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RESEARCH ARTICLE

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Social–ecological feedbacks drive spatial exploitation in a northern freshwater fishery: A halo of depletion

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Abstract

1. Freshwater fisheries are complex social–ecological systems spatially structured by coupled feedbacks between people and nature. Spatial exploitation dynamics depend on angler preferences for multiple attributes that influence their site choices. Anglers then reciprocally impact local fish populations through size-selective catch and harvest. Thus, feedbacks among angler site choices, their capture efficiency (i.e. catchability) and fish population dynamics permeate through whole landscapes.
2. We studied the coupled feedbacks and effects of spatial exploitation in an iconic northern freshwater fishery of conservation concern. Specifically, we evaluated several coupled feedbacks in the spatially structured Yukon lake trout fishery using a Bayesian multinomial choice model fitted to onsite interviews and fishery-independent population assessments to identify whether: (a) trip context (day vs. multi-day trips) shaped angler preferences and site choices, (b) catch-based quality was influenced by a size–numbers trade-off and density-dependent catchability and (c) fish population structure was associated with the gravity of resource usage resulting from spatial exploitation.
3. Overall, we found that angler site choices were shaped by preferences for multiple characteristics including travel time and catch-based quality. Angler preferences also varied with trip contexts—for example, anglers on day trips were less willing to travel than anglers on multi-day trips. We detected strong density-dependent catchability, which led to hyperstable catches and relatively few anglers dominated most of the catch.
4. There was a strong demographic trade-off between lake trout body size and abundance that appeared to dynamically interact with anglers' size-selective preferences for larger lake trout. Coupled feedbacks among angler site choices, size-selective and hyperstable catches, and density-dependent growth and survival appeared to structure spatial exploitation patterns leading to a halo of depletion in fish body sizes and fishing quality near urban centres.
5. *Synthesis and applications*. Feedbacks between fish and anglers affected spatial exploitation patterns leading to a halo of depletion in Yukon lake trout. We recommend

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fisheries' managers consider the size, distance and behaviours of nearby angler communities using measures of gravity to craft policies aligning expected resource usage with spatial conservation risks. Such approaches may help managers balance stakeholder needs with conservation targets across whole ecosystems.

KEYWORDS
angler behaviour, bioeconomics, recreational fisheries, *Salvelinus namaycush*, site choice, size-selective harvest, social–ecological systems

1 | INTRODUCTION

Social–ecological system dynamics emerge from coupled feedbacks between people and nature (Arlinghaus et al., 2017; Levin et al., 2013; Ward et al., 2016). These feedbacks often result from bio-economic behaviours: consumers weigh costs against benefits to maximize their net currency when choosing where to exploit a heterogeneous set of resources (ecological fitness—Orians & Pearson, 1979; socio-economic utility—Train, 2009). Both social and ecological theory suggest that compensatory feedbacks within a system (e.g. price-setting or density-dependence) alter site characteristics, thereby shaping subsequent consumer choices and whole-system dynamics (Arlinghaus et al., 2017; Carpenter & Brock, 2004; Levin et al., 2013). Understanding what drives consumer behaviour helps to identify the impacts of spatial exploitation on ecosystem outcomes, and to develop best practices for balancing stakeholder needs with conservation (Sanchirico & Wilen, 1999; van Poorten & Camp, 2019).

Recreational fisheries are example of social–ecological systems where spatial exploitation jointly affects human well-being and aquatic conservation (Arlinghaus et al., 2017, 2019). Recreational fisheries are often spatially structured—a landscape of waterbodies offers diverse fishing opportunities shaped by catch and non-catch characteristics. Fishers of that landscape, in our case anglers, can vary in preferences and skill that may change with trip contexts (Dabrowska, Hunt, & Haider, 2017; Hunt, Camp, van Poorten, & Arlinghaus, 2019). Because anglers directly impact fish populations through catch and harvest (Lewin, Arlinghaus, & Mehner, 2006), their aggregate choices feedback through the system to structure macroscale outcomes and fishery resilience (Carruthers et al., 2018; Kaemingk, Chizinski, Hurley, & Pope, 2018; Matsumura, Beardmore, Haider, Dieckmann, & Arlinghaus, 2019). These behavioural feedbacks structure entire landscapes by prompting density-dependent responses (e.g. growth, survival and catchability) that regulate the catch-based fishing quality shaping angler choices in the first place (Wilson et al., 2016).

Travel costs constrain consumer choices, including those of recreational anglers, and consumers often return to central origins after trips (natural foragers—Boyd et al., 2017; Orians & Pearson, 1979; outdoor recreationalists—Freund & Wilson, 1974; McConnell & Strand, 1981). The spatial range of sites considered by centrally placed consumers is associated with the relative weight of a site's expected benefits against travel costs. Central-place models commonly predict that consumers expand their selection to include low-ranked sites when high-ranked sites are scarce and contract their selection when high-ranked sites are abundant (Carpenter & Brock, 2004; Orians & Pearson, 1979). The balance between costs and benefits drives an expanding and contracting halo of exploitation around consumers' central origin observed in both social (Winterhalder, 2001) and ecological systems (Boyd et al., 2017). For example, colonial birds prefer foraging in patches closest to local colonies over distant patches but expand their ranges to include distant patches upon local depletions (Ashmole, 1963; Storer, 1952). The social–ecological model in Carpenter and Brock (2004) predicts similar dynamics in a lake district: anglers select local lakes first (minimizing travel costs) and choose more distant lakes once the benefits of fishing distant lakes outweigh travel costs. This leads to sequential population collapses that 'resemble the collapse of a line of dominoes' as the halo of exploitation expands (Carpenter & Brock, 2004). The halo contracts once local fisheries recover, or distant patches are depleted. Such processes are associated with fishery collapses globally (Cinner et al., 2018; Keppeler et al., 2018; Letessier et al., 2019; Post et al., 2002).

Understanding behavioural feedbacks between fish and anglers can help to predict effort dynamics and advise spatial management (Camp, Ahrens, Crandall, & Lorenzen, 2018; Carruthers et al., 2018; Matsumura et al., 2019). These feedbacks are influenced by angler preferences that depend on biotic and abiotic characteristics and trip contexts (Beardmore, Haider, Hunt, & Arlinghaus, 2011; Chizinski, Martin, Shizuka, & Pope, 2018; Hunt, 2005; Hunt et al., 2019). For example, anglers on multi-day trips may be willing to travel further for better fishing than anglers on day trips. We were interested in understanding these coupled feedbacks in the Yukon lake trout *Salvelinus namaycush* fishery where management is currently challenged with balancing angler well-being and lake trout conservation (Environment Yukon, 2010). The fishery is spatially structured: lakes are patchily distributed, watershed connectivity is low, fish production tracks landscape clines and the regional road network connects major towns to most freshwater lakes (Wilson, De Gisi, Cahill, Barker, & Post, 2019). Additionally, the fisher community is composed of both resident and tourism anglers that may vary in their preferences, behaviour and trip contexts. We assessed several coupled social–ecological feedbacks using a Bayesian multinomial choice model and nonlinear size–numbers trade-off to jointly estimate the revealed preferences of 2,250 interviewed lake trout anglers across 34 lake-years and fish population structure across 99 lakes (Table S1). Our specific objectives were to determine: (a) angler capture efficiency and fishing impacts on lake trout populations, (b) angler preferences for site characteristics and whether preferences varied with trip contexts and (c) whether areas of higher fishing pressure led to a halo-like effect of depleted fish populations. We then discuss these findings in the context of spatial exploitation theory and fisheries management, particularly for lake trout conservation.

