

MANAGEMENT BRIEF

# Efficacy of Using Data from Angler-Caught Burbot to Estimate Population Rate Functions

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**Abstract**

The effective management of a fish population depends on the collection of accurate demographic data from that population. Since demographic data are often expensive and difficult to obtain, developing cost-effective and efficient collection methods is a high priority. This research evaluates the efficacy of using angler-supplied data to monitor a nonnative population of Burbot *Lota lota*. Age and growth estimates were compared between Burbot collected by anglers and those collected in trammel nets from two Wyoming reservoirs. Collection methods produced different length-frequency distributions, but no difference was observed in age-frequency distributions. Mean back-calculated lengths at age revealed that netted Burbot grew faster than angled Burbot in Fontenelle Reservoir. In contrast, angled Burbot grew slightly faster than netted Burbot in Flaming Gorge Reservoir. Von Bertalanffy growth models differed between collection methods, but differences in parameter estimates were minor. Estimates of total annual mortality ( $A$ ) of Burbot in Fontenelle Reservoir were comparable between angled ( $A = 35.4\%$ ) and netted fish (33.9%); similar results were observed in Flaming Gorge Reservoir for angled (29.3%) and netted fish (30.5%). Beverton–Holt yield-per-recruit models were fit using data from both collection methods. Estimated yield differed by less than 15% between data sources and reservoir. Spawning potential ratios indicated that an exploitation rate of 20% would be required to induce recruitment overfishing in either reservoir,

regardless of data source. Results of this study suggest that angler-supplied data are useful for monitoring Burbot population dynamics in Wyoming and may be an option to efficiently monitor other fish populations in North America.

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Population demographic data are the basis of fisheries management as they provide insight into the recruitment dynamics, trophic interactions, and growth of fish populations (Allen and Hightower 2010; Quist et al. 2012). Accurate data on fish population dynamics are important for monitoring sport fish populations and are especially critical for monitoring introduced fish populations prior to and in response to removal efforts (Cambray 2003; Simberloff 2003). Because collecting demographic data is expensive and time consuming, developing cost-effective techniques is a high priority. A potential cost-effective technique to monitor populations is to use information from fish caught by anglers.

Management agencies often employ anglers to gather data on fish populations and to monitor angler effort and harvest (Willis and Hartmann 1986; Dolman 1991; Cooke

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et al. 2000; Park 2007). Angler-catch data provide an alternative to fishery-independent data (e.g., standard population surveys) used by natural resource agencies. For example, Travnicek and Clemons (2001) used long-term data from fishing tournaments to evaluate changes in Flathead Catfish *Pylodictis olivaris* populations after the closure of the commercial harvest in the Missouri River. Ebbers (1987) found that age-frequency distributions, growth rates, and mortality rates estimated for Largemouth Bass *Micropterus salmoides* in Minnesota lakes were similar between angler-supplied data and electrofishing surveys. In contrast, a number of studies suggest that fishery-dependent data should be used with caution. Gabelhouse and Willis (1986) concluded that biases related to angling technique (e.g., gear size and type) and season limited the use of data from Largemouth Bass tournaments in Kansas. Similarly, Miranda et al. (1987) found that angler-catch data tended to overestimate Largemouth Bass growth rates compared with data collected using standard survey methods (i.e., electrofishing, cove rotenone). Substantial length bias in angler-supplied data has also been reported in crappies *Poxomis* spp. (Miranda and Dorr 2000) and Northern Pike *Esox lucius* (Arlinghaus et al. 2008) populations. The majority of studies that have investigated the use of angler-catch data have focused on popular sport fishes. Although less common, anglers that target introduced species have the potential to provide valuable information at a fraction of the cost of standard monitoring regimes. Angling tournaments targeting illegally introduced Burbot *Lota lota* in the Green River basin of Wyoming provide an excellent opportunity to evaluate whether data from angling can be used to monitor fish populations.

