Application - Discovery Grants Program - Individual

Identification

Applicant

Family Name: van Poorten

First Name: Brett

Middle Names: Theodore

Current Position: Assistant professor

Applicant Category

Suggested Applicant Category Early Career Researcher (ECR)

Explanation

Assistant Professor [Simon Fraser University]
I began my position as an independent researcher at Simon Fraser University in April 2020. In this university faculty appointment I have had autonomy over the direction and scope of my research and have been authorized to supervise the research of undergraduate and graduate students, as well as postdoctoral fellows.

Honorary Professor [University of British Columbia]
I held this position from April 2017 to March 2020. Although this university appointment allowed me autonomy, I did NOT have independence over the direction and scope of my research because of my employment with the BC government. This position was only available to me as a government employee, where the research I conducted was under the direction of my supervisors within the BC Ministry of Environment and Climate Change Strategy. There were many times I was told that a particular project of my interest was not within the mandate of our section of the Ministry and I could not continue to pursue it. Although my relationship with the university through this appointment did not permit me any autonomy over the direction of my research, it did authorize me to co-supervise the research of graduate students whose research was within the mandate of my government position.

Adjunct Professor [Simon Fraser University]
I held this position from April 2013 to March 2020. Although this university appointment allowed me autonomy, I did NOT have independence over the direction and scope of my research because of my employment with the BC government.This position was only available to me as a government employee, where the research I conducted was under the direction of my supervisors within the BC Ministry of Environment and Climate Change Strategy. Although my relationship with the university through this appointment did not permit me any autonomy over the direction of my research, it did authorize me to co-supervise the research of graduate students whose research was within the mandate of my government position.

Adjunct Professor [University of British Columbia]
I held this position from January 2014 to March 2017. Although this university appointment allowed me autonomy, I did NOT have independence over the direction and scope of my research because of my employment with the BC government.This position was only available to me as a government employee, where the research I conducted was under the direction of my supervisors within the BC Ministry of Environment and Climate Change Strategy. Although my relationship with the university through this appointment did not permit me any autonomy over the direction of my research, it did authorize me to co-supervise the research of graduate students whose research was within the mandate of my government position.

If NSERC offers you a Discovery Grant as an Early Career Researcher, would you accept a Discovery Launch Supplement and would you be able to use all of the supplement funds on your Discovery Grant research program?

(•) Yes ( ) No

Administering Organization

Organization Simon Fraser University

Department/Division Resource and Environmental Management

Application

Application Title Can you trust your data? Causes and consequences of non-proportionality between fishery catch rates and abundance

Language of the Application (•) English ( ) French

Suggested Evaluation Group 1503 Evolution and Ecology

Hours per month to be devoted to the research/activity, or use of equipment or facility 28

Supplements/Joint Initiatives

To be considered for one or more Supplements or Joint Initiatives, select all that apply

DND/NSERC Discovery Grant Supplement	( ) Yes	(•) No
Northern Research Supplement (NRS)	( ) Yes	(•) No

Leaves of absence

I entered one or more eligible leaves of absence in my Canadian Common CV for this application (required) ( ) Yes (•) No

Summary of Proposal

Summary

Estimating abundance is a core focus of ecology and necessary for management decisions aimed at conservation. Yet abundance in most small inland fisheries is not monitored using standardized surveys because of excessive costs. Instead, management often relies on fishery catch rates (number caught per unit of fishing effort) under the dubious assumption that such rates are a proportional index of abundance. This approach is notoriously prone to failure and risks masking potentially important declines if the proportion of fish abundance captured per unit fishing effort (termed catchability) is actually density dependent.

Although recreational fishery catchability has been observed to be density dependent, there has been no evaluation of how frequently this occurs, and therefore no sense of the risk of using catch rate data for management. Further, while there are several causes of density-dependent catchability, few have experimentally tested for single mechanisms. Our research program seeks to improve decision-making of managed ecological systems by determining the frequency of density-dependent catchability, experimentally evaluating causal mechanisms in recreationally fished systems and evaluating policies that may be robust to the problem.

Objective 1: **Determine the frequency of density-dependent catchability in North American recreational fisheries.** We will develop a database of recreational fisheries to house fisher catch rates and fishery-independent estimates of abundance. We will estimate the degree of density dependence in catchability across fisheries and correlate this with mitigating conditions that may increase risk and therefore collapse. Rationale: density-dependent catchability is a recognized conservation risk, but it is not known whether risk is equal across fisheries, or whether there are conditions under which fisheries may be robust to causal mechanisms.

Objective 2: **Experimentally evaluate different mechanisms of density-dependent catchability and their influence on conservation**. We will alter fish densities in whole-lake experiments and monitor system dynamics to determine the relative strength and interaction among causal mechanisms leading to density-dependent catchability. Rationale: Observational studies have been challenged to find density-dependent catchability due to observation error and poor contrast in abundance. We will estimate the strength of various mechanisms to better understand conditions leading to density-dependent catchability. We will apply our findings in a policy analysis to determine best approaches to managing under uncertainty.

This research program directly addresses many unsubstantiated claims related to density-dependent catchability, including the probability of occurrence, mitigating conditions and strength of different causal mechanisms. This program will improve fisheries management monitoring choices and decisions, leading to improved conservation of wild populations for Canadians.

Second Official Language Translation

Proposed Expenditures

	Year 1 Qty	Year 1 Amount	Year 2 Qty	Year 2 Amount	Year 3 Qty	Year 3 Amount	Year 4 Qty	Year 4 Amount	Year 5 Qty	Year 5 Amount
Salaries and benefits										
Undergraduate	2	$13,320	2	$31,080	1	$15,540	2	$31,080	0	$0
Master's	1	$11,000	2	$29,000	2	$29,000	1	$18,000	0	$0
Doctoral	0	$0	1	$13,000	1	$20,000	1	$20,000	1	$20,000
Subtotal		$24,320		$73,080		$64,540		$69,080		$20,000
	0	$0	0	$0	0	$0	0	$0	0	$0
Subtotal		$0		$0		$0		$0		$0
Equipment or facility										
Purchase or rental		$0		$19,000		$12,000		$0		$0
Subtotal		$0		$19,000		$12,000		$0		$0
Materials and supplies										
Field consumables		$0		$2,000		$2,000		$2,000		$0
Subtotal		$0		$2,000		$2,000		$2,000		$0

	Year 1 Qty	Year 1 Amount	Year 2 Qty	Year 2 Amount	Year 3 Qty	Year 3 Amount	Year 4 Qty	Year 4 Amount	Year 5 Qty	Year 5 Amount
Travel										
Field work		$0		$24,000		$24,000		$24,000		$0
Conferences		$0		$1,900		$1,900		$3,800		$1,900
Subtotal		$0		$25,900		$25,900		$27,800		$1,900
Dissemination Costs										
Publication costs		$0		$2,500		$2,500		$5,000		$5,000
Subtotal		$0		$2,500		$2,500		$5,000		$5,000
Other (specify)										
		$0		$0		$0		$0		$0
Subtotal		$0		$0		$0		$0		$0
TOTAL PROPOSED EXPENDITURES		$24,320		$122,480		$106,940		$103,880		$26,900
Total Cash Contribution from industry (if applicable)		$0		$0		$0		$0		$0
Total Cash Contribution from university (if applicable)		$0		$0		$0		$0		$0
Total Cash Contribution from other sources (if applicable)		$0		$0		$0		$0		$0
Total amount requested from NSERC		$24,320		$122,480		$106,940		$103,880		$26,900

Relationship to Other Research Support

Grants Held

1. Agency/Program: Fisheries and Oceans Canada/C68 Implementation and Support Funds

Title: Co-developing management goals, reference points and sustainable harvest rates for anadromous Dolly Varden using Indigenous knowledge and western science

Funding period: 04/2022 – 03/2025

Funds Awarded: $175,000

Budgetary overlap: None

Conceptual overlap: There is no conceptual overlap.

This grant looks at evaluating community objectives for a fishery co-managed between DFO and local Indigenous communities. Specifically, we will be evaluating traditional ecological knowledge and fisheries data within the context of community motivations for fishing to inform fisheries management decision-making and conservation outcomes, consistent with the long-term goal of my research program.

2. Agency/Program: Fisheries and Oceans Canada/DFO Competitive Science Research Funds

Title: Development and evaluation of a stage-structured model and alternative management procedures for recreational spot-prawn management

Funding period: 04/2022 – 03/2025

Funds Awarded: $260,000

Budgetary overlap: None

Conceptual overlap: There is no conceptual overlap.

This grant will evaluate data available on the dynamics of spot prawn and its recreational fishery to inform fisheries management. We will build fisheries models and conduct decision analysis to evaluate different monitoring programs. In this way, we are informing decision-making processes in this fishery, consistent with the long-term goal of my research program.

3. Agency/Program: BC Ministry of Environment

Title: Habitat suitability evaluation of white sturgeon spawning in the Nechako River

Funding period: 09/2021 – 03/2023

Funds Awarded: $60,000

Budgetary overlap: None

Conceptual overlap: There is no conceptual overlap.

We are using simulation studies to propose spatial sampling designs aimed at determining spawning locations and habitat associations for white sturgeon. This work will incorporate generalized additive models to estimate habitat suitability, consistent with the models used in Objective 2, Task 2 of this research program. Further, this work will help inform management by better understanding how sampling design provides informative data with which to make decisions.

4. Agency/Program: Parks Canada

Title: Evaluation of social value of lakes

Funding period: 09/2022 – 03/2024

Funds Awarded: $50,000

Budgetary overlap: None

Conceptual overlap: There is no conceptual overlap.

We are conducting a discrete choice experiment to determine utility for different lake attributes as determined from different user groups in Jasper National Park. This work will help provide useful social utility with which to contrast gains in ecological utility if various conservation actions are taken, thereby avoiding politically costly errors in management when proposing limiting access or other mitigative measures to different areas. The stated preference survey designed will be similar in concept and implementation to that proposed in Objective 2, Task 3.

5. Agency/Program: BC Ministry of Forests, Lands, Natural Resource Operations and Rural Development

Title: Meziadin Lake fisheries assessment and management recommendations

Funding period: 04/2022 – 03/2023

Funds Awarded: $32,000

Budgetary overlap: None

Conceptual overlap: There is no conceptual overlap.

This project takes information from creel survey interviews (catch rates, fishing effort, harvest rates), and acoustic telemetry to evaluate total fishing mortality under different management conditions (opening or closing co-occurring fisheries on another species). This information will be used to simulate different management regulations to determine how to best manage the lake under uncertainty in fishing effort and future management of co-occurring fisheries. This project will analyse fisheries data consistent with Objective 2, Task 1; spatial positions of fish, consistent with Objective 2, Task 2 and simulate management policies, consistent with Objective 2, Task 5.

Do you hold or have applied for CIHR and/or SSHRC funding? No

HQP Training Plan

Over the next 5 years, I plan to train 11 HQP (1 PhD; 3 MRM; 7 BSc) to work towards this research program. Each will acquire a skillset appropriate for their level, which will position them to progress into their career as natural resource managers, policy makers and environmental consultants.

Training Philosophy

Our lab focuses on providing unique career-related skills and training in a safe, inclusive environment. The fisheries profession has historically been dominated by Caucasian males, and change has been slow. For example, in 2017 it was reported that over a 20-year period, the American Fisheries Society decreased from 91% male and 94% Caucasian to 75% and 92%, respectively. This compared to 70% male and 70% Caucasian in the STEM workforce (and much lower in the population overall; Penaluna et al., “Nine proposed action areas to enhance diversity and inclusion in the American Fisheries Society”, Fisheries, 2017). This reflects a general underrepresentation of diverse students graduating with advanced degrees. For example, in 2014, only 36 and 31% of students graduating with Master’s or Doctoral degrees in the sciences and engineering were awarded to women (NSERC, “Women in science and engineering in Canada”, 2017). Our group addresses challenges in promoting equity in the workforce and enhancing research training of HQPs through three approaches: (1) recruiting and training people of diverse backgrounds; (2) providing skills and opportunities; (3) and individualized supervision for HQP.

1. Recruiting and Training: The first step in tackling diversity and inclusion within fisheries and STEM is recruitment at the university level. By recruiting diverse students and technicians into our research group, we affect the talent base of individuals in the workforce available for promotion into, and throughout the profession. Moreover, by recruiting diverse students, incoming students will find relatable peers that can help them navigate and meet barriers they face throughout their time in academia and beyond. As a start to addressing this issue, our group will adopt university-level recruitment protocols for faculty recruitment and adapt them for recruitment at the graduate student and technician level. These actions include implicit bias training for members of the research team and crafting advertisements with input from the entire research team and soliciting critical feedback from colleagues in the department to encourage diverse applicants, and posting ads in forums targeting diverse genders and ethnic backgrounds, as well as distributing ads as broadly as possible through traditional means (e.g., emails to STEM universities, word of mouth, Twitter, etc.), as these have been found to be equally effective at attracting underrepresented minority applicants (Shadding et al. "Cost effective recruitment strategies that attract underrepresented minority undergraduates who persist to STEM doctorates", SAGE Open, 2016). These actions add to work we have undertaken to create an inclusive environment for members of the research team with different life circumstances by offering family-friendly actions that promote career development, such as finding funds to allow parents to find childcare when travel to meetings or conferences is desired or allowing flexible work schedules. We intend to build on this work and codify it in a written lab policy, helping to demonstrate to potential candidates our work to ease the burden of advancing research careers - starting in our research group.

2. Skills and Opportunities: The SFU School of Resource and Environmental Management (REM) is a course-intensive program, where Masters of Resource Management (MRM) students may either enroll in a thesis (25 course credits) or project (38 course credits) program; PhD students are required to take 18 course credits. Courses cover the three pillars of our program: natural science, social science, and policy. This program provides a solid background in career-related training and an important context for the research to be completed by each student.

I emphasize skills development that will be useful outside academia by creating opportunities for HQP to interact and work directly with collaborators in public and private agencies through short contracts, internships, and participation in workshops. Further, I provide support for HQP to attend scientific conferences and create connections between them and other attendees where possible and encourage HQP to be active contributors and authors on manuscripts. These opportunities contribute to the skills of all HQP in the lab.

3. Individualized Supervision: An important aspect in my lab is interaction. Our entire lab meets weekly to discuss issues and barriers of inclusion, and discipline-relevant literature; we also peer review articles submitted to research journals as a group. In addition, I meet individually with each of my HQP regularly (usually every two weeks) to discuss any research-related issues, review progress, and work together to solve problems and direct research activities. Finally, I encourage social interaction outside of the lab, by engaging in off-campus activities, where family and friends are encouraged to join. All these efforts help to build an inclusive, energized, and interactive atmosphere that promotes mental wellness and inclusivity.

Research Training Plan

Research Objective 1 (BSc 1-2; MRM 1: Determine the frequency of density-dependent catchability in North American recreational fisheries) requires BSc students assisting the MRM student to facilitate collection of data from across North America (accessing datasets from existing databases, as well as contacting and collecting data from individual agencies). Together with MRM 1, these individuals will develop skills in database development and management as large quantities of data will be collected and stored internally. Further, MRM 1 will develop skills in meta-analysis of large datasets. This program of research is narrow, well-defined, and appropriately sized for MRM students in our department.

Research Objective 2 (BSc 3-7; MRM 2-3; PhD 1: Experimentally evaluate different mechanisms of density-dependent catchability and their influence on conservation) will be an extensive field-based research program evaluating demographic and ecological responses to changes in abundance at individual lakes. This will include deployment of acoustic telemetry receivers, monitoring position of boats, conducting creel surveys of anglers and performing mark-recapture surveys of fish abundance across multiple lakes per year. PhD 1, MRM 2 and BSc 3-4 will collect data in year-2. MRM 2 will focus on evaluating the extent to which fish associate with different habitat types and the extent to which anglers find those aggregations, and will learn skills in fisheries data collection and analysis, GIS, habitat suitability modelling of fish and home range overlap between fish positions and anglers, in addition to scientific writing. MRM 3 will focus on angler behavioural responses to catch- and noncatch-related fishery attributes as well as response to management restrictions. MRM 3 will learn skills in fisheries data collection, as well as stated preference survey development, analysis, and scientific writing. MRM 2-3 will have focused projects that are appropriately sized for the expectations of our department. PhD 1 will focus on various mechanisms leading to density-dependent catchability, including effort sorting, and the exchange of fish between vulnerable and invulnerable states, as well as interactions among mechanisms leading to density-dependent catchability. PhD 1 will also create simulation models to evaluate how different management actions may lead to improvements in management outcomes. PhD 1 will develop skills in field data collection, nonlinear parameter estimation, simulation modelling, decision analysis and scientific writing. The research program of PhD 1 is broad, open-ended and spans multiple disciplines (natural science and policy), which is a requirement of our department. Each BSc student will assist the PhD and MRM students in field data collection, learning skills in multiple forms of fisheries sampling, data analysis and scientific writing. Work in the field will help BSc students identify their own research questions, which can then develop into honours theses.

All HQP will benefit from experience working in recreational fisheries from the perspectives of both fish dynamics and angler dynamics, as they play out across a landscape of distinct fishing opportunities. These students will contribute to a more complete understanding of the mechanisms leading to density-dependent catchability, interactions among mechanisms, and policy implications for them. More broadly, this information and its communication back to fisheries professionals to improve decision-making is an overarching theme of our research program.

Past Contributions to HQP Training

I am committed to working with students on applied and experimental projects that lead to gainful future employment. Since starting my first tenure-track position at Simon Fraser University (SFU) in April 2020, I have been primary supervisor for one postdoctoral-level researcher (Cahill) and eight MRM (Master of Resource Management) students (Hunter, Lemp, More O'Farrell, Schaefer, Tousignant, Ross, Ofoe, Townend) in addition to co-supervising one other MRM student (Watson).

I also serve on supervisory committees (1 PhD at SFU, 1 MSc and 3 PhD at University of British Columbia, 1 MA at University of Northern British Columbia). Prior to joining SFU, I co-supervised 2 PhD students (Chudnow, Woodruff), one MSc student (Brydle) and 2 MRM students (Demsar, Barrett).

Training Environment

Our lab is focused on developing skills and expertise that will carry HQP to rewarding and successful careers in public and private sectors. Many student projects undertaken have been with government partners to address applied problems. My HQP currently have active collaborations with Alberta Environment and Parks, BC Ministry of Forests, BC Ministry of Environment and Climate Change Strategy, Nebraska Cooperative Fish and Wildlife Unity, Fisheries and Oceans Canada, and the Freshwater Fisheries Society of BC.

Our group also works across disciplines, consistent with the mandate of my department. I have students that use qualitative tools to determine fishery objectives (Tousignant; Townend), economic models to determine social values (Demsar, Ross), decision-theoretic approaches to evaluate management actions and policies that will achieve a mixture of ecological and social objectives (Schaefer, Hunter, Chudnow), and simulation modelling to evaluate sampling or management processes (Lemp, More O'Ferrall, Ofoe, Barrett).

I am committed to acting on issues related to diversity, equity, and inclusion to support the recruitment of diverse HQP into my research group, and to support a safe and emotionally resilient work environment. Over the past 6 years, I have participated in several workshops and training opportunities focused on issues of equity and inclusion. I lead an annual workshop with fisheries labs in my department around personal values to identify conditions that promote a healthy work environment and positive interactions with peers and partners. This work has contributed our Equity, Diversity and Inclusion statement and ethic.

Part of providing an inclusive research and training environment is listening to HQP, being flexible in my approach, and working with them to overcome barriers. One frequent issue I see with my own HQP, and those from other labs, is mental health issues, which is common in graduate school in general (Evans et al. "Evidence for a mental health crisis in graduate education", Nature, 2018). I try to provide consistent, positive, and constructive feedback, flexible timelines, administrative support (including arranging for health leaves), directing them to on-campus resources and support, and understanding when needed. While mental health problems are not specific barriers to inclusion, they can keep students from participating in group activities, accepting help, or completing their degree. Being on the lookout for mental health struggles, particularly where they intersect with other barriers, is an important aspect of my role.

HQP Awards and Research Contributions

My research group at SFU has submitted one HQP-led manuscript (Lemp et al., in review), which is now undergoing revisions. My senior MRM student will present outcomes of her thesis to the BC Fisheries Managers meeting in Winter 2023. Many of my completed HQP produced peer-reviewed manuscripts from their thesis (Woodruff et al. 2021a, 2021b; Chudnow et al. 2019, Barrett et al. 2017), as well as through interactions with myself and my collaborators (Taylor et al. 2021, van Poorten and Brydle 2018, van Poorten et al. 2017).

My HQP are often recognized for their academic skills. Lemp (MRM) was awarded a stock assessment scholarship from Fisheries and Oceans Canada in 2022, as well as the annual Freshwater Fisheries Society scholarship for outstanding academic commitment in freshwater fisheries in 2021. Tousignant (MRM) was awarded the SFU Paul Higgins Award for excellence in fisheries in 20X2.

Outcomes and skills gained by HQP

My HQP receive extensive training in quantitative modelling and analysis, as well as manuscript preparation. Field research is not always a component of my HQP research (many applied problems have data to be analysed and interpreted), but I endeavour to provide opportunities in the field, or with agencies where they arise to round out their training. For example, Lemp (MRM) and Schaefer (MRM) conducted creel surveys for BC Ministry of Forests, Lemp (MRM) and Watson (MRM) are working as a co-op students for DFO, and Hunter (MRM) won an internship at Freshwater Fisheries Society of BC. These skills build their qualifications as future candidates for management-oriented positions within and outside of government and academia.

Woodruff (PhD) learned significant skills in ecosystem analysis and management during her PhD, where they used data to parameterize an ecosystem simulation model of multiple aquatic systems across British Columbia. They are now a postdoctoral fellow working at the University of British Columbia Institute for Oceans and Fisheries, creating simulation models of the Burrard Inlet (Vancouver) ecosystem pre-contact based on traditional ecological knowledge of Tsleil-Waututh Nation knowledge-holders.

Chudnow (PhD) gained experience and skills in fisheries and data analysis generally and specifically became an expert on population dynamics and regulation of bull trout. They now work for an environmental consulting company where they are regularly called upon to advise and participate in field and desktop processes to recover bull trout populations across British Columbia.

Most Significant Contributions

Most Significant Contribution

My research over the past 6 years has been consistent with the long-term goal of my research program: to understand dynamic interactions between fish populations and harvesters to improve management decision-making. Within that context, themes of my research have fallen into the following categories: (1) understanding density-dependent catchability; (2) social-ecological systems; and (3) applying decision-theoretic approaches to fisheries management.

1. Density-dependent catchability

Nieman, C.L., C. Iwicki, A.J. Lynch, G.G. Sass, C.T. Solomon, A. Trudeau, B. van Poorten. 2021. Creel surveys for social-ecological systems focused on fisheries management. Reviews in Fisheries Science & Aquaculture 29(4): 749-752.

- I contributed to concept, content, and writing

Dassow, C.J., S.E. Jones, C.T. Solomon, A.J. Ross, O.P. Jensen, G.G. Sass, B.T. van Poorten. 2020. Experimental demonstration of catch hyperstability from habitat aggregation, not effort sorting, in a recreational fishery. Canadian Journal of Fisheries and Aquatic Sciences 77(4):762-769.

- I contributed to experimental design, analysis, and writing

van Poorten, B.T., C.J. Walters, H.G.M. Ward. 2016. Prediction of changes in the catchability coefficient as less skilled fishermen drop out during stock declines. Fisheries Research. 183:379-384.

- I led all aspects of this study

Contribution: It is appropriate that I propose to work on density-dependent catchability, because I feel I have made real gains in understanding some of the causal mechanisms in recent years. For example, van Poorten et al. (2016) was the first attempt to estimate parameters for minimum catch rates and catchability variability among anglers associated with effort sorting from standard fisheries data. This work formed the basis for much of the proposed work on effort sorting. Further, it helped highlight the issue of effort sorting and density-dependent catchability generally, leading to several recent investigations into hyperstability in recreational fisheries and building the case for the importance of fisheries-independent surveys of abundance. This led to the recognition that each fishery will be differentially affected by the various mechanisms, leading to density-dependent catchability (Dassow et al. 2021), and has highlighted the importance of understanding social dynamics in fisheries management (Nieman et al. 2021).

Significance: Collectively, these works have redirected thoughts on density-dependent catchability. Effort sorting was rarely recognized as a mechanism prior to van Poorten et al. 2016, yet is now considered regularly among academics, and is leading to a re-examination of how we interact with anglers (e.g., Nieman et al. 2021), and an understanding of how variation in angler skill and motivation can have serious consequences for fishery sustainability. Significance of this work is still preliminary; outcomes from this proposal will build on these outcomes to change perspectives and approaches by fisheries managers.

2. Social-ecological systems

Golden, A.S., B.T. van Poorten, O.P. Jensen. 2022. Focusing on what matters most: Evaluating multiple challenges to stability in recreational fisheries. Fish and Fisheries 23(6):1418-1438.

- I mentored the lead author in all aspects of this study

Solomon, C.T., C.J. Dassow, C. Iwicki, O.P. Jensen, S.E. Jones, G.G. Sass, A. Trudeau, B.T. van Poorten, D. Whittaker. 2020. Frontiers in modeling social-ecological dynamics of recreational fisheries: a review and synthesis. Fish and Fisheries 21(5):973-999.

- I contributed to concept, literature review, and writing

van Poorten, B.T., E.V. Camp. 2019. Addressing challenges common to modern recreational fisheries with a buffet-style landscape management approach. Reviews in Fisheries Science and Aquaculture 27(4):393-416.

- I led all aspects of this study

Carruthers, T.R., K. Dabrowska, W. Haider, E. Parkinson, D. Varkey, H. Ward, M.K. McAllister, T. Godin, B. van Poorten, P. Askey, K.L. Wilson, L. Hunt, A. Clarke, E. Newton, C. Walters, J.R. Post 2019. Landscape-scale social and ecological outcomes of dynamic angler and fish behaviours: processes, data, and patterns. Canadian Journal of Fisheries and Aquatic Sciences 76(6):970-988.

- I advised on model development and liaised between researchers and government end users

Contribution: Recreational fisheries are excellent examples of social-ecological systems (SES), where social and social, ecological and governance systems interact, leading to unexpected outcomes if one or more of these systems is ignored. Much of recreational fisheries management acts directly on the anglers, rather than the fish, yet behavioural decisions by anglers are often overlooked or underappreciated. My colleagues and I have used SES models to understand how these systems interact, ways they can be used to improve decision making and where uncertainties still lie. For example, Golden et al. (2022) used an empirically based model to demonstrate that many of the mechanisms that we assume lead to overfishing in recreational fisheries are actually relatively benign on their own but can quickly lead to reduced social or ecological outcomes when interacting with one another. Carruthers et al. (2019) developed the first applied SES model to provide policy advice based on expected angler redistribution across the landscape and their influence on fishery objectives. van Poorten and Camp 2019 built on this idea by demonstrating how regulation diversity is necessary to address and satisfy the diverse motivations and skills present in the angler community. Finally, Solomon et al. 2020 has conducted a literature review of all such recreational fisheries SES models to determine where we are, and which gaps are most critical to address.

Significance: Collectively, these works motivate much of the current proposal as well as crucially redirecting the field of study for academia. As a result of this work, we have now summarized an extensive literature, considered next steps, helped take a theoretical concept and apply it to real fisheries and re-imagine management with feedbacks between the social, ecological and governance systems in mind. The BC government uses the outcomes from Carruthers et al. 2019 and van Poorten and Camp 2019 as the basis for their decision to create four separate categories of stocked lakes (urban, family, trophy, and regional) to provide diverse fishing opportunities for diverse anglers. Further, the model developed in Carruthers et al. 2019 now forms the basis for some of their management plans.

3. Decision-theoretic approaches to management

van Poorten, B.T. 2020. Evaluating recovery tactics and the role of research for sockeye blocked from anadromy. Fisheries Research 230: 105666. DOI: 10.1016/j.fishres.2020.105666.

- I led all aspects of this study

van Poorten, B.T., M. Beck. 2021. Getting to a decision: using structured decision making to gain consensus on approaches to invasive species control. Management of Biological Invasions 12(1):25-48.

- I led all aspects of this study

van Poorten, B.T., C.J.A. MacKenzie. 2020. Balancing angler utility and conservation in a recreational fishery using decision analysis. North American Journal of Fisheries Management 40(1):29-47.

- I led all aspects of this study

van Poorten, B.T., S. Harris, A. Hebert. 2018. Sockeye recovery projections for a highly managed mixed kokanee-sockeye system. Canadian Journal of Fisheries and Aquatic Sciences 75(12): 2280-2290.

- I led all aspects of this study

Contribution: Decisions in natural resource management are complicated by multiple objectives and significant uncertainty in predicted outcomes of any management action. I have worked to demonstrate how decision analysis and structured decision-making can help clarify decisions and communicate why decisions are made. van Poorten and MacKenzie 2020 demonstrated how management advice in a very uncertain fishery can be generated in a step-by-step process to provide clear outcomes; van Poorten and Beck 2021 did the same for structured decision-making.

Significance: These papers are helping to improve decision making in recreational fisheries. Moreover, people are using these outcomes and studies as the basis for important decisions. The fishery examined in van Poorten and MacKenzie 2020 is being managed consistent with our recommendations. A non-native smallmouth bass population is being controlled using methods suggested in van Poorten and Beck; we are currently following up on this work to determine how to learn from this experience. Additionally, significant headway is being made on how to recover a controversial sockeye salmon population trapped in a reservoir after a decision analysis demonstrated the difficulty in recovering the population without intervention (van Poorten et al. 2018; van Poorten 2020).

Additional Information on Contributions

Impact summary

I am an early-career researcher and started my first tenure-track position in April 2020. Although I have not completed a postdoctoral fellowship, I focused on gaining research experience while working in government. My dedication to research and scholarship has led to the publication of 50 articles in high-impact journals (e.g., Proceedings of the National Academy of Sciences; Fish and Fisheries), and a high citation rate (914 citations to date; top 89% of ResearchGate members). This experience and scholarship increased my prominence within the research community. The significance of this is exemplified by my being asked to join an editorial team creating an interdisciplinary book (including fields such as fisheries, ecology, economics, social psychology) aimed at collecting and interpreting information on recreational fisheries.

Publication and authorship philosophy

Until recently, I have always been first or second author, reflecting my primary role in the development of ideas, data collection, analysis, and writing. However, as I have grown my network and experience, I have started taking on secondary roles, instead contributing effort to the development of younger scholars. This is particularly evident in several of the papers I have written as part of a National Science Foundation working group, where I served as the recreational fisheries expert on the team (e.g., Solomon et al. 2020, Ziegler et al. 2021, Trudeau et al. 2021, Nieman et al. 2021, Golden et al. 2022; all in CCV). As I now start to re-focus my efforts on my own research lab, I intend to take on a final author role reflecting my focus on project design but allowing and encouraging my HQP to take ownership of the work.

Service to the field

In the past 6 years, I have served as a reviewer for 19 journals, including Fish and Fisheries (Impact Factor 7.1), Ecological Applications (6.1), and Canadian Journal of Fisheries and Aquatic Sciences (3.1). I have hosted or co-hosted symposia at 1 national and 2 international conferences, and have held regional workshops, often aimed at improving decision-making regarding control options for invasive species.

Activity Details

Certification Requirements

Does the proposed research involve humans as research participants?	(●) Yes ( ) No
Does the proposed research involve animals?	(●) Yes ( ) No
Does the proposed research involve human pluripotent stem cells?	( ) Yes (●) No
Does the proposed research involve harzardous substances?	( ) Yes (●) No

Does the proposed research involve human totipotent stem cells? ○ Yes ◉ No

Impact Assessment

Will any phase of the proposed research take place outdoors? ◉ Yes ○ No

(A) Will any phase of the proposed research take place on federal lands in Canada, other than lands under the administration and control of the Commissioner of Yukon, the Northwest Territories or Nunavut, as interpreted in section 2 (1) of the *Impact Assessment Act* (IAA)? ○ Yes ◉ No

(B) Will any phase of the proposed research take place in a country other than Canada? ○ Yes ◉ No

(C) Will the grant permit a designated project (listed in the *Physical Activities Regulations*) to be carried out in whole or in part? ○ Yes ◉ No

(D) Will any phase of the proposed research depend on a designated project (listed in the *Physical Activities Regulations*) being led and carried out by an organization other than NSERC? ○ Yes ◉ No

Research Subject Codes

Please select at least one research subject code

1. EVOLUTION AND ECOLOGY Wildlife management
2.

Area of Application Codes

Please select at least one area of application codes

1. Wildlife management
2. Oceans and inland waters

Keywords

List up to 10 keywords that best describe the proposal.