2 | MATERIALS AND METHODS

2.1 | Study design, data and site characteristics

Lake trout are among the few native game fishes accessible year-round in northern North American freshwaters with a long-lived life history sensitive to overfishing (Shuter, Jones, Korver, & Lester, 1998; Wilson et al., 2019). Sustainable lake trout fishing poses 'the greatest fisheries management challenge' to the Yukon government with dozens of populations managed under conservation or special concern regulations caused by overfishing (Environment Yukon, 2010). The Yukon government adopted creel survey methodology developed by the Ontario Ministry of Natural Resources (Lester & Trippel, 1985) and conducted 3,674 angler interviews (Box S1) across 37 lake-years in Yukon from 2005 to 2017 to understand angler behaviour (Figure 1). Sampled lakes were chosen non-randomly as places of conservation concern. Field workers interviewed all willing anglers with standardized questionnaires regarding their trip experience, including time spent fishing, fishing gear, originating location, trip type (e.g. day or multi-day, tourist), targeted species, and number of fish caught and released (Box S1). All interviews occurred at angler access points (e.g. boat launch) after completed trips. Survey timing depended on season and began at ice out and ended in early fall. Field workers sampled ≥20% of the season's total days (stratified for weekends) with interviews occurring 14 hr each day (08.00–22.00 hr).

We subset interviews based on fish species targeted (or caught) and whether anglers' originating town was known. Of the 3,674 interviews, 2,250 anglers sought or caught lake trout on 34 of the 37 lake-years (Table S2). We included 115 anglers (of 2,250 total) that caught but were not seeking lake trout as these anglers expressed no species preference and fished similar to lake trout anglers on popular lakes (Tarfu or Snafu lakes). Local origin was known for 1,885 interviewed anglers and the minimum distance travelled on the regional road network was calculated between the coordinates of the lake access point (typically a boat launch) and the downtown coordinates of their stated originating town (Figure 1; Table S3). We estimated one-way travel times (our metric for travel cost) for each trip with known origin by assuming anglers travelled at the legal speed limit to a lake's closest point of access, often a boat launch parking lot; larger lakes had multiple access points. We created a regional road network for Yukon and British Columbia to calculate least-cost travel times between all pairwise combinations of lakes and regional towns using ArcGIS (ESRI, 2017).

Each lake and trip were described by a set of environmental characteristics (e.g. travel times, presence/absence of campgrounds or lodges) hypothesized to influence angler utility (Table S1; Hunt, 2005; Hunt et al., 2019). Annual population assessments conducted after interview seasons measured relative population abundance (gillnet catch per unit effort [CPUE]) and expected size of catch (mean fork length in mm). We measured trophy-sized fish occurrence as the reporting of any fish ≥650 mm caught since 2005. Abiotic site characteristics included travel time, lake area (ha), angler congestion (i.e. crowding; rod hours·day^{-1}·ha^{-1}), fishing lodge and the presence of a campground that could accommodate recreational vehicles.

2.2 | Catch and catchability

We estimated anglers' capture efficiency (i.e. catchability) and their expected total catch per trip to understand impacts from fishing. We calculated catchability for each lake-year for the subset of lakes that were sampled by SPIN gillnetting (Table S1) by calculating population densities from gillnet CPUE following Sandstrom and Lester (2009). We described area-specific catchability (ha/hr) of an average angler using the following form:

$$q_j = \frac{\mathrm{CPUE}_j}{D_j} \quad (1)$$

with angler catch per unit effort (CPUE) described as:

$$\mathrm{CPUE}_j = \frac{\sum_t^T C_{jt}}{\sum_t^T E_{jt}} \quad (2)$$

with C_{jt} as the total catch for trip t among T total angler trips of lake j and E_{jt} as total rod hours. We used the Akaike information criterion (AIC) to test between two forms of catchability: (a) constant density-independent and (b) negative density-dependent (i.e. higher densities reducing angler efficiency). Density-dependent catchability was estimated following Shuter et al. (1998):

$$\hat{q}_j = \frac{a}{1 + bD_j} \quad (3)$$

Both models were fitted to catchability data (Equation 1) by minimizing the sum-of-squared errors using the *port* algorithm in the *nls* function in R (R Core Team, 2017). We excluded guided trips because they were uncommon and likely did not reflect anglers' typical catchability (Table 1). Catchability estimates were compared when including and excluding data from high-density and small-bodied lake trout populations (associated with the absence of suitable prey species, e.g. *Coregonus* spp.) because these populations may vary in foraging behaviour.

Anglers' average expected total catch per trip $\overline{C_{jt}}$ was estimated as:

$$\overline{C_{jt}} = \hat{q}_j E_{jt} D_j \quad (4)$$

with the form of $\hat{q}$ (i.e. constant or density-dependent) depending on the AIC-selected model from above. While a few angler trips dominated

