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Empirical estimation of recreational exploitation of burbot, *Lota lota*, in the Wind River drainage of Wyoming using a multistate capture–recapture model

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Abstract

Burbot, *Lota lota* (Linnaeus), is a regionally popular sportfish in the Wind River drainage of Wyoming, USA, at the southern boundary of the range of the species. Recent declines in burbot abundances were hypothesised to be caused by overexploitation, entrainment in irrigation canals and habitat loss. This study addressed the overexploitation hypothesis using tagging data to generate reliable exploitation, abundance and density estimates from a multistate capture–recapture model that accounted for incomplete angler reporting and tag loss. Exploitation rate μ was variable among the study lakes and inversely correlated with density. Exploitation thresholds μ_{40} associated with population densities remaining above 40% of carrying capacity were generated to characterise risk of overharvest using exploitation and density estimates from tagging data and a logistic surplus-production model parameterised with data from other burbot populations. Bull Lake ($\mu = 0.06$, 95% CI: 0.03–0.11; $\mu_{40} = 0.18$) and Torrey Lake ($\mu = 0.02$, 95% CI: 0.00–0.11; $\mu_{40} = 0.18$) had a low risk of overfishing, Upper Dinwoody Lake had intermediate risk ($\mu = 0.08$, 95% CI: 0.02–0.32; $\mu_{40} = 0.18$) and Lower Dinwoody Lake had high risk ($\mu = 0.32$, 95% CI: 0.10–0.67; $\mu_{40} = 0.08$). These exploitation and density estimates can be used to guide sustainable management of the Wind River drainage recreational burbot fishery and inform management of other burbot fisheries elsewhere.

KEYWORDS

burbot, exploitation, multistate capture–recapture model, population density, recreational fishery, tagging

1 | INTRODUCTION

Burbot, *Lota lota* (Linnaeus), is the only freshwater member of the otherwise exclusively marine Gadidae. It inhabits a wide variety of freshwater Holarctic ecosystems because of variable life history strategies (Jude, Wang, Hensler & Janssen, 2013) and physiological adaptations (Holker, Volkmann, Wolter, Van Diik & Hardewig, 2004). As top predators, it is an indicator of freshwater ecosystem function and drivers of trophic interactions (Cott, Johnston & Gunn, 2011). Globally, many burbot populations are stable (Stapanian et al., 2010), but some are at critically low levels (Hardy & Paragamian, 2013) or extirpated (Krueger & Hubert, 1997; Worthington, Kemp, Osborne, Howes & Easton, 2010). Habitat alteration and pollution are the primary stressors on burbot populations (Stapanian et al., 2010), but overexploitation has caused reduced abundances (Ahrens & Korman, 2002; Bernard, Parker & Lafferty, 1993). Burbot exploited throughout most of its range, although its popularity as a sport fish varies considerably by geographic location (Quinn, 2000; Stapanian et al., 2010). Yet, the influence of exploitation on burbot populations is largely unknown because few stock assessments targeting burbot have been conducted (Stapanian et al., 2010).

The Wind River drainage of Wyoming is the south-western extent of the native range of burbot in North America. Burbot is an important cultural resource for the Eastern Shoshone and Northern Arapahoe tribes in the Wind River drainage and is commonly harvested by anglers (Hubert, Dufek, Deromedi & Johnson, 2008). Based on its popularity as a sport fish and its aggregative behaviour, researchers hypothesised that exploitation could reduce population densities below sustainable thresholds (Hubert et al., 2008). However, exploitation levels and population densities have not been measured. Therefore, tagging data were used to estimate exploitation and population density of burbot in the Wind River drainage, Wyoming.

Angler-reported tag-return data commonly are used to estimate exploitation rates but require information on angler reporting rates (Pollock, Hoenig, Hearn & Calingaert, 2001). Additionally, tag loss and reduced survival caused by tagging and handling can bias estimates. The multistate capture–recapture model framework is advantageous for estimating exploitation because both tag-return and live-recapture data can be used (Lebreton, Nichols, Barker, Pradel & Spendelow, 2009), and parameters for angler reporting and tag loss can be included in the model. Accordingly, a multistate capture–recapture model was developed that incorporated live-recapture, tag-return, tag-loss and angler reporting data to estimate burbot exploitation in the upper Wind River drainage.

Exploitation rates that could drive population density below conservation levels were predicted to be common given the fishing effort, especially during the winter, and because catchability was hypothesised to be high due to burbot aggregating behaviour during the winter spawning period (Hubert et al., 2008). This prediction was investigated by simulating burbot populations with density-dependent population growth and harvest using a logistic surplus-production model. The model was parameterised using data from other exploited burbot populations and population density and exploitation estimates from this study. Using this approach, the sustainability of current exploitation rates was explored and exploitation thresholds for burbot in the Wind River drainage were established.

2 | MATERIALS AND METHODS

2.1 | Study site and field methods

Burbot were sampled from six glacially formed lakes in the upper Wind River drainage (Figure 1). The Dinwoody lakes were modified by a low head dam at the outlet of the lower lake, and the construction of a large dam on Bull Lake in 1938 raised the water level at full pool by 15 m; water levels in Torrey, Ring and Trail lakes are unaltered (Hubert et al., 2008). The nearest human population centres (Dubois, Fort Washakie, and Lander) are small to moderate size (971–7,487 inhabitants), but anglers from outside the region also travel to the Wind River drainage to fish (Miller, 1970).

Burbot were sampled from September through November of 2011, 2012 and 2013. Random sampling was facilitated by dividing each lake into areas of approximately equal size using scaled maps with an overlaid grid. A random subset of the areas was selected during each sampling occasion, and a bottom-set trammel net was fished in each selected area. Trammel nets were 48.8-m long, 1.8-m deep and had outer panels of 25.4-cm bar mesh and inner panels of 2.5-cm bar mesh. Trammel nets were set in the morning and allowed to fish for 24 hr. A maximum sampling depth was set at 22.9 m to decrease the probability of injury to captured burbot because, as physoclistous fish, they are susceptible to barotrauma if forced to the surface from deep depths (Neufeld & Spence, 2004). A weighted wire basket was used to return burbot to the lake bottom after processing (Neufeld & Spence, 2004). In total, 2166 trammel nets were set during the three seasons of sampling. Bull Lake was sampled for 46 days (median sets/day = 22), Lower Dinwoody Lake was sampled for 39 days (median sets/day = 12), Upper Dinwoody Lake was sampled for 30 days (median sets/day = 10), Torrey Lake was sampled for 35 days (median sets/day = 10), Ring Lake was sampled for 10 days (median sets/day = 3), and Trail Lake was sampled for 23 days (median sets/day = 8).

