

Landscape-scale social and ecological outcomes of dynamic angler and fish behaviours: processes, data, and patterns

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Abstract: The first relatively complete landscape-scale social–ecological system (SES) model of a recreational fishery was developed and ground-truthed with independent angling effort data. Based on the British Columbia multistock recreational fishery for rainbow trout (*Oncorhynchus mykiss*), the model includes hundreds of individual lake fisheries, hundreds of thousands of anglers, originating from tens of communities, connected by complex road and trail networks, all distributed over a landscape of approximately half a million square kilometres. The approach is unique in that it incorporates realistic and empirically derived behavioural interactions within and among the three key components of the SES: angler communities, fish populations, and management policies. Current management policies were characterized and alternate policies assessed by simulation. We examined spatial patterns in ecological and social properties of the SES and used simulations to investigate the impacts of alternate management policies on these patterns. Simulation outcomes strongly depended on the spatial redistribution of anglers across the landscape, existing road networks, heterogeneity in angler behaviours, and the spatial pattern of fish population productivity.

Résumé : Le premier modèle relativement complet de système socioécologique (SSE) à l'échelle du paysage d'une pêche sportive a été développé et vérifié à la lumière de données indépendantes sur l'effort de pêche. Reposant sur la pêche sportive aux truites arc-en-ciel (*Oncorhynchus mykiss*), de stocks multiples en Colombie-Britannique, le modèle intègre des centaines de pêches dans différents lacs, des centaines de milliers de pêcheurs de dizaines de collectivités reliées par des réseaux de routes et de sentiers complexes, le tout réparti dans un paysage couvrant environ un demi-million de kilomètres carrés. L'approche est unique en cela qu'elle intègre des interactions comportementales réaliste et dérivées empiriquement au sein des trois composantes clés du SSE (les communautés de pêcheurs, les populations de poissons et les politiques de gestion) et entre ces composantes. Les politiques de gestion actuelles ont été caractérisées et d'autres politiques possibles évaluées par simulation. Nous avons examiné les motifs spatiaux des propriétés écologiques et sociales du SSE et utilisé des simulations pour étudier les effets de différentes politiques de gestion sur ces motifs. Les résultats des simulations dépendent fortement de la redistribution spatiale des pêcheurs dans le paysage, des réseaux de routes existants, de l'hétérogénéité des comportements des pêcheurs et de la répartition spatiale de la productivité des populations de poissons. [Traduit par La Rédaction]

Introduction

Spatially structured consumer–resource systems exhibit complex and hierarchical dynamics that may be interpreted under the metapopulation paradigm (Wu and Loucks 1995; Hanski 1999; Sanchirico and Wilen 2005). This complexity and spatial hierarchy is particularly evident at the intersection of management, governance, and natural systems (i.e., social–ecological systems (SESS; Cash et al. 2006; Liu et al. 2007; Levin et al. 2013; McGinnis and Ostrom 2014; Arlinghaus et al. 2017). Obtaining accurate SES predictions can be difficult because consumers are mobile, resources are patchy, and the dynamics of the holistic system depends on the behaviour of many interdependent parts; this

includes heterogeneous behaviour of humans (Liu et al. 2007) and metapopulation dynamics among a patchy resource landscape (Sanchirico and Wilen 2005). Despite these difficulties, SESS require a mechanistic understanding of the processes driving system dynamics to advise natural resource decision-making.

Theoretical frameworks have been developed that formally link bioeconomic, landscape, metapopulation, and social–ecological processes (Sanchirico and Wilen 1999, 2005; Ostrom 2009; Folke et al. 2010) to inform management of SESSs. Such theory has guided development of models to predict patterns in resource exploitation based on a mechanistic understanding of human, ecological, and abiotic behaviour (Fulton et al. 2011; Cenek and Franklin 2017). Application of such mechanistic models has occurred fre-

Received 26 April 2018. Accepted 12 July 2018.

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quently for marine fisheries but is less common in freshwater recreational fisheries (see, e.g., Post et al. 2008; Hunt et al. 2011).

SES models contain ecological, social, and management (governance) components, which are linked by behavioural feedbacks (Ostrom 2009). Both terrestrial and aquatic SESs can be spatially structured and spatially managed (Synes et al. 2016). Hence, any SES model must explicitly capture the key processes that regulate these feedbacks and, as in any spatially complex system, also make credible predictions across space and time (Carpenter and Brock 2004; Sanchirico and Wilen 2005; Synes et al. 2016). Similarly to terrestrial environments, freshwater fisheries typically exhibit discrete spatial patchiness. While the population dynamics of freshwater and marine fisheries are similar (e.g., growth, reproduction, survival), both consumer behaviour (e.g., angler behaviour, preferences, and associated effort responses) and fish populations are generally easier to observe in freshwater fisheries than marine fisheries, which often operate offshore and over much larger geographic ranges. It follows that SESs for freshwater fisheries offer a bridge between marine and terrestrial case studies. Lastly, and of interest to many spatial ecologists, the dispersal processes in many inland fisheries are asymmetrical, as the consumers (anglers) are comparatively more mobile than the resource (i.e., recreational anglers travel long distances, while inland fishes are often precluded from large migrations).

It is increasingly recognised that managing recreational fisheries should consider the wider SES accounting for the complex interdependence among management measures, angler preference, fish population dynamics, and the spatial distribution of anglers in relation to angling opportunities (Radomski et al. 2001; Post et al. 2008; Johnston et al. 2010; Hunt et al. 2011; Lester et al. 2014). The potential benefits of doing so include more appropriate measures of management performance (Carpenter and Brock 2004) and improved prediction of system responses to management measures (Cox et al. 2003; Beardmore et al. 2011; Arlinghaus et al. 2017). While previous SES models have included components for biological and human dimensions, these have produced only simulated predictions of spatial angler effort and catch rates, for example (Sanchirico and Wilen 1999, 2005; Post et al. 2008; Fulton et al. 2011; Hunt et al. 2011). Two primary obstacles in creating defensible, empirically derived SES models include the high data requirements (e.g., surveying anglers, lake monitoring of angling effort) and efficient computation of the predicted state of the system for a proposed management option (Synes et al. 2016). The latter is required to allow the SES model to be run iteratively when fitted to data but is challenging because recreational systems often include thousands of lakes and hundreds of thousands of anglers (e.g., Post et al. 2008; Hunt et al. 2011).

The aim of this research is to understand spatial SES outcomes given heterogeneity in human behaviour, ecological dynamics, and management actions and also given spatial heterogeneity in resource abundance, resource quality, users, and user access. We developed and tested this approach for the British Columbia rainbow trout (*Oncorhynchus mykiss*) recreational fishing landscape. This system offers an ideal case study due to the availability of robust fish population surveys and assessments for many lakes (see Parkinson et al. 2004; Askey et al. 2013; Wilson et al. 2016). Additionally, the system includes heterogeneity in angler behaviour and preferences originating from multiple population centres (e.g., Ward et al. 2013a, 2013b; Dabrowska et al. 2014, 2017) that can be used to characterize the ecological and social factors influencing SES dynamics across the landscape. Unlike previous SES modelling, we aimed to develop an SES model that could be fitted to empirical data.

A principal goal of the empirical SES modelling was to characterize the ecological outcomes (e.g., spatial fish density, spatial fishing pressure) and social outcomes (e.g., effort distribution, spatial distribution of angling utility, equity among angler classes) of current management interventions. An additional goal

was to evaluate alternative management interventions of large increases in the stocking of particular lakes, increased stocking of lakes near population centres, and the imposition of trophy fishing regulations in the form of new bag limits.

Methods

Fishery landscape

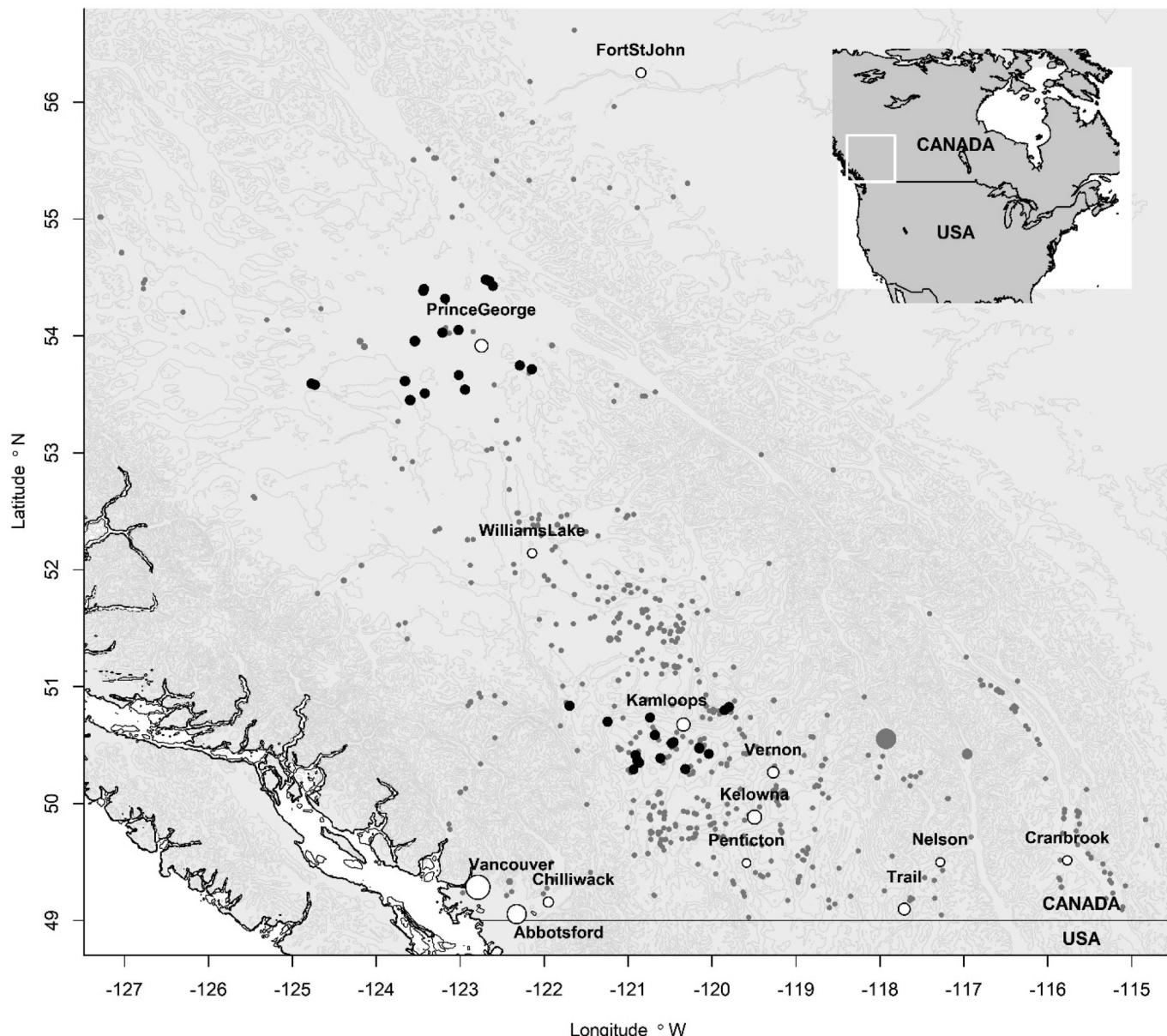
Rainbow trout provide an important multistock recreational fishery to inland British Columbia, a landscape of approximately 500 000 km² that includes over 4000 lakes, of which nearly 600 are stocked annually with hatchery-raised wild-strain rainbow trout (Fig. 1). This fishery landscape is highly connected with a complex road and trail network and hundreds of population centres.

The recreational fishery is managed by the British Columbia provincial government and attracts about 2.5 million angler-days per year (DFO 2010) worth an estimated value of approximately US\$800 million per year (Bailey and Sumaila 2012). The primary management objectives as articulated by the British Columbia provincial government are to “conserve wild fish and their habitats” and to “optimize recreational opportunities based on the fishery resource”. Measures of success associated with these objectives include angler satisfaction, fishing effort, and license sales (MOE 2007).

Travel distance is one of the primary factors influencing fishing effort (Post et al. 2008). The road network in British Columbia is convoluted, and there are multiple routes that can be taken from each population center to each fishing site. Least travel time distance was calculated among the centroids of lakes and population centres along paved, gravel, and foot paths with spatial data extracted from the Digital Road Atlas of the British Columbia Geographic Warehouse (<http://www2.gov.bc.ca/gov/content/data/geographic-data-services/bc-spatial-data-infrastructure/bc-geographic-warehouse>). Least travel time for larger lakes was calculated for each access point, rather than the centroid of the lake, and the closest access point was used for travel time calculations.

