Path-dependent institutions drive alternative stable states in conservation

Edward W. Tekwa\textsuperscript{a,b,1,2}, Eli P. Fenichel\textsuperscript{a}, Simon A. Levin\textsuperscript{b}, and Malin L. Pinsky\textsuperscript{a}

\textsuperscript{a}Department of Ecology, Evolution, and Natural Resources, Rutgers University, New Brunswick, NJ 08901; \textsuperscript{b}Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544-1003; and \textsuperscript{1}School of Forestry and Environmental Studies, Yale University, New Haven, CT 06460

Edited by Pablo A. Marquet, Pontificia Universidad del Chile, Santiago, Chile, and accepted by Editorial Board Member B. L. Turner November 19, 2018 (received for review May 8, 2018)

Understanding why some renewable resources are overharvested while others are conserved remains an important challenge. Most explanations focus on institutional or ecological differences among resources. Here, we provide theoretical and empirical evidence that conservation and overharvest can be alternative stable states within the same exclusive-resource management system because of path-dependent processes, including slow institutional adaptation. Surprisingly, this theory predicts that the alternative states of strong conservation or overharvest are most likely for resources that were previously thought to be easily conserved under optimal management or even open access. Quantitative analyses of harvest rates from 217 intensely managed fisheries supports the predictions. Fisheries’ harvest rates also showed transient dynamics characteristic of path dependence, as well as convergence to the alternative stable state after unexpected transitions. This statistical evidence for path dependence differs from previous empirical support that was based largely on case studies, experiments, and distributional analyses. Alternative stable states in conservation appear likely outcomes for many cooperatively managed renewable resources, which implies that achieving conservation outcomes hinges on harnessing existing policy tools to navigate transitions.

Significance

Intrinsic institutional or ecological differences are often invoked to explain resource conservation success or failure. However, alternative conservation outcomes instead may be caused by path-dependent processes, where historical contingencies trap similar institutions in dramatically different, but predictable, states. We model social-ecological processes in cooperatively managed natural resources and show that institutional path dependence can create alternative stable states of conservation or overharvesting. We find that the model significantly explains a large dataset of well-studied marine fisheries. Highly productive and costly resources are, unexpectedly, most likely to exhibit the alternative stable states of strong depletion or conservation. Path dependence presents challenges and opportunities, including the possibility that short but intensive harvest reduction efforts can generate self-perpetuating conservation outcomes.


The authors declare no conflict of interest.

This article is a PNAS Direct Submission. P.A.M. is a guest editor invited by the Editorial Board.

This open access article is distributed under Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 (CC BY-NC-ND).

Data deposition: The data and code reported in this paper have been deposited in a Figshare repository (10.6084/m9.figshare.5813934).

\textsuperscript{1}Present address: Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON M5S 3B2, Canada.

\textsuperscript{2}To whom correspondence should be addressed. Email: wongtekwa@gmail.com.

This article contains supporting information online at www.pnas.orglookup/ suppl/doi:10.1073/pnas.1806852116/DCSupplemental.

Published online December 19, 2018.

www.pnas.org/cgi/doi/10.1073/pnas.1806852116

PNAS | January 8, 2019 | vol. 116 | no. 2 | 689–694
harvested) relatively slowly (25) due to fixed costs or political cost of change (akin to friction) (1, 28), while stocks equilibrate to size $S^*$ relatively quickly in response to harvest ($SI$ Appendix, Ecological Response to Harvest Rate and Figs. S1B and S3). Generalized variations in the functional forms of stock growth dynamics (29, 30), of diminishing benefits (20, 31), and of cost around the stated assumptions do not qualitatively affect the model’s main predictions ($SI$ Appendix, Generalized Model and Figs. S4 and S5). Therefore, in our main analyses we employ Schaefer (19) or logistic growth (with intrinsic growth rate $r$, $S_{\text{MAX}} = r/a$, and $S_{\text{MSY}} = S_{\text{MAX}}/2$, Eq. 1), natural log benefits (with marginal benefit parameter $F$ and shape parameter $w$, Eq. 2 and Materials and Methods, Model), and constant marginal cost $I$:

