Title:

Leveraging species interactions to creatively maintain desired stable states in multi-species recreational fisheries

Accounting for positive feedback loops and stable states can improve management outcomes in recreational fisheries

Managing recreational fisheries from a multi-species perspective: Leveraging species interactions to maintain desired ecosystem states

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**Keywords**

**Statement of Significance**

**Abstract**

# Introduction

Interspecific interactions are often not heavily considered in natural resource management in order to simplify complex management problems (Walters and Martell 2004, Baum and Worm 2009). This simplification may lead to decisions that in hindsight prove to be ineffective or even detrimental (Walters et al. 2000; Springer et al. 2003; Myers et al. 2007; Hansen et al. 2015; Sass and Shaw 2020). For example, Barents Sea capelin (*Mallotus villosus*) stocks have crashed due to interacting effects of overfishing and predation by Atlantic herring (*Clupea harengus*), and subsequent predation of Atlantic herring by Atlantic cod (*Gadus morhua*) delayed the stock’s recovery (Hjermann et al. 2004). These unexpected outcomes have occurred at least in part because decision makers failed to consider interactions between multiple species and life stages (Walters et al. 2000; Jackson et al. 2001; Hansen et al. 2017; Embke et al. 2019; Hutchings 2000). Although challenging, ecosystem-based management (i.e., holistic approaches to manage natural resources that includes accounting for inter-specific interactions and human decision making) can help decision makers avoid unexpected, and often undesirable, outcomes (Pine et al. 2009).

Perhaps the most undesirable scenario for a decision maker whose single-species focused intervention has led to an unexpected response is one that pushes the system to an undesirable alternative stable state. Regime shifts have been well documented in aquatic systems and are often exceedingly difficult to reverse once they have occurred (Carpenter and Kinne 2003). Regime shifts represent an abrupt change in ecosystem configuration that can be self-reinforcing (Carpenter and Kinne 2003). 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 decision makers to change the stable state may not have their intended effects. For instance, Walters and Kitchell (2001) described how positive feedback loops due to cultivation effects could create two alternative stable states in a “trophic triangle” food web consisting of adult and juvenile stages of a top predator and a forage species. Further, size- and food-dependent individual growth can result in depensatory population growth, also known as an ‘Allee Effect’ (De Roos and Persson, 2002). 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. Depensatory growth effects on the predator population further limit its ability to rebound and become abundant again.

In addition to interactions with non-targeted species as in the simple trophic triangle models described above, exploited populations are often embedded in a larger community in which harvest of multiple species takes place (Hansen et al. 2015). The tradeoffs between competing management goals for several co-occurring exploited species in recreational fisheries are often not considered; however, some notable exceptions do exist in commercial fisheries (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). Decision makers accounting for inter-specific interactions could leverage these dynamics to creatively achieve their goals and thereby reduce unexpected outcomes and decrease the probability of catastrophic regime shifts.

Recreational fisheries are ideal study systems where decision makers can take advantage of inter-specific interactions to solve complex problems through an ecosystem-based or adaptive management approach. Inland recreational fisheries are specifically amenable to these approaches because of their well-defined boundaries and widespread occurrence across the landscape, which allows for replication and comparison (Walters 1986). An adaptive approach using experimental management actions across many independent systems could allow decision makers to generate new knowledge about how to creatively manage these systems; however, this is not always feasible. Management goals, in systems that have the potential to exhibit multiple stable states, often aim to maintain fisheries in the ‘desired’ stable state or the state in which the species most desired by anglers dominates the system. Although these desired stable states exist within a broader safe operating space, certain management interventions could result in shifts into ‘undesired’ states – or states outside a safe operating space. Decision makers are limited in the ways in which they can influence recreational fisheries (i.e., fishing regulations, stocking, effort limitation, habitat alteration, valuation), yet fisheries users have diverse goals. Given recreational fishery complexity, understanding and leveraging ecological interactions may allow decision makers 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 recreational fishery users in the system (Carpenter et al. 2017).

