

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

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Author contributions

All authors have approved the submitted manuscript and agreed to be listed as such. C.D. and C.L.N. formulated the theoretical framework. S.J., C.T.S., and G.S. helped C.D. and C.L.N. to develop the model and the manuscript.

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Abstract

Historically, recreational fisheries have been managed through a single-species framework where fish species are considered in isolation. This single-species framework can lead to unintended consequences for fisheries, potentially resulting in fishery collapses or regime shift. A common factor leading to regime shift and preventing population recovery are interspecific interactions between the collapsed species and their competitors. Increasingly, ecosystem-based management has been advocated in recreational fisheries where users have a diverse set of goals, however, in practice, ecosystem-based management can be difficult in systems subject to non-linearity. We use a modeled recreational fishery to describe how interactions between two harvested species can drive shifts in the stable state of the system, and seek to understand how interactions can be leveraged for efficient management. These experiments explore 1) the effectiveness of single-species management actions at maintaining the desired stable state as compared to multi-species management 2) the diversity of decision making paths that can lead to positive outcomes when leveraging certain interspecific interactions, and 3) how interspecific interactions can be leveraged to maintain a system in a safe-operating-space despite stable state drivers outside of a managers control. This model demonstrates how interspecific interactions within a system can lead to non-linear outcomes, and when these interactions are unaccounted for, result in regime shifts. Accounting for interspecific action 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.

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44 **Introduction**

45 Interspecific interactions are often not heavily considered in natural resource
46 management in order to simplify complex management problems (Walters and Martell 2004;
47 Baum and Worm 2009). This simplification may lead to decisions that in hindsight prove to be
48 ineffective or even detrimental (Walters et al. 2000; Myers et al. 2007; Hansen et al. 2015; Sass
49 and Shaw 2020). For example, Atlantic Cod (*Gadus morhua*) stocks in the Baltic Sea collapsed
50 in the late 1980's and the population failed to recover during the 20 years after collapse despite
51 strong restrictions on harvest, suggesting a shift in stable state (ICES 2006). Subsequent research
52 identified ecological interactions with Sprat (*Sprattus sprattus*) as the factor limiting cod
53 recovery and called for a more holistic plan that accounts for these interspecific interactions in
54 the cod recovery strategy (Casini et al. 2009). These unexpected outcomes have occurred at least
55 in part because earlier management decisions were unable to account for interactions between
56 multiple species and life stages (Walters et al. 2000; Jackson et al. 2001; Hansen et al. 2017;
57 Embke et al. 2019; Hutchings 2000). Although challenging, ecosystem-based management (i.e.,
58 holistic approaches to manage natural resources that includes accounting for interspecific
59 interactions and human decision making) can help decision makers avoid unexpected, and often
60 undesirable, outcomes (Pine et al. 2009).

61 While in many instances, ecosystem-based management may result in unexpected
62 outcomes with a wide variety of potentially negative effects, here, we focus on unexpected
63 regime shifts that push the system to an undesirable alternative stable state. Regime shifts have
64 been well documented in aquatic systems and are often exceedingly difficult to reverse once they
65 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 resource-dependent individual growth can result in depensatory population growth, also known as an ‘Allee Effect’ (De Roos and Persson 2002). Under low exploitation, in this model, 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 to examine how decision makers could 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. Of course large-scale experimental and adaptive management approaches are not always feasible and other approaches, such as model-based experiments, may be a useful first step toward this goal.

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. Indeed, decision makers are limited in the ways in which they can influence recreational fisheries (i.e., fishing regulations, stocking, effort limitation, habitat alteration, valuation) and fisheries users have diverse goals. Given the complexity of recreational fisheries, 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 (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' 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 a series of 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 are often not feasible for addressing questions about alternate stable states in fisheries (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 and state-maintaining positive feedbacks 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 subject 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

$$\frac{dA_1}{dt} = s_1 J_1 - m_1 A_1 - q E_1 A_1 \quad \text{Eq. 1}$$

$$\frac{dA_2}{dt} = s_2 J_2 - m_2 A_2 - q E_2 A_2 \quad \text{Eq. 2}$$

Adults of Species 1 or Species 2 are produced through the maturation of juveniles at a constant rate s_1 or s_2 . Adults undergo natural mortality, m_1 and m_2 , and are harvested at rates qE_1 and qE_2 . Harvest rate can be either constant or vary as a function of time.

