**Path Dependence in Global Fishing Patterns**

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[*Nature Letters guideline for first paragraph:* One or two sentences providing a basic introduction to the field, comprehensible to a scientist in any discipline. Two to three sentences of more detailed background, comprehensible to scientists in related disciplines. One sentence clearly stating the general problem being addressed by this particular study. One sentence summarizing the main result (with the words “here we show” or their equivalent). Two or three sentences explaining what the main result reveals in direct comparison to what was thought to be the case previously, or how the main result adds to previous knowledge. One or two sentences to put the results into a more general context. Two or three sentences to provide a broader perspective, readily comprehensible to a scientist in any discipline, may be included in the first paragraph if the editor considers that the accessibility of the paper is significantly enhanced by their inclusion. Under these circumstances, the length of the paragraph can be up to 300 words.]

Many complex systems in evolutionary biology1,2, developmental biology3–5, ecology6–10, and social science11–13 are path dependent, meaning that small initial differences can lead to great divergence in subsequent outcomes. In particular, socioecological systems14 such as fisheries15,16 may exhibit path dependence because local managements are constrained17,18 and adapt gradually, which may explain surprisingly persistent overharvesting even with exclusive control of stocks. Path dependence has been shown experimentally4,5,7,19 and inferred from single populations through time in nature6,8,15,16, but cross-system patterns have been inferred only descriptively2,9–13,20. Here we test whether the wide variations in global fish harvest rates exhibit a model-specific path dependence towards two harvest strategies rather than a single optimum that we expect of rational institutional agents. If we assume that institutional change occurs slower than resource dynamics14, data from 217 global fisheries21 strongly support the theoretical prediction of a path-dependent harvesting regime occurring at high cost/benefit ratios and large potential resource yields (R2=0.311, p=3.0e-5). The surprisingly simple one-parameter model demonstrates that diverging harvest patterns across the globe, which critically impact resource sustainability, can arise from similar institutional agents following simple bioeconomic rules with no differences in foresight or resource valuation. Path dependence implies that undesirable policies can be hard to shake, but also leaves hope for large and nearly-irreversible shifts toward desirable policies and resource sustainability.

Surveying marine fishery harvest patterns and the related literature suggests the possibility that path dependence may explain the variation in fishery harvest rates. In an era where resource sustainability is increasingly recognized22 and mandated23, harvest rates remain highly heterogeneous, with 31.4% of global fisheries still overharvesting24. Path dependent harvest rate is different from the issue of multiple stability in fish stock due to complex (non-unimodal) growth dynamics25 or a constant harvest policy26. The possibility of high harvest rate policies where a lower optimum exists is often explained using high discounting27 or open access and failure to cooperate28. However, another line of reasoning seeks to explain overharvesting without directly invoking discounting and cooperation, and indeed alludes to path dependence. This is articulated as a *shifting baseline*29, where fishery managements set targets and limits based on the prevailing harvests, or as a *ratchet effect*23, where institutions are politically pressured against decreasing established harvest rates even when it is otherwise socioeconomically desirable. In formal economic theory, rational managers are expected to arrive at a single optimal harvest rate30, but limited management control can lead to multiple attractors17,18. In the following single-stock model, management limitation comes through attraction to local peaks in rent (benefit minus cost) as a function of harvest rate, rather than through convergence to a globally optimal strategy.

