Threshold Effects
in Coral Reef Fisheries

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Summary

Coral reefs may naturally flip between coral-dominated and algae-dominated states, when species' stocks trespass some threshold levels. This essay uses a stylized model of a coral reef to show how fishing may induce flips towards more algae-dominated states. Threshold effects have consequences for fisheries management, which are analyzed for open access fisheries and sole ownership.

Keywords: Multiple Steady States, Fisheries, Threshold Effects, Coral Reefs, Skiba Points

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1   Introduction

Coral reefs are significant for human welfare because they produce a wide range of natural resources and ecosystem services. They are crucial for fisheries because they provide essential shelter for reproduction of many fish species that live as adults in the open sea. They also offer services such as recreation opportunities, nutrient cleaning, and protection from sea erosion. Recent concerns about bleaching, overfishing, and eutrophication indicate that human activities may affect the way in which coral reefs evolve over time. This may jeopardize future use of goods and services produced within reefs.

This paper focuses on the effects of fishing in coral reefs and the reefs' potential for sustainable resource production. Coral reefs may have at least two stable states: coral-dominated and algae-dominated. Scheffer et al. [34] pointed out that sudden drastic changes to a contrasting state can interrupt smooth changes in such ecosystems. Such shifts typically occur when some kind of threshold is crossed. Shifts between coral-dominated and algae-dominated states affect the reefs' capacities to sustain production of resources and services. This paper models the economics of fisheries in a coral reef that may shift between two different states. Classic results for open access and sole ownership are revisited. Though the analysis focuses on coral reefs, it could apply to any fisheries where there are threshold effects similar to the ones observed in coral reefs.

The economics of fisheries tends to rely upon Schaefer-type biological models (Schaefer [32]), which usually represent fish biomass growth using a logistic function. This is the case in the two seminal papers that modeled the economics of fisheries in a static and a dynamic setting, respectively (Gordon [13] and Scott [35]). Smith [39] provided a theoretical ground for dynamic open-access models of natural resources.

Plourdes [30] used optimal control to determine the optimal rate of harvest for a renewable resource such as fisheries. In 1976, Clark [8] attempted to study multi-cohort fisheries but pointed out that analytic solutions were difficult to produce. Munro and Scott [26] reviewed the principal results in the economics of fisheries and drew attention to problems that the common property nature of fishery resources creates.

Research inspired mainly by Holling [18] [19] presented new ways to model ecosystems. Scheffer [33] and Carpenter and Cottingham [6] studied shallow lakes. These researchers–independently of one another–derived a nonlinear model with one state variable, where the nonlinearity had a sigmoid form. Using this model, they showed that large nutrient loads into a lake could induce a flip from a clear to a turbid state. Several economists, working in collaboration with ecologists, have used this model to produce new results for management of such lakes.[1] In particular, Brock and Starrett [4] gave a complete treatment of the optimal management of a deterministic version of a lake model. Mäler et al. [25] and Xepapadeas et al. [42] derived the resource use that would result if the lake was managed under common property. They also provided conditions under which the optimal management solution could be obtained using taxes. Wagener [41] showed that heteroclinic bifurcation[2] manifolds limit the parameter region for which Skiba points[3] occur—for one state control systems with one co-state variable. He gave a local criterion that ensures the existence of Skiba points in systems with small discount rates.

All these papers modeled thresholds using a flipping mechanism that smoothly went between a low and a high level, without jumps. In contrast, Nævdal [28] modeled optimal regulation of eutrophying lakes, fjords, and rivers in the presence of what could be called hard thresholds. He used a dichotomous function that instantaneously jumped between a high and low level when the threshold was crossed. This implied that there must be jumps in shadow prices when the threshold was trespassed. Smooth thresholds seem more appealing for at least two reasons: One convenient reason is that while the functional form is more complicated for a smooth

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[1]See Carpenter, Ludwig and Brock [7], Carpenter, Brock and Hansson [5], Mäler, Xepapadeas and de Zeeuw [25], Brock and Starrett [4], and Xepapadeas, de Zeeuw, and Mäler [42].

[2]A heteroclinic bifurcation occurs when the unstable separatrix of a saddle becomes the stable separatrix of another saddle (Hubbard and West [20]).

[3]Initial states for which trajectories going to different steady states yield the same welfare level (Skiba [38]).

threshold, jumps in variables can be avoided. They would require using heavy modeling tools. Another reason is that natural scientists, who should be better informed about the topic than economists, seem to prefer a smooth way of modeling thresholds[4].

Section 2 explains typical features of coral reefs and presents a model where algae and fish play a major role in coral reefs' dynamics. Section 3 shows how to model fishing and how uncertainty about some parameter values may affect the outcome. Section 4 models and discusses the effects of open access fisheries. Section 5 models sole ownership. Section 6 simulates both management models using a specific cost function. Section 7 contains concluding remarks.

2 The coral reef ecosystem

2.1 Typical features[5]

A typical coral reef is a colony of up to tens of thousands of tiny animals (polyps). Inside each animal lives a microscopic form of algae, the zooxanthellae, which color the corals and provide them with food through photosynthesis. In exchange, the corals contribute with food for the microscopic algae and with protection from many predators that live in the reefs. Reefs, in turn, supply a habitat for many marine species. Reefs also act as nurseries for several thousand species that can spend the rest of their lives in the oceans' open waters (Davidson [11]).

Coral reefs are known for their beauty, high biological diversity, high productivity, and complex dynamics. Their high productivity makes them indispensable to some tropical marine ecosystems and hence to local people. Coral reefs produce many goods and services, such as tourism, fish, coastal protection, and ingredients for medicines. They also sustain other ecosystems such as mangroves (Hoegh and Guldberg [17]).

Coral reef specialists generally agree that coral reefs can assume at least two stable forms: coral-dominated and algae-dominated. The algae-dominated state can eventually lead to mass coral mortality, possibly followed by depletions of reef

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[4]See Murray [27], Gurney and Nisbet [14], Scheffer [33], and Carpenter and Cottingham [6].

[5]I thank Miriam Huitric from the Beijer Institute for many discussions on coral reefs and hints about relevant literature. Any mistakes are mine.
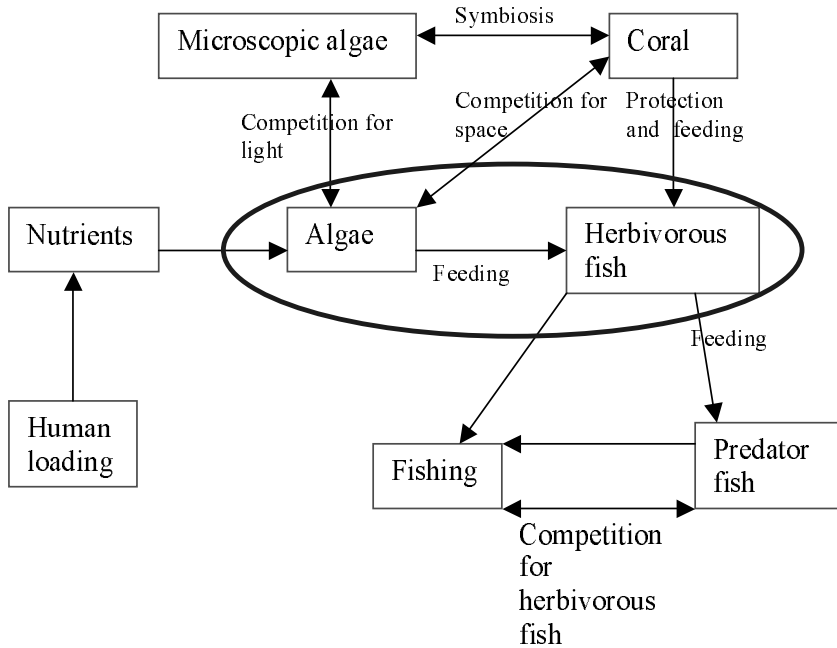
Figure 1: Coral reef model

fisheries. Physical and biological erosion may then make it difficult for the coral population to recover[6] (Done [12]). The algae-eating fish are pointed out as an important factor for regulating algae through grazing (Hughes [21]).

2.2   Modeling a coral reef

The complexity that characterizes coral reefs implies that it is difficult to model their dynamics in a simple way. Figure 1 shows a flow model of what seem to be the main interactions in a coral reef. This paper focuses on the areas that are circled. Except for fishing, the remaining parts enter as parameters.

Two differential equations build a coral reef model. They show changes in biomass of algae (A) and fish (H) at time (t), respectively. Fish play a crucial role because they feed on algae, thereby limiting their biomass. Appendix A contains

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[6]In Jamaica, for example, a combination of overfishing, damage from hurricanes, and diseases mostly threaten the corals. Latent damages due to overfishing implied that the synergistic effects of hurricanes and diseases lead to a major shift in the reef, toward an algae-dominated state (Hughes [21]).

the model developed for the purpose of this paper[7]. For computational purposes, the model is rewritten in a dimensionless form to reduce the number of parameters to those necessary for the dynamics.

