

# The Beijer Institute of Ecological Economics

## DISCUSSION PAPER

Beijer Discussion Paper Series No. 185

## Using fast and slow processes to manage coral reef series with threshold effects

Anne-Sophie Crépin. 2004.

# Using fast and slow processes to manage coral reef fisheries with threshold effects

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February 27, 2004

## Abstract

Coral reefs may naturally flip between coral-dominated and algae-dominated states, when species' stocks trespass some threshold levels. This has consequences for fisheries management, which are analyzed here. This article shows how fishing can affect the location of ecosystem thresholds and provoke an ecosystem flip. In particular, the interplay between fast (algae and fish) and slow (coral) variables has an important role in the dynamics of these flips. The analysis of slow and fast processes gives insights about the mechanisms underlying an ecosystem flip. The article shows also how these insights could be useful to detect thresholds and find new variables to control the reef's dynamics.

Keywords: multiple steady states, fisheries management, non-convexities, slow and fast processes.

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\*Thanks to Karl-Göran Mäler, Stephen Carpenter, Miriam Huitric, and Anastasios Xepapadeas for many discussions and suggestions about the paper. Grants from FORMAS are gratefully acknowledged.

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# 1 Introduction

Sometimes, algae that seem to come out of nowhere invade coral reefs. If they shade the corals for too long, they may kill them and the previously diverse coral reef becomes dominated by algae and few other species. Such changes occur rapidly and are called ecosystem shifts. Recent research<sup>1</sup> shows that ecosystems like lakes, forests or savannas can experience similar shifts.

Ecosystem shifts affect the services that people derive from the reefs and hence people's well being. A coral reef produces, for example, much less fish and tourist sites after an algae invasion. These ecosystems are difficult to manage because marginal changes in management methods could have huge effects on the ecosystem, hence on future management opportunities. Due to multiple steady states, several strategy paths may fulfill marginal conditions derived using optimal control theory or dynamic programming, but some of them may be suboptimal. Following such a path would lead to a much-undesired outcome.<sup>2</sup> The best management paths may depend on previous actions so to avoid huge mistakes we must calculate all future costs and benefits of each alternative path. Such calculations require a lot of information about the future, which highlights the need to come up with alternative ways of handling this kind of resource management problems in practice. Recent research discusses many alternative strategies to manage complex adaptive ecosystems. Unfortunately few of them seem well suited to manage ecosystems with thresholds.

Ecosystem shifts seem to be linked to their resilience—their capacity to cope with changes in the environment. Resilience often derives from slow variables, such as reservoirs of soil nutrients, heterogeneity of ecosystems on a landscape, or variety of genotypes and species. (Folke et al. 2002). This article highlights the role of slow variables that trigger shifts between coral-dominated and algae-dominated states. This produces new insights on the coral reef dynamics and also on management opportunities for such ecosystems.

The technique used here is called geometric singular perturbation theory (Fenichel 1979). Similar techniques are often used in ecology (See for example Ludwig, Jones and Holling 1978). Milik and coauthors (1996) seems to be the only example in economics. With this method they line up the characteristics of their system that would characterize the beginning of a sustainability loss. Knowing this enabled

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<sup>1</sup>See for example Crépin 2002, Dasgupta and Mäler 2003 and the thresholds database of the Resilience Alliance, <http://www.resalliance.org>.

<sup>2</sup>See Brock and Starrett 2003, Mäler, Xepapadeas and de Zeeuw 2003, Crépin 2002 and 2003, Wagener 2003, Dasgupta and Mäler 2003.

them to react before a crash occurred.

Section 2 describes typical characteristics of coral reefs and proposes a rather general way to model their dynamics. Singular perturbation theory is used to highlight the reefs' fast and slow processes and the mechanisms that trigger shifts between alternative states. Section 3 shows how fishing affects the threshold location. Section 4 derives more specific results on optimal fisheries. In particular it shows that even optimized fisheries make the reef more prone to shifts. This section also shows that similar to the natural ecosystem, changes in the ecosystem dynamics occurred before the system has shifted to a less favorable state. Section 5 discusses how a manager can use the insights from the previous sections to better manage the coral reefs and maybe get warning signals that the system is about to shift. Section 6 concludes.

## 2 Coral reef ecosystems

A typical coral reef is made up of slowly growing coral colonies — animals that consist of up to tens of thousands of tiny polyps. (Davidson 1998). The combination of fast and slow processes characterizes coral reef dynamics: algae and fish populations are fast variables that adapt quickly to changes. In contrast, coral can be viewed as a slow variable.

Consider a coral reef at time  $t$  with non-negative populations of algae ( $x(t)$ ), herbivores<sup>3</sup> ( $y(t)$ ) and coral ( $z(t)$ ). Fish have a logistic growth with growth rate  $R_y$  and carrying capacity  $Kx$  that depends linearly on the amount of algae available.<sup>4</sup> There are abundant indications that *transient predators* — who come to spots where prey is abundant and leave spots where prey is scarce — play an important role in the mortality of herbivores.<sup>5</sup> Following Turchin (2003), a *Holling type III functional response* (Holling 1959) models such behavior: predation is low below a threshold value at which a switch occurs and predation becomes high and reaches a saturation value.<sup>6</sup> Let  $\frac{F}{z}$  be the maximum average number of fish that predators, not including humans, catch per unit of time. This is a decreasing function of coral because corals provide shelter against predators. Let  $Y$  be the threshold between low and high predation<sup>7</sup>. Predation can be written  $\frac{F}{z} \frac{y^\theta}{Y^\theta + y^\theta}$ , where  $\theta > 1$  indicates how sharp the

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<sup>3</sup>Algae-eating fish.

<sup>4</sup>This way of modeling food availability is discussed for example in Turchin (2003 p.99).

<sup>5</sup>Indications of that kind of behavior are discussed for example in Roberts (1995), Jennings and Polunin (1997) and Stewart and Jones (2000).

<sup>6</sup>So the herbivore equation fully include predator dynamics.

<sup>7</sup>It is also called the half-saturation herbivore population: for a herbivore population of size  $Y$ , predators could catch half as many herbivores as they would have caught if herbivores were

threshold is between high and low predation; a higher  $\theta$  corresponding to a sharper threshold. When  $\theta$  is infinitely large, predation makes a discrete jump between 0 and  $\frac{F}{z}$  when the threshold is crossed. The equation of motion for fish is:

$$\frac{dy}{dt} = R_y y \left(1 - \frac{y}{Kx}\right) - \frac{F}{z} \frac{y^\theta}{Y^\theta + y^\theta} \quad (1)$$

Coral and algae compete for light. This is modeled using a simplified version of the competition model for floating and submerged aquatic plants, which Scheffer with coauthors (2003) proposed. In the stylized model constructed here, the negative impact of coral on algae goes only via fish consumption. A load of nutrients  $N$  gives  $N$  new algae. Algae die naturally at a rate  $D$ . Fish consume algae at a rate  $P$  per fish. So the equation of motion for algae is:

$$\frac{dx}{dt} = N - Dx - Pxy \quad (2)$$

Algae shade the coral but they do not affect the coral's intake of nutrient very much. Let  $R_z$  be the coral growth rate,  $\frac{1}{I}$  is the density of coral cover at which its growth rate becomes reduced by 50%,  $W$  is light attenuation in the water column,  $S$  is the shading coefficient by algae and  $L$  is the coral loss:

$$\dot{z} = R_z \frac{z}{1 + Iz + Sx + W} - Lz \quad (3)$$

Following Segel (1972), the system (1-3) was rewritten in a dimensionless form, which has the same dynamic properties and is easier to analyze. Let  $u_x$ ,  $u_y$  and  $u_z$  be the units in which algae, fish and coral are measured. Let  $A \equiv \frac{x}{u_x}$ ,  $H \equiv \frac{y}{u_y}$ ,  $C \equiv \frac{z}{u_z}$ ,  $n = \frac{YN}{R_y K}$ ,  $d = \frac{D}{R_y}$ ,  $p = \frac{PY}{R_y}$ ,  $\varepsilon r = \frac{R_z}{R_y}$ ,  $i = \frac{IF}{Y R_y}$ ,  $s = \frac{SK}{Y}$ ,  $w = 1 + W$  and  $\varepsilon l = \frac{L}{R_y}$ . We obtain the system (4a-4c):

$$\frac{dA}{dt} = n - dA - eAH \quad (4a)$$

$$\frac{dH}{dt} = H \left(1 - \frac{H}{A}\right) - \frac{1}{C} \frac{H^\theta}{1 + H^\theta} \quad (4b)$$

$$\frac{dC}{dt} = \varepsilon r \frac{C}{iC + sA + w} - \varepsilon l C \quad (4c)$$

$\varepsilon$  is a small ( $0 < \varepsilon \ll 1$ ) perturbation parameter that highlights the difference in the velocity between the system's equations. (4a-4c) is expressed in the scale of the fast variable: variations in coral biomass are very small compared to variations

