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Interaction of ecological and angler processes: experimental stocking in an open access, spatially structured fishery

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Abstract. Effective management of socioecological systems requires an understanding of the complex interactions between people and the environment. In recreational fisheries, which are prime examples of socioecological systems, anglers are analogous to mobile predators in natural predator–prey systems, and individual fisheries in lakes across a region are analogous to a spatially structured landscape of prey patches. Hence, effective management of recreational fisheries across large spatial scales requires an understanding of the dynamic interactions among ecological density dependent processes, landscape-level characteristics, and angler behaviors. We focused on the stocked component of the open access rainbow trout (*Oncorhynchus mykiss*) fishery in British Columbia (BC), and we used an experimental approach wherein we manipulated stocking densities in a subset of 34 lakes in which we monitored angler effort, fish abundance, and fish size for up to seven consecutive years. We used an empirically derived relationship between fish abundance and fish size across rainbow trout populations in BC to provide a measure of catch-based fishing quality that accounts for the size-abundance trade off in this system. We replicated our experimental manipulation in two regions known to have different angler populations and broad-scale access costs. We hypothesized that angler effort would respond to variation in stocking density, resulting in spatial heterogeneity in angler effort but homogeneity in catch-based fishing quality within regions. We found that there is an intermediate stocking density for a given lake or region at which angler effort is maximized (i.e., an optimal stocking density), and that this stocking density depends on latent effort and lake accessibility. Furthermore, we found no clear effect of stocking density on our measure of catch-based fishing quality, suggesting that angler effort homogenizes catch-related attributes leading to an eroded relationship between stocking density and catch-based fishing quality at the timescale of annual surveys. We conclude that declines in fishing quality resulting from understocking (due to declines in catch rate with low fish abundance) and overstocking (due to suppressed growth and limited recruitment at high density) give an optimal stocking rate that depends on accessibility and latent effort.

Key words: angler effort; culture-based fishery; experiment; fishing quality; freshwater; management; open access fishery; rainbow trout, Oncorhynchus mykiss; *recreational fishery; stocking density.*

Introduction

Outcomes of conservation and natural resource management actions depend on complex interactions between people and the environment. Effective management of fisheries, forest resource extraction, ecological preserves, and hunting, for example, depends on the consideration of both social and ecological aspects of the system (Berkes and Folke 1998, Liu et al. 2007, Carter et al. 2014). Recreational fisheries, in particular, are prime examples of socioecological systems (Arlinghaus et al. 2013). Negative system outcomes in recreational fisheries, generally judged by fisheries managers or conservationists, include regional-scale overfishing, fish population collapse, declines in angler satisfaction, and loss of angling license revenue. These outcomes are dependent on the three main components of any recreational fishery: individual fish populations, regionally mobile anglers, and the managers acting across the region (including the relevant policies and governance within the region). Whereas the processes, interactions, and feedbacks among all three components must be considered for effective management (Ward et al., *in press*), there are several critical uncertainties that are limiting effective management and that point to key research needs. In particular, there is an outstanding need to empirically evaluate the factors that control consumer effort and to quantify variability in the effort response as a function of resource quality (Ward et al., in press). This need can be addressed by measuring actual responses in angler effort and fishing quality to experimentally induced changes in management practices.

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Understanding how foraging animals are distributed across a spatially structured landscape is a central focus for both basic and applied ecologists. Many recreational fisheries are spatially structured, with multiple stocks patchily distributed across landscapes linked by a common pool of highly mobile anglers (Hunt et al. 2011, Post and Parkinson 2012, Post 2013, Lester et al. 2014). This structure is, in many ways, analogous to spatial predator–prey dynamics (Fretwell 1972, Sutherland 1983) where individual fisheries in lakes can be considered prey patches among which mobile predators (i.e., anglers) forage (Johnson and Carpenter 1994). Within lakes, sustainable exploitation theory assumes that there are ecological processes that compensate for some level of harvest based on density dependent processes of growth, survival, and recruitment (Walters and Martell 2004, Clark 2006). This theory posits that maximum yield occurs at the nexus of exploitation rate and ecological compensatory capacity (Lester et al. 2014). Assessing sustainable exploitation across a landscape of multiple lakes in open access recreational fisheries is complex because biological, geographic, and angler behavioral traits can vary between lakes, and biological and angler behavioral traits can vary within lakes (Johnston et al. 2010, 2013, 2015, Horan et al. 2011, Post and Parkinson 2012, Abbott and Fenichel 2013, Fenichel et al. 2013*a*,b, Lester et al. 2014).

At the scale of the patch, ecological processes of recruitment, density dependent growth, and size-dependent survival control the local production and compensatory ability of populations to sustain harvest (Walters and Post 1993, Post et al. 1999, Lorenzen 2000, Lorenzen and Enberg 2002, Lester et al. 2014). At the landscape scale, spatial configuration of lakes and angler behavior combine to exert local harvest pressure (Post et al. 2008, Johnston et al. 2010, 2013, Hunt et al. 2011, Ward et al. 2013*b*). But, angler behavior is complex and heterogeneous across landscapes, and anglers in different regions can have different utility functions (Bryan 1977, Ditton et al. 1992, Aas et al. 2000, Dorow et al. 2010, Johnston et al. 2010, 2013, 2015, Beardmore et al. 2013). Even within a region with a relatively homogenous angler population, variation among patches in travel distance and other non-catch-related site attributes (e.g., campsites, aesthetics, crowding, regulations) interacts with variability in fish size and abundance to influence anglers' decisions of how much to fish and where to fish (Hunt 2005, Matsumura et al. 2010, Horan et al. 2011, Hunt et al. 2011, Abbott and Fenichel 2013, Fenichel et al. 2013*a*,b, Ward et al. 2013*b*, Chizinski et al. 2014). Local harvest dynamics therefore depend on catch-dependent and catch-independent attributes of patches, as well as on anglers' utility functions. In the context of predator–prey systems, angler effort dynamics have been characterized as the emergent response of anglers to measures of fish abundance (Johnson and Carpenter 1994, Chizinski et al. 2014) or to aggregate measures of fishing quality incorporating both fish abundance and fish size (Post et al. 2008, Post and Parkinson 2012, Wilson et al., in press), as well as non-catch attributes (such as accessibility and crowding) and angler utility functions (Arlinghaus et al. 2013). In the context of economics, the reward sought by anglers across fishing patches is called utility or economic rent, whereas, in the context of social psychology, the reward is called expected satisfaction. Fisheries biologists use the term fishing quality to encompass both the bioeconomic and social psychology aspects of angler reward (Conrad and Bjorndal 1991, Sanchirico and Wilen 1999).

