Supply and demand drive a critical transition to dysfunctional fisheries

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There is growing awareness of the need for fishery management policies that are robust to changing environmental, social, and economic pressures. Here we use conventional bioeconomic theory to demonstrate that inherent biological constraints combined with nonlinear supply–demand relationships can generate threshold effects due to harvesting. As a result, increases in overall demand due to human population growth or improvement in real income would be expected to induce critical transitions from high-yield/low-price fisheries to low-yield/high-price fisheries, generating severe strains on social and economic systems as well as compromising resource conservation goals. As a proof of concept, we show that key predictions of the critical transition hypothesis are borne out in oceanic fisheries (cod and pollock) that have experienced substantial increase in fishing pressure over the past 60 y. A hump-shaped relationship between price and historical harvest returns, well demonstrated in these empirical examples, is particularly diagnostic of fishery degradation. Fortunately, the same heuristic can also be used to identify reliable targets for fishery restoration yielding optimal bioeconomic returns while safely conserving resource abundance.

bioeconomic | equilibria | time series | overfishing | critical transition

There has been considerable debate in recent years about the extent of overharvesting of wild fish stocks (1–3). While population declines may involve multiple causal factors that vary among different fish stocks (3–6), it is often claimed that a substantial fraction of fish stocks are currently maintained well below their maximum sustainable yield and an even larger fraction are below the level necessary to maximize economic returns (2–9). There is growing recognition that such perturbations can have serious ecological repercussions for entire marine ecosystems as well as the social and economic welfare of humans who depend on these ecosystems (1–10). Here we extend an existing body of theory (11–18) to develop a model of fishery dynamics based on bioeconomic relationships among renewable resource supply, resource price, and consumer demand. Our model is based on conventional assumptions regarding density-dependent feedbacks on fish stock recruitment linked to commercial harvest dictated by profitability, stock abundance, and effort exerted by the fishing industry (11–18). Based on recent studies demonstrating dynamical changes in effort in other harvested systems (19), we assume that the rate of change in effort from year to year is a positive function of fishery revenue, but is negatively influenced by fishing costs and constraints on the amount of capital and labor that are available. This model is used to consider how a steady rise in consumer demand coupled with biological limitations on resource renewal can generate a rapid and surprising transition to low-yielding, unsustainable, and costly fisheries that poorly serve the interests of nature, economy, or social welfare. Given uncertainty about the most realistic way to mathematically represent the composite bioeconomic relationships, we also consider the qualitative impact of generalized nonlinear modifications to the functions for stock recruitment, price elasticity, and marginal costs.

Model

We assumed that stock abundance increases from year to year according to net recruitment defined by a Ricker logistic function minus the annual harvest,

$$N_{t+1} = N_t \exp\left[r_{max}\left(1 - \frac{N_t}{K}\right)\right] - qE_tN_t$$

$$E_{t+1} = E_t \exp\left(a\left[\gamma^{\frac{1}{\beta}}(qE_tN_t)^{\frac{\beta-1}{\beta}} - cE_t\right]\right),$$

where r_{max} is the exponential rate of growth, K is carrying capacity of the fish stock in the absence of fishing, and N is stock abundance. We assume that effort increases at a rate proportional to the difference between revenue, calculated as the landed price (P) multiplied by harvest (H), and cost per unit effort (c) multiplied by effort (E), where a scales the rate of response. Harvest is proportionate to catchability (q) multiplied by harvest effort and stock abundance, such that $H = qEN$. We assume that price is isoelastic (13), meaning that price flexibility (β) is fixed over time, and price rapidly adjusts to catch level in any given year (7, 11–13),

$$P_t = \left(\frac{\gamma}{H_t}\right)^{\frac{1}{\beta}},$$

where γ is a scaling coefficient defined as the unit price when harvest = 1. Rising demand is indexed by an increase in γ.

