is the predicted surplus production under each model for year t ; σ is the standard deviation of the surplus production about the model-prediction; $\hat{\theta}$ are the parameters for each model.

The parameters (B_∞ , m , and σ) of the Fox model were estimated by nonlinear function minimization in AD Model Builder (ADMB) v10.1 (<http://admb-project.org/>).

Parameters of the productivity regime model (\bar{S}_i , f_i , σ) were estimated using a sequential t-test analysis in R with two “tuning parameters” used as inputs: the minimum duration of a regime, known as “cut-off-length” and the significance level for the t-tests. I used a cut-off-length of 10 years and the significance level for the t-test of 0.1 (e.g. Rodionov and Overland, 2005). Thus, the shifts are more likely to be at least a decade long although the algorithm often chose shorter regimes at the beginning and end of the time series. Once the break points were determined, the average production during each regime was calculated and the value of σ determined analytically.

The parameters ($B_{\infty}/B_{\infty,i}$, m_i , and σ) of the Mixed model were estimated by nonlinear function minimization in ADMB v10.1 using the regime change break points estimated in the regime change model.

For the random model, the average production was calculated from equation 5 and σ was determined analytically.

Model selection

The most parsimonious of the four models was identified using the Akaike Information Criterion corrected for small sample size (AICc) (Burnham and Anderson, 2002). AICc weights (Burnham and Anderson, 2002) were also calculated and can be interpreted as the relative support of data for each model (Hobbs and Hilborn, 2006). The AICc was calculated as:

$$8) \quad AICc = -2 \log(L) + 2k + \frac{2k(k+1)}{N-k-1}$$

where L is the likelihood of the data given the parameters; k is the number of parameters; N is the number of data points.

The preferred model is the one with the lowest AICc.

The Fox model has three parameters (m , B_{∞} and σ). The number of parameters in the Productivity regime model varies, with one parameter for the average surplus production during each regime, one parameter for each breakpoint and the value of σ . The mixed model has 1 parameter for each break point, 1 parameter for each m , and two additional parameters B_{∞} and σ . The null model has two parameters, the average surplus

production and σ . To calculate the AICc weights, I first calculate the difference between the best model and each model i (Δ_i).

$$9) \Delta_i = AICc_i - \min(AICc)$$

and then the weights for each model (w_i) were calculated from the Δ_i .

$$10) w_i = \frac{e^{-0.5\Delta_i}}{\sum_{j=1}^4 e^{-0.5\Delta_j}}$$

Testing of the methods

To verify the reliability of the model selection method and correct for expected misclassification, four simulation-based evaluations were run using data generated from the biomass, the productivity regime, the mixed and the null model and then subject to evaluation using each of these four models. The simulation procedure is described below using process errors.

Data sets were generated for each of the four hypotheses. For each simulation the parameters were drawn from stocks that were best explained by the particular underlying hypothesis. Thus, I selected data for 37 stocks for the biomass model, 95 stocks for the productivity regime model, 33 for the random model and 65 for the mixed model. Then, 20 stochastic replicate data sets were generated for each stock. The initial biomass of each simulation was the value of the initial biomass in the first year of the data set. The exploitation rate U_t for every year was calculated from the data used in our analysis.

$$11) U_t = \frac{C_t}{B_t}$$

where U_t is the exploitation rate at time t.

The biomass was simulated for the Fox model using equation 12.

$$12) \tilde{B}_{t+1} = \tilde{B}_t + \left(-em \left(\frac{\tilde{B}_t}{B_\infty} \right) \ln \left(\frac{\tilde{B}_t}{B_\infty} \right) + \tilde{\varepsilon}_t \right) - \left(\tilde{B}_t U_t \right)$$

where \tilde{B}_{t+1} is the simulated biomass at time $t+1$; the biomass is set to always be positive ; m is the maximum sustainable yield obtained by fitting the Fox model; B_∞ is the carrying capacity obtained by fitting the Fox model; $\tilde{\varepsilon}$ is normal process error; $\tilde{\varepsilon} \sim N(0, \sigma)$; σ is the parameter obtain by fitting the Fox model.

The biomass for the productivity regime and random models was calculated from equation 13.

$$13) \begin{aligned} \tilde{B}_{t+1} &= \tilde{B}_t + \left(\hat{S}_t + \tilde{\varepsilon}_t \right) - \tilde{C}_t \\ \tilde{C}_t &= \tilde{B}_t U_t \end{aligned}$$

where \hat{S}_t is the mean regime in which year t occurs obtained by fitting the productivity regime model or random model.

The biomass was simulated for the mixed model using equation 14

$$14) \tilde{B}_{t+1} = \tilde{B}_t + \left(-em_i \left(\frac{\tilde{B}_t}{B_\infty} \right) \ln \left(\frac{\tilde{B}_t}{B_\infty} \right) + \tilde{\varepsilon}_t \right) - \left(\tilde{B}_t * U_t \right)$$

where m_i is the maximum sustainable yield for period i obtained by fitting the mixed model; B_∞ is the carrying capacity obtained by fitting the mixed model; $\tilde{\varepsilon}$ is normal process error; $\tilde{\varepsilon} \sim N(0, \sigma)$; σ is the parameter obtain by fitting the mixed model.

Given the new series of \tilde{C} and \tilde{B} , the surplus production from the simulated data was calculated, using equation 1.

The null, the productivity regime, mixed and biomass models were fitted to the simulated series of surplus production and AICc was used to select a best model for each data set. The “classification rate” was calculated as the number of stocks best explained by each model divided by the number of stocks simulated. Thus, I obtain a four by four matrix (Table 1.1) of the classification rates, E_{ij} , where i is the true model and j is the model selected by AICc.

The matrix is then used to solve for the vector of proportions of stocks selected for each model (P) that would result in the observed proportions from the fitting section (\hat{P}_t):

$$15) P = \mathbf{E}_{ij}^{-1} \hat{P}_t$$

Results

Annual production of a stock can be depicted as a function of population abundance (biomass) only (Figure 1.1, left column), population abundance with regime varying parameters (Figure 1.1, center column), or time with shifting production regimes (Figure 1.1, right column). Using a “winner takes all” approach, 38.6% of stocks are best explained by periodic changes in production (e.g., Icelandic cod, Figure 1.1A-C). For 18.3% of stocks, production was best explained by changes in population abundance (e.g., Kattegat and Skagerrak cod, Figure 1.1D-F). For 30.5% of stocks, production was best explained by periodic changes combined with changes in population abundance (e.g., Petrale sole from the U.S. southern Pacific coast, Figure 1.1G-I), and the random production hypothesis received most support for 12.6% of stocks (e.g., common sole in the Kattegat and Skagerrak, Figure 1.1J-L).

Using the “relative support” approach where AICc weights are summed for each hypothesis (pie charts Figure 1.1), the relative support for the four hypotheses was similar (Table 1.3), with 41.3% of the weight for the regime change for 12.6% of stocks, 16.1% for the population abundance hypothesis, 28.3% for the mixed effect hypothesis, and 14.3% for the random hypothesis. The selection process seems independent from the variance present in biomass (Figure 1.2).

I found that the estimated true proportion, using equation 15 and the classification matrix (Table 1.1) to be 27% biomass, 24% productivity regime, 45% mixed and 4% random.

Applying all four models to simulated data suggests that there is a slight tendency to over-classify stocks as being from the productivity regime or random models and to under-classify stocks as being from the biomass and mixed models (Table 1.2). Nevertheless, models that include regime changes in production, either with or without an abundance effect, constitute 72% of the stocks after adjusting for estimation bias, compared to 69% before the correction (Table 1.3) and for the mixed model 80% of the variation in production explained by the model is attributed to the regime changes.

It is possible that model selection is dependent on the intensity of exploitation. For instance, if a stock has never been intensively exploited or it has not varied over a significant range of stock sizes, then we would not expect biomass to explain differences in production. I classified stocks into four categories of abundance based on the ratio of their abundance in the last year (B) of the time series to the equilibrium biomass at maximum sustainable yield (B_{MSY}): collapsed ($B < 0.2B_{MSY}$), overfished ($B \geq 0.2B_{MSY}$ and $B < 0.5B_{MSY}$), fully exploited ($B \geq 0.5B_{MSY}$ and $B < 1.5B_{MSY}$), and developing ($B \geq 1.5B_{MSY}$). Contrary to expectation, the proportion of stocks best explained by changes in population abundance is actually lower for collapsed and overfished stocks (14% and 10% respectively) than for stocks that are less depleted (22% for fully exploited and 13% for developing). Also, for all models, the mean coefficient of variation for the total biomass is close to 40%. There is no significant relationship between historical variability in abundance and the proportion of stocks explained by alternative models (Figure 1.3, Table 1.4). There is a significant relationship between life history traits and proportion of stocks explained by alternative models for the biomass, productivity and random models (Figure 1.4, Table 1.5).

I identified a total of 314 regime changes from the 160 stocks where the preferred model was either regime change or mixed. I calculated the relative change in production between regimes as the absolute change (in tonnes) divided by the average production across all years for that stock. I found that positive changes were as common as negative ones (160 increases vs 154 declines Figure 1.5). The bimodality in Figure 1.5 is due to the fact that the algorithm for selecting regime changes does not readily identify small changes.

Discussion

Caddy and Gulland (1983) suggested that the production of fish stocks could be divided into four classes, regular, cyclical, irregular and spasmodic and that “To be successful, fishery assessment and management must take these patterns into account.” Caddy and Gulland’s regular stocks were characterized by repeatable relationships between stock size and production. Our analysis suggests that the “regular” stocks constitute about $\frac{1}{4}$ of all fish stock for which I have data.

The fishery management system in the U.S., and increasingly elsewhere, is based upon biomass-related reference points that reduce exploitation rates as stock sizes decline and generally attempt to stop all directed harvesting when stocks reach low abundance. The exploitation rates and biomass targets are primarily designed to maintain the stock biomass in the range that is estimated to produce maximum sustained yield. Increasingly, however, the exploitation rate and biomass targets are being shifted to increase economic profitability by higher biomass and reduce ecosystem impact by reducing fishing effort

(Hilborn, 2010). The conventional wisdom, and scientific and political expectation, is that maintaining these levels of biomass will assure the production of the stocks. Moreover, the population abundance hypothesis predicts that reductions in catch to rebuild stocks provides for increased sustainable harvest once stocks were rebuilt.

However, if the production of a stock is determined by periodic regimes and the assessment of the stock does not recognize the shift in regimes, then the current management system with respect to sustainable yield is incorrect. Holding stocks at high levels of abundance and rebuilding depleted stocks will not necessarily result in increased yields in the future. While the economic and environmental benefits of rebuilding abundance and reducing fishing pressure remain, the cost-benefit calculus of rebuilding plans is seriously changed

In current U.S. management, the allowable catches of many species are limited by incidental catch of stocks under rebuilding plans. Current legal mandates to include many more species in the regulatory system, combined with the overfishing definitions and rebuilding requirements suggest that existing fisheries will be increasingly constrained and limited by stocks at low abundance. Our analysis suggests the possibility of many stocks being at low abundance because of periodic shifts in production. Thus, unless the management system changes, the current legal mandates threaten major reductions in fisheries yields.

However, when production changes from high to low, the catch need to decrease. Stocks in a low production regime cannot support the same yield as stocks in high production regimes. Theoretical studies have suggested that the best approach to non-stationary

production may be to harvest a constant fraction of the stock with that fraction determined by averaging across the range of production (Parma, 1990, Walters and Parma, 1996) or to have the exploitation rate adjusted based on recent recruitment (A'mar et al., 2009). All of these studies found that harvest control rules that dramatically decrease exploitation rate at low population size resulted in significant foregone harvest.

