ABSTRACT OF THE DISSERTATION

INTEGRATING HUMAN AND ECOLOGICAL DIMENSIONS OF RECREATIONAL FISHERIES

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Recreational fisheries are complex adaptive systems (CAS) that possess emergent properties and the potential to surprise us. In this dissertation, I investigate the social and ecological components of recreational fisheries, plus their interactions, to understand how these components might affect the sustainability of fishery systems as a whole. I start by exploring the motivations and preferences of participants in an unusual fishery, the Mongolian trophy fly-fishery for taimen (*Hucho taimen*), the largest salmonid in the world (Chapter 1). These anglers pay thousands of dollars and travel thousands of miles to catch-and-release a fish known for exceptionally low catch rates, making them an extreme example of the non-economic motives of recreational anglers. I find that taimen anglers are motivated almost as much by travel-related factors as by the expectation of catching fish and are mostly “bucket list” anglers who rarely return to the same destination twice. This means that fishing pressure for taimen depends far
more how anglers choose among an international landscape of similarly remote trophy fisheries than they do on the population status of taimen themselves.

In Chapter 2, I build on this knowledge about the social dimensions about recreational fisheries in Mongolia to ask how climate change might alter the way salmonids interact with fishing gear in this system. I find that hydrological changes caused by thunderstorms, which are increasing in Mongolia because of climate change, reduce the catchability of the Mongolian salmonids lenok (*Brachymystax lenok*) and Arctic grayling (*Thymallus arcticus arcticus*). These impacts depend on species feeding ecology and gear type in ways that suggest that international fly fishermen may maintain higher catch rates under climate change conditions than the Mongolian hobbyists who primarily fish with spinning gear, creating “winners” and “losers” under climate change.

In Chapter 3, I ask whether factors that are theoretically thought to erode recreational fisheries’ stability actually do so when present at the levels that are observed in real-world systems. I synthesize data on four well-studied mechanisms: 1) depensatory population dynamics, 2) environmentally-driven variability in recruitment, 3) density-dependent catchability, and 4) anglers’ responsiveness to changing catch rates. Incorporating these mechanisms at empirically-relevant levels into mathematical simulations of a generic recreational fishery reveals that interactions involving the two social mechanisms (#3-4) have the greatest implications for system stability. In particular, anglers’ degree of responsiveness to catch determines whether other factors have the potential to collapse the recreational fishery CAS.
Together, these chapters highlight the complexity of recreational fisheries and the importance of interdisciplinary research in understanding and managing this complexity.
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INTRODUCTION

Recreational fisheries have become the dominant way that most people interact with fish and fishing (Arlinghaus et al., 2019), engaging about 220 million people worldwide compared to the world’s approximately 40 million commercial fishermen (FAO, 2018; World Bank, 2012). They provide significant economic and social benefits (Cooke et al., 2016; Pawson et al., 2008), and in many ecosystems, a fish caught recreationally provides many times more economic value than the same fish harvested commercially (Lamine et al., 2018; Stage & Kirchner, 2005). Because of these multifaceted social and economic benefits, recreational fisheries also present unique management challenges at the nexus of ecological dynamics and human behavior. Unlike commercial fisheries, whose value resides in pounds of protein landed or the dollar value of catch, recreational fisheries must be managed to balance the competing benefits of catch, fishing effort, and other non-catch-related aspects of fishing valued by anglers, many of which are hard to quantify (Hunt et al., 2019; Stoeven, 2014).

This complexity presents a double-edged sword. On the one hand, as complex adaptive systems (CAS), recreational fisheries possess emergent properties and feedback loops that could, in theory, make them resilient to collapse even in the absence of management (Arlinghaus et al., 2017; Carmichael & Hadžikadić, 2019). Specifically, recreational fisheries are theorized to exhibit a negative feedback loop in which angler effort responds to population abundance (Figure 1): if abundance decreases, anglers’ expectations for their fishing experience are not met, and they leave the fishery. This reduction in effort allows the fish population to recover, making it an
attractive fishing target once again (McConnell, & Sutinen, 1979; Bishop & Samples, 1980; Carpenter et al., 1994). The above self-regulatory process has been observed in at least one real-world fishery (Askey & Johnston, 2013), but in many other systems anglers have had significant negative impacts on fish populations and aquatic ecosystems, including the collapse of targeted populations (Hunt et al., 2011; Lewin et al., 2006; Post et al., 2002).

In general, this self-regulatory potential is balanced out by another aspect of recreational fisheries’ complexity: the diversity of anglers’ goals. This diversity means that managers are in fact regulating multiple types of common-pool resource, each subject to scarcity and conflict (Arlinghaus et al., 2019). As well as fish population size, these are the availability of fishing sites with desired characteristics (a preferred mix of target species, lack of crowding, etc.) and the population’s catchability, which can be reduced by hook learning and the skewed removal of bold phenotypes even if overall population size stays the same. Managing fisheries to maximize one of these common-pool resources can jeopardize one or more the others. For instance, catch-and-release regulations intended to increase or sustain the populations of targeted fishes can still have negative impacts on anglers’ experiences by creating an invulnerable pool of previously caught fish (Camp et al., 2015). These tradeoffs, however, are rarely made explicit in the management process and in communications with anglers, contributing to the conflict and other unintended outcomes that are all too common in recreational fisheries.
My dissertation adds to our understanding of these two aspects of recreational fisheries—the availability of preferred fishing opportunities and the catchability of targeted populations—as scarce common-pool resources and investigates the tradeoffs that can occur when managing recreational fisheries for multiple goals. My first two chapters present case studies that explore 1) the factors that contribute to the desirability of an unusual fishing opportunity, and 2) how gear types, feeding ecology, and climate interact to determine the catchability of recreationally targeted species. The third chapter synthesizes data from studies worldwide to assess the extent to which hypothetically destabilizing mechanisms in recreational fisheries actually affect the tradeoffs between the social benefits and/or biological stability of fisheries and contribute to potential collapse of the fishery CAS.

The two case study chapters focus on northern Mongolia, which represents a valuable model system for a number of reasons. Recreational fishers in Mongolia inhabit the extremes of the angler specialization gradient originally defined by Bryan (1977), being primarily divided between extremely specialized trophy fly fishermen willing to spend thousands of dollars for a week of fishing (Golden et al., 2019) and generalist hobbyist anglers with no target preferences. However, the country had little history or culture of fishing for food or recreation before the last few decades (FAO 2007), meaning that target species are not heavily exploited. In addition, the country has already warmed at a rate about double the global average (Nandintsetseg et al., 2007), making it a valuable sentinel of changes predicted to occur more broadly in the rest of the world. In contrast, though, waterways in northern Mongolia have experienced few
of the compounding anthropogenic impacts present in many other ecosystems, such as
damming, stocking, and pollution from mining and agriculture. This combination of
traits means that northern Mongolia can teach us a great deal about the ongoing
impacts of recreational fisheries and climate change—and their interactions—without
the risk of compounding these impacts with those caused by other anthropogenic
stressors or historical overfishing.

In Chapter 1, I investigate the motivations and fishing preferences of the
specialized international fly fishermen who travel to Mongolia to fish for taimen, *Hucho
taimen*, the largest species of salmonid in the world. This fishery is unusual in that it is
extremely remote, costly, and difficult to participate in, requiring specialized gear and a
high level of skill. I coin the phrase “high-threshold fishery” to describe this fishery and
others that present similarly high barriers to entry. These fisheries occur throughout the
world but are generally understudied, with some exceptions (Pinder & Raghavan, 2013).
Given the high investment required to participate in them, and the low benefits (in
terms of catch and harvest) that they often entail, it becomes interesting to ask: What
motivates anglers to participate in one of these fisheries? What determines their
satisfaction with their fishing experience? And finally, does satisfaction translate into
repeated participation, as in more conventional fisheries? I use mixed quantitative-
qualitative social science methods to answer these questions and consider their
implications for anglers’ choices among a landscape of internationally distributed “high-
threshold” fisheries.
Chapter 2 clarifies how angling gear and indirect effects of climate change interact to modulate the catchability of two species of Mongolian salmonids with different feeding ecologies. Along with warming, northern Mongolia is experiencing increasingly frequent and intense thunderstorms because of climate change (Goulden et al., 2016), which impact aquatic ecosystems by increasing their 1) turbidity and 2) flow/water level. These mechanisms affect salmonids’ feeding behavior by 1) reducing their reaction distance to visual cues or 2) reducing their ability to observe auditory cues and/or increasing the distance over which they must search to find food. Since angling gears imitate prey items, meaning that fish must be actively foraging in order to be vulnerable to fishing, these thunderstorm-related impacts can hypothetically also affect Mongolian fishes’ catchability, with different effects for different species depending on their feeding ecology. I conduct experimental angling to determine how two salmonid species’ catchability varied based on species and gear type under a wide range of hydrological conditions caused by a sequence of severe thunderstorms.

I shift to a broad theoretical approach in Chapter 3, which synthesizes data on mechanisms that are theorized to reduce the stability of recreational fisheries and uses mathematical modeling to determine the extent to which they can 1) erode stability at their observed strength in real systems and 2) interact to dampen or intensify each other’s effects. The chapter highlights four biological and social mechanisms of instability: 1) depensatory population dynamics, 2) environmentally-driven variability in recruitment, 3) density-dependent catchability, and 4) anglers’ responsiveness to changing catch rates when deciding where and how much to fish. I evaluate these
mechanisms’ impact on both the social benefits and the biological sustainability of the system as well as variability in both aspects in order to address the issue of tradeoffs between competing goals when managing recreational fisheries.

Together, these chapters apply a range of complementary methods to increase our understanding of recreational fisheries as complex adaptive systems dependent on the thoughtful management of common-pool resources.

References


**Figure 1.** The social-ecological feedback loop hypothesized to self-regulate recreational fisheries sustainably. Starting from the top and moving clockwise, abundant fish populations attract many anglers. Fishing pressure reduces the size of the fish
population, making it a less attractive target to anglers. Anglers switch targets or stop fishing, reducing the fishing pressure and enabling the population to recover.
CHAPTER 1

ANGLER PREFERENCES AND SATISFACTION IN A HIGH-THRESHOLD BUCKET-LIST RECREATIONAL FISHERY*

Abstract

It is important to understand recreational anglers' motivations for fishing in order to predict when, where, and how they interact with species that can be sensitive to overfishing. So far, few studies have investigated angler motivation in recreational fisheries that are extremely distant from their angler population, require specialized angler skill, and pose other barriers to participation like high travel and equipment costs. We collectively refer to these as “high-threshold” fisheries and explore angler motivation and its implications for anglers’ decision-making in one particularly remote example, the Mongolian fly fishery for endangered taimen, Hucho taimen, the largest salmonid in the world. We used a mixed-methods approach that enriched discrete choice experiments with in-depth qualitative interview data to investigate anglers’ motivations for participating in the taimen fishery, their satisfaction with the fishing experience, and their stated interest in participating in the fishery in the future. We found that anglers preferred fewer high-quality, trophy-sized fish to a higher catch rate of smaller taimen, but that activity-general factors like the opportunity to travel to an “exotic” wilderness destination were also highly motivating. The anglers we sampled

were all first-time taimen fishermen and many were bucket-list anglers who sought a wide variety of fishing tourism experiences throughout their lifetime and therefore and had no intention to return to the taimen fishery. Instead, these fishermen selected their future trips from among a set of similarly remote, specialized, and costly fisheries throughout the world, especially in developing countries. We argue that these high-threshold fisheries should not be studied in isolation but instead would benefit from a unified research approach that accounts for their unique traits and shared angler population.

1. Introduction

Recreational anglers are the primary users of many freshwater fish stocks and can provide significant economic, social, and environmental benefits (Arlinghaus et al., 2002; Parkkila et al., 2010). Recreational fisheries can be important economic engines at the local and regional scale (Hyder et al., 2018) and they engage an estimated 220 million people worldwide (World Bank 2012), not to mention accounting for a significant fraction of the global fish harvest (Cooke and Cowx, 2004). They also present unique management challenges. Fishing effort in recreational fisheries tends to be geographically diffuse and to include diverse targets and gear types even within a single fishery (Arlinghaus et al., 2014; Post et al., 2002). These factors can make it difficult to collect accurate catch statistics, enforce regulations, and predict how biological and regulatory changes might impact future effort. A large body of literature and theory has emerged to address these challenges and especially to understand the dynamics that control angler effort. For instance, many researchers have modeled angler behavior as a
predator-prey interaction in which anglers intensify their effort when they encounter rich patches of “prey,” causing effort to equalize across a landscape (Johnson and Carpenter, 1994; Post et al., 2008; Wilson et al., 2016).

This understanding of anglers as human predators works well in fisheries where anglers are uniformly catch-oriented to the exclusion of other goals, but many fisheries cater to a spectrum of anglers who range from catch-oriented to trophy-seeking to casual recreationists (Arlinghaus et al., 2008; Bryan, 1977; Magee et al., 2018). In these fisheries, the connection between current fishery status and future fishery participation is more complex. Anglers are motivated by a diverse set of factors that include not only their preferred catch rate and target species but also activity-general elements that are common to many forms of outdoor recreation, such as experiencing nature, enjoying solitude, and socializing (Arlinghaus, 2006; Oh and Ditton, 2008; Oh et al., 2013). These preferences and motivations set the expectations that determine anglers’ satisfaction and consequently their future fishing effort (Arlinghaus, 2006). Therefore, if anglers are motivated to fish partly or primarily by activity-general characteristics of the activity, their satisfaction may depend heavily on factors other than the number and perceived quality (size, species, etc.) of the fish they catch (Curtis and Breen, 2017; Fedler and Ditton, 1994; Greiner et al., 2016). For instance, a recent study of angler satisfaction in a German multispecies fishery found that the contribution of catch-related factors to satisfaction plateaued above a certain threshold for most species, demonstrating that catch provides diminishing returns in satisfaction (Beardmore et al., 2015). In another case, 90% of surveyed anglers reported that they would be satisfied with a trip even if
they did not catch any fish. These minimally catch-oriented anglers instead valued “relaxing in the outdoors at the water side and fishing in pleasant company” (Arlinghaus, 2006).

Random utility theory provides one framework for understanding this heterogeneity in preferences and weighing the relative importance of different catch-related and activity-general factors (Aas et al., 2000; Hunt, 2005). The theory states that anglers choose fishing options by subconsciously integrating the costs and benefits of different options in a way that maximizes their overall utility, or benefit, from the fishing opportunity. This utility metric includes a set of deterministic components that can be measured by the researcher and a stochastic term that represents individual variation in taste, missing variables, and other unmeasured factors (Train, 2002). Studies that use the framework of random utility theory draw on stated or revealed preference data to characterize the utility of different options and the marginal contribution of each aspect of an option to its overall utility (Hunt, 2005). Discrete choice experiments used to elicit anglers’ stated preferences can incorporate a wide variety of catch-related preferences and activity-general factors like travel costs and crowding by other recreationists (e.g. Beardmore et al., 2015). Combining these stated preference surveys with qualitative methods such as in-depth interviews and focus groups is less common, but this mixed-method approach can draw an even more nuanced picture of fishermen’s preferences and behavior (Carr and Heyman, 2016; Magee et al., 2018).

The angler preference literature that uses this framework is dominated by studies that investigate anglers’ decision-making in local- or regional-scale fisheries that
include a range of generalist and specialized anglers (e.g. Duffield et al. 2012; Arlinghaus et al. 2014; Curtis and Breen 2017). However, few studies investigate the behavior of anglers in distant, high-cost recreational fisheries that require specialized angler skill, where one can expect different relationships between catch and participation simply because the commitment required to participate is so high (but see Nguyen et al., 2013; Pinder and Raghavan, 2013). In many of these fisheries, the targeted fish are highly desirable for their size, appearance, or behavior, attracting avid and generally wealthy anglers from around the world. These fisheries often require highly skilled fishing techniques and specialized gear and have either formal regulations or informal norms that enforce catch-and-release practices. One example is the bonefish (*Albula vulpes*) fisheries of the Caribbean, which provide millions of dollars annually to local economies and are primarily catch-and-release (Adams et al., 2014). Bonefish are highly valued by international sport fishermen for their speed and aggressive behavior when hooked, such that a single bonefish has been estimated to be worth US$3,500 to the local economy (Santos et al., 2017). Other examples include peacock bass (*Cichla spp.*) in the Amazon (Holley et al., 2008), tigerfish (*Hydrocynus vittatus*) in Africa (Smit et al., 2009), mahseer (*Tor spp.*) in India (Pinder and Raghavan, 2013), and high-cost pelagic trophy fisheries for marlin, tuna, and other highly migratory species (Duffield et al. 2012). Collectively, we categorize these fisheries as “high-threshold” fisheries, where economic, biological, and social factors combine to raise the barriers required to participate.
In northern Mongolia, abundant populations of taimen (*Hucho taimen*) attract wealthy fly fishermen willing to pay up to US$7,000 per week, excluding travel costs, for the chance to catch the largest salmonid in the world (Jensen et al., 2009). Taimen can reach lengths of up to two meters and weigh up to 100 kg, and at about one meter total length they undergo an ontogenetic shift that enlarges the head and jaw disproportionately to the body (Holcik et al. 1988). This large size, unusual appearance, and status as the world’s largest salmonid make them a valued target for some highly specialized recreational anglers. Many of these anglers travel to Mongolia with dedicated fly-fishing outfitting companies. The large size and selective feeding behavior of taimen combine to make them hard to catch on fly fishing gear, inspiring fishing guides to call them “the fish of a thousand casts.” The high cost, low catch rate, and specialized skills required of anglers in the international taimen fishery make it an excellent place to investigate the preferences and behavior that characterize anglers in such high-threshold recreational fisheries.

This study investigates the preferences, satisfaction, and behavior of international anglers in the taimen fishery in northern Mongolia. Using a mixed-methods approach that enriches discrete choice methodology with in-depth qualitative interview data, we ask the following three general questions: 1) What factors contribute to anglers’ motivation to participate in the taimen fishery, and what preferences do they have for their taimen fishing experience? 2) Based on these motivating factors, are sampled anglers generally satisfied with their experience in the taimen fishery, and what factors drive satisfaction most strongly? And finally, 3) How does satisfaction translate
into future participation; namely, do satisfied anglers express more interest in a return trip?

2. Methods

2.1 Study System

This study focuses on recreational taimen fishing in the Eg-Uur watershed in northern Mongolia, which is remote and relatively pristine (Gilroy et al., 2010). The watershed is located primarily in the Khövsgöl, Bulgan, and Selenge provinces in the transition zone between Mongolia’s steppe ecosystem and Siberian taiga forest. The Eg River, and its tributary, the Uur River, drain into the transboundary Selenge River, the largest tributary of Lake Baikal (Figure 1). The rivers support a fish community dominated by the salmonids lenok (*Brachymystax lenok*) and Arctic grayling (*Thymallus arcticus arcticus*), with taimen as the apex predator (Mercado-Silva et al., 2008). Taimen are relatively long-lived, large-bodied omnivorous fish with extensive habitat needs; some individuals have been observed to traverse home ranges of over 100 km (Gilroy et al., 2010; Kaus et al., 2016). Mongolian rivers like the Eg, Uur, and Selenge have historically served as refuge habitat for taimen because of Mongolia’s limited culture of fishing and fish consumption (FAO 2007). However, in the mid-1990s, the first foreign outfitting companies began bringing fly fishermen to Mongolia to fish for taimen (D. Vermilion, pers. comm.). Now, taimen are the primary object of a growing recreational fishery that includes both foreign fly fishermen (Vander Zanden et al., 2007) and, increasingly, Mongolian fishermen (Chandra et al., 2005). The American and European-
based outfitting companies that cater to many of these foreign fly fishermen enforce strict catch-and-release policies, while Mongolian recreational anglers vary in their adherence to catch-and-release practices.

