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ARTICLE

Evaluating Short Openings as a Management Tool to Maximize Catch-Related Utility in Catch-and-Release Fisheries

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Abstract
Catch and release (CR) is an increasingly common strategy for recreational fisheries in which sustaining high catch rates is important. The success of this strategy is reduced if the released fish are temporarily invulnerable to capture due to behavioral changes, as recent research suggests. Here, we explore how temporary fishing closures with short openings might be used in CR fisheries to increase the catch-related utility associated with angler satisfaction from catches. We simulated generic fisheries in single-lake and multiple-lake systems and found that regular, temporary closures could increase catch-related utility—but predominately under the key assumption that angler satisfaction increases disproportionately with increasing catch rates. In the multiple-lake case, a strategy of rotating temporary closures could provide greater catch-related utility than continuously open fisheries, but this would depend upon anglers' willingness to redistribute effort from closed waters to open waters. A key implication of these results is that even in CR fisheries, effort limitation may be necessary to provide quality angling opportunities. Our results also emphasize the importance of understanding how vulnerable pool dynamics can differ across fisheries and potentially interact with other processes and mechanisms that drive the observed changes in catchability and catch rates.

For most recreational fisheries, the fundamental management objective is to achieve high socioeconomic value—generally measured as the total utility (aggregated satisfaction) obtained by anglers from fishing—without impairing fish population sustainability (Radomski et al. 2001; Cox et al. 2002; Pereira and Hanson 2003). Satisfaction can be derived from catch-related and non-catch-related dimensions of fishing trips (Hunt 2005; Beardmore et al. 2015). Although both dimensions are important, overall satisfaction generally depends on catch-related elements, in part because anglers have more control (via site choice in open-access systems) over their non-catch-related satisfaction (Arlinghaus 2006; Beardmore et al. 2011, 2015). Catch rate is often considered the primary determinant of catch-related satisfaction and thus overall utility (Cox et al. 2003; Arlinghaus 2006), and it remains a key metric targeted by managers (Martin 1976; Malvestuto and Hudgins 1996; Beardmore et al. 2015). Catch rate targets present an inherent challenge. By their nature as ratios, catch rates will be expected to decrease with increasing effort, ceteris paribus, but greater aggregate effort would potentially allow for more total catch-related utility throughout a season. Even under constant effort, the actual rates at which fish are caught depend on many factors, including fish behavior, angler behavior and skill, and abiotic factors, such as weather and temperature

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(van Poorten and Post 2005; Kuparinen et al. 2010). Because only some of these factors can be (indirectly) influenced by managers, the number of strategies that are useful for controlling catch rates is limited (Cox et al. 2002; van Poorten et al. 2013). Two potent strategies for maintaining desired catch rates are (1) mandatory catch-and-release (CR) fishing, wherein fish abundance can be maintained despite high effort as long as discard mortality is minimal (Coggins et al. 2006; Arlinghaus et al. 2007); and (2) effort restrictions, such as periodic fishery closures, which limit the amount of effort over which capture-vulnerable fish are divided (Cox et al. 2003; Walters and Martell 2004).

Catch-and-release regulations are often used as a way of maintaining the quality of fishing in situations where harvest might lead to quality overfishing or to conservation concerns (Barnhart 1989; Radomski et al. 2001; Askey et al. 2006; Arlinghaus et al. 2007); CR has also gained prominence with many anglers as a voluntary practice (Cooke and Suski 2005; Myers et al. 2008). Although CR can reduce mortality and make fish available for repeated capture, it may also produce unintended consequences (Askey et al. 2006; Arlinghaus et al. 2009). One such consequence is that the released fish may become increasingly difficult to catch again. For example, fish may behaviorally respond to catch and subsequent release by becoming temporarily unreactive to fishing gear (Cox et al. 2002; Askey et al. 2006) or even by learning to avoid fishing gear (e.g., Beukema 1970; Askey et al. 2006; Arlinghaus et al. 2009; Klefoth et al. 2013). This response of fish can be represented by using vulnerable pool dynamics theory (Walters and Juanes 1993; S. P. Cox and Walters 2002), which states that a fish population is composed of capture-vulnerable and capture-invulnerable individuals. The transition of released fish to the "invulnerable pool" may be partially responsible for observed temporally declining catch rates in some species-specific fisheries with high CR rates or mandatory CR (van Poorten and Post 2005), as these invulnerable fish are unavailable to anglers.

Previous recognition of vulnerable pool dynamics in largely harvest-oriented fisheries has suggested that utility may be maintained by periodic effort closures (Cox et al. 2002, 2003). Such closures "fallow" the fishery and allow the vulnerable pool to repopulate. However, evaluation of this idea has yet to be extended to CR fisheries. The effects of such closures on the utility of CR fisheries are not necessarily intuitive: substantial fishery closures would limit the overall number of trips taken (a scalar of catch-related utility), whereas few or no closures may depress catch rates (and thus the utility per trip) as the fishing season progresses. The usefulness of closures becomes more complex across a landscape of discrete fishing sites, which is common to many freshwater recreational fisheries (Carpenter and Brock 2004). In such a landscape, it may be beneficial to implement CR regulations with infrequent, spatially stratified, and temporally staggered fishery openings. Doing so could theoretically support daily fishing effort while still maintaining high catch rates and associated utility. These rotating closures have the potential to produce more utility across a landscape than would be obtained from continuously open fisheries on all lakes.

The primary objective of the present work was to extend the existing theory of vulnerable pool dynamics to simulated CR fisheries so as to evaluate the use of short openings and temporary closures as a management tactic. Under these conditions, we explored how catch-related utility for anglers might be altered by periodic closures of different durations; this was done by using a simple simulation model that was generalized to single-lake and multiple-lake (landscape) fisheries. We further assessed how these outcomes could be mediated by key angler characteristics, including relationships between catch-related satisfaction, catch rates, and anglers' willingness to redistribute their fishing effort across the landscape. Based on these simulation results, we discuss key areas for future investigation.

METHODS

Model development.—The model extends previous work on vulnerable pool dynamics, which considered a fish population to be composed of vulnerable individuals and invulnerable individuals (S. P. Cox and Walters 2002; Cox et al. 2002, 2003), a notion that enjoys empirical support (Philipp et al. 2009; Klefoth et al. 2013; Alós et al. 2015). Our model assumes that there are three primary states with respect to fish vulnerability to capture by anglers: vulnerable, invulnerable, and refractory (Figure 1). Vulnerable fish (V; Figure 1) occupy areas of the system where they are available to anglers and are in a behavioral state where they will react to the fishing gear. Invulnerable fish (I; Figure 1) are unavailable to anglers because they occupy an area of the system or are in a behavioral state where they will not be captured by anglers. Vulnerable fish that have been captured and released are in the refractory state (R; Figure 1), where they are unwilling to react to fishing gear even if they are otherwise available for capture. These refractory fish will eventually move into one of the other states. The explicit separation of fish in the invulnerable state (regardless of exposure to fishing) from fish in the refractory state (as a response to previous release) is an important component of our model and has not been included in previous harvest-only models (e.g., S. P. Cox and Walters 2002, S. Cox and Walters 2002; Cox et al. 2003). Importantly, altered behavior after catch and subsequent release (Cooke et al. 2002; Ridgway 2002; Baktoft et al. 2013) as well as a gradual return to pre-capture behavior have been documented empirically for multiple fish species (Young and Hayes 2004; Klefoth et al. 2008).

