Fast behavioral feedbacks make ecosystems sensitive to pace and not just magnitude of anthropogenic environmental change

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Anthropogenic environmental change is altering the behavior of animals in ecosystems around the world. Although behavior typically occurs on much faster timescales than demography, it can nevertheless influence demographic processes. Here, we use detailed data on behavior and empirical estimates of demography from a coral reef ecosystem to develop a coupled behavioral–demographic ecosystem model. Analysis of the model reveals that behavior and demography feed back on one another to determine how the ecosystem responds to anthropogenic forcing. In particular, an empirically observed feedback between the density and foraging behavior of herbivorous fish leads to alternative stable ecosystem states of coral population persistence or collapse (and complete algal dominance). This feedback makes the ecosystem more prone to coral collapse under fishing pressure but also more prone to recovery as fishing is reduced. Moreover, because of the behavioral feedback, the response of the ecosystem to changes in fishing pressure depends not only on the magnitude of changes in fishing but also on the pace at which changes are imposed. For example, quickly increasing fishing to a given level can collapse an ecosystem that would persist under more gradual change. Our results reveal conditions under which the pace and not just the magnitude of external forcing can dictate the response of ecosystems to environmental change. More generally, our multiscale behavioral–demographic framework demonstrates how high-resolution behavioral data can be incorporated into ecological models to better understand how ecosystems will respond to perturbations.

animal decision making | hysteresis | transient dynamics | Allee effect | functional response

Understanding how anthropogenic environmental change affects natural systems upon which humans rely is a pressing scientific challenge (1, 2). Among the most rapid ways environmental change can affect natural systems is by altering the behavior of organisms (3, 4). For example, human land use is increasing the nocturnality of large mammal species globally (5); warming is altering settlement, foraging, and predator avoidance behavior of fish and invertebrates in the world's oceans (6); and changes in the abundance of predator species due to hunting and habitat loss in terrestrial and aquatic ecosystems (7) are causing cascading effects on the behavior of individuals at lower trophic levels (8, 9). How organisms behave, including how they find mates, consume resources or prey, and avoid danger, governs their population's demographic rates (10). Because of the connections between behavior and demography, changes in the environment that alter behavior also have the potential to affect population growth and persistence (11), the structure of communities (12), and the function of ecosystems (4, 6, 13).

Through its effect on demography (e.g., refs. 13–16), behavior also has the potential to affect the dynamics of ecosystem state, for example by creating the conditions necessary for the existence

of alternative stable ecosystem states, that is, distinct ecosystem states that are stable under the same environmental conditions (17). The existence of alternative stable states and the properties of transitions between those states depend on the functional relationships that relate the growth and mortality rates of a population to its density (17–19). For example, in models of savanna ecosystems, the form of the relationship between the severity of fires and grass density determines whether the system exhibits abrupt thresholds between tree- and grass-dominated states or whether there is a smooth transition between the two (20). Similarly, shifting the form of consumer functional response from saturating (type II) to sigmoidal (type III) causes abrupt transitions from consumer-dominated to plant-dominated ecosystem states in response to resource pulses in generic population models (18). Analogous density-dependent dynamics due to behavior (11, 16, 21) might therefore also underlie ecosystem state transitions.

Understanding the drivers of ecosystem state transitions and when and where thresholds between distinct states can manifest requires rigorously quantifying ecological interactions from empirical data (13, 22, 23). This means deriving demographic rates directly from measurements or empirically validated models of behavior (21, 24). Collecting the kinds of large, in situ behavioral datasets necessary to make this connection has only recently become feasible with technological advancements in the ability

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to gather and analyze large amounts of video, audio, and tagging data (25, 26). This advancement has opened the possibility of scaling up, from behaviors at the resolution of individual organisms and on the timescale of seconds [e.g., active search behavior (27) or social interactions (12, 28)] to functional relationships that can determine the long-term, ecosystem-level consequences of such behavior (4, 13).

Coral reefs are a fitting system in which to explore the role behavior may play in ecosystem state transitions. Over the last half-century, coral reefs in many locations around the world have undergone structural shifts, in which populations of foundation coral species decline or disappear and algae come to dominate the benthic habitat (29). If unchecked, algae can rapidly colonize open space, preventing the expansion of existing coral colonies or the settlement and growth of new corals (30, 31). The loss of coral is often associated with a significant loss of biodiversity and ecosystem services (29, 32). Demographic models suggest that shifts from coral to algal dominance can hinge on the consumption of algae by the herbivorous fish community (33–36), and, indeed, the harvest of herbivorous fish has been proposed by both empiricists and theoreticians as a major contributor to ecosystem shifts (37, 38). However, there has been considerable debate about whether or not coral-dominated and macroalgal-dominated states represent alternative stable states (i.e., both states stable under the same environmental conditions versus shifts between states due to different environmental conditions) and, if so, the precise mechanisms that generate thresholds between states (23, 39, 40). Much of this debate has centered on how grazing behavior by herbivores feeds back on demography, and how anthropogenic forcing, particularly fishing, influences grazing (23, 39, 40). Determining the relevance of alternative stable states and identifying the mechanisms that govern thresholds remains a major goal in coral reef ecology, restoration, and management (1, 41).

Here, we develop an approach that takes advantage of extensive field measurements of reef fish foraging behavior (42, 43) to create a model of herbivory in coral reefs. We use this model to derive the density dependence of herbivory and introduce this functional form into a model of coral–algal–herbivore demography. We then show how this empirically measured behavioral feedback

(42) can scale up to produce alternative stable ecosystem states. In addition, our analysis reveals that when we include behavioral feedbacks, transitions from coral-dominated reefs to algal dominance and the collapse of coral and fish populations depend on how quickly fishing changes and not just on the magnitude of fishing. Our multiscale approach provides a conduit for "big behavioral data" (25), which are becoming available in many systems (26), to inform demographic models and to help resolve debates over the presence and mechanisms of ecosystem thresholds. Resolving these mechanisms can guide management decisions about not just the amount of management adjustment but also the time course of management changes needed to achieve a target outcome.