Regardless of the importance of non-catch-related patch attributes and variation in angler utility functions, anglers, among other fishers, appear to track variation in fish abundance and fish size across space leading to heterogeneity in the magnitude and spatial distribution of angler effort (Parkinson et al. 2004, Post and Parkinson 2012, Askey et al. 2013, Chizinski et al. 2014). This heterogeneity of angler effort and the application of the concept of ideal free distribution (IFD; Fretwell 1972, Sutherland 1983, Tregenza 1995) to spatially structured fisheries with mobile anglers has resulted in inferences of homogenization of fish abundance (or other measures of fishing quality) among fishing lakes of equal access cost (Matsumura et al. 2010, Hunt et al. 2011). Some empirical and modeling studies addressing spatially structured recreational fisheries have suggested that spatial patterns of harvest dynamics are consistent with IFD predictions (Cox and Walters 2002, Cox et al. 2002, 2003, Post et al. 2002, Parkinson et al. 2004), whereas other modeling studies suggest IFD predictions at the landscape scale are only expected when latent effort is high and access costs are taken into account (Matsumura et al. 2010, Hunt et al. 2011).

The pattern of angler effort across a landscape responds to variation in patch utility (i.e., the fishing quality of each patch) and emerges as the aggregate outcome of variation across patches in ecological processes (e.g., the effect of fish population density on fish size and abundance) and non-catch-based attributes (e.g., accessibility), regional variation in angler population attributes (e.g., population size and perception of fishing quality), and individual variation in angler behaviors and preferences (i.e., utility functions). Figure 1 summarizes how variation in fishing effort emerges from these aggregate effects. We single out the catch-based component of patch utility by controlling for other determinants of patch utility (i.e., access costs, latent effort, and regional variation in utility functions), and we provide an empirical assessment of the emergent pattern of angler effort across a landscape in response to experimentally induced changes in management practices for rainbow trout, *Oncorhynchus mykiss* (Walbaum, 1792), which is the centerpiece of a large, open access, spatially structured recreational fishery in British Columbia, Canada. We focused only on the stocked component of this fishery (i.e., in lakes with no natural recruitment, where populations are

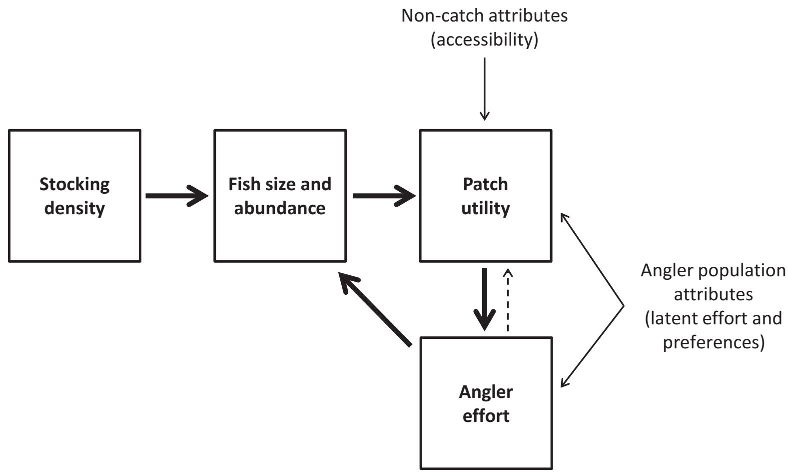

Fig. 1. The effect of stocking density on angler effort emerges via dynamic feedbacks between angler effort and patch utility. Fish size and abundance, which are affected by density dependent growth and recruitment, and which are influenced by angling, constitute the catch-based component of patch utility. We focused on this catch-based component of utility (which we call fishing quality) and on the effects shown with thick arrows. Patch utility can also be affected directly by angler effort (due to crowding), non-catch attributes (e.g., patch accessibility), and angler population attributes (e.g., angler population size). These latter effects were either non-existent (dashed arrow) or controlled for (solid thin arrows) in the present study.

dependent entirely on hatchery fish), which allowed us to experimentally decouple spatial patterns of fishing effort from natural recruitment at the local scale. This decoupling was crucial in facilitating our goal of drawing robust inferences from empirical data regarding landscape scale patterns in fish populations and angler populations in response to our experimental manipulation of management activities (i.e., stocking rates). An additional goal was to advise fishery managers on whether increasing stocking rates will always attract additional angler effort or whether high levels of stocking can, if stocking rates are too high, degrade the utility of a fishing patch by decreasing fish size at the expense of abundance (e.g., due to density dependent ecological processes in the fish population), thereby reducing fishing quality and repelling anglers. We aimed to advise managers on what stocking rate should give maximal effort and on how this optimal stocking rate is expected to vary over a landscape composed of lakes with varying ease of access (e.g., depending on driving distance) and regionally variable latent effort and angler utility functions.

Our experimental approach, with controls, involved the manipulation of stocking rate in a subset of lakes after a period of unchanged stocking and replication of this manipulation in two pre-defined regions known to differ substantially in latent fishing effort (i.e., the total population of anglers), driving distance to the biggest angler population in the province (in the Fraser River Valley, including Vancouver), and the average anglers' perception of fishing quality (Wilson et al., in press). We hypothesized that a dynamic angler effort response to variation in fish abundance and size, created through manipulation of stocking rates, would result in spatial heterogeneity in angler effort across lakes with equivalent accessibility within a region. Furthermore, we hypothesized that, across lakes with equivalent accessibility within a region, a dynamic angler effort response would result in maximal angler effort at intermediate stocking rates due to declines in fishing quality at low stocking rates (if fewer fish result in lower fishing quality) and high stocking rates (if high density suppresses growth, or even prevents recruitment into the fishery). Hence, we tested the predictions that (1) there is a stocking density for a given lake at which attraction of angler effort is maximized (i.e., there is an optimal stocking density), (2) angler effort is highest in the most accessible lakes within a region with the highest latent effort, and (3) the effect of stocking density on angler effort interacts with accessibility and latent effort such that the stocking density at which attraction of angler effort is maximized is highest in the most accessible lakes in a region with the highest latent effort.

We also hypothesized that the effect of stocking density on angler effort likely emerges as a result of the proximate effect of stocking density on fish size and abundance in combination with the dynamic feedback between angler effort and fish size and abundance across landscapes (Fig. 1). We used an empirically derived relationship between fish abundance and fish size across rainbow trout populations in BC (Wilson et al., in press) to provide a measure of catch-related fishing quality that accounts for the size–abundance trade-off in this system, and is expected to contribute, to some degree, to overall patch utility (Fig. 1). We refer to this aggregate measure as "fishing quality" (or, for brevity, "quality") for the remainder of our paper. Our experimental design, however, was not intended to reveal the mechanisms underlying the dynamic effort–quality feedback (as depicted in Fig. 1), as such a design would require direct experimental manipulation of angler effort, and this control on effort has been investigated in the experimental simulation models by Hunt et al. (2011) and others. We can, nonetheless, gain insight into how catch-based aspects of patch utility influence angler effort (e.g., proposed in Matsumura et al. 2010, Hunt et al. 2011) because we control for access costs and latent effort and observe equilibrium outcomes. Hence, by analyzing empirical patterns of fishing quality in response to our experimental manipulation of stocking rate, we can make the connection between stocking density and angler effort via the effect of catch-based patch utility (i.e., fishing quality). We tested the predictions that (4) across lakes of equivalent access costs, reduced fishing quality results from understocking (if low abundance results in lower catch rates) and overstocking (if high density limits growth and/or prevent recruitment into the fishery), (5) anglers degrade fishing quality most quickly when accessibility and latent effort are highest, and (6) anglers homogenize fishing quality across lakes with equivalent accessibility most quickly when latent effort is highest (Matsumura et al. 2010, Hunt et al. 2011).