A range of management options are available for managing the British Columbia recreational trout fishery, including size, number and species of stocked fish, fishing regulations (e.g., bag limits, boat engine restrictions), amenities (e.g., boat ramps, toilets, campsites), and access (e.g., footpaths, trails, paved roads). Currently, management decisions for British Columbia trout lakes are made primarily at the level of individual lakes, and therefore these ignore a body of research on the ecology and angler behaviour that suggests that management decisions, ecological processes, and human behaviour are interdependent over the wider landscape scale (Cox et al. 2003; Carpenter and Brock 2004; Fenichel et al. 2013). For example, increasing the stocking rate of a particular lake may draw anglers away from other lakes due to higher expected catch rates (Post et al. 2008; Post and Parkinson 2012; Mee et al. 2016). An increase in angler density may also dissuade certain classes of anglers that now exploit opportunities at other lakes (Dabrowska et al. 2014, 2017). Because angler classes have varying fishing efficiencies (Ward et al. 2013b), catch rates, and therefore exploitation levels, may be altered across a wider set of lakes. These changes in exploitation level may lead to changes in the growth rate and size composition of fish in these lakes (Walters and Post 1993; Askey et al. 2013; Ward et al. 2013b) and alter attractiveness for some angler classes (Aas et al. 2000). Because various classes of angler are not distributed evenly across British Columbia (e.g., casual anglers are most predominant in the urban centres of southern British Columbia; Dabrowska et al. 2014), improving angling opportunities in any given lake is likely to have an uneven benefit across angler classes. In this hypothetical scenario, a single management action has important wider consequences for both angling pressure over a wider range of lakes and equality of opportunity among anglers.

Fig. 1. Map of the British Columbia recreational trout fishery. Solid circles on the map represent 584 lakes that are stocked with at least 200 trout per year and are over 5 hectares in surface area. Black solid circles are the 34 “training lakes” that were used to condition the landscape model. A total of 24 human population centres were modelled. The labelled white circles represent 8 of the 24 population centres that are large discrete towns or cities. The area of these circles is proportional to the number of license sales by population centre.



Overview of the S-SES model

In this paper, we describe a novel landscape-scale spatial SES model (referred to as the S-SES model hereinafter) that brings together extensive research into the human dimensions of British Columbia trout anglers (Dabrowska et al. 2014, 2017) with lake-specific biological models of harvest compensation through density-dependent growth (Walters and Post 1993; Parkinson et al. 2004; Askey et al. 2013; Lester et al. 2014; Ward et al. 2017; Fig. 2). We validated the S-SES model based on detailed angling effort data gathered from whole-lake management experiments (Mee et al. 2016) and demonstrate how the approach can be used to inform management policy across a diverse range of management options and performance metrics.

The S-SES has three principal components to capture the processes that characterize the behavioural feedbacks and nodes of

a generalized SES relevant to this and many other recreational fisheries:

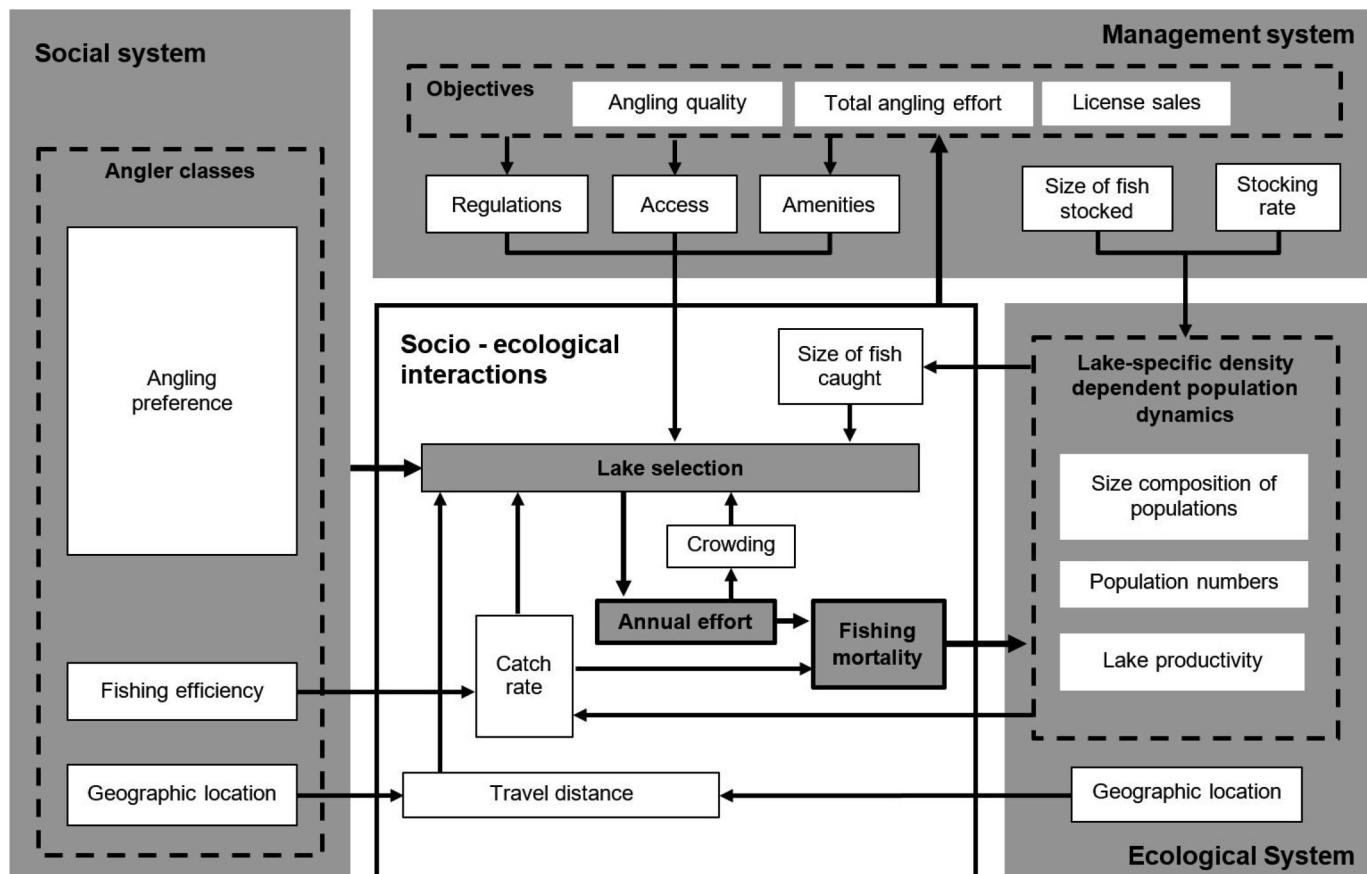
(1) an angler behaviour model that predicts the amount of angler effort on multiple lakes for multiple angler classes residing in multiple population centres;

(2) a biological model that predicts the impact of stocking rate options and fishing mortality rate on survival and growth of fish in each lake; and

(3) a numerical approach for converging on a stable distribution of angling effort over the landscape.

At the heart of S-SES is a logit choice model that calculates angler effort $E_{A,p,l}$ as the number of days of fishing lake l , for a class of anglers A , residing in a population centre p (Table 1 contains a summary of all model parameters, variables, and indexes):

Fig. 2. The social, ecological, and management components of the spatial social–ecological system (S-SES) model and their interactions.



$$(1) \quad E_{A,p,l} = m_A \cdot n_{A,p} \cdot \frac{G_{A,p,l}}{\tau_{A,p} + \sum_l G_{A,p,l}} = n_{A,p} \cdot \bar{E}_{A,p} \cdot \frac{G_{A,p,l}}{\sum_l G_{A,p,l}}$$

where m_A is the maximum number of days of effort in a year per angler, n is the number of licenses sold, τ is the weight of not angling in the landscape of modelled lakes for individuals who have already purchased a license (which includes all other leisure opportunities, including angling opportunities not modelled) and is specific to each management region r , G is the weight of a particular lake, \bar{E} is the mean effort (days per year) of an angler of class A in population centre p , and E is the participation rate of anglers on each lake (days per year per license).

We used the right-hand expression of eq. 1 to fit a landscape model and calculate G terms using data regarding mean effort \bar{E} . This formulation is designed to reallocate a fixed amount of effort ($n \times \bar{E}$). To predict increases in landscape-wide effort, it is necessary to move towards the formulation of the central expression that includes the τ term. Once G terms are calculated, it is simple to calculate the weight of not angling the landscape of modelled lakes τ :

$$(2) \quad \tau_{A,p} = \frac{m_A \cdot \sum_l G_{A,p,l}}{\bar{E}_{A,p}} - \sum_l G_{A,p,l}$$

Figure 1 illustrates the location and size of the population centres and 584 lakes included in the S-SES model (details of the lakes and

population centres are included in Table 2; also refer to the online Supplementary material, Tables S1–S3¹). The S-SES model was implemented in the statistical environment R (R Core Team 2017).

Angler behaviour

Angler behaviour was characterized by a latent class choice model (Swait 1994) based on hypothetical (stated) choices of British Columbia anglers. The model was based on utility maximization and random utility theories (Ben-Akiva and Lerman 1985), which assume that anglers choose fishing sites to maximize their well-being (utility). Following convention, utility for a fishing site was assumed to arise from a function of attributes that describe the trip such as catch rate and travel distance. Parameter estimates for attributes and attribute levels (e.g., a specific type of boat launch) were interpreted as preferences, and the product of preferences and attributes provided a part worth utility for a fishing site. Heterogeneity among anglers was accounted for by the latent class part of the model and the observable trait of fishing license purchase fidelity. Here, we jointly estimated class-specific preferences for attributes and attribute levels and the probability that each angler would belong to a class (Swait 1994). A detailed assessment of several angler behaviour model types, including the model used here, are presented in Dabrowska et al. (2017).

The choice for a responding angler was to select a fishing trip for rainbow trout to hypothetical lakes in British Columbia. Attributes and levels focused on both catch and non-catch-related factors that are reported to affect fishing site choices by anglers (Hunt 2005; Dabrowska et al. 2017). Through pretests with British Columbia fisheries biologists, managers, and anglers, we selected

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2018-0168>.

Table 1. Equation parameters, variables, and indexes in order of their appearance in this article.

	Description	Unit	Eq.
Parameter or variable			
<i>E</i>	Angler effort	days	1
<i>m</i>	Maximum effort for a class of anglers	days	1
<i>G</i>	Weight of a lake	—	1
<i>τ</i>	Weight of not angling modelled lakes	—	1
<i>n</i>	No. of licenses sold	licenses	1
\bar{E}	Mean effort of an angler class	days·year ⁻¹	1
<i>d</i>	Lake distance (travel distance)	km	3
<i>C</i>	Expected catch rate	fish·ha ⁻¹ ·day ⁻¹	3
<i>S</i>	Expected size of fish caught	mm	3
<i>X</i>	Angler crowding	anglers·ha ⁻¹	3
<i>H</i>	A set of categorical lake attributes	—	3
<i>W</i>	An accessibility score	—	3
<i>D</i>	Fish population density	10 ⁻⁶ mm ² ·ha ⁻¹	4
<i>N</i>	Predicted number of fish	fish	4
<i>L</i>	Predicted length of fish	mm	4
<i>v</i>	Lake surface area	ha	4
\hat{G}	Growing degree-days	days·year ⁻¹	5
<i>Q</i>	Thermal age	1000 days	5
L^*	Maximum length	mm	6
<i>K</i>	Slope of growth at the origin	mm·year ⁻¹	6
t_0	Theoretical age at length zero	years	6
<i>Y</i>	Thermal age at maturation	1000 days	6
<i>h</i>	Density-dependent juvenile growth	mm·year ⁻¹	6
L_s	Length at the time of stocking	mm	6
γ	Slope parameter for calculation of <i>Y</i> from <i>h</i>	—	7
δ	Exponent parameter for calculation of <i>Y</i> from <i>h</i>	—	7
Δ	Slope parameter for calculation of <i>h</i> from <i>D</i> , <i>G</i> , and L_s	—	8
β	Exponent parameter for calculation of <i>h</i> from <i>D</i> , <i>G</i> , and L_s	—	8
α	Exponent parameter for calculation of <i>h</i> from <i>D</i> , <i>G</i> , and L_s	—	8
<i>g</i>	Proportion of surplus energy allocated to reproduction	—	9
<i>R</i>	Total fraction of fish removed by anglers	fish ⁻¹	10
<i>q</i>	Catchability	ha·day ⁻¹	12
<i>s</i>	Selectivity (fraction of maximum harvest rate at age)	—	12
Φ	Fraction of trips exceeding the bag limit	year ⁻¹	13
<i>B</i>	Daily bag limit	fish·day ⁻¹	13
<i>F</i>	Instantaneous annual fishing mortality rate	year ⁻¹	14
<i>V</i>	Voluntary release rate	year ⁻¹	14
ψ	Postrelease mortality rate	year ⁻¹	14
<i>Z</i>	Total instantaneous annual mortality rate	year ⁻¹	15
<i>M</i>	Natural mortality rate at age	year ⁻¹	15
<i>N⁰</i>	Stocking numbers	fish	16
θ	Relaxation parameter for numerical effort calculation	—	20
E_{trial}	Proposed effort from numerical effort calculation	days	20
Ω	Dissimilarity matrix based on lake distances	km	21
κ	Slope parameter controlling contribution of <i>W</i> to <i>G</i>	—	22
gravel	Distance on gravel roads	km	23
4WD	Distance on roads suitable for all-terrain vehicles	km	23
foot	Distance by footpath	km	23
OBJ	Global objective minimized when fitting observed effort	—	24
E_{obs}	Observed angling effort	days	24
E_{pred}	Model-predicted angling effort	days	24
Index			
<i>A</i>	Angler class	—	1
<i>p</i>	Population centre	—	1
<i>l</i>	Lake	—	1
<i>T</i>	Stocking type (e.g. fry, catchable)	—	4
<i>a</i>	Age of fish (integer)	years	4
<i>j</i>	A discrete catch rate of fish	fish·day ⁻¹	13
<i>i</i>	Iteration of the numerical effort calculation	—	20
\bar{p}	Population centre for pairwise comparison	—	21

Note: "Eq." refers to the first equation where the symbol was used.

four plausible levels for all attributes except for distance to the lake over paved road. Eight levels were selected for road distance given the broad range of travel distances from all angler population centres to all lakes across the landscape (Post et al. 2008).

