

Supporting Information

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SI Methods

Are There Trends in Stock Collapses? We evaluated whether years in which stocks underwent population collapse (population biomass less than 25% of mean) were random across decades. For each stock that collapsed, we identified the first year that the population dropped below the biomass threshold and called that the collapse year. We tabulated the number of stocks that had collapse years in each decade beginning in the 1950s and extending to the 2000s. We then tabulated the total number of stocks for which we had at least 5 y of population biomass estimates for each decade. Based on these two metrics, we asked whether the collapse years were distributed randomly with respect to the stock data coverage by decade. This analysis was done using a binomial generalized linear model with number of stock collapses and number of stocks with data as a bivariate response variable and decade as a categorical predictor variable. To confirm that the results were not driven by our biomass thresholds, we repeated the analysis for collapse thresholds equal to 50% and 15%. At the high threshold, there was no difference in collapse frequency by decade ($P = 0.21$), but at the lower threshold, we found evidence for greater collapse frequency in 1960s and 1980s, with similar collapse frequency in the other decades ($P = 0.02$). We used the same generalized linear modeling approach to ask whether collapse frequency varied among five main regions for which we had suitable population time series. There was no difference in collapse frequency (where collapse threshold = 25% of average biomass) among regions for either the high or low collapse threshold ($P = 1.0$ or $P = 0.48$, respectively). We repeated this analysis for even finer-scale regional classification: Northeast Atlantic, Northwest Atlantic, Northeast Pacific, Northwest Pacific, South Atlantic, South Pacific, and Mediterranean. We did not have sufficient numbers of stocks in southern hemisphere ocean basins to permit east–west distinctions. This analysis also revealed no difference in collapse frequency among regions ($P = 0.83$).

Because a few highly variable stocks might be driving trends (e.g., perhaps only a few stocks were sufficiently variable to have collapses and bonanzas), we repeated this analysis with time series that were standardized by their variance. Specifically, for each stock and year, we calculated the log $[B(t)]$, where $B(t)$ is the mean-standardized stock biomass in year t , so that increases and decreases in biomass were on the same scale; then, we standardized the log-transformed time series so that each had a mean = 0 and an SD = 1. Under this data transformation, collapse threshold was set to -2 . We found evidence for significantly fewer collapses during the 1950s and the 1990s but similar frequency of collapses in all other decades ($P = 0.017$). There was no difference in collapse frequency by region using either the coarse ($P = 0.96$) or finer ($P = 0.97$) regional definitions.

What Are Characteristics of Stock Collapse? We examined temporal dynamics of fishing and population productivity rates for stocks that exhibited population collapses. We had at least 4 y of total population biomass and fishing rate estimates before collapse for 17 collapsed stocks. Fishing rate (F) was calculated as the ratio of catch to total biomass, except for three cases where either total biomass or catch was unavailable (Chub Mackerel Pacific Coast, Atlantic Herring North Atlantic Fisheries Organization Area 4VWX, and Atlantic Herring International Council for the Exploration of the Sea Area VIaVIIbc). In these cases, we used the stock assessment-based estimate of the instantaneous exploitation rate (F_{inst} ; in years) to generate an approximate catch to biomass ratio of $1 - \exp(-F_{\text{inst}})$. This expression presumes that

natural mortality and somatic growth rate are approximately equal. We then calculated the annual surplus production using conventional methods (1–3), which follows from the population model $\Delta B_t/\Delta t = SP_t - F_t B_t$. Namely, SP_t equals the difference in biomass from year t to $t + 1$ plus fishery catches in year t .

This method of estimating population productivity assumes that surplus production is independent population biomass stock biomass. For instance, an alternative model could assume that surplus production depends linearly on population size, so that population dynamics are equal to

$$\frac{\Delta B_t}{\Delta t} = (\lambda_t - F_t)B_t, \quad \text{[S1]}$$

where λ_t is the population growth rate estimated from the ratio B_{t+1} to B_t and the rate F_t , because $B_{t+1} = (1 + \lambda_t - F_t)B_t$, such that

$$\lambda_t = \frac{B_{t+1}}{B_t} + F_t - 1. \quad \text{[S2]}$$

We used SP_t instead of λ_t , because it produced the most conservative results (i.e., the projected benefits from setting $F_t = 0$ for $t - 2$, $t - 1$, and t were even greater when we applied calculated λ_t values from Eq. S2 and used those in Eq. S1).