Materials and Methods

Study system

To investigate the effects of stocking density on angler effort, we conducted a multiyear experiment using 34 lakes that are managed as recreational rainbow trout fisheries and that had been stocked with rainbow trout at consistent densities for several years preceding our experiment. These lakes were selected because they all have similar physical characteristics, similar angling regulations, and are all dependent on stocking for recruitment (i.e., there are no suitable spawning locations for rainbow

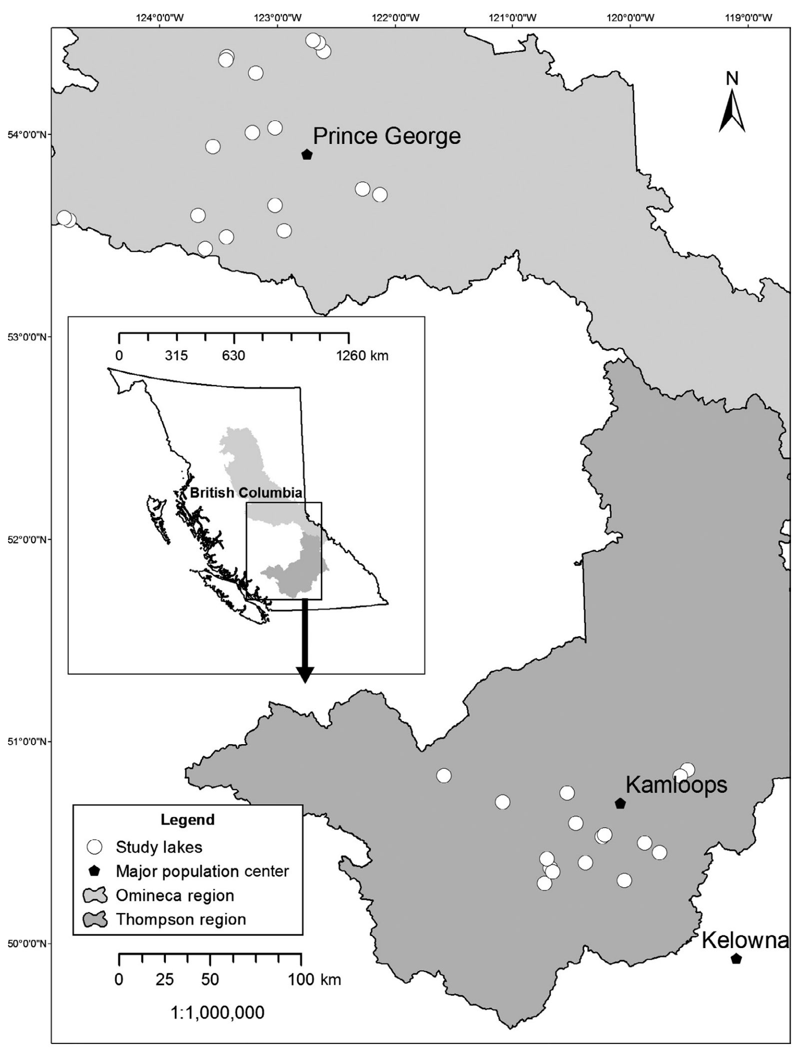

Fig. 2. Locations of 34 natural study lakes in the Omineca (northern) and Thompson (southern) regions of British Columbia.

trout in these lakes). These lakes are distributed across two geographically separate management regions (Fig. 2) with significantly different communities of anglers (Ward et al. 2013*b*, Wilson et al., *in press*). The northern region is characterized by low human population density, and lakes in this region are relatively distant from the largest urban centers in the province (i.e., Vancouver and surrounding municipalities). The southern region is characterized by high human population density, and lakes in this region are relatively closer to several of the major urban centers in the province (e.g., Vancouver, Kelowna, and Kamloops). Hence, we expect higher latent effort in the southern region than in the northern region as a result of the broad-scale difference in access cost (e.g., it takes upwards of 10 h to drive from Vancouver to many lakes in the northern region) and latent effort (e.g., population density is very low in northern BC). We also expected some within-region variation in accessibility among lakes based on variables such as road distance from urban centers (i.e., travel cost) and campsite availability.

Measuring angler effort

Angling effort during the open water season was measured at each lake using time-lapse cameras set at a 1-h interval. The total number of anglers per hour was counted using the specially developed software Time Lapse (Greenberg and Godin 2012, 2013). Annual summer (May–September) angling effort density (h/ha) was obtained by aggregating hourly effort across the whole season and standardizing for lake area. We used instantaneous counts from creel surveys to correct for anglers not captured by cameras (van Poorten et al. 2015).

Estimating fishing quality

Rainbow trout populations were sampled annually using the British Columbia provincial standard protocol. Gillnet samples provided a standard method to assess fish size and density across lakes. One floating and one sinking multimesh gillnet was set overnight in each lake. Fish density in each lake was estimated using the sampling methodology outlined in Ward et al. (2012), and this estimate of fish density was used to calculate the catch per unit effort (CPUE) that would be experienced by anglers based on the Ward et al. (2013*a*) catchability model. Mean fish length of rainbow trout above 250 mm was estimated from gillnet samples. This measure of fish size is based on the minimum length at which rainbow trout are fully vulnerable to angling (Cox 2000, Askey et al. 2006).

There is a trade-off between fish size and abundance due to density dependent growth and survival, and this size–numbers trade-off influences the relative attractiveness (i.e., catch-based utility; Fig. 1) of a lake to recreational anglers (Parkinson et al. 2004, Askey et al. 2013, Wilson et al., *in press*). Wilson et al. (*in press*) analyzed size and abundance data across British Columbia and found that average fishing quality for lakes in northern British Columbia is higher than average fishing quality in southern British Columbia. We used the parameter estimates from Wilson et al. (*in press*) for the trade-off between average fish size (L cm) and CPUE across lakes to calculate the expected value of CPUE for a given value of L

$$\mathrm{CPUE}[L] = \alpha \times L^{-\beta}, \tag{1}$$

where α is a region-specific constant, and β denotes the curvature of the size–numbers trade-off. Wilson et al. (*in press*) estimated an α_{north} of 775953, an α_{south} of 276434, and a β of 3.61. We then used the ratio between observed CPUE (based on observed fish densities) and expected CPUE (from Eq. 1) to estimate the contribution of fish abundance to fishing quality (Q_v) in each lake,

$$Q_v = \frac{\mathrm{CPUE}}{\mathrm{CPUE}[L]}, \tag{2}$$

and the ratio of observed size (from gill net samples) and predicted size (from Eq. 1) to estimate the contribution of average fish size to fishing quality (Q_h) in each lake,

$$Q_h = \frac{L}{L[\mathrm{CPUE}]}. \tag{3}$$

We then combined contributions of abundance and size to fishing quality for each lake (Q) using a weighted average:

$$Q = [Q_v \times (Q_v/(Q_v + Q_h))] + [Q_h \times (Q_v + Q_h)]. \tag{4}$$

We assumed that the predicted total CPUE corresponded to catch rate in our calculation of catch-dependent fishing quality (i.e., the predicted CPUE is the catch rate that influences angling effort) as we were unable to estimate kept fish catch rates and caught-and-released fish catch rates among the experimental lakes.