Catchability, Hyperstability, Hyperdepletion, Nonproportionality, Fisheries dependent data, Fisheries collapse, Monitoring, Value of information

Eligibility Profile

Academic Appointment

I hold an academic appointment at an eligible Canadian postsecondary institution. (•) Yes ( ) No

I will hold an academic appointment at an eligible Canadian postsecondary institution. ( ) Yes (•) No

Expected Start Date:

Academic Position

Official Title of Position Assistant professor/Professeur adjoint

Postsecondary Institution Simon Fraser University

Department/Division Resource and Environmental Management

The position I currently hold or will hold is a tenured, tenure-track or lifetime professor emeritus at an eligible Canadian university. (•) Yes ( ) No

The position I currently hold or will hold is an indeterminate (i.e. with no end date) academic position with an eligible Canadian university, other than tenured, tenure-track or lifetime professor emeritus. ( ) Yes (•) No

The position I currently hold or will hold is a term or contract academic position of no less than three years at an eligible Canadian university. ( ) Yes (•) No

From:

To:

In addition to the academic position named above, I hold a remunerated position at an eligible Canadian institution. ( ) Yes (•) No

In addition to the academic position named above, I hold a position outside the university sector.	Yes No
I hold a position outside of Canada.	Yes No
I am enrolled in a graduate program in the natural sciences or engineering, or I hold a postdoctoral position.	Yes No

Overview and Objectives

Many ecological rates across all species are determined by population abundance and/or density. Conservation decisions are similarly dependent on indices of abundance to detect trends and conservation status. Actions emanating from this information may range from initiating habitat improvements, modifying harvest levels or triggering species assessments and federal protections. However, accurate measures of abundance are often unavailable and indices must be used under the assumption that capture probability is constant (or measurable) over time and space. For example, the sheer number of inland recreational fisheries within a management jurisdiction makes timely monitoring of even a small fraction of lakes and rivers nearly impossible [1]. Managers frequently rely on catch rates (number caught per unit of fishing effort) of recreational fishers (henceforth anglers) as the basis of management decisions, assuming catch rates are proportional to abundance [2]. This system breaks down if catch rates are not proportional to abundance, particularly if the constant of proportionality, or 'catchability' between catch rates and abundance is actually density dependent. If catch rates remain high as abundance declines, anglers primarily motivated by catching fish will continue fishing on low density populations, and managers will be unaware of population declines until densities reach critical levels. In their seminal paper, Post et al. [1] warned density-dependent catchability was a frequent and key risk to the invisible collapse of recreational fisheries and predicted several causal conditions that may exacerbate the problem. Yet 20 years on, those claims have yet to be tested.

The **long-term goal of my research program is to advance our understanding of the dynamic interactions between harvested populations and their human predators as a basis for knowledgeable management decisions and improved conservation**. Such understanding starts with accurate measures of the state of the harvested population. The importance of catch rate as an attribute contributing to site choice and eventual satisfaction by anglers [3], and as a signal leading to management scrutiny and intervention, means it is critical to understand conditions leading to density-dependent catchability and its causal mechanisms. Though individual studies searching for density-dependent catchability, or evaluating isolated mechanisms have occurred in the past, there has been no evaluation of the relative frequency of hyperstability across a wide range of recreational fisheries, nor has the relative importance and magnitude of different mechanisms contributing to this problem been explored. To address this gap, my research program will advance two short-term objectives: **Objective 1,** to determine the frequency of density-dependent catchability in North American recreational fisheries; and **Objective 2,** to experimentally evaluate different mechanisms of density-dependent catchability and their influence on conservation.

Literature Review and Recent Progress

Fisheries scientists focusing on commercial fisheries recognized the danger of relying on catch rate data early in the development of the discipline [4]. It was recognized that fish do not distribute randomly throughout a fished area, but form aggregations due to variation in food density and habitat quality, spawning and nest guarding, or various other behavioural processes. Likewise, commercial fishing boats can preferentially target high-density aggregations through communication within the fleet and improvements in fishing technology [5], which help to improve catch efficiency and therefore profit as abundance drops, improving short-term viability of the fishery [6]. Despite these early warnings, incomplete analysis and misinterpretation of catch rate data have still occasionally contributed to overfishing or even collapse of important fisheries, such as northern cod (*Gadus morhua*; [7]). As a result of these warnings and occasional high profile failures in commercial fisheries, many nations and international fisheries management organizations (e.g., International Council for the Exploration of the Seas; ICES) prioritize spatially stratified fisheries-independent surveys of abundance (sometimes several overlapping indices), which help account for changes in spatial distribution or aggregations among fish (though nonproportionality between survey catch rates and abundance can still occur: [8]). Similarly, geospatial catch data are also used in assessing fish populations for setting catch limits in future years.

Recreational fisheries are often managed using less informative data regarding fish abundance and removals than commercial fisheries, largely due to governance differences between these fisheries [9]. Many commercial fisheries have reporting requirements associated with fishing licenses, so catch and effort data are relatively accurate and complete. Small-scale fisheries, particularly inland fisheries that are not targeted by commercial fisheries, do not have reported catch and effort data due to open-access rights to all licensed fishers with no reporting requirements [9]. These fisheries are difficult to independently monitor because there are many hundreds to thousands of waterbodies in a management region, and there is rarely sufficient staff or budget to monitor even a small fraction of them [1]; consequently, knowledge of landings and other fishery-related data is poor [10]. These fisheries may be surveyed using standardized gear on a rolling basis (e.g., every 10 or more years), or in response to complaints of poor catch rates by fishers, particularly recreational anglers. Therefore, fisheries management must make decisions based on incomplete information, often relying on perceptions of anglers rather than independent time series.

Recreational fisheries differ from commercial fisheries in several important ways. First, as a leisure activity, anglers are motivated by a wide range of catch- (e.g., numbers, species, size, and harvest opportunities) and noncatch-related attributes (e.g., relaxation, time with friends/family, amenities, and distance; [3]). Motivations for fishing also vary across anglers and context [3], and as such, skill varies tremendously among anglers [11]. Hook-and-line gear commonly used by recreational anglers are passive in that fish must decide to attack fishing gear based on a number of biotic and abiotic factors [12]. These factors all contribute to an increased likelihood that catch rates will not vary proportionally with fish abundance.

There are multiple implications of a nonproportional relationship between catch rates and abundance. Catch rates may remain high as catch rates decline (i.e., hyperstability; red lines in Figure 1), or decline more rapidly than abundance (i.e., blue lines in Figure 1). Hyperstability masks declines in abundance if anglers and managers assume catch rates to be proportional to abundance because catch rates remain high until abundance has declined to extremely low levels. Hyperdepletion may lead to unnecessary management action as abundance rapidly declines or, if initial depletion is not monitored, may hide true habitat capacity. These density-dependent outcomes are based on three key mechanisms: (1) aggregation of fish and targeting by anglers; (2) variation in capture probability among fish; and (3) variation in angler skill.

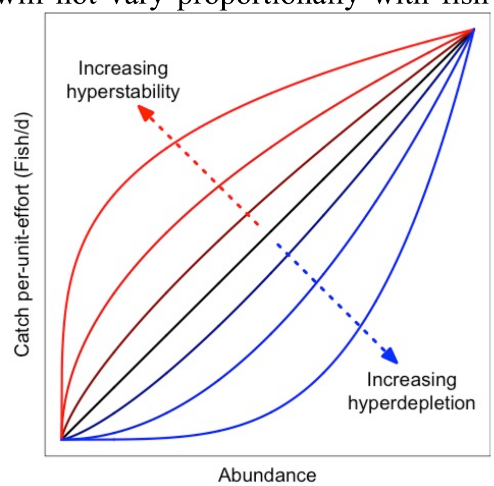

Figure 1: Relationship between abundance and catch rate measured in fish per day. Solid red lines indicate increasing levels of hyperstability; solid blue lines indicate increasing levels of hyperdepletion

Fish aggregate due to several motivations, including spawning, feeding, habitat associations and protection. The degree of aggregation differs across species, within a species, and over time. For example, some species form tight aggregations during courtship and spawning, only to disperse for the remainder of the year [13]. Fish also associate with different habitats throughout the year. Aggregations are known and targeted by anglers so that even as abundance declines, they are often not recognized by anglers because aggregation density stays constant [13–18]. Experiments show that as abundance declines, fish continued to use profitable habitat (as expected from IFD; [11]), resulting in hyperstable catch rates [19].

Fish also vary in their propensity to react to fishing gear, leading to a variation in capture probability [20]. The result is more catchable fish being removed from the population and catch rates declining faster than abundance: hyperdepletion [21]. This issue has been known as a violation of mark-recapture assumptions for many years, leading to persistent errors in abundance estimates [20]. Fish may also learn to avoid fishing gear, which affects their capture probability resulting in rapid depletion of catch rates correlated with total fishing effort [22]. Fish may also alternate between states of vulnerability and invulnerability depending on appetite, space-use, or injury, leading to rapid declines in catch rate [23].

Finally, hyperstable catch rates occur due to angler behavioural decisions. For example, interference competition between anglers, where unskilled anglers inadvertently exclude skilled anglers from good fishing spots, will reduce mean catch rates across all anglers. Further, if poorly skilled anglers leave fisheries with poor catch rates, catch rates will stay high if only skilled anglers remain [11]. This process is called effort sorting [11,24,25], which is a strong social mechanism leading to hyperstability. Hyperstability may also occur if anglers increasingly exaggerate catch rates as abundance declines [26].

All these mechanisms cause catch rate to be nonproportional with abundance: hyperstability and hyperdepletion. Hyperstability in particular has been demonstrated to collapse some recreational fisheries [15] and has been detected in others through observational studies [18,25,27,28] and induced in experimental studies [19]. Density-dependent catchability may not always be strong enough to lead to collapse on its own, but strongly interacts with other destabilizing impacts on fisheries [29]. Density-dependent catchability was identified as strongly influencing the probability of collapse [1], yet a recent meta-analysis highlights that the scale and impact of density-dependent catchability is still understudied [30]. Further, the recent interest in collecting and applying information from fishing smartphone apps [31] may exacerbate the problem [32]. Understanding mechanisms leading to density-dependent catchability will be important in addressing or reducing potential bias in catch rate data.

Recent progress: This research proposal builds on several studies aimed at understanding mechanisms and impact of density-dependent catchability. For example, Dassow et al. 2020 experimentally manipulated fish abundance to determine whether habitat association leads to hyperstability, while van Poorten et al. 2016 developed a novel model of effort sorting that will contribute to the analysis of data to be collected in my proposed research. Further, while van Poorten and Camp 2019 included hyperstability in a social-ecological systems model of recreational fisheries to determine the importance of this rate in fisheries resilience, Solomon et al. 2020 suggested these investigations need to be incorporated more broadly in our understanding of social-ecological systems, which directly motivates this study.

METHODOLOGY

<u>Objective 1:</u> Determine the frequency of density-dependent catchability in North American recreational fisheries (BSc1-2; MRM1; Years 1-2)

<u>Methods:</u> Several studies have examined specific recreational fisheries for evidence of density-dependent catchability (e.g., [24,25]), and a limited number have examined multiple fisheries within a particular jurisdiction (e.g., [27,28]). However, while a broad-scale evaluation of commercial fisheries has been conducted to raise awareness of the problem of nonproportionality [8], none has been conducted for recreational fisheries despite increasing reliance on catch rate data. Conducting a broad survey of fisheries across species, jurisdiction and regulations will provide a more fulsome overview of the problem. We will extend the research done to date through the following tasks:

1-Recreational fisheries database: We will build a database of recreational catch, fishing effort, and annual abundance across a broad suite of species and individual waterbodies (e.g., marine jurisdictions, lakes, rivers) from across North America. For each fishery, we will include metrics that may influence the degree of density-dependent catchability, such as species life history, fishing regulations and proximity to population centers. To build this dataset, we will start with the US Inland Creel and Angler Survey Catalog (CreelCat [33]) database, which includes information on catch, effort and associated information collected during angler interviews (creel surveys). We will also include information from the Marine Recreational Information Program (MRIP), which collects and store catch and effort data from marine recreational fisheries along the US coast. Many species targeted by commercial fisheries also have estimated time series of abundance, often found in the RAM Legacy Database [34], which will be incorporated within our database. Much of the recreational fisheries data included in CreelCat and MRIP are based on US fisheries; to supplement this dataset, we will also work with other researchers and staff at Canadian provincial, and federal agencies who have access to catch rate or abundance indices. We will build on Canadian data already compiled by another research group, who has agreed to work with us on this task (Sean Simmons, Anglers Atlas, *pers. comm.*). Our database will be securely stored on SFU servers.

2-Estimate density-dependent catchability: We will use the database developed in Task (1) to estimate the relationship between catch rate and abundance in each population using the power function [14]

(Equation 1) $CPUE = q_0\, N^{\beta}$,

where *CPUE* is catch per unit of fishing effort, q_0 is maximum catchability at low abundance and β describes the degree of nonlinearity between *CPUE* and abundance. Instances where $\beta = 1$ imply proportional declines of *CPUE* with *N*; when $\beta < 1$, hyperstability occurs; and when $\beta > 1$, hyperdepletion occurs. Past work has found that bias in β occurs depending on the relative error in *C*/*E* and *N* [2]. We will guard against this using Monte Carlo methods to improve our ability to correctly estimate β. Previous work on commercial fisheries [8] and subsets of recreational fisheries [18,27,28], suggest that some degree of density-dependent catchability should be evident in most fisheries examined.

3-Predict mitigating factors: We will explore how life history, fishing regulations, and proximity to population centers are correlated with the degree of density-dependent catchability (β) to test predictions posed in [1]. We will use a mixed effects model of the form

(Equation 2) $CPUE_{i,j} = q_0\, N^{X\beta_i + Zu_j + \varepsilon}$,

where β_i and u_j are respectively fixed and random effects, *X* and *Z* are vectors of estimated parameters and ε is process error. This model allows population to be a random effect while estimating fixed effect coefficients. This approach has been used to detect habitat- or species-level differences in hyperstability [27]; we will build on this approach to identify conditions that suggest a risk of density-dependent catchability for these and similar fisheries.

Potential impact: There has never been an evaluation of density-dependent catchability across recreational fisheries spanning multiple species, jurisdictions, and management regimes. This work will expose the relative probability and conditions in which density-dependent catchability is most likely in recreational fisheries. Results will expose the risks involved in under-monitored fisheries that are at least partially reliant on fisheries-dependent data, leading to policy change with respect to the use of fishery-dependent data. I expect one peer-reviewed paper for Objective 1.

<u>Objective 2:</u> Experimentally evaluate different mechanisms of density-dependent catchability and their influence on conservation (BSc3-7; MRM2-3, PhD1; Years 2-5)

<u>Methods:</u> Several studies have experimentally isolated individual mechanisms leading to density-dependent catchability in controlled fisheries to demonstrate their effects on catch rates (e.g., [19,22]). We will build on this work by experimentally evaluate multiple mechanisms in real fisheries to estimate their relative importance and interactions. We will build on past research through the following tasks.

1-Experimental fisheries: Conduct experiments over 3 years across many (8-10) fished lakes of stocked rainbow trout (*Oncorhynchus mykiss*) to evaluate recreational fishery dynamics. Selected lakes will have similar size, fishing regulations, and be relatively close together so they reasonably represent alternative fishing choices for anglers. We will seek consent from Indigenous nations in which these lakes reside, discussing our intentions, outcomes and seeking feedback on study design and perspectives. We have worked closely with multiple Indigenous groups and believe we can achieve consent in year-1 for experiments to start in year-2. Some lakes will have stocking reduced or ceased while others will remain constant to act as controls. All lakes will be open to public fishing. Monitoring will include:

- **a.** Creel surveys (angler interviews based on existing provincial standards to monitor catch, harvest, and fishing effort of trips; additional questions will be added to collect information on demography, fishing history and factors they use to decide fishing locations within a lake) of anglers fishing research lakes on each lake twice a week, stratified by time of day and day type (weekend/weekday). Anglers will be provided details of the study and asked to consent to interviews prior to being surveyed; anglers are assigned anonymized codes for identification by researchers. Past experience suggests ~200 interviews per lake per year. Surveys will include all anglers present, regardless of race, gender, or ability.
- **b.** Structured research angling on each lake every other week to evaluate seasonal shifts in vulnerability.
- **c.** Mark-recapture studies throughout the experiment to evaluate abundance, size selectivity and seasonal fishing mortality as well as to determine variation in capture probability among fish.

2-Evaluate aggregation and targeting: Spatially track fish and angler locations in two fished lakes per year (one with stocking decreased, one control) to determine spatial refugia by fish, transition rates between vulnerable and invulnerable states, and targeting by anglers. Fish will be tracked using acoustic transmitters and a 2D acoustic array in each lake; habitat suitability will be determined through GAM models relating fish location with habitat conditions, including vegetation, depth, slope, and substrate. angler fishing locations and capture locations will be manually monitored by researchers. Estimates of fish targeting will be identified using analysis of home range overlap [35] as well as comparisons of habitat suitability and angler interviews to understand their site choice for fishing. This work builds on work of [17]; insights will provide context to the contribution of targeting as a mechanism for density-dependent catchability compared to other mechanisms identified in Tasks 1 and 3.

3-Discrete choice experiments: Randomly distribute stated preference surveys to licensed anglers (database available through BC government) to evaluate their utility for various fishing attributes (e.g., catch rate, crowding) and fishing regulations (e.g., harvest tags, size limits). This discrete choice experiment will build on similar work in BC, while providing unique information on angler direct response to regulations. Outcomes will also inform Tasks 4 and 5.

4-Estimate effort sorting: Creel interviews in Task 1 will be used to characterize individual angler skill as in [36], and movement summaries across lakes will be correlated with angler skill. Effort sorting will be identified using methods in [24,25], as well as through simulation based on outcomes from Task 3.

5-Evaluate interactions among mechanisms: Information from Tasks 1-4 will be used to evaluate mechanisms contributing to density-dependent catchability across a fished landscape. The relative contribution of effort sorting, variation in individual catchability, fish aggregation, and angler targeting will be used to estimate overall density-dependent catchability. Estimating all mechanisms concurrently using custom Bayesian state-space models will allow for an evaluation of the relative contribution and trade-offs across mechanisms. Simulation models will be used to evaluate how different management regulations or monitoring actions may be used to account for some mechanisms using a decision-theoretic approach and how this may affect overall hyperstability in the fished system.

Potential Impact: This work will demonstrate how all mechanisms interact to facilitate or mediate one another. Through this work, fisheries scientists and managers will see how ecological and social dynamics interact to affect fisheries outcomes and how different regulation policies may help mitigate the problem. I anticipate at least 5 peer-reviewed papers from this objective.

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1. Salaries and benefits (Total $251,020; Average $50,204/year)
Graduate students: The graduate program in the School of Resource and Environmental Management does not have a minimum student salary; to account for the high cost of living, I promise a minimum of $18,000/year for MRM students, and $20,000/year for PhD students (including benefits). Our graduate program is very course-intensive; MRM students in the thesis stream must take at least 7 courses in their first year. Therefore, to balance research, course load, and completion time, I request that all students TA once per year, thereby increasing their annual salary by $3,700 at no cost to NSERC. Additionally, most incoming students earn a $7,000 Graduate Fellowship upon entering the program, which further offsets NSERC costs. Therefore, I request the following funds to support 3 MRM and 1 PhD students:

MRM students: Total of $87,000 = ($11,000 + $18,000) x 3 students

PhD student: Total of $73,000 = $13,000 + $20,000 x 4 years

Undergraduate students: Six (6) undergraduate research assistants will help advance the proposed research: two part-time students will assist in Objective 1 in year-1 at $1,000/mo; two per year for years 2 and 4, and one in year-3 will assist in Objective 2 at $3,500/mo for 4 months = $14,000.

BSc students: Total of $91,020 = ($1,000 x 2 BSc x 6 mo + $14,000 x 5 BSc) + 11% benefits

Table 1: Annual salary costs to achieve Objectives 1 and 2.

Position	2023-24	2024-25	Year 2025-26	2026-27	2027-28
BSc1	$6,660				
BSc2	$6,660				
BSc3		$15,540			
BSc4		$15,540			
BSc5			$15,540		
BSc6				$15,540	
BSc7				$15,540	
MRM1	$11,000	$18,000			
MRM2		$11,000	$18,000		
MRM3			$11,000	$18,000	
PhD1		$13,000	$20,000	$20,000	$20,000
Total	**$24,320**	**$73,080**	**$64,540**	**$69,080**	**$20,000**

2. Equipment (Total $31,000; Average $6,200/year)
Acoustic telemetry: Objective 2, Task 2 requires active tracking of fish in two lakes. We require 30 tags per year for 2 years in each of 2 lakes (120 tags). We will borrow receivers from collaborators in the BC government.

Telemetry equipment: Total of $24,000 = 120 tags @ $200

Motor: Objective 2, Task 1 requires working on lakes to monitor angler activity and location, use research anglers to fish known locations, and conduct mark-recapture and index netting. Therefore, we require a motor to move around lakes.

Motor: Total of $3,000

Field safety gear: Our fieldwork will occur in the Interior of British Columbia, which often has no cellular coverage; we therefor require satellite communication including 2 lone worker check-in devices

(SPOT; one for each crew), and a satellite phone. Additionally, unobtrusive personal floatation devices (PDF) will be required for work on water.

Field safety: Total of $4,000 = 2 SPOT @ $500 + 1 sat phone @ $2000 + 4 PDFs @ $250

3. Materials and supplies (Total $6,000; Average $1,200/year)
For materials and supplies, I budget $2,000/year for years in the field (years 3-5) for consumables such as batteries, first-aid anchors, oars, net replacement etc.

4. Travel (Total $81,500; Average $16,300)
Conferences: Each MRM will present once, and the PhD will present twice at a national or international meeting (5 total). For each conference, funds are requested for round trip from Vancouver ($750), conference registration ($400) and meals and lodging ($150/d for 5 days).

Conference travel: Total of $9,500 = 5 trips @ $1,900

Field work: Field work in the interior of British Columbia include vehicle rental and fuel costs ($2,000/mo), and accommodation ($4,000/mo).

Field travel: Total of $72,000 = ($2,000 + $4,000) x 4 months/yr x 3 years

5. Dissemination costs (Total $15,000; Average $3,000/year)
The proposed work is anticipated to lead to 6 peer-reviewed publications, one for each of the three MRM HQP, and three from the PhD HQP. The budget assumes approximately $2,500 in open-access publication fees per article.

Dissemination costs: Total of $15,000 = $2,500 x 6 peer-reviewed articles

<u>Total funds requested: $384,520; average $76,904 per year</u>

Received: 6 October 2021 | Revised: 13 July 2022 | Accepted: 16 July 2022

DOI: 10.1111/faf.12697

ORIGINAL ARTICLE

FISH and FISHERIES 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 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 & 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 low catch rates, they may inadvertently contribute to overfishing by maintaining or intensifying fishing pressure as stock sizes decline.

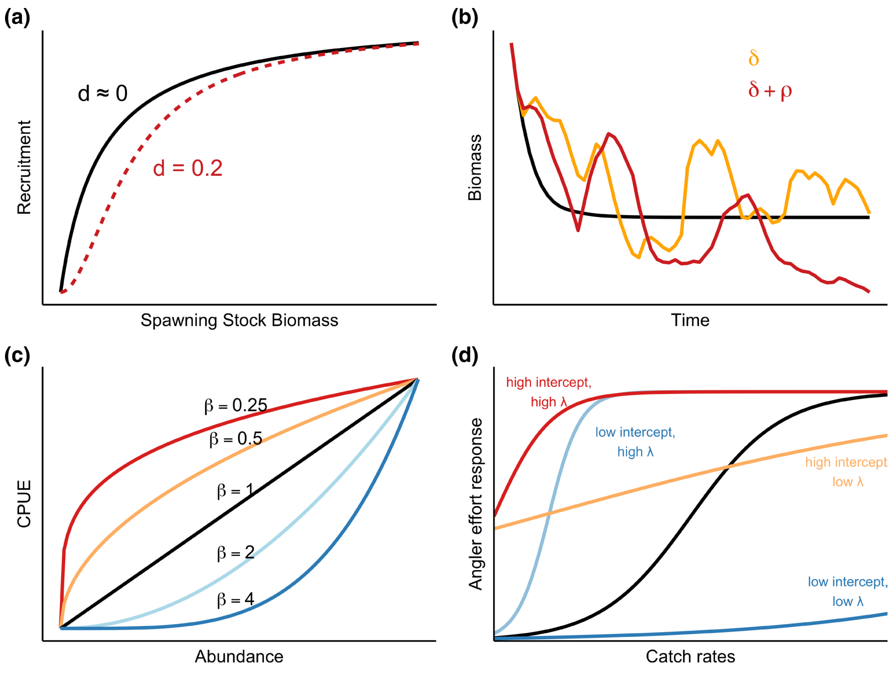

FIGURE 1 Conceptual figure illustrating four potential mechanisms of instability in recreational fisheries. Parameter values or combinations hypothesized to be moderately destabilizing are in orange; strongly destabilizing values are in red; and stabilizing ones are in blue. Black lines indicate the 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.

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)

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

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 $g \to \infty$, 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 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

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

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:

$$C = qEN^{\beta} \tag{4}$$

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 (*Micropterus salmoides*, Centrarchidae)	Wisconsin, USA	0.47	Hyperstable
Erisman et al. (2011)	Kelp bass (*Paralabrax clathratus*, Serranidae)	California, USA	0.46	Hyperstable
Giacomini et al. (2020)	Walleye (*Sander vitreus*, Percidae)	Ontario and Quebec, Canada	1.017	No evidence for non-linearity
Hansen et al. (2005)	Walleye (*Sander vitreus*, Percidae)	Wisconsin, USA	0.825 (angling) 0.659 (spearing)	Hyperstable
Mrnak et al. (2018)	Walleye (*Sander vitreus*, Percidae)	Wisconsin, USA	0.53 (angling) 0.41 (spearing)	Hyperstable
Pierce and Tomcko (2003)	Northern pike (*Esox lucius*, Esocidae)	Minnesota, USA	1.7	Hyperdeplete
Ward et al. (2013)	Rainbow trout (*Oncorhynchus mykiss*, 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:

$$U_{ij} = V_{ij} + \zeta_{ij}. \tag{5}$$

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:

$$V_{ij} = \boldsymbol{\eta} \mathbf{X}_{ij} \tag{6}$$

where $\mathbf{X}_{ij}$ is a vector of the observed attributes of alternative j for angler i and $\boldsymbol{\eta}$ 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

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

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 turns 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:

$$\lambda = \frac{\overline{C}}{C_{P_{im}=0.6} - C_{P_{im}=0.5}} \tag{8}$$

where $C_{P_{im}=0.6}$ indicates the value of CPUE that produce a 60% probability of generic angler i fishing at mean site m using Equation 7; $C_{P_{im}=0.5}$ is defined similarly for a 50% probability of fishing; and $\overline{C}$ 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 = −.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, *Morone saxatalis*, 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)	2.216	0.4214
					Coastal migratory species (1.9405)	0.125	0.4087
					Highly migratory species (1.7687)	0.071	0.4335
					Inshore species (1.5734)	0.036	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, *Oncorhynchus mykiss*, Salmonidae; brown trout, *Salmo trutta*, Salmonidae; brook trout, *Salvelinus fontinalis*, Salmonidae; tiger trout, *Salmo trutta x Salvelinus fontinalis*, 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)	0.003	0.0191
					Key sports fish (1.39)	0.089	0.0195
					Prize fish (1.28)	0.173	0.0186
					Reef fish (1.47)	0.017	0.0205
					Table fish (1.97)	0.038	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)	3304.693	0.1276
					Coastal migratory pelagic fish (2)	0.816	0.0624
					Mackerel, *Scomberomorus cavalla* and *S. maculatus*, Scombridae (1)	1.159	0.1351
					Snapper-grouper (1)	2.755	0.171
					Other fish (4)	0.030	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

[a]See citation for definition of these species groups.

[b]Excluded from analysis because parameter estimate was negative, suggesting the presence of unobserved covariates.

[c]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.