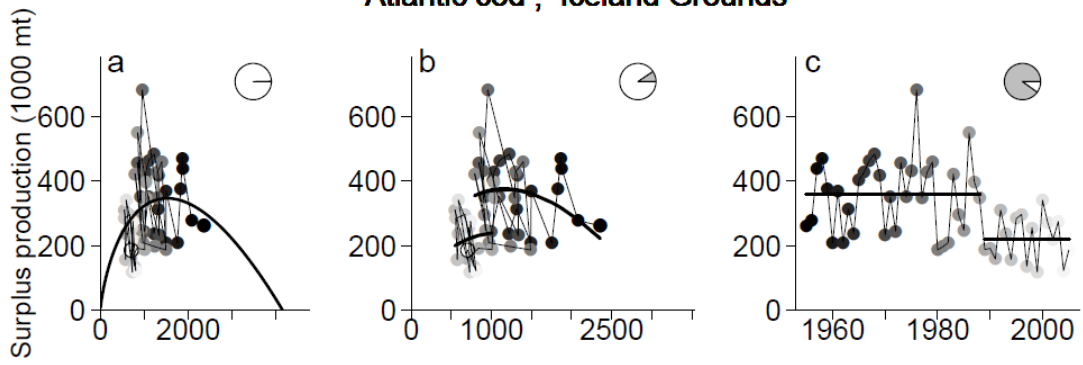
Oceanographic regime shifts have been identified as important drivers of fish production in many regions, including the North Pacific (Mantua and Hare, 2002), Tropical Pacific (Lehodey et al., 1997) and North Atlantic (Parsons and Lear, 2001). However, if regime shifts are the dominant driver of fish population dynamics, why haven't more of them been identified? First, even for stocks where the productivity regime hypothesis received the most support, there was substantial unexplained variability, with the productivity regime model explaining an average of 38.6% of the variability in production. Second, the regime shifts described here are shifts in production of a single stock and may not correspond to observable oceanographic changes or changes in production of other species within the ecosystem.

The stock assessment database on which this analysis is based is a non-random sample of fish populations (Ricard et al., 2011) and is dominated by heavily exploited stocks. The biases this might create, however, would generally be in the opposite direction of the observed results. Heavily exploited stocks presumably have undergone more declines in abundance than lightly exploited stocks and thus provide more contrast for the population abundance model to explain. Stock assessments are generally more available for developed countries, and may thus under-represent fish populations in tropical regions.

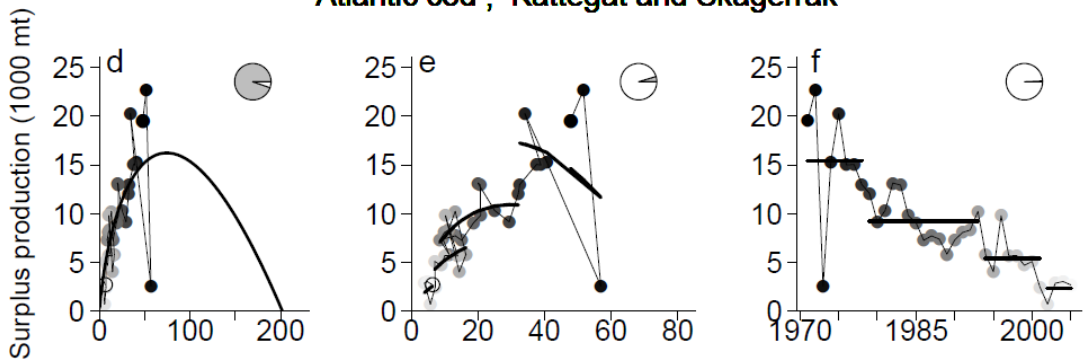
Future work should evaluate a wide range of harvest strategies for robustness to uncertainty in the basic causes of production. Additional work should also look to the physical and biological factors that explain the changes in production and examine if these occur synchronously across species in an ecosystem. Finally it is possible that state-space modelling might provide more insight on the mix of observation and process error in the model fitting.

Figures

Atlantic cod , Iceland Grounds



Atlantic cod , Kattegat and Skagerrak



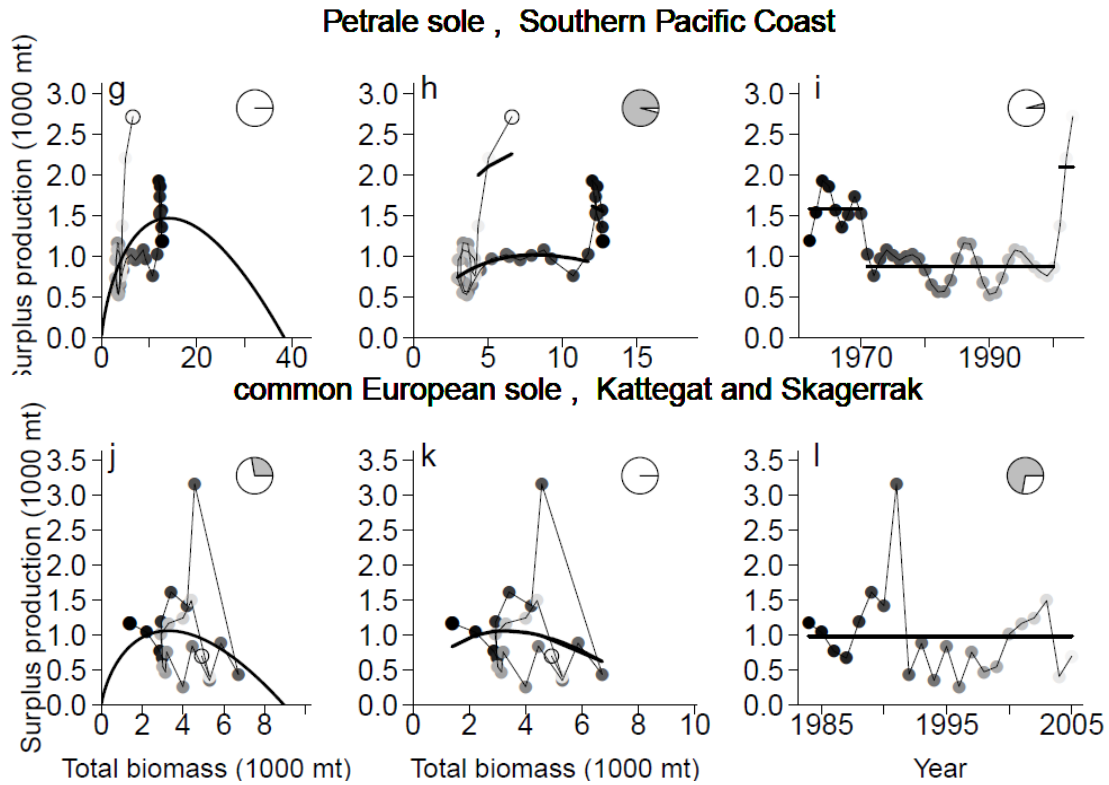


Figure 1.1. Examples of alternative model fits. Annual production of a stock can be depicted as a function of stock size (biomass) only (left column), stock size with regime varying parameters (center column), or time (going from past years in dark gray to present years in light gray) with shifting production regimes (right column). In panels a-c the Icelandic cod stock is used to illustrate a stock best explained by a productivity regime. In panels d-f the Kattegat cod stock illustrates a stock best explained by changes in population abundance. In panels g-i the (Petrale sole from the southern Pacific coast illustrates a stock best explained by periodic changes combined with population abundance changes and in panels j-l the European sole stock in ICEAS area IIIa (Kattegat) illustrates a stock that is best explained by the random model. The “relative support” approach where AICc weights are summed for each hypothesis is represented by pie charts.

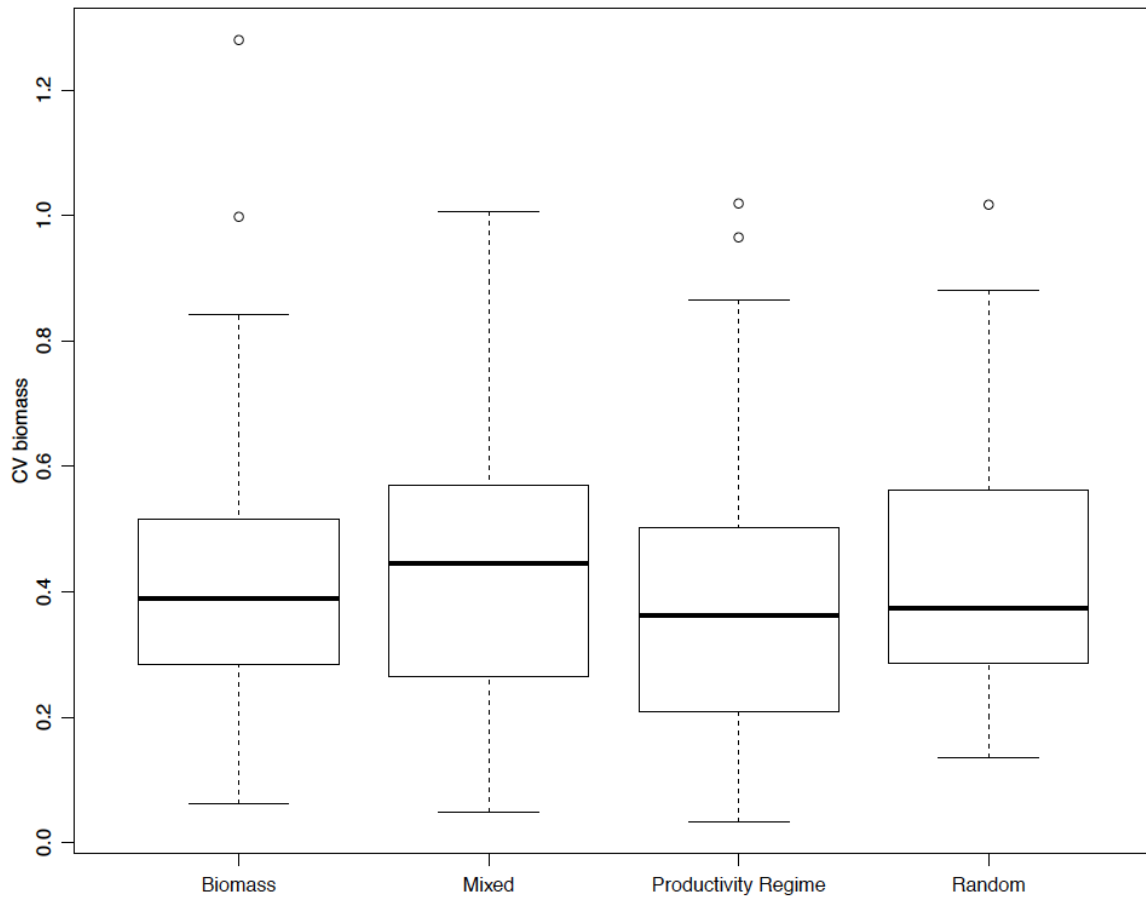


Figure 1.2. Coefficient of variation of total biomass for the different model selected.

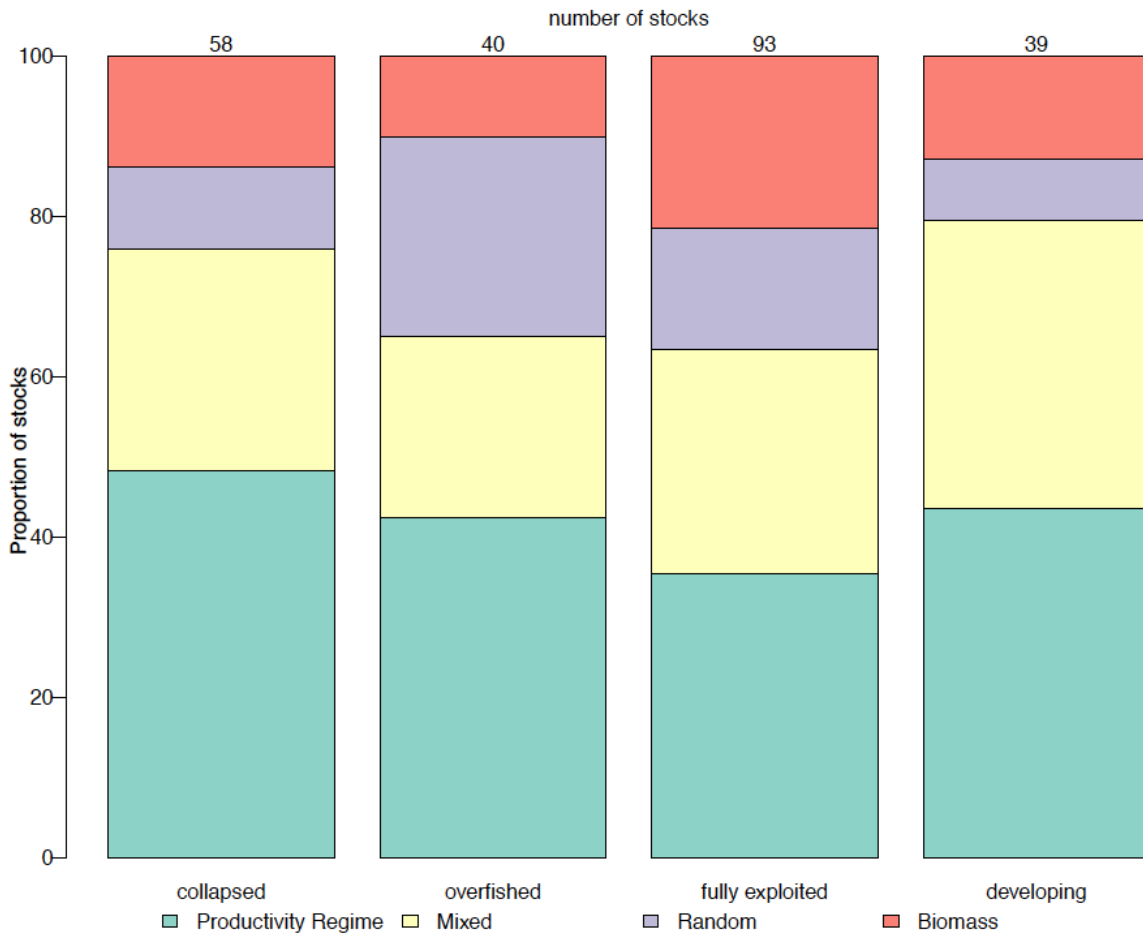


Figure 1.3. Model selection given four categories of abundance - collapsed, overfished, fully exploited, and developing - based on the ratio of their abundance in the last year of the time series to the equilibrium biomass at maximum sustainable yield (BMSY).