Results

Our modeling framework involves several steps. We 1) derive a data-driven model of fish behavior (dynamics occurring on the order of seconds to minutes) to determine the functional relationship between fish density and per-capita feeding rate (Fig. 1 *A* and *B*) then 2) use that relationship in a demographic model that follows fish, algae, and coral interactions (dynamics occurring on the order of months to years; Fig. 1*C*) to determine the ecosystem-scale consequences of behavior (see *Materials and Methods* for details). Our behavioral model (System **1**) tracks movements of fish between open foraging habitat and shelter-rich (i.e., coral-dominated) habitat. It captures the empirical observation that fish follow each other into and out of foraging areas and reduce their tendency to exit productive but dangerous foraging habitat when many neighbors are present (42, 43). As a result of these behaviors, the per-capita feeding rate of herbivorous fish is an increasing function of fish density, which leads to longer feeding bouts and greater algal consumption per bout (Fig. 1*B* shows empirical consumption per foraging bout alongside model prediction). This model reveals a fast behavioral feedback of herbivorous fish density, H, on per capita feeding rate, which we describe with the function $\lambda(H)$. We incorporate this functional relationship into a simple ecosystem model, a coral–algae–herbivore demographic model, by assuming a separation of time scales by which behavior equilibrates rapidly relative to demography. The demographic model (Eqs. **2–4**) follows herbivorous fish consumption of benthic algae, which
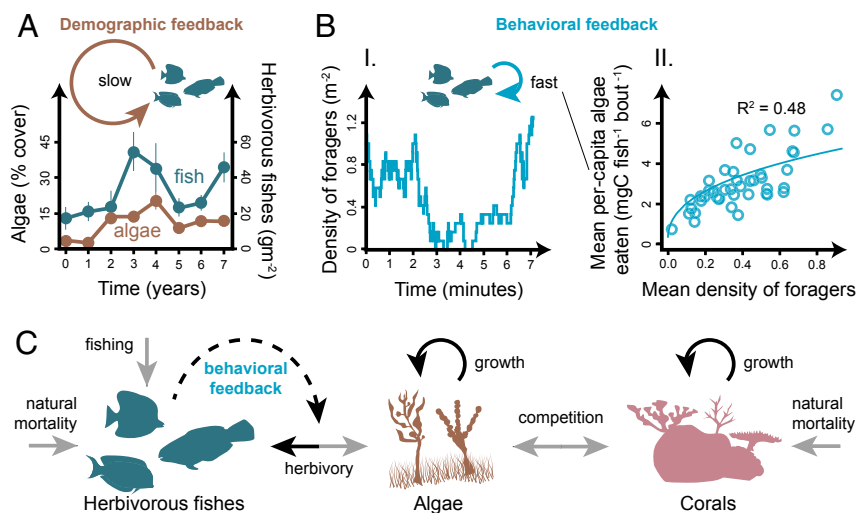
Fig. 1. Demographic and behavioral feedbacks in a coral reef ecosystem. The herbivorous fish population experiences two distinct feedbacks: demographic feedback of fish density on fish population growth driven by changes in availability of algae (*A*; mean ± 95% CI, data provided with permission by refs. 107 and 108; algae = brown, fish = blue) and behavioral feedback caused by changes in local fish density (*B*, *I*) driving changes in mean fish feeding behavior (*B*, *II*, $n = 44$; data from ref. 42, modeled in System **1**; blue curve = model predictions, $R^2 = 0.48$). The relationships that comprise the demographic coral reef model (*C*; Eqs. **2–4**), including positive (black arrows) and negative (gray arrows) effects. To test its ecological consequences, we include or exclude the behavioral feedback in the demographic coral reef model (dashed arrow in *C*).

compete with corals for limited open space on the reef. The herbivorous fish in the model experience both natural and fishing mortality.

Empirically Observed Foraging Behavior Involves a Feedback between Fish Density and Algal Consumption. We fitted a behavioral model to data and model predictions from a previous study (42) in which we used large camera arrays to measure the foraging behavior (initiation and cessation of foraging and bite rate) of herbivorous fish in a coral reef. The fitted behavioral model reproduced observed fish behavior (*SI Appendix, Solving & Fitting Behavioral Model*), and the resulting functional form for the steady-state per-capita feeding rate, $\lambda(H)$, was an increasing, saturating function of total herbivore density, H. In other words, the behavioral rules that herbivorous fish follow when foraging cause each fish to eat more, on average, at higher population densities. Although the structure and parameters of this relationship are determined by fine-scale behavioral parameters, once known, this relationship can be well approximated by an offset Michaelis–Menten function of the form $\lambda(H) = \lambda_0(d + \frac{H}{1+zH})$, where the product of λ_0 and d sets the minimum per-capita feeding rate and z determines how per-capita feeding rate changes with herbivore abundance (*SI Appendix, Fig. S1*; see also our similar approach for deriving the demographic effect of greater risk aversion in fished populations: *SI Appendix, Direct Effects of Fishing on Fish Behavioral Traits*). Through its effect on foraging behavior, changes in fish population density, H, feed back on per-capita feeding rate. We, therefore, refer to this effect as a behavioral feedback.

Behavioral Feedbacks Can Increase Ecosystem Sensitivity to Fishing. To understand the effect of the behavioral feedback, we compare the outcome of the demographic (fish–algae–coral) model with this feedback in the algae–fish interaction [$\lambda(H) = \lambda_0(d + \frac{H}{1+zH})$ in Eq. **2**] to the case with constant, density-independent per-capita feeding rate ($\lambda(H) = \lambda_{no\ beh}$). The model with behavioral feedbacks exhibits alternative stable states, which do not occur in the model without behavioral feedbacks (see *SI Appendix, Testing for Alternative Stable States in Demographic Model*; note that we do not include a nonlinear feedback between coral cover and herbivory rate as in refs. 33–35). Therefore, the ecosystem collapses or begins to recover at the same level of fishing pressure for a given feeding rate in the model without behavioral feedbacks but at different levels of fishing pressure in the model with behavioral feedbacks (*SI Appendix, Fig. S2*). To compare the expected collapse point with and without behavioral feedbacks, we first started in an unfished system with an abundant herbivorous fish population (i.e., the system is run to equilibrium with no fishing, $f = 0$; Eq. **2**), where the fish per-capita feeding rate (λ in Eqs. **2** and **3**) is expected to be relatively high, a pattern that aligns with field surveys and experiments (refs. 42–45 and Fig. 2*A*). We then increased fishing by raising f by 0.01 fish biomass year^{-1} to a maximum level that ranged from 0.003 to 0.5 fish biomass year^{-1} (*SI Appendix, Sensitivity to Magnitude of Fishing*). If the per-capita feeding rate remains constant across herbivorous fish population sizes as in the model without behavioral feedbacks, then the ecosystem is more resistant to state shifts that result from increasing fishing (i.e., the fish and coral populations can withstand a higher fishing level before they collapse) than in the model with behaviorally driven reductions in the per-capita feeding rate with decreasing fish density (Fig. 2 and see *SI Appendix, Fig. S3A and Sensitivity to Magnitude of Fishing*). In *SI Appendix*, we compare the recovery point with and without behavioral feedbacks by starting in a heavily fished coral reef with a sparse herbivorous fish population (i.e., we run the system to equilibrium with a high fishing rate, $f = 0.5$, Eq. **2**, but use a very small nonzero initial fish biomass for subsequent numerical