(Continues)

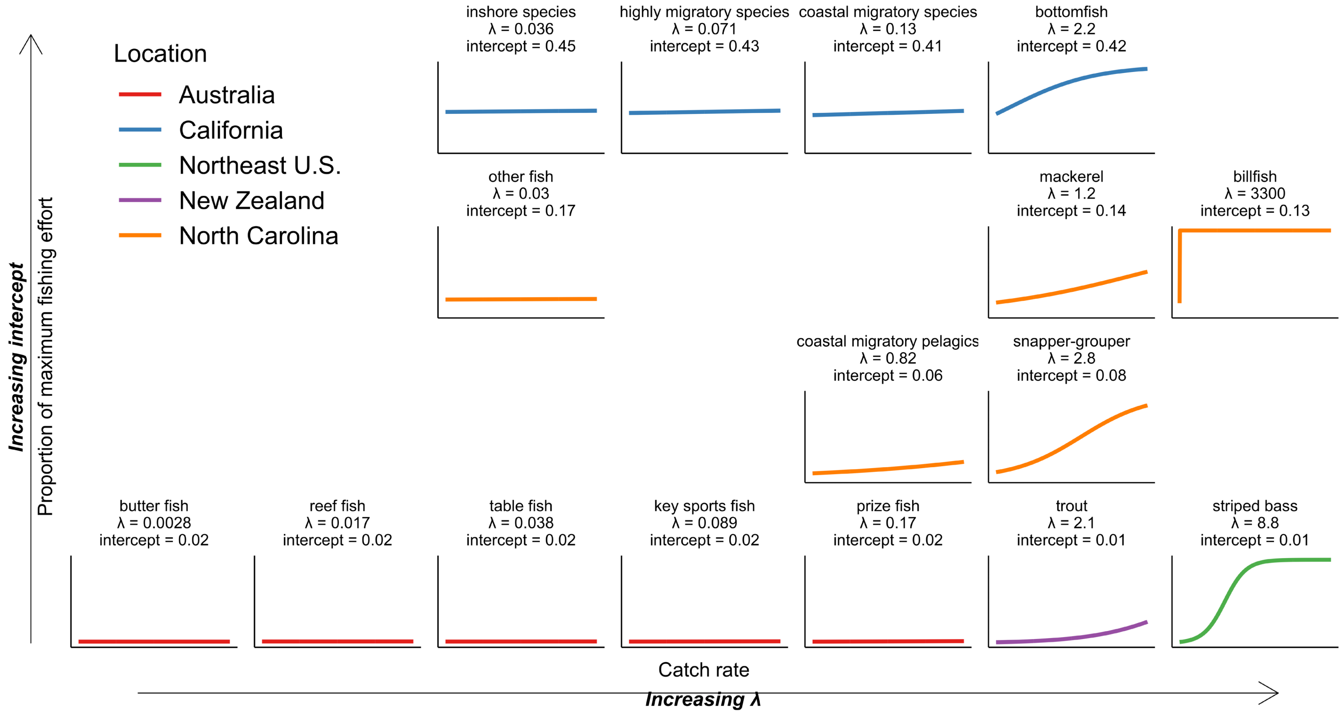

FIGURE 2 Empirically observed functional forms of the relationship between catch rate and anglers' fishing effort from five studies of angler utility. Study location is indicated with line colour and plots are arranged from low to high steepness of the angler effort response (λ; x-axis) and with increasing 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:

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

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):

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

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, $\overline{V}$. 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

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

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

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

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 $0.5 \times B_{MSY}$ 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, $E_{extinction}$ = 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, $E_{extinction}$ = 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

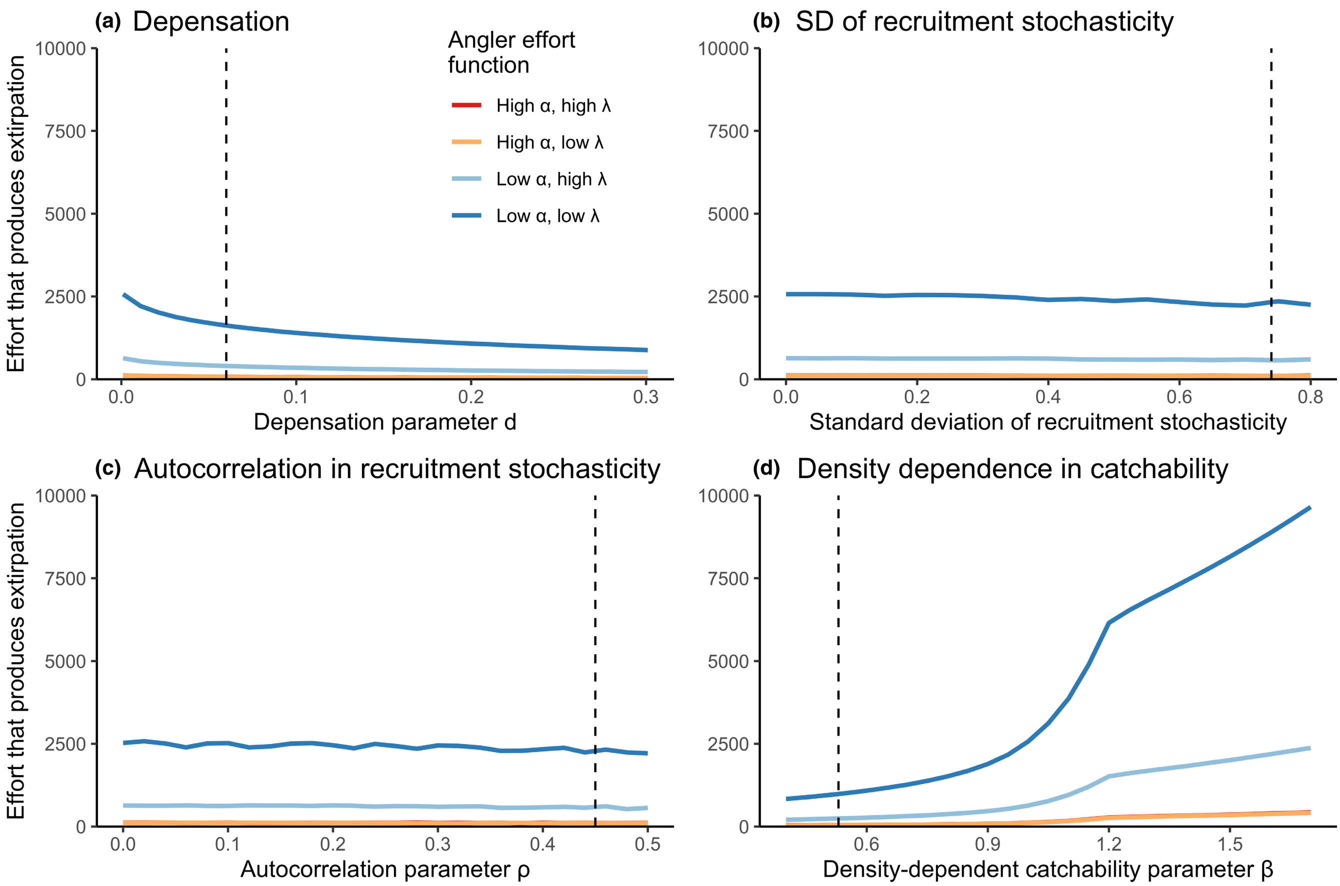

FIGURE 3 Amount of latent effort (E_{max}) required to extirpate the modelled population across the empirically observed range of values of depensation (a), normally distributed recruitment stochasticity (b), autocorrelated recruitment stochasticity (c) and density-dependence in catchability (d) across 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

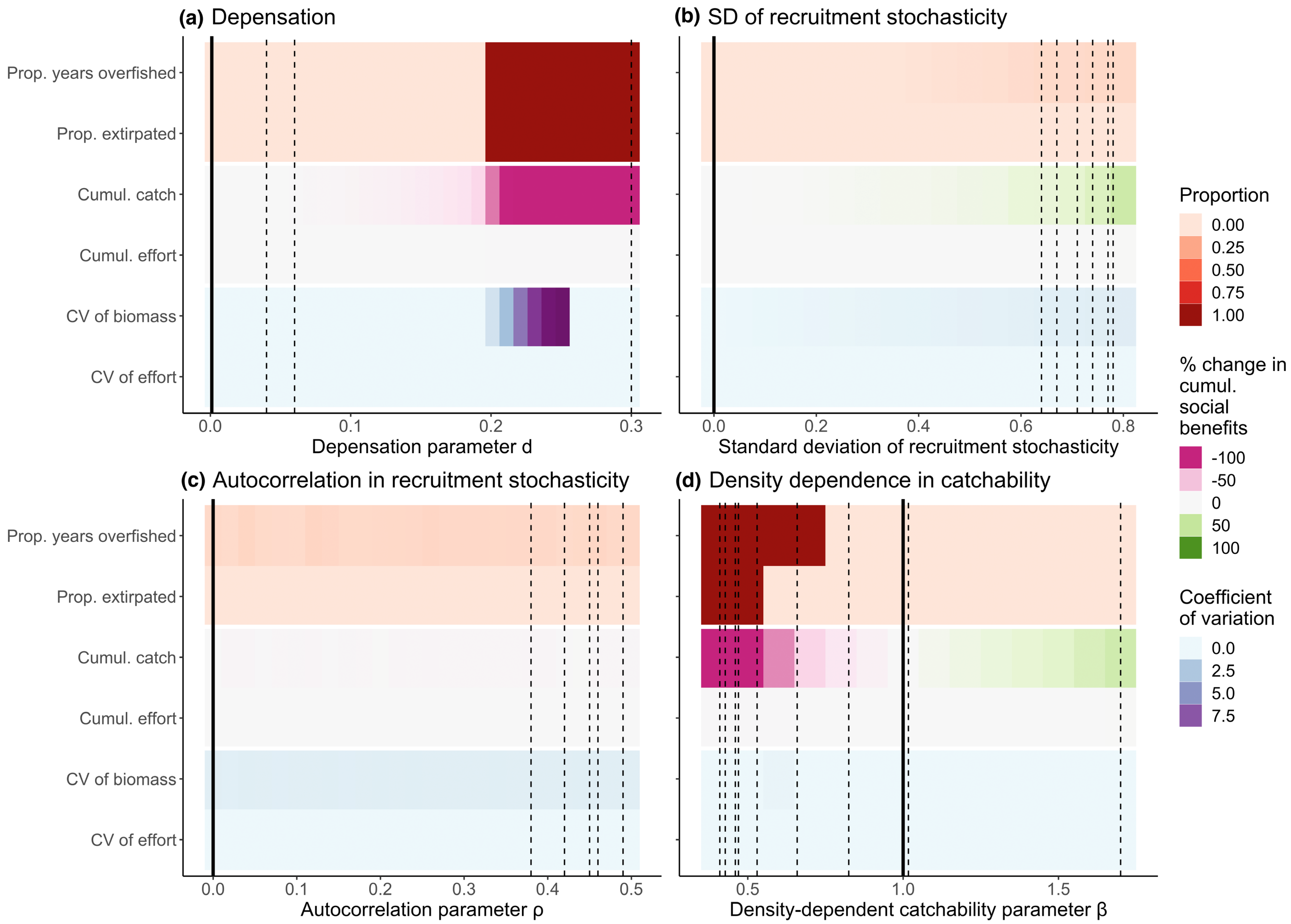

FIGURE 4 Heatmaps showing the effects of each of the three mechanisms of interest (depensation (a), normally distributed recruitment stochasticity (b), autocorrelated recruitment stochasticity (c) and density-dependence in catchability (d)) on three aspects of model behavior: Biological sustainability (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 ($E_{extinction}$) for each species-specific angler effort function in our analysis. The table is organized in increasing order of $E_{extinction}$

Citation	Species	$E_{extinction}$
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 (ρ = .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

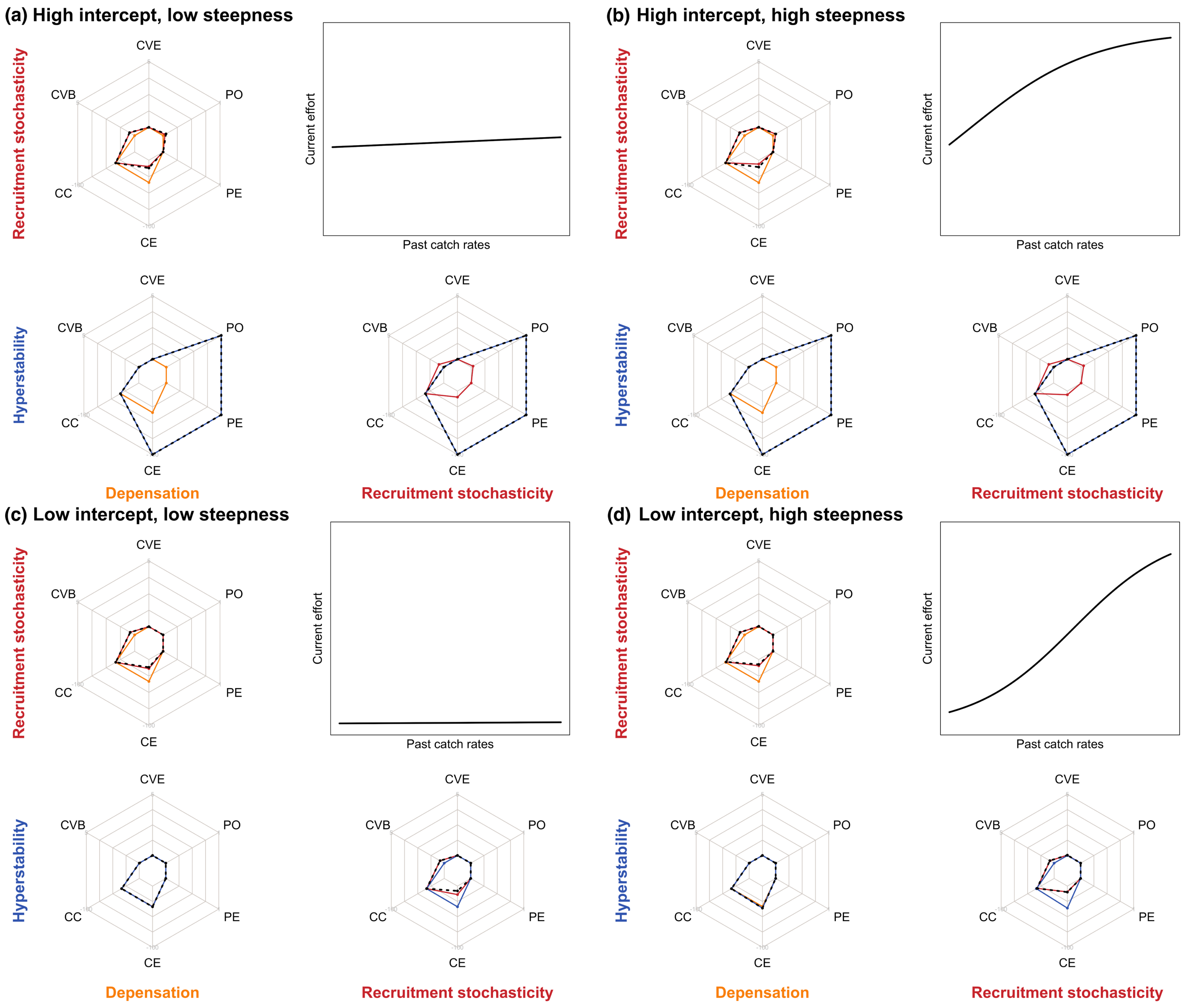

FIGURE 5 Radar plots indicating the effects of interactions between depensation (orange), recruitment stochasticity (red) and hyperstability (blue) on model behavior at their median observed levels. Six outcome variables are represented on each radar plot (CC, cumulative catch; CE, cumulative effort; 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 depensatory 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 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 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*, *23*, 1418–1438. https://doi.org/10.1111/faf.12697

North American Journal of Fisheries Management

ISSN: 0275-5947 print / 1548-8675 online
DOI: 10.1002/nafm.10377

FEATURED PAPER

Using Decision Analysis to Balance Angler Utility and Conservation in a Recreational Fishery

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Abstract
Recreational fisheries are often managed to provide satisfying fishing experiences for anglers while conserving wild fish stocks. However, managing recreational fisheries is difficult because fish populations are often infrequently monitored and fishing effort is uncontrolled; moreover, a satisfying fishery may draw many anglers, which may lead to enhanced risk of overfishing. Furthermore, external pressures will also affect fisheries, leading to fishery collapses despite the best intentions of management. Any management decision about regulations and habitat alteration will have effects on angler satisfaction and conservation. Decisions should be made with the intention of achieving fisheries objectives despite the uncertainties that arise from sampling data, ecosystem processes, and external factors, yet they must be defensible to stakeholders and the public. We show herein how decision analysis can be used to evaluate and communicate the relative efficacy of management decisions that are made to achieve fisheries management objectives by using a variety of commonly collected field data. We used a wild kokanee population at risk of overfishing as a case study and evaluated the medium-term effects of fishing regulations and habitat alterations on conservation and angler utility objectives. Using a flexible age-structured model, we determined that these two objectives are often at odds, where management actions leading to high angler utility in this fishery also lead to high conservation risk. Overall, decision analysis helps to communicate these tradeoffs and makes it clear how particular decisions were made. Decision analysis is not new, but it is often underused in recreational fisheries. This work demonstrates how it may streamline decisions, even for infrequently monitored fisheries, and lead to better fisheries overall.

Recreational fisheries on wild fish populations are typically managed with the paired goals of satisfying anglers and ensuring that fish populations are healthy (Powers and Lackey 1976; Radomski et al. 2001; Pereira and Hanson 2003; Cowx et al. 2010). While it is convenient to believe that recreational fisheries are self-regulating (in that anglers leave if catch rates get too low, thereby conserving the stock), this will not be true if anglers are not primarily motivated by catch rates (Post et al. 2002). Research has demonstrated that anglers are actually motivated by several fishery attributes that contribute to their satisfaction (e.g., catch rates, fish size, social interactions), and the importance of each of these attributes varies among anglers (Bryan 1977; Beardmore et al. 2014) and fisheries (Beardmore et al. 2011). This diversity of motivations means that recreational fisheries are not self-regulating; effort may stay high even as abundance declines (Post et al. 2002; van Poorten et al. 2016). Moreover, not all of the attributes that contribute to angler utility and satisfaction are under the control of fishery managers.

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Received January 10, 2019; accepted October 7, 2019

Managing a fishery such that it provides a satisfying fishing experience while conserving the stock requires an integrated understanding of angler expectations so that it is viable to predict angler response to management changes.

The suite of management tools that is available to freshwater fisheries management is relatively broad (Nielsen 1999). They can include manipulating angler efficiency through regulations or manipulating ecosystems through stocking, habitat alteration, nutrient enhancement, and predator control. The responses to these actions of a fish population may be counterintuitive due to density-dependent changes in growth and survival and subsequent changes in size structure. For example, increasing minimum harvest size limits may increase the abundance of spawning individuals and boost total egg production and recruitment (Allen et al. 2013). Alternatively, increasing juvenile survival through habitat improvements may lead to an increase in total biomass but an undesirable shift in size structure to smaller individuals and increased "stunting" (Rinne 1982). Anglers similarly exhibit complex responses to such management changes in the fishery either through direct behavior responses to regulation changes (Aas et al. 2000; Beard et al. 2003) or indirect responses due to changes in catch rates and sizes (Johnson and Carpenter 1994; van Poorten and Post 2005). Uncertainty in the type and magnitude of system response can only truly be considered by using quantitative models.

While there is considerable uncertainty in how a fishery will respond to management actions, external stressors affect the system as well. For example, human population growth continues to exert pressure on natural systems through urbanization (Wang et al. 2001; Seilheimer et al. 2007), changes in land use (Evans et al. 1996), and even increases in fishing capacity (Post et al. 2002). Changes to nutrient loading may occur indirectly due to changes in upstream flow regimes (Prowse et al. 2006) or directly due to agricultural and urban runoff (Blann et al. 2009). How these inputs affect the natural system dynamics on any single waterbody over time is subject to considerable uncertainty and needs to be assessed with a systematic approach to management.

In the face of obvious process and observation error and even changes in underlying productivity, it is easy for a decision maker to become overwhelmed and just rely on past experience and expert judgment (Powers et al. 1975; Powers and Lackey 1976). However, it is important for decision makers to understand and embrace the limited ways that managers can control the system and make decisions that are robust to this uncertainty (Jones and Bence 2009). Decision analysis provides a structured approach to providing management advice (Walters 1986; Peterman and Anderson 1999) by simply evaluating which management actions are robust to uncertainty while providing the best possible outcomes (Robb and Peterman 1998; Harwood 2000; Jones and Bence 2009). Defining the "best possible outcomes" depends on identifying measurable objectives, a key prerequisite to any decision and a necessary part of decision analysis. Decision analysis has been used in a variety of environmental and natural resource contexts, including recreational (Peterson and Evans 2003; Varkey et al. 2016) and commercial fisheries (Punt and Hilborn 1997; Robb and Peterman 1998), forestry (Cohan et al. 1984; Crome et al. 1996), conservation (Harwood 2000; Dreschler and Burgman 2004), and the response of invasive species (Maguire 2004). Decision analysis allows trade-offs between the objectives (e.g., biological and social objectives) that are to be visualized and understood; the end result is a decision that is clear, understandable, and defensible.

We present a framework for deciding which changes to the management or habitat in a recreational fishery are most appropriate by demonstrating the tradeoffs between conservation and use objectives. We develop a model that predicts changes in the size structure and abundance of a fished population by including density-dependent growth and survival. While many population models are concerned with maximizing catch-based outcomes, we take a more nuanced approach and examine how angler utility and resulting fishing effort will change as a result of changes to the population. Finally, the model feeds into a decision analysis, thereby providing managers and decision makers with the tools that are necessary to evaluate the tradeoffs.

METHODS

Study site.— Kawkawa Lake is a 72-ha coastal montane lake that is approximately 150 km from Vancouver, British Columbia (BC). The lake is used by anglers that are fishing for wild kokanee *Oncorhynchus nerka*, Coho Salmon *O. kisutch*, Rainbow Trout *O. mykiss*, and Cutthroat Trout *O. clarkii* as well as by nonangling boaters. Kokanee are the most commonly targeted species of the fishery, primarily because they grow to uncharacteristically large sizes (asymptotic length >400 mm) and because they are abundant. Fishing regulations limit kokanee harvest to four per angler per day with no size restrictions. The large body size of kokanee in this population, which is attractive to anglers, combined with the relatively close proximity to a large metropolitan area (metropolitan Vancouver) may cause stress on the fish population due to high fishing pressure and harvest.

Kawkawa Lake is surrounded on two sides by steep, unstable terrain; the other two sides have residential and recreational development. The kokanee population spawns in four spring-fed streams that flow through the residential community and enter the lake along the eastern end of it. Habitat in all of the streams is affected to varying degrees by residential development including channel realignment, streambed disturbance, sediment inputs, and invasive plant species. All of the buildings in the area were connected to the district sewer system in the 1970s (Kevin Dicken, Director of Operations, District of Hope), but there is concern that now unused septic tanks and/or lawn fertilizer are contributing to nutrient eutrophication in the lake (Michael Willcox, BC Ministry of Forests, Lands, Natural Resource Operations and Rural Development, personal communication).

Data collection and analysis.— The kokanee population and fishery in Kawkawa Lake were monitored in 2016. A fixed-point completed trip creel survey was performed three to four times per week from May to October. The surveys were stratified by time of day (0800 to 1400 hours; 1400 to 2000 hours) and day of the week (i.e., weekday, weekend, or holidays). Angling parties leaving via the single public boat launch were asked how many were in their fishing party, the number of kokanee that were released and retained, and how long they had been fishing. The fork length of the harvested fish was recorded and scales were removed for later age assignment.

Interviews were also used as an opportunity to gain insight into the catch-related fishing utilities that were perceived by anglers. Each angler that was interviewed in the creel survey was asked two sets of questions to bound their level of interest in catch rates and fish size in a trip. Specifically, each angler was asked open-ended questions regarding his or her ideal number of landed kokanee per day of fishing (i.e., that which would maximize their satisfaction) and what catch rate would cause them to be disinterested in fishing on the lake again (i.e., that which would minimize their satisfaction). Similarly, the anglers were asked what size of kokanee would be ideal and what size would make them want to stop fishing the lake. The answers to these questions were used to parameterize the utility functions that were related to angler satisfaction.

Angler utility for both daily harvest and mean size was described by using a logistic function. We assigned a utility of 0.05 to the daily harvest rates and mean sizes that the anglers stated would result in their leaving the fishery unsatisfied. Likewise, the harvest rates and sizes that the anglers stated would result in high satisfaction were assigned a utility of 0.95. We estimated the posterior distribution for the harvest rate at 50% utility ($H_{50[N]}$) and logit transformed the standard deviation in utility for harvest rate ($\sigma_{[N]}$) by fitting the resultant logistic model to all of the coded angler responses regarding harvest rates that were obtained in the creel survey (Table 1). The posterior estimates for harvested fish length mean ($H_{50[L]}$) and standard deviation ($\sigma_{[L]}$) were similarly obtained by fitting the resultant logistic model to the coded angler responses regarding fish size that were obtained in the creel survey (Table 1). The posterior distributions were numerically approximated in JAGS 3.4.0 (Plummer 2003) by using a Markov chain–Monte Carlo simulation. The posterior distributions were calculated from 10,000 iterations after an initial burn-in of 5,000,000 iterations and further thinned to provide a final sample of 10,000 iterations from each of three Markov simulation chains. The simulated parameters were used to define the effort response function and the stated preference utility function that was later used as a fishery objective (see the *Decision analysis* section).

Fishing effort was estimated by using a combination of traffic counters that were installed along the single access road to the boat ramp and independent visual observations of anglers and boat traffic. Two traffic counters were installed in April 2016 and remained in place through the following January. Visual counts of traffic were conducted during the creel survey days at the ramp to count traffic with and without boats and to count boats on the lake that were fishing and those that were not fishing. Methods for estimating fishing effort and the resulting posterior estimate for annual fishing effort are described in van Poorten and Brydle (2018). Briefly, this method estimated daily angler arrivals and departures by fitting to traffic counter data, boat and nonboat traffic observations, and fishing and nonfishing boat counts on the lake that were taken during the creel surveys. The daily angler estimates were summed over the season to provide an estimate of seasonal fishing effort. The posterior estimate for fishing effort (in angler-days per year; AD/year) was multiplied by the mean observed harvest per unit effort from the creel survey to provide an estimate of total annual harvest.

The growth parameters for kokanee were estimated by fitting a two-parameter von Bertalanffy growth model (i.e., L_∞ and K) to the length-at-age data that were collected from the harvested fish that were sampled during the creel survey (Table 1). It was not possible to estimate both parameters without prior information due to the limited age range of the fish in the fishery (mean = 2.9 years, SD = 0.4). Therefore, the model was estimated by using a normally distributed prior probability distribution on the metabolic parameter, K, based on the estimate for kokanee from a nearby lake (van Poorten et al. 2018a), which helped reduce the correlation among the two growth parameters. The posterior distributions for the von Bertalanffy parameters were approximated as above.

A hydroacoustic survey of kokanee in the lake was performed on July 21, 2016, by using a 120-kHz split-beam sounder, set at 2–5 pings/s and towed at ~2 m/s at a depth of 1 m. The echograms for each transect were analyzed at 10-m equal depth layers. Depth-stratified pelagic gill nets were used the following evening to characterize the species and size composition of the fish by depth stratum. Based on this supplemental information, only targets that were sampled from depths between 5 and 15 m were used and

TABLE 1. Bayesian models that were used to estimate the key population parameters from the field data. The prior probability distributions and likelihood functions that were used to calculate the posterior estimates for each parameter of interest are shown.

Variables and models	Prior probability distribution	Likelihood
Angler utility		
$U_{(N\|HPUE)} = \frac{1}{1+\exp\left[\frac{-\left(HPUE-H_{50(H)}\right)}{\sigma_{(H)}}\right]}$	$H_{50(H)} \sim N$ (0, 1,000) $\sigma_{(H)} \sim N$ (0, 1,000) $\tau_u \sim G$ (0.01, 0.01)	$0.05 \sim N\left(U_{low}, \tau_u^{-0.5}\right)$
$U_{(L\|\bar{L})} = \frac{1}{1+\exp\left[\frac{-\left(\bar{L}-H_{50(L)}\right)}{\sigma_{(L)}}\right]}$	$H_{50(L)} \sim N$ (0, 1,000) $\sigma_{(L)} \sim N$ (0, 1,000) $\tau_u \sim G$ (0.01, 0.01)	$0.95 \sim N\left(U_{high}, \tau_u^{-0.5}\right)$
Kokanee growth function		
$\hat{L}_{age=a} = \dot{L}_\infty(1-e^{-Ka})$	$\dot{L}_\infty \sim N$ (500, 1,000) $K \sim N$ (0.51, 0.017) $\tau_L \sim G$ (0.01, 0.01)	$L_a \sim N(\hat{L}_a, \tau_L^{-0.5})$
Spawner abundance		
$A_{t,stream=i} = Esc_i \int_{j=0}^{t} \left[\frac{1}{\sigma\sqrt{2\pi}} e^{\frac{\tau_a(j-m_i)^2}{2}}\right]$	$Esc_{stream=i} \sim N(0, 1{,}000)$	$S_{t,i} \sim N(\nu\hat{S}_{t,i}, \tau_S^{-0.5})$
$D_{t,stream=i} = Esc_i \int_{j=0}^{t-s} \left[\frac{1}{\sigma\sqrt{2\pi}} e^{\frac{\tau_a(j-m_i)^2}{2}}\right]$	$m_{stream=i} \sim N(280, 20)$	
$\hat{S}_{t,stream=i} = A_{t,i} - D_{t,i}$	$\nu \sim B$ (1, 1) $\tau_a \sim G$ (0.01, 0.01) $\tau_s \sim G$ (0.01, 0.01)	

of these 51% were kokanee. Age 0 kokanee could reliably be distinguished from older age-classes based on target strength, although there was uncertainty about the proportion of small targets that were small kokanee versus invertebrates and air bubbles (D. Johner, BC Ministry of Forests, Lands, Natural Resource Operations, and Rural Development, personal communication). We represented this uncertainty by multiplying the estimated number of small targets (p_{juv}) by a beta-distributed random variable with shape parameters 50 and 5, providing a mean value of 0.91 ± 0.03. This choice of the prior distribution and shape parameters that were used reflects the professional opinion of the hydroacoustic technicians who performed the survey.

Each inlet stream was surveyed weekly from early October to mid-November 2016 to index spawning kokanee. Live spawners were counted in an upstream orientation from the confluence with the lake until the first contiguous 50 m, where no spawners were seen. Spawning kokanee were found in four of the five inlet streams; one of these only had a low number of spawners present on two occasions (21 total), so it was dropped from further analysis. The remaining three streams were used to estimate total spawner abundance by using the statistical escapement model from Hilborn et al. (1999; Table 1). Arrival timing was assumed to be normally distributed; survey life (the length of time that kokanee remained in the stream) was set to 10.2 based on observations in Andrusak et al. (2004). The posterior distributions were approximated as above.

Stable isotope ratios that were measured in particulate organic matter were used to determine whether nutrient enrichment was occurring in the lake. Three replicate water samples were taken on August 1, 2016, at various locations: mid-lake (at 2-, 7-, and 14-m depths), at the outlet, and at the two largest inlet streams (Kopp and Menz). The water samples were filtered in the field and stored in a refrigerated, opaque container until analysis, For the nutrient analysis, $\delta^{15}N$ was measured at the University of British Columbia by using an elemental analyzer that was coupled to a gas chromatograph and reported with respect to air.

Operating model.— The effects of different management actions on both angling utility and population conservation were evaluated by using a density-dependent, age-structured simulation model (Table 2). The model includes parameter estimates that were derived from the survey data in Kawkawa Lake (T2.1) and estimates based on values that have been reported in the literature and the expert judgment of the authors (T2.2). All of the indices, parameters, and variables are described in detail in Table 3. The model was initialized assuming that the fishery is currently at equilibrium; therefore, equilibrium recruitment

($R_{[F]0}$) was set to the estimated age 0 abundance from the hydroacoustic survey (i.e., the number of small hydroacoustic targets multiplied by p_{juv}). Equations T2.3–T2.10 sequentially define the current fished state of the kokanee population in Kawkawa Lake. The von Bertalanffy growth function was used to estimate length at age (T2.3), which in turn was used to predict fecundity at age 3 (T2.4). Capture selectivity was assumed to be a logistic function of length (T2.5). Initial vulnerable abundance at the middle of the fishing season was approximated by estimating the remaining spawner abundance after accounting for half a season of natural mortality and adding back half of the estimated harvest (T2.6) for the same time interval. Estimating abundance at the middle of the fishing season is necessary to estimate the season-wide fishing mortality rate from the total harvest rate more accurately. The initial fishing mortality rate was calculated to include release mortality (T2.7). Unfished survivorship was assumed to be constant over ages (T2.8), and fished survivorship included a parameter that incorporates fishing mortality (T2.9). Initial abundance by age-class (T2.10) was calculated by using estimates of equilibrium fished recruitment and fished survivorship multiplied by a log-normal recruitment deviate (e^{Ω_a}), where Ω_a is normally distributed with a standard deviation of 0.4.

Model initialization was necessary to calculate several of the derived variables. The unfished and fished incidence functions (T2.11 and T2.12, respectively; Walters and Martell 2004) were used to predict unfished recruitment (T2.13) as well as the equilibrium Beverton–Holt recruitment parameters (T2.14 and T2.15). Equations T2.16 through T2.18 calculate the parameters of a food-dependent recruitment function, assuming that the proportion of recruit survival is influenced by variation in food density (z_t), based on van Poorten et al. (2018b). Food density was set relative to that measured in 2016 (i.e., $z_{2016} = 1.0$). Catchability was calculated by dividing the predicted fishing mortality rate by the observed fishing effort (T2.19). Finally, the density-dependence parameter of the annual asymptotic length function was calculated by solving T2.22 for $\beta_{L\infty}$ at initial conditions based on surface area (SA) = 72 ha (T2.20).

With initial population parameters, the operating model was used to make projections of age-structured population dynamics, harvest dynamics, and angler utility over the next 20 years, considering uncertainty in the fitted population parameters and process error. The model evaluated how changes in fishery management controls affect both the population and the fishery. Possible management controls included daily bag limits (BL), minimum length limits (MLL), and changes to the available spawning habitat (HAB) through spawning habitat improvements or exclusions to available spawning habitat. Additionally, the model evaluated how progressive changes in fishing effort capacity (through regional demographic growth) and lake productivity (through changes in land use) affect the system.

Predicting abundance at age proceeded in a similar manner to estimating the initial values; however, proposed controls were included to simulate changes to bag limits on numbers harvested, minimum length limits for harvest, and changes to available spawning habitat. Length at age was predicted from von Bertalanffy growth parameters, where K is assumed to remain constant and $L_{\infty,t}$ varies positively with available food density (T2.23); the parameters for the density-dependent function for predicting asymptotic length (T2.22) were generated assuming that the maximum asymptotic length at current food rates would extend to 1,000 mm. Selectivity to retention based on the minimum length limit was modeled as a logistic approximation to the cumulative normal distribution, thereby accounting for variability in length at age within an age-class (T2.24). Landed catch for each year and age-class were predicted by using the standard catch equation (T2.25). The proportion of angler days resulting in catch in excess of the bag limit was predicted assuming that the daily catch rate is Poisson distributed (T2.26), which was then used to calculate the proportion of captured fish that are legal for harvest. The rates for harvested fish for each year and age-class were predicted by modifying the catch equation by the proportion of fish harvested and assuming that length-based selection to harvest is a function of both the selection to the fishery and the minimum length limit (T2.27). The mean annual length of harvested fish was simply calculated as length-at-age weighted by the relative distribution of captured ages (T2.28). Total fishing mortality on the kokanee population is a function of both harvest and release mortality (T2.29). Abundance in the following year was modeled separately for recruits (age 0) and older fish (ages 1 to 3) that are subjected to fishing mortality. The Beverton–Holt recruitment function (T2.30) positively varies both maximum survival rate at low abundance and asymptotic recruitment based on the simplified prey-dependent recruitment function proposed in van Poorten et al. (2018b). Effective density (the total consumptive pressure on the shared food resource; Walters and Post 1993; Post et al. 1999), which was used in the density-dependent growth function (T2.22), was calculated as the squared sum of lengths of individuals per area (T2.31). Finally, angling utility was a weighted average of the utility that anglers have for both daily harvest and harvested lengths (T2.32). Both utilities were weighted equally, assuming that size and catch rates are of equal importance to anglers. Fishing effort the following year was expressed simply as the utility multiplied by the maximum possible fishing effort ($E_{max,t}$; T2.33). Note that the utility function that was used in this application (T2.32) recognizes that although these two metrics are not necessarily independent, the questions that were

TABLE 2. Fishery operating model for generating age-structured population dynamics, harvest dynamics, and angler utility for the kokanee fishery in Kawkawa Lake.

