**Managing recreational fisheries from a multi-species perspective: Leveraging species interactions and accounting for positive feedback loops to maintain desired ecosystem states**

Colin J. Dassow1, Chelsey L. Nieman2, Chris T. Solomon2, Greg G. Sass3, and Stuart E. Jones1

1. Dept. of Biological Sciences, University of Notre Dame, Notre Dame, IN, USA.
2. Cary Institute of Ecosystem Studies, Millbrook, NY, USA.
3. Wisconsin Dept. of Natural Resources, Boulder Junction, WI, USA.

**Keywords**

**Statement of Significance**

**Abstract**

Historically, recreational fisheries have been managed through a single-species framework where fish species are considered in isolation. Overharvest and subsequent regime shifts preventing populations from recovering characterizes many of the most prolific commercial fishery collapses. A common factor leading to regime shifts and preventing population recovery is interspecific interactions between the collapsed species and its competitors. Increasingly, ecosystem-based management has been advocated in recreational fisheries where users have a more diverse set of goals than commercial fisheries where profit maximization is prioritized. We use a modeled recreational fishery to describe how interspecific interactions between two harvested species can drive shifts in the dominant species using modeling experiments. These experiments explore 1) the effectiveness of single-species management actions at maintaining the desired stable state is compared to multispecies actions 2) the diversity of paths that can lead to positive outcomes when leveraging interspecific interactions, and 3) how interspecific interactions can be leverage to keep a system in a safe-operating-space despite stable state drivers that are outside a managers control. Accounting for interspecific actions allows decision makers to meet their goals through a diverse and cost-effective combination of direct (i.e., managing the focal species through stocking and harvest limitation) and indirect (i.e. managing the competitor) means.

# 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; Myers et al. 2007; Hansen et al. 2015; Sass and Shaw 2020). For example, Atlantic cod (*Gadus morhua*) stocks in the Baltic Sea collapsed in the late 1980’s and the population failed to recover during the 20 years after collapse despite the restriction in harvest (ICES 2006). Subsequent research identified ecological interactions with sprat as the factor limiting cod recovery and called for a more holistic plan that accounts for these interspecific interactions in the cod recovery strategy (Casini et al. 2009). These unexpected outcomes have occurred at least in part because decision unable to account for 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 interspecific interactions and human decision making) can help decision makers avoid unexpected, and often undesirable, outcomes (Pine et al. 2009).

While in many instances, ecosystem-based management may result in unexpected outcomes with a wide variety of potentially negative effects, here, we focus on unexpected regime shifts that push 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 interspecific 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. 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 and Essington 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 interspecific 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 interspecific 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. In these systems certain drivers of regime shifts may be outside a decision maker’s control such as slow moving changes in climate. 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 despite slow moving changes outside their control (e.g., changes to fecundity, loss of refuge, etc.), 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 interspecific interactions to achieve desired outcomes. The hypothetical decision makers’s motivation in our model 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. With this model, we compare and contrast outcomes of management actions under scenarios when interspecific interactions are considered and when they are not. 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

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). Instead, we use a dynamic model to explore the implications and opportunities of a systems-based approach to managing regime shifts in recreational fisheries. Our theoretical framework allowed us to conduct a series of modeling experiments exploring the benefits of considering interspecific interactions in management, and potential opportunities afforded by an ecosystem-based management approach. For example, we used our model to explore management outcomes for scenarios in which the hypothetical decision maker either ignores or accounts for interspecific interactions.