Significance

Recent years have witnessed strenuous ongoing debate about the sustainability of many commercial fisheries. Here we apply commonly accepted principles of fishery science to consider the impact of price flexibility on long-term fishery sustainability in an era of increasing demand due to population increase and rising economic expectations. We apply this model to two commercial oceanic fisheries (cod and pollock) to demonstrate that harvest and price statistics that are commonly available for commercial fisheries can be used to diagnose the degree to which a given fishery has been overharvested. More importantly, the same heuristic can also be used to identify plausible targets for fishery rehabilitation and evaluate the effectiveness of alternative policy options to achieve those goals.

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In an open access fishery, participants will continue to be added until revenues equal marginal costs, such that $PqEN = cE$, at which point the equilibrium level of abundance $N = c/Pq$. Substituting this ratio into the Ricker recruitment function, the equilibrium harvest [$\Psi(P)$] in relation to price can be calculated as follows (12):

$$\psi(P) = \left(\frac{c}{qP}\right) \exp\left(r_{\max}\left[1 - \frac{\left(\frac{c}{qP}\right)}{K}\right]\right) - \left(\frac{c}{qP}\right).$$

We used local stability analysis to evaluate how the dynamics of human consumer resource systems would change with respect to demand (scaled by γ) and the degree of price elasticity (β) in relation to fish harvest rates. The first step of local stability analysis is to linearize the equations of change around local equilibria,

$$n = N_{eq} - \Delta N$$

$$\varepsilon = E_{eq} - \Delta E.$$

The equations of change for these linearly transformed variables are calculated as follows:

$$\begin{pmatrix} n(t+1) \\ \varepsilon(t+1) \end{pmatrix} = \begin{pmatrix} \alpha_{11} & \alpha_{12} \\ \alpha_{21} & \alpha_{22} \end{pmatrix} \begin{pmatrix} n(t) \\ \varepsilon(t) \end{pmatrix},$$

where the Jacobian matrix coefficient α_{ij} represents ∂(rate of change of variable i)/∂(variable j) measured at equilibrium. Nontrivial equilibria for our system occur at points of intersection of the nullclines for stock abundance and effort. The Jacobian matrix coefficients are calculated as follows:

$$\alpha_{11} = \exp\left(-r_{\max}\left[\frac{n}{K} - 1\right]\right) - \varepsilon q - \left(\frac{n r_{\max} \exp\left[-r_{\max}\left(\frac{n}{K} - 1\right)\right]}{K}\right)$$

$$\alpha_{12} = -qn$$

$$\alpha_{21} = \left(\frac{1}{\beta}\right)\gamma^{\frac{1}{\beta}} a\varepsilon^2 q \exp\left(-a\left[\varepsilon c - \gamma^{\frac{1}{\beta}}(q\varepsilon n)^{\frac{\beta-1}{\beta}}\right]\right)(\beta - 1)(q\varepsilon n)^{\frac{-1}{\beta}}$$

$$\alpha_{22} = \left(1 - a\varepsilon\left[c - \left(\frac{1}{\beta}\right)\gamma^{\frac{1}{\beta}} nq(\beta - 1)(q\varepsilon n)^{\frac{-1}{\beta}}\right]\right)$$
$$\times \exp\left(-a\left[\varepsilon c - \gamma^{\frac{1}{\beta}}(q\varepsilon n)^{\frac{\beta-1}{\beta}}\right]\right).$$

If the absolute value of all eigenvalues (λ) of the Jacobian matrix is <1 calculated at the points of equilibrium, then the equilibrium is stable. For complex eigenvalues ($\lambda = \Phi \pm \Theta i$), which are typical for this system for many parameter values, stability requires that $|\Phi^2 + \Theta^2|^{1/2} < 1$ for all eigenvalues; otherwise, the system shows damped oscillations of length $= 2\pi/\arctan(\Theta/\Phi)$.

