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Supply–demand equilibria and the size–number trade-off in spatially structured recreational fisheries

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Abstract. Recreational fishing effort varies across complex inland landscapes (e.g., lake-districts) and appears influenced by both angler preferences and qualities of the fishery resource, like fish size and abundance. However, fish size and abundance have an ecological trade-off within a population, thereby structuring equal-quality isopleths expressing this trade-off across the fishing landscape. Since expressed preferences of recreational anglers (i.e., site-selection of high-quality fishing opportunities among many lakes) can be analogous to optimal foraging strategies of natural predators, adopting such concepts can aid in understanding scale-dependence in fish–angler interactions and impacts of fishing across broad landscapes. Here, we assumed a fish supply–angler demand equilibria and adapted a novel bivariate measure of fishing quality based on fish size and catch rates to assess how recreational anglers influence fishing quality among a complex inland landscape. We then applied this metric to evaluate (1) angler preferences for caught and released fish compared to harvested fish, (2) the nonlinear size–numbers trade-off with uncertainty in both traits, and (3) the spatial-scale of the equilibria across 62 lakes and four independent management regions in British Columbia's (BC) rainbow trout *Oncorhynchus mykiss* fishery. We found anglers had low preference for caught and released fish (~10% of the value compared to harvested fish), which modified anglers' perception of fishing quality. Hence, fishing quality and angler effort was not influenced simply by total fish caught, but largely by harvested fish catch rates. Fishing quality varied from BC's northern regions (larger fish and more abundant) compared to southern regions (smaller fish and less abundant) directly associated with a 2.5 times increase in annual fishing effort in southern regions, suggesting that latent fishing pressure can structure the size–numbers trade-off in rainbow trout populations. The presence of two different equal-quality isopleths suggests at least two effective landscapes support co-occurring ideal free distributions of recreational fishing effort in BC's rainbow fishery. Anglers' expressed preferences among lakes interacted with density dependent growth and survival within lakes to structure a size–numbers trade-off influencing how anglers perceive fishing quality and, ultimately, distribute across complex inland landscapes.

Key words: angler effort dynamics; creel sampling; fishing quality; ideal free distribution; inland fisheries; Oncorhynchus mykiss.

Introduction

The distribution of highly mobile predators among complex landscapes is influenced by the relative qualities of targeted resource patches (e.g., prey populations) and by predator behavior (Stephens and Krebs 1986, Wiens et al. 1993, Alos et al. 2012). Prey species diversity, numerical abundance, and population size-structure can vary among patches and, assuming a rate-optimizing predation strategy, this variability influences prey choice, capture rate, and the predators' perception of patch quality (Mittelbach 1988, Osenberg et al. 1988, Osenberg and Mittelbach 1989). Predator populations are composed of individuals that behave heterogeneously and specialize on different prey types (e.g., Leibold et al. 2004, Chaplin-Kramer et al. 2011). The numerical response of predators among a landscape interacts dynamically with landscape-level characteristics of prey populations, and this response can vary depending on behaviors and preferences of the predator, e.g., generalist vs. specialist predators (Elliott et al. 2002, Hamer et al. 2006). Recreational anglers are, in many ways, analogous to natural predators in terms of target species

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specialization, harvest behavior, and responses to variation in patch quality (or fishing quality) among complex landscapes (Johnson and Carpenter 1994, Carpenter and Brock 2004, Hunt et al. 2011, Alos et al. 2012, Ward et al. 2013*a,b*, Dabrowska et al. 2014). As a prey population is depleted via predation or harvest, and as the quality of that site declines, the benefits to the predator or angler of continuing to forage or fish in that patch decrease, and mobile predators or anglers in an openly accessible landscape will typically search for more beneficial opportunities among other patches (e.g., Sanchirico and Wilen 1999, Fauchald et al. 2000). Increased growth and survival in prey populations after predators or anglers leave a patch should typically lead to improvements in patch quality, depending on density dependent processes within the prey population. Since the numerical response of predators or anglers is dependent on prey production, a dynamic feedback emerges between the size structure and abundance of prey and the distribution of predators or anglers among the landscape that leads to variation in patch quality, which is analogous to supply–demand relationships between resource quality and total consumptive pressure occurring across discrete patches (Fig. 1; Johnson and Carpenter 1994, Sanchirico and Wilen 1999, Salamolard et al. 2000, Winder et al. 2001, Carpenter and Brock 2004, Post et al. 2008).

Like natural predators foraging among a patchy landscape (Sims et al. 2006), recreational anglers must select lakes among many competing lakes that vary in fishing quality (Sanchirico and Wilen 1999). Similar to natural predators, anglers within a broad landscape also vary in terms of their tendencies to catch different sizes, abundances, and species of fish (Arlinghaus 2006, Beardmore et al. 2011, Beardmore et al. 2013). Unlike natural predators, however, some anglers optimize total harvestable catch while others target large trophy fish for catch and release (Ward et al. 2013a). Despite this key difference, angler catch rates provide a suitable analogue for prey capture rates, as catch rates track resource abundance (Johnson and Carpenter 1994), variation in catch rate strongly influences variation in angler effort across fishing patches, and both fish size and catch rate tradeoff to influence anglers' perception of fishing quality (Parkinson et al. 2004, Askey et al. 2013). Given that recreational fisheries are important from both a conservation and economic perspective, there is great interest to apply concepts from spatially structured predator–prey dynamics to the management of sustainable fisheries (Carpenter and Brock 2004, Post and Parkinson 2012).

