Social-ecological interactions, management panaceas, and the future of wild fish populations

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We explored the social and ecological outcomes associated with emergence of a management panacea designed to govern a stochastic renewable natural resource. To that end, we constructed a model of a coupled social-ecological system of recreational fisheries in which a manager supports naturally fluctuating stocks by stocking fish in response to harvest-driven satisfaction of resource users. The realistic assumption of users remembering past harvest experiences when exploiting a stochastically fluctuating fish population facilitates the emergence of a stocking-based management panacea over time. The social benefits of panacea formation involve dampening natural population fluctuations and generating stability of user satisfaction. It also maintains the resource but promotes the eventual replacement of wild fish by hatchery-descended fish. Our analyses show this outcome is particularly likely when hatchery-descended fish are reasonably fit (e.g., characterized by similar survival relative to wild fish) and/or when natural recruitment of the wild population is low (e.g., attributable to habitat deterioration), which leaves the wild population with little buffer against competition by stocked fish. The potential for release-based panacea formation is particularly likely under user-based management regimes and should be common in a range of social-ecological systems (e.g., fisheries, forestry), whenever user groups are entitled to engage in release or replanting strategies. The net result will be the preservation of a renewable resource through user-based incentives, but the once natural populations are likely to be altered and to host nonnative genotypes. This risks other ecosystem services and the future of wild populations.

stocking panacea | wild population collapse | angler satisfaction | social-ecological model | cultural ecosystem service

A panacea refers to a blueprint for a single type of governance (e.g., private property) or management action [e.g., release of cultured organisms to restore declining natural stocks (1)] that is applied across a variety of social-ecological (SE) contexts (2–4). Assuming they help deal with complex resource-management problems, many decision makers and stakeholders advocate for, and subsequently apply, a certain panacea across situations (2, 4). Broadly prescribed solutions to complex problems are usually problematic (2, 3, 5), but more work is needed to understand the causes and consequences of panaceas for coupled social-ecological systems (SESs), for theory development and to gauge solutions (2, 5). Integrated models constitute a tool to understand further the importance of feedbacks between humans and nature in driving emergent properties of SESs, including formation of management panaceas and associated outcomes, such as overuse, loss of natural resources, or erosion of system resilience (2, 3). Such understanding is ultimately needed for developing sustainable resource-management policies, which are to remain flexible and adaptive to change (2, 3, 6).

Against this background, our objectives are, first, to construct a conceptually realistic and empirically informed SE model of recreational fisheries to study conditions that promote the emergence of fish stocking as a management panacea in the face of natural stochasticity and, second, to explore the long-term con-

sequences of stocking panacea formation for both the managed wild population and the social system. Stocking, defined here as the repeated injection of juvenile fish from various sources (mainly hatchery-bred offspring from hatchery or wild spawners) to support wild fish populations (7, 8), is a common management practice in fisheries involving billions of individuals released annually across the world (7, 9). Stocking is perceived by many as the most obvious solution to declining populations (10, 11), but conservation biologists increasingly warn against unintended and often irreversible repercussions for aquatic biodiversity, ranging from genetic to community scales (e.g., 1, 12–14). Therefore, understanding the evolution of stocking as a panacea-like management tool in the coupled SES of recreational fisheries and studying its impacts on wild fish populations are globally relevant (15), particularly because in many industrialized countries, fishing for recreational rather than commercial or subsistence purposes constitutes the dominant use of wild freshwater fish populations (16).

Recreational fisheries are governed using a diversity of property-rights regimes, ranging from public property in North America to private property in much of Europe (17, 18). Irrespective of the property rights regime, normative pressure exerted by resource users (e.g., anglers) on managers to maintain stocks in the face of exploitation and other threats influences management decisions, such as stocking (10, 18, 19). Peer pressure may be particularly direct and intense under the private rights regime, where managers usually operate voluntarily in the interest of the angler constituency (e.g., in angling clubs and associations) as leaseholders of fisheries in central Europe (17). Indeed, semi-structured interviews with numerous recreational fisheries management boards in German angling clubs revealed that many water bodies managed by them were regularly stocked and that social norms exerted by anglers affected stocking decisions (*SI Text* and Table S1). These interviews also revealed that the degree of peer pressure for fish stocking on managers depended on angler satisfaction, which is strongly catch/harvest-dependent across most angler groups (20). Angler satisfaction may be affected by past catch/harvest experiences and the resulting expectations about future rewards (21). Natural fish stocks usually exhibit large between-year fluctuations in recruitment (22), which has an impact on angler catch/harvest levels and angler satisfaction. The dynamic interplay between naturally fluctuating resources, satisfaction, and angler norms for adjusting management intervention may constitute a mechanistic explanation driving the development of a fish stocking panacea in the recreational fishing SES. Although possibly maintaining or stabilizing angler satisfaction (compare with

