Colin Dassow, Chelsey Nieman, Chris Solomon, Greg Sass, and Stuart Jones

12/18/2020

# Introduction

Interactions between species are often not considered in natural resource management in order to simplify complex management problems (Walters and Martell 2004, Baum and Worm 2009). This simplification may lead managers to make decisions that in hindsight, were ineffective or even detrimental (Walters et al. 2000; Springer et al. 2003; Myers et al. 2007; Hansen et al. 2015; Sass and Shaw 2020). These unexpected outcomes are akin in that they all failed to consider interactions between multiple species and life stages (Walters et al. 2000). Overfishing has interacted with climate change and inter-specific interactions to cause dramatic shifts in dominant species in coastal ecosystems around the world and in north-temperate lakes (Jackson et al. 2001; Hansen et al. 2017; Embke et al. 2019). Barents Sea capelin (*Mallotus villosus*) stock collapsed due to overfishing and predation by herring (*Clupea harengus*) while subsequent predation on herring by cod (*Gadus morhua*) delays the stock’s ability to recover (Hjermann et al. 2004). However, as human influences on ecosystems continue to grow, so will the need to avoid undesirable outcomes. Consideration of the interactions between species can help managers avoid unexpected, and often undesirable, outcomes (Pine et al. 2009). Ecosystem-based management uses a holistic approach to manage natural resources that includes accounting for inter-specific interactions and human decision making. Further, these complex social-ecological systems are integrated within larger systems ranging across governance boundaries from local to international. Although implementing ecosystem-based management may be difficult, it is nevertheless warranted as humans seek to maintain desired stable states to provide ecosystem services. Aquatic social-ecological systems, including fisheries, provide excellent examples to explore the potential benefits of implementing ecosystem-based management. Counterintuitive responses by fish populations to management have shown that in many cases a linear, single-species focused view of these systems can lead to actions that result in undesirable stable states (Hutchings 2000).

Complex intra- and inter-specific interactions in aquatic systems can result in positive feedback loops that allow a stable state to reinforce itself such that efforts by managers to change the stable state may have no or unintended effects. Walters and Kitchell (2001) described how positive feedback loops can create two alternative stable states in a food web consisting of a top predator and a forage species through cultivation-depensation effects. Under low exploitation, the top predator is abundant and able to cultivate conditions to increase survival of its juveniles by preying on the predators of its juveniles, namely the forage species. Alternatively, the forage species may dominate when exploitation of the top predator is high (as is the case in many fisheries), allowing the forage species to cultivate conditions for itself through predation on juveniles of the top predator. When top predator abundance declines below a critical threshold (depensation), recruitment of new juveniles may be compromised through elevated mortality rates (in contrast to the commonly assumed density-dependent compensatory recruitment and elevated survivorship above the critical threshold) (Liermann and Hilborn 1997; 2001; Carpenter 2003; Hilborn et al. 2014; Sass et al. 2021). If the forage species dominates, simply increasing the abundance and survival of adult predators (even through fishery closure) may have no effect, or possibly a negative effect if the associated increase in juvenile production further increases foraging opportunities for the forage species, leading to further increases in their biomass with the increased prey availability. Regime shifts driven by overfishing are one example of the persistence of these new stable states where fish populations are unable to recover even when the fishery is closed for decades (Hutchings 2000).

In fisheries, it is common to focus applied research and management on a single focal species, even though this species is embedded in a larger community where harvest of multiple species takes place (Hansen et al. 2015). The tradeoffs between competing management goals for several co-occurring exploited species are often not considered; however, some notable exceptions do exist (e.g., Essington et al. 2015, Oken et al. 2016). Essington et al. (2015) used competing objectives for a predator fishery (Atlantic cod, *Gadus morhua*) and a forage species fishery (Atlantic herring, *Clupea harengus*) and showed how ecological interactions between the two and the market price of each species could be combined to determine the appropriate level of mortality for each species given specific management goals (maximizing combined profit of both species at equilibrium). In contrast to commercial fisheries where users aim to maximize profit, recreational fishery users vary along multiple axes of species preference, catch rate, fish size, location, valuation, utility, avidity, and harvest opportunity (e.g., Johnston et al., 2010; Beardmore et al., 2015; Arlinghaus et al., 2017). Users place differing levels of importance on each of these aspects of the fishing experience, leading to divergent, and in some cases, competing desires by fishery users and ultimately complex management problems. Given the limited ways in which managers can influence recreational fisheries (i.e., fishing regulations, stocking, habitat alteration, valuation), understanding and leveraging ecological interactions may allow managers to make the most of the limited tools at their disposal to keep systems within a safe operating space and to meet the diverse goals of users in the system (Carpenter et al. 2017).