Both social and ecological processes influence fishing quality (Weithman and Anderson 1978). Density dependent growth and size-dependent survival are influenced by angler harvest, and these processes regulate population abundance and size-structure, which are key components of fishing quality (Tonn et al. 1994, Post et al. 1999). Furthermore, an emergent property of density dependent growth and size-dependent survival is the demographic trade-off between the number of fish

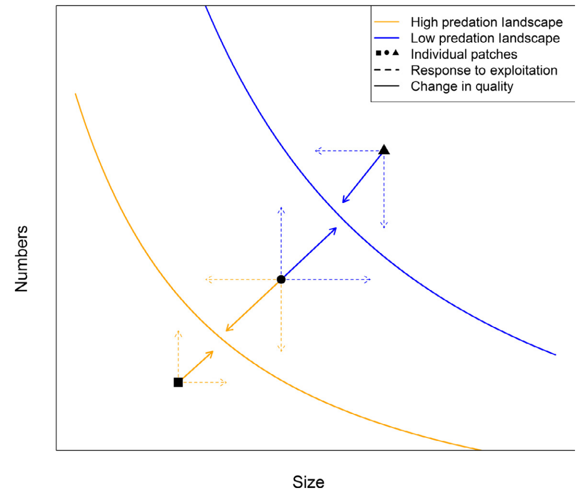

FIG. 1. Prey size and abundance trade-off due to density dependent growth/survival, the numerical response of predators, and predator preference for large prey items. Mobile predators–prey dynamics within and across patches structure a size–numbers trade-off, but these dynamics depend upon characteristics of the prey's landscape. In a high predation landscape prey populations are depleted quickly and patch quality is generally lower compared to a low predation landscape. As individual patch quality is reduced below the landscape's average quality, predators leave the patch to search for higher quality patches elsewhere. This allows for improvements in the prey population from either density dependent growth, which increases size, or density dependent survival, which increases abundance both of which improve patch quality. These dynamics change depending on whether a patch is embedded in the high predation landscape compared to the low predation landscape. If a patch's quality were above the landscape's average quality (orange isopleth), then that patch would attract predators, which would then selectively feed on larger prey items and deplete prey abundance (reducing numbers) thereby reducing quality. If the same patch were within the low predation landscape, and thus below the landscape's average quality, that patch would attract few predators which would allow for improvements in size, numbers, and quality over time.

and the size of the fish within a given population. Density dependent processes and harvest pressures vary among lakes, and this is expected to result in variable fishing quality among lakes on the landscape (Post et al. 2008, Hunt et al. 2011). The size-numbers trade-off has rarely been quantified across a fishing landscape (but see Parkinson et al. 2004 and Askey et al. 2013) where quality and effort are spatially variable and dynamic, and where fish production and anglers (i.e., their behavior, expectations, motivation, and perception of quality) also vary throughout the landscape (Ward et al. 2013a, Beardmore et al. 2013). Previous attempts to model this size–numbers trade-off (Parkinson et al. 2004, Askey et al. 2013) ignored scale dependency that could occur among a broad landscape, allowed for quality to be measured based only on changes in catch rates but not size, and did not estimate differences in angler preferences (Parkinson et al. 2004, but not Askey et al. 2013). Relying on simple assumptions about angler behavior can preclude adequate understanding of the drivers of fishery dynamics (Post et al. 2008, Hunt et al. 2011); while failing to analyze a mosaic of resource patches within a landscape-scope can mask relative changes to resource quality (Turner 1989) and fail to link population-level outcomes to the spatial-scale of management (Hilborn et al. 2005). Since fishing quality provides the key link between within-lake fish population dynamics and landscape-scale angler effort dynamics, these models should consider further realism in socioecological processes.

Understanding patterns in fishing quality can help predict the landscape distribution and numerical response of fishing effort and spatial patterns in the impacts of fishing (Post et al. 2002, Allan et al. 2005, Post 2013). Fishing quality could be defined as a combination of ecological and non-ecological characteristics of a fishing site that attracts effort depending on cost–benefit ratios (Dabrowska et al. 2014). Hence, fishing quality, which may be a combination of several social factors (e.g., presence/absence of lodges, driving distance, scenery, anglers' harvest expectations, angler motivations) or ecological factors (e.g., number of fish, size of fish, species diversity), affects the amount of fishing effort in particular lakes (Carpenter and Brock 2004, Hunt 2005). The non-ecological components of fishing quality (e.g., lodges and travel distance), though important for selecting which sites to fish (Hunt 2005), are constrained by fiscal budgets and technologies that change infrequently (i.e., periodically) and appear less responsive than fish population structure within a temporal snapshot. Therefore, dynamic feedbacks between fishing effort and fishing quality within a given time period likely depends mostly upon the ecological component of quality. In other words, fishing quality (i.e., the number and average size of fish) in a particular lake is influenced by the amount of fishing effort in that lake, while fishing effort is, in turn, influenced by fishing quality (Post et al. 2008). Any measure of fishing quality among a landscape is therefore inherently intertwined with variation in effort among the landscape. It is often assumed that anglers have perfect knowledge of the distribution of fishing quality among lakes and that anglers allocate their effort to the highest quality lakes until all lakes are of equal quality among the landscape resulting in what is known as the "ideal free distribution" (IFD) of effort (Parkinson et al. 2004, Post et al. 2008, Askey et al. 2013). Although perfect knowledge of resource quality is obviously untrue, recreational anglers have an immense capacity for communication, learning, and mobility such that anglers can test the quality of many lakes directly or indirectly, thus helping approximate a perfect knowledge assumption (Post et al. 2002, Parkinson et al. 2004).

We addressed the hypotheses that (1) there is a size–numbers trade-off in fishing quality, (2) equilibrium fishing quality will vary across spatial scales, and (3) the equilibria will be associated with differences in social or ecological factors detectable at those scales. We addressed two specific questions related to these hypotheses. First, how do social factors regarding catch-and-release preferences and latent angler effort (i.e., the total population of anglers) interact with ecological factors in the determination of fishing quality at the landscape scale? Second, is variation in quality at the landscape scale consistent with the expected outcome of an IFD of angler effort? In order to answer these questions, we developed a novel approach to estimate perceived fishing quality (hereafter referred to as fishing quality) that takes into account the size–numbers trade-off as well as the anglers' preferences for catch and release vs. harvested fish. Then, we estimated fishing quality across a diverse landscape of isolated, independent lakes. Our study system is the rainbow trout (*Oncorhynchus mykiss*) fishery in British Columbia. This is an ideal system for our study because robust fish life-history and size-abundance data (i.e., creel data) across a multitude of lakes, as well as data on variation in angler preferences and harvest tendencies for multiple regions, help characterize the ecological and social factors that influence fishing quality throughout the province (Parkinson et al. 2004, Askey et al. 2013, Ward et al. 2013*a*).