Taimen are IUCN Red Listed throughout their range because of overfishing and habitat degradation (Hogan and Jensen, 2013), and Mongolian law prohibits the harvest and consumption of taimen. Research has shown that purely catch-and-release fishing for taimen can be sustainable, but that even limited consumptive fishing could lead to local extirpation of taimen populations (Jensen et al., 2009). As a result, foreign outfitting companies and Mongolian conservation activists have found common cause in supporting catch-and-release angling by foreigners, which provides economic revenues to rural, isolated areas, and thus discourages consumptive fishing by local herders and urban, middle-class Mongolians. The outfitting companies provide funding to several non-profit conservation organizations for research and enforcement of Mongolia’s fishing laws and permitting regulations. These efforts have been concentrated in the Eg-Uur watershed, which was also one of the earliest areas of Mongolia to see foreign fly-fishing effort. As a result, the watershed has become known for its abundant taimen population.

2.2 Research sites and study population

Fieldwork was conducted throughout the six-week 2017 fishing season (August to October) at two fishing camps operated by the Mongolian-run Hovsgol Travel Company in partnership with the American-based Sweetwater Travel Company. One
camp is located on the Uur River, 9 km above its confluence with the Eg, and the other is located 89 kilometers downstream of the Eg-Uur confluence on the Lower Eg (Figure 1). Data were collected for approximately three weeks at each camp to ensure roughly equal sampling of respondents. The two fishing camps hosted 60 clients over the 6-week fishing season, of which 38 overlapped with the research team. Of these 38 anglers, 30 completed paper surveys and 26 participated in semi-structured interviews for a 79% and 68% response rate, respectively. An additional angler who had recently completed a fishing trip at another camp completed a survey and interview at the travel company’s headquarters in Ulaanbaatar. Although the 60-person sampling frame is small in absolute numbers, so is the overall population of foreign anglers who fly-fish for taimen in Mongolia each year. This research protocol was approved by the Rutgers Institutional Review Board (Protocol #E17-714).

2.3 Survey design and implementation

Anglers were surveyed using a brief (15 minute) paper survey instrument that included two components: 1) a series of six discrete choice scenarios designed to elicit preferences and motivations for participating in a Mongolian fishing trip, and 2) questions about respondent’s demographic characteristics (e.g., age, location, and past fishing trips) and fishing experience. Discrete choice experiments (DCEs) present respondents with multiple hypothetical scenarios involving tradeoffs between desired attributes of an experience and ask them to rank or choose their most preferred option (Train, 2002). These data allowed us to assess the relative importance of different
attributes of the experience to respondents, analyze decision-making, and evaluate the utility of different options. In this case, anglers were presented with three options within each scenario: two alternative fishing trips that varied in the number of taimen caught and the size of the largest fish, and a third option in which they did not travel to Mongolia to fish, following the survey design of Carter and Liese (2012). The size attribute had six levels, ranging from 0 cm (i.e., no fish caught) to 150 cm, which were presented in both centimeters and inches (Table S1). The catch attribute had seven levels ranging from zero taimen (no fish caught) per week to eighteen, representing a maximum catch rate of about three fish per day. Attribute levels were developed to represent the whole range of outcomes possible on a taimen fishing trip based on our knowledge of the fishery. We chose to include only two attributes because we anticipated a small pool of respondents, which would limit our sample size and force us to focus on a small number of attributes of high interest. Although including a cost attribute would have enabled us to estimate anglers’ willingness to pay (WTP) for a taimen fishing experience, we deemed the tradeoff between size and catch rate in anglers’ preferences to be a higher research priority for this fishery given the high WTP already demonstrated by taimen anglers.

Anglers were asked to select the best and worst alternatives (Figure 2), allowing for a full ranking of the three alternatives as implemented by Lew and Larson (2012). Discrete choice experiments often do not use a full factorial design because the number of unique combinations would be prohibitively large (Fox, 2007; Kuhfeld, 2010). In this case, a fractional factorial design was developed from a full factorial design representing
the entire set of combinations of attribute levels. Illogical choices within the full factorial
design (i.e., a catch rate of zero with a non-zero maximum size) were then discarded.
Since most of the remaining scenarios were non-informative in that they possessed a
logically superior option that was better in terms of both size and catch (e.g., a choice
between 10 fish with a maximum size of 100 cm versus five fish at 50 cm), we followed
Train et al. (1987) in narrowing down our fractional design to focus on the scenarios that
presented informative choices. Scenarios were divided into “control” scenarios (those
with an obviously superior option as described above) and “experimental” ones that
present a meaningful tradeoff (e.g., a choice between 10 fish with a maximum size of 50
cm and two fish with a maximum size of 100 cm). Thirty unique survey variants were
developed in order to include all of the experimental scenarios. Each survey variant
included five experimental scenarios and one control scenario, selected from the large
pool of potential control scenarios, to screen for survey fatigue and respondent
disengagement.

Survey disengagement is a well-established concern in the implementation of
discrete choice experiments (Petrik et al. 2013), and the interview portion of this
project, combined with the inclusion of control questions, provided a unique
opportunity to address this potential source of bias. To take advantage of this
opportunity, respondents who failed the control scenario (n = 3) or displayed
preferences that were notably different from the majority of survey responses (n = 7 out
of 31) were asked about their DCE responses during the interview stage. One angler
revealed that he had failed the control due to disengagement and his responses were
removed from the data. The other two anglers who failed the control revealed that they had misunderstood the survey questions in an easily resolved way (circled their best and second-best choices instead of best and worst), and their responses were amended to reflect this. The remainder were asked about their responses because their choices suggested unusual preferences which could be profitably explored in the qualitative interview phase, like the frequent choice of the “no trip” option even when catch rates were high. These respondents’ clarifications were included in the interview data but did not affect the DCE analysis in any way.

Surveys were distributed at the beginning of the anglers’ trip and anglers completed them at their leisure throughout the fishing week. Some completed and returned them immediately, and some returned them when they left a week later. The day that anglers returned the survey did not have a significant effect on their choices and did not improve the model fit (Table 1).

2.4 Semi-structured interviews

In-person, semi-structured interviews were conducted with anglers to expand on discrete choice experiment results. An interview guide was designed based on 10+ years of experience working on the Mongolian taimen fishery and following best practices in qualitative research techniques (Roller and Lavrakas, 2015). The guide was modified several times in the field to address unforeseen circumstances and saturation of some interview questions (that is, reaching a point when no new insights emerge from further responses) (Appendix). Interviews were conducted at both fishing camps and during breaks on the river during the fishing day. Most interviews lasted 15 to 30 minutes, with
outliers ranging from 8 minutes to over an hour. All interviews were audio recorded and transcribed by a professional transcriber, following which the transcripts were checked for accuracy by the researchers. Twenty-six interviews were conducted in English and one was conducted in French; this was translated and transcribed by a native English speaker with an advanced degree in French.

2.5 Additional data sources

A researcher accompanied anglers and guides throughout the fishing day for 26 of the 43 days of the fishing season and recorded catch and effort data in units of angler hours per day. Limited catch logs were also maintained by some fishing guides. These were used to estimate the size structure of captured taimen. Unstructured key informant interviews were conducted with fishing guides and outfitting company staff members (n = 8) to assess longer-term fishery dynamics.

2.6 Data analysis

2.6.1 Modeling angler preferences

A multinomial logit model was fit to anglers’ ranked choices using the mlogit package (Croissant 2018) in R v.3.4.3 (R Core Team 2017). Candidate models included catch, size, both catch and size, and an interaction term between catch and size as parameters. One candidate model included a natural log-transformed catch rate and natural log transformation of the catch component in the catch-size interaction term because the observed data showed a diminishing effect of catch rate on utility (Figure 3).
and other studies have found diminishing returns of high catch rate (Beardmore et al., 2015). We also included trip day as an individual-specific variable to test whether the day the survey was returned affected anglers’ responses. Models were competed using Akaike’s Information Criterion (AIC; Akaike, 1974) (Table 1). Individual-specific parameters like fly fishing experience and days fished per year (a proxy for angler avidity) were not included because the interview portion of the project allowed us to explore the importance of these characteristics in a richer, albeit more qualitative, way, and because drawing valid conclusions about these parameters in DCE analysis generally requires larger sample sizes (Louviere, Hensher, and Swait, Joffre D. 2000: 110).

2.6.2 Qualitative analysis of interview responses

Interviews were coded for themes using the qualitative coding software NVivo 12.1.0 (NVivo qualitative data analysis Software; QSR International Pty Ltd. Version 12, 2018).

Themes used for this analysis were divided into the general categories of angler demography, angler preferences/satisfaction, and trip choice, and sub-themes were developed inductively during the coding process; that is, guided by the themes that emerged throughout participants’ responses rather than a priori assumptions about which factors would be important (Roller and Lavrakas, 2015). References to angler preference subthemes were quantified by their frequency in responses to questions about angler motivation (e.g., “What appealed to you about coming to Mongolia to fish for taimen?”) and satisfaction (e.g., “How do you feel about the trip so far?”). These
preference themes were identified as either catch-related or activity-general. Anglers were also classed into groups based on their expressed interest in returning to the fishery in future years.

3. Results

3.1 Angler demography

Surveyed anglers were primarily male (87%), white (100%), and middle-aged, with a median age of 52. The majority (51%) had a professional degree, with another 32 percent possessing a bachelor’s degree or some college education. Forty percent of anglers were American, 23 percent were European, and the rest were from Canada, Australia, and Morocco. Key informant interviews with fishing guides suggest that the majority of Sweetwater’s clientele are American, although the outfitter sometimes hosts large groups of anglers from countries not represented in this sample, such as Russia. Angler experience and avidity, as measured by frequency of fishing (Beardmore et al., 2015; Ferter et al., 2013), varied widely among surveyed anglers. The median angler had 30 years of fishing experience and 18 years of fly-fishing experience; however, several were novices who had never fly fished before and a few had over 50 years of experience as fly fishermen. The surveyed anglers spent an average of 29 days per year fishing (interquartile range = 14-38 days). All the anglers in the surveyed population were first-time taimen fishermen, although guide interviews indicate that typically about 25 percent of Sweetwater’s clientele are repeat visitors.
3.2 Angler preferences and motivation

The best fit model included size of largest fish, natural log-transformed catch rate, and an interaction term between size and natural log-transformed catch (Table 1). The size term, catch term, and the interaction term were statistically significant ($p = 0.000$, $p = 0.048$, and $p = 0.005$ respectively), as was the intercept for the no-trip option ($p = 0.002$) (Table 2). The no-trip intercept represents the utility of not traveling to Mongolia to fish compared to a trip with the lowest levels of each attribute—that is, a trip in which no fish are caught. The mean probability of choosing a trip with a catch rate of six fish per week and a maximum size of 50 cm was 0.32, while the mean probability of choosing a trip with a catch rate of 12 and a largest fish of 100 cm was 0.63, an increase of 31%. Doubling only the maximum fish size while maintaining the catch rate at six fish per week moderated this impact to some degree, increasing the probability of choosing a trip by only 24% instead of 31%. In contrast, doubling the expected catch rate while maintaining the size of largest fish constant at 50 cm increased the probability of choosing an option by only two percent. Overall, the effect of catch rate was low at small maximum fish size and stronger at high maximum fish size (Figure 3c). The best fitting model had a McFadden’s Pseudo $R^2$ value of 0.475. McFadden’s Pseudo $R^2$ is analogous to a standard $R^2$ statistic but generally produces lower values (Ben-Akiva and Lerman 1985). This is considerably better than the 20% standard of fit proposed as a benchmark in Hensher and Johnson (1981:50).

In interviews, anglers’ discussion of their motivations for traveling to Mongolia confirmed and expanded on this result. Anglers were motivated by catch quality over
catch rate, with quality defined mostly by size but also by the interaction between size and other factors, such as the way the fish fought on the line. As one 49-year-old Canadian angler said,

If the largest you catch is 30 inches and you get a dozen fish, that wouldn’t be enough to motivate me...they’re cool fish, but there’s not a spectacular run, there’s not a spectacular jump. Frankly, you’re hand-lining in a 30-inch fish...you’re basically just dragging them in.

Overall, anglers expressed a desire for 40- to 50-inch (100- to 125-cm) “trophy”-sized fish in interviews; this size class represents the 98th percentile of the fish caught during the season (Supplemental Figure 1). Catch rate expectations were more heterogeneous, but most anglers expected to hook one or two fish per 8-hour fishing day. Anglers were split between being frustrated with these low catch rates and valuing the fish more highly because they were difficult to catch. One 53-year-old British angler who typified the latter view said that landing a fish is more enjoyable when “you [have] to work a bit harder, wade a bit deeper, cast a bit further, fight the weather.”

More broadly, interviews reflected anglers’ interest in a variety of catch-related motivators beyond size and catch rate, as well as in factors related to the overall experience of the trip. Slightly over half of anglers’ references to their motivation for traveling to Mongolia mentioned these catch-related factors, which included not only taimen size and catch rates, but also being able to catch a diversity of species and the desire to catch specific species (primarily taimen, but also lenok, Arctic grayling, and northern pike) (Figure 4). Anglers valued taimen in particular for its size, its
aggressiveness, its “interesting-looking” morphology, its evolutionary lineage as an “ancient fish,” and its status as the “largest salmonid in the world.” Although a few anglers mentioned taimen’s rarity and endemism as a draw, many did not know that the species was endangered, and its conservation status was not a factor in their fishing decision: “I didn’t know if there were a million fish a mile, or two, no idea. I don’t know any more now.” Some even assumed that if anglers knew taimen’s conservation status, it would be a less appealing target. As one 48-year-old British fisherman speculated, it would hurt the operators’ interest to share the information because “they’re going to want people to think, there’s loads of them: you’re going to come, you’re going to catch loads every day, and they’re going to be huge.”

Interview responses revealed that a nuanced interaction between catch-related factors and aspects of the broader trip experience combined to draw anglers to the taimen fishery. These activity-general motivating factors included the social aspect of fishing with friends, the lure of travel to an exotic or “pristine” wilderness destination, and the experience of a novel culture. Anglers mentioned these activity-general factors almost as often as their catch-related expectations and motivations for the trip; approximately 44 percent of motivation-related references fell in this group (Figure 4). Thus, the very aspects of the taimen fishery that create barriers to participation—its distance, its remoteness, and its skill requirements—were also strong motivators for many anglers. As one 72-year-old American angler said,

Probably, if these taimen were in Bakersfield, California, I wouldn’t go there. But because they’re in Mongolia—there’s a certain flair where people say, ‘Where’re
you going?’ and you say, ‘I’m going to Mongolia’—their eyes kind of light up and they go, ‘Oh, that’s cool.’

For some anglers, these factors even outweighed their interest in trophy-sized taimen.

One 56-year-old American fisherman had recently begun fly fishing and spoke passionately about his new sport. He said,

It’s not about catching fish, it’s about fishing. It’s about the challenge. Can you get everything lined up to where you can get that hit? You know, get the fly in the right place, in the right fashion, at the right time? So it’s cool [that] there’s big fish here, but I would have come if there weren’t big fish. I would have come if it were just lenok and grayling.

3.3 Angler satisfaction

A different set of catch-related factors emerged in interviews when anglers spoke about their satisfaction with their ongoing trip, rather than their motivation for taking it. The size and number of fish that they had caught still mattered, but for many, catching a single taimen was enough to fulfil their goals for the trip: one seventy-year-old British fisherman said, “If I don’t catch another taimen, I’m not going to go home and say to friends and family, ‘Well, that was a waste of time, I only caught one taimen.’” A minority were frustrated by the pace or difficulty of the fishing, and especially by “blanking” or “skunking”—the experience of spending a day on the water without encountering any fish. One Australian angler, who came with a group of friends
who were all finding the fishing more difficult than they expected, said on his fourth evening:

After the first day, I didn’t take a fish. And I thought, my god, these are the fish of ten thousand casts. People said to me, how’s your day? And I said, look, it was a beautiful day, in that you’re out there and enjoying the environment, the wilderness, but it was really a hard day’s fishing…very, very different to my anticipation and expectation of coming here.

For him, the frustration of going multiple days without seeing a fish on the line outweighed the experience of “enjoying the environment, the wilderness.” Overall, as typified by this interview, catch-related themes like this one dominated anglers’ responses to questions about satisfaction, while activity-general themes were secondary. This contrasted with their responses about motivation, where catch-related and activity-general themes were almost equally prominent (Figure 4).

3.4 Anglers' intentions to return

The model indicated significant negative utility for the alternative of not traveling to Mongolia to fish for taimen (p = 0.02), showing that anglers strongly preferred even an unsuccessful taimen fishing trip to no trip (Table 2). This would be a surprising result in many catch-oriented recreational fisheries, but the high prevalence of activity-general motivations in the taimen fishery revealed by the interview data suggest that it is realistic for taimen anglers to have a positive utility for a Mongolia fishing trip even if they catch no fish. However, this tolerance for unsuccessful trips did
not translate into equivalent interest in future taimen trips. In interviews, only one angler expressed a definite intention to return to Mongolia to fish. Of the rest, thirteen said they would not return, eleven said they might under the right circumstances, and one was undecided (Figure 5).

The anglers who stated some intention to return mostly did so in vague terms, or only if certain conditions were met; for instance, if their children or friends became interested in the trip, or if they could expect better fishing in the future. Some weighed their mixed satisfaction with the experience against the longer-term population dynamics described by the guides, like one 53-year-old Welsh fisherman who had been frustrated with several “blank” days before catching four taimen in the span of an hour, including a 42-inch trophy fish:

I get the sense that this week has been quite slow compared to what the guides normally expect. And so I wouldn’t come back to repeat the week, but I would be interested in coming back to something that [had] more action, and bigger fish around.

The anglers who said they would not return were mostly bucket-list travelers; that is, those who wished to collect a variety of experiences and achievements during their lifetime (Thurnell-Read, 2017), and who therefore rarely traveled to the same place twice regardless of their satisfaction with a particular fishing destination. One 53-year-old Englishman typified the bucket-list view:

Probably, I won’t ever come back. Too big a world, too many places. And there’s a finite amount of time physically I can do it, because this [kind of fishing] is quite
a physical job; I won’t be on this water when I’m seventy years old. [So] I don’t go on holiday anywhere twice in my life.

While overcoming logistical and physical challenges was part of his motivation for this first trip—“the fishing is the bit you do on the river, [but] there’s [also] the traveling to it, preparing for it, planning for it, trying new places, new airports”—those same challenges posed a high barrier to a second trip.

As evident above, many anglers felt that the time and resources for a second trip could just as well go toward another bucket-list destination. They had many destinations to choose from; the more avid and experienced anglers in the study group participated in a wide range of recreational fisheries around the world. Common targets were bonefish and tarpon (*Megalops atlanticus*) in the Caribbean, sea run brown trout (*Salmo trutta*) in Patagonia, tropical reef fish like milkfish (*Chanos chanos*) and giant trevally (*Caranx ignobilis*) in the Seychelles, and a variety of salmonids in Alaska, Canada, and northern Europe. Some bucket-list anglers saved money to travel every two or three years, while others took expensive international trips multiple times a year to a mix of old and new destinations. Though these anglers’ target species were diverse, they were united in being large, visually unusual, aggressive, and best caught on specialized fly-fishing gear. They were also found in a range of scenic destinations in remote parts of low-income countries where anglers could experience a “human culture that is outside your normal experience, a long way from civilization.” These traits matched the activity-general factors that motivated anglers to fish for taimen in Mongolia.
4. Discussion

This paper aims to investigate anglers’ motivations for participating in a remote, high-threshold recreational fishery and to understand how these motivations could impact future fishery participation. We found a strong link to the “bucket list” cultural phenomenon (Thurnell-Read, 2017), where anglers were motivated largely by the prospect of accumulating a novel and exotic travel experience to catch an unusual fish. The size and morphological traits of the fish contributed to its appeal, while its perceived abundance and catchability were less important. This focus on size over expected catch rate adds to a growing literature assessing the catch-related preferences of anglers across a diverse range of fisheries (Hunt et al. 2019) and provides important information for guiding fishery-specific management, because strategies that maximize catch often require giving up size and vice versa (Hansen et al. 2015). More broadly, the importance of this “one and done” travel and fishing experience to anglers’ motivations meant that satisfaction with the fishing itself was, for many anglers, a poor predictor of future participation in the fishery. The majority of anglers did not intend to return to the taimen fishery, and even those who expressed some interest in future participation were not strongly motivated to do so. We found that the high barriers to entry in the taimen fishery, especially its difficult logistics and physical demands, contributed to the appeal of a single trip but discouraged anglers from seeking out further experiences.