## *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 2004; Roth et al. 2007; Carpenter et al. 2008; Biggs et al. 2009). The original model used a trophic triangle structure that included interactions among 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 predation on juveniles occurs in the foraging arena where adults can prey on their own juveniles and on juveniles of the competing species. 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 (Beverton and Holt 1957). 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, and . 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. Refuge availability is commonly assumed to decrease predation risk (Walters and Juanes 1993; Ahrens et al. 2012; but see Ziegler et al. 2018). 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 foraging arena | 1 |
|  | rate at which species 1 juveniles leave foraging arena | 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 foraging arena | 1 |
|  | rate at which species 2 juveniles leave foraging arena | 8 |
|  | stocking, species 2 | 0-4000 |
|  | harvest rate, species 2 | 0-8 |

## *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 modeling experiments were designed to mimic this situation. Species 1 in our models represents the initially 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 for the focal species only; as opposed to controlling harvest and stocking for both species respectively when managing from a whole-ecosystem perspective. Given the hypothetical goals of decision makers in our simulations, species 2 management will always take the form of setting harvest limits and not include stocking.

After exploring its basic dynamics and validating that the model produced alternate stable states, we focused on three different modeling 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 influence of leveraging ecological interactions to achieve decision maker’s goals related to retaining a desired stable state. In this experiment, while species 2 is not the focal species, harvest of species 2 is likely to occur, however, in the first part of the experiment (species 1 active management), species 2 is managed for species 2 alone (no interaction considered). In the second part, species 2 is managed explicitly with these ecological interactions in mind.

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 shift 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 theoretical model was loosely based on interactions between walleye (*Sander vitreus*) and largemouth bass (*Micropterus salmoides*) in North American north-temperate lakes. However, we have retained the conceptual interactions and have generalized the model parameterization so that it applies to many interacting, exploited species. As such, the abundances, stocking rates, and harvest rates presented here are meant to illustrate the ideas represented therein, and not meant to be interpreted literally. The stocking and harvest rates in our experiments are relatively small in order to avoid extreme values that overpower ecological interactions within the system and represent influences a decision maker might realistically have, given other constraints. For all experiments, a species was only considered dominant when its abundance exceeded that of its competitor by a minimum of 100 individuals. We set this threshold in order to avoid situations where abundances for the two species were close enough that neither species could reasonably be considered ‘dominant’. Model simulations were performed in R using RStudio and the deSolve package (RStudio Team; Soetaert et al. 2010; R Core 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. Equilibrium abundances of the two species were influenced both by their initial abundances and by the harvest rate on species 1. When species 1 was initially dominant, there was a much wider range of harvest rates over which species 1 remained dominant. 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 (Fig. S4). Harvest rates at which the system transitioned differed with variation in parameter values (Fig. S4). Increasing juvenile survival to adulthood () for example, shifts the threshold higher indicating that the range of harvests over which alternative stable states occur is increased (Fig. S4). The model was most sensitive to changes in competition amongst juveniles, and to Beverton-Holt stock-recruitment parameters (**)**.

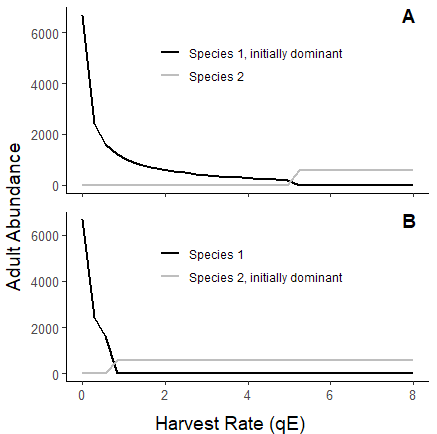


Fig. 1. Model exhibits alternative stable states. The model is run to equilibrium over a range of harvest rates for species 1, while harvest of species 2 is held constant (qE2=2). Panels show equilibrium results when (A) species 1 is initially dominant or (B) species 2 is initially dominant. The region 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 was the initially dominant species. This dominance was maintained for all combinations of stocking and harvest levels that occur above isoclines (Fig. 2). Leveraging interspecific interactions expands the range of management options that can achieve the management goal. The decision maker can manage species 1 in isolation without any consideration of its competitor species 2, or they can manage them together as a system that accounts for their competitive interactions. The dashed and solid lines in Fig.. 2 are isoclines separating combinations of species 1 harvesting and stocking rates that yield species 1 dominance (area above each isocline) from combinations that yield species 2 dominance (below each isocline). If the manager considers only the focal species (species 1) when setting harvest and stocking rates, the ranges of those rates that produce the desired outcome of species 1 dominance are relatively limited (Fig. 2). Generally, as more harvest is allowed for species 1, more stocking is required to maintain the system. When the decision maker uses species 2 harvest rate as an additional tool for maintaining the desired state, the range of species 1 harvest and stocking rates that produce the desired outcome is greatly expanded (Fig. 2). More harvest can be tolerated for species 1 while requiring less stocking when harvest is increased for species 2. Similar analyses were also conducted in a modeling scenario in which 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 Fig. 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.

