

ORIGINAL ARTICLE



WILEY

Focusing on what matters most: Evaluating multiple challenges to stability in recreational fisheries

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Funding information

Freshwater Fisheries Society of British Columbia; National Science Foundation, Grant/Award Number: CNH #1716066 and NSF DGE-1842213

Abstract

Recreational fisheries were traditionally theorized to self-regulate in a sustainable feedback loop in which recreational anglers moderate their fishing effort in response to population declines. However, several mechanisms are hypothesized to break down this self-regulatory process, including recruitment variability and depensatory population dynamics. Although many of these mechanisms of instability have been estimated in empirical systems and explored using modelling, 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) recruitment stochasticity, (3) density-dependent catchability 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 a simplified recreational fishery model. We find that at moderate fishing effort none of the mechanisms was destabilizing enough on its own to collapse the modelled population, but that an angler population that was likely to keep fishing when catch rates approached zero was a key element of interactions that caused collapse. The strongest interaction was between an angler population with this characteristic and a fish population with hyperstable catch rates. Our results highlight the need for more consistent and widespread estimation of utility-based angler effort functions as well as the importance of interdisciplinary teams that can gather both social and ecological data.

KEYWORDS

angler effort, depensation, hyperdepletion, hyperstability, random utility site choice modelling, recruitment variability

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

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ecological and social subsystems (Carmichael & Hadžikadić, 2019). One key emergent property of SESs is their potential to self-regulate and maintain a desirable system state (i.e. abundant biomass and consistent harvests) over the long term without creating instability and ecological collapse (Ostrom, 2009; Post et al., 2002). Systems with this ability should be relatively easy to manage, while ones that tend towards instability may require intensive, costly management interventions (Camp et al., 2020). Knowledge of a system's ability to self-regulate in the absence of management is, therefore, a key to understanding whether managing for any given outcome is cost-effective or even possible.

This self-regulating potential depends on a negative feedback loop between angler behaviour 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 (Bishop & Samples, 1980; Carpenter et al., 1994; McConnell & Sutinen, 1979). However, extensive research using both empirical data and theoretical modelling, driven by hypotheses first posed in Post et al. (2002), 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 behaviour in fish that generates hyperstable catch rates (i.e. catch rates that remain high even as abundance declines) 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 one's 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 adult abundance. In particular, fish stocks are commonly assumed to exhibit compensatory or negative density-dependent recruitment dynamics, in which offspring survival rates increase as adult population size decreases (Walters & Martell, 2004). If this assumption is met, populations that have been reduced to low levels by harvest will recover rapidly as long as harvest rates are not too high, enabling a return to a high-biomass system state. This assumption seems to hold for most stocks as long as other stressors (e.g. habitat loss, invasive species) do not prevent recovery (Chagaris et al., 2020; Johnson et al., 2022), but a number of species exhibit positive density-dependence at very low population sizes, also known as depensation (Hilborn et al., 2014; Perälä & Kuparinen, 2017; Rowe et al., 2004) (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 &

1. INTRODUCTION	1
2. METHODS	4
2.1. Literature review and data synthesis	4
2.1.1. Depensation in the stock-recruit relationship	4
2.1.2. Recruitment variability	5
2.1.3. Density-dependent catchability	5
2.1.4. Angler responsiveness to catch rates	6
2.2. Model overview	7
2.2.1. Biological model	9
2.2.2. Angler effort model	9
2.2.3. Outcome variables	11
3. RESULTS	11
3.1. Latent fishing effort	11
3.2. Depensation	11
3.3. Recruitment stochasticity	12
3.4. Density-dependent catchability	12
3.5. Angler responsiveness to catch rates	12
3.6. Interactions	12
4. DISCUSSION	13
ACKNOWLEDGEMENTS	18
DATA AVAILABILITY STATEMENT	19
REFERENCES	19

Hilborn, 2001). Species with depensatory population dynamics exhibit an upper, stable equilibrium population size (carrying capacity) as well as a lower, unstable equilibrium; below this unstable equilibrium they exhibit *critical depensation*, in which population growth becomes negative and the population declines to extinction (Liermann & Hilborn, 2001; Post et al., 2002). If an exploited fish population possesses depensatory dynamics but is modelled 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 often varies 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 behaviour 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 declining 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

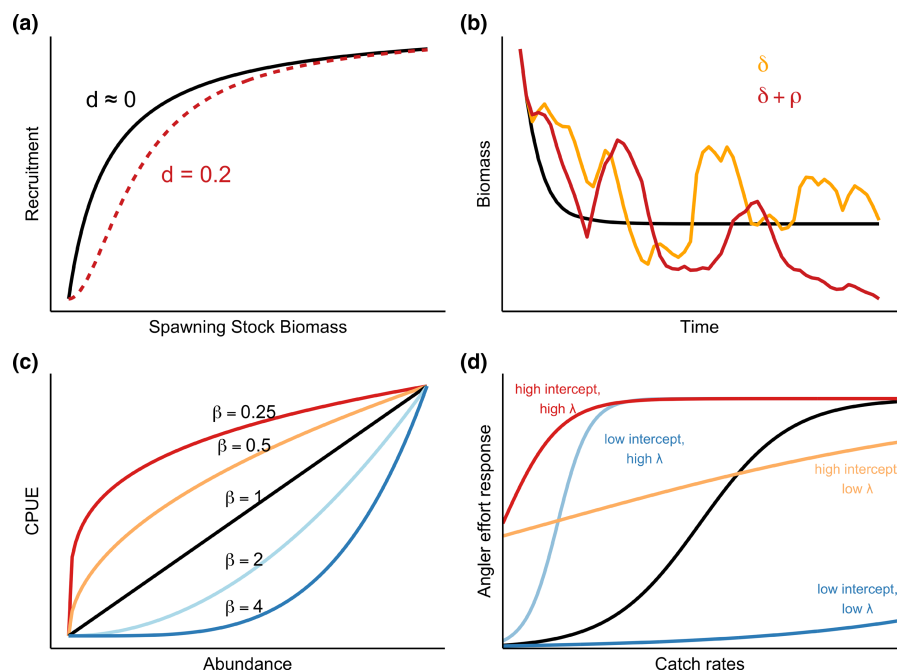


FIGURE 1 Conceptual figure illustrating four potential mechanisms of instability in recreational fisheries. Parameter values or combinations hypothesized to be moderately destabilizing are in orange; strongly destabilizing values are in red; and stabilizing ones are in blue. Black lines indicate the 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 Equation 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 autocorrelated recruitment stochasticity that has produced a persistent downward trend (red line). See Equation 3 for definitions of δ (stochasticity) and ρ (autocorrelation). (c) Illustrates the relationship between population abundance and catch per unit effort when catchability is density-independent (black; $\beta = 1$, Equation 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 (λ ; Equation 8) and the location where it intercepts the y-axis (indicating the amount of effort anglers allocate when catch rates are zero). Angler effort functions with a higher intercept are expected to destabilize the fishery SES.

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 not adequately perceive declines in abundance, and thus may not reduce their effort (anglers) or introduce precautionary regulations (managers) in response. Hyperstability can be caused by fish aggregation behaviour (Dassow et al., 2020; Erisman et al., 2011) or by effort sorting patterns in which more highly skilled anglers, who tend to have higher catch rates, continue fishing longer as stocks decline (van Poorten et al., 2016; Ward et al., 2013).

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 (Walters & Martell, 2004). 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 behaviour and preferences, reviewed in Hunt, Camp, 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 behaviour 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.