solutions, *SI Appendix, Sensitivity to Magnitude of Fishing*) and a low per-capita feeding rate (refs. 42–44 and *SI Appendix, Figs. S3B and S4*). We then decreased fishing linearly (we reduced f by 0.01 y^{-1}) to a minimum level that ranged from 0.497 to 0 y^{-1}. In this case, the no-behavioral-feedbacks model with constant herbivory across fish population size predicts the ecosystem needs greater reductions in fishing to recover than does the behavioral feedbacks model where per-capita feeding depends on fish density (*SI Appendix, Fig. S4*). In sum, we find that behavioral feedbacks cause ecosystem collapse (i.e., fish and coral population collapse) at a lower level of fishing pressure and ecosystem recovery (i.e., recovery of the fish and coral populations) at a higher level of fishing pressure than would be expected under the standard assumption (33–36) that fish behave independently of one another (Fig. 2 and *SI Appendix, Figs. S3 and S4*).

To illustrate the utility of explicitly modeling behavior, we use our framework to explore the ecosystem consequences of another fish behavior that has been observed in coral reef systems: that predation (including fishing) can directly alter individual fish behavior by increasing risk aversion during foraging ("behavioral feedbacks + trait shift" model, *SI Appendix, Direct Effects of Fishing on Fish Behavioral Traits*, refs. 44–47). When we implement a simple adjustment to our behavioral model to represent such fishing-induced shifts in behavioral traits (Fig. 2*A*, purple [square] curve; see *SI Appendix, Direct Effects of Fishing on Fish Behavioral Traits* and Fig. S1), this compounds the aforementioned effect of behavioral feedbacks, further increasing ecosystem sensitivity to fishing by reducing the fishing level that causes fish and coral population collapse under increasing fishing pressure (Fig. 2*B*, purple, square points).

By calculating the Jacobian for the model with behavioral feedbacks (*SI Appendix, Testing for Alternative Stable States in Demographic Model*), we find that the "algae only" ecosystem state is stable only when the minimum per-capita feeding rate of herbivores falls below the ratio of the sum of natural and fishing mortality over the algae assimilation parameter: $\lambda(0) < \frac{\mu+f}{b}$ (Eqs. **2** and **3**). In other words, the greater the fishing mortality, f (or natural mortality, μ), or the lesser the assimilation rate of algae by fish (b; Eq. **3**), the larger the region of initial conditions that lead to the ecosystem state with only algae and no fish or coral remaining.

Across a wide, empirically derived range of model parameters, the behavioral feedback captured by System **1** makes the reef ecosystem more sensitive to changes in fish abundance (Fig. 2 and *SI Appendix, Fig. S5*). However, the effect of behavioral feedbacks lowering the fishing level that causes coral collapse (i.e., increasing ecosystem sensitivity) is greatest when coral and algal growth rates are low (*SI Appendix, Fig. S5*). Furthermore, the collapse and recovery points predicted from our numerical analysis with fishing increasing or decreasing to a target level over time differ from those predicted by an equilibrium bifurcation analysis (*SI Appendix, Fig. S2*). This motivated us to further explore the importance of the pace of change of fishing pressure.

Behavioral Feedbacks Can Make the Ecosystem Sensitive to the Pace of Change in Fishing Mortality, Not Just the Magnitude. In addition to increasing the ecosystem's sensitivity to the magnitude of fishing, the behavioral feedback on per-capita feeding rate (Fig. 1*B* and System **1**) causes the ecosystem to be sensitive to how quickly the fishing rate changes. By allowing fishing mortality to increase linearly up to a target level, at which it is then held constant (*SI Appendix, Sensitivity to Pace of Fishing*), we find that increasing how quickly a target fishing level is reached (i.e., raising the initial slope in the f function shown at the top in Fig. 3 *A* and *B*) can cause the ecosystem to undergo a state shift,
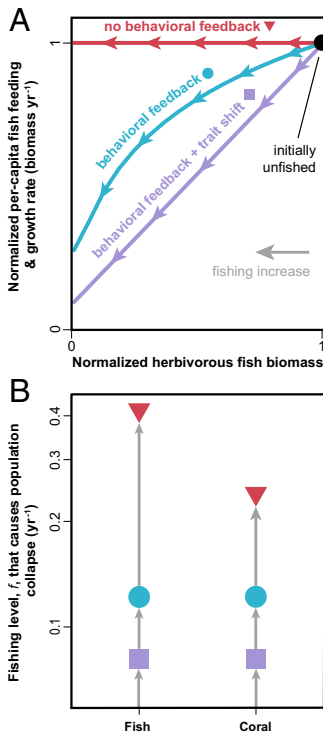
Fig. 2. Behavioral feedbacks can alter ecosystem responses to fishing. Changes in the abundance of herbivorous fish also affect density-dependent behavioral feedbacks on the per-capita feeding and growth rates of herbivores (*A*: blue curve [circle] derived from behavioral model (System **1**) and included as $\lambda(H)$ in Eqs. **2** and **3**, *Materials and Methods*, and *SI Appendix, Solving & Fitting Behavioral Model*). Fishing can also directly affect individual behavior through trait shifts toward greater risk aversion (*A*: purple line [square] derived from fitted System **1** parameters but with spontaneous exit rate increasing linearly with *f*, up to 100% at $\lambda(0)$, *SI Appendix, Direct Effects of Fishing on Fish Behavioral Traits*). (*B*) Given an initially unfished system, fish and coral populations collapse (i.e., drop below 0.01) under lower fishing levels when behavioral feedbacks are present (blue circles) and even lower levels when behavioral feedbacks and behavioral trait shifts are present (purple squares), relative to the model with no behavioral feedbacks or trait shifts (red triangles; i.e., initially high feeding rate held constant: *A*; see *SI Appendix, Sensitivity to Magnitude of Fishing* and Fig. S3 for details). Model results presented in *B* provide an example, from a single parameterization; however, this qualitative pattern holds across the full empirically determined range of parameters explored (*SI Appendix*, Fig. S5).

from coral and fish persistence to the collapse of both populations. This state shift can be avoided if the same target fishing level is approached more slowly (Figs. 3 and 4). This kind of sensitivity to the pace of change in a control parameter has recently been referred to as "rate-dependent tipping" or, hereafter, "R-tipping" (18, 48, 49).