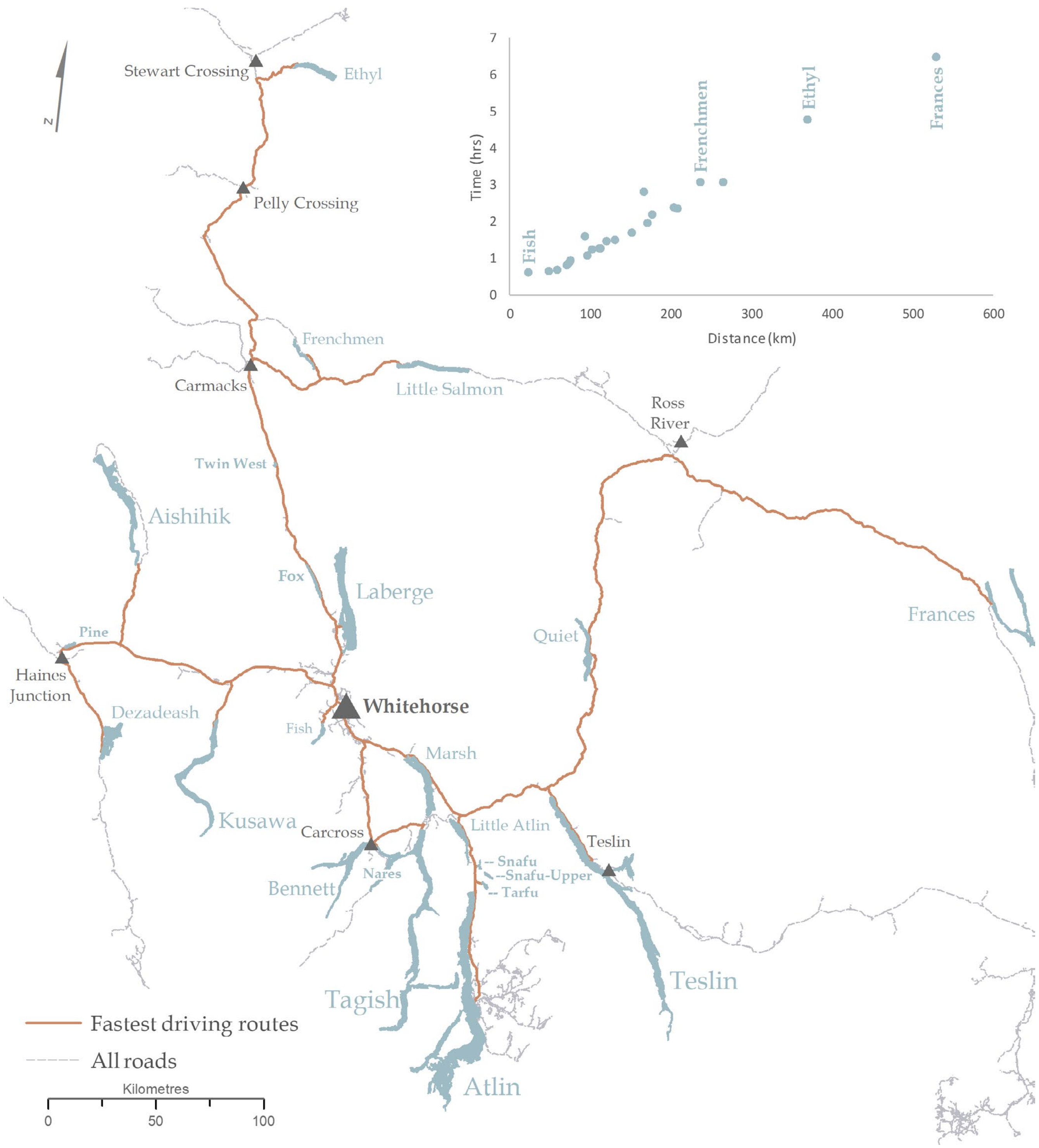

FIGURE 1 Yukon lake trout fishery and regional road network. Inset shows travel times between Whitehorse and all sampled lakes. Size of lake names (blue text) proportional to lake area (ha). Size of town names (black text and triangles) proportional to town population size

the catch (1.8% of trips caught ≥10 fish), most trips (52%) caught zero fish. We tested for alternative distributions explaining observed catches C_{jt} from trips during SPIN sampled lake-years (N = 1,937) by comparing average catches $\overline{C_{jt}}$ estimated from a Poisson, negative binomial, zero-inflated Poisson or zero-inflated negative binomial model. We then used AIC to select the best-fitting distribution and compared observed and predicted catch distributions from 1,000 bootstrap samples.

2.3 | Size–numbers trade-off

We modelled fishing quality using equal-quality isopleths to account for trade-offs between fish body size and abundance (Wilson et al., 2016). This approach assumes that (a) a common response to density-dependent growth and survival regulates lake trout populations (Wilson et al., 2019) and (b) anglers

TABLE 1 Number of anglers interviewed by trip context, resident status and guided activity with proportion of trips catching at least one lake trout in parentheses

	Urban		Rural		Tourist		
Context	Unguided	Guided	Unguided	Guided	Unguided	Guided	Total
Day	675 (0.44)	4 (1.0)	442 (0.40)	8 (0.88)	101 (0.44)	8 (0.63)	1,238 (0.43)
Multi-day	677 (0.58)	4 (0.75)	91 (0.65)	4 (0.75)	216 (0.63)	20 (1.0)	1,012 (0.61)
Total	1,352 (0.51)	8 (0.88)	533 (0.44)	12 (0.83)	317 (0.57)	28 (0.89)	2,250 (0.51)

may be simultaneously attracted to fish size and perceived abundance. However, onsite interviews lacked information on fish size, and there were far more populations surveyed with standardized gillnetting (N = 99) than with creel (N = 23). We assumed relative abundance from standardized gillnetting approximated true fish densities $D \approx \text{CPUE}_{\text{GN}}$ and estimated anglers' relative effective catch rates eCPUE_j by multiplying CPUE_{GN} by area-specific catchability for lake j:

$$\text{eCPUE}_j = \hat{q}_j \text{CPUE}_{\text{GN}_j} \approx \hat{q}_j D_j \quad (5)$$

We then modelled the size–numbers trade-off that standardized eCPUE_j by length with a negative exponential model:

$$\text{eCPUE}\,(L)_j = \alpha\,(L_j - L_q)^{-\beta} \quad (6)$$

where L_j is the average lake trout fork length (cm), L_q is the minimum size of a quality fish, and α and β are shape parameters.

Given that exploitation impacts fish densities and fish size through reducing competitors or size-selective harvest, quality may also change in either direction (see Wilson et al., 2016). We defined fishing quality Q_{cj} as the average distance between a lake's demography and the equal-quality isopleth, combining both numbers (vertical) and size (horizontal) directions. Quality in the vertical direction (i.e. catch rate) Q_{vj} followed:

$$Q_{vj} = \frac{\text{eCPUE}_j}{\text{eCPUE}\,(L_j - L_q)} \quad (7)$$

where eCPUE_j is the effective catch rate, and $\text{eCPUE}\,(L_j - L_q)$ is that population's catch rate conditioned on size. Quality measured in the horizontal direction (i.e. size) Q_{hj} followed:

$$Q_{hj} = \left(\frac{L_j - L_q}{e^{(\ln(\alpha) - \ln(\text{eCPUE}_j))/\beta}} \right) \quad (8)$$

where $e^{(\ln(\alpha) - \ln(\text{eCPUE}_j))/\beta}$ is the average fish size conditioned on catch rate. Fishing quality became bivariate by combining the weighted average of the Equations 7 and 8 relative to the slope (β) of the log-transformed Equation 3 and solve for the log of α:

$$Q_{cj} = Q_{vj} \left(\frac{Q_{vj}}{Q_{vj} + Q_{hj}} \right) + Q_{hj} \left(\frac{Q_{hj}}{Q_{vj} + Q_{hj}} \right) \quad (9)$$

where Q_{cj} reflects the weighted sum of catch rate (Q_{vj}) and size (Q_{hj}). Assuming a common response in density-dependent growth and survival across lake trout populations (Wilson et al., 2019) and an ideal free distribution of angling effort (Wilson et al., 2016), we expected combined fishing quality to equilibrate at 1.0 and estimated the shape parameters (α, β and L_q) by modelling the residuals $(1.0 - Q_{cj})^2$ within a log-normal likelihood in the integrated Bayesian model.

2.4 | Choice model

We modelled the angler site choice process using a multinomial-logit model consistent with utility theory (Train, 2009). Utility theory assumes anglers choose fishing sites among a set of sites that maximizes their utility (e.g. well-being or satisfaction). This utility arises from interactions between anglers' preferences for site characteristics and the provisioning of those characteristics among the set of sites. Because neither utility nor the choice process was directly observable, we described utility via a probabilistic choice model assuming angler utility was estimable through their revealed choices.

