Q2: Hysteresis and Management

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8/3/2020

# Introduction

Recreational angling has a major influence on the ecology of freshwater ecosystems and is likely to structure community dynamics through selective or lack of harvest of certain individuals and species from the system (Curry, Brady, and Morgan 2003; Sass and Shaw 2020). In recognition of the influence anglers have on freshwater fish communities, ecosystem-based fisheries management, adaptive management, and safe operating space concepts have all been invoked in an effort to better manage freshwater resources. In order to successfully manage fish populations, applied management must account for the intricate dynamics of multiple species that are targeted in recreataional fisheries (Johnston, Arlinghaus, and Dieckmann 2013). A central theme of these management strategies is a holistic view of the ecosystem and the rejection of single species management strategies applied broadly in favor of flexibility that allows managers to consider the full context of the systems they work in and tailor their actions appropriately (Collie et al. 2016; Camp and van Poorten 2019?).

Regime shifts (i.e., abrupt and persistent changes in ecosystem state) are likely to have major influences on aquatic systems and the recreational fisheries that rely on these systems. Increasingly, efforts have been made to incorporate ecosystem states and regime shifts into fisheries management (King, McFarlane, and Punt 2015). Current research to incorporate ecosystem-based fisheries management has focused on ecosystem change, such as climate change and cultural eutrophication, and management strategies to maintain stable states of a system in light of ecosystem change (Liu et al. 2015). Management of ecologically driven regime shifts tend to focus on identifying the underlying cause of change, and, in many cases, adapting to those changes **(citation)** or mitigating the effects of those changes through increased systemic resilience **(Carpenter et al. 2017citation)**. Although increased resilience has been shown to decrease the likelihood of rapid shifts in the stable state of a system (Scheffer et al. 2001), many of these regime shifts are initiated by drivers that are not ecological. One such driver, harvest driven regime shifts, is of particular interest in fisheries systems (Steele 1996; Post et al. 2002; Rothschild and Shannon 2004).

Harvest driven regime shifts have been studied in commercial and marine fisheries when ecosystem-based management has been implemented (Oken and Essington 2016; Essington et al. 2015). The recognition of the role of inter-specific and trophic interactions between species, and the hysteretic behavior that may follow, has helped foster the adoption of ecosystem-based management (Walters and Kitchell 2001; Blackwood, Hastings, and Mumby 2012). Crowder et al. (2008) has also explored the simultaneous influences of multiple fished species on marine systems. This type of ecosystem-based management plays an import role in maintaining a desired stable state, often in the form of a specific fish community structure. This stands in contrast to more traditional, single-species? management decisions which take a linear view of the system (e.g., fish population is overexploited, so managers attempt reduce mortality rates through regulations or stock in response) (Sass et al. 2017). Instances where these simple solutions have had no effect, or even a negative effect, are abundant and demonstrate a need to consider alternative stable states and the hysteretic behavior that is often present in complex aquatic communities (Pine et al. 2009).

One of the commonly hypothesized reasons for these depensatory counterintuitive responses to management actions was formalized as ‘cultivation-depensation’ effects by Walters and Kitchell (2001) and similarly by DeRoos and Persson (2002). They described how intraguild predation can lead to alternative, self-reinforcing, states that can be transitioned between through the intensity of harvest on the adults of the top predator species which is an intraguild predator with the forage fish species. Cultivation-depensation mechanisms have been empirically demonstrated in marine fisheries resulting in alternative stable states, thereby reducing the ability for recovery of some exploited species (Gårdmark et al. 2015). In freshwater systems however, there has been limited focus on the effects of harvesting multiple interacting species and the consequences it may have for maintaining a desired stable state in the system (but see Sass et al. 2020). The hysteretic behaviors of many freshwater communities have, to date, focused on ‘trophic triangle’ models where a single harvested species is an intraguild predator with a second species that is not part of the fishery or mortality rates are mediated by harvest and the availability of refuge (Roth et al. 2007), while in reality most freshwater systems are subject to multiple harvested fish species which often interact with each other in various ways (Walters and Kitchell 2001; Biggs, Carpenter, and Brock 2009).