$$\frac{dS}{dt} = S(r - aS - F),$$

$$u = \frac{1}{\ln(wFS^*)} - IFS^*.$$  

Our model, when expanded to account for market substitutability between stocks, can be solved analytically. The solution shows that harvest rate expectations (Fig. 1A and B) are determined by three factors: the maximum yield $\ln(MSY\gamma)$, the cost/benefit ratio ($\gamma$), and the average number of substitutable stocks ($N$) (Materials and Methods, Connecting Solutions to Data). The cost/benefit ratio ($\gamma$) is defined as the ratio of net costs (including subsidies) to net benefits of harvesting from stocks in a region, which can be related to $I$, $V$, and $N$ (Eq. 6).

The model predicts that harvest rates form a path-dependent pitchfork bifurcation, trapping similar institutions in either overharvesting or conservation regimes (Fig. 1A and B). Consider the institutional objective of maximum economic yield (MEY), which is the harvest volume that maximizes rent. When costs are low, the greatest sustained harvest is preferred but is limited by stock growth (maximized at MSY). Thus, the institution is “ecologically constrained” to cap MEY at MSY by harvesting at rate $F_{\text{MSY}}$. On the other hand, an institution with a resource supporting a greater MEY—the institution objective of maximum economic yield ($MEY$)—will monotonically adjust harvest rates to approach the $S^*$ equilibrium, while open access additionally implies overharvesting instead of $F_{\text{MSY}}$ for small and initial stocks ($\ln(MSY) < N$). Whether the two key conditions are typical is an empirical question.

We examined a global database (21) containing MSY and harvest rate assessments spanning 1961–2009 for 217 fisheries managed by 21 national and international institutions. These fisheries, accounting for the majority of total harvest volume from the developed world, are considered cooperatively managed (21) and likely satisfy both the exclusive-access and slow-institution assumptions (but see $SI$ Appendix, Ecological Response to Harvest Rate) for evidence of certain violations. We used country-level economic costs (variable cost plus subsidy and benefits (funding value)) for 1990–2000 (22) (Materials and Methods, Evaluating the Model with Data) to estimate a constant $\gamma$ for each fishery. We used the first reported (not necessarily inception) harvest rate of each fishery (the binary of whether $F_0 > F_{\text{MSY}}$) as its initial condition.

Aggregate harvest rate data did not suggest bimodality [mean $\log_{2}(F/F_{\text{MSY}}) = -0.50$; Fig. 2D]. This unimodality also held for the subset of fisheries with low MSY and cost/benefit ratios (“ecologically constrained” fisheries), including smaller northeastern and West Coast US fisheries. These fisheries had long-run (up to 2002–2009) harvest rates distributed evenly around $F_{\text{MSY}}$ regardless of initial conditions (from 1961 to 2000, Fig. 2A). In contrast, fisheries with high MSY and cost/benefit ratios (such as cod and herring) revealed bimodality (“ecologically constrained” fisheries, Fig. 2B and C). These fisheries included many northeastern US and European fisheries that overharvested initially (1961–1991) and continued to do so ($F^*_{0}$, up to 2007–2009), as well as many West Coast US, multinational Atlantic, and Indian Ocean fisheries that harvested at lower levels initially (1961–1989) and remained at low levels through time ($F^*$, up to 2002–2009; $SI$ Appendix, Tables S1 and S2).

We tested for conditional path dependence by iteratively fitting our model (Materials and Methods, Evaluating the Model with Data) with one free parameter ($N$, Eq. 8) to the observed mean harvest rates, cost/benefit ratios, and MSY values (Fig. 2E). The initial condition ($F_0 > F_{\text{MSY}}$) determined whether $F^*_{0}$ was
the expected solution in the path-dependent regime. The fitted model explained 29% of the variation in mean harvest rates [bootstrapped 95% CI, 19–39%], with an estimated $n = 11.2$ [10.3–12.2] (SI Appendix, Fig. S7 for sensitivity analysis). This $n$ is close to independent proxies for the number of substitutable fisheries (10.3; SI Appendix, Independent Proxies of $N$) and places 93% [84–96%] of fisheries in the path-dependent regime (SI Appendix, Fig. S8). A permutation test (Fig. 3A) revealed that the model explained the observations significantly better than under a null hypothesis of no relationship between $\gamma \ln(\text{MSY})$ and harvest rates ($P = 0.7 \times 10^{-4}$).

