The frequency and intensity of productivity regime shifts in marine fish stocks.

Katyana A. Vert pre[1], Ricardo O. Amoroso[2], Olaf P. Jensen[3], Ray Hilborn[1]

[1]School of Aquatic and Fishery Sciences Box 355020
University of Washington
Seattle, WA 98195 USA

[2]Centro Nacional Patagónico,

9120 Puerto Madryn, Argentina

[3]Institute of Marine & Coastal Sciences

Rutgers University

New Brunswick, NJ 08901 USA

Corresponding Author:
Ray Hilborn

School of Aquatic and Fishery Sciences Box 355020

University of Washington

Seattle, WA 98195 USA

Email: rayh@uw.edu

Classification: Biological Sciences; Population Biology

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 regimes have been described, their frequency and intensity have not previously been assessed. We 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. We evaluated the statistical support for four hypotheses: (1) the Abundance Hypothesis, where production is always related to population abundance, (2) the Regimes 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. We found that 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%. 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.

\body

Introduction

Modern fisheries management is predicated on a repeatable relationship between stock size and the long term yield of fish stocks (1), and that population production (and thus, long term yield) is best served by holding stocks within a specific range of abundance. In the U.S. and some other developed countries, stocks are classified as overfished when their abundance falls below this target range. At that point, fishing pressure is reduced to rebuild stocks to levels that are thought to produce long term maximum sustainable yield (2). Many other national and international fishery management organizations have adopted similar approaches.

However, fish stock production often shifts between high and low productivity regimes unrelated to population size (3-6). Mullon et al. (7) explored the pattern of fisheries collapses and concluded that there were often patterns "that seem to reflect interdecadal pseudoperiodic variability which remains largely unexplained." This pseudoperiodic variability could arise from a broad range of ecological factors including changes in predator, prey or competitor abundance, or changes in physical habitats. We term this variability "productivity regimes" not to be equated or confused with the physical oceanographic regime shifts such as the Pacific Decadal Oscillation (8). One well-known example of such shifts in productivity is the collapse of Northwest Atlantic cod stocks, which, for several of these stocks, was preceded by a sharp decline in productivity at relatively high abundance (9-11). There has been substantial debate about the causes and consequences of productivity regimes across a range of fish stocks, but no systematic attempt has been made to assess the frequency and intensity of changes in productivity regimes.

Despite the dramatic example of the cod collapse and the rise of non-equilibrium or multiple-equilibrium perspectives in ecology (12), fisheries management is still based largely on a single equilibrium worldview. Within this paradigm, inter-annual fluctuations of vital rates (and thus productivity) are centered on a stationary mean, and under a fixed harvest rate populations vary around a long-term equilibrium. This paradigm, and alternatives that include regime changes in productivity, and random productivity, should be challenged with data.

If changes in productivity were generally unrelated to abundance, this would have significant consequences for fisheries management. First, one of the primary economic arguments for rebuilding overfished stocks would be negated; if greater population biomass is not associated with higher sustainable harvests, then there is much less economic reward to offset the cost (in forgone harvest) of rebuilding. Even though there are often other reasons that larger stock sizes and low fishing pressure provide economic or ecological benefits (13), a major argument for rebuilding depleted stocks has been the promise of higher sustained yield in the future. Second, if fish populations experience substantial shifts in productivity unrelated to stock size, then management based on a single set of management targets (e.g., maximum sustainable yield) will be either inefficient or risky. If the targets are based on a higher productivity regime, then a shift to low productivity regime will result in increased risk of overfishing. Conversely, management targets based on a lower productivity phase will result in overly cautious harvest during regimes of high productivity.

There was a lively debate about the relationship between population size and resulting number of young fish that began in 1950 and lasted into the 1990s. Many argued that there was little relationship between the two and fishing down stocks to low abundance did not lower the number of new fish that subsequently entered the population (recruitment) (14). In the 1990s, Myers used several hundred data sets of stock size and recruitment to show there was indeed a statistical relationship between the two – very low abundance begat lower recruitment (15, 16). Gilbert (6) challenged Myers' conclusions and argued that the apparent relationship between stock size and recruitment was often spurious. Periods of high and low recruitment that are unrelated to abundance result in high stock size during high recruitment and low stock size during low recruitment. Gilbert noted that in many of Myers' data sets recruitment dropped to low levels even though stock sizes were high, and it is the low recruitment that causes the decline in stock size rather than the other way around.

