Path-dependent institutions drive alternative stable states in conservation

Edward W. Tekwa[a,b,1,2], Eli P. Fenichel[c], Simon A. Levin[b], and Malin L. Pinsky[a]

[a]Department of Ecology, Evolution, and Natural Resources, Rutgers University, New Brunswick, NJ 08901; [b]Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544-1003; and [c]School of Forestry and Environmental Studies, Yale University, New Haven, CT 06460

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.

path dependence | alternative stable states | conservation | institution | fishery

The path dependence hypothesis suggests that alternative stable outcomes result from historical contingencies rather than intrinsic differences. This hypothesis has sparked substantial theoretical investigation in social (1, 2) and natural sciences (3–5). Case studies (2, 6, 7), experiments (5), and global studies (8, 9) suggest the existence of alternative stable states, but the explanatory significance of specific path-dependent processes in nature remains less clear. In social-ecological systems, path dependence due to complexity (10, 11) or limited control (12, 13) can hinder resource conservation even when conservation is economically desirable (14, 15). Alternatively, path dependence means conservation can be self-sustaining once achieved. Path dependence for social-ecological systems, however, is largely theoretical and contrasts with the classical focus on institutional differences—such as management type, excludability, leadership, and incentives (16–18)—and single equilibrium expectations to explain why some resources are overharvested and others conserved (19, 20). Cooperatively managed marine fisheries are well documented (21, 22) and important social-ecological systems (16) with potential path-dependent processes that are ripe for evaluation. The last half-century's overfishing (15, 23) (*SI Appendix,* Fig. S1A) has been explained informally using the "shifting baselines" (24) and "ratchet effects" (16) concepts, which are political processes that maintain status quo policies. Conversely, the evolution of prosocial norms could lock in conservative harvest rates (19). Here, we show that a simple institutional adaptation (25) model with realistic features generates path-dependent outcomes and outperforms a wide range of alternative explanations for global fishing patterns. This institutional perspective, coupled with statistical tests designed for multisolution models, quantifies how history can sway societies toward or away from resource conservation.

Results

We explain patterns of resource harvest rate based on the idea that institutions maximize rent (net benefit function u) (19). Rent is to society, which includes fishers and managers. We assume four features common to many institutions managing a renewable resource, and we test how sensitive the outcomes are to these assumptions. First, the institution has exclusive access to a resource stock, which describes the idealized social planner, cooperative, or market system (26). Second, stock growth (dS/dt) is concave with S_{MSY} generating a maximum sustainable yield (MSY) and a carrying capacity S_{MAX}. Third, social utility (or rent) diminishes with harvest volume. This can take the form of consumer satiation, with the marginal benefits of harvesting the stock diminishing with increased harvest volume. Given diminishing benefits, it would be sufficient for the marginal costs of harvest to not fall with harvest volume, which is consistent with global evidence (27) (*SI Appendix, Alternative Cost Models* and Fig. S2). Finally, the institutions adjust harvest rates or effort (F, the portion of a stock

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, $S_{MAX} = r/a$, and $S_{MSY} = S_{MAX}/2$, Eq. 1), natural log benefits (with marginal benefit parameter V and shape parameter w, Eq. 2 and *Materials and Methods, Model*), and constant marginal cost I:

$$\frac{dS}{dt} = S(r - aS - F),\qquad [1]$$

$$u = V ln(wFS^*) - IFS^*.\qquad [2]$$

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 Eq. 8) are determined by three factors: the maximum yield $ln(MSY_{kg})$, the cost/benefit ratio (γ), and the average number of substitutable stocks (N) (*Materials and Methods, Connecting Solutions to Data*). The cost/benefit ratio (γ) 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. 1 A 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_{MSY}. On the other hand, an institution with a resource supporting a greater *MSY* and/or with a larger cost/benefit ratio [$\gamma ln(MSY) > N$] is "economically constrained" because harvesting *MSY* becomes too costly due to diminishing marginal benefits—at the extreme, harvesting too much can yield negative rent. In this parameter space, *MEY* < *MSY* and *MEY* intercepts the surplus production curve at two equilibria (S^{F^*+} and S^{F^*-}) (Fig. 1B). Institutions monotonically adjust harvest rates to F^{*+} (overharvesting) or F^{*-} (conservative harvesting) to approach the S^{F^*+} or S^{F^*-} equilibrium. The intuition behind these alternative stable states is that harvest rate and stock size lock into a positive social-ecological feedback: a large stock encourages conservative harvesting, but a small stock encourages overharvesting. F_{MSY} is a common management target or legal mandate (16, 32), but is often unstable