Experimental design and analyses

Our experimental manipulation involved changing stocking density mid-way through our series of yearly estimates of angler effort and fishing quality. Stocking density ranged from 26 to 370 yearlings equivalent per ha prior to our stocking manipulation, and from 41 to 740 yearlings equivalent per ha after our stocking manipulation. The amount of change in stocking density was determined on a lake-by-lake basis in collaboration with local fisheries managers and varied between an 11% and 632% increase in stocking density (Appendix S1: *Stocking densities for each year in each lake*). Stocking density was left unchanged in eight lakes, and we used these lakes to account for potential annual trends in angler effort and fishing quality by estimating the slope of the year-effort and year-quality relationships in linear mixed models. We used the logarithm of effort and quality to remove any correlation between magnitude and variance in the data (we also tried analyzing the data without log transformation, and the results, not shown, were not qualitatively different from those presented herein), and we used our estimate of the year-effort and year-quality slopes to adjust our measurements of effort and quality to remove the year-over-year trend. In seven additional lakes, there were inconsistent changes in stocking density between years (i.e., there were increases and decreases in stocking density over this time period, and/or stocking did not occur in some years), and we used the combined set of 15 control lakes (i.e., the eight lakes with no stocking change, plus the seven lakes with inconsistent changes in stocking density) to predict the effects of variables, such as road distance and campsite availability on lake accessibility, and to construct an accessibility measure. We calculated mean effort (across all years) for each control lake and then calculated the residual effort among lakes after accounting for the mean difference in effort between regions using a linear model. Residual effort in each lake was then used to predict how effort varies in relation to four lake-specific access variables: (1) distance from the nearest urban center to the lake on paved road, (2) distance to the lake on gravel road, (3) distance to the lake on four-wheel-drive road, and (4) number of campsites at the lake (Appendix S1: *Road distances and number of campsites for each lake*). We then used a linear model to estimate how many angler h/ha are gained or lost for each additional km of road or for each additional campsite. These estimates were then used to calculate an accessibility measure (i.e., predicted accessibility; "AccessP" in Appendix S2) for each lake.

To evaluate our predictions regarding the effects of stocking density on angler effort, we used the 19 lakes in our data set with a clear stocking manipulation (e.g., an increase in stocking density as of 2010, and no prior or subsequent changes in stocking density). Fishing quality was measured for a subset of the years in which angler effort was measured, and five of our 19 treatment lakes did not have a sufficiently long time series of quality measurements to overlap with the stocking manipulation (i.e., <1 yr pre- or post-manipulation). Hence, for our evaluation of the effects of stocking density on fishing quality, we used 14 lakes with both a stocking manipulation and at least 1 yr of gillnet surveys pre- and post-treatment. We employed an information criterion approach to assess the fit of linear mixed effects models with subsets of the following fixed effects (Table 1):

$$\begin{aligned}(\text{Effort or Quality}) \sim & \text{Region} + \text{Access} + \text{Stocking} \\ & + \text{Stocking}^2 + \text{Region} \times \text{Stocking} \\ & + \text{Region} \times \text{Stocking}^2 + \text{Access} \\ & \times \text{Stocking} + \text{Access} \times \text{Stocking}^2.\end{aligned}$$

We centered stocking density measures on the mean stocking density across all lakes and years in order to remove collinearity between stocking and stocking^2 (Kutner et al. 2005). Year and lake were modeled as a random effect so that yearly estimates of effort and quality were treated as repeated measures on lakes. Model fit was assessed based on the corrected Akaike's information criterion corrected for small sample size (AIC_c) with the number of observations (the sum of all years across all treatment lakes) set to 91 for models of effort and to 57 for models of quality (quality was measured in fewer years than was effort). We used the

Table 1. Model comparison for effects of region, accessibility, and stocking density (with a 0-, 1-, and 2-yr lag) on angler effort.

Model	No lag		1-yr lag		2-yr lag	
	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c
1) Region	**216.5**	**0.6**	216.5	12.9	216.5	9.3
2) Region + access	**217.4**	**1.4**	217.4	13.7	217.4	10.1
3) Region + stocking	218.3	2.3	215.3	11.6	214.2	6.9
4) Region + stocking + region : stocking	**216.0**	**0.0**	211.8	8.1	214.1	6.8
5) Region + access + stocking	219.1	3.1	216.1	12.4	215.1	7.8
6) Region + access + stocking + region : stocking	**216.8**	**0.8**	212.5	8.8	214.8	7.5
7) Region + access + stocking + access : stocking	220.8	4.9	217.9	14.2	215.5	8.2
8) Region + access + stocking + region : stocking + access : stocking	219.2	3.3	211.6	7.9	212.4	5.1
9) Region + stocking + stocking^2	220.6	4.6	215.1	11.4	213.9	6.6
10) Region + stocking + stocking^2 + region : stocking + region : stocking^2	**217.4**	**1.4**	**203.7**	**0.0**	**207.3**	**0.0**
11) Region + access + stocking + stocking^2	221.5	5.5	215.8	12.1	214.8	7.5
12) Region + access + stocking + stocking^2 + region : stocking + region : stocking^2	218.1	2.1	**204.2**	**0.5**	**208.3**	**1.1**
13) Region + access + stocking + stocking^2 + access : stocking + access : stocking^2	219.9	3.9	220.5	16.9	219.1	11.8
14) Region + access + stocking + stocking^2 + region : stocking + region : stocking^2 + access : stocking + access : stocking^2	222.5	6.6	207.6	3.9	212.7	5.4

Note: Models with $\Delta AIC_c < 2$ are shown in bold.

log-likelihood optimization method (as opposed to reduced maximum likelihood) to fit the models so that models could be compared using AIC_c in a statistically valid manner (Pinheiro et al. 1994, Pinheiro and Bates 1996). Models with $\Delta AIC_c < 2$ relative to the best model were considered to have substantial and equivalent support (Sugiura 1978, Hurvich and Tsai 1991, Burnham and Anderson 2004), and we focused our subsequent analyses on these models, although models with $\Delta AIC_c < 4$ were also included in our interpretation of fixed effects. Because 1-yr-old fish typically recruit into the fishery within 1–2 yr post-stocking, we assessed models using three different stocking time lags: stocking in the same year as effort and quality were measured (lag = 0), stocking the year prior to measurement (lag = 1), and stocking 2-yr prior to measurement (lag = 2). All analyses were performed in R (R Core Team 2014). We used the lme4 package to fit linear mixed-effects models (Bates et al. 2014), and we used the AICcmodavg package to compute AIC_c values (Mazerolle 2015). To further interpret the models with $\Delta AIC_c < 2$, the statistical significance of the fixed effects included in these models was computed using the lmerTest package with Satterthwaite approximation for denominator degrees of freedom (Kuznetsova et al. 2014).