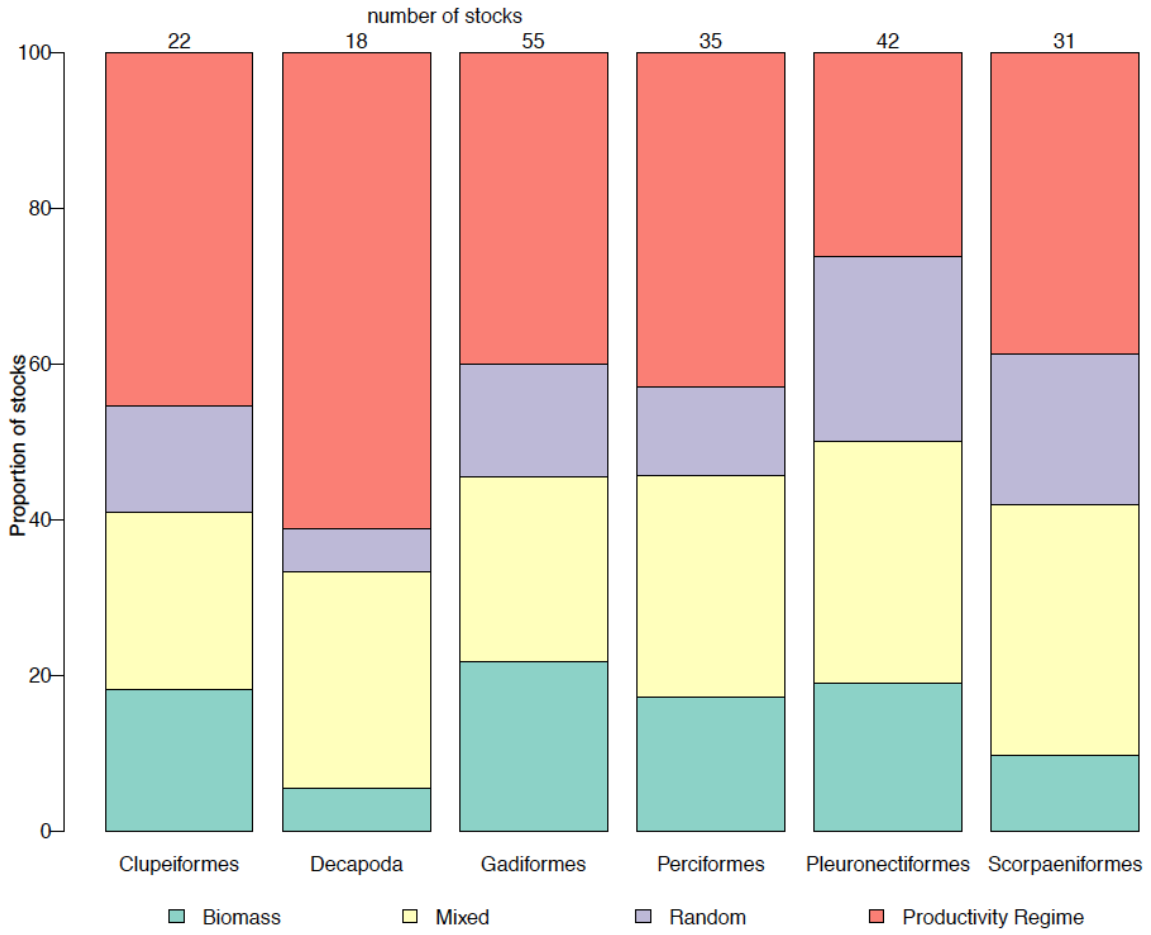


Figure 1.4. Model selection given six orders: Clupeiformes, Decapodes, Gadiformes, Perciformes, Pleuronectiformes, Scorpaeniformes.

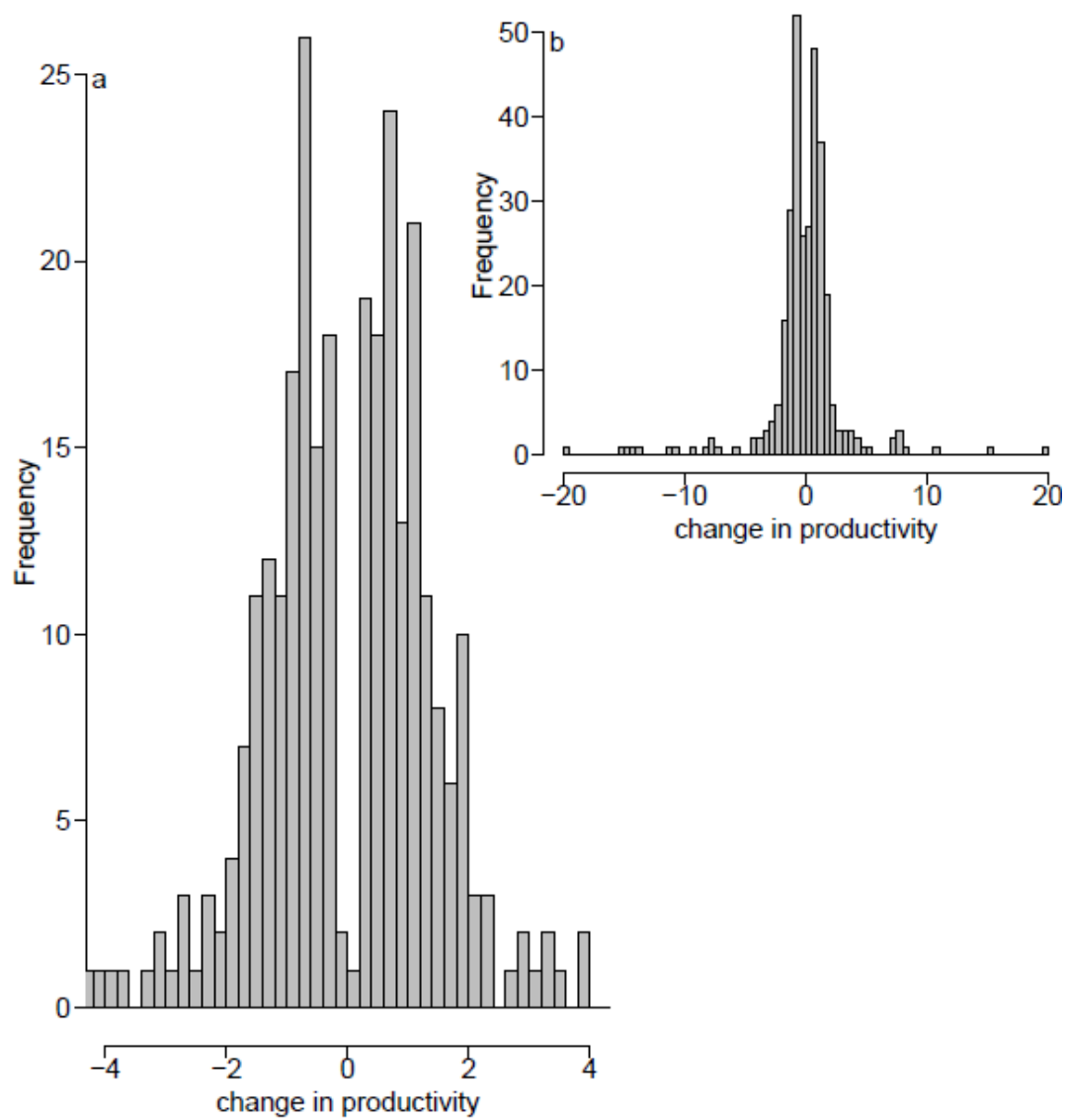


Figure 1.5. The frequency distribution of shifts in production. In panel a the shifts are plotted from -4 to 4 which excludes some extreme values. In panel b all the shifts are plotted in the range -20 to 20 and includes all outliers.

Tables

	Best Fit Model			
Real model	Biomass	Productivity Regime	Mixed	Random
Biomass	0.54	0.14	0.08	0.24
Productivity regime	0.04	0.81	0.11	0.04
Mixed	0.05	0.33	0.57	0.04
Random	0.12	0.13	0.04	0.71

Table 1.1. Probability that a data set generated from a “real” model would be best explained by each kind of model for simulation.

Model	Percentage of stocks best explained by this model
Productivity regime	27%
Biomass	24%
Mixed	45%
Random	4%

Table 1.2. Classification of stocks corrected for classification bias using the classification matrix in Table 1.1

Hypothesis	% stocks with the highest support	# of stocks best supported	% total AICc weight	% of stocks best supported after correction for estimation bias
Productivity regime	38.6%	95	41.3%	27%
Biomass	18.3%	37	16.1%	24%
Mixed	30.5%	65	28.3%	45%
Random	12.6%	33	14.3%	4%

Table 1.3. The percentage of stocks and number of stocks that are best explained by each hypothesis and the total AICc weight for each.

Model	p-value
Productivity regime	0.58
Biomass	0.17
Mixed	0.36
Random	0.01

Table 1.4. Pearson's chi square test for each model selected across stock status. Comparing the mean number of stock for each selection across stock status.

Model	p-value
Productivity regime	0.01
Biomass	0.02
Mixed	0.75
Random	0.02

Table 1.5. Pearson's chi square test for each model selected across stock order. Comparing the mean number of stock for each selection across stock order.

Chapter II: Do spawning stock abundance or environmental conditions determine the recruitment of fish stocks?

Abstract

The assembly of a large data base on spawner-recruitment relationships by Ransom Myers in the 1990s led to considerable advances in large scale evaluation of the relationship between spawning stock and recruitment for marine fishes and showed that recruitment overfishing was indeed common when spawning stocks were driven to low levels. An alternative hypothesis proposed by Gilbert is that recruitment comes in periods of high and low recruitment driven by environmental regimes. During periods of high recruitment, spawning stock is higher, and during periods of low recruitment spawning stock is lower. Thus, Gilbert proposed that what appears to be a relationship between spawning stock affecting recruitment, may in fact be a relationship between recruitment affecting spawning stock, and that concern about recruitment overfishing may be overestimated. I conducted a meta-analysis of marine stock-recruitment relationships, using a traditional spawner-recruitment model against a regime shift model as proposed by Gilbert. I found that there is far more support for the regime shift hypothesis than for recruitment depending upon spawning stock biomass. The stock-recruitment Hypothesis best explains 17% of stocks, the Regimes Hypothesis 45%, the Mixed Hypothesis 21% and the Random Hypothesis 18%. These results have strong implications for fisheries management. Indeed, policies not recognizing shifts in recruitment might not assure high and sustained recruitment. Thus, future work should identify and evaluate management strategies that would be robust to irregular jumps in average productivity.

Introduction

Understanding the relationship between fish stock abundance and subsequent recruitment has been one of the key questions in fisheries science for over a century (e.g. Hjort, 1914; Ricker, 1954; Cushing, 1990; Myers and Barrowman, 1996). Using a database of 364 time series of spawning stock biomass and recruitment, Myers and Barrowman (1996) showed that there generally was a relationship between spawning biomass and subsequent recruitment. Recruitment will be the lowest, and the per capita growth rate highest, at low spawning stock biomass. Once spawning stock increases, the per capita growth rate decreases because of compensatory or over-compensatory mechanisms (e.g., cannibalism and habitat restriction). These mechanisms assume no direct environmental impact on recruitment.