The predicted path dependence explained observed harvest rates, and $R^2$ dropped to $-0.11$ when $F^+ - F^-$ was eliminated. Dropping $F^+$ is equivalent to assuming that institutions are relatively fast (SI Appendix, Comparison to Previous Theories). An analysis of interannual changes also supported the slow-institution assumption at $\gamma = 0.7$ (SI Appendix, Southern Europe, Mediterranean, and Caribbean). In addition, single-equilibrium economic models (19) that included cost in other forms (that is, not proportional to harvest volume) explained less of the variation in the data (maximum $R^2 = 0.027$; SI Appendix, Alternative Cost Models). Our model outperformed a more flexible statistical model with separate means for the two initial condition groups (“statistical bimodality,” $R^2 = 0.27$, $\Delta AIC = 7.9$; SI Appendix, Path-Dependence and Bimodality). Additional robustness checks to control for temporal autocorrelation (SI Appendix, Figs. S9 and S10), regional autocorrelation (nonindependence), and multiple productivity states (30) (SI Appendix, Fig. S11A) showed that the model remained significant with nearly identical $N$ estimates (SI Appendix, Model Time Delay and Autocorrelation, Regional Autocorrelation and Permutation, and Alternative Productivity States).

Temporal variances and autocorrelations may be elevated near certain thresholds—low $\gamma \ln(\text{MSY})$ in our case—where the system has a shallow basin of attraction (35). We found greater temporal harvest rate variances near the bifurcation threshold at low $\gamma \ln(\text{MSY})$ ($P = 0.014$; Fig. 3C), as expected, but no evidence of elevated autocorrelation ($P = 0.86$). The higher variance may represent within-fishery signals of conditional path dependence.

The model predicts that transitions, defined as crossing $F_{\text{MSY}}$, are rare in the path-dependent regime where $F_{\text{MSY}}$ becomes unstable. We found that 40% of relatively path-independent fisheries [$\gamma \ln(\text{MSY}) < 13$] transitioned. In contrast, only 15% of strongly path-dependent fisheries [$\gamma \ln(\text{MSY}) \geq 13$] transitioned, in agreement with predictions. In recent years (1995–2009) that have seen more concerted conservation efforts (16, 18, 36), the overall transition rates were similar to the full sample, but transitions to conservation became more frequent than transitions to overharvesting (SI Appendix, Table S3).

We truncated the dataset to different time periods and tested the sensitivity of the model to major political events (SI Appendix, Different Initial and Final Years and Fig. S11 B–D). We found that the 1995–2009 harvest rates were more difficult to explain ($R^2 = 0.25$, $P = 0.67$, SI Appendix, Fig. S11D), particularly for weakly economically constrained fisheries that exhibited fast
institutional dynamics (Fig. 3B) and likely experienced stronger conservation mandates (SI Appendix, Table S3) (16, 18, 36). However, once fisheries transitioned across $F_{\text{MSY}}$, they again strongly converged on the alternative stable state—including both conservation and overharvesting. Using the information that a transition occurred, an informed path-dependent model could significantly explain the 40 transitioning fisheries’ eventual harvest rates ($n = 10.9, R^2 = 0.47, P = 0.050$, SI Appendix, Different Initial and Final Years). Even though transitions are unexpected, it appears that fisheries subsequently relaxed into the business-as-usual dynamics of path dependence.

**Discussion**

Our model predicted that harvest rates will be path dependent and display alternative stable states, conditional on cost, benefit, and stock productivity when institutions adapt slowly relative to resource dynamics under exclusive resource access conditions. We used a comprehensive statistical procedure to reveal that the predictions based on a single global parameter representing the average number of substitutable stocks ($N$) are parsimonious, significant, and explain more variation in the state of global, intensively managed fisheries than a wide range of alternative models, including an optimization model (20).