The production of sustainable yield depends not only on recruitment but also on the growth of young fish and survival from natural mortality. To understand changes in productivity we 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 recruitment, growth and natural mortality and can easily be calculated from available fish stock assessments (17).

Worm et al. (18) assembled a data base with the history of abundance and catch from published assessments that now includes 355 stocks (19). There is sufficient information on 230 stocks in these data to calculate the history of surplus production for each year, defined as the change in total biomass plus the catch for the year. We pose four competing hypotheses: (1) the Abundance Hypothesis, where production is always related to population abundance through a biomass dynamics model, (2) the Regimes Hypothesis, where production shifts irregularly between high and low productivity 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 and not explained either by productivity regime changes or population abundance. These four models can best be thought of as broad classes of models, imbedded within each is a range of different ecological relationships and processes that could lead to the dynamics described by the model. Our fundamental question is how frequently does each hypothesis provide the best explanation for the changes in observed production. The statistical support for each hypothesis was assessed using AICc, and simulation tests were also performed to evaluate the robustness and bias of the model selection criteria used here.

Results

Using a “winner takes all” approach, for 18.3% of stocks, production was best explained by the abundance hypothesis (e.g., Kattegat and Skagerrak cod, Fig. 1A-C), 38.6% of stocks are best explained by regimes (e.g., Icelandic cod, Fig. 1D-F). For 30.5% of stocks, production was best explained by the mixed hypothesis (e.g., Petrale sole from Southern California, Fig. 1G-I),, and for 12.6% of stocks the random hypothesis received most support (e.g., Common sole in the Kattegat and Skagerrak, Fig. 1J-L). Using the “relative support” approach where AICc weights are summed for each hypothesis, the relative support for the four hypotheses was similar to the winner takes all approach

(Table 1), with 16.1% for abundance, 41.3% for the regimes hypothesis, 28.3% for the mixed hypothesis, and 14.3% for the random hypothesis.

Results from simulation testing of the hypothesis testing statistics suggest that there is a slight tendency to over-classify stocks as being from the regimes and random hypotheses and to under-classify stocks as being from the abundance and the mixed hypotheses (Table 2). Nevertheless, models that include shifts in regimes in production between high and low states, either with or without an abundance effect (regimes and mixed models), constitute 72% of the stocks after adjusting for estimation bias, compared to 69% before the correction (Table 1). For the mixed hypothesis 80% of the variation in production explained by the model is attributed to the changes in the productivity relationship, and only 20% due to changes in abundance.

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 abundance to explain differences in production. We classified stocks into 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 abundance at maximum sustainable yield. Contrary to expectation, the proportion of stocks best explained by the abundance hypothesis 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, there is no significant relationship between historical variability in abundance and proportion of stocks explained by alternative models.

We identified a total of 314 productivity shifts from the 160 stocks where the preferred model included changes in productivity (regimes and mixed). We calculated the relative change in production as the absolute change (in tonnes) between high and low productivity periods divided by the average production across all years for that stock. We found that positive changes were as common as negative ones (160 increases vs. 154 declines, Fig. 2). The bimodality in Figure 2 is due to the fact that the algorithm for selecting changes does not readily identify small changes.

Discussion

Caddy and Gulland (20) 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 these “regular” stocks are only about ¼ of all the fish stocks for which we have data.

Fisheries management in the U.S., and increasingly elsewhere, uses biomass as management targets and consequently will reduce exploitation when stock sizes decline and generally will attempt to stop all directed harvesting when stocks reach low abundance. Exploitation and biomass targets are primarily designed to maintain the stock biomass in a range that will produce maximum sustained yield. Increasingly, however, these targets are being shifted toward higher biomass to increase profit and lower fishing effort to reduce ecosystem impact (21). Conventional wisdom and scientific and political expectations tell us that maintaining these levels of biomass will assure production of the stocks. In the same vein, the population abundance hypothesis predicts that if we lower the catch to rebuild stocks, higher sustainable harvests will follow once stocks are rebuilt.

However, if the production of a stock is determined by productivity regimes and stock assessments do not account for the shift in productivity, then the underlying management theory with respect to sustainable yield is incorrect. In this case, 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 are certainly valid, the benefits of increasing abundance are significantly changed.