Through further analysis (*SI Appendix*, Eqs. S11–S16) of our demographic model with behavioral feedbacks, we can infer four key features of the initial transient dynamics that cause R-tipping (*SI Appendix, Analysis of R-Tipping*). First, more rapid increases in fishing pressure (i.e., greater *df*/*dt*; *SI Appendix*, Eq. S12) lead to more rapid declines in the realized per-capita feeding rate $\lambda(H)$, relative to the critical per-capita feeding rate needed to sustain the herbivore population [$\lambda_c(t)$; *SI Appendix*, Eq. S11]. This leads to more rapid loss of herbivores when fishing pressure increases quickly. Second, steeper per-capita feeding rate functions—that is, functions, $\lambda(H)$, for which $\frac{d\lambda(H)}{dH}$ is large—lead to faster loss of herbivores [i.e., more rapid changes in $\lambda(H) - \lambda_c(t)$; *SI Appendix*, Eq. S11]. In other words, stronger positive density dependence leads to faster declines in herbivore density as fishing pressure is increased, a result evident in

Fig. 4*D*. Third, the loss rate of herbivores grows most rapidly when growth of the algal population, *dA*/*dt*, is low, consistent with the intuition that slower algal growth limits the capacity for algal growth to compensate for herbivore mortality due to fishing. Fourth, there is a threshold of algal cover needed to prevent the collapse of a fish population suffering an abrupt increase in fishing pressure (*SI Appendix, Analysis of R-Tipping*). Thus, rapid increases in fishing pressure cause transient dynamics that reach lower herbivore population sizes but also, critically, lower algal cover (Fig. 3). The latter phenomenon is due to the finite rate of algal growth and competition between algae and coral for space. Algal growth is minimal when the standing algal cover is low and coral and algae occupy most of the free space on the reef (Eqs. **3** and **4**). Under these conditions, the slow expansion of algae (limited by coral mortality rate: *m* in Eq. **4**) is unable to rescue an herbivore population declining due to rapid increases in fishing (*SI Appendix*, Fig. S6). However, algae can compensate for fish mortality when fishing pressure is increased slowly. Slow increases in fishing pressure, even toward relatively high target fishing levels, can sustain a biomass of the herbivorous fish population equal to, or even temporarily above, the equilibrium biomass under no fishing, although with substantial differences in turnover (e.g., turnover rate increases ninefold from initially no fishing to the equilibrium at *f* = 0.18; Fig. 3*A*).

In our model, when alternative stable states exist for a given fishing level, one set of initial conditions (i.e., initial coral and algal cover and herbivore density) leads to coral persistence, while a different set of initial conditions leads to coral extinction. These different "basins of attraction" to distinct ecosystem states are separated by a boundary (i.e., a separatrix) in state space. When fishing is increased from an unfished state, faster paces of change push the system into the basin of attraction that leads to fish and coral population collapse, whereas slow increases in fishing pressure allow the system to remain in the basin of attraction that leads to fish and coral persistence (Fig. 4 and *SI Appendix*, Fig. S7). Because the model without behavioral feedbacks does not exhibit alternative stable states (*SI Appendix, Testing for Alternative Stable States in Demographic Model*), it cannot exhibit R-tipping of this kind. Therefore, in the presence but not in the absence of behavioral feedbacks, the pace of change in fishing pressure can have qualitative effects on the fate of the ecosystem (Figs. 3 and 4) that would not be predicted by naïvely applying traditional bifurcation analyses (Fig. 4 *A–C* and *SI Appendix*, Figs. S2 and S7). For a given target fishing level, there is a critical pace of change in fishing pressure that pushes the system across the separatrix (i.e., the negative slope in Fig. 4*E*). In this region of parameter space, the fate of the ecosystem is extremely sensitive to small changes in the pace of increase in fishing pressure. For example, in one realistic region of parameter space, our model suggests that reaching a target fishing level just a few years faster (e.g., in 2 vs. 6 y; *SI Appendix*, Fig. S8) can cause the collapse of fish and coral populations that would otherwise persist.

R-tipping is a general property of the demographic coral reef model when behavioral feedbacks are present. It occurs in both the case of the monotonically increasing, saturating functional form for per-capita herbivory shown here (Fig. 4 and *SI Appendix*, Fig. S9) and also under a unimodal functional form (*SI Appendix*, Fig. S10) with negative density dependence (*SI Appendix*, Fig. S11, discussed in *SI Appendix, Functional Sensitivity: Including Negative Density Dependence*). For a given functional form of the behavioral feedback, the ranges of target fishing levels and paces of approach over which R-tipping occurs depend on model parameters (*SI Appendix*, Figs. S9 and S11). For example, with a behavioral feedback that causes saturating positive density dependence (Fig. 2*A*, blue [circle] curve), when coral growth rates are at the low end of their observed range (34), R-tipping occurs over a low and narrow range of paces of

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Fishing raised to target level (f_T) over...
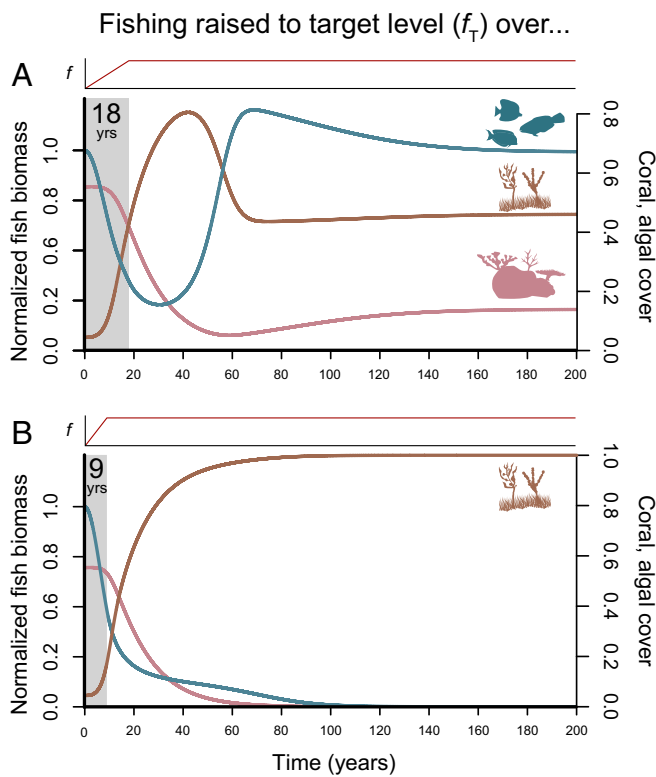
Fig. 3. Small changes in fishing effort can determine whether coral and fish populations persist or collapse. Model results illustrating a system undergoing an increase in fishing effort from no harvest ($f = 0$) to $f = 0.18$ (Eq. 2). (A) Coral (pink), algae (brown), and fish (blue) population dynamics when target fishing level is reached over a period of 18 y. (B) Populations when same target harvest level is reached over a shorter period of 9 y. Slower increase in harvest (A) results in persistence of fish and coral populations; more rapid change in harvest (B) causes fish and coral population collapse.