In our choice model, utility u for an angler on trip t considering site j is composed of observable deterministic utility v and random unobservable utility ϵ such that:

$$u_{jt} = v_{jt} + \epsilon_{jt} \quad (10)$$

Deterministic utility is then composed of characteristics hypothesized to influence angler choices:

$$v_{jt} = \beta x_{jt} \quad (11)$$

where β is a vector of coefficients for the set of characteristics x. Assuming errors ϵ_{jt} are *iid*, the probability of an angler choosing site j from a set of J becomes the conditional multinomial-logit:

$$P_{jt} = \frac{e^{v_{jt}}}{\sum_j^J e^{v_{jt}}} \quad (12)$$

Estimating angler utility from onsite interviews can be endogenously biased from choice-based sampling (Hindsley, Landry, & Gentner, 2011; Kuriyama, Hilger, & Hanemann, 2013). We addressed this using a weighted likelihood that adjusted angler choices by strata thought to reflect biases in the lake-sampling process. We presumed pure choice-based sampling and ignored avidity bias because the seasonal duration of sampling likely interviewed both avid and occasional anglers (25%–30% of the summer season days were each sampled for ≥14 hr). The weight $w_s(j)$ for lake j was:

$$w_s(j) = \frac{F_s(j)}{H_s(j)} \tag{13}$$

where $F_s(j)$ and $H_s(j)$ are the frequency of strata s among all Yukon lakes and sampled lakes respectively (Hindsley et al., 2011; Kuriyama et al., 2013). Strata were defined by categorizing lakes as: (a) greater than versus lesser than a 2-hr one-way trip from Whitehorse (the major urban centre in the region; Figure 1), (b) managed under general versus stringent regulations and (c) small versus large lakes (surface area >1,000 ha). Our expectation was that large lakes with stringent regulations (implying fishery or conservation concerns) close to the predominant source of harvest (Whitehorse) would be sampled more frequently when compared to small lakes with general regulations (implying less cause for concern) far from Whitehorse (Figure S1). Thus, these lakes should be weighted differently in the choice model than they were represented in the creel interviews such that:

$$P_{jt} = \frac{e^{v_{jt}} w_s(j)}{\sum_j^J e^{v_{jt}} w_s(j)} \tag{14}$$

As the multinomial-logit reduces to the Poisson distribution, weighting on $e^{v_{jt}}$ becomes equivalent to weighting the expected counts of a Poisson process (Kuriyama et al., 2013).

Trip context can alter angler preferences (Dabrowska et al., 2017; Hunt et al., 2019). To account for this, coefficients in the design matrix of the multinomial-logit regression were allowed to vary by angler t on trip type k such that:

$$v_{jt} = \beta_{k_t} x_{jt} \tag{15}$$

where k indicates a day or a multi-day trip. We considered the same set of characteristics for both trip types including: (a) travel time for an angler on trip t to site j; (b) trophy fish presence; (c) presence of lodges; (d) presence of campground; (e) lake area; (f) fishing quality; and (h) bag limit regulation. All covariates had variance inflation factors ≤4.0 suggesting no problematic collinearity between site characteristics (Zuur, Ieno, & Elphick, 2009). As trip contexts may alter angler preferences for catch-based quality (e.g. day-trip anglers may prefer many fish while multi-day anglers prefer large fish), we allowed the measure of fishing quality in Equation 15 to vary with trip type t following a categorical choice:

$$Q_{jt} = \begin{cases} Q_{vjt} | y_t = 1 \\ Q_{hjt} | y_t = 2 \\ Q_{cjt} | y_t = 3 \end{cases} \tag{16}$$

$$y_t \sim \text{categorical}\left(\frac{\pi_{nt}}{\sum_{n=1}^{3} \pi_{nt}}\right) \tag{17}$$

where variable $y_t = 1$ indicates fishing quality in CPUE, $y_t = 2$ indicates quality in fish body size and $y_t = 3$ indicates quality in both CPUE and body size with each given equal prior probability $\pi_t = \frac{1}{3}$. We excluded year-effects in the choice model because most temporal variations in angler choices were explained by variable site characteristics (e.g. regulation changes) and not year-effects (Figure S2). To show preferences on a common scale, we portrayed the above β coefficients as anglers' willingness to travel (WTT, in hr) for an increase in a characteristic following:

$$\text{WTT}_{Xk} = \frac{\beta_{Xk} x - \beta_{Xk} x^*}{-\beta_{TTk}} \tag{18}$$

where β_{Xk} is the preference an angler on trip type k has for the characteristic X (e.g. fishing quality), x is the value of that characteristic, x^* is the baseline value and $-\beta_{TTk}$ is the travel time coefficient. The negative sign in the denominator was done for interpretability such that positive WTT_{Xk} indicates that the anglers were willing to travel longer for increases in X, and a negative WTT_{Xk} indicates that the anglers were unwilling. We used a baseline of 1.0 for angler preference for fishing quality (i.e. IFD equilibrium) and 0 for all other characteristics.

We assessed whether spatial exploitation and the gravity of fishing pressure (a measure of potential resource use as function of the size and distance of the nearby angler population) influenced a halo-like effect on fish population structure by fitting a GLM between gravity and mean body size, catch rates and fishing quality. Gravity G was defined as the number of potential anglers expected to visit lake j among J lakes (i.e. the 47 of 99 lakes with both standardized gillnetting and road access):

$$G_j = \sum_k^K \sum_m^M p_R N_{A_m} p_{km} \frac{e^{\beta_{TT_k} d_{mj}}}{\sum_j^J e^{\beta_{TT_k} d_{mj}}} \tag{19}$$

where p_R is the proportion of trips made by residents (rather than tourists), N_{A_m} the number of resident anglers from town m, k is trip context (day vs. multi-day), p_{km} the proportion of trips of trip type k for town m, d_{mj} the travel time between town m and site j, and β_{TT_k} the travel time coefficient for trip type k. The halo of depletion would be supported if the slope of these models were negative, suggesting that increased fishing pressure from nearby towns led to reduced fish body sizes, abundance and/or quality consistent with predictions from spatial exploitation theory.

2.5 | Statistical validation

We jointly estimated the choice model and the size–numbers trade-off in JAGS with four Markov chain Monte Carlo (MCMC) chains using *runjags* in R (Denwood, 2016; Plummer, 2003). Each chain took 2,000 posterior samples, thinning every three, with a burn-in period of 30% for 10,000 iterations total. Starting parameter values were jittered for each chain. We used several complementary methods to diagnose model suitability. MCMC chain convergence was inspected visually on traceplots. In addition, we ensured the posterior distribution for each parameter had low percent error relative to their *SD* (Gelman et al., 2013). We used the Gelman–Rubin diagnostic test on each parameter to determine whether independent chains converged to a common posterior mode, with potential scale reduction factors (PSRF) <1.1 suggesting convergence. We then used graphical posterior predictive checks to test for model misspecification by simulating random site choices for each posterior sample for each angler and comparing predicted to observed site choices.