23), the stocking panacea may have negative consequences for wild fish populations, thus creating relevant tradeoffs between wild fish conservation objectives and angler welfare. We test this prediction using an integrated SE model. Although the SE interactions and feedbacks in our model have been informed by properties of recreational fisheries, we contend the mechanisms leading to panacea formation are more general and are present in other user- and incentive-based natural resource governance systems, such as community-based hunting and forestry management systems.

Model Overview

Our model incorporated the key interactions between anglers, a managed fish population, and a management response involving stocking, as formalized in a generic coupled SES of recreational fisheries (Fig. 1). The model was structured following a newly developed framework for the analysis of SESs (4) distinguishing stochastic natural resource units (fish) striving in a resource system (e.g., a lake) that is exploited by local resource users (anglers) and affected by management institutions and the governance system (fisheries manager responding to angler-formed norms for management interventions). The social submodel represented two salient social-psychological processes inherent in many SESs: (*i*) reward-seeking behavior by users (i.e., angler satisfaction) and (*ii*) a management response (i.e., stocking) to feedback signals about the resource state in terms of user (dis)satisfaction with current rewards (i.e., harvest). Satisfaction by anglers in our model was formed in light of past reward levels [as is typical in human reinforcement learning (24)] and was conceptualized as the difference between expected and realized harvest (20, 25). Actual harvest levels were affected by natural stochastic fish population fluctuations (26). Annual harvest expectation in-

tegrated remembered past fishing rewards based on a default memory model (MM), where past harvest levels were forgotten based on a standard forgetting rate (27, 28). Humans tend to recall particularly emotionally rewarding stimuli from the past [so-called positivity effect in attention and memory (29)] when judging current rewards (e.g., harvest levels); thus, a second plausible variant memory model (MM*) was also tested, where exceptional fishing successes in terms of harvest were weighed more heavily (*SI Text*). To represent fisheries managers reacting to social norms exerted by (dis)satisfied anglers, the number of fish stocked annually was determined by a hypothetical manager responding to an aggregate level of angler satisfaction. Accordingly, stocking decisions followed a default stocking decision model (SDM), where fish stocking numbers stayed constant when angler satisfaction was neutral, increased when it was negative, and decreased when it was positive. Again, a second plausible scenario, the variant stocking decision model (SDM*), with stocking numbers remaining constant at positive satisfaction levels, is presented in *SI Text*.

The ecological submodel consisted of a generic single species, stage-structured model of a stocking-enhanced and recreational angling-exploited fish population (Fig. 1). Similar to the study by Lorenzen (7), the model separately tracked the wild and stocking-descended subpopulations of the same hypothetical fish species under varying stocking rates (determined by angler satisfaction dynamics) with density-dependent ecological competition and interbreeding between wild and hatchery fish (Fig. 1). This allowed examination of stocking impacts both in terms of density dependence (7) and hybridization-induced fitness depression (30). The stocking-descended subpopulation (for simplicity, hereafter called hatchery fish) consisted of recently stocked young of the year (YOY), a life stage often stocked in recreational fisheries (7, 8), and naturally spawned hatchery fish. Progeny from both pure hatchery and hatchery-wild crosses were assigned to the hatchery subpopulation to account for the often-reported reduced fitness in hatchery fish or hybrids relative to wild fish (30, 31). Prestocking early YOY numbers of each subpopulation were determined by a Ricker stock-recruitment function (22), resulting in density-dependent survival regulated by ecological competition, as is typical in nature (7, 32). A recruitment deviate added stochasticity that propagated through later life stages, resulting in natural population fluctuation (26). Stocking was subsequently conducted at the early YOY stage, resulting in a second density-dependent regulation through competition between stocked and naturally spawned YOY directly after stocking (7). Surviving late juveniles and adults were regulated by density-independent factors, as is common in nature (7, 32). Only adults were subjected to harvesting, mimicking exploitation using minimum-sized limits larger than size at maturation (16). The biological submodel was parameterized for a generic fish species and informed by meta-analyses on stock-recruitment relationships across important recreationally exploited taxa (Table S2).