Pretests revealed that anglers from the Lower Mainland region (i.e., Vancouver) would normally travel farther than would other anglers, and consequently, the attribute levels for paved distance were specific to the angler origin.

Table 2. Regional lake attributes.

Region	Lake area (ha)		Growing degree-days		Total lake-years of data	Angler effort density (days·ha ⁻¹ ·year ⁻¹)		Stocking rate (fish·ha ⁻¹)	
	Mean	SD	Mean	SD		Mean	SD	Mean	SD
Lower Mainland	113	359	1853	262	11	NA	NA	42	49
Thompson	56	100	1168	268	415	47.2	34.0	125	103
Kootenay	518	3625	1413	242	180	25.7	13.9	138	126
Cariboo	206	407	1237	166	352	8.9	9.6	105	72
Skeena	52	92	1226	188	0	NA	NA	68	46
Omineca	162	397	1247	152	175	6.7	7.9	84	55
Okanagan	34	58	1188	315	475	20.0	16.5	176	150
Peace	52	60	1143	150	0	NA	NA	67	47

Note: The number and names or regions are indicated with mean and standard deviation of attributes of lakes in the regions.

A total of 96 choice sets were developed from a fractional factorial design. Each choice set included three alternative fishing experience options: Lake A, Lake B, and neither Lake A nor Lake B. This design was used to populate attribute levels for Lake A and Lake B alternatives in a way to estimate all main effects (preferences for the attributes) independently from one another. A random sample of British Columbia licensed anglers was drawn in two ways. First, 10 000 anglers were randomly selected and contacted who had previously provided e-mail addresses to the province of British Columbia. Second, another 2500 anglers were randomly drawn and contacted by mail. Each respondent was asked to complete a longer questionnaire (see Dabrowska et al. 2014, 2017 for details) that included six choice sets. For each choice set, respondents were asked to select Lake A, Lake B, or neither Lake A or B for a day fishing trip. For respondents who had reported fishing for multiple days in the previous year, we presented the choices for both day and multiple day contexts because trip duration influences fishing site preferences (Hunt et al. 2011).

A total of 2848 online and 597 mail survey responses were obtained for an effective response rate of 28%. Only individuals targeting rainbow trout and (or) kokanee (*Oncorhynchus nerka*) in non-urban lake settings in the past year were asked to complete the choice tasks. This requirement reduced the sample size to 2106 individuals, from which complete choice set responses were made by 1854 individuals and 2763 day and multiple day contexts.

The latent class choice model was selected in two steps. First, anglers who had not purchased a fishing license every year from 2005 to 2010 were separated from the sample, and a simple conditional logit model was fitted to uncover preferences for the attributes and levels. For the remaining sample (77%) of committed fishers (i.e., ones purchasing a license every year between 2005 and 2010), a latent class choice model was fitted. We selected three latent classes along with the one known class for a total of four classes for the model. Although an Akaike information criterion (AIC) provided support for models with more than four classes, models with more than four classes exhibited nonsensible parameter estimates such as a preference for fishing sites with lower catch rates, *ceteris paribus*. Given that no standard approach exists for model selection for latent class choice models (Provencher and Bishop 2004), our choice of three latent and one known class was guided by both information statistics and the validity of the parameter estimates obtained.

We focused on six attributes to guide fishing site choice by anglers: lake distance (*d*); expected catch rates (*C*); expected size of fish caught (*S*); angler crowding (*X*); a set of categorical lake attributes (*H*), which included boat launch facilities, engine restrictions, the stocked species of fish, and the take limit (the number of fish that may be caught and killed per day); and finally lodging and accessibility (*W*). The utility for any fishing site was determined from:

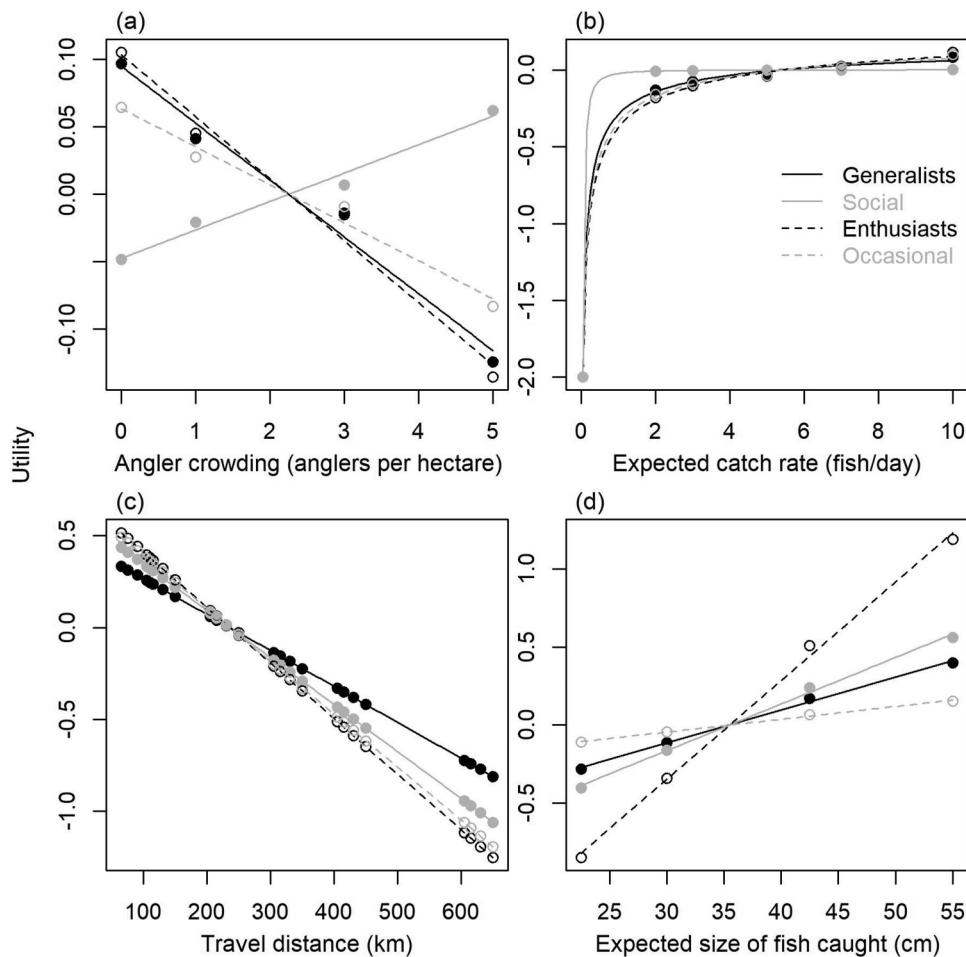
$$(3) \quad \log(G_{A,p,l}) = f(d_{p,l}, \dots) + f(C_{A,l}, \dots) + f(S_l, \dots) + f(X_l, \dots) \\ + f(H_l, \dots) + f(W_l, \dots)$$

The first four attributes of the S-SES model (lake distance, expected catch rates, expected size of fish, angler crowding) are continuous variables. Except for expected catch rate, we used the estimated linear relationships from the latent class choice model (Fig. 3). In the case of expected catch rates, we used a nonlinear relationship to extrapolate preferences for catch rates beyond the range of attribute levels that we presented to the survey respondents. This decision to alter the relationship was informed by increasing evidence that expected catch rates have a strong yet diminishing effect on fishing site choice (Arlinghaus et al. 2014) and angler satisfaction or well-being (Beardmore et al. 2011). Therefore, utility *U* was assumed to follow a nonlinear relationship with expected catch rate *C*: $U = aC^b + d$ (Fig. 3b). A single metric of access and lodging was developed, and the S-SES model was then fitted to observations of angling effort.

We labelled the four classes as “occasional” anglers (the known class), “generalists”, “social anglers”, and “enthusiasts” that represented 23%, 36%, 24%, and 17% of the sample, respectively (see Figs. 3 and 4). The site choice decisions for occasional anglers were least influenced by the expected size of fish and were most negatively influenced by any fly-fishing regulation instead, with class members strongly preferring a barbless hook only or no gear regulation. Generalists were responsive to all lake characteristics sensitive to expected size of fish, possession limit, and travel distance affecting their fishing site choice. Site choices, however, were strongly negatively influenced by fly-fishing-only regulations and crowding by other anglers. Social anglers preferred fishing sites with more anglers and larger-sized lakes. Despite their label, social anglers placed greater importance on take limits of fish than did most other classes of anglers. The final class of anglers, enthusiasts, showed a very strong preference for sites with larger expected sizes of fish and those allowing fly-fishing only. Like the occasional anglers, enthusiasts were more sensitive to the effects of travel distance than were anglers from other classes.

Besides the catch and non-catch traits of individual lake fisheries to which the heterogeneous angler population responded, we estimated differential catchabilities for angler groups using a discriminant function analysis and observations from Ward et al. (2013a, 2013b). Survey respondents were assigned to the four angler clusters developed in Ward et al. (2013a) based on three variables: distance traveled, harvest to catch ratio, and catchability. Individual angler catchability was estimated as a function of angler experience (days fished per year) based on the parameters in Ward et al. (2013b).

Fig. 3. Continuous utility models (plotted lines) for four classes of angler in respect to (a) angler crowding, (b) expected catch rate, (c) travel distance to lake, and (d) expected size of fish. Circles represent the results of the choice experiment of Dabrowska et al. (2014).



Biological processes

Somatic growth was assumed to follow a biphasic model that accounts for energy allocation before and after maturation (Lester et al. 2004). In the first phase, the model approximates juvenile growth linearly according to a growth rate h ($\text{mm} \cdot \text{year}^{-1}$) that varies with climate and the density of fish. In the second phase, adult growth was approximated by an asymptotic von Bertalanffy model (see Table 3 for details). In this model, natural mortality shaped known energetic trade-offs between growth and reproduction (see L^∞ , t_0 , and K below), and natural mortality was calculated based on allocation of energy to reproduction as parameterized by Ward et al. (2017).