3 | RESULTS

Interviewed lake trout anglers were typically residents of Yukon with relatively few tourist anglers and even fewer guided trips (Table 1). While 78% of all Yukon residents reside in Whitehorse, only 56% of anglers were from Whitehorse suggesting high rural participation. Day trips were slightly more common than multi-day trips (55% day vs. 45% multi-day trips) and the frequency of day trips was similar between urban and tourist anglers but not rural (Table 1; Table S3). On average, trips were composed of two people (range: 1–6) fishing for 3.3 hr (range: 0.1–24 hr) for an average of 5.05 rod hours·per trip. Anglers varied in their ability to catch lake trout—multi-day trips generally had higher success than day trips (61%–43% respectively). However, anglers on multi-day trips harvested similar portions of their catch as day trips (50% vs. 59% respectively) suggesting trip contexts did not modify harvest tendencies.

Angler catchability appeared strongly density-dependent and catches were hyperstable and overdispered (Figure 2; Tables 2 and 3). Both density-dependent models (this study and the model from Shuter et al., 1998) had strong support according to ΔAIC. Our best-fit model suggested slightly steeper density-dependent catchability in Yukon lake trout compared to Ontario lake trout (Figure 2). Including or excluding the limited data on small-bodied morphs led to similar estimates of the two shape parameters suggesting catchability did not change among lake trout morphs (Figure 2a,b; Table 2). Hyperstability caused angler CPUE to maximize at 0.28 fish per hour (Figure 2c). This low CPUE was compensated for by anglers fishing with more than one rod or fishing with another person. Angler catches were best described (according to ΔAIC) by an overdispersed negative binomial distribution (Table 3; Figure 2c). The negative binomial distribution adequately predicted the observed proportion of zero-catch trips (0.55 predicted to 0.52 observed), mean angler catch (1.48 fish·per trip predicted to 1.44 observed) and the upper 97.5th percentile in angler catch (8 fish·per trip predicted to 8 observed) suggesting a reasonable model fit. This suggests that, while most anglers often fail to catch fish, some anglers were able to maintain high catches despite low catchability (Figure 2c; Figure S3).

Overall, angler site choices were influenced by preferences for multiple site characteristics that changed with trip contexts (Figure 3; Table S4). Estimated model parameters passed all diagnostic and MCMC convergence checks (e.g. all PSRFs <1.1) with low percent error, and the posterior predictive distribution indicated reasonable model fit to observed site choices (R^2 = .50; Figure S4). Travel time had a strong

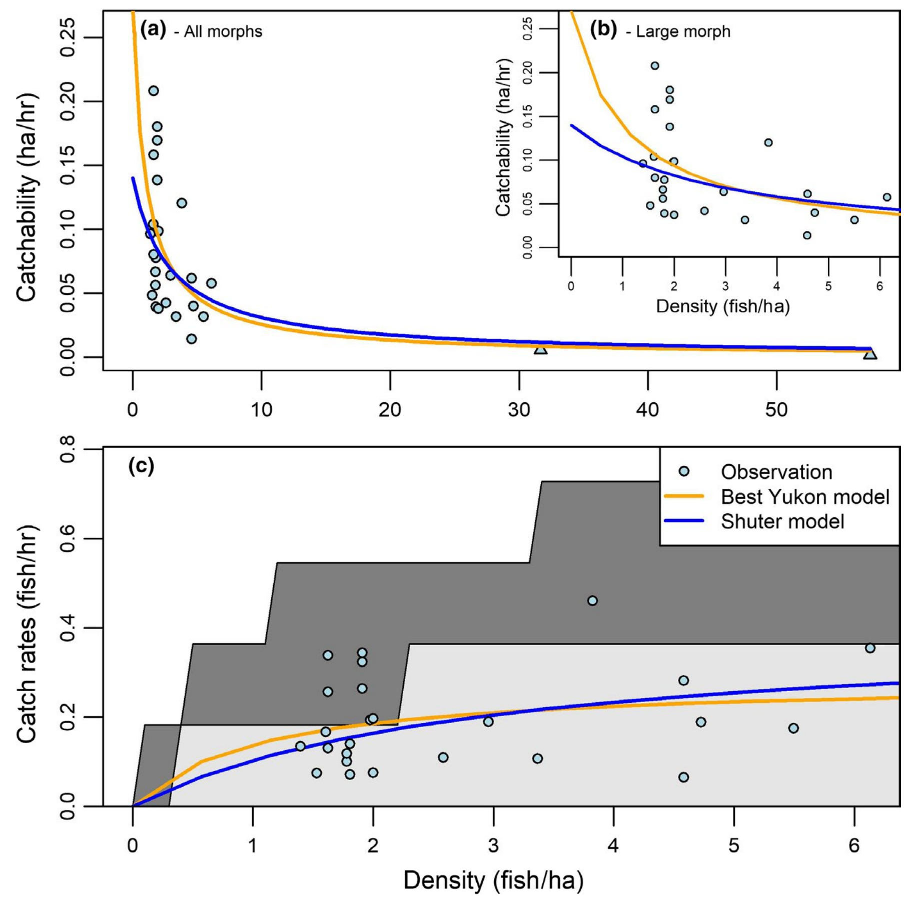

FIGURE 2 Angler catchability (a, b) and catch rates (c) along lake trout density gradients for large- and small-bodied populations (circles and triangles respectively). Best Yukon model selected from Akaike information criterion depended on inclusion (a) or exclusion (b) of small-bodied morphs. Catchability model from Shuter et al. (1998) taken from their figure 4b. Shaded regions in (c) depict interquartile and 80% interval (light and dark grey respectively) from best Yukon model

TABLE 2 Candidate models of area-specific angler catchability (q in ha/hr) using data that either excluded or included small-bodied morphs (lakes that lack suitable prey fish, e.g. *Coregonus* spp.). Models fitted by maximum likelihood (ML) and ranked by ΔAIC. The model from Shuter et al. (1998) taken from their figure 4b

Model	ML estimates	AIC	ΔAIC
Excluding small-bodied morphs (N = 25)			
Density-dependent	$q=\frac{0.27}{1+0.95D}$	−78.0181	0
Shuter et al. (1998)	$q=\frac{0.14}{1+0.35D}$	−76.4317	1.58642
Density-independent	$q=0.08488$	−73.917	4.10109
Including small-bodied morphs (N = 27)			
Density-dependent	$q=\frac{0.2728}{1+0.9656D}$	−86.8084	0
Shuter et al. (1998)	$q=\frac{0.14}{1+0.35D}$	−85.0732	1.7352
Density-independent	$q=0.07887$	−77.5843	9.22406

TABLE 3 Candidate models for distributions of angler catch per trip t in lake-year j fitted by maximum likelihood and ranked by ΔAIC. Distributions included negative binomial (*NB*), zero-inflated negative binomial (*ZINB*), zero-inflated Poisson (*ZIP*) and Poisson (*P*). Mean catch for each model is $\overline{C_{jt}}=\hat{q}_j E_t D_j$ where E_t is trip effort (rod hours), D_j is fish population density (ha^{-1}) and $\hat{q}_j$ (ha/hr) comes from selected model in Table 3. Note that $\frac{1}{\alpha}$ is the negative binomial dispersion parameter and ω is the zero-inflation parameter