from a socio-ecological perspective. Many institutions will drift toward either overharvesting or stronger conservation. This result contrasts with the optimal control path, which is to continue harvesting *MEY* even when the stock grows larger than S^{F^*+} (20). Maintaining the harvest at *MEY* in such cases eliminates path dependence and requires fast institutional adjustment from F^{*+} to F^{*-} (*Materials and Methods, Institution Speed* and Inequality 9).

Two aspects of our model are critical for path dependence. Path-dependent harvest rates hold (*i*) if the institution is sufficiently slow relative to ecological dynamics (14, 20, 33, 34) (see Fig. 3B and *SI Appendix, Ecological Response to Harvest Rate*), and (*ii*) if resource access is exclusive (19, 20) (*SI Appendix, Comparison to Previous Theories*). Specifically, fast institutions can avoid the overharvesting solution (F^{*+}), while open access additionally implies overharvesting instead of F_{MSY} for small and valuable stocks [$\gamma ln(MSY) < N$]. 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 (landing value) for 1990–2000 (22) (*Materials and Methods, Evaluating the Model with Data*) to estimate a constant γ for each fishery. We used the first reported (not necessarily inception) harvest rate of each fishery (the binary of whether $F_o > F_{MSY}$) as its initial condition.

Aggregate harvest rate data did not suggest bimodality [mean $log_2(F/F_{MSY}) = -0.50$; 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_{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 ("economically constrained" fisheries, Fig. 2 B and C). These fisheries included many northeastern US and European fisheries that overharvested initially (1961–1991) and continued to do so (F^{*+}, 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 ($F_o > F_{MSY}$) determined whether F^{*+} or F^{*-} was
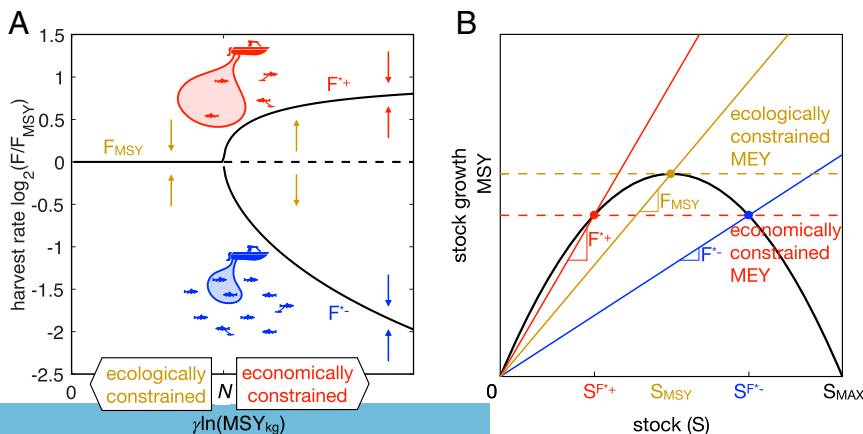