Captured burbot were measured to the nearest millimetre total length and tagged. A Carlin tag (2.54 cm × 0.95 cm) was attached behind the anterior dorsal fin of each captured burbot > 389 mm not injured by the netting process. Standard tags were blaze orange and inscribed with the Montana Cooperative Fishery Research Unit phone number, a unique index number and *Reward $10*. High-reward tags (same as standard tags but fluorescent yellow and inscribed with *Reward $100*) were used in Bull Lake concurrently with standard-reward tags in 2012 and 2013. Burbot receiving high-reward tags were systematically selected (every other fish until all high-reward tags were used), but efforts were made to ensure that length distributions of standard-tagged and high-reward-tagged burbot were similar. Furthermore, using this approach, captured burbot tagged with standard- and high-reward tags were sampled from the same set of randomly distributed lake areas. Unhealed wounds from tag loss identified burbot that were marked, lost their tag and subsequently recaptured within the same sampling season. Distinctive scars resulting from tags pulling through the dorsal musculature identified previously tagged burbot that had lost their Carlin tag. In 2012, a small section of the pectoral fin was removed from all burbot that received a Carlin tag. Untagged burbot with tag-loss scars were thereby assigned to the 2011 or 2012 tagging cohort.

Effects of tagging and handling on short-term survival were measured by holding tagged burbot in closed cod traps placed on the lake bottom (Miranda, Brock & Dorr, 2002). Cod traps had 2.5-cm bar mesh panels and were 60 cm tall with a 96-cm diameter base and a 66-cm diameter top. One to five burbot were placed in each trap. The percentage of surviving fish was recorded 48 hr later. Short-term survival was estimated using nonparametric bootstrapping with trap as the sampling unit; confidence intervals were constructed with the percentile method (Efron, 1979).

Anglers were informed about the research through local media and signs around the study lakes. Tag-return envelopes were available at each lake access along with information on how to return tags. Tags could be returned by mail to the Montana Cooperative Fishery Research Unit; at local Wyoming Game and Fish Department, U.S. Fish

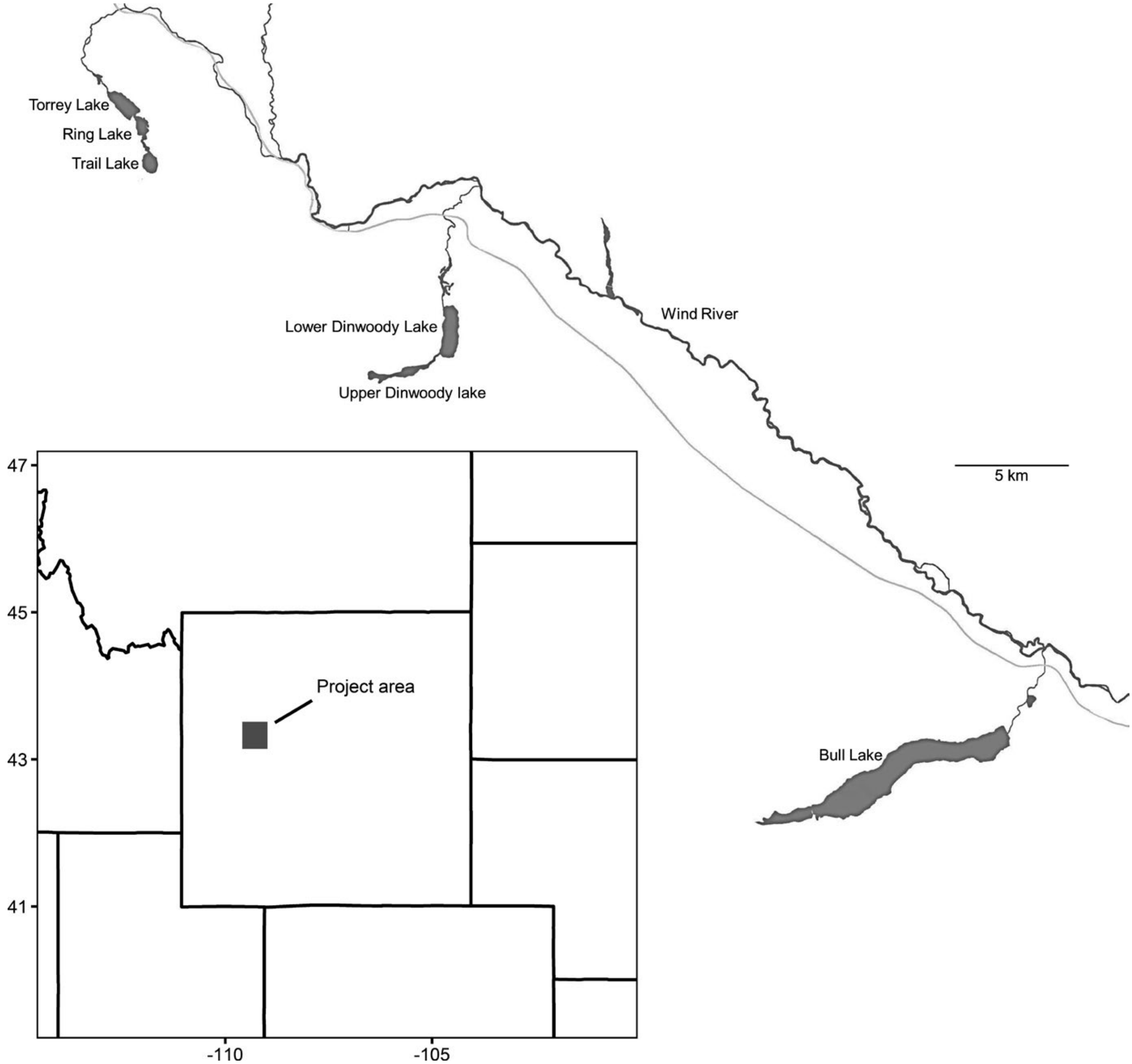

FIGURE 1 Map of study lakes located in the upper Wind River drainage of Wyoming

and Wildlife Service or Wind River Fish and Game offices; or tag information could be entered online.