Juvenile Dynamics

$$\frac{dJ_1}{dt} = a_1 A_1 e^{-b_1 A_1} + k_1 - \frac{c_{J_1, A_1} v_1 J_1 A_1}{h_1 + v_1 + c_{J_1, A_1}} - \frac{c_{J_1, A_2} v_1 J_1 A_2}{h_1 + v_1 + c_{J_1, A_2} A_2} - c_{J_1, J_2} J_1 J_2 - s_1 J_1 \quad \text{Eq. 3}$$

$$\frac{dJ_2}{dt} = a_2 A_2 e^{-b_2 A_2} + k_2 - \frac{c_{J_2, A_2} v_2 J_2 A_2}{h_2 + v_2 + c_{J_2, A_2}} - \frac{c_{J_2, A_1} v_2 J_2 A_1}{h_2 + v_2 + c_{J_2, A_1} A_1} - c_{J_2, J_1} J_2 J_1 - s_2 J_2 \quad \text{Eq. 4}$$

Juveniles are produced through Beverton-Holt stock-recruitment relationships (Beverton and Holt 1957). Additionally, stocking of juveniles can be imposed through k_1 and k_2 . Juveniles are removed from the population in one of three ways. The strength of each mortality source is represented by the parameter c , 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 $c_{J_1, A_1} J_1 A_1$ (read this as ‘the effect of A_1 on J_1 ’), which is dependent on refuge dynamics. Second, juveniles can be removed through predation by adults of the opposite species, $c_{J_1, A_1} J_1 A_2$ and $c_{J_1, A_1} J_2 A_1$. These dynamics are dependent on refuge and are controlled by two rates, h , the rate at which juveniles leave refuge and enter the foraging arena and v , 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. Remaining juveniles not claimed by the three sources of mortality mature to adults at the rate (s/J).

196 Table 1. Model parameterization

Term	Definitions	Value/Range
s_1	survival, species 1 juvenile	0.1
m_1	natural mortality, species 1 adult	0.1
c_{J_1,A_1}	cannibalism, species 1	0.001
c_{J_1,A_2}	predation by species 2 on species 1	0.05
c_{J_1,J_2}	juvenile competition	0.003
v_1	rate at which species 1 juveniles enter foraging arena	1
h_1	rate at which species 1 juveniles leave foraging arena	8
k_1	stocking, species 1	0-4000
qE_1	harvest rate, species 1	0-8
s_2	survival, species 2 juvenile	0.1
m_2	natural mortality, species 2 adult	0.1
c_{J_2,A_2}	cannibalism, species 2	0.001
c_{J_2,A_1}	predation by species 1 on species 2	0.03
c_{J_2,J_1}	juvenile competition	0.003
v_2	rate at which species 2 juveniles enter foraging arena	1

h_2	rate at which species 2 juveniles leave foraging arena	8
k_2	stocking, species 2	0-4000
qE_2	harvest rate, species 2	0-8

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212 ***Model Experiments***

213 Recreational fisheries are complex systems in which human influences and ecological
214 interactions feed back on each other to make applied management of any species challenging. A
215 key challenge facing many decision makers is how to maintain or improve abundances of highly
216 valued and exploited species in the face of competition with other less valued and exploited
217 species. Our modeling experiments were designed to mimic this situation. Species 1 in our
218 models represents the initially dominant, highly valued and highly exploited species that
219 managers are seeking to maintain, while species 2 represents a less valued and less exploited
220 species. When managing the focal species (species 1) alone, decision makers have control over
221 harvest limits and stocking rates for the focal species only; as opposed to controlling harvest and
222 stocking for both species respectively when managing from a whole-ecosystem perspective.
223 Given the hypothetical goals of decision makers in our simulations, species 2 management will
224 always take the form of setting harvest limits and not include stocking.

225 After exploring its basic dynamics and validating that the model produced alternate stable
226 states, we focused on three different modeling experiments that reflect scenarios commonly
227 encountered by fisheries decision makers (Table S1).