Results and Discussion

The interplay of social dynamics and resource stochasticity in our model affected the formation of a stocking-based management panacea, along with its effect on human well-being and potential repercussions for the wild fish population (Fig. 2). In particular, users (here, anglers) remembering past harvest experiences when exploiting a stochastically fluctuating renewable resource (here, fish) facilitated the emergence of a management panacea (here, stocking) over time. An example from our base scenario (MM/SDM; parameters are shown in Table S2) is visualized in Fig. 2 for a reasonably productive and stochastically varying wild fish population under conditions of stocking reasonably fit (i.e., relative survival of stocked to wild fish of 0.9) fish of the same species. At an unrealistically high (λ = 0.9) or medium (λ = 0.5) forgetting rate of past harvest levels by anglers (Fig. 2, *Left* and *Center*), fairly
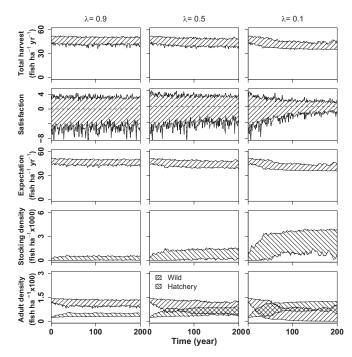

Fig. 1. Schematic representation of the life cycle of the wild and hatchery fish subpopulations and their interactions. The default decision models are in bold. YOY, young-of-the-year. Details are provided in *Methods*, and parameters are defined in Table S2.
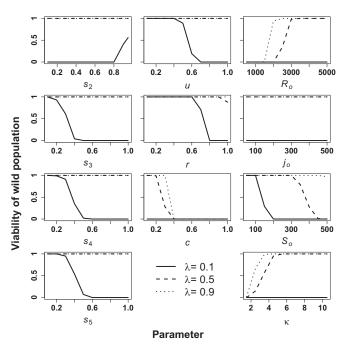
Fig. 2. Influence of the forgetting rate of past harvest (λ) for determining total harvest, angler satisfaction, expected harvest, stocking density, and adult density of wild and hatchery-descended subpopulations under the MM and the SDM. The range of 100 model runs over 200 y is shown for three levels of λ. A low λ means that all previous years are equally remembered; at a high λ, only the last few years are taken into account. Maximum memory length of anglers is fixed at 15 y, and the stocking response to angler satisfaction is set at 50 fish ha^{-1}.

Fig. 3. Viability of the wild subpopulation across a range of values for each parameter and three forgetting rates of past harvest levels by anglers (λ) under the MM and the SDM. Maximum memory length is fixed at 15 y, and parameters are defined in Table S2.

low stocking rates emerged through SE interactions over time and the wild component was maintained over all 200 simulated years. Under the more realistic assumption of anglers remembering all past experiences up to 15 y with nearly equal clarity (λ = 0.1) and basing future harvest expectation on them (Fig. 2, *Right*), regular and high annual stocking rates were developed as a panacea. The main mechanism for panacea formation was the initially highly variable and often negative angler satisfaction attributable to stochastic natural recruitment (Fig. 2), which then stimulated the manager to increase stocking rates. Coincident with panacea development, angler expectation and satisfaction declined over time, but satisfaction variability was reduced because of the dampening effect of stocking on top of stochastic natural recruitment (Fig. 2), providing a substantial social benefit attributable to increased stability. Increased stocking over time maintained the exploitable resource but had ecological consequences by changing the composition of the fish population toward a greater proportion of hatchery fish, eventually even resulting in extirpation of the wild population in as few as 100 y (Fig. 2) under certain parameter settings (Fig. 3 and Figs. S1 and S2). Such replacement was not caused by development of unrealistically high stocking densities relative to wild recruitment in our model. For example, when the wild population started to collapse in the base simulation (Fig. 2), the median stocking rate was only about 60% of natural recruitment levels (Table S3), which is similar to ratios of stocked to natural densities reported in various recreationally important freshwater species (Table S4). Put differently, our model predicted the development of stocking ratios that aligned with empirical values reported in the literature, suggesting the model predictions reflect realistic situations.