Here, we use a model of a recreational fishery with two managed species to explore whether decision makers can leverage ecological, interspecific interactions to achieve desired outcomes. The hypothetical decision makers’s motivation in our modeling experiments is to promote stable states in which the desired species dominates, resulting in higher economic benefits and user satisfaction. Our model, like all models, makes simplifying assumptions to balance tractability with realism. We use a relatively simple fishery model that allows for the interaction and harvest of two species. Our model imagines that decision makers can take advantage of inter-specific interactions to creatively influence system dynamics to meet their goals. We hypothesize that management activities taking species interactions into account will be more successful at keeping a system in a ‘desired’ state. As such, we predict that consideration of these interspecific interactions and the resulting non-linear dynamics will lead to more positive, predictable, and desired outcomes. We use modeling experiments to understand the influence of simultaneous management of two species in a recreational fishery, the increased diversity of management options when accounting for species interactions, and the effects of slow change on the stable state of the system.

# Methods

To explore the implications and opportunities of a systems-based approach to managing regime shifts in recreational fisheries, we used a modeling approach. Given the long time scales over which management decisions and fisheries dynamics operate, alternative avenues of inference such as long-term observations, comparative surveys, or experiments were not feasible (Carpenter 1998). Our modeling framework allowed us to conduct a series of modeling experiments to explore the risks of not considering inter-specific interactions, including harvest of multiple species, and potential opportunities afforded by an ecosystem-based management approach. For example, we used our model to explore management outcomes for scenarios where the hypothetical decision maker either ignores or accounts for inter-specific interactions. Our theoretical model was based on interactions between walleye (*Sander vitreus*) and largemouth bass (*Micropterus salmoides*) in North American north-temperate lakes, but we have adopted a general model parameterization that should apply to many interacting, exploited species.

## *Model*

For our modeling experiments, we adapted a stage-structured food web model previously used to explore alternative stable states in lake ecosystems (Carpenter and Brock 2005, Roth et al. 2007; Carpenter et al. 2008, Biggs et al. 2009). The original model used a trophic triangle structure that included interactions between the juvenile and adult stages of a harvested sport fish and a single-stage planktivorous fish not subjected to harvest. We modified this model to include two stage-structured fish populations that are both harvested. Our model contains basic foraging arena dynamics in which juveniles move between the foraging arena and refuge (Walters and Juanes 1993, Walters and Martell 2004, Ahrens et al. 2012). In our model, adults can prey on their own juveniles and on juveniles of the competing 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, but adults have asymmetrical effects on the juveniles of the opposite species (Table 1). Unless noted, all parameters are constant through time.

### *Adult Dynamics*

Eq. 1

Eq. 2

Adults of Species 1 or Species 2 are produced through the maturation of juveniles at a constant rate or . Adults undergo natural mortality, and , and are harvested at rates and . Harvest rate can be either constant or time-dependent.

### *Juvenile Dynamics*

Eq. 3

Eq. 4

Juveniles are produced through Beverton-Holt stock-recruitment relationships (Ricker, 1975). Additionally, stocking of juveniles can be imposed through and . Juveniles are removed from the population in 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. First, juvenile mortality can occur through cannibalism, for example (read this as ‘the effect of on ’), which is dependent on refuge dynamics. Second, juveniles can be removed 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. However, it is important to note that the influence of refuge availability on juvenile mortality is still debated in some systems (Zeigler et al. 2018). Refuge availability is commonly assumed to decrease predation risk (Walters and Juanes 1993, Ahrens et al. 2012). Last, juvenile mortality is imposed through direct competition with juveniles of the opposite species, such as might occur through competition for resources or direct predation. This competition occurs independent of refuge dynamics; all juveniles compete in all areas. We assumed that juveniles of both species occupy the same refuge and same foraging arena. All juveniles not claimed by the three sources of mortality then mature to adults at some proportion ().