2.2 | Model development and parameter estimation

A multistate model developed in program MARK (White & Burnham, 1999) integrated data from live recaptures of marked burbot, tag returns, tag losses and tag-reporting rate information (Lebreton & Pradel, 2002) to estimate exploitation and natural mortality. This approach accounted for uncertainty in exploitation and natural mortality estimates caused by tag loss and incomplete angler reporting (Miranda et al., 2002) and efficiently used multiple sources of information to increase the precision of parameter estimates (Kendall, Conn & Hines, 2006).

Multi-state capture–recapture models generate maximum likelihood estimates of apparent survival, detection probability and transition probability (Horton, Letcher & Kendall, 2011; Lebreton & Pradel, 2002). The model used four states: live, live-untagged (tagged burbot that became untagged), harvested and harvested-untagged (unobservable). Transition probabilities from live to live-untagged (tag loss) and from live to harvested (exploitation) were estimated. Live-untagged to harvested-untagged transition probabilities were constrained to be equal to respective live to harvested transition probabilities. All other possible state transitions could not logically occur within the model framework and were fixed at zero.

The fishery was assumed to occur immediately after the tagging period (an instantaneous pulse fishery) because burbot are targeted by anglers when lakes are frozen (typically December through February in the Wind River drainage) and are rarely targeted during the remainder of the year. Given this model structure and assuming no emigration or immigration, natural mortality (M) is equal to the complement of survival because the survival estimate is conditioned on not being harvested. Natural mortality and tag loss were assumed to occur between the end of the fishing season and the beginning of the next tagging period.

Two capture occasions occurred per year: a live-capture occasion and a tag-recovery period for harvested fish. Live captures were obtained from burbot captured in trammel net sets, and all tag recoveries were angler-reported tags from harvested burbot. The tag-recovery probability was fixed at zero during live-capture occasions, and capture probability was fixed at zero during tag-recovery periods. During tag-recovery periods, the high-reward tag-reporting rate was fixed at 1.0 [a $100 reward value is enough to elicit a 100% reporting rate in recreational fisheries (Meyer, Elle, Lamansky, Mamer & Butts, 2012)], and the standard-tag-reporting rate was estimated by assuming that standard- and high-reward-tagged burbot were exploited at the same rate (Pollock et al., 2001). High-reward tags were only applied in Bull Lake; consequently, the reporting rates estimated from the Bull Lake fishery were applied to all fisheries.

Recaptured burbot that lost their tags could be assigned to a lake and tagging cohort, but individual identification was not possible (burbot were assumed to not move among lakes, see 3). Accordingly, tag-loss data were incorporated into the MARK input file by adding recapture events of burbot in the untagged-live state to capture histories from the corresponding lake and cohort. Using these data and assuming symmetrical survival and capture probability for tagged and untagged burbot, annual tag loss was estimated as the probability of transitioning from a live to untagged-live state (Conn, Kendall & Samuel, 2004; Lebreton et al., 2009).

The most general model had a single natural mortality parameter and time-varying capture probability. Exploitation was allowed to vary by lake and year. Because of low tag-return rates from the lakes in the Torrey Creek drainage (Torrey Lake, Ring Lake and Trail Lake) and their close proximity (Figure 1), data from these lakes were pooled and exploitation was estimated for the drainage. Annual tag loss was modelled based on tagging cohort, and separate tag-reporting rates for the 2012 and 2013 seasons were estimated. The 2012 tag-reporting rate was applied to the 2011 data because tag-reporting information was not collected during the first year of the study. Goodness of fit for the most general model was estimated using the median c-hat method in program MARK (Cooch & White, 2006; Horton et al., 2011), and the resulting estimate (c-hat = 2.27) was used to adjust standard errors for overdispersion. Reduced models with a single tag-loss rate for both cohorts and time-invariant exploitation and tag-reporting rates were constructed. Model selection was conducted using AIC_C corrected for overdispersion bias ($QAIC_c$) (Burnham & Anderson, 2002).

An abundance estimation model that grouped data by year and constrained abundance to be equal among years was constructed in program MARK using the closed captures full likelihood option. The parameter constrained was the number of animals never caught (Cooch & White, 2006); the bias this introduced was minimal because the variation in number of burbot captured each year was much smaller than estimated population abundances. Too few fish were recaptured in the Dinwoody lakes to reliably estimate abundance using a closed population estimator; therefore, abundances were calculated from the multi-state model capture probabilities using

$$\hat{N} = \frac{C}{p},$$

where, $\hat{N}$ is abundance of burbot > 389 mm, p is capture probability, and C is the number of captured burbot > 389 mm. Abundances in Ring Lake and Trail Lake were not estimated because of limited recaptures. All abundance estimates were converted to densities ($\hat{N}$/ha) using lake areas.

2.3 | Fishery dynamics simulations

The effects of exploitation on burbot populations in the Wind River drainage were explored by simulating population dynamics under a range of exploitation rates. A logistic surplus-production model was used to simulate density-dependent population growth with annual harvest (Hunt, Arlinghaus, Lester & Kushneriuk, 2011) using the equation:

$$D_{t+1} = D_t + D_t r\left(1 - \frac{D_t}{K}\right) - (\mu \cdot D_t),$$

where D is density of burbot > 389 mm per ha at time t, r is the intrinsic population growth rate, K is carrying capacity, and μ is annual exploitation. The time series stock and recruitment data needed to estimate intrinsic population growth r (Ricker, 1975; Tsehaye, Catalano, Sass, Glover & Roth, 2013) for burbot populations in the Wind River drainage were unavailable. Therefore, following the advice of Myers, Bowen and Barrowman (1999), data from other stock assessments of similar populations were incorporated into the model. Specifically, r was estimated by fitting a logistic surplus-production model to time series burbot abundance and harvest estimates from Tolsona Lake, Alaska (n = 25; Schwanke, 2014). Intrinsic population growth rate and biological carrying capacity parameters were estimated by minimising the sum of squared residuals using the *nls* function in R (version 3.2.2). Abundance and harvest were assumed to be known without error for this simple analysis. Estimated r and associated variance ($\bar{x}$ = 0.55; SE = 0.19) were used to simulate population dynamics of burbot in the Wind River drainage. Carrying capacity was estimated for each lake by modelling population dynamics using r = 0.55 and assuming that population densities were at equilibrium from being exploited at the mean exploitation rates estimated from tagging data (Jensen et al., 2009). Using this approach, exploited density to unexploited density ratios were calculated for each population, and carrying capacity was estimated using the equation:

$$K = \frac{D_{\mathrm{est}}}{B*},$$

where D_{est} = mean density estimated from tagging data and B^* = exploited density to unexploited density ratio.