Model Predictions

Under the assumption that fishing costs scale with effort and that resource growth is logistically constrained, our bioeconomic model produces an asymmetric hump-shaped manifold relating equilibrium fishery yield to landed price (Fig. 1). Such a manifold can be thought of as being functionally equivalent to supply curves commonly discussed in the economics literature, although, in this case, the curve is derived from biological, rather than purely economic, principles. We assume a hyperbolic relationship between price and fish harvest, such that small catches command much higher prices per item than do large catches (7–13, 17). The shape of this functional relationship is indexed by price flexibility (a concept closely related to demand elasticity), with a price flexibility of 0.5 implying that a 10% increase in price leads to a 5%
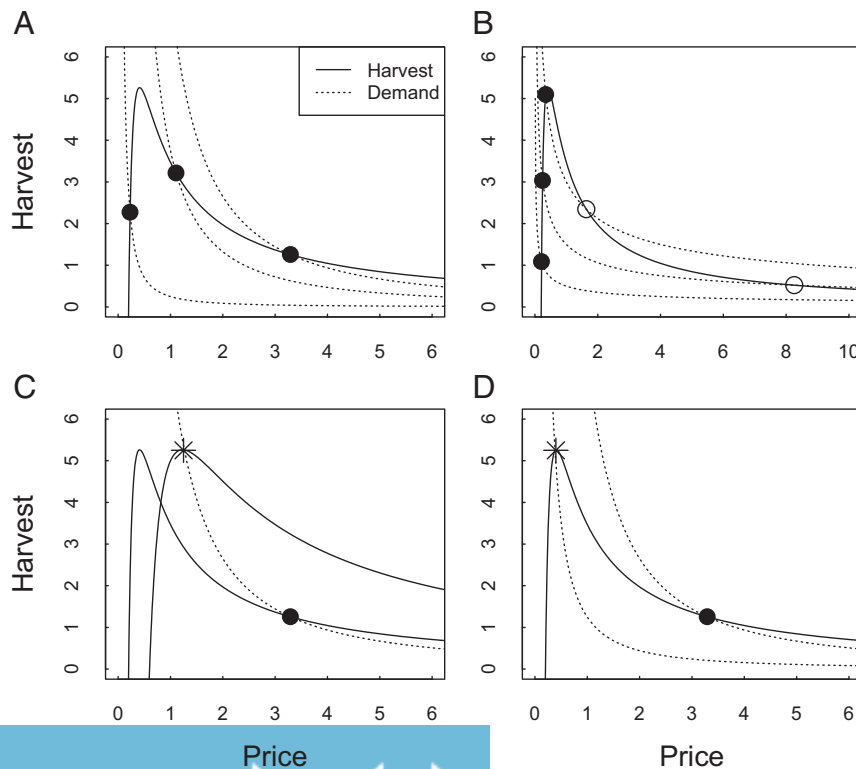

Fig. 1. Equilibrium supply and demand curves based on the bioeconomic model (parameters: $\gamma = 0.25$, $r_{max} = 0.20$, $c = 0.04$, $q = 0.002$, and $K = 100$). In A, price is assumed to be highly sensitive to year-to-year variation in catches ($\beta = 1.5$), whereas, in B, price is assumed to be relatively inelastic with respect to variation in catches ($\beta = 0.5$). Locally stable equilibria are indicated by filled symbols, whereas unstable equilibria are indicated by open symbols. In C and D, we show how changes in model equilibria can be achieved through (C) tripling c, the cost per unit effort, or (D) flooding the market with alternative fish produced via aquaculture to halve γ, the level of consumer demand. In each case, the original equilibrium is shown as a filled circle, whereas the equilibrium following policy intervention is shown as an asterisk.

reduction in consumer demand. Market forces would accordingly dictate changes in price according to the magnitude of catches in any given year. Similar to supply and demand relationships for other commodities, such bioeconomic equilibria identify points of intersection of the supply manifold with the corresponding hyperbolic price curve in relation to supply (Fig. 1). Demand curves with a hyperbolic shape could have one, two, or even three points of intersection with fish supply curves, suggesting the strong possibility for both critical transitions and multiple equilibria in the system. Bifurcation analysis (described in *Supporting Information*) can then be used to assess the dynamic properties of the system in the neighborhood of each equilibrium point.