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unlimited.

in the other variables. Rescaling (4a-4c) by  $t \rightarrow \tau\varepsilon$  yields instead the system in the scale of the slow variable:

$$\varepsilon \frac{dA}{d\tau} = n - dA - eAH \quad (5a)$$

$$\varepsilon \frac{dH}{d\tau} = H \left( 1 - \frac{H}{A} \right) - \frac{1}{C} \frac{H^\theta}{1 + H^\theta} \quad (5b)$$

$$\frac{dC}{d\tau} = r \frac{C}{iC + sA + w} - lC \quad (5c)$$

In this form, which is in the standard form of singular perturbation theory, it is obvious that unless the right hand side of (5a:5b) is large,  $A$  and  $H$  evolve much faster than  $C$ . For  $\varepsilon > 0$ , both systems are equivalent to SYS but in the limit  $\varepsilon \rightarrow 0$  we obtain two essentially different systems: the fast system and the slow system (see Table 1):

Table 1: Fast and slow systems	
Fast	Slow
$\frac{dA}{dt} = n - dA - eAH$	$0 = n - dA - eAH$
$\frac{dH}{dt} = H \left( 1 - \frac{H}{A} \right) - \frac{1}{C} \frac{H^\theta}{1 + H^\theta}$	$0 = H \left( 1 - \frac{H}{A} \right) - \frac{1}{C} \frac{H^\theta}{1 + H^\theta}$
$\frac{dC}{dt} = 0$	$\frac{dC}{d\tau} = r \frac{C}{iC + sA + w} - lC$

The phase diagrams of these two subsystems have limited validity but studying them separately and putting the solutions together may give a good global picture of what happens. Ludwig, Jones and Holling (1978) used a similar technique to study budworm outbreaks in spruce forests.

## 2.1 The fast processes

The graphs of functions  $u(H) = \frac{n}{d+eH}$  and  $v(H)|_C = \frac{H(1+H^\theta)}{1+H^\theta - \frac{H^{\theta-1}}{C}}$  represent points in the plane for which algae and fish biomass respectively are invariant ( $\frac{dA}{dt} = 0$  respectively  $\frac{dH}{dt} = 0$ ). For  $H = 0$ ,  $\frac{dH}{dt} = 0$  regardless of the value of  $A$ . It is easy to verify that  $u$  is continuously decreasing and convex;  $u(0) = \frac{n}{d}$  and  $\lim_{H \rightarrow +\infty} u(H) = 0$ .

If  $C$  is large one can show<sup>8</sup> that  $v$  is increasing in  $H$  until it reaches a local maximum and then decreases to a local minimum before it starts increase again for large values of  $H$ . If  $C$  is small (for some values of  $H$  we have  $1 + H^\theta - \frac{H^{\theta-1}}{C} < 0$ ),  $v$  has two vertical asymptotes: it is increasing and convex before the first asymptote. Between the asymptotes,  $v$  is negative and concave and after the second asymptote,  $v$  decreases to a local minimum and then increases again.

<sup>8</sup>See mathematical appendix B for the intuition for the shape of  $v$ .

This means that in both cases  $u$  and  $v$  may intersect 2 or 4 times depending on their location.<sup>9</sup> Figure 1 shows the possible outline for the fast processes with

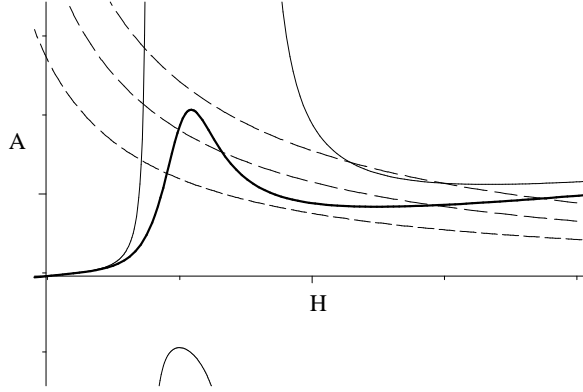


Figure 1: Alternative locations of  $u$  and  $v$ .

alternative locations of  $v$  in plain and  $u$  in dashed. The fat plain curve represents a large coral reef biomass, the thin one a small. Note that the case with only one stable coral dominated steady state is only possible if  $C$  is large (fat curve intersecting once with the highest dotted curve in figure 1). Figure 2 pictures the phase diagram for the case with four steady states and relatively high  $C$ . The cases with 2 steady states are straightforward to analyze and are not represented here.

Let  $H_0^*$ ,  $H_1^*$ ,  $H_2^*$  and  $H_3^*$  denote the four steady states ordered in decreasing value of the sustained fish population.  $H_0^*$  is a boundary state in which fish are extinct. We can verify graphically that it is a saddle point and can only be reached from points on the vertical axes: states with no fish. We can also verify graphically that  $H_1^*$  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 curve, the *separatrix*, separates the two stable steady states' *basins of attraction* — i.e. the regions in space from which any starting trajectory goes asymptotically toward the same steady state (Kuznetsov 1995). The separatrix goes through saddle point  $H_2^*$  and constitutes here the stable manifold of  $H_2^*$ . Any initial state to the right (left) of this curve evolves toward steady state  $H_3^*$  ( $H_1^*$ ). So the separatrix defines a threshold between coral-dominated and algae-dominated states. Figure 2 illustrates some trajectories (thin curves with arrows) and the approximate location of the separatrix (fat dashed curve).

<sup>9</sup>Of course at the bifurcation point they intersect in 2 points and are tangent to each other in a third point.



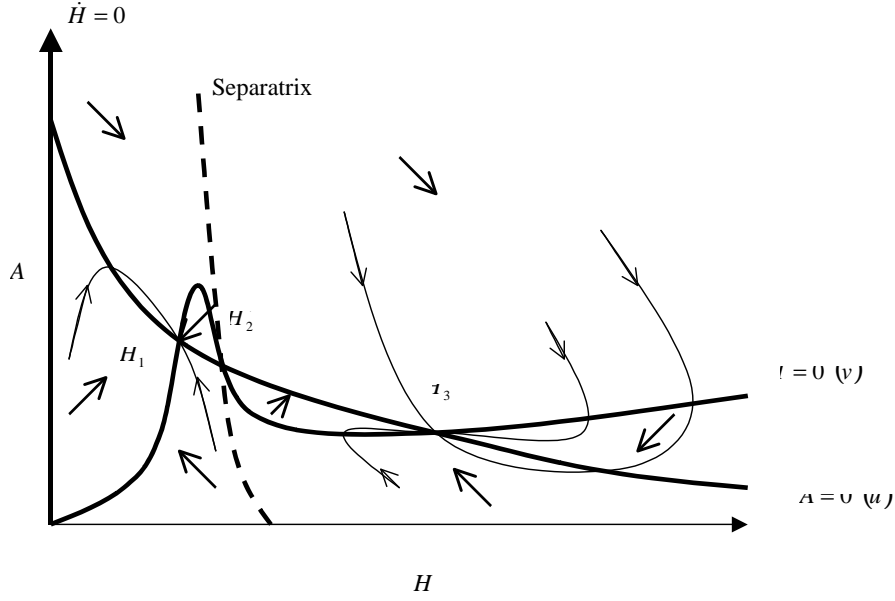


Figure 2: Phase diagram for the ecosystem

Changes in parameter values affect the levels of the graphs of  $u$  and  $v$  and hence the number of steady states. For relatively low (high)  $u$  compared to  $v$ , only  $H_0^*$  and  $H_1^*$  ( $H_3^*$ ) remain. This occurs when nutrient load  $n$  or coral biomass  $C$  are relatively low (high), or when death rate  $d$  or consumption rate  $e$  are relatively high (low). When there are only two steady states, the interior state is the only stable state.

## 2.2 The slow processes

In the time scale of the coral, algae and fish are in steady state and only coral change following the coral equation. In steady state  $C = 0$  or  $C = \frac{1}{i} (\frac{r}{l} - sA - w)$  so the interior coral steady state is a linear decreasing function of algae  $A$ . Let  $\Gamma$  represent the graph of this straight line. The interior steady state disappears when  $A \geq \frac{r-wl}{sl} \equiv \bar{A}$ . The maximum coral biomass is  $C^{\max} = \frac{1}{i} (\frac{r}{l} - w)$ . One can also verify that the interior steady state is stable whereas the boundary state  $C = 0$  is unstable.

Let the ecosystem start in  $H_3^*$ , a unique interior steady state and let  $C$  decrease along  $\Gamma$  so that  $v$  shifts upwards. For small changes in  $C$  the system tracks the steady state  $H_3^*$ , which becomes gradually more algae-dominated. Eventually for some value of  $C \equiv \bar{C}$ , two new steady states,  $H_1^*$  and  $H_2^*$ , appear but the system

remains around  $H_3^*$ . For  $C$  even smaller ( $\equiv \underline{C}$ ),  $H_2^*$  and  $H_3^*$  merge and disappear and the system heads towards  $H_1^*$  instead.