Methods

Study site and data

Rainbow trout are a commonly sought after fish species that occur naturally or by stocking of hatchery-reared fish, and provide an important inland recreational fishery in British Columbia (BC). The provincial management of BC's rainbow trout fishery is divided into eight independently administered Management Regions (Fig. 2). Since 1989, the Freshwater Fishery Society of British Columbia (FFSBC) and the British Columbia Ministry of the Environment periodically sampled angler catches (i.e., creel sampling) across four of these Management Regions: 3, 5, 7, and 8 (Parkinson et al. 2004) to understand fish–angler interactions and the impacts of fishing throughout the province. This data was made accessible in the FFSBC's long-term Small Lakes Assessment Management (SLAM) database. The angler catch data consisted of average size of harvested fish in addition to the total catch per unit effort, the harvested fish per unit effort, and the fish caught and released per unit effort, where effort was measured as the number of hours an individual angler spent fishing per trip (see Appendix S1: Table S1). Differentiating between harvested fish catch rates and released fish catch rates afforded an understanding of the relative importance of harvested fish compared to catch-and-release fish in characterizing fishing quality.

For the purposes of this study, all lakes with ≤100 angler-hours and all hike-in lakes (e.g., lacking a forestry road) were excluded due to unreliable effort snapshots over the time period of the sampling. Hence, creel samples came from the remaining 62 open-access lakes in the SLAM database and represented lakes where access was developed (e.g., forestry roads were built, lodges were

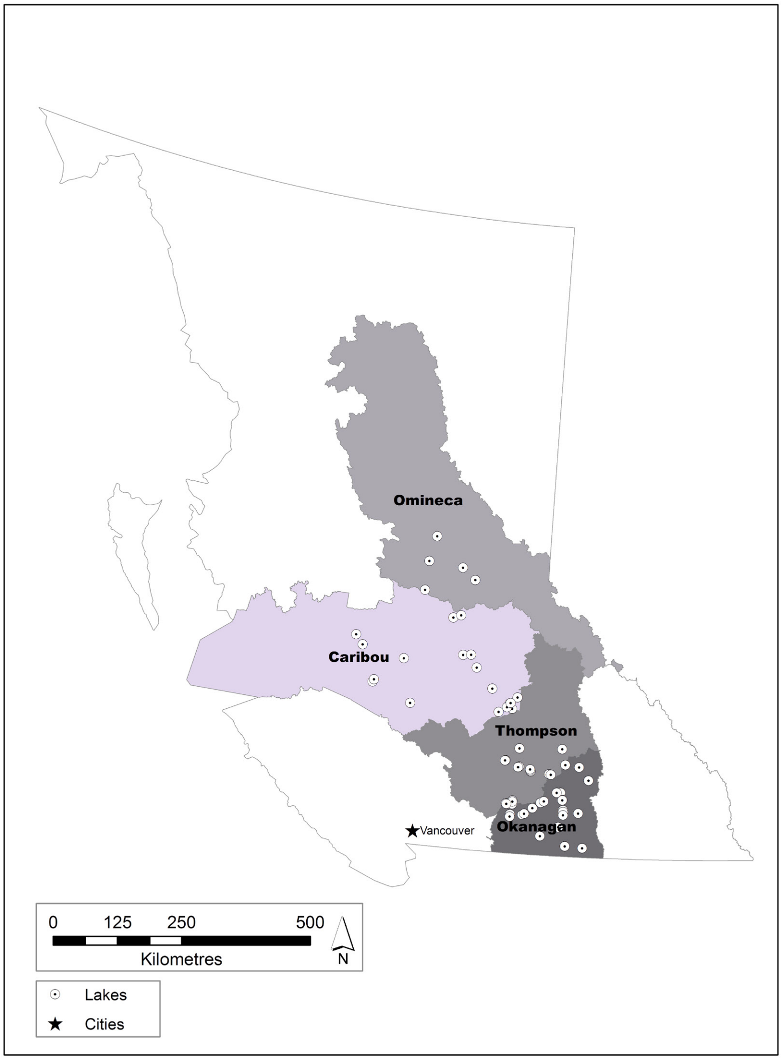

Fig. 2. The British Columbia rainbow trout fishery divided into eight independently administered management regions. Samples of angler catch data from 62 lakes were taken from the four regions shown to understand landscape-level dynamics between mobile anglers and individual rainbow trout stocks.

constructed, boat ramps were installed) prior to the creel sampling and effort monitoring program. This allowed us to assume that non-catch related aspects to site-selection, such as lodges, boat ramps, and road access, had negligible changes over this time. Nine of the lakes were within Region 3, 18 lakes from Region 5, six lakes from Region 7, and 29 lakes from Region 8, representing 3%, 8%, 4%, and 11% of managed lakes (i.e., lakes recognized with official management regulations) in each region, respectively, during this time period. In total, the creel dataset contained over 10000 intercept-surveys (i.e., agency personnel intercepted boats on the water or anglers onshore and their daily catches were surveyed) sampling over 19000 rainbow trout anglers across the 62 lakes, a total fishing effort of more than 39000 h, and over 34000 fish caught with over 19000 fish harvested. Management regulations varied across the 62 lakes. The maximum number of harvested fish per angler per day (i.e., the bag limit) ranged from one to eight fish, but 58 of the lakes had bag limits of five to six throughout the sampling period (see Appendix S1: Table S1). Further data for many of the lakes was made available including mean annual stocking densities per hectare (i.e., supplemental stocking) during this time period and lake productivity as measured by mean total dissolved solids (see Appendix S1: Table S1).

Samples over the 25-year period were pooled for each lake relying on an assumption that fish CPUE (catch per unit effort) and size equilibrated over time and represented a snapshot that would be reflective of an IFD. While assuming conditions were static (i.e., in an ideal free distribution) precluded evaluating changes in the size–numbers trade-off over this time period, an IFD of angler effort appears empirically supported in these management regions (Cox 2000) and regional size- and age-structured models assuming the IFD in effort dynamics recreate empirical patterns in aerial effort surveys, fish demography, and angler CPUE in the British Columbia rainbow trout fishery (Parkinson et al. 2004, Askey et al. 2013).