Fig. 1. Harvest model with path dependence. (A) Equilibrium harvest rates F^* as functions of the cost/benefit ratio (γ) multiplied by ln maximum sustainable yield [ln (MSY)]. The quantity $log_2(F^*/F_{MSY}) = 0$ is maximum sustainable harvesting, while $log_2(F^*/F_{MSY}) = 1$ produces stock collapse. Arrows indicate transient trajectories converging on F_{MSY}, F^{*-} or F^{*+}. Illustrated net sizes represent harvest rates (portions of the stock harvested), adult fish represent stock size, and small fish represent density-dependent population growth that balances harvest. Ecologically or economically constrained regimes correspond to less or more costly harvests, respectively (demarcated by N, the number of substitutable stocks per fish). (B) Stock growth (black line) as a function of stock size. Growth falls to zero when the stock is 0 or S_{MAX}. Ecologically constrained fisheries [yellow maximum economic yield (*MEY*)] converge on F_{MSY} (yellow) with stock S_{MSY}, while economically constrained fisheries (red *MEY*) converge on F^{*+} (red) with stock S^{F^*+} or on F^{*-} (blue) with stock S^{F^*-}.
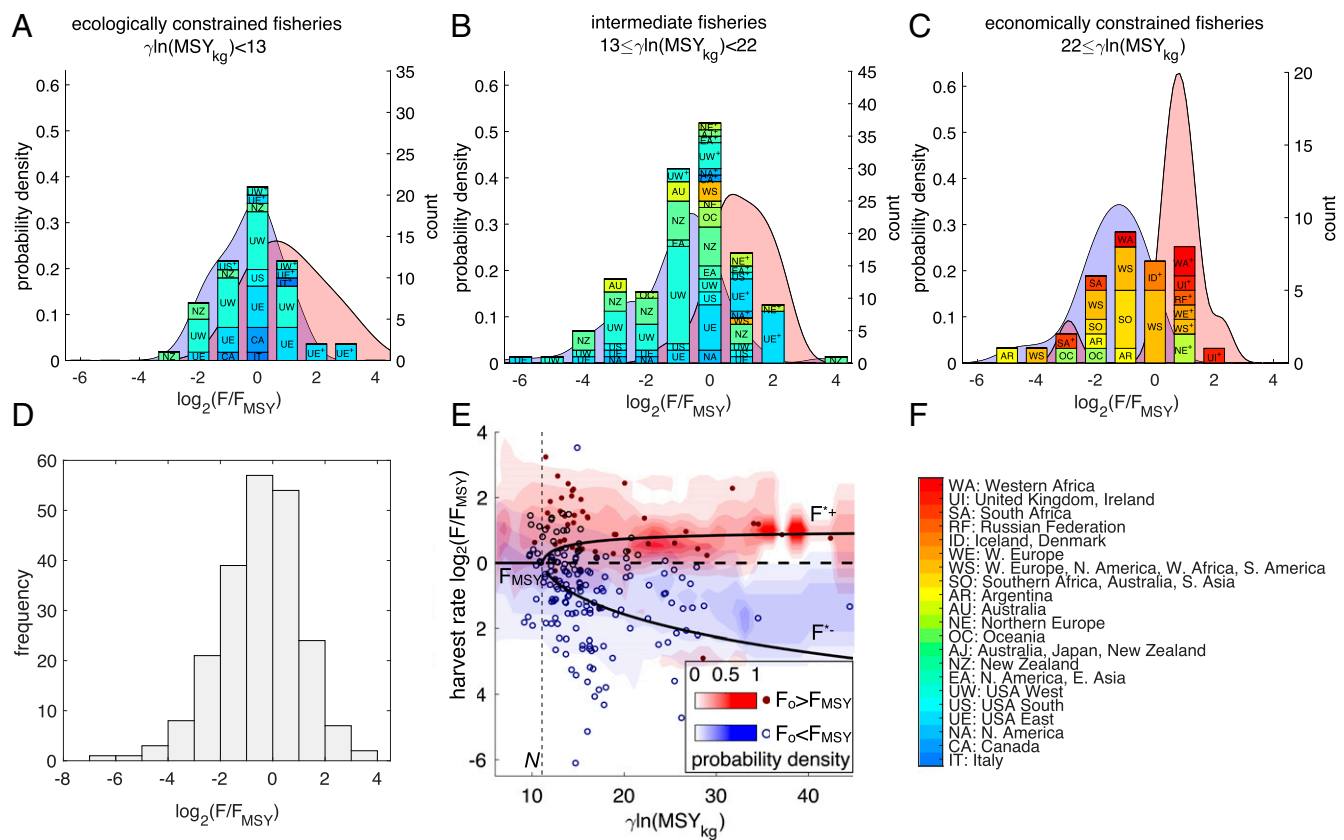
Fig. 2. Harvest rates and model fit. (*A–C*) Harvest rates (217 fisheries; 1961–2009) separated into three groups according to increasing cost/benefit ratio (γ) multiplied by ln maximum sustainable yield [ln(*MSY*)]. Harvest rate probability densities are displayed separately by initial conditions (blue for $F_o < F_{MSY}$, red for $F_o > F_{MSY}$; left axis). Stacked histograms (right axis) represent regional count (see *F*). Fisheries with $F_o > F_{MSY}$ are appended with the superscript $^+$. (*D*) Mean relative harvest rates $\log_2(F/F_{MSY})$ for all 217 stocks. (*E*) Modeled stable (solid) and unstable (dash) harvest rates as functions of γln(*MSY*). F^{*+} is unique to the slow-institution assumption, while F^{*-} and F_{MSY} are insensitive to institution speed. Mean harvest rates (circles) and probability densities are separated by initial conditions (blue or red, legend). The model with one free parameter N (the number of substitutable stocks per fish) was fit to the mean harvest rates (excluding initial year). (*F*) Regional color and label arranged with highest cost/benefit ratio γ on top.