Model	AIC	ΔAIC
$C_{jt} \sim NB\left(\mu=\overline{C_{jt}}, \alpha=1.68\right)$	5,756.198	0
$C_{jt} \sim ZINB\left(\mu=\overline{C_{jt}}, \alpha=1.68, \omega=2.88\text{e}-09\right)$	5,758.198	2
$C_{jt} \sim ZIP\left(\lambda=\overline{C_{jt}}, \omega=0.27\right)$	7,043.103	1,286.905
$C_{jt} \sim P\left(\lambda=\overline{C_{jt}}\right)$	7,585.476	1,829.278

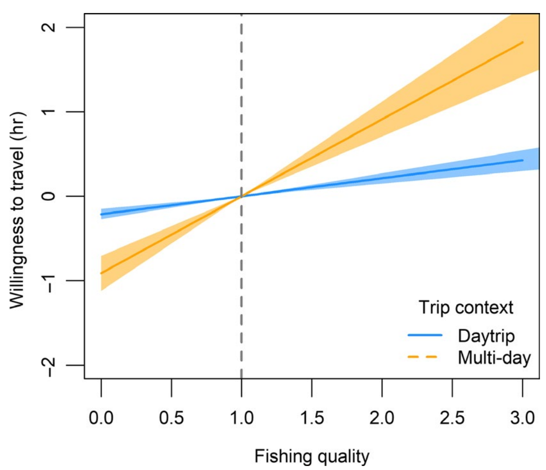

FIGURE 3 Angler willingness to travel for increased catch-based fishing quality (median and 95% highest posterior density interval in shaded region) across trip contexts. Vertical dashed line shows average fishing quality (1.0)

but varied effect—anglers on day trips were less willing to travel than multi-day trips (Table S4). However, angler preferences for fishing quality were similar between trip types. Both trip types had ≥99% of the posterior distribution favouring fishing quality in body size, rather than catch rates or combined, suggesting a strong preference for larger fish over more fish. This resulted in anglers on multi-day trips more willing to travel further for larger lake trout than anglers on day trips (Figure 3). Two cost–benefit trade-offs composed of multiple characteristics influenced spatial dynamics—one for each trip type. For simplicity, we portray these trade-offs by showing, all else equal, the marginal rate of anglers substituting travel time for fishing quality suggesting equal substitution for average fishing quality at 0.21 and 0.91 hr for day and multi-day trips respectively. Site choices were shaped by other characteristics that varied with contexts (Figure 4). For example, anglers on multi-day trips were willing to travel longer for campgrounds and/or lower crowding than anglers on day trips (Figure 4a,f).

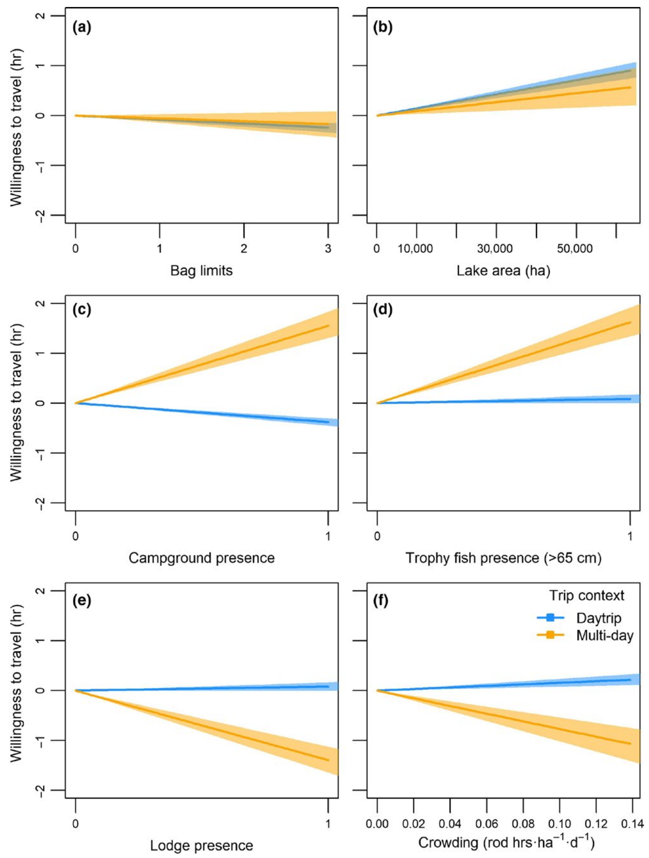

FIGURE 4 Angler willingness (a–f) to travel for multiple site attributes (median and 95% highest posterior density interval in shaded region) across trip contexts

Lake trout abundance and body size displayed a strong trade-off across Yukon populations (Figure 5). Posterior mean estimates of the shape parameters describing this trade-off were α = 22,025 (95% credible intervals [CI]: 21,960–22,085), β = 2.2 (95% CI: 2.14–2.22) and L_q = 197 mm (95% CI: 181–214 mm). Fork lengths of ≥197 mm represent lake trout body sizes that begin increasing angler utility. Results from the above choice model and Equation 5 imply the size–numbers trade-off was partly maintained by anglers' size-selective preferences and hyperstable catches.

We observed evidence for a halo of depletion in fishing quality and body size, but not catch rates, for lake trout populations near

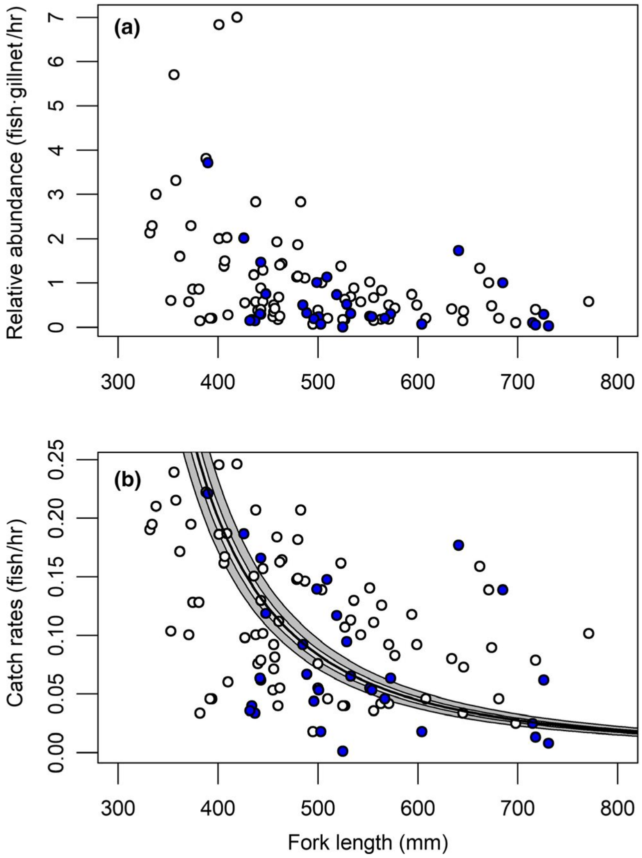

FIGURE 5 Fish population structure and the size–numbers trade-off for lake trout populations with (blue) and without (open) onsite angler interviews. Multiplying relative abundances from gillnet assessments (a) by angler catchability used to approximate angler catch rates (b). Black line shows posterior mean relationship describing trade-off with 75% and 95% credible intervals shown in light and dark grey respectively

high gravity (Figure 6). Consistent with spatial exploitation theory, the slope for body size (-1.51×10^{-4}, $p = .003$) and fishing quality (-4.41×10^{-4}, $p = .05$) were both negative suggesting that increased fishing pressure reduced lake trout body size and fishing quality. Furthermore, the average fishing quality for inaccessible and low gravity populations (1.36 and 1.24 respectively) were both above the landscape average for fishing quality (1.0) indicating low gravity led to higher fishing quality. Interestingly, catch rates increased with gravity (2.74×10^{-4}, $p = .02$) suggesting that feedbacks structuring the size–numbers trade-off compensated for reduced body sizes with increased catch rates. Increased gravity resulting from spatial exploitation appeared to filter lake trout population structure from their natural variation (see inaccessible populations in Figure 6) favouring small-bodied populations that eroded fishing quality.