To evaluate the interacting effects of biological and social factors on the stability of recreational fishery SESs, many studies have modelled a landscape of discrete fish populations (in lakes, rivers, etc.) across which anglers can allocate their effort freely. This landscape-scale approach provides information at the geographic scale most relevant to management and also enables the comparison of regulatory options that would be onerous or impractical to implement experimentally (Cox et al., 2003; Post & Parkinson, 2012; van Poorten & Camp, 2019). Landscape studies have also been particularly valuable as a way to explore nuanced interactions between angler behaviour and biological factors. For instance, numerous studies have demonstrated the existence of a gradient of angler effort and overfishing from urban centres to rural areas, moderated by factors including density-dependent catch rates, angler preferences and biological productivity (Hunt et al., 2011; Matsumura et al., 2019; Post et al., 2008; Wilson et al., 2020). Despite their value and increasing popularity, though, one potential application of landscape site choice models is underexplored in the literature. The current trend in fishery landscape modelling has been towards increasing realism and empirical grounding (e.g. Carruthers et al., 2019; Wilson et al., 2020) and even more abstract models tend to be based on a single, well-studied empirical system (Cox et al., 2003; Matsumura et al., 2019). What is missing is simple, abstract models whose parameters can be modified to reflect conditions in a variety of systems and compare them (although see Post et al. (2008) for an example of this kind of extrapolation).

The objectives of this study are, therefore, as follows: (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 modelled 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 to catch rates. We approached the first objective by reviewing the literature on case studies of mechanisms 3 and 4 and referring 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 modelled 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 key parameters of this expression from empirical data. For mechanisms that are at least partially related to angler behaviour (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 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. Using Allee effects as an example of a depensatory process, they operationalize depensation as a parameter d , representing the population size at which 50% of the population is able to find mates 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 (Figure 1a). Depensation parameter d informs a depensation term D_t that represents the fraction of females in the population who are mated at time t :

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

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)

$$R_{t+1} = \frac{aD_tB_t}{(1+bD_tB_t)^g} \exp(\epsilon_t), \quad (2)$$

where recruitment in the following time step, R_{t+1} , depends on B_t , constants a , b and g , and some stochasticity ϵ_t . The Deriso stock-recruit function simplifies to the Beverton-Holt stock-recruit function when

$g = 1$ and the Ricker function when $g \rightarrow \infty$, 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 AIC_C for only four of the analysed stocks, with the remaining 109 having values of d indistinguishable from zero. Of the four populations with significant depensation, three were finfish and fall within the scope of our study. These were North Sea herring (*Clupea harengus*, Clupeidae; $d = 0.04$), Atlantic cod (*Gadus morhua*, Gadidae; $d = 0.06$) and Atlantic menhaden (*Brevoortia tyrannus*, Clupeidae; $d = 0.30$). The median value of d for these three stocks was 0.06 and the mean was 0.13; note that we do not include the zero values in the calculation of the mean and median, because we are interested in evaluating the strength of depensation where it occurs. Although Hilborn et al. (2014) fit stock-recruit models to the data using both maximum likelihood and hierarchical Bayesian analyses, only the maximum likelihood 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 modelled the observed residuals around the curve as including both an autocorrelated component and uncorrelated, normally distributed stochasticity, such that

$$\epsilon_t = \rho \epsilon_{t-1} + \sqrt{1 - \rho^2} \delta_t \quad (3)$$

where ρ is the first-order autocorrelation coefficient, ϵ_t and ϵ_{t-1} are observed residuals around the stock-recruit curve in years t and $t-1$, respectively, and δ_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 δ that ranged from 0.64 for Pleuronectiformes to 0.78 for Perciformes and Scorpaeniformes (Table 1). They observed values of autocorrelation coefficient ρ ranging from .38 for Salmoniformes to .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) and Harley et al. (2001), in

TABLE 1 Empirical estimates of the standard deviation of normally distributed recruitment variability and autocorrelation coefficient ρ used to parameterize the model. Adapted from Thorson et al. (2014)

Order	Marginal SD	ρ
Aulopiformes	0.67	.49
Clupeiformes	0.77	.46
Gadiformes	0.75	.42
Perciformes	0.78	.49
Pleuronectiformes	0.64	.46
Salmoniformes	0.71	.38
Scorpaeniformes	0.78	.46
Median	0.74	.45
Mean	0.72	.44

which abundance N in the catch equation is modified by a shape parameter that governs the type and magnitude of non-linearity:

$$C = qEN^\beta \quad (4)$$

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 $\beta \neq 1$, the slope of CPUE vs. abundance 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 β , so that values of hyperstability and hyperdepletion could be compared across disparate systems. Some papers estimated β 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 2). Nine β 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 of America 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 β that indicate hyperstable catch rates; the median value of β 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.

TABLE 2 Empirical estimates of density-dependent catchability parameter β used to parameterize the model. For each study, the study species and location are included as well as the estimated value for β . When studies estimate β for multiple gear types, values for each gear are included in the relevant row of the table, with parentheses identifying the gear

Citation	Study species	Study location	β	Hyperstable or Hyperdeplete?
Dassow et al. (2020)	Largemouth bass (<i>Micropterus salmoides</i> , Centrarchidae)	Wisconsin, USA	0.47	Hyperstable
Erismann et al. (2011)	Kelp bass (<i>Paralabrax clathratus</i> , Serranidae)	California, USA	0.46	Hyperstable
Giacomini et al. (2020)	Walleye (<i>Sander vitreus</i> , Percidae)	Ontario and Quebec, Canada	1.017	No evidence for non-linearity
Hansen et al. (2005)	Walleye (<i>Sander vitreus</i> , Percidae)	Wisconsin, USA	0.825 (angling) 0.659 (spearing)	Hyperstable
Mrnak et al. (2018)	Walleye (<i>Sander vitreus</i> , Percidae)	Wisconsin, USA	0.53 (angling) 0.41 (spearing)	Hyperstable
Pierce and Tomcko (2003)	Northern pike (<i>Esox lucius</i> , Esocidae)	Minnesota, USA	1.7	Hyperdeplete
Ward et al. (2013)	Rainbow trout (<i>Oncorhynchus mykiss</i> , Salmonidae)	British Columbia, Canada	0.4276	Hyperstable
Median			0.53	
Mean			0.72	

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 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 modelled, utility estimates include both an observed component V and a random component ζ , such that the utility U of alternative j for angler i can be expressed as:

$$U_{ij} = V_{ij} + \zeta_{ij}. \quad (5)$$

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:

$$V_{ij} = \eta \mathbf{X}_{ij} \quad (6)$$

where $\mathbf{X}_{ij}$ is a vector of the observed attributes of alternative j for angler i and η 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 ζ_{ij} are distributed as type I extreme values and thus are independent of each other (Train, 2002). The probability P_{ij} that individual i chooses site j can, therefore, be expressed as the logistic function

$$P_{ij} = \frac{\exp(V_{ij})}{\sum_{j=1}^J \exp(V_{ij})}. \quad (7)$$

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, Camp, 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 a generic angler's functional response to catch rates for each RUM study in our dataset, which we call anglers' *responsiveness to catch* (Figure 1D). Anglers' responsiveness to catch is discussed extensively in the recreational fisheries literature, usually with the implicit context of exploring how anglers behave as fish abundance declines to low levels (e.g. Post, 2013; Post et al., 2002). However, anglers' responsiveness to catch actually includes two related (but independent) components: (1) how steeply angler effort increases in response to high abundance or catch rates and (2) how high effort remains as catch rates approach zero and what level of population decline triggers the minimum amount of effort (i.e. do anglers stop fishing entirely when

catch rates drop to zero, or do they maintain some level of effort at this point?). Our approach operationalizes both of these two components, which we refer to throughout this paper as the *steepness* of anglers' response to catch, or λ , and the angler effort function's *zero-catch intercept*, which we call α (Figure 1D). Steepness, λ , can be derived by calculating the difference between the catch rate that produces a 50% probability of fishing and the probability that produces a 60% probability of fishing (Figure S1). Note that the choice of these specific probabilities is arbitrary; steepness can be defined in terms of any two probabilities of fishing. This difference is divided by the mean observed catch rate, to standardize steepness values across studies, and then inverted, so that larger values indicate steeper angler effort functions. Steepness or λ can thus be expressed as:

$$\lambda = \frac{\bar{C}}{C_{p_{m=0.6}} - C_{p_{m=0.5}}} \quad (8)$$

where $C_{p_{m=0.6}}$ indicates the value of CPUE that produce a 60% probability of generic angler i fishing at mean site m using Equation 7; $C_{p_{m=0.5}}$ is defined similarly for a 50% probability of fishing; and $\bar{C}$ is the mean observed catch rate in the relevant study. 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. The zero-catch intercept is simply the probability of fishing (Equation 7) when catch is set to zero. Throughout this paper, references to anglers' responsiveness to catch include both of these two components (steepness and zero-catch intercept), since they cannot be calculated independently of one another and are generated from the same underlying random utility model in each study.