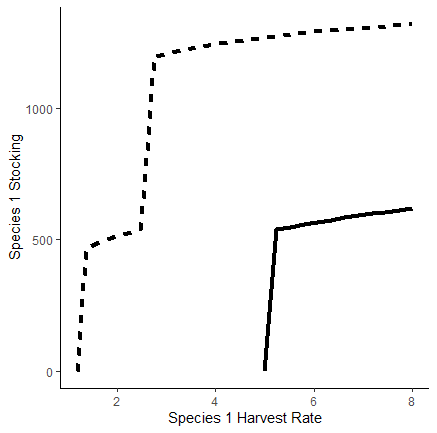


Fig. 2. Leveraging interspecific interactions expands the range of management options that can achieve the management goal. In this experiment, species 1 is initially dominant and the goal is to maintain that dominance. The dashed and solid lines are isoclines separating combinations of species 1 harvesting and stocking rates that yield species 1 dominance (above each line) from combinations that yield species 2 dominance (below each line). Dominance is only assigned when abundances differ by >100 individuals. 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. Combining direct management action (i.e., stocking) with indirect management action (i.e., managing a competitor) creates a diverse set of options for the decision maker allowing them to tradeoff less direct management action for more indirect action or vice versa (Fig. 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 in which 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.

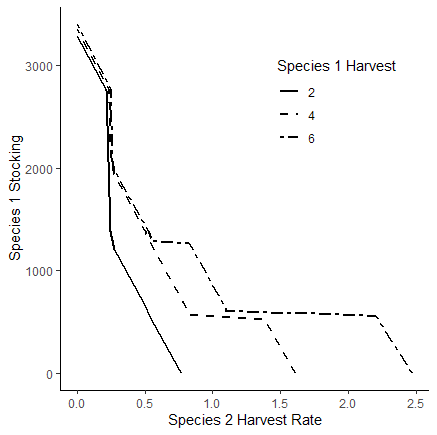


Fig. 3. Stocking of species 1 and harvest of species 2 can, on their own, result in maintaining the desired stable state of a system (species 1 dominance) in the Alternative Approaches Experiment. Tradeoff between stocking and competitor harvest are presented for various levels of harvest on species 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. Dominance is only assigned when abundances differ by >100 individuals. 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 actions implemented singularly may delay a transition through either harvesting species 2 (Fig. 4b) or stocking species 1 (Fig. 4c). In combination however, 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 as a driver outside managerial control pushes the system towards species 2. When no management action is taken, the stable state changes after 40 years (Fig. 4a). Minimal harvesting (=0.5) alone was able to delay the transition by 111 years (Fig 4b). Adding 500 juveniles annually through stocking delayed the change in stable state by 18 years (Fig. 4c). Management action here was chosen to avoid excessively high stocking and harvest rates which can on their own prevent regime shifts but are uninformative when examining how to creatively maintain the system given the constraints decision makers often face.