228 In our first experiment (Leveraging Interactions Experiment), we sought to understand
229 the implications of active management of only one species (species 1) *versus* both species
230 (species 1 and 2) on the “desired state” of the system. In this experiment, we sought to explore
231 the influence of leveraging ecological interactions to achieve decision maker’s goals related to
232 retaining a desired stable state. In this experiment, while species 2 is not the focal species,
233 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. 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 focused on the conceptual interactions rather than quantitative resemblance to that system in order to maximize generality of our model. As such, we only interpret the

qualitative dynamics of model simulations. For example, in order to define dominance and the presence of a system in the desired or undesired state we chose a threshold of one population's abundance exceeding that of its competitor by a minimum of 100 individuals. Model simulations were performed in R using RStudio and the deSolve package (RStudio Team; Soetaert et al. 2010; R Core Team 2020).

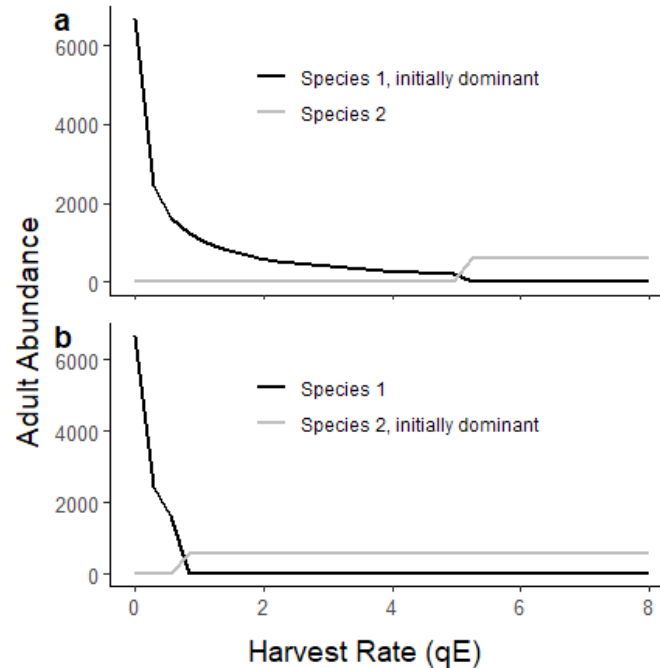
Results

Model Validation

Our model of a two-species recreational fishery exhibited alternative stable states. Initial species abundances and species harvest rates determined stable state outcomes (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.

Alternative stable states persisted across all but the most extreme values for species interaction strengths, mortality, survival, and fecundity (Fig. S1). However, the harvest rates at which the system transitioned differed with variation in parameter values (Fig. S1). Increasing juvenile survival to adulthood (s_1) for example, shifts the threshold higher indicating that the range of harvests over which alternative stable states occur is increased (Fig. S1). The model was

most sensitive to changes in competition amongst juveniles, and to Beverton-Holt stock-recruitment parameters (c_{J_1, J_2} , c_{J_2, J_1} , a , b).



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281 *Fig. 1. Model exhibits alternative stable states. The model is run to equilibrium over a range of*
 282 *harvest rates for species 1, while harvest of species 2 is held constant ($qE_2=2$). Panels show*
 283 *equilibrium results when (a) species 1 is initially dominant or (a) species 2 is initially dominant.*
 284 *The region of the x-axis between the thresholds in panels a and b represents the range of harvest*
 285 *rates over which alternative outcomes can occur; over this range of harvest rates it is the initial*
 286 *abundances, not the harvest rates, that determine equilibrium abundances.*

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288 *Modeling Experiment 1: Leveraging Interactions*

289 Managing both species simultaneously produced different outcomes than single species
 290 management (Fig. 2). In the Leveraging Interactions Experiment, species 1 was the initially

dominant species. This dominance tended to be maintained for simulations where stocking rates were sufficiently high and/or harvest levels were sufficiently low. The combination of stocking and harvest rates for species one that represented a boundary condition for maintenance of Species 1 dominance can be seen as the dashed isocline in Fig. 2. 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 (solid isocline in 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. S2). 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 much higher.