To examine the conditions of a self-organized SES of recreational fisheries that affect the potentially most serious ecological outcome of stocking panacea formation, replacement of wild fish

by hatchery fish, fully, we explored population viability against key parameter and structural uncertainties. When forgetting rates of past harvest levels by anglers were unrealistically high or intermediate (λ = 0.9 or 0.5), the wild stock's viability (definitions provided in *SI Text*) was largely insensitive to variation in most parameters and no replacement of wild fish occurred as in the base simulation (Figs. 2 and 3 and Figs. S1 and S2). At a more realistic low forgetting rate, a systematic pattern of rapid shifts from viable to unviable wild populations emerged for most biological model parameters (Fig. 3 and Fig. S2). In the face of panacea formation, wild fish persisted only at low relative survival (i.e., fitness) of hatchery fish relative to wild fish (as represented by parameters $s3$, $s4$, and $s5$) or at low immediate poststocking survival (u) and poor relative recruitment (r) of stocked fish (Fig. 3). Because the survival and reproductive success of stocked fish are often low in the wild (30), this may help to explain why wild genotypes are still found in many systems despite a long stocking history (examples are provided in Table S5). The viability of the wild population was also sensitive to the proportion of wild fish crossing with hatchery fish (c). There was also a strong impact of natural population productivity parameters, including the density of unfished early YOY (R_o), unfished spawners (S_o), and the compensation ratio (κ), in affecting wild population viabilities. Low S_o and high R_o and κ indicate a highly productive wild population, meaning adult abundance is relatively insensitive to harvest or competition stress attributable to relatively high reproductive and juvenile survival rates, and such conditions favored the viability of the wild population (Fig. 3). An interaction between population productivity parameters and relative fitness of stocked fish also existed, demonstrating that as fitness of stocked fish increased, the wild population must be increasingly productive to be maintained (*SI Text* and Fig. S2). These results suggest that conservation of the wild fish population is possible in nature but that shifts to hatchery fish-dominated states are equally plausible depending on a suite of factors (Fig. 3 and Figs. S1 and S2), which is in agreement with the vulnerability of other

SESs to slowly changing variables that drive system dynamics (6, 33). The possibility of wild fish replacement was found to be robust against the choice of the memory (i.e., MM/MM*) and stocking decision (i.e., SDM/SDM*) models (Figs. S3–S5).

Our model suggests that the SES of recreational fisheries is prone to stocking developing as a management panacea as a result of the reward-seeking behavior of anglers in a stochastic world and corresponding social dynamics between anglers and managers. This panacea will likely maintain an exploitable resource and stabilize angler satisfaction in the long term, which may be positively perceived from a fisheries perspective (23) and considered a success of incentive-driven resource conservation by fisher groups (34). However, the potential of stocked fish interbreeding with wild fish or otherwise impairing them through ecological competition is real and widespread (1), indicating tradeoffs between stability of user well-being and wild population conservation objectives. Such tradeoffs have been similarly reported from forestry systems (35) and likely take place in other resource-management contexts (e.g., hunting), where technical fixes, such as planting trees or releasing animals, can be used by local user groups to counter declining resources (1). From a management and governance perspective, the problem is particularly insidious under user-based management regimes, because the general willingness of local users to preserve, restore, and enhance the resource base through releases may indeed help conserve the stock; however, as our model has shown, it may also become a serious issue from a genetic conservation perspective if alien genotypes are used in supportive plantings (1). This is particularly problematic if users have a different awareness of the risk associated with introducing alien genotypes into a given ecosystem, as is often the case (15).