A fishery with highly flexible pricing with respect to catch ($\beta > 1$) will generally have a single equilibrium at a given level of overall demand that is typically both economically viable and dynamically stable. Both human population growth and improvements in real income have clearly generated substantial increase in total food demand over time, with demand curves accordingly shifting away from the origin. On the other hand, there is no reason to expect the biotic potential of wild fish stocks to increase in commensurate fashion. As a result of this disparity in constraints on supply versus demand, there is considerable potential for shifts over time in the location and number of bionomic equilibrium at which revenues balance costs (Fig. 1). Even though it may be sustainable, the equilibrium associated with high demand levels would be socially undesirable and arguably inefficient in several key respects, representing a highly diminished fish stock that meets the requirements of a small group of consumers.

Fisheries with low price flexibility ($\beta < 1$) create more serious issues. The flatter profile of an inflexible demand curve (Fig. 1B) implies that multiple equilibria will emerge. As overall demand increases over time, both equilibria will inevitably come into play (Fig. 1B). The upper equilibrium (open symbol in Fig. 1B) represents a dynamically unstable threshold, beyond which minor perturbations in price or variation in fish stocks due to environmental stochasticity would lead to increasing year-to-year variation in prices, runaway price increase over time, and eventual stock collapse (Fig. 2). As in other systems with potential for

critical transitions (20–25), the most reliable indicator of a runaway process may be increased amplitude of price and harvest variation near the critical point (Fig. 2).

Our model makes a number of predictions that are testable using conventional fisheries data that span both the initial phase of fishery development and a later phase at which the fishery has reached full capacity (Fig. 2). First, historical trends in fish harvest would be expected to show slow but steady initial increase as the fishery tracks the lower end of the equilibrium harvest manifold. After briefly peaking, subsequent catches should exhibit long-term decline as the system shifts into a new high-price, low-yield regime (Fig. 2 A and C). As stocks collapse, we would expect pronounced variability in both harvests and prices over time, with a tendency for increasingly cyclic fluctuations as harvest and price levels approach the unstable equilibrium. Scatterplots of harvest versus price should be sharply peaked at low price levels, with a decelerating slope as prices reach higher levels, reconstructing the shape of the equilibrium harvest supply manifold (Fig. 2 B and D).