In current U.S. management, the allowable catches of many species are limited by incidental catch of stocks that are 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 that are at low abundance. Our analysis suggests that many stocks will be at low abundance because of shifts in production. Thus, unless the management system changes or we greatly improve our ability to target individual species, current legal mandates will likely lead to major reductions in fisheries yields.

However, when production changes from high to low, the catch must be lowered. Stocks in low production regimes cannot support the same yield as stocks in high production regimes. Theoretical studies have suggested that the best approach to fluctuating production may be to harvest a constant fraction of the stock that is determined by averaging across the range of production (22, 23) or to adjust the exploitation rate based on recent recruitment (24, 25). All these studies found that rigid harvest control rules that dramatically lower exploitation rates at low population sizes sacrifice a significant amount of harvest.

Oceanographic regime shifts have been identified as important drivers of fish production in many regions, including the North Pacific (8), Tropical Pacific (26) and North Atlantic (27). However, we have found no obvious correlation between oceanic regime shifts and changes in productivity of individual stocks. Changes in a single stock’s productivity can be due to a wide range of factors influencing recruitment, survival or growth. Each of these may be influenced both by physical changes in the environment as well as changes associated with food, competitors or predators. Since we know from the long term historical record that fish stocks fluctuate considerably in abundance in the absence of fishing (5, 28), it should be expected that changes in abundance or predators and prey of any species would lead to changes in their productivity. It is not at all clear that one should expect a direct causal relationship between physical changes associated with oceanic regime shifts and shifts in productivity of fish stocks

Each of our four models describes a general class of behavior that can arise from a wide variety of mechanisms. For instance the regimes or mixed models could result from a major change in prey or predator abundance and the impact of prey and predators on recruitment, growth and survival could be explicitly modeled. A wide range of such models could generate what we interpret as shifts in productivity. Ecologists have long used such general models (for instance the logistic growth model) that incorporate a wide range of mechanisms that have similar population level consequences. The logistic growth model, for instance can represent density dependence in births, survival or individual growth rates. It also seems likely that shifts in productivity are not necessarily step functions, but might occur more gradually. Our regimes and mixed models are simplifications necessary to confine our analysis to a manageable number of competing hypotheses.

The stock assessment database on which this analysis is based is a non-random sample of fish populations (19) 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 that the population abundance model must explain. Stock assessments are generally more available for developed countries, and 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 patterns of covariance (positive or negative) in productivity across populations (29, 30) or species (31) in an ecosystem. Although there may be little that fishery managers can do to avert shifts to a lower productivity state, improved methods for early detection of such shifts (32) may permit managers to reduce harvest in time to avoid collapse.

Methods

Data

Time series of biomass, catch and fishing rate were extracted from the RAM Legacy Stock Assessment Database (19) 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; for 8 stocks the units of biomass and catch were not in the same units, 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 completed with 230 stocks.

Alternative models considered

Surplus production is defined as the net change in biomass, plus harvest (17).

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

Where S_t is the surplus production over 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 (33) was fitted to the data. The Fox model was chosen rather than the more well-known Schaefer (logistic) model as recent meta-analysis has determined that the shape of the productivity vs. biomass relationship is closer to that specified in the Fox model (34). The Fox model can be written as (35):

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

Where $\hat{S}_t$ is the predicted surplus production over year *t*; B_∞ is the carrying capacity; and *m* is the maximum sustainable yield and *e* is the base of the Naperian logarithm (2.718).

Productivity shifts are defined for our use as the change in surplus production from one state to another. For the regimes hypothesis, the challenge is to estimate the years when the productivity shifted (called break-points). We used the sequential t-test analysis of regime shifts (STARS) (36, 37), which has been widely used in similar applications (25). The STARS method estimates a series of break points that mark the first year of each flip in productivity. In general, this method involves searching over all possible breakpoints, using the Student's t-test to identify candidate breakpoints by testing for a significant change in the mean value of the time series, and then reevaluating these candidate points in the context of all other break points. This algorithm is described in detail by (36). The predicted surplus production for each year within regime *i* is simply the average surplus production during that regime.

$$(3) \qquad \overline{S_i} = \frac{\sum_{j=f_i}^{f_{i+1}-1} S_j}{f_{i+1} - f_i}$$

Where f_i is the first year of period *i;* $\overline{S}_i$ is the predicted average surplus production in period i; S_j is the surplus production in year *j*.