Our model suggests continuous stocking on top of naturally reproducing populations may eventually extirpate wild populations (Fig. 2), yet we acknowledge that the actual impacts of a stocking panacea on wild fish stocks will depend on various biological (Fig. 3 and Fig. S6) and social factors (Table S5), many of which were outside the scope of our model. The most crucial aspects, however, were explicitly or implicitly inherent in our model formulation, such as the importance of natural productivity providing a buffer against stocking impacts and stocking success being a function of the relative fitness of stocked fish (Fig. 3 and Fig. S2). The share of cultured fish in wild stocks after continued stocking has been empirically found to vary from near zero to almost complete displacement of wild populations (Table S5). Near-complete replacement of the wild stock seems to be especially likely in populations experiencing habitat impairments (36) (Table S5), which have an impact on population production. This finding was also present in our sensitivity analyses, because full replacement of the wild stock was most likely when natural productivity was low (which is equivalent to impaired natural recruitment attributable to habitat loss) (37) (Fig. 3 and Fig. S2). Many natural water bodies have been impaired by habitat changes (16) (Table S5), increasing the likelihood of wild population replacement after formation of stocking as a panacea. Almost ironically, habitat impairments often motivate stocking programs (8, 11), such that stocking practices may actually put an additional burden on already threatened or declining wild stocks. Generally, our prediction that long-term replacement of wild by planted organisms can occur in a self-organized SES, such as recreational fisheries, forestry, or hunting, should be considered a worst-case yet plausible scenario. Our findings also suggest that the cases of observed replacement might increase over time because they may take at least 100 y to materialize (Fig. 2), and intensive stocking has taken place for less than a century in much of the world. Thus, in many cases, replacement of wild fish by stocking-descendant fish may either not happen because of stocking with "unfit" fish (i.e., low relative survival in the wild) or because the natural population exhibits a high degree of resiliency (i.e., high pro-

ductivity). Alternatively, replacement may not have been recognized yet because of the lack of genetic tools or samples from the unstocked past (38). However, our findings should not be misinterpreted as a call against all forms of stocking, because under particular conditions (e.g., following irreversible habitat destruction or in artificial fisheries), stocking can be the only tool to maintain stocks and fisheries (37, 39).

Our prediction that the stocking panacea can lead to replacement of wild fish may be criticized because stocking decisions in our model directly and exclusively tracked angler satisfaction. Actual stocking decisions will often take into account a variety of factors, and will therefore be more cautious than in our base simulation, reducing the likelihood of impact on the wild fish stock (Fig. S7). Indeed, the German angling clubs we surveyed acknowledged a variety of factors influencing stocking decisions. In all clubs, however, angler desires were important determinants of stocking (Table S1), and angler pressure has similarly been found to influence decisions by North American management agencies to stock fish (19). Therefore, despite the simplification of actual stocking decision making in our model, emergence of stocking as a panacea in response to social norms reflecting reward expectations may still be a reasonably robust prediction and explain the widespread use of cultured fish in fisheries worldwide (1, 7, 8, 11). There is room for testing alternative specifications and processes and for expanding the model to represent more comprehensive decision-making scenarios, but that was not our purpose. We aimed to ask generally how memory of the past and reward-seeking behavior by humans act in a stochastic world to form management panaceas that may unwillingly prove deleterious for wild populations. Based on our model, we contend that one of the most important mechanisms explaining this feature is the interaction of social and ecological systems when fraught with natural stochasticity, and the human tendency of striving to control variability in the face of uncertainty. Our results should thus be viewed as a mechanistic approach to explain why the specific management panacea of releasing animals (or plants) is to be expected across many SESs, particularly those where local users are empowered to influence management decisions involving releasing organisms—a governance panacea often believed to result in sustainable trajectories (34, 35). Outcomes of such a panacea, however, include replacement of wild fish by stocking-descended fish, which often represent alien genotypes from different localities (1, 40), and homogenization of wild gene pools attributable to interbreeding (Table S5). Such outcomes are usually regarded as socially unacceptable from a biodiversity conservation perspective (15) and can penalize the stability of yields in the long term (41) (Fig. S8), despite providing obvious social benefits through dampening of natural variability and increased stability of user satisfaction.

The susceptibility of SESs to panaceas is a reaction to the difficulty of decision making under pervasive uncertainty (3). Panaceas are often easier to communicate to resource users than more complex approaches, and people tend to trust a simpler message over a more complex message (42). Often, as in the case of stocking (19), a panacea has been heavily relied on and advocated for by managers over extended periods of time, and it is then difficult to engage in novel solutions. Some have suggested that improved monitoring information on the population status and the fate of stocked fish might increase the adaptive capacity of fisheries governance systems to deal sustainably with ecological systems in the face of nonlinearity and stochasticity (43, 44). Monitoring, however, does not necessarily avoid the stocking panacea for two reasons. First, as shown in our model, stocking dampens natural stochasticity and stabilizes angler satisfaction, the main cultural ecosystem service sought by users. In the absence of fishery-independent monitoring information (e.g., information on true fish stock size and composition) and when the system variables monitored change slowly, panacea development

is difficult to be avoided even in the presence of monitoring and adaptive learning (2). Second, improved monitoring will only result in more cautious stocking if anglers or managers appreciate preservation of locally adapted populations as generating more aggregate utility than the benefits generated by stabilized harvest and angler satisfaction. In many recreational fisheries, this is probably not the case (45).