Algae grow by absorbing a given load of nutrients n. In this stylized model, a load of nutrients n gives n new algae. Algae die naturally at a rate d. Fish eat algae at a rate e per fish. So the equation of motion for algae is:

$$\dot{A} = n - dA - eAH$$

Fish have a logistic growth with the growth rate normalized to 1. The fish biomass that is sustainable in absence of any predation, also called carrying capacity, is equal to the algae biomass A. The logistic term $H\left(1 - \frac{H}{A}\right)$ represents fish biomass growth.

Predators consume fish. They are usually very mobile and search for spots where prey are abundant and abandon spots where prey are scarce. A model that includes spatial aspects and predator migration between different spots would be a realistic way to represent coral reef dynamics. Such a model would also be rather complex. For simplicity, predator biomass is assumed constant in time and enters the model only through a predation rate. The effects of a variable predator population can be partly controlled by analyzing changes in predation rate.

Predation has a sigmoid form. It is low below a threshold value at which a switch occurs and predation becomes high, reaching its saturation value. When fish biomasses are small, predators spend most of the time searching for food. When the biomasses increase, the propensity to find food increases and is convex. When the threshold is realized fish are so abundant that searching for food requires little time. Rather, most time can be spent ingesting food. If fish biomasses further increase, the saturation point is reached, and time is spent ingesting food. The propensity to find food is still increasing, but it is now concave.

Let f be the rate of predation defined in appendix A. The threshold between low and high predation, also called half-saturation fish biomass, is normalized to 1. In other words, for a fish population of one unit, predators could catch half the amount of food they would have caught if they did not have to spend time searching for food. Predation can be written $\frac{fH^q}{1+H^q}$, where $q > 1$ is a constant that affects the curvature of the sigmoid function. The higher the q, the steeper the predation is around the

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threshold. At the limit, when q goes toward infinity, predation makes a discrete jump between 0 and 1 when the threshold is crossed. If $f = 0$ (no predation), there is no threshold effect in the coral reef. The equation of motion for fish is:

$$\dot{H} = H\left(1 - \frac{H}{A}\right) - \frac{fH^q}{1 + H^q}$$

Populations of algae and fish evolve over time, following the system of differential equations SYS1:

$$\dot{A} = n - dA - eAH \tag{SYS1:1}$$

$$\dot{H} = H\left(1 - \frac{H}{A}\right) - \frac{fH^q}{1 + H^q} \tag{SYS1:2}$$

Hirsh and Smale [16], Kuznetsov [24], and Takeuchi [40] presented methods to study such dynamic systems. Appendix B shows that the ecosystem may have one, two, or three interior steady states and one boundary steady state: $H = 0$, $A = \frac{n}{d}$.
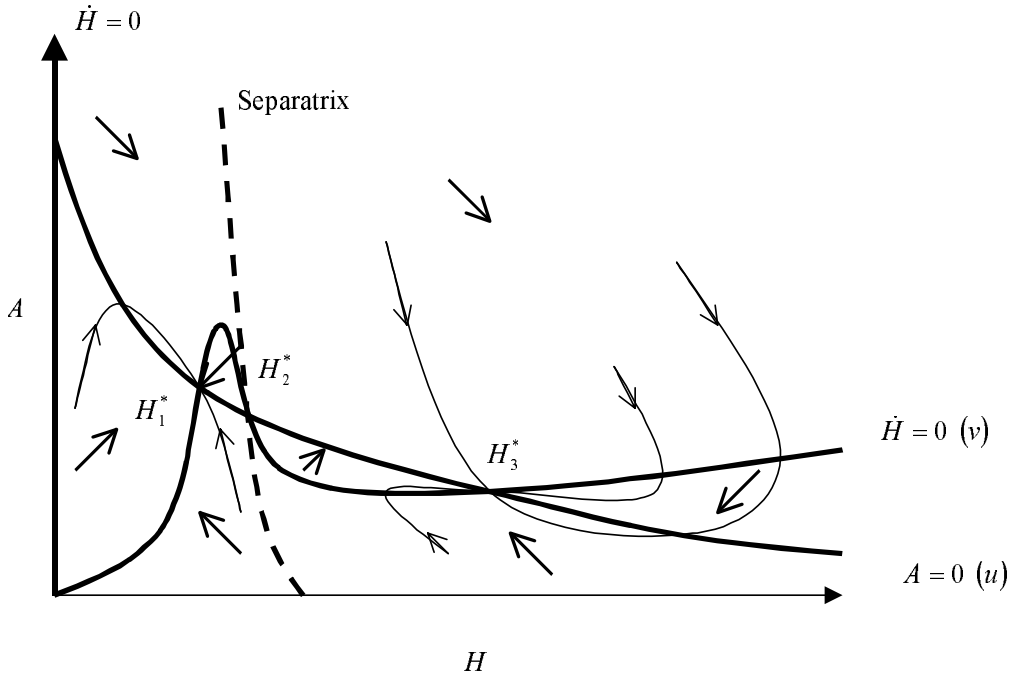

Figure 2: Phase diagram for the ecosystem

Figure 2 analyzes the system's dynamics for the case with four steady states, in a phase diagram drawn in the (H, A) plane. Let $\zeta(H) = H(1 + H^q)$ and $\xi(H) =$

$1 + H^q - fH^{q-1}$. The graphs of functions $u(H) = \frac{n}{d+eH}$ and $v(H) = \frac{\zeta(H)}{\xi(H)}$ represent points in the plane for which algae and fish biomass respectively are invariant ($\dot{A} = 0$ respectively $\dot{H} = 0$). For $H = 0$, $\dot{H} = 0$ regardless of the value of A. It is easy to see that u is monotonically increasing in n and decreasing in d and e. The function v is monotonically increasing in f and decreasing in q if $H < 1$, it otherwise increases.

The phase diagram is drawn for the parameter values in appendix D.[8] Let H_0^*, H_1^*, H_2^* and H_3^* denote the four steady states ordered in decreasing value of the sustained fish population. Steady state H_0^* is a boundary state in which fish are extinct. It is a saddle point and can only be reached from points on the vertical axes; that is, states with no fish. H_1^* and H_3^* are stable. H_1^* represents a state with many algae and few fish in contrast to H_3^*, which is a state with many fish and few algae. State H_2^* is a saddle point. A trajectory that starts from any initial point in the interior of $\mathbb{R}_+^2$ goes asymptotically toward one of the stable steady states. A curve, called the separatrix, separates the two stable steady states' basins of attraction[9] (Kuznetsov [24]). The separatrix goes through saddle point H_2^*.[10] Any initial state to the right of this curve evolves toward steady state H_3^*. Any initial state to the left of it evolves toward H_1^*. So the separatrix defines a threshold between coral-dominated and algae-dominated states. Figure 2 illustrates some trajectories and the approximate location of the separatrix.

Changes in parameter values affect the graph levels of u and v and the number of steady states. For relatively low u compared to v, only H_0^* and H_1^* remain. This occurs when the nutrient load n is relatively low or when death rate d, consumption rate e, or predation rate f are relatively high. For a relatively high u compared to v, only H_0^* and H_3^* remain. This occurs when the nutrient load n is high enough or when death rate d, consumption rate e, or predation rate f are relatively low.

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[8]Note that for some parameter values (if $f = \frac{1+H^q}{H^{q-1}}$ for some feasible value of H), the graph of $v(H)$ has discontinuities in some points; this does not seem to affect characteristics of steady states.

[9]These are the regions in space from which any starting trajectory goes asymptotically toward the same steady state.

[10]The separatrix is the stable manifold of saddle point H_2^*.