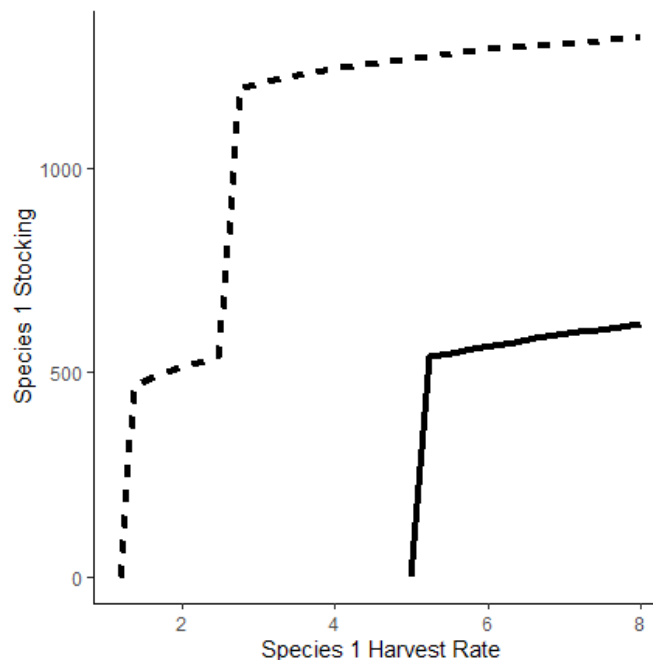
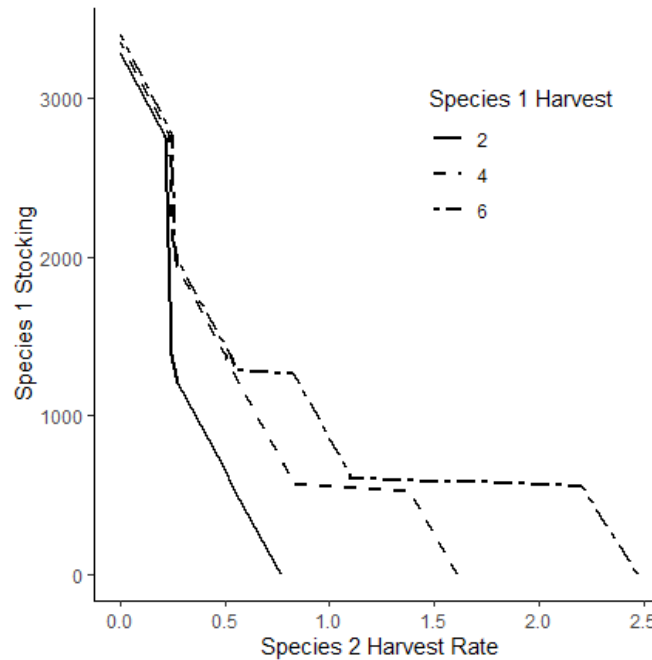


Fig. 2. Leveraging interspecific interactions expands the range of management options that can achieve the management goal. In this experiment, species 1 is initially dominant and the goal is to maintain that dominance. The dashed and solid lines are isoclines separating combinations of species 1 harvesting 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 at a rate of 2 (solid line), the range of species 1 harvest and stocking rates that produce the desired outcome is greatly expanded (above solid line).

Modeling Experiment 2: 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 tradeoff 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

328 stable state from species 2 dominance toward species 1 (Fig. S3). Because of the initial
 329 dominance of species 2 in this scenario, the magnitude of management action (stocking or
 330 harvest) needed to change the stable state towards species 1 was higher to account for initial
 331 dominance of species 2.



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333 *Fig. 3. Stocking of species 1 and harvest of species 2 can, on their own, maintain the desired*
 334 *stable state of a system (species 1 dominance) in the Alternative Approaches Experiment.*
 335 *Tradeoff between stocking and competitor harvest are presented for various levels of harvest on*
 336 *species 1 (solid and dashed lines). Areas above/to the right of the lines represent positive*
 337 *outcomes (species 1 dominance), areas below/to the left represent regime shifts to species 2.*
 338 *Dominance is only assigned when abundances differ by >100 individuals. The negative*
 339 *relationship between stocking species 1 and harvesting species 2 allows managers to achieve*
 340 *similar outcomes through implementation of either strategy or a combination of both.*

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342 *Modeling Experiment 3: Safe Operating Space*

343 Investigation of slow change towards a threshold in the system revealed the effectiveness
344 of management intervention for the prevention of shifts to alternate stable states (Fig. 4a).
345 Management actions implemented singularly may delay a transition through either harvesting
346 species 2 (Fig. 4b) or stocking species 1 (Fig. 4c). In combination however, managing both
347 species (through stocking of species 1 and harvest of species 2) prevented a regime shift
348 altogether (Fig. 4d). A combination of strategies still led to a decrease in species 1 abundance but
349 avoided a compensatory increase in species 2, thereby effectively maintaining conditions for
350 species 1 even as a driver outside managerial control pushes the system towards species 2
351 dominance. When no management action is taken, the stable state changes after 40 years (Fig.
352 4a). Minimal harvesting ($qE_2=0.5$) alone was able to delay the transition by 111 years (Fig 4b).
353 Adding 500 juveniles annually through stocking delayed the change in stable state by 18 years
354 (Fig. 4c).