Fish population density was modelled as the effective density D ($10^{-6} \text{ mm}^2 \cdot \text{ha}^{-1}$) of fish in a particular lake l of all stocking types T (e.g., fry, catchables) calculated by

$$(4) \quad D_l = \frac{\sum_T \sum_a N_{l,T,a} \cdot L_{l,T,a}^2}{(10^{-6} \cdot v_l)}$$

where N is the predicted number of fish at stocking at age a , L is the predicted length of fish (mm), and v is the surface area of the lake (ha). Both growth phases depended on lake productivity according to the annual growing degree-days \hat{G} . Annual growing degree-days are an index of thermal energy and are correlated with fish growth rates (Neuheimer and Taggart 2007; Ward et al. 2017). Growing degree-days were estimated based on latitude, lon-

gitude, and elevation data based on ClimateBC v5.10 program developed by Wang et al. (2015). For any day of the year, growing degrees are the number of degrees Celsius over a threshold level of 5°C necessary for growth (Lester et al. 2014). The annual growing degree-days \hat{G} is the summation of these growing degrees over a year. Thermal age Q (expected number of growing degree-days experienced by a given age class a in units of 1000 days) was calculated as

$$(5) \quad Q_{l,a} = \frac{1}{1000} \cdot \hat{G}_l \cdot (a - 0.5)$$

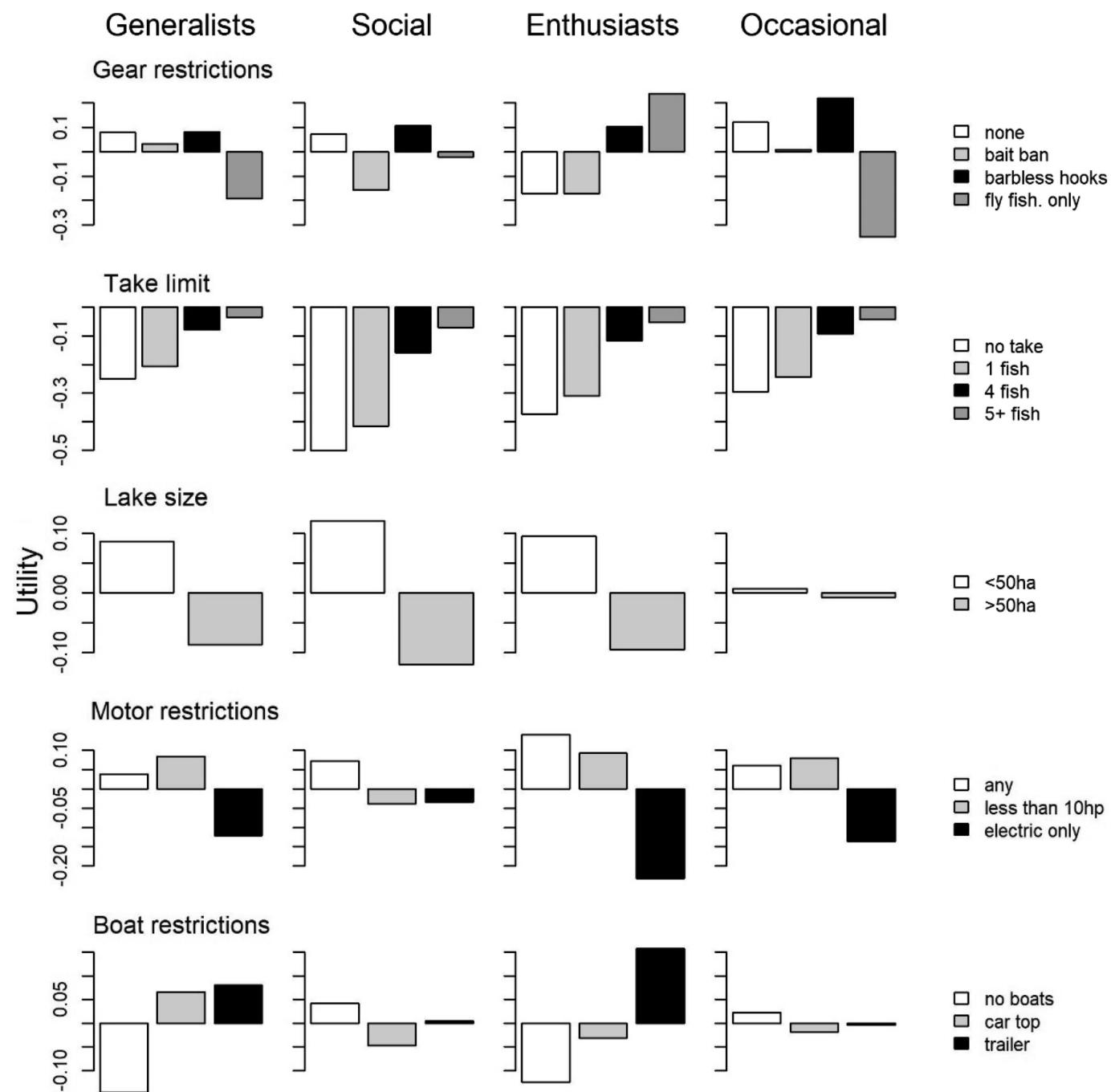
For each stock type T , the biphasic model described the change in length at age L_a (mm) between juvenile and adult growth occurring when the thermal age Q of age class a exceeded the thermal age at maturation Y such that

$$(6) \quad L_{l,T,a} = \begin{cases} L_{l,T}^\infty \cdot \{1 - \exp[-K \cdot (Q_{l,a} - t_{0,l})]\} & Q_{l,a} > Y_{l,T} \\ h_{l,T} \cdot Q_{l,a} + L_{s,T} & Q_{l,a} \leq Y_{l,T} \end{cases}$$

$$(7) \quad Y_{l,T} = \gamma \cdot h_{l,T}^{-\delta}$$

where γ and δ are shape parameters that describe how age, juvenile growth, and degree-days influence thermal age at maturity (Table 3), and L_s is the length at the time of stocking (mm). Density-dependent juvenile growth h ($\text{mm} \cdot \text{year}^{-1}$) was calculated as

Fig. 4. Estimated part worth utility of categorical lake attributes by angler class, including gear restrictions, take limit (maximum number of fish that may be caught and harvested per day), lake size, motor restrictions, and boat restrictions.



$$(8) \quad h_{l,T} = \Delta \cdot L_{s,T}^{\beta} \cdot \exp(\alpha \cdot D_l) / (10^{-3} \cdot \hat{G}_l)$$

where D was the effective density of fish ($10^{-6} \text{ mm}^2 \cdot \text{ha}^{-1}$; eq. 3), and the parameters α , Δ , and β were shape parameters for density dependence (Table 3).

Maximum length L^∞ (mm) and theoretical age at zero length t_0 were assumed to be density-dependent such that

$$(9) \quad L_{l,T}^\infty = 3 \cdot h_{l,T} / g_T$$

$$(10) \quad t_{0,l,T} = Y_{l,T} + \ln \left[1 - \frac{g_T \cdot (h_{l,T} \cdot Y_{l,T} + R_T)}{3 \cdot h_{l,T}} \right] \ln \left(1 + \frac{g_T}{3} \right)$$

The slope of growth at the origin K ($\text{mm} \cdot \text{year}^{-1}$) was assumed to be determined by the proportion of surplus energy allocated into reproduction g (Table 3):

$$(11) \quad K_T = \ln(1 + g_T)/3$$

To predict numbers, it was necessary to calculate total fraction of fish removed by anglers R (that could be either retained or released). For a given lake l , R was given by

$$(12) \quad R_{l,T,a} = \sum_p \sum_A \left(\frac{E_{A,p,l}}{365 \cdot v_l} \cdot q_A \cdot s_a \right)$$

Table 3. The values assigned to parameters of the rainbow trout population dynamics model.

	Parameter							
Value	γ	δ	Δ	β	α	g	V	Ψ
Age class								
	0–1	1–2	2–3	3–4	4–5	5–6		
Natural mortality rate M (year $^{-1}$)	0.5	0.025	0.025	0.7	0.8	0.8		
Selectivity s	0	0.5	1	1	1	1		
Stocking type								
	Fry	Yearling	Catchable					
Age at release	0–1	1–2	2–3					
Length at stocking R (mm)	50	100	200					
Angler class								
	Generalist	Social	Enthusiast	Occasional				
Catchability q (ha·day $^{-1}$)	0.0705	0.0687	0.0739	0.0348				
Maximum effort per year m (days·year $^{-1}$)	97	95	100	48				

where s is the selectivity at age a , and the catchability coefficient q (ha·day $^{-1}$) is specific to each angler class and derived from the relationship with days fished per year (Ward et al. 2013b; Table 3).

A fraction of these fish is released according to the bag limit B . Given an expected (mean) catch rate C (eq. 17), the fraction of trips exceeding the bag limit Φ was calculated by the cumulative Poisson distribution:

$$(13) \quad \Phi_{A,l} = 1 - \left[\exp(-C_{A,l}) \left(1 + \sum_{j=1}^{\lfloor B_l \rfloor} \frac{C_{A,l}^j}{j!} \right) \right]$$

where $\lfloor \cdot \rfloor$ is the floor function.

The total fishing mortality rate accounting fish released due to exceeding the bag limit Φ , those released voluntarily V , and those that die after release ψ was calculated as follows:

$$(14) \quad F_{l,T,a} = (1 - V)(1 - \Phi_{A,l})R_{l,T,a} + [1 - (1 - V)(1 - \Phi_{A,l})]R_{l,T,a} \cdot \psi$$

Total mortality rate Z , which includes natural mortality rate M (Table 3), was given by

$$(15) \quad Z_{l,T,a} = F_{l,T,a} + M_{T,a}$$

The parameter V , which represents the voluntary release rate of anglers, was determined by numerical optimization.

For any lake, expected numbers at age for a given stocking type T and age a could then be calculated according to the stocking numbers N^0 :

$$(16) \quad N_{l,T,a} = N_{l,T}^0 \cdot \exp\left(-\sum_{i=1}^{a-1} Z_{T,i} - \frac{Z_{T,a}}{2}\right)$$

Three of the central variables in the effort prediction model of eq. 3 are expected catch rates by angler class (C ; fish·ha $^{-1}$ ·day $^{-1}$), expected size of fish caught by lake (S ; mm) and angler crowding (X ; anglers·ha $^{-1}$) by lake l . These were given by

$$(17) \quad C_{l,A} = \sum_T \sum_a N_{l,T,a} \cdot v_l^{-1} [1 - \exp(q_A \cdot s_a)]$$

$$(18) \quad S_{l,A} = \sum_T \sum_a N_{l,T,a} \cdot L_{l,T,a} [1 - \exp(q_A \cdot s_a)] / C_{l,A}$$

$$(19) \quad X_l = \sum_A \sum_p E_{A,p,l} / (365 \cdot v_l)$$

Numerical approximation to the ideal free distribution (IFD) of angling effort

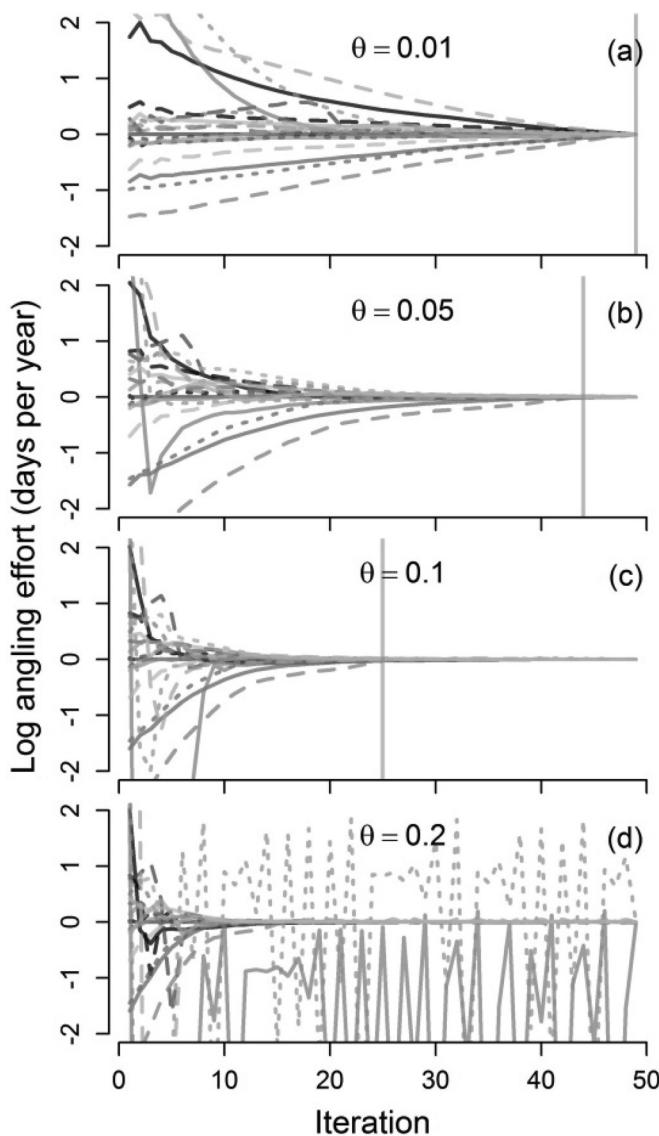
For a given set of management options, we calculated the predicted distribution of angling effort on the landscape such that for any class of anglers in each population centre, a change in distribution led to homogenization of overall utility. This state is referred to as the IFD of angling effort where no additional increase in utility is possible by anglers moving to alternate lakes in which to fish (Kennedy and Gray 1993; Parkinson et al. 2004; Askey et al. 2013).

