Supporting Information

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SI Text

Sources of Data. We used Myers et al. (1) meta-analysis of stock–recruitment relationships for species-specific mean estimates of the maximum reproductive rate (α).

Because Myers et al. (1) used a mixed-effects model to combine estimates from multiple fish populations to obtain species-level estimates of α, they report two types of uncertainty associated with mean estimates of α: the SEM estimate and the among-population variation within a given species. Among-population estimates of variance are only available for species that had stock–recruitment data from at least two populations. We report the SEM in Table S1 and Fig. 1 (main text) and the among population variation in Fig. S1.

We gathered estimates of the natural mortality rate for biomass, M_p, from a diverse array of published and gray literature sources. Where available, we collected published estimates of biomass natural mortality, M_p. However, published estimates of mortality were frequently derived from age-structured stock assessments and were in terms of individuals, M_a, not biomass mortality, M_p. M_p represents the net effect of mortality and growth into a single term, so as long as fish do not shrink as they age, $M_a \geq M_p$. Thus, M_a is a conservative proxy for M_p—our estimates of M_p are larger than the actual M_p. In addition, some species had age- or size-specific estimates of M_a. In such cases, we used the maximum literature value of M_a for fish older (or larger) than the age (or size) at maturity for the analysis. This approach also introduces a positive bias to our estimates of M_p. For completeness, we report maximum and minimum values of M_p (where available) from the literature (Table S1) and repeated all analyses using both minimum and maximum estimates of M_p. Using maximum vs. minimum values of M_p made no qualitative difference in the results.

For fishing mortality, F, estimates of biomass mortality were more readily available. Because published estimates of F varied so much among stocks within each species, and we wished to ensure that the effects of fishing mortality were at comparable levels across species, we elected to model the consequences of fishing at standardized fishing level. Thus, we model the predicted consequences of fishing mortality in all species when that species is fished at a level expected to produce maximum sustained yield, F_{MSY}. For populations in which fishing mortality occurs only on mature individuals, M_p is an accepted approximation of F_{MSY} (2). However, exploration of alternate approximations of F_{MSY} had no qualitative effects on the results.

The mean F may not be the only important aspect of fishing mortality: the temporal variability in fishing mortality may play an important role in fish population fluctuations. To document observed variation in F in fish populations, we collected published or gray literature sources for time series of F. Not all fisheries stock assessments estimate much less publish annual estimates of fishing mortality, but we were able to uncover time series for annual estimates of F for 66 stocks representing 22 species (Table S2). All time series were at least 19 y long. Observed variability in F, expressed as the coefficient of variation of F, $\left(\mathrm{CV}(F) = \frac{\mathrm{sd}(F)}{\bar{F}}\right)$, ranged from a minimum of 0.08 to a maximum of 0.96 across stocks and species, with a cross-species average of ≈0.4. Because the availability of estimates of F is not representative of fish stocks—available time series of F were overrepresented by stocks from the North Atlantic—our estimates of CV(F) are necessarily approximate. However, we view the range of CV(F) from 0 to 1.0 as a reasonable, empirically justified range over which to explore the consequences of variability in fishing mortality on the variability of populations (*Stochastic simulation of the Ricker model*).

We calculated the recruitment lag, τ, as the age at which 50% of individuals were estimated to be mature (A_{50}) for each species. In cases for which distinct maturity curves were available for each sex, we used the A_{50} for females, and where multiple estimates for a single species were found we took the largest reasonable published lag. Additionally, when age at maturity was reported in noninteger years, we rounded up to the nearest year (e.g., age at maturity of 1.3 y was classified as $\tau = 2$). However, we acknowledge that for some species, τ may vary greatly among species, and our literature-derived estimates of τ may not be representative for all populations within a species. Our estimates of τ are approximate.

In total we found estimates of α and M_p for 45 species that span many important fisheries species (Table S1). We excluded the four salmon species in the analysis of the consequences of fishing because our model is not appropriate for estimating the fisheries effect on salmon dynamics (*Alternative Models of Fisheries*). Our data collection and filtering procedures produce slightly high estimates of M_p and τ. Because higher morality rates and longer recruitment lags are associated with increasing the probability deterministic population cycles or chaos (3), our data selection procedures increase the probability of identifying species as having deterministic fluctuations.

In addition to our examination of the Ricker model, we analyzed a related production model, the Deriso-Schnute model, to ensure that our results do not simply arise from our choice of the Ricker model (*Alternative Production Models*). The Deriso-Schnute model requires additional biological data, namely the von Bertalanffy growth coefficient, k. Therefore, we collected published estimates of k for each species. We used FishBase (www.fishbase.org), gray literature stock assessments, and journal publications to estimate the range of k. We discovered that estimates of von Bertalanffy k are highly variable within a species, so we present a range of published values of k that bracket the likely range of this parameter for each species and perform multiple simulations to explore the effect of uncertainty in k on our results (Table S1). Although we explored the literature for estimates of temporal variability in k, we were unsuccessful in finding statistically robust estimates of temporal variation in k.

Simulation Details. ***Deterministic simulation of the Ricker model.*** To calculate stability directly, we simulated Eq. **6** (main text) for each species for 3,000 y for estimated natural mortality (M_p) and maximum reproductive rate (α). We fixed $\beta = 0.001$ because it only serves to scale steady-state biomass (Eq. **4**, main text). We discarded the first 100 y as burn-in and calculated the coefficient of variation, CV(B), for years 101 to $N + 100$, where N is the desired simulation length. Nonzero CVs were taken to be indicative of cyclical or chaotic dynamics. Inspection of simulated time series confirmed the presence of persistent fluctuations. We repeated this analysis for populations in the presence of constant fishing mortality for each species (total mortality, $Z = M_p + F_{MSY}$) and for both maximum and minimum estimates of M_p [Fig. 1 (main text), Fig. S1, and Table S1].

Stochastic simulation of the Ricker model. Simulations of unexploited populations. We conducted a series of stochastic simulations under a range of parameter combinations of the mean of maximum per capita reproduction and natural mortality, $\bar{\alpha}$, $\overline{M}_p$, and their variances and correlation, Var(α), Var(M_p), and Cor (α, M_p), to understand the effect of environmental variability on population variability in the absence of fishing mortality. Our simulations spanned plausible ranges for $\overline{\alpha}$ (0.01–15) (1) and $\overline{M}_p$ (0.01–2) for iteroparous species, and we used a lognormal distribution to describe variation in both parameters (4). We bracketed published estimates of temporal variability of α [CV(α) range: 0.2–1.4] (5, 6) by simulating populations with CV(α) of 0.2–1.5. The variability of M_p in fish populations is poorly understood and in many stock assessments assumed to be a constant. However, in practice, natural mortality must vary (7), so we simulated a range of CV(M_p) that spans a biologically plausible range (0.001–1.0). Finally, we considered a range *Cor* (α, M_p) from −0.7 to 0.7. For the log-normal distribution, $Var(M_p) = \log(CV(M_p)^2 + 1)$ so we simulate $M_p \sim LogNormal\left(\overline{M}_p - \frac{Var(M_p)}{2}, Var(M_p)\right)$. This formulation maintains a constant mean across simulations. The variance and log-normal distribution of α adopt an analogous form. For simplicity, we first assumed that parameter variability was white noise; parameters for each year represent independent realizations from a stationary joint distribution of α and M_p. We also relaxed this assumption and simulated populations with positive temporal autocorrelation in vital rates (see *Adding autocorrelation to simulations*). We present the consequences of environmental variation for the temporal variability of populations (Fig. S2).

