What we know:

* In a simple 2 species pred-prey model, not stage structured, May (1977) predicts alternate stable states should be fairly common depending on predation rates and prey growth rates. Harvesting of the predator will change where the tipping points are but not eliminate the hysteresis altogether.
* Polis et al. (1989) describes intraguild predation, its variances, and its prevalence across many taxonomic units. Intraguild predation occurs among members of the same guild which they define as a group of species that use the same resources in similar ways. These resources can be food or space. It’s competition and predation all rolled into one interaction. Asymmetrical intraguild predation occurs when one species is always the predator and the other is always the prey. Symmetrical intraguild predation occurs when both species can predate upon each other. Age structure is important for intraguild predation as well as substantial dietary overlap. “Most IGP occurs in systems with size-structured populations by generalist predators that are usually larger than their intraguild prey. Many of these IG predators are also cannibalistic on smaller conspecifics”. In some systems intraguild predation increases when other, nonguild, prey options decline.
  + Asymmetrical intraguild predation is especially common in species that eat classes of prey like any kind of insect or any kind of fish. Species that select prey based primarily on size are also likely to be intraguild predators. Asymmetrical intraguild predation where the species diet shifts with size increases is noted as widespread with examples from bass, trout, walleye, sauger, minnows, anchovies, and sardines. Perch-walleye, perch-bass,bluegill-bass systems are all noted (pg 303).
  + Symmetrical intraguild predation – noted as surprisingly common and dynamically important. Developmental timing asynchronies can allow for both large adults and small juveniles of the two species to occur simultaneously which allows for feedback loops.
  + Population implications – red shad – rainbow trout example where the negative competitive effects of red shad on juvenile trout outweighed the positive effects of predation by adult rainbows on adult shad. Ultimately introduction led to declines in rainbow trout. Same was observed for threadfin-bass interactions. Bluegill-bass interactions lead to developmental bottlenecks when bluegill are abundant and can limit bass recruitment to adulthood through competition with juvenile bass.
  + Bass bluegill work is cited a lot (refs 80,149,150)
  + Direct evidence of alternative stable states through intraguild predation comes mainly from planktonic communities, one example in a newt-salamander system as well. Whelk-lobster interactions are another well studied system.
* Polis & Holt 1992, field experiments testing the effects of intraguild predation can have counterintuitive results depending on the relative strength of indirect and direct effects of intraguild predation on the intraguild prey species.
  + Stocking of fish in brought up as an example of counterintuitive responses of management actions because of intraguild predation.
    - Can be overcome when stocking is done at the right time to reduce intraguild predation by taking advantage of life history changes or seasonal changes.
* Hart (2002) posits that simple food chain models can give false predictions of the effects of top-down or bottom-up trophic cascades when the system food web contains intraguild predation and cannot easily be approximated by a food chain. Both strength and direction of cascade effects can be incorrectly predicted without including IGP in the systems where it’s important.
  + She describes the general behavior of her models at equilibrium then constructs a simulation model that she parameterizes to approximate a specific system for which she can then make predictions.
* Beisner et al. (2003) – There are 2 kinds of alternative stable states, those that arise from changes in state variables and those that come from changes in parameter values (changes in state variables amounts to moving the ball around a static landscape, changes in parameter values amounts to changing the landscape itself and watching the ball react)
  + Good sections on hysteresis and what it takes to demonstrate alternative stable states in experiments.
  + Interesting point about whether or not angler harvest is intrinsic or external to the system, in other words, it it a constant that we treat as a parameter or is it a state variable. I think what Chelsea and I are proposing is that with two harvested species it can’t be treated as extrinsic and instead should be modeled dynamically
    - Is an interesting question, and maybe this is question 3, how does the inclusion of dynamics anglers change the stable states in the system? Does it dampen angler effort redistribution of anglers just switch species and stay in the same location?
* Schroder et al. (2005) reviewed empirical studies that sought evidence of alternative stable states and outline which studies were successful and which ones weren’t. Field experiments and those using longer-lived organisms generally did not see alternative stable states while lab experiments and those with short generations were more successful. Those two conditions are fairly confounded, long-lived organisms are hard to work with in the lab and take longer to see effects of manipulations which is harder to get funding for, many experiments using these organisms may not have run long enough to see strong effects. Field experiments are notoriously hard to control and this too may have contributed to the lack of support.