Managed commercial fisheries largely fit our predictions, but exceptions illustrate how social-ecological feedbacks enforce path dependence. For example, the New Zealand midwater stack of orange roughy was initially (<1983) harvested below $F_{\text{MSY}}$ even though there was no catch limit (37). This state did not last, however, and trawlers subsequently overharvested the stock [open circle near log$_2(F/F_{\text{MSY}}) = 3$; Fig. 2E] after extensive marketing campaigns (38) and erroneous growth rate estimates. In contrast, the South African Patagonian toothfish stock initially (<1997) was harvested above $F_{\text{MSY}}$, but harvest rates fell [filled circle near log$_2(F/F_{\text{MSY}}) = -3$; Fig. 2E] after political pressure and the initiation of a large marine protected area (MPA) in late 1996 (39, 40). Both examples violated our model’s assumption that institutional dynamics are slow relatively to ecological dynamics, which helps explain their unexpected transitions. For orange roughy, the species’ extreme slow growth made management action relatively fast. The South African case is an example of a sudden MPA-induced transition to conservation, illustrating the potential value but also the high transaction costs that often prevent such implementation (41). Despite these temporarily fast institutional dynamics, the fisheries subsequently converged on an alternative stable state that yielded nearly maximum economic rent (42), conforming to our predictions. Modern stock rebuilding efforts [e.g., under the 1996 and 2006 revisions to the US Magnuson–Stevens Act (36)] also appear to have initiated a higher transition rate to conservation, with transitioning fisheries converging on the predicted alternative state. Such acts, even when subject to revision and interpretation (36), can facilitate lasting conservation because of path dependence.

Among the 35 fisheries in the strongly path-dependent region [$\gamma(\text{ln}(\text{MSY})) \geq 22$], only one transitioned to conservation (the Patagonian toothfish), and 11 fisheries persistently overharvested. These overharvested, but highly productive, stocks included haddock and pollock in Northern Europe and sardinella in West Africa (SI Appendix, Table S2), which would be conservation priorities because they can be harvested at much lower rates while achieving similar rents.

Subsidies and investments are important management considerations (22), but their effects can be surprising under path dependence. A subsidy increases cost to society (higher $\gamma$, moving a resource toward the right of Fig. 2E), causing overharvested resources to become even more overharvested, while conserved resources become even more conserved. On the other hand, investment in research and gear [sometimes called a “bad-subsidy” (22) because it dampens the effectiveness of gear restriction policies (18)] can reduce harvesting costs (lower $\gamma$) and therefore reduce path dependence (toward $F_{\text{MSY}}$, left of Fig. 2E).

Researchers have traditionally identified intrinsic differences, including management type, excludability, leadership, and incentives (16–18), to explain why some resources are overharvested while others are conserved (43). These are important sources of unexplained variation. Slow institutions and excludability in particular are reasonable assumptions in the fisheries we analyzed, but they are sometimes violated even within our data. Such violations in part explain why our model explained only 29% of the variation in global fishing rates. In addition, these assumptions are not expected to hold in open-access institutions elsewhere. Nevertheless, our simple path-dependent model provides a unique and significant explanation for conservation outcomes in resources with clear access boundaries. We found that highly productive, costly-to-harvest resources are paradoxically most susceptible to strong depletion, but also most receptive to strong conservation because of prevailing economic incentives. For depleted resources to switch states and become conserved, institutions would need to implement fast but controlled management campaigns that reduce harvest rates below $F_{\text{MSY}}$. Such conservation opportunities may be present in many renewable resources beyond fisheries (20, 26, 34). The challenge will be to
acknowledge institutional speed limitations and understand how the costs of corrective actions (15, 22) can be mitigated to transition out of undesirable states and lock into desirable states.

Materials and Methods

Model. In Eq. 1, the biomass that supports maximum sustainable yield (MSY), defined as the stock size that yields the greatest harvestable surplus production, is \( F_{\text{MSY}} = rI1 \), and the associated harvest rate is \( F_{\text{MSY}} = rI2 \). MSY is \( S_{\text{MSY}}F_{\text{MSY}} = rI1(a) \). Harvest rates are scaled as \( F_{\text{FSY}} = (2a)I \), which is 1 when a stock is harvested at \( F_{\text{MSY}} \). We assumed a timescale separation such that ecological dynamics are faster than management; that is, \( F \) appears constant (as is common in practice and in fishery literatures (32)) in Eq. 1. While harvest rate \( F \)—the policy choice—changes slowly, harvest volume (FS) adjusts quickly to stock size. Contrasting timescales are common in complex systems (14) and bioeconomic theories (33), but analyses often assume management response is fast without empirical justifications. See Materials and Methods, Institution Speed for a justification of our assumption.