Our model is described in Table 1, and its parameters and variables are defined in Table 2. We assumed a landscape of multiple lakes at different distances that were accessed by anglers from a single population center (sensu Cox et al. 2003;

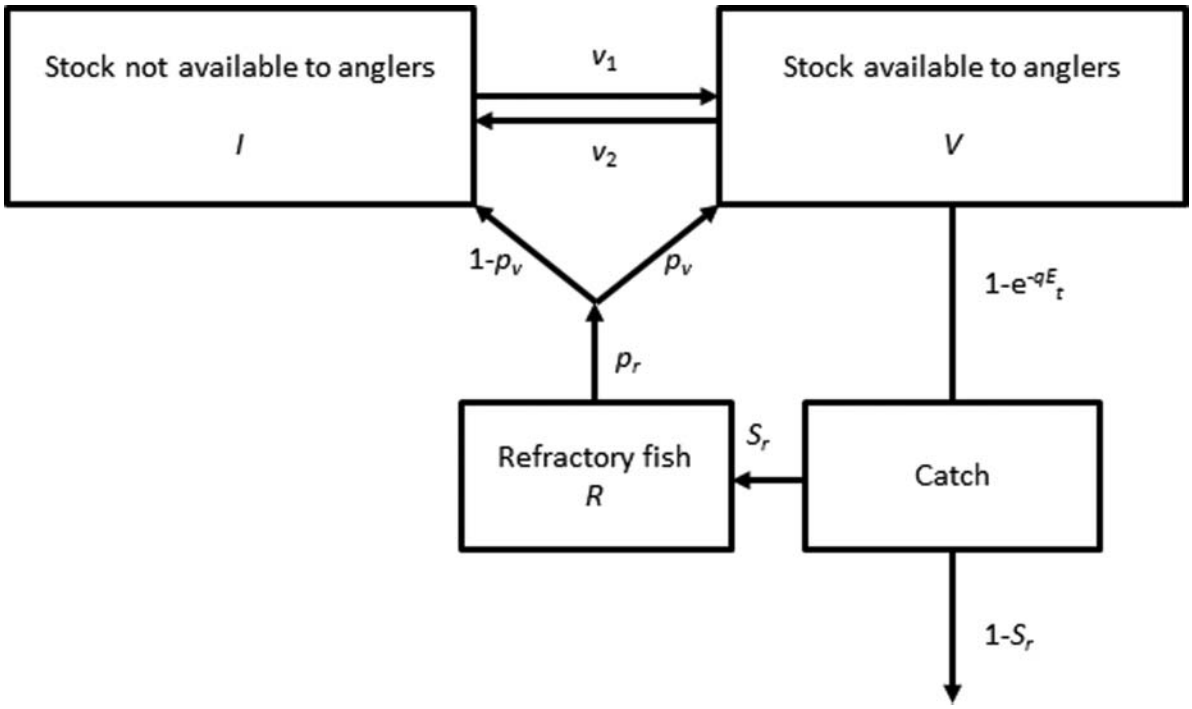

FIGURE 1. Schematic representation of the recreational fishery, with three states for individuals of the target species: vulnerable to fishing (V), invulnerable to fishing (I), and refractory (R). Exchange rates between vulnerable and invulnerable states are represented by v_1 and v_2. Catch on day t is proportional to effort on that day. All captured fish are released; some could potentially die from release mortality (at a rate of 1 – S_r) or they may survive (at a rate of S_r), subsequently enter the refactory state (R) and eventually leave the refractory state at a rate of p_r. Fish leaving the refractory state may return to the vulnerable pool at a rate of p_v or the invulnerable pool at a rate of $1 - p_v$.

Post et al. 2008; Post and Parkinson 2012). For simplicity, we characterized lakes as belonging to one of three distance classes (d_l = 10, 100, or 250 km; Table 2) affecting both the total effort and its distribution. Parameter values were chosen to represent a hypothetical fishery with reasonable catch rates (∼2 fish/angler-day [AD]) that do not result in overharvest. Rate parameters were based on literature values from lake fisheries where possible, and those references are listed in Table 2. Notably, the population is considered closed such that (1) no juveniles grow into the fishery throughout the season and (2) neither natural mortality (M) nor discard mortality is considered to operate (survival after catch and release [S_r] = 1.0; Table 2). This abstraction facilitates interpretation of results as the effects of vulnerable pool dynamics rather than as mortality associated with time or capture.

At the start of the year, all fish populations are assumed to be in equilibrium: fish are distributed across the vulnerable and invulnerable states according to the vulnerability exchange rates, and no fish are in the refractory state (Table 1, equations 1.2–1.4). Empirical studies suggest that even in an unfished population, a sizeable proportion of the fish may not be immediately vulnerable to fishing (van Poorten and Post 2005; Matthias et al. 2014). Effort exerted daily on each lake is predicted via a multistage process. First, the regionwide daily effort that would be exerted if all lakes were open to fishing ($E_{pmax,t}$; Table 2) on a given day t is represented by a logistic function (Table 1, equation 1.5) that (1) depends on the mean number of vulnerable fish across all lakes ($\hat{V}_{l,t}$; Table 1, equation 1.6), with each lake weighted by its distance from the population center; and (2) scales to the total number of anglers that are willing to redistribute between lakes. This distance weighting approach assumes that for two lakes with the same number of vulnerable fish (and thus potential catch rates), the lake that is closer to the population center will generate more effort. Importantly, a non-zero intercept was used to calculate the proportion of maximum effort (χ; Table 1, equation 1.5), representing the idea that due to non-catch-related motivations, some minimum proportion of effort will be exerted even at very low catch rates. Each lake's attractiveness to anglers is determined via a gravity model (Bonfil and Walters 1999; Walters et al. 2007) that partitions effort according to a gravity weight ($G_{l,t}$; Table 1, equation 1.7)—a function of the ratio of maximum benefit (represented by potential catch rates) per cost (represented by distance). The weights used here assume a log utility function, implying that the probabilities of fishing a given lake have a less-extreme distribution than a strictly multinomial logit choice model (Walters et al. 2007). The latter is most appropriately applied to individual angler choices, whereas the methods followed for this work describe a simplified and phenomenological approach for representing the aggregate of population-scale choices (Walters and Martell 2004).

TABLE 1. Notation and equations used for the recreational fishing model (Θ = parameters set) incorporating vulnerable pool dynamics. Parameter symbols are defined in Table 2.

Equation number	Equation	Description
	Parameters	
1.1	$\Theta = \left(N_{l,0}, v_1, v_2, S_r, v_r, p_v, C_0, \beta, C_{50}, C_\sigma, E_{max}, \{O_t\}_{t=1}^{T},\ \chi\right)$	
	Initial population	
1.2	$V_{l,t=1} = V_{l,0}\left(\frac{v_1}{v_1+v_2}\right)$	Initial vulnerable subpopulation
1.3	$I_{l,t=1} = N_{l,0}\left(\frac{v_2}{v_1+v_2}\right)$	Initial invulnerable subpopulation
1.4	$R_{l,t=1} = 0$	Initial refractory subpopulation
	State dynamics	
1.5	$E_{pmax,t} = \sum_l \left[\text{EM}_{l,t}O_{l,t} + r\text{EM}_{l,t}\left(1-O_{l,t}\right)\right] \times \left(\chi + (1-\chi)\left\{1+e^{-\left[\left(q\hat{V}_{l,t}-C_{50}\right)/C_\sigma\right]}\right\}^{-1}\right)$	Proportion of maximum effort exerted if all lakes are open
1.6	$\hat{V}_{l,t} = \overline{V}_t\left[\frac{\max(d_l)-d_l}{\max(d_l)}\right]$	Mean density of vulnerable fish, weighted by distance
1.7	$G_{l,t} = \left(\frac{qV_{l,t}}{d_l}\right)^g$	Gravity weight of each lake
1.8	$E_{l,t} = E_{pmax,t}\left[\frac{O_{l,t}G_{l,t}}{\sum_l\left(O_{l,t}G_{l,t}\right)}\right]$	Realized effort exerted on each lake per day
1.9	$C_{l,t} = V_{l,t}\left(1-e^{-qE_{l,t}}\right)$	Catch
1.10	$V_{l,t} = \left[\left(V_{l,t-1}-C_{l,t-1}\right)(1-v_2)\right] + I_{l,t-1}v_1 + \left[\left(R_{l,t-1}+C_{l,t-1}S_r\right)p_rp_v\right]$	Density of vulnerable fish
1.11	$I_{l,t} = \left[I_{l,t-1}(1-v_1)\right] + V_{l,t-1}v_2 + \left[\left(R_{l,t-1}+C_{l,t-1}S_r\right)p_r(1-p_v)\right]$	Density of invulnerable fish
1.12	$R_{l,t} = \left(R_{l,t-1}+C_{l,t-1}S_r\right)(1-p_r)$	Density of refractory fish