Table 1. Model parameterization

|  |  |  |
| --- | --- | --- |
| Term | Definitions | Value/Range |
|  | survival, species 1 juvenile | 0.1 |
|  | natural mortality, species 1 adult | 0.1 |
|  | cannibalism, species 1 | 0.001 |
|  | predation by species 2 on species 1 | 0.05 |
|  | juvenile competition | 0.003 |
|  | rate at which species 1 juveniles enter FA\* | 1 |
|  | rate at which species 1 juveniles leave FA | 8 |
|  | stocking, species 1 | 0-4000 |
|  | harvest rate, species 1 | 0-8 |
|  | survival, species 2 juvenile | 0.1 |
|  | natural mortality, species 2 adult | 0.1 |
|  | cannibalism, species 2 | 0.001 |
|  | predation by species 1 on species 2 | 0.03 |
|  | juvenile competition | 0.003 |
|  | rate at which species 2 juveniles enter FA | 1 |
|  | rate at which species 2 juveniles leave FA | 8 |
|  | stocking, species 2 | 0-4000 |
|  | harvest rate, species 2 | 0-8 |

\*foraging arena

## *Model Experiments*

Recreational fisheries are complex systems in which human influences and ecological interactions feed back on each other to make applied management of any species challenging. A key challenge facing many decision makers is how to maintain or improve abundances of highly valued and exploited species in the face of competition with other less valued and exploited species. Our model experiments were 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. When managing the focal species (species 1) alone, decision makers have control over harvest limits and stocking rates. When managing both species simultaneously, decision makers have control over harvest limits and stocking rates for both species. Given the hypothetical goals of decision makers in our simulations, managing species 2 will always take the form of setting harvest limits and not stocking.

After exploring its basic dynamics and validating that the model produced alternate stable states , we focused on three different model experiments that reflect scenarios commonly encountered by fisheries decision makers.

In our first experiment (Leveraging Interactions Experiment), we sought to understand the implications of active management of only one species (species 1) *versus* both species (species 1 and 2) on the “desired state” of the system. In this experiment, we sought to explore the infuence of leveraging ecological interactions to achieve decision maker’s goals related to retaining a desired stable state.

Our second modeling experiment focused on the diversity of management options available to decision makers when accounting for interspecific interactions (Alternative Approaches Experiment). Here, we sought to understand the different paths decision makers may take to the same outcome through managing one or both species using available management tools (i.e., stocking and harvest regulation).

Finally, we explored the influences of slow changes (i.e., those outside of managerial control) in adult fecundity and the resultant effects on stable states (Safe Operating Space Experiment). This experiment used a safe-operating space approach in which decision makers use the tools at their disposal, including leveraging species interactions, to keep the system in a desired stable state despite slow moving changes outside of managerial control (Carpenter et al. 2017). We explored a scenario in which slow changes to fecundity of species 1 may drive an eventual flip in stable state from species 1 to species 2, mimicking recruitment declines that have been observed in fisheries for a wide array of reasons (Walters and Martell 2004, Lynch et al. 2016). Similar slow-moving changes may occur in other parameters such as juvenile refuge availability (though in some cases managers may be able to control this variable) or angler preferences. Different modeling runs used slightly different parameterizations for harvest, stocking, and fecundity (Table S1).

Species interaction strengths, mortality, survival, and habitat availability were held constant across simulations (Table 1). Our model is based on walleye-largemouth bass interactions, but generalizable as to not be representative of a specific population of fish. As such, the abundances, stocking rates, and harvest rates presented here are not meant to be interpreted literally. The stocking and harvest rates in this experiment are relatively small and represent influences a decision maker might realistically have given other constraints. Model simulations were performed in R using RStudio and the deSolve package (Soetaert et al. 2010, R Core Team 2020, RStudio Team 2020).

**Results**

*Model Validation*

The model exhibited alternative stable states in this simulated two species fishery. Initial species abundances and species harvest determined stable state outcomes (Fig. 1). Alternative stable states persisted across all but the most extreme values for species interaction strengths, mortality, survival, and fecundity. When run to equilibrium across the range of harvest rates, the model outcomes differed depending on the initial system state, demonstrating alternative stable states (Fig. 1). For example, a moderate harvest rate on species 1 resulted in scenarios in which species 1 dominates over species 2 or vice versa depending on initial system state. In general, in scenarios where species 2 initially dominated, increasing harvest on species 1 resulted in a stable state where species 2 remains dominant. However, when reversing this scenario (initial system dominated by species 1), increasing harvest on species 1 resulted in the eventual transition to an alternate stable state where species 2 dominated. Harvesting in the model decreased the target species’ abundance and eventually led to a regime shift (Fig. S1). Sensitivity analysis showed that alternative stable states persisted across different values for species interaction strengths, mortality, survival, and fecundity with a few exceptions for extreme parameter values (Figs S5-13). Harvest rates at which the system flipped differed with variation in parameter values (Figs S5-13). The point at which the lines for species 1 and 2 cross represents a stable state change. Increasing juvenile survival to adulthood ( or ), for example, shifts the threshold further right indicating that the range of harvests over which alternative stable states occur is increased (Fig. S5). The model was most sensitive to changes in competition amongst juveniles, and to Ricker stock-recruitment parameters (Figs S9, S10, S12, S13**)**.