Gilbert (1997) presented an alternative view arguing that recruitment comes in successive periods of high and low recruitment, and that recruitment determines spawning stock biomass, rather than spawning biomass determining recruitment. Favorable environmental conditions will induce high recruitment that will lead to high abundance. Unfavorable environmental conditions will lead to a low average recruitment and hence low abundance. Gilbert argued that this creates the appearance of a stock-recruit relationship, whereas the underlying causal mechanism is environment-driven recruitment that then affects the spawning biomass.

There is a large literature that relates fluctuations in recruitment to environmental conditions (e.g. Bell and Puter, 1958; Cushing, 1982; Genner et al., 2004; Miller et al., 2011). Long-term scales, both inter-annual and decadal, have well been established

(Fogarty et al., 1991; Walters and Parma, 1996; Hsieh et al., 2009). These patterns can be caused by seasonal, climatic, inter-annual events such as the El Niño Southern Oscillation (ENSO) that lasts from 6 to 18 months, or multi-decadal climate regimes such as the Pacific Decadal Oscillation (PDO), lasting between 10 to 30 years (Mantua et al., 1997; Zhang et al., 1997). Baumgartner et al., (1992) found that anchovies and sardines vary over periods of approximately 60 years. In the North Pacific, important ecosystem changes have been associated with the PDO (Francis et al., 1998). Salmon productivity in Alaska was positively correlated with warm PDO phases, whereas salmon productivity in California, Oregon and Washington was negatively correlated, with the opposite relationship observed during cold PDO phases (Hare, 1996; Hare et al., 1999). Some studies revealed that clupeid productivity was modulated by the PDO and inter-annual variations such as ENSO (Chavez et al., 2003). Many other studies have identified that shifts in environmental factors are linked with fluctuations in fish abundance and population dynamics (Hare and Mantua, 2000; Mueter et al., 2007). Many studies (e.g. Megrey et al. 1996; Caley et al., 1996; Wilderbuer et al., 2002; Ciannelli et al., 2005) have focused on these large-scale variations at an ecosystem level, as they need to be considered for the management of marine resources.

This chapter will identify a range of hypotheses regarding the relationship between spawning biomass, regime changes, and recruitment, and will evaluate the support for each hypothesis using a data base of 256 spawner-recruit time series. The data from the RAM Legacy Stock Assessment Database (Ricard et al., 2011) and a model selection method, the Akaike information criterion (AIC), are applied. The AICc is used in two

ways, either a “winner takes all” approach in which the hypothesis that had the highest support from the data is determined for each stock, or a “relative support” approach in which the relative support for each hypothesis for each stock is calculated. The methods were tested by simulating data where the true underlying determinant of recruitment was one of four: spawning stock biomass, environmental regimes, a mixed effect, or simply random.

Materials and Methods

Data and choice of stocks

Time series of spawning stock biomass and recruitment as well as taxonomy, location and large marine ecosystem were extracted from the RAM Legacy Stock Assessment Database (Ricard et al., 2011) for 417 stocks on December 10th 2010. The stocks come from 29 large marine ecosystems.

Only 256 stocks with complete spawning stock biomass and recruitment time series were initially selected for analysis. A total of 43 of the 256 data sets were excluded from the analysis for the following reasons; 26 stocks had fewer than 20 data points and the estimated stock total biomass was the result of a deterministic model for 17 stocks. The analysis was thus conducted using data for 213 stocks.

Alternative models considered

To test if recruitment is related to spawning stock biomass, a stock-recruitment model was fitted to the data using a linear version of the Ricker model. The Ricker model (1954) can be written as

$$1) \widehat{R}_t = S_t e^{a+bS_t}$$

where \widehat{R}_t is the predicted recruitment in year t ; S_t is the spawning stock biomass during year t ; $\log a$ is the maximum survival rate; and b is the density-dependent effect on survival to recruitment.

Gilbert (1997) proposed an alternative to the conventional stock-recruitment paradigm where recruitment alternates between high and low recruitment regimes and vice versa. A central component of Gilbert's hypothesis is that periods of good and poor recruitment must persist for a sufficient period of time to create the appearance of a stock-recruit relationship via the adjustment of spawning stock to shifting recruitment levels. This hypothesis will be referred to as "recruitment regime". The challenge for this hypothesis is to estimate the years when the recruitment regime shifted (called break-points). The sequential t-test analysis of regime shifts (STARS) (Rodionov, 2004) estimates a series of break points that mark the first year of each regime, with two "tuning parameters" used as inputs: the minimum duration of a regime, known as "cut-off-length" and the significance level for the t-tests. As STARS was fitted to the logarithm of recruitment, the predicted recruitment for each year within regime i is the geometric mean recruitment during that regime (Equation 2). I used a cut-off-length of 10 years and the significance level for the t-test of 0.1. Thus, the shifts are more likely to be at least a decade long although the algorithm often chose shorter regimes at the start and end of the time series. When the length of the last regime was less than two years, the final years of the time-series were assumed to be part of the previous regime. This method has been widely applied to abiotic and biotic time-series (Rodionov & Overland, 2005; A'mar et al., 2009). The

STARS method does not assume any number of shifts *a priori*, and searches for shifts of decadal and multi-decadal scale.

$$2) \bar{R}_i = e^{\frac{\sum_{j=f_i}^{f_{i+1}} \log(R_j)}{f_{i+1}-f_i}}$$

where f_i is the first year of regime i ; \bar{R}_i is the predicted average recruitment during regime i ; and R_j the recruitment during year j .

The effect of spawning stock biomass on the stock and changes in environmental regime are combined in the “mixed model” in which an underlying spawner-recruit relationship is assumed, but the parameters of that relationship vary among regimes. For the mixed model, the estimated years at which break-points occurred were determined using STARS applied to log-recruitment, even though there are other ways to select regimes for the mixed model. The first alternative approach would be to first fit a stock-recruitment model and then a regime shift model to the residuals. This would give an idea of how much of the variability is explained by a stock-recruitment relationship and then how much is explained by a regime model. A single likelihood cannot be calculated for the two steps of the fitting process. Thus, this method, while realistic statistically, did not allow for model selection. The second alternative approach would be to fit an autoregressive stock-recruitment model. This method, while realistic ecologically, only takes into account the autocorrelation present in the data, but do not provide information on changes in regime. Three variants of the mixed approach as it was implemented were explored: (a) a shifts between regimes, but b is regime independent (Equation 3), (b) a is regime-independent, but that b is regime-dependent (Equation 4), and (c) both a and b

are regime-dependent (Equation 5). The break points are identical in each variant of the mixed model.

$$3) \widehat{R}_{t,i} = S_t e^{a_i + b_i S_t}$$

where a_i is the maximum log-survival rate during regime i

$$4) \widehat{R}_{t,i} = S_t e^{a + b_i S_t}$$

where b_i is the density dependent effect during regime i

$$5) \widehat{R}_{t,i} = S_t e^{a_i + b_i S_t}$$

The random recruitment model (Equation 6) assumes that the variability in recruitment is neither driven by spawning stock biomass nor by changes in recruitment regime so that the predicted recruitment in any year (y) is the geometric mean recruitment over all years.

$$6) \hat{R}_t = \left(\prod_{t=1}^y R_t \right)^{1/y}$$

Parameter estimation

The parameters of the stock-recruitment and mixed models were fitted assuming lognormal error using equation 7.

$$7) L = \sum_t \log(R_t) + \frac{1}{2} \log(2\pi\sigma^2) + \frac{((\log(\widehat{R}_t) - \log(R_t))^2}{2\sigma^2}$$

where L is the likelihood of the data given the parameters; and σ is calculated analytically:

$$8) \sigma = \sqrt{\frac{1}{n} \sum_t (\log(R_t) - \log(\widehat{R}_t))^2}$$

The parameters (a , and b) of the Ricker model were estimated using the nonlinear function minimizer in AD Model Builder (ADMB) v10.1 (<http://admb-project.org/>) and the value of σ was determined analytically using equation 8.

For the regime and mixed models, the breakpoints (f_i) were estimated using the STARS approach (Rodionov, 2004). Once the break points were determined, the geometric average recruitment during each regime was calculated and the value of σ determined analytically using equation 8.

The parameters of the recruitment regime model are the number of breakpoints, the average recruitment for each identified regime, and the variance. The breakpoints and regimes identified by STARS depend on the STARS tuning parameters, therefore multiple possible breakpoints and regimes combinations could be consider as parameters. For the purpose of this study I did not consider potential breakpoints and regimes other than those found by the STARS method with the cut-off-length of 10 years and the significance level for the t-test of 0.1.

The parameters of the three mixed models (a_i, b_i), (a, b_i), (a_i, b) were estimated by nonlinear function minimization using ADMB v10.1 based the regime change break points estimated for the recruitment regime model. The value of σ was determined analytically using equation 8.

For the random model, the average recruitment was calculated using equation 6 and σ using equation 8.

Model selection

The comparison of the six models was based on the Akaike Information Criterion corrected for small sample size (AICc) (Burnham and Anderson, 2002) which identified the most parsimonious model. AICc weights were also calculated and can be interpreted as the relative support of data for each model (Hobbs and Hilborn, 2006). The AICc is:

$$9) \quad AICc = -2 \log(L) + 2k + \frac{2k(k+1)}{N-k-1}$$

where k is the number of parameters; and N is the number of data points.

The preferred model is the one with the lowest AICc. The AICc weights are calculated using the formula:

$$10) \quad w_i = \frac{e^{\frac{AIC_{c,i} - \min(AIC_{c,i})}{2}}}{\sum_{j=1}^6 e^{\frac{AIC_{c,j} - \min(AIC_{c,j})}{2}}}$$

Testing of the methods

Data were simulated from each alternative hypothesis, each model fitted, model selection applied to identify the best model and the frequency of misclassification calculated. The exercise allowed the model selection method to be verified and corrected for expected misclassification probability. The data simulated for each hypothesis were drawn from stocks that were best explained by that hypothesis. Thus, we generated recruitment data

for 84 stocks for the Regime model, for 25 stocks for the stock-recruitment model, for 72 stocks for the random model, for 12 stocks for the mixed-*ab* model, for 11 stocks for the mixed-*a* model, and for 9 stocks for the mixed-*b* model. 100 stochastic replicate data sets were generated for each stock by adding measurement error (based on the estimate of σ) to recruitment predicted by the hypothesis:

$$11) \tilde{R}_t = \widehat{R}_t e^{\tilde{\varepsilon}_t - \frac{\sigma^2}{2}} \quad \text{where } \tilde{\varepsilon} \sim N(0, \sigma)$$

where \widehat{R}_t is generated using Equations 1-6. Spawning biomass was assumed to be measured exactly.

The “classification rate” was calculated by dividing the number of times each model was selected by the total number of stocks simulated. Thus, we obtain a 6 x 6 matrix of classification rates, E_{ij} , where i is the true model and j is the model selected by AICc. The matrix is then used to solve for the vector of proportions of stocks selected for each model (P) that would result in the observed proportions from the fitting section (\widehat{P}_i):

$$12) P = \mathbf{E}_{ij}^{-1} \widehat{P}_i$$

Results

The results of the meta-analysis are presented as the proportion of stocks selected using AICc, the weights assigned to each model using the AICc weights, and the corresponding figures for each model. Examples of model fits are presented in Figures 2.1 to 2.6. The relative support (AICc weights) compared to the proportion of stocks selected (AICc) is

substantially different for the regime, Ricker, and random hypotheses, but quite similar for the mixed models (Table 1).

In the RAM II legacy database, the mean coefficients of variation (CV) in recruitment and spawning biomass are 0.67 and 0.47 respectively. As suggested by the bias correction (Table 2), the method over-classifies stocks as being from the Ricker, mixed-*a* and mixed-*b* hypothesis. The method under-classifies stocks as being from the recruitment regime hypothesis and the mixed-*ab* hypothesis. The random hypothesis is classified identically before and after bias correction. Nevertheless, models assuming regime change in recruitment represent 50% of the stocks and, when assuming pure environmental influence, either random or regimes are the preferred model for 68% of the stocks (Table 1).

According to a Pearson's chi square test the model selection is significantly different across regions ($p=0.037$; Figure 2.7). The Pearson's chi square test is reliable as there is a non-significant number of cells under five counts. Two hypotheses could explain these results. The first would be that model selection depends on the level of depletion and the exploitation history of the stock. Some stocks have been heavily fished for a long time (e.g., those off the Canadian east coast and the US northeast coast) whereas others have been well managed for a long time (e.g. Alaska) and yet others are subject to recently-developed fisheries (e.g., New Zealand) (Figure 2.7). Stocks that have been less heavily fished tend to be selected more often as being driven by recruitment regimes, whereas the stock-recruitment hypothesis is more often selected for stocks that are highly fished and heavily depleted.