In our model, we assume that each fishery has exclusive access to a fish stock, that stocks quickly equilibrate in response to harvest, and that fisheries change their harvest rates slowly by small increments. With no discounting, these appear to be ideal conditions for managers to implement sustainable policies. Harvest rate is defined as the portion of the current stock that is harvested per year31. The fishery includes fishers and governing bodies of the stock, thus rents are defined as landing value minus variable operating cost and government subsidy32. The stock grows logistically, while the benefit from harvest exhibits diminishing return. This scenario exhibits the hallmarks of complex adaptive systems14: individual fisheries adapt locally, with a time-scale separation between resource and strategy dynamics, resulting in global patterns that are not necessarily optimal or unimodal. The model solutions (see Methods) are expressed in Equation 1 as =log2(*F\**/*FMSY*), or the log ratio of harvest rates *F\** over the harvest rate of maximum sustainable yield (*FMSY*), the rate that results in the highest possible sustained harvest. This normalized form makes different fisheries comparable; conveniently, it takes the value of 0 when the fishery harvests at *FMSY*, is negative when harvesting below *FMSY*, and is positive when harvesting above *FMSY*, taking on the value 1 if the stock is deterministically harvested to extinction in finite time. The solutions are determined by three factors: 1.) ln(MSY[kg]), 2.) *γ* , the cost/benefit ratio (operating cost+subsidy)/landing value), and 3.) a scaling factor *ξ* that approximates the number of fisheries in each geopolitical region (see Methods).

Equation

The harvest rate solutions and their stabilities are illustrated in Figure *1*a with respect to *γ*. At low MSY and *γ*, *FMSY* is the single attractor. At high MSY and *γ* (*ln*(MSY)*γ*=*ξ*), the solutions are path dependent, with basins of attraction at *F\*+* and *F\*-* now divided by the repeller *FMSY*. These solutions form a pitchfork bifurcation with a critical point *ξ*, and can be understood using an economic phase diagram (Figure *1*b). From a rent perspective, the optimal economic yield (OEY) is determined by cost and benefit (*γ*). When cost is relatively low, a fishery would like to harvest a lot but is limited by resource recruitment, or how fast the stock can grow (MSY). Thus, at low *γ*, the fishery is stock-limited and operates at *FMSY*. As the relative cost goes up, the OEY moves down past MSY along the resource recruitment y-axis, intercepting the hump-shaped stock growth curve at two points that correspond to *SF\*+*, or higher than MSY stock (*SMSY*) and *SF\*-*, or lower than MSY stock. These can be achieved using two linear consumption paths, defined by the harvest rates *F\*+* and *F\*-* respectively. Both strategies are ecologically and strategically attracting in the long run, and can be obtained using traditional economic techniques33 (see Supplementary Material). This is in fact a less sophisticated approach than modern economic optimization34, which generally produces a single, non-linear, and time-dependent consumption path that maximizes the present value of harvest at all time points. The non-linear consumption path leads to a socially optimal harvest rate of *F\*-*, or the lower equilibrium in our model35. The difference in our approach is the assumption that fisheries do not optimize through time, but rather gradually change their strategies based on long-run rents. The model can be generalized using more complex resource growth functions, diminishing return functions, and additional bias to strategy change, with no qualitative change in harvest rate predictions (see Supplementary Material).

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Figure 1. a. Model predictions on harvest rate attractors (solid curves) and repeller (dotted line) as a function of cost/benefit γ times ln(MSY). A pitchfork bifurcation occurs with a critical point at ξ. b. Economic phase diagram of resource recruitment (or harvest) versus stock. The thick solid curve represents the natural growth or recruitment curve of the stock as a function of stock. The recruitment is the MSY at SMSY, and is 0 at either 0 or stock carrying capacity (SMAX). The economically optimal equilibrium, accounting for cost, is to maintain the stock that yields the optimal economic yield (OEY) (horizontal dotted line). This can be achieved by adopting a constant harvest rate, or harvest per stock unit (slopes of linear paths), that is either high (F\*+) or low (F\*-). These rates result in either a low (SF\*+) or high (SF\*-) stable stock.