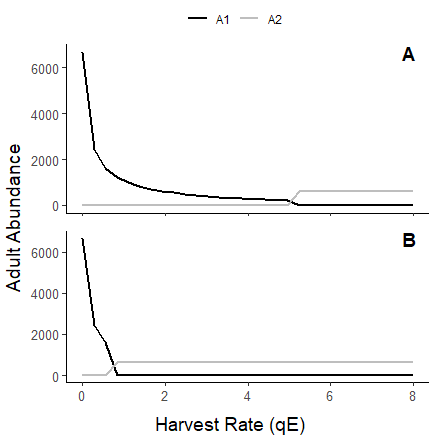


Figure 1. Model exhibits alternative stable states. The model is run to equilibrium over a range of harvest rates for species 1, while harvest of species 2 is held constant (qE2=2). Panels show equilibrium results when (A) species 1 is initially dominant or (B) species 2 is initially dominant. The region of the x-axis between the thresholds in panels A and B represents the range of harvest rates over which alternative outcomes can occur; over this range of harvest rates it is the initial abundances, not the harvest rates, that determine equilibrium abundances.

*Leveraging Interactions*

Managing both species simultaneously produced different outcomes than single species management (Fig. 2). In the Leveraging Interactions Experiment, species 1 began as the dominant species where the areas above the isoclines described stocking and harvest reductions which could be used separately or in combination and at different magnitudes to maintain species 1 dominance. As harvest increased, stocking was required to maintain the stable state and retain dominance; higher harvest resulted in greater stocking need. When managing only species 1, stocking species 1 resulted in a regime shift when the number of fish stocked was too low (dashed line, Fig 2). This occurred under all species 1 harvest levels except the very lowest (Fig 2). However, when the manager considers the interaction between species (solid line, Fig. 2), the options expanded from stocking and harvest regulations for species 1 to stocking and harvest regulations for both species, doubling the number of management options available. When species 1 is established as the dominant species and a small amount of fishing mortality is applied on species 2, the system can maintain species 1 dominance under all but the most intense harvest scenarios on species 1 with no stocking necessary (solid line, Fig 2). Allowing increased harvest on species 2, in combination with a small amount of species 1 stocking, overcame extreme harvest effects on species 1 allowing it to dominate across any harvest rate (solid line, Fig. 2). Accounting for the ecological interactions between species allowed the decision maker to use harvest of species 2 to increase the number of species 1 management options that would maintain its dominance. Similar analyses were also conducted in a modeling scenario where the undesirable species (species 2) was initially dominant and the management goal was to change the stable state to favor species 1 (Fig. S3). The dynamics in this 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 change the stable state towards species 1 was higher to account for initial dominance of species 2.

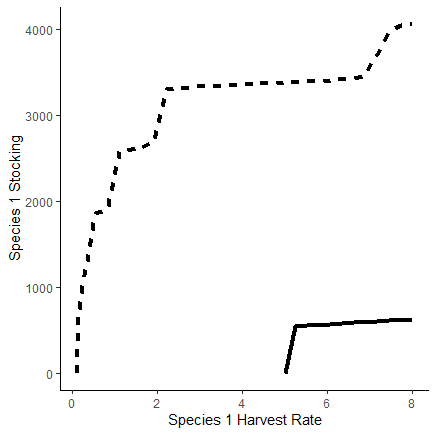


Figure 2. Leveraging interspecific interactions expands the range of management options that can achieve the management goal. In this experiment, species 1 is initially dominant and the goal is to maintain that dominance. The dashed and solid lines are isoclines separating combinations of species 1 harvesting and stocking rates that yield species 1 dominance (above each line) from combinations that yield species 2 dominance (below each line). If the manager only controls species 1 harvesting and stocking rates (dashed line), the ranges of those rates that produce the desired outcome of species 1 dominance are relatively limited (above dashed line). If the manager also imposes harvest on species 2 (solid line), the range of species 1 harvest and stocking rates that produce the desired outcome is greatly expanded (above solid line).