Are Observed Minimum Stock Biomass Levels Unusual? We evaluated whether the observed range of stock biomass levels—specifically, the observed minimum biomass—would be expected if stocks were fluctuating randomly with the same variance properties of the observed stocks. Because it is not possible to model population trajectories by complex age- or stage-structured models based solely on the stock assessment output that we compiled, we, instead, adapted a simple density-independent model commonly used in conservation biology to assess extinction risk (4). Namely, we characterize the observed dynamics of stock biomass according to Eq. S1. We, therefore, calculate λ_t as described in Eq. S2 and translate this into $r_t = \ln(\lambda_t + 1)$. By using this formulation, the expected value of $B_{t+T} = B_t \exp(\bar{r}T)$, where \bar{r} is the mean of r_t . Thus, if $\bar{r} = 0$, the expectation is no population growth or decline. We used this model form, because it is commonly used in simulating the probability of low population sizes and requires the fewest number of assumptions about parameters. Below, we describe an alternative model that is more complex, but it assumes that production is independent of population biomass. We use the second model only as a basis for comparison, because the first model (described here) provided the most conservative results (e.g., the weakest evidence for nonrandom fluctuations) and required the fewest assumptions.

We simulated trajectories of population growth rate based on properties of the observed time series of r_t . In this way, we can generate biomass time series of length T_k for each of the k stocks using Eq. S1, calculate the minimum biomass for each simulated stock, and compare the resulting simulations to the actual data. To generate realistic trends in simulated populations, we calculated both the spectral scaling (β_r) and the SD (σ_r) of r_t for each stock. The former is important, because low-frequency variation can greatly increase the range of population fluctuations (5). Variance scales with frequency (f ; in years) according to a $1/f^\beta$ law (6), and β_r was estimated using the multiple segment method to account for the short lengths of these time series (7). We only considered stocks that had more than 32 y of biomass and fishing rate data (40 stocks), because shorter time series cannot be used

to reliably estimate β_r . When β_r was estimated to be below zero, we set it equal to zero based on the assumption that the non-positive value reflects the imprecision of the estimate (there were no cases where a negative value of β_r was statistically different from zero). We then used a 2D kernel smoother to calculate the bivariate probability density surface of (β_r, σ_r) using the `bkde2D` function in the `KernSmooth` (8) package implemented in R (9). These results are provided in Fig. S2.

Stock biomass simulation proceeded according to the following four steps. First, σ_r and β_r were drawn from the bivariate smoothed density function, and a time series of r_t of length 200 with equivalent β_r was generated (5, 10). We scaled these draws to have a mean of zero and an SD equal to σ_r . Second, we generated the biomass time series by applying Eq. S1 and setting F_t equal to zero. It was necessary to filter the time series at this point to ensure that the simulated stock biomass had similar properties (spectral scaling and variance) as the observed time series. Namely, we required the simulated biomass time series to have spectral scaling between 0.5 and 3.5 and a coefficient of variation between 0.1 and 1.25. Third, we used the final T years of the full simulated time series as the simulated observation time series, where T was drawn from the actual time series lengths. Each simulated time series was standardized to its mean: we expressed each year's stock biomass as the ratio of B to average B over the final T years. The result of one iteration of this process is illustrated in Fig. S2. Fourth, we calculated the minimum standardized biomass over the last T years. These steps were repeated to generate simulated time series of K stocks, where K is the actual number of time series that we used in our calculations. We calculated the cumulative probability density of minimum biomass over the K stocks and then, repeated the entire process to generate 1,000 random cumulative probability densities of minimum stock biomass.