Results

In the northern region, for all study years (2008–2014), median effort was 22.16 angler $h \cdot ha^{-1} \cdot yr^{-1}$ (range, 0.88–161.9), whereas median effort was 99.37 angler $h \cdot ha^{-1} \cdot yr^{-1}$ in the southern region (14.05–691.96). The median expected CPUE was 0.883 fish caught per angler hour (0.477–3.26) in the northern region and 0.781 fish caught per angler hour (0.479–2.79) in the southern region. Median fish size was 327.67 mm (266.48–438.93) in the northern region and 321.60 mm (278.90–433.20) in the southern region.

Temporal trends

There was evidence for an annual trend in both angler effort and fishing quality in control lakes (Fig. 3). The slope of log(effort) over years was significantly different between regions ($F_{1,26} = 6.73$, $P = 0.015$). Our estimates of the slope for effort in the southern and northern regions were −1.15 and 1.05 $h \cdot ha^{-1} \cdot yr^{-1}$, respectively. The slope of log(quality) over years was not significantly different between regions ($F_{1,14} = 0.131$, $P = 0.723$). Our estimate of the slope for quality was 1.02/yr. In subsequent analyses, below, the annual trend was accounted for (i.e., detrended) in the time series of angler effort and fishing quality data.

Spatial pattern in access

We used angler effort from 14 control lakes to infer the effects of road distances from urban centers and number of campsites on accessibility. Road distances and the number of campsites had a significant effect on residual log(effort) after accounting for regional effects (multiple $R^2 = 0.6275$, $F_{4,11} = 4.63$, $P = 0.019$). We estimated that (1) a lake loses 1.017 angler h/ha for every km of paved road, (2) a lake loses 1.007 h/ha for every km of gravel road, (3) a lake loses 1.048 h/ha for every km of four-wheel-drive road, and (4) a lake gains 1.025 h/ha for every campsite. These estimates were used to calculate an accessibility measure (i.e., predicted accessibility, AccessP in our data set) for each lake (Appendix S1: *Road distances and number of campsites for each lake*).

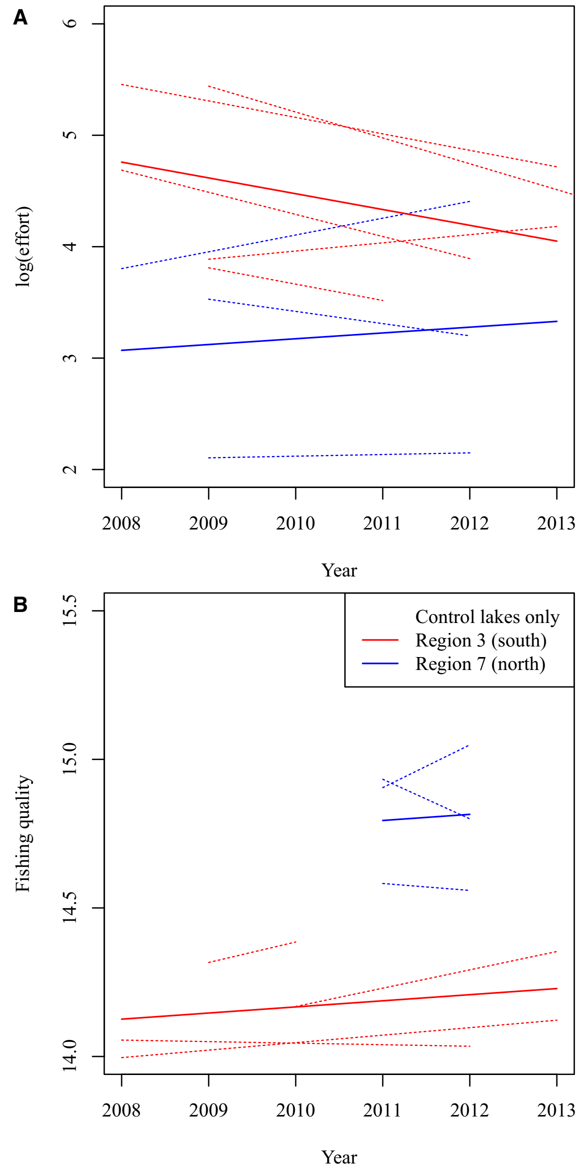

Fig. 3. Temporal trends in angler effort ($h \cdot ha^{-1} \cdot yr^{-1}$) (panel A) and fishing quality (panel B). Dashed lines are fitted trends for individual control lakes. Solid lines are regional trends (fitted linear models) across all control lakes.

Angler effort

Changes in stocking density appeared to influence angler effort after a 1- or 2-yr time lag. Models using 0-yr lagged data had consistently worse fits (minimum AIC_c = 216.0) than models with other lag times (1-yr lag, minimum AIC_c = 203.7; 2-yr lag, minimum AIC_c = 207.3; Table 1). The same set of models resulted in the best fits for both the 1-yr lag data and 2-yr lag data (models 10 and 12), whereas the simplest model, with no stocking effect, resulted in the best fit for 0-yr lag data (Table 1). Hence, for simplicity of presentation of the results from our analysis of the effect of stocking manipulation on angler effort, we only present details for the results from 1- to 2-yr lags between stocking and measurement of angler effort (Fig. 4). Also, these lags make the most biological sense in terms of the effect of stocking on angler effort (1-yr-old fish should typically recruit into the fishery 1–2 yr post-stocking).

We predicted that there is a stocking density for a given lake at which attraction of angler effort is maximized (prediction 1). Hence, we expected the best models to include a negative coefficient for the quadratic stocking effect (which results in a hump-shaped curve with a maximum value of $-b/(2a)$, where a and b are coefficients in the quadratic equation: effort = $a(\text{stocking})^2 + b(\text{stocking}) + c$). We found that the best model for both the 1- and 2-yr lag data (Table 1) included a significant quadratic stocking effect with a negative coefficient (Table 2, Fig. 4). All models with ΔAIC_c <4 relative to the best model, for both 1- and 2-yr lag data (Table 1), also included a significant quadratic stocking effect with a negative coefficient (Table 2). Thus, prediction 1 was supported with strong evidence.

We predicted that angler effort should be highest in the most accessible lakes within a region with the highest latent effort (prediction 2). Hence, we expected the best models to include a positive coefficient for the effect of access and lower effort in the northern region relative to the southern region. An effect of access was not included in the best model for either the 1-yr lag data or the 2-yr lag data (Table 1). An effect of access was included in all the other models with ΔAIC_c < 4 relative to the best model for both 1- and 2-yr lag data (Table 1), and access had a positive, although non-significant, coefficient in models with ΔAIC_c < 2 (Table 2). There was a large regional effect on effort, with lower angler effort in the northern region relative to the southern region (Fig. 4). Unsurprisingly, removing the effect of region drastically reduced model fits (results not shown), and all the models for both the 1- and 2-yr lag data with ΔAIC_c < 4 included a significant effect of region on effort (Table 2). Thus, prediction 2 was supported with evidence across both regions for lower angler effort with lower local-scale accessibility and for higher angler effort in the southern region where latent effort is highest and province-wide accessibility is highest.