Equation number	Equation	Conditions
Parameters		
T2.1	$\Theta = \{\dot{L}_\infty, K, H_{2016}, Sp_{2016}, p_{(r)1}, R_{(F)0}, H_{50}, \sigma H, HL_{50}, \sigma L\}$	
T2.2	$\varphi = \{\alpha_f, \beta_f, \alpha_s, \beta_s, M_{(r)}, M, E_{2016}, \kappa, p_c, \alpha_{L_\infty}, \mathrm{cv}_1\}$	
Initial population		
T2.3	$L_{2016,a} = \dot{L}_\infty(1 - e^{-K \cdot a})$	
T2.4	$f_t = \alpha_f L_{2016,a=A}^{\beta_f}$	
T2.5	$sc_{t,a} = \left[1 + \exp\left(-\frac{L_{t,a} - \beta_s}{\alpha_s}\right)\right]^{-1}$	
T2.6	$V_{(F)} = Sp_{2016} e^{0.5M} + 0.5 \cdot H_{2016}$	
T2.7	$F_{2016} = \log_n\left(1 - \frac{H_{2016}}{V_{(F)}}\right)\left[p_{(r)1} + \left(1 - p_{(r)1}\right) M_{(r)}\right]$	
T2.8	$lx_{(U)a} = \begin{cases} 1 \\ lx_{(U)a-1} e^{-M} \end{cases}$	$a = 0.25$ $0.25 < a \leq A$
T2.9	$lx_{(F)a} = \begin{cases} 1 \\ lx_{(F)a-1} e^{-M - s_{1,a-1} F_{2016}} \end{cases}$	$a = 0.25$ $0.25 < a \leq A$
T2.10	$N_{1,a} = R_{(F)0} lx_{(F)a} e^{\Omega_a}$	
Derived parameters		
T2.11	$\phi_{(U)0} = \sum_{a=0}^{A} lx_{(U)a} f_{t=1}$	
T2.12	$\phi_{(F)0} = \sum_{a=0}^{A} lx_{(F)a} f_{t=1}$	
T2.13	$R_{(U)0} = R_{(F)0} \frac{\phi_{(F)0}}{\phi_{(U)0}} \frac{(\kappa - 1)}{\left[\kappa \frac{\phi_{(F)0}}{\phi_{(U)0}} - 1\right]}$	
T2.14	$\alpha_R = \frac{\kappa}{\phi_{(U)0}}$	
T2.15	$\beta_R = \frac{(\kappa - 1)}{R_{(U)0} \phi_{(U)0}}$	
T2.16	$c_{(1)R} = -\log_e(\alpha_R)(1 - p_c)$	
T2.17	$c_{(2)R} = -\log_e(\alpha_R) p_c z_{t=1}$	
T2.18	$c_{(3)R} = \beta_R z_{t=1}$	
T2.19	$q = \frac{F_{2016}}{E_{2016}}$	
T2.20	$\beta_{L_\infty} = \left(\frac{\alpha_{L_\infty}}{L_{\infty,t=1}} - 1\right) \frac{SA}{\sum\left(R_{(F)0} lx_{(F)a}\right)}$	
State dynamics		
T2.21	$Egg_t = N_{t,a} f_t$	
T2.22	$L_{\infty,t} = \frac{\alpha_{L_\infty} z_{t-1}}{1 + \beta_{L_\infty} L_{t-1}^2}$	

TABLE 2. Continued.

Equation number	Equation	Conditions
T2.23	$L_{t,a} = \begin{cases} L_{\infty,t}[1-\exp(-K\cdot a)] \\ L_{t-1,a-1}\exp(-K) + L_{\infty,t}[1-\exp(-K)] \end{cases}$	$a = 0.25$ $0.25 < a \leq A$
T2.24	$sr_{t,a} = \left\{1+\exp\left[-\frac{1.7(L_{t,a}-\mathrm{MLL})}{L_{t,a}\mathrm{cv}_l}\right]\right\}^{-1}$	
T2.25	$C_{t,a} = N_{t,a}\left[1-\exp\left(-qE_t sc_{t,a}\right)\right]$	
T2.26	$p_{(r)t} = \frac{\sum_{x=1}^{100}\left\{\min(x,BL)\frac{\left[\left(\frac{C_{t,a}}{E_t}\right)^x \exp\left(-\frac{C_{t,a}}{E_t}\right)\right]}{x!}\right\}}{\left(\frac{C_{t,a}}{E_t}\right)}$	
T2.27	$H_{t,a} = \sum_{a=0}^{A}\left\{N_{t,a}p_{(r)t}\left[1-\exp\left(-qE_t sc_{t,a} sr_{t,a}\right)\right]\right\}$	
T2.28	$HL_t = \frac{\sum_{a=0}^{A}\left\{H_{t,a}L_{t,a}\right\}}{\sum_{a=0}^{A} H_{t,a}}$	
T2.29	$F_{t,a} = qE_t sc_{t-1,a}\left[p_{(r)t-1}sr_{t-1,a} + \left(1-p_{(r)t-1}sr_{t-1,a}\right)M_{(r)}\right]$	
T2.30	$N_{t,a} = \begin{cases} \frac{Egg_{t-1}\exp\left(-c_{(1)R}-\frac{c_{(2)R}}{z_{t-1}}+\Omega_{t+A-1}\right)}{1+\frac{c_{(3)R}}{z_{t-1}\mathrm{HAB}}Egg_{t-1}} \\ N_{t-1,a-1}e^{-M-F_{t,a}} \end{cases}$	$a = 0.25$ $0.25 < a < A$
T2.31	$L_t^2 = \frac{\sum L_{t,a}N_{t,a}^2}{SA}$	
T2.32	$U_t = \frac{0.5}{1+\exp\left(-\frac{\frac{\sum_{a=0}^{A} H_{t,a}}{E_t}-H_{50(H)}}{\sigma_{(H)}}\right)} + \frac{0.5}{1+\exp\left(-\frac{HL_t-H_{50(L)}}{\sigma_{(L)}}\right)}$	
T2.33	$E_{t+1} = E_{max,t}U_t$	

used to parameterize each function did not suggest an interaction between catch rate and size. Therefore, the two logistic functions were integrated into an overall utility function by taking a weighted average of the two components to be consistent with the overall intent of respondents to the survey.

The deterministic model evaluations were repeated for each value that was sampled from the estimated posterior distributions. The parameters that were based on literature values or expert judgment of the authors were assumed to be normally distributed with a coefficient of variation of 0.1. This allowed the model to represent uncertainty across all of the parameters.

To initialize the population, it is necessary to define the proportion of captured fish that are harvested at fished equilibrium (i.e., the proportion of captured fish that were below the current bag limit of four fish per day; $p_{[r]1}$). This was accomplished for each random combination of parameters by using a simple grid search across values from 0 to 1 by increments of 0.01. Each $p_{(r)1}$ was chosen based on the value that minimized the calculated interannual variation in spawner abundance.

Decision analysis.— We evaluated various management actions in the face of parameter and process uncertainty by using a Bayesian decision analysis framework (Robb and Peterman 1998). Decision analysis determines and communicates the relevant performance of management options across a range of hypotheses about the state of the system (Walters 1986). Each hypothesis is assigned a prior probability that reflects the relative belief in the hypothesis compared with all of the others. Integrating the expected performance of each management option across

TABLE 3. Estimated and fixed parameters that were used in the fishery operating model. Note that the parameters with no range are assigned fixed values in the model. The index values are presented as a range of values. The parameter values are expressed as the estimated mean with standard deviation in parentheses.

Parameter	Value	Description	Source
		Indices	
t	{2016, 2017, … T}	Time step ($T = 2036$)	
a	{0.25, 1.25, … A}	Age-class ($A = 3.25$)	
		Parameters estimated from data	
L_∞	444.4 (11.5)	Initial von Bertalanffy asympotic length	
K	0.5 (0.02)	von Bertalanffy metabolic parameter	
H_{2016}	1,545.3 (65.4)	Harvest in 2016	
Sp_{2016}	2,801.3 (728.3)	Spawner abundance in 2016	
$R_{(F)0}$	19,034.3 (803.5)	Equilibrium recruits (set to 2016 fry estimates)	
$H_{50(N)}$	2.4 (0.25)	Mean number of harvested fish at 50% angler utility	
$\sigma_{(N)}$	0.64 (0.19)	Logistic slope in angler utility for harvested fish numbers	
$H_{50(L)}$	316.7 (6.8)	Mean length of harvested fish at 50% angler utility	
$\sigma_{(L)}$	12.0 (3.9)	Logistic slope in angler utility for harvested fish length	
$p_{(r)1}$	0.36 (0.43)	Initial proportion released	
		Parameters based on literature or expert judgement	
α_f	3.7 10^{-4} (3.7 10^{-5})	Scalar in length–fecundity function	McGurk 2000
β_f	2.5 (0.25)	Power parameter in length–fecundity function	McGurk 2000
M	0.6 (0.06)	Instantaneous natural mortality rate	McGurk 1999
$M_{(r)}$	0.3 (0.03)	Release mortality rate	Bartholomew and Bohnsack 2005
E_{2016}	6,786 (289.9)	Fishing effort in 2016	van Poorten and Brydle 2018
α_S	13.0 (1.30)	Slope parameter in logistic selectivity function	Expert judgement
β_S	310 (31.0)	Length at 50% selectivity to fishing gear	Expert judgement
κ	5.2 (0.52)	Goodyear compensation ratio	Myers et al. 1999
p_c	0.9 (0.04)	Proportion of recruit survival due to prey availability	Expert judgement
α_{L_∞}	1,000 (100.0)	Prey-dependent density-dependent growth parameter	Expert judgement
cv_l	0.1	Coefficient of variation in length at age	Expert judgement
p_{juv}	0.9 (0.04)	Proportion of juvenile target strength range that is kokanee juveniles	Expert judgement

all possible hypotheses multiplied by the prior belief in each hypothesis provides a posterior expected value for that management option, essentially identifying policy options that are robust to uncertainty in the state of nature (Walters and Martell 2004).

Our evaluation followed the six basic steps of decision analysis (modified from Robb and Peterman 1998): (1) identify available management actions; (2) identify management objectives; (3) identify alternative hypotheses regarding the state of nature; (4) assign prior probability to each hypothesis; (5) calculate outcomes for each management action–hypothesis combination; and (6) evaluate the management options. Here, we discuss each of these steps in turn.

First, we identified the available management actions that were possible for Kawkawa Lake. The simplest of these is to impose or adjust regulations on the recreational fishery. These included: daily harvest (bag) limits, which we determined to be four, two, or zero (catch-and-release) fish per day; or minimum length limits on harvestable fish, which were either not imposed or set at 35 cm. Another management action is to directly modify available spawning habitat, reflecting the desire of managers to address urban encroachment and invasive plant species in the streams. Alternately, managers may choose to limit access to spawning habitat to reduce densities and potentially improve growth. Therefore, we included management scenarios where spawning habitat was increased or decreased by 25% or unchanged.

We next identified management objectives for the fishery, which were used to rank the relative efficacy of different management actions in achieving fishery goals. Recreational fishery goals in British Columbia include both maintaining angler satisfaction and conserving the resource (British Columbia Ministry of Environment 2007). Therefore, we defined objectives that are related to angler satisfaction and conservation of the population. We assumed that utility of daily catch rates and size of captured fish could be used to represent overall angler satisfaction, based on observations that satisfaction is routinely based on catch-related attributes of recreational fisheries (Arlinghaus 2006) and a recent meta-analysis of angler preference demonstrating that these two metrics were often important considerations when measuring catch-related utility (Hunt et al. 2019). Angler utility in the operating model was calculated in each time step and each management scenario by using equation T2.32, which was parameterized by using the stated preferences of the anglers that were interviewed in the creel survey (see the *Data collection and analysis* section). Using this metric, we defined our angler objective as that of achieving an angler utility greater than 50%; in other words, our objective is to have a fishery with angler satisfaction that is greater than neutral. Conservation was measured by using the spawning potential ratio (SPR), the expected lifetime egg production per recruit in the fished relative to the unfished state (i.e., $\Phi_{(U)0}$). Walters and Martell (2004) suggest maintaining SPR > 0.3, while Clark (2002) suggests that less resilient species must maintain SPR > 0.4. Therefore, we imposed a conservative objective to maintain SPR > 0.4. Performance indicators are measureable values that are used within the decision analysis to determine the relative success of different management actions in their ability to influence the objectives of the fishery. Therefore the performance indicators that were used for the future projections were the proportion of model runs across all random variables that resulted in angler utility >0.5 and spawning potential ratio >0.4, calculated 20 years after changes to the regulations or spawning habitat availability have been made. When evaluating both objectives together, we recognize that there is likely a trade-off between conservation and recreational use. There are a number of ways to combine multiple objectives (Kiker et al. 2005); we chose to multiply the expected values for each management option across conservation and angler objectives. In doing so, no single goal (recreation or conservation) may be compromised while maximizing the overall objective. Note that the management objective is multiplicative while the angler utility (T2.32) is additive. This implies that while individual anglers chose their fishing activity based on either size or catch rates, management considers that across all anglers both are important and a decline in utility for size or catch rates is detrimental to the overall utility.

There are two primary concerns regarding the state of nature and how it may affect the fish and fishery of Kawkawa Lake. The first is the state of primary productivity in the lake, which may decline over time as nutrients from septic fields dissipate. Therefore, we evaluated situations where in-lake productivity (z_t) varies annually as $z_t \sim N(dz_{t-1}, 0.1)$, where d was used to modify the rate of change in productivity to either increase ($d > 0$), vary randomly ($d = 0$), or decrease ($d < 0$). Another primary concern is the potential for increased fishing effort due to human population growth. We hypothesized that maximum annual fishing effort may increase at the same rate as the regional population growth ($g = 1.7\%$/year over the past 20 years; Statistics Canada 2017) or may grow twice as fast as the regional average, which might reflect an increase in participation rate or a propensity for local residents to be more interested in fishing than is represented by the regional average. Therefore, maximum annual fishing effort is evaluated as (1) $E_{max,t} \sim N(g \cdot E_{max,t-1}, 0.1)$ or (2) $E_{max,t} \sim N(2\,g \cdot E_{max,t-1}, 0.1)$. Each combination of these hypothesized states of nature were given an equal prior probability of being true; therefore, $p(\text{model}_i) = 0.167$ for each of the six modeled combinations of system productivity and fishing effort.

For each management action and state of nature, we calculated the probability of angler utility's dropping below 0.5 and the spawner potential ratio's being below 0.4 across all random draws of the estimated parameter posterior distributions (T2.1) and across all years. We then calculated the expected value (i.e., the weighted average) of each performance indicator for each management action across all states of nature (the hypotheses about productivity and fishing effort). Expected values were used to evaluate the management actions in light of the two fishery objectives. The final multicriteria objective was calculated as the product of expected values under each management action across conservation and angler objectives:

$$U_{MV} = \frac{\sum_{i=1}^{SN} U_{(N|HPUE)i}}{SN} \cdot \frac{\sum_{i=1}^{SN} U_{(L|\bar{L})i}}{SN},$$

where each component on the right represents the expected value of utility for catch rate and fish size across all states of nature $(SN) = 6$. This multiplicative utility function assumes that the angling satisfaction subobjectives for catch size and catch rates are independent.

Lastly, a one-way sensitivity analysis was conducted to evaluate the relative influence that each parameter had on the multicriteria objective across all of the possible management interventions. This was done by systematically setting each parameter to a series of fixed values across the range of that parameter, while all of the other parameters were stochastic within their distribution. The range of objective values that was observed across all of the management actions was reported for each parameter (Conroy and Peterson 2013).

RESULTS

A total of 669 anglers were interviewed over 68 creel survey days in 2016, reporting a total of 2,830 hours of fishing. The anglers that were interviewed reported a mean catch per unit effort of 1.4 kokanee per day and a mean harvest per day of 1.0 kokanee per day. Based on the estimated 2016 fishing effort in van Poorten and Brydle (2018), the total annual harvest was 1,544 (95% quantiles: 1,415, 1,671) kokanee.

Angler opinions on the number of fish that were harvested and their mean size varied widely across individuals. Some anglers admitted that they would be happy to come back to Kawkawa Lake regardless of the fishing experience because of various noncatch related motivations. However, among all anglers, it was possible to estimate a mean utility function for daily harvest and size (Figure 1). These functions predict a 50% utility for daily harvest of 2.4 fish with a mean size of 317 mm (Figure 1). Additionally, while anglers derive at least some utility for a wide range of daily harvest rates, they have a very low utility for small kokanee (Figure 1).

The size of the harvested kokanee ranged from 220–384 mm in length. Fifty fish from the fishery were assessed for age; of these, most (86%) were age 3, and the remainder were ages 2 and 4 (10% and 4%, respectively). Using an informative prior probability distribution for the von Bertalanffy K parameter, we calculated posterior predictions of growth parameters for use in the predictive model (Table 2).

The stable isotope analysis supported the hypothesis that nutrient enrichment was occurring at one of the two sampled inlet streams due to anthropogenic sources. The mean $\delta^{15}N$ was significantly higher in Kopp Creek than in any other location that was sampled and 3.4‰ higher than the mean value for the lake (Table 4). This highly elevated $\delta^{15}N$ suggests anthropogenic enrichment, although the influence on overall productivity will require further investigation.

A total of 2,058 spawning kokanee were observed in four of the five inlet streams between October and November 2016. The mean spawning date ranged from October 4–12 for the three streams that were analyzed. The median number of spawners that was estimated for each stream was 21, 699, 420, and 1,681, yielding a total of 2,801 spawners in 2016 (Sp_{2016}; Table 3).

The operating model provided useful baseline estimates of the current state of the fishery. Based on estimated vulnerable biomass (assuming the fishery primarily targets age 3 fish), the current fishing mortality is estimated to be 0.42/year (Figure 2A). Based on the value for fishing effort that was estimated in van Poorten and Brydle (2018), this leads to a catchability of 0.01 ha/angler day (Figure 2B). The current mean utility for the fishery that is derived by anglers was calculated as 0.44 (Figure 2C), which is largely driven by low average harvest rates across all of the anglers but large size of the harvested fish.

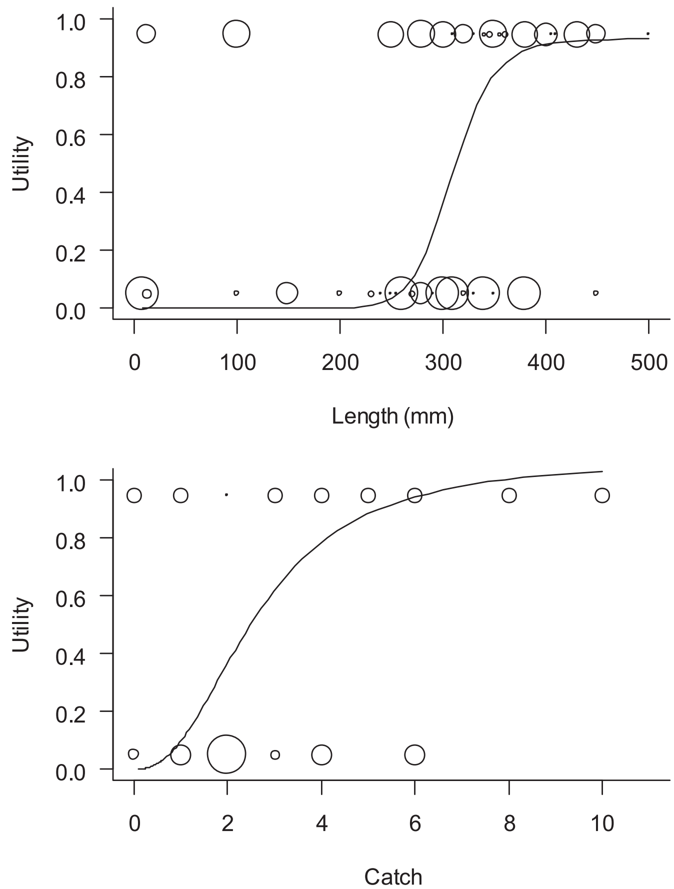

FIGURE 1. Logistic functions that were used to characterize angler utility for length of harvested fish (top panel) and daily catch rate (bottom panel). The dots represent aggregated angler responses to mean fish lengths and daily catch rates that lead to dissatisfaction (utility = 0.05) or complete satisfaction (utility = 0.95). The size of the dots corresponds to the number of responses for a particular length or catch rate. The lines represent the logistic function at the posterior parameter modes.

TABLE 4. Mean ± SE (sample size in parenthesis) δ^{15} values for particulate organic matter in the Kawkawa Lake samples.

	$\delta^{15}N$ (‰)	
Site	Mean	SE
Kopp Creek	5.4	1.0 (2)
Menz Creek	2.0	0.9 (3)
Mid lake	2.1	0.3 (3)
SE shore	2.0	0.1 (3)
Outlet	2.0	0.1 (3)

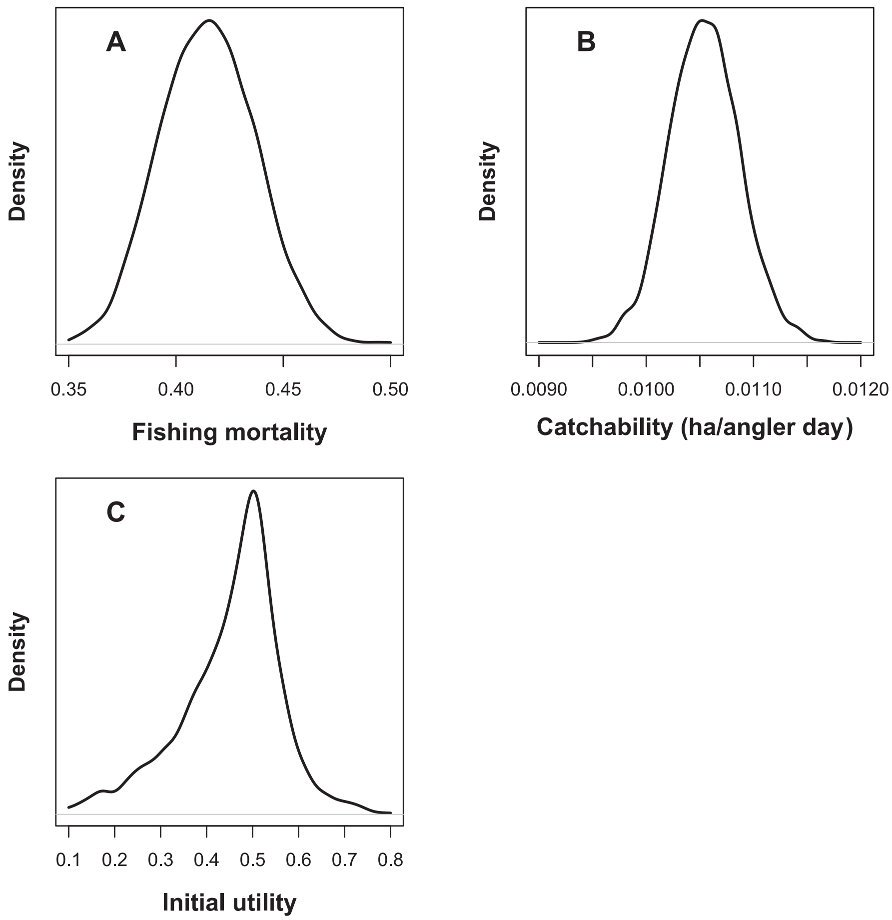

FIGURE 2. Calculated distribution of **(A)** fishing mortality, **(B)** catchability, and **(C)** angler utility for the Kawkawa Lake kokanee fishery in 2016 based on posterior parameter estimates input into the fishery model.

The operating model predicted that under the current management regulations of a daily harvest limit of four fish, if lake productivity maintains at the current level and maximum possible fishing effort tracks historic regional rates of population increase, the spawning stock will progressively decline due to increased fishing mortality (Figure 3). As population abundance declines, the mean length of harvested fish will increase, although marginally. Increases in fishing effort approximately offset increases in recruitment, resulting in stable harvest rates but a decline in spawner abundance by more than 50% (Figure 3). While effort increases due to increases in the number of anglers, utility remains relatively stable due to the very moderate change in the size and number of harvested fish.

If fishing effort increases faster than regional population growth or productivity declines over time, similar patterns will be seen in the fish population and the fishery when managing by using a daily harvest limit of four fish (Figure 3). If productivity declines at an annual rate of 2%, recruitment is impaired somewhat more than growth rate; therefore, the reduction in recruitment causes an overall moderate increase in fish size despite a reduction in prey availability. Spawner abundance in this scenario is approximately unchanged from the constant productivity scenario. If fishing effort increases at twice the regional population growth rate, spawner abundance declines by 75% over 20 years. In this scenario, the daily harvest rate begins to decline as a result of overharvest. If fishing effort increases at twice the regional population growth rate concurrently with declines in productivity, spawner abundance again declines by 75%, harvest rate begins to decline, and the mean size of fish increases to over 400 mm on average.

Optimal Management Action

Decision analysis was used to evaluate the performance of each management intervention across a series of hypotheses about how maximum fishing effort and system productivity may change over a 20-year horizon. If management and fishery productivity remain status quo (i.e., a four-fish bag limit and no other management actions; Table 5) and effort is assumed to increase continually with

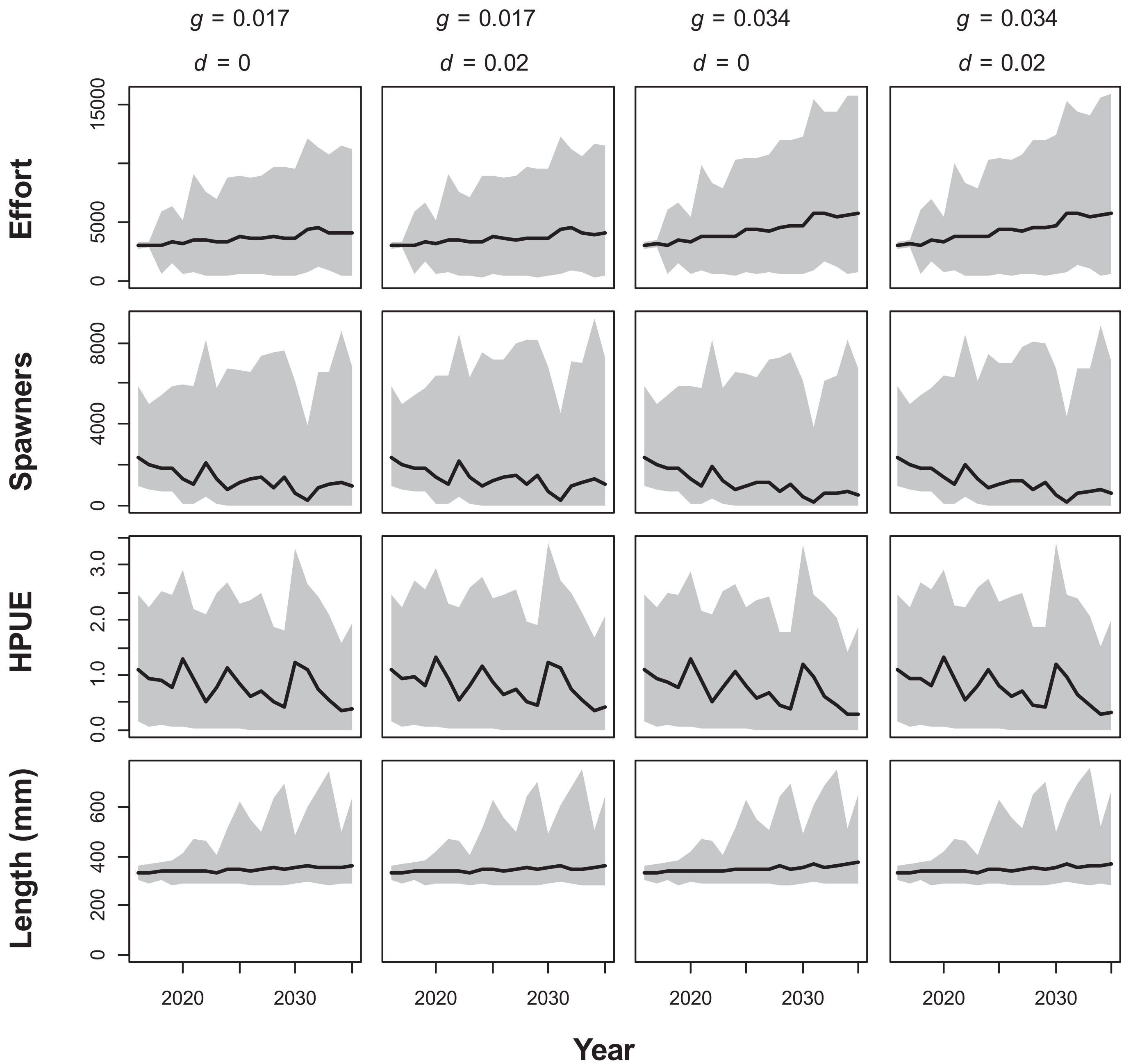

FIGURE 3. Projected time series of fishing effort (top row), spawner abundance (second row), mean daily harvest rate (third row), and mean length of harvested fish (bottom row) under different hypotheses (columns) for the rate of increase in angler capacity (g) and the rate of decrease in fish population productivity (d). The solid line represents the median projection; the gray shaded areas represent 80% quantiles.

regional population growth, marginal improvements in angler utility are predicted. However, angler utility is generally insensitive to changes in productivity and increasing effort; changes in long-term angler utility are most influenced by management actions. Reducing the daily harvest limit to two fish reduces angler utility, as highly skilled anglers are restricted in the number of fish that they can harvest. Catch and release regulations (zero fish may be harvested) universally result in the lowest angler utility under all scenarios. Similarly, size restrictions also lead to low angler utility, as many fish that would normally be harvested must now be returned. Increasing the available spawning habitat uniformly reduces angler utility due to an increase in recruitment, reducing density-dependent growth and the mean size of harvested fish. Conversely, the highest angler utility was predicted when spawning habitat was reduced due to the indirect effects on fish size.

TABLE 5. Probability of exceeding the angler utility threshold (i.e., $U > 0.4$), given different hypotheses regarding future trends in ecosystem productivity and capacity in fishing effort (columns) and management actions taken to achieve the angler satisfaction management goals (rows). The values in bold italics indicate the maximum expected values.

			No change in fishing effort			Increase in fishing effort			
Habitat	Size limit	Catch limit	Decrease in productivity	No change in productivity	Increase in productivity	Decrease in productivity	No change in productivity	Increase in productivity	Expected value
No change	None	4	0.59	0.58	0.57	0.63	0.62	0.62	0.6
	None	2	0.55	0.53	0.52	0.6	0.58	0.57	0.56
	None	0	0.31	0.3	0.29	0.33	0.32	0.31	0.31
	35 cm	4	0.43	0.42	0.4	0.46	0.45	0.43	0.43
	35 cm	2	0.42	0.41	0.4	0.46	0.44	0.42	0.42
Increase	None	4	0.46	0.45	0.44	0.5	0.49	0.47	0.47
	None	2	0.44	0.42	0.4	0.47	0.46	0.44	0.44
	None	0	0.26	0.24	0.23	0.28	0.26	0.25	0.25
	35 cm	4	0.35	0.34	0.33	0.38	0.36	0.35	0.35
	35 cm	2	0.35	0.35	0.32	0.37	0.36	0.35	0.35
Decrease	None	4	***0.78***	***0.78***	***0.78***	***0.83***	***0.82***	***0.82***	***0.8***
	None	2	0.75	0.73	0.72	0.8	0.79	0.77	0.76
	None	0	0.42	0.41	0.4	0.45	0.44	0.42	0.42
	35 cm	4	0.6	0.58	0.57	0.64	0.63	0.61	0.6
	35 cm	2	0.59	0.57	0.55	0.63	0.61	0.6	0.59

TABLE 6. Probability of exceeding the angler conservation threshold (i.e., SPR > 0.4), given different hypotheses regarding future trends in ecosystem productivity and capacity in fishing effort (columns) and management actions taken to achieve the conservation management goals (rows). The values in bold italics indicate the maximum expected values.