*Alternative Approaches*

The Alternative Approaches Experiment showed that species 1 dominance can be maintained through diverse management actions when accounting for interspecific interactions. Consideration of species interactions allowed decision makers to combine direct management action (i.e., stocking) with indirect action (i.e. managing a competitor); these strategies can be implemented individually or in combination to achieve the same outcome (Figure 3). The trade-off between stocking and harvest of the competitor was consistent across different levels of harvest on the desired species; only the magnitude of management action necessary changed. At low levels of species 2 harvest, more stocking was required to maintain the stable state of the system where species 1 remained dominant. Decision makers can decrease stocking effort by encouraging harvest of species 2 in order to maintain the stable state of a system. These dynamics were also explored for a scenario in which the decision maker aimed to change the stable state from species 2 dominance toward species 1 (Fig. S4). Because of the initial dominance of species 2 in this scenario, the magnitude of management action (stocking or harvest) needed to change the stable state towards species 1 was higher to account for initial dominance of species 2.

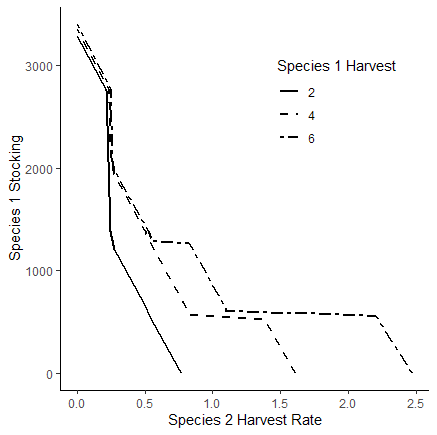


Figure 3. Stocking of species 1 and harvest of species 2 can, on their own, result in maintaining the desired stable state of a system (species 1 dominance) in the Alternative Approaches Experiment. Tradeoff between stocking and competitor harvest are presented for various levels of harvest on species 1 (solid and dashed lines). Areas above/to the right of the lines represent positive outcomes (species 1 dominance), areas below/to the left represent regime shifts to species 2. 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.

Safe Operating Space

Investigation of slow change towards a threshold in the system revealed the effectiveness of management intervention for the prevention of shifts to alternate stable states. Management action delayed an inevitable transition through either harvesting species 2 (Fig. 4b) or stocking species 1 (Fig. 4c). In combination, managing both species (through stocking of species 1 and harvest of species 2) prevented a regime shift altogether (Fig. 4d). A combination of strategies still led to a decrease in species 1 abundance but avoided a compensatory increase in species 2, thereby effectively maintaining conditions for species 1 even under slow change scenarios. When no management action is taken, the stable state changes after 41 years (Fig. 4a). Minimal harvesting (=0.5) alone was able to delay the transition by 130 years (Fig 4b). Adding 500 juveniles annually through stocking delayed the change in stable state by 18 years (Fig. 4c). Management action here was limited to what might be feasible given time and budget constraints for most decision makers within the parameterization of our hypothetical two species system (i.e., harvest control and stocking).