Burbot are top predators, aggregate spawners, and occupy a diversity of lotic and lentic habitats (Hewson 1955; McPhail and Paragamian 2000). Throughout their native distribution in Wyoming, Burbot populations are in decline or have been extirpated (Krueger and Hubert 1997; Hubert et al. 2008; Stapanian et al. 2010). Despite poor status in their native distribution, a population established through illegal introduction is thriving in the Green River basin. The presence of Burbot in the Green River system is a concern due to their potential negative effects on socially and economically important fishes (Gardunio et al. 2011). In response, the Wyoming Game and Fish Department (WGFD) has implemented regulations in the Green River basin that are designed to maximize fishing mortality (WGFD 2010). The WGFD is also investigating the efficacy of suppression programs (Klein et al. 2015a, 2015b, 2016). Anglers have become interested in participating in suppression efforts and have organized multiple ice-fishing tournaments for Burbot on Fontenelle and Flaming Gorge reservoirs, the two primary reservoirs in the system. Tournaments were organized as a means to

reduce Burbot numbers and have resulted in the removal of approximately 34,000 Burbot since tournaments began in 2010 (J. D. Walrath, unpublished data). In addition to their effectiveness as a removal tool, angling tournaments provide fish that can be used to evaluate and monitor Burbot age structure and growth.

Age and growth data are of utmost importance to fishery managers. Age-structure data provide insight into the mortality rates and recruitment dynamics of fish populations. Growth data are especially important because growth has direct and indirect effects on recruitment, mortality, maturity, and length structure of a population (Quist et al. 2012). Given the importance of age and growth data, new sampling methods should be assessed to evaluate concordance with standardized sampling methods. This study was conducted to compare age and growth estimates of Burbot from fishery-dependent (i.e., angler-caught) and fishery-independent (i.e., standard trammel netting survey) data sources in two Wyoming reservoirs. Given the results of previous studies addressing this topic, we hypothesized that fishery-dependent data would overestimate growth compared with estimates from fishery-independent data sources, and that population models fit to both data types would differ substantially in their results.

## METHODS

**Study area.**—This research took place on Fontenelle and Flaming Gorge reservoirs, both of which are located in the Green River basin, Wyoming. Fontenelle Reservoir is an artificial impoundment of the Green River located in Lincoln County. The reservoir is primarily used for flood protection with a secondary use of hydroelectric power generation. At capacity, the reservoir has a surface area of approximately 3,200 ha and a maximum depth of approximately 30 m. Flaming Gorge Reservoir is located 125 km downstream from Fontenelle Reservoir and is primarily located in Sweetwater County, Wyoming, with the southernmost portion of the reservoir located in Daggett County, Utah (Figure 1). As such, the Flaming Gorge Reservoir fishery is managed by both the WGFD and the Utah Division of Wildlife Resources. The reservoir is primarily used for hydroelectric power generation. At capacity, the reservoir has a surface area of approximately 17,000 ha and a maximum depth of 133 m.

**Data collection.**—Tournament data were collected from Fontenelle and Flaming Gorge reservoirs during January 2016 and 2017. Data were collected from one tournament on Fontenelle Reservoir and two tournaments on Flaming Gorge Reservoir. The tournament on Fontenelle Reservoir occurred over one night, whereas tournaments on Flaming Gorge Reservoir each spanned two nights. Tournaments offered cash prizes for the largest Burbot, smallest Burbot,