This finding contrasts with our usual understanding of angler participation in recreational fisheries as a functional response by individual anglers to their past experiences of catching fish “prey,” mediated by the mechanism of satisfaction or
dissatisfaction with prior fishing trips (Johnson and Carpenter, 1994). There has been a trend toward emphasizing specific catch-related goals and catch satisfaction, rather than general fishing motivations, as the primary drivers of future fishing effort (e.g. Robert Arlinghaus 2006; Beardmore et al. 2011). However, our results show that in some contexts, anglers’ general motivations for fishing, or for taking a particular kind of fishing trip, can be crucial to understanding their future fishery participation. In settings like the Mongolian taimen fishery, the desire to experience a bucket-list vacation and encounter a unique fish can outweigh expected catch rates and the availability of trophy fish in driving participant behavior. Therefore, we must tailor our theoretical assumptions about angler behavior and participation to the individual fisheries we study and especially to the goals and demography of participants, as previously argued by Beardmore et al. (2015).

Our study represents a first step toward filling a gap in the conceptual scope of the angler satisfaction literature. There is a large body of research on the relationship between angler site choice and travel distance, recently reviewed by Hunt et al. (2019), but few studies focus on fisheries characterized by extreme travel distances, difficult logistics, high costs, and intensive skill requirements. The Mongolian taimen fishery provides an excellent example of this high-threshold dynamic, given that the average angler surveyed here traveled thousands of kilometers to participate and paid approximately US$7,000 plus travel expenses for a week of fishing. Additionally, its participants have access to a network of similar high-threshold bucket-list fisheries throughout the world, including sea run brown trout in Argentina, the salmon fisheries
of Alaska and Canada, and tropical reef fisheries in the Caribbean and the Indian Ocean. The variety of options available to these anglers suggests that participation in a fishery like Mongolia’s taimen fishery is best modeled not as a binary choice between participation and non-participation but as a multivariate decision about how to allocate fishing days among a set of globally distributed fishing options. Consequently, future participation in the taimen fishery, and other fisheries like it, may depend just as much on difficult-to-measure climatological and geopolitical factors as they do on maintaining abundant populations of the target species, as posited in the metacoupling framework proposed by Liu (2017). Water conditions in Argentina, the length of hurricane season in the Bahamas, and volatility in global financial markets, to give a few examples, could all have unseen ramifications for the year-to-year fishing effort in the Mongolian taimen fishery halfway around the world.

These dynamics are worth investigating because fishery participation by international anglers can have important local-scale economic and conservation consequences. Many high-threshold fisheries are in remote rural areas, meaning that the fisheries are significant economic drivers in places with few other sources of employment and income (Zwirn et al., 2005). But if fishery participation is in fact driven by global forces, these economic benefits could be unstable, causing unintended consequences like the employment precarity observed among tourist industry employees in the Seychelles (Lee et al., 2015). In addition, these specialized catch-and-release sport fisheries are particularly suited to being channeled into conservation solutions, as described by Cooke et al. (2016), because of the wealth and avidity of their
participants and the resource stewardship norms that often accompany catch-and-release practices. One example is the growing fishery for mahseer (*Tor* spp.) in southern India, where catch-and-release angling organizations that place high value on this large and aggressive species have supported research and retrained former poachers as fishing guides (Pinder et al., 2015; Pinder and Raghavan, 2013; Raghavan et al., 2011). But if fishery participation by wealthy international anglers varies greatly from year to year, funding and human capital for these efforts will fluctuate as well, and the community of anglers may be too fragmented to share the social norms and best practices that enable good conservation outcomes.

Fisheries that attract bucket-list anglers pose particular sampling and generalizability challenges in human dimensions research because they possess a high proportion of anglers who, by definition, are unlikely to return. Much of the angler satisfaction and recreational fishing participation literature describes—or assumes—a relationship between future effort and aspects of the angler experience on previous fishing trips (Johnson and Carpenter 1994). The bucket list angler has no plans to return, regardless of the experience, and the current pool of bucket list anglers will not necessarily reflect the demography and decision-making process of future participants. Therefore, the population of potential anglers for a fishery of this type is inherently diffuse and poorly defined, requiring researchers to reach for creative sampling and data collection methods to understand and anticipate future fishery participation. One possible avenue is to compensate by collecting richer data on the sampling pool that is available, for instance by combining conventional surveys with qualitative techniques
like focus groups and interviews. This approach has been used extensively to inform and enrich discrete choice experiment results in health (Coast and Horrocks, 2007), transportation (Pineda Jaramillo et al., 2016), and other fields (Que et al., 2017).

However, there are still relatively few examples of research combining discrete choice methods and semi-structured interviews in fisheries, especially in a recreational context (Carr and Heyman, 2016). In addition, the examples that do exist tend to use interviews mostly to gather quantitative data or guide survey development (e.g Ward et al., 2013). While this is a useful approach, it does not take advantage of the key strength of qualitative data: the rich insight it provides into the thoughts and motivations of others (Weiss, 1995). Our approach of pairing surveys with simultaneous in-depth interviews allowed us to harness this strength and compensate for the limited sample size by gathering rich, in-depth data from each individual participant using mixed quantitative-qualitative methods.

5. Conclusion

In summary, we found that anglers are motivated to fish for taimen in Mongolia by a mix of catch-related and activity-general factors, particularly the size and morphology of the species and the chance to fish in a destination perceived as an exotic, pristine wilderness. Many anglers were bucket-list travelers who rarely fished in the same place twice but instead allocated their fishing effort among a variety of expensive, remote, and specialized fisheries for unusual fish, often in developing countries. We collectively label these fisheries as “high-threshold” fisheries because of the barriers to
participation posed by their location, cost, skill requirements, and other factors. We argue that the populations of anglers who surmount these barriers are qualitatively different from their counterparts in more accessible fisheries and that fisheries with these traits require research approaches that recognize the unique niche they occupy. Such study is especially urgent since many of these high-threshold fisheries are in developing countries with little funding for proactive research and fishery management, leaving scientists at risk of “following fisheries around” (Neis, 2011) and focusing attention only where crises have already occurred.

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Tables and Figures

**Table 1.** Candidate models with explanatory variables, number of parameters (K), log likelihood (LL), Akaike Information Criterion (AIC) score, and difference in AIC score relative to the model with the lowest AIC score (ΔAIC). Models with a ΔAIC <2 are similarly supported.

<table>
<thead>
<tr>
<th>Model</th>
<th>K</th>
<th>LL</th>
<th>AIC</th>
<th>ΔAIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>size + ln(catch) + size * ln(catch)</td>
<td>5</td>
<td>-163.1</td>
<td>336.1</td>
<td>0</td>
</tr>
<tr>
<td>size + catch + size * catch</td>
<td>5</td>
<td>-164.6</td>
<td>339.1</td>
<td>3</td>
</tr>
<tr>
<td>size</td>
<td>3</td>
<td>-167.3</td>
<td>340.6</td>
<td>4.5</td>
</tr>
<tr>
<td>size + catch + trip-day + size* catch</td>
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<td>-163.4</td>
<td>340.7</td>
<td>4.6</td>
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<tr>
<td>size + ln(catch)</td>
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<td>-167.2</td>
<td>342.3</td>
<td>6.2</td>
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<tr>
<td>size + catch</td>
<td>4</td>
<td>-167.2</td>
<td>342.4</td>
<td>6.3</td>
</tr>
<tr>
<td>catch</td>
<td>3</td>
<td>-188.4</td>
<td>382.8</td>
<td>46.7</td>
</tr>
</tbody>
</table>
Table 2. List of parameters in best-fit model with the parameter estimates, standard error, p-values, and significance.

| Parameter      | Attribute                        | $\beta$  | Std. Error | Pr(>|z|) |
|----------------|----------------------------------|----------|------------|---------|
| **Alternative-specific coefficients** | | | | |
| generic trip intercept | | 0.0712 | 0.1673 | 0.6703 |
| no-trip intercept | no trip | -2.2739 | 0.9778 | 0.0200* |
| **Generic coefficients** | | | | |
| size | size of largest fish caught | 0.0140 | 0.0039 | 0.0003*** |
| Ln(catch) | catch rate per week | -0.2195 | 0.1108 | 0.0475* |
| size x ln(catch) | interaction between catch rate and size | 0.0066 | 0.0024 | 0.0054** |

N = 180  
McFadden $R^2$: 0.475

* Significant to $p < 0.05$  
** Significant to $p < 0.01$  
***Significant to $p < 0.001$
**Figure 1. Study sites.** Map of the Eg and Uur Rivers in northern Mongolia’s Eg-Uur watershed showing the two fishing camps where research was conducted (black triangles). The Sweetwater/Hovsgol Travel companies have exclusive rights to fish the river section emphasized in grey, which occupies a total of 219 river kilometers. The black dotted line marks the boundary between waters fished by the upper camp (109 river km) and lower camp (110 river km).
Figure 2. Sample discrete choice scenario.

This section presents six scenarios. In each scenario, imagine that you could either take one of the two taimen fishing trips described in the box, or choose not to go fishing for taimen in Mongolia at all. Excluding the catch rates and sizes described below, assume that the trip price, outfitting company, and all other characteristics of the trip are identical to those of your CURRENT trip.

For each scenario, which of the three options (Trip A, Trip B, or No Trip) do you like the BEST, and which do you like the LEAST?

<table>
<thead>
<tr>
<th>SCENARIO #1</th>
<th>Trip A</th>
<th>Trip B</th>
<th>No Trip</th>
</tr>
</thead>
<tbody>
<tr>
<td>In one week, you catch</td>
<td>In one week, you catch</td>
<td>You do not go to Mongolia to fish for taimen.</td>
<td></td>
</tr>
<tr>
<td>3 taimen</td>
<td>18 taimen</td>
<td></td>
<td></td>
</tr>
<tr>
<td>of which the largest one is</td>
<td>of which the largest one is</td>
<td></td>
<td></td>
</tr>
<tr>
<td>125 cm / 50 in long</td>
<td>75 cm / 30 in long</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Which option do you like the BEST? Circle only one:  
Trip A  Trip B  No Trip

Which option do you like the LEAST? Circle only one:  
Trip A  Trip B  No Trip
**Figure 3. Discrete choice model results.** The marginal effect at the mean of (a) size of largest fish available and (b) expected catch rate per week on the predicted probability that anglers will choose a trip option in a discrete choice experiment. The black points show the observed proportion of trips selected with each level of the size and catch rate attributes. Panel c) shows the predicted probability of trip choice based on the interaction between size of largest fish and catch rate per week (deeper blues indicate higher probabilities of selection).
Figure 4. Interview themes related to angler motivation and satisfaction. Proportion of interview text that refers to catch-related (blue) and activity-general (orange) themes in responses to questions about angler motivation and satisfaction.
Figure 5. Angler attitudes to a return trip. Bar plot showing the frequency of different attitudes to taking a return trip to Mongolia as expressed in interviews. On the right are selected quotes representative of each attitude.

- **no return**
  - $n = 13$
  - "I never go anywhere twice. It's too big a world"

- **possible return**
  - $n = 11$
  - "Maybe three or four years from now, someone will want to go, and I'll tag along"

- **definite return**
  - "I'd like to, absolutely"

- **undecided**
  - "I just don't know"
Supplemental Tables and Figures

**Supplemental Table 1. Attribute levels in the choice experiment experimental design.**

<table>
<thead>
<tr>
<th>Size of largest fish caught (cm)</th>
<th>Catch rate per week</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zero fish caught</td>
<td>0</td>
</tr>
<tr>
<td>50</td>
<td>3</td>
</tr>
<tr>
<td>75</td>
<td>6</td>
</tr>
<tr>
<td>100</td>
<td>9</td>
</tr>
<tr>
<td>125</td>
<td>12</td>
</tr>
<tr>
<td>150</td>
<td></td>
</tr>
</tbody>
</table>
Supplemental Figure 1. Size structure of taimen caught during the 2017 fishing season. Black line shows size of desired “trophy” fish as revealed in angler interviews.
Appendix: Semi-Structured Interview Guides

Starting Interview Guide (as of 08/24/17)

How has your trip been so far?
What brought you to Mongolia?
How do you feel about today’s fishing?
Tell me about the last taimen you caught.
What is it that made you interested in the experience of coming to Mongolia and catching taimen?
Do you think you’ll come back to Mongolia again?
Where do you do most of your fishing?
What do you know about taimen conservation?

Ending Interview Guide (as of 9/30/17)

How was the fishing today / How do you feel about today’s fishing?
Tell me about the process of deciding to come on this trip.
What is it that appealed to you about the idea of coming to Mongolia and catching taimen?
What would your ideal day of taimen fishing look like?*
Where do you do most of your fishing?
What did you know about taimen conservation before coming here?
Do you think you’ll come back to Mongolia again?
What will you tell people about this trip when you’re back home?*

*These questions were added to the interview guide when it became clear that most anglers were bucket list travelers whose motivations were not based on previous experience of the fishery.
CHAPTER 2

THUNDERSTORMS HAVE SPECIES AND GEAR-SPECIFIC INDIRECT EFFECTS ON THE CATCHABILITY OF MONGOLIAN SALMONIDS*

Abstract:

Climate change is predicted to cause increasingly frequent and intense storms. Northern Mongolia is already warming at a rate twice the global average, and thunderstorms, defined as intense, short, patchy rains associated with thunder, lightning, and high precipitation rates, are becoming more frequent. Because Mongolia’s fish populations are lightly exploited, Mongolia provides a model system in which to study the effects of storms on fish behavior and fishing vulnerability. The impacts of thunderstorm-related hydrological changes on fishes’ vulnerability to two fishing gears were evaluated. Two thunderstorm-related factors, turbidity and river stage, reduced catch rates of the salmonids lenok (*Brachymystax lenok* Pallas) and Baikal grayling (*Thymallus baicalensis* Dybowskii). Fly fishing gear was more effective than spinning gear in this fishery, and retained higher catch rates in extreme conditions. These gear-specific effects suggest that turbidity and rising river stage affect fishing vulnerability by influencing feeding behavior.

1. Introduction

Climate change is altering the freshwater ecosystems that support inland recreational fisheries by increasing surface temperatures, changing precipitation patterns, and increasing the frequency of extreme storm events (Hartmann et al. 2013). The state of knowledge on the ways in which climate change might affect inland recreational fisheries is growing but uneven. For instance, a large body of research has investigated how warming waters will change fish population abundance and shift species distributions over the long term (Ficke et al., 2007; Kovach et al., 2016). Much less well understood are the more abrupt, short-term hydrological changes associated with storm events (Hartmann et al. 2013), which can also have significant effects on fish populations and human communities (Santos et al., 2016). In addition, several papers have predicted how fish and anglers will each respond to new temperature regimes and weather patterns (Kerr et al., 2009; Townhill et al., 2019), but few investigate how climate change might alter fishes’ vulnerability to fishing gear.

One way that climate change could affect these fishery interactions in the immediate future is through storm events, which are expected to become more frequent and severe as climate change intensifies (Hartmann et al. 2013). Extreme storm events like thunderstorms can be expected to change salmonids’ behavior, and therefore their interactions with fishing gear, in a number of ways. Turbidity resulting from sediment loading increases reaction distance to prey (Vogel and Beauchamp, 1999; Mazur and Beauchamp, 2003) and lowers feeding rates (Rowe et al., 2003) in visually foraging fish. Pulses of high river flow, such as those produced by precipitation runoff,
reduce fish activity and swimming speed (Larranaga et al., 2018). Increased river stage following thunderstorms also increases the volume of water within which a fish must search for prey. Unless there is a corresponding increase in prey available (e.g., from terrestrial prey washed into the river), then prey density, and encounter rates, will decrease.

A number of confounding environmental factors can also affect fish behavior and catchability, making it hard to isolate the effects of storm-related factors. Catch rates change with season (van Poorten and Post, 2005), and diel cycles, with many fish species more active and therefore more vulnerable to fishing gear at dawn and dusk (Kuparinen et al., 2010; Arlinghaus et al., 2017). Factors relating to anglers’ behavior and gear choices can also affect catchability, because fishermen’s skill influences their catch rates (Arlinghaus et al. 2017), and different types of angling gear vary in their efficiency in catching fish and in their selectivity for different species and sizes of gear.

For several reasons, Mongolia is a valuable model system in which to study interactions between fish and angling gear under climate change. First, air temperature records show that Mongolia has warmed by almost 2°C since 1940 (Nandintsetseg et al., 2007), a rate about double the global average (Hartmann et al. 2013). Along with warming, Mongolia is also experiencing new precipitation patterns: the gentle, long-lasting rains typical of summer precipitation in northern Mongolia are being replaced with thunderstorms, defined by Goulden et al. (2016) in a Mongolian context as “intense, short, patchy rains with large drops...associated with thunder, lightning, and precipitation rates greater than 7.6 mm hr\(^{-1}\).” These thunderstorms produce sudden
pulses of runoff and sediment erosion into rivers, dramatically altering the habitat in which Mongolian fishes move, forage, and interact with fishing gear. Second, Mongolia’s rivers are relatively untouched by other disturbances that are expected to confound the effects of climate change, such as stocking, flow control, and invasive species (Hunt et al., 2016; Kovach et al., 2016). Finally, Mongolia’s Eg-Selenge watershed contains healthy populations of the coldwater salmonids lenok (*Brachymystax lenok* Pallas) and Baikal grayling (*Thymallus baicalensis* Dybowski) (Mercado-Silva et al., 2008). These two species are already experiencing temperatures near their upper limits for growth in the summer in Northern Mongolia (Hartman and Jensen, 2017).

Because active angling gears, like fly and spinning gears, imitate prey items, changes in fishes’ feeding behavior caused by thunderstorms should also control their encounter rate with spinning and fly gear (Lennox et al., 2017). Although lenok and Baikal grayling are both drift feeders, lenok have a higher proportion of benthic invertebrates and fish in their diet than grayling do (Olson et al., 2016). This means that compared to grayling, they should be more vulnerable to lures that imitate prey fish, such as spinners. Since spinners may attract fish using sound as well as a visual cue, these lures may remain effective even in highly turbid water, while catch rates on purely visual lures, like the majority of artificial flies used in fly fishing, should be much more sensitive to turbidity. In Mongolia, these gear-specific interactions with river conditions could result in different levels of fishing success for different angler populations, creating winners and losers among Mongolia’s recreational anglers.
This study evaluates how the thunderstorm-associated factors turbidity and river stage affected Mongolian salmonids’ vulnerability to fishing on two different angling gears. A standardized experimental fishing approach that rotated spinning and fly gears equally among a team of anglers, following Arlinghaus et al. (2017), was used to estimate how thunderstorms affect catch rates on different gears. Three predictions were made: 1) that increased turbidity and increased river stage both reduce catch rates of lenok and grayling, 2) that turbidity has a greater effect on catch rates with fly than with spinning gear, while the effect of stage does not depend on gear, and 3) that lenok remain more vulnerable to capture on spinning gear than grayling during turbid conditions, while the two species are equally likely to be caught on fly gear during the same conditions.