change in fishing but over a wide range of target fishing levels (steep negative slopes in left panels of *SI Appendix*, Fig. S9, where the red horizontal line represents the boundary between basins of attraction for the model without behavioral feedbacks for each of these parameterizations). In contrast, when coral growth rates are higher (e.g., Fig. 4*E* and *SI Appendix*, Fig. S9), R-tipping occurs over a much wider range of paces of change in fishing but over a narrower range of target fishing levels (shallow negative slopes in right panels of *SI Appendix*, Fig. S9); however, in these cases, R-tipping does not manifest when target fishing levels are approached very slowly (shown by the flat part of the separatrix in Fig. 4*E* and right panels in *SI Appendix*, Fig. S9).

Discussion

Our analysis reveals that, despite the distinct timescales of behavior and demography (Fig. 1 *A* and *B*), feedbacks between the two can qualitatively affect how ecosystems respond to anthropogenic change. Specifically, our analysis reveals that interactions among herbivorous reef fish produce a behavioral density-dependence that feeds back on fish demography. This feedback gives rise to alternative stable states and changes the conditions under which the coral reef ecosystem will collapse in response to fishing pressure, a ubiquitous source of anthropogenic forcing linked to shifts in ecosystem state in aquatic environments (50–52). However, any externally driven perturbation, anthropogenic or natural, that changes fish mortality sufficiently could also cause state shifts. In our case, by altering the density of fish, fishing changes the feeding behavior of remaining individuals

(42, 43), which, in turn, alters the growth rate of the population. Higher algal growth rates better buffer herbivores against fishing-induced drops in population size that are particularly detrimental when behavioral feedbacks are present. When algal growth rates and coral turnover rates are at the lower ends of their observed ranges (34), behavioral feedbacks cause the ecosystem to collapse under less than half the level of fishing that one would expect to cause collapse if behavioral feedbacks were not considered (shown for a single parameterization in Fig. 2*B* and across parameter values in *SI Appendix*, Fig. S5).This effect could be compounded if exposure to fishing also directly affects individual behavior by making individuals less prone to feed due to the perceived risk of mortality (44–47), an empirically documented effect that we can incorporate because long-term feeding rates emerge from a mechanistic model of feeding behavior in our framework (Fig. 2 and *SI Appendix, Direct Effects of Fishing on Fish Behavioral Traits*). Our finding that behavioral feedbacks can both generate demographic thresholds and affect the amount of fishing an ecosystem can withstand before crossing a threshold suggests that models that ignore such feedbacks could mischaracterize how fishing affects ecosystem state.

The mechanism that gives rise to a behavioral feedback, and ultimately produces the rich dynamics in our ecosystem model, is the fact that foraging behavior of individual fish is strongly nonindependent (Fig. 1 and ref. 42): Individuals graze for longer periods of time and enter dangerous, open foraging areas more readily when the overall density of fish in the area is higher (Fig. 1*B*). Similar facilitative interactions among consumers, either through enhanced predator avoidance (53–56), increased resource consumption (57–60), or other mechanisms has been documented in a diverse range of ecosystems. For example, there is strong empirical support for the "individual risk hypothesis" (57), within which the "many eyes" (58, 61), "risk dilution" (62), and "confusion" (63) effects are nested: In many species of birds, mammals, and fish, the fraction of time any given individual devotes to vigilance typically decreases as the number of surrounding conspecifics or heterospecifics increases (64). Less time spent being vigilant typically translates to more time feeding when foraging in larger groups (57–59, 65). Positive density dependence of resource uptake is also widespread in microbial systems, where metabolic cooperativity (e.g., ref. 66) and cross-feeding (67) can allow individual microbes to more effectively exploit resources as the density of conspecifics or mutualist partners increases. Consequently, for many species, and for guilds of interacting mutualists, it is likely that per-capita population growth rates increase with density, at least at low densities, before plateauing or decreasing as density becomes high (4, 68, 69). Moreover, in mixed-species communities of savanna herbivores, not only do individuals benefit from the presence and densities of conspecifics and heterospecifics [e.g., through alarm-communication networks (70)], but, by grazing the landscape, they reinforce a characteristic, putatively stable grass-dominated ecosystem state, rather than an alternative, putatively stable state of tree dominance (71). Thus, these and other systems with highly social consumers whose control of primary producers can determine the state of the ecosystem [e.g., ungulates in forest (72) and riparian systems (73), rabbits in grasslands (74), geese in arctic marshes (75), and planktivorous fish in freshwater lakes (50)] could exhibit the same kind of behaviorally mediated density dependence proposed here to govern ecosystem dynamics in coral reefs. While the potential for positive density dependence to destabilize ecological systems has long been known in the context of Allee effects (e.g., ref. 16) and mutualistic interactions, determining how positive interactions play out in the context of the more diverse ensemble of ecological interactions that occur in real ecosystems remains a nascent but important research area (13, 68, 76).
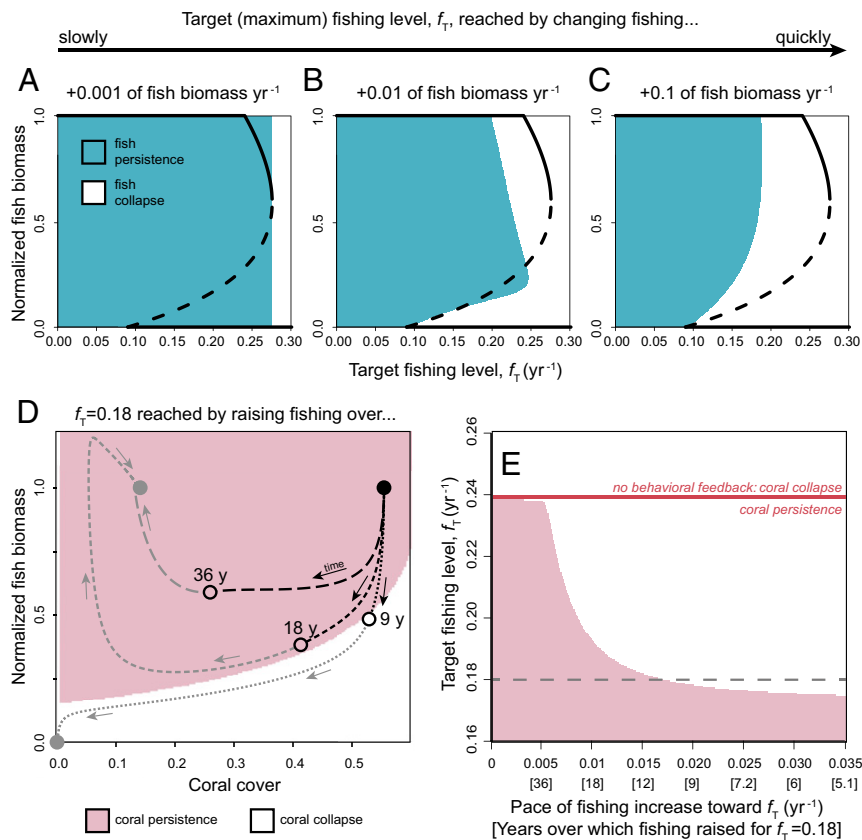
Fig. 4. Behavioral feedbacks cause pace of anthropogenic change to shape coral reef dynamics. In the model with behavioral feedbacks, the pace at which fishing changes determines (*A–C*) the combinations of initial fish biomass and target fishing level, f_T, that lead to either the persistence (blue) or collapse (white) of the fish population (comparable to predictions from full equilibrium analysis of model with constant fishing = f_T: black curves indicate stable [solid] or unstable [dashed] equilibria), and (*D*) the trajectory of the system through state space, beginning with no fishing at $t = 0$ (black closed circle, *A*). We denote the state variable (*H*, *C*) values when the target fishing level is first reached (open circles), and we denote the points at which equilibrium (gray closed circles) is reached by the three simulated trajectories: slow changes in fishing, long-dashed curve; intermediate changes in fishing, short-dashed curve; and fast changes in fishing, dotted curve. Faster paces of change can cause the system to cross the boundary between basins of attraction for coral persistence (pink) and coral collapse (white). (*E*) R-tipping can occur over a range of target fishing levels (f_T from *A* denoted with horizontal dashed line) and paces of change in fishing for a given set of ecosystem parameters but does not occur in the absence of behavioral feedbacks (e.g., the red horizontal line represents the boundary between basins of attraction for the model without behavioral feedbacks for this same parameterization). R-tipping exists over the full range of empirically determined parameters in the coral reef model with behavioral feedbacks (*SI Appendix*, Fig. S9).