Suppose now that  $C$  started to increase again, then  $H_2^*$  and  $H_3^*$  would reappear but because the system was near  $H_1^*$  it would remain there even for  $C \in [\underline{C}, \overline{C}]$ ! We would need  $C$  to increase back to  $\overline{C}$  for the system to head back towards  $H_3^*$ . This phenomenon, called *hysteresis*, occurs in lakes too — see Brock and Starrett (2003) or Wagener (2003). Figure 3 illustrates the bifurcation points  $\overline{C}$  and  $\underline{C}$ . The lower full curve represents  $v(H)|_{\overline{C}}$  and the upper full curve  $v(H)|_{\underline{C}}$ .

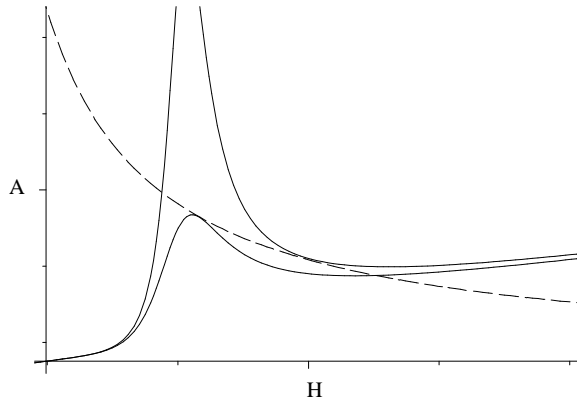


Figure 3: Threshold coral biomasses

Figure 4 summarizes coral dynamics showing the steady state level of coral as a function of algae, and the number and nature of the possible corresponding steady states for the fast variables.

### 3 The 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. A positive harvest term  $h^{10}$  represents fish harvest. The equation of motion for fish is then:

$$\frac{dH}{dt} = H \left( 1 - \frac{H}{A} \right) - \frac{1}{C} \frac{H^\theta}{1 + H^\theta} - h$$

For positive harvest, fishing implies that the curve representing  $\frac{dH}{dt} = 0$ , now called  $w(H) = \frac{H^2(1+H^\theta)}{(H-h)(1+H^\theta) - \frac{1}{C}H^\theta}$ , is always situated above  $v$ . The larger the harvest,

<sup>10</sup>See e.g. Clark. One could also model fishing as a function of effort and some catchability coefficient but this would complicate the model without giving much new insight.

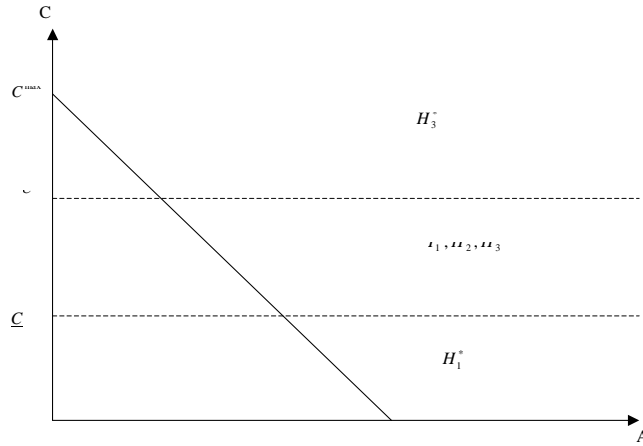


Figure 4: Coral biomass as a function of algae

the higher above  $w$  is. Figure 5 represents a phase diagram of the fast processes with fishing. The non-fishing situation is drawn as the thinnest curves. The directions of motion are the same as without fishing.

This figure helps predict potential effects of fishing. If fishing pressure is relatively low, the phase diagrams with and without fishing are topologically equivalent<sup>11</sup>. So for most initial points, the ecosystem would end up in a topologically equivalent but more algae-dominated steady state. The separatrix would shift to the right and the algae-dominated state's basin of attraction increase. An increase in fishing may also cause a bifurcation because  $w$  shifts upwards so that  $H_3^*$ , the coral-dominated state, may disappear.<sup>12</sup> The only remaining stable state would be algae-dominated and would attract all trajectories with strictly positive fish populations.

What are then the long-term effects on the coral? Consider a steady state with high coral biomass  $C^*$ , low algae biomass and high fish population ( $H_3^*$ ) and introduce fishing. This results in a shift from the  $v$  curve to the  $w$  curve so the short-term steady state becomes more algae-dominated. More algae harm corals and  $C^*$  decreases, so herbivores becomes more vulnerable to predation, which results in an even more algae-dominated equilibrium. If this *feedback* effect is large, even little fishing may result in a bifurcation and a flip towards an algae-dominated reef. Hysteresis effects observed in section 2.2 imply then that harvest must decrease substantially to recover a coral-dominated state.

<sup>11</sup>See Kuznetsov (Kuznetsov 1995) for a definition of topologically equivalent dynamic systems.

<sup>12</sup>To simplify notation the steady states are called the same as in the non fishing situation.

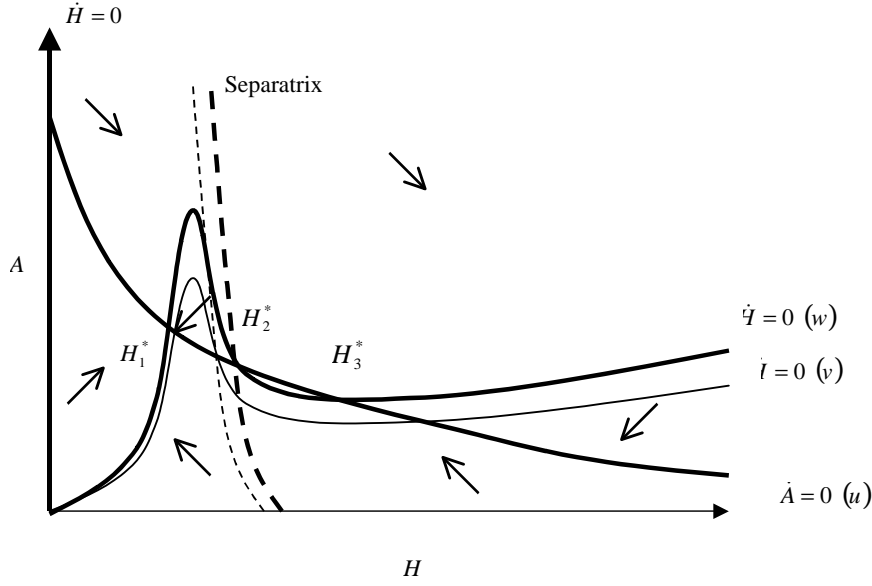


Figure 5: The effects of fishing

To get an idea of potential harvest sizes assume that algae biomass adjusts instantaneously to changes in the fish biomass in the short run. This means that we can replace for steady state algae biomass in the fish equation and solve for steady state harvest as a function of fish stocks:

$$h(H) = H \left( 1 - \frac{H(d + eH)}{n} \right) - \frac{1}{C} \frac{H^\theta}{1 + H^\theta}$$

Appendix C shows that for relatively high and relatively low coral biomasses,  $h$  is concave with a unique maximum as figure 6's highest and lowest curve illustrate. Lower coral biomasses imply lower curves. For intermediate coral biomasses, a second lower peak appears at low value of fish biomass. As coral decreases further the high fish biomass peak becomes lower than the low fish biomass peak. For very low values of coral only the low peak remains.

Figure 7 shows a double-peaked potential harvest curve with the thin arrows representing the direction of motion of fish biomass. Harvest below the curve increases fish stocks and harvest above decreases fish stocks. If harvest is represented by the fat straight line parallel to the  $H$  axes starting with a high fish biomass, the steady state would then be in  $H_3^*$ . If harvest increased marginally so that the harvest line would shift upward in the direction of the fat arrow, then the ecosystem would flip and the only equilibrium harvest left would be algae-dominated  $H_1^*$ .

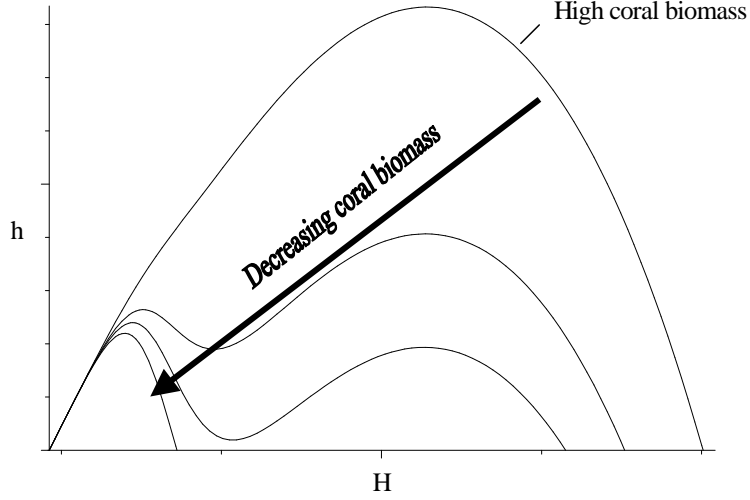


Figure 6: Potential harvest as a function of fish stock

Thus far, fishing is exogenous. The remainder of the paper considers endogenous harvest.