The amount of effort (i.e., number of fishing trips) distributed to each lake on each day ($E_{l,t}$; Table 1, equation 1.8) is a function of maximum total effort possible ($\text{EM}_{l,t}$; Table 2), the above-described $E_{pmax,t}$ and $G_{l,t}$, the probability of angler redistribution between lakes (r; Table 2), and the sequence in which the lakes are open for fishing ($O_{l,t,}$; Table 2). Here, full redistribution ($r = 1$) would represent anglers freely redistributing to whatever lakes are open. Similarly, anything less than full redistribution ($r < 1$) involves the assumption that some anglers who would have otherwise fished choose to not fish due to temporary closures on a particular lake. This represents the intuitive idea that due to their affinity for a specific lake, their distaste of crowding, and other factors, some anglers may be unwilling to change their plans and fish different waters (Hunt 2005, 2008). Realized effort for lake l on day t will be zero if the lake is closed to fishing on a particular day ($O_{l,t} = 0$; Table 1, equation 1.8). Abundance of fish in each vulnerability state (i.e., vulnerable, invulnerable, or refractory) is updated daily by accounting for catches (Table 1, equation 1.9). Additionally, captured fish that are released back into the lake immediately move into the refractory subpopulation (Table 1, equation 1.12). These refractory fish eventually recover at rate p_r; a proportion (p_v) of these recovered fish will be immediately reactive to fishing gear, and the remainder ($1 - p_v$) will be invulnerable to fishing (Figure 1; Table 1, equations 1.10–1.12; Table 2). Finally, fish that are not captured in the fishery will naturally move between vulnerable and invulnerable states at rates v_1 and v_2, respectively (Figure 1; Table 2).

Response metrics.—The utility of recreational fisheries is often perceived differently from the utility of commercial fisheries. While total catch (i.e., yield) is an important attribute of recreational fisheries, other factors may be more important, particularly in a CR fishery. Fisheries managers often view CPUE as a key metric for tracking the success of their management actions (Beardmore et al. 2015), as it is one of the few outputs over which they have some level of control (Bennett et al. 1978; S. P. Cox and Walters 2002). Likewise, aggregate fishing effort is often viewed as an important measure of management success under the presumption that a greater number of fishing trips implies more potential utility (Hilborn and Walters 1992).

Satisfaction achieved from a recreational fishing trip is considered the difference between expected and realized outcomes of specific determinants of utility, such as CPUE or catch size (Holland and Ditton 1992; Arlinghaus 2006). Representing the satisfaction achieved requires describing the functional relationship between total or catch-related utility and its determinants; these functional relationships have been empirically described for several fisheries, and catch rates and sizes have been shown to comprise important parts of overall utility (Arlinghaus et al. 2014; Beardmore et al. 2015). A commonly made simplifying assumption is that the catch-related satisfaction per trip and the overall catch-related utility of the fishery (satisfaction per trip scaled by the number of trips) are directly related to CPUE (Cox et al. 2003; Camp et al. 2014). However, catch-related utility increases as an accelerating, linear, or saturating (i.e., representing diminishing marginal returns) function with increasing catch rates depending on the species (Beardmore et al. 2015). Accordingly, we propose an adaptation of the Cox et al. (2003) function (describing value) by relaxing the assumption that utility increases linearly:

$$U_{l,t} = \left(\frac{\mathrm{CPUE}_{l,t}}{C_0}\right)^{\beta}, \tag{1}$$

where $U_{l,t}$ is the average satisfaction (per lake and AD) associated with the realized catch rate (CPUE, fish/AD; Cox et al. 2003); C_0 (Table 2) is the CPUE at which no more effort is attracted; and β (Table 2) describes whether satisfaction increases exponentially ($\beta > 1$), remains linear ($\beta = 1$), or becomes saturated ($\beta < 1$) as CPUE increases (Figure 2). Using equation (1.8) from Table 1, the total catch-related utility of the fishery is the product of daily satisfaction (utility per AD) multiplied by effort on days when the fishery is open:

$$A = \sum_{l=1}^{L} \sum_{t=1}^{T} U_{l,t} \cdot E_{l,t}. \tag{2}$$

Model evaluation.—To understand how temporary closures might affect utility in CR fisheries, we evaluated our model for two general cases: (1) a single-lake case, where all fishing effort is dedicated to a single water body (i.e., $L = 1$); and (2) a multiple-lake system, where anglers can choose between multiple waters characterized by potentially different catch-related satisfaction and travel-related costs ($L = 21$). For the multiple-lake case, 21 lakes were distributed across the landscape, with seven replicate lakes assumed for each of three distances from the population center. Evaluation of these two cases was designed to consider the influence of angler site choice on short openings in CR fisheries, as the single-lake case represents an extreme "choice-poor" environment for comparison with the multiple-lake system. For both scenarios, we evaluated alternative management strategies (frequency and duration of temporary closures) in terms of response metrics, and we describe how these results were sensitive to key assumptions of the model.

Both the single-lake and multiple-lake cases were evaluated over a fishing season ($T = 180$ d) while assuming no seasonality in fish behavior or fishing effort. For the single-lake case, we compared six candidate opening schedules in terms of total annual catch, effort, average CPUE, and satisfaction. These candidate schedules included opening the fishery (1) 1 d/week; (2) 2 d/week; (3) 1 d every 2 weeks; (4) two consecutive days every 2 weeks; (5) 1 d/month; or (6) continuously. The schedule with the highest utility was used for subsequent sensitivity analysis. For the multiple-lake case, an additional strategy—rotational closures—was evaluated. This strategy consisted of systematically closing and opening different lakes in rotation such that for any given day, at least one lake in each distance class was open. Theoretically, rotating closures may allow for overall increases in utility over non-rotational methods by ensuring that at least some lakes are open for fishing while also ensuring that the vulnerable populations in those lakes will have sufficient time to rebuild.

Model behavior was evaluated using two methods. First, the elasticity of total catch-related utility for the single-lake case was evaluated against small changes in each of the parameters. Elasticity was calculated as the proportional change in total fishery catch-related utility associated with a 10% increase or 10% decrease in each parameter. Both positive and negative changes were necessary because the influence of a parameter on a function may be nonlinear (van Poorten et al. 2011). The second evaluation of model behavior was to determine how catch-related utility varied as maximum effort increased substantially up to 25 AD/ha.

The performance of the temporary-closure management tactic has so far been predicated on the exchange of targeted fish between vulnerable and invulnerable states. Although there are multiple empirical suggestions that such a dynamic system is common in many fisheries, the prevalence of this type of system is largely unknown. To explore the influence of vulnerable exchange dynamics on our results, we evaluated a single-lake case with or without temporary closures and under three alternative scenarios of subpopulation dynamics: (1) with no invulnerable pool and no refractory pool, such that all fish were vulnerable at all times (accomplished by setting $v_1 = 1$, $v_2 = 0$, and $p_r = 1$); (2) without an invulnerable pool but with a refractory pool, from which all fish returned to the vulnerable state upon recovery ($p_v = 1$; accomplished by setting $v_1 = 1$ and $v_2 = 0$); and (3) the full vulnerability exchange as described in Table 2.