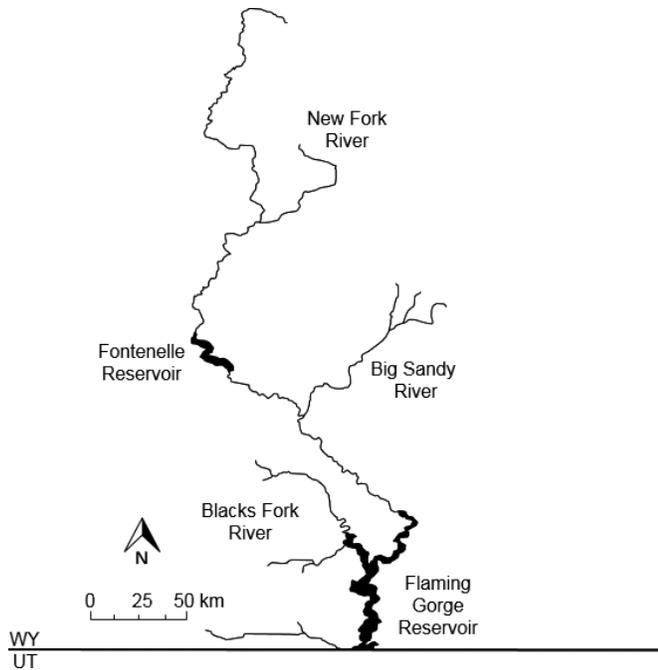


FIGURE 1. The Green River basin including its major tributaries and associated reservoirs. Burbot were sampled from Fontenelle Reservoir and Flaming Gorge Reservoir, Wyoming, during 2016 and 2017.

and most Burbot caught by one fishing team. The rules of the competition indicated that all Burbot had to be euthanized and checked in to be eligible for judging.

At each tournament check-in site, anglers were informed that a study was being conducted, and the premise of the study was explained. Anglers were invited to donate their catch. Due to logistical constraints, biological data were only collected from donated fish, not from the total tournament catch. Donated fish were enumerated, and TL (mm) and weight (g) were measured. Sex was determined for all fish by visual observation of the gonads. Collection of ovaries from mature female Burbot was attempted, but all had spawned prior to sampling. Sagittal otoliths were taken from up to 10 fish per 1-cm length group (Quist et al. 2012; Klein et al. 2014).

Burbot were collected from Fontenelle and Flaming Gorge reservoirs in October and November 2016 using trammel nets. Trammel nets have been found to be effective at capturing lentic Burbot during spring and fall and have become the standard gear for sampling Burbot in lentic waters in Wyoming (WGFD, unpublished data). Trammel nets measured 48.8 m long and 1.8 m deep and consisted of 25.4-cm (bar measure) outer mesh and 2.5-cm (bar measure) inner mesh. Nets were placed perpendicular to the shore at varying depths and anchored to the substrate at both ends. Trammel nets were placed in locations used annually by the WGFD during fall Burbot sampling. All netted fish were

counted, and TL (mm) and weight (g) were measured. Sex was determined by visual observation of the gonads. Ovaries were removed from up to five mature female Burbot per 5-cm length group, preserved in a solution of 5% formalin and stored for fecundity analysis. Sagittal otoliths were removed from up to ten fish per 1-cm length group. All otoliths were dried, stored in 2.0-mL centrifuge vials, and returned to the University of Idaho for processing.

Otoliths were mounted in epoxy and transversely sectioned about the nucleus (Koch and Quist 2007; Edwards et al. 2011; Klein et al. 2014). Otolith cross sections were examined under a dissecting microscope with transmitted light and an image analysis system. Otoliths were examined by a single reader that had previous experience ageing otoliths. If an age estimate could not be reached for a fish, that fish was removed from further analyses. Ovaries were blotted dry and weighed to the nearest 0.01 g. One ovary was randomly selected for subsampling. Subsamples of oocytes (0.01–0.02 g) were taken from the anterior, central, and posterior portions of the ovary. Oocyte subsamples were then counted under a dissecting microscope, and an average of subsample counts was calculated. Averages were then used to determine total fecundities based on total ovary weight (Klibansky and Juanes 2007; Klein et al. 2016).

*Data analysis.*—Mean back-calculated lengths were estimated using the Dahl–Lea method (Quist et al. 2012). Burbot growth rates were described using a von Bertalanffy growth model:

$$L_t = L_\infty [1 - e^{-k(t-t_0)}],$$

where  $L_t$  (mm) is length at time  $t$ ,  $L_\infty$  is average maximum length,  $k$  is a growth coefficient, and  $t_0$  is the theoretical age when length is zero (Quist et al. 2012). All analyses were conducted using the FSA package in R version 3.2.2 (R Core Development Team, see Ogle 2015). Proportional size distribution (PSD) was calculated for each reservoir and collection method (Gabelhouse 1984; Fisher et al. 1996; Neumann et al. 2012). Total annual mortality ( $A$ ) was calculated using a Chapman–Robson estimator and peak plus one criterion (Smith et al. 2012). Mortality rates were calculated for angled fish using only those fish that were donated by anglers, netted fish mortality rates were calculated using all sampled fish in which ages were assigned using an age–length key (Quist et al. 2012).