TABLE 1 Numbers (n) of tagged burbot released and subsequently recovered by lake and release cohort. Values in parenthesis are numbers of tags returned by anglers. Burbot tagged in Bull Lake are separated by tag type (i.e. standard and high reward [HR])

			Recapture year		
Lake	Cohort	n	2011	2012	2013
Bull	2011	389	7 (8)	17 (2)	10 (0)
	2012	237	–	3 (6)	6 (0)
	2013	183	–	–	2 (1)
Bull (HR)	2012	150	–	2 (16)	5 (2)
	2013	71	–	–	1 (1)
Lower Dinwoody	2011	94	0 (14)	1 (4)	5 (1)
	2012	31	–	0 (0)	1 (0)
	2013	37	–	–	0 (0)
Upper Dinwoody	2011	59	0 (0)	16 (1)	8 (0)
	2012	49	–	0 (1)	9 (1)
	2013	47	–	–	0 (2)
Torrey Creek drainage	2011	212	10 (1)	51 (0)	7 (0)
	2012	198	–	8 (1)	18 (0)
	2013	95	–	–	2 (2)

Simulated burbot populations were initialised at current estimated population density (mean estimate from tagging data) and projected for 10 years with exploitation rates ranging from 0.0 to 0.80. Short-term population projections were implemented because the effects of exploitation on time scales relevant to management were of interest. Within the Torrey Creek drainage, simulations were only conducted for Torrey Lake because density estimates for Ring and Trail Lakes were unavailable. For each harvest scenario, 1,000 Monte Carlo simulations were run with r equal to a random deviate drawn from a normal distribution with $\bar{x}$ = 0.55 and SE = 0.19. From these simulations, mean final population density and associated quantile-based 90% confidence intervals were calculated for each harvest scenario.

Depensatory mechanisms that occur at low population densities can lead to fishery collapse (Mullon, Fréon & Cury, 2005). Maintaining population densities above the threshold at which these mechanisms take place is imperative for sustainable fishery management (Post et al., 2002). Using this heuristic principle, a simple biological reference point (B_{40}) set to 40% of carrying capacity was established. The capacity of current exploitation rates to drive population density below B_{40} was investigated and exploitation thresholds (μ_{40}) associated with 0.95 probability of population density remaining above B_{40} were calculated from simulation results.

3 | RESULTS

Most of the 1852 burbot were captured, tagged and released in Bull Lake, including 221 burbot with high-reward tags (Table 1). No movements among lakes were detected (i.e. all recaptured burbot were recaptured in the lake in which they were released). Mean lengths of tagged burbot varied by lake with the largest burbot in the Dinwoody lakes and smallest burbot in the Torrey Creek drainage (Table 2). The length distributions of standard-tagged and high-reward-tagged burbot in Bull Lake were similar, suggesting that the equal exploitation of standard-tagged and high-reward-tagged burbot assumption was robust to length-dependent catchability.

Standard-tag-reporting rate was 0.33 in 2011–2012 (95% CI: 0.12–0.63) and 0.13 in 2013 (95% CI: 0.03–0.42), and annual tag-loss rate was estimated at 0.15 (95% CI: 0.08–0.27). The estimated 48-hr survival probability after tagging and handling was 0.98 (95% CI: 0.95–1.00); thus, the mortality estimation model was not biased from short-term tagging and handling mortality, and a correction for short-term mortality was not included in the multistate mortality estimation model. All models with time-invariant exploitation were well supported by the data ($\Delta QAIC_c$ < 2; Table 3). Parameter estimates from the top model were reported rather than parameter estimates derived through model averaging techniques because exploitation estimates were similar among all well-supported models.

Exploitation varied from 0.02 to 0.32 in the study lakes (Table 4). Lower Dinwoody had the highest exploitation and the widest 95% confidence interval. The annual natural mortality estimate for all study lakes was 0.43 (95% CI: 0.20–0.70), but the precision of this estimate was low.

Burbot abundance varied by an order of magnitude; Bull Lake had the highest abundance and Upper Dinwoody had the lowest (Table 4). Burbot density was highest in Torrey Lake and lowest in Lower Dinwoody Lake. Finally, mean density was negatively associated with exploitation rate (Kendall's rank correlation = −1.0).

Overharvest was not ubiquitous among burbot populations in the Wind River drainage. The highest exploitation rate that could be sustained without driving population density below B_{40} at the 95%

TABLE 2 Numbers (n) and mean total lengths (2.5 and 97.5% quantiles in parenthesis) of tagged burbot and tagged burbot captured by anglers, by lake. Burbot tagged in Bull Lake are separated by tag type (i.e. standard and high reward [HR])

	Tagged		Captured	
Lake	n	Length (mm)	n	Length (mm)
Bull	809	577 (393–856)	17	598 (425–756)
Bull (HR)	221	562 (392–875)	19	593 (392–840)
Lower Dinwoody	162	694 (336–963)	19	656 (395–920)
Upper Dinwoody	155	689 (414–940)	5	799 (529–905)
Torrey Creek drainage	505	500 (325–756)	4	436 (404–493)

TABLE 3 Model selection results for burbot tagging data from the Wind River drainage. Constant natural mortality (*M*) was assumed for all models; lake-specific annual exploitation rates (μ) were constant or allowed to vary by year (yr); angler tag reporting (ψ) was constant (.) or varied by year; and annual tag loss (φ) was constant or varied by tagging cohort (cohort). Capture probability in all models varied by year and lake