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. 3*A*) revealed that the model explained the observations significantly better than under a null hypothesis of no relationship between γln(*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^{*-} or 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 γln(*MSY*) > 13.5, which is where the path-dependent model strongly differs from fast-institution models (*Materials and Methods, Institution Speed* and Fig. 3*B*). 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," $R^2 = 0.27$, ΔAIC = 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. S11*A*) 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 γln(*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 γln(*MSY*) ($P = 0.014$; Fig. 3*C*), 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_{MSY}, are rare in the path-dependent regime where F_{MSY} becomes unstable. We found that 40% of relatively path-independent fisheries [γln(*MSY*) < 13] transitioned. In contrast, only 15% of strongly path-dependent fisheries [γln(*MSY*) ≥ 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 over-harvesting (*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. S11*D*), particularly for weakly economically constrained fisheries that exhibited fast

Tekwa et al.

www.manaraa.com
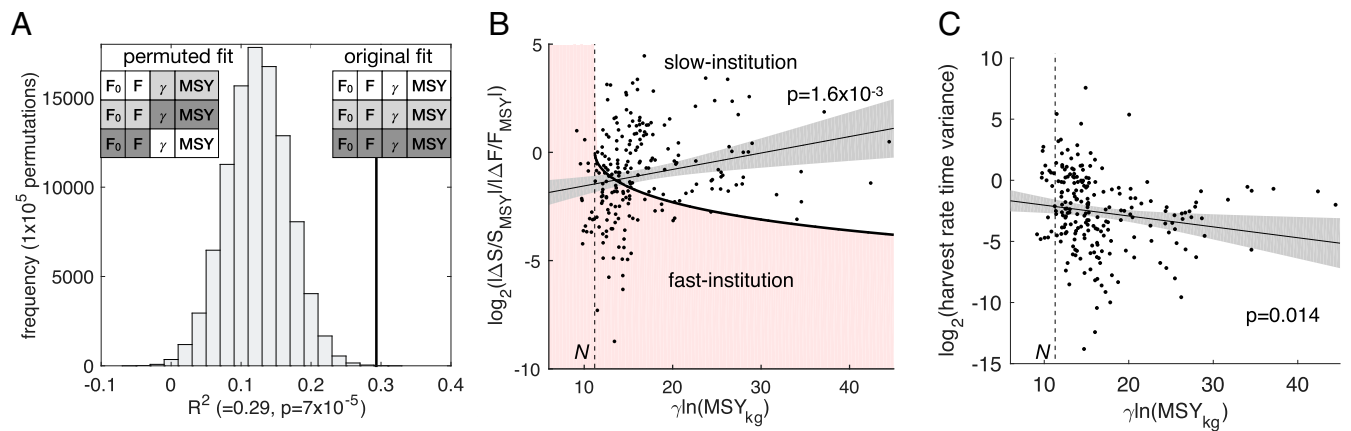
Fig. 3. Evidence for path dependence. (A) Model R^2 for permuted data (histogram) compared with R^2 for original data (line) ($P = 7 \times 10^{-5}$). The *Insets* illustrate the permutation procedure, which maintains the γ and MSY structure but disassociates these from F and F_o. (B) Empirical estimates of stock elasticity from interannual changes $\log_2(|\Delta S/S_{MSY}|/|\Delta F/F_{MSY}|)$, which is high when institution is slow (dots). The pink region indicates the institutional speeds required to avoid path dependence. The observed average stock elasticity increases with $\gamma \ln(MSY)$ (least-squares linear regression line with 95% CI in gray; $R^2 = 0.045$; $n = 217$). Institutions are too slow to avoid path dependence for $\gamma \ln(MSY) > 13.5$ [95% CI = 12.6–14.5]. (C) Elevated temporal variance (in F/F_{MSY}) can be a signature of an approaching critical threshold, and the path dependence model predicts a critical threshold (N) at small $\ln(MSY)$. The least-squares linear regression shows higher harvest rate variance at small $\gamma \ln(MSY)$ ($R^2 = 0.028$; $n = 217$).