			No change in fishing effort			Increase in fishing effort			
Habitat	Size limit	Catch limit	Decrease in productivity	No change in productivity	Increase in productivity	Decrease in productivity	No change in productivity	Increase in productivity	Expected value
No change	None	4	0.69	0.7	0.7	0.5	0.51	0.52	0.6
	None	2	0.73	0.74	0.75	0.53	0.56	0.55	0.64
	None	0	***0.99***	***0.99***	***0.99***	***0.98***	***0.98***	***0.98***	***0.98***
	35 cm	4	0.91	0.91	0.91	0.78	0.79	0.8	0.85
	35 cm	2	0.9	0.9	0.91	0.78	0.78	0.79	0.84
Increase	None	4	0.75	0.75	0.76	0.6	0.61	0.62	0.68
	None	2	0.78	0.79	0.79	0.62	0.64	0.65	0.71
	None	0	***0.98***	***0.98***	***0.98***	***0.98***	***0.97***	***0.98***	***0.98***
	35 cm	4	0.92	0.92	0.92	0.82	0.83	0.83	0.87
	35 cm	2	0.91	0.91	0.91	0.81	0.82	0.83	0.87
Decrease	None	4	0.64	0.64	0.64	0.38	0.39	0.4	0.51
	None	2	0.67	0.68	0.68	0.41	0.42	0.43	0.55
	None	0	***0.98***	***0.98***	***0.98***	***0.97***	***0.97***	***0.97***	***0.98***
	35 cm	4	0.87	0.88	0.88	0.68	0.69	0.7	0.78
	35 cm	2	0.86	0.86	0.86	0.67	0.69	0.7	0.78

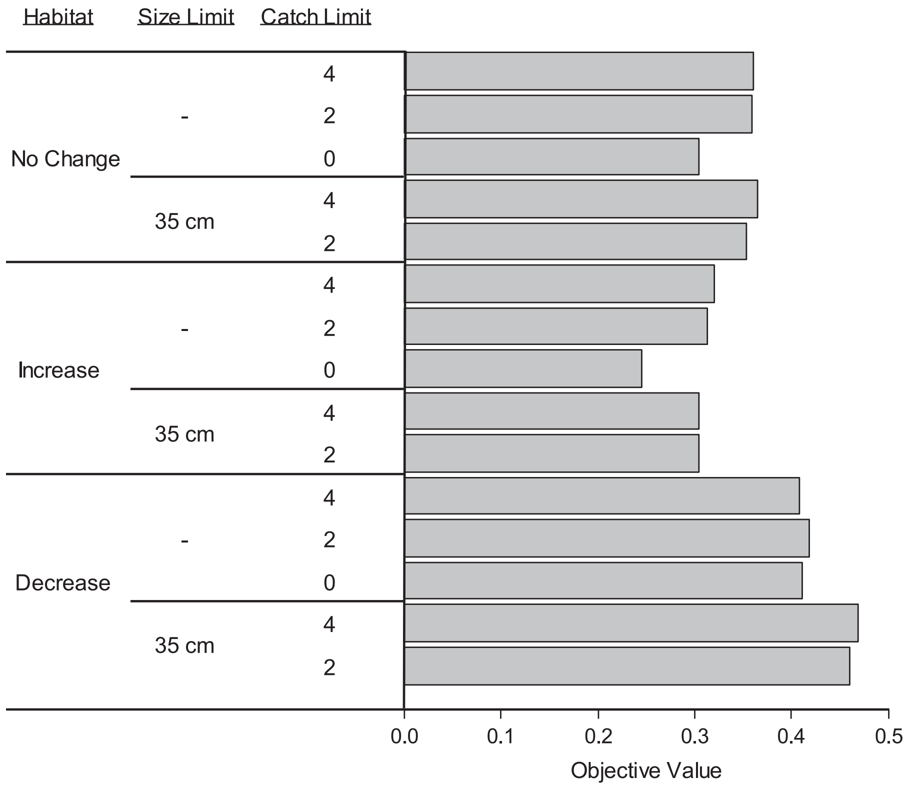

FIGURE 4. Multiattribute objective value for each management action, calculated as the product of the expected value for each management action across utility objectives for conservation and angler use.

Considering the expected value across all states of nature allows us to determine which management actions are robust to uncertainty about how fishing effort or system productivity may change over time. The model predicts that angler utility is highest with four- or two-fish bag limits, and bag limits are preferred to either catch-and-release regulations or size limits. Increasing spawning habitat is strongly discouraged in this context (i.e., maximizing angler utility) and reducing spawning habitat has the best overall outcome.

Evaluating the conservation indicator (the probability of the spawner potential ratio's declining to below 0.4) produced nearly opposite outcomes to evaluating the angler indicator (Table 6). Bag limits were much less effective at meeting conservation objectives than were catch-and-release or size limits. Increasing or retaining available spawning habitat had better conservation outcomes than did reducing current spawning habitat, except when paired with catch-and-release regulations because increased fish size led to increased egg production per fish. Overall, success at meeting the conservation objective was far more sensitive to changes in angler effort. The probability of falling below the conservation threshold decreased significantly if angler effort increased over time except for scenarios where catch-and-release regulations were implemented. Changes in productivity had no effect on the conservation indicator.

The multiplicative multicriteria objective was used to minimize a trade-off between the two objectives. If spawning habitat were to be maintained, limiting harvest by using a four- or two-fish bag limit would produce the highest management outcomes, especially when paired with a conservative minimum length limit (Figure 4). However, if management were willing to reduce spawning habitat, thereby increasing fish size, any fishing regulation will provide reasonable management outcomes. The best overall performance is with a four-fish bag limit and reduced spawning habitat.

The parameters that are related to size had the most influence on the multicriteria objective (Figure 5). Specifically, the median length of fishing selectivity and the slope of the fecundity relationship could each result in over a 20% increase in value or over a 70% decrease in the objective value. Most of the other parameters had a similar range in influence on the objective value.

DISCUSSION

Fisheries management strives to make choices among uncertain actions (Walters and Martell 2004). This

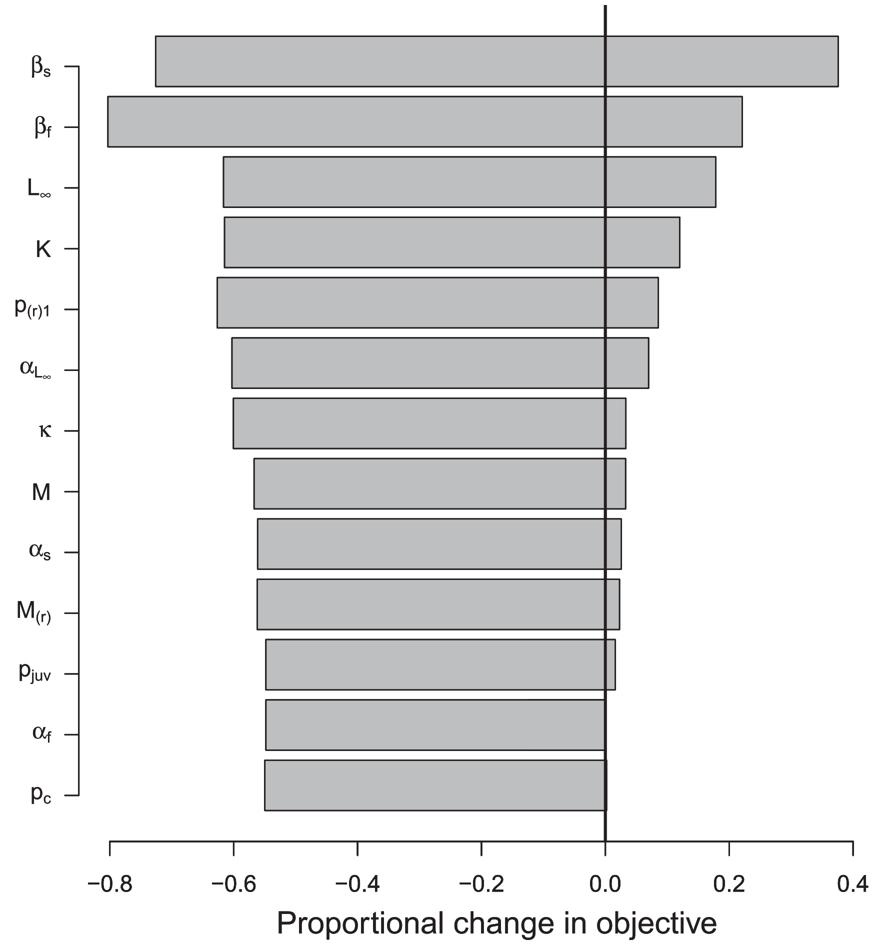

FIGURE 5. Tornado plot showing the proportional change in objective function that is possible across a range of actual values for each parameter.

involves explicitly stating management objectives, admitting which aspects of the system are uncertain, and predicting how each choice might affect the system. Decision analysis captures all aspects of this process by evaluating how the model predictions for different management actions affect management objectives amid uncertainty (Hilborn and Walters 1992; Robb and Peterman 1998). Decision analysis is a routine part of many commercial stock assessments, but it is relatively underused in recreational fisheries management applications (Peterson and Evans 2003; but see examples in Irwin et al. 2008; Jones and Bence 2009). For the Kawkawa Lake case study, decision analysis forced us to recognize the trade-offs that exist in our system, specifically the desire to improve abundance by increasing spawning habitat (a conservation argument) versus the desire to satisfy anglers by allowing harvest. The overall best management option in any decision where multiple attributes are considered within the objective function will depend on how various subobjectives are weighted. Managers can now use these results to make a clearly rationalized decision that can be communicated to stakeholders.

We have presented simplified management objectives, both for social and ecological outcomes, based on the stated preferences of anglers who were already on the lake (we do not know the views of anglers who may already be dissatisfied and not fishing; Lynch et al. 2017) and commonly agreed-upon conservation metrics (e.g., spawner potential ratio). Creating simplified management objectives was necessary, as there are no quantitative objectives for recreational fisheries in British Columbia or for most recreational fisheries generally (Lackey 1998). Our fishing objectives were based on the broad goals that are set out for recreational fisheries management in BC (British Columbia Ministry of Environment 2007), reflecting both ecological and social values. We feel that identifying and quantifying fishery objectives that match management goals is perhaps the most important step in a decision analysis and will help to avoid important pitfalls in the future (Barber and Taylor 1990; Hilborn 2007).

Our method for establishing catch-based angler utility is rudimentary, but it is consistent with the recreational management goals of the fishery (British Columbia Ministry of Environment 2007) and many other fisheries (Radomski et al. 2001; Pereira and Hanson 2003). The data that were used to parameterize our utility functions and the outcomes of these functions are easily interpretable by managers and stakeholders, which is important in any decision context. Although many recreational fisheries are guided by the goals of angler satisfaction and conservation, evaluating the human dimension of recreational fisheries is often lacking in many field-based assessments. We have incorporated empirically derived angler utility functions to quickly represent the heterogeneity of angler perceptions of various catch-related aspects of the fishery. Incorporating angler feedback to determine stated preferences for current and future fishery conditions in the fishery is entirely novel in recreational fisheries, and while we accept that there are many more appropriate methods for assessing angler utility and satisfaction (e.g., discrete choice experiments; Aas et al. 2000) we see this as a reasonable alternative that is easily conducted and interpreted by managers that are employing typical survey techniques that are common to small recreational fisheries.

Our results suggest that maintaining angler utility and satisfied anglers will not necessarily coincide with meeting conservation objectives. This reinforces the point that recreational fisheries often will not achieve a suitable bionomic equilibrium because of the multiple, often contradictory, objectives that are being evaluated by anglers (Hunt et al. 2011). For example, if anglers were only interested in catch rates, it is reasonable to expect that as catch rates decline effort would dissipate, resulting in a sustainable fishery. However, because kokanee anglers at Kawkawa Lake were more interested in fish size and because density-dependent growth results in extreme increases in body size at low density (Post et al. 1999), angler utility is maximized at low densities. Managers must carefully acknowledge the resultant trade-off between angler utility and conservation outcomes. Decision analysis helps to expose these trade-offs and facilitates discussion of these important outcomes.

Our system model incorporates density-dependent growth, which helped to produce some plausible, if somewhat counterintuitive, results. For example, without density-dependent growth, reducing spawning habitat would have merely affected catch rates but not size. This increase in growth results in a higher level of satisfaction with fish size as well as fecundity, thereby buffering the conservation outcome of reduced abundance. Therefore, including density-dependent growth changed the outcomes of our decision analysis, more accurately reflecting the conservation and satisfaction implications of management decisions. These results highlight the importance of including density-dependent processes when considering social-ecological fishery outcomes (Lorenzen 2016).

Monitoring effort is generally spread thinly across waterbodies because recreational fisheries managers are often responsible for hundreds to thousands of directed fisheries on individual waterbodies (Shuter et al. 1998). As such, time series analyses of fisheries data, as is typically available for many commercial stocks, are notably rare among all but the most economically and politically valuable recreational fisheries (De Graaf et al. 2015; Fitzgerald et al. 2018). We did not base our decision analysis on a typical stock assessment model (e.g., virtual population analysis, statistical catch-at-age analysis; Hilborn and Walters 1992) because we did not have a time series of data to fit to. Instead, we took information from a variety of sources to parameterize a plausible description of the Kawkawa Lake fishery. Further, we assumed that the population was at equilibrium prior to the initiation of monitoring, which is never technically true. Although we explicitly considered a slow change in system productivity, we would argue that this does not greatly influence our overall assumption of equilibrium due to the relative dynamic rates of populations and modeled productivity. Similar models that simulate interactions among ecosystem components with very different dynamic rates (e.g., phytoplankton and fish) can be appropriately approximated by setting one component as constant relative to the other, a process called variable speed splitting (Walters and Korman 1999), which we have essentially done here. While our modeling method may have oversimplified or poorly predicted some interactive processes, we feel that this is an appropriate method for leveraging the available data to make better and more informed decisions. As is common in decision analysis applications, we were able to combine information from different sources (Peterman and Anderson 1999) and thereby represent uncertainty in both our model parameters and the underlying states of nature with a fair amount of realism. Further work should consider the sensitivity analysis that was conducted (Figure 5) to prioritize important aspects of the system and model that have a large influence on objective values and decisions. Reducing uncertainty in these variables, particularly the length at 50% selectivity to the fishery and the fecundity relationship, would reduce uncertainty in the overall model predictions.

Recreational fisheries management is about much more than setting fishery regulations. It may involve (among other things) controlling invasive species, adding nutrients to a reservoir, creating spawning habitat, and recovering species at risk (Nielsen 1999). Engaging in any of these activities involves tradeoffs, among either stakeholders or objectives. Our work highlights the need for setting quantitative objectives; creating defensible, quantitative models (even simple ones, provided they address the problem at hand); and admitting uncertainty in both parameters and our presumption of the state of nature. Decision analysis allows a decision maker to clearly view how any suite of management actions will affect objective indicators and how each action compares against all others, improving the odds of creating robust and attractive recreational fisheries.

ACKNOWLEDGMENTS

The intensive field work for this project was carried out by Scott Brydle who, along with great assistance from Jesse Wood, interviewed the anglers and sampled fish in all conditions with patience and grace. Extensive input on all things limnological was provided by Shannon Harris, Jen Sarchuk, and Heather Vainionpaa (BC Ministry of Environment and Climate Change Strategy). The hydroacoustic sampling was conducted by Tyler Weir and Dave Johner. Impetus and encouragement (and gear) for this study was provided by Mike Willcox (BC Ministry of Forests, Lands, Natural Resource Operations and Rural Development). This work was funded by a grant from the Freshwater Fisheries Society of BC through the Small Lakes Technical Committee. There is no conflict of interest declared in this article.

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REVIEWS IN FISHERIES SCIENCE & AQUACULTURE
https://doi.org/10.1080/23308249.2019.1619071

Addressing Challenges Common to Modern Recreational Fisheries with a Buffet-Style Landscape Management Approach

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ABSTRACT

Recreational fisheries management strives to provide satisfying fishing experiences to heterogeneous anglers while conserving fish stocks of varying productivity. Achieving this balance with one-size-fits-all regulatory strategies is challenging; but complex, waterbody-specific regulations may be onerous to anglers and managers. An alternative strategy is a limited but specifically diverse "buffet" of regulations across a landscape of discrete fisheries to improve outcomes over existing regulation strategies. This approach is tested using a landscape bioeconomic model with density dependent growth and survival feedbacks in fish populations and dynamic angler behavior. Sources of heterogeneity in angler behavior and biological processes are considered to select and apply an optimal suite of fishing regulations. At a regional level, the buffet-style strategy offers improvements over other management strategies by recognizing tradeoffs among the utility and effort patterns of diverse angler types. Furthermore, these benefits are generally maintained even when limited to only five regulations to ease implementation logistics. Additional requirements for management agencies using the buffet strategy are discussed, such as assessing angler heterogeneity and determining which regulations are implemented on which waters. Some of these challenges may be overcome because this approach is imminently compatible with active-adaptive and cooperative management ideas.

KEYWORDS
Angler heterogeneity; buffet management; conservation; fishing motivations; participation; satisfaction

Introduction

Recreational fisheries comprise a dominant use of many fresh and coastal waters throughout the world (Lewin et al., 2006), and provide substantial socio-economic benefits to anglers (Toivonen et al., 2004; Arlinghaus and Cooke, 2009; Ihde et al., 2011) who, through the act of fishing, catching, and harvesting fish, exert mortality on fish populations that can sometimes be unsustainable (Post et al., 2002; Coleman et al., 2004; Arlinghaus and Cooke, 2005). Thus, providing anglers with satisfactory with fishing experiences, without sacrificing the long-term sustainability of the fish populations is the primary aim of institutions charged with governing recreational fisheries (Royce, 1983; Hilborn, 2007; Koehn, 2010).

Fisheries management agencies have traditionally tried to regulate fishing mortality by implementing closed seasons and/or harvest regulations limiting the size and number of fish removed to ensure adequate spawning fish for sustainable recruitment (Cowx, 2002; Pereira and Hansen, 2003; Walters and Martell, 2004). Harvest regulations that maximize long term catch or harvest may be poorly suited for recreational fisheries where angler satisfaction may not be closely tied to aggregate biomass harvested (Malvestuto and Hudgins, 1996; Radomski et al., 2001), and humans fish for leisure (Arlinghaus and Cooke, 2009; Cowx and van Anrooy, 2010). With this in mind, management agencies make decisions with the dual goals of satisfying anglers while still conserving fish populations. Certainly, in low-risk fisheries, increasing attention is paid to satisfying anglers. Angler satisfaction is a social construct derived from expectations and actual fishing experiences that include catch (size, numbers) and non-catch (crowding, esthetics, facilities) related attributes (Arlinghaus, 2006; Hunt et al., 2013a, Beardmore et al., 2015). But angling populations are diverse in how they achieve satisfaction (Holland and Ditton, 1992; Oh and Ditton, 2006), and

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this heterogeneity complicates managing for angler satisfaction (Johnston et al., 2010; Gwinn et al., 2013).

Angler heterogeneity stems from diverse motivations for engaging in and gaining satisfaction from recreational fishing (e.g. Fedler and Ditton, 1994; Massey et al., 2006; Oh and Ditton, 2006). Motivations (e.g. ex ante anticipations of expected outcomes) that stimulate anglers to engage in recreational fishing are notably diverse, including attaining harvest for consumption or sale, social interactions, challenge, time in nature, and trophy opportunities (e.g. Beardmore et al., 2011, 2015; Arlinghaus et al., 2016). Diverse angler motivations relate to the multiple functions by which anglers achieve satisfaction from fishing—i.e. the *ex post* psychological state associated with achieving expectations (Holland and Ditton, 1992; Arlinghaus, 2006; Beardmore et al., 2015). The relative importance of the variety of catch and non-catch motivations and determinants of satisfaction can vary among anglers (Holland and Ditton, 1992; Johnston et al., 2010). The prominence of certain fishing aspects for overall satisfaction are often used to group anglers into "angler types," such as "trophy oriented" and "catch rate oriented" (Johnston et al., 2010; Beardmore et al., 2011; Carruthers et al., 2018). Critically, the existence of multiple angler types implies multiple and potentially competing objectives for managing angler satisfaction, since management actions that most benefit one angler type may have little positive or even a negative effect on the satisfaction derived by another (Aas et al., 2000; Johnston et al., 2010; Ihde et al., 2011). For example, length-based harvest restrictions may promote larger catch size and the satisfaction of trophy-oriented anglers, but the same actions may produce suboptimal outcomes for harvest-oriented anglers (Gwinn et al., 2013). Such scenarios would produce tradeoffs, where improvement in the satisfaction achieved by one angler type in a single water body and temporal period could have the opportunity cost of reduced satisfaction for another type (Johnston et al., 2010; Garcia-Asorey et al., 2011). Thus it is extremely difficult and unlikely to simultaneously satisfy diverse angler types who fish for different reasons, with different expectation and exhibit different behaviors (Johnston et al., 2010).

A related challenge is that heterogeneous angler types will likely behave and impact fisheries in particular patterns (Ward et al., 2013b) that may deplete fish populations. For example, a trophy-oriented angler type targeting larger fish is apt to select particular angling locations, gear, techniques, and harvesting choices (e.g. Arterburn et al., 2002; Hutt and Bettoli, 2007). Such behaviors affect selective fishing mortality, which in turn structures the fish population and thereby provides a feedback to the catch-related aspects of the fishery (Ward et al., 2013a, Hansen et al., 2015b, van Poorten et al., 2016). This means heterogeneous angler behavior can shape the fishing opportunities available to all anglers and may exacerbate tradeoffs among angler types. But it also implies that as the fishery becomes unattractive to one angler type due to declining catch rates, another type may find the fishery increasingly attractive due to, for example, increasing mean size (van Poorten et al., 2016). This process of effort switching between angler types is referred to as "effort sorting" and may act to keep fishing mortality rate high even as fish abundance precipitously declines (Walters and Martell, 2004; Ward et al., 2013a, van Poorten et al., 2016); one of many mechanisms leading to hyperstability (Hilborn and Walters, 1992). Although the concept of angler diversity in motivations and attributes has been well-studied in the human dimensions literature (Bryan, 1977; Chipman and Helfrich, 1988; Fedler and Ditton, 1994; Arlinghaus, 2006; Beardmore et al., 2011), it has been relatively underappreciated among fisheries biologists and managers (Fulton et al., 2011; Hunt et al., 2013b, Ward et al., 2016) and is one potential mechanism for the "invisible collapse" of many recreational fisheries (Post et al., 2002; Post, 2013), which obviously is a threat when managing to conserve fish populations. As such, the mere existence of angler heterogeneity creates the potential for a significant conservation risk for fisheries landscapes (Hunt et al., 2011; van Poorten et al., 2016).

Addressing potentially competing objectives among angler types while preventing overharvest presents a formidable management challenge (Radomski et al., 2001; Hunt et al., 2011), which until recently has been the subject of comparatively few studies assessing alternative management approaches (Johnston et al., 2010, 2013, 2015; Gwinn et al., 2013). These studies demonstrate how it is necessary to consider angler heterogeneity to appropriately select regulation options, but generally do not offer a solution to the tradeoff among angler types. This is understandable because some tradeoffs may not permit easy compromises—i.e. there may be no single regulation that simultaneously maximizes satisfaction of trophy and catch-rate oriented angler types (Knoche and Lupi, 2016). This was recognized by Johnston et al. (2010), who stated "Managers are likely to encounter difficulties in jointly satisfying the interests of the entire angling public." While this is true for any single fishery (i.e. discrete water body), management agencies regulating multiple discrete waters or fishing sites throughout a region often have the option of selecting different regulations for these waters (Cowx, 2002; Parkinson et al., 2004; Post and Parkinson, 2012). Waterbody-specific regulations can and sometimes are implemented to ensure conservation of differently productive and harvested fish populations and/or to provide different types of fishing opportunities (e.g. Shetter and Alexander, 1966; Schill, 1996; Margenau and Petchenik, 2004). While special, waterbody-specific regulations are not rare, research assessing their efficacy is. In one of the few studies considering this issue, Carpenter and Brock (2004) suggested that diversified policies for overall lake management can offer broad advantages over "One-Size-Fits-All" (OSFA) strategies, though the study focused on a broad suite of ecosystem services beyond fishing, and did not explicitly consider many of the socioecological and behavioral feedbacks that are now understood to operate in recreational fisheries (Ward et al., 2016; Arlinghaus et al., 2017). Furthermore, implementing waterbody specific regulations also has challenges (Radomski et al., 2001). Numerous and complex different regulations may frustrate anglers or law enforcement agents, and establishing science-based waterbody-specific regulations can require overwhelming monitoring or research (Lester et al., 2003). What does not exist are studies assessing how diversified angling regulations should be designed to be practically applied to landscapes in a way that specifically satisfies heterogeneous anglers while also sustaining fish populations.

This work seeks to evaluate the expected outcomes of a spatially diversified approach to recreational fisheries management using an integrated bioeconomic landscape model. This approach, which involves effectively offering a buffet of regulation options to meet the diverse motivations of a heterogeneous angling community, is wholly different from previously explored objectives of identifying the best single action to be applied to heterogeneous fisheries (Johnston et al., 2010; Fenichel and Abbott, 2014). The model is used to assess the efficacy of buffet management strategy of setting management regulations for achieving desired outcomes at a regional level. The potential gain in recreational fisheries objectives is evaluated over other management approaches as heterogeneity of fishing opportunities and anglers increases. An additional zoned-approach with a small subset of regulation options (a reduced buffet of options) is tested to see if this might be an appropriate compromise between one-size-fits-all and lake-by-lake management.

Model overview

A bioeconomic landscape simulation model was used to test for the effects of different angling regulation strategies on each independent fish population in a landscape of fisheries (e.g. lakes) and in turn, the aggregate value of the fishing experience. To evaluate and compare the aggregate value achieved across all fisheries and angler types a landscape of fisheries (51 total fish populations) with a variety of unfished density and size structure attributes is simulated. This creates a variety of unique fisheries, which will each change with fishing pressure due to density dependent recruitment compensation and growth. The landscape of fisheries was recreationally fished by a population of anglers equally composed of four types, each uniquely defined by their interest in catch rates, harvest opportunities and size of fish captured, as well as their dissatisfaction in crowding and travel distance to a fishing site (Figure 1). Additionally, each angler type had a different impact on the fishery due to different efficiency (catchability), size-selectivity and discard mortality rate. The model was used to show the implications of ignoring heterogeneity in lake biology across a landscape and heterogeneity in angler preferences and attributes across the population, and go on to illustrate how a diversified buffet approach can better satisfy diverse anglers without impinging on fish population sustainability. The model further demonstrates that similar outcomes can be attained with a limited suite of regulations applied across a landscape to still provide a range of fishing experiences.

Model formulation

The landscape of fish populations (e.g. a lake region) was composed of lakes each containing the same single species of targeted fish. Each fish population (l) had a unique productivity based on unfished recruitment ($R_{0,l}$) and size structure based on unfished asymptotic length ($\overline{L}_{\infty,l}$). Fish populations were distributed among three distance classes from the main angler population center: 50, 150, and 400 km. Unfished equilibrium densities for each population were calculated using life history incidence functions (Botsford, 1981; Walters and Martell, 2004; Table 1). These equilibrium states were used as the starting points for the dynamic model. Parameters used to characterize the state of the model are shown in Table 2.

The model first simulated an unfished state for each lake based on a population-specific unfished recruit density and asymptotic length (Table 1). These

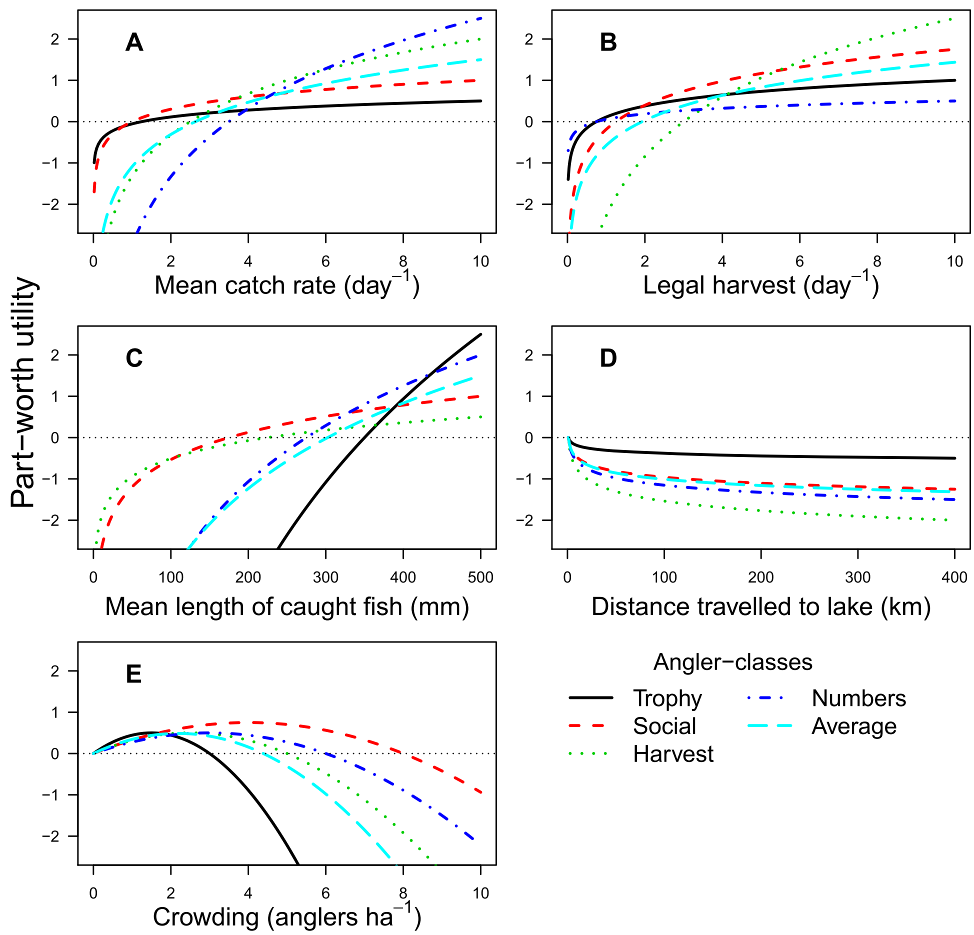

Figure 1. Part-worth utility functions describing the preferences of trophy, harvest, social, and catch angler types to daily legal harvest, daily catch, and mean length of captured fish.

two states (productivity and growth rate) were negatively correlated across populations (T2.2-T2.6). Asymptotic length was used to estimate length- and weight-at-age (T2.7, T2.8) and weight-at-maturity (T2.9). Weight-at-age was then used to estimate age-specific fecundity (T2.10). Survival of recruited fish was assumed constant (T2.11) Based on these variables, it is possible to estimate unfished equilibrium states for eggs-per-recruit (T2.12), egg density (T2.13), numbers-at-age (T2.14) and effective density (calculated as the sum of squared lengths; T2.17; Post et al., 1999; Walters and Post, 1993) for each population. Using a common recruitment compensation ratio (κ) and the population-specific equilibrium eggs per recruit and egg density, it was then possible to calculate parameters for Beverton-Holt recruitment functions for each population (T2.18-T2.19; Walters and Martell, 2004). Finally, parameters for a density-dependent growth function were calculated using lake-specific equilibrium effective density and asymptotic length (T2.20-T2.21; van Poorten and Walters, 2016).

The angling population was made up of four angler types whose total annual fishing effort and the distribution of effort among lakes is based on expected utility gained from fishing each lake. These angler types are designed to be consistent with the theory of recreational specialization (Bryan, 1977), ranging from the casually involved to the specialist angler. As specialization level increases, skills (e.g. catchability, survival upon release) improve, size is of greater importance for targeting and motivation, and harvest is of less importance (influencing release behavior and motivation; Bryan, 1977). Each angler type was named based on the primary motives for fishing: trophy anglers (fishing for large fish); harvest anglers (fishing for the opportunity to harvest many fish per trip); social anglers (fishing with others; not driven by any particular catch-related aspect); and catch anglers (fishing to maximize catch per unit effort, but not necessarily interested in harvest). Angler types had a unique set of part-worth utility functions for catch rates, harvest rates, fish length, travel distance, and crowding (Table 3; Figure 1). All part-worth utilities

Table 1. Initial states of size structure and abundance in each of the fish populations in the recreational fishing model.