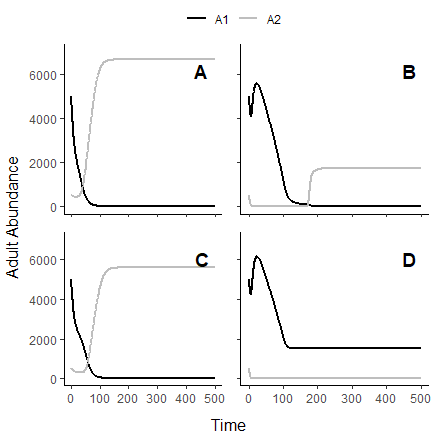


Fig. 4. Delaying transitions in the Safe Operating Space Experiment. Slow declines in recruitment represents a factor outside of managerial control, which will inevitably change the stable state from sp1 dominated to sp2 (no action; panel A). The change in system state can be delayed through either harvest 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. When 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 (Hjermann 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 (Fig. 4c). Here, we highlight how interspecific 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 (Fig.s 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 III et al. 2019), 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 (Secord 2003; Hoddle 2004; 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 allow for the management of complexity, we highlight managing such complexity explicitly through consideration of interspecific interactions. 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 interspecific 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 (Solomon et al. 2020). 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 in which 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. 2015; 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 interspecific interactions, decision makers may be able to achieve both goals.

Integration of ecological dynamics, interspecific 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, 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.

**Acknowledgements**

This work was funded by the U.S. National Science Foundation under grant 176066. We thank C. Mosely, A. Trudeau, C. Iwicki, O. Jensen, and B. van Poorten for their constructive feedback during the development of this paper. (I could so see us acknowledging the Walters and Kitchell paper that was sort of the genesis of this work. Or maybe people don’t really do that sort of thing since it’s already cited.)

**References**

Ahrens, R. N. M., C. J. Walters, and V. Christensen. 2012. Foraging arena theory: Foraging arena theory. Fish and Fisheries **13**: 41–59. doi:10.1111/j.1467-2979.2011.00432.x

Allen, C. R., and L. H. Gunderson. 2011. Pathology and failure in the design and implementation of adaptive management. Journal of Environmental Management **92**: 1379–1384. doi:https://doi.org/10.1016/j.jenvman.2010.10.063

Arlinghaus, R., J. Alós, B. Beardmore, and others. 2017. Understanding and Managing Freshwater Recreational Fisheries as Complex Adaptive Social-Ecological Systems. Reviews in Fisheries Science & Aquaculture **25**: 1–41. doi:10.1080/23308249.2016.1209160

Baum, J. K., and B. Worm. 2009. Cascading top-down effects of changing oceanic predator abundances. Journal of Animal Ecology **78**: 699–714. doi:10.1111/j.1365-2656.2009.01531.x

Beardmore, B., L. M. Hunt, W. Haider, M. Dorow, and R. Arlinghaus. 2015. Effectively managing angler satisfaction in recreational fisheries requires understanding the fish species and the anglers C. Ramcharan [ed.]. Can. J. Fish. Aquat. Sci. **72**: 500–513. doi:10.1139/cjfas-2014-0177

Beverton, R. J., and S. J. Holt. 1957. On the dynamics of exploited fish populations, U.K. Ministry of Agriculture and Fisheries.

Biggs, R., S. R. Carpenter, and W. A. Brock. 2009. Turning back from the brink: Detecting an impending regime shift in time to avert it. PNAS **106**: 826–831. doi:10.1073/pnas.0811729106

Carpenter, S., and W. Brock. 2004. Spatial Complexity, Resilience, and Policy Diversity: Fishing on Lake-rich Landscapes. Ecology and Society **9**. doi:10.5751/ES-00622-090108

Carpenter, S. R. 1998. The Need for Large-Scale Experiments to Assess and Predict the Response of Ecosystems to Perturbation, p. 287–312. *In* M.L. Pace and P.M. Groffman [eds.], Successes, Limitations, and Frontiers in Ecosystem Science. Springer.

Carpenter, S. R., W. A. Brock, J. J. Cole, J. F. Kitchell, and M. L. Pace. 2008. Leading indicators of trophic cascades. Ecology Letters **11**: 128–138. doi:https://doi.org/10.1111/j.1461-0248.2007.01131.x

Carpenter, S. R., W. A. Brock, G. J. A. Hansen, and others. 2017. Defining a Safe Operating Space for inland recreational fisheries. Fish Fish **18**: 1150–1160. doi:10.1111/faf.12230

Carpenter, S. R., and O. Kinne. 2003. Regime shifts in lake ecosystems,.

