Frequency and intensity of productivity regime shifts in marine fish stocks

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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. Although shifts in productivity regimes have been described, their frequency and intensity have not previously been assessed. We use a database of trends in harvest and abundance of 230 fish stocks to evaluate the proportion of fish stocks in which productivity is primarily related to abundance vs. those that appear to manifest regimes of high or low productivity. We evaluated the statistical support for four hypotheses: (*i*) the abundance hypothesis, where production is always related to population abundance; (*ii*) the regimes hypothesis, where production shifts irregularly between regimes that are unrelated to abundance; (*iii*) the mixed hypothesis, where even though production is related to population abundance, there are irregular changes in this relationship; and (*iv*) 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.

fish productivity | multiple stable states | regime change | surplus production models | population dynamics

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 United States 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 the 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 collapses of fisheries 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 nonequilibrium or multiple-equilibrium perspectives in ecology (12), fisheries management is still based largely on a single equilibrium worldview. Within this paradigm, interannual 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, there is much less economic reward to offset the cost (in foregone harvest) of rebuilding. Even though there are often other reasons why 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, 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, a shift to a 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 the 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 that 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 and coworkers (15, 16) used several hundred datasets of stock size and recruitment to show there was indeed a statistical relationship between the two: Very low abundance begat lower recruitment. Gilbert (6) challenged these 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 (6) noted that in many of Myers and coworkers' datasets (15, 16), 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.

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The production of sustainable yield depends not only on recruitment but 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 it can easily be calculated from available fish stock assessments (17).

Worm et al. (18) assembled a database 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: (*i*) the abundance hypothesis, where production is always related to population abundance through a biomass dynamics model; (*ii*) the regimes hypothesis, where production shifts irregularly between high- and low-productivity regimes that are unrelated to abundance; (*iii*) the mixed hypothesis, where even though production is related to population abundance, there are irregular changes in this relationship; and (*iv*) the random hypothesis, where production is random from year to year and is not explained by either productivity regime changes or population abundance. These four models can best be thought of as broad classes of models, and embedded within each is a range of different ecological

Fig. 1. Surplus production data plotted against model predictions showing individual fish stocks best explained by the abundance (*A–C*; Atlantic cod in the Kattegat and Skagerrak), regimes (*D–F*; Atlantic cod in Iceland), mixed (*G–I*; Petrale sole from Southern California), and random (*J–L*; common European sole in the Kattegat and Skagerrak) hypotheses. The first column is the fit under the abundance model, the second column is the fit under the mixed model, and the third column is the fit under the regimes model or, if no breakpoints are found, the random model (*I*). The area shaded in each pie diagram shows the AIC weight assigned to each model, such that a pie diagram that is 90% shaded indicates that 90% of the AIC weight was assigned to that model. mt metric tons. Points are shaded from dark (earliest data) to light (latest data).

Table 1. 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	No. of stocks best supported	Total AICc weight	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%

relationships and processes that could lead to the dynamics described by the model. Our fundamental question is how frequently each hypothesis provides the best explanation for the changes in observed production. The statistical support for each hypothesis was assessed using the Akaike Information Criterion corrected for small sample size (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. 1 *A–C*), and 38.6% of stocks were best explained by the regimes hypothesis (e.g., Icelandic cod; Fig. 1 *D–F*). For 30.5% of stocks, production was best explained by the mixed hypothesis (e.g., Petrale sole from Southern California; Fig. 1 *G–I*), and for 12.6% of stocks, the random hypothesis received the most support (e.g., common European sole in the Kattegat and Skagerrak; Fig. 1 *J–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 the abundance hypothesis, 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 overclassify stocks as being from the regimes and random hypotheses and to underclassify stocks as being from the abundance and 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 with 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% is 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, 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 their abundance at the 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 the proportion of stocks explained by alternative models.

We identified a total of 314 productivity shifts from the 160 stocks in which the preferred model included changes in productivity (regimes and mixed). We calculated the relative change in production as the absolute change (in tons) 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 Fig. 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 (20). Our analysis suggests that these "regular" stocks are only about one-quarter of all the fish stocks for which we have data.