For understanding the ecosystem-level consequences of additional behavioral interactions, the approach taken in this paper of deriving demographic rate functions from fast-timescale behavioral data on consumer–resource interactions is generalizable (24) and extends well beyond this system. Similar approaches have recently been applied, for example, to predator–prey (27, 77) and disease–host (78) systems. This approach has the advantage of relating demographic rates to measurable, individual-level behaviors, which are becoming increasingly accessible through developments in behavioral data acquisition (25, 26, 79).

One principal outcome of the behavioral feedback in our demographic model is that the pace of anthropogenic change matters: Whether an ecosystem undergoes a transition from one alternative stable state to another depends on how quickly fishing changes (Figs. 3 and 4). This type of R-tipping (48) was recently hypothesized to be a general property of dynamical systems in which a state variable or parameter of an otherwise autonomous system is externally forced through time (49). In our model, the ecosystem exhibits R-tipping because of two properties. First, as we described above, the behavioral feedback leads to bistability, in which alternative stable states of coral population persistence or collapse (and complete algal dominance) occur at the same level of fishing (Fig. 4; *SI Appendix*,

Testing for Alternative Stable States in Demographic Model). Second, density-dependent herbivore feeding, finite algal growth rate, and competition between corals and algae limit the rate of growth of the algal and herbivore populations, as herbivores are subjected to increasing fishing pressure (*SI Appendix, Analysis of R-Tipping*). When fishing pressure is rapidly imposed, algae increase but this rise in herbivore food supply is not fast enough to compensate for fishing-induced mortality (*SI Appendix*, Fig. S7), and herbivores are fished to extinction, while algae competitively exclude corals (Figs. 3*B* and 4 and *SI Appendix*, Fig. S8*B*). In contrast, increasing fishing pressure slowly allows for greater algal growth earlier in the timeline, and the herbivore population recovers through greater food availability (Figs. 3*A* and 4 and *SI Appendix*, Figs. S7 and S8*A*), though with much higher turnover (Fig. 3*A*). Although our model does not contain size or age structure, these higher herbivore turnover rates would likely translate to an herbivore population consisting, on average, of younger, smaller fish size classes, typically less desirable for fisheries (80).

The possibility that shifts in ecosystem state could depend on the pace of change of a parameter and not just the magnitude of change has been proposed in past work (18). However, to date, the great majority of published analyses of transitions among

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ecosystem states do not consider this possibility (13, 19, 81). For ecosystems that exhibit such R-tipping, standard analyses that are often applied to understand ecosystem dynamics can give misleading results (*SI Appendix*, Fig. S2). For example, bifurcation analysis is widely used to determine the existence and location of alternative stable states in ecosystem models; however, conducting a bifurcation analysis of our demographic model at a target fishing level (black lines and curves in Fig. 4 *A–C*) yields expectations that are violated (compare with blue-white boundary, or separatrix, in Fig. 4 *A–C*) by the dynamics of the system when the same fishing level is reached through continuous changes in fishing pressure over time. From an ecological or management perspective, this finding indicates that knowing the two system features that are most often considered when assessing the potential impact of harvesting a population—the initial conditions of the ecosystem and the target level of harvest—is insufficient to predict how the system will respond to being harvested; the pace of the change in harvest must also be considered (Fig. 4 *A–C*).