The second hypothesis is that the method could be sensitive to the way recruitment is estimated in the assessment. Recruitment deviates can be estimated as either free or constrained parameters to follow a stock-recruitment relationship. Estimation methods vary among regions and large marine ecosystems. Assessments for groundfish stocks in the California Current system assume an underlying stock-recruitment relationship, but contrary to expectation, the stock-recruitment relationship hypothesis was not often selected for these stocks. In Alaska, recruitment deviates are estimated as free parameters and the stock-recruitment relationship hypothesis was selected often (Figure 2.8). We conclude that the method used to estimate recruitment deviates does not influence our results. Also contrary to expectation, model selection seems independent of life history traits since the Pearson's chi square test showed no significant difference across order ($p=0.6$) (Figure 2.9).

263 regimes are identified for the 139 stocks where the preferred model was regime or mixed. The relative change in recruitment between regimes was calculated as the absolute change (in units) divided by the average recruitment across all years for that stock. The proportion of positive to negative shifts is unbalanced with 158 negative shifts and 105 positive shifts. The median absolute value of regime change was 0.5, and 90% of regime changes were between 7% and 104% of the average productivity (Figure 2.10). The bimodality in Figure 2.10 arises because the STARS algorithm for selecting regime changes does not readily identify small changes. The results from the first chapter show that the median absolute value of regime changes was 1.3 for surplus production. It seems likely, therefore, that in addition to changes in recruitment, the changes in surplus

production were due to changes in somatic growth, and potentially natural mortality (although natural mortality is assumed constant in the majority of stock assessments).

Discussion

There is still an intense debate in the scientific community on the relative importance of spawning stock biomass and environmental change for driving recruitment *inter alia* because it is of primary importance for fisheries managers. Nevertheless, while sporadic analysis has been conducted, no meta-analysis has been performed to answer this question. Here we address this shortcoming by analyzing 213 stocks from the RAM Legacy database using a set of models allowing us to compare the support provided for four alternative hypotheses. The first hypothesis assumes that recruitment is related to spawning stock biomass. It assumes that low spawning stock biomass leads to low recruitment and is tested by fitting the Ricker model. Alternatively, a period of environmentally-caused low recruitment would lead to low spawning stock biomass and a period of high recruitment would lead to high spawning stock biomass (Gilbert, 1997). The recruitment regimes hypothesis assumes that recruitment comes in successive periods of high and low values. In that case, recruitment regimes are identified using the STARS method. The third hypothesis, referred to as the mixed hypothesis, assumes a combined effect of spawning stock biomass and environmental regimes on recruitment, and is represented using three alternative mixed models. The fourth hypothesis assumes

that recruitments are random and independent events, described as the null hypothesis in Gilbert's analysis and as the random hypothesis in this analysis.

Among the 213 marine fish stocks considered, 50% of the stocks were best explained by the recruitment regime hypothesis. Hence recruitment is explained by successive periods of high and low values as suggested by Gilbert (1997). Indeed some stocks selected as regime recruitment showed what Gilbert called the "time series effect," that recruitment and spawning stock biomass are independent, but low recruitment will induce low spawning stock biomass. Only 15% of the stocks were best explained by the density-dependent stock-recruitment relationship. Our results thus contradict those of Myers and Barrowman (1996) who stated "the hypothesis that there is no practical relationship between spawners and subsequent recruitment can be rejected," since recruitment of almost 2/3 of the stocks appears to be independent of spawning stock biomass. Contrary to Gilbert's results, this analysis also found some evidence for the Null/Random hypothesis. Indeed, for 18% of stocks, recruitment appeared to be random and independent of spawning stocks biomass.

This work suggests that recruitment is less frequently driven by spawning stock size and more frequently by environmental conditions. Stock recovery will then commonly depend primarily on environmental conditions (Brander, 2005). There are many reasons to maintain stocks at high abundance including economic efficiency (Hilborn and Walters, 1992) and lower ecosystem impacts. Maintaining stocks at high abundance will provide more resilience to fishing and environmental change (Folke et al., 2004). Therefore, this paper does not suggest that we should abandon the goal of maintaining

fish stocks at high abundance. Rather, we show that it is unlikely that policies assuring high abundance will assure high and sustained recruitment.

These results are consistent with the results on surplus production dynamics (Vert-pre et al., 2013). In both analyses, the majority of stocks were best explained by regimes (recruitment 80%; surplus production 75%). The traditional assumption that biomass determines recruitment was the preferred hypothesis for only 14% of stocks, and that biomass determines surplus production was the preferred hypothesis for 25% of stocks. The agreement between the results from both studies reinforce one another. Indeed, since recruitment is one of the main drivers of surplus production, we would expect that stocks showing recruitment regimes would also show production regimes. In this study I have not attempted to provide any explanatory mechanisms for the shifts in recruitment, nor did the earlier work on surplus production (Vert-pre et al., 2013) attempt to explain shifts in surplus production. Changes in all life history parameters (recruitment, growth, natural mortality) are expected to be influenced by changes in food and predator populations (Drinkwater et al., 2010), and thus given the dynamic changes in marine ecosystems we should not be surprised that both recruitment and surplus production show periodic shifts.

The data used in this analysis are model outputs from worldwide stock assessments. Stock-assessment methods and how recruitment deviates are estimated vary widely among countries and agencies. Recruitment deviates can be estimated either as deviates from an underlying stock recruitment relationship or as annual deviates from a global mean recruitment. It would seem likely that the recruitment pattern is explained by a spawner-recruitment relationship when the stock assessment has an underlying assumption of a spawner-recruitment relationship. Thus, we would expect assessments

from regions where assessments assume an underlying spawner-recruit relationship to lead to stronger support for the hypotheses that there is a spawner-recruitment relationship. Therefore the specific pattern of preferred hypothesis found by region might depend on the level of depletion and the exploitation history of the stock. Less heavily fished stocks tend to follow a regime pattern, whereas highly fished and heavily depleted stocks follow a stock-recruitment pattern.

The goal of management agencies is to maintain stocks at a sustainable level of biomass and rebuild depleted stocks. This paper shows how rarely spawning stock biomass is driving recruitment. Thus, biological reference points described in Gabriel and Mace (1999) related to maximum sustainable yield (e.g., B_{MSY} and F_{MSY}), are likely to change between recruitment regimes. A stock-recruitment relationship can be used to set target reference points, but the uncertainty in the spawner-recruit relationship has led management agencies to favor the use of proxies (e.g. Clark, 1993). These proxies do not rely directly on a specific stock-recruitment relationship but are based on an average expectation of fishing rate at which MSY would be achieved, assuming a direct dependence of recruitment on spawning biomass (e.g. Gabriel and Mace, 1999; NPFMC, 2011). Given the results of our simulation testing, it does not appear that change point analysis is reliable enough for management agencies to assess the probability of a stock being in a new regime. Thus, I suggest that management agencies find harvest control rules that are robust to regime shifts.

Several studies have explored management strategies that explicitly include environmental change, but the performance of these strategies has generally not been much better than strategies that ignore such change (Punt et al., in press). The

management of Pacific sardine, *Sardinops sagax*, is one of the few that has included an environmental variable in the harvest control rule (Anon, 1998). Studies (e.g. Szuwalski and Punt, In press) have shown that shifts in environment lead to uncertainty in the outcomes of management strategies, and some studies suggest dealing with uncertainty by simulating different scenarios of the dynamics of the fishery being managed (Punt, 2007). For example, A'mar et al. (2009) simulations show that when, assuming future regime shifts, the highest catch with the lowest inter-annual variation was achieved but with a higher probability of fishing mortality exceeding the overfishing limit. These evaluations conclude that including environmental changes to management leads to non-robust risky outputs. Management strategy outcomes given regime shifts are more robust with fishing rate target than biomass target (Punt et al., in press).

Future work should identify the mechanisms that lead to these regimes and whether they are coordinated among stocks in the same region. Additional effort should be put into determining when it is necessary for time-varying natural mortality and growth parameters to be included in stock assessments, given that they are likely to be influenced by environmental changes. While it is generally accepted that regime recruitment is mostly relevant for small pelagic species, this analysis found no relationship between life history characteristics and the likelihood of recruitment being regime driven. Thus, regardless of life history traits, studies should focus on integrating out the effect of recruitment regimes on management outcomes perhaps using target fishing mortality reference points based on per recruit analysis.

Figures

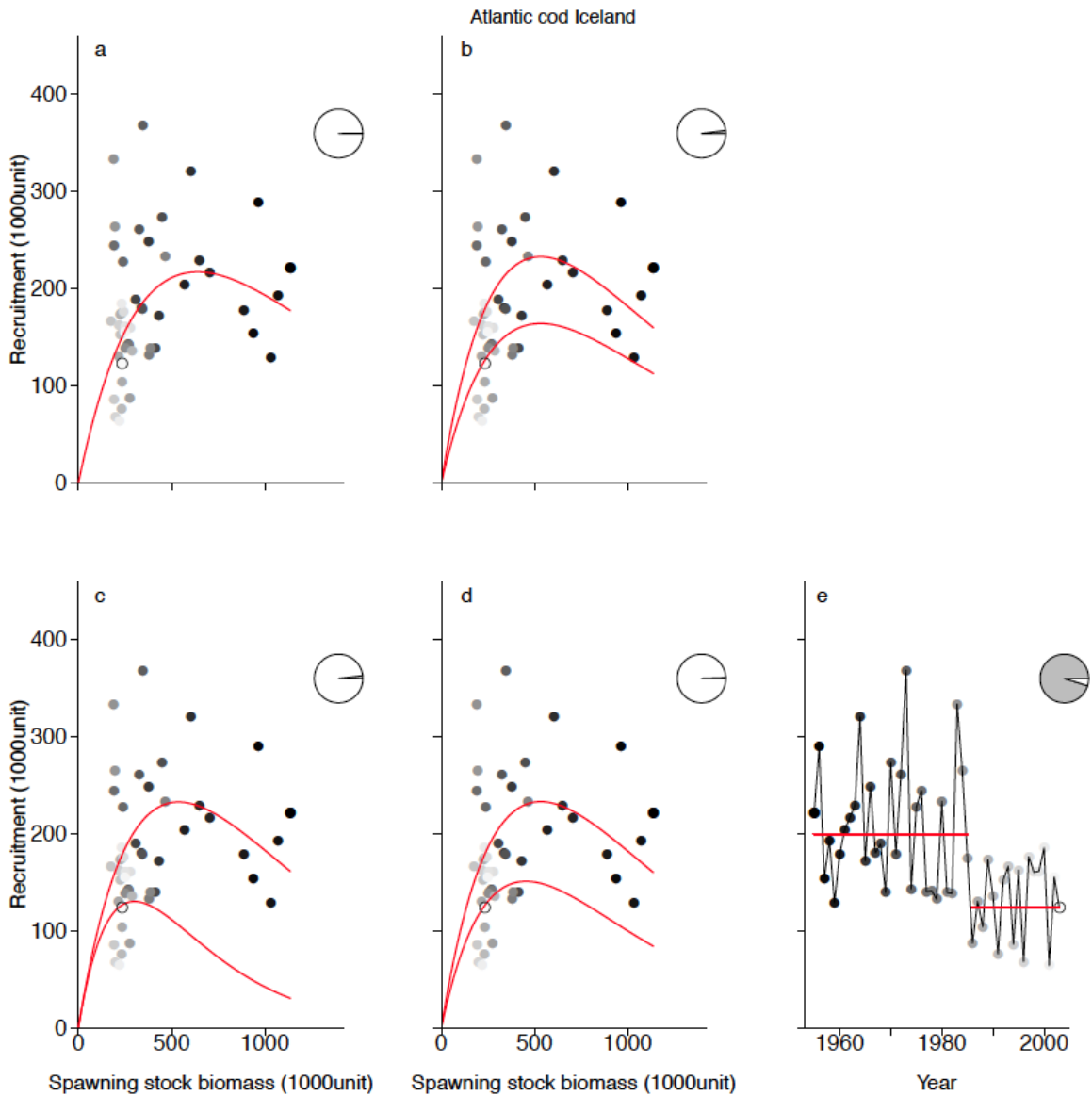


Figure 2.1. Atlantic cod from Iceland is used to illustrate recruitment of a stock as a regime function of time (recruitment regime model). Recruitment regime can be depicted as a function of spawning stock biomass (Ricker model in panel a), as a combined effect of spawning stock biomass and recruitment regime (mixed model *a* in panel b, mixed model *b* in panel c, and mixed model *ab* in panel d, for each mixed model the different

stock recruit function is plotted as it would be in each regime detected), or time (going from past years in dark gray to present years in light gray) with shifting recruitment regimes (panel e). For each hypothesis the “relative support” approach using AICc weights is represented by pie charts. The pie charts sum to 100% across all hypotheses. Recruitment and spawning stock biomass are in units which could be, metric tons, thousands, relative or thousands per eggs.