Model	*df*	QAICc	ΔQAICc	Likelihood
M (.) + μ (lake) + ψ (yr) + φ (.)	16	678.9612	0	1
M (.) + μ (lake) + ψ (.) + φ (.)	15	679.4294	0.4682	0.7913
M (.) + μ (lake) + ψ (yr) + φ (cohort)	17	679.6648	0.7036	0.7034
M (.) + μ (lake) + ψ (.) + φ (cohort)	16	680.2446	1.2834	0.5264
M (.) + μ (lake·yr) + ψ (.) + φ (.)	23	683.8152	4.854	0.0883
M (.) + μ (lake·yr) + ψ (.) + φ (cohort)	24	684.3261	5.3649	0.0684
M (.) + μ (lake·yr) + ψ (yr) + φ (.)	24	685.5832	6.622	0.0365
M (.) + μ (lake·yr) + ψ (yr) + φ (cohort)	25	686.1105	7.1493	0.028

TABLE 4 Burbot exploitation rate, abundance of >389 mm burbot, lake area and density, for lakes in the Wind River drainage of Wyoming. Values in parenthesis are 95% confidence intervals

Lake	Annual exploitation rate	Abundance ($\hat{N}$)	Lake area (ha)	Density ($\hat{N}$ ha^{-1})
Bull	0.06 (0.03–0.11)	6,433 (3,924–10,582)	1,300	4.95 (3.01–8.14)
Lower Dinwoody	0.32 (0.10–0.67)	262 (84–1,183)	149	1.76 (0.56–7.94)
Upper Dinwoody	0.08 (0.02–0.32)	177 (92–450)	77	2.30 (1.19–5.84)
Torrey	0.02 (0.00–0.11)	966 (616–1,558)	94	10.28 (6.55–16.57)

confidence level (μ_{40}) was 0.18 for Bull Lake, Torrey Lake and Upper Dinwoody Lake. Exploitation estimates were below these thresholds for both Torrey Lake and Bull Lake (Figure 2), indicating that these populations were not overharvested. Mean estimated exploitation was below μ_{40} for Upper Dinwoody Lake, but exploitation rates within a large portion of the 95% CI exceeded this threshold suggesting a substantial risk for overharvest (Figure 2). Lower Dinwoody had a lower μ_{40} compared to the other lakes (0.08) and the highest mean exploitation rate. Although the 95% CI for Lower Dinwoody exploitation was wide, the entire interval was above μ_{40} and risk of overharvest was high.

4 | DISCUSSION

Burbot populations at the southern extent of their range have been suggested to be highly vulnerable to exploitation (Hubert et al., 2008), but empirical estimates of burbot exploitation in recreational fisheries were not available prior to this research. Based on estimated exploitation rates and population projection modelling, risk of overharvest varied among burbot populations. The upper 95% confidence bound of exploitation rates from Bull Lake and Torrey Lake populations were below rates predicted to cause population densities to decline below conservation levels, whereas exploitation rates in the Dinwoody system could cause population densities to fall below conservation levels. These results suggest that implementing further harvest restrictions in the Bull Lake and Torrey Lake fisheries would not substantially improve the sustainability of the fishery. However, the potential for overharvest was greater for Upper Dinwoody Lake and Lower Dinwoody Lake. Management strategies that reduce harvest could decrease risk of fishery collapse and promote conservation of these lentic burbot populations.

The multi-state capture–recapture model developed to estimate exploitation and apparent natural mortality allowed tag-reporting and tag-loss data to be incorporated into the modelling framework, efficiently used information from live recapture and tag returns (Kendall et al., 2006) and eliminated the need for ad hoc methods to estimate exploitation (Cowen, Walsh, Schwarz, Cadigan & Morgan, 2009). Furthermore, using this approach, models that account for time-varying tag loss and angler reporting rates or associations between these rates and biological covariates can be constructed easily in program MARK. Miranda et al. (2002) noted that the precision of exploitation estimates increases substantially as variance associated with tag loss and tag reporting are accounted for using ad hoc methods. Thus, using a capture–recapture model that accounts for tag loss and incomplete tag reporting within the likelihood function appears advantageous.

The annual natural mortality estimate of burbot in the Wind River drainage (*M* = 0.43) was higher than the majority of values reported in the literature for burbot populations (*M* = 0.20–0.60; Worthington & Osborne, 2011). Permanent emigration from the study area or reduced long-term survival caused by tagging and handling could have biased our natural mortality estimate. Permanent emigration is possible because barriers constructed on the outlets of Bull Lake and Lower Dinwoody Lake prevent returns, and cascades on Torrey Creek probably limit returns. A movement study found limited to no downstream emigration from Bull Lake and Torrey Lake (Z. Underwood, University of Wyoming, personal communication); therefore, permanent emigration from Bull Lake and Torrey Lake is probably minimal. However, adult burbot have been observed entrained in the irrigation canal below Lower Dinwoody Lake (Hubert et al., 2008). Connected waterways were not sampled and emigration rates were expected to be estimated from angler reports of locations where anglers caught tagged