3   Effects of fishing

This paper does not consider fishing methods that affect coral or algae biomass directly. Thus fishing only enters the equation of motion for fish. Fish harvest $h(t)$ is traditionally modeled as a function of catchability coefficient η, fishing effort E, the stock of fish, the number of fishermen or vessels (K), and some constants α and β, usually both equal to 1(Munro and Scott [26]):[11]

$$h(t) = K\eta E^{\alpha} H^{\beta}$$

With $\alpha = \beta = 1$, the fish harvest is $h(t) = K\eta EH$ and the equation of motion for fish becomes:

$$\dot{H} = H\left(1 - \frac{H}{A}\right) - f\frac{H^q}{1 + H^q} - K\eta EH$$

For positive effort and catchability, fishing implies that the curve representing $\dot{H} = 0$ shifts upward. This upward shift increases in effort and catchability. Figure 3
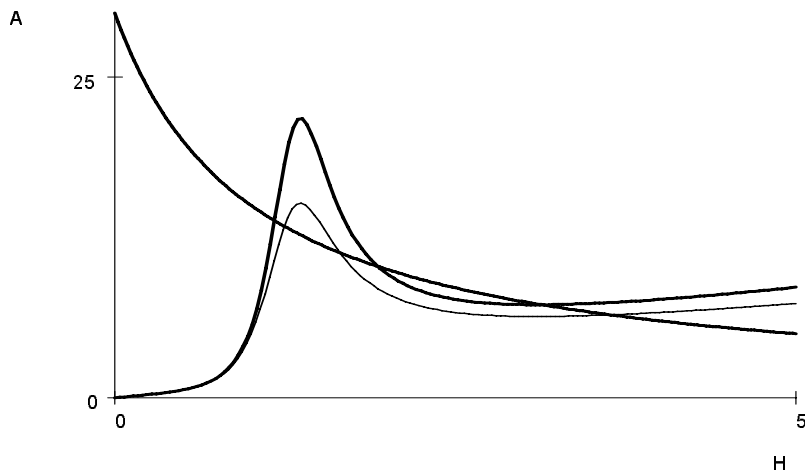

Figure 3: Effects of fishing

represents a phase diagram with fishing. The non-fishing situation is drawn as the thinnest line. This figure helps predict some potential effects of fishing.

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[11]One could also argue for modeling catchability as dependent on herbivore stocks in the ecosystem. But to allow for comparisons with more traditional fishery models, catchability is assumed constant.

- If fishing pressure is relatively low, the phase diagram that represents the fishing ecosystem is topologically equivalent[12] to the phase diagram for the ecosystem without fishing. So for most initial points, fishing implies that the ecosystem ends up in a topologically equivalent steady state. The only difference is that the steady state is slightly more algae-dominated.

- The saddle point H_2^* becomes less algae-dominated so the separatrix shifts to the right. This implies that the algae-dominated state's basin of attraction increases to the detriment of the coral-dominated state's basin. Even small changes in fishing efforts may then have large, long-term effects on the ecosystem. Suppose the sizes of algae and fish biomasses corresponded to the crossed ring in figure 4. If the fishing effort was relatively low, so that the
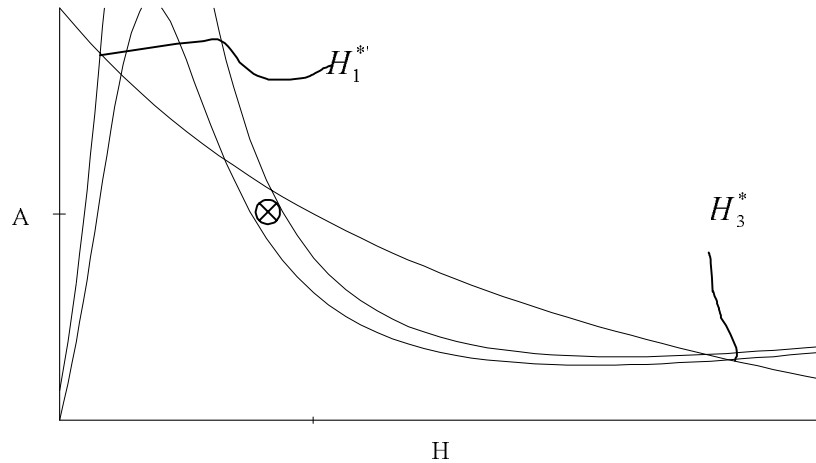

Figure 4: Flipping mechanisms

lower curve represented $\dot{H} = 0$, algae and fish biomasses would evolve toward the coral-dominated steady state and end up in H_3^*. Suppose that fishing increased so that the upper curve represented $\dot{H} = 0$. Suppose further that the system was in a state near the separatrix. The separatrix would shift to the right, the initial state ending up in the algae-dominated state $H_1^{*\prime}$'s basin of attraction. In the end the increase in fishing effort would induce a shift from coral-domination to algae-domination. Even when fishing did not cause

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[12]See Kuznetsov [24] for a definition of topologically equivalent dynamic systems.

a shift, the increase of the algae-dominated steady state's basin of attraction would imply higher flipping risks after external shocks. Such external shocks are, for example, fish disease and nutrient shortage.

- An increase in fishing efforts could have even larger effects if the harvest becomes so large that a bifurcation occurs and the coral-dominated state disappears. The only remaining stable state would be algae-dominated and would attract all trajectories with strictly positive fish populations.

These mechanisms presume a world of complete knowledge. But in the real world, complete knowledge may not be possible. There are many sources of uncertainty; assume (without loss of generality) that one parameter is uncertain, for example, consumption rate e, for which only the probability distribution is known. Uncertainty about the consumption rate implies that the level of curve $A = 0$ is unknown. Knowledge of e's probability distribution can only be used to state that there is a possible 90% chance that the u graph is found between the bold curves in figure 5. Fishing may then have different effects, depending on the initial state and
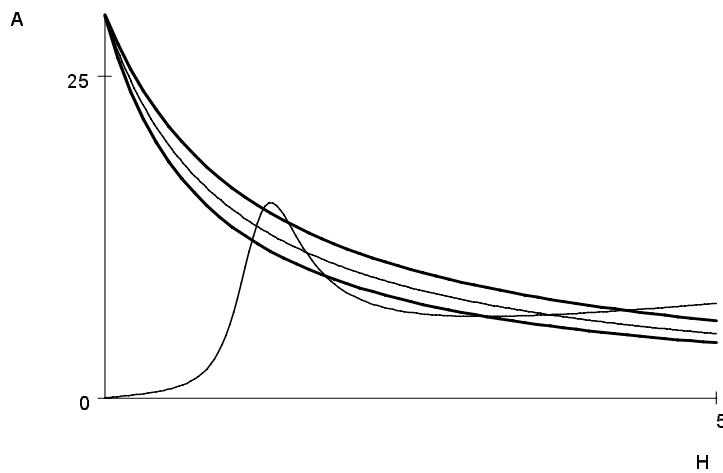

Figure 5: Effects of uncertainty

the true location of u's graph. Suppose the true location was such that it was close to the highest bold curve. Then a small harvest would only cause a slight shift in the curve representing $H = 0$ and would not affect the phase diagram's topological

properties. The system would still go toward a steady state near the no-fishing steady state, unless the initial state was very close to the separatrix to begin with. If u's graph was situated near the lowest bold curve instead, then a dramatic change could occur, even if the system was not near the separatrix to begin with. In that case, the harvest need not be very large to cause bifurcation, and there would be only one stable algae-dominated state left.

When there is uncertainty, a flip can occur in a situation that is perceived as *business as usual* and may not be observable before long after it has occurred. When the flip is observed, the intervention needed to return to the coral-dominated state's basin of attraction is much greater than if it would have been discovered earlier. If a bifurcation has occurred, returning to a coral-dominated state might not be possible unless fishing is completely prohibited and new fish are introduced. These restorations imply welfare costs for society.

To deal with parameter uncertainties, one can simulate the model with an entire set of possible parameter values. Such simulations produce the steady states' distribution, given the parameter values' distributions. This enables an opportunity to localize bifurcations and determine the risks of flipping.

Thus far, the fishing effort is exogenous. The remainder of the paper studies management models for fisheries, in which the fishing effort is endogenously determined. Even if all parameters are known, thresholds complicate the dynamics of ecosystems. The analysis focuses on the effects of the ecosystems' complexities, particularly the existence of thresholds on open access (section 4) and sole ownership (section 5).