Fisheries management in the United States, 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 the 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 ensure 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, 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. Although 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 US 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

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

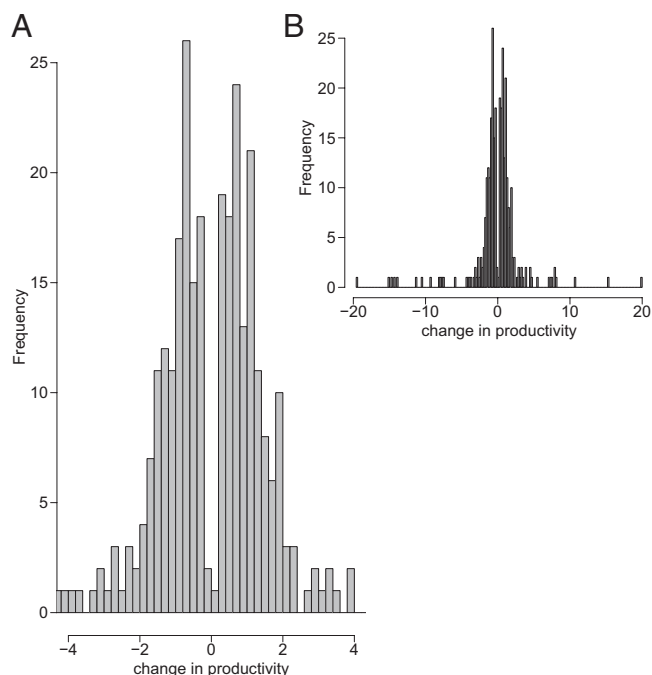| Real model	Best-fit model			
	Abundance	Regimes	Mixed	Random
Abundance	0.54	0.14	0.08	0.24
Regimes	0.04	0.81	0.11	0.04
Mixed	0.05	0.33	0.57	0.04
Random	0.12	0.13	0.04	0.71

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Fig. 2. Frequency distribution of shifts in production. (*A*) Shifts are plotted in the range from −4 to 4, which excludes some extreme values. (*B*) Shifts are plotted in the range from −20 to 20 and include all outliers.

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 by physical changes in the environment as well as by changes associated with food, competitors, or predators. Because 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 in 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 model or mixed model 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 (e.g., the logistic growth model), which 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 model and mixed model 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 nonrandom sample of fish populations (19), and it 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 underrepresent 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 10, 2010. Only 279 stocks had no missing data points within the time series; thus, these stocks were initially selected for analysis. A total of 49 of the 279 datasets 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 y; 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 because recent metaanalysis has determined that the shape of the productivity vs. biomass relationship is closer to that specified in the Fox model (34). The Fox model (35) can be written as follows:

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

where $\hat{S}_t$ is the predicted surplus production over year t, B_∞ is the carrying capacity, 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 breakpoints). We used the sequential t test analysis of regime shifts (STARS) (36, 37), which has been widely employed in similar applications (25). The STARS method estimates a series of breakpoints that mark the first year of each flip in productivity. In general, this method involves searching over all possible breakpoints, using the Student t test to identify candidate breakpoints by testing for a significant change in the mean value of the time series, and

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then reevaluating these candidate points in the context of all other breakpoints. This algorithm is described in detail by Rodionov (36). The predicted surplus production for each year within regime i is simply the average surplus production during that regime:

$$\overline{S}_i = \frac{\sum_{j=f_i}^{f_{i+1}-1} S_j}{f_{i+1}-f_i},$$ [3]

where f_i is the first year of period i, $\overline{S}_i$ is the predicted average surplus production in period i, and 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 breakpoints 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 independent of time but maximum sustainable yield is shifting between alternative regimes states; thus, the exploitation rate that produces a maximum sustainable yield shifts between higher and lower values:

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

where m_i is the maximum sustainable yield in each period i.

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

$$\hat{S}_t = \frac{\sum_{t=1}^{y} S_t}{y}.$$ [5]

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

$$L\left(S|\hat{\theta}\right) = L = \prod_t \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(s_t-\hat{s}_t)^2}{2\sigma^2}},$$ [6]

where $\hat{S}_t$ is the predicted surplus production under each model for year t; σ is the SD of the surplus production about the model prediction, and $\hat{\theta}$ 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, and 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 the "cutoff-length," and the significance level for the t tests. We used a cutoff-length of 10 y and a 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 breakpoints were determined, the average production during each period was calculated and the value of σ was 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 breakpoints estimated in the regimes model.

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

Model Selection. The comparison of the four models used the 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 follows:

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

where L is the likelihood of the data given the parameters, 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 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 an additional parameter representing the value of σ. The mixed model has one parameter for each breakpoint, 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):

$$\Delta_i = AICc_i - min(AICc).$$ [8]

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

$$w_i = \frac{e^{-0.5\Delta_i}}{\sum_{j=1}^{4} e^{-0.5\Delta_j}}.$$ [9]

Fig. 1 shows examples of datasets in which each of the alternative models was preferred.

Testing of the Methods. To verify the reliability of the model selection method and to correct for any misclassification, four simulation-based evaluations were run using data generated from the abundance, regimes, mixed, and random models and were then subjected to evaluation using each of these four models. The simulation procedure is described below using process errors.