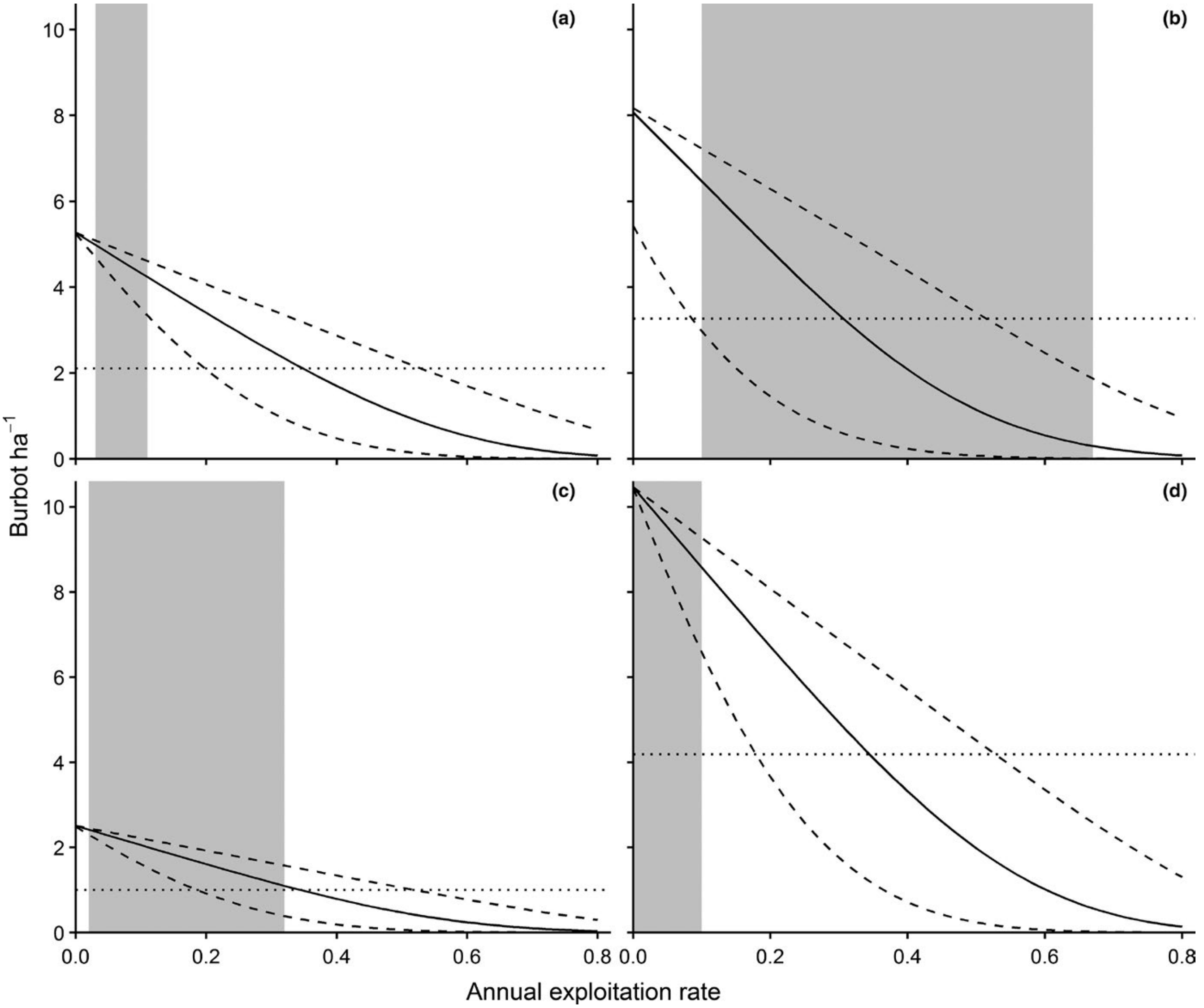

FIGURE 2 Projected burbot population density after 10 years of exploitation for Bull Lake (a), Lower Dinwoody Lake (b), Upper Dinwoody Lake (c) and Torry Lake (d) for annual exploitation rates ranging from 0.00 to 0.80. The broken lines are the 90% quantile confidence intervals of projected population density, the shaded area depicts 95% confidence bounds of estimated exploitation rates, and the dotted line is the biological reference point B^{40} (population density at 40% of carrying capacity)

fish. Only one tagged burbot caught in the irrigation canal near the outlet of Lower Dinwoody Lake was reported from outside the study lakes. However, low reporting rates or low angler effort in areas outside of the study lakes may have masked emigration. Sampling in connected waterways or placement of fixed receiver arrays at the outlets to detect telemetered burbot could provide data on emigration rates from Lower Dinwoody Lake (Horton et al., 2011; Weber, Flammang & Schultz, 2013).

The effects of exploitation on burbot populations in the Wind River drainage were modelled using a logistic surplus-production model. Model predictions could be inaccurate if r of burbot populations in the Wind River drainage was substantially different from the value used in the model. Estimates of r from the literature suggest that the values used in the population projection model ($\bar{x}$ = 0.55; SE = 0.19) calculated from burbot time series abundance estimates were reasonable for gadoid populations. Burbot population growth in the Green River drainage of Wyoming (where burbot are a recently introduced non-native and population growth is expected to be near maximum) was calculated by estimating growth, survival and fecundity and using values of early-life survival from the literature (Klein, Quist, Rhea & Senecal, 2016). Using high early-life survival, r = 0.73; and assuming low early-life survival, r = 0.10 (annual population growth estimates were converted to instantaneous population growth). Estimates of r for 20 Atlantic cod, *Gadus morhua* Linnaeus, populations ranged from 0.15 to 1.03 ($\bar{x}$ = 0.46; SE = 0.06; Myers, Mertz & Fowlow, 1997). Consistency in r among populations from the same taxonomic group is common for a variety of fishes (Myers et al., 1999) and, therefore, population growth rate at low population sizes may be similar among burbot populations. However, variability in life history traits and population dynamics among geographically disparate burbot populations is less clear. Stock-specific data on r of burbot populations in the Wind River drainage would increase the confidence in population projections, but recreational fishery managers seldom have access to the stock-specific data required to estimate this parameter empirically (Post et al., 2002), and modelling strategies that incorporate data from other stock assessments are often useful (Jensen et al., 2009).

Carrying capacity was estimated using population density and exploitation estimates by assuming that populations were at equilibrium from being exploited at the current rate. However, while this approach leveraged available data, the realism of this assumption is unknown and biased estimates of K could result in recommended exploitation thresholds (μ_{40}) that are overly cautious or risky. Further research into burbot K in lentic systems could increase confidence in the predictive ability of population dynamics models.

In addition to understanding the population-level response of burbot populations to exploitation, accurately predicting population density trajectory given an initial exploitation rate and population density requires understanding of the mechanisms that drive changes in exploitation rates over time. The simple harvest scenarios considered in this research all included constant exploitation. The implicit assumption of these scenarios is that angler effort and catchability remain constant over time. Hunt et al. (2011) suggested that some degree of inverse density-dependent catchability (i.e. increasing catchability as population density decreases) is expected in all recreational fisheries and, therefore, that angler catch rates are not linearly related to population density. Additionally, Post et al. (2002) demonstrated that recreational fisheries are vulnerable to collapse under the condition that catch rates remain high at low population densities (hyperstability). In burbot recreational fisheries, the majority of angler effort occurs during the winter when lakes are iced over and coincides with burbot aggregating behaviour associated with pre-spawning and spawning activities. Anglers can probably target burbot aggregations more frequently than would be expected by chance due to local knowledge of the spatial distribution of catch rates and lake bathymetry. The combination of fish and angler behaviour is a probable mechanism for elevated density-dependent catchability (Erisman et al., 2011). Furthermore, Ahrens and Korman (2002) analysed catch and effort data from Kootenay Lake and determined that angler catchability of burbot was probably density-dependent.