Assume that fishermen cannot influence the market outcome and sell their harvests at a constant price p. The fishing effort E is costly and can only take values in its domain ($E \in \Xi$). The cost of fishing $C(E)$ is assumed to be increasing and convex in effort, so $C'(E) > 0$, $C''(E) > 0$. The harvesting revenue is the price multiplied by the individual harvest. So a fisherman's profit from harvesting at time t is:

$$\Pi(E, H, K) = p\eta E H - C(E)$$

4   Open access

4.1   The model

This section uses Smith [39] to analyze open access fisheries using the model developed in section 3. Assume that reef fisheries are open access. Fishermen choose the effort level to maximize their profit. The condition $p\eta H = C'(E)$ is necessary and sufficient for profit maximization, because profit is concave in fishing efforts. This means that profit maximization requires the marginal cost of effort to equal the market value of the total amount of available fish. Positive profits attract new fishermen while negative profits drive them away. By assumption, the flow of fishermen is proportional to pure profit, where $\phi > 0$ is a behavioral constant[13] for the fishery:

$$\dot{K} = \phi\left(p\eta EH - C(E)\right)$$

The equations of motion (SYS2) and the profit maximizing condition (1) characterize the open access ecosystem.

$$\dot{A} = n - dA - eAH \tag{SYS2:1}$$

$$\dot{H} = H\left(1 - \frac{H}{A}\right) - f\frac{H^q}{1 + H^q} - K\eta EH \tag{SYS2:2}$$

$$\dot{K} = \phi\left(p\eta HE - C(E)\right) \tag{SYS2:3}$$

$$p\eta H = C'(E) \tag{1}$$

With cost of effort being strictly convex, the marginal cost of effort is an invertible function. Equation (1) offers then a unique solution: the optimal fishing effort is uniquely determined for a given fish biomass. Let $E^o(H) \equiv (C')^{-1}(p\eta H)$. It can be replaced for in SYS2. This gives:

$$\dot{A} = n - dA - eAH$$

$$\dot{H} = H\left(1 - \frac{H}{A}\right) - f\frac{H^q}{1 + H^q} - K\eta E^o(H)H$$

$$\dot{K} = \phi\left(p\eta HE^o(H) - C(E^o(H))\right)$$

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[13]ϕ could also represent some function of profit. For example, a large profit would give fishermen incentives to rapidly enter the market, while a small profit would not attract them as quickly.

Let K^o, A^o and H^o be respectively the number of fishermen, and the stocks of algae and fish. Assuming $H^o \neq 0$ in steady state:

$$E^o = E^o\left(H^o\right) \tag{2}$$

$$A^o = \frac{n}{d + cH^o} \tag{3}$$

$$H^o = \frac{C\left(E^o\left(H^o\right)\right)}{p\eta E^o\left(H^o\right)} \tag{4}$$

$$K^o = \frac{1}{\eta E^o\left(H^o\right)} \left(1 - \frac{H^o}{n}\left(d + cH^o\right) - f\frac{H^{oq-1}}{1 + H^{oq}}\right) \tag{5}$$

The number of steady states in open access depends only on the fishery's cost function as stated in proposition 1.

Proposition 1 *A steady state exists if and only if the average cost is lower than the market value of the total available fish stock for some levels of fish stock while the opposite is true for other levels of fish stock. The steady state is unique if the average cost is monotonous.*

Proof. Once H^o and E^o are given, equations (3) and (5) uniquely determine the algae population and number of vessels. So the number of steady states depends on the number of positive solutions in E to equation (1) and the number of positive solutions in H to the equation (4). Convexity of costs insures that (1) has a unique solution. Thus the number of steady states depends on the number of fix points of equation (4).

This depends on the average cost of effort as a function of fish stock. Define $\overline{C} : \mathbb{R}^{++} \to \mathbb{R}^{++}, H \to \overline{C}\left(H\right) = \frac{C\left(E^o\left(H\right)\right)}{E^o\left(H\right)}$, as the average cost as a function of fish stock. Note that $\overline{C}$ is continuous by assumptions on C if fishing effort does not equal zero. It is easy to graphically verify that (4) has a fix point if and only if there are at least two different levels of fish stocks H_1 and H_2 such that $p\eta H_1 < \overline{C}\left(H_1\right)$ and $p\eta H_2 > \overline{C}\left(H_2\right)$. Moreover, if the average cost is monotonous, the fix point is obviously unique, which means that the system has a unique steady state. ∎

The predation term drives threshold effects in the model. This term appears only in equation (5) for $f \neq 0$. The case $f = 0$ corresponds to a fishery model with no threshold effects. Proposition 2 follows directly from equations (2-5).

Proposition 2 *Steady state levels of algae, fish and effort remain as if there were no threshold effects but there are fewer fishermen.*

This result is not too surprising because fishermen do not account for ecosystem dynamics in open access. Rather, they maximize profits and then decide about entering the market depending on whether the profit is positive or negative. This means that threshold effects can only affect the decisions of fishermen through changes in profits. Thus the zero profit condition implies that only the number of fishermen or vessels is affected.

4.2 Comparison with unexploited reefs

The effect of open-access fishery on the ecosystem is better understood by comparing SYS2 with the corresponding system SYS1 when there is no fishing activity. Assume
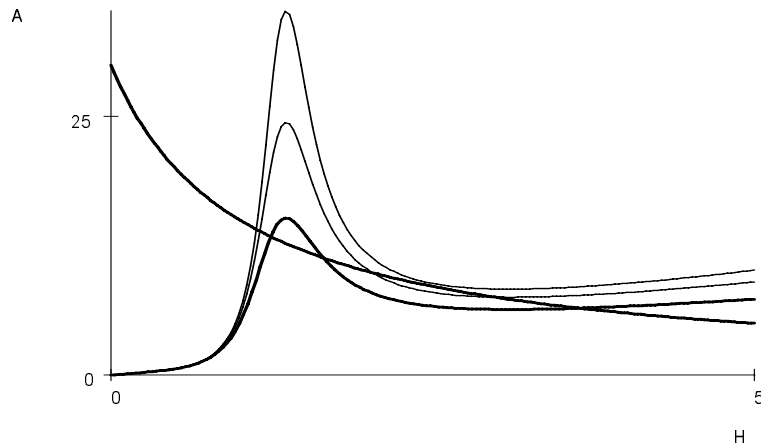
Figure 6: Fishing with different price levels for fish, $K = 10$

the same conditions as in proposition 1 so that the steady state is unique. Let $w(H) = \frac{\zeta(H)}{\xi(H) - K\eta E^o(1+H^q)}$. w's graph represents a projection of manifold $\dot{H} = 0$ for open access fishery in the (H, A)-plane. The function u's graph represents a projection of manifold $\dot{A} = 0$. A projection of manifold $\dot{K} = 0$ is a vertical line in the (H, A) plane. Assume that the predation rate is so small that $\xi(H) > 0$, that is, $f < \frac{1+H^q}{H^{q-1}}$.[14] For strictly positive levels of fish populations,

$$w(H) \; > \; v(H) \Leftrightarrow \xi(H) > K\eta E^o(1+H^q)$$
$$w(H) \; < \; 0 < v(H) \Leftrightarrow \xi(H) < K\eta E^o(1+H^q)$$

[14]If this assumption did not hold we would have $v(H) < 0$ on some interval where herbivore population would decrease.

Note that in intervals where $\xi(H) < K\eta E^o(1 + H^q)$, fish populations continuously decrease. If this occurs when H is small, fish may become depleted in the long run. Note that there is a discontinuity for values of H such that $\xi(H) = K\eta E^o(1 + H^q)$, corresponding to vertical asymptotes in w's graph.

Figure 6 represents functions u, v, and w. The thin curves represent a price level of 0.2 (lower curve) and 0.3 (higher curve). The number of fishermen (vessels) is arbitrarily set to $K = 10$. The fat curve represents the corresponding situation when there is no fishing. The dynamics in the (H, A) plane are similar in open access and in the unexploited ecosystem. Figure 7 draws an equivalent diagram for $K = 15$,
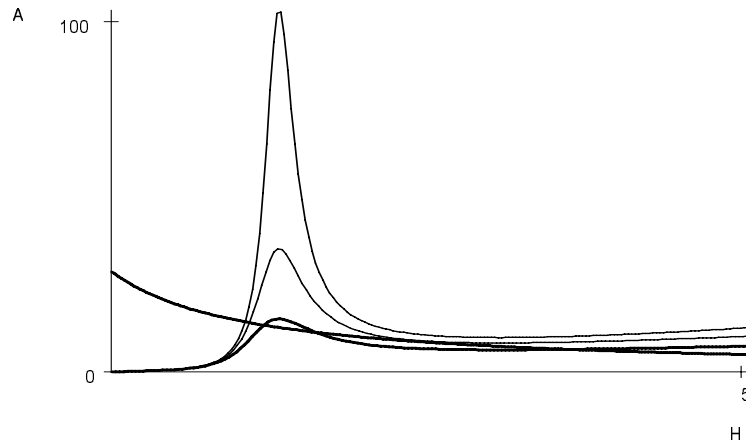
Figure 7: Fishing with different price levels for fish, $K = 15$

showing that the level of w increases with the number of fishermen.

A steady state occurs at the point where u, w and the vertical line that represents $\dot{K} = 0$ in plane (H, A) intersect. Typically, there is a maximum of one such steady state in a plane, but there might be several such planes depending on whether or not the cost function meets the assumptions in proposition 1. Whether such a steady state is algae-dominated or coral-dominated depends on the cost function, which determines where $\dot{K} = 0$ intersect with the other curves.

In any case, the steady states are more algae-dominated compared to the un-exploited ecosystem because for any positive number of vessels K, the w graph lies either above the v graph or in the negative part of space. When proposition 1 holds, the only steady-state candidate is more algae-dominated than any other

algae-dominated state in the unexploited ecosystem.