To better understand the dynamics and interactions of multi-species recreational fisheries, we expand on the model presented in Biggs et al. (2009) and present a two species, stage-structured fisheries model. In keeping with the tenets of ecosystem-based management, our model moves away from a single harvested species management scenario and towards a more realistic system where multiple harvested sportfish species compete with each other. The outcome of this trophic interaction affects and is affected by the effects of humans on the ecosystem through fishing activities (*I’m not sure if we want to limit this to just fishing or also thing about shoreline development, climate change as human effects too*). Adults and juveniles of both species trophically interact with each other and are simultaneously harvested, but to different degrees. We parameterized our model to represent largemouth bass (*Micropterus salmoides*) or a generalized centrarchid complex (bluegill *Lepomis macrochirus*, black crappie *Pomoxis nigromaculatus*) and walleye (*Sander vitreus*) trophic interactions in north temperate lakes. Our model is unique in that it examines hysteresis and management in: (1) a freshwater ecosystem; and (2) a multi-species system where both species and/or species complex are sport fish targeted by anglers. The goals of our modeling exercises were to: (1) better understand the role hysteresis plays in the type and magnitude of management responses necessary to maintain a system in a desired state; and (2) to investigate the role management responses can play in reverting to an alternative configuration. We accomplish this by modeling species-specific responses to regulations and stocking in a system where hysteresis is present or absent. We perform our modeling experiments in systems where a manager’s goal is to either maintain a desired stable state or push the system to a desired stable state from an undesired one.

# Methods

## *Base model*

We used a stage-structured fishery model adapted from Biggs et al. (2009). Their model contained trophic triangle dynamics between a harvested sport fish with juvenile and adult stages, and a single-stage planktivorous fish that was not part of the fishery. The model also contained basic foraging arena dynamics where juvenile sportfish and planktivores move between the foraging arena and refuge. In this model, adult sportfish can prey on planktivores or cannibalize their own juveniles when they are in the foraging arena. Planktivores can prey on juvenile sportfish in the refuge and the foraging arena. Harvest rate and the amount of refuge available to fish are both externally controlled.

We modified this model by replacing the single-stage planktivore with a second two-stage sport fish species or species complex. Adults of both species can cannibalize their own juveniles and juveniles of the opposite species when juveniles are present in the foraging arena. Juveniles of both species also interact with each other for resources. Harvest rate and the amount of refuge available to fish are both externally controlled. Our model is set up as a series of differential equations where adults are removed through catch and subsequent harvest () and natural mortality (). New adults are produced by juveniles maturing at a constant rate(). As an example we provide the equations for species 1 adults () and juveniles (). The equations for species 2 are identical with reversed subscripts.

The model displays hysteretic behavior typical of systems where interacting species are limited more strongly by each other than by themselves. This manifests itself in what is typically called a ‘priority effect’, where the initial abundance is what determines which species dominates. Here, the more abundant species is able to cultivate conditions for itself through predation on and competition with juveniles of the opposite species. The equilibrium abundances of the two competing species will depend on the strength of harvest on each species and the strength of their effects on each other. When the species limit themselves more than they limit each other there is only one stable equilibrium point and hysteresis is gone from the system.

## *Simulations*

Simulations were run using the ‘deSolve’ package in R (Team 2020; Soetaert, Petzoldt, and Setzer 2010). We varied management scenarios of stocking and harvest rate within the system in order to understand the influence of management on the maintenance of alternate stable states. Stocking is included in our version of the Biggs et al. (2009, 2009) model through the term . Stocking takes the form of a yearly addition of a number of juveniles to the system. Harvest rate control in our model is done through setting harvest rate to a given level (*Note to us: this results in a proption of the population removed each time step, at smaller pop size fewer fish are removed and vis versa*). This can be set as a constant level across time or can be allowed to vary between years. Similarly, stocking of juveniles by managers can be held constant through time or allowed to vary through time. A third management option which we do not address here is variable availability of refuge () leading to increased or decreased juvenile survival rates. Simulation were run in order to examine the magnitude of management intervention necessary to maintain or alter the state of a system.