In addition to the general simulation, we performed simulations for each species using available estimates of M_p and α. Variation in α among populations of a single species can be substantial (6), and we assume that variation in M_p with a species is similarly variable even though no empirical estimates are available. Rather than making specific assumptions about the variability in M_p and α for each species, we adopted a more general simulation approach to understand what patterns in temporal variability will appear under a range of potential temporal variability patterns and examined our simulations for general patterns. We simulated each species across the following parameter ranges: CV(α) range: 0.2–1.5; CV(M_p) range: 0.001–1.0; *Cor*(α, M_p) range: –0.7 to 0.7. To conduct simulations for populations in the absence of fishing, we drew pairs of log(M_p) and log(α) from a bivariate normal distribution with appropriate variance–covariance matrix and simulated each scenario. To calculate a population's CV we estimate the population's mean and SD from the simulated time series. We use long simulations (≥3,000 y) to improve the estimation of CV(B). We avoid the effect of simulation burn-in by not including the first 100 y of simulation in the calculation of CV(B). In summary, we ran simulations for each species across all possible combinations of CV(α), CV(M_p), and Cor(α, M_p) and used CV(B) as our response variable.

Simulations of exploited populations. Adding fishing mortality to the simulation of fish populations is relatively straightforward. The simulations for distributions of α and M_p are identical to the simulations for unexploited populations (see above). Like M_p, fishing mortality, F, was also considered to be log-normally distributed, $F \sim LogNormal\left(\overline{F} - \frac{Var(F)}{2}, Var(F)\right)$. Each year, F was considered to be independent of M_p and α. Given that fishing harvest levels typically are established well before any estimate of natural mortality is available for a given year, this assumption is reasonable. Total mortality, Z, is the sum of natural and fishing mortality, $Z = M_p + F$. Unfortunately, the sum of two log-normal random variables has no closed form solution, and therefore we cannot simply write down a distribution for Z and simulate it. However, simulating the distributions of F and M_p is straightforward as long as M_p and F can be considered to be independent. We used our empirical estimates of temporal variability in F (Table S2) to bound reasonable levels of variability in F [range CV(F): 0–1.0]. As noted in the main text (*Methods*, *Interaction Between Environmental Variability and Fisheries*), the temporal variability of F is very difficult to estimate empirically. To simplify our analysis, ensure generality, and enhance interpretability, we simulated all species at the fishing effort that approximates maximum sustained yield, F_{MSY}. For populations in which fishing mortality occurs only on mature individuals, M_p approximates F_{MSY} (2). Therefore, we simulated each of our species with $\overline{F}_{MSY} = \overline{M}_p$ to explore the consequence of fishing at F_{MSY} for the variability of populations. Exploratory simulations of other possible relationships between F_{MSY} and M_p (e.g., $F_{MSY} = M_p/2$) produced qualitatively similar results. In summary, we ran simulations for each species across all possible combinations of CV(α), CV(M_p), Cor(α, M_p), and CV(F). Compared with the simulation results from the unexploited population, our simulations can be interpreted as examining the consequences of fishing at maximum sustained yield for the temporal variability of populations. In simulations that compare CV(B) for unexploited and exploited populations, we excluded the small number of species for which the addition of fishing mortality moved populations to parameters with a negative equilibrium biomass.

Adding autocorrelation to simulations. As noted earlier, the basic simulations considered environmentally driven parameters α and M_p to follow log-normal distributions with white noise; each year of simulated values of α and M_p are independent of the previous year. However, there is increasing evidence that many environments are positively autocorrelated (8). In terms of the model used here, positive autocorrelations can arise from either autocorrelation in the abiotic environment (e.g., temperature variability) or via autocorrelation in the biotic environment (e.g., the abundance of predator or prey species). Because the magnitude and mechanistic causes of positive temporal autocorrelation are almost wholly unknown in real-world systems, we simulated our populations under three autocorrelation scenarios to understand how the addition of temporal autocorrelation affects our results.

In all cases we generated autocorrelated time series of α and M_p using standard Markov chain Monte Carlo (MCMC) techniques. Because we wanted to maintain a specified variance–covariance structure between α and M_p, we used a Metropolis-Hastings algorithm to MCMC sample their distribution. The joint distribution of log(α) and log(M_p) is bivariate normal with a variance–covariance matrix Σ. For notational convenience in the following we denote this probability distribution function $h(\alpha, M_p)$ or even more briefly $h()$. There are three components in creating a MCMC sampler for $h()$. First, given a current value of the two parameters, α^c and M_p^c, propose new values of the parameters to determine the next proposed position of α^* and M_p^*. In all simulations we use a symmetric proposal distribution identical to distribution $h()$. Second, calculate the probability of proposed values relative to the current values, q, given the distribution $h()$; $q = min\left(1, \frac{h(\alpha^*, M_p^*)}{h(\alpha^c, M_p^c)}\right)$. Third, accept the proposed values with probability q. Repeating this process many times, this procedure generates the distribution $h(\alpha, M_p)$. Further, the time series of accepted values in the MCMC chain are autocorrelated samples from $h(\alpha, M_p)$. By varying the proposal distribution and thinning the MCMC chain to various degrees we can obtain different lag-one autocorrelations of α and M_p for use in simulations. For illustration, Fig. S3 illustrates how the MCMC chain can be thinned to produce a lag-one autocorrelation of 0.4 and thinned further to produce independent draws from $h(\alpha, M_p)$.

Essentially, we designed a poorly mixing MCMC sampler of the joint distribution of α and M_p and thinned the MCMC chain until we obtained a series of the parameters with the approximate temporal autocorrelation of interest. Because this process is computationally intensive and we had to simulated this process over many values of α, M_p, F, and affiliated variances and covariances, we only conducted three autocorrelation scenarios, $\phi = 0$, 0.4, and 0.8.