5 Sole ownership

5.1 The model

Suppose a sole profit-maximizing fisherman owned a coral reef fishery: $K = 1$. She controlled the fish biomass levels through a fishing effort E, which was her unique control variable. Recall that harvest is $h(t) = E\eta H$ for $K = 1$.

Assume further that the owner was knowledgeable about coral reef dynamics and had an infinite horizon (powerful but usual, convenient assumptions). She wanted to maximize the present value of discounted profits from fishing given the reef dynamics. Algae and fish biomasses cannot be negative. The problem is:

$$\max_{E \in \Xi} \int_0^\infty (pE\eta H - C(E)) e^{-\rho t} dt \tag{6}$$

$$\text{s.t } \dot{A} = n - dA - eAH \tag{7}$$

$$\dot{H} = H\left(1 - \frac{H}{A}\right) - f\frac{H^q}{1 + H^q} - E\eta H \tag{8}$$

$$A \geq 0, H \geq 0, h = E\eta H \tag{9}$$

Pontryagin's maximum principle helps solve this problem. Note that $\limsup_{A \to 0} \dot{A} = n$ and $\limsup_{H \to 0} \dot{H} = 0$, so the non-negativity constraints are probably not binding. Arrow and Kurz [1], Hestenes [15], and Seierstad and Sydsæter [37] developed methods to solve such problems when there are constraints on state variables. Crépin [9] shows in appendix how such constraints can be treated in a similar problem where there are binding constraints. To simplify this problem's solution, assume that no constraint is ever binding. The presentation below follows Seierstad and Sydsæter. Let $\mathcal{H}(E, A, H, \lambda)$ be the current-value Hamiltonian and $\lambda \equiv \lambda(t)$ represent a vector of shadow prices:

$$\mathcal{H}(E, A, H, \lambda) = pE\eta H - C(E) \tag{10}$$

$$+\lambda_A (n - dA - eAH) + \lambda_H \left(H\left(1 - \frac{H}{A}\right) - f\frac{H^q}{1 + H^q} - E\eta H\right)$$

The necessary conditions for E^* to be optimal are:

- For v.e.[15] $t \in \mathbb{R}^+$, $E^* \equiv E^*(t)$ maximizes $\mathcal{H}(E, A^*, H^*, \lambda)$ for all $E \in \Xi$. Assume that at least one effort level is optimal and yields a positive discounted sum of all future profit.[16] Given that the Hamiltonian is concave in E, E^* is such a maximum if and only if:

$$p\eta H - C'(E^*) - \lambda_H \eta H \leq 0 \tag{11}$$

This remains with equality for an interior solution, which means that optimal harvest is such that net marginal benefits from harvesting equal marginal costs. Marginal benefits consist of the market value of the available fish stock $(p\eta H)$. Marginal costs are the sum of the marginal cost of effort $C'(E^*)$ and the total value of the available fish stock if it remains in the ecosystem $(\lambda_H \eta H)$.

- λ is continuous and has a derivative v.e. given by

$$\dot{\lambda}_A(t) = \lambda_A \rho + \lambda_A(d + eH) - \lambda_H \frac{H^2}{A^2} \tag{12}$$

$$\dot{\lambda}_H(t) = \lambda_H \rho - pE\eta + \lambda_A eA \tag{13}$$
$$-\lambda_H \left(1 - \frac{2H}{A} - fq\frac{H^{q-1}}{(1+H^q)^2} - E\eta\right)$$

These conditions are also sufficient, if for all admissible $j(t) \equiv (H(t), A(t))^T$:

- $\liminf\limits_{t \to +\infty} \lambda(t)(j(t) - j^*(t)) \geq 0$

- $\widehat{\mathcal{H}}(A, H, \lambda) = \max\limits_{E \in \Xi} \mathcal{H}(E, A, H, \lambda)$ is concave in (A, H).

Let $\widehat{\mathcal{H}}_{HH}$ be the maximized Hamiltonian's second derivative with regard to H. Appendix C shows that $\widehat{\mathcal{H}}(A, H, \lambda)$ is concave if and only if conditions (14) and (15) remain:

$$\lambda_H \geq 0 \tag{14}$$

$$\widehat{\mathcal{H}}_{HH} \leq -A^3 \frac{\left(2\lambda_H \frac{H}{A^2} - \lambda_A e\right)^2}{2\lambda_H H^2} \tag{15}$$

---

[15] Following Seierstad and Sydsæter, let v.e. represent *virtually every* or *virtually everywhere*, which includes all points except a finite, countable number.

[16] $\int_0^\infty (pE^*\eta H - C(E^*)) e^{-\rho t} dt > 0$ for some E^*.

With the cost of effort being strictly convex, the marginal cost of effort is an invertible function. Equation (11) then has a unique solution and the optimal fishing effort is uniquely determined for a given fish biomass:

$$E^* \left(H, \lambda_H \right) \equiv \left(C' \right)^{-1} \left(\eta H \left(p - \lambda_H \right) \right) \tag{16}$$

Because C' is monotonously increasing, E^* is also monotonously increasing in η, H, and p and decreasing in λ_H. The equations of motion (SYS3) of the modified dynamic Hamiltonian system are:

$$\dot{A} \; = \; n - dA - eAH \tag{SYS3:1}$$

$$\dot{H} \; = \; H \left(1 - \frac{H}{A} \right) - f \frac{H^q}{1 + H^q} - E^* \left(H, \lambda_H \right) \eta H \tag{SYS3:2}$$

$$\dot{\lambda}_A \; = \; \lambda_A \rho + \lambda_A \left(d + eH \right) - \lambda_H \frac{H^2}{A^2} \tag{SYS3:3}$$

$$\dot{\lambda}_H \; = \; \lambda_H \left(\rho - 1 + \frac{2H}{A} + fq \frac{H^{q-1}}{\left(1 + H^q \right)^2} \right) + \lambda_A eA - \left(p - \lambda_H \right) E^* \left(H, \lambda_H \right) \eta \tag{SYS3:4}$$

It is challenging to determine how many potential steady states this system may have. One can easily see that the partial equation system (SYS3:1, SYS3:3) has a unique steady state in (A, λ_A) expressed as a function of H and λ_H. Replacing this solution in equations SYS3:2 and SYS3:4 gives a two-dimensional system. Normally this is difficult to solve because both equations involve polynomials of higher order in H (and possibly in λ_H, depending on the cost function). So there will typically be several values of H, which solve the system SYS3. Each of these corresponds to a steady state of SYS3. Numerical simulations (section 6) give better ideas about the number and characteristics of such steady states.

If there is a steady state, then it is such that $\dot{A} = \dot{H} = \dot{\lambda}_A = \dot{\lambda}_H = 0$; obviously λ_A and λ_H must have the same sign, otherwise $\dot{\lambda}_A \neq 0$. The concavity conditions require that $\lambda_H > 0$ so both shadow prices are most probably positive in an optimal steady state's neighborhood. This leads to proposition 3:

Proposition 3 *Both algae and fish have a positive shadow price near an optimal steady state.*

5.2 Comparisons with open access and unexploited ecosystems

How does the exploited ecosystem behave compared with the natural ecosystem SYS1? Methods for analyzing such dynamic systems can be found in Brock and Malliaris [3]. They present a series of stability results, which are difficult to apply here because the ecosystem equations are rather complicated. But it is easy to show that the saddle-path property proven in Kurz [23] still holds true even when the ecosystem equations are not concave. This is done in Crépin [10].

A proper phase diagram for the system would require four dimensions, but one can imagine projections in the algae/fish plane. Recall the functions $u\left(H\right)$, $v\left(H\right)$, and $w\left(H\right)$ representing manifolds $\dot{A} = 0$ and $\dot{H} = 0$ in the unexploited ecosystem (SYS1) and in open access (SYS2) respectively (see sections 2.2 and 4.2). These functions can represent steady algae and fish biomasses in a four-dimensional phase diagram. They are two-dimensional manifolds in a four-dimensional space because the dynamics of algae and fish biomasses are uncoupled from the dynamics of shadow prices. What happens in the (H, A) plane is independent of the shadow prices in SYS1 and SYS2.