To find studies that would enable us to estimate anglers' responsiveness to catch in real-world fisheries, we conducted a Web of Science search with the search terms '(angl* OR "recreation* fish*") AND (choice* OR behaviour OR preference* OR satisfaction OR motivation) AND utility AND (catch* OR "catch-related" OR "fishing quality" OR harvest*)'. Following Hunt, Camp, 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 multi-species fisheries in which catch rates of multiple species contributed to the utility function, λ and the zero-catch intercept were calculated for each species using Equations (7) and (8) above.

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 of America. 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 in their steepness by seven orders of magnitude, from $\lambda = 0.0028$ for butter fish (a species group that includes garfish, *Belone belone*, Belonidae; Australian herring, *Arripis georgianus*, Arripidae; blue mackerel, *Scomber australasicus*, Scombridae; and other species; see Raguragavan et al., 2013 for full definition) in Western Australia to $\lambda = 3304$ for billfishes (Istiophoridae and Xiphidae) in North Carolina (Whitehead et al., 2013). The zero-catch intercept ranged from a 1.1% probability of fishing when catch rates were zero for salmonids in New Zealand lakes (Mkwara et al., 2015) to a 44.7% probability for inshore species in southern California (Kuriyama et al., 2013; see citation for definition of 'inshore' species group) and was uncorrelated with λ (correlation coefficient = -0.04). These angler responsiveness values represent a wide range of relationships between catch rates and angler effort (Figure 2). Note especially that steepness, λ , varies a great deal by species or species group even within a single study; that is, angler effort functions from a single study occupy a wide range of positions on the x-axis of Figure 2. In contrast, the zero-catch intercept tends to be relatively similar for species within a given fishery (angler effort functions from a single study tend to be grouped together on the y-axis of Figure 2). This can be attributed to the fact that λ represents, in part, the strength of anglers' satisfaction from catching one additional fish of a given species, which varies widely with species. As one hypothetical example, a pike angler would be expected to be more strongly influenced by catching one more pike (a species with low catch rates) than she expects than a panfish angler on the same lake would be influenced by catching one more panfish (a group of species with high catch rates). In contrast, the zero-catch intercept reflects other attributes of the fishing experience, such as amenities, travel costs and the availability of non-focal species, which theory predicts should remain relatively stable within a given fishery regardless of the focal species.

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. This population was initiated at unfished equilibrium with a Beverton-Holt recruitment function whose parameters were derived from first principles following Botsford and Wickham (1978). Starting in time $t = 2$, fish were harvested by a homogeneous population of anglers that was assumed to allocate its fishing effort between the modelled lake and an unmodelled 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

TABLE 3 List of papers used to define the relationship between past catch rates and the current probability of fishing in the model

Citation	Study location	Model	Utility attributes	N sites	Species (mean CPUE)	λ	Intercept
Gentner (2006)	Northeast U.S.A.	Conditional logit site choice model	Travel cost, travel time, catch-and-keep rate, aggregation variable indicating number of sites used in model	63	Striped bass, <i>Morone saxatilis</i> , Moronidae (0.19)	8.782	0.014
Kuriyama et al. (2013)	Southern California, U.S.A.	Random parameter logit model weighted by sampling effort	Round trip cost, CPUE of bottomfish, CPUE of coastal migratory species, CPUE of highly migratory species, CPUE of inshore species, ^a CPUE of trips with no target species, ^b availability of beach fishing, availability of boat fishing	37	Bottomfish (0.3931) Coastal migratory species (1.9405) Highly migratory species (1.7687) Inshore species (1.5734)	2.216 0.125 0.071 0.036	0.4214 0.4087 0.4335 0.4466
Mkwara et al. (2015)	Rotorua Lakes, New Zealand	conditional logit site choice model	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	11	Rainbow trout, <i>Oncorhynchus mykiss</i> , Salmonidae; brown trout, <i>Salmo trutta</i> , Salmonidae; brook trout, <i>Salvelinus fontinalis</i> , Salmonidae; tiger trout, <i>Salmo trutta</i> x <i>Salvelinus fontinalis</i> , Salmonidae (1.6)	2.121	0.0109
Raguragavan et al. (2013)	Western Australia	random utility site choice model	Travel cost, catch rate of butter fish, ^a 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)	48	Butter fish (8.86) Key sports fish (1.39) Prize fish (1.28) Reef fish (1.47) Table fish (1.97)	0.003 0.089 0.173 0.017 0.038	0.0191 0.0195 0.0186 0.0205 0.0197
Whitehead et al. (2013)	North Carolina, U.S.A.	Nested logit site choice model ^c	Trip cost, billfish kept, coastal migratory pelagic fish kept, ^a mackerel kept, snapper-grouper kept, ^a other fish kept, ^a site-specific intercepts, mode-specific intercepts, inclusive value	5	Billfish (Istiophoridae and Xiphidae) (0.02) Coastal migratory pelagic fish (2) Mackerel, <i>Scomberomorus cavalla</i> and <i>S. maculatus</i> , Scombridae (1) Snapper-grouper (1) Other fish (4)	3304.693 0.816 1.159 2.755 0.030	0.1276 0.0624 0.1351 0.171 0.0756

Note: 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. Steepness parameter λ (defined in Equation 8) 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. The mean catch per unit effort is listed in parentheses next to each species name or species group

^aSee citation for definition of these species groups.

^bExcluded from analysis because parameter estimate was negative, suggesting the presence of unobserved covariates.

^cThe 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.