Alternative Production Models. ***Deriso-Schnute model.*** In the main text we use analytic and stochastic modeling approaches to investigate a ubiquitous population model, the discrete-time Ricker model, and understand the causes of fluctuations in fish populations. However, the Ricker model is far from the only possible population model for fish. In this section we investigate the sensitivity of our results to our use of the Ricker model. Specifically, we repeated our stability analysis on the Deriso-Schnute model (9 and 10, p 212). The Deriso-Schunte formulation models the processes of recruitment, somatic growth, natural mortality, and fisheries mortality separately, whereas somatic growth and natural mortality are combined in the Ricker model. However, the model is unfamiliar to most readers outside of fisheries science and is not as straightforward to interpret as the Ricker formulation.

If annual growth (described by the von Bertalanffy growth coefficient, k) and total mortality ($Z = M + F$) are constant across years, and recruitment is a function of spawning biomass τ years in the past and follows the Ricker recruitment, biomass in year B_t is:

$$B_t = (1+e^{-k})e^{-Z}B_{t-1} - e^{-k-2Z}B_{t-2} + \alpha B_{t-\tau}e^{-\beta B_{t-\tau}}, \qquad \textbf{[S1]}$$

the steady state biomass of this model is

$$B_0 = \frac{1}{\beta}\log\left(\frac{\alpha}{1+e^{-k-2Z}-(1-e^{-k})e^{-Z}}\right), \qquad \textbf{[S2]}$$

and the linear stability criteria of this model at B_0 is

$$g'(B_0) = \Bigg(1+e^{-k-2Z} - \left(1-e^{-k}\right)e^{-Z}\Bigg)\log\left(\frac{\alpha}{1+e^{-k-2Z}-(1-e^{-k})e^{-Z}}\right). \qquad \textbf{[S3]}$$

Thus, the stability condition $|g'(B_0)| < 1$ is determined by the ratio of the maximum reproductive rate, α, to a complicated term including the von Bertalanffy growth coefficient, k, and total adult mortality rate, Z, but not the density-dependent parameter β [see also Quinn and Deriso (10)]. Note also that as k becomes very large, $k \to \infty$, the Deriso-Schnute model collapses to the Ricker model.

To determine whether this model generated different results than the discrete Ricker, we collected published estimates of the von Bertalanffy growth coefficient and used simulation to examine the stability properties for species in our data set. Mortality estimates and estimates of k are uncertain for some species. To account for this uncertainty, we performed a range of simulations, from using the minimum estimates for parameters, M and k, to using the maximum estimates of each parameter, and all other possible combinations. As with Ricker model, we performed simulations in the absence of fishing mortality ($Z = M$) and in the presence of fishing mortality ($Z = M + F$) to ask whether the addition of fishing mortality moved populations from stable, equilibrial dynamics to deterministically fluctuating or chaotic dynamics, as has been suggested by Anderson et al. (11).

Because the stability criteria are a function of three parameters (α, Z, and k) in the Deriso-Schnute model instead of the two in the Ricker, the Deriso-Schnute model does not lend itself to easy graphical representation [unlike Fig. 1 (main text)]. Instead we summarize the results of these simulations for the extreme cases; the first simulating parameters at the minimum of their reported range [min (M) and min (k); hereafter "minimum scenario"] and the second simulating populations at the maximum of their range [max (M) and max (k); hereafter "maximum scenario"]. We exclude salmon from this analysis because the form of the Deriso-Schnute model used is formulated for iteroparous species. For both maximum and minimum scenarios, the results for the Deriso-Schnute model are broadly in alignment with the results of the Ricker. In the absence of fishing, very few species exhibited deterministic fluctuations: five of 41 species for the minimum scenario and four of 41 species for the maximum scenario. Three species were identified in both simulations (Atlantic menhaden, Greenland halibut, and swordfish), whereas the minimum scenario also included black anglerfish and striped bass and the maximum scenario included gold-spotted grenadier anchovy. Note that the three species identified by the Ricker model as potentially fluctuating in the absence of fishing mortality are identified as having the potential for deterministic fluctuations by the Deriso-Schnute model (Atlantic mendhaden, swordfish, and gold-spotted grenadier anchovy). When fishing mortality is added to the minimum scenario, two additional species exhibit deterministic fluctuations (scup and gold-spotted grenadier anchovy). However, when fishing mortality is included in the maximum scenario, no additional species show fluctuating dynamics. Again the simulations in the presence of fishing match previous results with the species moving from stable to fluctuating dynamics in response to fishing including the species identified in the Ricker model (scup).

Results from the Deriso-Schnute model are in agreement with our analysis of the Ricker model and suggest that additional mortality from fishing is very unlikely to change species dynamics from a single stable equilibrium to deterministic fluctuations (cycles or chaos). As mentioned in the main text, the maximum reproductive rate for each of these species identified (except Greenland halibut) is derived from a single population's stock-recruit data and may be estimated with uncertainty. The Deriso-Schnute model does identify a few additional species as having the potential for cyclic or chaotic dynamics. However, these additional species tend to be species with long lags between reproduction and maturity ($\tau \geq 5$). Indeed species with $\tau \geq 5$ are overrepresented in the species suggested to have fluctuating dynamics by our simulations (four of eight species with $\tau \geq 5$; black anglerfish, Greenland halibut, striped bass, and swordfish). Because the parameter ranges of α, M, and k that produce stable equilibria shrink rapidly as τ increases, we suggest that bias and uncertainty in estimating any of the parameters will tend to cause our simulations to identify fluctuating dynamics even where none exist. However, as with all species that our models identify as fluctuating deterministically, we cannot rule out strong density dependence as a driver of population fluctuations. In practice, because species with long recruitment lags are particularly long-lived, actually detecting any fluctuating dynamical behavior in real populations will require much longer time series than are currently available for any of these species.

We did not compliment our deterministic analysis of the Deriso-Schnute model with stochastic simulations such as those performed on the Ricker model. Therefore, we cannot partition the variability of populations as a result of the four main biological components: recruitment, natural mortality, somatic growth, and fishing mortality. However, as evidenced by our discussion of the Ricker (*Stochastic simulation of the Ricker model*), there is a great deal of uncertainty regarding the variability of α, M, and F, as well as the correlation between these parameters. To make the Deriso-Schnute model stochastic in the absence of fishing mortality would require adding to the Ricker not only the specification of the variability of the von Bertalanffy growth coefficient, k, but also the correlation between k and α, as well as the correlation between k and M. We know of very few estimates of the variability of k over time and of no estimates of the correlation between k and the other parameters. Further, we have little idea about how temporal autocorrelation should be included in these models. When added to the already substantial uncertainty in estimates of M, α, and F, we view simulation across so many dimensions of uncertainty as unlikely to contribute to our understanding of fish population dynamics beyond that which arises from the analysis of the simpler Ricker model. Thus, our work should encourage better estimates of each biological parameter and the correlations among them so that future researchers can perform such detailed and important analyses.