The mixed model combines the effect of the biomass on the stock and productivity shifts. For the mixed model, the estimated years at which break-points happened were determined using the regimes model. To test if surplus production is related to biomass and productivity shifts, a productivity shifting surplus production model was fitted to the data. It assumes that carrying capacity is time independent, but maximum sustainable yield is shifting between alternative regimes states thus the exploitation rate that produces maximum sustainable yield shifts between higher and lower values.

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

m_i is the maximum sustainable yield in each period i;

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

$$(5) \qquad \hat{S}_t = \frac{\sum_{t=1}^{y} S_t}{y}$$

Parameter estimation

For all models, the set of parameters that maximizes the likelihood was found by assuming process error and the observed surplus production is normally distributed:

$$(6) \qquad L\left(S \mid \hat{\theta}\right) = L = \prod_t \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{\left(S_t - \hat{S}_t\right)^2}{2\sigma^2}}$$

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 regimes model ($\overline{S_i}$, 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. We 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 beginning and end of the time series. Once the break points were determined the average production during each period was calculated and the value of σ determined analytically.

The parameters (B_∞, m_i, and σ) of the Mixed model were estimated by nonlinear function minimization in ADMB v10.1 using the break points estimated in the regimes model.

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

Model selection

The comparison of the four models used the Akaike Information Criterion corrected for small sample size (AICc)(38) which identified the most parsimonious model. AICc weights were also calculated and can be interpreted as the relative support of data for each model (39). The AICc was calculated as:

$$(7) \qquad AICc = -2\log(L) + 2k + \frac{2k(k+1)}{N-k-1}$$

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 regimes model varies, with one parameter for the average surplus production during each period, one parameter for each breakpoint and the value of σ. The mixed model has one parameter for each break point, one 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, we first calculate the difference between the best model and each model i (Δ_i).

$$(8) \qquad \Delta_i = AICc_i - \min(AICc)$$

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

$$(9) \qquad w_i = \frac{e^{-0.5\Delta_i}}{\sum_{j=1}^{4} e^{-0.5\Delta_j}}$$

Figure 1 shows examples of data sets where each of the alternative models was preferred.

Testing of the methods

To verify the reliability of the model selection method and correct for any mis-classification, four simulation-based evaluations were run using data generated from the abundance, the regimes, the mixed and the random 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, we selected data from 37 stocks for the abundance model, 95 stocks for the regimes model, 33 for the random model and 65 for the mixed model. Then for each stock 20 stochastic replicate data sets were generated. 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.

$$(10) \qquad U_t = \frac{C_t}{B_t}$$

Where

U_t is the exploitation rate at time t.

The biomass was simulated for the Fox model using equation 11.

$$(11) \qquad \tilde{B}_{t+1} = \tilde{B}_t + \left(-em\left(\frac{\tilde{B}_t}{B_\infty}\right)\ln\left(\frac{\tilde{B}}{B_\infty}\right) + \tilde{\varepsilon}_t \right) - \left(\tilde{B}_t U_t\right)$$

Where

$\tilde{B}_{t+1}$ is the simulated biomass at time t+1;

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 regimes and random models was calculated from equation 12.

$$(12) \qquad \begin{aligned} \tilde{B}_{t+1} &= \tilde{B}_t + \left(\hat{S}_t + \tilde{\varepsilon}_t\right) - \tilde{C}_t \\ \tilde{C}_t &= \tilde{B}_t U_t \end{aligned}$$

where

$\hat{S}_t$ is the predicted values obtain by fitting the regimes model or random model.

The biomass was simulated for the mixed model using equation 13

$$(13) \qquad \tilde{B}_{t+1} = \tilde{B}_t + \left(-em_i\left(\frac{\tilde{B}_t}{B_\infty}\right)\ln\left(\frac{\tilde{B}_t}{B_\infty}\right) + \tilde{\varepsilon}_t\right) - \left(\tilde{B}_t * U_t\right)$$

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 random, the regimes, the mixed and abundance 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, we obtain a four by four matrix (Table 2) of the classification rates, E_{ij}, where i is the true model and j is the model selected by AICc.