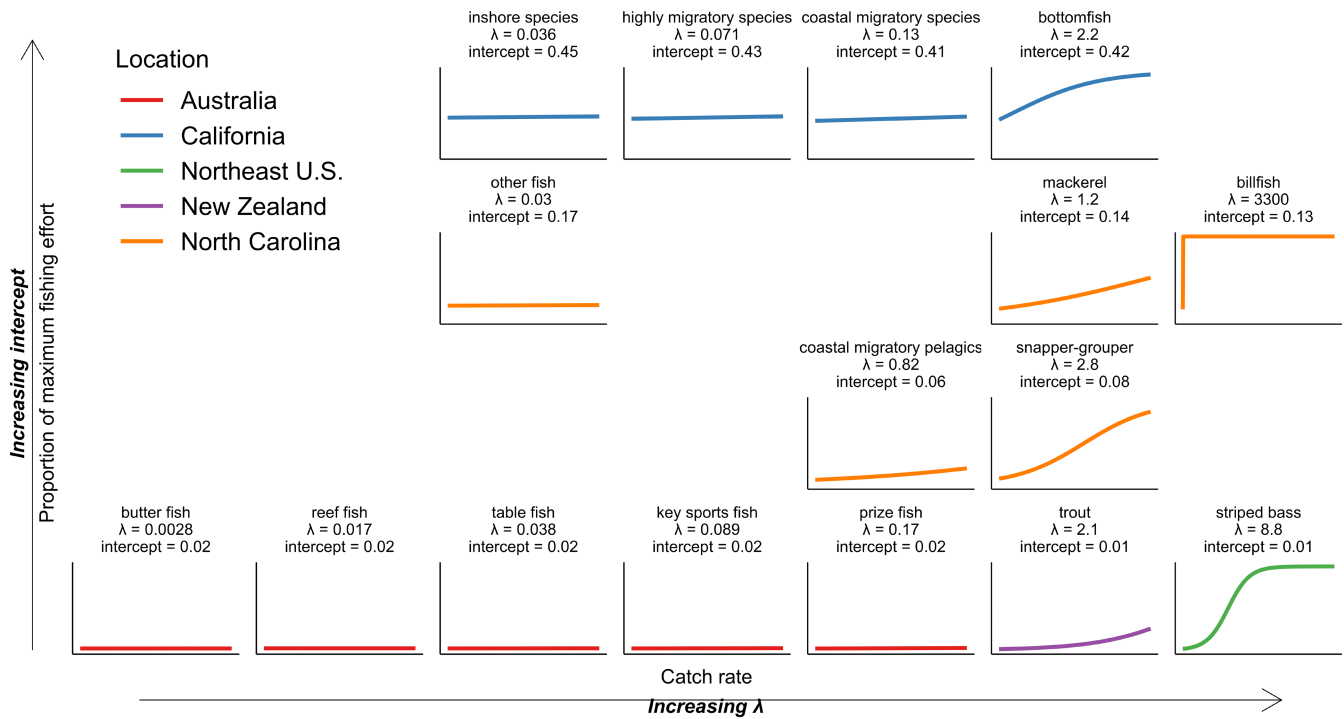


FIGURE 2 Empirically observed functional forms of the relationship between catch rate and anglers' fishing effort from five studies of angler utility. Study location is indicated with line colour and plots are arranged from low to high steepness of the angler effort response (λ ; x-axis) and with increasing no-catch intercept (y-axis). Axes are not to scale.

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. Model parameters and values are listed in Table S1 and the full set of equations making up the model is listed in Table S2.

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:

$$N_{a,t} = [N_{a-1,t-1} - qE_t v_a (N_{a-1,t-1})^\beta] s_a \quad (9)$$

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 , which accounts for natural mortality, is constant across age classes. Abundance is truncated at zero and considered to be extirpated if it drops below zero (i.e. abundance and catch remain at zero for the remaining years of the model run) to address the fact that the catch equation used here can potentially produce negative population abundances as an artefact. Catchability shape parameter β

can be modified to produce hyperstability ($\beta < 1$), hyperdepletion ($\beta > 1$) or the null expectation, density-independent catchability ($\beta = 1$). Captured fish are assumed to have a 100% retention rate, with no discards.

Spawning stock biomass is calculated from the abundance of mature fish and weight-at-age from a von Bertalanffy growth curve and a length-weight relationship (parameters given in Table S2):

$$B_t = \sum_{i=1}^a N_{a,t} w_a m_a \quad (10)$$

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 be 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):

$$R_t = N_{a=1,t} = \frac{aD_{t-1}B_{t-1}}{(1+bD_{t-1}B_{t-1})^g} \exp(\rho e_{t-1} + \sqrt{1-\rho^2}\delta_t) \quad (11)$$

where depensation term D_t is calculated using Equation 1 and g is set to 1 to produce a Beverton-Holt stock-recruit relationship. Recruitment stochasticity can be turned 'off' by setting ρ and the standard deviation of δ equal to zero. The null expectation of no depensatory dynamics in the stock-recruit relationship was represented by setting d close to zero.

TABLE 4 Mechanisms included in the model, with the parameter(s) used to operationalize them and the mean, median, and standard deviation of the parameters' observed values. The 'null value' column indicates the value of each parameter that represents the null hypothesis for that mechanism (that is, that there is no depensation in the stock-recruit relationship, that the stock-recruit relationship is deterministic rather than stochastic, and that catchability is density-independent). Note that there is no obvious null value for anglers' behavior in response to catch

Mechanism	Model component	Parameter(s)	Null value	Median	Mean	Standard deviation
Depensation	Biological submodel	d	$d \approx 0$	0.06	0.13	0.14
Recruitment stochasticity	Biological submodel	SD, ρ	$SD = 0$	0.74	0.72	0.07
			$\rho = 0$	0.45	0.44	0.28
Density-dependent catchability	Catch equation	β	$\beta = 1$	0.53	0.72	0.05
Angler responsiveness to catch	Angler effort model	λ , intercept	NA	0.01	0.39	1.45
				0.07	0.15	0.17

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. Researchers typically 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 catch rate in the previous time step, $CPUE_{t-1}$ and the probability of angler i fishing at time t , $P_{i,t}$. Specifically, for each study in Table 3, 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 7, 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 modelled site was treated as a focal fishing option in a landscape consisting of the modelled site plus $n-1$ unmodelled sites, where n is the number of sites observed in the study of interest. All $n-1$ unmodelled sites were assumed to have the mean value of each site attribute, including catch, such that overall utility at each of the unmodelled 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 unmodelled sites can, therefore, be calculated as

$$P_{i,t} = \frac{\exp(V_{i,t})}{\exp(V_{i,t}) + (n-1)(\exp(\bar{V}))} \quad (12)$$

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; $V_{i,t} = f(CPUE_{t-1})$. Although Equation 12 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 generated versions of Equation 12 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 five species groups could inform our model with five potential choice probability functions.

Since we assume that the angler population is homogeneous, the probability of generic angler i fishing at the modelled 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 $E_{\max}$, so that

$$E_t = P_t * E_{\max} \quad (13)$$

This proportion P_t was set equal to the probability of any generic angler i choosing to fish at the modelled site (P_{im}). For example, in a time step where the site choice probability for the generic angler i was 0.2, the overall effort across the modelled 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} . The parameter $E_{\max}$, representing the total amount of latent fishing effort in the modelled system, can take a wide range of plausible values because of the extensive variation in fisheries' accessibility and level of latent effort in real-world fisheries. The influence of $E_{\max}$ on model behavior was first explored via a sensitivity analysis in which we evaluated model behavior for values of $E_{\max}$ up to 3000 for each angler effort function and up to 200 for the interactions between angler effort and the other three mechanisms (depensation, recruitment stochasticity and density-dependent catchability). A reasonable constant value of $E_{\max}$ was then selected to explore the effects of

the mechanisms of interest in greater detail, since greater amounts of latent effort tended to extirpate the modelled population regardless of the magnitude of the focal mechanisms explored in this study. This value of $E_{\max}$ (one that was large enough for anglers to *potentially* extirpate the modelled fish population, but not so large that they extirpated the population at a small fraction of $E_{\max}$) was selected by conducting a sensitivity analysis in which the model was run with constant effort E across all time steps (Appendix S1). The smallest value of constant E that extirpated the fish population was selected as $E_{\max}$ in our analysis of the effects of depensation, recruitment stochasticity, density-dependent catchability and angler responsiveness to catch rates.

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 λ and the no-catch intercept (Figure 2).

2.2.3 | Outcome variables

We assessed model outcomes across three axes: (1) biological sustainability, (2) socio-economic benefits and (3) stability/variability of biological and socio-economic 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 $t = 100$ (i.e. after a burn-in period of transient dynamics) in which population biomass was below $0.5 \times B_{\text{MSY}}$ 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 starting at $t = 100$ 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 for all time steps starting at $t = 100$ and then averaged across simulations. To assess the impact of each mechanism (or combination of mechanisms) of interest, the outcome variables above were averaged across 100 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. Because outcome variables were only calculated for the stable state represented by the last 100 time steps of the simulation, model runs in which the population was extirpated before this point would exhibit zero cumulative catch, cumulative effort and coefficient of variation of biomass and effort.

3 | RESULTS

Model behaviour depended strongly on the latent effort present in the system ($E_{\max}$) and secondarily on the mechanisms of interest, which mediated the degree of effort required to extirpate the modelled population (Figure 3). 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 (Figure 4). At moderate levels of $E_{\max}$, 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, even when overall effort was moderate.