Delta Method. We are interested in understanding the consequences of environmental variation for fish populations. In particular, we want to understand the consequences of the variation in the parameters α and M_p, the maximum reproductive rate and instantaneous mortality, respectively, for variation in population abundance. The steady state biomass at $\overline{\alpha}$ and $\overline{M}_p$ is:

$$\overline{B}_0\left(\overline{\alpha}, \overline{M}_p, \beta\right) \equiv \overline{B}_0 = \frac{1}{\beta}\log\left(\frac{\overline{\alpha}}{1-e^{-\overline{M}_p}}\right). \qquad \textbf{[S4]}$$

To approximate the expected value of B_0, as a function of the variability in α and M_p, (considering β fixed) we use the second-order Taylor series expansion of (4),

$$\begin{aligned} E(B_0) \approx \overline{B}_0 &+ \frac{1}{2}\frac{\partial^2\overline{B}_0}{\partial\alpha^2}\operatorname{Var}(\alpha) \\ &+ \frac{1}{2}\frac{\partial^2\overline{B}_0}{\partial M_p^2}\operatorname{Var}(M_p) \qquad \textbf{[S5]} \\ &+ \frac{\partial^2\overline{B}_0}{\partial\alpha\partial M_p}\operatorname{Cov}(\alpha, M_p), \end{aligned}$$

where the derivatives are evaluated at the mean values for their parameters. The required derivatives are:

$$\frac{\partial^2\overline{B}_0}{\partial\alpha^2} = -\frac{1}{\beta\overline{\alpha}^2} \qquad \textbf{[S6]}$$

$$\frac{\partial^2\overline{B}_0}{\partial M_p^2} = \frac{e^{-\overline{M}_p}}{\beta(1-e^{-\overline{M}_p})^2} \qquad \textbf{[S7]}$$

$$\frac{\partial^2\overline{B}_0}{\partial\alpha\partial M_p} = 0, \qquad \textbf{[S8]}$$

and so the expected value of B_0 with variation in α and M_p is:

$$\begin{aligned} E(B_0) \approx \overline{B}_0 & \\ &- \frac{1}{2}\frac{1}{\beta\overline{\alpha}^2}\operatorname{Var}(\alpha) \\ &+ \frac{1}{2}\frac{e^{-\overline{M}_p}}{\beta(1-e^{-\overline{M}_p})^2}\operatorname{Var}(M_p) \qquad \textbf{[S9]} \end{aligned}$$

because α, β, and M_p are positive parameters, and variances of α and M_p are positive, variation in α decreases the expected value of B_0, whereas variation in M_p will increase the expected value of B_0.

The variance of B_0, $\operatorname{Var}(B_0) = E(b_0^2) - E((B_0))^2$. We have previously calculated $E(B_0)$, so we now calculate $E(B_0^2)$:

$$\begin{aligned} \overline{B}_0^2 &= \left(\frac{1}{\beta}\log\left(\frac{\overline{\alpha}}{1-e^{-\overline{M}_p}}\right)\right)^2 \\ &= \frac{1}{\beta}\left[(\log\overline{\alpha})^2 - 2(\log\overline{\alpha})\log\left(1-e^{-\overline{M}_p}\right) + \left(\log\left(1-e^{-\overline{M}_p}\right)\right)^2\right]. \end{aligned} \qquad \textbf{[S10]}$$

The second-order Taylor series approximation for $E(B_0^2)$ is:

$$\begin{aligned} E(B_0^2) \approx \overline{B}_0^2 & \\ &+ \frac{1}{2}\frac{\partial^2\overline{B}_0^2}{\partial\alpha^2}\operatorname{Var}(\alpha) \\ &+ \frac{1}{2}\frac{\partial^2\overline{B}_0^2}{\partial M_P^2}\operatorname{Var}(M_p) \\ &+ \frac{\partial^2\overline{B}_0^2}{\partial\alpha\partial M_p}\operatorname{Cov}(\alpha, M_p). \qquad \textbf{[S11]} \end{aligned}$$

The required second derivatives are:

$$\frac{\partial^2\overline{B}_0^2}{\partial\alpha^2} = \frac{2}{\beta^2\alpha^2}\left[1 + \log\left(\frac{1-e^{-M_p}}{\alpha}\right)\right] \qquad \textbf{[S12]}$$

$$\frac{\partial^2\overline{B}_0^2}{\partial M_p^2} = \frac{2e^{-M_p}}{\beta^2\left(1-e^{-M_p}\right)^2}\left[\log\left(\frac{\alpha}{1-e^{-M_p}}\right) + e^{-M_p}\right] \qquad \textbf{[S13]}$$

$$\frac{\partial^2\overline{B}_0^2}{\partial\alpha\partial M_p} = -\frac{2e^{-M_p}}{\beta^2\alpha\left(1-e^{-M_p}\right)}, \qquad \textbf{[S14]}$$

and so $E(B_0^2)$ with variation in α and M_p is:

$$\begin{aligned} E(B_0^2) \approx \overline{B}_0^2 & \\ &+ \frac{1}{\beta^2\overline{\alpha}^2}\left[1 + \log\left(\frac{1-e^{-\overline{M}_p}}{\overline{\alpha}}\right)\right]\operatorname{Var}(\alpha) \\ &+ \frac{e^{-\overline{M}_p}}{\beta^2(1-e^{-\overline{M}_p})^2}\left[\log\left(\frac{\overline{\alpha}}{1-e^{-\overline{M}_p}}\right) + e^{-\overline{M}_p}\right]\operatorname{Var}(M_p) \\ &- \frac{2e^{-\overline{M}_p}}{\beta^2\overline{\alpha}(1-e^{-\overline{M}_p})}\operatorname{Cov}(\alpha, M_p). \end{aligned} \qquad \textbf{[S15]}$$

Note that the coefficients associated with the covariance terms in $E(B_0)$ and $E(B_0^2)$, respectively,

$$\frac{\partial^2 B_0}{\partial\alpha\partial M_p} = 0 \qquad \textbf{[S16]}$$

$$\frac{\partial^2 B_0^2}{\partial\alpha\partial M_p} = -\frac{2e^{-\overline{M}_p}}{\beta^2\overline{\alpha}\left(1-e^{-\overline{M}_p}\right)}. \qquad \textbf{[S17]}$$

For all values of α, β, and M_p, Eq. **S14** is always negative. Therefore, for any values of $\overline{\alpha}$, $\operatorname{Var}(\alpha)$, $\overline{M}_p$, $\operatorname{Var}(M_p)$, and β, the approximate variance of B_0 is:

$$\begin{aligned}\mathrm{Var}(B_0) &= \mathrm{E}(B_0^2) - \mathrm{E}(B_0)^2 \\ &\approx c - \frac{2e^{-\overline{M}_p}}{\beta^2\overline{\alpha}(1-e^{-\overline{M}_p})}\,\mathrm{Cov}\,(\alpha, M_p) \\ &\approx c - \frac{2e^{-\overline{M}_p}}{\beta^2\overline{\alpha}(1-e^{-\overline{M}_p})}\,\mathrm{Cor}\,(\alpha, M_p)\,[\mathrm{Var}(\alpha)\mathrm{Var}(M_P)]^{0.5},\end{aligned} \qquad \textbf{[S18]}$$

where c is a constant including all terms in $E(B_0) - E(B_0)^2$ but those including $\mathrm{Cov}(\alpha, M_p)$. So a positive correlation between α and M_p will result in decreased variance around the equilibrium abundance, and a negative correlation will increase variance.