Although based on assumptions commonly applied in the fishery science literature, there is no compelling reason to expect real fisheries to conform perfectly to the parametric form of the simple bioeconomic model we have outlined (26, 27). To evaluate the generality of our conclusions, we accordingly modified the basic model to consider the impact of changes in the maximum rate of fish growth rate (r_{max}) and nonlinear modification of the functions used to represent stock recruitment [$N_{t+1} = N_t \exp[r_{max}(1 - [N_t/K]^\theta)]$], harvest in relation to stock abundance ($H = qEN^\omega$), price elasticity in relation to changes in harvest levels ($P = [\gamma/H^\zeta]^{1/\beta}$, and profit in relation to effort ($\Pi = PH - cE^\kappa$). To assess the impact of these nonlinear changes in functional relationships, we compared deterministic outcomes over time for models with accelerating vs. decelerating nonlinear formulations (exponent of <1 and >1) to the simpler original model variant (exponent = 1). The nonlinear modifications preclude closed-form solutions for nullclines, but equilibrium outcomes can be approximated numerically using deterministic time series simulation.
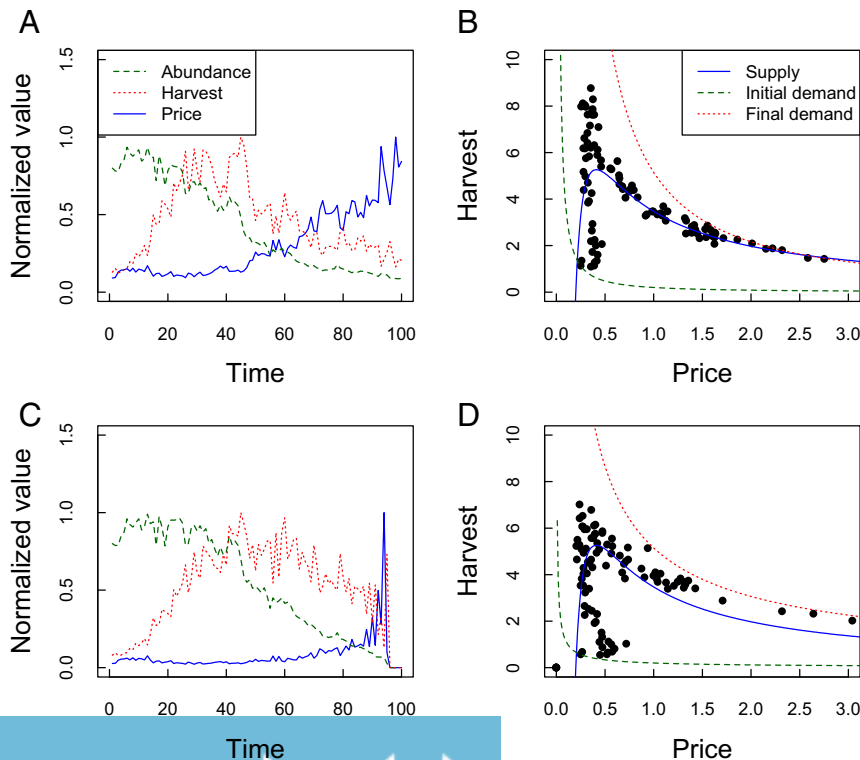
Fig. 2. (*A* and *C*) Simulated dynamics for fish abundance (dashed line), harvests (dotted line), and price (solid line) over time, and (*B* and *D*) scatterplot of annual harvest levels in relation to price (filled symbols) obtained from those simulations. In *B* and *D*, equilibrium supply (solid line) and demand curves (dashed line for initial demand and dotted line for final demand) are also shown, based on the bioeconomic model (parameters: $a = 0.3$, $r_{max} = 0.20$, $c = 0.04$, $q = 0.002$, and $K = 100$). In the simulations shown in *A* and *B*, price is assumed to be highly sensitive to year-to-year variation in catches ($\beta = 1.25$), whereas, in *C* and *D*, price is assumed to be relatively inelastic with respect to variation in catches ($\beta = 0.75$). In all simulations, demand is assumed to climb at a constant rate over a 100-y period (innermost curve, $\gamma = 0.2$; outermost curve, $\gamma = 5.2$). Both simulations are based on an identical time series for Gaussian stochastic deviation in both fish recruitment and harvest.

Fryxell et al.

Although changes in the maximum rate of growth or nonlinear modifications to harvest, recruitment, elasticity, and profit functions have substantial impact on the height and curvature of the equilibrium manifold, the expectation for the evolution of harvest in relation to price is always hump-shaped, provided that overall demand has risen sufficiently (Figs. S4–S8). This qualitatively consistent pattern suggests that the shape of historical harvest−price relationships provides a robust general signature of underlying bioeconomic relationships. Nonlinear modification of the underlying relationship can alter system stability via changes in the shape of the harvest manifold relative to the price flexibility curve. For example, fish stocks with high maximum growth rates might well remain locally stable despite substantial increase in demand, even in systems with low price flexibility (Fig. S4), whereas fish populations with lower growth rates are more vulnerable to collapse due to runaway increase in prices. Similar forms of ecological destabilization are more likely when exponential growth rates for fish stocks decline with changes in abundance at a decelerating rate ($\theta < 1$; Fig. S5), harvest has a positive accelerating relationship with stock abundance ($\omega > 1$; Fig. S6), price flexibility becomes less elastic as harvest declines ($\zeta < 1$; Fig. S7), and per unit costs decelerate with increasing levels of effort ($\kappa < 1$; Fig. S8). These examples reiterate the importance of nonlinear processes in shaping trophic dynamics, even when humans are the top consumer (24).