Casini, M., J. Hjelm, J.-C. Molinero, J. Lövgren, M. Cardinale, V. Bartolino, A. Belgrano, and G. Kornilovs. 2009. Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. PNAS **106**: 197–202. doi:10.1073/pnas.0806649105

Cowx, I. G. 1994. Stocking strategies. Fisheries Management and Ecology **1**: 15–30. doi:https://doi.org/10.1111/j.1365-2400.1970.tb00003.x

Cowx, I. G. 1999. An appraisal of stocking strategies in the light of developing country constraints. Fisheries Management and Ecology **6**: 21–34. doi:https://doi.org/10.1046/j.1365-2400.1999.00139.x

De Roos, A. M., and L. Persson. 2002. Size-dependent life-history traits promote catastrophic collapses of top predators. PNAS **99**: 12907–12912. doi:10.1073/pnas.192174199

Essington, T. E., M. L. Baskett, J. N. Sanchirico, and C. Walters. 2015. A novel model of predator-prey interactions reveals the sensitivity of forage fish: piscivore fishery trade-off to ecological conditions. ICES Journal of Marine Science **72**: 1349–1358. doi:doi:10.1093/icesjms/fsu242

Gaeta, J. W., T. R. Hrabik, G. G. Sass, B. M. Roth, S. J. Gilbert, and M. J. Vander Zanden. 2015. A whole-lake experiment to control invasive rainbow smelt (Actinoperygii, Osmeridae) via overharvest and a food web manipulation. Hydrobiologia **746**: 433–444. doi:10.1007/s10750-014-1916-3

Hansen, G. J. A., J. W. Gaeta, J. F. Hansen, and S. R. Carpenter. 2015. Learning to Manage and Managing to Learn: Sustaining Freshwater Recreational Fisheries in a Changing Environment. Fisheries **40**: 56–64. doi:10.1080/03632415.2014.996804

Hansen, G. J. A., J. S. Read, J. F. Hansen, and L. A. Winslow. 2017. Projected shifts in fish species dominance in Wisconsin lakes under climate change. Global Change Biology **23**: 1463–1476. doi:10.1111/gcb.13462

Hansen, G. J. A., L. A. Winslow, J. S. Read, M. Treml, P. J. Schmalz, and S. R. Carpenter. 2019. Water clarity and temperature effects on walleye safe harvest: an empirical test of the safe operating space concept. Ecosphere **10**: e02737. doi:https://doi.org/10.1002/ecs2.2737

Hjermann, D. Ø., G. Ottersen, and N. C. Stenseth. 2004. Competition among fishermen and fish causes the collapse of Barents Sea capelin. PNAS **101**: 11679–11684. doi:10.1073/pnas.0402904101

Hoddle, M. S. 2004. Restoring Balance: Using Exotic Species to Control Invasive Exotic Species. Conservation Biology **18**: 38–49. doi:https://doi.org/10.1111/j.1523-1739.2004.00249.x

Jennings, M. J., M. A. Bozek, G. R. Hatzenbeler, E. E. Emmons, and M. D. Staggs. 1999. Cumulative Effects of Incremental Shoreline Habitat Modification on Fish Assemblages in North Temperate Lakes. North American Journal of Fisheries Management **19**: 18–27. doi:https://doi.org/10.1577/1548-8675(1999)019<0018:CEOISH>2.0.CO;2

Johnson, B. M., and P. J. Martinez. 1995. Selecting Harvest Regulations for Recreational Fisheries: Opportunities for Research/Management Cooperation. Fisheries **20**: 22–29. doi:https://doi.org/10.1577/1548-8446(1995)020<0022:SHRFRF>2.0.CO;2

Johnston, F. D., R. Arlinghaus, and U. Dieckmann. 2010. Erratum: Diversity and complexity of angler behaviour drive socially optimal input and output regulations in a bioeconomic recreational-fisheries model. Can. J. Fish. Aquat. Sci. **67**: 1897–1898. doi:10.1139/F10-113

Lorenzen, K. 2014. Managing Fisheries Enhancements, p. 649–657. *In* Foundations of Fisheries Science. American Fisheries Society.