The utility function, \( u \), defines the benefits minus costs (in millions of US dollars per year) to a society over time in Eq. 2. Adapting this holistic, institutional perspective implies that harvesting decisions are aligned with social utility (44) and that the manager’s legal or conservation objectives are subject to continual revision and interpretation (36, 45–47). \( v \) is the initial marginal benefit when the harvest (\( wFS \)) is near 1 (since \( \ln(F + wFS) - \ln(wFS) \ll 1 \)). \( w \) (in per-kilogram) is a constant controlling the shape of the marginal benefit function (with a greater \( w \) implying marginal benefit diminishes faster) and renders the term \( wFS \) dimensionless. Assuming the resource is essential for institutional survival implies the marginal utility of the first unit of \( S \) is infinite. The equilibrium stock \( S^* \) was used in the utility function because we assume fast ecological dynamics. \( I \) is a constant marginal cost of harvesting a unit of stock (in millions of US dollars per kilogram per year). This cost definition (20) matches a but differs from the effort (27, 28). These assumptions were made because data for specifying individual fishery \( I \) and \( V \) were unavailable, and substitutability was difficult to confirm directly across a large number of species. The result was that each fishery had a harvesting cost \( I \), an initial marginal benefit \( V/I \) (as opposed to \( V \) for the aggregate substitutable stocks), and a marginal benefit that diminished with the harvests from \( N \) stocks, rather than diminishing only with its own harvest:

\[
\frac{dF}{dt} = \frac{\partial}{\partial F} \left[ \ln(wFS) - IFS \right] = -r2F \frac{Va}{F(F - r)}.
\]

We restrict the validity of Eq. 3 to \( F < r \); beyond this value, the stock is deterministically driven to extinction, in which case we define utility to be negative infinite. The solutions \( F^* \) (from setting Eq. 3 to zero) are either stable or unstable harvesting strategies (SI Appendix, Generalized Model and Alternative Cost Models).

The change in harvesting strategy over time, \( dF/dt \), is gradual and is proportional to the change in utility (Eq. 2) as a function of change in strategy, \( du/dF \). That is, institutions change \( F \) to maximize:

\[
\frac{d}{dF} \left[ \int \ln(wFS) - IFS \right] = \frac{-2F}{F(F - r)}.
\]

As \( I/V \) passes the critical threshold 4, a pitchfork bifurcation occurs. The critical bifurcation threshold can be understood in the form \( V = 1/MSY \), which is when the reference marginal benefit equals the cost of harvesting at MSY. As MSY of the stock increases, the bifurcation point along the \( I/V \) axis shifts to the left (to a smaller cost/benefit ratio), and the region of \( I/V \) where harvesting at \( F_{\text{MSY}} \) is stable shrinks as MSY increases. As \( I/V \) approaches infinity, the stable solutions asymptotically approach \( r \) and 0. We use the logarithms of relative harvest rates \( F^* = \ln(F/F_{\text{MSY}}) \) to facilitate comparisons across fisheries. The use of log base 2 normalizes the quantity so that it is 0 when harvests are at \( F_{\text{MSY}} - 1 \) when harvests are at \( 1/2F_{\text{MSY}} \) and 1 for deterministic extinction:

\[
F^* = \left\{ \begin{array}{ll}
0 & \text{if } F < r/2 \\
\log_2 \left( 1 + \frac{1}{V - FMSY} \right) & \text{if } F = r/2 \\
\log_2 \left( \frac{1}{V - FMSY} \right) & \text{if } F = 1/2FMSY \\
\end{array} \right.
\]

A stable harvest strategy gives the maximum economic yield or rent (MEY) over the long run, which in the zero-discounting case equals the optimal economic yield.