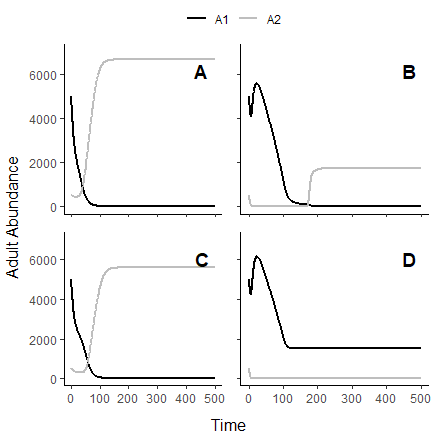


Figure 4. Delaying transitions in the Safe Operating Space Experiment. Slow declines in recruitment represents a factor outside of managerial control, which will inevitably change the stable state from sp1 dominated to sp2 (no action; panel A). The change in system state can be delayed through either harvest of species 2 (panel B), or stocking of the desired species (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 grow and erode ecosystem resilience (De Roos and Persson 2002, Carpenter and Kinne 2003, Persson et al. 2007). We demonstrated how management interventions could be used to maintain stable states of a system through careful consideration of human influences and interspecific interactions as drivers of regime shifts within a system. Where a single species management approach is infeasible or unable to achieve the desired stable state, our relatively simple model of a multi-species recreational fishery demonstrated how species interactions could allow a decision maker to creatively manage a system to reach desired outcomes. Although interspecific interactions have long been known to exert influences on a system, here we showed how direct management can use those interactions in order to influence fishery outcomes, including changing the stable state of a system. Although our model is a simplification of a complex system, it demonstrated the need to incorporate drivers of stable state dynamics into the management of these important resources. In practice, this is challenging to do as interactions within aquatic communities and our understanding of them continue to change; however, integration of species interactions is a step in the right direction towards a more holistic view of inland recreational fishery systems.

Fisheries have often been managed through a single species lens (Hjerman et al. 2004, Walters et al. 2005, Carpenter et al. 2017); however, this practice has not always resulted in positive outcomes. Our results, and the research of others, have demonstrated why positive feedback loops, which are often unaccounted for, sometimes produce unexpected outcomes in the eyes of decision makers (Tonn et al. 1992, Pine et al. 2009, Solomon et al. 2020). In our model, the key feedback loop was through juvenile competition and predation by adults. When maintaining the abundance of species 1, the decision maker’s ultimate goal is to conserve or increase the number of maturing to adulthood. Although this result can be achieved directly through stocking, this may not be the most effective management strategy; limitations to stocking include density-dependent mortality and high costs associated with adding individuals (Cowx, 1999). Furthermore, our model demonstrated how stocking can be rendered ineffective when a portion of the stocked fish will feed species 2, thereby promoting species 2 abundance and beginning a feedback loop wherein their own juveniles, , increase in abundance (Fig 4c). Thus, the magnitude of stocking that was necessary to maintain the system was greatly increased when solely stocking was implemented, which may not be feasible given other limitations associated with stocking (Fig. 2). Alternatively, if fishing mortality was increased on species 2, with or without stocking, survival increased as predation pressure was alleviated, allowing to maintain dominance (Figs. 2 &3). An understanding of how ecological interactions create positive feedback loops (e.g., Pine et al., 2009) that result in stable ecosystem states can allow decision makers to make choices that leverage these feedback loops to increase the probability of maintaining the desired stable state.

Decision makers are limited by political, monetary, mechanical, and technological constraints when confronting complex management problems. Most commonly, fishery decision makers turn to one of four different tools for preventing or mitigating the negative influences of humans on a 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, Sass et al. 2017); and/or (4) fishery closure (either temporary or permanent). Although each of these management interventions has a history of success in certain circumstances, management responses in complex systems (beyond single species) are not always straightforward. Often, these actions produce no response or a counterintuitive response when species interactions are not acknowledged (Fig. 2). For example, stocking of lake trout (Salvelinus namaycush) in Lake Granby, Colorado resulted in declines in Kokanee salmon (Oncorhynchus nerka) and other meso-predator species (Johnson and Martinez, 1995). However, by investigating feedbacks in these interactions, we provide a strategy for using those tools already available in innovative ways to produce positive fishery outcomes. Not only must a decision maker consider direct and indirect management, but timing of management interventions and lags in implementation have also been shown to influence the outcome of action (Biggs et al. 2009, Martin et al. 2020).