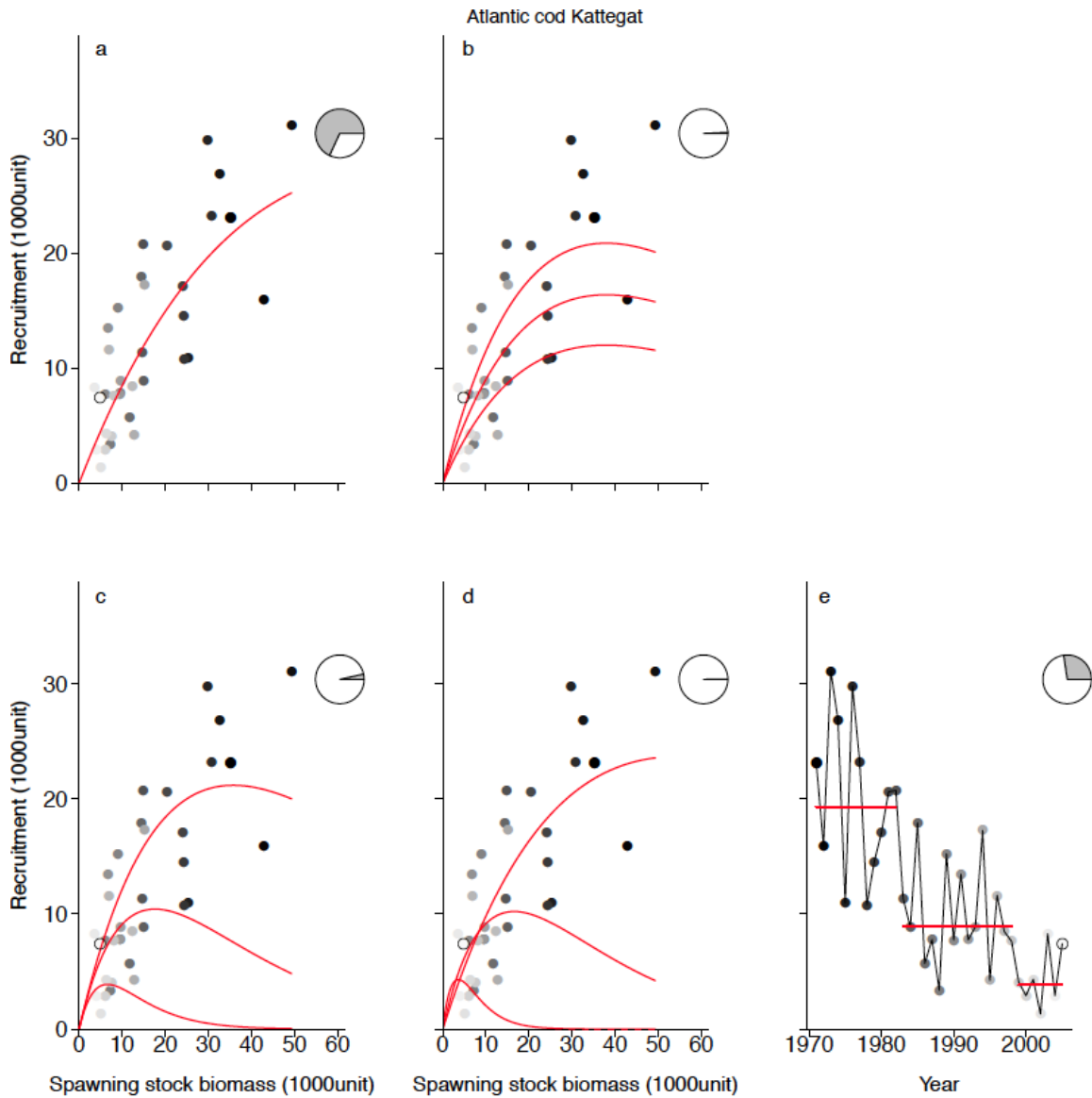


Figure 2.2. As for Figure 2.1, except the results pertain to Atlantic cod from Kattegat used to illustrate recruitment as related to stock (spawning stock biomass model).

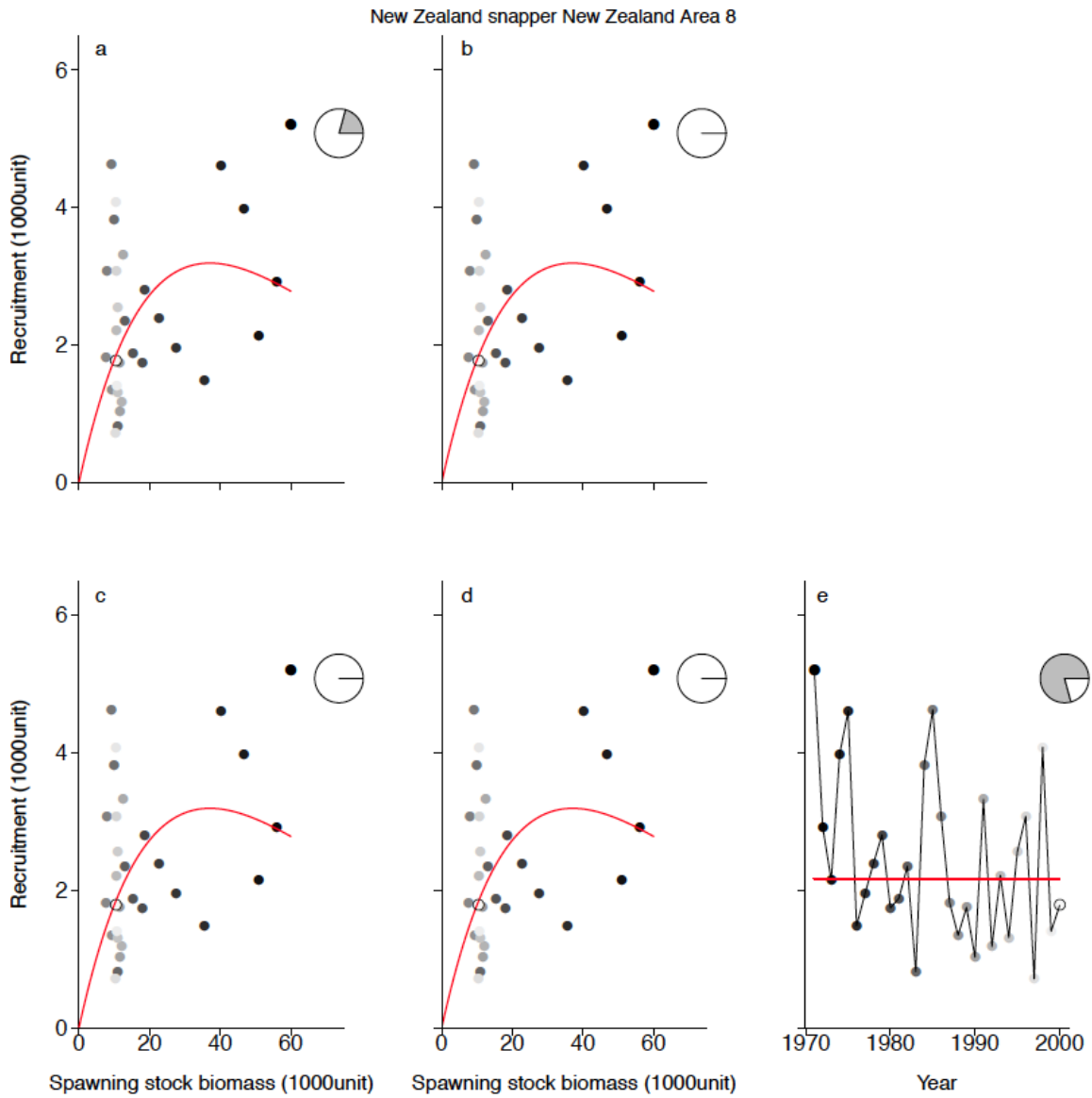


Figure 2.3. As for Figure 2.1, except the results pertain to snapper from New Zealand, used to illustrate recruitment of a stock as a random function of time (random model).

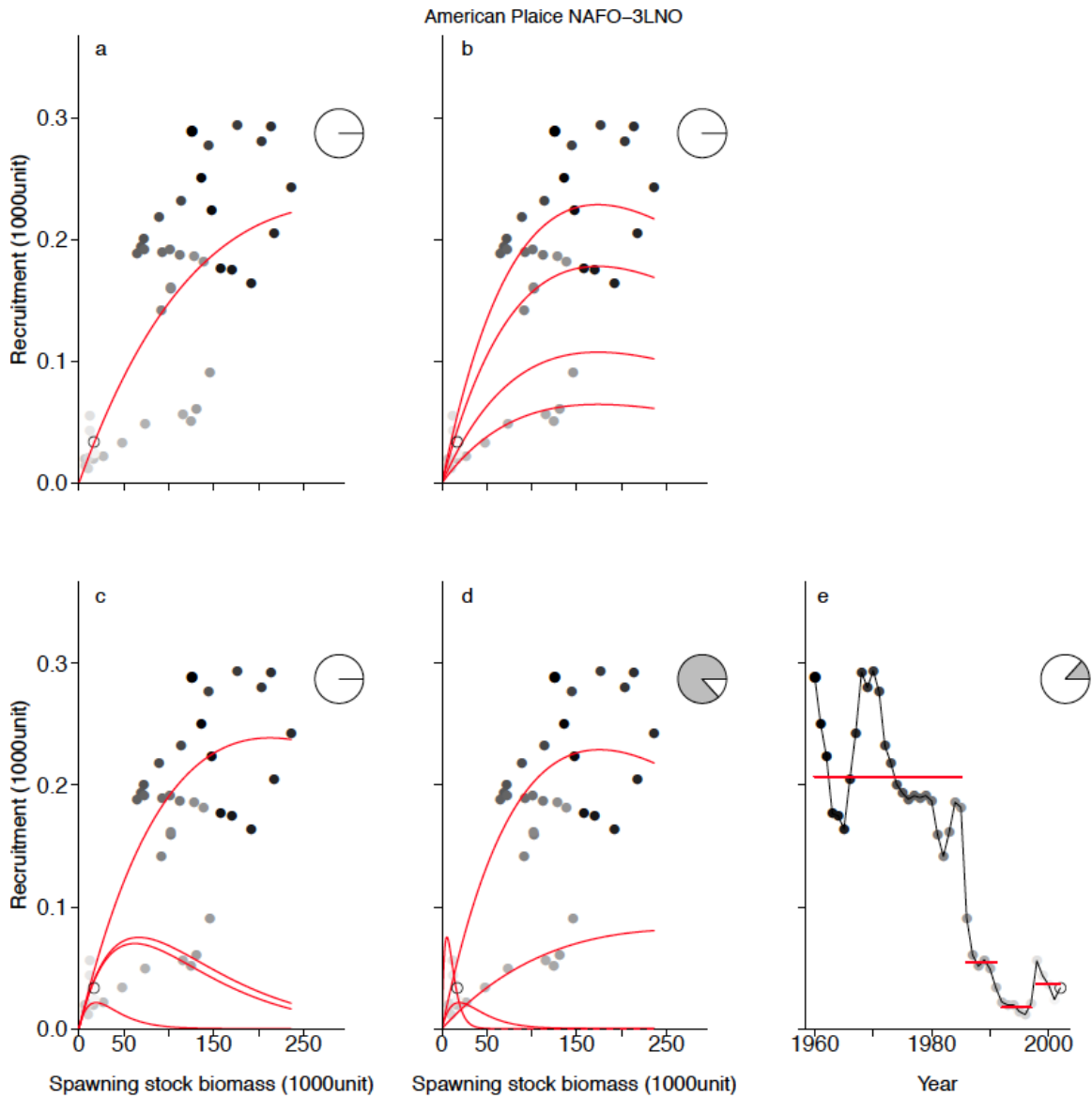


Figure 2.4. As for Figure 2.1, except the results pertain to American plaice from NAFO-3LNO used to illustrate recruitment of a stock as a combined function of spawning stock biomass and recruitment regime assuming parameters a and b regime-varying (mixed ab model).