Analytical rationale

Four issues were encountered when attempting to estimate fishing (patch) quality among the British Columbia rainbow trout landscape. The first problem is that the IFD predators' assessment of quality is based, in part, on a catch rate that is composed of both harvested fish and fish caught and released. Similar to how preferences of natural predators determines landscape-level predator–prey interactions (e.g., Chaplin-Kramer et al. 2011), harvest preferences and angler behavior vary both within lakes and across landscapes and these preferences motivate angler effort in different ways (Ward et al. 2013a). Estimates of quality therefore need to account for how differences in angler preferences might influence the perception of fishing quality potentially making total catch rates (i.e., all harvested fish + all released fish) a poor characterization of fishing quality. Askey et al. (2013) concluded that an effective catch rate for fishing quality (i.e., a catch rate that reflects how anglers are motivated by numbers of fish caught) will be one that allows for the relative value of a released fish (value pertaining to anglers' preference for catching a fish that is then released) to be different than the relative value of a harvested fish, and that, generally, released fish will be valued equal to or less than harvested fish.

The second issue encountered was that the consumers' perception of resource quality is not composed of only resource abundance. The use of IFD in predator–prey dynamics (including in fisheries) often assumes that predators' assessment of patch quality correlates to prey or resource abundance (Kennedy and Gray 1993, Tregenza 1995, Gillis 2003). However, quality in many systems is composed of two traits: the average size of prey captured and prey capture rate; this has been demonstrated in both predator–prey (Osenberg and Mittelbach 1989) and fish–angler systems (Parkinson et al. 2004). For spatially structured recreational fisheries, Parkinson et al. (2004) and Askey et al. (2013) demonstrated that fish size and catch rates trade off with each other due to within lake ecological processes (i.e., density dependent growth and survival) interacting with predation of fish populations via angler harvest. Therefore, we incorporated a more accurate effective catch rate (i.e., one that accounts for harvest vs. catch-and-release preferences) into the size–numbers trade-off, and we determined quality by modeling the trade-off between average fish size and the effective catch rate, which incorporates the relative values of harvested and released fish (Parkinson et al. 2004, Askey et al. 2013).

The third issue encountered was how to statistically fit estimates of fishing quality knowing that density dependent growth and survival modifies both prey size and prey numbers dynamically. Previous attempts to characterize fishing quality with a two-trait isopleth only allowed quality to be measured as the residual distance of lake-specific catch rates from the landscape's average catch rate (Askey et al. 2013, highlighted in Fig. 1 with the vertical arrows). This distance therefore only measured residuals along the vertical axis (i.e., catch rates). This did not allow quality to change with changes to both catch rates and fish size. Therefore, we created an estimator for quality that allowed for the distance from patch-specific characteristics to be measured as residual distances along both the horizontal axis (fish size) and the vertical axis (catch rates) as shown with the diagonal arrows in Fig. 1.

The fourth and final issue was that the IFD of angler effort and the emergent properties of these dynamics can vary across spatial scales (Parkinson et al. 2004). Since creel data existed from four Management Regions where the populations of mobile anglers may or may not be responding independent of each other, we wanted to determine the spatial scale at which the IFD is occurring. This meant creating analyses where angler preferences (i.e., the effective catch rate) and the shape and characterization of the size–numbers trade-off could vary across these spatial scales. For example, an IFD-based equilibrium between mobile anglers and fish could occur at four unique "regional scales" (i.e., four IFDs), across the entire BC province-scale (i.e., one IFD), or at some intermediate scale (i.e., two IFDs). We created these analyses using an information theoretic approach to compare models where the estimated parameters of the size–numbers trade-off and angler preference for released fish vs. harvested fish were grouped differently across these different spatial-scales.

Effective catch rate and the size–numbers trade-off

Total catch rate is the sum of catch rates of fish that are harvested and the catch rates of fish that are released:

$$\mathrm{CPUE}_i = \mathrm{RPUE}_i + \mathrm{KPUE}_i, \tag{1}$$

where CPUE_i is the total catch per unit effort for lake i, RPUE_i is the released fish per unit effort, and KPUE_i is the harvested (kept) fish per unit effort. However, total catch rate may overestimate the number of fish that motivates angling effort because, while anglers prefer more fish than fewer fish, anglers behave heterogeneously with regard to preferences for harvested fish compared to fish caught and released (Fedler and Ditton 1994, Fisher 1997, Arlinghaus 2006, Beardmore et al. 2011, Ward et al. 2013a). Askey et al. (2013) used a parameter ($\hat{r}$) that modifies total catch rates to be an effective catch rate for anglers that takes into account the average angler's value for fish caught and released. To estimate the effective catch rate from both harvest and catch-and-release fish, we defined the effective catch rate (ECUE) for lake i as

$$\mathrm{ECUE}_i = \hat{r} \times \mathrm{RPUE}_i + \mathrm{KPUE}_i \tag{2}$$

where $\hat{r}$ is the average value of catch-and-release fish. This assumes that the value of harvested fish is 1 and $\hat{r}$ can be greater than, equal to, or less than 1. By assuming an average value for catch-and-release fish, we can then evaluate how fishing quality varies among a landscape that is fished by a shared population of highly mobile anglers.