Here, we use an example of a recreational fishery with two managed species to explore how managers can leverage ecological interactions between species to achieve their goals. Outcomes that are of specific interest arise from stable states where the desired species dominates, resulting in higher economic benefits and user satisfaction. Our model, like all models, makes necessary simplifying assumptions to balance tractability with realism. We use a relatively simple fishery model that allows for the interaction and harvest of two species, which is an improvement over many of the single species models used to date. We use this two species model to explore how ecological interactions can be leveraged, in combination with human intervention, to maintain desired stable states that otherwise could not be maintained using single species approaches. Our hypothesis that inter-specific interactions play an important role in determining the appropriate management action leads us to predict that consideration of these interactions and the resulting non-linear dynamics can lead to more positive and predictable outcomes.

# Methods

## Overview

In order to understand how accounting for interspecific interactions can improve our ability to predict and manage important ecosystem services we developed a simple fishery model where two species simultaneously compete with each other and are harvested by humans. We then use this model to explore management outcomes for scenarios where the hypothetical manager either ignores or accounts for the interspecific interactions. A modeling approach, such as the one we’ve adopted here, is better suited to explore these dynamics because of the longer time scales at which they operate. Stocking and harvest regulations are, at their fastest, adjusted on an annual basis. Furthermore, the effects of any management action on a fish population take several years to become apparent for even relatively short lived species. The species in our model are parameterized such that their juveniles overlap completely in their use of the refuge while the adults do not. One species’ adults uses the refuge and associated foraging arena more than the other. This is designed to mimic the walleye (*Sander vitreus*) and largemouth bass (*Micropterus salmoides*) relationship in north temperate lakes where walleye have historically outcompeted largemouth bass.

## Model

We used a modified version of a stage-structured food web model that has previously been used to explore alternative stable states in lake ecosystems (Carpenter and Brock 2005, Carpenter et al. 2008, Biggs et al. 2009). The original model contained interactions between a harvested sport fish with juvenile and adult stages, and a single-stage planktivorous fish not subjected to harvest. We modified this model to include two stage-structured fish populations that are simultaneously harvested. The model contains basic foraging arena dynamics where juvenile sportfish move between the foraging arena and refuge. In our model, adult sportfish can prey upon their own juveniles and juveniles of the competing sportfish species when they are in the foraging arena. The survival and fecundity of the two species are identical while the competition coefficients are not. Juveniles of both species have equal effects on each other while adults have asymmetrical effects on the juveniles of the opposite species (**table** ref). Unless noted, all parameters are constant through time.

### Adult Dynamics

Eq. 1

Eq. 2

Adults are produced through the maturation of juveniles at a constant rate or . Adults undergo natural mortality, and , and are harvested at rate and . Harvest rate can be either constant or time-dependent in our model.

### Juvenile Dynamics

Eq. 3

Eq. 4

Juveniles are produced through density-dependent recruitment based on Ricker stock-recruitment relationships. Additionally, stocking of juveniles can be imposed through and . Juveniles are removed from the population by one of three ways. The strength of each mortality source is represented by the parameter which can be thought of in general terms as the ‘effect’ of one species/life stage on another. Juvenile mortality occurs through cannibalism (read this as ‘the effect of on ’), which is dependent on refuge dynamics. Second, juveniles undergo mortality through predation by adults of the opposite species . These dynamics are dependent on refuge and are controlled by two rates, the rate at which juveniles leave refuge and enter the foraging arena, and the rate at which they leave the forage arena and enter refuge. Changes in the amount of refuge available to fish are simulated through changes in the parameter, which determines how many juveniles are in the foraging arena. The last juvenile mortality source is through direct competition with juveniles of the opposite species either through competition for resources or direct predation. This competition occurs independent of refuge dynamics such that all juveniles compete in all areas. We assumed that juveniles of both species occupy the same refuge and same foraging arena. The three processes described above account for all juvenile mortality in the system. All juveniles not claimed by the three sources of mortality above then mature to adults. These fish then survive at some proportion to join the adult population ().