Datasets 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 datasets were generated. The initial biomass of each simulation was the value of the initial biomass in the first year of the dataset. The exploitation rate, U_t, for every year was calculated from the data used in our analysis:

$$U_t = \frac{C_t}{B_t},$$ [10]

where U_t is the exploitation rate at time t.

The biomass was simulated for the Fox model using Eq. **11**:

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

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 the normal process error [$\tilde{\varepsilon} \sim N(0,\sigma)$], and σ is the parameter obtained by fitting the Fox model.

The biomass for the regimes and random models was calculated from Eq. **12**:

$$\tilde{B}_{t+1} = \tilde{B}_t + \left(\hat{S}_t + \tilde{\varepsilon}_t\right) - \tilde{C}_t$$
$$\tilde{C}_t = \tilde{B}_t U_t,$$ [12]

where $\hat{S}_t$ is the predicted value obtained by fitting the regimes model or the random model.

The biomass was simulated for the mixed model using Eq. **13**:

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

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 the normal process error [$\tilde{\varepsilon} \sim N(0,\sigma)$], and σ is the parameter obtained by fitting the mixed model.

Given the new series of $\tilde{C}$ and $\tilde{B}$, the surplus production from the simulated data were calculated using Eq. **1**.

The random, regimes, mixed, and abundance models were fitted to the simulated series of surplus production, and the AICc was used to select a best model for each dataset. The "classification rate" was calculated as the number of stocks best explained by each model divided by the number of stocks simulated.

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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 the 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 non-linear search over p_i to minimize the difference between the observed and predicted $\hat{p}_j$:

$$\hat{p}_j = \sum_i p_i E_{ij}. \qquad [14]$$

We found the estimated true proportion (p_i) to be 27% for the abundance model, 24% for the regimes model, 45% for the mixed model, and 4% for the random model.

1. Beddington JR, Agnew DJ, Clark CW (2007) Current problems in the management of marine fisheries. *Science* 316(5832):1713–1716.
2. Murawski SA (2010) Rebuilding depleted fish stocks: The good, the bad, and, mostly, the ugly. *ICES Journal of Marine Science* 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(3):300–310.
4. Burkenroad MD (1946) Fluctuations in abundance of marine animals. *Science* 103(2684):684–686.
5. Cushing D (1982) *Climate and Fisheries* (Academic, London).
6. Gilbert DJ (1997) Towards a new recruitment paradigm for fish stocks. *Can J Fish Aquat Sci* 54(4):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. *J Oceanogr* 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(2):235–238.
10. Rothschild B (2007) Coherence of Atlantic cod stock dynamics in the Northwest Atlantic ocean. *Trans Am Fish Soc* 136(3):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. *Q Rev Biol* 70(4):439–466.
13. Hilborn R (2007) Defining success in fisheries and conflicts in objectives. *Marine Policy* 31(2):153–158.
14. Gulland JA (1983) *Fish Stock Assessment: A Manual of Basic Methods* (Wiley, New York).
15. Myers RA, Rosenberg AA, Mace PM, Barrowman N, Restrepo VR (1994) In search of thresholds for recruitment overfishing. *ICES Journal of Marine Science* 51(2):191–205.
16. Myers RA, Barrowman NJ (1996) Is fish recruitment related to spawner abundance? *Fishery Bulletin* 94(4):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(5940):578–585.
19. Ricard D, Minto D, Jensen OP, Baum JK (2012) 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. *Marine Policy* 7(4):267–278.
21. Hilborn R (2010) Pretty good yield and exploited fisheries. *Marine Policy* 34(1):193–196.
22. Parma AM (1990) Optimal harvesting of fish populations with non-stationary stock-recruitment relationships. *Nat Resour Model* 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(1):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 Journal of Marine Science* 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. *Prog Oceanogr* 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):609–612.
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) Turning back from the brink: Detecting an impending regime shift in time to avert it. *Proc Natl Acad Sci USA* 106(3):826–831.
33. Fox WW (1975) Fitting the generalized stock production model by least-squares and equilibrium approximation. *Fish Bull* 73(1):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 Univ Press, New York).
36. Rodionov SN (2004) A sequential algorithm for testing climate regime shifts. *Geophys Res Lett* 31(9), 10.1029/2004GL019448.
37. Rodionov S, Overland JE (2005) Application of a sequential regime shift detection method to the Bering Sea ecosystem. *ICES Journal of Marine Science* 62(3):328–332.
38. Burnham KP, Anderson DR (2002) *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach* (Springer, New York).
39. Hobbs NT, Hilborn R (2006) Alternatives to statistical hypothesis testing in ecology: A guide to self teaching. *Ecol Appl* 16(1):5–19.