Paramater Values

|  |  |
| --- | --- |
|  | Value |
| s1 | 0.100 |
| cJ1A1 | 0.002 |
| cJ1A2 | 0.500 |
| cJ1J2 | 0.003 |
| v1 | 1.000 |
| f1 | 2.000 |
| s2 | 0.100 |
| cJ2A2 | 0.002 |
| cJ2A1 | 0.500 |
| cJ2J1 | 0.003 |
| v2 | 1.000 |
| f2 | 2.000 |

# Results

### *Base Model Behavior*

The base model shows the presence of alternative stable states occurring with dominance of species 1 and species 2 based on initial conditions (Figure 1). When initial abundance of species 1 is high and species 2 is low, low harvest will maintain high abundance of species 1 and low abundance of species 2 (when harvest of species 2 remains constant). At high harvest of species 1, the model eventually results in functional extirpation of species 1, while maintaining a moderate abundance of species 2. However, when we alternate these (species 2 is initially dominant), even low levels of harvest of species 1 result in functional extirpation of species 1, and maintenance of species 2 (again with harvest of species 2 remaining constant).

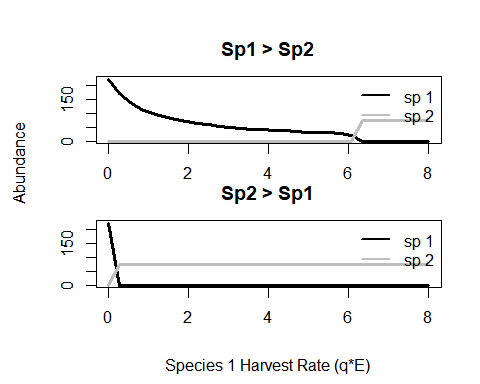


Figure 1. Model run to equilibrium over a range of harvest parameters, no stocking. Top panel shows equilibrium abundances for the range of harvests when species 1 is initially dominant. Bottom panel shows equilibrium abundances for the range of harvests when species 2 is initially dominant.

### *Influence of stocking on system dynamics*

At low levels of stocking of Species 1, increased harvest resulted in dominance of Species 2. However, when stocking was increased, dominance of Species 1 also increased (Figure 2). In model simulations in which Species 1 initially dominated in the system, low levels of stocking were all that were necessary to maintain the stable state of Species 1 dominance. Here, hysteresis resulted in increased likelihood that Species 2 would dominate the system at low levels of stocking. In systems in which Species 2 initially dominated, we found that low levels of stocking were not enough to result in an alternative stable state in which Species 1 dominates. In these systems, the presence of hysteresis resulted in higher levels of stocking necessary in order to result in a shift in stable state. These results indicate that in order to manipulate the stable state of a system, it may be necessary to increase the magnitude of the stocking intervention.