Table 1. Parameter definitions used

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| --- | --- |
| Term | Definitions |
| s1 | Juvenile survival sp1 |
| m1 | adult natural mortality |
| cJ1A1 | cannibalism |
| cJ1A2 | predation by sp2 |
| cJ1J2 | Juvenile competition |
| v1 | rate sp1 juveniles enter FA |
| h1 | rate sp1 juveniles leave FA |
| k1 | stocking species 1 |
| qE1 | harvest rate sp1 |
| s2 | Juvenile survival sp2 |
| m2 | adult natural mortality |
| cJ2A2 | cannibalism |
| cJ2A1 | predation by sp1 |
| cJ2J1 | Juvenile competition |
| v2 | rate sp2 juveniles enter FA |
| h2 | rate sp2 juveniles leave FA |
| k2 | stocking species 2 |
| qE2 | harvest rate sp2 |

## Model Experiments

Recreational fisheries are complex systems where human impacts and ecological interactions feedback on each other to make management of any one species difficult. A key challenge facing many managers is how to maintain or improve abundances of certain highly valued, and exploited, species in the face of competition with other less valued, and exploited, species. The modeling experiments are designed to mimic this situation. Species 1 in our models represents the dominant, highly valued, and highly exploited species that managers are seeking to maintain while species 2 represents a less valued, and less exploited species. We focused on four different model experiments that reflect scenarios that are likely commonly encountered by fisheries managers. While not an experiment, first, we sought to understand how the fishery in this model functioned over a range of harvest levels (both species 1 and 2). The aim of this simulation was to understand species dynamics and the stable states that are present in our simulated fishery system. In our first experiment, we sought to the implications of active management of only one species (species 1) *versus* both species (species 1 and 2), and the resultant influence on species dynamics. Our second model experiment focused on the interactive effects of management on both species in the system. Here, we sought to understand the different paths managers may take to the same outcome through managing one or both species. Finally, we explored the influences of slow changes in habitat availability and the resultant influences on stable states. Within this model experiment, we take a safe-operating space approach where managers use the tools at their disposal to keep a system in the desired stable state despite slow moving changes outside their control. Different modeling runs used slightly different parameterizations for harvest, stocking, and habitat availability (Appendix/Supplement). Species interaction strengths, mortality, survival, and fecundity were held constant across simulations (Appendix/Supplement). Model simulations were performed in R using RStudio and the deSolve package (Soetaert et al. 2010, R Core Team 2020, RStudio Team 2020).

# Results

The model demonstrated alternative stable states (Fig. 1). Across the range of harvest rates when run to equilibrium, the model outcomes differed depending on the initial system state. For example, a harvest rate of approximately 5 fish per unit effort on species 1 resulted in scenarios where species 1 dominates over species 2 or vice versa depending on initial system state. In general, in scenarios in which species 2 initially dominates, increasing harvest on species 1 results in results in a stable state in which species 2 remains dominant, however, reversing this scenario resulted (initial system dominated by species 1), increasing harvest on species 1 results in the eventual transition to an alternate stable state in which species 2 dominates. Model behavior suggests that in this two species system, alternative stable states are driven largely by initial conditions and species harvest.



Figure 1. Model exhibits alternative stable states. The model is run to equilibrium over a range of harvest rates for species 1, species 2 harvest is held constant at 2. Top panel shows equilibrium abundances for the range of harvests when species 1 is initially dominant. Bottom panel represents outcomes when species 2 is initially dominant.

Our first model experiment focused on the implications of single species *versus* two-species management in our model system. Managing both species simultaneously produced drastically different outcomes than single species management. In scenarios in which species 1 began as the dominant species, stocking and harvest reductions could be used separately or in combination to maintain the dominance of this species. As harvest increased, stocking was required to maintain the stable state and retain dominance; higher harvest resulted in greater stocking need. However, when management of species 1 and species 2 co-occurs, the options for managers expanded from stocking and harvest regulations for species 1 to stocking and harvest regulations for both species, doubling the number of options available to achieve desired outcomes. In this scenario in which both species are managed (Figure 2), the manager can regulate harvest on both species and stocks species 1 in order to allow species 1 to dominate over species 2. When species 1 is established as the dominant species and a small amount of fishing mortality is applied on species 2, the system is able to maintain species 1 dominance under all but the most intense harvest pressure scenarios on species 1 with no stocking necessary. A small amount of stocking was able to overcome extreme harvest effects and allow for species 1 to dominate across any harvest rate (Fig. 2). These analyses were also conducted in a model scenario where the undesirable species (species 2) was initially dominant and the management goal was to flip the system to favor species 1. The dynamics in that scenario mirror those presented in figure 2, but because of the initial dominance of species 2, the magnitude of management action (stocking or harvest) needed to flip to system towards species 1 is higher in order to overcome the initial dominance of species 2.