We performed three checks on the simulated time series to ensure that they adequately captured properties of the observed time series. First, we calculated the spectral scaling of the stock biomass time series, β_B , for each stock, calculated the cumulative density function of β_B , and compared this with the range of cumulative density functions of the simulated β_B . Second, we performed the same check on the coefficient of variation on B . We found that the simulations matched the observed estimates well in terms of the coefficient of variation but that the simulations produced a narrower range of β_B than was observed (Fig. S2). Our interpretation is that fishing (which is not explicitly included in our simulation) acts to introduce both high-frequency variation through interannual fluctuations in fishing mortality and low-frequency variation through patterns of fishery development and decline. Third, we also compared the range of maximum biomasses produced by the randomization procedure with the observed distribution of maximum biomasses and found only small differences in the distributions.

Alternative Model. Because stock productivity is often not related to stock biomass (3), the randomization test described above is potentially biased. To assess this possibility, we also conducted the same randomization test but with a different population model that assumed that population production was independent of population size. A typical way to evaluate productivity in fish stocks is to calculate annual surplus production (the difference between growth plus reproduction and mortality; e.g., SP_t in Eq. S3). In this way, surplus production is calculated from annual changes in population size after correcting for fishery catch (C_t): $SP_t = B_{t+1} - B_t + C_t$. Although surplus production is easily calculated, it is difficult to use these in simulations, because the values of SP_t are unconstrained and thereby, can produce biologically implausible dynamics. The smallest possible rate of decline is MB_t , where M is the natural mortality rate, but random draws using spectral synthesis produce values of SP_t that

are independent of stock size so that it is possible to generate negative population biomass.

Our solution is to decompose surplus production into two components: natural mortality (always negative) and production (always positive; $SP_t = MB_t + P_t$). We estimated plausible values of natural mortality, which was assumed constant across years, whereby the loss caused by natural deaths equaled MB_t . For each stock, we used the SP_t and B_t to find the best-fitting M (constrained to be within -0.8 to -0.2). We reasoned that P_t is not likely to ever equal 0, and therefore, we defined an arbitrarily small minimum value of 0.01 (units are standardized biomasses per year). From this assumption, we found the value of M for each stock that made the smallest P_t to be equal to 0.01. Estimated values of M were between 0.2 and 0.7. This process then produced time series of P_t for each stock, which we log-transformed, and then, we estimated the SD and spectral scaling of the $\log(P_t)$. Log transformation was necessary so that generation of random series of $\log(P_t)$ through spectral synthesis would produce time series of P_t that were positive. We used the kernel density smoothers to generate (i) bivariate densities of SD and β and (ii) univariate densities of M (Fig. S3). We used these in the randomization test in the same manner as described above.

To ensure that the models had no long-term growth trend, we made the mean of the simulated P_t equal to the M drawn for that simulation. This calculation means that, at average biomass density, mortality is perfectly matched with production. Because conversion from $\log(P_t)$ to P_t requires an adjustment to account for the fact that $\log(\text{mean of } P_1, P_2, \dots, P_n)$ does not equal $\exp(\text{mean of } \log(P_1), \log(P_2), \dots, \log(P_n))$, some adjusted P_t values dropped below our minimum value of 0.01. In these cases, we adjusted any P_t below 0.01 to equal 0.01 and then, reduced the largest jP_t by the same magnitudes (where j is the number of P_t that had to be adjusted to meet minimum value) to ensure that the overall mean of the P_t was unchanged. Similar to the randomization test above, this procedure generated population dynamics with very similar characteristics (variance and spectral scaling) as the true population dynamics. Importantly, this more complex model produced minimum biomass levels that were generally greater than those produced by our base model (Fig. S3). We, therefore, conclude that our results are robust to the underlying assumptions regarding the relationship between production and stock biomass.

What Are Possible Consequences of Precautionary Fishing Management?