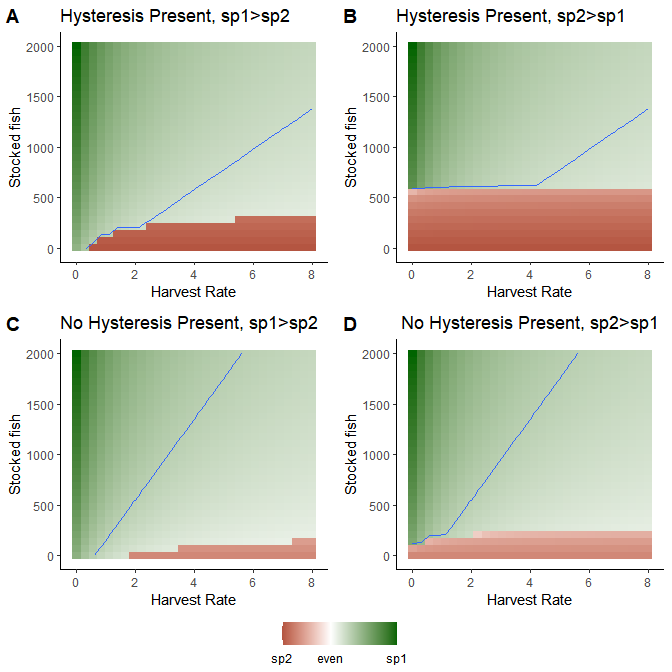


Fig 2. Effect of hysteresis on either maintaining sp1 dominance (A&C) or flipping to a state where sp 1 dominates (B&D). This is described for systems with and without hysteresis. Green = sp1 >sp2, red = sp2 > sp1. Blue line marks boundary where sp1 > sp2 by at least 100 individuals. This is shown as an exmaple of what a manager may care about, not just the sp1 is a little more abundant than sp2 but that the diffferent meets some minimum requirement.

### *Influence of management on system dynamics*

* optimal strategy and magnitude - How harvest control can influence the stable state of the system (Figure 3).
* influence of hysteresis

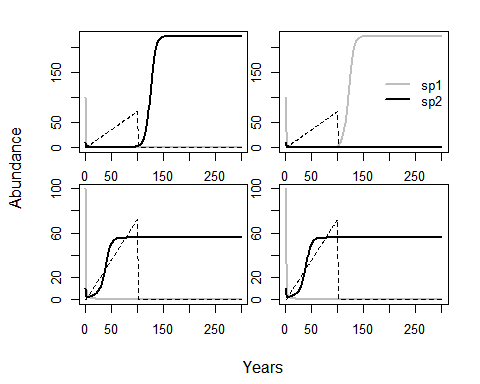


Figure 3. Top row of figures show effect of management response in a system where hysteresis is considered. Bottom row shows effect of management without hysteresis. The left column is for a scenario where the goal is to flip the state from sp1 to sp2 dominating at equilibrium. The right column is for a scenario where the goal is to maintain the system in a state where sp1 dominates at equilibrium.

Refuge (or declines in available refuge) also play a role in maintaining the stable state of the system, although the influence can be mitigated through increased stocking interventions. Declines in refuge can result in a transition to alternative stables states, especially in those instances where refuge declines are disproportionate between the two species. However, we found that this transition can be halted by managers through stocking interventions (Figure 4b).

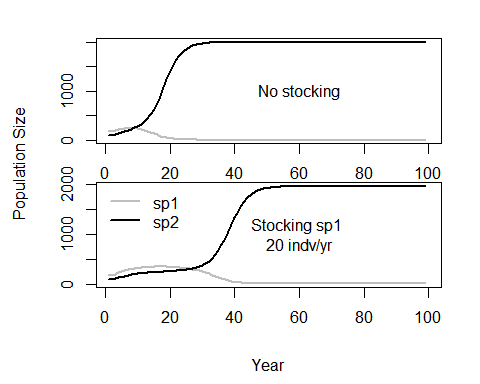


Figure 4. Top panel shows a switch in dominant species in a scenario with no stocking. Bottom panel shows the effect of stocking at delaying the transition. For both model runs, no harvest just slow declines in refuge. Both species experience a decline in refuge availability but for sp1 the decline is more significant while sp2 experiences less of a decline.

### *Optimal strategies/management and stocking*

Modeling the combination of stocking and harvest control on the system,the hysteretic behavior of these systems significantly alters what management actions are necessary to either keep a system in a desired state (Fig 2. a & c) or flip a system into a desirable state (Fig 2. b & d). Depending on the species desired and the type of management intervention, management control is likely to strongly influence the dominance of desired species and maintenance of the desired stable state.



Figure 5. System dynamics over a range of management interventions, including stocking and harvest. Solid lines indicate no stocking, long dashes indicate stocking of species 1, short dashes indicate stocking of species 2.