RESULTS

The developed model illustrates how vulnerable pool dynamics in a mandatory CR fishery might generate rapid declines in vulnerable fish, catch rates, and, ultimately, angler

TABLE 2. Model parameter values, description, units, and justification (references) for the recreational fishing model incorporating vulnerable pool dynamics.

Symbol	Value	Description	Units	Reference
		Indices		
t	$\{1,2,...T\}$	Daily time step ($T = 180$ d)	d	
l	$\{1,2,...L\}$	Lake ($L = 1$ for the single-lake system or 21 for the multiple-lake system)	Lake	
		Model parameters		
$N_{l,0}$	250	Initial density of catchable fish	Number of fish	
M	0	Natural mortality	Rate	
q	0.05	Catchability coefficient for recreational fishing gear	Rate	Shuter et al. 1998; Cox 2000; Hansen et al. 2000; Newby et al. 2000; Ward et al. 2013a
v_1	$2\Delta t$	Rate of exchange from the invulnerable subpopulation into the vulnerable subpopulation	Rate	Cox 2000
v_2	$2\Delta t$	Rate of exchange from the vulnerable subpopulation into the invulnerable subpopulation	Rate	Cox 2000
S_r	1.0	Survival after catch and release	Rate	
p_r	0.2	Rate of recovery out of the refractory subpopulation	Rate	
p_v	0.5	Proportion of fish leaving the refractory state that become vulnerable to the fishery	Rate	
C_0	0.5	Base catch rate required for obtaining 1 unit of angler satisfaction	CPUE	
β	2	Power parameter defining the increase in satisfaction with increasing catch rate	Unitless	
C_{50}	2.0	Catch rate that attracts half of total available effort	CPUE	
C_σ	0.5	Inverse of the proportional rate of increase in effort with increasing catch rate	Rate	
r	0.5	Rate of effort redistribution from closed lakes to open lakes	Rate	
g	0.2	Gravity power for the gravity model	Unitless	
$EM_{l,t}$	10	Maximum effort on any given day for lake l	Number of trips	
$E_{pmax,t}$	Calculated	Proportion of maximum effort on any given day across all lakes	Proportion	
χ	0.1	Minimum value for proportion of maximum effort at very low catch rates	Proportion	
$O_{l,t}$	$\{0, 1\}$	Opening switch across days of the year	Unitless	
d_l	10, 100, or 250	Distance of lake l from the population center	Km	
max (d_l)	400	Assumed maximum distance	Km	
$\overline{V}_t$	Calculated	Mean number of vulnerable fish per lake	Number of fish	
		Derived states		
Δt	1/180	Daily time step	d	
		State variables		
$V_{l,t}$		Abundance of fish that are vulnerable to the recreational fishery	Number of fish	
$I_{l,t}$		Abundance of fish that are invulnerable to the fishery	Number of fish	

TABLE 2. Continued.

Symbol	Value	Description	Units	Reference
$R_{l,t}$		Abundance of fish that are recovering from catch and release (i.e., refractory)	Number of fish	
		State variables		
G_l		Gravity weight for each lake	Number of fish per unit distance	
$E_{l,t}$		Daily fishing effort	Angler-days	
$C_{l,t}$		Total daily catch in the recreational fishery	Number of fish	

catch-related utility throughout the year. Under the assumed scenario for a single lake, a sizeable proportion of all targeted fish are invulnerable to fishing at the start of the year (Figure 3, left panels). When fishing commences, fish are caught and released into the refractory state, and they eventually recover into the vulnerable pool or the invulnerable pool (Figure 1). Once fishing begins, the vulnerable pool rapidly becomes depleted, and it never has a chance to recover (Figure 3). The CPUE immediately declines as a result of the reduction in vulnerable fish; effort and satisfaction quickly fall in response (Figure 3). In the hypothetical fishery demonstrated here, the greatest amount of satisfaction is realized during the first week, and mandatory CR management is not sufficient to sustain moderate catch rates or much angler satisfaction throughout the season.

The behavior of this typified CR fishery changes when temporary closures restrict how often the lake is available for fishing. In the example presented in Figure 3 (right panels), the fishery is only open 1 d/week, and as a result the density of vulnerable fish declines more gradually and stabilizes at a higher mean density because fewer fish are being caught and released. During open fishery days, effort per day remains at the maximum because the pool of vulnerable fish remains large enough—and thus the CPUE remains high enough—to attract effort. Utility does not approach the minimum for nearly 2 months, and on days the fishery is open, utility stays higher than that observed for the continuously open fishery. The temporary closures allow effort, catch rates, and angler utility to be sustained at greater levels throughout the fishing season when the fishery is open, but obviously the values of these metrics are zero on closed days.

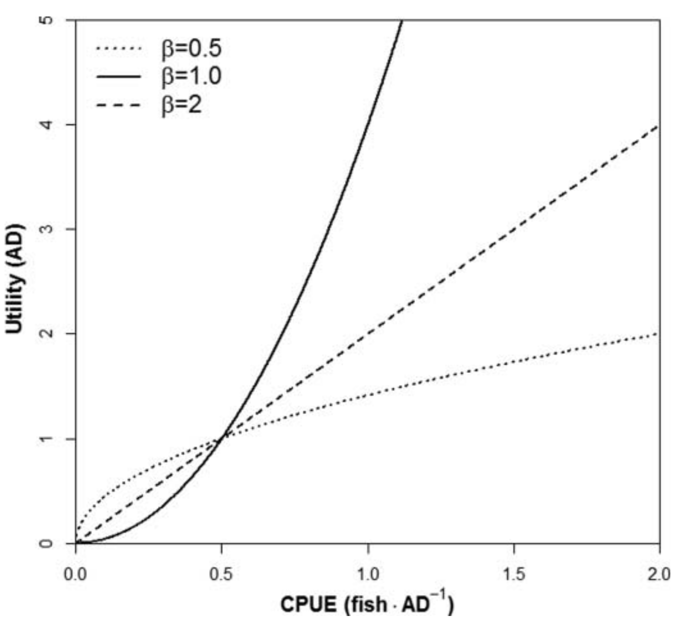

FIGURE 2. Catch-related utility per angler-day (AD) as a function of CPUE (fish/AD) in a single lake. The value β determines the degree to which catch-related utility is nonlinear with catch rate (adapted from Cox et al. 2003).

In the single-lake case, decreasing the number of open fishery days (represented by alternative scenarios of temporary closures) produced three distinct trends in the four response metrics (Figure 4). As would be expected, total catch and fishing effort over the season declined as the total number of open fishery days per month decreased (Figure 4). However, due to the vulnerable pool dynamics (i.e., fish recovery from invulnerable and refractory subpopulations to the vulnerable subpopulation), the declines in catch were less severe than the declines in effort. Consequently, the CPUE on open fishery days increased as the frequency of open days during the season decreased; thus, the greatest catch rates for the lake would be expected from implementing only one open day per month (Figure 4). Because the total catch-related utility of the fishery is evaluated as a function of CPUE per AD summed across fishing effort, utility is maximized by some intermediate intensity of closures (under the assumption of $\beta = 2$). In this hypothetical fishery, catch-related utility was maximized when the fishery was open 1 d/week, providing 23.6% greater utility than the alternative of a continuously open fishery (i.e., under the assumptions given; Figure 4).