## 4 An optimally managed coral reef

Consider rational social planners who are knowledgeable of coral reefs' dynamics and have infinite time horizon. They seek to maximize social welfare by maximizing the present value of discounted utilities from harvesting herbivores given the ecosystem's dynamics. Assume that the utility ( $U$ ) derived from coral reef services is additively separable so that  $U(h, A, H, C) = U^h(h) + U^e(A, H, C)$ , where  $U^h$  represent the utility of harvest and  $U^e$  represents the utility derived from coral reef species. The problem to solve is:

$$\max_h \int_0^{\infty} U(h, A, H, C) e^{-\rho t} dt \quad (6)$$

$$s.t. \quad \frac{dA}{dt} = n - dA - eAH \quad (7)$$

$$\frac{dH}{dt} = H \left( 1 - \frac{H}{A} \right) - \frac{1}{C} \frac{H^\theta}{1 + H^\theta} - h \quad (8)$$

$$\frac{dC}{dt} = \varepsilon \left( r \frac{C}{iC + sA + w} - lC \right) \quad (9)$$

$$A \geq 0, H \geq 0, C \geq 0 \quad (10)$$

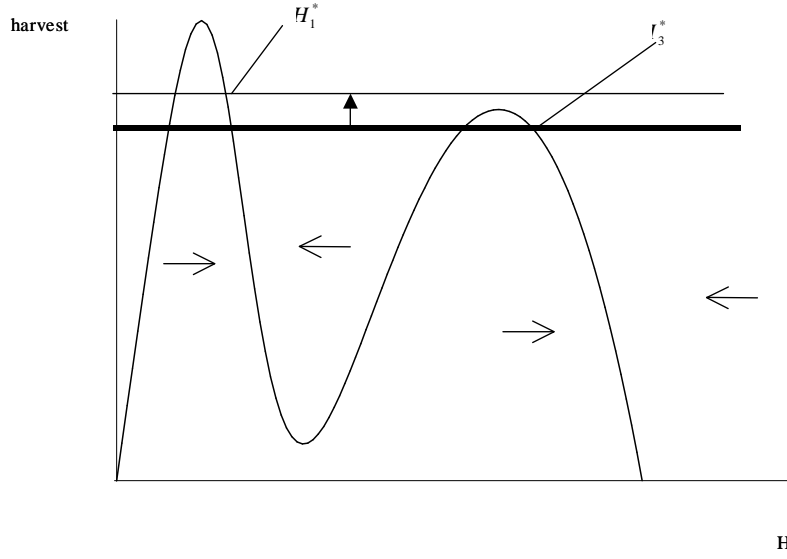


Figure 7: Harvest dynamics

Define the current value Hamiltonian ( $\mathcal{H}$ ) using  $\lambda_A$ ,  $\lambda_H$  and  $\lambda_C$  as shadow prices for algae, fish and coral stocks respectively:

$$\begin{aligned} \mathcal{H}(A, H, C, h, \lambda) = & U(h, A, H, C) + \lambda_A(n - dA - eAH) \\ & + \lambda_H \left( H \left( 1 - \frac{H}{A} \right) - \frac{1}{C} \frac{H^\theta}{1 + H^\theta} - h \right) \\ & + \lambda_C \varepsilon \left( r \frac{C}{iC + sA + w} - lC \right) \end{aligned}$$

Pontryagin's maximum principle states that the necessary condition for an optimal harvest and the equation of motion for herbivore shadow price are

$$\begin{aligned} \frac{dU^h}{dh} & \geq \lambda_H \\ \frac{d\lambda_H}{dt} & = \lambda_A eA - \lambda_H \left( 1 - \frac{2H}{A} - \frac{1}{C} \frac{\theta H^{\theta-1}}{(1 + H^\theta)^2} - \rho \right) - \frac{\partial U^e}{\partial H} \end{aligned}$$

Assuming an interior solution and replacing for optimal harvest, Pontryagin's necessary conditions for an optimal harvest form a six-dimensional dynamic system (11).

$$\begin{aligned} \frac{dA}{dt} & = n - dA - eAH \\ \frac{dH}{dt} & = H \left( 1 - \frac{H}{A} \right) - \frac{1}{C} \frac{H^\theta}{1 + H^\theta} - h \end{aligned} \tag{11}$$

$$\begin{aligned}
\frac{dC}{dt} &= \varepsilon \left( r \frac{C}{iC + sA + w} - lC \right) \\
\frac{d\lambda_A}{dt} &= \lambda_A (\rho + d + eH) - \frac{dU^h}{dh} \frac{H^2}{A^2} + \lambda_C \frac{\varepsilon r C s}{(iC + sA + w)^2} - \frac{\partial U^e}{\partial A} \\
\frac{dh}{dt} &= \frac{1}{\frac{d^2 U^h}{dh^2}} \left( \lambda_A e A - \frac{dU^h}{dh} \left( 1 - \rho - \frac{2H}{A} - \frac{1}{C} \frac{\theta H^{\theta-1}}{(1+H^\theta)^2} \right) - \frac{\partial U^e}{\partial H} \right) \\
\frac{d\lambda_C}{dt} &= \lambda_C \left( \rho - \frac{\varepsilon r (sA + w)}{(iC + sA + w)^2} + \varepsilon l \right) - \frac{dU^h}{dh} \left( \frac{1}{C^2} \frac{H^\theta}{1+H^\theta} \right) - \frac{\partial U^e}{\partial C}
\end{aligned}$$

#### 4.1 The fast variables dynamics

In the short run  $\varepsilon \rightarrow 0$  implying that coral is in steady state and the shadow price for coral does not affect the other variables so the managed coral reef follows the dynamics of system (12):

$$\begin{aligned}
\frac{dA}{dt} &= n - dA - eAH & (12) \\
\frac{dH}{dt} &= H \left( 1 - \frac{H}{A} \right) - \frac{1}{C} \frac{H^\theta}{1+H^\theta} - h \\
\frac{d\lambda_A}{dt} &= \lambda_A (\rho + d + eH) - \frac{dU^h}{dh} \frac{H^2}{A^2} - \frac{\partial U^e}{\partial A} \\
\frac{dh}{dt} &= \frac{1}{\frac{d^2 U^h}{dh^2}} \left( \lambda_A e A - \frac{dU^h}{dh} \left( 1 - \rho - \frac{2H}{A} - \frac{1}{C} \frac{\theta H^{\theta-1}}{(1+H^\theta)^2} \right) - \frac{\partial U^e}{\partial H} \right)
\end{aligned}$$

Appendix D shows that under the assumption that utility doesn't depend on algae and fish biomasses ( $\frac{\partial U^e}{\partial A} = \frac{\partial U^e}{\partial H} = 0$ )<sup>13</sup>, this controlled ecosystem may have 0, 1 or 3 steady states depending on parameter values and on the level of coral reef biomass. The number of steady states and the levels of fish, algae and harvest depend on natural parameters only, not on the utility function. The shadow price for algae is the only variable that depends on utility, through a term involving the marginal utility of harvest. If this assumption did not hold, the number of steady states would depend on  $\frac{\partial U^e}{\partial A}$  and  $\frac{\partial U^e}{\partial H}$ . Appendix E verifies the classical result that steady states of the system are either saddle points or totally unstable.

<sup>13</sup>This assumption is reasonable because the fish that are valuable for harvest are not necessarily the fish that are valuable for contemplation in the coral reef. Also it should not be too restrictive to assume that algae do not have any value per se, their only value could very well be as a necessary component for the ecosystem to work.