2. Methods

2.1 Materials and Methodology

Standardized fishing was conducted on 30 kilometers of the Uur River directly above its confluence with the Upper Eg River and on 30 kilometers of the Lower Eg River above its confluence with the Selenge (Figure 1). The two fishing areas are located 251 river kilometers apart in the Hovsgol and Bulgan provinces of north-central Mongolia, which occupy the ecotone between Mongolian steppe and Siberian taiga forest. The Uur is predominantly fed by groundwater and precipitation runoff and is characterized by a mixed riparian habitat and large meanders in a wide floodplain valley. Below their confluence, the combined Eg and Uur rivers are known as the Lower Eg and have a similar riparian habitat but with increased width and reaches with large boulders (Gilroy
et al., 2010). Mongolia’s summer rainy seasons last from late June to late August (Goulden et al., 2016). Therefore, fishing on the Uur River was conducted throughout the 10-day period from July 21 to July 30, 2019 and fishing on the Lower Eg was conducted from August 2 to August 14, 2019.

Twelve fishing sites were selected on each river, equally divided between three 10-km segments to ensure uniform fishing effort throughout the 30-km stretch. The fishing sites were selected by a local fishing guide with more than a decade of experience fishing on the two rivers as good lenok and grayling habitat, generally riffles or runs. Compared to unselected sites, they tended to have coarser substrate (gravel or cobble rather than silt or sand) and sparser riparian vegetation. One 10-km segment was selected randomly for fishing each day, and three or four sites within the segment were fished depending on time constraints. To avoid confounding site effects with time of day, the order in which sites were fished (starting either downstream or upstream) was determined using a coin toss.

Spin fishing was conducted with standardized medium-fast action rods (6½’ Shakespeare UglyStik and Abu Garcia Vendetta) and standard reels (Abu Garcia, Silvermax 40 and Blackmax 20). Spinning lures were restricted to #1 and #2 dressed Mepps aglia treble hook spinners in silver and gold, with two hooks removed and the remaining barb crimped to comply with Mongolian law, which requires single barbless hooks. Anglers used Trilene 8-lb test monofilament line and a barrel swivel was fixed 50 cm above the lure. Fly fishing was conducted with an 8.5’ 5-wt Orvis fly rod and a Clearwater Classic III fly reel with 5X tippet (Rio Powerflex brand). Dry flies were
restricted to size 14 and 16 Parachute Adams and Royal Wulff patterns and nymphs were restricted to a beadhead Prince Nymph and a non-beadhead Hare’s Ear pattern of the same size (Figure S1). For both species, there were minimal differences in catch rates (Figure S2) and size selectivity (Figure S3) between the dry fly and nymph patterns.

Fishing events consisted of 40 minutes of active angling by two fishermen at a single site, equally divided between spinning and fly fishing. Time spent processing captured fish and changing lures and gear was not included in the total fishing time to avoid artificially creating hyperstable catch rates due to handling time limitations (Korman and Yard, 2017). Fishing was carried out by four skilled recreational anglers with an average of 31 years of experience fishing on spinning gear and 25 years of experience fly fishing. This is similar to the median of 30 years of overall fishing experience and 18 years of fly-fishing experience observed in international ecotourist anglers in Mongolia (Golden et al. 2019). For each fishing event, two anglers fished the site simultaneously such that both gear types were presented to the fish at the same time, rotating rods after 20 minutes to control for angler skill with each gear following Arlinghaus et al. (2017). The angler using fly fishing gear changed between a nymph and a dry fly halfway through each 20-minute period. The gear each angler started with, and the type of fly (dry fly vs. nymph) used by the fly fisherman in the initial 10-minute period, were randomized with a coin flip to control for the possibility that catch rates decreased over the course of a fishing event, regardless of gear type and angler skill. Anglers were instructed to fish as they normally would within the constraints imposed
by the study to maximize their fishing success in terms of total length of fish caught per fishing event.

Each fish caught was landed, measured (total length in millimeters), and the anal fin was clipped to permit identification of previously captured fish. Time of capture, site, angler identity, gear used, species, and the number of casts from the beginning of the 10-minute period using that gear type were recorded by dedicated note takers. As in most recreational angling, some fish were lost before they could be landed, and these were recorded and the loss noted. The recreational fishing protocol was approved by Rutgers University’s Institutional Animal Care and Use Committee (Protocol # PROTO201900052).

Environmental variables were measured immediately before each fishing event. Water and air temperature (°C), barometric pressure (mmHg), dissolved oxygen (mg/L and % saturation), conductivity (µS/cm) and total dissolved solids (mg/L) were measured using a YSI Professional Series probe. Water turbidity was measured in formazin nephelometric units (FNU) using a Hach 2100Qis portable turbidimeter. YSI measurements and turbidity samples were taken in midstream adjacent to each fishing site. Weather (sunny, partly cloudy, cloudy, rain) was recorded from visual observation before each fishing event. River stage (cm) was recorded at the beginning and end of each fishing day.

2.2 Statistical analysis
Generalized linear mixed effects models (GLMMs) were fit to the catch data to explain variation in 1) overall catch rates and 2) species-specific catch rates for lenok and grayling. Because they were in the form of count data (Figure 2), catch rates were modeled using a Poisson distribution. For all models, the response variable was in the form of landed fish per angler per 20-minute interval, allowing us to account for angler-specific variation as a random effect and gear type as a fixed effect. All models were fit in R version 3.6.0 using the ‘lme4’ package version 1.1-21 (Bates et al. 2015; R Core Team, 2019). A principal component analysis (PCA) was conducted on the environmental covariates and the first principal component was extracted and used as a candidate explanatory variable in the model selection process described below (see Appendix). River stage was included as a candidate explanatory variable in the form of the standardized difference in stage from the previous day (referred to throughout as “change in river stage”) in order to capture the known importance of changes in river level on fish movement and foraging.

After determining the best random effect structure using AICc (corrected Akaike Information Criterion; Hurvich and Tsai, 1989), maximal models were fit that included standardized turbidity, change in river stage, time of day, weather, Julian day, gear type, and the first principal component of the PCA. For overall catch rate and lenok catch rates, interactions between turbidity and change in river stage with gear type were also incorporated into candidate models, reflecting the a priori hypothesis that the effect of these environmental factors depends on fishing gear. However, gear interactions were not tested for grayling catch rates because the majority (90.9%) of grayling were caught
on fly fishing gear. Nested candidate models that represented different hypotheses about the importance of key variables turbidity, change in river stage, and gear and the interaction between them were competed using AICc following Betini et al. (2017). Model fit was assessed using marginal and conditional coefficients of determination calculated with the trigamma method ($R^2$; Nakagawa and Schielzeth, 2013) and the ‘DHARMa’ package version 0.2.6 in R (Hartig 2019). The partial effects of each parameter included in the best-fit model were calculated and plotted using the ‘effects’ package version 4.1-3 in R (Fox 2003; Fox and Weisberg 2019).

3. Results

3.1 Overall catch rates

Eighty 40-minute fishing events were conducted across 24 sites for a total of 320 observations (two 20-minute observations per angler in each fishing event). 398 total fish were landed across 5 species, with grayling and lenok accounting for 27% and 32% of the total catch, respectively (Table S1). The majority of captures were on fly fishing gear ($n = 305$), with about a quarter of fish caught on spinning gear ($n = 93$). Captures on fly fishing gear were relatively evenly distributed between dace ($Leuciscus leuciscus$ Linnaeus) ($n = 139$, a non-target species), grayling ($n = 100$), and lenok ($n = 66$). In contrast, 70% of spinning gear captures were lenok ($n = 65$), with ten or fewer captures each of grayling, dace, perch ($Perca fluviatilis$ Linnaeus), and taimen ($Hucho taimen$ Pallas). Of the 398 landed fish, only two grayling and one perch were previously captured during the study, as indicated by the presence of a fin clip. An additional 97
fish were hooked but not landed. Since most of these could not be identified to species, they were excluded from the analysis.

The model that best explained patterns of variation in overall catch rates of landed fish included main effects for turbidity, change in river stage, gear, and interaction terms between turbidity and gear and between change in river stage and gear (Table S2). It included an angler random effect and a random effect for fishing site nested within sampling location (Eg-Uur or Eg-Selenge). A candidate model that included all of these variables and a fixed effect for time of day was similarly supported by ΔAIC<sub>C</sub> (ΔAIC<sub>C</sub> = 1.90) but it included an additional parameter that did not improve model likelihood, so this model was rejected following Arnold (2010). All other candidate models had ΔAIC<sub>C</sub> > 2 (Table S2). All fixed effects in the best-fit model were significant at the p < 0.01 level except for change in river stage (p = 0.27), which was retained because its interaction with gear type was significant (p = 0.009) (Table 1).

The effect of both turbidity (p = 0.005) and change in river stage (p = 0.009) depended on gear type. Specifically, increased turbidity and positive change in river stage reduced catch rates on fly fishing gear, while for spinning gear, catch rates declined exponentially with increased turbidity but were unaffected by increases in river stage from the previous day (Figure 3). For an increase in turbidity from 5 to 35 FNU and an increase in river stage from -10 to 15 cm from the previous day, such as occurred during the study period following three days of continual rain, the model predicted a decrease in fly fishing captures from 1.7 to 0.8 fish per 20 minutes for an average angler at an average site. For spinning gear, the model predicted a decrease from 0.9 to 0.3 fish
per 20 minutes for the same change in conditions. Overall, the random effects, which represented variability among anglers and fishing locations, explained about the same amount of variation in catch rates as the variables of interest did. Specifically, the fixed effects of turbidity, change in river stage, and fishing gear explained 28% of the variation in catch rates (marginal adjusted $R^2$) while the model as a whole (fixed and random effects; conditional adjusted $R^2$) explained 59% of the variation (Table 1).

3.2 Species-specific catch rates

Grayling were much more vulnerable to fly fishing gear than to spinning gear, with 91% of grayling captures occurring on fly gear ($n = 110$) and only 9% on spinning gear ($n = 10$) (Table S1). For this reason, a model explaining grayling catch rates was only fit to captures on fly fishing gear. Four candidate models to explain grayling catch rates were similarly supported by AIC$_C$, with $\Delta$AIC$_C$ < 2. All of these models included a highly significant turbidity term ($p < 0.001$), with some also including non-significant terms for the first principal component of the environmental variables, time of day, and change in river stage from previous day (Table S3). Since the coefficient estimates for turbidity were similar across all supported models, and the additional parameters improved the model likelihoods only marginally, only the parameter estimates from the most parsimonious model are reported following (Arnold, 2010). This model included a turbidity fixed effect and random effects for angler and for fishing event nested within fishing site (Table 2). Grayling catch rates on fly fishing gear decreased exponentially as turbidity increased ($p = 0.001$) (Figure 4a). An increase in turbidity from 5 FNU to 35 FNU decreased catch rates from 0.8 to 0.2 fish per 20 minutes. The model’s fixed effects
explained 17% of the variation in grayling catch rates, and the model as a whole explained 41% of the variation.

Lenok were caught equally often on spinning gear and fly gear (49.6% and 50.4%, respectively) (Table S1). Variation in lenok catch rates was best explained by a model that included fixed effects for turbidity, gear type, change in river stage, an interaction between turbidity and gear, and random effects for angler and fishing event (Table S4). The effects of turbidity (p = 0.003) and the turbidity/gear interaction (p = 0.004) were significant, while the main effect of change in river stage was marginally non-significant (p = 0.06) (Table 3). Increased turbidity reduced catch rates on spinning gear exponentially, with the greatest effect occurring at low values of turbidity. Catch rates on fly were stable across the range of observed values for turbidity (Figure 4b).

Increased river stage from the previous day decreased catch rates slightly, and this effect did not depend on gear type (Figure 4c). On spinning gear, the model predicted catch rates of 0.5 fish per 20 minutes when turbidity was 5 FNU and river stage had dropped by 10 cm from the previous day. When turbidity was 35 FNU and river stage had increased 15 cm from the previous day, such as occurred after three days of rain during the study period, the model predicted catching only 0.1 lenok per 20 minutes. In contrast, the model predicted fly catch rates of 0.2 and 0.1 fish per 20 minutes for the same interval. Overall, the fixed effects explained only 5.3% of the variation in lenok catch rates, while the model as a whole explained 23% of the variation.
4. Discussion

Standardized experimental fishing observations showed that, as predicted, both increased turbidity and increased river stage reduced catch rates for lenok and grayling on both gear types. Across the board, turbidity had a greater effect on catch rates than changes in river stage. The influence of turbidity was greatest in relatively clear water, with the greatest declines in catch rates occurring when turbidity increased from near zero to about 40 FNU. Contrary to expectations, fly fishing gear outperformed spinning gear in this fishery, retaining higher catch rates than spinning gear across a range of environmental conditions (Figure 3). For example, the overall catch rates model predicted that catch rates of all fish would decline 86% on spinning gear and only 44% on fly fishing gear with an increase in turbidity from 0 to 40 FNU. For lenok, spinning gear was more effective under normal water conditions, but above a low threshold of turbidity, fly fishing gear was more effective (Figure 4b). Fly fishing was even more effective for grayling than for lenok, accounting for 91% of grayling captures in this study regardless of environmental conditions. The most parsimonious model fit to grayling catch rates, which had fewer observations, only included a single fixed effect for turbidity. This suggests that changing river stage had a weaker influence on catch rates that could only be detected with greater statistical power. For all models, the random effects for angler and fishing location explained a greater proportion of the variation in catch rates than the fixed effects did. The degree of variability explained by the fixed effects (marginal adjusted $R^2$) and the model as a whole (conditional adjusted $R^2$) varied greatly among models. The model fit to overall catch rates had the most explanatory
power, with the fixed effects explaining 27% of the variation (marginal adjusted $R^2$). The model fit to lenok catch rates alone had the least, with the model as a whole only accounting for 23% of the variation in catch rates and the fixed effects explaining 5%.

None of the covariates that might have confounded the variables of interest, such as Julian day, time of day, barometric pressure, and weather, significantly improved model fit.

Turbidity’s importance in explaining catch rates matches previous experimental evidence that turbid water reduces many fishes’ feeding rates and reaction distance to prey (Chapman et al., 2014). Because the angling gears used here passively imitate fish and invertebrate prey items moving on the surface and in the water column, fishes’ encounter rate with these gears depends on the distance from which they can identify and react to prey. Mazur and Beauchamp (2003) found that some piscivorous salmonids’ reaction distance declined almost 20% when turbidity was increased from 0.08 to 1.5 nephelometric turbidity units (NTU) in controlled experiments; note that the turbidity units NTU and FNU are considered equivalent (WHO 2017). Across a wider range of observed values, Harvey and White (2008) found that salmonids’ feeding success on benthic invertebrate prey declined by nearly 60% when turbidity was increased from 0 to 100 NTU in an experimental setting. In the present study, catch rates declined exponentially with increasing turbidity, which matches the well-established experimental finding that turbidity and reaction distance are exponentially related (Vogel and Beauchamp, 1999; Hansen et al., 2013). Declines in reaction distance are likely to have outsize impacts on encounter rates with prey as reaction distance is a
squared term in most foraging models (e.g. Jensen et al., 2006), i.e., a decline in reaction distance of 50% would yield a decline in prey encounter rates of 75%.

Lenok were more vulnerable to fly fishing than spinning gear under extreme water conditions, although lenok catch rates on spinning gear were higher under normal conditions. This contradicted the hypothesis that lenok would remain more vulnerable to spin fishing at high turbidities because of spinning lures’ auditory/vibratory component, which was hypothesized to remain effective regardless of water clarity. One possible explanation for this unexpected result is provided by contrast degradation theory, which predicts that turbidity should reduce the visibility of distant objects more than that of objects that are nearby. Therefore, a given increase in turbidity should reduce the visibility of large prey items like fish, which can be observed from a distance, more than small prey items like invertebrates or plankton that are only visible within a small visual range (Utne-Palm, 2002). Consistent with this theory, De Robertis et al. (2003) found that turbidity had a greater effect on feeding rates of piscivorous fish than planktivorous fish in a controlled experiment. One can extend this theory to lure types that imitate differently sized prey items and hypothesize that spinning lures, which imitate larger prey, should be more sensitive to turbidity than the smaller fly-fishing lures used here. This suggests that the visual component of spinning lures may be more important than originally assumed, or that lenok forage primarily using visual cues.

Although its effect was smaller and less consistent than that of turbidity, change in river stage also affected catch rates. Change in river stage from the previous day, the metric used here, provides a proxy for river flow, which has well-established effects on
fishes’ activity levels and movement patterns. Many studies of fishes’ movement patterns in artificially manipulated waterways, like the tailraces of hydropower dams, have established that pulses of flow increase variability in fish movement and feeding behavior (Larranaga et al., 2018; Rocaspana et al., 2019). For example, Larranaga et al. (2018) found that juvenile Arctic charr (*Salvelinus alpinus* Linnaeus) increased their activity rate, swam more quickly, and attacked prey at longer distances in low-flow conditions, and that they stopped moving entirely in high flow. This pattern could be explained by opportunistic feeding on the increased drift of invertebrates produced by high-flow events and could underlie the increased catch rates observed in the present study on days when river stage had dropped from the previous day. Supporting this explanation, the estimated effect of changes in river stage was greatest for overall catch rates on fly fishing gear (Figure 3), which imitate drifting invertebrate prey. These results suggest that thunderstorms could make Mongolian salmonids’ feeding behavior more varied, producing more uncertain catch rates for anglers, and that periods after thunderstorms when water levels drop may be hotspots of fish feeding activity and susceptibility to fishing gear. These findings are relevant in the context of the proposed Egiin Gol Hydropower Project (EGHPP), which would construct an 82 m high hydropower dam immediately downstream of the Eg-Selenge fishing site (Figure 1). Artificially manipulated flow, along with the obvious stressor of habitat fragmentation produced by dam construction, could intensify the stressors of climate change-induced extreme water conditions for these fish.
The two gear types evaluated here are strongly associated with two distinct demographic groups of anglers in this fishery. Gear effectiveness under extreme water conditions could influence these two groups' future fishing success as climate change intensifies. The demographic that most often uses fly-fishing gear in Mongolia is international ecotourist anglers (Golden et al., 2019), who primarily target taimen but also occasionally fish for lenok and grayling when taimen are not available. Taimen are listed as Vulnerable on the IUCN Red List of Endangered Species (Hogan and Jensen 2013), and as threats against them intensify, international taimen anglers may rely more heavily on the fallback option of lenok and grayling. Less is known about the spin fishermen who target these species. However, fishing is becoming a more popular hobby among Mongolians, and most of the Mongolians observed fishing in the Eg-Selenge Watershed between 2016 and 2019 used spinning gear (Golden, unpubl. data). In this fishery, fly fishing by international ecotourists is generally associated with catch and release, and spin fishing by Mongolian anglers is associated with fishing for harvest. Therefore, this division between gears may also represent a tipping point between sustainable and unsustainable fishing (Jensen et al., 2009). However, some Mongolian activists are trying to promote the combination of fly fishing and catch and release practices to Mongolian fishermen (B. Baatar, pers. comm.). The results reported here suggest that fly fishing is a more effective technique for fishing in these rivers in adverse conditions, which in theory could help accelerate a transition toward more sustainable practices among Mongolia anglers.
This study is somewhat limited by the nature of the standardized observations. The catch rates observed here are likely lower than true recreational anglers would experience, because fishing was conducted in a randomized manner and was continued for a set duration regardless of fishing success. Additionally, the data included one extreme outlier, a fishing event conducted on a day when river stage had increased by 36 cm from the previous day and the turbidity was 122 FNU, twice the magnitude of the next highest turbidity observation (see Figure 3). Only one experimental fishing event was possible that day because of logistical challenges associated with the high water event. However, rerunning the analysis without this outlier did not change the outcome of the model selection process or the pattern of results (Figure S4).