We simulated the outcome in terms of total catch and minimum population stock size if all fisheries adopted a policy where fishing was suspended whenever the standardized population biomass was below 0.5 (biomass is $<50\%$ of the mean). This simulation relied on projecting population biomass through a population dynamics model based on observed trends in productivity and actual fishing rates combined with the precautionary rule. We used a model that generated the most conservative estimate of ecological benefits and the most liberal estimate of foregone catch by making annual surplus production, SP_t , independent of stock biomass:

$$B_{t+1} = \begin{cases} B_t + SP_t - F_t B_t, & \text{if } B_t > 0.5 \\ B_t + SP_t, & \text{otherwise} \end{cases} \quad [\text{S3}]$$

In all simulations, we set exploitation rate equal to the actual exploitation rate unless $B_t < 0.5$. Catch in any year was equal to $B_t F_t$ when $B_t > 0.5$, and it was $B_t = 0$ otherwise. Annual surplus production was calculated from the difference in population biomass from year t to $t + 1$ plus fishery catches in year t . We only simulated population dynamics over a 10-y period beginning with the first year that $B_t < 0.5$. We chose this short time period, because the model was not appropriate for predicting population biomass trajectories over long time periods.

As a sensitivity test, we also used a density-independent model analogous to our simulation (base) modeling:

$$B_{t+1} = \begin{cases} (1 + \lambda_t - F_t) B_t, & \text{if } B_t > 0.5 \\ (1 + \lambda_t) B_t, & \text{otherwise} \end{cases} \quad [\text{S4}]$$

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This model predicted that, on average, the harvest rule would lead to an overall 58% increase in landings, with a 78% increase in minimum forage fish stock biomass. Thus, our predictions about the ecological benefits are not particularly sensitive to the choice of model, but our calculations of lost catches may be biased high if production is related to stock biomass.

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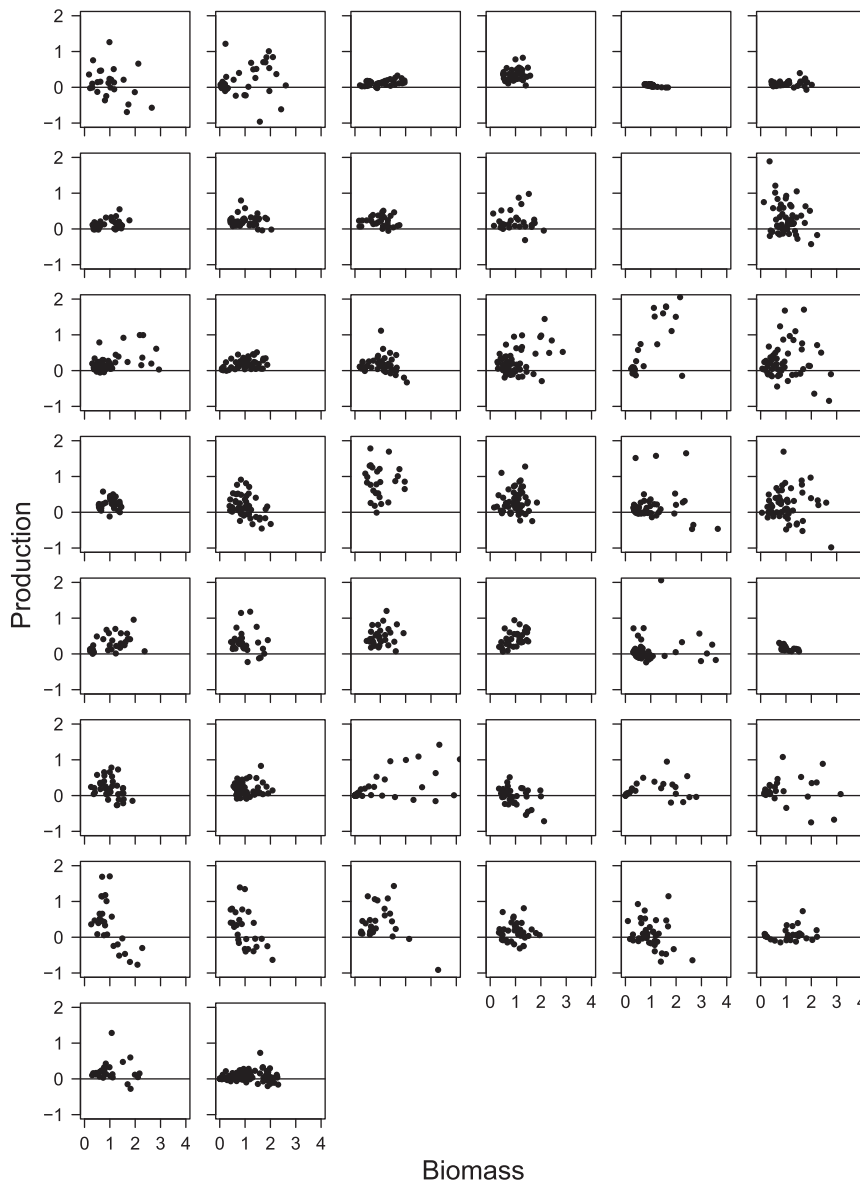