## 4.2 The slow variables dynamics

To account for long run dynamics only, the system (13) is rewritten using a new time unit:  $t \rightarrow \tau\varepsilon$ . This gives:

$$\begin{aligned}
\varepsilon \frac{dA}{d\tau} &= n - dA - eAH & (13) \\
\varepsilon \frac{dH}{d\tau} &= H \left( 1 - \frac{H}{A} \right) - \frac{1}{C} \frac{H^\theta}{1 + H^\theta} - h \\
\frac{dC}{d\tau} &= r \frac{C}{iC + sA + w} - lC \\
\varepsilon \frac{d\lambda_A}{d\tau} &= \lambda_A (\rho + d + eH) - U'(h) \frac{H^2}{A^2} + \lambda_C \frac{\varepsilon r C s}{(iC + sA + w)^2} - \frac{\partial U^e}{\partial A} \\
\varepsilon \frac{dh}{d\tau} &= \frac{1}{\frac{d^2 U^h}{dh^2}} \left( \lambda_A eA - \frac{dU^h}{dh} \left( 1 - \rho - \frac{2H}{A} - \frac{1}{C} \frac{\theta H^{\theta-1}}{(1 + H^\theta)^2} \right) - \frac{\partial U^e}{\partial H} \right) \\
\varepsilon \frac{d\lambda_C}{d\tau} &= \lambda_C \left( \rho - \frac{\varepsilon r (sA + w)}{(iC + sA + w)^2} + \varepsilon l \right) - U'(h) \left( \frac{1}{C^2} \frac{H^\theta}{1 + H^\theta} \right) - \frac{\partial U^e}{\partial C}
\end{aligned}$$

Letting the perturbation parameter  $\varepsilon$  go to zero we obtain the long run dynamics in the ecosystem. Only the coral is evolving following its natural motion. Note that the last equation can be solved for the coral shadow price:  $\rho\lambda_C = \left( \frac{U'(h)}{C^2} \frac{H^\theta}{1 + H^\theta} + \frac{\partial U^e}{\partial C} \right)$ . The discounted shadow price of coral equals the marginal value of coral for increased harvest thanks to predator protection  $\left( \frac{U'(h)}{C^2} \frac{H^\theta}{1 + H^\theta} \right)$  plus the marginal utility of coral itself. The shadow price for coral does not affect any other variable in the long run so we can just skip the last equation and obtain a system of one differential equation for coral (14) and the reduced system (12) from section (4.1) in steady state.

$$\frac{dC}{dt} = r \frac{C}{iC + sA + w} - lC \quad (14)$$

The coral dynamics were analyzed graphically in section 2.2. These results still hold but now that the ecosystem is exploited, the steady state levels of the fast variables differ implying that the bifurcation points  $\underline{C}$  and  $\bar{C}$  are not the same. To see why, consider a projection of the four dimensional phase diagram for the fast variables on the  $(A, H)$  plane. The graph of function  $u(H) = \frac{n}{d + eH}$  can still represent the nullcline for algae but the nullcline for fish is instead the graph of function  $w(H)|_C = \frac{H^2(1 + H^\theta)}{(H - h)(1 + H^\theta) - \frac{1}{C} H^\theta}$ , which lies always above  $v$  for any given fish and coral biomass level if harvest  $h$  is positive. This means that  $w(H)|_{\bar{C}} > v(H)|_{\bar{C}}$  and  $w(H)|_{\underline{C}} > v(H)|_{\underline{C}}$  so the exploited ecosystem reaches the bifurcation points for higher levels of coral biomass (because  $w(H)|_C$  is decreasing in  $C$ ). This result holds for any specification of the utility function but a given utility function will



correspond to a given level.

So coral reef fisheries, even if they are optimally undertaken, flip at higher coral reef biomasses. This means that even optimal fisheries lead to loss of resilience because, compared to a pristine reef, smaller shocks can make an exploited coral reef flip toward an algae-dominated state. Furthermore the specification for the utility function will determine how much resilience is lost because it determines the level of the curve  $w(H)|_C$  above  $v(H)|_C$  through the harvest term.

## 5 Management strategies

For a long time, poorly developed technology, high costs and relatively low demand restricted coral reef fisheries, so that fishing pressures high enough to cause a bifurcation were never profitable. A logistic differential equation for fish was then enough to approximate coral reef dynamics and find an optimal management strategy. Today, better technologies, higher demand and lower costs have increased fishing pressure on coral reefs a lot. Many coral reefs may have passed the first bifurcation point  $\bar{C}$  and are then close to shift to an alternative stable state. In such a situation, accounting for fish dynamics only is not enough. Social planners can no longer rely on simple rules like marginal cost should equal marginal benefits from fishing. To find the optimal management strategy, the social planners must calculate all future costs and benefits that each potentially optimal strategy would generate. This is not realistic because in practice gathering knowledge about these costs and benefits would require a huge amount of resources and also most of these costs and benefits are uncertain. Highlighting the fast and slow dynamics in a coral reef gives a lot of useful information that could help find satisfying management practices. This section shows how knowledge of slow processes can be useful for coral reef management. In particular knowledge of slow processes seems particularly useful to help detect thresholds and find new ways of controlling the system.

### 5.1 Detect thresholds

Study of the slow dynamics in sections 2.2 and 4.2 show that coral reefs can trespass not one but three different thresholds. The separatrix between the basins of attraction of coral-dominated and algae dominated states is the threshold that decides whether the coral will end up in one state or the other. But the bifurcation points form also some kind of thresholds. To see how consider a situation with one

coral dominated state, the ecosystem can never flip before the bifurcation point  $\bar{C}$  is trespassed. This point marks some kind of frontier between situations where the reef can flip and situation where it cannot. If  $\bar{C}$  is trespassed, the reef can very well stay coral-dominated for a very long time: the separatrix can only be crossed if an external chock occurs. This was observed in practice when reefs flipped after unusual events such as violent hurricanes and fish pests' outbreak. If no external chock occurs, the reef must pass bifurcation point  $\underline{C}$  to flip so this defines still another threshold.

In practice, social planners do not have all information necessary to make the best choice but they probably have some kind of clue of whether it would be best to keep the reef coral-dominated or algae-dominated. Trying to detect ecosystem thresholds would then be a way of acquiring enough information to enable satisfying management tactics. If social planners know the long run dynamics and use that knowledge in management, they obtain long run limiting coral reef biomasses that correspond to their short run management tactics. Comparing these to the threshold biomasses  $\bar{C}$  and  $\underline{C}$  can help them diagnose the reef before a flip has occurred.

A flip to an algae dominated state could occur in two situations: either if the system is between  $\bar{C}$  and  $\underline{C}$  and an external shock pushes it on the other side of the separatrix or if the system crosses the bifurcation point  $\underline{C}$ . Obviously these two ways of flipping differ a lot from each other and might be avoided or cured in different ways.

It seems that much of the research on threshold detection has aimed to detect either the separatrix or the point  $\underline{C}$ , which are points at which the system really shifts. Such threshold detection is problematic because one typically needs to shift the system to detect the threshold, which is precisely what planners want to avoid. Detecting point  $\bar{C}$  instead would give tremendous information to the planners without implying changes that are irreversible or hardly restorable. They would know whether the reef is safe or whether it is a ticking bomb that may flip at any time.

Detecting thresholds is problematic. Problems arise from the fact that thresholds are typically not fixed so trying to detect them might lead to resilience loss and increased flipping risks. Planners need to find good testing methods, which involve controls that are easy to adapt and relatively cheap as well as knowledge about suitable variable to monitor. The phase diagrams and figure 7 indicate that monitoring the direction of motion of herbivorous fish stocks could be a way to go. Around the separatrix the direction of motion change and if social planners can monitor that, they may be able to reverse a shift before it has gone too far. De-

tecting bifurcation point  $\bar{C}$  seems more problematic because this bifurcation goes unnoticed in the neighborhood of the coral dominated state, the radical changes occur around the separatrix and the algae dominated state.

## 5.2 Find new controls

So far, fish harvest was the only way to control the coral reef. In practice other controls are available. Knowledge about ecosystem dynamics provides planners with ideas about new controls that may be useful. In the ecosystem model at hand, coral seems difficult to control in practice. In Florida, old dumped vessel carcasses build artificial reefs that coral have started to colonize but such measures can only help increase the number of areas where coral can develop. They cannot help restore an algae-dominated reef because no coral could survive or colonize as long as algae dominate.

Controlling algae may be easier and useful given their important role. McClanahan with coauthors (2000) experimented large-scale algae removal on Glover Reef in Belize. It turned out to be very labor consuming and might thus not be a good control alternative.<sup>14</sup> One may instead try to limit the nutrient load from land. This would probably be a cheaper alternative at least for regions where sewage treatment has not developed very much yet. Nutrient cleaning could be a cheaper way than lower harvest to obtain a marginal increase in fish biomass.

Intuitively, a combination of several available controls should increase the basin of attraction of the coral-dominated state because that may increase the number of initial states for which remaining in the coral-dominate state is cheap enough to be optimal. To see why consider a social planner who use harvest and nutrient cleaning ( $k$ ) to control a reef. The problem is:

$$\begin{aligned} & \max_{h,k} \int_0^{\infty} U(h, k, A, H, C) e^{-\rho t} dt \\ \text{s.t. } & \frac{dA}{dt} = n - k - dA - eAH \\ & \frac{dH}{dt} = H \left( 1 - \frac{H}{A} \right) - \frac{1}{C} \frac{H^\theta}{1 + H^\theta} - h \\ & \frac{dC}{dt} = \varepsilon \left( r \frac{C}{iC + sA + w} - lC \right) \\ & A \geq 0, H \geq 0, C \geq 0 \end{aligned}$$

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<sup>14</sup>Personal communication with Miriam Huitric one of the authors.