institutional dynamics (Fig. 3B) and likely experienced stronger conservation mandates (*SI Appendix*, Table S3) (16, 18, 36). However, once fisheries transitioned across F_{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, intensely 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 mideast stock of orange roughy was initially (<1983) harvested below F_{MSY} even though there was no catch limit (37). This state did not last, however, and trawlers subsequently overharvested the stock [open circle near $\log_2(F/F_{MSY}) = 3$; 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_{MSY}, but harvest rates fell [filled circle near $\log_2(F/F_{MSY}) = -3$; 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 [$\gamma \ln(MSY) \geq 22$], 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 γ, 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 γ) and therefore reduce path dependence (toward F_{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_{MSY}. Such conservation opportunities may be present in many renewable resources beyond fisheries (20, 26, 34). The challenge will be to

www.manaraa.com

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 $S_{MSY} = r/(2a)$, and the associated harvest rate is $F_{MSY} = r/2$. *MSY* is $S_{MSY}F_{MSY} = r^2/(4a)$. Harvest rates are scaled as $F/F_{MSY} = (2F)/r$, which is 1 when a stock is harvested at F_{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 $\ln(1 + \Delta wFS) \sim \Delta wFS^*$ when $\Delta wFS^* \ll 1$]. *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 standard reported unit (27) and is empirically supported (*SI Appendix*, Fig. S2), but differs from the effort (*F*)-based cost common in fisheries literature (19) (that is, our utility is proportional to *F* instead of FS^*). As long as some costs rise with harvest volume, our main results hold (*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, $\partial u/\partial F$. That is, institutions change *F* to maximize *u*:

$$\frac{\partial u}{\partial F} = \frac{\partial}{\partial F}\left(V\ln(wFS^*) - IFS^*\right) = \frac{r - 2F}{a}\left(\frac{Va}{F(r - F)} - I\right). \quad [3]$$

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, Stability Analysis*):

$$F^* = \begin{cases} r/2 \\ \left(r \pm \sqrt{r^2 - \dfrac{4aV}{I}}\right)\Big/2 \end{cases}. \quad [4]$$

As *I/V* passes the critical threshold $4a/r^2$ ($=1/MSY$), a pitchfork bifurcation occurs. The critical bifurcation threshold can be understood in the form $V = I \cdot MSY$, 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_{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 $\widehat{F^*} = \log_2(F^*/F_{MSY})$ to facilitate comparisons across fisheries. The use of log base 2 normalizes the quantity so that it is 0 when harvests are at F_{MSY}, −1 when harvests are at $1/2 \; F_{MSY}$, and 1 for deterministic extinction:

$$\widehat{F^*} = \begin{cases} 0 \\ \log_2\left(1 \pm \sqrt{1 - \dfrac{1}{MSY \cdot I/V}}\right) \end{cases}. \quad [5]$$