The total annual catch-related utility of the fishery as calculated by the model was most sensitive to β, S_r, and the parameters used in the satisfaction function (Figure 5, top panel). Note that (1) the base value of β in the elasticity calculation was evaluated at 1.0 rather than 2.0 to demonstrate how the model responds to an exponential or saturating function for

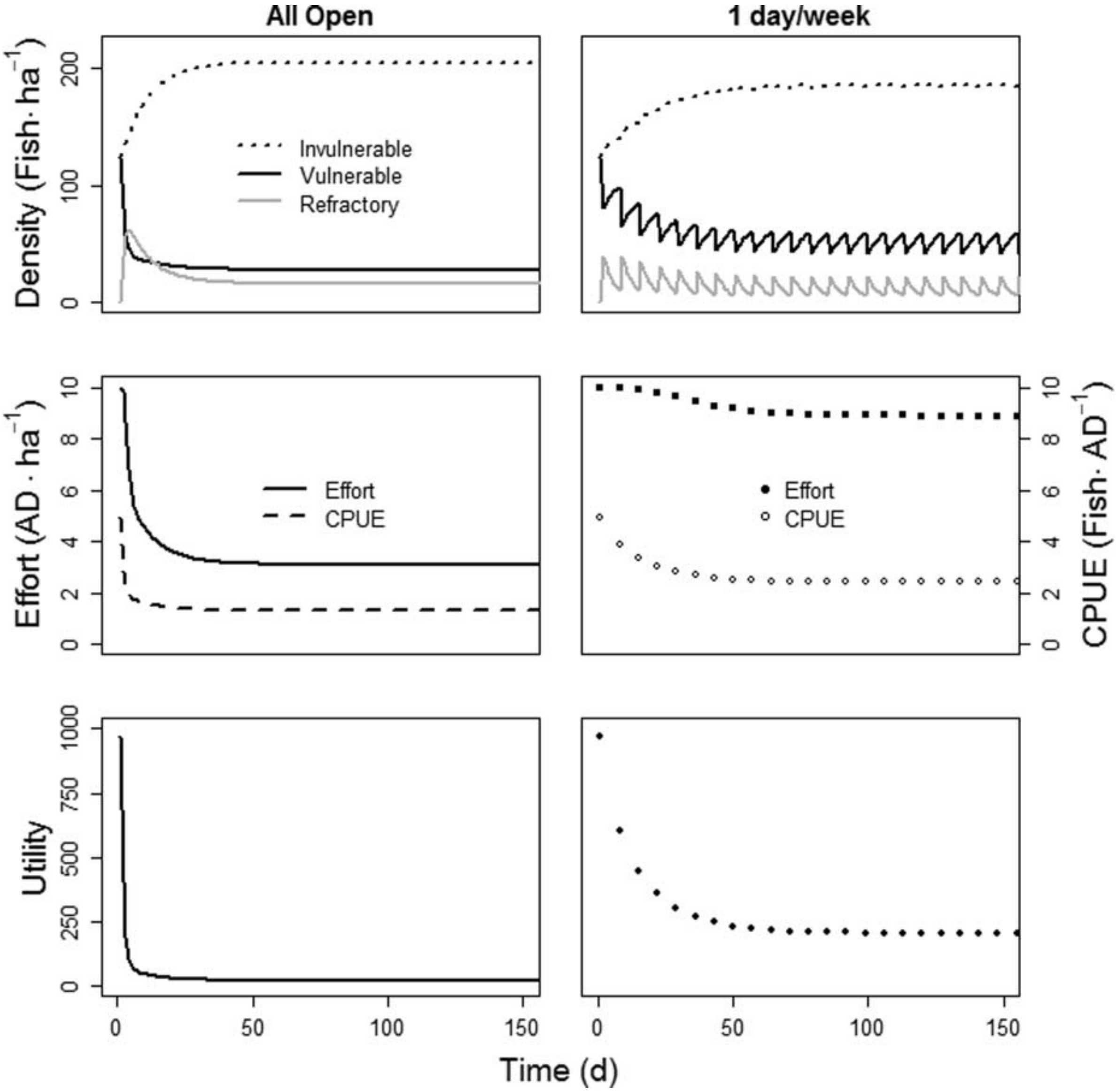

FIGURE 3. Within-season dynamics of two fishery management tactics for the case of a single lake: a catch-and-release fishery that is open year-round (left panels); and a catch-and-release fishery that is only open 1 d/week (right panels). Temporal patterns are depicted for fish abundance in the vulnerable, invulnerable, and refractory pools (upper panels); effort (angler-days [AD]/ha) and CPUE (fish/AD; middle panels); and catch-related utility (lower panels).

satisfaction and (2) the sensitivity of utility to S_r was evaluated only for a 10% decrease in S_r. The sensitivity of overall utility to β demonstrates the sensitivity of our findings to assumptions about how satisfaction scales with catch rates. Provided that angler satisfaction has a disproportionately positive relationship with catch rate (i.e., $\beta > 1$), the temporary-closure strategy contributes to a greater total catch-related utility than the continuously open fishery strategy across a wide range of maximum daily fishing effort values (Figure 5, bottom panel). At extremely low maximum effort, there is little benefit from implementing temporary closures, but catch-related utility for temporary-closure tactics quickly increases and reaches a maximum at moderate levels of maximum effort. For a continuously open CR fishery, catch-related utility declines almost linearly with increasing maximum effort because daily CPUE and effort decline after catches early in the season.

The effects of temporary closures depend largely on assumptions about (1) whether invulnerable or refractory subpopulations exist and (2) the exchange between those subpopulations and the vulnerable subpopulation (Table 3). Under the assumptions regarding vulnerability exchange rates and mortality, greater catch-related utility depended upon the existence of invulnerable and refractory subpopulations. This result is exclusively attributable to the recovery of fish from the invulnerable and refractory states to the vulnerable state, as closure of the fishery for several days allows nearly all of