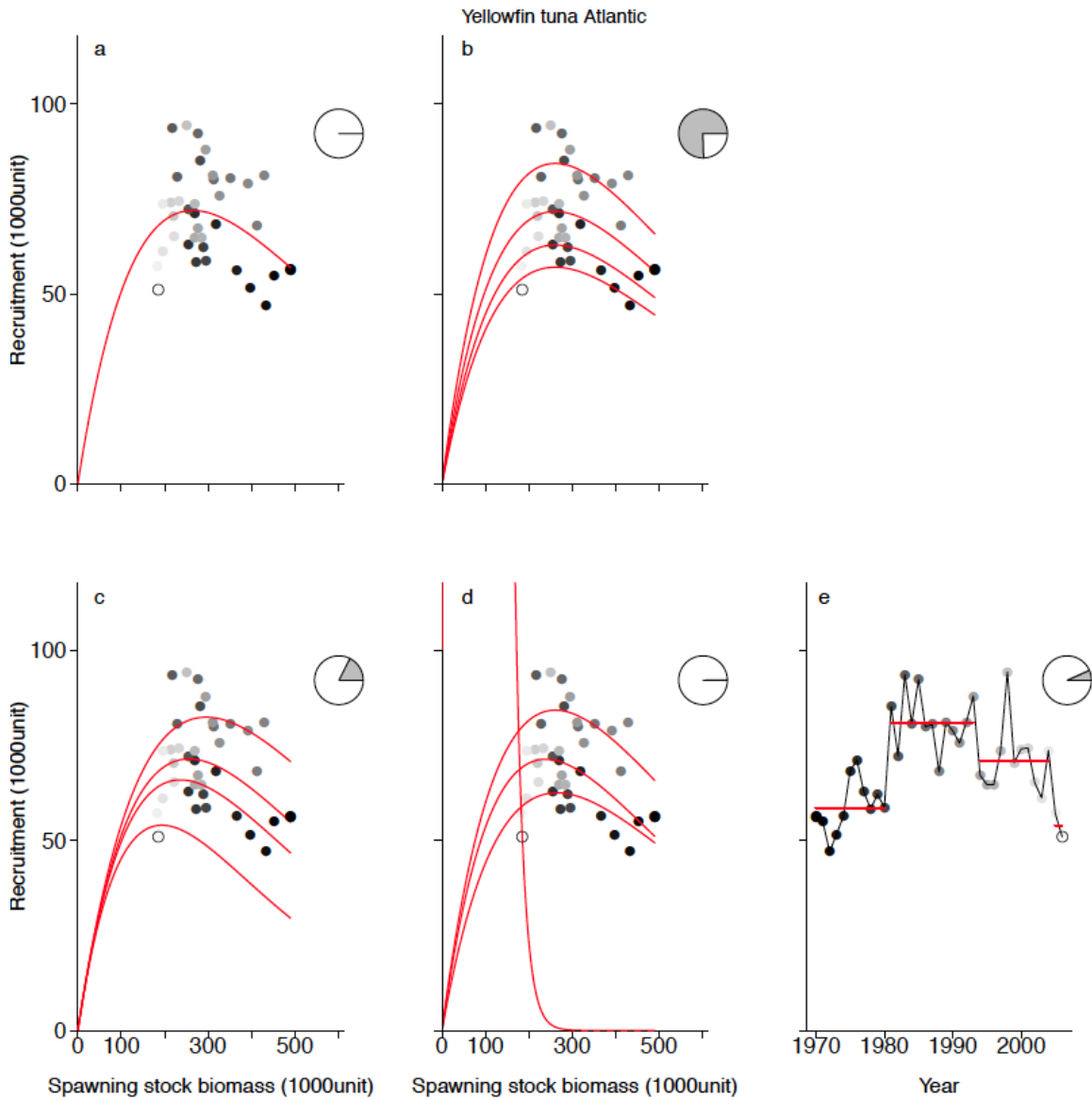


Figure 2.5. As for Figure 2.1, except the results pertain to Yellowfin tuna from the Atlantic high seas used to illustrate recruitment of a stock as a combined function of spawning stock biomass and recruitment regime assuming parameters a as regime-varying and b as invariant (mixed a model).

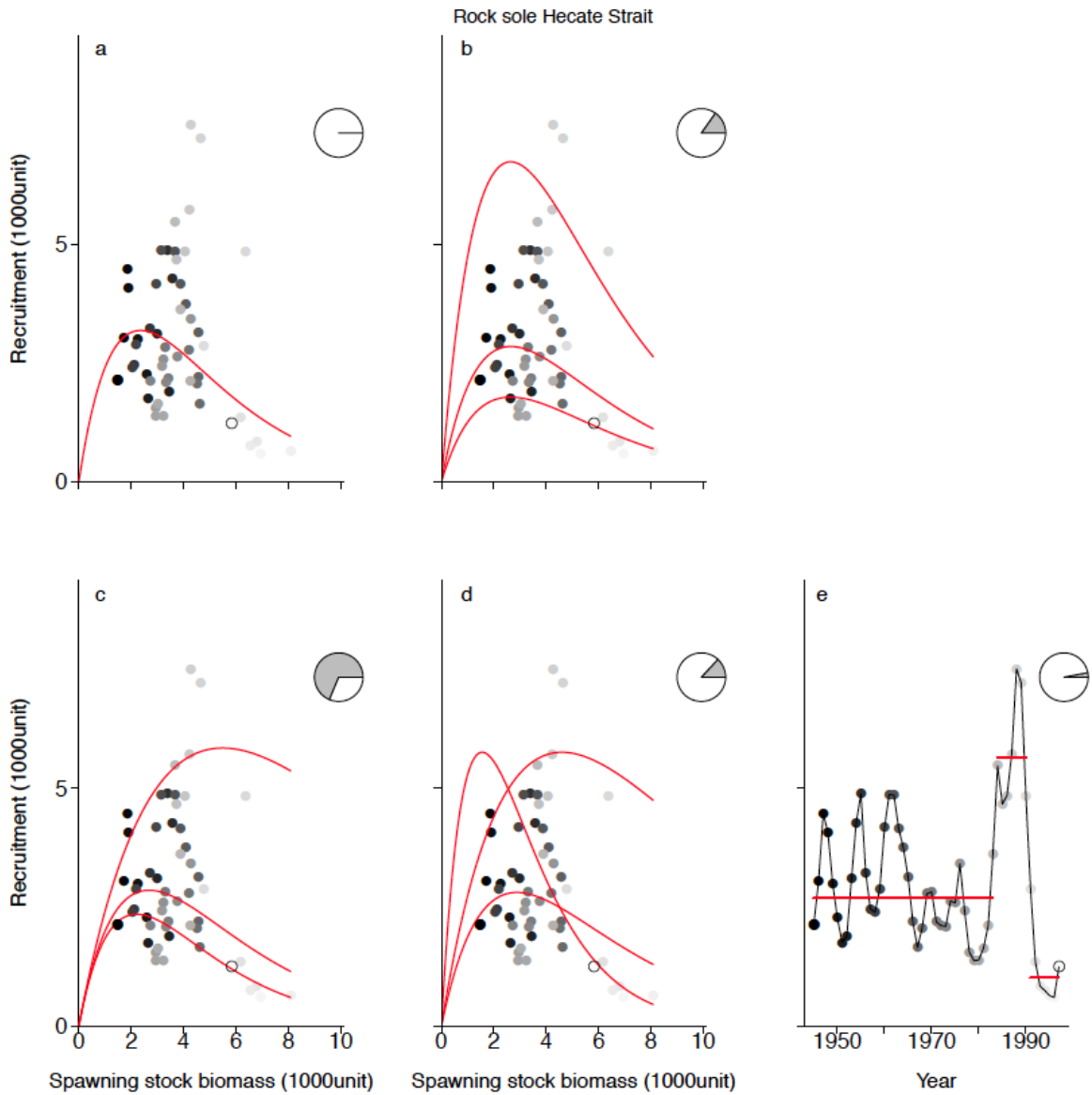


Figure 2.6. As for Figure 2.1, except the results pertain to rock sole from Hecate Strait used to illustrate recruitment of a stock as a combined function of spawning stock biomass and recruitment regime assuming parameters a as invariant and b as regime-varying (mixed b model).

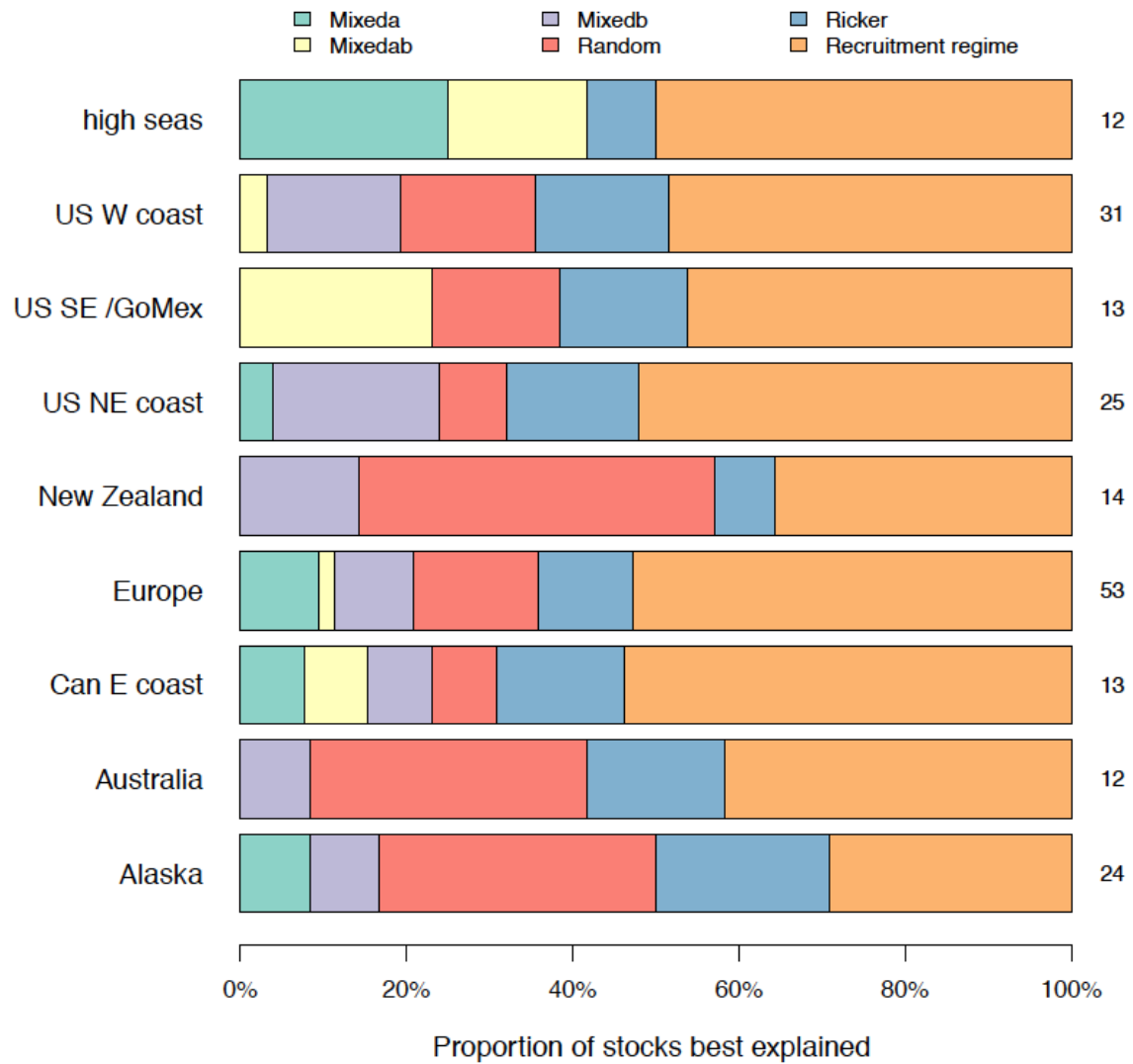


Figure 2.7. Model selection given nine regions across the world (regions with less than 12 stocks were removed).