Fig. S1. Relationship between surplus production and stock biomass for 44 small pelagic fish populations. Surplus production is calculated for populations for which we have both total biomass and fishing rate or catches. Each plot represents one population, and data points represent the estimate of biomass and surplus production for 1 y. Biomass and surplus production for each population are standardized as a proportion of long-term mean biomass.

Table S1. Summary of stocks and measurements used in analysis

Common name	Location/stock	Scientific name	Years	TB/SSB	Exploitation rate?
Anchovy	Adriatic Sea	<i>Engraulis encrasicolus</i>	1976–2007	TB	Yes
Anchovy	South Africa	<i>Engraulis encrasicolus</i>	1984–2011	TB	Yes
Anchovy (Anchovetta)	North Central Peru	<i>Engraulis ringens</i>	1963–2004	SSB	No
Anchovy, Japanese	Inland Sea of Japan	<i>Engraulis japonicus</i>	1981–2010	TB	Yes
Anchovy, Japanese	Pacific Coast	<i>Engraulis japonicus</i>	1978–2009	TB	Yes
Anchovy, Japanese	Tsushima Strait	<i>Engraulis japonicus</i>	1977–2010	TB	Yes
Anchovy, Northern	East Pacific	<i>Engraulis mordax</i>	1981–2009	SSB	No
Capelin	Barents Sea	<i>Mallotus villosus</i>	1972–2007	TB	Yes
Capelin	Iceland	<i>Mallotus villosus</i>	1979–2010	SSB	No
Herring, Atlantic	Gulf of Maine/Georges Bank	<i>Clupea harengus</i>	1965–2011	TB	Yes
Herring, Atlantic	ICES Area 28	<i>Clupea harengus</i>	1977–2010	TB	Yes
Herring, Atlantic	ICES Area 30	<i>Clupea harengus</i>	1973–2010	TB	Yes
Herring, Atlantic	ICES Area 31	<i>Clupea harengus</i>	1980–2010	TB	Yes
Herring, Atlantic	ICES Area VIa	<i>Clupea harengus</i>	1957–2010	TB	Yes
Herring, Atlantic	ICES Areas 25–32	<i>Clupea harengus</i>	1974–2010	TB	Yes
Herring, Atlantic	ICES Areas VIa-VIIIbc	<i>Clupea harengus</i>	1957–2010	TB	Yes
Herring, Atlantic	ICES Areas VIIa-g-h-j	<i>Clupea harengus</i>	1958–2010	TB	Yes
Herring, Atlantic	NAFO 4R Fall Spawners	<i>Clupea harengus</i>	1973–2003	SSB	Yes
Herring, Atlantic	NAFO 4R Spring Spawners	<i>Clupea harengus</i>	1965–2004	TB	Yes
Herring, Atlantic	NAFO 4T Fall Spawners	<i>Clupea harengus</i>	1978–2007	TB	Yes
Herring, Atlantic	North Sea	<i>Clupea harengus</i>	1960–2011	TB	Yes
Herring, Atlantic	Northern Irish Sea	<i>Clupea harengus</i>	1961–2010	TB	Yes
Herring, Atlantic	Norwegian Spring Spawners	<i>Clupea pallasii</i>	1907–2012	TB	Yes
Herring, Atlantic	Scotian Shelf and Bay of Fundy	<i>Clupea harengus</i>	1965–2006	TB	Yes
Herring, Atlantic	NAFO 4T Spring Spawners	<i>Clupea harengus</i>	1978–2007	TB	Yes