As storm events become more frequent globally (Hartmann et al. 2013), the results presented here suggest that they could have significant and complex impacts on the interactions between fish and fishing gear. In the focal ecosystem of northern Mongolia, turbidity and increased river stage reduced catch rates for both lenok and grayling, regardless of gear type. Turbidity had the greatest effect on catch rates, suggesting that other sources of sediment loading, like bank erosion caused by overgrazing, could also impact these fishes’ catchability. The number of grazing animals in Mongolia has increased dramatically in the last 30 years, and cashmere goats, whose browsing behaviors can cause severe overgrazing, represent the greatest increase (Lkhagvadorj et al. 2013). The effects of turbidity on Mongolian salmonids are therefore relevant beyond the context of thunderstorms. Additionally, the gear-specific outcomes observed here could translate into divergent outcomes for two distinct angler
demographic groups, or potentially into the adoption of new gears. Along with the more well-known threat of rising temperatures, climate change-induced increases in thunderstorm frequency and severity will have nuanced effects whose net results will depend on interactions between environmental change and social change.

Acknowledgments:

We gratefully acknowledge our volunteer anglers Dr. David Putnam and Samuel St. John, who fished without complaint in inclement weather conditions and under unusual experimental constraints. Additional field assistance was provided by Suvd Sarantsetseg and Bud Mendsaikhan. We would like to thank the entire MAAERI 2019 field team for logistical and moral support during fieldwork. Emily Slesinger, Zoe Kitchel, and the Jensen Lab at Rutgers University provided extremely helpful feedback on the analysis and manuscript. This research was supported by NSF IRES grant #1658251 to OPJ, a Lewis and Clark Field Scholarship from the American Philosophical Society to ASG, and a Field Research Fellowship from the American Center for Mongolian Studies to ASG. Additional support was provided by NSF grants OISE #1658251, CNH #1716066, and DEB #1442436 to OPJ. ASG is supported by the National Science Foundation Graduate Research Fellowship Program under Grant No. NSF DGE-1842213. Any opinions, findings, conclusions, or recommendations expressed in this paper are those of the authors and do not necessarily reflect the views of the National Science Foundation.

References
Arlinghaus, Robert, Alós, J., Pieterek, T., & Klefoth, T. (2017). Determinants of angling catch of northern pike (Esox lucius) as revealed by a controlled whole-lake catch-


Tables and Figures

Table 1. Fixed and random effects of the model that best explained variation in log-transformed catch rates of all fish. Coefficient estimates (β) and standard errors (s.e.) of fixed effects are shown, and number of observations and variance of random effects is shown. Marginal and conditional adjusted \( R^2 \) values were calculated using the trigamma function.

<table>
<thead>
<tr>
<th>Fixed effects</th>
<th>β (s.e.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-1.11 (0.46)*</td>
</tr>
<tr>
<td>Standardized turbidity</td>
<td>-0.94 (0.25)***</td>
</tr>
<tr>
<td>Standardized difference in stage from previous day</td>
<td>0.19 (0.17)</td>
</tr>
<tr>
<td>Gear (fly)</td>
<td>1.22 (0.15)***</td>
</tr>
<tr>
<td>Turbidity * Gear (fly)</td>
<td>0.66 (0.24)**</td>
</tr>
<tr>
<td>Difference in stage * Gear (fly)</td>
<td>-0.41 (0.16)**</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Random effects</th>
<th>Num. obs.</th>
<th>Variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Event:camp</td>
<td>76</td>
<td>0.35</td>
</tr>
<tr>
<td>Angler</td>
<td>4</td>
<td>0.22</td>
</tr>
<tr>
<td>Camp</td>
<td>2</td>
<td>0.25</td>
</tr>
</tbody>
</table>

\( n = 304 \)

Marginal Adj \( R^2 = 0.27 \)

Conditional Adj \( R^2 = 0.57 \)

\*p < 0.001, \**p < 0.01, \*p < 0.05
Table 2. Fixed and random effects of the model that best explained variation in log-transformed catch rates of grayling on fly fishing gear. Coefficient estimates (β) and standard errors (s.e.) of fixed effects are shown, along with number of observations and the variance of random effects.

<table>
<thead>
<tr>
<th>Fixed effects</th>
<th>β (s.e.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-1.47 (0.38)***</td>
</tr>
<tr>
<td>Standardized turbidity</td>
<td>-1.04 (0.32)***</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Random effects</th>
<th>Num. obs.</th>
<th>Variance</th>
</tr>
</thead>
<tbody>
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<td>Event:site</td>
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</tr>
<tr>
<td>Site</td>
<td>24</td>
<td>0.66</td>
</tr>
<tr>
<td>Angler</td>
<td>4</td>
<td>0.14</td>
</tr>
</tbody>
</table>

n = 152
Marginal Adj $R^2 = 0.16$
Conditional Adj $R^2 = 0.41$

*** p < 0.001, ** p < 0.01, * p < 0.05
Table 3. Fixed and random effects of the model that best explained variation in log-transformed catch rates of lenok on fly and spinning gear. Coefficient estimates (β) and standard errors (s.e.) of fixed effects are shown, along with number of observations and the variance of random effects.

<table>
<thead>
<tr>
<th>Fixed effects</th>
<th>β (s.e.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-1.95 (0.45)***</td>
</tr>
<tr>
<td>Standardized turbidity</td>
<td>-0.92 (0.31)**</td>
</tr>
<tr>
<td>Standardized difference in stage from previous day</td>
<td>-0.31 (0.17)</td>
</tr>
<tr>
<td>Gear (fly)</td>
<td>0.28 (0.21)</td>
</tr>
<tr>
<td>Turbidity * Gear (fly)</td>
<td>0.86 (0.30)**</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Random effects</th>
<th>Num. obs.</th>
<th>Variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Event</td>
<td>76</td>
<td>0.95</td>
</tr>
<tr>
<td>Angler</td>
<td>4</td>
<td>0.53</td>
</tr>
</tbody>
</table>

n = 304

Marginal Adj R² = 0.05
Conditional Adj R² = 0.23

*** p < 0.001, ** p < 0.01, * p < 0.05
Figure 1. Study sites. Experimental fishing was conducted in north-central Mongolia (inset) at 24 sites spanning a total of 60 km of river distance. The Eg-Uur site is located in the upper left area and the Eg-Selenge site is located in the bottom right area of the map.
Figure 2. Histogram of a) overall catch rates per 20 minutes of experimental fishing, b) catch rates of grayling, and c) catch rates of lenok. All plots are divided into catches on spinning gear (dark blue) and fly gear (orange).
Figure 3. The partial effects of both turbidity (formazin nephelometric units, FNU) and change in river stage from the previous day (centimeters) on overall catch rates per angler per 20 minutes of experimental fishing. Partial effects for fly fishing gear are indicated with an orange dashed line and spinning gear is indicated with a solid dark blue line. 95% confidence intervals are indicated with shaded bands. The distribution of observations is indicated with a rug at the bottom of each plot.
**Figure 4.** The partial effects of turbidity (formazin nephelometric units, FNU) and change in river stage from the previous day (centimeters) on catch rates of A) grayling and B,C) lenok per angler per 20 minutes of experimental fishing. Partial effects for fly fishing gear are indicated with an orange dashed line and spinning gear is indicated with a solid dark blue line. 95% confidence intervals are indicated with shaded bands. Partial effects plots with a single blue line do not depend on an interaction with fishing gear.
Supplemental Table 1. Count and proportion of each species captured on each gear.

<table>
<thead>
<tr>
<th>Common name</th>
<th>Scientific name</th>
<th>Overall</th>
<th>Spin gear</th>
<th>Fly gear</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Captures</td>
<td>Proportion</td>
<td>Captures</td>
<td>Proportion</td>
</tr>
<tr>
<td>Dace</td>
<td>Leuciscus leuciscus</td>
<td>143</td>
<td>0.351</td>
<td>4</td>
</tr>
<tr>
<td>Grayling</td>
<td>Thymallus baicalensis</td>
<td>110</td>
<td>0.270</td>
<td>10</td>
</tr>
<tr>
<td>Lenok</td>
<td>Brachymystax lenok</td>
<td>131</td>
<td>0.322</td>
<td>65</td>
</tr>
<tr>
<td>Perch</td>
<td>Perca fluviatilis</td>
<td>10</td>
<td>0.025</td>
<td>10</td>
</tr>
<tr>
<td>Taimen</td>
<td>Hucho taimen</td>
<td>4</td>
<td>0.010</td>
<td>4</td>
</tr>
<tr>
<td>Total</td>
<td>398</td>
<td>0.010</td>
<td>93</td>
<td>0.043</td>
</tr>
</tbody>
</table>
**Supplemental Table 2.** Candidate models evaluated for their ability to explain overall catch rates on spinning gear and fly-fishing gear. All models are Poisson-distributed with a log link and include the random effect structure (1 | angler) + (1 | camp/event). Best-fit model and models with a value of $\Delta AIC_c < 2$ from the best-fit model are indicated in bold.

<table>
<thead>
<tr>
<th>Model</th>
<th>K</th>
<th>AIC&lt;sub&gt;C&lt;/sub&gt;</th>
<th>$\Delta$AIC&lt;sub&gt;C&lt;/sub&gt;</th>
<th>AIC&lt;sub&gt;C&lt;/sub&gt; Weight</th>
<th>LL</th>
</tr>
</thead>
<tbody>
<tr>
<td>turbidity<em>gear + stage</em>gear</td>
<td>9</td>
<td>863.872</td>
<td>0</td>
<td>0.543</td>
<td>-422.63</td>
</tr>
<tr>
<td>turbidity<em>gear + stage</em>gear + time of day</td>
<td>10</td>
<td>865.838</td>
<td>1.966</td>
<td>0.203</td>
<td>-</td>
</tr>
<tr>
<td>turbidity*gear</td>
<td>7</td>
<td>867.022</td>
<td>3.15</td>
<td>0.112</td>
<td>-</td>
</tr>
<tr>
<td>turbidity*gear + stage</td>
<td>8</td>
<td>867.977</td>
<td>4.105</td>
<td>0.07</td>
<td>-</td>
</tr>
<tr>
<td>turbidity + stage*gear</td>
<td>8</td>
<td>869.582</td>
<td>5.71</td>
<td>0.031</td>
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<tr>
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<td>9</td>
<td>869.949</td>
<td>6.077</td>
<td>0.026</td>
<td>-</td>
</tr>
<tr>
<td>turbidity + stage*gear + time of day</td>
<td>9</td>
<td>871.537</td>
<td>7.665</td>
<td>0.012</td>
<td>-</td>
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<tr>
<td>stage*gear</td>
<td>7</td>
<td>876.752</td>
<td>12.88</td>
<td>0.001</td>
<td>-</td>
</tr>
<tr>
<td>turbidity + stage*gear + weather + time of day</td>
<td>12</td>
<td>876.845</td>
<td>12.973</td>
<td>0.001</td>
<td>-</td>
</tr>
<tr>
<td>turbidity + gear</td>
<td>6</td>
<td>880.813</td>
<td>16.941</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>turbidity + stage + gear</td>
<td>7</td>
<td>881.694</td>
<td>17.822</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>turbidity + stage + gear + time of day</td>
<td>8</td>
<td>883.632</td>
<td>19.76</td>
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<td>-</td>
</tr>
<tr>
<td>gear</td>
<td>5</td>
<td>886.931</td>
<td>23.059</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>stage + gear</td>
<td>6</td>
<td>887.612</td>
<td>23.74</td>
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</tr>
<tr>
<td>turbidity</td>
<td>5</td>
<td>977.5</td>
<td>113.628</td>
<td>0</td>
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</tr>
<tr>
<td>turbidity + stage</td>
<td>6</td>
<td>978.367</td>
<td>114.495</td>
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</tr>
<tr>
<td>stage</td>
<td>5</td>
<td>984.299</td>
<td>120.427</td>
<td>0</td>
<td>-</td>
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</tbody>
</table>


**Supplemental Table 3.** Candidate models evaluated for their ability to explain catch rates of grayling on fly fishing gear. All models are Poisson-distributed with a log link and include the random effect structure (1 | angler) + (1 | site/event). Best-fit model and models with a value of ΔAICc < 2 from the best-fit model are indicated in bold.

<table>
<thead>
<tr>
<th>Model</th>
<th>K</th>
<th>ΔAICc</th>
<th>ΔAIC</th>
<th>AICc</th>
<th>Weight</th>
<th>LL</th>
</tr>
</thead>
<tbody>
<tr>
<td>turbidity + stage</td>
<td>6</td>
<td>4</td>
<td>0</td>
<td>0.223</td>
<td>146.958</td>
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<tr>
<td>turbidity</td>
<td>5</td>
<td>2</td>
<td>7</td>
<td>0.215</td>
<td>-148.08</td>
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</tr>
<tr>
<td>turbidity + stage + PC1</td>
<td>7</td>
<td>3</td>
<td>8</td>
<td>0.129</td>
<td>146.408</td>
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<tr>
<td>turbidity + stage + time of day</td>
<td>7</td>
<td>6</td>
<td>1</td>
<td>0.122</td>
<td>146.459</td>
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<tr>
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<td>7</td>
<td>2</td>
<td>7</td>
<td>0.077</td>
<td>146.922</td>
<td></td>
</tr>
<tr>
<td>turbidity*stage</td>
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<td>3</td>
<td>8</td>
<td>0.074</td>
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<tr>
<td>turbidity + stage + PC1 + time of day</td>
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<td>1</td>
<td>6</td>
<td>0.069</td>
<td>145.917</td>
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<tr>
<td>turbidity + stage + Julian day + time of day</td>
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<td>3</td>
<td>9</td>
<td>0.046</td>
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<td>turbidity*stage + PC1</td>
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<td>stage</td>
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<td>4</td>
<td>2</td>
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<td>154.552</td>
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</table>
**Supplemental Table 4.** Candidate models evaluated for their ability to explain catch rates of lenok on fly and spinning gear. All models are Poisson-distributed with a log link and include the random effect structure (1 | angler) + (1 | event).

<table>
<thead>
<tr>
<th>Models</th>
<th>K</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>AICc Weight</th>
<th>LL</th>
</tr>
</thead>
<tbody>
<tr>
<td>turbidity*gear + stage</td>
<td>7</td>
<td>500.12</td>
<td>0</td>
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<td></td>
<td></td>
<td>242.874</td>
<td>-</td>
</tr>
<tr>
<td>turbidity<em>gear + stage</em>gear</td>
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<td>500.86</td>
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<td>-</td>
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<tr>
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<td>3</td>
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</tr>
<tr>
<td>turbidity*gear + stage + Julian day</td>
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<td>501.56</td>
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<td>-242.54</td>
</tr>
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<td>8</td>
<td></td>
<td></td>
<td>242.187</td>
<td>-</td>
</tr>
<tr>
<td>turbidity<em>gear + stage</em>gear + Julian day</td>
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<td></td>
<td></td>
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<td>-</td>
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<td></td>
<td>247.678</td>
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</tr>
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<td>0.022</td>
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<td>1</td>
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<td></td>
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<td></td>
<td>247.662</td>
<td>-</td>
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<tr>
<td>turbidity + PC1 + Julian day + time of day</td>
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<td>509.53</td>
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<td>-</td>
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<td></td>
<td></td>
<td>247.576</td>
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<td>turbidity + stage + gear + PC1 + Julian day</td>
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<td>510.28</td>
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</tbody>
</table>
Supplemental Figure 1. The fly and spinning lures used for standardized experimental fishing. A) Parachute Adams dry fly, B) Gold #2 Mepps dressed aglia treble hook spinning lure with two hooks removed in compliance with Mongolian law, C) Royal Wulff dry fly, D) Beadhead Prince Nymph pattern, E) Non-beadhead Hare’s Ear nymph pattern.
Supplemental Figure 2. Fly fishing catch rates on dry fly and nymph patterns for A) all species, B) grayling, and C) lenok.
Supplemental Figure 3. Length distribution of grayling and lenok captured on dry fly (dark brown) and nymph (beige) patterns. Vertical lines indicate the median length of fish captured on dry flies (solid lines) and nymph patterns (dashed lines). Grayling captured on both patterns had a median size of 170 mm (note the single line in the top panel).
Supplemental Figure 4. Partial effects of turbidity (formazin nephelometric units, FNU) and change in river stage (centimeters) on overall catch rate with an outlier removed.
Appendix: Principal Components Analysis

A principal components analysis was conducted on the environmental variables dissolved oxygen (% saturation), conductivity, total dissolved solids, and barometric pressure to reduce the number of these correlated environmental variables. Conductivity, barometric pressure, and total dissolved solids were highly positively correlated with each other and uncorrelated with percent saturation of dissolved oxygen. Observations were strongly clustered along the first principal component according to the river where fishing events occurred (Eg-Uur versus Eg-Selenge). The biplot below indicates the first two principal components of the PCA. The variables are depicted as vectors, with the angle between any two vectors representing the correlation between the corresponding variables: an angle of 180, 0, or 90° represents a correlation coefficient of -1, 1, or 0, respectively. Points represent individual fishing events and are labeled according to their location on the Uur River above its confluence with the Eg (blue points; Eg-Uur site) and on the Eg River above its confluence with the Selenge (pink points; Eg-Selenge site). The labeled outliers were observations from a single site, 5.3, which was at the mouth of a groundwater-fed creek and therefore had highly variable dissolved oxygen saturation over time.
CHAPTER 3

FOCUSING ON WHAT MATTERS MOST: EVALUATING MULTIPLE CHALLENGES TO STABILITY IN RECREATIONAL FISHERIES

Abstract:
Recreational fisheries are theorized to self-regulate in a sustainable feedback loop in which recreational anglers moderate their fishing effort in response to population declines. However, a number of mechanisms are hypothesized to break down this self-regulatory process, including density-dependent catchability and depensatory population dynamics. Although many of these mechanisms of instability have been estimated in empirical systems and explored using modeling, we still do not know the extent to which these mechanisms can 1) erode stability at their observed strength in real systems and 2) interact to dampen or intensify each other’s effects. In this study, we synthesize existing data on four of these mechanisms: 1) depensation in the stock-recruit relationship, 2) environmentally driven recruitment variability, 3) hyperstability in catch rates, and 4) the strength of anglers’ responsiveness to changing catch rates. We report the range of observed values for these four mechanisms in real-world fisheries and observe their effect on the behavior of a simplified recreational fishery model. We find that none of the mechanisms was destabilizing enough on its own to collapse the modeled population, but that an angler population that was highly responsive to catch rates was a key element of interactions that resulted in collapse. The strongest interaction was between a responsive angler population and a fish population with hyperstable catch rates. Our results highlight the need for more
consistent and widespread estimation of angler utility functions in recreational fisheries as well as the importance of interdisciplinary teams that can gather both social and ecological data.

1. Introduction

Fisheries management is complicated by the fact that fisheries are social-ecological systems (SES), in which an ecological system (fish) interacts with a social system (anglers and managers) to produce a whole that is more complex than the sum of its parts (Ostrom, 2009). Social-ecological systems possess emergent properties that accrue from the micro-scale interactions of many individual actors in both the ecological and social subsystems (Carmichael & Hadžikadić, 2019). One key emergent property of SESs is their ability to exhibit resilience, frequently operationalized as the magnitude of disturbance a system can withstand without collapse (Gunderson, 2000). Stable, resilient systems should be easy to maintain, while ones that tend toward instability may require intensive, costly management (Camp et al., 2020). Knowledge of a system’s level of resilience is therefore key to understanding whether managing for any given outcome is cost-effective or even possible.