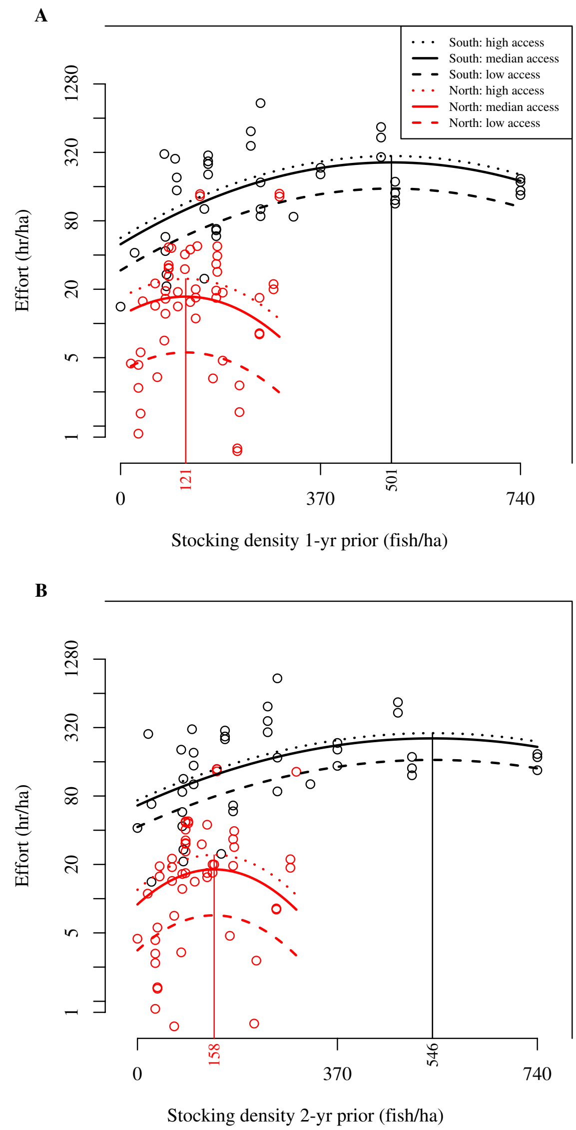

FIG. 4. The response of angler effort (h/ha) to stocking density (A) 1-yr prior or (B) 2-yr prior. Note the log scale on the y-axis. Lines show the linear fit based on Model 12 in Table 1.

We predicted that the effect of stocking density on angler effort interacts with accessibility and latent effort such that the stocking density at which attraction of angler effort is maximized is highest in the most accessible lakes in a region with the highest latent effort (prediction 3). In our models with a quadratic stocking effect (i.e., those with an optimal stocking density), any term interacting with stocking and/or stocking^2 will influence the optimal stocking density (i.e., the stocking density that gives the maximum angler effort). Hence, we expected the best models to include interaction effects between stocking and access, as well as between stocking and region. We found that the best models for both the 1- and 2-yr lag data included region-by-stocking and

Table 2. Values of coefficients (coef) and statistics for tests of significance for effects included in the best fit models ($\Delta AIC_c < 2$) for lagged stocking effect on ln(angler effort).

	1-yr lag						2-yr lag					
	Model 10			Model 12			Model 10			Model 12		
	coef	df	F	coef	df	F	coef	df	F	coef	df	F
Intercept	4.9	…	…	5.3	…	…	4.8	…	…	5.2	…	…
Region	**−2.3**	**1**	**20.3**	**−2.0**	**20.1**	**15.2**	**−2.0**	**20.0**	**16.4**	**−1.8**	**18.5**	**12.9**
Access	…	…	…	9.5E-03	18.9	2.1	…	…	…	7.8E-03	16.2	1.5
Stocking	3.9E-03	1	75.3	3.9E-03	75.7	0.1	3.4E-03	5.7	0.8	3.4E-03	2.4	0.6
Stocking^2	**−6.5E-06**	**1**	**73.5**	**−6.6E-06**	**73.6**	**7.1**	**−4.5E-06**	**66.5**	**9.9**	**−4.6E-06**	**60.5**	**9.3**
Region : stocking	**−8.4E-03**	**1**	**75.3**	**−8.4E-03**	**75.5**	**19.6**	**−5.3E-03**	**65.0**	**10.7**	**−5.6E-03**	**53.3**	**11.7**
Region : stocking^2	−2.1E-05	1	73.5	−2.0E-05	73.6	2.6	**−3.2E-05**	**62.8**	**6.1**	**−3.1E-05**	**54.0**	**5.5**

Notes: Significant effects ($P < 0.05$) are shown in bold. Denominator degrees of freedom (df) were estimated with Satterthwaite approximation. Coefficients for the effects associated with region apply to values in the northern region relative to the southern region.

region-by-stocking^2 interactions (Table 1, Fig. 4). Significant region-by-stocking interactions were included in all models with $\Delta AIC_c < 4$ for both the 1- and 2-yr lag data, and there was a significant region-by-stocking^2 interaction for all models with $\Delta AIC_c < 2$ for the 2-yr lag data (Table 2). None of the models with $\Delta AIC_c < 2$ for the 1- or 2-yr lag data included an access-by-stocking interaction, although such an interaction was included in model 14 for 1-yr lag data ($\Delta AIC_c = 3.9$; Table 1). Thus, prediction 3 was not fully supported with our experimental results. We found weak evidence for an effect of local-scale accessibility on optimal stocking density and strong evidence for an effect of regional differences in latent effort and broad-scale differences in accessibility on optimal stocking density.

Fishing quality

We predicted that overstocking and understocking both cause decreases in fishing quality (prediction 4). Hence, we expected the best models to include a negative coefficient for the quadratic stocking effect. Contrary to this expectation, none of the models with $\Delta AIC_c < 4$ for 0-, 1-, or 2-yr lag data included a quadratic stocking effect (Table 3, Fig. 5).

We predicted that anglers degrade fishing quality most quickly when accessibility and latent effort are highest (prediction 5). Hence, we expected the best models to include a negative coefficient for the effect of access and a significant effect of region. Region had a significant effect in all models with $\Delta AIC_c < 2$ (Table 4). Access was included in model 2 for 0-, 1-, or 2-yr lag data ($\Delta AIC_c = 1.3$; Table 3) and had a non-significant negative coefficient in all these cases (Table 4, Fig. 5). Thus, prediction 5 was supported with our experimental results.

We predicted that anglers homogenize fishing quality across lakes with equivalent accessibility most quickly when latent effort is highest (prediction 6). Hence, we expected that the best models would include an interaction between access and stocking^2 and between region and stocking^2. Contrary to our prediction (6), none of the models with $\Delta AIC_c < 2$ included an interaction between access and stocking^2 or between region and stocking^2 (Table 3, Fig. 5), although model 4 ($\Delta AIC_c = 3.9$) included an interaction between region and stocking. There was also a trend of greater variability in fishing quality in the northern region compared to the southern region (Fig. 5), suggesting less homogenization in the northern region (with lower latent effort). Hence, we observed only weak support for our prediction (6).