For sole ownership, the $\dot{A} = 0$ manifold is also a graphic representation of $u\left(H\right)$. Representing the $\dot{H} = 0$ manifold is more challenging because it depends on shadow prices; for that reason, it is four-dimensional. Let z be the level of algae stocks such that $\dot{H} = 0$ for given fish stocks and shadow prices. Using previous notations from section 2.2:

$$z\left(A, H, \dot{\lambda}\right) = \frac{\zeta\left(H\right)}{\xi\left(H\right) - E^{*}\left(H, \lambda_{H}\left(A, H, \dot{\lambda}\right)\right) \eta\left(1 + H^{q}\right)}$$

implicitly defines z and $\lambda_{H}\left(A, H, \dot{\lambda}\right)$ solves the partial equation system (SYS3:3-SYS3:4). The levels of algae and fish biomasses in a sole-owner managed coral reef depend on the optimal effort level and on the difference between market and shadow prices for fish. If the market price is higher than the shadow price, a steady level of fish population requires a larger algae population than in an unexploited ecosystem. This means that if SYS3 has several steady states, the one that is more algae-dominated and the one that is less algae-dominated will both become more algae-dominated compared to corresponding steady states in the unexploited

ecosystem. If the market price is lower than the shadow price, the opposite is true, which may result in a negative fishing effort. If the market price for fish is low, the owner may want to implant or insert new fish and abstain from fishing for a period of time to secure future opportunities.

Comparison with the ecosystem in open access involves comparing $KE^o(H)$ with $E^*(H, \lambda_H)$. Recall that $K > 1$ and $(C')^{-1}$ increases monotonously because C' does. This means that unless λ_H is very large and negative, $K(C')^{-1}(p\eta H) > (C')^{-1}(\eta H(p - \lambda_H))$ so $KE^o(H) > E^*(H, \lambda_H)$. For that reason, z is typically found below w if the shadow price for fish is positive or not too negative. When concavity conditions are verified, z is always below w. So under *usual* circumstances, such as when fish have a positive value in the ecosystem, the optimal steady level for fish stocks is found above the corresponding level in open access.

Compared to more traditional fishery models, the threshold term enters SYS3:2 and SYS3:4, so it should affect the steady state levels and the number of feasible steady states.

6   Simulations

The systems are simulated with an ad hoc cost function: $C(E) = aE^2 + F$, where a is a positive constant, and F is a fixed cost. The parameter values used for benchmark simulation are in appendix D. With this specific cost function, the optimal effort in open access is $E^o(H) = \frac{p\eta H}{2a}$ and SYS2 becomes:

$$\dot{A} = n - dA - eAH \tag{SYS2:1}$$

$$\dot{H} = H\left(1 - \frac{H}{A}\right) - f\frac{H^q}{1 + H^q} - K\frac{p(\eta H)^2}{2a} \tag{SYS2:2}$$

$$\dot{K} = \phi\left(\frac{(p\eta H)^2}{4a} - F\right) \tag{SYS2:3}$$

The optimal effort in sole ownership is $E^*(H, \lambda_H) = \frac{(p - \lambda_H)\eta H}{2a}$ and SYS3 becomes:

$$\dot{A} = n - dA - eAH \tag{SYS3:1}$$

$$\dot{H} = H\left(1 - \frac{H}{A}\right) - f\frac{H^q}{1 + H^q} - \frac{(p - \lambda_H)(\eta H)^2}{2a} \tag{SYS3:2}$$

$$\dot{\lambda}_A = \lambda_A \rho + \lambda_A \left(d + eH \right) - \lambda_H \frac{H^2}{A^2} \tag{SYS3:3}$$

$$\dot{\lambda}_H = \lambda_H \left(\rho - 1 + \frac{2H}{A} + fq\frac{H^{q-1}}{\left(1+H^q\right)^2} \right) + \lambda_A eA - \frac{\left(p - \lambda_H\right)^2 \eta^2 H}{2a} \tag{SYS3:4}$$

SYS2's and SYS3's steady states were simulated using MATHCAD[17]. Appendix E contains a table with the values of all steady states, given the parameter values in appendix D. The sole-owner ecosystem (SYS3) has four feasible steady states: $S3.1 - S3.4$. The number of steady states varies with parameter values. All feasible steady states are saddle points. Changes in the fixed cost F do not affect the sole-owner system, but parameter a does. When a increases, fish biomass tends to increase and for $a > 0.05$, two new steady states appear. The unique open-access steady state $S2$ greatly depends on cost variables. If the fixed cost is large enough (about 0.17, given other parameter values), fishermen do not find it profitable to fish, which means that there are no feasible open-access steady states. The same is true when a is larger than about 8.28.

This shows that the cost function affects both management models in different ways. Also note that $S2$ is more algae-dominated than any of the feasible interior steady states in sole ownership, which are more algae-dominated than the corresponding states in the natural ecosystem. This verifies the expected results from comparisons in sections 4 and 5.

MATHCAD was used to simulate trajectories in the sole-ownership case. Using the method of reverse shooting[18], the stable manifold for each steady state could be derived for the sole-owner ecosystem. This is pictured in figure 8.

Simulations[19] using the method developed in Beyn, Pampel, and Semmler [2] indicate the existence of Skiba points in SYS3. Skiba points are threshold points at which trajectories toward two different steady states yield the same welfare. Such a point is, for example, somewhere around $P = (0.1, 3.57)$. Starting from P and following the optimal path toward $S3.1$ or $S3.3$ yields the same welfare of 0.033 units. For all initial points that were tested, trajectories toward $S3.2$ yielded a

---

[17]MATHCAD is a computer program that can perform numeric calculations or find general symbolic solutions to mathematical problems.

[18]See Judd [22] for details on this method.

[19]The program codes in MATLAB can be acquired from the author
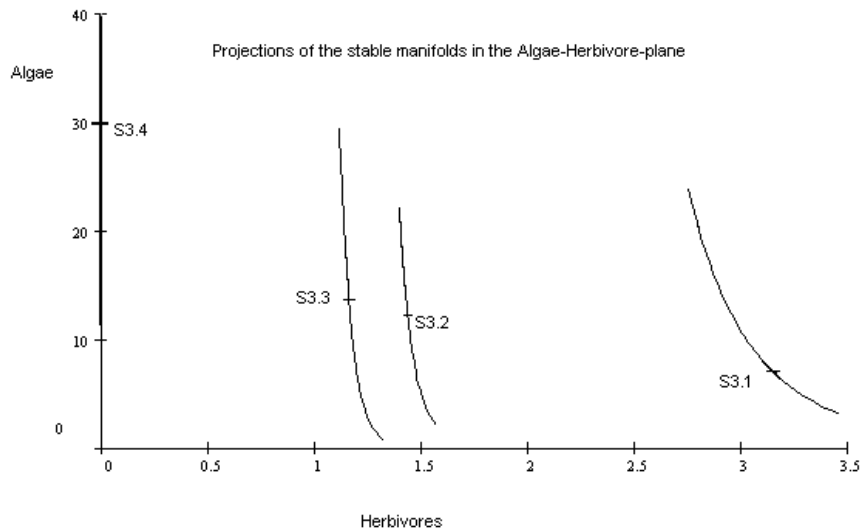
Figure 8: Stable manifolds in SYS3

negative expected welfare. This indicates that $S3.2$ may never be an optimal steady state. Simulations of trajectories toward $S3.4$ are difficult to test because three of the variables are equal to zero. This steady state may also be suboptimal because once the stable manifold is reached, from then on, social welfare is equal to zero.

The sets of all Skiba points form this system's Skiba manifolds. There is one Skiba manifold for each pair of optimal steady states. Only some of these Skiba points have been located; the task of locating them all would be too tedious. According to Beyn et al. [2], the Skiba manifolds' dimension should equal the number of state variables. So a Skiba manifold should be of dimension 2.[20] To approximate the Skiba manifolds, one can use the initial state variables as continuation parameters.

The parameters chosen for the simulation are improvised and have nothing to do with the empirical data. Meanwhile, if the model's general features are correct, use of ad hoc parameters still gives qualitative results, which should be reliable for the case studied. For the natural ecosystem and the open-access case, it is relatively easy to check how the parameter values affect the curves when varied, which may lead to bifurcations.

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[20]Except when there are more than two optimal trajectories from a Skiba point or when the dimension of the stable manifold differs from the number of state variables (Beyn et al [2, p. 266]).

In the case of sole ownership, the results' sensibility to variations of economic parameters was studied. This showed the occurrence of bifurcations for every parameter tested. For some parameter values, steady states may appear or disappear. In general, higher parameter values lead to the disappearance of some steady states. The saddle point property seemed more robust to changes in parameter values, except for variations in effort and discount rate. For discount rates higher than about 0.4, the steady state S3.2 had three positive eigenvalues. For discount rates higher than 1, S3.4 also had three positive eigenvalues. For high catchability ($\eta \geq 2$), steady state S3.3 became less stable (three eigenvalues with positive real parts).

7   Concluding remarks

This paper shows that accounting for threshold effects substantially changes the dynamics and steady states of coral reefs in open access and sole ownership.