In theory, recreational fisheries SES should be highly resilient at relatively high levels of biomass and effort, under the right conditions. Specifically, given some key assumptions, fisheries should self-regulate through a negative feedback loop between angler behavior and population dynamics. The feedback is as follows: angler effort responds to population abundance. If abundance decreases, anglers’ expectations for their fishing experience are not met, and they leave the fishery. This reduction in effort
allows the fish population to recover, making it an attractive fishing target once again (McConnell, & Sutinen, 1979; Bishop & Samples, 1980; Carpenter et al., 1994). However, extensive research using both empirical data and theoretical modeling has revealed a variety of mechanisms that can violate these assumptions and break down this self-regulating process (Post, 2013). Some of these are fairly well understood, like aggregating behavior in fish that generates inversely density-dependent catch rates and prevents anglers and managers from perceiving and responding to declining abundance (Rose & Kulka, 1999). Other potential mechanisms have hardly been studied, like the role of imperfect information sharing among anglers in delaying the reallocation of angler effort in response to changing abundance (Solomon et al., 2020). Because these mechanisms have usually been studied in isolation, the current literature provides little guidance about which mechanisms are likely to be most influential in a given fishery, all else being equal, and, therefore, which ones managers should invest time and resources in understanding or possibly controlling.

In the biological subcomponent of the system, the negative feedback loop between fishing pressure and abundance requires that recruitment to the fish population responds in a predictable way to changes in abundance. In particular, fish stocks are commonly assumed to exhibit compensatory or negative density-dependent recruitment dynamics, in which per-capita population growth rates increase as population size decreases (Walters & Martell, 2004). If this assumption is met, populations that have been reduced to low levels by harvest will recover rapidly, enabling a return to a high-biomass system state. This assumption seems to hold for
most stocks, but a number of species exhibit positive density-dependence, also known as depensation, at very low population sizes (Rowe et al., 2004; Hilborn et al., 2014; Perälä & Kuparinen, 2017) (Figure 1A). Depensation can occur if individuals in a population fail to encounter mates or have trouble evading predators below some threshold population size (Liermann & Hilborn, 2001). If an exploited fish population possesses depensatory dynamics but is modeled and managed as though it has a purely compensatory stock-recruitment relationship, fishing pressure could theoretically reduce the population to levels from which it cannot recover. An additional source of complexity is the fact that recruitment can vary significantly from year to year due to environmental conditions, even without changes in population size or reproductive output (Hjort, 1926; Morgan et al., 2011) (Figure 1B). This natural stochasticity includes temporally autocorrelated error, which can produce persistent deviations from the deterministic expectation (Thorson et al., 2014). If these deviations are negative, they may produce persistent population declines even in the absence of overfishing.

Angler behavior can also violate the assumptions required for recreational fisheries to self-regulate in a sustainable way. The stabilizing, self-regulating feedback described above depends on anglers responding to decreased population abundance—as experienced through catch rates—by reducing their fishing effort. If catch rates are not a linear function of abundance, or if anglers are not highly motivated by increasing their catch rates and/or avoiding low catch rates, they may inadvertently contribute to overfishing by maintaining or intensifying fishing pressure as stock sizes decline. A number of mechanisms can produce non-linear relationships between catch rates and
abundance, known as either hyperstability, in which catch rates remain higher than expected as abundance declines, or hyperdepletion, in which catch rates decline more quickly than expected (Harley et al., 2001) (Figure 1C). In fisheries with hyperstable catch rates, anglers and managers may never perceive declines in abundance, and may never reduce their effort (anglers) or introduce precautionary regulations (managers) in response. Hyperstability can be caused by fish aggregation behavior (Erisman et al., 2011; Dassow et al., 2020) or by effort sorting patterns in which more highly skilled anglers, who tend to have higher catch rates, continue fishing longer as stocks decline (Ward et al., 2013; van Poorten et al., 2016).

Even if anglers accurately perceive changes in population abundance, they must voluntarily reduce their effort as stocks decline in order to produce a self-regulatory response in open-access fisheries. This voluntary reduction is expected in fisheries where anglers are mostly motivated by catching fish and maintaining a high catch per unit effort, and therefore leave the fishery when catch rates are too low (Bishop & Samples, 1980). However, a large body of literature on angler behavior and preferences, reviewed in Hunt et al. (2019), has shown that recreational anglers are motivated to fish by a wide range of catch and non-catch-related factors. The relative importance of these factors to anglers’ fishing preferences and behavior varies widely within and across fisheries (for example, Arlinghaus et al., 2008; Bryan, 1977; Curtis & Breen, 2017; Jiménez-Alvarado et al., 2019). In some trophy fisheries characterized by low catch rates and specialized gear, anglers are motivated more by activity-general goals, such as experiencing a new fishing destination or testing their fishing skill, than they are by
maximizing catch rates (Beardmore et al., 2011; Golden et al., 2019). In fisheries where anglers are not primarily motivated by catch rates, anglers may continue fishing even as stocks approach collapse because they remain satisfied with other aspects of their fishing trips.

Each of these mechanisms described above can, in theory, contribute to the instability of recreational fisheries SES. There is also substantial empirical evidence from case studies that these mechanisms have contributed to specific fishery declines. For example, hyperstable catch rates contributed to the collapse of barred sand bass (Paralabrax nebulifer, Serranidae) and kelp bass (Paralabrax clathratus, Serranidae) populations in southern California (Erisman et al., 2011). Similarly, Mullon et al. (2005) found that about 20% of global fisheries collapses could be mechanistically explained by the presence of depensation, although their analysis did not observe depensatory mechanisms directly. However, what is currently missing in the literature on fisheries SES is an understanding of (1) the extent to which these mechanisms can erode stability at levels that are commonly observed across systems and (2) how interactions among these mechanisms might exacerbate risk of collapse.

The objectives of this study are therefore: (1) to conduct a quantitative review and synthesis of the strength of four mechanisms theorized to erode resilience in recreational fisheries as measured in empirical studies and (2) evaluate the impacts of these mechanisms on the stability of a modeled recreational fishery SES when parameterized at these empirically observed levels. The mechanisms are 1) depensation in the stock-recruitment relationship, 2) autocorrelated stochasticity in recruitment, 3)
density-dependent catchability, and 4) the responsiveness of angler effort dynamics to catch rates. We approached the first objective by reviewing the literature on case studies of mechanisms 3 and 4 and refer to existing comprehensive meta-analyses for mechanisms 1 and 2. We addressed the second objective by exploring the effects of these mechanisms in a coupled social-ecological model of a simplified recreational fishery, in which a single generic fish stock with age-structured dynamics is exploited by a homogeneous angler population that allocates effort between a focal modeled lake and a landscape of unobserved alternatives. Each mechanism’s effect on the measures of sustainability and stability is evaluated in isolation and in combination to evaluate possible dampening, amplifying, or synergistic interactions between mechanisms.

2. Methods

2.1 Literature review and data synthesis

Where possible, we leveraged existing data synthesis efforts to parameterize the four mechanisms of interest. When a comprehensive data synthesis was not available for a given mechanism, the most common mathematical expression for that mechanism was identified, and a Web of Science search was conducted to find papers that calculated this value from empirical data. For mechanisms that are at least partially related to angler behavior (density-dependent catchability and angler responsiveness to catch), only studies conducted on recreational fisheries were included. Conversely, for mechanisms that solely relate to biological processes (depensation and recruitment variability), we included studies conducted for both recreationally and commercially exploited fishes. Both marine and freshwater vertebrate fishes were included, but
studies on invertebrates were excluded. All Web of Science searches were conducted on July 19, 2020 and spanned the years 2000 to 2020 inclusive.

2.1.1. Depensation in the stock-recruit relationship

Estimates for depensation in the stock-recruit relationship were drawn from Hilborn et al. (2014), which synthesizes global data from the RAM Legacy Stock Assessment Database (Ricard et al., 2012). The authors use time series of spawning stock biomass and recruitment for stocks that dropped below 20% of their maximum observed biomass in the RAM database to fit stock-recruit models with and without a depensation term. They operationalize depensation as a parameter \( d \), representing the population size at which 50% of the population is mated relative to the population size at carrying capacity \( K \). This parameter can take values between zero and one, with \( d \approx 0 \) indicating no depensatory dynamics and increasing values of \( d \) greater than zero indicating a higher degree of depensation. Depensation parameter \( d \) informs a depensation term \( D_t \) that represents the fraction of females in the population who are mated at time \( t \):

\[
D_t = 1 - \exp \left( \frac{\log(0.5) B_t}{dK} \right),
\]

where \( B_t \) is spawning stock biomass at time \( t \). Depensation term \( D_t \) is used to modify the biomass term in a conventional stock-recruit relationship, in this case the Deriso stock-recruit function (Deriso, 1980)

\[
R_t = \frac{aD_tB_t}{(1 + bD_tB_t)^g} \exp(\epsilon_t),
\]
where recruitment $R_t$ depends on $B_t$, constants $a$, $b$, and $g$, and some stochasticity $\epsilon_t$.

The Deriso stock-recruit function simplifies to the Beverton-Holt stock-recruit function when $g = 1$ and the Ricker function when $g \to \infty$, allowing researchers to estimate the stock-recruit function without making a priori assumptions about its form.

Hilborn et al. (2014) estimated a Deriso stock-recruit function with and without a depensation term $D_t$ for 113 stocks using maximum likelihood estimation. They found that the depensation term improved model performance as measured by $\text{AIC}_C$ for four of the analyzed stocks. Of these, three were finfish and fall within the scope of our study. The median value of $d$ for these three stocks was 0.06, with a range of 0.04-0.3 (Table 2). Although Hilborn et al. (2014) fit stock-recruit models to the data using both maximum likelihood (ML) and hierarchical Bayesian analyses, only the ML estimates were used for this project because they provide more precise values for the depensation term.

2.1.2. Recruitment variability

Natural variability in recruitment was parameterized from Thorson et al. (2014), which estimated the degree of variability and autocorrelation in recruitment for 154 stocks from the Myers et al. (1995) repository of spawning biomass and recruitment estimates from stocks worldwide. The authors fit a stock-recruit relationship for each stock and then modeled the observed residuals around the curve as including both an autocorrelated component and uncorrelated, normally distributed stochasticity, such that

$$
\epsilon_t = \rho\epsilon_{t-1} + \sqrt{1 - \rho^2}\delta_t
$$
where $\rho$ is the first-order autocorrelation coefficient, $\epsilon_t$ and $\epsilon_{t-1}$ are observed residuals around the stock-recruit curve in years $t$ and $t-1$, respectively, and $\delta_t$ is normally distributed random error in year $t$. Across the taxa included in their analysis, the authors found values of the standard deviation of $\delta$ that ranged from 0.64 for Pleuronectiformes to 0.78 for Perciformes and Scorpaeniformes (Table 1). They observed values of autocorrelation coefficient $\rho$ ranging from 0.38 for Salmoniformes to 0.49 for Aulopiformes and Perciformes.

2.1.3. Density-dependent catchability

Unlike the recruitment-related mechanisms, a comprehensive meta-analysis does not exist for estimates of density-dependent catchability in recreational fisheries. However, the majority of studies that estimate the magnitude of this phenomenon use the mathematical framework described in (Gulland, 1977; Harley et al., 2001), in which abundance $N$ in the catch equation is modified by a shape parameter that governs the type and magnitude of nonlinearity:

$$C = qE \beta N$$

where $C$ is catch, $E$ is effort, and $q$ is the catchability coefficient. When $\beta = 1$, equation (4) reduces to the conventional linear form of the catch equation, $C = qEN$, but if $\beta \neq 1$, catchability varies with abundance. Values of $\beta < 1$ produce hyperstability, in which catch declines more slowly than expected as abundance declines, while conversely, $\beta > 1$ produces hyperdepletion, in which catch declines more rapidly than expected (Figure 1C).
We conducted a Web of Science search for papers that estimate density-dependent catchability in recreationally targeted populations of finfish using the search terms “(hyperstab* OR hyperdeplet*) AND (catch* OR CPUE) AND fish* AND (recreation* OR angl*).” Search results were then manually screened to include only studies that use equation (4) and report a value for $\beta$, so that values of hyperstability and hyperdepletion could be compared across disparate systems. Some papers estimated $\beta$ for multiple gear types; in these cases, we extracted the value for each gear type.

Estimates from seven studies met the search criteria and are reported here (Table 3). Nine $\beta$ estimates are reported from these seven studies because two studies estimated density-dependent catchability for both spearing and angling gear in the same fishery. The studies were all conducted in the United States and Canada, with Wisconsin being the most common study location. Freshwater species heavily dominate the dataset, with walleye ($Sander vitreus$, Percidae) alone representing five of the nine estimates. Most studies produced estimates of $\beta$ that indicate hyperstable catch rates; the median value of $\beta$ was 0.53, and the mean was 0.72. Only one population, Northern pike ($Esox lucius$, Esocidae) in Minnesota, exhibited hyperdepletion ($\beta = 1.7$). Additionally, one study reported no evidence of non-linear catchability in walleye in Ontario and Quebec ($\beta = 1.02$), in contrast with studies of walleye in the U.S. that reported hyperstability ranging in magnitude from 0.4 to 0.8.

2.1.4. Angler responsiveness to catch rates
There is no comprehensive data synthesis of the importance of catch rates to anglers’ fishing preferences and decision making. A wide variety of tools have been used to estimate anglers’ preferences and predict their fishing choices, including gravity models (Freund & Wilson, 1974; Hunt, Morris, et al., 2019), conjoint analysis (Gillis & Ditton, 2002), and Kuhn-Tucker demand models (Abbott & Fenichel, 2013; Von Haefen & Phaneuf, 2005). By far the most common tool, however, is derived from random utility theory, which states that anglers (or other consumers) choose the option that best maximizes their utility (i.e., the benefits they receive) from fishing or some other activity (McFadden, 1973). The theory further assumes that anglers make this choice by subconsciously integrating the benefits and costs they accrue from each aspect of the activity and weighting them based on their preferences. This assumption enables researchers to develop random utility models (RUM) that predict anglers’ choices by estimating the utility $U$ that they would derive from different fishing options. Because utility is latent and not all the factors that influence individuals’ preferences can be fully observed and modeled, utility estimates include both an observed component $V$ and a random component $\zeta$, such that the utility $U$ of alternative $j$ for angler $i$ can be expressed as:

$$U_{ij} = V_{ij} + \zeta_{ij}.$$  

The observed component $V$ in turn includes the marginal utilities for a variety of attributes that can influence angler preference, including catch rates, site characteristics, and individual traits like income and catch orientation:

$$V_{ij} = \beta X_{ij}.$$
where \( X_{ij} \) is a vector of the observed attributes of alternative \( j \) for angler \( i \) and \( \beta \) is a vector of marginal utility weights for those attributes (Fiebig et al., 2010). These utility values allow researchers to predict anglers’ choices, most commonly using a multinomial logit model (MNL), which assumes that the error terms \( \zeta_{ij} \) are independent and identically distributed as type I extreme values. The probability \( P_{ij} \) that individual \( i \) chooses site \( j \) can therefore be expressed as the logistic function

\[
P_{ij} = \frac{\exp(V_{ij})}{\sum_{j=1}^{J} \exp(V_{ij})}.\]

Random utility models are used to estimate anglers’ probability of fishing, their site choice among a landscape of options, or the joint probability that they will both choose to fish and fish at a particular site.

The RUM angler choice literature spans multiple disciplines and statistical approaches (Fenichel et al., 2013), making it more difficult to synthesize than other mechanisms explored in this paper. In addition, (Hunt et al., 2019) found that a wide variety of catch-related and non-catch-related factors influence where anglers choose to fish, adding to the field’s complexity. In our synthesis effort, we sought to preserve the diversity of attributes and functional forms that are used to understand anglers’ choices while enabling comparison across studies. To do this, we calculated the responsiveness of a generic angler’s site choices to catch rates for each study, which we label \( \lambda \). This value can be expressed as the partial derivative of the probability function \( P \) with respect to catch rate:
\[ \lambda = \frac{\partial P_{im}}{\partial x} = \beta_x P_{im} (1 - P_{im}) \]

where \( x \) is the catch rate or other equivalent catch-related attribute used in the study, \( \beta_x \) is the marginal utility estimate associated with that catch attribute, and \( P_{im} \) is the probability of generic angler \( i \) fishing at the mean site \( m \). Generic angler \( i \) is assumed to possess the mean level of all individual-specific attributes (or the modal value, for categorical attributes), and mean site \( m \) is assumed to have the mean value for all site-specific attributes, including catch rate.

To calculate anglers’ responsiveness to catch across studies, we conducted a Web of Science search with the search terms “(angl* OR "recreation* fish*") AND (choice* OR behavior OR preference* OR satisfaction OR motivation) AND utility AND (catch* OR "catch-related" OR "fishing quality" OR harvest*).” Following (Hunt, et al., 2019), we limited our analysis to papers that predict angler fishing effort allocation across sites in a multi-site choice model, since this is the most common application for angler RUMs. Papers were therefore manually filtered to include only studies that 1) calculated an angler utility function for fishing effort allocation across sites in a multi-site choice model, 2) were empirically derived from stated or revealed preference data, 3) included catch rates or an equivalent catch-related attribute in the utility function, and 4) provided sample means for all attributes that were included in the angler utility function. For studies of multispecies fisheries in which catch rates of multiple species contributed to the utility function, angler responsiveness \( \lambda \) was calculated for each species using equation (9).
Five studies met the search criteria and provided enough information to calculate angler responsiveness to catch (Table 3). They represent a wide geographic scope, ranging from Western Australia to New Zealand to the east and west coasts of the United States. Three of the studies included separate catch rates for multiple species groups in their utility estimates, so that the five papers yielded a total of 16 angler responsiveness estimates. These estimates varied by five orders of magnitude, from $\lambda = 0.00019$ for butter fish (a species group that includes Belone belone, Belonidae; Arripis georgianus, Arripidae; Scomber australasicus, Scombridae; and other species; see Raguragavan et al., 2013) in Western Australia to $\lambda = 5.8$ for billfishes (Istiophoridae and Xiphiidae) in North Carolina (Whitehead et al., 2013). These angler responsiveness values represent a wide range of relationships between catch rates and probability of fishing at a site (Figure 2), which are defined by both $\lambda$ and the y-intercept of the logistic curve. This intercept represents the probability of fishing when catch rates are zero. This value ranged from a 1% probability of fishing when catch rates were zero for salmonids in New Zealand lakes (Mkwara et al., 2015) to a 45% probability for inshore species in southern California (Kuriyama et al., 2013), and was uncorrelated with $\lambda$ (correlation coefficient = -0.03).

2.2. Model Overview

We incorporated the four mechanisms outlined above into a dynamic social-ecological model of a highly simplified recreational fishery. A biological submodel was developed to represent a single age-structured population occupying a single waterbody. Fish were harvested by a homogeneous population of anglers that was
assumed to allocate its fishing effort between the modeled lake and an unmodeled landscape of alternative fishing sites, in order to remain consistent with the angler site choice literature used to estimate angler responsiveness to catch across sites. The model is a discrete-time model run for 200 yearly time steps. For depensation, autocorrelated recruitment error, and density-dependent catchability, simulations were run across the range of values observed empirically, keeping the other mechanisms at the null expectation (Table 4). In addition, we evaluated two-way interactions between mechanisms of interest by running simulations in which each pair of mechanisms was set at the median observed value and the remaining ones were kept at the null.

2.2.1 Biological model

The biological submodel is conceptualized as a single age-structured population exhibiting knife-edge maturity and fishing vulnerability at age 2. In each yearly time step \( t \), the abundance \( N \) of each age class \( a \) is censused following harvest and natural mortality:

\[
N_{a,t} = \left[ N_{a-1,t-1} - q E_t v_a (N_{a-1,t-1})^\beta \right] s_a
\]

where catchability \( q \) is a constant, effort \( E_t \) is informed by the angler effort model, fishing vulnerability \( v \) is zero below age at maturity and one at and above the age of maturity, and survival \( s \) is constant across age classes. Catchability shape parameter \( \beta \) can be modified to produce hyperstability (\( \beta < 1 \)), hyperdepletion (\( \beta > 1 \)), or the null expectation, density-independent catchability (\( \beta = 1 \)).