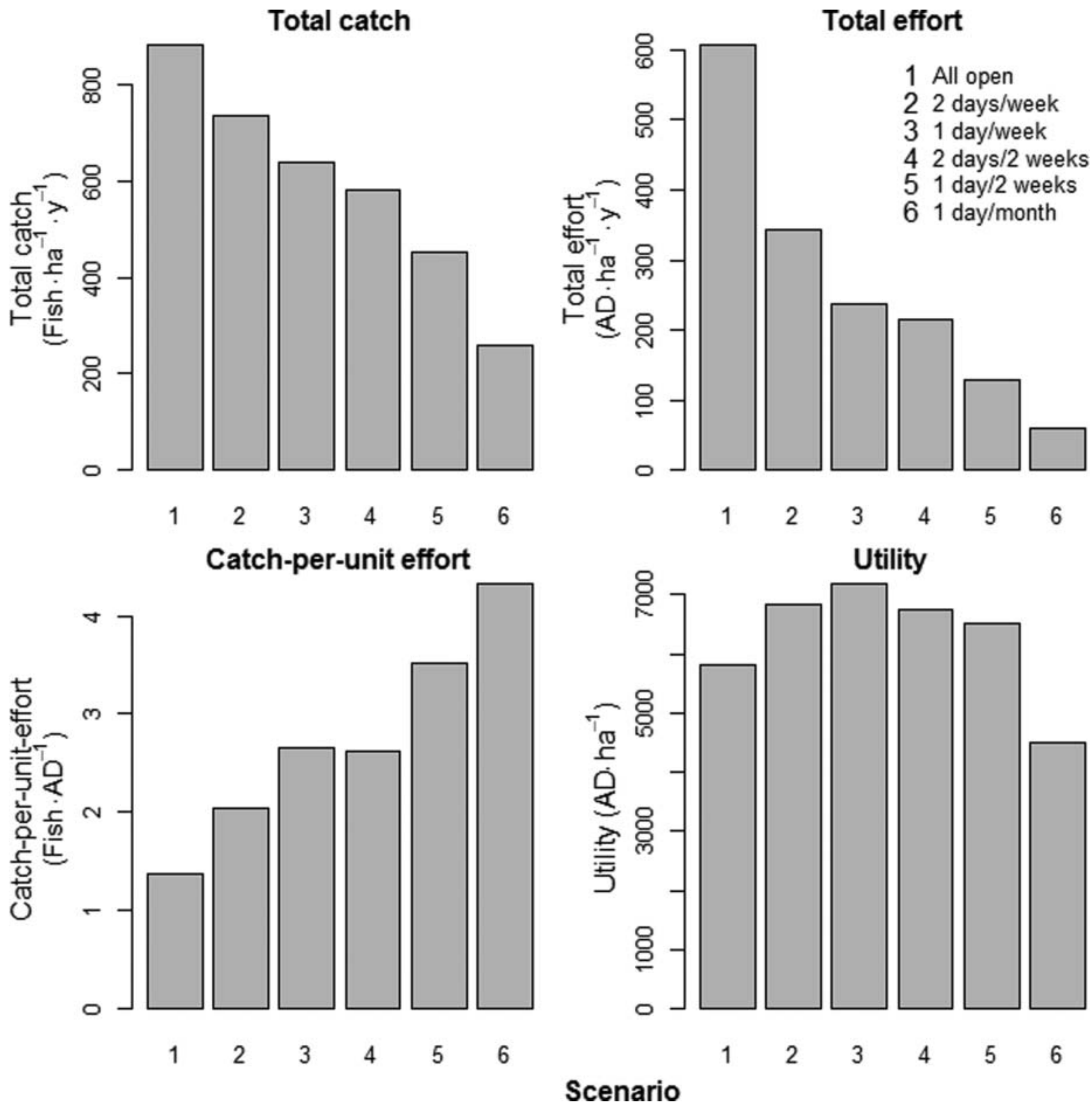

FIGURE 4. Bar plots showing differences in key recreational fishery metrics (mean total annual catch, total annual effort, CPUE [fish/angler-day, AD], and catch-related utility) associated with different opening scenarios for the case of a single lake. Opening schedules corresponding to each scenario number are described in the legend (all open = continuously open fishery).

the fish to return to the fishery and be captured again, thus sustaining much higher catch rates and attracting effort (Table 3). However, if there is an assumption of (1) no invulnerable subpopulation or (2) no invulnerable or refractory subpopulation, greater catch-related utility is generated from having a continuously open fishery.

The overall patterns in the results were similar when the single-lake case was extended to represent multiple lakes across a landscape. Under most assumptions, the rotational-closure strategy for multiple lakes provided lower catch-related utility than the optimal strategy for the single-lake case (1 d/week) and sometimes produced similar or lower catch-related utility than the continuously open fishery scenario (Figure 6). These results were due largely to assumptions about the redistribution of angler effort from closed lakes to open lakes; such assumptions were not a consideration for the single-lake case. If effort was assumed to fully redistribute, the resulting effort displaced by closures was concentrated toward the open lakes (Figure 7). This produced greater effort under the rotating-closure scenario relative to other temporary closures, reducing the number of vulnerable fish, the catch rate, and the seasonal utility (Figure 6, right panels). Alternatively, under the assumption that anglers were unwilling to redistribute their effort in response to fishery closures ($r = 0$),

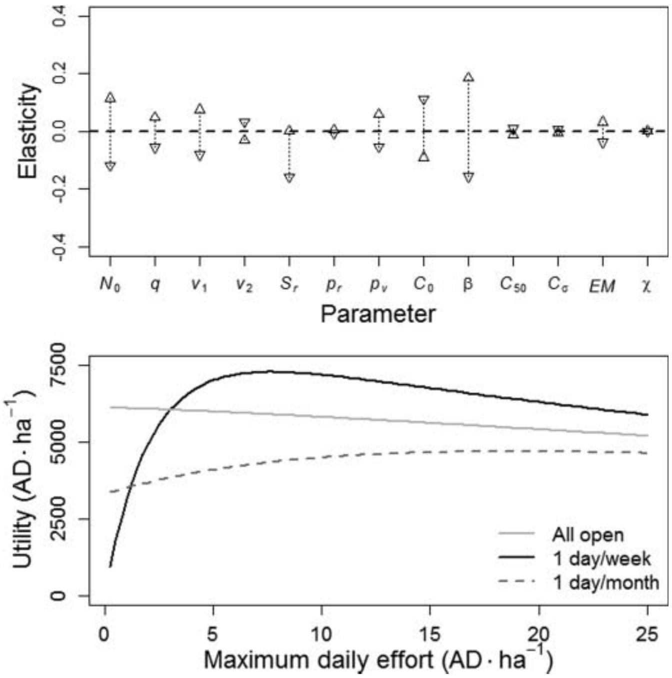

FIGURE 5. Elasticity of catch-related utility (angler-days [AD]/ha) to changes in the key model parameters (upper panel) and sensitivity of catch-related utility to maximum daily effort (lower panel) for the case of a single lake. Elasticity was calculated as the proportional change in catch-related utility resulting from a 10% increase or decrease in the parameter value from the base rate (parameters are defined in Table 2). The exception was β (the exponent of the satisfaction function), which was varied as a ±10% deviation from 1.0, allowing the function to be exponential or saturating. Upward-pointing arrows represent elasticity in response to parameter increases; downward-pointing arrows represent elasticity in response to parameter decreases. Total annual catch-related utility (lower panel) derived from a catch-and-release fishery that is open continuously (solid gray line), 1 d/week (solid black line), or 1 d/month (dashed gray line) was calculated across a range of maximum daily effort values from 1 to 25 AD/ha.

the rotational scenario produced utility similar to that of the best single-lake model (1 d/week); this is because the multiple-lake system was essentially functioning as many independent systems. Such a pattern was most apparent under the assumption of disproportionately high angler satisfaction from increased catch rates (β = 2; Figure 6, bottom row, left panel).

Within the temporary-closure scenarios, the multiple-lake system revealed an interesting interaction between angler satisfaction and catch rate (controlled by β). When angler satisfaction was less related to catch rate, the rotational scenario actually out-performed other temporary closures in terms of catch-related utility, nearly matching or even exceeding the utility of the continuously open fishery scenario (Figure 6, top row, right and middle panels). An assumption that angler satisfaction is less responsive to catch rate implicitly increases the relative importance of anglers being able to fish regardless of whether catch rates are low; therefore, strategies that give anglers some open lakes (i.e., rotational strategies) will allow for greater catch-related utility, especially if the anglers are willing to travel to those lakes (i.e., at least some redistribution of effort occurs).

DISCUSSION

The dynamics of vulnerable fish populations in recreational fisheries may have meaningful effects on CR fishery management. Mandatory CR is considered a relatively restrictive and powerful policy for sustaining catch rates (Barnhart 1989; Arlinghaus et al. 2007; Cooke and Schramm 2007), but alone it is insufficient to preserve the desired catch rates and associated utility. So long as fish require some meaningful time frame before returning to the vulnerable state, the population of fish that are vulnerable to anglers will decline throughout a continuously open season. These vulnerable pool dynamics alone can cause exactly the seasonal declines in catch rate and catchability that have been observed in multiple recreational fisheries (van Poorten and Post 2005; Askey et al. 2006). However, two critical points must be recognized. First, decreased catchability due to vulnerable pool dynamics is only one of several potential processes (e.g., harvest, effort, and environmental dynamics) that are responsible for the persistently declining catch rates observed throughout a season (Lux and Smith 1960; Askey et al. 2006), and these multiple processes may have an additive or interactive effect on catchability. Therefore, although the present results suggest that vulnerable

TABLE 3. Response metrics for a continuously open fishery (fully open) and a fishery with short openings (1 d/week) assuming populations with (1) vulnerability exchanges; (2) a refractory subpopulation but no invulnerable subpopulation; or (3) no invulnerable or refractory subpopulation (AD = angler-days).