Alternative Models of Fishing. ***Harvest of juveniles.*** Our basic model assumes that fishing mortality occurs only on mature individuals

$$B_t = B_{t-1}e^{-M_p-F} + R(B_{t-\tau}). \qquad \textbf{[S19]}$$

This assumption is reasonable because fisheries tend to focus on the largest and most valuable fish in a population (mature individuals); however, some fisheries do catch immature individuals even if they are not targeted. An extreme example of harvest on individuals that are not reproductive are species of fish that die immediately after reproduction (e.g., Pacific salmon) and are therefore unavailable or undesirable for harvest after reproduction. For fish that experience harvest on both mature and immature stages, a more appropriate production model is

$$B_t = B_{t-1}e^{-M_p-F_a} + R(B_{t-\tau})e^{-F_j}, \qquad \textbf{[S20]}$$

where F_j and F_a represent the fishing mortality for juvenile and adult individuals, respectively. Note that whereas F_a is an annual morality rate, F_j represents the mortality rate during the τ years of the juvenile phase. For the most extreme case—semelparous fish like Pacific salmon—the model reduces to (assuming a Ricker recruitment function),

$$B_t = \alpha B_{t-\tau}e^{-\beta B_{t-\tau}}e^{-F_j}, \qquad \textbf{[S21]}$$

which can be rewritten as:

$$B_t = \left(\alpha e^{-F_j}\right)B_{t-\tau}e^{-\beta B_{t-\tau}} \qquad \textbf{[S22]}$$

with equilibrium biomass, B_0:

$$B_0 = \frac{1}{\beta}\log\left(\alpha e^{-F_j}\right). \qquad \textbf{[S23]}$$

The linear stability criteria of this model at B_0 is:

$$g'(B_0) = 1 - \log\left(\alpha e^{-F_j}\right), \qquad \textbf{[S24]}$$

where $|g'(B_0)| > 1$ produces cyclic or chaotic dynamics. Thus, for any given value of α, increased fishing should result in the increased stability of the population (i.e., population moves toward parameter space with equilibrial dynamics) (12).

For our work, this result generates a significant question: are the salmon recruitment curves analyzed by Myers et al. (1) generating estimates of α or the product αe^{-F_j}? Given that all of the salmon stocks in the Myers database were derived from fished populations, we believe they are likely closer to αe^{-F_j}. Because $\alpha e^{-F_j} < \alpha$, values of α from Myers et al. (1) for the four Pacific salmon are likely underestimates. Larger values of α suggest that Pacific salmon are likely among the fish species most likely to exhibit complex dynamics as a result of nonlinear dynamics. This matches salmon biology whereby several populations have evidence of complex dynamics (e.g., ref. 13). For almost all other species, we regard F_j as a trivial component of fishing mortality. However, we suspect that the harvest of juvenile individuals would be most likely to occur in species with long maturation time. We note that many of the longest-lived species are clustered at the low α (e.g., sablefish, deepwater redfish) and speculate that low estimates of α for these long lived species may be attributable, in part, to juvenile harvest that is not accounted for in the Myers et al. analysis (1).

We emphasize that although imposing fishing mortality on juvenile fish will slightly reduce the expected variability observed at equilibrium abundance, it has a large negative effect on the equilibrium abundance of the population. In short, harvesting prereproductive fish as a management strategy is a very bad idea and a recipe for driving fish species extinct.

Timing of harvest within years. An additional assumption of our basic model is that all fishing mortality occurs after each year's reproduction. For many species, fisheries may occur partially or entirely before fish reproduce in a given year. An extreme example of fishing on prereproductive individuals is fisheries that target the roe of mature fish (e.g., some Pacific herring fisheries). In such fisheries all fishing pressure occurs immediately before individuals can reproduce. A model in which fishing that occurs before reproduction is:

$$B_t = B_{t-1}e^{-M_p-F} + R\left(B_{t-\tau}e^{-F}\right). \qquad \textbf{[S25]}$$

Assuming Ricker recruitment and a single year between reproduction and recruitment, the model becomes:

$$B_t = B_{t-1}e^{-M_p-F} + \alpha e^{-F}B_{t-1}\exp\left(-\beta B_{t-1}e^{-F}\right), \qquad \textbf{[S26]}$$

with equilibrium biomass,

$$B_0 = \frac{1}{\beta e^{-F}}\log\left(\frac{\alpha e^{-F}}{1-e^{-M_p-F}}\right). \qquad \textbf{[S27]}$$

The linear stability criteria of this model at B_0 is:

$$g'(B_0) = 1 - \log\left(\frac{\alpha e^{-F}}{1-e^{-M_p-F}}\right)\left(1-e^{-M_p-F}\right). \qquad \textbf{[S28]}$$

Again, $|g'(B_0)| > 1$ result in cyclic or chaotic dynamics. The stability criteria are very similar to Eq. **5** in the main text. However, the timing of fishing relative to reproduction has two notable consequences. First, for equivalent fishing mortality, fishing before reproduction causes significant declines in equilibrium biomass relative to fishing after reproduction and increases the parameter space resulting in the extinction of populations. Second, the range of α that results in stable equilibria increases. Thus, considering alternate timing of fishing mortality does not change our main conclusions. In the absence of environmental variation fish populations have stable dynamics, and the addition of fishing mortality does not markedly affect the stability properties of populations.