# Discussion

Here, we present evidence to suggest that the hysteretic behavior that characterizes the transition between states plays an important role in determining what level of management action is necessary to achieve a manager’s goals. Our models, which include and exclude hysteresis, generally show that when we assume hysteretic dynamics are absent from the system, we will underestimate the magnitude of action necessary to either maintain or flip a system. Our results highlight the importance of understanding the ecological interactions of fishes in a multi-species fishery. Further, our results indicate the importance of ecosystem-based multi-species management in systems where multiple species are targeted by recreational anglers.

Impact of hysteresis in our model  
How timing of management and stocking are important factors to consider.  
extrapolate to freshwater fish dynamics  
\* How our model is/is not a good representation of freshwater systems.  
+ Right now the parameter values, abundances, harvest and stocking rates, etc. are pretty abstract. We can still do more to ground this. + The effect of refuge on model dynamics isn’t as strong as the effect of stocking or harvesting, maybe we should’ve expected this?  
\* What is missing from our model.  
+ Fishing effort is controlled externally, it’s not responsive to changes in catch rate. It’s maybe not important to add in just to note that the model is set up this way (in q3 we change this and allow effort to respond to abundance within the model)

Optimal Management Strategies  
\* What did we learn from comparing stocking and controlling harvest?  
\* Management implications - do we use models like this to identify ‘Early Warning Signs’ of potential regime shift? (Litzow and Hunsicker 2016).

How can this be used by managers  
\* Strategies for maintaining a desired stable state

Future work  
\* Ground truth this model with empirical data  
\* Think about how angler dynamics can impact fisheries outcomes  
*I’m just adding these to show that the need to understand these is there (and to put a plug for our other two papers)*  
Conclusions

# Supplemental

## Figure graveyard

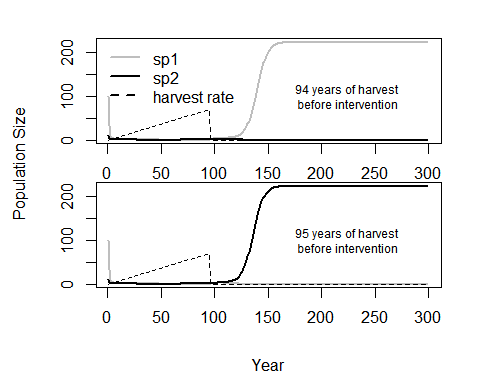


Figure 2. Temporal influence of management interventions. Intervention to stop harvest one year too late can allow for regime shift to undesired state

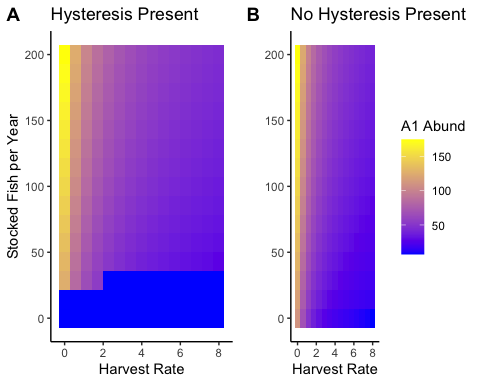


Figure 3. Effect of stocking at different harvest rates. (a) with hysteresis, (b) without hysteresis

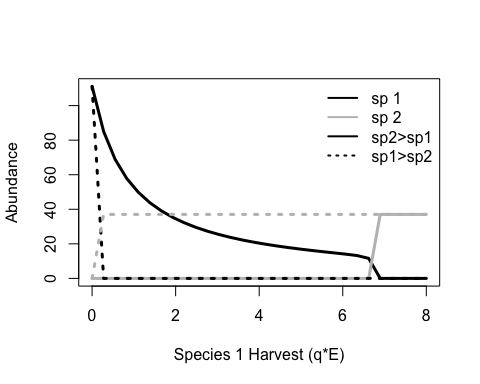


Figure 1. Basic model behavior. When species are equal in all interactions, alternate stable states can be produced by through harvest. The stable state will depend on the combination of harvest rate and the species with the higher initial abundance.

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