To calculate the IFD of angling effort, we started with an initial calculation of effort E_1 for each lake that was the same as eq. 1 but was calculated using the weight terms G , without accounting for the predicted size and catch rate of fish on each lake (the S and C terms of eq. 3, respectively). This initial effort distribution E_1 allows fishing mortality rate to be calculated, and hence, it is possible to obtain the initial predictions of expected size of catches S and catch rate C . This initialization enables the calculation of the full weight term G including utility components for S and C and hence an updated predicted effort distribution, E_1^{trial} . The next calculation of effort, E_2 , is based on a weighted combination of the previous effort distribution E_1 and its update E_1^{trial} with the degree of relaxation determined by the parameter θ :

$$(20) \quad E_i = (1 - \theta) \cdot E_{i-1} + \theta \cdot E_{i-1}^{\text{trial}}$$

When operating correctly, this numerical procedure may be iterated until convergence on an approximation to the IFD of effort has been achieved ($E_i \approx E_{i-1}$). We define successful convergence when the effort of all angler classes from all population centres on all lakes ($E_{A,p,l}$; eq. 1) are all within half an angler day of the previous iteration. Our SES model reliably converged within 200 iterations given a θ value of 5%. This value was sufficient to calculate a stable solution within a few seconds, enabling the model to be used iteratively, for example, in numerical optimization of parameters to fit observed effort data. This iterative approach (a relaxation method) is required to prevent oscillation in predicted effort or “flip-flopping” between alternate states. Figure 5 shows the convergence to a numerical approximation of the IFD of an-

Fig. 5. Numerical convergence to the ideal free distribution of effort given alternative values for the relaxation parameter θ . The vertical grey line represents the iteration in which convergence has been achieved (all effort predictions are now within 0.1 day of the previous iteration).



gling effort for the SES model given different values of θ ; panel *d* shows the oscillation phenomenon at high θ values.

As illustrated by Fig. 5, the value of θ determines the trade-off in convergence speed (number of iterations to reach “convergence”) against angling effort instability. Unfortunately, there are no general rules for selecting an appropriate level of θ because convergence depends on the configuration of the particular landscape. For example, it is possible to describe a landscape in which there are two population centres composed of similar proportions of angler classes that are approximately equidistant from the lakes in the model. It follows that effort from the anglers of one population centre are interchangeable with effort from anglers of the other population centre, and thus the problem is poorly defined and highly unstable, requiring very low values of θ . Note that the predicted total effort on a modelled lake may be stable while the effort from each population centre and angler class are perfectly traded off and are therefore unstable.

Simplifying the landscape of anglers and fitting to data

As described above, it is necessary to have contrast in the location of population centres and lakes to calculate a stable approximation to the IFD of effort. The most complex landscape model included 24 population centres, some of which are situated near each other. In such a case, the effort from one population centre would be confounded with that of the adjacent population centre, and it would not be possible to calculate a stable IFD of effort. To address this problem, population centres were clustered to ensure that they were distinct relative to the landscape of lakes. Firstly, a dissimilarity matrix Ω was calculated to capture the difference among the population centres in their location relative to the landscape of lakes.

$$(21) \quad \Omega_{p,\bar{p}} = \sum_l |d_{p,l} - d_{\bar{p},l}|$$

This definition of dissimilarity is more appropriate than simply using the geographic distance among population centres, as it accounts for travel distance and is therefore considerate of both the distribution of lakes and the configuration of the British Columbia road network. The hierarchical cluster analysis function “*hclust*” (of the “*stats*” R package) was then used to group population centres into nine clusters using Ward’s criterion (Murtagh and Legendre 2014) (Fig. S1¹). When combined, the attributes of the clustered population centres were either summed (e.g., angler numbers) or calculated as a weighted mean according to angler numbers in component population centres (e.g., distance to lakes).

There were two stages to the process of model fitting. We divided the landscape model into two sets of lakes: a training set and a British Columbia-wide set (Fig. 1). The training set was made up of 34 lakes that were subject to recent experimental manipulations (Mee et al. 2016) for which we have a wider selection of high-quality data available. The British Columbia-wide set includes these lakes and a further 550 (584 in total) over a much wider spatial range that have fewer covariate data and less precise observations of angling effort.

We initially fitted the model to observations of effort for the training set to estimate two parameters that were not available from the angler behaviour or biological model components: the mean release rate of captured fish by catch-and-release anglers V (eq. 14) and the slope in angler utility relative to lodging and access κ . The utility component for lodging and access (eq. 3) was calculated:

$$(22) \quad f(W_l, \kappa) = \kappa \cdot W_l$$

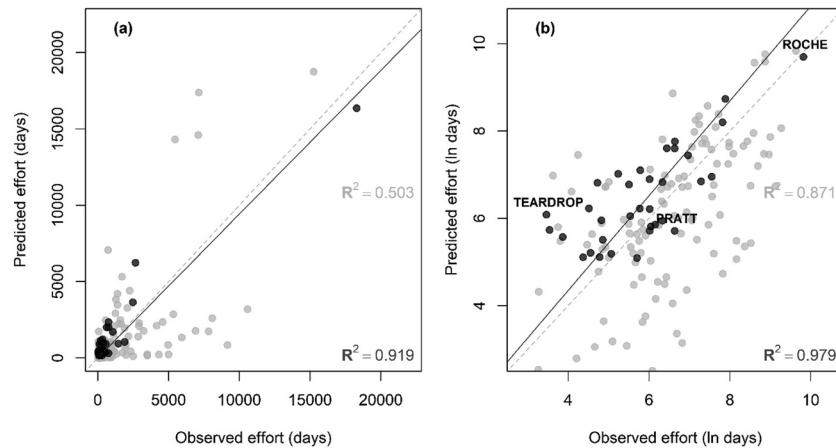
where the access and lodging covariate W , for each lake l , was calculated as

$$(23) \quad W_l = \exp\left(-\frac{\text{gravel}_l}{55} - \frac{4\text{WD}_l}{15} - \frac{\text{foot}_l}{3}\right) \cdot (\text{campsites}_l + \text{lodgebeds}_l)$$

where gravel is the distance (km) to the lake on a gravel road, 4WD is the distance to the lake on a rough off-road surface, and foot is the distance to the lake by footpath only (these are divided by 55, 15, and 3, respectively, which represent the expected average speed of travel on these surfaces; km·h⁻¹). Following applications that have predicted recreational fishing activity (e.g., Drake and Mandrak 2010; Muirhead and MacIsaac 2011), we multiplied the nonlinear effect travel (time) by site attractiveness, which we defined as the sum of campsites and lodge beds at each lake.

To fit the model, observed annual effort at a lake E^{obs} was assumed to follow a lognormal observation error model with a stan-

Fig. 6. The fit of the model to observed effort and the natural logarithm of effort for the experimental lakes (black) and British Columbia-wide lakes (grey). The black line represents a best-fit linear model through the observed and predicted data for the experimental lakes (with zero intercept). The dashed grey line represents a line of slope 1. R^2 statistics are provided for the experimental lakes (black) and British Columbia-wide lakes (grey).



dard deviation of 0.5. The objective function OBJ to be minimized was the negative log-likelihood:

$$(24) \quad OBJ = \sum_l 2\log(0.5) + [\log(E_l^{obs}) - \log(E_l^{pred})]^2$$

Predicted total effort on a lake E_l^{pred} was simply model-predicted effort summed over angler classes and population centres:

$$(25) \quad E_l^{pred} = \sum_A \sum_p E_{A,p,l}$$

The maximum likelihood estimates of the mean release rate V and the slope in log utility with lodging and access k were 0.83 and 1.15, respectively.

Results

Fit to experimental data

The S-SES model fitted observed effort well for the training set of lakes ($R^2 = 0.979$) and for the British Columbia-wide lakes set ($R^2 = 0.871$; Fig. 6b). The greater variance in the British Columbia-wide lake set is expected, as we lack data on access and lodging for this broader data set, and the observations of effort are less precise. Of the training set of lakes, one lake, Roche Lake, attracted the most angling effort. It was important to fit this lake correctly, as a failure to do so could erroneously redistribute a large amount of effort onto or away from other nearby modelled lakes. The model exhibited a general tendency to overestimate effort for small lakes at the edges of the landscape, such as Teardrop Lake (Fig. 6b), which is among the most northerly of the training lake set. Conversely, the model tended to underestimate the effort on small lakes closer to the centre of the landscape, such as Pratt Lake (Fig. 6). There are several possible explanations for this that point to a limitation of the S-SES. Smaller distant lakes, such as Teardrop Lake, may often have restricted fishing seasons and are surrounded by other fishing opportunities that are not accounted for by the landscape model. In this situation, we would expect to overestimate effort compared with realized effort. This apparent attenuation is a limitation of our logit choice model and the spatial configuration of our landscape model.

Nonindependence in effort redistribution

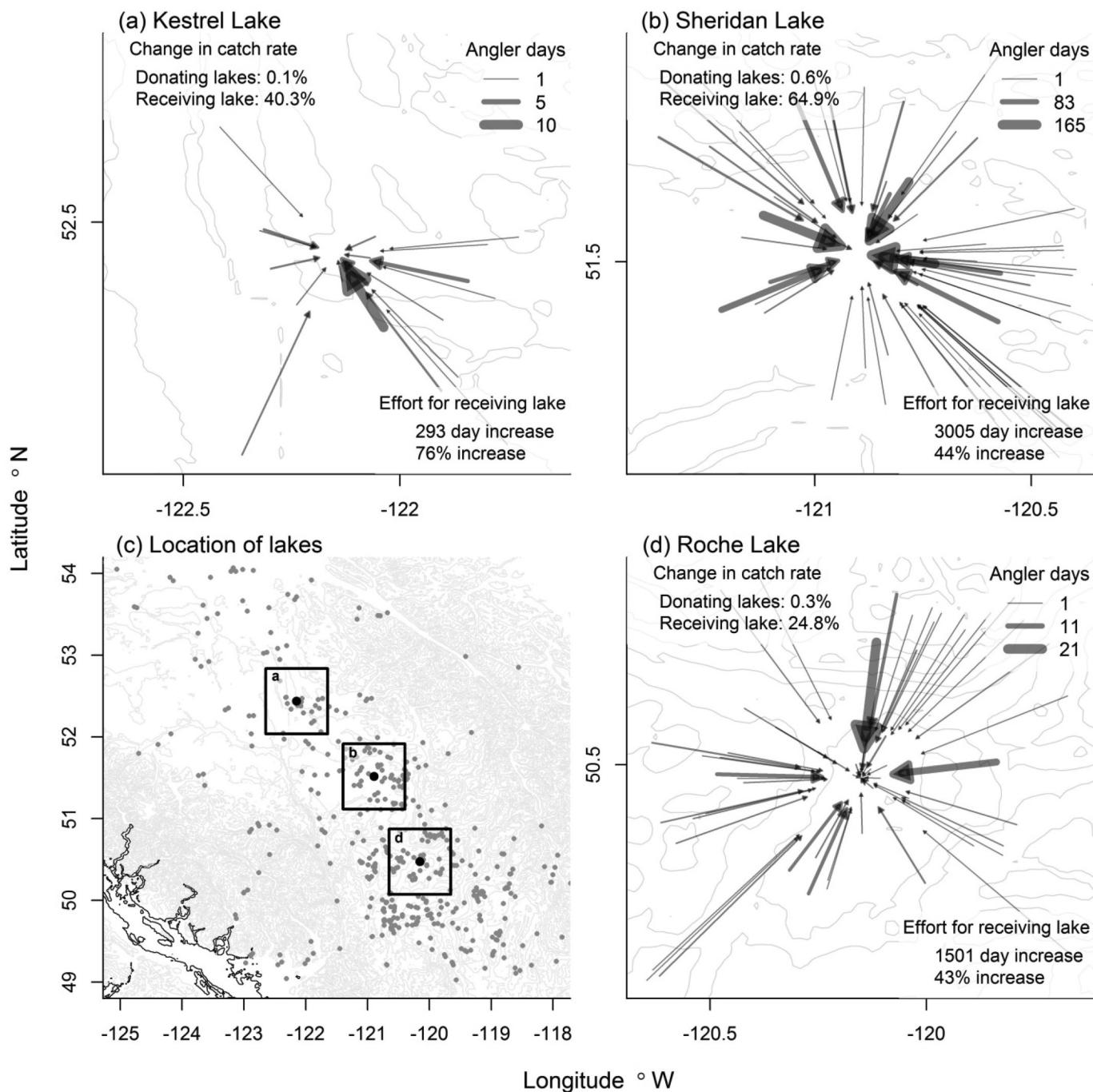
A principal advantage of the S-SES model is that it can predict instances where altering the angling quality of a single lake leads

to reallocation of effort among lakes on the landscape. To demonstrate these spatial dynamics, we arbitrarily doubled the stocking rate of three lakes, including a high-effort southern lake and a low-effort northern lake (Fig. 7c), and calculated the movement of effort among local lakes (Figs. 7a, 7b, 7d). The magnitude of effort redistribution varied considerably among the three experimental lakes (according to their size, landscape location, and current stocking rate), but in all three cases much of the redistributed effort originated from a small fraction of relatively nearby lakes. The magnitude of the absolute effort response to doubling stocking rates was related to lake size, with the greatest increase in Sheridan Lake (1650 ha surface area), smallest in Kestrel Lake (58 ha), and intermediate in Roche Lake (162 ha). The proportional increase in effort was greatest in Kestrel Lake, suggesting that this area has the greatest latent demand for fishing opportunities created by the simulated stocking rate increase and lower but similar demand in the other two areas. The stocking rate doubling had the greatest improvement in fishing quality, as represented by catch rates, for Sheridan Lake and its surrounding donating lakes. This outcome makes sense because a stocking rate doubling on a large lake has a greater local and regional-scale response simply because it represents a greater infusion of fishing opportunities than does a doubling of stocking rate on a small lake. The impact of doubling stocking rates on the smaller lake had lower impacts on donating lakes, in proportion to the lake's size receiving the augmentation. Overall, increasing stocking rates appears to have diminishing returns in terms of both effort and fishing quality due to the dynamic spatial effort response (i.e., doubling stocking does not double effort or quality), but is expected to increase both. This effect is strongest in the enhanced lake, but also is felt in adjacent lakes, which experience a reduction in their effort due to the local redistribution of anglers to the enhanced lake. This decline in local effort is manifest in an increase in quality as local harvest is reduced. However, keep in mind that these simulations characterize a redistribution of effort in response to increased fish availability but do not address the question of whether we would expect an overall regional increase in effort in response to increased investment in enhanced hatchery capacity.