	Vulnerability exchange		No invulnerable subpopulation		No refractory or invulnerable subpopulation	
Metric	Fully open	Open 1 d/week	Fully open	Open 1 d/week	Fully open	Open 1 d/week
Total catch (fish/ha)	881	638	6,990	2,326	17,706	2,558
Total effort (AD/ha)	606	238	1,795	260	1,800	260
Mean CPUE (fish/AD)	1.4	2.7	3.9	9.0	9.8	9.8
Utility (AD/ha)	5,805	7,174	110,744	83,298	696,682	100,632

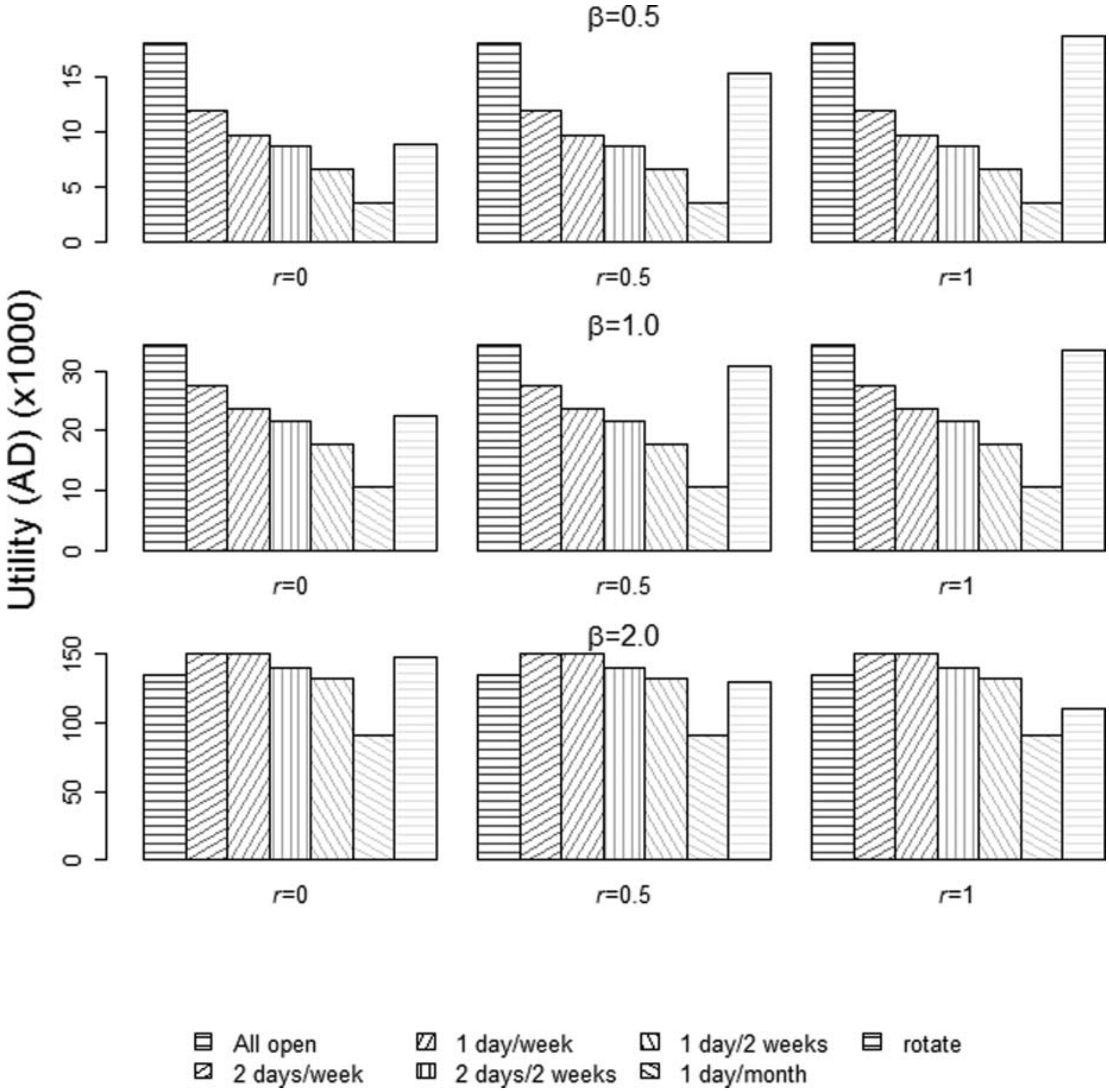

FIGURE 6. Evaluation of how catch-related utility (angler-days [AD]) for a multiple-lake system is affected by the relationship between angler catch rate and satisfaction (β) and by assumptions about how angler effort is redistributed from closed lakes to open lakes (r = effort redistribution parameter). Opening schedules are described in the legend (all open = continuously open fishery; rotate = rotating closures [see Methods]).

pool dynamics can generate this common catch rate pattern even in CR fisheries, further work is needed to distinguish the role of vulnerability exchanges from the roles of other processes. Second, the vulnerable pool dynamics described here are general enough to support various behavioral mechanisms that lead to decreased catchability. Several such mechanisms include fish movement and feeding responses to angling (Young and Hayes 2004), fish learning from angling (Young and Hayes 2004; Askey et al. 2006), and environmental effects on fish behavior (van Poorten and Post 2005). Vulnerable pool dynamics are particularly compatible with angling-driven mechanisms for seasonal changes in fish catchability (since the refractory subpopulation consists of caught-and-released fish) and thus provide a simple, theoretically based, empirically testable representation of changing catchability that does not depend on a detailed mechanistic understanding of the underlying behavioral mechanisms. However, angling-driven mechanisms can occur simultaneously with and potentially interact with environmentally driven mechanisms (van Poorten and Post 2005), and their relative importance in fisheries will be a crucial management question for future studies.

The primary management implication of this work is that effort limitation in the form of temporary closures may be warranted to sustain season-long catch-related utility of CR

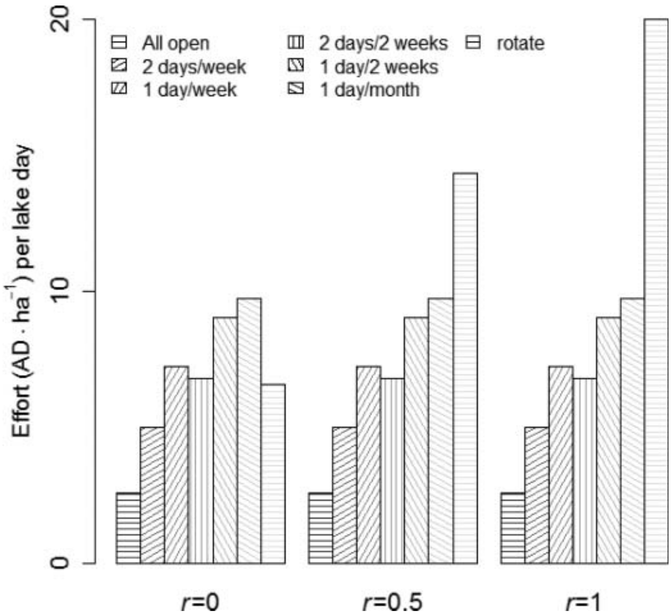

FIGURE 7. Realized effort (angler-days [AD]/ha) per lake-day (i.e., a function of opening schedule) under different assumptions of angler effort redistribution (r). Opening schedules are described in the legend (all open = continuously open fishery; rotate = rotating closures [see Methods]).

fisheries. Input controls have been recommended for both commercial fisheries (Walters and Pearse 1996; Stefansson and Rosenberg 2005) and harvest-oriented recreational fisheries (S. P. Cox and Walters 2002) as a means of controlling exploitation and preserving catch-related utility, but we are unaware of any example of their use for open-access CR fisheries. Here lies the challenge. Effort control is widely considered to be unpopular in many recreational fisheries (Sullivan 2003), and the "right to fish" is revered by anglers as well as by managers (Dorow et al. 2010; McClenachan 2013), who are understandably interested in stakeholder support and license sales (Cox et al. 2002). If stakeholders have a strong dislike for regulated effort limitation, the effect may subtract from the gains in catch-related utility that could be achieved by temporary closures. Such a dilemma may necessitate strong stakeholder engagement and human dimensions research to ensure the eventual success of drastic management tactics like short fishery openings (Arlinghaus 2006).