Discussion

Our goal was to draw inferences from empirical data regarding landscape-scale patterns in fish populations and angler populations in response to an experimental manipulation of stocking rates. We also aimed to improve the ability of fisheries managers to manage and predict angler effort across inland freshwater fisheries. We found that there is a stocking density for a given lake or region at which attraction of angler effort is maximized and that this optimal stocking density depends largely on differences in lake accessibility and latent effort. If maximum effort occurs at a higher stocking density when latent effort and accessibility are higher (as suggested by our results), managers may be able to increase angler effort by increasing lake accessibility (e.g., by building campsites or improving roads) and increasing stocking density.

Whereas stocking density had a clear effect on angler effort, we did not detect a clear analogous effect of stocking density on fishing quality. The best models in our analysis did not include any effect of stocking on fishing quality, and we found no support for a curvilinear relationship (with a maximum) between stocking

TABLE 3. Model comparison for effects of region, accessibility, and stocking density (with a 0-, 1-, and 2-yr lag) on fishing quality.

Model	No lag		1-yr lag		2-yr lag	
	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c
1) Region	**−6.8**	**0.0**	**−6.8**	**0.0**	**−6.8**	**0.0**
2) Region + access	**−5.5**	**1.3**	**−5.5**	**1.3**	**−5.5**	**1.3**
3) Region + stocking	−4.8	2.1	−4.7	2.1	−4.6	2.3
4) Region + stocking + region : stocking	−2.4	4.4	−2.6	4.2	−3.0	3.9
5) Region + access + stocking	−3.7	3.1	−3.5	3.3	−3.3	3.6
6) Region + access + stocking + region : stocking	−1.3	5.5	−1.5	5.4	−1.6	5.2
7) Region + access + stocking + access : stocking	−1.2	5.6	−0.9	5.9	−0.6	6.2
8) Region + access + stocking + region : stocking + access : stocking	1.3	8.2	1.3	8.1	1.2	8.0
9) Region + stocking + stocking^2	−2.2	4.7	−2.1	4.7	−2.0	4.8
10) Region + stocking + stocking^2 + region : stocking + region : stocking^2	1.8	8.6	2.0	8.8	2.5	9.3
11) Region + access + stocking + stocking^2	−1.3	5.5	−1.1	5.7	−0.9	6.0
12) Region + access + stocking + stocking^2 + region : stocking + region : stocking^2	3.8	10.7	3.8	10.6	4.1	11.0
13) Region + access + stocking + stocking^2 + access : stocking + access : stocking^2	4.3	11.2	4.6	11.5	4.9	11.8
14) Region + access + stocking + stocking^2 + region : stocking + region : stocking^2 + access : stocking + access : stocking^2	10.1	16.9	10.1	16.9	10.2	17.1

Note: Models with $\Delta AIC_c < 2$ are shown in bold.

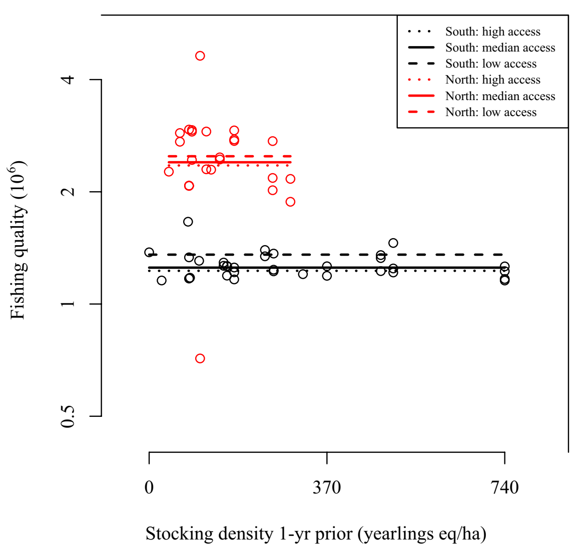

FIG. 5. The response of fishing quality to stocking density 1-yr prior. Note the log scale on the *y*-axis. Lines show the linear fit based on Model 2 in Table 3.

density and fishing quality. The pattern of variation in fishing quality that we detected is, we conclude, likely the result of an ideal free distribution (IFD) of angler effort, which homogenizes fishing quality across lakes within regions (lines with zero slope in Fig. 5). Hence, we were able to detect an effect of stocking density on angler effort, but the feedback between angler effort and fishing quality (wherein more angling reduces fish size and abundance; Fig. 1) eroded the relationship between stocking density and fishing quality by the time we conducted our sampling to estimate fishing quality. There is, however, a trend in our data (Fig. 5) of greater variation in fishing quality in the northern region, which suggests that the feedback between angler effort and fishing quality is weaker (occurs more slowly) where latent effort is lower (such as in the northern region). This trend is consistent with the expectation from the simulation study by Hunt et al. (2011), where low latent effort resulted in greater variation in catch rates, and higher latent effort resulted in more homogenization within zones of equivalent travel times. Several mechanistic explanations for slower homogenization when latent effort is lower have been suggested (Matsumura et al. 2010, Hunt et al. 2011): (1) probabilistic patch choice by anglers is more likely to lead to suboptimal patch selection when there are fewer anglers, (2) heterogeneity in angler preferences and habits lead to more sorting of effort when latent effort is low and all lakes are less affected by angler exploitation, and (3) anglers are less efficient at gathering information on patch quality when there are few anglers on the landscape.

We examined the landscape-scale pattern of angler effort and fishing quality that emerged from ecological and angler behavioral processes interacting in a large, open-access, spatially structured recreational fishery. Our experimental approach facilitated controlling for underlying temporal trends and ecological time lags that would have otherwise limited the power to test hypotheses about the outcomes that emerge from these dynamic

Table 4. Values of coefficients (coef) and statistics for tests of significance for effects included in the best fit models ($\Delta AIC_c < 2$) for stocking effect on ln(fishing quality).

	Model 1			Model 2		
	coef	df	F	coef	df	F
Intercept	1.5	…	…	1.5	…	…
Region	**−3.9E-01**	**56.6**	**46.8**	**−4.0E-01**	**56.5**	**48.8**
Access	…	…	…	−1.4E-03	53.0	1.1

Notes: Significant effects ($P < 0.001$) are shown in bold. Denominator degrees of freedom (df) were estimated with Satterthwaite approximation. Coefficients for the effects associated with region apply to values in the northern region relative to the southern region.

processes. Our stocking rate manipulations simulated variation in recruitment, which is one of the ecological processes that combine with density dependent growth and size-dependent survival to control production of fish available for harvest (i.e., recruitment into the fishery). Stocking rate variation produced the predicted quadratic fishing effort response where low stocking rate attracts few anglers, and high stocking rates reduce growth and survival, with the net effect of also attracting low angler effort. This stocking rate variation results in a pattern of maximum angling effort at intermediate stocking rates.