3.1 | Latent fishing effort

Model behaviour was highly sensitive to the overall level of latent effort in the system, with sustained effort (that is, anglers expending 100% of their possible latent fishing effort in each time step) extirpating the population at $E_{\max} = 48$. When angler effort responded dynamically to catch, the amount of overall latent effort required to extirpate the fished population increased dramatically (for instance, for Australian prize fish, $E_{\text{extinction}} = 2596$; note that units of effort are arbitrary), indicating that anglers' dynamic response to catch does indeed have a self-regulating effect (Figure 3, Table 5). The strength of this self-regulating effect depended on the magnitude of the angler effort function's zero-catch intercept (Figure 3), with the highest zero-catch intercepts yielding the least effective self-regulation, regardless of the angler effort function's steepness. However, even the most destabilizing angler effort functions required much higher levels of latent effort to produce extirpation than when effort remained constant through time (e.g. for California highly migratory species, $E_{\text{extinction}} = 111$).

3.2 | Depensation

The highest magnitudes of depensation reduced the amount of latent effort required to extirpate the modelled population about threefold, with the most noticeable effect occurring in combination with a low intercept, low steepness angler effort function (Figure 3a). When latent effort was held constant at a moderate level ($E_{\max} = 48$), this inflection point occurred at a value of $d = 0.2$ in the presence of a high-intercept angler effort function (Figure 4a). This extirpation resulted in 80% less cumulative catch relative to the null scenario of $d \approx 0$ and increased the coefficient of variation of biomass to 10 as d increased above 0.2. Moderate levels of effort, which could extirpate the population if sustained through time, did not produce extirpation at any value of d when a low-intercept angler effort function was used (Figure S2C,D). For all angler effort

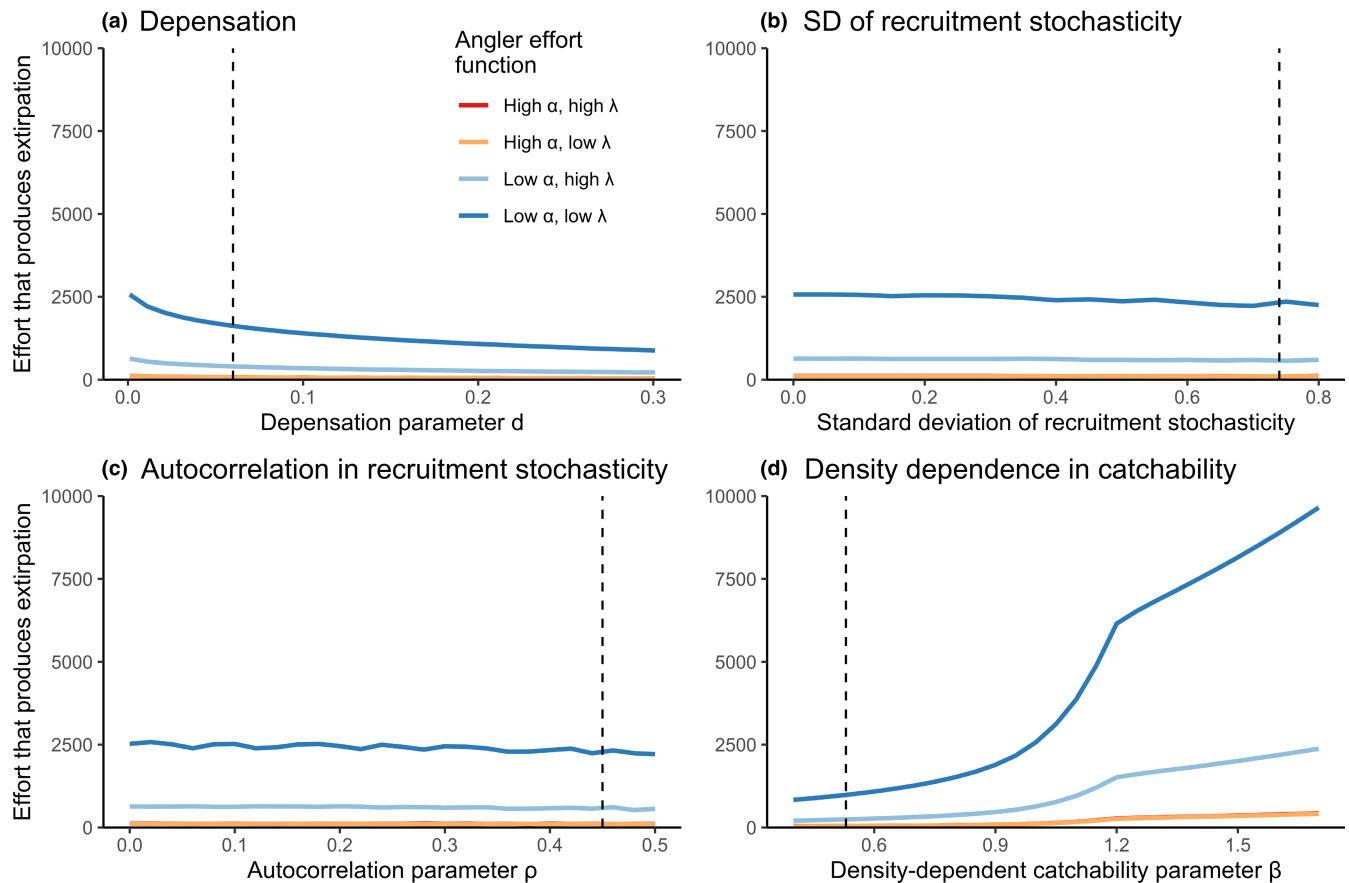


FIGURE 3 Amount of latent effort ($E_{\max}$) required to extirpate the modelled population across the empirically observed range of values of depensation (a), normally distributed recruitment stochasticity (b), autocorrelated recruitment stochasticity (c) and density-dependence in catchability (d) across four representative angler effort functions (red = high α , high λ ; orange = high α , low λ ; light blue = low α , high λ ; dark blue = low α , low λ). Vertical dashed lines indicate the median empirically observed value for each mechanism.

functions and at moderate effort, depensation only produced serious negative effects at levels greater than the median observed value of d ($d = 0.06$), indicating that this mechanism alone is not likely to be strongly destabilizing in most real recreational fisheries if regional latent fishing effort remains at or below E_{MSY} . Note that the depensation sensitivity analysis—like all other scenarios without recruitment variability—did not include any form of stochasticity, so its behaviour 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 .

3.3 | Recruitment stochasticity

Recruitment stochasticity had minimal impacts on model behaviour and stability, regardless of the angler effort function or the degree of latent effort (Figures 3b,c and 4b,c). At moderate $E_{\max}$, for instance, increasing the normally distributed standard deviation of stochasticity had the greatest effect on cumulative catch, producing a 41% increase in cumulative catch from the null expectation for the highest

observed standard deviations (Figure S3). However, it had no effect on overfishing or the probability of extirpation and only slightly increased the coefficient of variation of biomass. The magnitude of autocorrelation coefficient ρ had no effect on model behavior at the levels observed in empirical data, regardless of the angler effort function used (Figure 3D; Figure S3E–H).