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 γ, 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 γ [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/N* (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:

$$\gamma = \overbrace{\frac{\sum_i^{nN} I_i C_i}{\sum_j^{nN} V_j \ln(wC_j)}}^{(1)} = \overbrace{\frac{\sum_i^{n} I_i N \cdot MSY_i}{\sum_j^{n} V_j \ln(wN \cdot MSY_j)}}^{(2)} = \overbrace{\frac{I \cdot MSY}{\frac{V}{N}\ln(wN \cdot MSY)}}^{(3)}. \quad [6]$$

Holding γ 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 *wN* with an aggregate shape parameter ω yields the following:

$$\frac{1}{MSY \, I/V} = \frac{N}{\gamma \ln(\omega \cdot MSY)}. \quad [7]$$

The right-hand side of Eq. **7** was substituted into Eq. **5**, yielding the solutions:

$$\widehat{F^*} = \begin{cases} 0 \\ \log_2\left(1 \pm \sqrt{1 - \dfrac{N}{\gamma\ln(\omega \cdot MSY)}}\right) \end{cases}. \quad [8]$$

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 $|\Delta S/S_{MSY}|/|\Delta F/F_{MSY}|$, or stock elasticity, that still produces path dependence (black curve in Fig. 3*B*) 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 *S* 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. S3). The elasticity condition for path dependence is thus as follows:

$$\frac{|\Delta S/S_{MSY}|}{|\Delta F/F_{MSY}|} > 1 - 2\Big/\left(1 + \sqrt{1 - \frac{N}{\gamma\ln(\omega \cdot MSY)}}\right). \quad [9]$$

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. 3*B* includes all 217 stocks, and the mean and 95% CI of $\gamma\ln(MSY)$ beyond which institutions are slow enough for path dependence are estimated from where the empirical confidence band crosses above the theoretical condition (Inequality 9). Eliminating stocks with elasticity >1, which suggests independence from harvest, preserves the same negative trend ($P = 5.5 \times 10^{-3}$, $R^2 = 0.050$, $n = 152$), with institutions being slow enough for path dependence for $\gamma\ln(MSY) > 17.5$ [95% CI = 16.3–18.9].

Evaluating the Model with Data. The distributions of cost/benefit ratios γ, stock *MSY*, and mean harvest rates for fisheries in the RAM Legacy database (version 3.0) (21) are presented in Fig. 2*D* and *SI Appendix*, Fig. S6. 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)]. γ was computed as the simple average of the (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 γ estimator was derived by ref. 27 from various sources (European Commission, Food and Agriculture

Tekwa et al.

Organization, websites, gray literature, and survey), and captured predominantly 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 γ between fisheries [coefficient of variation (CV) = 0.071] and between gear types [weighted by number of records (27); CV = 0.097] are comparable. We treated $\gamma\ln(MSY)$ as constant for each fishery as we lack temporal data.

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

We initially estimated N and ω (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 $\ln(\omega MSY_{kg}) > N$, 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_o was below F_{MSY}, then the model predicted that the fishery would subsequently converge to F^{*-}. Conversely, if the initial harvest rate was above F_{MSY}, then the fishery was expected to converge to F^{*+}. For the model analysis, the dependent variable was the average F/F_{MSY} of each fishery for all years excluding the first, which averaged out any oscillatory patterns.

While ω 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. S7A). We thus set the unit to the standard kilogram ($\omega = 1$).

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) of the data. The significance of the model fit 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 γ 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 $\gamma\ln(MSY)$. 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 $\gamma\ln(MSY)$.