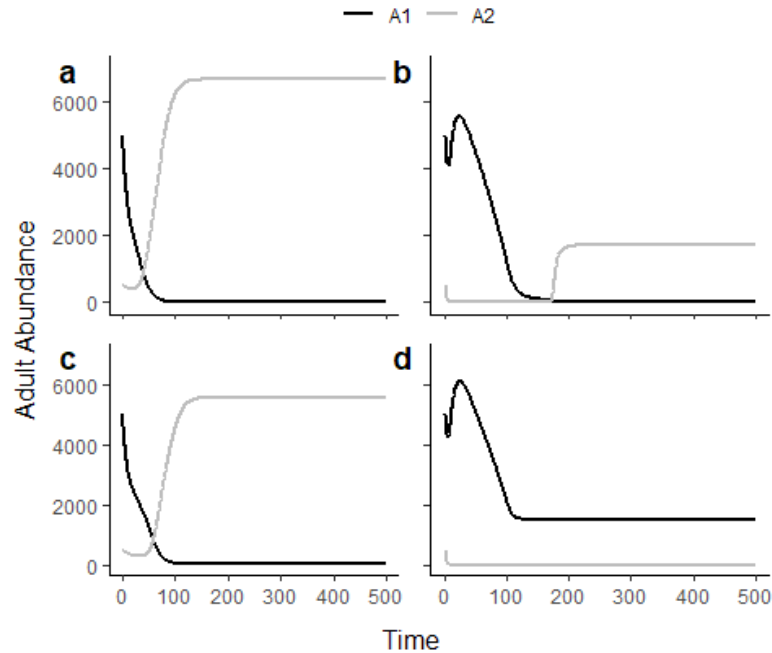


Fig. 4. Delaying transitions in the Safe Operating Space Experiment. Slow declines in recruitment represents a factor outside of managerial control, which will inevitably change the stable state from sp1 dominated to sp2 (no action; panel a). The change in system state can be delayed through either harvest 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.

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 species 1 juveniles 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, species 1 juvenile survival increased as predation pressure was alleviated, allowing species 1 adults 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).

414 Consideration of alternative management strategies, such as leveraging ecological
415 interactions, can aid decision makers in reinforcing the desired stable state of a system. Although
416 the limited set of options available to decision makers may be ineffective or even detrimental
417 when implemented without consideration of species interactions, these interactions can be
418 leveraged to create more avenues for maintenance of a stable state. For example, stocking has the
419 potential to be ineffective at maintaining the stable state of a system (Fig. 4c). Here, we highlight
420 how interspecific interactions can be a reason for stocking ineffectiveness at times. Our model
421 showed that alternatives such as harvest controls of the target species or management of a
422 competitor species can often be more effective than stocking in the production of favorable
423 outcomes (Fig.s 2 & 3). Although there are other drivers that influence the effectiveness of
424 stocking in a system (e.g., habitat loss, climate change, genetics; Lorenzen 2014; Hansen et al.
425 2015; Ziegler et al. 2017; Tingley III et al. 2019), our research emphasizes the critical need to
426 integrate species interactions into management scenarios. This idea is not entirely novel; indeed,
427 invasive species management has long included introducing ‘biocontrol’ agents into a system in
428 an effort to reduce invasive species abundance (Secord 2003; Hoddle 2004; Roth et al. 2010). A
429 key distinction between our multi-species fishery and invasive species management was the use
430 of existing ecological interactions between the species already present, as opposed to the
431 introduction of a novel agent.

432 Certain drivers of regime shifts in ecosystems may be outside of managerial control, such
433 as slow moving changes in recruitment as a result of climate change (Hansen et al. 2017).
434 Increasing consideration of these drivers has resulted in the emergence of a safe operating space
435 concept, increasing the call for adapting management to respond to ecological variables and
436 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 captured 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-dependence 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.

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-dependensation 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.

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