Trade-offs between average fish size and $CPUE_i$ have been described with equal-quality isopleths calculated with a negative-exponential relationship (Parkinson et al. 2004, Askey et al. 2013). Fishing quality isopleths were estimated using modifications to Eqs. 11, 12, and 13 from Askey et al. (2013). We then estimated a size-numbers isopleth that standardized $ECUE_i$ by length with

$$\mathrm{ECUE}(L)_i = \alpha \times L_i^{-\beta} \tag{3}$$

where L_i is the average size (in cm) of fish caught at lake i, and α and β are shape parameters that estimate the trade-off between catch rates and average size. We then define quality (Q_i) as the average distance of lake-specific characteristics (a point) compared to the equilibria defined with Eq. 3 size-numbers isopleth (i.e., the length of the solid arrows in Fig. 1). Given that changes in effort modify both fish size and catch rates by reducing competitors or harvesting fish of a certain size, quality can also change in the two directions. Therefore, quality will need to incorporate the average distance from the $ECUE_i$ (a point) to the ECUE $(L)_i$ (a curve) in both the numbers (vertical) and size (horizontal) directions (Fig. 1). We thereby define quality as the combination of these two traits measured with the average distance of the point to the log-transformed isopleth:

$$Q_{v,i} = \mathrm{ECUE}_i / \mathrm{ECUE}(L)_i \tag{4}$$

where $Q_{v,i}$ is quality as measured in the vertical direction (i.e., catch rate) for lake i, $ECUE_i$ is the observed catch rate, and $ECUE(L)_i$ is the catch rate predicted for that fish size. The distance from the point to the isopleth in the horizontal direction is measured with

$$Q_{h,i} = (L_i / e^{([\ln(\alpha) - \ln(\mathrm{ECUE}_i)]/\beta)}) \tag{5}$$

where $Q_{h,i}$ is quality measured in the horizontal direction (i.e., size) for lake i, L_i is the observed average fish size (in cm), $ECUE_i$ is the catch rate, and $e^{([\ln(\alpha)-\ln(ECUE_i)]/\beta)}$ is the predicted average fish size for that catch rate. We then combine these two traits of quality with a weighted average relative to the slope (β) of the log-transformed Eq. 3 and solve for the log of α:

$$Q_i = [Q_{v,i} \times (Q_{v,i}/(Q_{v,i} + Q_{h,i}))] + [Q_{h,i} \times (Q_{v,i} + Q_{h,i})] \tag{6}$$

where Q_i is the lakes total quality, which reflects the weighted combination of the magnitude of catch rate ($Q_{v,i}$) compared to size($Q_{h,i}$). Taking the log of Eq. 3 linearized the curved isopleth and allowed for the weighted average to better estimate the two shape parameters α and β (compared to a simple average) where the weight is applied relative to the slope (β) of the line. If the slope of the isopleth were equal to a 45° line, then the catch rate and size would be weighted equivalently, a steeper slope would indicate that catch rate has more weight than fish size when estimating quality, and a shallower slope would indicate that fish size has more weight than catch rate. Given an ideal free distribution of angling effort (Parkinson et al. 2004, Askey et al. 2013), we expected the average quality in Eq. 6 (i.e., the weighted sum of the two ratios) to approach 1.0 over time. Therefore, in order to have our predicted quality reflect the outcome of an IFD, we used Eq. 6 to estimate the parameters α, β, and $\hat{r}$ from Eqs. 2 and 3 above by minimizing the sum of squares $(Q_i - 1)^2$.

Spatial scale of the IFD

The spatial scale that reflected the outcome of an IFD for estimating fishing quality among the rainbow trout fishery was uncertain. To determine this spatial scale, we allowed for the three parameters influencing fishing quality in Eq. 6 to vary with spatial scale (s):

$$Q_i \sim \{\alpha_s, \beta_s, \hat{r}_s\} \tag{7}$$

such that s = 1, 2, or 4 where an s = 1 corresponded to a province-wide fishing landscape (i.e., there is one size-numbers trade-off and one average value for released fish among all of British Columbia), an s = 2 corresponded to an intermediate spatial-scale larger than individual management regions but smaller than a province-wide landscape, and an s = 4 corresponded to a landscape specific to each individual management region (i.e., four co-occurring IFDs, one for each of the four sampled regions). To determine the most likely value for s, we evaluated nine candidate models for estimating fishing quality across spatial scales using Akaike's information criterion (Akaike 1974) corrected for small sample size (AIC_c) by calculating

$$\mathrm{AIC}_c = n \times \ln(\mathrm{RSS}/n) + 2 \times K + (2 \times K \times (K+1))/(n - K - 1) \tag{8}$$

where n is the number of observations, RSS is the residual sum of squares from model fitting, and K is the number of parameters in the candidate model. Therefore, the best candidate model allowed us to determine the appropriate scale for the rainbow trout landscape, whether anglers in different regions have different preferences for released fish, and whether the size–numbers trade-off is similar across the four management regions, the entire province, or at some intermediate scale. Specifically, the intermediate spatial scale grouped lakes based on the North/South (i.e., latitudinal) grouping of the four management regions assuming that Regions 5 and 7 share similar effort–quality characteristics and Regions 3 and 8 share characteristics (Table 1). Models with ΔAIC_c values of <10.0 have support and <2.0 have substantial support and are considered equivalent at explaining the data; if models were equivalent (i.e., the two models were differentiated by <2.0 ΔAIC_c), we selected the model with the highest weighted AIC_c (w_i) calculated as

$$w_i = \exp\left(-0.5 \times \Delta \mathrm{AIC}c_i\right) / \sum_{r=1}^{R} \exp\left(-0.5 \times \Delta \mathrm{AIC}c_r\right) \tag{9}$$

Table 1. Nine candidate models used to determine the spatial scale structuring an ideal free distribution (IFD) between mobile anglers and rainbow trout in British Columbia, Canada.

Model type	AIC_c	K	ΔAIC_c	w_i
Global β, Global α, Global $\hat{r}$	−145.58	3	33.43	<0.00
Global β, Latitude α, Global $\hat{r}$	**−179.01**	**4**	**0.00**	**0.62**
Global β, Global α, Latitude $\hat{r}$	−142.79	4	36.22	<0.00
Global β, Latitude α, Latitude $\hat{r}$	−176.68	5	2.33	0.19
Latitude β, Latitude α, Latitude $\hat{r}$	−174.17	6	4.84	0.05
Global β, Regional α, Global $\hat{r}$	−175.88	6	3.13	0.13
Global β, Global α, Regional $\hat{r}$	−140.97	6	38.04	<0.00
Global β, Regional α, Regional $\hat{r}$	−169.20	9	9.81	<0.00
Regional β, Regional α, Regional $\hat{r}$	−161.29	12	17.72	<0.00

Notes: The models estimated fishing quality by estimating anglers preference for catch-and-release fish ($\hat{r}$ parameter) and the size–numbers trade-off (α and β shape parameters) across the fishing landscape. The models are ordered by their spatial complexity (i.e.,. *K*, the number of estimated parameters) from a province-wide IFD (Global) to an intermediate-scale grouping (Latitude) to a region-wide grouping by the independently administered management regions (Regional). Models were ranked according to Akaike's information criterion corrected for small sample size (AIC_c) and the relative explanatory weight (w_i; Burnham and Anderson 2004) amongst all candidate models. The model with the lowest delta-AIC_c and most explanatory weight (wi) highlighted in bold.

where *R* is the number of fishing quality models ranked (Burnham and Anderson 2004).