Spawning stock biomass is calculated from the abundance of mature fish using a von Bertalanffy growth curve and the length-weight relationship:
where weight-at-age \( w_a \) depends on length-at-age and shape parameters and maturity at age \( m_a \) is a dummy variable with the value of 0 for immature age classes and 1 for age classes at or above the age of maturity. Recruitment to the first age class can then calculated based on the previous year’s biomass. Depensatory recruitment dynamics and autocorrelated stochasticity can be incorporated here by inserting equations 1 and 3 into the Deriso stock-recruit function (equation 2):

\[
R_t = N_{a=1,t} = \frac{aD_{t-1}B_{t-1}}{(1 + bD_{t-1}B_{t-1})^g} \exp \left( \rho \epsilon_{t-1} + \sqrt{1 - \rho^2} \delta_t \right)
\]

where depensation term \( D_t \) is calculated using equation 1. Recruitment stochasticity can be turned “off” by setting \( \rho \) and the standard deviation of \( \delta \) equal to zero. The null expectation of no depensatory dynamics in the stock-recruit relationship was represented by setting \( d \) close to zero.

2.2.2 Angler effort model

Random utility estimates are uniquely difficult to apply outside their original context or compare across systems because utility is unit-less, meaning that the absolute magnitude of utility estimates is uninformative. Instead, researchers draw conclusions based on the differences in observed utility between the alternatives within a study; these differences would be meaningless across studies (Train, 2002). In addition, random utility studies of fishing site choice almost never report enough information about site-specific attributes to fully contextualize anglers’ utility gained from a given site compared to others. To solve this problem, we developed a novel
approach that preserves the wide range of attributes and functional forms for anglers’ site choice utility that exist in the literature while enabling comparison across studies.

In our approach, the range of empirical values for anglers’ responsiveness to catch was incorporated into the model by estimating study-specific random utility models of fishing site choice that represent different degrees of angler catch responsiveness to link $C_{t-1}$ and the probability of angler $i$ fishing at time $t$, $P_{i,t}$.

Specifically, for each paper in Table S1, we generated a simplified probability function that treated the site described in our model as a modified version of the mean site $m$ from equation 9, where all the utility attributes were set at the sample mean for the study except for the catch-related attribute, which was set equal to the model’s time-varying catch function. The modeled site was treated as a focal fishing option in a landscape consisting of the modeled site plus $n - 1$ unmodeled sites, where $n$ is the number of sites observed in the study of interest. All $n - 1$ unmodeled sites were assumed to have the mean value of each site attribute, including catch, such that overall utility at each of the unmodeled sites can be considered the generic angler’s observed utility for the mean site in the study, $\bar{V}$. The probability of a generic angler choosing to fish at the focal site at a given time step, rather than at one of the unmodeled sites, can therefore be calculated as

$$P_{i,t} = \frac{\exp(V_{i,t})}{\exp(V_{i,t}) + (n - 1)(\exp(\bar{V}))}$$

where $V_{i,t}$ is the observed utility of generic angler for the focal site $i$ in time step $t$ based on the catch rate in the previous time step; $V_{i,t} = f(C_{t-1})$. Although equation 13
represents a multinomial logit model, the same simplification is easily applied to other probability functions used in angler utility studies, including the nested logit, the random parameters logit, and the probit model. For studies that evaluated the catch utility for multiple species or species groups, we created versions of equation 13 in which each of those species was assumed to be represented in the model, with the others held at the mean. For example, a paper that estimated utility for 5 species groups could inform our model with 5 potential choice probability functions.

Since we assume that the angler population is homogeneous, the probability of generic angler $i$ fishing at the modeled site at a given time informs the total angler effort in that time step, $E_t$. We treat $E_t$ as a proportion of some maximum fishing effort $E_{max}$, which represents a level of fishing effort large enough to extirpate the fish population if sustained at equilibrium. This proportion was assumed to be directly proportional to the probability of any generic angler $i$ choosing to fish at the modeled site ($P_{tm}$). For example, in a time step where the site choice probability for the generic angler $i$ was 0.2, the overall effort across the modeled angler population (all of which share the preferences of angler $i$) would be $0.2 \times E_{max}$. This approach enabled us to model angler effort $E_t$ as a function of anglers’ site choice probability based on their utility from catch in the previous time step, $C_{t-1}$.

Unlike the other three mechanisms evaluated in this paper, there is no simple, empirically based null expectation for anglers’ responsiveness to catch rates. Any approach that assumes that anglers respond dynamically to catch based on their utility from catching fish requires a functional form for that response, and the steepness and
zero-catch intercept of that function can vary widely (Figure 2). Therefore, the model’s performance was evaluated using a subset of the empirically derived functions that represented each quadrant of the two-dimensional parameter space defined by the steepness $\lambda$ and the no-catch intercept (Figure S1).

### 2.2.3 Outcome variables

We assessed model outcomes across three axes: 1) biological sustainability, 2) socioeconomic benefits, and 3) stability/variability of biological and socioeconomic outcomes through time. Biological sustainability was evaluated using two metrics: the proportion of simulations in which the fish population was extirpated by the final time step, and the mean proportion of time steps starting at $t = 100$ in which population biomass was below $0.5*B_{\text{MSY}}$ across simulations, a common metric of overfishing (Hunt et al., 2011). Since anglers receive benefits both from catching fish and from fishing effort (Stoeven, 2014), social outcomes were assessed by measuring the average cumulative fishing effort $E$ and catch $C$ for all time steps across simulations. To assess the stability of these biological and social outcomes, the coefficient of variation (CV) of biomass and effort through time were calculated and then averaged across simulations. To assess the impact of each mechanism (or combination of mechanisms), 100 simulations were run for each scenario of interest and the outcome variables above were averaged across these simulations. Stochasticity was only introduced into the model through the mechanism of autocorrelated recruitment variability, so scenarios without this mechanism were purely deterministic, with identical outcomes across simulations.
3. Results

Overall, the mechanisms of interest had a stronger impact on the biological subsystem than on the angler subsystem, creating greater changes in cumulative catch and the coefficient of variation of biomass than they did in cumulative effort or the CV of effort. None of the four mechanisms were destabilizing enough on their own to collapse the fish population without the influence of other mechanisms. However, when mechanisms were explored in combination, some exhibited interactions that produced extirpation in the biological system.

3.1 Depensation

Depensation had no effect on the system’s stability when an anglers’ no-catch probability of fishing was low and their utility increased shallowly with increasing catch (low λ) (Figure S1C). It had the greatest impact when anglers’ utility function from catch both had a high no-catch intercept and was very steep (Figure 3A). In this scenario, anglers overfished the population (B < 0.5B_{MSY}) for all values of \(d\), and extirpated the population when \(d\) had a value greater than or equal to 0.17. Note that the depensation sensitivity analysis—like all other scenarios without recruitment variability—did not include any form of stochasticity, so its behavior was entirely deterministic and the biological outcome variables either had a value of zero (no simulations overfished/extirpated) or one (all simulations overfished/extirpated) depending on the value of \(d\). This extirpation resulted in a 70% loss of cumulative catch relative to the null scenario of \(d \approx 0\), and a 7% loss of cumulative effort. In scenarios where anglers had either a steep effort responsiveness function or one with a high intercept, but not both,
Depensation had weaker negative effects and these negative impacts occurred at higher levels of \( d \) (Figure S1A,D). For all utility functions, depensation only produced serious negative effects at levels greater than the median and mean observed values of \( d \) (0.06 and 0.13, respectively), indicating that this mechanism alone is not likely to be strongly destabilizing in real recreational fisheries.

### 3.2 Recruitment stochasticity

Recruitment stochasticity had minimal impacts on model behavior and stability (Figure 3C). Increasing the normally distributed standard deviation of stochasticity had the greatest effect on cumulative catch, producing a 45% increase in cumulative catch from the null expectation for the highest observed standard deviations (Figure S2). When a low-intercept and shallow utility function was used, increases in the standard deviation of recruitment slightly increased the coefficient of variation of biomass and effort, but with more responsive utility functions, this effect disappeared (Figure S2C). Similarly, with a high intercept, low steepness utility function, overfishing increased along with the standard deviation of recruitment stochasticity (Figure S2A), but with a high intercept, high steepness function, overfishing was inversely related to the magnitude of uncorrelated recruitment stochasticity (Figure 3C, S2B). In contrast, the magnitude of autocorrelation coefficient \( \rho \) had very little effect on model behavior at the levels observed in empirical data, regardless of the utility function used (Figure 3D; S2E-S2H).

### 3.3 Density-dependent catchability
Hyperstability in catch per unit effort was strongly destabilizing at commonly observed empirical values (Figure 3B). When modeled in combination with a catch utility function possessing a high no-catch intercept, values of $\beta$ below 0.6 produced extirpation of the modeled fish population (Figures S3A-S3B). This value of $\beta$ is above the median observed value of 0.53, meaning that more than half of the observations of this parameter in the real world indicate magnitudes of hyperstability sufficient to produce extirpation if combined with an angler population that has a high probability of fishing when catch rates are low. The parameter combinations that produce extirpation also increase the variability of the biological system (CV of biomass > 3) and reduce the social benefits available from catch (9-35% decline in cumulative catch), without influencing cumulative effort or the variability of effort.

Hyperdepletion, in contrast, stabilized the system and increased the social benefits of the fishery in the form of catch and fishing effort. The highest levels of hyperdepletion produced over a 100% increase in cumulative catch and 60% more cumulative effort than occurred with density-independent catchability (Figure 3B). Values of $\beta$ consistent with hyperdepletion never produced extirpation, although when a utility function with a low intercept and high steepness value was used, they did produce a greater prevalence of overfishing compared to models run with hyperstable values of $\beta$. This is because the low-intercept, high-steepness utility function normally produces a stable limit cycle in which the model alternates between a high effort, low biomass state and a low biomass, high effort state, such that the modeled population is in an overfished state about 60% of the time (Figure S4). Hyperstability amplifies this
cycle, slightly increasing the amount of time the population spends below the overfishing threshold to up to 70%. In contrast, hyperdepletion dampens it so biomass and effort reach a stable equilibrium just below the overfishing threshold, such that the population is overfished 100% of the time but the model is more stable overall (Figure S3D).

3.4 Angler responsiveness to catch rates

Although the model structure allowed a level of angler effort that would extirpate the population if sustained through time, none of the empirical angler utility functions we incorporated into the model sustained this level of effort long enough to produce extirpation in the absence of other mechanisms (Figure 4B). This indicates that dynamic utility-based angler effort responses based on empirical measures of angler utility do, in fact, produce the self-regulatory feedback behavior that is predicted by theory, in the absence of other destabilizing mechanisms. However, the small number of utility functions representing fisheries where anglers were highly responsive to catch ($\lambda > 0.08$) did produce overfishing over half the time (Figure 4A). Social benefits of fishing in the form of cumulative catch were maximized at intermediate levels of $\lambda$ (0.005 to 0.06) and no-catch probabilities above a low threshold (>6% probability of fishing when catch is zero) (Figure 4D). In contrast, cumulative effort was maximized for the functions with the highest levels of $\lambda$ (Figure 4C). Most utility functions produced highly stable effort and biomass time series ($CV < 1$) with the exception of the one with the highest steepness value by an order of magnitude (North Carolina billfishes, $\lambda = 5.8$), whose biomass time series was highly variable ($CV = 3.9$) (Figure 4E,F).
3.5 Interactions

There are important interactions between social and biological components of the system. The strongest interacting factor was the angler effort response, which was necessary but not sufficient to collapse the fish population and, by extension, the social-ecological system as a whole. Most strikingly, when the model included an angler population with a high probability of fishing with zero catch (i.e., high intercept), median levels of hyperstability ($\beta = 0.53$) crashed the fish population, while the same degree of hyperstability had minimal effects when a low-intercept angler effort response was used (Figure 5). As well as producing greater effects of the other mechanisms individually, the shape and intercept of the angler effort function determined whether and to what degree the other three mechanisms interacted with each other. When a low-intercept, shallow effort function was modeled, almost no interactions occurred between the other mechanisms (Figure 5C). With a high-intercept effort function, interactions occurred but did not fundamentally change the system’s end state: model runs that included hyperstability crashed the system, while those where catchability was density-independent did not, regardless of the presence of depensation or recruitment stochasticity (Figure 5A,B). Only when a low-intercept, highly responsive angler effort function was used did interactions change the fundamental outcomes for the fishery. In this scenario, the combination of depensation and hyperstability extirpated the population, increased variability, and reduced catch and effort by more than 80%. In contrast, both depensation and hyperstability alone produced a low but stable
population size and at least 50% of the social benefits that would have accrued when
neither of those factors were present (Figure 5D).

Recruitment stochasticity behaved most consistently in interactions, tending to
moderate the negative effects of the other two mechanisms. It reduced the loss of catch
and effort produced by hyperstability in some scenarios and slightly dampened the
variability in biomass caused by hyperstability when a high-intercept utility function was
used. When a steep (high \( \lambda \)) angler utility function was used, it also moderated the
negative effects of depensation on cumulative catch and effort and lowered the
proportion of time the population was overfished. In contrast, depensation had a
stabilizing effect when combined with hyperstability if a high-intercept, shallow angler
effort function was used, but combined with hyperstability to collapse the system in the
presence of a steep effort function (Figure 5A,D).

4. Discussion

The human behavioral mechanisms (anglers’ responsiveness to catch and density
dependence in catchability) that we evaluated in our model generally had a stronger
influence on system stability than the biological mechanisms (depensation and
recruitment variability). Anglers’ responsiveness to catch was particularly important,
being necessary but not sufficient on its own to destabilize the SES. This result highlights
the importance of interactions between the social and biological components of the
modeled system. Specifically, the effects of depensation, recruitment stochasticity, and
density-dependent catchability all depended strongly on their interaction with anglers’
response to catch. Except for recruitment stochasticity, which had minimal effects on
model behavior, the combination of these mechanisms with a high-intercept and steep utility function enabled overfishing and even extirpation of the modeled population. The strongest of these interactions was the one between hyperstability and an angler population that was highly responsive to catch, which extirpated the population at levels of hyperstability commonly observed in empirical systems (Figure 3B). In contrast, while depensation is highlighted as a potential mechanism of instability in the literature (Hunt et al., 2011; Post, 2013), our findings show that it is only significantly destabilizing at unrealistically high levels (Figure 3A).

This paper introduces a novel approach to modeling angler effort based on empirical estimates of angler utility. Our approach enables us to ground the model’s behavior in real-world estimates of anglers’ preferences for catch and compare the effects of angler behavior across systems in the form of utility estimates from a wide range of real-world fisheries (Table S1). Although the concept of incorporating angler utility into mathematical models is not new, previous fishery SES models have either relied on abstract utility functions that represent arbitrary but reasonable relationships between CPUE and utility (e.g. Carpenter & Brock, 2004; Cox et al., 2003; Johnston et al., 2010) or have parameterized utility functions from a single well-studied system (e.g. Carruthers et al., 2019). The first approach provides generalizable results but may not represent anglers’ utility from catch in the real world, while the second approach is empirically validated but not easily generalizable across systems. In addition to reconciling these competing goals, our approach also reveals a wide range of functional forms for the relationship between catch and angler effort (Figure 2). The steepness of
the relationship varied by five orders of magnitude, from almost horizontal (no relationship between catch and effort) to almost vertical (anglers increase their effort to the maximum amount in response to very small increases in catch). Our results also reveal that the angler effort response varies widely in its y-intercept, from close to zero to 0.45; that is, when anglers experience zero catch, they exert between 0% and 45% of their maximum possible effort, depending on the system being modeled. This result represents the first synthesis of empirical data on the concept that Post (2013) labels the “giving-up density” of anglers, or the density of fish at which anglers choose to abandon the resource. Post (2013) hypothesized that this intercept could be positive, indicating that angler effort persists even as population declines to zero (destabilizing), or negative, meaning that anglers stop fishing at some low but positive population size (stabilizing) (Figure 1D). However, he made no a priori assumptions about the value of this intercept one should expect in most real-life systems. All of the studies we synthesized had angler utility functions with a positive y-intercept, suggesting that destabilizing patterns are common in anglers’ response to catch, while stabilizing negative intercepts are rare or nonexistent.

Our results provide guidance about how to set research priorities in a way that can most effectively inform recreational fishery management. Anglers’ preferences, specifically their response to changes in catch rates, have the strongest effects on fishery stability and should be a top research priority. The functional form of this response then will inform whether and to what degree other factors may be destabilizing as well. For example, if anglers in a particular fishery have a low probability
of fishing when catch rates are zero, and their response to increasing catch rates is moderate, the fishery should meet the self-regulating expectation and have limited possibility of collapse. In contrast, either a high no-catch probability or a steeper catch response increases the chances that other factors will be destabilizing, and an angler response function that combines both (high steepness, high intercept) makes destabilizing interactions much more likely. If the angler effort response does provide the conditions for instability, the most important potential interacting factor is hyperstability, which should therefore be the second highest priority for research. Only if both of these two mechanisms (high responsiveness to catch and hyperstability) are present may further research into the presence and magnitude of depensation and recruitment variability be necessary.

These recommendations should not be prohibitive to implement in terms of time and expertise. Although research is needed to estimate these factors precisely, several of them can be “guessed” with minimal data, using only basic information about target species’ biology and angler motivations. For instance, schooling behavior and strong habitat associations in fish often results in hyperstable catch rates, so the presence of this behavior in a targeted species makes it likely that catch rates will be hyperstable (Dassow et al., 2020; Erisman et al., 2011), at least to some degree. In addition, some species may be known to have highly variable recruitment (Jenkins et al., 2010) or to have mating or predator avoidance strategies that put them at risk for depensation at low stock sizes (Rowe et al., 2004). Similarly, in a multi-species fishery, one can expect anglers to be most responsive to catch rates of trophy species, such as billfishes
(Istiophoridae and Xiphidae) in North Carolina, than they are to less highly valued species. They are also unlikely to stop fishing as catch rates decline for any single species, producing a high-intercept catch response curve. With these basic heuristics in hand, managers can preliminarily assess whether a given fishery may be prone to instability, and then follow up with more intensive research once any precautionary measures are in place.

The amount and quality of data available on each of our four mechanisms of interest somewhat limits the conclusions presented here. For example, only about 4% of stocks in the synthesis used to inform this study exhibited any depressantory dynamics (Hilborn et al., 2014), and depression is notoriously difficult to measure because it can only be observed in populations that have been reduced to very low stock sizes (Liermann & Hilborn, 2001; Perälä & Kuparinen, 2017). Similarly, our literature review on density dependence in catchability yielded almost no examples of density independence \( \beta \approx 1 \), with most empirical estimates of \( \beta \) indicating either hyperstability or hyperdepletion (Table 3). This likely reflects the difficulty of publishing null results rather than an actual lack of density-independent catchability in real fisheries. In both cases, since we are primarily interested in evaluating the effects of these mechanisms at empirical levels where they exist, rather than measuring their overall prevalence, these biases does not affect our conclusions greatly. Conversely, though, biases related to the magnitude of a given mechanism could have much greater impacts. For example, the density-dependent catchability dataset was unexpectedly dominated by a single species, walleye \( (Sander vitreus) \). If walleye catch rates are in fact
significantly more hyperstable than other species because of some species- or fishery-
specific factors, this could mean that destabilizing levels of $\beta$ are less common than we
thought. However, excluding walleye from the dataset did not substantially alter the
mean and median values of $\beta$ (Mann-Whitney U test, $p = 0.8$), suggesting that our
conclusion that hyperstability is destabilizing at commonly observed levels does not
depend too strongly on this single species.