The classification matrix can then be used to solve for the vector model proportions (p_i) that would result in the observed proportions ($\hat{p_i}$) by nonlinear search over p_i to minimize the difference between observed and predicted $\hat{p}_j$

$$(14) \qquad \hat{p}_j = \sum_i p_i E_{ij}$$

We found that the estimated true proportion (p_i) as 27% abundance, 24% regimes, 45% mixed and 4% random.

Acknowledgements. This work was supported by the National Science Foundation and NOAA through the CAMEO (grant numbers 1041570 and 1041678). The authors thank Ana Parma, Brandon Chasco, Trevor Branch and Ulrike Hilborn for assistance during this work.

Author Contributions K.V-P. did the majority of analysis with the assistance of O.J., R.A. and R.H. R.H designed the study and assisted in the analysis. All authors contributed to the writing.

400

References

1. Beddington JR, Agnew DJ, & Clark CW (2007) Current Problems in the Management of Marine Fisheries. Science 316:1713-1716.

2. Murawski SA (2010) Rebuilding depleted fish stocks: the good, the bad, and, mostly, the ugly. ICES J. Mar. Sci. 67(9):1830-1840.

3. Burkenroad MD (1953) Theory and practice of marine fishery management. Journal du Conseil. Conseil International pour l'Exploration de la Mer 18:300-310.

4. Burkenroad MD (1946) Fluctuations in abundance of marine animals. *Science* 103:684-686.

5. Cushing D (1982) Climate and Fisheries (Academic Press, London) p 373.

6. Gilbert DJ (1997) Towards a new recruitment paradigm for fish stocks. *Can. J. Fish. Aquat. Sci.* 54:969-977.

7. Mullon C, Freon P, & Cury P (2005) The dynamics of collapse in world fisheries. *Fish and Fisheries* 6(2):111-120.

8. Mantua NJ & Hare SR (2002) The Pacific decadal oscillation. *Journal of Oceanography* 58(1):35-44.

9. Shelton PA, Sinclair AF, Chouinard GA, Mohn R, & Duplisea DE (2006) Fishing under low productivity conditions is further delaying recovery of Northwest Atlantic cod (Gadus morhua). *Can. J. Fish. Aquat. Sci.* 63:235-238.

10. Rothschild B (2007) Coherence of Atlantic cod stock dynamics in the Northwest Atlantic ocean. *Trans. Am. Fish. Soc.* 136:858-874.

11. Hilborn R & Litsinger E (2009) Cause of Decline and Potential for Recovery of Atlantic Cod Populations. *The Open Fish Science Journal* 2:32-38.

12. Wu JG & Loucks OL (1995) From balance of nature to hierarchical patch dynamics: A paradigm shift in ecology. *Quarterly Review of Biology* 70(4):439-466.

13. Hilborn R (2007) Defining success in fisheries and conflicts in objectives *Mar. Pol.* 31:153-158.

14. Gulland JA (1983) Fish stock assessment: a manual of basic methods. (John Wiley & Sons, New York) p 223 p.

15. Myers RA, Rosenberg AA, Mace PM, Barrowman N, & Restrepo VR (1994) In search of thresholds for recruitment overfishing. *ICES J. Mar. Sci.* 51:191-205.

16. Myers RA & Barrowman NJ (1996) Is fish recruitment related to spawner abundance? *Fish. Bull.* 94:707-724.

17. Hilborn R (2001) Calculation of biomass trend, exploitation rate, and surplus production from survey and catch data. *Can. J. Fish. Aquat. Sci.* 58(3):579-584.

18. Worm B, et al. (2009) Rebuilding Global Fisheries. *Science* 325:578-585.

19. Ricard D, Minto D, Jensen OP, & Baum JK (2011) Examining the knowledge base and status of commercially exploited marine species with the RAM Legacy Stock Assessment Database. *Fish and Fisheries* 13:380-398.

20. Caddy JF & Gulland JA (1983) Historical patterns of fish stocks. *Mar. Pol.* 7:267-278.

21. Hilborn R (2010) Pretty Good Yield and exploited fisheries. *Mar. Pol.* 34:193-196.

22. Parma AM (1990) Optimal harvesting of fish populations with non-stationary stock-recruitment relationships. *Natural Resource Modeling* 4(1):39-77.