The term  $-k$  in the equation for algae is the only difference with the problem treated in section 4. So as soon as it is optimal to clean ( $k > 0$ ), algae biomass will be lower in steady state for a given fish biomass and hence fish biomass will be higher in steady state. Consider for example a situation in which the optimal fishing pressure is such that the ecosystem is almost at the threshold, about to flip. If social planner start to control nutrient inflow and if this control is cheaper on the margin than the social cost of reducing fish harvest, then, controlling nutrient will help keep a high level of harvest while leaving the proximity of the threshold.

## 6 Conclusions

This article deals with coral reefs but the same kind of mechanisms should be useful for any ecosystem where slow variables play a role, like shallow lakes for example. Analyzing slow and fast processes in coral reefs certainly gives many answers on the reef's dynamics and on different ways to manage them.

This article produces coral reef model that highlights slow and fast dynamics. It shows how fishing affects threshold location in reefs: even optimized fisheries make the reef more prone to shift to an algae-dominated state. In the natural and in the exploited ecosystem, changes in the ecosystem dynamics occurred before the system had shifted to a less favorable state. This insight is used to discuss how planners could better manage the reef and maybe get warning signals that the system is about to shift. Knowledge of slow and fast dynamics also gives indications about other ways of controlling the reef than fishing. Nutrient control was used as an example but a better knowledge of ecosystem dynamics could give information about other kind of relevant control that managers have not thought about yet.

Finding a good way to manage ecosystems with threshold effects is still not obvious though. There are many potential different solutions to such management problem but none of them stands alone as the best one. It seems more than ever that social planners will have to pick management strategies for such ecosystems after having acquired as much knowledge as possible about the ecosystem. Sometimes, applying marginal rules may still be the best way to go. In other situations, managing other variables in addition to harvest or creating protections areas may be better.

## A System transformation

Let  $u_x$ ,  $u_y$  and  $u_z$  be the units in which algae, fish and coral are measured. Let  $u_\tau$  be the time unit and let  $A \equiv \frac{x}{u_x}$ ,  $H \equiv \frac{y}{u_y}$ ,  $C \equiv \frac{z}{u_z}$ ,  $t \equiv \frac{\tau}{u_\tau}$ . The system (1-3) can be rewritten:

$$\begin{aligned}\frac{dA}{d\tau} &= \frac{dx}{d\tau} \frac{d\tau}{dt} = \frac{u_\tau}{u_x} N - u_\tau D A - u_\tau P A H u_y \\ \frac{dH}{d\tau} &= \frac{dy}{d\tau} \frac{d\tau}{dt} = u_\tau R_y H \left( 1 - \frac{H u_y}{K A u_x} \right) - \frac{u_\tau}{u_y} \frac{F}{C u_z} \frac{H^\theta}{\left( \frac{Y}{u_y} \right)^\theta + H^\theta} \\ \frac{dC}{d\tau} &= \frac{dz}{d\tau} \frac{d\tau}{dt} = u_\tau R_z \frac{C}{1 + I C u_z + S A u_x + W} - u_\tau L C\end{aligned}$$

Choose  $u_x = \frac{K}{Y}$ ,  $u_y = Y$ ,  $u_z = \frac{F}{Y R_y}$  and  $u_\tau = \frac{1}{R_y}$

$$\begin{aligned}\frac{dA}{d\tau} &= \frac{Y N}{R_y K} - \frac{D}{R_y} A - \frac{P Y}{R_y} A H \\ \frac{dH}{d\tau} &= H \left( 1 - \frac{H}{A} \right) - \frac{1}{C} \frac{H^\theta}{1 + H^\theta} \\ \frac{dC}{d\tau} &= \frac{R_z}{R_y} \frac{C}{1 + I C \frac{F}{Y R_y} + S A \frac{K}{Y} + W} - \frac{L}{R_y} C\end{aligned}$$

Let  $n = \frac{Y N}{R_y K}$ ,  $d = \frac{D}{R_y}$ ,  $p = \frac{P Y}{R_y}$ ,  $\varepsilon r = \frac{R_z}{R_y}$ ,  $i = \frac{I F}{Y R_y}$ ,  $s = \frac{S K}{Y}$ ,  $w = 1 + W$ ,  $t = \tau$  and  $\varepsilon l = \frac{L}{R_y}$  we obtain the ecosystem equations:

$$\begin{aligned}\frac{dA}{dt} &= n - dA - pAH \\ \frac{dH}{dt} &= H \left( 1 - \frac{H}{A} \right) - \frac{1}{C} \frac{H^\theta}{1 + H^\theta} \\ \frac{dC}{dt} &= \varepsilon r \frac{C}{iC + sA + w} - \varepsilon l C\end{aligned}$$

## B Phase diagram characteristics

Note that  $v(H) = \frac{H}{1 - \frac{1}{C} \frac{H^{\theta-1}}{1+H^\theta}}$ . Let  $\alpha(H) = \frac{H^{\theta-1}}{1+H^\theta}$ . It is easy to verify that  $\alpha$  has two fix points at  $H = 0$  and  $H = \sqrt[\theta]{\theta - 1}$  and two inflection points at  $H = \sqrt[\theta]{\frac{1}{4}\theta \left( 3 + \theta \pm \sqrt{6\theta - 7 + \theta^2} \right)}$ .  $\alpha$  is increasing between 0 and  $\sqrt[\theta]{\theta - 1}$  and decreasing for larger  $H$  with  $\lim_{H \rightarrow +\infty} \alpha(H) = 0$ . Figure 8 shows the graph of  $\alpha$ . So  $v(H) = \frac{H}{1 - \frac{\alpha(H)}{C}}$  where  $\alpha(H)$  has the shape depicted in figure 8. This means that for very small and very large values of  $H$ ,  $v(H)$  behaves similarly to  $H$ . For values in between these

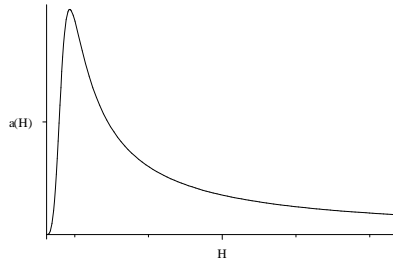


Figure 8:  $\alpha(H)$

two extremes, there are obviously two cases:

1. For all values of  $H$ ,  $C > \alpha(H)$ . In that case it is obvious that  $v(H) > H$  for all possible values of  $H$ . Furthermore,  $\alpha$  increases for low values of  $H$  so  $v$  must be increasing as well. Eventually,  $\alpha$  reaches its maximum and starts decreasing implying that  $v(H)$  is not increasing as quickly and eventually starts decreasing as well until  $\alpha(H)$  becomes so small that the term  $H$  dominates and  $v(H)$  starts increasing again towards the asymptote  $H$ . In this case the graph of  $v$  will look like in figure 9 with the asymptote  $H$  in fat.

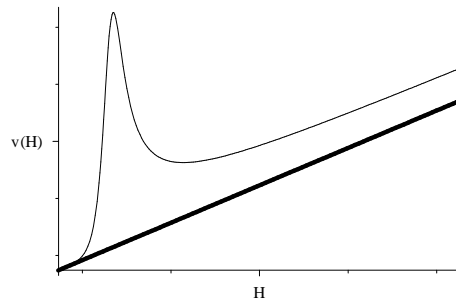


Figure 9:  $v$  with high  $C$

2. For some values of  $H$ ,  $C < \alpha(H)$ . This means that there must be some values of  $H$  such that  $1 - \frac{\alpha(H)}{C} = 0$  and because  $\alpha$  is single-peaked, there can be at most two such values. For those values the graph of  $v$  has obviously two vertical asymptotes and in between those asymptotes,  $v$  must be concave and negative. Outside the asymptotes the graph of  $v$  is similar to the case with no asymptotes. Figure 10 shows the graph of  $v$  in this case.