Ecological outcomes across the landscape

The landscape patterns of fish density and size are an outcome of the status quo stocking rates (Table S1), landscape patterns of environmental conditions (as measured as growing degree-days), and the spatial distribution of lakes and anglers (Fig. 1). These spatial patterns and dynamics result in a characteristically non-

Fig. 7. Local angling effort redistribution arising from doubling the number of stocked fish for three lakes across the landscape. Grey circles on panel c represent lakes, black boxes correspond with the regions of panels a, b, and d. The width of arrows is proportional to the amount of effort that was redistributed from local lakes.

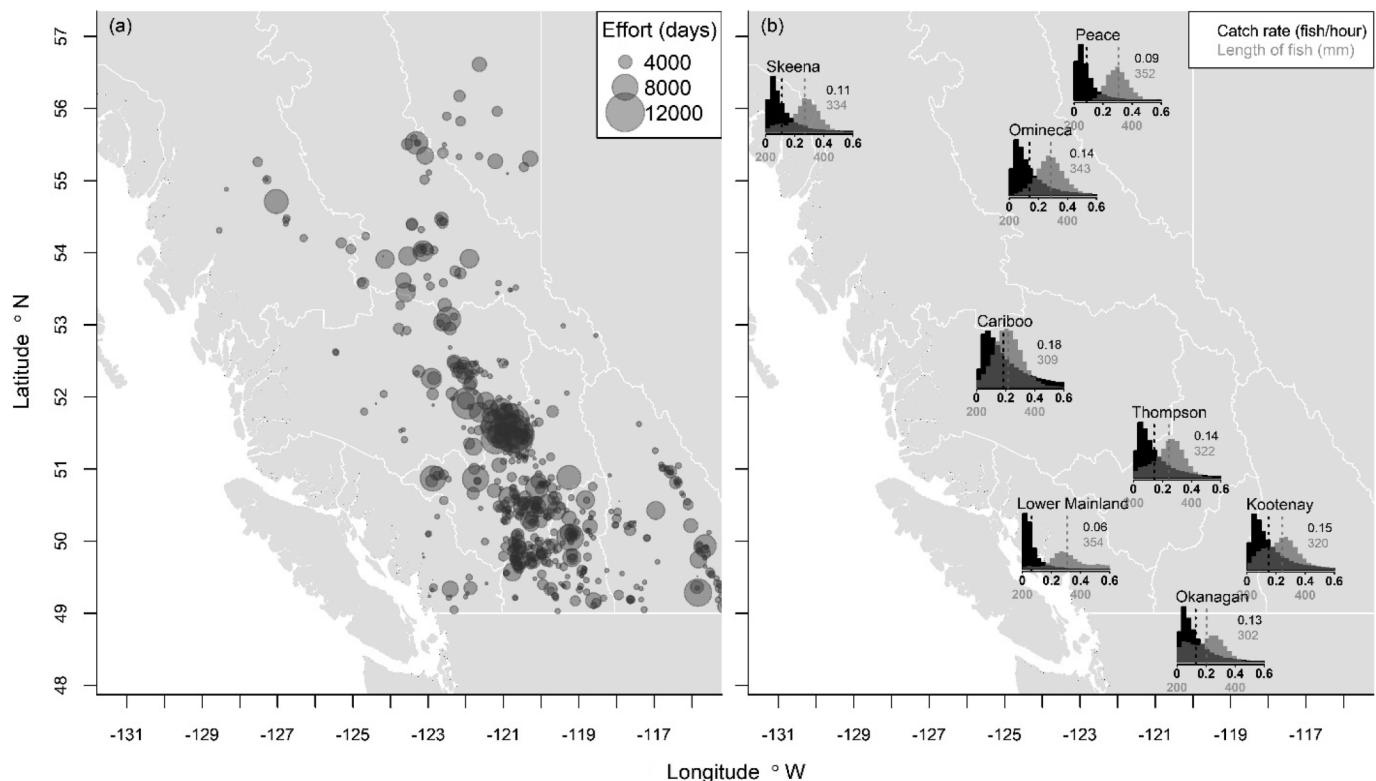


homogeneous distribution of angler effort across the landscape (Fig. 8a). Catch rates, as a measure of fish abundance, varied three-fold, from a low in the Lower Mainland region to the highest in the Cariboo region (Fig. 8b). Fish abundance is determined in these lakes by stocking and harvest rates. Harvest rates are a function of landscape characteristics: human abundance, angler participation rates, lake area, and accessibility. Therefore, the emergent spatial pattern is due to management decisions on stocking rates, the movement of anglers from origins to lakes based on accessibility, and the dynamic interaction among fish populations, harvest, and angler preferences for both catch and non-catch attributes of individual lakes. Not only do the regions differ in

mean abundance of fish and lakes, but there is substantial difference in variability in abundance in regions. All regions have some lakes supporting only low densities, but few have lakes supporting high fish densities. For example, the Lower Mainland region has no lakes supporting high abundance (i.e., a catch rate of more than 0.3 fish per hour), whereas the Kootenay, Thompson, and Cariboo regions have many lakes with higher densities of fish. Other regions have intermediate variability among lakes and intermediate fish abundance.

Mean size of fish in lakes also varies across the landscape. This population characteristic is a function of density-dependent fish growth, which is determined by the combination of management

Fig. 8. The model-predicted catch rate and size of fish caught by anglers in each management region. The vertical dashed lines correspond to the mean value, which is also given as a number in the top right-hand corner of each plot.



decisions on stocking rates, geographic patterns in growing degree-days, and harvest rates that modify abundance and size structure. The landscape pattern across the region (Fig. 8b) shows a strong negative correlation between fish abundance and mean size ($r = -0.76$, $n = 8$), suggesting that density-dependent ecological processes dominate.

Social outcomes across the landscape

Perhaps not surprisingly, the model predicts the highest angling effort on lakes that are adjacent to the largest population centres, represented by the Abbotsford population centre (the British Columbia Lower Mainland region including the City of Vancouver; Fig. 9a). The Lower Mainland region has the lowest participation rate (2.7% per capita license sales) but 72% of the population of British Columbia, resulting in 42% of the total provincial license sales. The majority of the highest effort lakes are within approximately 300 km of the Lower Mainland region (see Fig. 3c where these travel distances have positive part worth utilities). These south-central regions also have several intermediate-sized cities (e.g., Kamloops, Kelowna, and Penticton; Fig. 1) with much higher per capita participation rates (12.0%) than in the Lower Mainland. More northerly lakes, despite being in regions with higher per capita participation, have much lower human population density and are prohibitively distant for most nonlocal anglers (see Fig. 3c where travel distances greater than 300 km have negative part worth utilities).

The numerical response of the angler population to spatial variation in the availability of fishing opportunities, as linked dynamically through harvest, varies substantially across the fishery (Fig. 9a). Clearly, most angling effort in British Columbia emanates from the Lower Mainland (as characterized by Abbotsford), where despite low participation rates the population is high and within 300 km of abundant opportunities. The second greatest fishing effort emanates from the Thompson and Okanagan regions (characterized by Kamloops), where the population is sub-

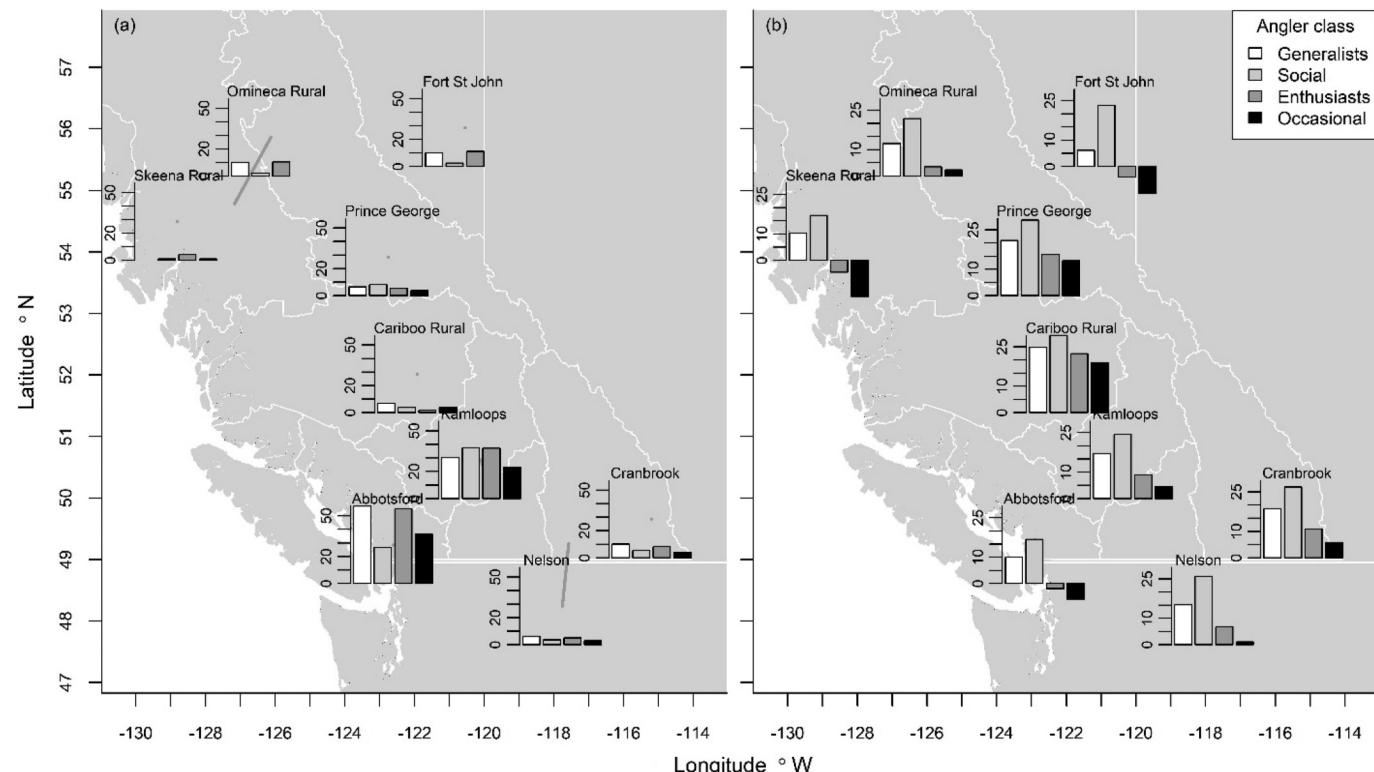
stantially lower but participation rate is high and there is an abundance of short distance angling opportunities (Fig. 9a).

The angler population is not homogeneous in its behaviour (Fig. 9a). Overall, enthusiast anglers spent the greatest amount of time angling across all regions. The utility of the best fishing opportunities varies widely by region (Fig. 9b), where anglers living in central areas enjoy the best quality of angling by some margin (i.e., Kamloops, Cariboo Rural, Prince George). Anglers from the Lower Mainland region, as characterized by anglers living in Abbotsford, spend the least time fishing and have few local lakes, requiring commuting several hundred kilometres to the central regions (reflected by low regional utility even for the top 20 lakes; Fig. 9b).