23. Walters C & Parma AM (1996) Fixed exploitation rate strategies for coping with effects of climate change. *Can. J. Fish. Aquat. Sci.* 53:148-158.

24. A'Mar ZT, Punt AE, & Dorn MW (2009) The impact of regime shifts on the performance of management strategies for the Gulf of Alaska walleye pollock (*Theragra chalcogramma*) fishery. *Can. J. Fish. Aquat. Sci.* 66(12):2222-2242.

25. A'Mar ZT, Punt AE, & Dorn MW (2009) The evaluation of two management strategies for the Gulf of Alaska walleye pollock fishery under climate change. *ICES J. Mar. Sci.* 66(7):1614-1632.

26. Lehodey P, Bertignac M, Hampton J, Lewis A, & Picaut J (1997) El Nino Southern Oscillation and tuna in the western Pacific. *Nature* 389(6652):715-718.

27. Parsons LS & Lear WH (2001) Climate variability and marine ecosystem impacts: a North Atlantic perspective. *Progress in Oceanography* 49(1-4):167-188.

28. Soutar A & Isaacs JD (1974) Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediment off the Californias. *Fish. Bull.* 72(2):257-274.

29. Peterman RM, Pyper BJ, Lapointe MF, Adkison MD, & Walters CJ (1998) Patterns of covariation in survival rates of British Columbian and Alaskan sockeye salmon (Oncorhynchus nerka) stocks. *Can. J. Fish. Aquat. Sci.* 55(11):2503-2517.

30. Schindler DE, et al. (2010) Population diversity and the portfolio effect in an exploited species. *Nature* 465(7298):609-613.

31. Mueter FJ, Boldt JL, Megrey BA, & Peterman RM (2007) Recruitment and survival of Northeast Pacific Ocean fish stocks: temporal trends, covariation, and regime shifts. *Can. J. Fish. Aquat. Sci.* 64(6):911-927.

32. Biggs R, Carpenter SR, & Brock WA (2009) Spurious Certainty: How Ignoring Measurement Error and Environmental Heterogeneity May Contribute to Environmental Controversies. *BioScience* 59(1):65-76.

33. Fox WW (1975) Fitting the generalized stock production model by least-squares and equilibrium approximation. *Fish. Bull.* 73:23-37.

34. Thorson JT, Cope JM, Branch TA, & Jensen OP (2012) Spawning biomass reference points for exploited marine fishes, incorporating taxonomic and body size information. *Can. J. Fish. Aquat. Sci.* 69(9):1556-1568.

35. Quinn TJ, Jr. & Deriso RB (1999) Quantitative Fish Dynamics (Oxford University Press, New York) p 542.

36. Rodionov SN (2004) A sequential algorithm for testing climate regime shifts. *Geophysical Research Letters* 31(9).

37. Rodionov S & Overland JE (2005) Application of a sequential regime shift detection method to the Bering Sea ecosystem. *ICES J. Mar. Sci.* 62(3):328-332.

38. Burnham KP & Anderson DR (2002) Model selection and multi-model inference: a practical information-theoretic approach (Springer-Verlag, New York).

39. Hobbs NT & Hilborn R (2006) Alternatives to statistical hypothesis testing in ecology: a guide to self teaching. *Ecol. Apps.* 16:5-19.

Figure Captions

Figure 1. Surplus production data plotted against model predictions, showing individual fish stocks best explained by abundance (Atlantic cod in the Kattegat and Skagerrak panels a-c), regimes (Atlantic cod in Iceland panels d-f), the mixed hypothesis (Petrale sole from Southern California panels g-i) and random (sole from the Kattegat and Skagerrak panels j-l). The first column is the fit under the abundance model, the second column the fit under the mixed model, and the third column the regimes model, or, if no breakpoints are found, the random model (panel l). The area shaded in each pie diagram shows the AIC weight assigned to each model, so that a pie diagram that is 90% shaded indicates that 90% of the AIC weight was assigned to that model.