R-tipping arises in our analysis because, when external forcing and demography occur on similar timescales, transient forcing can push a system into a new basin of attraction from which it cannot recover. We show that the strength of the behavioral feedback [i.e., $d\lambda(H)/dH$] and the growth rate of algae are crucial in determining demographic transients and, thus, whether the system exhibits R-tipping (*SI Appendix, Analysis of R-Tipping*). Similar approaches applied to evolutionary dynamics have shown that fast versus slow evolution or coupled fast–slow eco-evolutionary feedbacks can drive distinct evolutionary and ecological outcomes, emphasizing the importance of analogous transient phenomena on evolutionary timescales (82–84).

The type of behavioral feedback that generates R-tipping in our system (a positive density-dependent rate of resource consumption) is likely relevant to many other systems (4, 12, 85), and other systems that exhibit alternative stable states could also exhibit R-tipping (18, 48, 49). When R-tipping is relevant, the management decisions necessary to arrive at a target state depend on not only the value of a management control such as fishing but also the path to that target value. In the case of our coral reef system, this would mean considering how to change fishing over time, in addition to the eventual target level of fishing. Perhaps counterintuitively, our analysis suggests that the coral reefs most vulnerable to R-tipping are those that fit the description of a healthy reef: high coral cover and little free space on the reef (*SI Appendix*, Fig. S6). Such reefs are vulnerable because when fishing increases there is little space available for the algal growth needed to rescue the herbivorous fish population from fishing-induced collapse (Fig. 3), and the growth rate of algae is limited by the mortality rate of coral. Moreover, we find that reefs with lower mean algal growth rates and/or coral turnover rates appear particularly sensitive to the magnitude and pace of fishing (*SI Appendix*, Figs. S5 and S9). Such reefs would include those with a coral population dominated by slower-growing, typically more stressor-resistant mounding taxa [shown to be selected for by global climate change (86)], and/or an algal population in which slower-growing macroalgae represent a greater proportion relative to faster growing filamentous algal turf, a pattern typically correlated with anthropogenic nutrient enrichment (30). Furthermore, our findings suggest that management strategies that prioritize the maintenance or restoration of high herbivore densities, such as no-take marine reserves, could reduce the susceptibility of coral reef ecosystems to a change in state in response to fish mortality. In addition to the potential to increase the overall system resilience (i.e., basin of attraction for the target state for a given fishing effort) by allowing for more fish within reserve boundaries [as occurs

in a model where size-dependent predator-prey interactions drive alternative stable states (87)], reserves might reduce the likelihood of R-tipping inside and outside reserves by reducing the spatially averaged pace at which fishing effort increases in the system as a whole.

For fisheries more generally, our results highlight that considering the pace of change in fishing pressure may be necessary to achieve an "ecologically sustainable yield," targeted at maintaining a particular ecological state [a component of ecosystem-based management (88)] when fished species exhibit dynamics that can cause R-tipping. The specific behaviorally driven dynamics we reveal could apply to other fisheries but may hold less relevance to obligate shoaling fish taxa [which can dominate many open-ocean fisheries (51, 52)] due to grouping behavior that can maintain the same local density despite population declines (89). While classic fisheries management has focused on equilibrium harvest without considering the path to reach it (80), considering harvest trajectories over time is a central element of approaches such as optimal control analysis (90) and some multiannual plans (91). In single-species fisheries models, when the population dynamics and catch depend linearly on fishing effort, the optimal strategy is to approach the population size that produces the maximum sustainable yield as quickly as possible; doing anything else prolongs the time over which yields are lower than the maximum (92). In contrast, incorporating nonlinear dynamics that lead to alternative stable states into optimal control analysis leads to optimal pathways with delayed implementation of such strategies (93). Our results provide an additional motivation for employing an approach such as optimal control that considers fishing trajectories over time: Subtle differences in the pace of change of fishing could lead to significant differences in the long-term yield and viability of the fishery. Moreover, because the feedbacks studied here can cause the fate of harvested fish populations to depend on the pace of change in fishing pressure, our findings indicate a need to understand the social and economic processes that influence changes in harvest. While our analysis treats changes in harvest as extrinsic to the ecological system (Eq. **2**), harvest is perhaps better viewed as the outcome of coupled social-ecological dynamics in which the timescales of stock management and conservation policy implementation are also important considerations (94). Finally, while incorporating species interactions has long been a goal of ecosystem-based fishery management (95), application to on-the-ground fishery management decisions remains limited due to the complexity of marine food webs and the associated model uncertainty and data limitations (96). In considering which aspects of that complexity are most crucial to incorporate into fisheries models, our paper, based on empirical findings of facilitative interactions among fish in a community, adds to a growing literature that indicates that behavioral considerations can substantially alter how we expect a system will respond to harvest (47, 97).

Our results reveal the potential importance of behavioral feedbacks in modifying the location and nature (e.g., smooth vs. abrupt) of ecosystem transitions. Although too simplistic to generate quantitative predictions for any specific reef, we consider this work an important early step toward directly linking demography and behavior. Additional complexities such as species diversity (98, 99) or demographic stochasticity (100) that can dampen positive feedbacks and increase ecological resiliency should be considered in the context of behavioral feedbacks in the future to further assess the robustness of our findings (101). Coral reefs and many other ecosystems can also exhibit complex trophic structure, strong functional dependence on species diversity, and various levels of demographic openness that are not considered here (48, 102, 103). Furthermore, past models of coral reefs have shown that multiple positive feedback mechanisms that are not included in our model can, in isolation (e.g., refs. 33, 36, and 104) or in combination (22),

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cause alternative stable states, albeit typically between controversial "coral and fish only" vs. "algae only" states (39) and over a relatively narrow region of demographic parameter space (34, 98). Finally, including dynamic mesopredator and apex predator populations or allowing human fishing pressure to emerge from a dynamic process would introduce additional direct and indirect effects (105) and demographic feedback loops but could also introduce behavioral feedbacks within and among populations. Determining how these mechanisms interact with the behavioral feedbacks included in our model will be an important future step in the analysis of ecosystem dynamics.

Our work illustrates the potential to begin to understand how quantifiable animal behaviors influence the ecology and conservation of natural ecosystems. We stress that our approach of unifying the disparate timescales of the behavior of individuals and the demography of coupled populations can and should be applied to other systems, especially those that putatively exhibit thresholds. This line of inquiry holds promise to inform not only the methods and guiding questions of theoretical work on ecosystem state transitions but also strategies for on-the-ground management in the face of anthropogenic change.