  + System complexity doesn’t necessarily mean it’s harder to detect alternatives table states than simple systems.
  + If variability of natural systems really does make it harder for alternative stable states and it’s not the case they they’re just harder to detect for researchers then the concept of alternative stable states would be limited in it’s importance
* Baskett et al. (2006) presents a trophic triangle model (like the conceptual figure in Walters and Kitchell 2001) of a rockfish community that follows the cultivation-depensation dynamics of Walters and Kitchell (2001). Here only the predator is fished while the competitor is unfished, as in Walters and Kitchell. She notes that When predation and competition between community members is removed the model has only 1 stable state and the predator is predicted to recover with reductions in fishing mortality no matter what. When predation and competition between community members is included the stable state to which the system goes following a reduction in fishing mortality depends on both the size of the marine reserve and the initial densities of predator and competitor.
  + Their goal is qualitative predictions not quantitative ones, they note that many parameters in their model are hard to measure in the field or unknown
  + “..our model indicates that community interactions substantially alter the conditions necessary for recovery of overfished species within marine reserves.”
* Persson et al. (2007) manipulated a lake food web which exhibited low predator densities, dominance by a prey species (including stunted sizes because of high densities). They culled larger, old prey fish allowing for the increased survival of smaller prey fish which promoted recovery of the predator population. The food web then shifted to being dominated by the predator and this shift has been maintained for 15 years after the manipulation.
  + Strong empirical evidence for alternative stables states in a lake fishery.
* Baum & Worm (2009) review evidence for top down effects of predators on food webs in ocean environments. Historically oceanographers have thought ocean food webs were dominated by bottom-up processes. They find evidence in the papers they review that oceanic food webs an be controlled by top down processes. They use the overexploitation of many top predators as natural experiments to demonstrate this. (This is a good way of thinking about bass-walleye interactions too, as a natural experiment).
  + 3 properties of human exploitation lead to top-down trophic effects of fishing.
    - Exploitation is sufficiently intense so as to reduce predator abundance in a meaningful way
    - Targeting top predators removes species that are likely to be strong interactors
    - Even when top predator diversity is high and prey populations are controlled by diffuse predation across predators, the nonselective nature of commercial fishing gear reduces the abundance of the whole functional group.
  + Simultaneous exploitation of predator and prey species in ocean environments prevent cultivation-depensation scenarios from happenings (Shepard & Myers 2005). The study they describe showed that shrimp trawling yields significant bycatch of benthic elasmobranchs whose predators are large sharks. In these areas both large sharks and elasmobranchs declined and no mesopredator release happened. Along the east coast where shrimp trawling is rare the decline of elasmobranchs did not occur alongside large shark declines. In those areas elasmobranch increased in abundance significantly.
* Huss et al. (2013) describes the dynamics of a model of two competing fish species that consume zooplankton and benthic invertebrates. Size dependent mortality on each of the species altered the dynamics of the system. Alternative stable states occurred when the following conditions were met:
  + - Populations exhibiting cohort-driven dynamics
    - Different maturation sizes for the two species (leading to different population cycle lengths
    - Strong interspecific competition
  + They note: “to better be able to predict changes in community structure in exploited communities of competing fish, the roles of food-dependent growth and size-dependent interactions are crucial”
* Gardmark et al. (2015) present a method of deducing the mechanism behind a regime shift by studying the body growth of different life stages of the piscivore population in question to determine if the cause is cultivation-depensation or overcompensation. This is important for managers to understand how to tailor their responses to the regime shift and try to reverse it.
  + This paper is especially useful in understanding empirical data like we may have for walleye and bass
* Essington et al. (2015) proposes a model where both the forage species and piscivore are fished, commercially, and explains how the policy that maximizes profits summed across the two fisheries depends on the ecological interaction between the two species (egg predation, bottom-up trophic control, top-down trophic control). They explore how best to divide up fishing mortality between the two species to maximize profits.
* Onken & Essignton (2016) is an application of some of the principles outlined in Essington et al. (2015). Onken & Essington describe scenarios where opening of a marine protection area to fishing for a specific species may be permissible depending on the ecological interactions between the fished species and the species of conservation concern and the gear selectivity for the fished species over the threatened species.
* Nilsson et al. (2019) Pike-stickleback interactions in the Baltic Sea, pretty strong example of traditional cultivation-depensation dynamics using both lab experiments and field data.