Consideration of alternative management strategies, such as leveraging ecological interactions, can aid decision makers in reinforcing the desired stable state of a system. Although the limited set of options available to decision makers may be 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 4c). Here, we highlight how inter-specific interactions can be a reason for stocking ineffectiveness at times. Our model showed that alternatives such as harvest controls of the target species or management of a competitor species can often be more effective than stocking in the production of favorable outcomes (Figures 2 & 3). Although there are other drivers that influence the effectiveness of stocking in a system (e.g., habitat loss, climate change, genetics; Lorenzen, 2014; Hansen et al., 2015; Ziegler et al. 2017; Tingley et al. 2020), our research emphasizes the critical need to integrate species interactions into management scenarios. This idea is not entirely novel; indeed, invasive species management has long included introducing ‘biocontrol’ agents into a system in an effort to reduce invasive species abundance (Krueger and Hrabik 2005; Messing and Wright, 2006; Roth et al. 2010; Gaeta et al. 2015). A key distinction between our multi-species fishery and invasive species management was the use of existing ecological interactions between the species already present, as opposed to the introduction of a novel agent.

Certain drivers of regime shifts in ecosystems may be outside of managerial control, such as slow moving changes in recruitment as a result of climate change (Hansen et al. 2017). Increasing consideration of these drivers has resulted in the emergence of a safe operating space concept, increasing the call for adapting management to respond to ecological variables and complexity in the system (Carpenter et al., 2017, Hansen et al. 2019). Although safe operating space concepts allows for the 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, a better understanding of those interactions is likely to increase predictive ability when proposing alternative management options. Incorporation of the feedbacks and complexity contained within inter-specific ecological interactions can provide decision makers with a new dimension to maintain a system in a safe operating space, even in the face of other slowly changing variables.

Our two-species model, although relatively simple, illustrates the need to incorporate ecological interactions in fisheries management within complex fishery systems. Human influences on ecosystems will continue to increase (Sih et al., 2011), and understanding species interactions can help to creatively manage these systems given the constraints that decision makers face. Although our model added a layer of complexity not usually considered in most fisheries management models (Solomon et al. 2020), we acknowledge that there is still significant complexity inherent in these systems that was not simulated here. Further exploration of this complexity will allow the integration of multiple ecological and social interactions into fisheries management, as well as provide decision makers with the tools necessary to sustainably manage fisheries in the most efficient ways possible. Future research incorporating cultivation-depensation effects of species interactions, or other ecological interactions that induce alternate stable states, may provide empirical evidence supporting the importance of considering these dynamics in managing complex systems. Increasing complexity of these models to include energetics may also reveal the consequences of alternative stable states on the life histories of the dominant and subordinate species.

Another layer of complexity to consider is the social component of fisheries (Solomon et al. 2020). 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-orientation (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. For example, anglers may choose to voluntarily catch and release certain species (Gaeta et al. 2013; Sass and Shaw 2020). When managers try to promote harvest of a given species (e.g.,through liberalized bag and length limits), anglers may simply choose to continue releasing their catch, rendering this management strategy ineffective (Miranda et al. 2017; Sass and Shaw 2020). Management goals are often focused on maintaining a system in a ‘desired’ stable state; however, what is ‘desired’ is determined by human desires and may conflict with overall sustainability of the resource. Appropriate responses or management to changing demands from stakeholders in their system will be reliant on a foundational understanding of ecological interactions (specifically through cultivation-depensation mechanisms) and the resultant shifts towards a more ‘desirable’ stable state. Ultimately, sustainability of the resource in the long-term should trump human desires. Sustainable resource use and meeting human desires need not be in conflict, and by accounting for inter-specific interactions, decision makers may be able to achieve both goals.

Integration of ecological dynamics, inter-specific interactions, and potential regime shifts into ecosystem-based freshwater fisheries management may increase a decision maker’s ability to maintain systems in a desired stable state and reduce 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 just one example of how our modeling results could be used to design an adaptive management experiment that generates new knowledge about creatively managing fisheries. In practice, adaptive management is challenging to implement and often fails; however, the causes of these failures have been well studied and allow for a way forward towards success (Walters 1998, Walters et al. 2007, Allen and Gunderson 2011). The wide breadth of knowledge accumulated can play an integral role in building resilient fisheries. By taking a more ecosystem-oriented view of management, outcomes can be improved, and areas can be identified for further exploration when actions produce unexpected outcomes.