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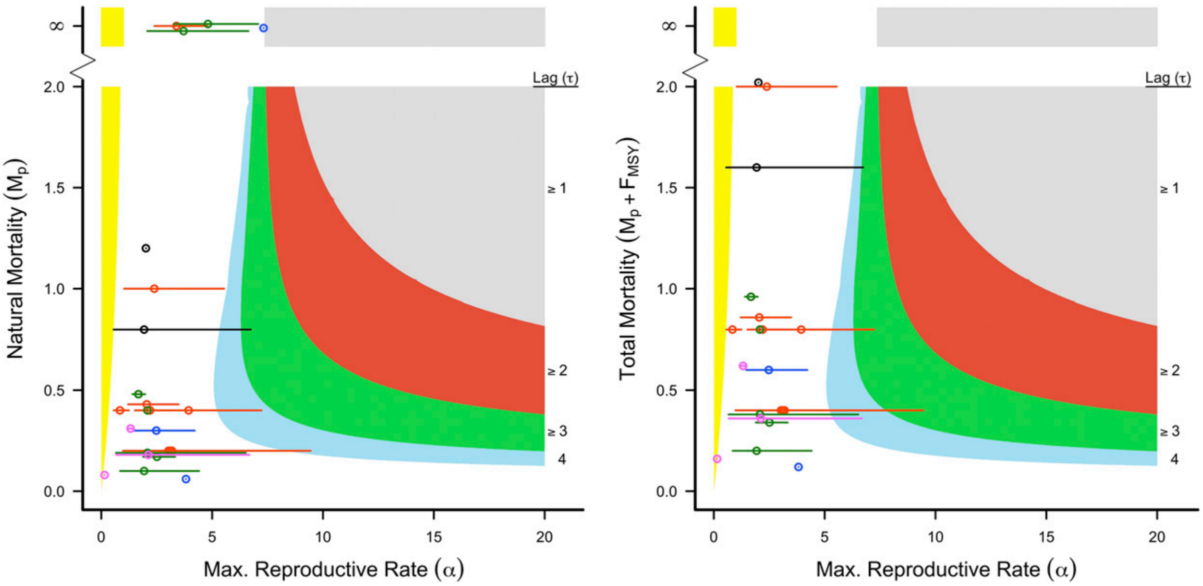

Fig. S1. Parameter estimates for a global sample of fish species and stability criteria for Eq. **6** (main text) in the absence (*Left*) and presence (*Right*) of fishing mortality. Only species in which at least two populations were used to estimate α are included. Shaded regions indicate areas with deterministic cycles or chaotic dynamics, for four recruitment lags (τ = 1, 2, 3, or 4). For example, deterministic cycles and chaos for τ = 1 includes only the gray region, whereas the deterministic cycles and chaos for τ = 2 includes both gray and red regions, and so on. For each lag, regions outside of shaded regions denote parameter space with stable equilibrium dynamics or damped oscillations. Yellow regions indicate parameter values that result in negative equilibrium biomass (i.e., population extinction). Points indicate individual species (± among-population SD) with color corresponding to the appropriate τ. Pink points indicate species for which $\tau > 4$. Mortality rates of ∞ are indicative of semelparous species, which die after reproduction. Iteroparous species with mortality rates >2 are plotted at $M_p = 2$ or $M_p + F_{MSY} = 2$ to enhance readability.

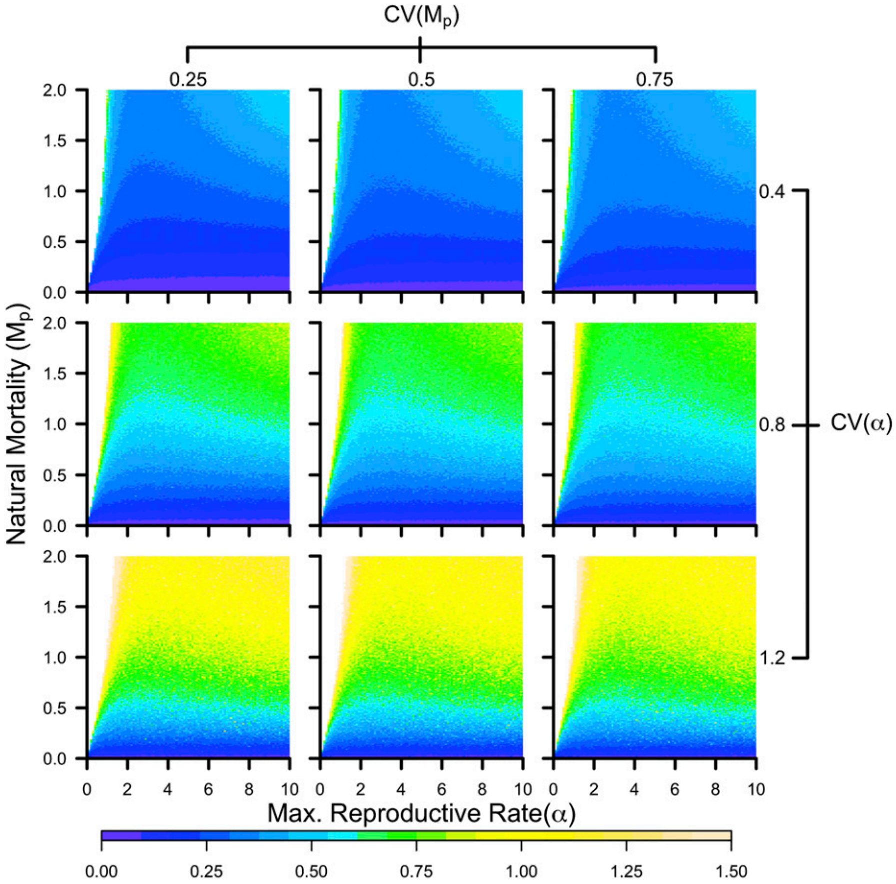

Fig. S2. Effect of environmental variation on the coefficient of variation of biomass, CV(*B*). Colors indicate CV(*B*) for simulations of three levels of CV(M_p) (columns) and three levels of CV(α) (rows). For all simulations shown, Cor(α, M_p) = 0. Increasing CV(α) dramatically increases CV(*B*), whereas increasing CV(M_p) only slightly affects *CV*(*B*).