Examples

As a proof of concept, we compared qualitative predictions of our generalized models against time series data for North American cod and pollock fisheries (https://www.st.nmfs.noaa.gov/commercial-fisheries/commercial-landings/annual-landings/index), each with 60 y of continuous time series data available on harvest levels as well as landed price of the catch, which we divided by the consumer price index to adjust for inflation. In each case, there was clear evidence of increasing catches over time, then

subsequent decline (Fig. 3). As predicted by our model (Figs. 1 and 2), inflation-corrected price was unresponsive or showed a mild increase as cod and pollock fisheries went through the initial phase of increase. Once the peak harvest had been reached, however, all stocks showed evidence of steady decline in catches, while inflation-corrected prices continued to increase. Each of these stocks experienced fivefold variation in both harvests and real price over time (Fig. 3 A and C). Scatterplots of catch yields against price demonstrate hump-shaped distributions in both the cod (Fig. 3B) and pollock (Fig. 3D) examples, with a humped shape clearly suggestive of the equilibrium fish harvest manifold in the bioeconomic model (Fig. 1 and Figs. S4–S8). Similar time series trajectories are common elsewhere in the fisheries literature. For example, California abalone catches showed historical patterns of initial increase, then rapid decline as average prices soared (17). A similar pattern is seen in global production and price pattern for caviar (17).

While our models are framed around bioeconomic models commonly applied to aquatic resources, particularly fisheries, the models are equally applicable to terrestrial systems with unrestricted access by harvesters in which profitability plays a key role in shaping changes in harvester effort. Recent models have considered the conservation challenges arising when rarity itself creates an insatiable demand for luxury commodities produced by naturally renewable terrestrial resources (17, 28). For example, both rhino horn and African elephant ivory markets have exhibited spiraling price as populations of rhinos and elephants collapsed across Africa due to poaching (29, 30). Similar bioeconomic narratives are consistent with rapid decline in a number of other threatened terrestrial species (28). The risk of extinction is further amplified when range contraction accompanies population collapse (17), because harvesting cost per unit effort would be expected to decline as a harvested population becomes increasingly restricted to a fraction of its original range.
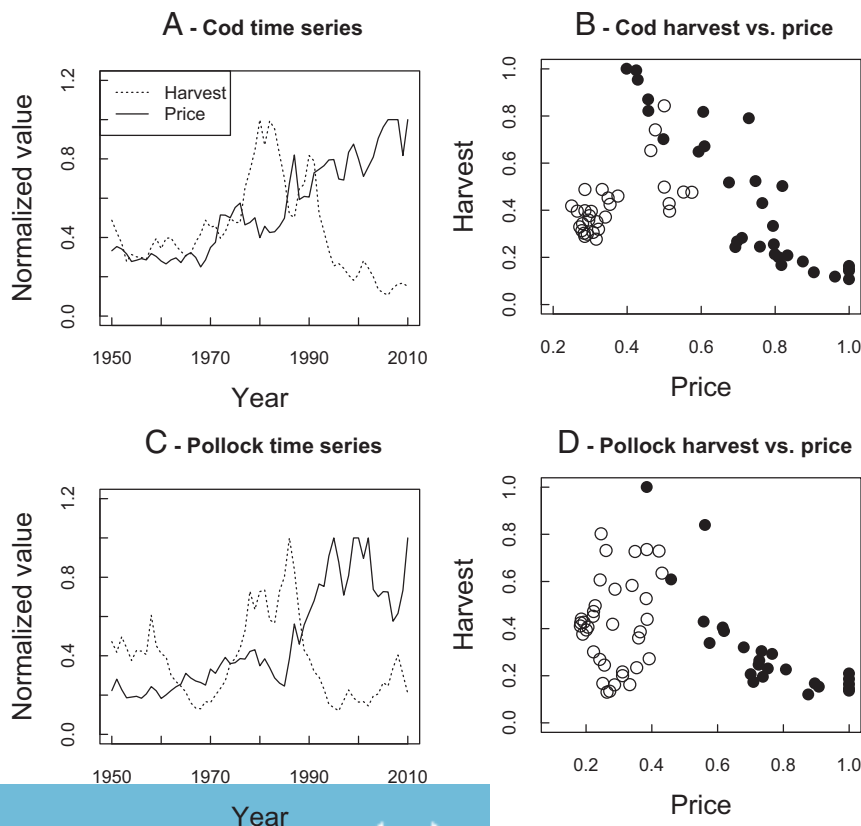