Results

The observed proportion of fish harvested varied substantially across the 62 lakes with a mean of 0.65 and 95% CI of 0.16–1.0. Across the four regions and 62 lakes, the average fish kept varied from 21 to 50 cm, observed total catch rates varied from 0.35 to 7.14 fish per angler hour, and observed harvested fish catch rates varied from 0.03 to 4.04 fish per angler hour (Fig. 3a). The effective catch rate was influenced by anglers' preference for released vs. harvested fish (i.e., the $\hat{r}$ parameter; Fig. 3b), such that the average angler preferred a mix of harvested and released fish (i.e., $0 < \hat{r} < 1$). A size–numbers trade-off emerged from the interactions between mobile anglers and rainbow trout populations but the position of this trade-off differed across British Columbia (Fig. 3b). The AIC-selected model had strong explanatory power ($r^2 = 0.65$) and carried 62% of the weighted AIC amongst the nine candidate models and suggested that the IFD of angling effort occurred at an intermediate scale, smaller than a single province-wide IFD but larger than four regional IFDs (Table 1). Overall, the equal-quality isopleths differed based on the northern (Regions 5 and 7) and the southern portion of the landscape (Regions 3 and 8) with the equal-quality isopleths in the northern landscape having a higher average for both size and catch rates compared to the southern landscape. These results suggested that anglers expected larger and more fish in northern lakes than in southern lakes (Fig. 3b). The AIC-selected model showed that, for the purposes of explaining fishing quality, the β (shape of the curvature, or slope, in the isopleth) and $\hat{r}$ (value of fish caught and released) parameters did not vary by region or latitude, while the α (constant, or intercept, that moves the isopleth up or down) parameter varied between northern and southern regions. The estimated equal-quality isopleth parameters were α = 775,953 and 276,434 (in northern and southern regions respectively), β = 3.61, and $\hat{r}$ = 0.09 (Fig. 3). The β estimates were similar across the nine candidate models

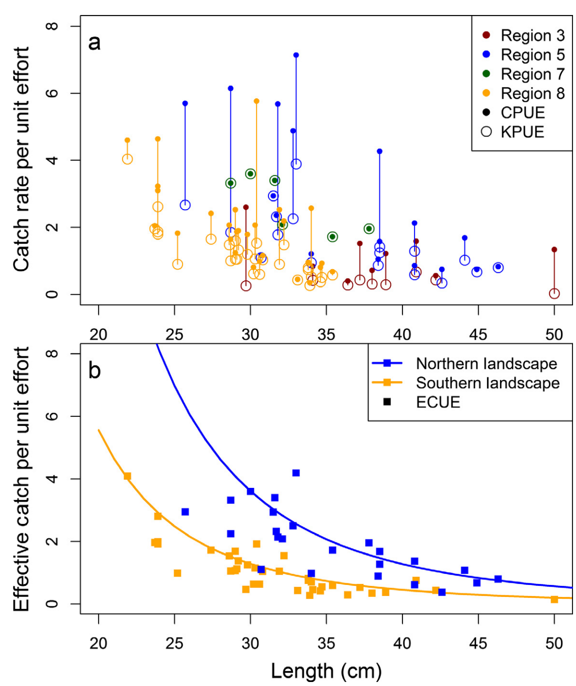

Fig. 3. The landscape-scale size–numbers trade-off across British Columbia's rainbow trout fishery. Panel (a) shows the observed total catch per unit effort (effort in angler hours; CPUE) and observed harvested fish per unit effort (KPUE) in 62 lakes across each of four management regions. Panel (b) shows model fits from the AIC-selected model to an effective catch rate (ECUE; which modifies catch rates depending upon anglers' preference for released fish) and the size–numbers trade-off in the northern landscape (Regions 5 and 7 combined; blue isopleth) compared to the southern landscape (Regions 3 and 8 combined; orange isopleth).

suggesting that the emergent shape of the trade-off behaved consistently. The model estimates for $\hat{r}$ of 0.09 was below the range estimated in Askey et al. (2013) of 0.16–0.20 and showed an effective catch rate that was dominated by harvested fish (Fig. 3b). Like the β parameter estimates, the $\hat{r}$ were similar across different candidate models (i.e., when $\hat{r}$ and α varied with latitude: $\hat{r}_{North} = 0.07$ and $\hat{r}_{South} = 0.10$) suggesting that the value of released fish was also consistent across the landscape. Therefore, the shape of the size-numbers trade-off was shared across the province, but the position of the trade-off changed so that average quality in the northern landscape was higher, both in numbers and average size of fish, than in the southern landscape.

Within the most parsimonious spatial grouping, there was variance in quality among individual lakes. The distance from fishing quality of individual lakes to each landscape's average quality varied, showing that fishing quality was heterogeneous across each landscape (Fig. 4). These results showed that within both the northern and southern regions, the majority of lakes had near or below average fishing quality with relatively few high quality lakes. With this heterogeneity, the equal-quality isopleths show a wide range of catch rates and a wide range of sizes that create equivalent fishing quality. The two region-specific, equal-quality isopleths converge toward large fish sizes, likely due to the asympototic size of individual fish that is approached at low fish numbers and is likely a function of the genetic and ecological similarities among rainbow trout across the lakes sampled in this study. Residuals from the selected model were negatively biased by 4% suggesting that the equal-quality isopleths were slightly overestimated. This is likely due to the log-transformation of the isopleth and fitting the model via minimizing sums of squares residuals, an approximation of a normal likelihood that can often bias linear models due the error structure of the model, resulting in slightly biased residuals.