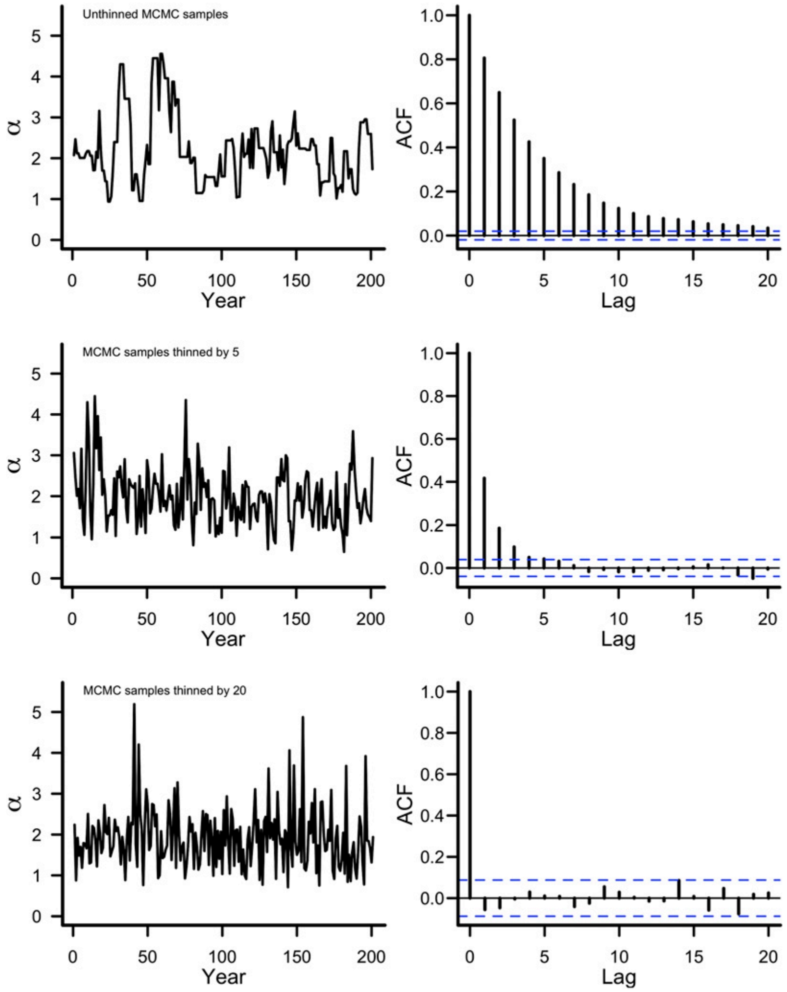

Fig. S3. Illustration of the process used to generate positively autocorrelated random variable using MCMC. This example was produced for an anchovy simulation with $\overline{\alpha} = 2.01$ and CV(α) = 0.4. *Left:* MCMC time series with no thinning of the MCMC chain (*Top*), thinning every 5 iterations (*Middle*), and thinning every 20 iterations (*Bottom*). *Right:* Empirical autocorrelation function for each time series.

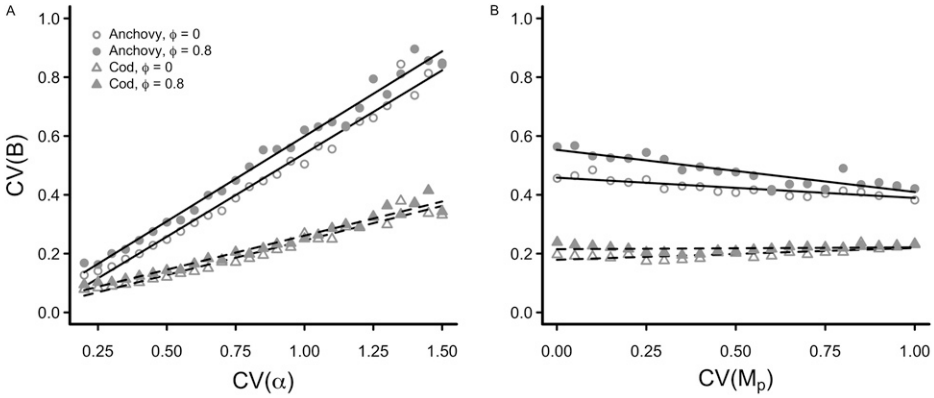

Fig. S4. Predicted consequences of variation in vital rate parameters on the coefficient of variation of biomass, CV(*B*), for two species, Atlantic cod (*Gadus morhua*) and anchovy (*Engraulis encrasicolus*) for both strongly autocorrelated environments, ϕ = 0.8, and uncorrelated environments, ϕ = 0. Each point represents the CV(*B*) from a 5,000-y simulation, and solid (anchovy) and dashed (cod) lines show linear trends. For both species in all simulations, mean values of α and M_p are held constant (Table S1) and Cor(α, M_p) = 0.5. See Fig. 2 (main text) for simulations under alternate correlation scenarios. (*A*) Increasing variation in maximum recruitment rate, CV(α), results in rapid increase in the variability of mature biomass. CV(M_p) = 0.4 in all simulations shown. (*B*) Increasing variation in natural mortality rate, CV(M_p), leads to decreased variability of CV(*B*) for anchovy but shows a flat or slightly increasing effect on CV(*B*) for cod. CV(α) = 0.8 in all simulations shown.

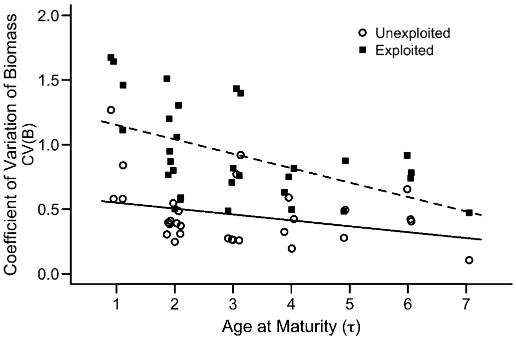

Fig. S5. Effect of age at maturity on population fluctuations for species in the absence (solid line) and presence (dashed line) of fishing mortality. Lines are best-fit linear regressions. Results shown are from simulations with CV(Z) = 0.1, CV(α) = 1.4. Points have been slightly jittered along the x axis to reduce overlap.