Spatial patterns in efficacy of management interventions

A common management response to complaints of poor angling quality is increased stocking by management agencies (Post et al. 2002; Arlinghaus and Mehner 2005). To identify spatial patterns in stocking opportunities, we ran 584 landscape models, one for each lake, where each lake in turn was subject to a 10% increase in stocking rate. In each case, the landscape-wide effort response relative to the stocking cost was calculated (Fig. 10). In some cases, the increased stocking attracted proportionally more effort for each dollar spent on stocking (the dark grey circles in Fig. 10). In other cases, the effort response did not appear to justify the additional stocking cost (white circles, Fig. 10). A positive change in fishing effort per dollar cost of stocking implies that the increased stocking improved the fishing quality, which is a combination of fish abundance and size as preferred by the aggregate angler population that are willing to travel to that particular lake. A negative change in effort with increased stocking implies that the ecological process of density-dependent growth results in reduced fish size and, therefore, attractiveness of the fishery. The overall spatial pattern in effort response to stocking alteration is a function of the status quo stocking rates, processes involved in

Fig. 9. Regional equity in landscape usage and utility: (a) the model-predicted effort originating from various regions on all lakes (thousand days); (b) the mean part worth utility of the highest 20 ranking lakes for each region and angler class. Note that in some regions there are no members of an angler class (for example, there are no occasional anglers in Omineca Rural and Fort St. John regions).



fish growth (density and growing degree-days), and the latent demand for fishing opportunities of anglers willing to travel to particular lakes and their preferences for fishing quality. Therefore, in some cases the money spent on increased stocking might be better spent elsewhere; the effort response relative to increase in stocking costs may not be favourable for management. In general, increasing the stocking of the central lakes closest to communities was most likely to be cost-effective. However, across regions on the landscape there were no clear spatial patterns or gradients in stocking opportunities, suggesting that management strategies may not be easily generalized at the scale of the whole fishery. This conclusion implies that considering how best to allocate stocking resources needs to be done at the regional scale, rather than a reallocation among regions.

We next examined policy options at the within-region spatial scale and assessed equality among angler groups at lakes of two types: near urban centres (within 100 km) and distant to urban centres (greater than 100 km; Fig. 11a). In the first example of a management action, we examined the consequences of a 10% increase in the stocking of lakes closer than 100 km travel distance to a major urban centre (Fig. 11b). In general, effort of all angler classes was increased, but the margin of increase was much higher for occasional anglers located in Prince George and rural Cariboo. In some cases, angler effort was fractionally reduced, for example, social anglers in Fort St. John. Because only two lakes were deemed to be within 100 km of an urban centre, effort was moved away leading to a reduction in angling quality for the social angler class that responds positively to increased angler densities. Increasing the stocking of lakes within 100 km of an urban centre led to very small increases in angling effort for the Lower Mainland area. The contrasting management option, a 10% stocking rate increase on lakes farther than 100 km from an urban centre, led to a very different pattern of effort increases, with almost no gains in Prince George and rural Cariboo (Fig. 11c). Effort

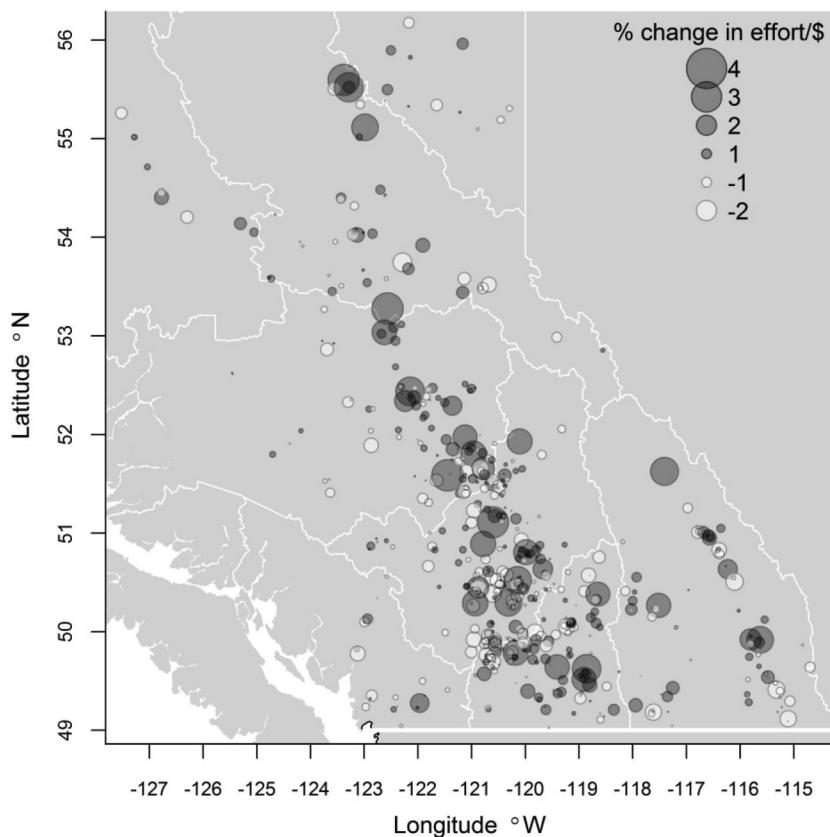
was only increased in a few cases, such as occasional anglers in rural Skeena and enthusiast anglers in Nelson.

Most current regulations impose a maximum bag limit of five fish per day. On some lakes, sometimes referred to as “trophy” lakes, bag limits are lower, typically two fish per day or catch and release only. To investigate the potential impacts of increasing the number of trophy lakes, 20% of lakes with an existing bag limit regulation of five fish per day were changed to a two fish per day bag limit (90 lakes in total). The most likely candidates for trophy lake regulations are productive lakes. Rather than arbitrarily selecting lakes for trophy regulation, the 90 lakes with the highest growing degree-days were selected (Fig. 12a). The increased number of trophy lakes generally increased effort, particularly for occasional anglers in Prince George, Cranbrook, and Nelson and for enthusiast anglers in rural Cariboo (Fig. 12b). The only substantial reduction in effort (-7%) was seen for social anglers in Fort St. John.

Discussion

Multistock recreational fisheries provide an excellent subject for the study of spatial social–ecological systems. The outcomes of the interactions among fish populations, fishers, and managers are governed by behavioural interactions overlain on the spatial landscape of the fishery (Ward et al. 2016; Arlinghaus et al. 2017). Processes occurring within and among these three players in the S-SES occur at a diversity of spatial scales, over a range of temporal scales, are often complex and nonlinear, and their dynamic outcomes are difficult to predict. To assess these social–ecological outcomes, we presented a dynamic model of the key behavioural processes across a large empirical landscape of fish populations, a behaviourally diverse angler community, and alternate policy options. Although built and parameterized for a particular fishery and its landscape, the qualitative dynamic outcomes should be

Fig. 10. Spatial pattern of cost-benefit from increased stocking. The map represents 584 independent runs of the landscape model (one run for each lake). In each model run, stocking on a particular lake is increased by 10%, and the cost-benefit of that manipulation is calculated as the total resulting landscape effort divided by the total cost of stocking. Black circles represent occasions where the increased stocking led to higher effort per dollar stocking costs. White circles represent occasions where the increased stocking led to lower effort per dollar stocking costs.



generalizable to other spatially structured recreational fisheries, which are common in many parts of the world (Post et al. 2002; Allan et al. 2005; Arlinghaus et al. 2017).

Previous models for predicting spatial patterns in angling effort have assumed that lakes are independent (Cox and Walters 2002; Post et al. 2008; Post and Parkinson 2012). Approaches that account for nonindependence in angling effort among lakes have concluded that ignoring this phenomenon could lead to poor management decisions over a wider spatial scale (Cox et al. 2003; Hunt et al. 2007, 2011). Our S-SES model addresses shortcomings of previous approaches by accounting for the complex interplay of management options, angler choice, density-dependent growth of fish, and the spatial distribution of anglers and angling opportunities. The model provides predictions of landscape-wide effort distributions that matched independent empirical observations reasonably well (Fig. 6). Therefore, we believe that the model could reliably be used to simulate and assess alternate management policy options.

Ecological dynamics in this S-SES occur at the lake (or patch) scale where fish recruitment, growth, and survival are locally determined, and in aggregate these define the production available for harvest across the landscape. Our modelled system was somewhat simplified; we bypassed the complexities involved in natural recruitment by using stocked fisheries. We retained, however, the important in-lake ecological functions of density- and climate-dependent growth and survival, which are key sources of compensation in the dynamics of harvest (Lester et al. 2014; Ward et al. 2017). At the landscape scale, nutrient richness and climate variables interact with lake-scale density dependence to control fish production.

Social dynamics in this S-SES are complex because there is substantial heterogeneity among anglers with behaviour modified by both catch- and non-catch-related attributes (Hunt 2005). In addition, landscape heterogeneity in angler population abundance, participation rates, distribution of behavioural types, and transportation networks result in substantial spatial heterogeneity of harvest demand by anglers across a fishery (e.g., Carson et al. 2009). Following convention, we used random utility and utility maximization theories to predict angler distribution across the landscape (e.g., Abbott and Fenichel 2013). We also observed an approximately twofold variation among angler groups in both catchability and maximum annual fishing days. Therefore, angler harvest behaviour, which is determined by their efficiency and maximum effort, differentially impacts harvest mortality and resulting feedback processes in the modelled system, as has been demonstrated empirically (Johnston et al. 2013; Ward et al. 2016).

The management component of the S-SES was not dynamically linked to the ecological and social processes in our simulations. For simplification, we started with a fixed status quo for the empirical landscape and then assessed the implications of altering management policy on ecological and social outcomes (through stocking rate changes at the lake and landscape scales). We did not simulate feedbacks between management policy and outcomes of these policy modifications. This may not be a substantial limitation, however, since feedbacks involving management policy are likely to be much slower than those related to ecological and angler behaviours (Ward et al. 2016; Arlinghaus et al. 2017).

At the landscape scale, we treated features as a static framework of fishing opportunities and angler demand. In particular, the spatial distribution of climate, human abundance in cities–towns–

Fig. 11. Model-predicted effort response to increased stocking of lakes nearer or farther than 100 km from an urban centre: (a) the manipulated lakes; (b) effort response (%) to increased stocking of lakes within 100 km of an urban centre; (c) effort response (%) to increased stocking of lakes farther than 100 km from an urban centre.

rural, and transportation network provides the linkages from all angler locations to all lakes on the landscape were held constant. The S-SES model could be adapted, however, to evaluate the implications of changing human population growth, climate, fish production, and transportation patterns across the landscape.

The S-SES outcomes presented here are the net result of the dynamic processes among fish populations and a heterogeneous angler population across the ecological, angler, and management landscape. The predictions from the S-SES do a reasonable job of characterizing the effort patterns across the landscape as assessed from an independent data set (i.e., mean predictions across many systems differ little). A priority for subsequent analyses is to characterize mechanisms behind the larger positive and negative residuals.

Ecological processes are a key determinant of the landscape patterns in fish populations and angler effort. Density- and climate-dependent processes result in within-lake trade-offs between fish density and body size (Ward et al. 2017). Density, in this case, is a function of stocking and harvest rates; natural mortality rate and size-at-age are functions of density and climate. Altering stocking rates results in a complex set of outcomes across the landscape. In some situations, increasing stocking rates had the net effect of attracting more anglers, implying that the manipulation increased local productivity that can be harvested by additional anglers. These lakes should be those that were originally stocked at rates whereby the net effect of an increase was to provide increased harvest opportunities, attracting anglers. The opposite situation was also encountered whereby increased stocking repelled anglers, suggesting that the densities were such that the ecological process of density-dependent growth reduced fish size to the point where the angling community assessed the fishing opportunity as less attractive, and anglers chose to fish elsewhere. These outcomes were therefore a function of the growth and survival of altered fish populations and effort and harvest behaviour by the heterogeneous angler population. We observed a similar dynamic experimentally where we identified an empirical optimum stocking density, which maximized total fishing effort (Mee et al. 2016). Interestingly, when this experiment was replicated across regions, optima were found in both regions, but at very different stocking densities. The region with the higher human density had a much higher optimum stocking density due to higher total harvest mortality than did a lower population density region. This result further supports the inference that the harvest dynamic works through a combination of density-dependent fish growth, harvest mortality, and angler behaviour driven by trade-offs between preferences for fish size and catch per unit effort (Parkinson et al. 2004; Wilson et al. 2016). Our landscape-scale model outcomes, based on behavioural interactions between fish populations and angler communities, corroborate these experimental observations (Mee et al. 2016).