Parameters		
T1.1	$\Theta = \{\mu_{R_0}, \sigma_{R_0}, \mu_{L\infty}, K, M, \kappa, p_m, w_{egg}, p_{fem}, \beta_{1,c}, \beta_{2,c}\}$	
Lake-specific variables		
T1.2	$R_{0,l} = N(\mu_{R_0}, \sigma_{R_0})$	Unfished recruitment
T1.3	$b_{L_\infty} = \frac{-\mu_{L\infty}}{2(\max(R_{0,l}) - \min(R_{0,l}))}$	Slope of mean asymptotic length vs. unfished recruitment
T1.4	$a_{L_\infty} = 0.75\mu_{L\infty} - b_{L_\infty}\max(R_{0,l})$	Intercept of mean asymptotic length vs. unfished recruitment
T1.5	$\hat{L}_{\infty,l} = a_{L_\infty} - b_{L_\infty} R_{0,l}$	Predicted asymptotic length
T1.6	$L_{\infty,l} = N\left(\hat{L}_{\infty,l}, 0.1 \cdot \hat{L}_{\infty,l}\right)$	Asymptotic length
Life history schedules		
T1.7	$\bar{L}_{l,a} = L_{\infty,l}\left(1 - e^{-K(a)}\right)$	Initial length-at-age
T1.8	$\bar{w}_{l,a} = 1e^{-5}\left(\bar{L}_{l,a}\right)^3$	Initial weight-at-age
T1.9	$\bar{w}_{(m)l} = 1e^{-5}\left(L_{\infty,l} p_m\right)^3$	Initial weight-at-50%-maturity
T1.10	$\bar{f}_{l,a} = \left[max\left(0, \bar{w}_{l,a} - \bar{w}_{(m)l,a}\right)/w_{egg}\right] p_{fem}$	Initial fecundity-at-age
T1.11	$\bar{lx}_{l,a} = \begin{cases} 1 & a = 1 \\ e^{-M(a-1)} & a > 1 \end{cases}$	Initial survivorship
Unfished equilibrium states		
T1.12	$\varphi_{(0)l} = \sum_{a=1}^{A} \bar{f}_{l,a} lx_{l,a}$	Unfished eggs per recruit
T1.13	$\bar{Egg}_l = R_{0,l}\varphi_l$	Unfished egg density
T1.14	$\bar{N}_{l,a} = R_{0,l}\bar{lx}_{l,a}$	Unfished density
T1.15	$\bar{sl}_{l,a,c} = \left(1 + e^{-\left(\bar{L}_{l,a} - \beta_{2,c}\right)/\beta_{1,c}}\right)^{-1}$	Initial fishery selectivity to angler type-*c*
T1.16	$\varphi_{(V)l,c} = \sum_{a=1}^{A}\left(\bar{N}_{l,a}\bar{sl}_{l,a,c}\right)$	Initial vulnerable density to angler type-*c*
T1.17	$\bar{L}_{(2)l} = \sum_{a=1}^{A}\left(\bar{N}_{l,a}\bar{L}_{l,a}{}^2\right)$	Initial effective density
Beverton–Holt recruitment parameters		
T1.18	$\alpha_{(1)l} = \frac{\kappa}{\varphi_{(0)l}}$	Maximum recruits per spawner
T1.19	$\alpha_{(2)l} = \frac{\kappa - 1}{\bar{Egg}_l}$	Recruitment density-dependence parameter
Density-dependent growth parameters		
T1.20	$\gamma_{(1),l} = 1.25 \cdot \bar{L}_{\infty,l}$	Maximum asymptotic length
T1.21	$\gamma_{(2),l} = \frac{\left(\frac{\gamma_{(1),l}}{L_{\infty,l}} - 1\right)}{\bar{L}_{(2)l}}$	Growth density-dependence parameter

were non-linear, described using either log-linear or quadratic functions. Shapes and parameters describing utilities and attributes were loosely based on empirical and estimated observations of different angler types in the literature (Ward et al., 2013b, Beardmore et al., 2015; Hunt et al., 2019). Total utility is based on the sum all part-worth utilities (T4.8). Each angler type also had different skills and attributes with respect to fishing. Specifically, catchability, size selectivity, hooking mortality, and probability of retaining a legal sized fish were unique to each angler type (Table 3).

Parameters for the four angler types reflected differential skill, motivation and impacts on fish populations (Table 3). Trophy-oriented anglers were (i) most likely to participate in fishing; (ii) least interested in catch rates; (iii) least interested in harvest; (iv) most interested in large fish size (with part-worth utility increasing nearly linearly with mean fish length); (v) least impacted by travel distance; and (vi) least tolerant of crowding (Figure 1). Trophy anglers also had the highest catchability of all angler types, low release mortality rates, intermediate voluntary release rates and had a selectivity function that targeted large fish (Table 3). Social-oriented anglers were (i) least likely to participate in fishing; (ii) intermediate in their interest in high catch rates but still tolerant of intermediate catch rates; (iii) high in their interest in any opportunity to harvest; (iv) least interested in fish size, but were more tolerant of small sizes than other angler types; (v) intolerant of travel distance; and (vi) most tolerant of crowding (Figure 1). Note that social anglers were described with a greater maximum part-worth utility for crowding, indicating they were less averse to crowding. Social anglers also had the lowest catchability, highest release mortality rate, low voluntary release rates, and had a selectivity function that was least size-selective (Table 3). Harvest-oriented anglers were (i) intermediate in their likelihood to participate in fishing; (ii) highly interested in catch rates and (iii) harvest rates; (iv) generally disinterested in size; (v) most intolerant of travel distance; and (vi) intermediate in their tolerance for crowding (Figure 1). Harvest anglers also have an intermediate catchability, low release mortality rate, harvest every legal fish they catch and have a selectivity function with relatively low size-selectivity (Table 3). Numbers-oriented anglers were (i) most likely to participate in fishing (the same as trophy anglers); (ii) most interested in high catch rates; (iii) relatively uninterested in harvest; (iv) interested in fish size, but less

Table 2. Model indices, variables, and parameter values used in the model with associated descriptions and units.

Symbol	Value	Description	Units
Indices			
l	$\{1, 2, \ldots, n_l\}$	Lake ($L = 51$)	lake
a	$\{1, 2, \ldots, A\}$	Age (A = 10)	year
c	$\{1, 2, \ldots, n_c\}$	Angler type ($n_c = 4$)	
Model parameters			
μ_{R_0}	750	Mean unfished recruitment across lakes	recruits
σ_{R_0}	150	Standard deviation in unfished recruitment across lakes	recruits
μ_{L_∞}	400	Mean asymptotic length across lakes	mm
K	0.3	Metabolic rate parameter of von Bertalanffy function	
M	0.3	Instantaneous natural mortality	yr^{-1}
κ	6.84[a]	Compensation ratio in recruitment	
p_m	0.6	Length at maturity (as a proportion of $L_{\infty,l}$)	
w_{egg}	0.1	Weight of a single egg	G
p_{fem}	0.5	Sex ratio	
$\beta_{1,c}$	see Table 3	Length at 50% selectivity for angler type-*c*	mm
$\beta_{2,c}$	see Table 3	Slope of selectivity at $\beta_{1,c}$ for angler type-*c* (logit-scaled)	mm^{-1}
$\alpha_{(x)c}$	see Table 3	Log-linear intercept of part-worth utility functions for component *x* for angler type-*c*	
$\beta_{(x)c}$	see Table 3	log-linear slope of part-worth utility functions for component *x* for angler type-*c*	units of *x*
$U_{(o)c}$	see Table 3	Utility gained from angler type-*c* choosing to fish	
U_n	2	Conditional indirect utility gained by an angler from choosing not to fish on the landscape	
d_l	{50, 150, 400}	Driving distances from population center to lake-*l*	Km
δ	0.8	Persistence of fishing effort	
$p_{(c)}$	{0.25,0.25,0.25,0.25}	Proportion of all anglers belonging to each angler type	
$E_{max,c}$	$500 \cdot p_{(c)} \sum AR_l$	Maximum fishing effort available for angler type-*c*	angler-days
cv	0.07	Variation in length at age	
q_c	see Table 3	Catchability for angler type-*c*	ha/angler-days
d	0.9	Degree of density dependence in catchability	
AR_l	U(10,5000)	Surface area of lake-*l*	Ha
$\bar{p}_{(r)c}$	see Table 3	Probability of retaining legal sized fish for angler type-*c*	
M_d	see Table 3	Hooking mortality for angler angler type-*c*	$fish^{-1}$
Management Controls			
BL_l	{CR,1,2,4, none}	Bag limit	fish/d
ML_l	{none,350,450,550}	Minimum length limit	Mm

[a]Based on mean compensation ratio for freshwater fish in Myers et al. 1999.

motivated by extreme size than trophy anglers; (v) fairly tolerant of travel distance and (vi) crowding (Figure 1). Numbers anglers also had high catchability, low release mortality, highest voluntary release rates and a selectivity function that targeted large fish more than social or harvest anglers (Table 3). In scenarios assuming no heterogeneity among anglers, the mean utility function and fishery impact across all angler types is assumed.

Numerical approximation of equilibrium state

To calculate fishing effort on each site, an initial estimate of total utility (T4.8) is used to distribute effort among lakes based on a multinomial logit utility function (T4.9). Equation T4.9 calculates the probability of fishing any given lake relative to the total utility for that angler type plus a probability of not fishing or fishing elsewhere (U_n). The probability of not fishing in the modeled landscape was set high ($U_n = 2.0$), reflecting an increasing understanding that anglers choose to fish by selecting from a suite of alternative leisure opportunities (e.g. fishing, golfing, camping). This importantly assumes that there is positive utility by choosing not to fish (Ditton and Sutton, 2004; Sutton, 2007). Total fishing effort in each model iteration is distributed among lakes by multiplying the probabilistic distribution of each angler type by the total number of anglers in each angler type (T4.10).

Each iteration begins with calculating density dependent growth as a result of intraspecific competition in the lake (T4.15-T4.16; van Poorten and Walters, 2016). Length at age is then used to calculate selectivity to capture (T4.13) and legal harvest (T4.14) based on the regulated minimum length limit. Expected capture of all fish (T4.18) and legal sized fish (T4.19) based on minimum length limits is calculated using the Baranov equation (Ricker, 1975) distributing catch across angler types based on density dependent catchability for each angler type (T4.17) and natural mortality experienced by fish. The resulting catch per unit effort (T4.20) is used to calculate the expected proportion of total catch that can be harvested within the bag limit assuming realized catch rates among anglers are Poisson distributed (T4.21; Porch and Fox, 1990). Because bag limits result in fish being returned to the population to be caught again, the bag limit sub-model has no closed-form solution. This is accounted for by breaking the fishing season into four time-steps where fish density, total fishing

Table 3. Angler types, their utility for various aspects of the fishery, which drives behavior, and their specific attributes.

		Parameter values describing angler types			
Variable	Symbol	Trophy ($c = 1$)	Social ($c = 2$)	Harvest ($c = 3$)	Catch ($c = 4$)
Preference for attributes of the fishing experience[a]					
PWU gained from angler type-c choosing to fish	$U_{(0)c}$	0.25	−0.15	0.15	0.25
PWU of daily catch rate for angler type-c	$U_{(C)l,c}$	$\alpha_{(C)l,c} = -0.08$ $\beta_{(C)l,c} = 0.83$	$\alpha_{(C)l,c} = 0.00$ $\beta_{(C)l,c} = 1.5$	$\alpha_{(C)l,c} = -1.65$ $\beta_{(C)l,c} = 4.15$	$\alpha_{(C)l,c} = -2.98$ $\beta_{(C)l,c} = 5.48$
PWU of daily harvest rate for angler type-c	$U_{(H)l\ ,c}$	$\alpha_{(H)l,c} = 0.11$ $\beta_{(H)l,c} = 0.89$	$\alpha_{(H)l,c} = -0.19$ $\beta_{(H)l,c} = 1.94$	$\alpha_{(H)l,c} = -1.65$ $\beta_{(H)l,c} = 4.15$	$\alpha_{(H)l,c} = 0.06$ $\beta_{(H)l,c} = 0.44$
PWU of mean length of captured fish for angler type-c	$U_{(S)l,c}$	$\alpha_{(S)l,c} = -41.06$ $\beta_{(S)l,c} = 16.14$	$\alpha_{(S)l,c} = -6.15$ $\beta_{(S)l,c} = 2.74$	$\alpha_{(S)l,c} = -11.74$ $\beta_{(S)l,c} = 4.81$	$\alpha_{(S)l,c} = -13.57$ $\beta_{(S)l,c} = 5.77$
PWU of distance for angler type-c	$U_{(D)l,c}$	$\beta_{(D)l,c} = -0.19$	$\beta_{(D)l,c} = -0.48$	$\beta_{(D)l,c} = -0.77$	$\beta_{(D)l,c} = -0.58$
PWU of crowding fish for angler type-c	$U_{(Cr)l,c}$	$\alpha_{(Cr)l,c} = 0.67$ $\beta_{(Cr)l,c} = 0.22$	$\alpha_{(Cr)l,c} = 0.75$ $\beta_{(Cr)l,c} = 0.09$	$\alpha_{(Cr)l,c} = 0.40$ $\beta_{(Cr)l,c} = 0.08$	$\alpha_{(Cr)l,c} = 0.33$ $\beta_{(Cr)l,c} = 0.06$
Fishing Attributes					
Skill level for angler type-c	q_c	0.09	0.03	0.06	0.08
Selectivity for angler type-c	$sl_{l,a,c}$	$\beta_{1,c} = 10$ $\beta_{2,c} = 350$	$\beta_{1,c} = 25$ $\beta_{2,c} = 250$	$\beta_{1,c} = 20$ $\beta_{2,c} = 250$	$\beta_{1,c} = 20$ $\beta_{2,c} = 300$
Probability of releasing legal fish for angler type-c	$\bar{p}_{(r)c}$	0.60	0.25	0.00	0.85
Hooking mortality for angler type-c	M_d	0.05	0.1	0.05	0.05

[a]See Table 4 for functional forms.

effort and the distribution of effort among lakes are iteratively calculated to account for losses due to release mortality. Using sub-year time-steps allows an accurate approximation of how bag and minimum length limits can affect overall harvest rates. Calculations within each iteration are not shown in Table 4 for clarity of presentation. Finally, harvest, release and natural mortality are removed from the population of fish in each lake based on the total effort from each angler type. Recruitment is calculated at the end of each iteration and each age-class is advanced one.

Predicted utility at the end of each iteration is calculated using T4.8, which updates the predicted distribution of angler types among lakes based on T4.9. Final probability distribution of angler types among lakes is calculated by updating the previous prediction with a degree of relaxation (δ; T4.10). The relaxation parameter prevents undue oscillation of effort among lakes to aid in convergence (Carruthers et al., 2018). Each model simulation was evaluated after the system reached equilibrium.

Management objective

The performance of management strategies was evaluated using a penalized total value, which maximizes recreational benefit until conservation risk is compromised. The conservation metric used was spawner potential ratio (SPR; Walters and Martell, 2004), which is the ratio of egg production per recruit under exploitation relative to the unexploited state. An SPR < 0.3 (Walters and Martell, 2004) is generally considered an early indication of recruitment overfishing (although (Clark, 2002) suggests 0.4 for sensitive and/or long-lived species). A penalty was calculated for each population l, calculated as

$$P_l = \frac{(min(SPR_l, 0.3) - 0.3)^2}{0.3}, \tag{1}$$

which increases from zero each time the population exceeds the conservation threshold of SPR = 0.3. The penalty for each lake was applied to the utility of each angler type for that lake. Penalized value for an angler type is simply the sum of penalized utility across lakes:

$$V_{(p)t,c} = \sum_{l=1}^{L} \left(U_{l,t,c}(1 - P_l)\right). \tag{2}$$

This formulation means landscape value increases with the sum of lake-specific utilities across the landscape, but utility for any lake will decline to zero as

Table 4. Dynamics of the recreational fishing bioeconomic model.

Parameters		
T4.1	$\omega = \left\{ \begin{array}{c} \alpha_{(C)c}, \alpha_{(H)c}, \alpha_{(S)c}, \alpha_{(D)c}, \alpha_{(Cr)c}, \beta_{(C)c}, \beta_{(H)c}, \beta_{(S)c}, \beta_{(D)c}, \beta_{(Cr)c}, U_{(o)c}, U_n, d_l, \delta, E_{max,c} \\ \beta_{1,c}, \beta_{2,c}, cv, q_c, d, K, M, AR_l, \bar{p}_{(r)c}, M_d, p_{fem}, w_{egg} \end{array} \right\}$	
Management controls		
T4.2	$\{\mathrm{BL}_l, \mathrm{ML}_l\}$	
Angler utility		
T4.3	$U_{(C)l,t,c} = \alpha_{(C)c} + \beta_{(C)c} log_{10}\left(\frac{C_{l,c}}{E_{l,c}}\right)$	Part-worth utility for catch rates for angler type-*c* on each lake *l* in year *t*
T4.4	$U_{(H)l,t,c} = \alpha_{(H)c} + \beta_{(H)c} log_{10}\left(\frac{H_{l,c}}{E_{l,c}}\right)$	Part worth utility for harvest rates for angler type-*c* on each lake *l* in year *t*
T4.5	$U_{(S)l,t,c} = \alpha_{(S)c} + \beta_{(S)c} log_{10}\left(\frac{sl_{l,a} N_{l,a} L_{l,a}}{\sum_a sl_{l,t} N_{l,a}}\right)$	Part worth utility for mean length of fish captured for angler type-*c* on each lake *l* in year *t*
T4.6	$U_{(D)l,c} = \beta_{(D)c} log_{10}(d_l)$	Part worth utility for distance for angler type-*c* on each lake *l*
T4.7	$U_{(Cr)l,t,c} = \alpha_{(Cr)c} + \beta_{(Cr)c}\left(\frac{\sum_c E_{(tot)c}}{365}\right)^2$	Part worth utility for crowding for angler type-*c* on each lake *l* in year *t*
T4.8	$U_{l,t,c} = U_{(0)c} + U_{(C)l,c} + U_{(H)l,c} + U_{(S)l,c} + U_{(D)l,c} + U_{(Cr)l,c}$	Conditional indirect utility of angler type-*c* for fishing in year *t*.
Angler effort dynamics		
T4.9	$\hat{p}_{l,c} = \frac{\exp(U_{l,c})}{\left(\exp(U_n) + \sum_{l=1}^{L} \exp(U_{l,c})\right)}$	Probability of angler type-*c* choosing to fish at lake *l*
T4.10	$p_{l,c,i} = \hat{p}_{l,c}(1-\delta) + p_{l,c,i-1}\delta$	Realized probability of angler type-*c* choosing to fish at lake *l*
T4.11	$E_{l,c} = E_{max,c} p_{l,c,i}$	Effort on each lake by angler type-*c*
Fishing catchability and selectivity		
T4.12	$sl_{l,a,c} = \left(1 + e^{-\left(L_{l,a} - \beta_{2,c}\right)/\beta_{1,c}}\right)^{-1}$	Size-based selectivity to capture
T4.13	$sl_{(H)l,a} = \left(1 + e^{-1.7(L_{l,a} - \mathrm{ML}_l)/(L_{\infty,l} cv)}\right)^{-1}$	Size-based selectivity to harvest based on minimum length limit (ML_l)
T4.14	$q_{l,c} = q_c \left(\frac{\sum_{a=1}^{A} N_{l,a} sl_a}{\varphi_{(V)l,c}}\right)^{d-1}$	Density-dependent catchability
Fish population dynamics		
T4.15	$L_{\infty,l} = \frac{\gamma_{(1)l}}{1 + \gamma_{(2)l} L_{(2)l}}$	Asymptotic length
T4.16	$L_{l,a} = \begin{cases} L_{\infty,l}(1 - e^{-K}) & a = 1 \\ L_{\infty,l} + (L_{l,a-1} - L_{\infty,l}) e^{-K} & a > 1 \end{cases}$	Length-at-age
T4.17	$Z_{l,a} = M + \sum_c q_{l,c} E_{l,c}$	Total instantaneous fishing mortality rate
T4.18	$C_{l,c,a} = \frac{N_{l,a} sl_{l,a} q_{l,c} E_{l,c} AR_l}{Z_{l,a}}\left(1 - e^{-Z_{l,a}}\right)$	Total catch
T4.19	$C_{(Leg)l,c,a} = C_{l,c,a} sl_{(H)l,a}$	Total legal catch
T4.20	$CPUE_{(Leg)l,c,a} = \frac{C_{(Leg)l,c,a}}{E_{l,c}}$	Legal catch per effort
T4.21	$p_{(ret)l,c,a} = \frac{\sum_{x=1}^{100}\left[\min(x, \mathrm{BL}_l)\left(\frac{CPUE_{l,c,a}{}^{x} e^{-CPUE_{l,c,a}}}{x!}\right)\right]}{CPUE_{(Leg)l,c,a}} \bar{p}_{(r)c}$	Exploitation rate due to retention given bag limit
T4.22	$H_{l,c,a} = p_{(ret)l,c,a} C_{(Leg)l,c,a}$	Total legal harvest
T4.23	$HM_{l,c,a} = H_{l,c,a} + M_d\left[\left(1 - p_{(ret)l,c,a}\right) C_{(Leg)l,c,a} + \left(1 - sl_{(H)l,a}\right) C_{l,c,a}\right]$	Total harvest and release mortality
T4.24	$f_{l,t} = max\left(0, \bar{w}_{l,a} - \bar{w}_{(m)l,a}\right)/w_{egg} p_{fem}$	Size-based fecundity
T4.25	$Egg_l = \sum_{a=1}^{A}(f_{l,a} N_{l,a})$	Egg density
T4.26	$N_{l,a} = \begin{cases} \frac{Egg_l \alpha_{(1)l}}{1 + Egg_l \alpha_{(2)l}} & a = 1 \\ \left(N_{l,a-1} - \frac{\sum_c HM_{l,c,a}}{AR_l}\right) e^{-M} & a > 1 \end{cases}$	Fish density

SPR for that population declines below 0.3. Multiplying the utility and conservation objectives effectively scales them to produce a single objective value for each angler type. Total landscape value of the fishery in year-t is given as the geometric mean of penalized values across angler types multiplied by the total fishing effort that year

$$V_{(p)t} = \prod_{c}^{n_c}\left(\sqrt{V_{(p)t,c} N_c}\right) \cdot \sum_{l=1}^{L}\sum_{c}^{n_c} E_{l,t,c}. \tag{3}$$

Taking the geometric mean of value across angler types ensures realized values of each types are traded off, promoting equity among angler types during optimization. Multiplying the geometric mean of value by total effort promotes strategies that increase angler participation.

Simulations

Fishing regulations were used as the primary control over fisheries across the landscape. Fisheries managers typically assign regulations from a few discrete choices rather than tightly linking regulations to biology (e.g. assigning a standard minimum length harvest limit rather than one relative to maximum length or size at maturity; van Poorten et al., 2013). Therefore, the regulation options considered were a combination of bag limits (0, 1, 2, 4, no limit) or minimum length harvest limits (no limit, 300 mm, 400 mm, 500 mm). These discrete options led to 17 regulation combinations (since a zero fish bag limit, or catch-and-release, does not interact with length limits) ranging from very liberal (unlimited bag limit; no minimum length) to very conservative (catch-and-release).

The landscape model was used to evaluate how different management strategies perform under a combination of scenarios representing variation in fish biology across lakes and angler heterogeneity. There were four management strategies evaluated. The first is a one-size-fits-all (OSFA) strategy, which is evaluated as the single best combination of bag and length limits to apply to all fish populations. The second is a biologically optimal strategy, which sets regulations based on the maximum length of fish in a lake. Biological regulations take advantage of the natural size-density gradient across populations to provide a variety of fishing experiences. Lakes within the top 25th percentile of unfished asymptotic lengths ($L_{\infty,l}$) were assigned a 500 mm length limit to promote large fish; lakes within the second 25th percentile of $L_{\infty,l}$ were assigned a 2-fish bag limit and 400 mm length limit to provide some harvest of larger fish; lakes within the third 25th percentile of $L_{\infty,l}$ were assigned no regulations to provide harvest opportunities in naturally high density lakes; and populations within the lower 25th percentile of $L_{\infty,l}$ were assigned catch-and-release regulations to preserve the naturally high density (and small body size) of fish. The third management strategy is a socially optimal strategy, which is evaluated as the best combination of bag and length limits if all anglers were of a single angler type. These four regulations (one for every angler type) are then applied randomly to lakes based on the proportional make-up of anglers. The final management strategy is the buffet of regulation combinations, evaluated using a simulated annealing algorithm, which allows optimization across discrete parameter combinations (such as bag and length limit options). The algorithm iteratively changes management combinations on each lake and evaluates the overall performance metric (total landscape value) at equilibrium until the best combination of regulations on each lake across the landscape is found. Regulations are optimized using the simulated annealing optimization algorithm within the rgenoud package (Mebane and Sekhon, 2011) in the R statistical programing language (R Core Development Team, 2016).

Managers are unlikely to use a wide variety of regulation combinations when choosing how to manage a fishery. Except in special circumstances, it is most likely that they favor a small subset of regulation combinations, likely those that provide a wide variety of harvest opportunities and safeguards against overfishing. This strategy also promotes regulation simplification, which is preferable to anglers (Lester et al., 2003). To reflect this, a fifth management strategy was considered, which was identical to the buffet management strategy above, but with only five extreme regulation combinations considered by the optimization algorithm. These regulation combinations ranged from catch-and-release to unregulated. As with the buffet strategy, the exact regulation applied to each lake was found using a simulated annealing optimization. This strategy is referred to as a reduced buffet management strategy.

Performance of the five management strategies was evaluated assuming three levels of social-ecological complexity, each representing a different hypothesis of variation in the system. The first level was an idealized system with all fish populations identical and all anglers of a single angler type. Fish population parameters were determined by setting all unfished recruits and asymptotic lengths to the mean value (e.g. $R_{0,l} = \mu_{R_0}$ and $L_{\infty,l} = \hat{L}_{\infty,l}$). Angler parameters were determined by setting all utility and attribute parameters to the mean value across angler types. The second level of complexity represented all anglers as a single angler type but each fish population was unique. The final level of complexity is the most realistic where there are four angler types, each with unique preferences and attributes, and a fully heterogenous fishery landscape where each fish population has a distinct size structure and abundance.

Sensitivity analyses were conducted to determine how sensitive the model is to parameter specification and how sensitive the system is to regulation choices. Model sensitivity was evaluated using elasticity, which is evaluated as the proportional change in landscape value with a ±10% change in a parameter. Elasticity was evaluated under one-size-fits-all catch-and-release regulations. Sensitivity of the system to misspecification of regulations was evaluated as the proportional change in landscape value between the optimal diversified buffet strategy and value calculated when 2–50 (in increments of 2) lakes are incorrectly assigned regulations. Random regulation misspecification for a random lake was repeated 100 times to demonstrate the range of possible changes in landscape value.

Results

The total landscape value of the recreational fishery under a single one-size-fits-all regulation was evaluated under three scenarios: (1) all fish populations are equivalent and no angler heterogeneity; (2) all fish populations are unique but no angler heterogeneity; and (3) all fish populations are unique and anglers are of four angler types. The single regulation for each of these scenarios that maximized penalized value was used as the one-size-fits-all strategy for later simulations. Under the simplest scenario, a one-fish bag limit combined with a 400 mm length limit ("one-over 400 mm regulation") provides the best landscape value (Figure 2; top row). It is largely unnecessary to protect smaller fish in this scenario using a minimum length limit because all lakes have the same size structure and anglers do not particularly target fish with large body sizes. The 500 mm length limit provided nearly the same landscape value as catch-and-release because few fish were large enough to exceed the minimum length limit. Bag limits alone or with low minimum length limits were not enough to protect against conservation concerns due to the potential to overfish some populations (Figure 2; top-right panel); the reduced value of these regulations was a reflection of conservation concerns and reduced catch rates, despite an increased opportunity for harvest and moderate increase in fish size due to density-dependent growth. When fish populations are unique but anglers are homogeneous in their multi-attribute utility functions and impacts, a one-over 400 mm regulation was once again the preferred regulation, which maintains catch rates over a wide range of fish population size structures and protects against overfishing, yet still

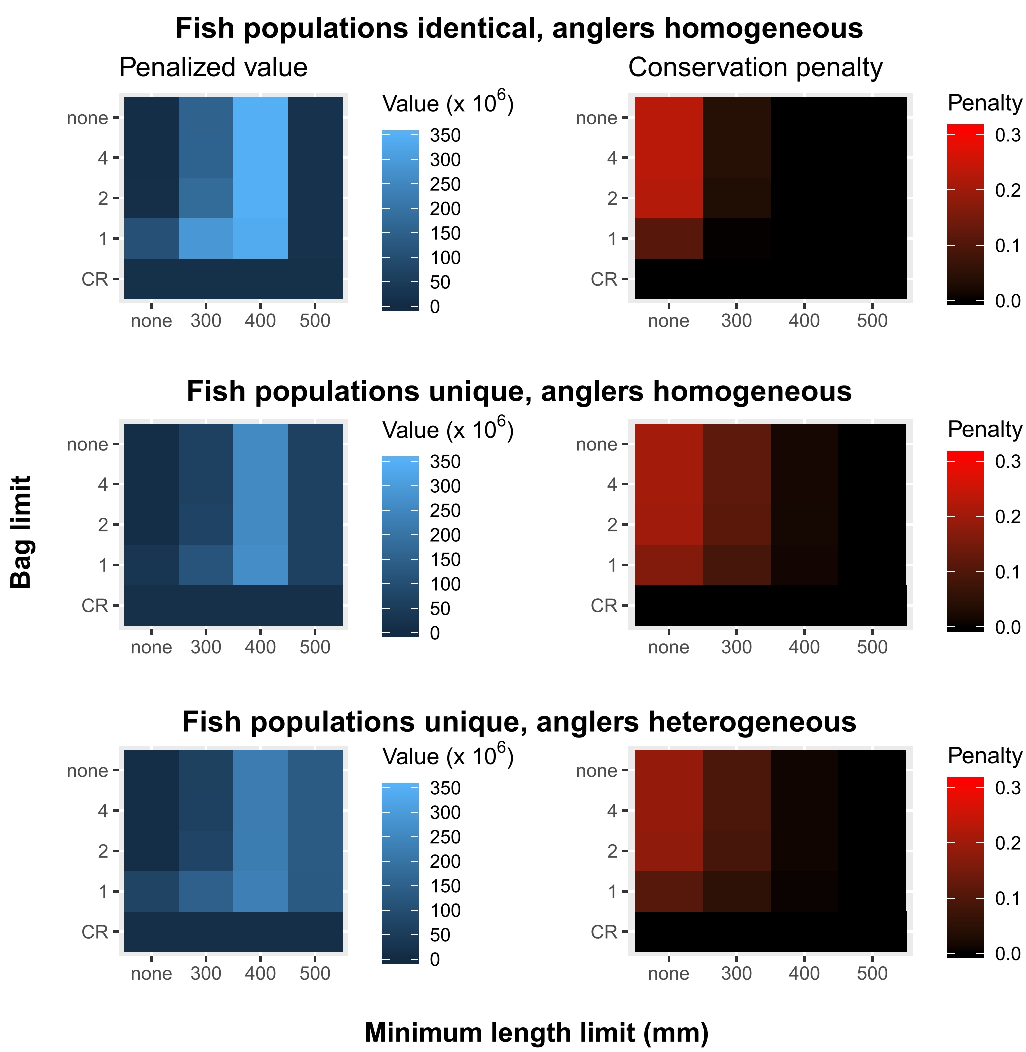

Figure 2. Penalized landscape value (left column) and conservation penalty applied to landscape value (right column) under combinations of bag limits (catch-and-release; 1, 2, or 4 daily harvest limit; no limit) and minimum length limit (no limit; 300, 400, or 500 mm minimum length limit). Panel rows refer to the complexity of the system. Top row: all fish populations are identical and all anglers are homogeneous; middle row: each fish population is unique and all anglers are homogeneous; bottom row: each fish population is unique and anglers belong to one of four homogeneous angler types.