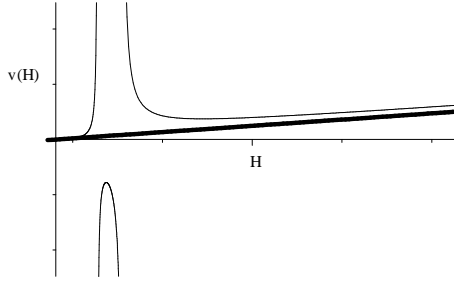


Figure 10:  $v$  with low coral

## C Characteristics of potential harvest

$$h = H \left( 1 - \frac{H(d + eH)}{n} \right) - \frac{1}{C} \frac{H^\theta}{1 + H^\theta}$$

$\frac{\partial h}{\partial H} = 1 - \frac{1}{C} \theta \frac{H^{\theta-1}}{(H^\theta + 1)^2} - \frac{H}{n} (2d + 3He)$ . Let  $\phi(H) = 1 - \frac{1}{C} \theta \frac{H^{\theta-1}}{(H^\theta + 1)^2}$  and  $\gamma(H) = \frac{H}{n} (2d + 3He)$ . Any extremum of  $h$  must be found at the intersection of  $\phi$  and  $\gamma$ . One can show that  $\frac{\partial \phi}{\partial H} = -\frac{1}{C} \theta H^{\theta} \frac{\theta(1-H^\theta) - (1+H^\theta)}{H^2(1+H^\theta)^3} > 0 \Leftrightarrow H^\theta > \frac{\theta-1}{(1+\theta)}$ . Because  $H$  must be positive this implies that  $\frac{\partial \phi}{\partial H} > 0 \Leftrightarrow H > \left( \frac{\theta-1}{(1+\theta)} \right)^{\frac{1}{\theta}}$ . So  $\phi(0) = 1$  and  $\phi$  is decreasing for  $H < \left( \frac{\theta-1}{(1+\theta)} \right)^{\frac{1}{\theta}}$  and reaches a minimum at  $\phi \left( \left( \frac{\theta-1}{(1+\theta)} \right)^{\frac{1}{\theta}} \right) = 1 - \frac{1}{C} \frac{\theta \left( \frac{\theta-1}{(1+\theta)} \right)^{\frac{\theta-1}{\theta}}}{\left( \frac{2\theta}{(1+\theta)} \right)^2}$  before it starts increasing for larger values of  $H$ ,  $\lim_{H \rightarrow +\infty} \phi = 1$ .  $\frac{\partial^2 \phi}{\partial H^2} = -\theta H^{\theta} \frac{\theta^2 - 4\theta^2 H^\theta + H^{2\theta} \theta^2 - 3\theta + 3H^{2\theta} \theta + 2 + 4H^\theta + 2H^{2\theta}}{CH^3(1+H^\theta)^4}$  implying that  $\frac{\partial^2 \phi}{\partial H^2} > 0 \Leftrightarrow \sqrt{(\theta^2 - 1)} \frac{(2\sqrt{\theta^2 - 1} + \theta\sqrt{3})}{(\theta^2 + 3\theta + 2)} > H^\theta > \sqrt{(\theta^2 - 1)} \frac{(2\sqrt{\theta^2 - 1} - \theta\sqrt{3})}{(\theta^2 + 3\theta + 2)}$ . Also  $\gamma$  is always positive and monotonously increasing from 0 for any positive value of  $H$ . So  $\phi$  and  $\gamma$  can intersect 1 or 3 times. For relatively large  $C$ ,  $\gamma$  is located high above the peak of  $\phi$  and the curves intersect once implying that  $h$  has one maximum for relatively high values of  $H$ . For relatively small values of  $C$ , the peak of  $\phi$  is located high above  $\gamma$  and the curve intersect once implying that  $h$  has one maximum for relatively low values of  $H$ . For intermediate values of  $C$ , the curve intersect three times implying that  $h$  has two local maxima and a local minimum in between them. For given parameter values when  $C$  decreases a second to begin with lower

## D Number of steady states of the exploited system in the short run

The exploited system (12) has steady states that solve:

$$\begin{aligned}
 A &= \frac{n}{d + eH} \\
 h &= H \left( 1 - \frac{H}{A} \right) - \frac{1}{C} \frac{H^\theta}{1 + H^\theta} \\
 \lambda_A &= \frac{1}{\rho + d + eH} \left( \frac{dU^h}{dh} \frac{H^2}{A^2} - \frac{\partial U^e}{\partial A} \right) \\
 &= \frac{dU^h}{dh} \left( \frac{H^2 (d + eH)}{(\rho + d + eH) n} e - \left( 1 - \rho - \frac{2H (d + eH)}{n} - \frac{1}{C} \frac{\theta H^{\theta-1}}{(1 + H^\theta)^2} \right) \right) \\
 &= \frac{\partial U^e}{\partial H} + \frac{en}{(\rho + d + eH)(d + eH)} \frac{\partial U^e}{\partial A}
 \end{aligned}$$

Finding solutions to this system is difficult so to come further we assume that utility did not depend on algae and fish biomasses. This exploited system has steady states that solve:

$$\begin{aligned}
 A &= \frac{n}{d + eH} \\
 h &= H \left( 1 - \frac{H}{A} \right) - \frac{1}{C} \frac{H^\theta}{1 + H^\theta} \\
 \lambda_A &= \frac{U'(h)}{\rho + d + eH} \frac{H^2}{A^2} \\
 0 &= \frac{H^2 (d + eH)}{(\rho + d + eH) n} e - \left( 1 - \rho - \frac{2H (d + eH)}{n} - \frac{1}{C} \frac{\theta H^{\theta-1}}{(1 + H^\theta)^2} \right) \quad (a)
 \end{aligned}$$

One can easily see that  $A$ ,  $h$  and  $\lambda_A$  are uniquely determined as soon as  $H$  is given so the number of steady states of this system must correspond to the number of solutions in  $H$  to equation (a). Furthermore the shadow price for algae is the only variable that depends on the form of the utility function in steady state. The other variables will have the same level no matter the utility function as long as utility only depends on harvest. Equation (a) does not depend on the utility function and transforms into

$$1 - \frac{1}{C} \frac{\theta H^{\theta-1}}{(1 + H^\theta)^2} = \frac{H^2 (d + eH)}{(\rho + d + eH) n} e + \frac{2H (d + eH)}{n} + \rho$$

An analytical solution is difficult to find but this equation can be analysed



graphically: the steady state values of  $H$  are found at the intersection of the graph of  $\phi(H) = 1 - \frac{1}{C} \frac{\theta H^{\theta-1}}{(1+H^\theta)^2}$  and  $\psi(H) = \frac{H^2(d+eH)}{(\rho+d+eH)n} e + \frac{2H(d+eH)}{n} + \rho$ . Note that  $\frac{\partial \psi}{\partial H} = eH \frac{2d(\rho+d)+(4d+3\rho)eH+2H^2e^2}{(\rho+d+eH)^2 n} + \frac{2(d+2eH)}{n} > 0$  for any  $H \geq 0$ , and  $\frac{\partial \phi}{\partial H} = -\frac{1}{C} \theta H^\theta \frac{\theta(1-H^\theta)-(1+H^\theta)}{H^2(1+H^\theta)^3} > 0 \Leftrightarrow H^\theta > \frac{\theta-1}{(1+\theta)}$ . Because  $H$  must be positive this implies that  $\frac{\partial \phi}{\partial H} > 0 \Leftrightarrow H > \left(\frac{\theta-1}{(1+\theta)}\right)^{\frac{1}{\theta}}$ . So  $\phi(0) = 1$  and  $\phi$  is decreasing for  $H < \left(\frac{\theta-1}{(1+\theta)}\right)^{\frac{1}{\theta}}$  and reaches a minimum at  $\phi\left(\left(\frac{\theta-1}{(1+\theta)}\right)^{\frac{1}{\theta}}\right) = 1 - \frac{1}{C} \frac{\theta \left(\frac{\theta-1}{(1+\theta)}\right)^{\frac{\theta-1}{\theta}}}{\left(\frac{2\theta}{(1+\theta)}\right)^2}$  before it starts increasing for larger values of  $H$ ,  $\lim_{H \rightarrow +\infty} \phi = 1$ .  $\frac{\partial^2 \phi}{\partial H^2} = -\theta H^\theta \frac{\theta^2 - 4\theta^2 H^\theta + H^{2\theta} \theta^2 - 3\theta + 3H^{2\theta} \theta + 2 + 4H^\theta + 2H^{2\theta}}{CH^3(1+H^\theta)^4}$  implying that  $\frac{\partial^2 \phi}{\partial H^2} > 0 \Leftrightarrow \sqrt{(\theta^2 - 1) \frac{(2\sqrt{\theta^2 - 1} + \theta\sqrt{3})}{(\theta^2 + 3\theta + 2)}} > H^\theta > \sqrt{(\theta^2 - 1) \frac{(2\sqrt{\theta^2 - 1} - \theta\sqrt{3})}{(\theta^2 + 3\theta + 2)}}$ . Also we have  $\psi(0) = \rho$  and  $\frac{\partial^2 \psi}{\partial H^2} = 2e \frac{7d\rho^2 + 8d^2\rho + 2\rho^3 + (\rho+d)^2 9eH + 3d^3 + 3H^3e^3 + 9e^2 H^2(\rho+d)}{(\rho+d+eH)^3 n} > 0$ . This implies that  $\phi$  and  $\psi$  can intersect one or three times so we may have one or three candidate steady states. There is a bifurcation when the two curves are tangent and the system goes from one to three steady states. The number of steady states depends on the parameter values and there are three different possibilities:

1. If  $C$  is large,  $\phi(H) \approx 1$  for all values of  $H$  because the second term becomes very small. In that case there will be one steady state for most values of the other parameters. Note that high values of  $e$  and  $d$  and low values of  $n$  make  $\psi$  steeper. High discount rates make  $\psi$  shift up and become flatter.