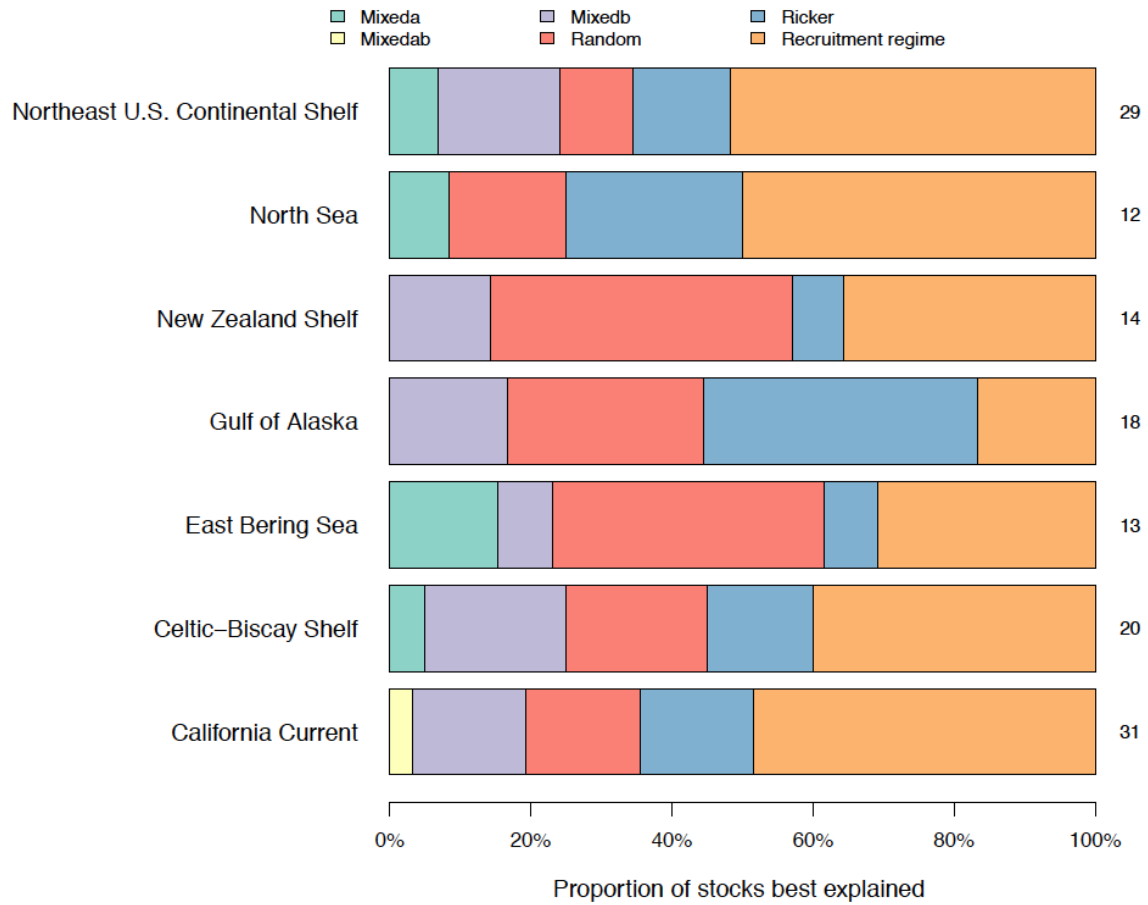


Figure 2.8. Model selection given 7 large marine ecosystems from the 29 large marine ecosystems available in the RAM II stock-recruitment database (large marine ecosystem with less than 12 stocks were removed).

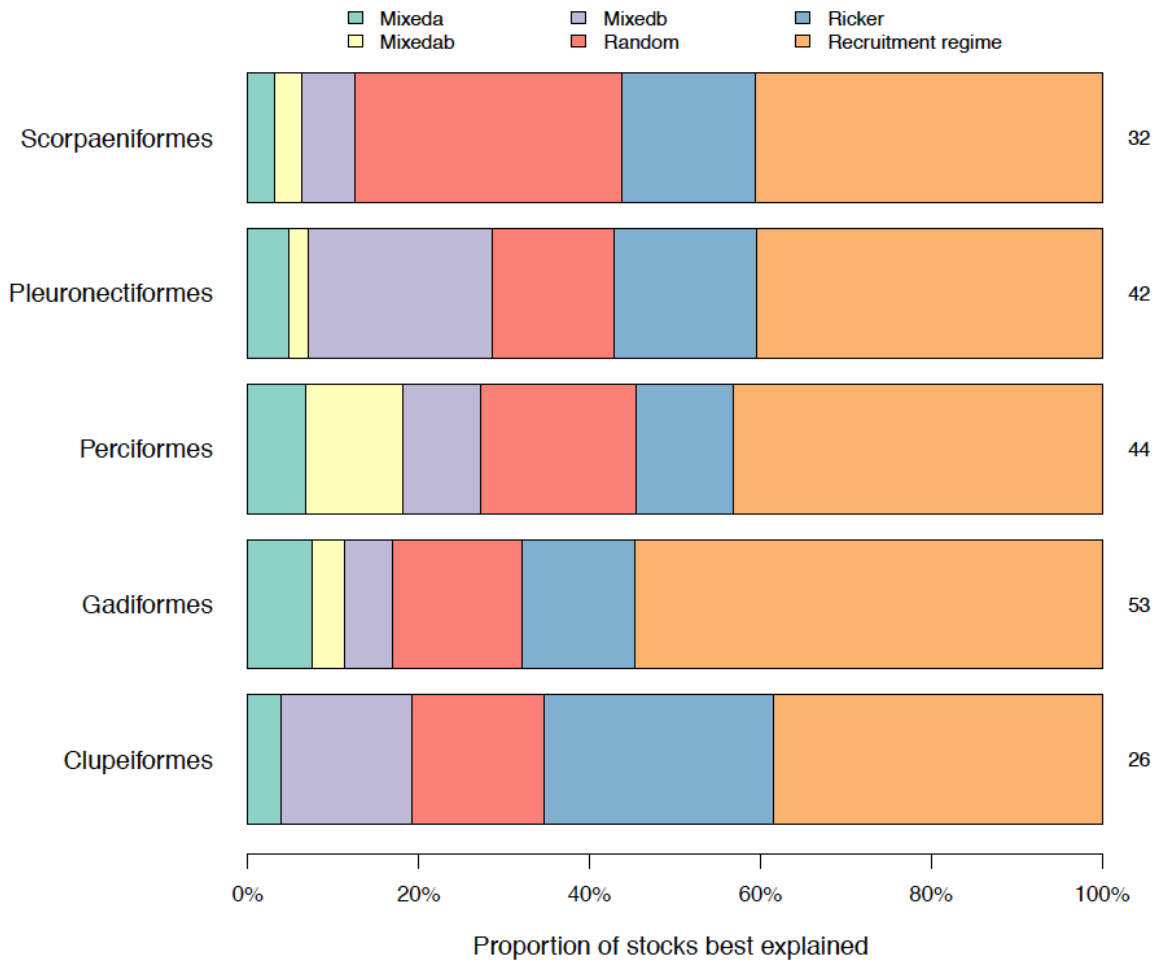


Figure 2.9. Model selection given five orders: Clupeiformes, Gadiformes, Perciformes, Pleuronectiformes, Scorpaeniformes (orders with less than 12 stocks were removed).

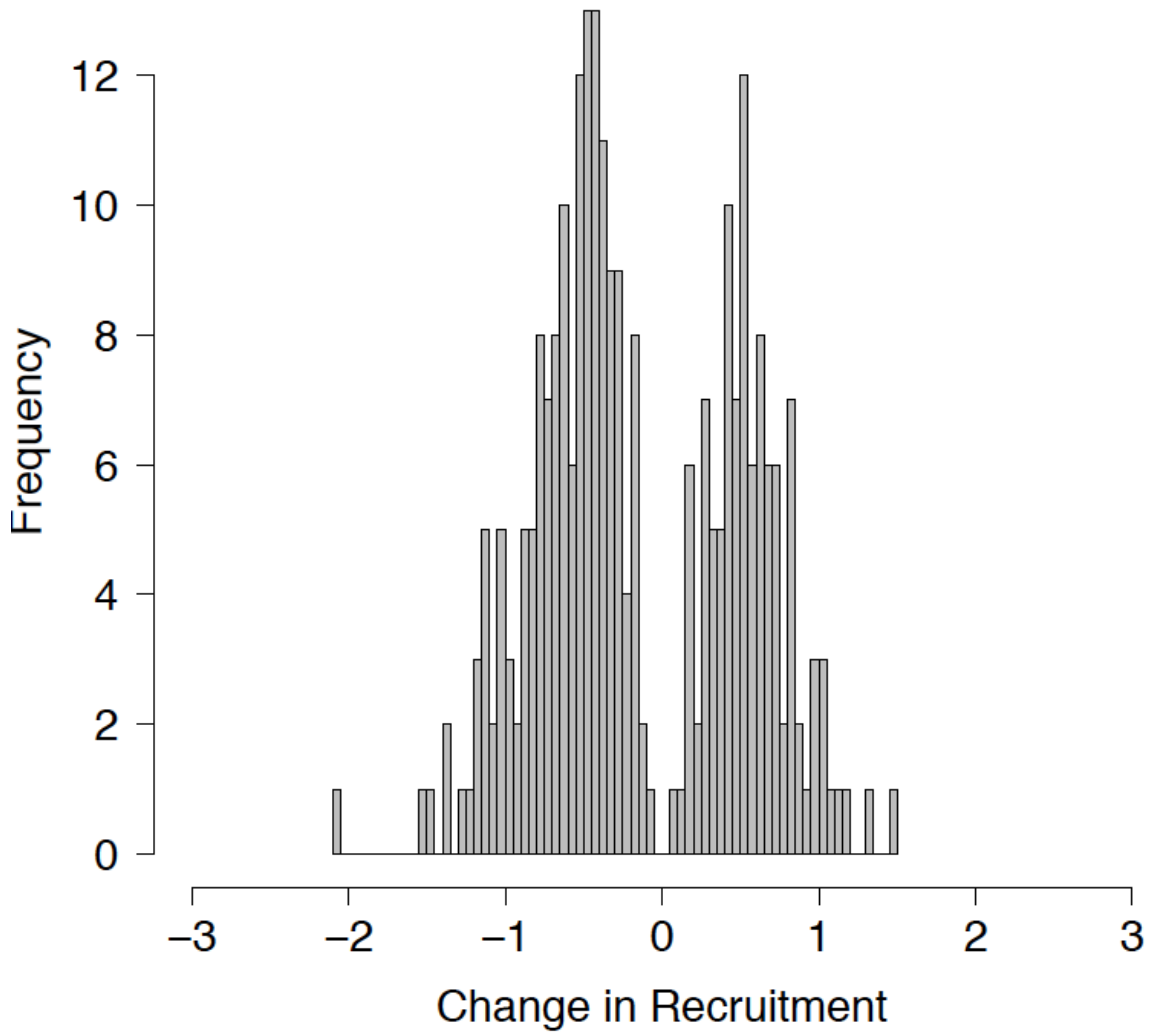


Figure 2.10. The frequency distribution of shifts in mean recruitment. The relative change was calculated as the change between regimes divided by the average recruitment across all years for that stock. Thus if the recruitment increased between regimes by 500 and the average recruitment across all years was 1000, the change was calculated as 0.5.

Tables

Hypothesis	% stocks with the highest support	# of stocks best supported	% total AICc weights	% of stocks best supported after correction for estimation bias	Corresponding Figure
Regime	45%	95	37%	50%	Figure 2.1e
Ricker	17%	36	15%	15%	Figure 2.2a
Random	18%	38	18%	18%	Figure 2.3e
Mixed <i>ab</i>	4%	9	6%	6%	Figure 2.4d
Mixed <i>a</i>	6%	12	11%	3%	Figure 2.5b
Mixed <i>b</i>	11%	23	13%	8%	Figure 2.6c

Table 2.1. The percentage of stocks and number of stocks that are best explained by each hypothesis and the total AICc weight for each.

	Best Fit Model					
Real model	Ricker	Regime	Random	Mixed <i>ab</i>	Mixed <i>a</i>	Mixed <i>b</i>
Ricker	0.80	0.00	0.10	0.00	0.00	0.10
Regime	0.01	0.85	0.05	0.01	0.05	0.03
Random	0.11	0.08	0.74	0.00	0.05	0.02
Mixed <i>ab</i>	0.12	0.00	0.00	0.5	0.13	0.25
Mixed <i>a</i>	0.27	0.00	0.09	0.00	0.55	0.09
Mixed <i>b</i>	0.13	0.09	0.05	0.05	0.00	0.68

Table 2.2. Probability that a data set generated from a “real” model would be best explained by each estimation model.

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