3.4 | Density-dependent catchability

Hyperstability in catch per unit effort was strongly destabilizing at commonly observed empirical values and moderate latent effort (Figure 4D). Similarly to depensation, the greatest magnitudes of hyperstability reduced the amount of latent effort required to produce extirpation threefold, regardless of angler effort function (Figure 3D). When modelled at moderate latent effort, this translated into values of β below 0.55 producing extirpation of the modelled fish population when combined with an angler effort function with a high zero-catch intercept (Figure S4A,B). This value of β is above the median observed value of 0.53, meaning that more than half of the estimates of this parameter found in the literature indicate

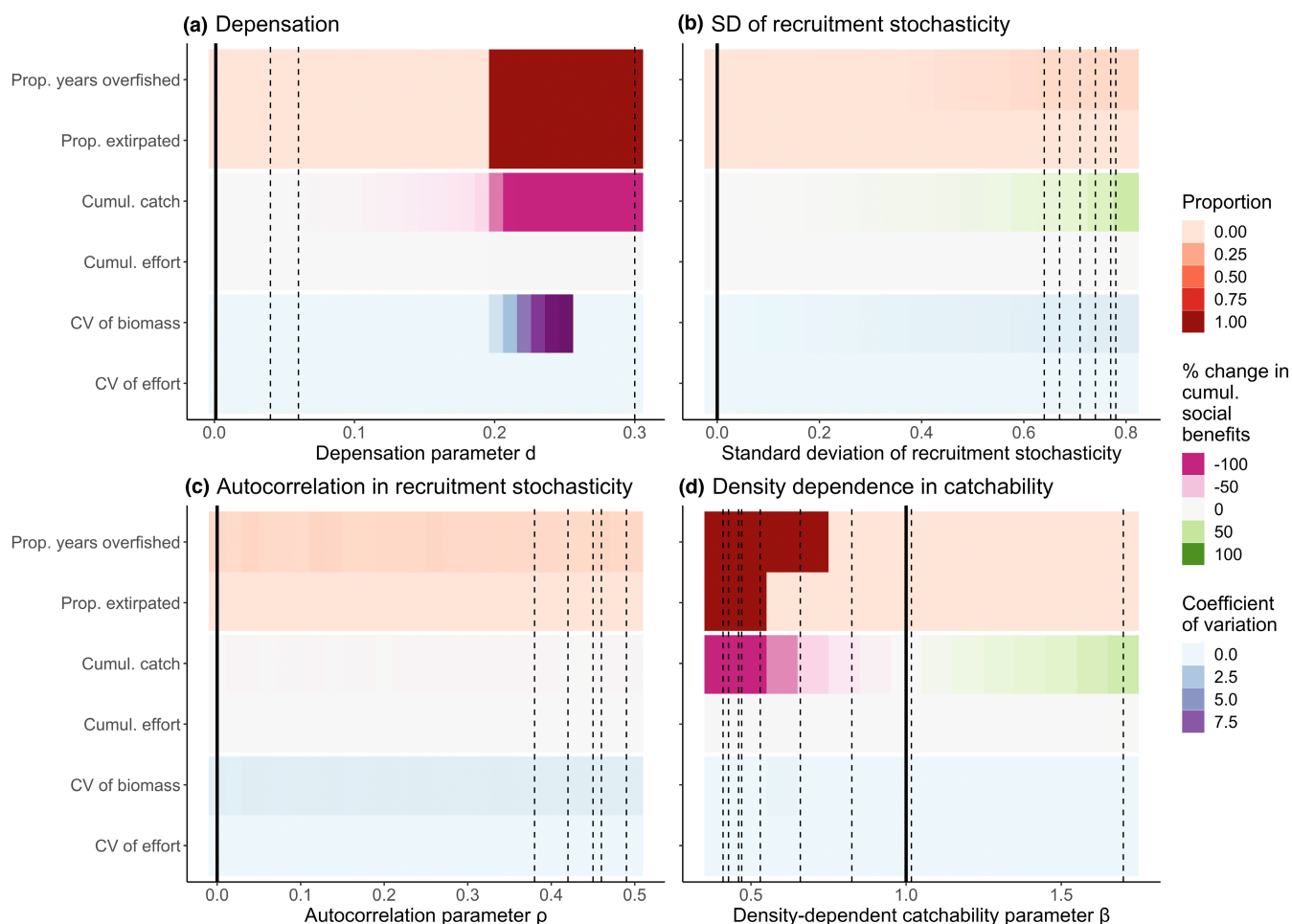


FIGURE 4 Heatmaps showing the effects of each of the three mechanisms of interest (depensation (a), normally distributed recruitment stochasticity (b), autocorrelated recruitment stochasticity (c) and density-dependence in catchability (d)) on three aspects of model behavior: Biological sustainability (red; top bar), social benefits (pink/green; middle bar) and variability (blue; bottom bar). Model behavior is shown for the entire observed range of values for depensation parameter d , catchability parameter β and the standard deviation and autocorrelation parameter of recruitment stochasticity at moderate effort ($E_{\max} = 48$). 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 an angler effort function representing high-catch responsiveness and high probability of fishing with zero catch (California bottomfish).

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 produced extirpation also reduced the social benefits available from catch (100% decline in cumulative catch), without influencing cumulative effort or increasing the coefficient of variation of biomass or effort. Hyperdepletion, in contrast, stabilized the system, increasing the amount of effort required to produce extirpation by up to 370% for the highest observed value of β (Figure 3D). Interestingly, this interaction between hyperdepletion and latent effort exhibited an inflection point at $\beta = 1.2$, in which below this point, the amount of effort required to produce extirpation increased exponentially, while above it, it increased linearly. At moderate $E_{\max}$, the highest levels of hyperdepletion produced over a 44% increase in cumulative catch (Figure 4D).

3.5 | Angler responsiveness to catch rates

Unsurprisingly, the level of effort that produced extirpation depended strongly on the angler effort function used to model anglers' responsiveness to catch. Angler effort functions with a high zero-catch intercept extirpated the population at much lower levels of overall effort, while a low-intercept, low-steepness function sustaining the highest level of latent angler effort. However, when $E_{\max}$ was set to 48, a moderate level 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 (Table 6). This indicates that dynamic utility-based angler effort responses based on empirical measures of angler utility do, in fact, produce the self-regulatory feedback behaviour that is predicted by

TABLE 5 The lowest level of $E_{\max}$ that extirpated the population ($E_{\text{extinction}}$) for each species-specific angler effort function in our analysis. The table is organized in increasing order of $E_{\text{extinction}}$

Citation	Species	$E_{\text{extinction}}$
Whitehead et al. (2013)	Billfish	100
Kuriyama et al. (2013)	Inshore species	108
Kuriyama et al. (2013)	Highly migratory species	111
Kuriyama et al. (2013)	Bottomfish	115
Kuriyama et al. (2013)	Coastal migratory species	118
Whitehead et al. (2013)	Other fish	282
Whitehead et al. (2013)	Mackerel	357
Whitehead et al. (2013)	Snapper-grouper	638
Whitehead et al. (2013)	Coastal migratory pelagics	774
Raguragavan et al. (2013)	Reef fish	2353
Raguragavan et al. (2013)	Table fish	2457
Raguragavan et al. (2013)	Key sports fish	2482
Raguragavan et al. (2013)	Butter fish	2529
Raguragavan et al. (2013)	Prize fish	2596
Gentner (2006)	Striped bass	3445
Mkwara et al. (2015)	Trout	4412

theory, in the absence of other destabilizing mechanisms. Only the angler effort function with the highest steepness by several orders of magnitude (North Carolina billfish, $\lambda = 3304$) produced overfishing at moderate latent effort. Social benefits of fishing in the form of cumulative catch were highest when anglers' no-catch probability of fishing was high and decreased slightly as anglers became more responsive to catch (i.e. higher λ ; Table 6). In contrast, cumulative effort was maximized for the functions with the highest levels of λ . All the utility functions produced highly stable effort and biomass time series ($CV < 1$).