In addition to density-dependent catchability, exploitation dynamics are also driven by changes in angler effort. Angler behaviour is a complex process driven by catch related and non-catch related aspects of angling (Hunt et al., 2011; Johnston, Arlinghaus & Dieckmann, 2010); therefore, angler effort can fluctuate independently of burbot population densities or in response to changes in burbot population density. Accessibility, a non-catch aspect of angling associated with angler effort may be a mechanism shaping the distribution of angling effort among the Dinwoody lakes and Bull Lake. The majority of anglers that fish Bull Lake target the eastern basin near Bull Lake Dam because it is easily accessible by road, whereas the western basin of the lake has no road access and receives little fishing effort. Based on this heterogeneous distribution of fishing effort, burbot inhabiting the western basin of the lake are probably invulnerable to the majority of anglers. If burbot movement rate from areas of the lake not targeted by anglers to targeted areas is low, then increased angler effort would drive up exploitation rate slower than expected (Cox & Walters, 2002). This mechanism may contribute to the apparent sustainability and low observed exploitation in Bull Lake. Lower Dinwoody Lake and Upper Dinwoody Lake are also road accessible, but lake areas are an order of magnitude smaller than Bull Lake. Therefore, sections of these lakes probably do not receive low angling effort consistently because accessibility is less of a constraint to anglers in this system. Data from a creel survey conducted during the 1977–1978 ice-fishing season support that the Dinwoody lakes typically receive higher densities of angler effort compared to Bull Lake. Substantially, fewer lines per hectare were observed on Bull Lake ($\bar{x}$ = 0.08; SE = 0.01; n = 17) compared to the Dinwoody lakes ($\bar{x}$ = 0.16; SE = 0.03; n = 14; Upper and Lower Dinwoody were combined for this survey).

The intent of this study was to measure exploitation and support proactive management of the burbot fishery in the Wind River drainage. Proactive management is important because lentic burbot populations are strongly genetically diverged among Wind River tributaries (Underwood, Mandeville & Walters, 2016) such that overexploitation causing extirpation from a single tributary would result in irreversible loss of burbot genetic diversity. Decreased regional heterozygosity could threaten the long-term persistence of burbot in the region and limit the efficacy of conservation propagation programmes should such programmes become necessary. Burbot populations in the Wind River drainage with high risk of overharvest and those with sustainable exploitation were identified using exploitation and abundance estimates from tagging data and simple population projection modelling. This characterisation of overharvest risk will help natural resource managers uphold sustainable burbot fisheries in the region that provide a valuable cultural resource to anglers and identify fisheries that are probably overfished and would benefit from reductions in harvest.

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REFERENCES

Ahrens, R., & Korman, J. (2002). *What happened to the West Arm Burbot stock in Kootenay Lake? Use of an age-structured population model to determine the possible causes for recruitment failure* (p. 30). Nelson, BC: British Columbia Ministry of Water, Land, and Air Protection.

Bernard, D. R., Parker, J. F., & Lafferty, R. (1993). Stock assessment of burbot populations in small and moderate-size lakes. *North American Journal of Fisheries Management*, *13*, 657–675.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*, 2nd ed. (p. 485). New York, NY: Springer-Verlag.

Conn, P. B., Kendall, W. L., & Samuel, M. D. (2004). A general model for the analysis of mark-resight, mark-recapture, and band-recovery data under tag loss. *Biometrics*, *60*, 900–909.

Cooch, E., & White, G. (2006). *Program MARK: A Gentle Introduction*. Retrieved from http://www.phidot.org/software/mark/docs/book/

Cott, P., Johnston, T., & Gunn, J. (2011). Food web position of burbot relative to lake trout, northern pike, and lake whitefish in four sub-Arctic boreal lakes. *Journal of Applied Ichthyology*, *27*, 49–56.

Cowen, L., Walsh, S. J., Schwarz, C. J., Cadigan, N., & Morgan, J. (2009). Estimating exploitation rates of migrating yellowtail flounder (*Limanda ferruginea*) using multistate mark–recapture methods incorporating tag loss and variable reporting rates. *Canadian Journal of Fisheries and Aquatic Sciences*, *66*, 1245–1255.

Cox, S. P., & Walters, C. (2002). Modeling exploitation in recreational fisheries and implications for effort management on British Columbia rainbow trout lakes. *North American Journal of Fisheries Management*, *22*, 21–34.

Efron, B. (1979). Bootstrap methods: Another look at the jackknife. *Annals of Statistics*, *7*, 1–26.

Erisman, B. E., Allen, L. G., Claisse, J. T., Pondella, D. J., Miller, E. F., Murray, J. H., & Walters, C. (2011). The illusion of plenty: Hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations. *Canadian Journal of Fisheries and Aquatic Sciences*, *68*, 1705–1716.

Hardy, R., & Paragamian, V. (2013). A synthesis of Kootenai River burbot stock history and future management goals. *Transactions of the American Fisheries Society*, *142*, 1662–1670.

Holker, F., Volkmann, S., Wolter, C., Van Diik, P., & Hardewig, I. (2004). Colonization of the freshwater environment by a marine invader: How to cope with warm summer temperatures? *Evolutionary Ecology Research*, *6*, 1123–1144.

Horton, G. E., Letcher, B. H., & Kendall, W. L. (2011). A multistate capture–recapture modeling strategy to separate true survival from permanent emigration for a passive integrated transponder tagged population of stream fish. *Transactions of the American Fisheries Society*, *140*, 320–333.

Hubert, W. A., Dufek, D., Deromedi, J., & Johnson, K. (2008). Burbot in the Wind River drainage of Wyoming: Knowledge of stocks and management issues. In V. L. Paragamian, & D. H. Bennett (Eds.), *Burbot: Ecology, management, and culture* (pp. 187–199). Bethesda, MD: American Fisheries Society.