In summary, our model hypothesizes increasingly suboptimal harvest rates at high MSY and high *γ*, whenever the initial harvest rate is above the unstable strategy (*FMSY*). To test this hypothesis, we use the RAM Legacy database, which contains data on 217 global fisheries with MSY and *FMSY* estimates in multiple years between 1961-200921. These can be considered closely managed fisheries by virtue of their data availability, and thus satisfy our model’s assumption of resource excludability. We combine these fisheries data with additional country-level data on economic costs (variable cost + subsidy) and benefits (landing value) for 1990-200032 (see Methods). We use the state of the first reported harvest rate of each fishery (the binary of whether *Finit*>*FMSY*) as the initial condition that determines the expected path. 52 fisheries initially harvested above *FMSY*, while 165 began below *FMSY*. We wish to explain the distribution in the temporal means of the harvest rates log2(*F/FMSY*), excluding the first reported year. The mean of log2(*F/FMSY*) is -0.511 (std=1.54). The data distributions are summarized in Figure 2, and can be accessed in the Supplementary dataset.

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Figure . Distributions of a. cost/benefit ratio γ, b.stock maximum sustainable yields (MSY), and c. relative harvest rates log2(F/FMSY) in the RAM Legacy database.

The predicted attractors of the model (Equation 1), with a single parameter *ξ,* are fitted to harvest rates using *γ*, MSY, and initial conditions as inputs. The model is severely constrained in term of how it can fit the data, as *ξ* can only move the bifurcation point along the single dimension of ln(MSY)*γ* (Figure 1a). With *ξ*=11.1, the model explains (as R2) 0.311 of the variations in harvest rates across the globe. Figure 3a shows the apparent data trends that fisheries initially harvesting below *FMSY* (open circles) generally converge to the decreasing harvest rate attractor (*F\*-*) with increasing ln(MSY)*γ*, while fisheries initially harvesting above *FMSY* (filled circles) generally converge to the increasing harvest rate attractor (*F\*+*) with increasing ln(MSY)*γ*. A permutation test shows that the model explained the observations significantly better than when fitted against randomized mean harvest rates (p=3.0e-5, Figure 3b). In other words, if the harvest rate data were to have no relationship with *γ*, MSY, and initial conditions as the model hypothesized, the fit would be much worse. The mean of the model R2 fitted to permuted data is R2rand=0.138 (std=0.0442, p=7.30e-4), which can be understood as the portion of variations in the pure distribution of harvest rates (Figure 2c) explained by the model’s bimodality predictions. This still leaves a large portion of variations (ΔR2=0.173, std=0.0442, p=3.0e-5) explained by the model’s hypothesis that fisheries should increasingly diverge from *FMSY* at higher *γ* and ln(MSY). Further, to test whether one economic optimum solution alone35 could explain the harvest rate variations when compared to the path-dependent model solutions, we fitted a version of our model that retains only the lower harvest rate solution regardless of initial conditions. This model variant and the converse variant (with only the upper solution retained) both explain less variation than the mean (R2=-0.111), indicating that the path-dependent solutions are warranted.

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Figure 3. a. Fitted model predictions on attracting (solid curves) and repelling (dotted line) harvest rates as a function of γln(MSY), or cost/benefit times log of maximum sustainable yield, with the RAM Legacy fishery data plotted as either filled or open dots depending on initial conditions. b. R2 of the model fitted to the actual data (vertical line) compared to the null R2 distribution obtained from fitting the model to permuted harvest rates (repeated 100000 times). c, d. Harvest rates and fitted model predictions as functions of γ, for subsets of fisheries centering around ln(MSY)=12 and 20 (±1)

The clearest path-dependent patterns are observed in fisheries with high stock (Figure 3d). These fisheries all belong to a path-dependent regime given their sufficiently high *γ*. Here, newer fisheries in Alaska, Pacific US, the Indian Ocean, Oceania, and Argentina harvest at the lower, socially optimal rates. In contrast, older fisheries in the Atlantic US, the North Sea, and Russia continue to harvest near the higher, suboptimal rates, which are expected given their histories of overharvesting before sustainability awareness became prevalent. The segregation of these fisheries, despite shared ecological and economic characteristics, illustrate the path dependence of local institutional change. In contrast, fisheries with small MSY and *γ* should be path independent, which is corroborated by the data scattered around *FMSY* even though most of them initially harvested below *FMSY* (Figure 3c). Interestingly, many of these fisheries historically overestimated their stock MSYs, and yet they converged around *FMSY* as we would expect in the path-independent regime.