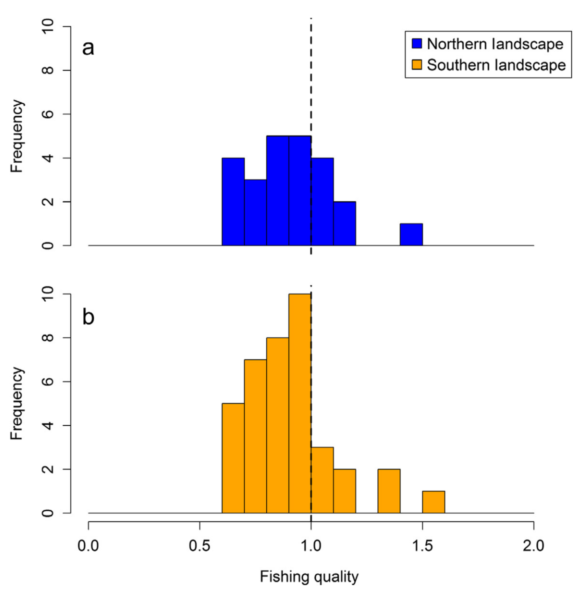

Fig. 4. Histogram highlighting variance in fishing quality in two landscapes across 62 rainbow trout lakes as a deviation from average fishing quality (vertical line at 1.0) assuming an ideal free distribution.

Discussion

Just as natural predation structures a size–numbers trade-off in prey populations (Osenberg and Mittelbach 1989, Post et al. 1999), angling structures a similar trade-off in fishing quality across numerous isolated lakes in inland British Columbia's rainbow trout fishery. Due to the manner in which highly mobile anglers distribute among and select lakes, this structuring pattern emerges from density dependent growth and size-dependent survival processes that occur at multiple spatial-scales both within lakes and across the fishing landscape (e.g., Parkinson et al. 2004). We showed that these patterns depended on the preferences for certain resource types (i.e., released fish vs. harvested fish) of the mobile anglers suggesting that the expressed preferences and behaviors of a mobile consumer can structure landscape-level patterns in a resource populations (e.g., Fauchald et al. 2000, Sims et al. 2006). Given that landscapes can have diverse resource assemblages, varying in prey species (Leibold et al. 2004) or varying in size, or bag regulations in a recreational fishery (Post and Parkinson 2012), these trade-offs may depend strongly on the selection and preferences for certain characteristics of the resource population and the total consumptive pressure within the landscape (Sanchirico and Wilen 1999).

Interestingly, the different position of the size–numbers trade-off and the higher average quality in northern regions compared to southern regions counters expectations given by productivity gradients. For example, average lake productivity in the south is ~50% higher than the north (southern TDS = 125; northern TDS = 77; see Appendix S1: Table S1). Climate is also warmer in the south (mean annual air temperature [MAT] in southern region = 3.9°C ± 2.6°C; northern region MAT = 2.8°C ± 1.6°C; Pike et al. 2010) and more favorable to fish growth as the growing season is longer in the south (southern landscape average growing degree days [DD] >5°C = 1172 ± 512; northern average DD = 1045 ± 334; Pike et al. 2010). Furthermore, management differences among lakes did not seem associated with any improvement in quality. For example, the three lakes with bag limits of two or fewer fish only had average or below average quality ranging from 0.8 to 1.1 (Appendix S1: Table S1). Stocking hatchery-raised rainbow trout to supplement natural recruitment also had no association with quality. Lakes with >200 fish/ha had an average quality of 0.84, while lakes with natural recruitment, i.e., no stocking management, had an average quality of 0.95. Given that stocking is a management tactic that can be intended to subsidize fishing quality in poor environments or high angling effort, the expected positive association between stocking densities and fishing quality can be nullified in either regard.

Hence, a key question left unaddressed thus far is, Why is fishing quality better in the northern landscape when both management tactics and climate seems more favorable in BC's southern interior? Such a counter-gradient pattern likely emerged due to differences in the composition of angler typology between the two landscapes and interactions between total angler effort and density dependent growth and survival. This empirical pattern is directly associated with angling pressure being concentrated in southern British Columbia, with a higher numerical response of anglers depleting fish populations more rapidly and removing most of the larger fish. Specifically, the southern landscape receives ~2.5 times more total fishing effort than the northern landscape (Post et al. 2002, 2008). Furthermore, the angler population in the south is composed of numerous rainbow trout specialists that prefer trophy-sized fish and travel long distances, while anglers in the north appear to be generalists that fish locally and prefer to keep what they catch (Dabrowska et al. 2012, Ward et al. 2013*a*). While generalists tend to target other fishes when fishing quality is demonstrably reduced (Dabrowska et al. 2012), rainbow trout enthusiasts often have high skill allowing them to maintain high catch rates even among depleted rainbow trout populations, which results in CPUE hyperstability (Ward et al. 2013*b*). These patterns reveal that factors related to mortality of the resource population (i.e., the numerical response) can counter productivity gradients to structure fish populations and that angling effort and specialization can be associated with landscape gradients. Overall, differences among angler behavior and increased total demand for a limited supply of above-average quality fishing patches in BC's southern landscape has likely lead to the observed pattern where the equal-quality isopleth averages smaller fish and lower catch rates compared to the northern landscape.