To conclude, although being specific to recreational fisheries, our analysis shows that the combination of generic psychological mechanisms and social processes, as well as the feedbacks between nature and humans in a stochastic world, helps in understanding the emergence of management panaceas that, in turn, drive the sustainability of a SES. The stocking panacea generates obvious benefits (i.e., preservation of the exploited stock, stabilized cultural ecosystem service), although potentially threatening conservation of the wild population in the long term. Stakeholders and policy makers interested in developing more adaptive and risk-averse stocking policies face the issue of confronting a complex policy system that involves multiple actors, institutions, conflicting goals, and competing notions of the problem (15). To achieve change and move to a more adaptive stocking policy, learning among coalitions of actors with different notions of the problem is important (15). This can best be achieved by redistributing authority among local level user organizations and higher governance levels (46). The resulting linkages may then help in dealing with multiple objectives by using multiple knowledge systems in the context of panacea management (46), with a view toward avoiding panacea development and facilitating development of adaptive management practices.

Methods

Ecological Submodel: Dynamics of a Stocking-Enhanced Fish Population. The density in the early YOY stage is based on the number of adults in each subpopulation, and survival is regulated by density-dependent competition as:

$$j_{1,1} = (1-c)z_1\alpha \cdot e^{-\beta[z_1 + r \cdot z_2] + \omega}$$
$$j_{1,2} = (c \cdot z_1 + r \cdot z_2)\alpha \cdot e^{-\beta[z_1 + r \cdot z_2] + \omega},$$

[1]

where $j_{1,g}$ is density (fish·ha^{-1}) of early YOY produced for subpopulation g (wild = 1, hatchery = 2); c is the proportion of wild adults that interbreed with hatchery adults, producing offspring considered to be part of the hatchery subpopulation [attributable to reduced fitness of hybrids (7, 30, 37)]; $z_g(t)$ is the density of adults from subpopulation g in year t; α is the recruits per spawner as spawner density approaches zero, β is the inverse of the density of spawners that produce the maximum density of recruits; and r is the relative recruitment success of hatchery fish (7, 37) (Table S2). This Ricker type stock-recruitment function (22) results in overcompensation at high density and is common in many recreationally important freshwater species (47, 48), accounting for competition among spawning adults for spawning sites, among early YOY for settling sites and intercohort cannibalism (22). The normally distributed recruitment deviate (ω) is set with an SD of 0.58 (Table S2).

Stocking is assumed to take place at the early YOY stage. Poststocking density-dependent survival to the late YOY stage is characterized using a Beverton–Holt type model (22):

$$x_g = \frac{r_o \cdot j_{1,g}}{1 + k\left(j_{1,1} + j_{1,2} + uS\right)},$$

[2]

where r_o is the maximum survival rate and the carrying capacity of recruits is given by r_o/k. The addition of uS in this model represents the competitive impact of stocked hatchery YOY fish (S) that immediately survive following stocking, given a stocking survival rate u. Initial stocking mortality (represented by u) is characteristic of most stocking events and is often attributed to, for example, poor foraging efficiency, underdeveloped predator avoidance behavior, or transportation-induced poststocking mortality (49). The use of a Beverton–Holt type survival in Eq. 2 implies that late YOY experience less extreme density-dependent mortality at high density, which has been observed in several important recreationally fished species (32, 47, 48).

Combining Eqs. 1 and 2 provides the density (fish·ha^{-1}) of wild (x_1) and hatchery (x_2) late YOY at the end of the first year as:

$$x_{1,t+1} = \frac{r_o\left[(1-c)z_{1,t}R\right]}{1 + k\left[R(z_{1,t} + r \cdot z_{2,t}) + uS\right]}$$

$$x_{2,t+1} = \frac{r_o s_3\left[(c \cdot z_{1,t} + r \cdot z_{2,t})R + uS\right]}{1 + k\left[R(z_{1,t} + r \cdot z_{2,t}) + uS\right]},$$

[3]

where R is the survival term from Eq. 1 and s_3 is the annual survival of hatchery fish relative to wild fish from the early to late YOY stage. Note that s_3 represents a fitness parameter that allows hatchery fish to perform worse than wild fish (7, 30).