Connecting Solutions to Data. We infer the fishery-specific parameters \( I/V \) with aggregated economic data. Suppose we know the regional cost/benefit ratio \( r \), which is the sum of variable fishing cost (plus subsidy) divided by the total landing value of all fish [each with harvest \( C_i \), indexed \( i \) within summations to emphasize fishery-specific variables, see term (1) in Eq. 6]. We then made the approximations that each of \( n \) fishes belonged to a group of \( N \) substitutable fishes, and they were harvested to the same \( MSY \) [term (2) in Eq. 6]. Finally, each group’s average cost/benefit was assumed the same as each other and the same as the regional \( r \) [term (3) in Eq. 6]. This simplification implied that stocks with a greater \( MSY \) than average within a region would also have a lower \( I/V \), that is, the stock is cheaper to catch and/or more valuable by weight because of abundance, compared with stocks with a smaller \( MSY \) within the region. These assumptions were made because data for specifying individual fishery \( I \) and \( V \) were unavailable, and substitutability was difficult to confirm directly across a large number of species. The result was that each fishery had a harvesting cost \( I \), an initial marginal benefit \( V/I \) (as opposed to \( V \) for the aggregate substitutable stocks), and a marginal benefit that diminished with the harvests from \( N \) stocks, rather than diminishing only with its own harvest:

\[
\gamma = \frac{\sum_{i=1}^{N} I_i}{\sum_{i=1}^{N} V_i \ln(MSY_i)} - \frac{\sum_{i=1}^{N} V_i \ln(MSY_i)}{\sum_{i=1}^{N} V_i \ln(MSY) - 1}.
\]

Holding \( r \) constant, an increase in \( N \) implies a decrease in \( I/V \), that is, each fish is relatively more profitable to catch. Rearranging Eq. 6 (3) and substituting the constant \( w \) with an aggregate shape parameter \( w \) yields the following:

\[
F^* = \left\{ \begin{array}{ll}
0 & \text{if } 1 + \frac{1}{V - MSY} < N \ln(MSY) \\
\log_2 \left( 1 + \frac{1}{V - MSY} \right) & \text{if } 1 + \frac{1}{V - MSY} \geq N \ln(MSY) \\
\end{array} \right.
\]

These solutions consisted entirely of dimensionless terms (48) and enabled a single analysis of vastly different fisheries. We have assumed a single global \( N \) to limit the number of free parameters.

Institution Speed. The minimum theoretical ratio of interannual changes in stock and harvest \( \Delta SS_{\text{MSY}}/\Delta F_{\text{MSY}} \), or stock elasticity, that still produces path dependence (black curve in Fig. 3B) was derived by exploring the stability of \( F^* \) in the economically constrained region (\( MEY < MSY \)). High elasticity implies slow institutions. The optimal institution must maintain the harvest volume \( MEY \) during the transition from \( F^* \) to \( F^+ \) (20) by adjusting \( F \) fast enough as \( F \) recovers; otherwise, the harvest volume will be above \( MEY \), which decreases rent and prompts a return to \( F^* \) (hence path dependence—SI Appendix, Ecological Response to Harvest Rate and Fig. 5B). The elasticity condition for path dependence is thus as follows:

\[
\frac{\Delta S/SS_{\text{MSY}}}{\Delta F/FS_{\text{MSY}}} > 1 - 2 \left( 1 + \frac{1}{V - MSY} \right) \frac{N}{\ln(MSY)}.
\]

An infinitely fast transition to \( F^* \) yields a harvest volume below \( MEY \) and thus also a lower rent and a likely return to \( F^* \). The empirical estimates of stock elasticity in Fig. 3B includes all 217 stocks, and the mean and 95% CI of \( \ln(MSY) \) beyond which institutions are slow enough for path dependence are estimated from where the empirical confidence band crosses above the theoretical condition (Inequality 10). Eliminating stocks with elasticity \( > 1 \), which suggests independence from harvest, preserves the same negative trend \( (P = 5.5 \times 10^{-5}, R^2 = 0.050, n = 152) \), with institutions being slow enough for path dependence for \( \ln(MSY) \) > 17.5 [95% CI = 16.3–18.9].