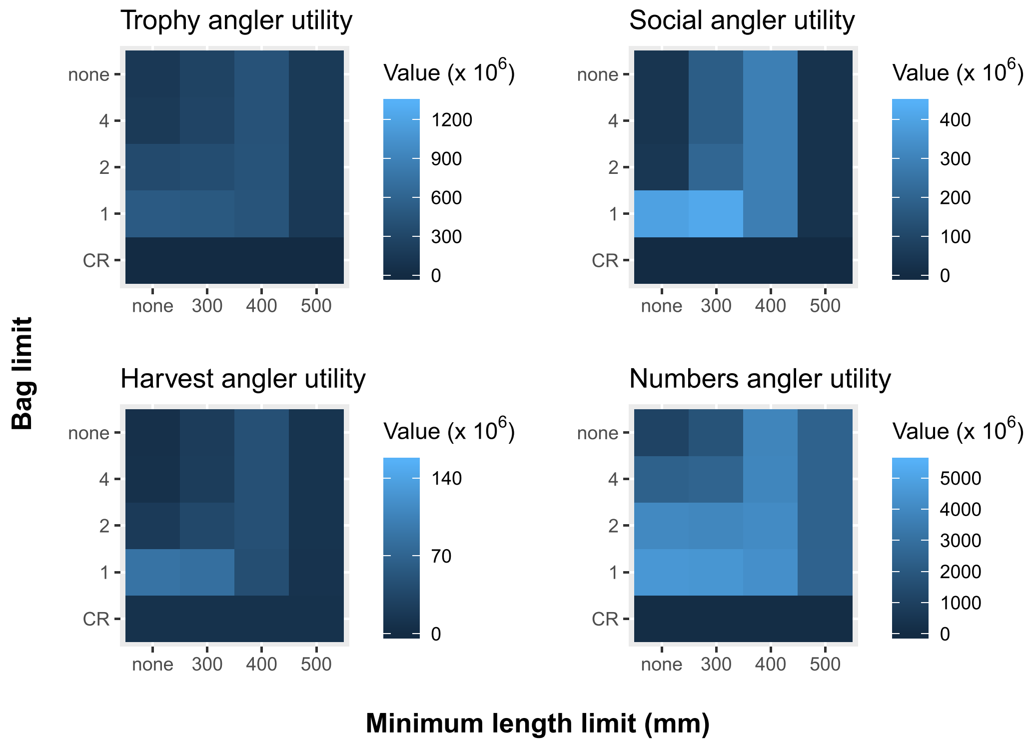

Figure 3. Penalized landscape value under combinations of bag limits (catch-and-release; 1, 2, or 4 daily harvest limit; no limit) and minimum length limit (no limit; 300, 400, or 500 mm minimum length limit). Each panel depicts a situation where all anglers are homogeneous and utility functions are that of either the trophy (top left), social (top right), harvest (bottom left), or catch (bottom right) angler type. Note scales differ among panels.

provides harvest opportunities (Figure 2; middle-left panel). Note the 500 mm minimum length limit provides much greater value in this scenario because the variation in size structure among fish populations means there are more opportunities to harvest large fish across the landscape. In this scenario anything less than a 400 mm minimum length limit can cause overfishing, resulting in a conservation penalty (Figure 2; middle-right panel). When fish populations are unique and anglers are heterogeneous the best single regulation to set on all lakes is again a one-over 400 regulation, which provides harvest opportunities for harvest-oriented anglers yet still effectively protects against overharvest (Figure 2; bottom row). Again, the 500 mm minimum length limit provides greater value still because there is now variation in utility for large fish among anglers in this scenario. Note that the exact combination of regulations that result in the maximum landscape value is entirely dependent on the parameterization used in the simulation model. Different parameter combinations may lead to changes in the relative value achieved across regulation combinations.

Four social regulations were identified by determining which single regulation would provide the greatest value if all anglers were of one of the four angler types (Figure 3). Based on the parameterization of anglers and the fishery landscape, the highest penalized landscape value was obtained with a one-fish bag limit for trophy, harvest, and numbers-oriented angler types, respectively. Social anglers prefer a one-over 300 mm regulation. The absolute landscape value achieved with these regulations varied substantially: numbers-oriented anglers had a penalized value nearly ten times that of any other angler type.

When fish populations were identical and anglers were of a single, average angler type, there was no improvement in value when providing lake-specific regulations over the one-size-fits-all (OSFA) strategy, determined to be the one-over 400 mm regulation (Figure 4; top left panel). The buffet strategy also applied the one-over 400 mm regulation to all lakes since all anglers uniformly preferred the same fishing experience. The reduced buffet strategy did not include a one-over 400 mm regulation, so optimal value was much lower; most lakes had a one-over 500 mm regulation or a one-fish bag limit. The proportion of the maximum possible effort exerted under the OSFA and buffet strategies was approximately equivalent (Figure 4; top center panel), and both resulted in similarly high spawner potential ratio (SPR) across populations and management strategies

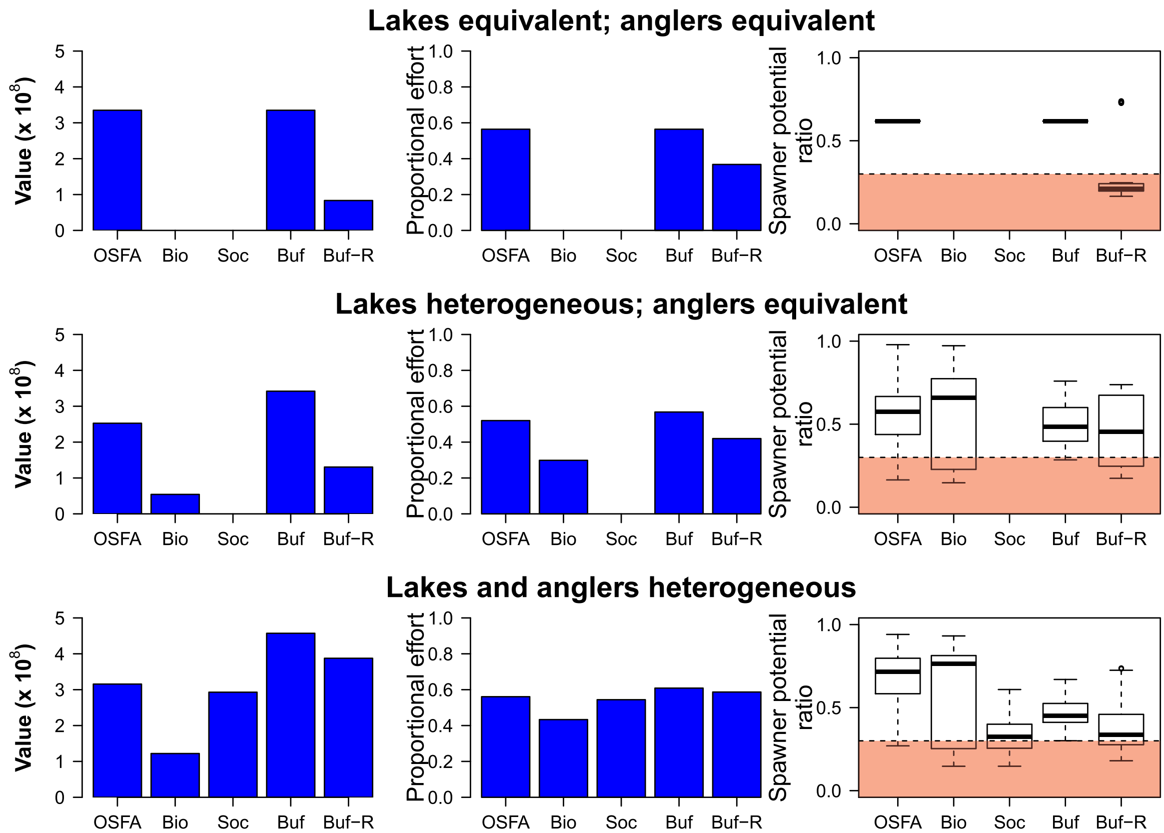

Figure 4. Landscape-level performance of five management strategies: one-size-fits-all (OSFA), biologically-based (Bio), socially-based (Soc), buffet (Buf), and reduced buffet (Buf-R) strategies. Top row of panels represents a situation where all fish populations are identical and all anglers are homogeneous; middle row represents a situation where each fish population is unique and all anglers are homogeneous; bottom row represents a situation where each fish population is unique and anglers belong to one of four homogeneous angler types. Left column shows relative penalized landscape value under each management strategy; center column shows the total proportion of possible fishing effort under each management strategy; right column shows the distribution of spawner potential ratio across lakes under each management strategy.

(Figure 4; top right panel). The reduced buffet option had lower effort and a high proportion of lakes below the conservation threshold. Biological and social strategies for setting regulations were not considered in this context because all lakes and anglers were identical. In a scenario where fish populations were each unique but anglers were homogeneous, the biological strategy had much lower value than the OSFA strategies, suggesting the choice of regulations applied to lakes in the biological strategy may not have led to high satisfaction (Figure 4; center left panel). The buffet strategy had much higher value than any other strategy. Again, because the reduced buffet strategy did not include the optimal OSFA strategy, it still had lower value than under then OSFA strategy. Proportional effort reflected patterns in value, with the buffet strategy resulting in the highest effort (Figure 4; center panel). The OSFA strategy resulted in only one lake below the conservation threshold; other strategies, particularly the biological and reduced buffet strategies, resulted in several populations below the conservation threshold ($SPR < 0.3$; Figure 4; center-right panel).

In the realistic scenario where fish populations were each different and the angling population was made up of four unique angler types, there was a marked difference in performance across fishery regulation strategies (Figure 4; bottom row). The buffet strategy resulted in a penalized value 45% greater than the OSFA strategy, and greater still than the biological and social strategies (Figure 4; bottom-left panel). Value achieved under the reduced buffet strategy was 22% greater than that achieved with the OSFA strategy, but less than under the buffet strategy. Proportional fishing effort was also highest under the buffet strategy, but the relative improvement over other strategies was low (Figure 4; bottom-center panel). The buffet strategies had the best overall conservation outcome, with no populations falling below the 0.3 SPR threshold (Figure 4; bottom-right panel).

The complexity of the social-ecological system where fish populations are unique and the angling population is heterogeneous means aggregate decisions by anglers on whether and where to fish are driven by the many site-specific variables offered by each fishing opportunity. Across all management strategies evaluated, the trophy angler type experienced the highest mean utility across fish populations of any angler type (Figure 5). This is largely a function of the type of landscape created and the high fishing effort, which reduced densities on many lakes, increasing mean body length of fish. The OSFA management strategy produced extremely low utility for harvest anglers because there was limited harvest opportunities offered across the landscape. Biological and social strategies affected each angler type differently. For example, harvest-oriented anglers had improved utility and effort under the social strategy, but trophy and numbers-oriented anglers had much lower utility and effort than under the OSFA strategy. The buffet strategy resulted in slight reductions in mean value for trophy- and numbers-oriented anglers, but improved landscape value by increasing the value of fishing opportunities for social and harvest-oriented anglers. The ability for the buffet strategies to provide relatively high utility opportunities for all angler types resulted in higher multiplicative utility for the fishery as a whole.

Several patterns emerge when examining where regulations applied to fish populations across the realistic landscape under the reduced buffet strategy (Figure 6). Angling pressure had a noticeable effect on density-dependent parameters (recruit density and asymptotic length) in fished (Figure 6; lower panels) versus unfished populations (Figure 6; upper panels). Most lakes, regardless of their proximity to the population center, were often regulated with a 1-fish bag limit. This regulation often protects against overharvest, yet still provides a diversity of fish size-number combinations. Populations with the largest fish were invariably regulated with one-over 500 mm regulations, which protects against removal of the largest fish. Some populations located close to, and at an intermediate distance from the population center, and with a high maximum size and high density, were occasionally regulated with a 500 mm minimum length limit, which also preserves the largest fish, but permits greater harvest opportunity. The pattern of exploitation and regulations also seems to shift the size-structure of populations. Most lakes are lower abundance than the unfished state, but this results in a larger size-structure, which favors a general desire for larger fish among all angler types. As noted above, this resulted in some populations dropping below the conservation threshold of SPR = 0.3, exposing a tradeoff between angler satisfaction and conservation.

Sensitivity of the model was evaluated by calculating elasticity to changes in parameters associated with each angler type and biology of fish populations separately. Penalized landscape value was relatively inelastic to utilities anglers derive from some aspects of fishing, namely the logistic inflection parameter for

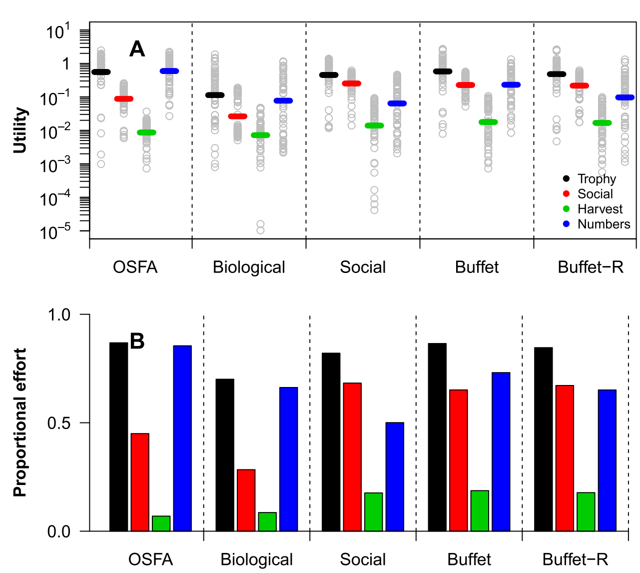

Figure 5. Angler type-level performance when each fish population is unique and anglers belong to one of four homogeneous angler types of five management strategies: one-size-fits-all (OSFA), biologically-based, socially-based, buffet, and reduced buffet (Buffet-R) strategies. Top panel shows the utility experienced by each angler type at each lake (open circles); colored bars represent the mean utility experienced by an angler type across all fish populations. Bottom panel shows the proportion of possible fishing effort exerted across the landscape by each angler type under each management strategy.

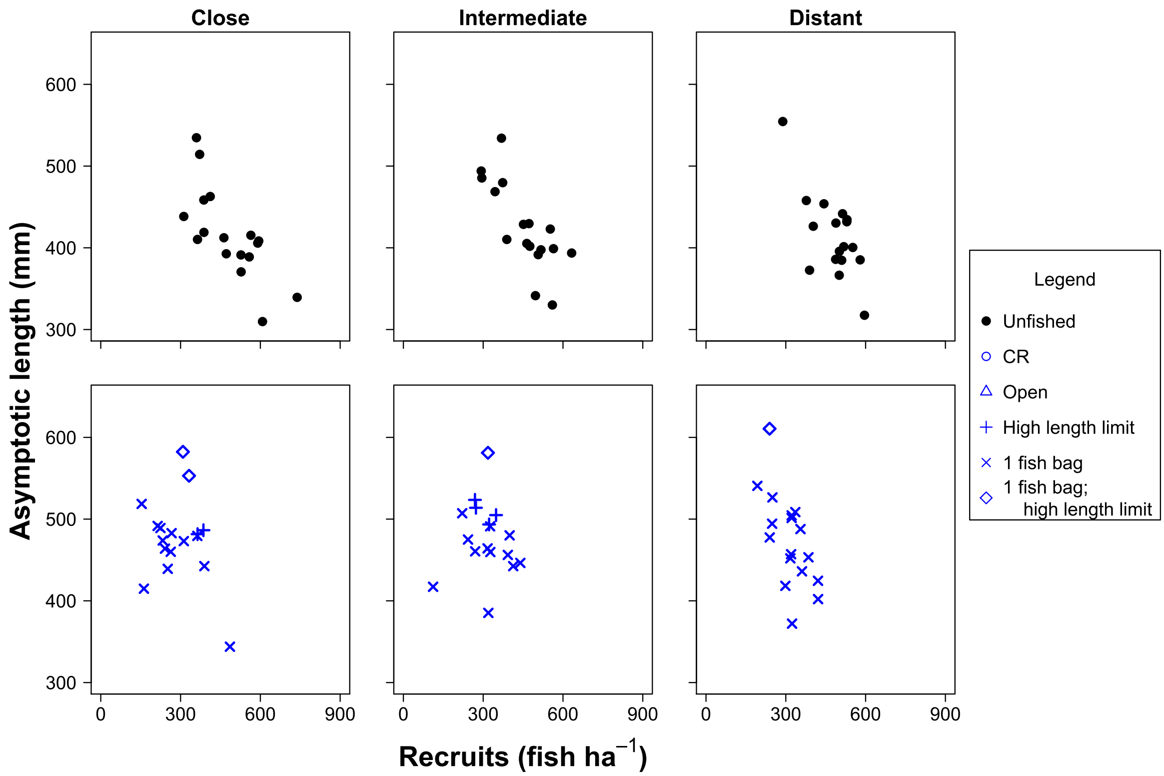

Figure 6. Top row: relative population-level asymptotic lengths and recruits under unfished conditions for populations close, intermediate and distant from the angler population source. Bottom row: relative population-level asymptotic lengths and recruits under equilibrium fished conditions for the same populations when a reduced buffet management strategy is employed on the landscape. Symbols in the bottom panels represent fishing tactics employed on each population under the reduced buffet management strategy.

mean daily harvest, catch and crowding (Figure 7A). Conversely, angler types with high logistic inflection parameters for any trait, especially fish length and distance to lakes, were most sensitive to those traits (i.e. angler types with high logistic inflection parameters were more elastic to those parameters). The model did have high and asymmetric elasticity to catchability with increases in catchability generally resulting in large reductions in landscape value. The model was inelastic to the selectivity and retention rate parameters. The model was sensitive to discard mortality imposed by each angler type, with increases in discard mortality often resulting in reductions in value (Figure 7A). Elasticity of the model to biological parameters revealed a general sensitivity to productivity parameters (R_0, L_∞, K, M), but insensitivity to others.

The relative change in landscape value when regulations are incorrectly applied was evaluated to determine how sensitive the system is to regulations and the relative importance of correctly identifying appropriate regulations. Figure 8 shows the distribution of landscape values calculated over 100 simulations when between two and 50 lakes had incorrect regulation

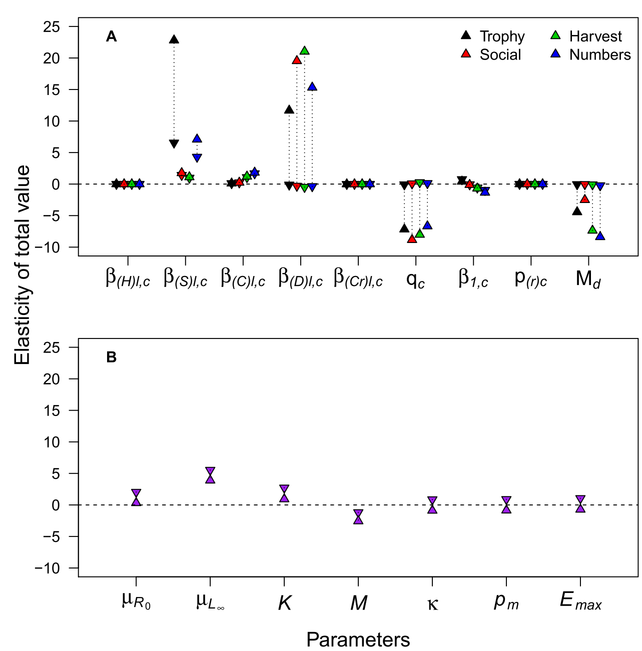

Figure 7. Elasticity of model landscape value relative to one-size-fits-all catch and release regulations. Panel A shows elasticity of social (length at 50% utility) and fishery parameters; panel B shows elasticity of ecological parameters. Up and down pointing parameters depict elasticity when specified parameters are increased or decreased by 10%, respectively.

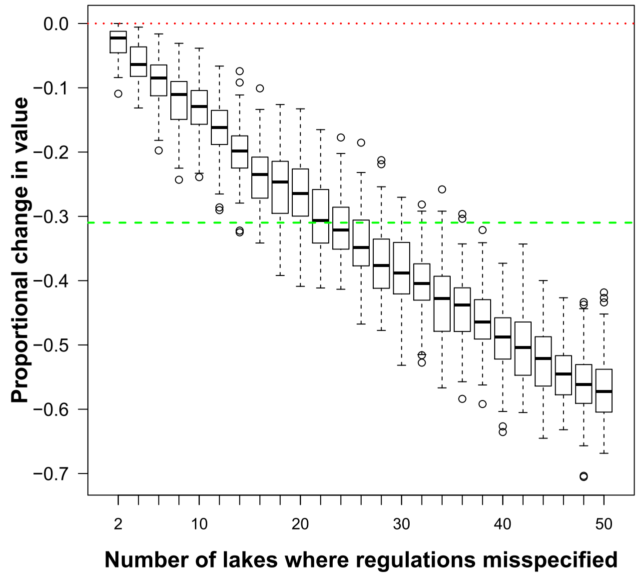

Figure 8. Proportional change in landscape value when regulations on two or more lakes are misspecified relative to the optimal set of regulations across lakes. Dotted horizontal line represents landscape value when all lakes are regulated in a way that results in optimal landscape value; dashed horizontal line represents landscape value achieved under the best one-size-fits-all (400 mm minimum length limit) regulations.

assignments relative to the optimal landscape value. Sensitivity is obviously influenced by which lakes are misspecified and which regulation was applied, with even two incorrectly regulated populations resulting in value ranging from being unchanged to over 10% lower than optimal. In the simulated landscape, only when more than 50% of lakes are incorrectly assigned regulations, did the median value decline to what would be achieved with a one-size-fits-all strategy.

Discussion

Overview of direct implications for fisheries management

This work demonstrates how spatially explicit, purposefully diversified buffet-style management strategies may offer broad improvements for diverse recreational fisheries. At a regional scale, buffet-style strategies outperformed optimally designed OSFA and other management strategies in terms of greater overall and more even (across angler types) utility and effort, generally without inducing substantial fishery overharvest. This means buffet style strategies can potentially simultaneously address the common recreational fisheries management objectives of satisfying anglers and conserving fish populations (Hilborn, 2007; Cowx et al., 2010). Since these objectives often have been traditionally thought to conflict and create tradeoffs (Cheung and Sumaila, 2008; Garcia-Asorey et al., 2011; Thebaud et al., 2014; Camp et al., 2017), these results should be particularly relevant to management agencies concerned with socioeconomic-conservation tradeoffs. Notably, the buffet-style approach has flexibility to be adapted to a diverse suite of multiple, potentially conflicting management objectives, but this will be easier if these multiple objectives are explicitly recognized.

Buffet-style strategies may be attractive to recreational fisheries management agencies for several secondary reasons. First, the buffet style strategies proved robust to imperfect implementation—i.e. applying a less-than-ideal regulation to any particular waterbody. Imperfect implementation of a full buffet style management strategy can occur if waterbody-specific fish populations and region-specific angler types are not thoroughly understood, which is likely in many areas (Radomski et al., 2001; Lester et al., 2003; Carpenter and Brock, 2004; Hansen et al., 2015a). Furthermore, improvements over optimal OSFA or other strategies are still possible under the reduced-buffet strategies. The simplicity of the reduced buffet strategy should make it attractive to agencies seeking to diversify angling experiences (Carpenter and Brock, 2004; Cooke et al., 2016) without implementing too many waterbody-specific regulations that may confuse anglers and law enforcement or prevent systematic learning (Lester et al., 2003; Hansen et al., 2015a). Finally, by supporting more even distributions of effort and utility across different types of anglers, buffet-style strategies may diminish dissatisfaction or disenfranchisement of angling groups, a prominent concern to managers and decision makers (Pope, 1983; Arlinghaus, 2005, 2007; Hilborn, 2007). More even effort across angler types may also facilitate recruiting and retaining a diversity of angling participants to sustain socio-ecological angling systems (Wightman et al., 2008; Aas and Arlinghaus, 2009), which is like to be especially important in the context of angler demographic shifts (Arlinghaus et al., 2015).

Mechanisms driving success of buffet-style strategies in recreational fisheries

Differences between buffet-style and alternative management strategies were partly due to how each addresses angler heterogeneity. The importance of heterogeneity has been established (Beardmore et al., 2013; Johnston et al., 2013), but past studies have largely addressed heterogeneity and resultant tradeoffs by searching for the single best compromise regulation (Johnston et al., 2010; Gwinn et al., 2013). These approaches, similar to the OSFA results of this study, will almost always be less-than-optimal for any single angler type because they are a compromise across all angler types. Buffet-style strategies avoid this by implementing regulations to purposefully vary fishing experiences that match motivations of all angler types. At a regional scale, this allows for increased utility over all types of angler, as well as a greater diversity of types of anglers achieving high degrees of utility, compared to even an optimal OSFA strategy. The concept of doing different things in different places is exceedingly simple and not new to natural resource management—indeed some management agencies implicitly apply this logic when implementing, for example, gear-specific regulations to provide different angling opportunities. However, diversified approaches rarely have been studied in recreational fisheries (Lester et al., 2003; Carpenter and Brock, 2004), and this likely hampers broader and more strategic implementation of such approaches. This work shows it seems to work particularly well in recreational fisheries because of the feedbacks by which collective angler behaviors sculpt angling experiences.

The diversity of fishing experiences created by buffet-style management promotes synergies with socio-ecological feedbacks common to recreational fisheries systems with diverse anglers (Hunt et al., 2013a, Ward et al., 2016; Arlinghaus et al., 2017). Heterogeneous angler types characterized by corresponding behaviors (e.g. catch and release) exert patterned influences on fish population dynamics, which allows anglers to further mold fishing opportunities (Johnston et al., 2010; Camp et al., 2015; Ward et al., 2016). In an OSFA strategy, identical regulations likely encourage multiple angler types to essentially shape a given fishery in potentially opposite ways. For example, the effects of catch-rate-oriented anglers releasing most of their catch might be largely undone if trophy-oriented anglers increase harvest of smaller fish to promote trophy growing conditions. As these competing feedbacks play out across landscapes, fish populations that may have initially been biologically diverse should become more homogenized (Cox et al., 2002; Camp et al., 2015), and result in lower diversity of angling opportunities. Despite these interactions, some sorting will occur across the landscape due to the effect on driving distance, where more distant populations have lower fishing mortality and concurrent changes in population structure (Parkinson et al., 2004; Askey et al., 2013; Wilson et al., 2016). Conversely, the purposefully diversified regulations of a buffet-style management strategy should better sustain diverse fishing opportunities by encouraging anglers to “self-sort” towards locations best suited to their desires. For example, implementing trophy regulations on any given water served to redirect harvest-oriented anglers from those waters and to others, better allowing trophy anglers to mold a larger size structure of the fish population. The key of buffet-style management is that these potentially competing fishery uses are spatially separated, similar to how Marine Spatial Planning or Coastal Zone Management (e.g. Tiller et al., 2012) functions. This lets each objective be maximized within a region, creating better options for different types of anglers and leading to greater fishing effort.

Buffet-style management in the context of previous studies

The buffet style management strategy described here builds off of a small number of previous studies as well as some established concepts in recreational fisheries management. Management agencies have long-recognized that different anglers have different preferences, and certainly some recreational fishery regulations are designed to promote different fishing experiences or to address biological differences in fish populations. For example, stream salmonid fisheries have a long history of being regulated with a subset of waters reserved for catch and release only, or special gear (e.g. fly fishing), while others allow more general gear and/or harvest (Gigliotti and Peyton, 1993; Aas et al., 2000). Such regulations are intended to promote a variety of opportunities for diverse anglers (Engstrom-Heg, 1981; Carpenter and Brock, 2004), as well as to protect more vulnerable fish populations (Post et al., 2003). While there is abundant literature describing angler diversity and preferences for diverse elements of the recreational fishery experience (Fisher, 1997; Wild et al., 1998; Oh and Ditton, 2006), and while the concept of using regulations to promote such diversity is likely familiar to many agencies (Radomski et al., 2001), very little literature exists describing how this ought to be accomplished (Carpenter and Brock, 2004). One-size-fits-all strategies are likely to leave diverse anglers dissatisfied (Carpenter and Brock, 2004), and risk overfishing, especially of easily accessible waters (Post et al., 2002; Hunt et al., 2011). But myriad, waterbody-specific regulations cannot be practically supported by scientific sampling (Shuter et al., 1998), while causing substantial confusion to anglers and law enforcement alike (Lester et al., 2003). What this work does is to introduce buffet-style strategies, especially reduced-buffet options, as a practical compromise between OSFA and overly complex strategies. Specifically, buffet-style management goes beyond randomly providing diverse opportunities to match angler motivations (e.g. the "social" strategy evaluated) to suggest quantitatively evaluating how to use regulations to improve angler utility and conservation outcomes, either through simulation or adaptive management. Equally importantly, this work provides a framework where none existed for agencies to design and implement strategies that serve diverse anglers.

This idea of spatially separating potentially competing uses has been sparsely invoked for recreational fisheries (Aas et al., 2000) but is not new to natural resource management. Buffet-style strategies largely borrows principles from marine spatial planning on zoning research (Crowder and Norse, 2008; Halpern et al., 2008). For example, a common application of marine spatial planning is siting marine protected areas and those intended for specific fisheries to minimize conflict and support multiple objectives (Walters et al., 2007; Agardy et al., 2011). Spatial separation is also common in inland waters, where zoning may separate, for example, swimming or diving areas from pleasure boating or fishing, from other industry such and energy generation (Rees et al., 2010; Christie et al., 2014). The application of these zoning and spatial planning principles has long been recognized in wildlife management to provide diverse opportunities to stakeholders hunting at different times of year or with varying weapons (Hendee, 1974; McCorquodale, 1997), as well as to sustain vulnerable populations of game and non-game species (e.g. Bodmer et al., 1994; Bennett et al., 2007). Similarly, spatially explicit strategies based on suitability mapping and land use planning (McHarg, 1969) have long been used to address conflict in outdoor recreation, such as results from competing uses like forestry, hiking, and wildlife conservation (Franklin, 1994; Harris et al., 1995; Kliskey, 2000). These principles have become commonplace in terrestrial and ocean management, while their application to recreational and especially inland fisheries has lagged, despite the seemingly high degree of compatibility with this sector.

Integration with other management approaches

Buffet style strategies compliment one of the most commonly invoked management approaches, adaptive management (Walters, 1986; Walters, 2007). A persistent challenge to learning from deliberate adaptive management experiments of recreational fisheries has been lack of replication of experimental treatments (Walters, 1998; Lester et al., 2003; Hansen et al., 2015a). This occurs when most waters receive individually-designed regulations (no replication; Lester et al., 2003), as well as when all waters receive the same or very similar regulations (no treatment separation; Hutchings et al., 1997; Walters, 1997). In contrast, substantial replication would be possible under reduced buffet strategies that implement a small number of diverse regulations. This could allow for learning about fish population and human behavioral responses to regulations, such as better understanding how anglers select fishing sites, or what types of opportunities are most desired for different types of anglers. This information can help refine buffet style strategies in the future to suit human and resource needs, to adjust to unpredictable but certain environmental changes or perturbations, or to help agencies more proactively understand and incorporate stakeholders in decision making (Carpenter et al., 2017).

Buffet-style management strategies are also imminently compatible with an increasing emphasis on incorporating stakeholders in the fisheries management process itself through collaborative or co-management (Jentoft, 1989; Pomeroy and Berkes, 1997; Granek et al., 2008; Pinkerton, 2011), and related place-based approaches (Young et al., 2007). Co-management promotes stakeholder investment in management that can further socio-ecological resilience

(Ostrom, 1990; Berkes, 2009), and is generally considered most effective when implemented at more local scales where stakeholders are well-connected to the resource (Cheng and Daniels, 2003; Gutierrez et al., 2011; Edwards and Stephenson, 2013). The flexibility and diversity of buffet-style strategies allows for, and would probably benefit from, agencies seeking greater local stakeholder input and involvement with recreational fisheries regulations. Potential examples could span a continuum of stakeholder inclusion, from involvement in assigning agency-determined regulations to specific waters, to stakeholders helping to define the suite of regulations to be applied. At a time when many recreational fisheries governance agencies are recognizing the need for greater stakeholder participations in the management process (Granek et al., 2008), buffet-style strategies may serve as a valuable tool to facilitate this in a flexible and progressive manner.

Assumptions, caveats, and limitations

One assumption central to this work and previous studies (e.g. Johnston et al., 2010) is the explicit formulation of a quantitative management objective. For this specific study, a management objective must be specified to select optimal OSFA strategies and to assign regulations to waterbodies under buffet-style management. Past studies have addressed the ambiguity of recreational fisheries management objectives differently. Johnston et al. (2010) compared how sociological objectives and overfishing risk trade off; Fenichel and Abbott (2014) used a suite of economic objectives. Here, a single, multi-attribute objective function (Kiker et al., 2005) was used as a simple representation of what is often considered important by management agencies: angler utility that leads to satisfaction, and risk of overfishing (Larkin, 1977). Clearly these are not the only aspects that could be considered, and does not include license sales, political expediency, or other less-often-stipulated attributes that are likely important to management agencies (Lackey, 1979; Hilborn, 2007). While otherwise-formulated objectives might result in different OSFA optimal regulations (with respect to length and bag limits), there is no reason to expect them to alter meaningfully the pattern of comparison between OSFA and buffet-style strategies. Notwithstanding, this does highlight the importance of future research better describing objectives of a recreational fisheries (Barber and Taylor, 1990).

Another set of assumptions affecting the results presented involve the complexity of the socioecological system represented, which could affect the efficacy of buffet-style strategies. This study assumed a regional recreational fishery system with a single population center, many discrete waters, and a single-species fishery. Many regions, however, have multi-species fisheries that can compete, such as between introduced and native species fisheries (e.g. Churchill et al., 2002; Carey et al., 2011), or between native species that ecologically interact (Rowe, 2007; Hansen et al., 2015b, 2017). Additional research is required, but buffet-style strategies may still function in multi-species fisheries if ecological interactions among species are not wholly mutually exclusive. Additional complexities would emerge with recreational use coexists with subsistence or commercial pressure; these situations would require careful thought and experimentation. A greater challenge is posed by landscapes with sparse and indivisible waters (e.g. reservoirs, rivers with migrating fish populations, marine systems). Landscapes with few, large waters lacking natural spatial “boundaries” should impede creating discrete angling opportunities. Indeed, these boundary issues are considered some of the most challenging for marine spatial planning approaches (Walters, 2000; Young et al., 2007; Kellner et al., 2007). Similarly, buffet style strategies should become unnecessary with increasing angler homogeneity, since in these cases OSFA strategies will perform as well as buffet style strategies, without the added cost of additional regulations (Johnston et al., 2010; Gwinn et al., 2013).