The observed effort–stocking relationship is consistent with ecological IFD theory in that variation in fishing effort (analogous to predator abundance) is explained by production (the combination of stocking and density dependent growth and survival), latent effort, and access costs. Furthermore, this observation was consistent across a range in production consistent with our understanding of density-dependence (Post et al. 1999, Parkinson et al. 2004, Askey et al. 2013). This experiment was replicated in two regions that have very different angler abundances and therefore different latent angler effort. The quadratic pattern was consistent between regions but the optimum production that maximized fishing effort differed substantially. Not only is effort substantially lower in the north, but also the stocking rate that maximizes effort is substantially lower. There is no reason to suggest that density dependent processes should differ across these regions. So, these differences between regions are due to the interactions between latent angler effort, angler behavior (e.g., harvest vs. catch and release), and local ecological processes. The ecological interpretation, therefore, is that in the northern region (with lower fishing effort and lower total harvest), the density at which growth and survival are reduced is reached at lower stocking rates because the stocked biomass is not being removed as quickly or extensively as in the southern region. Within a region, as would be predicted by IFD with access or travel costs (Bernstein et al. 1991, Tregenza 1995, Matsumura et al. 2010), accessibility is positively related to fishing effort when stocking (or productivity) is controlled, and this is consistent across regions. This result is also consistent with the simulation results of Hunt et al. (2011) showing that fishing pressure was higher near anglers' point of origin.

When assessing predato–prey dynamics over space, ecologists typically examine numerical or biomass abundance of each (Osenberg and Mittelbach 1989, Kennedy and Gray 1993, Gillis 2003, Sims et al. 2006). In the context of a fishery, fishing effort is the most common measure of the numerical response of the predator (Gillis et al. 1993, Gillis and Peterman 1998, Gillis 2003, Post et al. 2008, Gillis and van der Lee 2012, van der Lee et al. 2014) and fishing catch per unit effort (CPUE) is a metric of the abundance of prey. But, in recreational fisheries, CPUE alone rarely predicts the predator's numerical response, because fish size, in combination with non-catch attributes such as crowding, accessibility, and fishing regulations, can be equally important to anglers (Fisher 1997, Aas et al. 2000, Parkinson et al. 2004, Hunt 2005, Dorow et al. 2010, Askey et al. 2013, Beardmore et al. 2013, Arlinghaus et al. 2014, Wilson et al., *in press*). Fish size and abundance combined to determine anglers' perception of fishing quality within a region, and there were regional differences in anglers' perception of value for a fish of a given size and for a given CPUE (Wilson et al., *in press*). Given this metric of fishing quality, our stocking rate manipulations resulted in no measurable effect on fishing quality across broad ranges in stocking within regions. Fishing quality was higher in the region with lower latent effort (Fig. 5), and there was some evidence that quality was related to accessibility within regions (Table 4). The dynamic interpretation of this, which is again consistent with IFD theory, is that anglers distribute themselves across fishing opportunities in such a way as to maximize their utility function, thereby homogenizing catch-based fishing quality across lakes with equivalent access costs within a region. Our observation of homogenized fishing quality implies that the dynamics involving angler effort and fishing quality (Fig. 1) occur at a timescale faster than our stock status measurements. In a bioeconomic sense, the interpretation is that net rent (also called utility) is homogenous at equilibrium (Sanchirico and Wilen 1999).

Modeling studies of spatially structured recreational fisheries have produced variable results in terms of approximations to IFD (relating to catch-based attributes). Parkinson et al. (2004) summarized ecological process data and made the conceptual argument that catch-based IFD will be approximated in recreational fisheries. Askey et al. (2013) developed these ideas further with a modeling exercise, concluding that, if the management objective is to maximize effort, the appropriate measure of management success is be sustainable effort, not fishing quality. Hunt et al. (2011) concluded from a landscape model with a simplified fish production function and a more sophisticated angler behavior model that the IFD predictions of homogenization of angling quality within regions of similar latent effort was likely only in particular scenarios. Matsumura et al. (2010) suggest that a pattern consistent with IFD should be expected when the cost of travelling between patches is taken into account. The empirical results from our landscape-scale experiment support the idea that catch-based IFD with travel costs (or variation in accessibility) reasonably represents the pattern that we see in nature in this socioecological system.

Our experiments lead to several outcomes of interest to management of open access, spatially structured recreational fisheries managed via stocking. The first is the observation of maximal fishing effort at intermediate stocking rates. The second is that the stocking rate that results in maximal effort is strongly dependent on the lake accessibility and latent effort in a region. And third, that the stocking rate–effort dynamic is sufficiently fast that catch-based fishing quality is homogenized at the annual time scale. While the first two observations are useful to quantify, they likely won't be surprising to fishery managers. The third is particularly interesting because it implies that managers may not be capable of producing variability in fish size or abundance by varying stocking rate. Any increased production resulting in improvements in catch-based fishing quality can be rapidly depleted by a rapid numerical response of anglers if latent effort is high. Hence, in a culture based stocking system (where recruitment is dependent on stocking), evaluations of management success should not be based on measurements of fish size and abundance. This dynamic likely should apply to any management initiative designed to increase production to the sport fishery and would result in enhanced fishing effort, not enhanced fishing quality. It is this argument that Askey et al. (2013) developed, leading to the suggestion that management success should be evaluated by measuring angler variables (e.g., effort or utility functions) rather than fish variables (i.e., size and catch). Providing high-quality fisheries is often a goal of management and our work provides a prescription to do this by focusing on angler variable rather than fish variables (see also Johnston et al. 2010, 2013, 2015). Clearly, fishing effort must be controlled to modify fishing quality. Control over fishing effort can be achieved by either input regulations (e.g., tags or seasonal closures) or output regulations (e.g., daily or seasonal harvest limits or size at harvest limits; Walters and Martell 2004). But note that our results suggest that output controls on individual harvest behavior in open access fisheries can be rendered ineffective if there is sufficient latent effort and angler effort responses are present. Our observations, and those of others (Chizinski et al. 2014), imply that management of open-access, spatially structured fisheries must take a landscape perspective in the development of strategic management plans (Lewis et al. 1996, Lester et al. 2003, 2014).

Our quantitative empirical results emerge from a suite of ecological and angler behavioral processes that are particular to the fishery that we characterize. Results are a function of the spatial configuration and abundance of individual lake fisheries and demand by anglers on this landscape. Angler populations are heterogeneous in their behaviors and attributes, and our results are particular to the mix of angler typologies observed on this landscape (Ward et al. 2013*b*). Management initiatives that select for particular angler types, altering the community composition, may result in other outcomes (Fenichel and Abbott 2014, Johnston et al. 2015). But we suggest that the patterns that emerge from a combination of density dependent ecological processes and angler behaviors are likely general for open-access, spatially structured recreational fisheries. We also suggest that management policy evaluations should consider these dynamic processes when planning stocking or other enhancement programs, fish harvest regulations, access control and angling marketing initiatives.

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