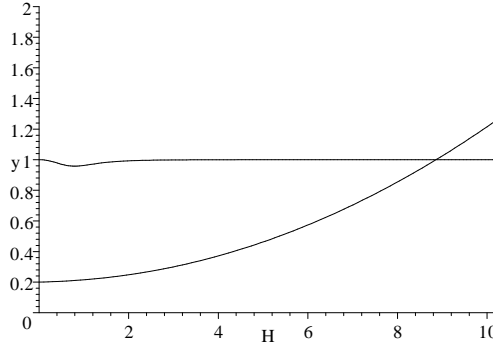


Figure 11: Graph of  $\psi$  and  $\phi$  with high coral biomass

2. If  $C$  is small,  $\phi$  is not approximately equal to one everywhere. Then the number of steady states depends on parameter values. If the parameter values imply that  $\psi$  is relatively low and flat there is one steady state with relatively high algae stock. If the parameter values imply that  $\psi$  is high and steep there

is also only one steady state with low algae stock or maybe even none if the discount rate is high. For values in between there may be three steady states implying that there are bifurcations.

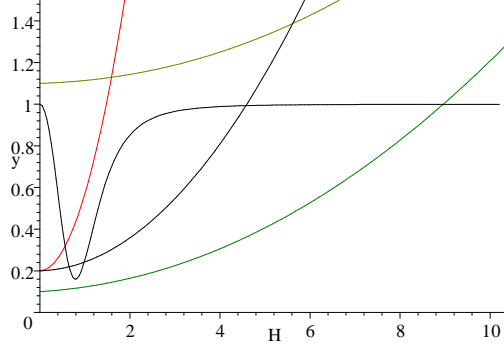


Figure 12: Graph of  $\phi$  and several alternatives of  $\psi$  for low coral biomasses

## E Dynamics around steady states in the short run

The Jacobian of the system (12) is<sup>15</sup>

$$\begin{pmatrix} \Psi & \frac{H^2}{A^2} & 2\frac{dU^h}{dh} \frac{H^2}{A^3} - \frac{\partial^2 U^e}{\partial A^2} & \frac{1}{\frac{d^2 U^h}{dh^2}} \Theta \\ -eA & \Lambda & \Theta & \Upsilon \\ 0 & 0 & \rho - \Psi & \frac{eA}{\frac{d^2 U^h}{dh^2}} \\ 0 & -1 & -\frac{d^2 U^h}{dh^2} \frac{H^2}{A^2} & \rho - \Lambda \end{pmatrix}$$

$$\text{Where } \Theta = \lambda_A e - \frac{dU^h}{dh} \frac{2H}{A^2} - \frac{\partial^2 U^e}{\partial A \partial H}; \Lambda = 1 - \frac{2H}{A} - \frac{\theta}{C} \frac{H^{\theta-1}}{(1+H^\theta)^2};$$

$$\Upsilon = -\frac{\frac{dU^h}{dh}}{\frac{d^2 U^h}{dh^2}} \left( -\frac{2}{A} - \frac{\theta(\theta-1)}{C} \frac{H^{\theta-2} - H^{2\theta-2}}{(1+H^\theta)^3} \right) - \frac{\frac{\partial^2 U^e}{\partial H^2}}{\frac{d^2 U^h}{dh^2}}; \Psi = -(d + eH)$$

Given the appearance of the diagonal of this Jacobian, it is obvious that if  $\mu$  is an eigenvalue of this Jacobian then  $\rho - \mu$  must be an eigenvalue as well. This result was expected due to the results in Birkhoff (1927), Kurz (1968) and Crépin (2002). So any steady state of this system is either a saddle point or is completely unstable.

<sup>15</sup> Assuming  $\frac{d^3 U^h}{dh^3} = 0$

## F Second order conditions

Here we use Arrow's sufficiency conditions, which state that the maximized Hamiltonian of the system must be concave with respect to the state variables. In the fast variables system this amounts to

$$\begin{aligned}\mathcal{H}(A, H, C, h, \lambda) &= U(h, A, H, C) + \lambda_A(n - dA - eAH) \\ &\quad + \frac{dU^h}{dh} \left( H \left( 1 - \frac{H}{A} \right) - \frac{1}{C} \frac{H^\theta}{1 + H^\theta} - h \right)\end{aligned}$$

being concave with respect to  $(A, H)$ . To check that we must calculate the Hessian matrix for the Hamiltonian:  $\begin{pmatrix} B & D \\ D & F \end{pmatrix}$ . Where  $A = \frac{\partial^2 U^e}{\partial A^2} - 2 \frac{dU^h}{dh} \frac{H^2}{A^3}$ ;  $B = \frac{\partial^2 U^e}{\partial H \partial A} - \lambda_A e + 2 \frac{dU^h}{dh} \frac{H}{A^2}$  and  $F = \frac{\partial^2 U^e}{\partial H^2} - \frac{dU^h}{dh} \left( \frac{2}{A} + \frac{\theta H^{\theta-2} (\theta-1) - (\theta+1) H^\theta}{(1+H^\theta)^3} \right)$

The hamiltonian is concave if  $(-1)^r D_r \geq 0$  for  $r = 1, 2$ , where  $D_r$  are the leading principal minors of order  $r$  of the hessian matrix. This is equivalent to

$$-A \geq 0 \text{ and}$$

$$AF - B^2 \geq 0$$

The first condition is always satisfied if utility is increasing in harvest and concave in algae – two reasonable assumptions. The second condition is only satisfied for certain values of fish biomasses. If  $\frac{\partial U^e}{\partial A} = \frac{\partial U^e}{\partial H} = 0$  and  $\frac{dU^h}{dh} \neq 0$  this last condition is:

$$\begin{aligned}2 \frac{H^2}{A^3} \left( \frac{2}{A} + \frac{\theta H^{\theta-2} (\theta-1) - (\theta+1) H^\theta}{(1+H^\theta)^3} \right) - \left( 2 \frac{H}{A^2} - \frac{\lambda_A}{\frac{dU^h}{dh}} e \right)^2 &\geq 0 \\ \Leftrightarrow 2\theta H^\theta \frac{(\theta-1) - (\theta+1) H^\theta}{(1+H^\theta)^3} &\geq A^3 C \frac{\lambda_A}{\frac{dU^h}{dh}} e \left( \frac{\lambda_A}{\frac{dU^h}{dh}} e - 4 \frac{H}{A^2} \right)\end{aligned}$$

$$\text{Define } \zeta(H) = A^3 C \frac{\lambda_A}{\frac{dU^h}{dh}} e \left( \frac{\lambda_A}{\frac{dU^h}{dh}} e - 4 \frac{H}{A^2} \right) \text{ and } \delta(H) = 2\theta H^\theta \frac{(\theta-1) - (\theta+1) H^\theta}{(1+H^\theta)^3}$$

Recall that in an equilibrium we must have

$$\begin{aligned}A &= \frac{n}{d + eH} \\ \lambda_A &= \frac{\frac{dU^h}{dh}}{\rho + d + eH} \frac{H^2}{\left( \frac{n}{d + eH} \right)^2}\end{aligned} \tag{15}$$

So  $\zeta(H) = -CH^3 e (d + eH) \frac{3eH + 4\rho + 4d}{(\rho + d + eH)^2 n}$ , which is negative, decreasing in  $H$  and concave with a maximum  $\zeta(0) = 0$ . One can easily verify that  $\delta(H)$  is decreasing in  $H$  if  $\frac{1}{2(\theta+1)} (4\theta - 2\sqrt{3\theta^2 + 1}) \leq H^\theta \leq \frac{1}{2(\theta+1)} (4\theta + 2\sqrt{3\theta^2 + 1})$  and increasing otherwise. Furthermore one can show that  $\delta$  increases from 0 to a maximum at  $\left( \frac{1}{2(\theta+1)} (4\theta - 2\sqrt{3\theta^2 + 1}) \right)^{\frac{1}{\theta}}$ , then decreases and reaches the value 0 at

$H = \left(\frac{\theta-1}{\theta+1}\right)^{\frac{1}{\theta}}$ , decreases further towards a minimum at  $\left(\frac{1}{2(\theta+1)} \left(4\theta + 2\sqrt{3\theta^2 + 1}\right)\right)^{\frac{1}{\theta}}$  and then increases for any large value of  $H$ . In the limit,  $\delta$  approaches 0 when  $H$  becomes very large. Figure 13 shows the graph of the projection of the curves  $\delta(H)$  and  $\zeta(H)$ .

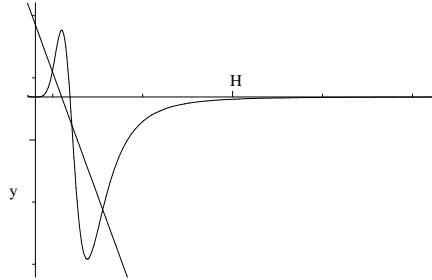


Figure 13: Graph of  $\delta$  and  $\zeta$

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