Figure 2. Species 1 dominance isocline where areas above line represent species 1 stocking and harvest combinations that allow species 1 to dominate. Areas below the isoclines represent scenarios where species 2 dominates. Species 1 is initially dominant and the management goal is to maintain this dominance. Solid line indicates scenario in which species 2 is not harvested, while the dashed line indicates a scenario in which species 2 is harvested.

Investigation of the interactive effects of management on both species revealed that there are different, and sometimes counter-intuitive management interventions that can lead to similar outcomes. Consideration of species interactions allow managers to combine direct management action (i.e. stocking) with indirect action (i.e. managing a competitor). Managers can use these strategies by themselves or in combination to achieve the same outcome (Figure 3). The trade-off between stocking and harvest of competitor is consistent across different levels of harvest on the desired species; only the magnitude of management action necessary changes. At low levels of species 2 harvest, stocking may be necessary to maintain the stable state of the system. However, as harvest of species 2 increases, stocking interventions may become less necessary. While this result may seem fairly intuitive, here we show the magnitude of stocking necessary to overcome. Additionally, the reverse is true: managers can decrease stocking effort by encouraging harvest of species 2 in order to maintain the stable state of a system.



Figure 3. Stocking of species 1 and harvest of species 2 can both result in maintaining the desired stable state of a system (species 1 dominance). Tradeoff between stocking and competitor harvest are presented for various levels of harvest on species 1 (solid and dashed lines). Areas above the lines represent positive outcomes (species 1 dominance), areas below represent negative outcomes (alternate stable state in which species 2 dominates). The negative relationship between stocking species 1 and harvesting species 2 allows managers to achieve similar outcomes through implementation of either strategy or a combination of both.

Finally, a scenario was explored where slow moving changes in habitat availability can drive an eventual flip in system state from species 1 to species 2. Investigation of slow change towards tipping points in a system revealed the effectiveness of management intervention for the prevention of shifts to alternate stable states. Management action can delay an inevitable transition through either stocking species 1 (Fig. 4b) or harvesting species 2 (Fig. 4c). In combination, managing both species (through stocking of species 1 and harvest of species 2) may be able to prevent a regime shift altogether (Fig. 4d). Our model results show that with a combination of strategies, species 1 population can decrease without a compensatory increase in species 2, thereby effectively maintaining conditions for species 1 even under slow change scenarios. Management action here was limited to what might be feasible given time and budget constraints for most managers.



Figure 4. Delaying transitions. Slow moving variable ’h’ represents changing habitat availability which will inevitably flip system from sp1 dominated to sp2 (panel A). The flip in system state can be delayed through either stocking of the desired species (panel B), harvest of its competitor (panel C), or perhaps prevented altogether by stocking and harvesting (panel D).

# Discussion

Sudden, unexpected regime shifts represent a growing threat to aquatic systems as human influences on these systems grow and erode system resilience. Here, we have illustrated how species interactions can result in non-linearity in a fisheries system, which can ultimately result in transition between alternative stable states. We further demonstrate how management interventions can be used to maintain stable states of a system through careful consideration of human influences and species interactions within the system. Where a single species management approach is infeasible or unable to reach those outcomes, our relatively simple model of a multi-species recreational fishery demonstrates how understanding the ecological interactions between species can allow a manager to creatively manage a system to reach desired outcomes. Although species interactions have long been known to exert influence on a system, here we show how direct management can use those interactions in order to influence fishery outcomes. While our model is a simplification of a complex system, it demonstrates the need to incorporate our understanding of the ecology of aquatic ecosystems into a holistic view of managing these important resources.

Traditionally, fisheries have been managed through a single species lens (Walters et al. 2005, Carpenter et al. 2017). Our results, and the work of others, demonstrates why positive feedback loops which are unaccounted for, often produce unexpected outcomes in the eyes of decision makers (Tonn et al. 1992, Pine et al. 2009). In our model the key feedback loop is through juvenile competition and predation by adults. When maintaining the abundance of species 1, the manager’s ultimate goal is to maintain or increase the number of maturing to adulthood. This can be done directly through stocking, adding more juveniles such that more survive to adulthood. Our model demonstrates how this may be less effective than expected because a portion of the stocked fish will feed species 2, promoting their abundance increase and beginning a feedback loop where their own juveniles, , grow more abundant (Fig 4). Thus the magnitude to stocking that is necessary to maintain the system is greatly increased when it is used in isolation (Fig. 2). Alternatively, if fishing mortality is increased on species 2, with or without stocking, survival increases as predation pressure is alleviated, allowing to maintain dominance (Figs. 2 &3). An understanding of how ecological interactions create positive feedback loops that result in stable ecosystem states can allow managers to make decisions that leverage these feedback loops to create the desired stable state.