Our results indicate that fisheries with socially desirable practices act out of the same motivations as overharvesting fisheries; their differences may largely be due to path dependence and not necessarily to differences in incentive36, discounting37, or stock valuation30,38. Path dependence here can be attributed to gradualism, or institutions’ inability to make drastic change, and imposes a strategy resilience that is not necessarily desirable39. Path dependence also leaves hope for seismic shifts toward desirable states, perhaps due to social innovations in incentives and valuation. However, it is not clear whether resource recovery (estimated at a decade32,40) is fast enough for local institutions to see the benefit of a large downward shift in harvest rate. New theoretical advances are required to address the mechanisms and sustainability of such a large strategy shift.

Marine fisheries are vital to cultures and economies41, but their path dependence also serves as natural experiments for even larger challenges, where the gradualism of human action may threaten sustainability everywhere42. Our work is a step toward addressing sustainability issues by asking not only what mangers should do, but also why they fail and when optimal policies can succeed.

**Methods**

***Model***

We assume that stock *S* grows logistically, with intrinsic growth rate *r* and self-competition *a*:

Equation

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The maximum sustainable yield, defined as the stock that yields the greatest flow, is *SMSY* = *r*/*2a*, and the harvest rate leading to this is *FMSY* = *r*/*2*. Harvest rates are thus normalized as 2*F*/*r* to obtain *F/FMSY*, which takes the value 1 when a stock is harvested at *FMSY*.

A simple utility function expresses the flow of utility *u* (such as money per year) to a community over time:

Equation

*u* = *Vφ* ln(*FS*) - *IFS*

*V* is the maximum positive marginal income from fishing and *I* is a constant marginal cost of harvesting a unit of stock. *φ* is a constant that scales the income (ln) function and allows *V* and *I* to share the same unit. The units for the variables in Equation 3 are:

Equation

[$/yr] = [$/kg][kg/yr][1] - [$/kg][1/yr][kg]

where $ is in millions US. The quantity ln(*FS*) is dimensionless because logarithms are transcendental functions43. These unit identifications will facilitate how we can insert empirical observations into Equation 3 later on.

Assuming that the resource is excludable within a community, the stock will converge to equilibrium *S\** (from solving Equation 2) according to the community’s strategy – the harvest rate – before harvest rate is compelled to change by small steps. In other words, there is a time -scale separation between fast ecological dynamics and slow strategy dynamics. The change in strategy over time, d*F*/d*t*, is proportional to the change in utility (Equation 3) as a function of change in strategy, ∂*u*/∂*F*, according to standard evolutionary game models based on the fitness (or utility) hill climbing analogy44–47.

Equation

The equilibria of Equation 5 are either evolutionarily stable or unstable harvesting strategies:

Equation

The first solution is stable for 0 ≤ *I/V* ≤ 4*aφ*/*r*2 since ∂2*u*/∂*F2*<0; for greater *I*, a pitchfork bifurcation occurs, where the second and third solutions are stable, while the first solution is unstable (Supplementary). The bifurcation point is thus 4*aφ*/*r*2, which is equivalent to *φ*/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). That is, the region of *I*/*V* where harvesting at MSY rate is stable shrinks as MSY increases. As *I/V* approaches infinity, the stable solutions asymptotically approach *r* and 0. A more enlightening formulation of the solutions in Equation 6 are the logarithms of relative harvest rates log2(*F\*/FMSY*):

Equation

Using standard economic optimization methods on the managed harvest of renewable resources33,48, we obtain the same equilibria as in Equation 6 and Equation 7 (see Supplementary Information).