Angler utility potentially presents more serious data limitations. Most of the
many papers that use random utility models to evaluate recreational anglers’ site choice
do not report enough information to enable us to apply the method we develop here.
This means that we do not know whether the distribution of values we observed for the
steepness and intercept of the angler effort response function is representative of the
empirical distribution of those values, or if it is specific to the five studies we
synthesized (Figure 2, Table S1). For example, anglers are an order of magnitude more
responsive to catches of billfishes (Istiophoridae and Xiphidae) in North Carolina than
any other species we observed. Based on our synthesis, this species group seems to be
an extreme outlier, but this may just be caused by the fact that no other papers on
extremely low-CPUE, high-value trophy species, like taimen ($Hucho taimen$, Salmonidae;
Golden et al., 2019) or bonefishes (Albulidae; Santos et al., 2017) fit our inclusion
criteria. We also lack the information to predict where a given fishery will fall in the two-
dimensional parameter space defined by the steepness and intercept of the angler
effort response. To understand the underlying factors that might determine these
parameters, we simply need more data, in the form of random utility site choice studies
that report all the necessary information for fitting this function. At a bare minimum, angler utility site choice studies should report 1) sample means for all covariates used to fit the RUM, 2) the number of sites evaluated, and 3) the specific model structure used to estimate site choice probabilities to facilitate comparisons across studies. The lack of reported sample means represents a particularly frustrating gap in the current literature, and one that is relatively easy to fill.

Finally, we make the necessary assumption that the parameters we incorporate in the model are static, while in practice, they can vary dynamically through time (Nieman & Solomon, 2021). As an example, the degree of hyperstability in a fishery might change over time as anglers adopt more efficient gear or fish finding technology, and in fact, density-dependent catchability parameter $\beta$ was observed to change on a multi-decadal scale in Wisconsin panfish fisheries (Feiner et al., 2020). Similarly, estimates of anglers’ utility from catch represent a snapshot of anglers’ preferences and behavior at the moment a given study was conducted. If social norms in a fishery change, or if the community of species available in a multispecies fishery grows or shrinks, the steepness and intercept of anglers’ responsiveness to catch for each available species will likely change as well. For example, a low-intercept, low-steepeess catch response curve for one species group in a multispecies fishery, such as the “other fish” category in Whitehead et al. (2013) (Figure 2), could reflect the fact that anglers are primarily motivated by fishing for more valued species and their probability of fishing depends very little on the unvalued species category. However, if more highly valued species (such as billfish or snapper-grouper in the Whitehead et al. example)
become unavailable because of regulations, range shifts, or other reasons, anglers’ effort might respond much more strongly to catch rates of the previously unvalued species as their baseline expectations shift (Post et al., 2002). To our knowledge, there are no studies that re-survey anglers about their trip choices at successive time points to determine how their utility from fishing might change through time. This represents an intriguing area for future study that could have consequences for how we understand the stabilizing or destabilizing role of the angler effort response.

In conclusion, our synthesis and modeling effort suggests that anglers’ responsiveness to catch is a key element of recreational fishery stability that should be prioritized in the research and management process. Of most concern is the fact that a highly responsive angler pool can interact with hyperstability to collapse a targeted species’ population, given relatively common values of hyperstability. The other two mechanisms we evaluated either had minimal effect on system behavior (recruitment variability) or only produced instability at unrealistically high levels or in combination with two other mechanisms (depensation). As well as providing guidance about how to set research priorities, our results highlight the importance of interdisciplinary collaborations in studying and managing recreational fisheries. In particular, the angler response function we estimate in this study requires random utility modeling of anglers’ site choices, typically the purview of fisheries social scientists. Hyperstability, on the other hand, is most readily estimated using ecological experiments. Our results show that both of these mechanisms are important components of system stability and
should be studied in tandem by teams that include both social science and ecological expertise.

**Acknowledgments**

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**References**


Tables and Figures

Table 1. Empirical estimates of the standard deviation of normally distributed recruitment variability and autocorrelation coefficient $\rho$ used to parameterize the model. Adapted from (Thorson et al., 2014).

<table>
<thead>
<tr>
<th>Order</th>
<th>Marginal SD</th>
<th>$\rho$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aulopiformes</td>
<td>0.67</td>
<td>0.49</td>
</tr>
<tr>
<td>Clupeiformes</td>
<td>0.77</td>
<td>0.46</td>
</tr>
<tr>
<td>Gadiformes</td>
<td>0.75</td>
<td>0.42</td>
</tr>
<tr>
<td>Perciformes</td>
<td>0.78</td>
<td>0.49</td>
</tr>
<tr>
<td>Pleuronectiformes</td>
<td>0.64</td>
<td>0.46</td>
</tr>
<tr>
<td>Salmoniformes</td>
<td>0.71</td>
<td>0.38</td>
</tr>
<tr>
<td>Scorpaeniformes</td>
<td>0.78</td>
<td>0.46</td>
</tr>
<tr>
<td><strong>Median</strong></td>
<td>0.74</td>
<td>0.45</td>
</tr>
<tr>
<td><strong>Mean</strong></td>
<td>0.72</td>
<td>0.44</td>
</tr>
</tbody>
</table>
Table 2. Empirical estimates of depensation parameter $d$ used to parameterize the model. Estimates are drawn from (Hilborn et al., 2014).

<table>
<thead>
<tr>
<th>Stock</th>
<th>$d$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herring North Sea</td>
<td>0.04</td>
</tr>
<tr>
<td>Atlantic cod NAFO 3NO</td>
<td>0.06</td>
</tr>
<tr>
<td>Atlantic menhaden Atlantic</td>
<td>0.30</td>
</tr>
<tr>
<td><strong>Median</strong></td>
<td>0.06</td>
</tr>
<tr>
<td><strong>Mean</strong></td>
<td>0.13</td>
</tr>
</tbody>
</table>
Table 3. Empirical estimates of density-dependent catchability parameter $\beta$ used to parameterize the model. For each study, the study species and location are included as well as the estimated value for $\beta$. When studies estimate $\beta$ for multiple gear types, values for each gear are included in the relevant row of the table, with parentheses identifying the gear.

<table>
<thead>
<tr>
<th>Citation</th>
<th>Study species</th>
<th>Study location</th>
<th>$\beta$</th>
<th>Hyperstable or hyperdeplete?</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Dassow et al., 2020)</td>
<td><em>Micropterus salmoides</em></td>
<td>Wisconsin, USA</td>
<td>0.47</td>
<td>Hyperstable</td>
</tr>
<tr>
<td>(Erisman et al., 2011)</td>
<td><em>Paralabrax clathratus</em></td>
<td>California, USA</td>
<td>0.46</td>
<td>Hyperstable</td>
</tr>
<tr>
<td>(Giacomini et al., 2020)</td>
<td><em>Sander vitreus</em></td>
<td>Ontario and Quebec, Canada</td>
<td>1.017</td>
<td>no evidence for non-linearity</td>
</tr>
<tr>
<td>(Hansen et al., 2005)</td>
<td><em>Sander vitreus</em></td>
<td>Wisconsin, USA</td>
<td>0.825 (angling)</td>
<td>Hyperstable</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.659 (spearing)</td>
<td></td>
</tr>
<tr>
<td>(Mrnak et al., 2018)</td>
<td><em>Sander vitreus</em></td>
<td>Wisconsin, USA</td>
<td>0.53 (angling)</td>
<td>Hyperstable</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.41 (spearing)</td>
<td></td>
</tr>
<tr>
<td>(Pierce &amp; Tomcko, 2003)</td>
<td><em>Esox lucius</em></td>
<td>Minnesota, USA</td>
<td>1.7</td>
<td>Hyperdeplete</td>
</tr>
<tr>
<td>(Ward et al., 2013)</td>
<td><em>Onchorhynchus mykiss</em></td>
<td>British Columbia, Canada</td>
<td>0.4276</td>
<td>Hyperstable</td>
</tr>
</tbody>
</table>

**Median** 0.53  
**Mean** 0.72
Table 4. Mechanisms included in the model, with the parameter(s) used to operationalize them, the null value of each parameter, and the mean, median, and standard deviation of the parameters' observed values.

<table>
<thead>
<tr>
<th>Mechanism</th>
<th>Model component</th>
<th>Parameter(s)</th>
<th>Null value</th>
<th>Median</th>
<th>Mean</th>
<th>Standard deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depensation</td>
<td>biological submodel</td>
<td>$d$</td>
<td>$d \approx 0$</td>
<td>0.06</td>
<td>0.13</td>
<td>0.14</td>
</tr>
<tr>
<td>Recruitment stochasticity</td>
<td>biological submodel</td>
<td>$\sigma^2, \rho$</td>
<td>$\sigma^2 = 0$</td>
<td>0.74</td>
<td>0.72</td>
<td>0.07</td>
</tr>
<tr>
<td>Density-dependent catchability</td>
<td>catch equation</td>
<td>$\beta_c$</td>
<td>$\beta_c = 1$</td>
<td>0.53</td>
<td>0.72</td>
<td>0.05</td>
</tr>
<tr>
<td>Angler responsiveness to catch</td>
<td>angler effort model</td>
<td>$\lambda$, intercept</td>
<td>NA</td>
<td>0.01</td>
<td>0.39</td>
<td>1.45</td>
</tr>
</tbody>
</table>


**Figure 1.** Conceptual figure illustrating four potential mechanisms of instability in recreational fisheries. Parameter values or combinations hypothesized to be moderately destabilizing are in orange; strongly destabilizing values are in red; and stabilizing ones are in blue. Black lines indicate the null expectation. A) shows the relationship between spawning stock biomass and subsequent recruitment with and without depensation (red dashed line and black solid line, respectively; $d$ is defined in eq. 1). B) shows time series of biomass in the absence of recruitment stochasticity (black line), with uncorrelated recruitment stochasticity (orange line) and with first-order autcorrelated recruitment stochasticity that has produced a persistent downward trend (red line). See eq. 3 for definitions of $\delta$ (stochasticity) and $\rho$ (autocorrelation). C) illustrates the relationship between population abundance and catch per unit effort when catchability is density-independent (black; $\beta = 1$, eq. 4), when catch rates exhibit hyperstability (red hues; $\beta < 1$), and when catch rates exhibit hyperdepletion (blue hues; $\beta > 1$). D) angler effort is often conceptualized as a logistic curve dependent on the catch rates anglers experience in a fishery (black line). Characteristics of the fishery and of the angler population can change the steepness of this curve (representing the strength of anglers’ response to catch, $\lambda$; eq. 9) and the location where it intercepts the y-axis (indicating the amount of effort anglers allocate when catch rates are zero). Higher intercept and steepness are both predicted to destabilize the fishery SES.
Figure 2. Empirically observed functional forms of the relationship between catch rate and anglers’ fishing effort from five studies of angler utility. Study location is indicated with line color and plots are arranged from low to high steepness of the angler effort response ($\lambda$; x axis) and with increasing no-catch intercept (y axis). Axes are not to scale.
Figure 3. Heatmaps showing the effects of each of the three mechanisms of interest (depensation (A), density-dependent catchability (B), and two components of recruitment stochasticity: the standard deviation (C) and autocorrelation (D) in recruitment deviations) on three aspects of model behavior: biological sustainability (red), social benefits (pink/green), and variability (blue). Model behavior is shown for the entire observed range of values for depensation parameter $d$, catchability parameter $\beta$, and the standard deviation and autocorrelation parameter of recruitment stochasticity. Empirical values of each parameter are indicated with vertical dashed lines, with a solid line indicating the “null” value for that parameter. All simulations were run with a utility function representing high catch responsiveness and high probability of fishing with zero catch (California bottomfish).
Figure 4. Scatterplots showing the effects of the angler effort function used to run the model on the model’s biological sustainability (A,B), social outcomes (C,D), and variability (E,F). Each point represents the mean value of the relevant outcome variable across a set of 100 simulations run with a given utility function. Points are arranged according to the steepness of the utility function’s response curve to catch ($\lambda$, x-axis) and y-intercept when catch is zero (y-axis). Dashed vertical and horizontal lines indicate the median values of $\lambda$ and zero-catch intercept, respectively. Note that the x-axis is on the log scale.
Figure 5. Radar plots indicating the effects of interactions between depensation (orange), recruitment stochasticity (red), and hyperstability (blue) on model behavior at their median observed levels. Model outputs with a single mechanism turned “on” at the median are indicated with thick colored lines. Model outputs for interactions between two mechanisms are indicated with a dotted black line. Simulations were run with an angler effort function representing A) low angler responsiveness to catch and high probability of fishing with zero catch (California highly migratory species), B) high angler responsiveness and no-catch fishing probability (California bottomfish), C) low angler responsiveness and no-catch fishing probability (Australia prize fish), and D) high angler responsiveness and low no-catch fishing probability (North Carolina snapper-grouper). The shape of the angler effort response is shown in the upper right portion of each panel.
Supplemental Table 1. List of papers used to define the relationship between past catch rates and the current probability of fishing in the model. For each article, the study location and model type are indicated, as well as the list of attributes that are used to define the angler utility function and the number of sites evaluated. Catch responsiveness parameter $\lambda$ (defined in Eq. 9) and the intercept of the probability function (that is, the probability of fishing when catch is zero) are listed for each species evaluated in each paper.

\[ \text{See citation for definition of these species groups} \]
\[ ^1 \text{Excluded from analysis because parameter estimate was negative, suggesting the presence of unobserved covariates.} \]
\[ ^4 \text{The authors fit two site choice models, one for primary-purpose anglers and one for secondary-purpose anglers. We used only the model for primary-purpose anglers to estimate responsiveness to catch, to avoid dominating the dataset with estimates from a single paper.} \]
<table>
<thead>
<tr>
<th>Citation</th>
<th>Study location</th>
<th>Model</th>
<th>Utility attributes</th>
<th>N sites</th>
<th>Species</th>
<th>$\lambda$</th>
<th>Intercept</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gentner 2006</td>
<td>Northeast U.S.A.</td>
<td>conditional logit site choice model</td>
<td>travel cost, travel time, catch-and-keep rate, aggregation variable indicating number of sites used in model</td>
<td>63</td>
<td>Morone saxatalis</td>
<td>0.00996</td>
<td>0.014</td>
</tr>
<tr>
<td>Kuriyama et al. 2013</td>
<td>southern California, U.S.A.</td>
<td>random parameter logit model weighted by sampling effort</td>
<td>round trip cost, CPUE of bottomfish, CPUE of coastal migratory species, CPUE of highly migratory species, CPUE of inshore species, CPUE of trips with no target species, availability of beach fishing, availability of boat fishing</td>
<td>37</td>
<td>bottomfish, coastal migratory species, highly migratory species, inshore species</td>
<td>0.08657</td>
<td>0.4214</td>
</tr>
<tr>
<td>Mkwara et al. 2015</td>
<td>Rotorua Lakes, New Zealand</td>
<td>conditional logit site choice model</td>
<td>travel cost, Secchi disk depth, average annual weight of fish, lake size, number of facility developments per lake, percentage of urban land surrounding each lake, percentage of forested land surrounding each lake, lake depth, presence of algal bloom health warnings</td>
<td>11</td>
<td>Oncorhyncus mykiss, Salmo trutta, Salvelinus fontinalis, Salmo trutta x Salvelinus fontinalis</td>
<td>0.01703</td>
<td>0.0109</td>
</tr>
<tr>
<td>Raguragavan et al. 2013</td>
<td>Western Australia</td>
<td>random utility site choice model</td>
<td>travel cost, catch rate of butter fish, catch rate of key sports fish, catch rate of prize fish, catch rate of reef fish, catch rate of table fish, coast length, biomass of reef fish (interacted with reef fish catch rate)</td>
<td>48</td>
<td>butter fish, key sports fish, prize fish, reef fish, table fish</td>
<td>0.00019</td>
<td>0.0191</td>
</tr>
<tr>
<td>Whitehead et al. 2013</td>
<td>North Carolina, U.S.A.</td>
<td>nested logit site choice model¹</td>
<td>trip cost, billfish kept, coastal migratory pelagic fish kept, mackerel kept, snapper-grouper kept, other fish kept, site-specific intercepts, mode-specific intercepts, inclusive value</td>
<td>5</td>
<td>billfish (Istiophoridae and Xiphidae), coastal migratory pelagic fish, mackerel (Scomberomorus cavalla and S. maccutus), snapper-grouper, other fish</td>
<td>5.82331</td>
<td>0.1276</td>
</tr>
</tbody>
</table>
Supplemental Figure 1. Sensitivity analysis showing effects of depensation on three aspects of model behavior: biological sustainability (red), social benefits (pink/green), and variability (blue). Model behavior is shown for the entire observed range of values for depensation parameter $d$ and using four representative utility scenarios: high intercept and low steepness (A), high intercept and steepness (B), low no-catch intercept and steepness (C), and low intercept and high steepness (D). Empirical values of each parameter are indicated with vertical dashed lines, with a solid line indicating the “null” value for that parameter.
Supplemental Figure 2. Sensitivity analysis showing effects of autocorrelated recruitment stochasticity on three aspects of model behavior: biological sustainability (red), social benefits (pink/green), and variability (blue). Model behavior is shown for the entire observed range of values for the standard deviation of normally distributed recruitment error (A-D) and autocorrelation parameter $\rho$ (E-H) and using four representative utility scenarios as in Figure S1. Empirical values of each parameter are indicated with vertical dashed lines, with a solid line indicating the “null” value for that parameter.
Supplemental Figure 3. Sensitivity analysis showing effects of hyperstability on three aspects of model behavior: biological sustainability (red), social benefits (pink/green), and variability (blue). Model behavior is shown for the entire observed range of values for density-dependent catchability parameter $\beta$ and using four representative utility scenarios as in Figures S1 and S2. Empirical values of each parameter are indicated with vertical dashed lines, with a solid line indicating the “null” value for that parameter.
Supplemental Figure 4. The dynamics of biomass in relation to effort (top) and catch (bottom) produced by models run using a low-intercept, high-steepness angler effort function (North Carolina snapper-grouper) in the presence and absence of hyperstability ($\beta = 0.8$) and hyperdepletion ($\beta = 1.2$). The overfishing threshold $0.5*B_{msy}$ is indicated with a dashed vertical line and the start point and end point of the model runs are marked with a filled circle and filled triangle, respectively.
CONCLUSION

Recreational fisheries present unique challenges, but also unique opportunities to understand how ecosystems and human behavior interact to form complex adaptive systems. In my first dissertation chapter, I show that participants in one remote high-threshold fishery are motivated almost as much by activity-general factors like travel as they are by catching trophy fish, and that many are “bucket list” travelers who will move on to new fishing opportunities regardless of the fishing quality they experience at a given site. This result reveals that the relevant unit for analysis of this type of fishery may be a global network of fishing opportunities, all remote and highly specialized, that could exhibit teleconnections because they share an angler pool. My second chapter reveals that catchability of two species of Mongolian salmonid depends on interactions between indirect effects of climate change, their feeding ecology, and whether they are caught on spinning gear or fly-fishing gear, with fly-fishing gear remaining more effective in the aftermath of thunderstorms. Since this fishery includes distinct demographic groups of anglers that are strongly associated with these two gear types, my results suggest that international anglers who fly fish may be climate change “winners,” while local hobbyists who spin fish will lose out. My third chapter demonstrates that anglers’ responsiveness to catch is a key but neglected contributor to the stability of recreational fishery CAS, especially when a fishery exhibits density-dependent catchability. As a whole, my dissertation highlights the importance of combining quantitative tools like field experiments and modeling with social science
research to gain a more holistic understanding of coupled social-ecological complex adaptive systems.