The inferences drawn from this work depend ultimately on assumptions of fish behavior—specifically, the vulnerability exchanges (i.e., transfer of fish among the vulnerable, invulnerable, and refractory states). There is theoretical and empirical support for the existence of vulnerable pool dynamics (S. P. Cox and Walters 2002; Cox et al. 2002) and alterations in fish vulnerability after capture and subsequent release (represented here by the refractory subpopulation; Young and Hayes 2004; Post et al. 2006; Alós et al. 2015). However, empirical estimates of the vulnerability parameters (e.g., v_1, v_2, and p_r; Table 2) are not common (Matthias et al. 2014). Further, it is reasonable to expect that vulnerability exchange parameters will vary among species, among fisheries, or even among angling practices, since catchability dynamics can also differ at these scales. For example, studies of some species (e.g., Rainbow Trout *Oncorhynchus mykiss* and Common Carp *Cyprinus carpio*) have suggested relatively strong changes in catchability (Beukema 1970; van Poorten and Post 2005; Askey et al. 2006; Klefoth et al. 2013), whereas other species (e.g., Northern Pike *Esox lucius*) appear to show weaker responses (Kuparinen et al. 2010). Values of the vulnerability parameters are important, since more rapid exchanges between states will eventually approximate a single-state system (i.e., no subpopulations based on vulnerability differences), and our results suggest that the gains to overall catch-related utility in CR fisheries (assuming no discard mortality) depend upon meaningful invulnerable and refractory subpopulations. The paucity of empirical estimates for vulnerability exchange rates and the importance of their magnitude emphasize the critical need for future empirical studies that evaluate vulnerability exchanges in recreational fisheries, particularly across different fish species or guilds.

This work highlights the importance of understanding relationships between angler catch-related utility and catch rate. In fact, temporary closures are predominately only useful if angler catch-related utility increases exponentially with increases in catch rate (akin to $\beta > 1$ in this model); such closures (with the potential exception of rotational closures and complete redistribution) are actually quite wasteful if angler utility instead features marginally decreasing gains in response to increasing catch rates ($\beta < 1$). This latter situation may be a more reasonable assumption for average angling populations, in accordance with the general economic theory of diminishing marginal returns. Empirical evaluations of this relationship are not common. However, Beardmore et al. (2015) found that anglers in northern Germany reported such decreasing marginal gains in overall satisfaction with increasing catch rates in five of six fisheries; accelerating increases in catch-related satisfaction (analogous to $\beta > 1$) were observed only for "coarse fish"—a suite of generally small, abundant cyprinid species. It is typically expected that a smaller proportion of anglers (likely the most avid anglers) will be interested in particularly high catch rates (Schramm et al. 1998; Dorow et al. 2010; Beardmore et al. 2015). Clearly, it will be necessary to gauge the importance of catch-related satisfaction for a particular fishery before implementing an extreme policy such as temporary closures, for which success is predicated on a particular angler type with a relatively rare level of catch-related satisfaction. Description of generalizable patterns in functional relationships between catch-related utility or total utility and catch rates across fish species and angler demographics represents an important area of future research.

The simplicity of our model with respect to socioeconomic processes and metrics leads to three key limitations. First, we describe daily regional effort via a logistic relationship depending on vulnerable fish and lake distance (following Allen et al. 2013 and Camp et al. 2014) without accounting for other elements (e.g., angler crowding) that could potentially influence the overall effort (Hunt 2005; Dabrowska et al. 2014). Inclusion of crowding effects in the effort dynamic process could result in fewer angler trips contributing to total catch-related utility under short-opening strategies in which fishing is spatiotemporally condensed. However, in this model, fewer trips taken to open lakes would have further increased the catch rates and the resultant catch-related utility achieved by those anglers who do fish. Second, we represent anglers' selection of fishing sites via a gravity model (based on a multinomial logit choice model) that does not allow for complex patterns of lake substitutability in the redistribution process (Hunt 2005), whereas such patterns might occur in reality due to angler preference for and attachment to particular sites (Hunt et al. 2007; Hunt 2008). Such preference patterns may be fishery specific and could be studied (1) via discrete-choice experiments conducted prior to potential implementation of a short-opening strategy (Beardmore et al. 2011) or (2) via site choice models that are revealed after implementation of this strategy (Hunt 2005; Hunt et al. 2011). Finally, we calculate catch-related utility based on catch rate, but we do not consider the size of fish caught, which can be important to anglers (Beardmore et al. 2015) and can affect other aspects of a fishery, such as differential hooking mortality (Johnston et al. 2015). This assumption allows for straightforward comparisons with past studies of vulnerable pool dynamics (S. P. Cox and Walters 2002; Cox et al. 2003) and is consistent both with the historical management focus on catch rates (Hudgins and Davies 1984; Schramm et al. 1998) and with recent recommendations (Beardmore et al. 2015). Furthermore, because we specifically represent CR fisheries throughout a season while assuming no discard mortality, the size structure of fish available to catch would not be clearly expected to change as a function of openings without fishery-specific information of how vulnerability exchanges are mediated by fish age or fish size. In reality, size-based exchange rates and the possibility that anglers will target larger fish could result in more rapid depletion of larger individuals from the available pool, especially if discard mortality is considered.

The implications discussed here should motivate thought on a critical element that was not quantitatively evaluated in this study: the likely heterogeneity of the anglers. Studies have suggested that angling populations are composed of multiple typologies (Johnston et al. 2010; Ward et al. 2013b), differing in terms of how they attain utility (e.g., the relationship between angler satisfaction and increasing catch rates; Pereira and Hanson 2003) and probably related to how they would be willing to redistribute effort when faced with temporary closures and potentially differing catch rates. We did not explore (1) how catch-related utility might be best achieved in an angler population composed of distinct typologies with respect to β or (2) the potential for anglers characterized by a certain β to be more or less willing to travel than other anglers (Fenichel and Abbott 2014). These assumptions are useful for understanding how angler characteristics can mediate the outcomes of management strategies in the context of fish vulnerability dynamics, but they do not allow us to explore the simultaneous implementation of multiple strategies that may appeal to a (possibly spatially nonrandom) mosaic of different angler typologies. This "portfolio approach" to management has gained some recognition (Sutinen and Johnston 2003) and represents a valuable area of future research.

In total, our work has extended the existing theory of vulnerable pool dynamics to encompass CR fisheries and has shown how such regulations might be ineffective at producing sustained high catch rates. Short openings, a relatively uncommon management strategy, could be coupled with CR regulations to potentially increase catch-related utility in single-lake and multiple-lake fisheries under certain conditions. Our simulations were overly simplistic, permitting us to explore the underlying socio-ecological implications under relatively optimistic conditions. More realistic conditions, which include variation in utility across anglers and site-specific variation in facilities (and even driving distances), will likely demonstrate that a short-opening strategy would be an effective tool in only a very limited set of circumstances. However, during an era in which effective management involves providing a variety of fishing opportunities that cater to a wide variety of angler utilities, this strategy provides another tool that could lead to high recreational benefits (in terms of catch rates) while conserving the resource. Actual changes to catch-related utility will depend on a series of assumptions regarding the biological and socioeconomic specifics of the fishery, and the present work represents a starting point for future investigation that may prove broadly meaningful for the management of catch-related utility in recreational fisheries.

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