Understanding the possible outcomes of systems that exhibit this non-linearity can result in more efficient management while utilizing those management tools that have been proven to be effective in single species management. Managers are limited by political, monetary, mechanical, and technological constraints when confronting complex management problems. Most commonly, fishery managers turn to one of four different tools for preventing or mitigating the negative influences of humans on the system; (1) Stocking (e.g., Cowx, 1994), (2) harvest regulation (e.g., length and bag limits; Post et al., 2003), (3) habitat modification (Jennings et al., 1999), and (4) fishery closure (either temporary or permanent). Although each of these management interventions has a history of success in certain circumstances, management response in systems with increased complexity (beyond single species) is not always straightforward. Often, these actions produce no response or a counterintuitive response when we don’t think about interactions between species (Fig. 2). For example, stocking of lake trout in Lake Granby, Colorado resulted in declines in kokanee and other mesopredator populations (Johnson and Martinez, 1995). However, by investigating feedbacks in species interactions, we provide a strategy for using those tools already available in innovative ways to produce positive fishery outcomes.

Consideration of alternative management strategies, such as leveraging ecological interactions, can aid managers in reinforcement of the desired stable state of a system. Although the limited set of options available to managers are often ineffective or even detrimental when implemented without consideration of species interactions, these interactions can be leveraged to create more avenues for maintenance of a stable state. For example, stocking has the potential to be ineffective at maintaining the stable state of a system (Figure 4b). Here, we highlight in particular how ecological interactions can be a reason why stocking is not effective at times. Our model shows that lower cost options, such as harvest controls of the target species, or through management of a competitor species can often be more effective than stocking in producing favorable outcomes (Figures 2 & 3). While there are other drivers that influence the effectiveness of stocking in a system (e.g., habitat loss, climate change; Hansen et al., 2015; Ziegler et al.,2017), this work emphasizes the need to integrate species interactions into management scenarios. Increasing consideration of variability and slow change that is outside a managers control in a system has resulted in the emergence of a safe operating space theory, increasing the call for adapting management to respond to ecological variables and complexity in the system (Carpenter et al., 2017). While safe operating space management allows for management of complexity, we highlight maintaining such a space through consideration of non-linear management strategies. Tradeoffs are likely to arise between directly managing a species or indirectly managing that species through its competitor, however, increasing our understanding of those interactions in likely to increase our predictive ability when proposing alternative management options.

Our two-species model, while relatively simple, illustrates the need to incorporate ecological interactions in fisheries management within complex fishery systems. Human influences on ecosystems will continue to increase, and understanding species interactions can help us creatively manage these systems given the constraints on what managers can feasibly do. While our model adds a layer of complexity not usually considered in most fisheries management models, we understand that there is still significant complexity inherent in these systems that is not modeled here. The exploration of this complexity will allow the integration of multiple ecological and social interactions into fisheries management, as well as provide managers with the tools necessary to sustainably manage fisheries in the most cost- and time-effective way possible. Future work incorporating the cultivation-depensation effects of species interactions can provide empirical evidence supporting the importance of considering ecological interactions in managing complex systems. Increasing complexity of these models to include energetics can also reveal the consequences of alternative stable states on the life history of both the dominant and non-dominant species. Another layer of complexity to consider is the social component of fisheries. Management goals, ultimately, are focused on maintaining a system in a ‘desired’ stable state, however, what is ‘desired’ is determined by human desires. An understanding of how ecological interactions (specifically through cultivation-depensation mechanisms) will respond to changing harvest pressure can reveal how managers can respond to changing demands from stakeholders in their system.

Integration of ecological dynamics into adaptive management of freshwater fisheries can increase managers’ ability to maintain systems in a desired stable state, reducing the likelihood of unexpected or undesirable outcomes, while using standard interventions and reducing overall costs. Experimental reductions in competitor abundance coupled with various stocking regimes is one example of how the knowledge here can be used to design an adaptive management experiment that generates new knowledge about how to creatively manage a fishery. Furthermore, our fairly robust kon ecological interactions and should While our understanding of ecological interactions between species remains incomplete, we do understand some food webs and species fairly well. The wide breadth of knowledge we do have can play an integral role in building resilient fisheries. By taking a more ecosystem-oriented view of management, we can improve outcomes and identify areas for further exploration when our actions produce unexpected outcomes.