Lynch, A. J., B. J. E. Myers, C. Chu, and others. 2016. Climate Change Effects on North American Inland Fish Populations and Assemblages. Fisheries **41**: 346–361. doi:10.1080/03632415.2016.1186016

Martin, R., M. Schlüter, and T. Blenckner. 2020. The importance of transient social dynamics for restoring ecosystems beyond ecological tipping points. PNAS **117**: 2717–2722. doi:10.1073/pnas.1817154117

Messing, R. H., and M. G. Wright. 2006. Biological control of invasive species: solution or pollution? Frontiers in Ecology and the Environment **4**: 132–140. doi:https://doi.org/10.1890/1540-9295(2006)004[0132:BCOISS]2.0.CO;2

Miranda, L. E., M. E. Colvin, A. C. Shamaskin, L. A. Bull, T. Holman, and R. Jones. 2017. Length Limits Fail to Restructure a Largemouth Bass Population: A 28-Year Case History. North American Journal of Fisheries Management **37**: 624–632. doi:https://doi.org/10.1080/02755947.2017.1308891

Myers, R. A., J. K. Baum, T. D. Shepherd, S. P. Powers, and C. H. Peterson. 2007. Cascading Effects of the Loss of Apex Predatory Sharks from a Coastal Ocean. Science **315**: 1846–1850. doi:10.1126/science.1138657

Oken, K. L., and T. E. Essington. 2016. Evaluating the effect of a selective piscivore fishery on rockfish recovery within marine protected areas. ICES Journal of Marine Science **73**: 2267–2277. doi:doi:10.1093/icesjms/fsw074 Original

Persson, L., P.-A. Amundsen, A. M. De Roos, A. Klemetsen, R. Knudsen, and R. Primicerio. 2007. Culling Prey Promotes Predator Recovery--Alternative States in a Whole-Lake Experiment. Science **316**: 1743–1746. doi:10.1126/science.1141412

Pine, W. E., S. J. D. Martell, C. J. Walters, and J. F. Kitchell. 2009. Counterintuitive Responses of Fish Populations to Management Actions. Fisheries **34**: 165–180. doi:10.1577/1548-8446-34.4.165

R Core Team. 2020. R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing.

Roth, B. M., T. R. Hrabik, C. T. Solomon, N. Mercado‐Silva, and J. F. Kitchell. 2010. A simulation of food-web interactions leading to rainbow smelt Osmerus mordax dominance in Sparkling Lake, Wisconsin. Journal of Fish Biology **77**: 1379–1405. doi:https://doi.org/10.1111/j.1095-8649.2010.02764.x

Roth, B. M., I. C. Kaplan, G. G. Sass, and others. 2007. Linking terrestrial and aquatic ecosystems: The role of woody habitat in lake food webs. Ecological Modelling **203**: 439–452. doi:10.1016/j.ecolmodel.2006.12.005

RStudio Team. RStudio | Open source & professional software for data science teams.

Sass, G. G., A. L. Rypel, and J. D. Stafford. 2017. Inland Fisheries Habitat Management: Lessons Learned from Wildlife Ecology and a Proposal for Change. Fisheries **42**: 197–209. doi:https://doi.org/10.1080/03632415.2017.1276344

Sass, G. G., and S. L. Shaw. 2020. Catch-and-Release Influences on Inland Recreational Fisheries. Reviews in Fisheries Science & Aquaculture **28**: 211–227. doi:10.1080/23308249.2019.1701407

Secord, D. 2003. Biological control of marine invasive species: cautionary tales and land-based lessons, p. 117–131. *In* J. Pederson [ed.], Marine Bioinvasions: Patterns, Processes and Perspectives. Springer Netherlands.