Open-access fisheries may typically cause a bifurcation toward a unique algae-dominated steady state. This state can support fewer fishermen than if there were no threshold effects. Traditional results on the inefficiency of open access are reinforced. In the real world, there is open access to many coral reef fisheries. In the context of this paper's results, the multiple concerns about eutrophication and shifting coral reefs are not surprising. They reflect that the open-access coral reef fisheries may be approaching their long-term steady state, which is algae-dominated compared to natural equilibria.

The results for sole ownership of the reefs' fisheries differ substantially from those obtained in traditional fishery models. Instead of a unique steady state, threshold effects imply that the controlled system can have several steady states. Depending on the initial state, the optimal path leads toward different optimal states. There are also some initial states for which several paths are optimal. This implies that even an optimized coral reef can shift between different states, such as after an external shock like disease or a hurricane.

The possibility of multiple steady states implies that policy recommendations for sole-owner fishermen cannot rely on simple marginal rules such as those calculated in traditional fishery models. Owners must calculate all future benefits from fisheries to rule out the paths toward steady states that are suboptimal. This is difficult in an uncertain and changing world. Meanwhile, failing to do so implies that owners face

the risk of choosing the wrong path, which could result in an even more detrimental steady state.

These results explain the need for new policy instruments in fisheries. Safe minimum standards, including fishing quotas, have been used; but as Munro and Scott [26] pointed out, this typically leads to excess capacity in the fishing fleet if there is open access. The task for policy makers is much harder than previous results indicated. They must find some way to solve the inefficiency problems related not only to open access but also to the difficulty in finding the best path when several steady states may be optimal.

It may take time before a shift is discovered. This is worrisome because even if the short-term effects of a shift are small, the long-term effects can be quite large and even irreversible. For these reasons, it is challenging to try and detect flips early to make available as many management opportunities as possible. This explains the need for work on new ways to treat such problems.

The results obtained in this paper depend on the model studied. The paper examines the effects of parameter uncertainty. In particular, mistakes about parameter values may be serious because parameter changes can cause bifurcations. This means that even if the model is correct, bad parameter estimates may lead to qualitatively misleading policy recommendations. In addition to that, the formulation of the model is a major uncertainty. Many of the mechanisms that govern coral reefs are still unknown to scientists, so the model used may have missed some aspects, such as an important category of variables or some important movement of motions. We need to better learn how to cope with this kind of uncertainty. An important task for natural scientists is to recognize key features in ecosystems and to be able to model them as simply as possible so that their models can become useful for natural resource management.

A   Dynamic model of coral reefs

These two differential equations may represent the dynamics in a coral reef:

$$
\begin{aligned}
\dot{x} &= N - Dx - Cxy \\
\dot{y} &= Gy\left(1 - \frac{y}{Kx}\right) - F\frac{y^q}{Y^q + y^q}
\end{aligned}
\qquad (17)
$$

where x and y are the populations of algae and fish, respectively, N is a load of nutrients, D is the natural death rate, and C is the rate of consumption by fish. The fish population has a growth rate G and carrying capacity K per unit of algae. F is the maximum average number of fish that predators, not including humans, catch per unit of time. Y is the half-saturation fish population and q is a positive constant that affects the sigmoid function's curvature.

Following Segel [36], I scaled the system to obtain a simpler dimensionless form, which was easier to analyze. Let x_u, y_u and t_u be the units in which algae, fish, and time are measured and let $A = \frac{x}{x_u}$, $H = \frac{y}{y_u}$ and $\tau = \frac{t}{t_u}$ be dimensionless populations of algae, fish, and time, respectively.

$$
\begin{aligned}
\dot{A} &= \frac{\partial A}{\partial \tau} = \frac{\frac{\partial x}{\partial t}}{x_u} t_u = t_u \left(\frac{N}{x_u} - DA - CAy_u H \right) \\
\dot{H} &= \frac{\partial H}{\partial \tau} = \frac{\frac{\partial y}{\partial t}}{y_u} t_u = t_u \left(GH \left(1 - \frac{Hy_u}{KAx_u} \right) - \frac{F}{y_u} \frac{H^q}{\left(\frac{Y}{y_u} \right)^q + H^q} \right)
\end{aligned}
$$

Choose $x_u = \frac{y_u}{K}, y_u = Y,\ t_u = \frac{1}{G}$ to find:

$$
\begin{aligned}
\dot{A} &= \frac{1}{G} \left(\frac{NK}{Y} - DA - CYAH \right) \\
\dot{H} &= H \left(1 - \frac{H}{A} \right) - \frac{F}{YG} \frac{H^q}{1 + H^q}
\end{aligned}
$$

Now let $n \equiv \frac{NK}{YG}, d \equiv \frac{D}{G}, e \equiv \frac{CY}{G}$, and $f \equiv \frac{F}{YG}$ and we obtain a dimensionless system with the dynamic properties similar to the original system (17):

$$
\begin{aligned}
\dot{A} &= (n - dA - eAH) & \text{(SYS1)} \\
\dot{H} &= H \left(1 - \frac{H}{A} \right) - f \frac{H^q}{1 + H^q}
\end{aligned}
$$

B Number of interior steady states

A steady state of SYS1 must solve

$$
\begin{aligned}
0 &= n - dA - eAH \\
0 &= H \left(1 - \frac{H}{A} \right) - f \frac{H^q}{1 + H^q}
\end{aligned}
$$

This equation system has one boundary steady state, $\left(\frac{n}{d}, 0 \right)$. If fish biomass is non-negative, $A^* = \frac{n}{d + eH^*}$ is the unique interior steady state of the algae biomass. Given

A^*, the fish biomass in an interior steady state solves: $1 - \frac{H}{n}(d + eH) = f\frac{H^{q-1}}{1+H^q}$. So the steady state fish biomass is the value(s) of H at the intersection(s) between the curves $\kappa(H) = 1 - \frac{H}{n}(d + eH)$ and $\gamma(H) = f\frac{H^{q-1}}{1+H^q}$. The parameters are all strictly positive, so κ is a concave function of H, and the graph of κ is a concave parabola with the maximum at $H = -\frac{d}{2e} < 0$. Only positive values of H are feasible so the relevant maximum is at $H = 0$, which gives the intercept on the vertical axis: $\kappa(0) = 1$. The curve cuts the horizontal axis when $H = \frac{1}{2e}\left(-d + \sqrt{(d^2 + 4cn)}\right)$. The graph of κ is plotted in figure 9 for $e = d = n = 1$.
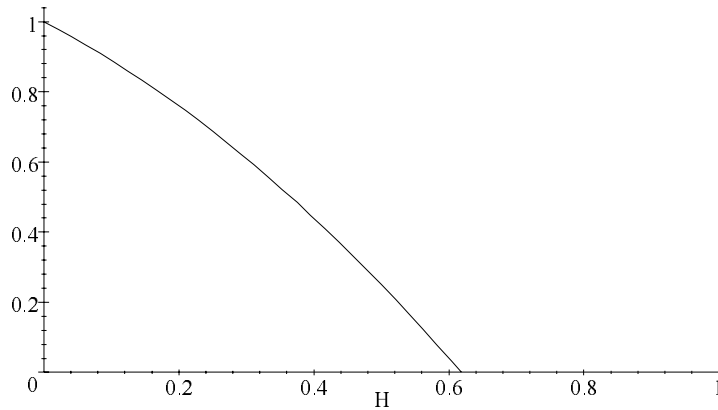
Figure 9: Graph of κ

Computation of the first and second derivatives of γ gives

$$\gamma'(H) = f\frac{H^q(q - 1 - H^q)}{H^2(1 + H^q)^2} \tag{18}$$

$$\gamma''(H) = f\frac{(q^2 - 3q + 2)H^q - (q^2 + 3q - 4)H^{2q} + 2H^{3q}}{H^3(1 + H^q)^3}$$

So γ has a maximum of one non-negative interior extremum at $H = (q - 1)^{\frac{1}{q}}$. Suppose $q \geq 2$, the function γ increases from 0 until it reaches its maximum at $Y = (q - 1)^{\frac{1}{q}}$ (where $\gamma\left((q - 1)^{\frac{1}{q}}\right) = \frac{(q-1)^{\frac{q-1}{q}}}{q}$) and starts to decrease toward the horizontal axis, which is an asymptote ($\lim\limits_{H \to +\infty} \gamma(H) = \lim\limits_{H \to +\infty} f\frac{1}{\frac{1}{H^{q-1}} + H} = 0^+$).

At most, the curve has two inflection points at

$H_1 = \left(\frac{1}{4}q^2 + \frac{3}{4}q - 1 - \frac{1}{4}q\sqrt{(q^2 + 6q - 7)}\right)^{\frac{1}{q}}$ and

$H_2 = \left(\frac{1}{4}q^2 + \frac{3}{4}q - 1 + \frac{1}{4}q\sqrt{(q^2 + 6q - 7)}\right)^{\frac{1}{q}}$.