Evaluating the Model with Data. The distributions of cost/benefit ratios \( r \), stock \( MSY \), and mean harvest rates for fisheries in the RAM Legacy database (version 3.0) (21) are presented in Fig. 2D and SI Appendix, Fig. 5D. The database contained 217 fisheries that met our criteria with 9,521 aggregate time points worldwide. We selected fisheries with at least 4 y of nonzero harvest rates (from stock assessments) and positive \( MSY \) estimates (from the assessment when available; otherwise from RAM Legacy model estimates (21)). \( r \) was computed as the simple average of the \( \partial \) variable cost + government subsidy/total landing value ratios from countries or regions involved in fishery management, averaged over the years 1990–2000 (22, 27). This \( r \) estimator was derived by ref. 27 from various sources (European Commission, Food and Agriculture
Organization, websites, gray literature, and survey), and captured predominately regional variability in subsidy, labor, fuel, and processing costs, and to some extent gear-specific costs, as gear types are correlated with regions (27). This was an incomplete but reasonable estimator, as the variation in some extent gear-specific costs, as gear types are correlated with regions (27).

The probability densities of harvest rates as a function of $\ln(\text{MSY}_{\text{opt}})$ (Fig. 2 A–C and E) were constructed using MatLab(R2017a)'s kernel smoothing function (ksdensity) with automatic bandwidth.

We initially estimated $N$ and $\omega$ (Eq. 8) as free model parameters using an iterative search procedure (fminsearch in MatLab R2017a) to minimize the nonlinear least squares. Since the model predicted two possible stable strategies for $\ln(\text{MSY}_{\text{opt}})} > \omega$, the expected solution was chosen in a binary fashion according to each fishery’s initial condition. If a fishery’s first reported harvest rate $F_0$ was below $F^*_0$, then the model predicted that the fishery would subsequently converge to $F^*_0$. Conversely, if the initial harvest rate was above $F^*_0$, then the fishery was expected to converge to $F^*$. For the model analysis, the dependent variable was the average $\text{Fish}_{\text{easy}}$ of each fishery for all years excluding the first, which averaged out any oscillatory patterns.

While we modified the unit of MSY (Eq. 8), it had little effect on the model fit, and $R^2$ changed by only 0.01 across 10 orders of magnitude (SI Appendix, Fig. S7). We tested the model using the standard kilogram ($w = 1$).

The 95% CIs of the parameter $N$ estimate and the resulting $R^2$ were obtained by refitting the model to 2,000 bootstraps (resampling with replacement) (49). The significance of the fit model and parameter estimate were evaluated using a permutation test (50). We permuted 100,000 times without replacement the mean harvest rate $F$. The initial harvest rate remained paired with the mean harvest rate, while the cost/benefit ratio $\gamma$ and MSY remained paired to retain the fishery data structure (Fig. 3A). Each permutation created a dataset that represented the null hypothesis of no relationship between $F$ and $\ln(\text{MSY})$. The model was then fit to each set of permuted data, generating null $R^2$ and $N$ distributions. The one-sided $P$ value of the model was the fraction of the permuted fits whose $R^2$ were larger than the original $R^2$ (50). A similar procedure was performed to obtain the two-sided $P$ value of the original $N$ estimate (SI Appendix, Fig. S7C). An insignificant parameter estimate for $N$ could occur even if the model fit was significant. Such a case indicates that $N$ fit the pure harvest rate distribution without being sensitive to $\ln(\text{MSY})$.

Data Availability. Code and data are available on a figshare repository (51).

ACKNOWLEDGMENTS. We thank Martin Krkosek, Dan Holland, Alex Paff, Ryan Batt, Partha Dasgupta, and Olaf Jensen for discussions. Research was funded by National Science Foundation Awards OCE-1426700, OCE-1426746, OCE-1426881, and DEB-1616821, New Jersey Sea Grant Award N6410-0011; the Keystone Family Foundation; an Alfred P. Sloan Research Fellowship; and the project, Green Growth Based on Marine Resources (GreenMAR, Nordforsk).

23. Food and Agriculture Organization (2016) The State of World Fisheries and Aquaculture (Food and Agriculture Organization, Rome).
33. Waddington CH (1942) Canalization of development and the inheritance of acquired shallow lakes.