4 | DISCUSSION

We examined several coupled feedbacks between fish and anglers thought to influence spatial exploitation dynamics in the Yukon lake trout fishery. Overall, we found that site choice was shaped by multiple attributes that varied with trip context, and that interactions between multiple social–ecological processes impacted fish population structure and, subsequently, angler site choices. For example, the trade-off between lake trout body size and catch rates appeared structured not by an IFD in fishing effort alone (Wilson et al., 2016), but by feedbacks between angler site preferences, size-selective harvest, density-dependent growth and survival favouring more fish over larger fish, and hyperstable catch rates maintained through density-dependent catchability. Although there were only limited snapshots, we argue our findings should be interpreted as temporally dynamic (e.g. Pitman et al., 2019). Our results agree with Hunt, Arlinghaus, Lester, and Kushneriuk (2011) and Matsumura et al. (2019) that the homogenization of fishing qualities across a landscape cannot be generalized as substantial variation in catch-based quality remains unexplained by an IFD in effort; however, quality may still oscillate around some equilibrium structured by the coupled feedbacks above. In our case, deviations from this equilibrium appeared associated with the gravity of resource usage. These findings help to understand angler site choice behaviour in this spatially structured fishery, allowing management to better assess the social and ecological consequences of alternative management tactics (Carpenter & Brock, 2004).

Many of our findings on angler preferences were intuitive and supported relationships found in other studies (Hunt, 2005; Hunt et al., 2019). Our study relied on anglers' travel time serving as a scarce resource because we lacked measures of total trip costs or willingness to pay, but the effect of travel time is not always linear nor directly related to leisure costs (Hunt et al., 2019). Nonetheless, travel times had strong negative effects on site choice consistent with findings across other fisheries (Camp et al., 2018; Curtis & Breen, 2017; Hunt et al., 2019). Some angler preferences varied with trip context, for example anglers on day trips fished closer to their origin than anglers on multi-day trips (Hunt et al., 2019). Anglers on both trip types expressed positive effects of increased fishing quality, lake area and trophy fish presence (Dabrowska et al., 2017; Kaemingk, Chizinski, Allen, & Pope, 2019). Some results were less intuitive, like how anglers on multi-day trips preferred less congestion than anglers on day trips (e.g. Pitman et al., 2019), while anglers on day trips had stronger preferences for lodges. Trip contexts can drive unusual variation in angler preferences (Beardmore et al., 2011; Dabrowska et al., 2017) with growing evidence of higher catch motivations (or lower cost constraints) for anglers on multi-day trips than anglers on day trips (Grilli, Landgraf, Curtis, & Hynes, 2018). Our findings that anglers on multi-day trips travelled further for increased fishing quality align with this hypothesis, although multi-day trips may aggregate preferences from multiple leisure activities (Deely, Hynes, & Curtis, 2019). Unlike Dabrowska et al. (2017), we found that anglers expressed no preference for increased bag limits possibly caused by anglers preferring larger, but not more, lake trout. Nonetheless, the high portion of multi-day trips (45% of all trips) echoes calls from Dabrowska et al. (2017) that understanding trip context is essential for managing sustainable fisheries as diverse anglers can have diverse impacts on fisheries. Given the high effort

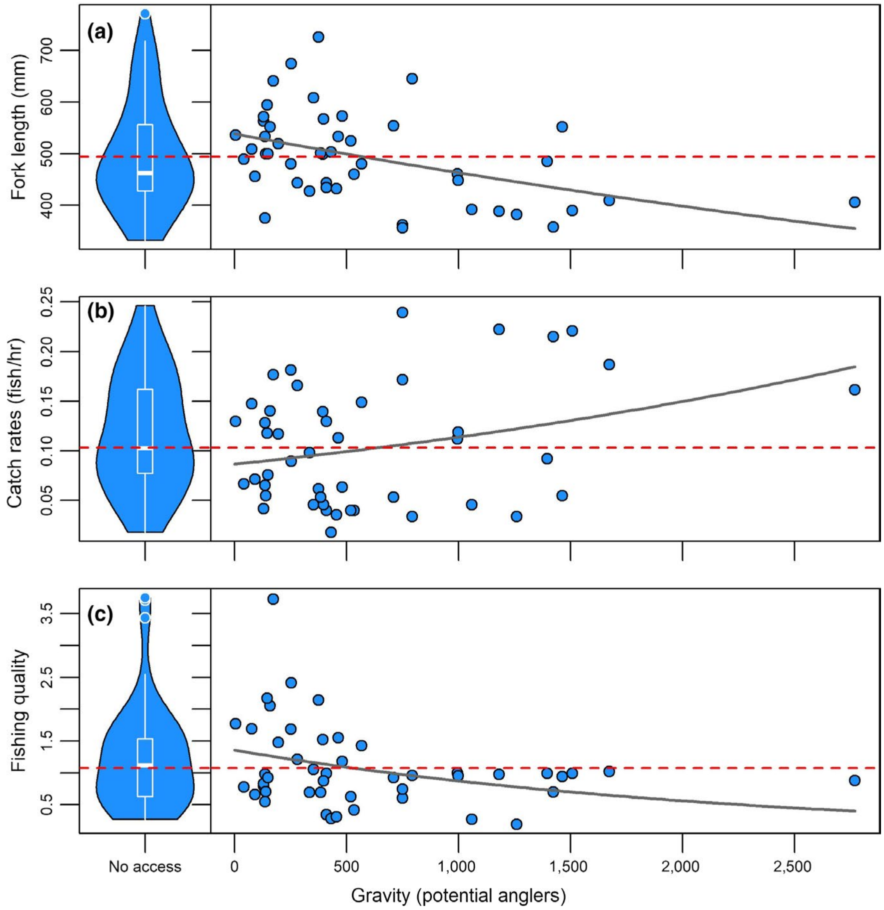

FIGURE 6 Fish population structure as measured by (a) fish body size, (b) angler catch rates and (c) the size–numbers trade-off along gradient of gravity (i.e. a measure of potential resource use as function of the size and distance of nearby angler populations) with inaccessible fish populations serving as baseline violin box plot. Red dash line indicates landscape average, grey line represents best-fit linear model to the data

from multi-day users in this fishery, some spatial impacts could go unnoticed if only one angler typology were managed for (Johnston, Arlinghaus, & Dieckmann, 2010; Post et al., 2002).