For $q = 3$, the curve has two inflection points: $H_1 = \frac{1}{2}\sqrt[3]{\left(28 - 12\sqrt{5}\right)}$ and $H_2 = \frac{1}{2}\sqrt[3]{\left(28 + 12\sqrt{5}\right)}$. For $q = 2$, the curve has one inflection point at $H = \sqrt{3}$. Note that when q becomes large, the two inflection points approach 1: H_1 from below and H_2 from above, which yield a steeper peak around the maximum at $\widehat{H} = (q-1)^{\frac{1}{q}}$. The graph of γ is plotted in figure 10 for $f = 1$ and $q = 1$ (thin
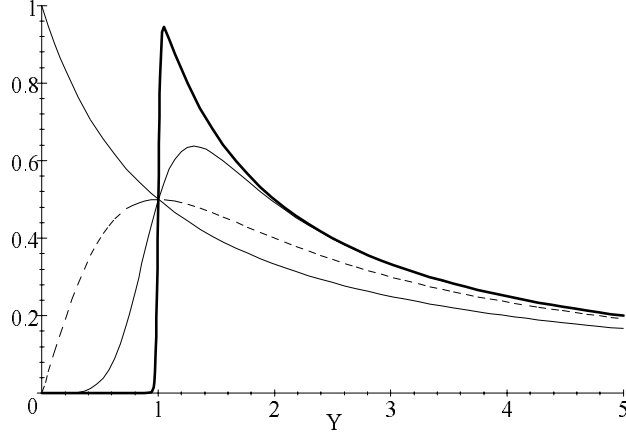
Figure 10: Graph of γ for several values of q

decreasing curve), $q = 2$ (dotted curve), $q = 6$ (thin convex-concave curve), and $q = 100$ (bold curve).

The characteristics of both functions imply that for $q > 1$, they can intersect once, twice, or three times, depending on the parameter values. This gives one, two, or three interior steady states.

C Concavity conditions

$\widehat{\mathcal{H}}(A, H, \lambda, \mu) \equiv \mathcal{H}(E^*, A, H, \lambda, \mu)$ is concave in A and H if $(-1)^r \Delta_r \geq 0$ for $r = 1, 2$ where Δ_r are the principal minors of order r in the Hessian for $\widehat{\mathcal{H}}(A, H, \lambda, \mu)$. (See Nikaido [29]). $E^*(H, \lambda_H) = (C')^{-1}(\eta H (p - \lambda_H))$ so

$$
\begin{aligned}
\widehat{\mathcal{H}}(A, H, \lambda, \mu) \equiv{} & (p - \lambda_H)(C')^{-1}(\eta H (p - \lambda_H)) \eta H - C\left((C')^{-1}(\eta H (p - \lambda_H))\right) \\
& + \lambda_A (n - dA - eAH) + \lambda_H \left(H\left(1 - \frac{H}{A}\right) - f\frac{H^q}{1 + H^q}\right)
\end{aligned}
$$

So the corresponding Hessian is:

$$
\begin{pmatrix}
\widehat{\mathcal{H}}_{AA} & \widehat{\mathcal{H}}_{AH} \\
\widehat{\mathcal{H}}_{HA} & \widehat{\mathcal{H}}_{HH}
\end{pmatrix}
$$
where $\widehat{\mathcal{H}}_{AH} = \widehat{\mathcal{H}}_{HA} = 2\lambda_H \frac{H}{A^2} - \lambda_A e$ and $\widehat{\mathcal{H}}_{AA} = -2\lambda_H \frac{H^2}{A^3}$.

The conditions for a concave Hamiltonian amount to:

- $\lambda_H \geq 0$

- $-2\lambda_H \frac{H^2}{A^3} \widehat{\mathcal{H}}_{HH} - \left(2\lambda_H \frac{H}{A^2} - \lambda_A e\right)^2 \geq 0$

So even if the shadow price of fish is positive, the second concavity condition is not necessarily satisfied unless $\widehat{\mathcal{H}}_{HH}$ is negative and large enough. These conditions can be rewritten:

$$
\begin{aligned}
\lambda_H &\geq 0 \\
\widehat{\mathcal{H}}_{HH} &\leq -A^3 \frac{\left(2\lambda_H \frac{H}{A^2} - \lambda_A e\right)^2}{2\lambda_H H^2}
\end{aligned}
$$

D   Parameters

d	1	algae death rate (per year)
e	1	share of algae eaten (per fish per year)
f	1.6	rate of predation
n	30	nutrient loading
q	4	curvature of the predation
p	0.1	price
ρ	0.02	discount rate
η	0.5	catchability
a	0.5	cost parameter
F	0.001	fixed cost

E Steady states

The feasible steady states (positive populations) are in bold.

System	name	A	H	λ_A	λ_H	K
SYS1		-5.335	-6.623			
	H_3^*	**6.466**	**3.64**			
	H_2^*	**11.315**	**1.651**			
	H_1^*	**13.378**	**1.243**			
	H_0^*	**30**	**0**			
SYS2	$S2$	**15.836**	**0.894**			**10.976**
		284.164	-0.89443			-76.082
SYS3		$-1.431E+3$	-1.021	$-3.795E-3$	7.212	
		-104.155	-1.288	$-3.422E-3$	5.997	
		-4.975	-7.03	$1.861E-3$	$-5.602E-3$	
	$S3.1$	**7.243**	**3.142**	**9.44E$-$4**	**0.021**	
	$S3.2$	**12.307**	**1.438**	**8.43E$-$4**	**0.152**	
	$S3.3$	**13.883**	**1.161**	**1.69E$-$5**	**5.272E$-$3**	
	$S3.4$	**30**	**0**	**0**	**0**	
		34.881	-0.14	$5.29E-4$	28.925	

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(li) This paper was presented at the Fourth Toulouse Conference on Environment and Resource Economics on "Property Rights, Institutions and Management of Environmental and Natural Resources", organised by Fondazione Eni Enrico Mattei, IDEI and INRA and sponsored by MATE, Toulouse, May 3-4, 2001

(lii) This paper was presented at the International Conference on "Economic Valuation of Environmental Goods", organised by Fondazione Eni Enrico Mattei in cooperation with CORILA, Venice, May 11, 2001

(liii) This paper was circulated at the International Conference on "Climate Policy – Do We Need a New Approach?", jointly organised by Fondazione Eni Enrico Mattei, Stanford University and Venice International University, Isola di San Servolo, Venice, September 6-8, 2001

(liv) This paper was presented at the Seventh Meeting of the Coalition Theory Network organised by the Fondazione Eni Enrico Mattei and the CORE, Université Catholique de Louvain, Venice, Italy, January 11-12, 2002

(lv) This paper was presented at the First Workshop of the Concerted Action on Tradable Emission Permits (CATEP) organised by the Fondazione Eni Enrico Mattei, Venice, Italy, December 3-4, 2001

(lvi) This paper was presented at the ESF EURESCO Conference on Environmental Policy in a Global Economy "The International Dimension of Environmental Policy", organised with the collaboration of the Fondazione Eni Enrico Mattei , Acquafredda di Maratea, October 6-11, 2001

(lvii) This paper was presented at the First Workshop of "CFEWE – Carbon Flows between Eastern and Western Europe", organised by the Fondazione Eni Enrico Mattei and Zentrum fur Europaische Integrationsforschung (ZEI), Milan, July 5-6, 2001

(lviii) This paper was presented at the Workshop on "Game Practice and the Environment", jointly organised by Università del Piemonte Orientale and Fondazione Eni Enrico Mattei, Alessandria, April 12-13, 2002

(lix) This paper was presented at the ENGIME Workshop on "Mapping Diversity", Leuven, May 16-17, 2002

(lx) This paper was presented at the EuroConference on "Auctions and Market Design: Theory, Evidence and Applications", organised by the Fondazione Eni Enrico Mattei, Milan, September 26-28, 2002

(lxi) This paper was presented at the Eighth Meeting of the Coalition Theory Network organised by the GREQAM, Aix-en-Provence, France, January 24-25, 2003

(lxii) This paper was presented at the ENGIME Workshop on "Communication across Cultures in Multicultural Cities", The Hague, November 7-8, 2002

(lxiii) This paper was presented at the ENGIME Workshop on "Social dynamics and conflicts in multicultural cities", Milan, March 20-21, 2003

(lxiv) This paper was presented at the International Conference on "Theoretical Topics in Ecological Economics", organised by the Abdus Salam International Centre for Theoretical Physics - ICTP, the Beijer International Institute of Ecological Economics, and Fondazione Eni Enrico Mattei – FEEM Trieste, February 10-21, 2003

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