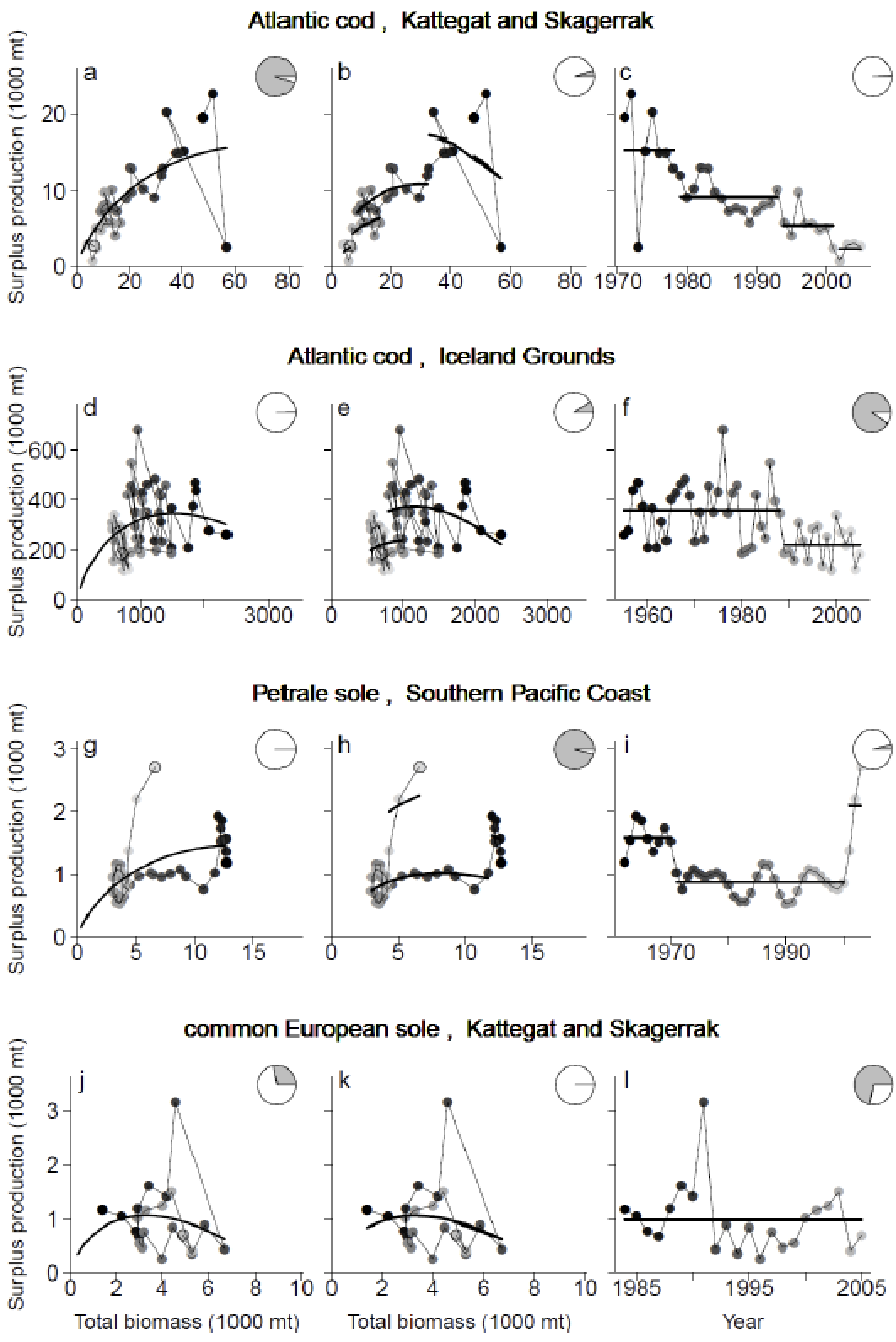
Figure 2. The frequency distribution of shifts in production. In panel a the shifts are plotted from -4 to 4 which excludes some extreme values. In panel b all the shifts are plotted in the range -20 to 20 and includes all outliers.

Table 1. The percentage of stocks and number of stocks that are best explained by each hypothesis and the total AICc weight for each.

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

Table 2: Probability that a data set generated from a "real" model would be best explained by each kind of model.