Anglers, like other mobile predators, are often assumed to distribute across isolated prey patches in order to maximize a utility function, but the optimum rate may vary depending on the system (e.g., total energy, total capture, or prey-encounter rates; Sims et al. 2006). For many mobile predator–prey systems, including recreational fisheries, there may be a bivariate trait function for the predator's utility (i.e., quality): prey size and prey catch rates (Osenberg and Mittelbach 1989). Increased complexity of angler behavior influences the numbers (i.e., catch rate) among these two traits and quality may not strictly be total numbers of fish harvested or total yield (i.e., size × catch of harvested fish only) but instead some combination of catch of harvested fish and catch of released fish, which added value in terms of fishing quality but only ~10% compared to harvested fish. This 10% value of released fish is lower than the 16% value estimated in Askey et al. (2013). However, the 16% value was estimated from a southern BC region of lakes where the angler population releases more fish, thus biasing value upwards (Ward et al. 2013a). Certainly, released fish appear less valuable than kept fish, as even specialist anglers harvest more frequently than previously believed (Beardmore et al. 2011), but how this translates to a specific estimate for released fish value remains uncertain. Stated preference surveys of BC rainbow trout anglers indicate a strong, positive relationship between social utility and fish harvest; for example, relative utility decreases by 50% when anglers must release all fish compared to when anglers can harvest at least five fish per trip, which occurred on 59 of 62 lakes in this study (Dabrowska et al. 2012). Adding anglers' value for released fish into fishing quality modified the effective capture rate and suggested that the rate that anglers maximize depends upon angler preferences for certain types of the resource. Without accounting for how anglers modified their perception of catch rates based on the value of released fish compared to harvested fish, the catch rate of anglers would overestimate patch quality (i.e., anglers' utility) for individual patches (Askey et al. 2013). When assuming a utility-maximizing tactic, both predator behavior and the preys' size–numbers trade-off need to be accounted for to determine patch quality and, ultimately, the predators' distribution patterns among the patchy prey landscape. Specific to recreational fisheries, Hunt et al. (2013) suggests that anglers may not adhere to maximization tactics to determine effort across many fishing sites, but instead anglers may seek to satisfy their well-being (i.e., improvements to fishing quality have diminishing returns to angler well-being), although the extent of this remains undetermined. Regardless, the strong landscape-level pattern shown here suggests that, though anglers may or may not maximize individual utility among the landscape (in the maximize vs. satisfy debate; Hunt et al. 2013), the aggregate behavior of the entire population of anglers in the fishing landscape does appear to maximize utility based on quality.

Fishing quality varied significantly among British Columbia's fishing landscape, and the average size and catch rates of fish were both higher in the north than the south. This suggests that estimating the numerical response of anglers across landscapes (e.g., Hunt et al. 2011, Allen et al. 2013) should include both ecological and social factors in order to capture regional differences in fishing quality among spatially structured fisheries, as a particular catch rate and average fish size may be perceived as high quality in one region but low quality in another. Currently, most models base fishing quality upon total vulnerable biomass, harvestable biomass, or total yield which has size-dependent characteristics but does not allow anglers' perception of quality to vary between subpopulations of anglers across regions. These results indicated that, at the scale of the province of British Columbia, the variation in fishing quality among lakes does not conform to the expected outcome of a single, province-wide ideal free-distribution of angler effort. Instead, there appears to be at least two IFDs co-occurring in BC's rainbow trout fishery, one for the northern management regions and another for the southern management regions.

The size–numbers isopleths for fishing quality presented here improves upon Askey et al. (2013) and can be incorporated relatively straightforwardly into fisheries' ecology models. Such an approach can be used to manage multi-stock fisheries based upon fishing quality and, ultimately, predict patterns in fishing effort and the dynamic responses between fish demography and effort across inland landscapes. Fisheries managers that utilize dynamic-effort modeling will have to evaluate how best to manage fishing quality to attract effort at the appropriate spatial scale at which fish–angler interactions influence fishing quality. Due to density dependent ecological processes affecting the fish population, no particular management strategy can optimize both catch rates and fish size for any individual patch. The equal-quality isopleths shown here highlight how social factors can partly determine the types of fisheries (e.g., trophy vs. harvest fishery) that can emerge across regions. For example, if anglers in BC's northern management regions tended to prefer larger fish for catch and release, then management strategies (e.g., increasing stocking rates) that aim to promote increased catch rates and harvest, which leads to smaller fish on average, may be counterproductive. As a fishery tips toward one direction vs. another (i.e., numerous small fish), managers may end up inadvertently reducing participation at that lake for certain types of anglers in favor of another angler group (Arlinghaus et al. 2013, Hunt et al. 2013). The isopleths also demonstrate that anglers within regions respond differently to changes in quality to create fishing landscapes that would appear to be scale-dependent responses (i.e., province-wide compared to region-wide). Askey et al. (2013) supported an assertion common to other landscape-level predator–prey studies that anglers respond to fishing quality in different patches across spatial-scales (i.e., the landscape). However, the different isopleths from cross-regional analyses indicate that the effective landscape to which anglers respond occurs at an intermediate spatial scale that is larger than individual management regions but smaller than the provincial scale (Fig. 2).

Fishing quality has long been viewed as a key connection between the biological aspects to fished populations and fishing pressure. Understanding fishing quality is an important tool for fisheries managers, as estimating quality helps to understand patterns of overfishing in inland and other spatially structured fisheries (Post et al. 2002, Allan et al. 2005, Hunt et al. 2011). However, quality has often been informally characterized as simply total yield, harvestable biomass, or numbers of vulnerable fish. Here, we formally characterized the dynamic, biological components of fishing quality. The relative importance of catch-based (e.g., fish size) vs. non-catch (e.g., travel distance; Morey et al. 1993, Parsons and Kealy 1994, Hunt 2005) characteristics of quality in predicting angling effort remain variable and uncertain (Hunt 2005, Post et al. 2008, Dabrowska et al. 2014). Nonetheless, fisheries biologists now have a formal structure to quantify a key intermediate step between the biological processes affecting the supply of fish and the human dimensions affecting the demand and behavior from anglers. This novel, landscape-level characterization of patch quality showed that the aggregate responses of predators, including recreational anglers, structure a trade-off between prey size and numbers that emerges due to density dependent growth and survival interacting with total consumptive pressure and consumer behaviors that all vary among the landscape. These findings continue to support the view that mobile angler–fish interactions occur within a hierarchical patch structure (Sanchirico and Wilen 1999, Carpenter and Brock 2004), similar to other mobile predator–prey dynamics (e.g., Fauchald 1999), that ultimately structures the landscape-level distribution of the anglers and the size–numbers trade-off in fish populations.

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