Hunt, L. M., Arlinghaus, R., Lester, N., & Kushneriuk, R. (2011). The effects of regional angling effort, angler behavior, and harvesting efficiency on landscape patterns of overfishing. *Ecological Applications*, *21*, 2555–2575.

Jensen, O. P., Gilroy, D. J., Hogan, Z., Allen, B. C., Hrabik, T. R., Weidel, B. C., … Vander Zanden, M. J. (2009). Evaluating recreational fisheries for an endangered species: A case study of taimen, *Hucho taimen*, in Mongolia. *Canadian Journal of Fisheries and Aquatic Sciences*, *66*, 1707–1718.

Johnston, F. D., Arlinghaus, R., & Dieckmann, U. (2010). Diversity and complexity of angler behaviour drive socially optimal input and output regulations in a bioeconomic recreational-fisheries model. *Canadian Journal of Fisheries and Aquatic Sciences*, *67*, 1507–1531.

Jude, D., Wang, Y., Hensler, S., & Janssen, J. (2013). Burbot early life history strategies in the Great Lakes. *Transactions of the American Fisheries Society*, *142*, 1733–1745.

Kendall, W. L., Conn, P. B., & Hines, J. E. (2006). Combining multistate capture-recapture data with tag recoveries to estimate demographic parameters. *Ecology*, *87*, 169–177.

Klein, Z. B., Quist, M. C., Rhea, D. T., & Senecal, A. C. (2016). Population characteristics and the suppression of nonnative burbot. *North American Journal of Fisheries Management*, *36*, 1006–1017.

Krueger, K., & Hubert, W. (1997). Assessment of lentic burbot populations in the Big Horn Wind River drainage, Wyoming. *Journal of Freshwater Ecology*, *12*, 453–463.

Lebreton, J. D., Nichols, J. D., Barker, R. J., Pradel, R., & Spendelow, J. A. (2009). Modeling individual animal histories with multistate capture–recapture models. *Advances in Ecological Research*, *41*, 87–173.

Lebreton, J. D., & Pradel, R. (2002). Multistate recapture models: Modelling incomplete individual histories. *Journal of Applied Statistics*, *29*, 353–369.

Meyer, K. A., Elle, F. S., Lamansky, J. A. Jr, Mamer, E. R., & Butts, A. E. (2012). A reward-recovery study to estimate tagged-fish reporting rates by Idaho anglers. *North American Journal of Fisheries Management*, *32*, 696–703.

Miller, D. D. (1970). A life history study of burbot in Ocean Lake and Torrey Creek. MSc Thesis, University of Wyoming, Laramie, WY, 194 pp.

Miranda, L., Brock, R., & Dorr, B. (2002). Uncertainty of exploitation estimates made from tag returns. *North American Journal of Fisheries Management*, *22*, 1358–1363.

Mullon, C., Fréon, P., & Cury, P. (2005). The dynamics of collapse in world fisheries. *Fish and Fisheries*, *6*, 111–120.

Myers, R. A., Bowen, K. G., & Barrowman, N. J. (1999). Maximum reproductive rate of fish at low population sizes. *Canadian Journal of Fisheries and Aquatic Sciences*, *56*, 2404–2419.

Myers, R. A., Mertz, G., & Fowlow, P. (1997). Maximum population growth rates and recovery times for Atlantic cod. *Fishery Bulletin*, *95*, 762–772.

Neufeld, M. D., & Spence, C. R. (2004). Evaluation of a simple decompression procedure to reduce decompression trauma in trap-caught burbot. *Transactions of the American Fisheries Society*, *133*, 1260–1263.

Pollock, K. H., Hoenig, J. M., Hearn, W. S., & Calingaert, B. (2001). Tag reporting rate estimation: 1. An evaluation of the high-reward tagging method. *North American Journal of Fisheries Management*, *21*, 521–532.

Post, J., Sullivan, M., Cox, S., Lester, N., Walters, C., Parkinson, E., … Shuter, B. (2002). Canada's recreational fisheries: The invisible collapse? *Fisheries*, *27*, 6–17.

Quinn, S. (2000). The status of recreational fisheries for burbot in the United States. In V. L. Paragamian, & D. W. Willis (Eds.), *Burbot: Biology, ecology, and management* (pp. 127–135). Bethesda, MD: American Fisheries Society.

Ricker, W. E. (1975). *Computation and interpretation of biological statistics of fish populations* (p. 382). Ottawa, ON: Department of the Environment, Fisheries and Marine Service.

Schwanke, C. J. (2014) *Stock assessment and biological characteristics of Burbot in Tolsona Lake, 2008–2011* (p. 28). Anchorage, AK: Department of Fish and Game, Fishery Data Series No. 14-11.

Stapanian, M., Paragamian, V., Madenjian, C., Jackson, J., Lappalainen, J., Evenson, M., & Neufeld, M. (2010). Worldwide status of burbot and conservation measures. *Fish and Fisheries*, *11*, 34–56.

Tsehaye, I., Catalano, M., Sass, G., Glover, D., & Roth, B. (2013). Prospects for fishery induced collapse of invasive Asian Carp in the Illinois River. *Fisheries*, *38*, 445–454.

Underwood, Z. E., Mandeville, E. G., & Walters, A. W. (2016). Population connectivity and genetic structure of burbot (*Lota lota*) populations in the Wind River Basin, Wyoming. *Hydrobiologia*, *765*, 329–342.

Weber, M. J., Flammang, M., & Schultz, R. (2013). Estimating and evaluating mechanisms related to walleye escapement from Rathbun Lake, Iowa. *North American Journal of Fisheries Management*, *33*, 642–651.

White, G. C., & Burnham, K. P. (1999). Program MARK: Survival estimation from populations of marked animals. *Bird Study*, *46*(Suppl. 1), 120–128.

Worthington, T., Kemp, P., Osborne, P., Howes, C., & Easton, K. (2010). Former distribution and decline of the burbot (*Lota lota*) in the UK. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *20*, 371–377.

Worthington, T., & Osborne, P. (2011). Factors affecting the population viability of the burbot, *Lota lota*. *Fisheries Management and Ecology*, *18*, 322–332.

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