	Best Fit Model			
Real model	Abundance	Regimes	Mixed	Random
Abundance	0.54	0.14	0.08	0.24
Regimes	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

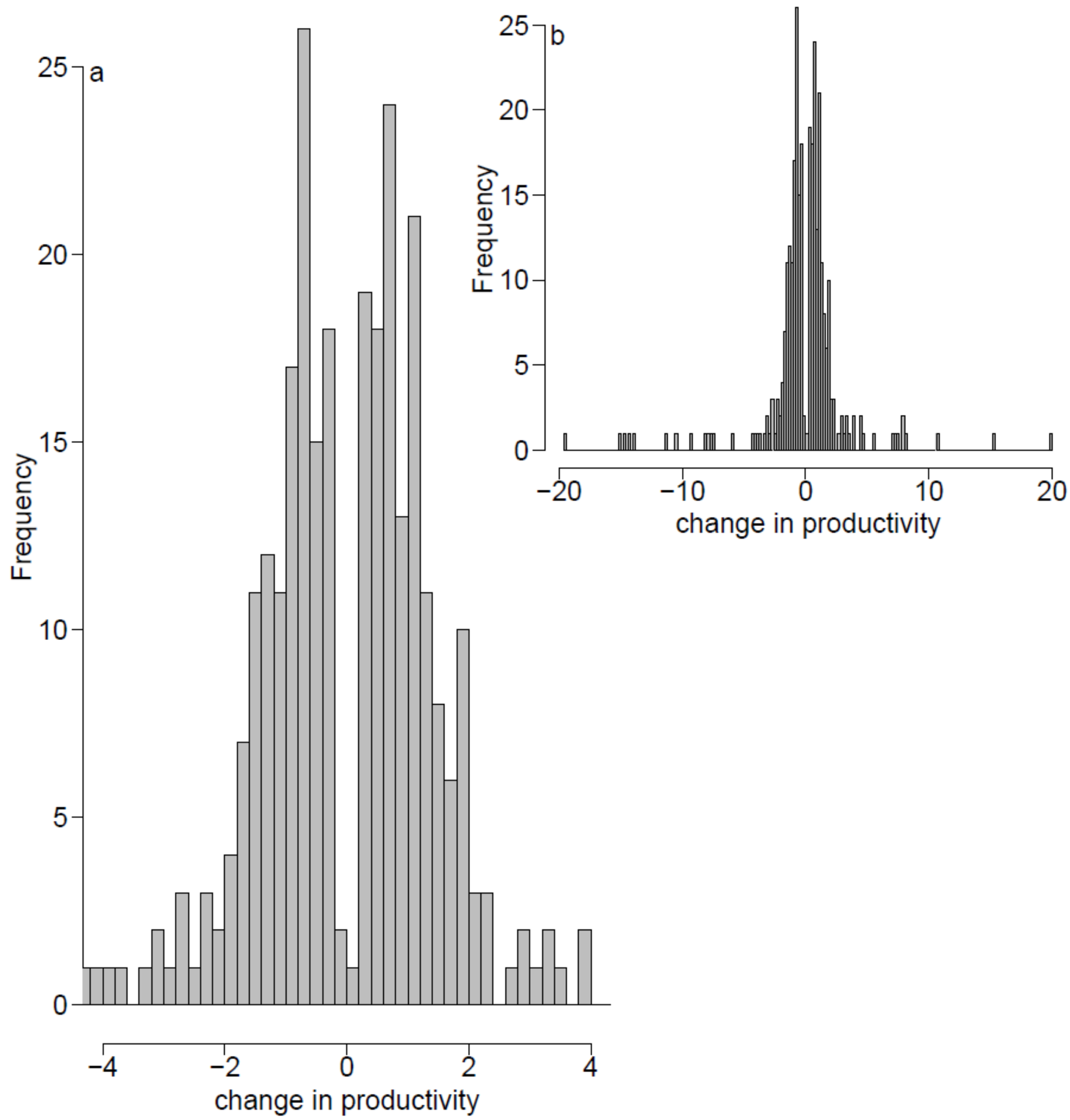


Atlantic cod , Kattegat and Skagerrak
Atlantic cod , Iceland Grounds
Petrale sole , Southern Pacific Coast
common European sole , Kattegat and Skagerrak
Surplus production (1000 mt)
Total biomass (1000 mt)
Year

516

517

518



a
Frequency
0
5
10
15
20
25
−4
−2
0
2
4
change in productivity
b
Frequency
0
5
10
15
20
25
−20
−10
0
10
20
change in productivity