Table S1. Species, parameters, and data sources used in all analyses

		log(α)		M_p		k			
Species	*n*	Mean	SE	Min	Max	Min	Max	τ	Refs.
Clupeiformes									
Anchovy (*Engraulis encrasicolus*)	2	0.70	0.13	0.8	1.2	0.35	0.90	1	1, 2
Atlantic herring (*Clupea harengus*)	18	0.73	0.28	0.1	0.19	0.44	0.66	3	3, 4, 5
Atlantic menhaden (*Brevoortia tyrannus*)	1	2.2	0.12	0.37	0.64	0.15	0.30	3	6, 7, 8, 9
Gold-spotted grenadier anchovy (*Collia dussumieri*)	1	2.73	0.19	1.3	2.02	0.80	1.30	1	10, 11, 12
Gulf menhaden (*Brevoortia partonus*)	1	1.25	0.16	0.8	1.1	0.29	0.51	3	13, 14, 15, 16
Northern anchovy (*Engraulis mordax*)	1	0.33	0.41	0.4	1.31	0.10	0.90	1	17, 18
Pacific sardine (*Sardinops sagax*)	2	0.66	0.89	0.4	0.80	0.46	0.91	1	1, 17, 19
Spanish sardine (*Sardina pilchardus*)	1	−0.56	0.75	0.33	0.33	0.18	0.93	1	20, 21,22
Sprat (*Sprattus sprattus*)	3	0.87	0.55	0.33	1	0.30	1.02	2	3, 23, 24
Gadiformes									
Atlantic cod (*Gadus morhua*)	21	1.37	0.15	0.18	0.40	0.09	0.39	3	3, 4, 25, 26, 27
Haddock (*Melanogrammus aeglefinus*)	9	0.72	0.21	0.2	0.43	0.08	0.28	2	4, 28, 29
Pacific hake (*Merluccius productus*)	1	−0.95	0.83	0.25	0.3	0.26	0.30	3	30, 31, 32, 33
Pollock or Saithe (*Pollachius virens*)	5	1.16	0.14	0.2	0.2	0.07	0.19	2	3, 20, 34
Silver hake (*Merluccius bilinearis*)	3	−0.18	0.29	0.14	0.4	0.25	0.74	2	4, 35, 36
Walleye pollock (*Theragra chalcogramma*)	2	0.28	0.24	0.24	0.31	0.20	0.44	5	37, 38, 39, 40
Whiting (*Merlangius merlangus*)	5	1.14	0.51	0.2	0.2	0.05	0.71	2	20, 41, 42
Lophiiformes									
Black anglerfish (*Lophius budegassa*)	1	−0.07	0.32	0.23	0.25	0.07	0.14	8	43, 44, 45
Perciformes									
Atlantic bluefin tuna (*Thunnus thynnus*)	1	−0.40	0.23	0.1	0.24	0.05	0.17	5	46, 47, 48
Atlantic mackerel (*Scomber scombrus*)	2	1.11	0.91	0.18	0.20	0.11	0.56	2	4, 49, 50
Bigeye tuna (*Thunnus obesus*)	2	0.73	0.08	0.1	0.4	0.10	0.37	3	51, 52, 53, 54
Chub mackerel (*Scomber japonicus*)	1	−0.05	0.33	0.1	0.4	0.16	0.50	3	55, 56, 57
Horse mackerel (*Trachurus trachurus*)	2	0.52	0.8	0.15	0.48	0.11	0.37	2	58, 59
New Zealand snapper (*Pagrus auratus*)	2	1.34	1.31	0.06	0.06	0.07	0.12	4	20, 60, 61, 62
Red snapper (*Lutjanus campechanus*)	1	1.9	0.9	0.078	0.35	0.11	0.25	2	63, 64
Scup (*Stenotomus chrysops*)	1	2.6	0.38	0.2	0.2	0.17	0.27	2	4, 45, 65, 66
Striped bass (*Morone saxatilis*)	1	0.95	0.16	0.13	0.62	0.12	0.27	6	67, 68, 69
Swordfish (*Xiphias gladius*)	1	1.7	0.05	0.2	0.3	0.05	0.24	6	51, 70, 71, 72
Walleye (*Sander vitreus*)	2	0.91	0.57	0.3	0.3	0.08	0.45	4	20, 73, 74
White croaker (*Pennahia argentata*)	1	1.88	0.28	0.85	0.93	0.18	0.42	1	75, 76, 77
Yellowfin tuna (*Thunnus albacares*)	1	1.43	0.21	0.1	0.4	0.18	0.39	2	51, 53, 78, 79, 80
Pleuronectiformes									
European flounder (*Platichthys flesus*)	1	−0.03	0.42	0.2	0.2	0.23	0.38	4	20, 81
Greenland halibut (*Reinhardtius hippoglossiodes*)	3	0.75	0.68	0.11	0.18	0.04	0.15	10	45, 82, 83, 84, 85
Plaice (*Pleuronectes platessa*)	8	0.92	0.17	0.1	0.17	0.06	0.19	3	3, 4
Sole (*Solea solea*)	7	0.66	0.35	0.1	0.1	0.13	0.50	3	34, 86, 87
Yellowtail flounder (*Pleuronectes ferrungineus*)	2	0.79	0.34	0.2	0.4	0.07	0.41	2	88, 89, 90
Salmoniformes									
Northern pike (*Esox lucius*)	2	0.51	0.19	0.48		0.07	0.33	3	91, 92
Chinook salmon (*Oncorhynchus tshawytscha*)	6	1.99	0.13	∞				4	
Chum salmon (*Oncorhynchus keta*)	7	1.31	0.24	∞				3	
Pink salmon (*Oncorhynchus gorbuscha*)	52	1.22	0.07	∞				2	
Sockeye salmon (*Oncorhynchus nerka*)	32	1.57	0.08	∞				3	
Scorpaeniformes									
Atka mackerel (*Pleurogrammus monopterygius*)	1	1.13	0.49	0.12	0.34	0.39	0.87	4	93, 94
Chilipepper (*Sebastes goodei*)	1	−0.85	0.57	0.02	0.08	0.11	0.30	3	3, 95, 96
Deepwater redfish (*Sebastes mentella*)	1	−1.93	0.18	0.02	0.10	0.05	0.15	10	20, 97, 98
Sablefish (*Anoplopoma fimbria*)	1	−2.35	0.47	0.07	0.10	0.11	0.47	6	99, 100, 101
Pacific ocean perch (*Sebastes alutus*)	5	−1.93	0.18	0.02	0.08	0.08	0.17	7	3, 20, 95

All estimates of log(α) are derived from Myers et al. (102). *n* indicates number of stocks included to estimate log(α) by Myers et al. (102).

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Table S2. Published estimates of fishing mortality for available species

		mean(*F*)		CV(*F*)		
Species	*n*	Min	Max	Min	Max	Ref.
Anchovy (*Engraulis encrasicolus*)	1	0.35		0.44		1
Atlantic herring (*Clupea harengus*)	9	0.12	0.56	0.21	0.70	2
Atlantic mackerel (*Scomber scombrus*)	1	0.26		0.31		2
Atlantic menhaden (*Brevoortia tyrannus*)	1	1.11		0.40		3
Atlantic cod (*Gadus morhua*)	9	0.37	1.09	0.08	0.33	2
Atka mackerel (*Pleurogrammus monopterygius*)	1	0.22		0.52		4
Greenland halibut (*Reinhardtius hippoglossiodes*)	1	0.27		0.43		2
Haddock (*Melanogrammus aeglefinus*)	7	0.36	0.76	0.18	0.41	2
Horse mackerel (*Trachurus trachurus*)	1	0.087		0.53		2
Pacific hake (*Merluccius productus*)	1	0.13		0.79		5
Pacific ocean perch (*Sebastes alutus*)	1	0.067		0.96		6
Plaice (*Pleuronectes platessa*)	5	0.50	0.68	0.13	0.43	2
Pollock or Saithe (*Pollachius virens*)	4	0.32	0.45	0.22	0.40	2
Red snapper (*Lutjanus campechanus*)	1	1.02		0.14		7
Sablefish (*Anoplopoma fimbria*)	1	0.066		0.42		8
Scup (*Stenotomus chrysops*)	1	0.49		0.78		9
Sole (*Solea solea*)	7	0.27	0.50	0.18	0.35	2
Spanish sardine (*Sardina pilchardus*)	1	0.28		0.21		2
Sprat (*Sprattus sprattus*)	1	0.32		0.37		2
Striped bass (*Morone saxatilis*)	1	0.21		0.47		10
Walleye pollock (*Theragra chalcogramma*)	1	0.085		0.46		11
Whiting (*Merlangius merlangus*)	2	0.52	0.83	0.35	0.38	2
Yellowtail flounder (*Pleuronectes ferrungineus*)	1	1.32		0.37		12
All species				0.08	0.96	

All estimates are derived from at least 19 y of data for each stock.

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