Fig. 3. Observed data on harvest versus price (corrected for consumer price index) for (*A* and *B*) cod and (*C* and *D*) pollock fisheries during 1950–2010. In each example, the relationship between harvest and price was either nonsignificant or positive during the increase phase (open symbols; cod: $H = 0.13 + 0.80P$, $F_{1,28} = 16.55$, $P < 0.001$; pollock: $H = 0.29 + 0.47P$, $F_{1,34} = 1.16$, $P = 0.290$), but negative during the decrease phase (filled symbols, cod: $H = 1.52 - 1.48P$, $F_{1,29} = 120.6$, $P < 0.001$; pollock: $H = 1.04 - 0.98P$, $F_{1,23} = 39.6$, $P < 0.001$).

Fryxell et al.

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Our modeling framework suggests that increasing demand over time due to population increase or rising economic expectations can itself contribute to stock collapse, even for naturally renewable commodities that have constant levels of price elasticity (Figs. 2 and 3). Whether rising demand will induce runaway collapse to extinction depends on the shape and magnitude of a number of bioeconomic functional relationships (Fig. 1 and Figs. S4–S8), but long-term harvest decline would seem inevitable in the absence of direct intervention. Perhaps the most critical factor influencing the long-term stability of harvested stocks is the degree of price flexibility in relation to catch. Demand is often predicted to be highly flexible for commodities for which substitutes are common, which seems a reasonable conjecture for most fish stocks. While some estimates of price flexibility for specific stocks in the fisheries literature are highly responsive ($\beta > 1$), recent metaanalyses of a large number of studies suggest that the demand elasticity of fish among US consumers ranged between 0.50 and 0.79 (31–34). This is clearly a key topic for further study, because our model suggests that price flexibility could be a common determinant of whether heavily exploited stocks may become increasingly unstable over time and therefore require urgent management intervention to prevent complete collapse.

Management Responses

Consideration of both the simple basic model and the nonlinear model variants suggests that the equilibrium manifold for harvests relative to price provides a diagnostic tool that could, in principle, be used to estimate the degree of bioeconomic degradation of a given fishery. The ratio of current yields relative to the maximum levels on the manifold expresses, in some sense, lost biotic potential of the harvested resource. Given that, by definition, the manifold reflects identical levels of net profitability, lost biotic potential also represents a useful measure of economic inefficiency. On a more positive note, the peak of the bioeconomic manifold also represents a realistic goal for fishery restoration. Since the bioeconomic maximum for a naturally regulated resource typically occurs at an intermediate level of resource abundance, targeting the ascending part of the manifold would restore the resource abundance to near-pristine levels. Such a scenario represents a win–win situation in the long run, sustaining efficient economic returns as well as meeting defensible conservation goals.

Our bioeconomic model also suggests practical measures by which dysfunctional fisheries might be improved. For example, tariffs scaled to effort levels might be used to reposition the resource renewal manifold at levels more favorable to meeting conservation goals (Fig. 1C). Alternatively, aquaculture or industrial sources of equivalent food protein could play an important indirect role in conserving wild fish stocks by enhancing the availability of suitable commodity substitutes that would help suppress the price of wild fish, thereby shifting the demand manifold closer to the origin (Fig. 1D). Since historical records of both landed price and yield are commonly available, in contrast to detailed biological parameters needed to estimate stock intrinsic growth rates, carrying capacity, and maximum sustainable yield (3, 8, 9) needed to identify more sophisticated fishery objectives (9), defensible bioeconomic goals should be readily attainable, at least in principle, for most commercial fisheries. Such transformational changes imposed through policy intervention may be increasingly required to restore the resilience of natural renewable resources in an era of increasing demand (35, 36).

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