3.6 | Interactions

There were only minimal three- or four-way interactions between the mechanisms of interest when they co-occurred at the median values observed in real-world fisheries and at moderate levels of latent effort. Depensation did not interact with any of the other three mechanisms when it was present at its median value of 0.06 (that is, much lower than the threshold at which it produced extirpation in combination with a high-intercept angler effort function, $d = 0.2$) (Figure 5). In general, when a high-intercept angler effort function was present, hyperstability caused extirpation regardless of the presence of the other two mechanisms (recruitment stochasticity and depensation) at their median values (Figure 5a,b). Recruitment stochasticity interacted with hyperstability to moderate its

destabilizing effect slightly and prevent extirpation, but only when a high-intercept, high-steepness angler effort function was present (Figure 5b). In contrast, in scenarios with a low-intercept angler effort function, in which hyperstability does not cause extirpation (Figure S4), the model's behaviour was most strongly affected by the presence or absence of recruitment stochasticity. Where recruitment stochasticity was present at its median value ($\rho = .45$, $SD = 0.74$), the model exhibited slightly more variability in biomass and slightly greater cumulative catch than when it was not (Figure 5c,d).

4 | DISCUSSION

The human behavioural 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, with an angler population that was willing to keep fishing when catch rates were zero being necessary but not sufficient on its own to destabilize the SES at moderate levels of latent effort. This result highlights the importance of interactions between the social and biological components of the modelled system. Specifically, the effects of depensation, recruitment stochasticity, and density-dependent catchability all depended strongly on their interaction with this aspect of anglers' behaviour. Except for recruitment stochasticity, which had minimal effects on model outcomes, the combination of these mechanisms with a high-intercept angler effort function enabled overfishing and even extirpation of the modelled population. The strongest of these interactions was the one between hyperstability and an angler population with a high zero-catch fishing probability, which extirpated the population at moderate latent effort and levels of hyperstability commonly observed in real fisheries (e.g. largemouth bass and walleye in Wisconsin, Dassow et al. (2020) and Mrnak et al. (2018); *Paralabrax clathratus* in California, Erisman et al. (2011); rainbow trout in British Columbia, Ward et al. (2013); Figure 4b). 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 levels higher than most empirical measurements of this mechanism unless latent effort in the fishery is extremely high, as can occur around urban centres (Hunt et al., 2011; Matsumura et al., 2019; Wilson et al., 2020; Figure 3a).

This paper introduces a novel approach to modelling angler effort based on empirical estimates of angler utility. Our approach enables us to ground the model's behaviour in real-world estimates of anglers' preferences for catch and compare the effects of angler behaviour across systems in the form of utility estimates from a wide range of real-world fisheries (Table 3). Although the concept of incorporating angler utility into fishery SES models is not new, previous attempts have either relied on abstract effort functions that represent reasonable but arbitrary relationships between CPUE and utility (e.g. Carpenter & Brock, 2004; Cox et al., 2003; Johnston

TABLE 6 Proportion of modelled years overfished, proportion of simulations extirpated, mean cumulative catch and effort and coefficient of variation of biomass and effort for each angler effort function derived from empirical studies

Citation	Species	λ	α	Prop. overfished	Prop. Extir-pated	Cumul. catch	Cumul. effort	CV biomass	CV effort
Gentner (2006)	Striped bass	8.782	0.01	0	0	11	2	0	0
Kuriyama et al. (2013)	Bottomfish	2.216	0.42	0	0	99	43	0	0
Kuriyama et al. (2013)	Coastal migratory species	0.125	0.41	0	0	100	41	0	0
Kuriyama et al. (2013)	Highly migratory species	0.071	0.43	0	0	99	43	0	0
Kuriyama et al. (2013)	Inshore species	0.036	0.45	0	0	98	45	0	0
Mkwara et al. (2015)	Trout	2.121	0.01	0	0	7	1	0	0
Raguragavan et al. (2013)	Butter fish	0.003	0.02	0	0	12	2	0	0
Raguragavan et al. (2013)	Key sports fish	0.089	0.02	0	0	12	2	0	0
Raguragavan et al. (2013)	Prize fish	0.173	0.02	0	0	12	2	0	0
Raguragavan et al. (2013)	Reef fish	0.017	0.02	0	0	13	2	0	0
Raguragavan et al. (2013)	Table fish	0.038	0.02	0	0	12	2	0	0
Whitehead et al. (2013)	Billfish	3304	0.13	1	0	32	89	0	0
Whitehead et al. (2013)	Coastal migratory pelagics	0.816	0.06	0	0	36	6	0	0
Whitehead et al. (2013)	Mackerel	1.159	0.14	0	0	66	14	0	0
Whitehead et al. (2013)	Other fish	0.03	0.17	0	0	76	17	0	0
Whitehead et al. (2013)	Snapper-grouper	2.755	0.08	0	0	44	8	0	0

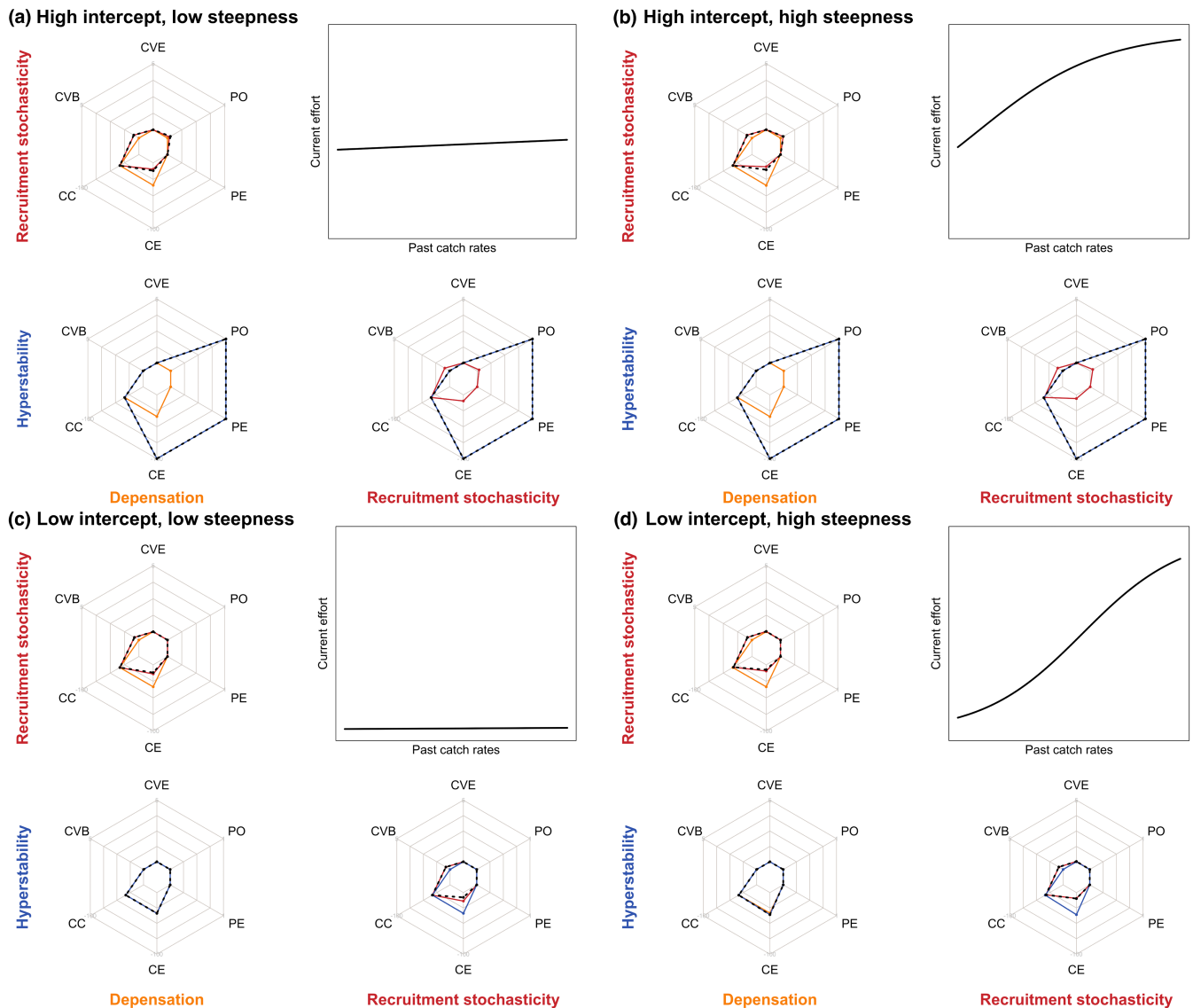


FIGURE 5 Radar plots indicating the effects of interactions between depensation (orange), recruitment stochasticity (red) and hyperstability (blue) on model behavior at their median observed levels. Six outcome variables are represented on each radar plot (CC, cumulative catch; CE, cumulative effort; CVB, coefficient of variation of biomass; CVE, coefficient of variation of effort; PE, proportion extirpated; PO, proportion overfished). Model outputs with a single mechanism present at the median and the others turned 'off' are indicated with thick coloured lines (see Table 4 for these median values). 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.