***Analysis***

To fit the model solutions in Equation 7 to data, we estimate the fishery-specific cost-benefit ratio *I*/*V* from the empirical community-wide cost-benefit ratio *γ.* In addition, since MSY is arbitrarily defined with a unit of kg, a multiplicative factor is inserted such that MSY=*ω*MSY[kg]. Suppose that each community’s total fish landing is *CT*=*ξω*MSY[kg], or *ξ* times the observed fishery’s potential, and that each community follows the utility function in Equation 3. Then, *γ* is the ratio of total community cost over benefit in terms of MSY, which contains the *I*/*V* ratio as derived below.

Equation

where = *ξω*, a multiplicative factor of MSY inside the *ln* function. The right hand side of the final expression in Equation 8 directly plugs into Equation 7, yielding the model solutions that can be fitted to data:

Equation

To fit the model to data, we can estimate *ξ* and as constant parameters using an iterative search procedure to minimize the non-linear least squares. Since the model (Equation 9) predicts two possible stable strategies for *γ* >*ξ*/(*ln*(MSY)), the expected solution is chosen according to each fishery’s initial condition. If a fishery’s first reported harvest rate *Finit* is below *FMSY* (which is the unstable solution in the bistable region), then the model predicts that the fishery will subsequently converge to the smaller . Conversely, if the initial harvest rate is above *FMSY*, then the fishery is expected to converge to the larger . The initial condition is thus binary (either above or below *FMSY*). For the model analysis, the dependent variable that we wish to predict is the average *F\*/FMSY* of each fishery over all available years between 1961 and 2009, excluding the first available year.

While modifies the unit of MSY, it does not strongly affect the value of *ξ*/*ln*(), which is the quantity that determines the model predictions on harvest rates, when *ξ* is fitted at the chosen unit. This is shown as the sensitivity of the model *R2* to the chosen unit of MSY (Figure 4). For all tested units where *ln*(MSY) is positive for all fisheries, the *R2* is close to the maximum. We set the unit to kg (=1), which is very close to the best fitting unit of 0.581 kg. In the main results, the model essentially contains a single parameter *ξ*, with MSY being understood to have the unit of kg.

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Figure . a. Sensitivity of model, as evaluated by R2, to MSY unit. b. Model R2 as a function of the parameter ξ with MSY in kg.

The significance of the model fit and parameter estimate are evaluated using a permutation test49–51. We permute, without replacement, the mean harvest rate *F*, which is what the model attempts to explain. To keep the time series of each fishery intact, the initial harvest rate remains paired with the mean harvest rate (which excludes the first year) through the permutation. The cost/benefit ratio *γ* and MSY remain as original pairs to retain the fishery data structure. The model is fitted to the permuted data, which generates an *R2* and a *ξ* estimate. By performing the permutation 100000 times, we generate null distributions of *R2* and *ξ* for the model, with the null hypothesis being that there is no relationship between harvest rate and the predictor variables (*γ* and MSY) in our model. The one-sided *p*-value of the original *R2*, fitted to the original data, is the fraction of the permuted fits whose *R2* are larger. This is the significance of the model. The one-sided *p*-value of the model fit to permuted harvest rate is the fraction of *R2* greater than 0 in the permuted set, and indicates the model’s fit to the pure harvest rate distribution without regard to *γ* and MSY. The two-sided *p*-value of the original *ξ* estimate is 2x the smaller of the fractions of permuted *ξ* estimates that are either larger or smaller. The result is shown in Figure 5. The insignificance of the estimate indicates that *ξ* fits to the pure harvest rate distribution, and that any additional variations explained by the full model comes from part of the model that is parameter-independent.

../BacteriaSim/RAManalysis%20fit%20100000%20permutations%20null%20distributions%20vs%20model.pdf

Figure . Estimated parameter ξ (black vertical line) compared to null distributions generated from permutation tests.

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