Sih, A., M. C. O. Ferrari, and D. J. Harris. 2011. Evolution and behavioural responses to human-induced rapid environmental change. Evolutionary Applications **4**: 367–387. doi:https://doi.org/10.1111/j.1752-4571.2010.00166.x

Soetaert, K., T. Petzoldt, and R. W. Setzer. 2010. Solving Differential Equations in R: Package deSolve,.

Solomon, C. T., C. J. Dassow, C. M. Iwicki, and others. 2020. Frontiers in modelling social–ecological dynamics of recreational fisheries: A review and synthesis. Fish and Fisheries **21**: 973–991. doi:https://doi.org/10.1111/faf.12482

Tingley III, R. W., C. Paukert, G. G. Sass, P. C. Jacobson, G. J. A. Hansen, A. J. Lynch, and P. D. Shannon. 2019. Adapting to climate change: guidance for the management of inland glacial lake fisheries. Lake and Reservoir Management **35**: 435–452. doi:10.1080/10402381.2019.1678535

Tonn, W. M., C. A. Paszkowski, and I. J. Holopainen. 1992. Piscivory and Recruitment: Mechanisms Structuring Prey Populations in Small Lakes. Ecology **73**: 951–958. doi:https://doi.org/10.2307/1940171

Walters, C. J. 1986. Adaptive management of renewable resources, Macmillian Publishing company.

Walters, C. J. 1998. Improving Links Between Ecosystem Scientists and Managers, p. 272–286. *In* M.L. Pace and P.M. Groffman [eds.], Successes, Limitations, and Frontiers in Ecosystem Science. Springer.

Walters, C. J. 2007. Is Adaptive Management Helping to Solve Fisheries Problems? ambi **36**: 304–307. doi:10.1579/0044-7447(2007)36[304:IAMHTS]2.0.CO;2

Walters, C. J., V. Christensen, S. J. Martell, and J. F. Kitchell. 2005. Possible ecosystem impacts of applying MSY policies from single-species assessment. ICES Journal of Marine Science **62**: 558–568. doi:10.1016/j.icesjms.2004.12.005

Walters, C. J., and F. Juanes. 1993. Recruitment Limitation as a Consequence of Natural Selection for Use of Restricted Feeding Habitats and Predation Risk Taking by Juvenile Fishes. Canadian Journal of Fisheries and Aquatic Sciences. doi:10.1139/f93-229

Walters, C. J., and S. J. D. Martell. 2004. Fisheries ecology and management, Princeton University Press.

Walters, C., and J. F. Kitchell. 2001. Cultivation/Depensation Effects on Juvenile Survival and Recruitment: Implications for the Theory of Fishing. Can. J. Fish. Aquat. Sci. **58**: 39–50. doi:10.1139/f00-160

Walters, C., D. Pauly, V. Christensen, and J. F. Kitchell. 2000. Representing Density Dependent Consequences of Life History Strategies in Aquatic Ecosystems: EcoSim II. Ecosystems **3**: 70–83. doi:10.1007/s100210000011

Ziegler, J. P., C. J. Dassow, S. E. Jones, A. J. Ross, and C. T. Solomon. 2018. Coarse woody habitat does not predict largemouth bass young of year mortality during the open-water season. Canadian Journal of Fisheries and Aquatic Sciences. doi:10.1139/cjfas-2018-0050

Ziegler, J. P., E. J. Golebie, S. E. Jones, B. C. Weidel, and C. T. Solomon. 2017. Social-ecological outcomes in recreational fisheries: the interaction of lakeshore development and stocking. Ecological Applications **27**: 56–65. doi:https://doi.org/10.1002/eap.1433

2006. International Council for the Exploration of the Sea. Report of the Baltic Fisheries Assessment Working Group **24**.