et al., 2010) or have used empirical 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' real-world responses to catch, 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, effectively ground-truthing the hypotheses about the potential forms of this relationship developed by Post (2013) (Figure 2). The steepness of the relationship varied by seven 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 modelled. 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 more common than might be expected in anglers' response to catch. Our results do not exclude the possibility that negative, stabilizing zero-catch intercepts exist, only that they did not appear in the small number of systems that are well-studied enough to be included here.

Our results provide guidance about how to set research priorities in a way that can most effectively inform recreational fishery management. Anglers' behaviour, specifically their willingness to keep fishing when they are no longer catching fish, has 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. At the most basic level, any angler effort function with a non-negative y-intercept can potentially extirpate the population if sufficient latent effort is present in the system. However, if effort is moderate, anglers have a low probability of fishing when catch rates are zero, and they respond moderately to increasing catch rates, the fishery should meet the self-regulating expectation and have limited possibility of collapse. In contrast, in systems where anglers are very likely to keep fishing as fishing quality declines, for instance in high-effort sites close to urban centres (Hunt et al., 2011; Matsumura et al., 2019; Wilson et al., 2020), the other factors we studied are generally more destabilizing. If the angler effort response does provide the conditions for instability, the most important potential interacting factor is hyperstability in catch rates, which should, therefore, be an additional priority for research. Only if both of these two mechanisms (a high zero-catch intercept 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 approximated with minimal data, using only basic information about target species' biology and angler motivations. For instance, schooling behaviour and strong habitat associations in fish often result in hyperstable catch rates, so the presence of this behaviour in a targeted species makes it likely that catch rates will be hyperstable (Dassow et al., 2020; Erisman et al., 2011). A compelling early example of this kind of heuristic approach with limited data is the analysis of CPUE data from 12 Ontario lake trout (*Salvelinus namaycush*, Salmonidae) fisheries to demonstrate the prevalence of hyperstability as a potential factor in the 'invisible collapse' of Canada's recreational fisheries (Post et al., 2002). Similarly, 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). As another example, in a

multi-species fishery, one can expect anglers to be more responsive to catch rates of trophy species than to those of less highly valued species and to continue fishing as catch rates decline for any single species as long as valued alternatives persist, 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, and the baseline assumptions of our model, somewhat limit the conclusions presented here. Most crucially, the data sources we draw on for this synthesis all represent recreational fisheries that are both stable and valuable enough to be studied by researchers, as well as exhibiting a bias towards the United States of America and other developed nations with robust fisheries management and research. Our results cannot speak to the behaviour of highly transient fisheries that have already collapsed or those that fly under the radar of management because of low participation, research capacity limitations, extreme remoteness or other factors. There are also mechanism-specific sources of potential bias. Only about 4% of stocks in the synthesis used to inform this study exhibited any compensatory dynamics (Hilborn et al., 2014), and depensation 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 almost all of the empirical estimates of β indicating hyperstability (Table 2). 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 do 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 β are less common than we thought. Excluding walleye from the dataset did not substantially alter the mean and median values of β (Mann-Whitney *U* test, $p = .8$), but the remaining non-walleye dataset was small (four species). Finally, our model assumed an open-access fishery, with no size or bag limits, season closures or voluntary catch-and-release by anglers. Harvest regulations and voluntary catch-and-release are effective tools for sustaining recreationally harvested populations and moderating angler effort (e.g. Jarvis et al., 2014; Post & Parkinson, 2012; Trudeau et al., 2022), so understanding how they affect these mechanisms' impacts on fishery stability is an important next step.

Angler behaviour potentially presents more serious data limitations due to the conventions and current state of the recreational angler behaviour literature. First, we were unable to model changes

in anglers' overall fishery participation rates directly, as would have been possible if we were able to draw on joint random utility estimates of both fishing allocation (where anglers decide to fish) and total regional effort (how likely they are to fish). These joint estimates are a known application of random utility modelling in recreational fisheries (Hutt et al., 2013; Lew & Larson, 2011). However, we were limited by the small number of studies that calculate these joint estimates and also provide enough documentation to be able to duplicate their methods. We identified only one joint estimation study that met the criteria outlined in Section 2.1.4, while five site allocation studies did so. The approach we develop here, which draws on fishing effort allocation estimates alone, therefore, has the potential to be influenced by the number of sites anglers are able to choose between, with the importance of catch declining as the number of alternatives increases. However, we will note that the number of sites in each study does not straightforwardly map onto the steepness values observed in this analysis (Figure 2, Table 3).

More broadly, the small number of angler site choice papers that met our inclusion criteria 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 3). For example, anglers are three orders of magnitude more responsive to catches of billfishes (Istiophoridae and Xiphiidae) 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 would be 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 β 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 behaviour at the moment a given study was conducted. If social norms in a fishery change, or if the community of species available in a multi-species

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-steepness catch response curve for one species group in a multi-species 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). For example, anglers in the New Jersey bottomfish charter boat fishery exhibit a willingness to substitute between black sea bass (*Centropristis striata*, Serranidae), summer flounder (*Paralichthys dentatus*, Paralichthyidae), scup (*Stenotomus chrysops*, Sparidae) and tautog (*Tautoga onitis*, Labridae), despite the varying perceived desirability of these species, and to continue fishing as long as one of these four species is available (Trudeau et al., 2022). 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 modelling effort provides guidance about how to prioritize research on recreational fisheries, which have been implicated in fish population declines worldwide (Cooke & Cowx, 2006; Post et al., 2002). Of most concern is the fact that a highly persistent angler population (i.e. one very likely to continue fishing when catch rates are zero) can interact with hyperstability to collapse a targeted species' population, given relatively common values of hyperstability. 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 modelling 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.

ACKNOWLEDGEMENTS

We are deeply grateful to Dr. Sunny L. Jardine and Dr. Adam L. Hayes for many fruitful discussions that led to the approach to the angler effort response described here. This project would not have been possible without the expertise they brought to bear in their thoughtful critiques and suggestions. We also thank Dr. Len Hunt for his feedback on an early version of the angler effort parameterization. Dr. John Post, Dr. Holden Harris and two anonymous reviewers thoughtfully reviewed this paper and materially improved

it with their suggestions. ASG is supported by the National Science Foundation Graduate Research Fellowship Program under Grant No. NSF DGE-1842213. BTVP is supported by a grant from the Freshwater Fisheries Society of British Columbia. Additional support was provided by NSF grant CNH #1716066 to OPJ. 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.

DATA AVAILABILITY STATEMENT

The code for the mathematical model and all the figures based on modelled data that are presented here are available in a public repository at https://github.com/abigailgolden/rec_fish_mechanisms_instability.

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How to cite this article: Golden, A. S., van Poorten, B., & Jensen, O. P. (2022). Focusing on what matters most: Evaluating multiple challenges to stability in recreational fisheries. *Fish and Fisheries*, 00, 1–21. <https://doi.org/10.1111/faf.12697>