Some of our preference relationships, like crowding and lake area, may be inherently intertwined because revealed choice data can suffer from collinearity (Hunt, 2005; Schuhmann & Schwabe, 2004). Although none of our covariates suffered from statistical collinearity (Zuur et al., 2009), the spatial complexity of the landscape (i.e. anglers with multiple origins or destinations) or the nature of the study design may cause some unobservable collinearity between lake and trip characteristics (Schuhmann & Schwabe, 2004). For example, our measure of crowding was the average total fishing effort per day during the study period, which may not reflect the congestion realized on actual trips and may be endogenous to resource usage in the first place (Deyak & Smith, 1978). Our results should be contrasted with stated preferences (sensu Deely et al., 2019) to help tease apart these coupled processes and to reduce potential biases reflected in onsite sampling (Hindsley et al., 2011; Kuriyama et al., 2013). For example, British Columbia rainbow trout anglers stated that they preferred catch-based quality more than that was revealed during onsite interviews (Dabrowska et al., 2017; Mee et al., 2016). Stated preference or angler diaries would help to further understand angler heterogeneity (Beardmore et al., 2011; Ward et al., 2016; Ward, Quinn, & Post, 2013). Understanding this heterogeneity is important as diverse anglers impact fisheries in unique ways potentially meriting alternative regulations for sustainable management (Pitman et al., 2019). Interestingly, the widespread usage of only a few angling gears (trolling and still-fishing accounted for ~90% of total effort) suggests these impacts may be less variable than fisheries with more diverse angler communities (e.g. Ward, Quinn, et al., 2013). Nonetheless, our model serves as a useful starting point for understanding angler effort dynamics in Yukon's lake trout fishery with direct application to resource management.

Angler catch appeared hyperstable because of inverse density-dependent catchability. Our estimates of catchability were similar to that observed on lake trout populations in Ontario suggesting hyperstability may be ubiquitous in lake trout fisheries (Shuter et al., 1998). Hyperstability can arise from several processes including angler skill heterogeneity and effort sorting (van Poorten, Walters, & Ward, 2016; Ward, Askey, & Post, 2013). Due to hyperstability, angler CPUE maximized around 0.28 fish·per hour—similar to the range in CPUE observed in the Lake Opeongo lake trout fishery for trips ≥4 hr (Shuter, Matuszek, & Regier, 1987). We found that angler catches closely followed a negative binomial process with relatively few trips dominating most of the catch and many trips resulting in no catch. Angler catch is often assumed to arise from a Poisson process (McConnell, Strand, & Blake-Hedges, 1995), but skill heterogeneity and effort sorting can underestimate total catch arising from a Poisson process as a few skilled individuals can maintain high catch despite low fish densities (Ward, Quinn, et al., 2013). Studies on the catch success of individual anglers across environmental conditions would help to understand mechanisms for overdispersion and hyperstability.

Spatial exploitation led to reduced body sizes and fishing quality near higher sources of fishing pressure. These results are strikingly similar to predictions from foraging theory whereby spatial exploitation can lead to a halo of depleted prey patches near consumer origins (Ashmole, 1963; Storer, 1952). Reduced body sizes and fishing quality of local fisheries are also consistent with empirical observations (Cinner et al., 2018; Kaufman, Snucins, Gunn, & Selinger, 2009; Keppeler et al., 2018; Letessier et al., 2019; Post et al., 2002) and predictions from spatial exploitation models, like Carpenter and Brock (2004) and Matsumura et al. (2019), that show expanding–contracting effort patterns most affects local fisheries. The combination of anglers' imperfect knowledge, hyperstable catches and low willingness to substitute travel times for improvements in other site characteristics may deplete fisheries nearest large sources of gravity as anglers are unwilling (or unable) to track biotic changes in resource quality (Johnston et al., 2010; Matsumura et al., 2019; Post et al., 2002). In our study, both angler trip types had similar positive effects from increased quality suggesting the two equilibria mostly depended on anglers' willingness to travel. Identifying the spatial extent of anglers' willingness to travel from choice models and subsequent risks for exploitation halos can be used to guide spatial management (Camp et al., 2018; Freund & Wilson, 1974; Kaufman et al., 2009). For example, lake trout populations near high 'gravity' of fishing pressure (e.g. ≥1,000 potential anglers in Figure 6) could be managed with reduced fishing seasons, stringent length-limits or effort control compared to populations outside the halo. Such approaches may better balance stakeholder needs with conservation goals for ecosystem-based management (Carruthers et al., 2018; Matsumura et al., 2019).

Our findings are both intriguing and alarming for fisheries management. They are intriguing because trip context modified angler preferences to create two cost–benefit equilibria resulting in exploitation patterns strikingly similar to foraging halos (Ashmole, 1963; Orians & Pearson, 1979; Storer, 1952). Halos of depletion may occur more frequently in landscapes with strong asymmetry in resource gravity compared to symmetrical landscapes, where angler effort may more evenly distributed in space (Matsumura et al., 2019). Asymmetry may lead to spatial modularity resulting in uneven social–ecological feedbacks, and may be a key process promoting patterns in local collapses (Cinner et al., 2018; Matsumura et al., 2019; Sanchirico & Wilen, 1999). Determining angler site choice preferences can allow managers to explore alternative policies to improve broad-scale management (Carruthers et al., 2018; Post & Parkinson, 2012; van Poorten & Camp, 2019).

Our findings are also alarming because catch was hyperstable and angler preferences for dynamic characteristics, like fishing quality, were low relative to fixed characteristics like travel times (Mee et al., 2016). The spatial exploitation feedbacks resulting from interactions between cost–benefit dynamics and hyperstable angler catches are one of the key mechanisms weakening the self-regulation of spatially structured fisheries—often these mechanisms lead to fishery collapses across whole landscapes (Hunt et al., 2011; Post et al., 2002). We observed such a pattern here: Yukon lake trout averaged lower fishing quality and body sizes in lakes nearest Whitehorse, the largest source of fishing pressure. The importance of catch-based quality is often underestimated in motivation research, and comparisons between revealed and stated preferences would help management to ground-truth angler preferences and then explore how alternative policies may improve whole-system management (Arlinghaus, 2006; Beardmore et al., 2011). Awareness of angler preferences can also help to engage stakeholders by identifying potential mismatches between angler preferences and management goals. If catch importance is low, it can render the primary management tactics of recreational fisheries ineffective because bag or size limits can only indirectly influence angler effort or preferences. As freshwater recreational fisheries exhibit complex dynamics (Arlinghaus et al., 2017), variation in individual-level preferences, like catch importance, can have strong effects on regional overexploitation (Hunt et al., 2011). This highlights a need for more spatially based management and/or effort controls (Post & Parkinson, 2012) as fishery managers may be unlikely to find robust panaceas in their current toolbox (van Poorten & Camp, 2019).

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AUTHORS' CONTRIBUTIONS

K.L.W. led the project and designed the methodology. K.L.W. and J.R.P. conceived the ideas for the manuscript. A.F.[1], J.D.G. and O.E.B. led field data. A.F.[2] conducted spatial analyses. All authors wrote the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

All data and the JAGS model used for this manuscript are available via Zenodo https://doi.org/10.5281/zenodo.3401646 (Wilson, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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