Materials and Methods

Behavioral Model of Fish Foraging. We constructed a dynamical model of reef fish foraging behavior based on findings from our previous field experiments (42, 43), which employed multimodel inference to determine the essential features required to accurately model fish foraging behavior. The model developed here captures these salient features. In particular, we follow the density of fish in two possible behavioral states: individuals feeding in highly productive, open foraging habitat (e.g., pavement or coral rubble in reef flats) easily accessible to predators (106), $P(t)$, and individuals traversing or hiding in relatively unproductive but shelter-rich (i.e., coral-covered) habitat outside primary foraging areas, $U(t)$. The total density of herbivores, H, is the sum of densities in the two states: $H = P(t) + U(t)$, where we assume that H is constant $\left(\frac{dH}{dt} = 0\right)$ on the relatively rapid timescale of behavior (Fig. 1B). Several factors influence movement of fish between the two states. First, fish follow one another into and out of foraging areas such that when a fish enters or exits foraging areas from adjacent, shelter-rich coral-dominated habitat, it temporarily raises the probability that other fish will also enter, at a rate α_γ, or exit, at a rate α_μ, respectively. To capture the observed effect of a fish's memory of its neighbors' past entrances and exits (42, 43), we introduce variables E and L, which track fish that recently entered or left the foraging area. The influence of past entries or exits decays exponentially with time at a per-capita rate $1/\tau_E$ and $1/\tau_L$, respectively [τ terms estimate the depth of time into a fish's memory over which past events are influential (42)]. Second, fish spontaneously enter or leave foraging areas at a per-capita rate γ_0 or μ_0, respectively, and we allow a minimum per-capita feeding rate >0 (e.g., due to the fact that a fish must feed at some minimum level to avoid starvation) by including a baseline entry rate β (42). Third, the probability that a fish will spontaneously exit the foraging area or follow the exits of other fish into less productive regions with more shelter (i.e., coral-dominated habitat) declines with the density of surrounding fish in the foraging area, via the exponential parameter $-\eta_\mu$ or $-\eta_\Phi$, respectively (42). Taken together, these behavioral dynamics are given by the following system:

$$\frac{dP}{dt} = U[\gamma_0 + \alpha_\gamma E] + \beta - P[\mu_0 P^{-\eta_\mu} + \alpha_\mu P^{-\eta_\Phi} L]$$

$$\frac{dU}{dt} = P[\mu_0 P^{-\eta_\mu} + \alpha_\mu P^{-\eta_\Phi} L] - U[\gamma_0 + \alpha_\gamma E] - \beta$$

$$\frac{dE}{dt} = U[\gamma_0 + \alpha_\gamma E] - \frac{1}{\tau_E} E$$

$$\frac{dL}{dt} = P[\mu_0 P^{-\eta_\mu} + \alpha_\mu P^{-\eta_\Phi} L] - \frac{1}{\tau_L} L. \qquad \text{[1]}$$

By solving System **1** at equilibrium (System **1** has a unique stable internal equilibrium in the parameter regime where it matches behavioral data: *SI Appendix, Testing for Alternative Stable States in Behavioral Model*), we calculate the long-run average number of herbivores foraging in the productive habitat, $\bar{P}$, and divide this by the total number of herbivores, H. We multiply this proportion by empirical constants to compute the average per-capita rate, λ, at which the herbivorous fish population consumes areal cover of algae per year (*SI Appendix, Solving & Fitting Behavioral Model*).

Demographic Model of a Coral Reef Ecosystem. To explore the influence of behavioral feedbacks on coral reef ecosystem dynamics and responses to fishing pressure, we adopted a demographic modeling framework similar to those used in past studies (33–36). The model tracks changes in the herbivorous fish, coral and algal populations using a system of ordinary differential equations, where H, A, and C denote herbivorous fish biomass, algal cover, and coral cover, respectively (Fig. 1C). Herbivorous fish consume algae at a per-capita rate $\lambda(H)$, determined from the behavioral model, and assimilate this algal cover to fish biomass via the parameter b. Herbivores also experience natural mortality at rate μ and fishing mortality at rate f (Eq. 2). Algal and coral populations each grow into free space at a rate r_A and r_C, respectively, and compete with one another for space with equivalent intraspecific and interspecific competition (Eqs. 3 and 4). Algae experience mortality by being consumed by herbivores at a per capita rate $\lambda(H)$, while corals experience natural mortality (e.g., due to corallivory, tissue damage from disturbances, etc.) at a rate m (Eqs. 3 and 4). Thus, our demographic model takes the form

$$\frac{dH}{dt} = b\lambda(H)AH - \mu H - fH \qquad \text{[2]}$$

$$\frac{dA}{dt} = r_A A(1 - A - C) - \lambda(H)AH \qquad \text{[3]}$$

$$\frac{dC}{dt} = r_C C(1 - A - C) - mC. \qquad \text{[4]}$$

We used empirically determined estimates to parameterize the model (*SI Appendix*, Table S1 and refs. 33–35).

Quantifying Effects of Behavioral Feedbacks. We compared two versions of the demographic model (Eqs. 2–4 and Fig. 1C): one with the conventional assumption of a constant fish feeding rate, $\lambda(H) = \lambda_{no\ beh}$ for all H (i.e., behavioral feedbacks absent), and one with behavioral feedbacks, where $\lambda(H) = \lambda_0\left(d + \frac{H}{1+zH}\right)$ based on the above-described approximation of the solution to System **1** (*SI Appendix, Solving & Fitting Behavioral Model*; functional forms shown in Fig. 2A, and *SI Appendix*, Fig. S1). For the model with behavioral feedbacks, the density of herbivorous fish, H, directly affects the population dynamics of herbivores and algae and indirectly affects the population dynamics of corals (Fig. 1).

We used these demographic models to evaluate the response of the reef ecosystem with behavioral feedbacks to two different directions of anthropogenic change: 1) an increase in fishing pressure on an initially unfished ($f = 0$) ecosystem and 2) a decrease in fishing pressure on an initially degraded ecosystem ($f = 0.5$). Then, for the analogous model without behavioral feedbacks in each analysis, we set the constant per-capita feeding rate equal to that with behavioral feedbacks, given the equilibrium biomass of herbivores, $\overline{H_0}$, under the initial fishing level, that is, $\lambda_{no\ beh} = \lambda_0\left(d + \frac{\overline{H_0}}{1+z\overline{H_0}}\right)$. All other parameters and parameter values were identical between the models. This approach allowed us to measure the influence of behavioral feedbacks on the ecosystem response to changes in fishing pressure.

Data Availability. Data and code used for modeling and analyses are available via a public repository on GitHub: https://github.com/m-gil/Gil_et_al_PNAS_2020.

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