Herring, Pacific	British Columbia Central Coast	<i>Clupea pallasii</i>	1951–2007	TB	Yes
Herring, Pacific	DFO Area 27	<i>Clupea pallasii</i>	1978–2012	SSB	No
Herring, Pacific	DFO Area 2W	<i>Clupea pallasii</i>	1978–2012	SSB	No
Herring, Pacific	Haida Gwaii	<i>Clupea pallasii</i>	1951–2012	SSB	No
Herring, Pacific	Prince Rupert District	<i>Clupea pallasii</i>	1951–2007	TB	Yes
Herring, Pacific	Prince William Sound	<i>Clupea pallasii</i>	1980–2006	TB	Yes
Herring, Pacific	Queen Charlotte Island	<i>Clupea pallasii</i>	1951–2007	TB	Yes
Herring, Pacific	Sitka	<i>Clupea pallasii</i>	1980–2007	TB	Yes
Herring, Pacific	Strait of Georgia	<i>Clupea pallasii</i>	1951–2007	TB	Yes
Herring, Pacific	West Coast of Vancouver Island	<i>Clupea pallasii</i>	1951–2007	TB	Yes
Mackerel, Atlantic	Gulf of Maine	<i>Scomber scombrus</i>	1962–2008	TB	Yes
Mackerel, Atlantic	Northeast Atlantic	<i>Scomber scombrus</i>	1972–2006	TB	Yes
Mackerel, Cape Horse	South Africa South Coast	<i>Trachurus capensis</i>	1950–2007	TB	Yes
Mackerel, Chub	Northeast Pacific Coast	<i>Scomber japonicus</i>	1929–2008	SSB	Yes
Mackerel, Chub	Tsushima Strait	<i>Scomber japonicus</i>	1973–2010	TB	Yes
Mackerel, Jack	Chile	<i>Trachurus murphyi</i>	1970–2010	TB	Yes
Mackerel, Japanese Jack	Tsushima Strait	<i>Trachurus japonicus</i>	1973–2010	TB	Yes
Menhaden, Atlantic	US Mid-Atlantic	<i>Brevoortia tyrannus</i>	1955–2011	TB	Yes
Menhaden, Gulf	Gulf of Mexico	<i>Brevoortia patronus</i>	1964–2004	TB	Yes
Pilchard, European	ICES Areas VIIIc-lxa	<i>Sardina pilchardus</i>	1978–2011	SSB	Yes
Pilchard, Japanese	Tsushima Strait	<i>Sardinops ringens</i>	1960–2010	TB	Yes
Round herring	Tsushima Strait	<i>Etrumeus teres</i>	1976–2010	TB	Yes
Sandeel	North Sea Area 1	<i>Ammodytes marinus</i>	1983–2010	TB	Yes
Sandeel	North Sea Area 2	<i>Ammodytes marinus</i>	1983–2010	TB	Yes
Sandeel	North Sea Area 3	<i>Ammodytes marinus</i>	1983–2010	TB	Yes
Sardine	Adriatic Sea	<i>Sardina pilchardus</i>	1975–2007	TB	Yes
Sardine	South Africa	<i>Sardinops sagax</i>	1984–2011	TB	Yes
Sardine	Northeast Pacific	<i>Sardinops sagax</i>	1981–2007	TB	Yes
Sprat	ICES Baltic Areas 22–32	<i>Sprattus sprattus</i>	1974–2010	TB	Yes
Sprat	North Sea	<i>Sprattus sprattus</i>	1974–2012	TB	Yes

Whether exploitation rate (fraction of fish captured annually) was available is indicated. DFO, Canada Department of Fisheries and Oceans; ICES, International Council for the Exploration of the Sea; NAFO, North Atlantic Fisheries Organization; SSB, spawning stock biomass; TB, total biomass.