Juvenile wild fish and hatchery fish (y_1 and y_2) that survive the first year of life experience constant survival and eventually mature at rate μ:

$$y_{1,t+1} = s_1\left[x_{1,t} + (1-\mu)y_{1,t}\right]$$
$$y_{2,t+1} = s_4 s_1\left[x_{2,t} + (1-\mu)y_{2,t}\right],$$

[4]

where s_1 is the annual survival rate of juvenile fish and s_4 is the annual survival rate of hatchery juvenile fish relative to wild juvenile fish, again interpreted as a relative fitness parameter (7). Adult wild fish and hatchery fish (z_1 and z_2) are represented as:

$$z_{1,t+1} = s_2\left[\mu \cdot y_{1,t} + (1-h)z_{1,t}\right]$$
$$z_{2,t+1} = s_5 s_2\left[\mu \cdot y_{2,t} + (1-h)z_{2,t}\right],$$

[5]

where s_2 is the annual adult survival rate, s_5 is the annual survival rate of hatchery adults relative to wild adults, and h is the annual harvest rate.

To parameterize the biological model, we defined the stock-recruitment function for a prototypical freshwater fish population targeted by anglers. We parameterized our stock-recruitment functions using unfished reference points and steepness, defined as the proportion of unfished recruitment when spawning stock is reduced to 20% of equilibrium unfished levels (50). Estimates of steepness from Salmonidae, Esocidae, and Percidae by Myers et al. (50) provided an average value of 0.63, which was converted to a compensation ratio (κ) to give $\kappa = 6.84$. From this, α and β in Eq. 1 can be estimated (22) as:

$$\alpha = \kappa \frac{R_o}{S_o},$$

[6]

$$\beta = \ln\left(\alpha \frac{S_o}{R_o}\right) \bigg/ S_o,$$

[7]

where R_o is the unfished density of recruits at an unfished spawner density, S_o. A similar procedure can be used to estimate r_o of Eq. 2, by replacing R_o and S_o in Eq. 6 with j_o and R_o, respectively, where j_o is the number of early YOY produced in an unfished population. The parameter k from Eq. 2 is estimated as (22):

$$k = \frac{\left(r_o\dfrac{R_o}{j_o} - 1\right)}{R_o}.$$

[8]

Given fixed population parameters and assuming equilibrium conditions when unfished (omitting stochastic recruitment), the first mortality parameter, s_1, can be solved directly.

Parameters used to describe the biology of the modeled fish population are compiled in Table S2; a robustness analysis is presented in SI Text.

Social Submodel: Human Stocking Decision-Making Dynamics. Average angler satisfaction (U_t) was assumed as the difference between average actual angling success (represented by actual harvest, H_t^{act}) and the angling success expected by the angler population (i.e., harvest, H_t^{exp}) in year t (Fig. 1). Actual harvest from the biological model above is simply the harvest rate times the density of vulnerable (i.e., adult) fish from both wild and hatchery fish. Expected harvest in year t is related to past harvest using the MM, defined as:

$$H_t^{exp} = \frac{\sum\limits_{i=1}^{T}\left[e^{-\lambda i}H_{t-i}^{act}\right]}{\sum\limits_{i=1}^{T} e^{-\lambda i}},$$

[9]

where λ is the relative importance of past harvest for determining current harvest expectations (i.e., forgetting rate) and i is a sequence of previous years up to a maximum memory about previous harvest of T years. In Eq. 9, λ can be any positive number: A value near 0 effectively weights all years

equally (i.e., all previous years are equally remembered), and a value greater than 2 effectively ignores all harvest before the past year.

When fishery managers decide on whether to stock and how much to stock based on satisfaction of the angler constituency and associated peer pressure (Fig. 1), the stocking density can be assumed to vary each year as $S_{t+1} = \max(0, S_t - dU_t)$, where d is the rate at which (dis)satisfaction leads to changes in stocking. This is the referred to as the SDM.

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