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

1. North DC (1990) *Institutions, Institutional Change and Economic Performance* (Cambridge Univ Press, Cambridge, UK).
2. David PA (2000) Path dependence, its critics and the quest for "historical economics." *Evolution and Path Dependence in Economic Ideas: Past and Present*, eds Garrouste P, Ioannides S (Edward Elgar, Cheltenham, UK), pp 15–36.
3. Waddington CH (1942) Canalization of development and the inheritance of acquired characters. *Nature* 150:563–565.
4. Jacob F (1977) Evolution and tinkering. *Science* 196:1161–1166.
5. Ferrell JE, Jr (2002) Self-perpetuating states in signal transduction: Positive feedback, double-negative feedback and bistability. *Curr Opin Cell Biol* 14:140–148.
6. Scheffer M, Hosper SH, Meijer ML, Moss B, Jeppesen E (1993) Alternative equilibria in shallow lakes. *Trends Ecol Evol* 8:275–279.
7. Mumby PJ, Hastings A, Edwards HJ (2007) Thresholds and the resilience of Caribbean coral reefs. *Nature* 450:98–101.
8. Staver AC, Archibald S, Levin SA (2011) The global extent and determinants of savanna and forest as alternative biome states. *Science* 334:230–232.
9. Ling SD, et al. (2015) Global regime shift dynamics of catastrophic sea urchin overgrazing. *Philos Trans R Soc Lond B Biol Sci* 370:20130269.
10. Quaas MF, van Soest D, Baumgärtner S (2013) Complementarity, impatience, and the resilience of natural-resource-dependent economies. *J Environ Econ Manage* 66:15–32.
11. Skiba AAK (1978) Optimal growth with a convex-concave production function. *Econometrica* 46:527–539.
12. Horan RD, Fenichel EP, Drury KLS, Lodge DM (2011) Managing ecological thresholds in coupled environmental–human systems. *Proc Natl Acad Sci USA* 108:7333–7338.
13. Fenichel EP, Horan RD (2016) Tinbergen and tipping points: Could some thresholds be policy-induced? *J Econ Behav Organ* 132:137–152.
14. Levin S, et al. (2013) Social-ecological systems as complex adaptive systems: Modeling and policy implications. *Environ Dev Econ* 18:111–132.
15. Costello C, et al. (2016) Global fishery prospects under contrasting management regimes. *Proc Natl Acad Sci USA* 113:5125–5129.
16. Botsford LW, Castilla JC, Peterson CH (1997) The management of fisheries and marine ecosystems. *Science* 277:509–515.
17. Gutiérrez NL, Hilborn R, Defeo O (2011) Leadership, social capital and incentives promote successful fisheries. *Nature* 470:386–389.
18. Lubchenco J, Cerny-Chipman EB, Reimer JN, Levin SA (2016) The right incentives enable ocean sustainability successes and provide hope for the future. *Proc Natl Acad Sci USA* 113:14507–14514.
19. Clark CW (2010) *Mathematical Bioeconomics* (Wiley, Hoboken, NJ), 3rd Ed.
20. Dasgupta P, Mitra T, Sorger G (January 25, 2018) Harvesting the commons. *Environ Resour Econ*, 10.1007/s10640-018-0221-4.
21. Ricard D, Minto C, Jensen OP, Baum JK (2012) Examining the knowledge base and status of commercially exploited marine species with the RAM Legacy Stock Assessment Database. *Fish Fish* 13:380–398.
22. Sumaila UR, et al. (2012) Benefits of rebuilding global marine fisheries outweigh costs. *PLoS One* 7:e40542.
23. Food and Agriculture Organization (2016) *The State of World Fisheries and Aquaculture* (Food and Agriculture Organization, Rome).
24. Pauly D (1995) Anecdotes and the shifting baseline syndrome of fisheries. *Trends Ecol Evol* 10:430.
25. Nelson RR, Winter SG (1982) *An Evolutionary Theory of Economic Change* (The Belknap Press of Harvard Univ Press, Cambridge, MA).
26. Ostrom E (1990) *Governing the Commons: The Evolution of Institutions for Collective Action* (Cambridge Univ Press, Cambridge, UK).