\*\* feels like the 2 spp model I’ve proposed should be expected to behave the same way other simple intraguild predation model perform which would make our idea just a variant of general intraguild predation. It’s an important variant to understand in fisheries where many species are harvested, and one that seems understudied.

When sp1 is heavily harvest and sp2 is not the system essentially reduces to 1 trophic triangle, where the double triangle comes in handy is for managers trying to change/maintain alternative stable states because fishing on sp2 can be used as a management lever. This is often left out of fisheries focused papers like (Baskett et al. 2006, Walters and Kitchell 2001). When both species are harvested at a non-trivial level, things will likely get confusing, slow moving system drivers may become more important then?

What we don’t know:

* How different are the dynamics of a two targeted species model from a single targeted species model? What predictions do they make about when coexistence should happen, when alternative stable states should happen?
  + How do these predictions line up with any empirical evidence we have?
* Long-lived species are still expected to exhibit alternative stable states but they are harder to observe because they take longer. This may be an area where models and data can work together to, in structured and efficient way, detect alternative stable states that empirical studies alone can’t because of time or logical constraints in manipulating driver variables.
* What is the optimal allocation of fishing mortality between the two species that maximizes the tradeoffs in satisfaction for anglers of each species?

**Some text I’ve generated**

Intraguild predation is widely documented across taxa and known to produces alternative stable states where the intraguild predator or prey dominates (May 1977; Polis et al. 1989; Polis and Holt 1992). This dominance is often maintained through processes of cultivation & depensation which Walters and Kitchell (2001) describe using a simple aquatic food web as an example. Alternative stable states have long interested researchers trying to understand to what degree are the communities we observe are products of random chance events or a slow steady march to some inevitable equilibrium state no matter what the initial conditions are (May 1977). More recently, researchers have applied what we know about alternative stable states to the conservation and management of valuable species or ecosystem services (Biggs et al. 2009). The sudden unexpected collapse of many animal populations and subsequent failure to recover despite management action have pushed resource managers to think about their systems as having multiple stable states that the system can transition between, given large enough perturbations. Fisheries provide compelling examples of the possibility of ecosystems to exhibit multiple stable equilibria (Olson et al. 1995; Persson et al. 2007; Nilsson et al. 2019). Aquatic systems are well situated for the study of alternative stable states because of their relatively well defined boundaries and complex food webs which allow for processes like intraguild predation that can produce alternative stable states. Furthermore, aquatic species like fishes are highly valued and so are of specific interest to researchers seeking to understand how to rehabilitate overexploited species or prevent currently abundant species form being overexploited (Myers et al. 1996; Carpenter et al. 2017).

Currently aquatic food webs have been employed extensively in models to demonstrate how a simple trophic triangle composed of adult and juvenile stages of a top predator interacting with a forage species can lead to alternative stable states. Walters and Kitchell (2001)describe how dominance by either the adult predator species or the forage species can arise through cultivation-depensation effects. Empirical evidence to support theoretical predictions has lagged. However, some empirical evidence of alternative stable states has been reviewed by Schröder et al. (2005)who summarize the results of 35 experiments. Generally, they found that lab studies and those using short-lived organisms were more successful at finding evidence for alternative stable states while field experiments and those using long-lived organisms were less successful. Interestingly they note that the complexity of the theoretical framework for the system studied did not seem to matter in detecting alternative stable states, both simple and complex systems exhibited alternative stable states.

What remains to be explored is the dynamics of multi-species fisheries where many species are harvested and those same species interact in the wild through processes like intraguild predation, though more recently these dynamics have been explored in commercial fisheries (Essington et al. 2015; Oken and Essington 2016). Importantly, the dynamics of these multispecies fisheries, including the effect of replacing the forage fish in a recreational fishery trophic triangle with a second harvested species, remains unstudied. The addition of this second harvested species represents a new ‘lever’ for managers to work with in trying to manage a focal species. It also represents mechanism by which the effects of management on one species may produce unexpected outcomes given that species’ interactions with a second harvested species and the dynamics of anglers targeting either of the two species. We present a model of a theoretical two species recreational fishery and use that model to make predictions about when we would expect alternative stable states to exist in these fisheries and what the outcomes of specific management actions might be. We then compare insights from this model, and previous work on cultivation-depensation in fisheries to highlight an example of intraguild predation leading to a shift in stable state through cultivation effects in a north temperate lake recreational fishery. While alternative stable states representing switches in the dominant species of the system are expected, empirical evidence remains rare.