Spatial patterns in fishing effort are the outcome, as measured by utility, of the effort–fishing quality dynamic, plus several human features of the landscape. The spatial distribution of human settlements and the transportation network provides the template for this dynamic to unfold (Carpenter and Brock 2004; Hunt et al. 2011). But, there is much more richness to the network as participation rates in the fishery differ substantially across the landscape, with clear contrasts among large cities and small

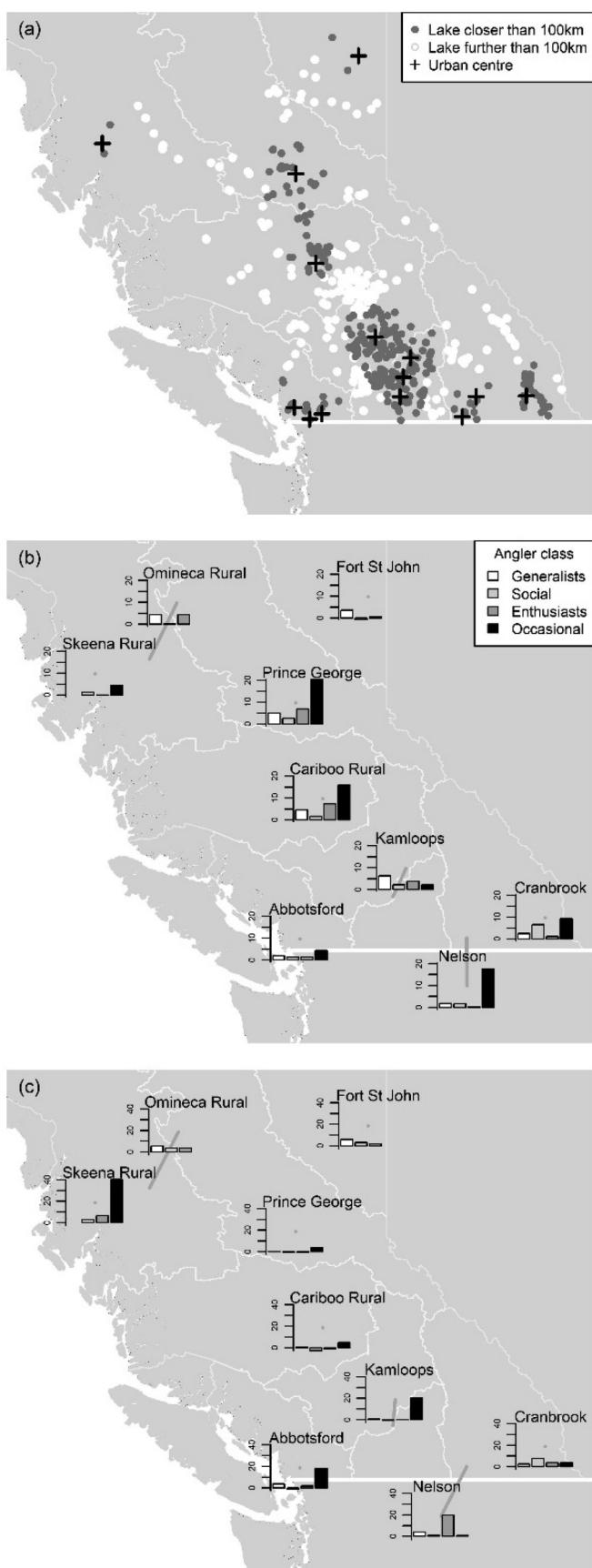
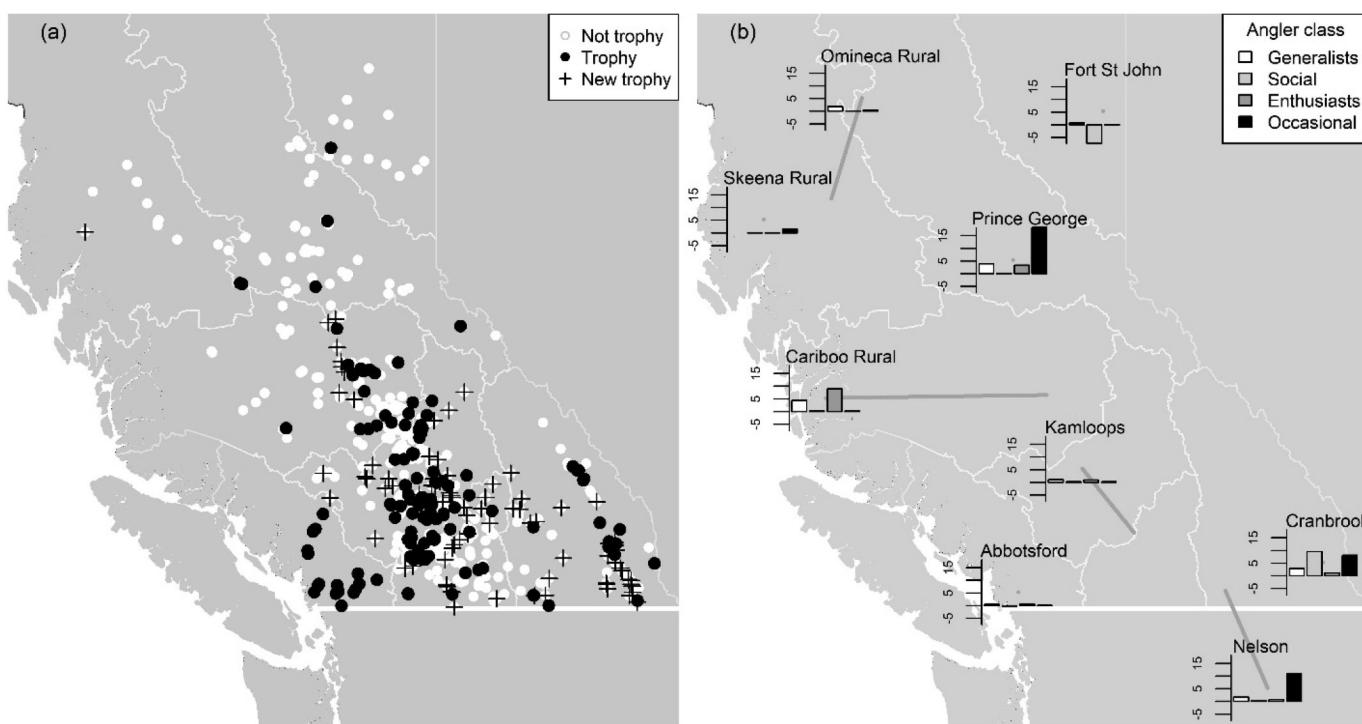


Fig. 12. Changes in angling effort (%) over the landscape in response to increasing the number of trophy lakes (in this example, lakes with a bag limit of two fish per day; panel a).



towns. In the British Columbia rainbow trout fishery, we observed participation rates varying from 3.7% in the primarily urban Lower Mainland region to 17.1% in the northern, least urbanized region, which is consistent with other landscape fisheries (Hunt et al. 2017). Although researchers often indict the process of urbanization and the disconnect of urban residents from nature as critical factors for reduced fishing participation (Arlinghaus et al. 2015; Hunt et al. 2017), an alternate explanation is that urban residents lack access to high-quality fishing opportunities within reasonable travel time, due to historical overfishing. This phenomenon has been described as producing low-quality fishing shadows around large cities, dissipating with distance, because of high urban effort, overfishing, and collapse (Post et al. 2002, 2008, 2012; Post 2013). It is hard to disentangle these competing hypotheses given snapshot observations, but we have experiments underway involving enhanced fishing in or near cities to assess the propensity of urbanites to fish if local opportunities are made available through stocking.

The spatial patterns in fishing effort and quality (catch rate and size) are much more heterogeneous across the landscape than considered in previous assessments of this fishery (Post et al. 2002, 2008; Post and Parkinson 2012). They presumed that most of the fishing effort emanated from the Lower Mainland–Vancouver area, which does contain by far the highest human density. However, it appears that substantial fishing effort also emanates from smaller communities throughout the interior of British Columbia, which although are much smaller centres, have higher participation rates. There is still an apparent south to north cline in effort and fishing quality, but this is less distinct than considered earlier due to the spatially diffuse nature of anglers' origin across the landscape.

Substantial heterogeneity in behaviour exists within the population of anglers who use this fishery. Four groups were identified with varying responses to the characteristics of the individual lake fisheries. This segmentation of angler types is common in many recreational fisheries (e.g., Beville et al. 2012; Carlin et al. 2012). Importantly, predictions of fishery outcomes in response to

management initiatives are sensitive to angler behavioural heterogeneity in their responses to variation in catch and non-catch in attributes (Johnston et al. 2010, 2013; Fenichel et al. 2013). Additionally, harvest dynamics are directly determined by the combination of angler behaviour and fish population compensatory processes of density-dependent growth and size-dependent natural and fishing mortality (Lester et al. 2014). Therefore, assessing alternate management policies aimed at optimizing outcomes requires the inclusion of these dynamics. Yet, mechanistic modelling approaches to fish–angler dynamics that incorporate both angler heterogeneity and realistic fish population structure are rare (Fenichel et al. 2013; Arlinghaus et al. 2017). Our simulations of management interventions involving stocking rates and harvest regulations revealed angler effort responses that varied substantially among angler groups and spatially. We would not have captured this heterogeneity in response to management policy changes if we modelled only the average angler.

While models such as S-SES may provide strategic benefits, their development is relatively costly. A large selection of data and models are required, such as choice models to characterize angler preference (Dabrowska et al. 2017), biological models to characterize growth, a complete account of management measures for all lakes, lake-specific information such as productivity and size, and geographic information systems for characterizing landscape features such as size of population centres, distances among lakes and population centres, and access to lakes. Depending on the landscape configuration, the S-SES approach can also be computationally intensive. The cost-efficacy analysis (Fig. 10) required the calculation of 584 simulated landscapes, which took 10 min on a contemporary workstation. Because the number of calculations required is the product of the number of population centres, angling classes, and lakes, a larger landscape model with double of each of these dimensions entails 32 times more calculations, which may prevent real-time exploration of the model in a management workshop.

There are several other limitations of the current S-SES approach that should be addressed by future model development.

Extensive verification of S-SES is vital and should go beyond fitting the model to independently estimated effort observations as we did. For example, S-SES predictions of effort changes from stocking experiments could be compared with observed effort changes where data are available. In our analyses, various simulations were undertaken in which stocking levels were altered arbitrarily, and some of these stocking options may not be possible given fish hatchery production constraints. Further versions of the model could aim to integrate hatchery production and cost models to ensure realistic management options are evaluated.

An important limitation of S-SES relates to our use of a simple stated preference choice model. This model does not include the importance of contextual factors such as proximity of an angler to lakes outside of the modelled system. Consequently, the predictions from the model can overstate effort in lakes near the boundary of the study area. Future applications could consider alternate models that (i) include important contextual factors in angler decision making by using information from stated and actual (revealed) choices by anglers (MacNair and Desvouges 2007); (ii) better connect fishing participation, effort, and site choices by anglers within more realistic time and budgetary constraints (e.g., Abbott and Fenichel 2013); and (iii) better understand how angler impacts on resources are influenced by gear and equipment selectivity.

The model also does not account for changes in license sales (n) and in this regard may underestimate responsiveness to angling opportunities. Using data from stocking experiments (Mee et al. 2016), future analyses could estimate limits on annual participation rate by angler class to better characterize effort response. In parallel to these stocking density experiments, the research team has also completed a series of experiments in which angling regulations were altered with controls and fishing effort monitored, providing additional potential to test landscape-scale prediction of this model. Additionally, historical license sales data may be investigated to attempt to relate predicted angling quality to a prediction of license sales (see Hunt et al. 2017 for such an application). Note that even if responsiveness was inaccurate, the S-SES model may still provide information regarding management priorities. For example, the patterns in the cost-efficacy maps of Fig. 10 are largely unaffected by alternative assumptions regarding the maximum annual participation rate of angler classes.

Future research on the dynamics of social–ecological recreational fishery systems could take three productive directions. First, enhancement of the framework that we developed for application to naturally recruiting fisheries would be a useful advance (Arlinghaus et al. 2017). This involves substantial complication of the ecological submodel in which mean recruitment and interannual variability in recruitment drives lake-scale fish production. Recruitment (as stocking) in our model was a management policy rather than an ecological process. In addition, this enhancement could include compensatory processes (Ward et al. 2013a; Perälä and Kuparinen 2017) and provide a more realistic assessment of the potential for overfishing and collapse with important management and conservation implications for wild-stock fisheries. A second and very useful research direction would be to subset the processes within the spatial SES to test hypotheses that result in the emergent properties of the system. For example, questions related to the importance of the spatial distribution of angler communities, lakes, and transportation networks could be assessed experimentally. Such an approach could help to generalize the patterns that emerge from dynamic SES interactions and could enhance our understanding in ways that are not possible with an empirically derived SES, as in our analyses. And third, development of a stochastic version of the model that incorporates variability of the key behavioural processes would be useful in assessment of the robustness of alternate management policy options under uncertainty and the value of additional information in optimizing outcomes of the S-SES.

Acknowledgements

We acknowledge the Natural Sciences and Engineering Research Council of Canada for funding a Collaborative Research and Development Grant in partnership with the Freshwater Fisheries Society of British Columbia and the Habitat Conservation Trust Foundation. We also acknowledge fishery biologists with the Freshwater Fisheries Society of British Columbia and the British Columbia Ministry of Forest, Lands, Natural Resource Operations and Rural Development who were instrumental in the planning and development of this landscape-scale adaptive and experimental management program, in particular Vicki Lewis, Cory Williamson, Steve Maricle, and Lee Williston. Thanks also to Natasha Carr and Dan Taillon for their helpful comments on an earlier version of this paper.

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