27. Lam VWY, Sumaila UR, Dyck A, Pauly D, Watson R (2011) Construction and first applications of a global cost of fishing database. *ICES J Mar Sci* 68:1996–2004.
28. Sims C, Finnoff D (2016) Opposing irreversibilities and tipping point uncertainty. *J Assoc Environ Resour Econ* 3:10–12.
29. Pella JJ, Tomlinson PK (1969) A generalized stock production model. *Inter Am Trop Tuna Comm Bull* 13:416–497.
30. Collie JS, Richardson K, Steele JH (2004) Regime shifts: Can ecological theory illuminate the mechanisms? *Prog Oceanogr* 60:281–302.
31. Smith VL (1968) Economics of production from natural resources. *Am Econ Rev* 58:409–431.
32. Deroba JJ, Bence JR (2008) A review of harvest policies: Understanding relative performance of control rules. *Fish Res* 94:210–223.
33. Crépin AS (2007) Using fast and slow processes to manage resources with thresholds. *Environ Resour Econ* 36:191–213.
34. Fryxell JM, Packer C, McCann K, Solberg EJ, Saether B-E (2010) Resource management cycles and the sustainability of harvested wildlife populations. *Science* 328:903–906.
35. Scheffer M, et al. (2009) Early-warning signals for critical transitions. *Nature* 461:53–59.
36. Gehan SM, Hallowell M (2012) Battle to determine the meaning of the Magnuson-Stevens Fisheries Conservation and Management Reauthorization Act of 2006: A survey of recent judicial decisions. *Ocean Coast Law J* 18:1–34.
37. Clark M (1995) Experience with management of orange roughy (*Hoplostethus atlanticus*) in New Zealand waters, and the effects of commercial fishing on stocks over the period 1980–1993. *Deep-Water Fisheries of the North Atlantic Oceanic Slope*, ed Hopper AG (Springer Netherlands, Dordrecht, The Netherlands), pp 251–266.
38. Jacquet JL, Pauly D (2008) Trade secrets: Renaming and mislabeling of seafood. *Mar Policy* 32:309–318.
39. Lombard AT, et al. (2007) Conserving pattern and process in the Southern Ocean: Designing a marine protected area for the Prince Edward Islands. *Antarct Sci* 19:39–54.
40. Österblom H, Folke C (2013) Emergence of global adaptive governance for stewardship of regional marine resources. *Ecol Soc* 18:4.
41. Edgar GJ, et al. (2014) Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506:216–220.
42. Hilborn R, Annala J, Holland DS (2006) The cost of overfishing and management strategies for new fisheries on slow-growing fish: Orange roughy *Hoplostethus atlanticus* in New Zealand. *Can J Fish Aquat Sci* 63:2149–2153.
43. Acemoglu D, Robinson JA (2012) *Why Nations Fail: The Origins of Power, Prosperity, and Poverty* (Crown, New York), 1st Ed.
44. Pinchot G (1910) *The Fight for Conservation* (Doubleday, Page and Company, New York).
45. Wilen JE, Homans FR (1998) What do regulators do? Dynamic behavior of resource managers in the North Pacific halibut fishery 1935–1978. *Ecol Econ* 24:289–298.
46. Hilborn R (2007) Defining success in fisheries and conflicts in objectives. *Mar Policy* 31:153–158.
47. Pershing AJ, et al. (2015) Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science* 350:809–812.
48. Stahl WR (1962) Similarity and dimensional methods in biology. *Science* 137:205–212.
49. Efron B, Tibshirani R (1986) Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. *Stat Sci* 1:54–77.
50. Anderson MJ (2001) Permutation tests for univariate or multivariate analysis of variance and regression. *Can J Fish Aquat Sci* 58:626–639.
51. Tekwa EW, Fenichel EP, Levin SA, Pinsky ML (2018) Data on "Path-dependent institutions drive alternative stable states in conservation." Figshare. Available at 10.6084/m9.figshare.5813934. Deposited November 1, 2018.

Tekwa et al.

www.manaraa.com