Buffet-style management strategies can create additional challenges to recreational fisheries management. Buffet-style management will require initial research to identify a suite of diverse potential regulations to implement across a region, especially given the model sensitivity to regulations considered. Selecting regulations types requires understanding angler characteristics and preferences, as well as biological attributes of fish populations. Assessing both is subject to observation and process error that may complicate assessments. For example, fish populations may not be at equilibrium when surveyed owing to past histories of harvest altering size structure and abundance (Barnett et al., 2017). Or, different angler types may be statistically assigned to the same group based on their utility to certain catch and non-catch attributes if using a latent class choice model, while they in fact have very different fishing behavior and targeting (Morey et al., 2006; Ward et al., 2013b). Such challenges, however, will exist whenever managers seek to consider human and biological information to support regulatory decision making, and are not exclusive to buffet-style strategies. This reinforces the need to make changes within an adaptive management cycle.

Future directions

There are many options for future expansion of the ideas and applications of buffet-style management strategies described here. While this study focused on fisheries harvest regulations specifically—i.e. length and bag limits—these are but a small component of the total management options available. Other actions such as stock enhancement (Lorenzen, 2008; Camp et al., 2013), habitat restoration (Bolding et al., 2004; Seaman, 2007; Poplar-Jeffers et al., 2009), fishing site facilities, or access improvements (Hunt, 2005; Salz and Loomis, 2005) may all have substantial effects on anglers and the utility they achieve (Hunt, 2005). These actions could easily be used in conjunction with length and bag regulations to create even more separation or diversity of fishing experiences, if desired. For example, regular stock enhancement of catchable-size fish might be employed in a limited number of discrete water bodies to which liberal harvest regulations would be applied (i.e. put-and-take fisheries or urban fisheries), or site facilities and access might be augmented in waters intended to appeal to more social or less specialized anglers. The expected benefit of such actions would not only be increased realized utility for the angler types towards which the action were directed (e.g. harvest oriented or social anglers) but likely also greater utility of other groups (e.g. catch-rate or trophy oriented, more specialized anglers) benefiting from the lesser congestion at other sites (Cox et al., 2003; Hunt, 2005; Salz and Loomis, 2005). Such additional management actions may also be useful for expanding buffet-style management to more readily achieve management objectives broader than sustainable satisfaction of anglers, but that are nonetheless related to recreational fisheries, such as the ecological conservation of rare non-targeted species or imperiled habitats (Pikitch et al., 2004; Lewin et al., 2006; Granek et al., 2008). For example, a combination of stock enhancement and harvest regulations could be used to "draw" anglers away from other waters more sensitive owing to their habitat or presence of endangered species (Martin and Pope, 2011; Carpenter et al., 2017). Specific details and ideally case studies exploring how buffet-style strategies can address these other objectives and management options, potentially in conjunction with adaptive management or co-management principles, is likely a verdant area for future research.

Conclusion

In concert, the buffet-style, spatially diversified management strategies described here offer promise for recreational fisheries management. While many management agencies currently provide intentionally diverse fisheries through a combination of stocking strategies, regulations, and amenities, buffet-style management goes further, where management actions on each lake are quantitatively considered, either through simulation or adaptive management, and have the potential to further improve angler utility while minimizing conservation risk. Such strategies can offer improvement over one-size-fits-all strategies by increasing the overall utility experienced by the angling population with minimal conservation concern to fish population. This is expected to promote greater satisfaction (to which utility is related) of current anglers, but should also decrease the proportions of anglers poorly served by existing one-size-fits-all strategies and thus minimize dissatisfaction. Both these are important for agencies interested in recruiting and retaining greater or more diverse participation in recreational fisheries, while sustaining ecological function of fisheries. Simultaneously, buffet style strategies promote simplification of the (likely common) situation in which hundreds of different regulations are applied to individual waters (Lester et al., 2003), which places a high cost on supporting science and enforcement. The theoretical benefits are possible specifically because buffet style strategies account for open access angler dynamics as well as multiple, potentially competing objectives of diverse stakeholders. Realizing the theoretic benefits of buffet style strategies will have challenges, especially related to assessing angler preferences and non-stationarity of fish populations or social norms that may influence fisheries (e.g. pervasive catch-and-release: Gilbert and Sass, 2016; Sass et al., 2018; Shaw et al., 2019). These challenges also offer opportunities to pair buffet style strategies with adaptive management ideals for learning about potentially changing social-ecological systems, and for explicitly incorporating anglers in regulatory decision making per cooperative management principles. Buffet style strategies are certainly not a panacea, but they may prove a useful compromise for agencies seeking to sustain recreational fisheries, while encouraging systemic learning and cooperative governance of resources valuable to many users, including but not limited to, anglers.

Acknowledgements

The original idea for this paper was formed through conversations with Fiona Johnston, Carl Walters, Kai Lorenzen, and Michael Allen. We would also like to thank Fiona Johnston and coauthors for breaking new ground with their 2010 conceptual paper, upon which this work is based.

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Fisheries Research 183 (2016) 379–384

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Predicting changes in the catchability coefficient through effort sorting as less skilled fishers exit the fishery during stock declines

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ARTICLE INFO

Article history:
Received 5 March 2016
Received in revised form 29 June 2016
Accepted 30 June 2016
Handled by A.E. Punt

Keywords:
Catchability
Effort sorting
Angler diversity
Recreational fishing

ABSTRACT

Effort sorting is a process in fisheries where fishers of various skill levels sort according to fish density so that the mean catchability of remaining fishers increases as stock size declines. The resulting hyperstability in catch rates masks declining density, sometimes until fish populations have effectively collapsed. Effort sorting as a potential mechanism leading to hyperstability has been known for a while, but the ability to detect it using existing fisheries data has been limited. We present a way to detect effort sorting in fisheries and evaluate it using published recreational fisheries data. Specifically, we propose that catchability among anglers is log-normally distributed, but the anglers remaining fishing on any particular lake will have catchabilities high enough to exceed a minimum acceptable catch rate given available stock size. It is then possible to discern between hypotheses about causes of hyperstability, namely effort sorting or range contraction. However, the fitted model cannot reliably be used to predict fish density from catch-per-unit effort (CPUE) data, reiterating the importance of fishery-independent data, and serving as a warning against using CPUE as an index of density in management.

1. Introduction

Catchability is a measure of the fishing efficiency per fish density or the fishing mortality rate per unit of fishing effort (Arreguin-Sanchez, 1996). Catchability is a function both of fish behavior (e.g., activity, aggregation, naiveté; Arreguin-Sanchez, 1996; Askey et al., 2006; Kuparinen et al., 2010; Alos et al., 2012) and fisher behavior (e.g., skill in finding and capturing fish; Jones et al., 1995; Gaertner et al., 1999; Ruttan, 2003; Salas and Gaertner, 2004). It is commonly assumed that catchability is constant across a wide range of fish densities, implying that catch-per-unit effort (CPUE) is directly proportional to density. Assuming constant catchability is important because in the absence of fishery-independent data CPUE is commonly used as an index of density (Hilborn and Walters, 1992; Quinn and Deriso, 1999). However, catchability in many (particularly recreational) fisheries is density-dependent and most often hyperstable (Erisman et al., 2011; Shuter et al., 1998; Ward et al., 2013a), meaning catchability increases as density declines. Density dependent catchability is problematic for managers monitoring catch rates because density declines more quickly than catch rates, masking potential fishery collapses (Hilborn and Walters, 1992; Post et al., 2002). Understanding the range of conditions under which catchability may vary is important for fisheries management and conservation (Fenichel et al., 2013; Hunt et al., 2011), especially in situations where fisheries-independent data are sparse or absent.

It is typical for the skill of recreational anglers to vary considerably (Abrahams and Healey, 1990; Baccante, 1995; Ruttan, 2003; Ward et al., 2013b), often seen as catch inequality across individuals. If there is a minimum success rate that anglers are willing to tolerate, then less skilled anglers will exit the fishery (or seek other recreational opportunities) before more skilled individuals during periods of stock decline (Post, 2013; Walters and Martell, 2004). This "effort sorting" process (Walters and Martell, 2004) will lead in turn to increases in the average catchability coefficient of the subset of anglers still actively participating. Such a perceived increase in average catchability coefficient can cause fishing morality rate to remain high despite effort decreases and cause CPUE to exhibit hyperstability even when other mechanisms that typically cause hyperstability (handling time, range contraction) are absent. Obviously, this process will also depend on the dynamics of other fishing opportunities, making direct observation difficult. The notion of effort sorting is not new, but the ability to detect it as a mechanism has been limited. The effort sorting mechanism is not specific to recreational fisheries. For example, commercial fisheries experi-

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http://dx.doi.org/10.1016/j.fishres.2016.06.023
0165-7836/

ence effort sorting near the end of a fishing season as less efficient boats leave early to balance revenue against costs. Vessel buyback programs are also more likely to attract less efficient skippers and owners. While the relative influence of effort sorting in different fisheries has not been evaluated, it seems likely that this mechanism is particularly strong in recreational fisheries, where skill and experience vary widely (Walters and Martell, 2004).

We propose a framework for predicting how the average catchability coefficient, i.e., the fishing mortality rate if effort is known, will change under the assumption that anglers have similar constraints that result in similar catch rates at which they cease fishing. Within this framework, we explore alternative hypotheses for variation in catchability. Namely, we suggest that effort sorting may occur due to one or more of the following mechanisms: 1) the basic effort sorting mechanism outlined above; 2) effort sorting exacerbated by tolerance for low catch rates being related to catchability, so skilled anglers will also accept lower catch rates than less skilled anglers due to factors such as increases in maximum fish size; or 3) effort sorting exacerbated by hyperstability in catchability due to spatial contraction of fish at low densities. We evaluate these models against catch rate data presented in Ward et al. (2013a) on freshwater recreational fisheries in British Columbia.

2. Characterizing change in catchability as less-skilled anglers leave the fishery

Anglers will only continue to fish if they believe there is a positive benefit. Suppose that catching fish is the primary motivation for fishing, and the catch rate at which anglers exit the fishery is c_o. An angler i, who has catchability coefficient q_i, will seek other options (either fishing elsewhere or not at all) when stock density N is low enough so that catch rate q_iN is less than c_0, or equivalently when that individual's q_i satisfies:

$$q_i < {}^{c_0}\!/\!N. \tag{1}$$

Next, suppose that the distribution of q_i's over the population of anglers is approximately log-normal (or the distribution of $q_i{}^* = \log_e(q_i)$ is normally distributed), with mean μ_q and standard deviation σ_q. That is, suppose that 50% of anglers will exit the fishery, so that effort drops below half its maximum value, when$q_i{}^* = \log_e(c_0) - \log_e(N) < \mu_q$. Highly heterogeneous angler populations are represented by high σ_q (Walters and Martell, 2004), potentially resulting in a few very skilled anglers. For the constant-catchability case (Eq. (1)), a normal distribution of $q_i{}^*$'s over anglers implies that the effort response (number of anglers fishing) to increasing N will have a sigmoidal shape, i.e., will be a cumulative log-normal distribution with cumulative probability 0.5 at the density for which catch rate is equal to c_0.

Given a density N, we can then predict the mean catchability coefficient of the anglers that will continue to fish at that density as the back-transformed mean of the truncated normal distribution with lower truncation limit q_{min} given by Eq. (1). That mean is given by (Greene, 2003)

$$q_e = \exp\left(\mu_q + \sigma_q \frac{n(d)}{1 - N(d)}\right) \tag{2}$$

where q_e is the mean of the remaining anglers with individual q_i's, $n(d)$ is the standard normal density function (mean 0, standard deviation 1.0) evaluated at the deviate

$$d = \frac{\left(\log_e(q_{min}) - \mu_q\right)}{\sigma_q} \tag{3}$$

using q_{min} equal to the q_i from Eq. (1) and $N(d)$ is the cumulative standard normal distribution function evaluated at standard deviate d.

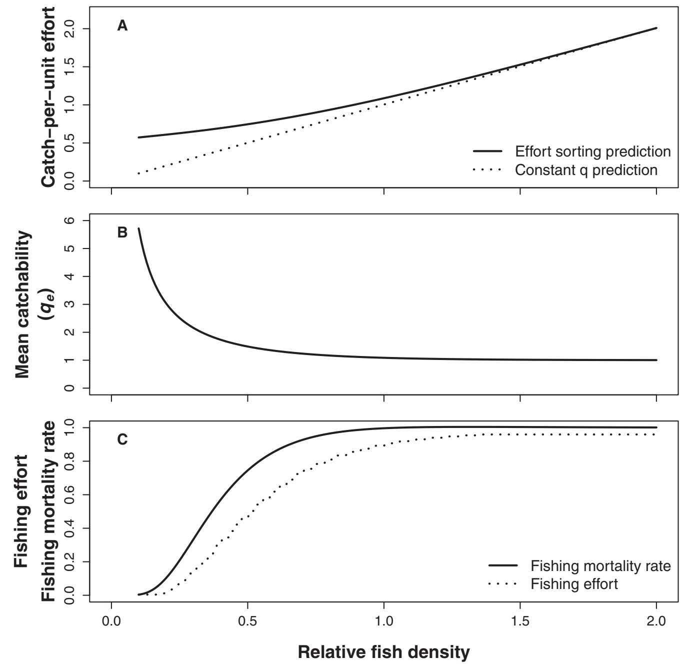

Fig. 1. (A) Hyperstability in CPUE caused by increases in mean q_i at low stock size due to effort sorting even assuming CPUE = qN, where q is catchability and N is fish density; (B) change in catchability as density declines due to effort sorting; (C) change in fishing mortality rate and fishing effort as fish density declines.

For illustrative purposes, when N changes from 0.0 to 2.0, $\mu_q = 0$, $\sigma_q = 0.25$ and $c_0 = 0.5$, effort sorting leads to differences in CPUE at low stock sizes (Fig. 1A) and increases in q_e at low stock sizes (Fig. 1B). However, fishing mortality, calculated as $F = q_e \times$ effort, does not increase at low stock sizes due to decreases in fishing effort (Fig. 1C). Note that the outcome of this process is that CPUE for this example would display dangerous hyperstability for stock sizes below 0.75.

It should not be difficult to obtain reasonable estimates of c_0 from observations of catch rates at which anglers exit the fishery and from economic analysis of the costs of fishing relative to catch per effort (Cinner et al., 2008; Daw et al., 2012). The catchability distribution parameters μ_q and σ_q are much more difficult to estimate. One possibility is to examine how observed CPUE changes with density estimates from various assessment methods (e.g. Fig. 1). Another possibility is to conduct experimental fishing with standardized q and to compare a standardized q to changes in mean q measured over the heterogeneous angler population as Ward et al. (2013a) did for recreational trout fishing in British Columbia.

Note that the q distribution cannot be estimated just by examining short term variation in catch rates among anglers; many factors contribute to that variation, especially chance variation in encounter rates (Ruttan, 2003). For example, in recreational fisheries we typically see Poisson or negative binomial distributions of catch rates across anglers over short sample periods (Seekell, 2011). This variation does not mean that catchability varies among anglers, or that the distribution of catchability among anglers is Poisson or negative binomial; rather, it means only that luck varies for every angler and "real" or persistent variation in catchability among anglers can only be seen by comparing average catch rates across anglers over long time periods (fishing seasons, years; Deriso and Parma, 1987). Over longer periods, we expect q_i for any given angler to increase with experience (Ward et al., 2013a,b) and accumulated information about best fishing sites and practices, then decrease with angler age for those old enough to have difficulty handling the physical rigors of fishing. An obvious statistical approach is to use a hierarchical modeling approach such as is commonly used in "standardizing" CPUE, with year effects representing density change and angler effects representing the "hyperdistribution" of q_i values. This analysis would need to be conducted on CPUE data collected over periods short enough for such cumulative learning effects to be negligible. Ward et al. (2013a) used this approach in a cross-lake comparison, where more experienced (presumably higher q_i) anglers were typically found to fish on lakes with lower fish densities. In the next section, we use this data to estimate parameters of our model and test several assumptions regarding the cause of hyperstability seen in their data.

3. Application to recreational fishery data from a landscape of lakes

While we argue that effort sorting is a potentially important mechanism driving variation in catchability and hyperstability in many fisheries, there are other competing mechanisms that will likely occur in concert. We propose three variations of related mechanisms that may explain effort distribution in BC lakes, as reported in Ward et al. (2013a). The base model (Model 1) supposes that effort sorting occurs due to anglers with lower catchability leaving as densities decline, as outlined above. Model 2 assumes that anglers with higher q_i's may also have lower fishing costs (or tolerance for low CPUE for various reasons, such as larger average fish size when density is low; Beardmore et al., 2015). This can be incorporated into the model structure by assuming a linear decrease in the cost of exiting the fishery with increasing q, i.e.:

$$c_{exit,i} = c_0 - c_1 q_i, \tag{4}$$

which changes the calculation of q_{min} for Eq. (1) from c_0/N to

$$q_{min} = {}^{c_0}\!/\!(N + c_1). \tag{5}$$

The variable c_1 represents the rate at which the cost of exiting the fishery changes across anglers as individual q_i changes. Model 3 assumes there is density dependence in catchability and/or a search-handling time effect on catchability (e.g. $CPUE = \frac{q_i N}{1+hN}$; Appendix A), so the condition where anglers exit the fishery becomes

$$q_{min} = c_0 \frac{(1 + hN)}{N}. \tag{6}$$

Note that density dependent catchability implies density must be lower by a factor determined by the handling time or range contraction parameter h before an individual will exit the fishery.

We evaluated each of the assumptions regarding the behaviors that lead to CPUE patterns (Models 1–3) using the data presented in Ward et al. (2013a). CPUE in the 18 lakes was assessed using a seasonally and weekly stratified creel survey where anglers were asked catch and effort upon trip completion. Fish densities were estimated in 16 of 18 lakes using a standardized gill net protocol (Ward et al., 2012). In the remaining two lakes, fish densities were estimated using a mark-recapture method (see details in Ward et al. (2013a)).

Each of the three proposed mechanistic models were fit to the CPUE data from Ward et al. (2013a) (Table 1). Prior probability distribution functions (PDF) for each of the estimated parameters were assumed uniform except for precision (τ), which was assumed to be gamma distributed. CPUE data were assumed normally distributed with estimated precision τ. Posterior distributions for each model were calculated from 100,000 Markov chain Monte Carlo iterations after an initial burn-in of 4,900,000 iterations and further thinned to provide a final sample of 1000 iterations from each of four chains (using JAGS 3.4.0; Plummer, 2003). Burn-in length and associated convergence were evaluated iteratively through examination of trace plots and using the Gelman-Rubin diagnostic for each parameter. Model parsimony and selection was determined using the Deviance Information Criterion (DIC; Spiegelhalter et al., 2002).

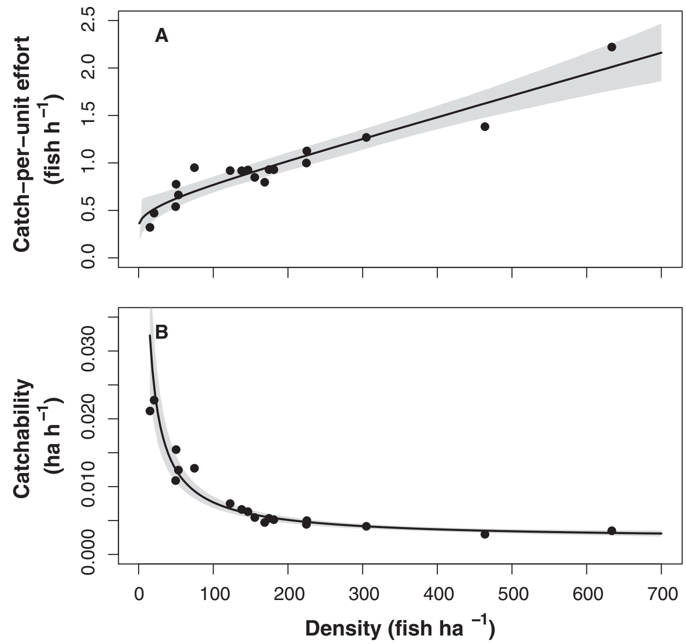

Fig. 2. Hyperstability in catch per effort caused by increases in mean catchability (q) at low stock size (N) due to effort sorting assuming CPUE = qN. Observations are shown as dots; median and 95% credible intervals from posterior prediction of Model 1 are shown as solid lines and shaded areas, respectively; Expectation given constant catchability shown as dotted line. Panel (A) shows observed and predicted catch per effort in BC lakes from Ward et al. (2013a). Panel (B) shows observed and predicted catchability of anglers fishing on the same lakes.

Fitting each of the three models to the data from Ward et al. (2013a) showed that the simplest model, which assumed hyperstability in CPUE occurred solely due to effort sorting as a function of fish density (Model 1) was selected using DIC (Table 2). Model 2, which accounted for increased tolerance for low CPUE as densities decline, was strongly rejected; Model 3, which accounts for density dependent catchability or handling time was also rejected based on the relative DIC values. (Burnham and Anderson, 2002). This suggests two things: first that the effort sorting mechanism proposed is appropriate for the data, as argued in Ward et al. (2013a); second is that including density dependent catchability or handling time does not help explain the data. The results of Model 1 explain the overall pattern in CPUE (Fig. 2A) and catchability (Fig. 2B) across the range of fish observed in the data from Ward et al. (2013a). Note that the fitted model shows that catchability in anglers remaining on low-density lakes must dramatically increase to account for the observed pattern in lake-wide catchability of anglers.

4. How can predicting effort sorting help us manage fisheries?

Unfortunately, knowing the shape of the CPUE-density relationship does not directly help us manage the fishery. First, the parameters of the model must be known before it can be used, i.e., there has to be spatial or temporal fish density data as well as CPUE data to 'calibrate' the function. This may take several years to accomplish and there is no guarantee that estimated parameters are stable over time. Second, there is no analytical solution to back-calculate fish density from observed CPUE using the model described above. This can be overcome using Bayes' theorem

Table 1
Prior and posterior probability distribution functions (PDF) for parameters of the three models fit to the Ward et al. (2013a) data when catchability among anglers is assumed to follow a log-normal distribution. Uniform distributions are denoted with U and gamma distributions are noted with G. Posterior probability distribution functions are described with means and 95% credible intervals.

Parameter	Prior PDF	Posterior PDF		
		Model 1	Model 2	Model 3
μ_q	U(0,10)	0.71 (−0.66,1.24)	0.62 (−6.75,1.28)	1.19 (−0.11,2.07)
σ_q	U(0,10)	1.65 (0.57,3.82)	0.71 (0.23,3.38)	1.28 (0.26,3.31)
c_o	U(0.01,10)	0.26 (0.03,0.57)	0.86 (0.14,1.82)	0.31 (0.04,0.64)
c_1	U(0,10)	–	0.05 (0.00,0.31)	–
h	U(0,10)	–	–	0.72 (0.01,2.91)
τ	G(0.001,0.001)	51.50 (22.17,94.50)	65.46 (15.14,130.61)	45.36 (18.41,85.53)

Table 2
Results of the three models fit to the Ward et al. (2013a) data, each model differentiated by the q^*_{min}. Here, catchability among anglers is assumed to follow a log-normal distribution. Models differ in the effective number of parameters (p_D), the deviance information critierion (DIC) and the relative difference between each DIC and the minimum DIC among tested models (ΔDIC).

Model	q^*_{min}	p_D	ΔDIC
1	$\log_e(c_o) - \log_e(N)$	5.0	0
2	$\log_e(c_o) - \log_e(N + c_1)$	30.7	21.8
3	$\log_e(c_o) - \log_e\left(\frac{N}{1+hN}\right)$	8.4	5.7

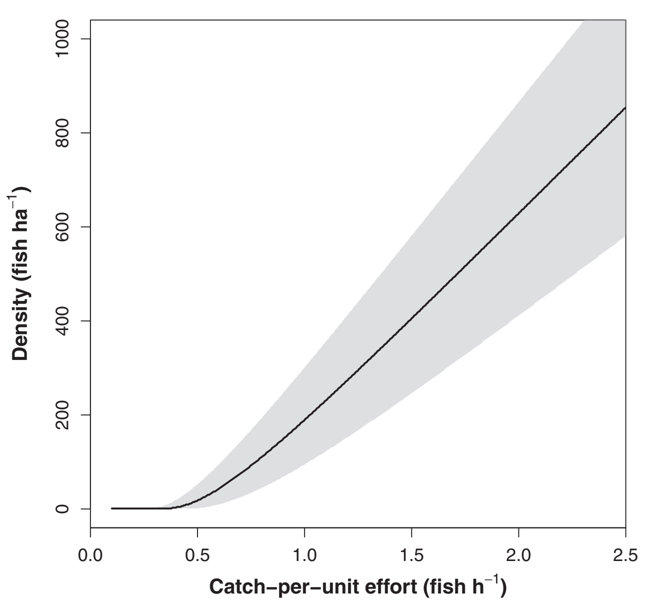

Fig. 3. Prediction of fish density given observed catch-per-unit effort as predicted using fitted Model 1. Dark line represents median predictions; shaded area represents 95% credible intervals. Dashed line represents prediction given constant catchability.

(Hilborn and Mangel, 1997), where a prediction of the distribution of density (N) given observed CPUE is given by

$$P(N|CPUE) = \frac{P(N)P(CPUE|N)}{\int P(N)P(CPUE|N)} \tag{7}$$

where $P(CPUE|N)$ is given by Eq. (3) and $P(N)$ is the prior probability density function in fish density.

Fish density on BC lakes similar to those evaluated in Ward et al. (2013a) was predicted by numerically integrating Eq. (7) using a uniform prior probability distribution for N ranging from 0 to 700 fish/ha. The resulting relationship (Fig. 3) shows that as with all fisheries with hyperstable CPUE, there is an range of fish density for which CPUE is relatively invariant to N and is hence uninformative (Hilborn and Walters, 1992). For instance, a CPUE of one fish per hour on BC lakes could mean a density ranging from 92 to 320 fish/ha; a 3-fold range. CPUE between 0.75 and 1.25 represents a wide range of fish density, while a similar range in CPUE from 0.25 to 0.50 indicates extremely low fish density and may signal near-collapse conditions (Fig. 3). Therefore, estimating the strength and mechanism of hyperstability, as we have done here for BC lakes, should not be used as a means to provide management recommendations. Rather, detecting hyperstability should be used as a signal that fishery independent data must be used to assess and monitor fisheries and make management decisions.

5. Discussion

The model framework presented here is intended to help interpret CPUE data collected over relatively short time periods during which density does not appreciably change. For prediction of average CPUE over longer time scales, e.g., over fishing seasons during which there is a substantial decrease in density due to high fishing effort, the mean CPUE will need to be calculated for a series of shorter time steps using the average density present during each of the steps. At this point, other sources of variation in catchability may need to be considered. Several authors have noted a seasonal pattern in fish catchability (Askey et al., 2006; Gordoa et al., 2000; Stoner, 2004; van Poorten and Post, 2005) primarily due to environmentally-driven variation in fish behavior. As finer time steps are considered, more detail on how catchability may change will likely be required.

One warning from this framework is that it does not predict observed changes in fishing effort (number of anglers fishing) across lakes. Our models assume effort declines as fish density declines because less skilled anglers drop out, yet, there is no pattern in observed fishing effort across the BC lakes in Ward et al. (2013a). There are several reasons for this, which the data are not able to appropriately discriminate. The first is that skilled anglers avoid lakes with many unskilled anglers. This may be strictly to avoid interference competition, whereby skilled anglers understand the biology and likely areas of fish concentrations but unskilled anglers may encroach on those areas by chance yet not have the skill to capitalize on their location. The implication here is that the distribution of individual q_i's is bimodal rather than lognormal. In this case, as fish density declines across lakes, total effort will remain relatively constant. Therefore, as catchability of remaining anglers increases across lakes, fishing mortality rate may actually increase: a type of "super-depensation". This will almost certainly lead to collapse in unregulated fisheries. Initial work showed this alternate model to fit equally well to the CPUE data, though the proportion of skilled anglers (the upper mode in the bimodal catchability distribution) could not be estimated without use of a strongly informative prior probability distribution function.

The second, more likely, reason why our model does not fit the observed effort pattern across lakes is that while anglers are attracted to catch rates, their primary motivations for fishing low density lakes becomes increasingly diverse. The BC lakes modeled here are both stocked (no natural reproduction) and regulated so as to specifically create particular fishing experiences (trophy – large maximum sizes; family – high densities; and regional regulations – average size and numbers). It may well be that anglers fishing on low density lakes are actually attracted to particular fishing regulations (Cook et al., 2001) and the expected fishing experience they will provide. The intention of these lake classifications is to attract particular angler typologies so it is not surprising that our theory breaks down for low density lakes that are intended to attract specific subsets of anglers. Moreover, because of the restrictive regulations on some lakes, high catchability combined with high effort will not necessarily lead to high fishing mortality, unless release mortality is particularly high (Coggins et al., 2007). Obviously our interpretation of fisheries dynamics integrates over several catch-related factors (through c_0, c_1 and h) that may drive decisions on where and when to fish. More importantly, this analysis assumes equal costs among anglers. For the recreational fishery examined here, costs are generally described among human-dimensions researchers as non-catch related motivations and constraints (Fedler and Ditton, 1994; Holland and Ditton, 1992). The most obvious non-catch related factors in recreational fisheries are travel distance and fishing regulations or quotas, which may restrict where and when anglers fish and, therefore, shape aspects of the fishing experience (Beard et al., 2003; Cook et al., 2001; Post et al., 2008; Radomski et al., 2001). Several authors have shown that regulations in recreational fisheries not only limit angler fishing behavior, but also directly influence where people fish by establishing expectations (Aas, 1995; Beard et al., 2003; Cook et al., 2001; Salas and Gaertner, 2004). For example, Cook et al. (2001) suggested that setting a high bag limit may signal to anglers that there are many fish to catch, thereby attracting anglers motivated by catch rates. Harvestable size limits send similar messages about the general size structure of fish populations. These additional sources of variation may somewhat obscure the true relationship between CPUE and fish density and serve to reinforce the unreliability of CPUE in driving management decisions.

Determining angler preferences and skill using angler interview data or surveys is difficult and prone to errors. Ward et al. (2013a) pointed out that it may be useful to collect ancillary information that can be correlated with angler skill as a means of detecting whether effort sorting is occurring in a fishery. This collection poses its own challenges, as there are no consistently accurate covariates of angler skill or preferences (Beardmore et al., 2013; Ward et al., 2013b). In some fisheries, it may be possible to examine relative fishing effort across space or time. However, this assumes costs are relatively equal across anglers. Because costs are rarely equal across anglers, there is a need to carefully consider and incorporate multivariate utility functions that mimic angler decision making when creating predictive models of angler effort and catch. The obvious overlap between the natural and social sciences in recreational fisheries management calls for a re-examination of how we view anglers and assess fisheries.

Fisheries are complex social-ecological systems made up of interacting fish populations and the anglers that affect them directly through harvest and indirectly through release mortality and the subtler physiological and behavioral consequences of capture and release (Arlinghaus et al., 2009; Camp et al., 2015; Carpenter and Brock, 2004; Johnson and Carpenter, 1994). Fisheries management is evolving from a field focused on fish population dynamics to one actively attempting to understand the primary motivations behind effort distribution and behavior. This is not a simple task: most fisheries managers are trained as biologists and much of the human dimensions behind fleet dynamics and angler satisfaction are difficult to grasp (Carpenter et al., 1994). Relatively simple mechanistic models that integrate over a variety of phenomenological sub-processes are necessary to help make management decisions that are robust to uncertainty about the details of human behavior (Fenichel et al., 2013). The model presented here should help managers recognize the extent to which hyperstability may be undermining their ability to sustainably manage fisheries and encourage thought on alternative monitoring activities with which to base decisions (Lester et al., 2003; Post et al., 2002; Shuter et al., 1998).

Acknowledgements

Collection of the data used here (originally published in Ward et al. (2003a,b)) was made possible by a Discovery and Collaborative Research and Development Grant from the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Freshwater Fisheries Society of British Columbia (FFSBC) to John R. Post (University of Calgary). The Habitat Conservation Trust Foundation (HCTF) also supported data collection through anglers, hunters, trappers and guides who contribute to the Trust. This manuscript was greatly improved by the helpful comments of two anonymous reviewers.+

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2016.06.023.

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