Chi-square tests were used to compare length–frequency and age–frequency distributions between collection methods in each reservoir ( $\alpha = 0.05$ ; Neumann and Allen 2007; Ogle 2015). Beverton–Holt yield-per-recruit models were used to describe differences in potential yield and spawning potential ratio (SPR) estimates between data collected by anglers and data collected using trammel nets. Models

were constructed using the Fishery Analysis and Modeling Simulator (FAMS) program version 1.64 (Slipke and Maccina 2014). Yield-per-recruit models required input parameters of growth, mortality, longevity, and length–weight relationship parameters specific to each collection method and reservoir. Spawning potential ratio calculations required additional parameters including fecundity–length relationship estimates, a maturation schedule, and estimates of spawning frequency (Table 1). Spawning potential ratio is used to index the influence of fishing on the productivity of a population and is calculated as the ratio of fished to unfished mature eggs that are produced in an average recruit’s lifetime. Populations were considered to be experiencing recruitment overfishing when SPR was below 0.20 (Goodyear 1993).

Conditional natural mortality ( $cm$ ) was held constant at 0.10 in all models. Conditional fishing mortality ( $cf$ ) was allowed to vary from 0 to 1.0 in increments of 0.05. An arbitrary initial population of 100,000 individuals was input into each model. Logarithmic length–weight relationship and fecundity–length relationship parameters were estimated from our data using linear regression. Since fecundity–length data were unavailable for angled fish, we used the fecundity–length relationships of netted fish for all simulations. Age at first maturation for females was 2 years in each reservoir based on observed maturity rates. We assumed that females comprised 50% of the population. Based on our observations when evaluating oocytes, we assumed that 100% of mature female Burbot spawned annually.

Models were run under a single management scenario that assumed no minimum length limit in either reservoir. Both reservoirs are currently managed with no length restrictions on Burbot harvest. Since Burbot smaller than 200 mm were absent from our sample, we used 200 mm as the “minimum length limit.”

## RESULTS

A total of 515 Burbot was sampled from Fontenelle Reservoir, 376 were collected using trammel nets and 139 were collected by anglers. Otoliths were collected from all angled fish and from 139 fish collected using trammel nets. In Flaming Gorge Reservoir, 417 Burbot were collected. Of these, 214 were collected by anglers and 203 were collected using trammel nets. Otoliths were collected from all angled fish and 155 netted fish. Ovaries were collected from 35 Burbot from Fontenelle Reservoir and from 42 Burbot from Flaming Gorge Reservoir.

Lengths of angled fish in Fontenelle Reservoir varied from 293 to 900 mm, whereas netted fish varied in length from 304 to 965 mm (Figure 2). Lengths of angled fish in Flaming Gorge Reservoir varied from 218 to 858 mm and lengths of netted fish varied from 317 to 853 mm (Figure 2). Although length distributions of angled and netted fish were significantly different in Fontenelle Reservoir ( $\chi^2 = 16.8$ ,  $df = 4$ ,  $P = 0.002$ ) and Flaming Gorge Reservoir ( $\chi^2 = 15.0$ ,  $df = 4$ ,  $P = 0.004$ ), PSD estimates were similar between collection methods in both reservoirs (Figure 2).

Angled fish in Fontenelle Reservoir varied in age from 1 to 11 years, whereas ages of netted fish varied from 1 to 12 years (Figure 3). Ages of Burbot in Flaming Gorge Reservoir varied from 1 to 10 years for angled fish and 2 to 11 years for netted fish (Figure 3). No significant difference in age distributions were observed between angled and netted fish in Fontenelle Reservoir ( $\chi^2 = 13.4$ ,  $df = 11$ ,  $P = 0.27$ ) or Flaming Gorge Reservoir ( $\chi^2 = 12.0$ ,  $df = 10$ ,  $P = 0.29$ ). Estimates of total annual mortality of Burbot in Fontenelle Reservoir were comparable between angled ( $A = 35.4\%$ ) and netted fish (33.9%). Mortality rates in Flaming Gorge Reservoir were also similar between angled (29.3%) and netted fish (30.5%).

TABLE 1. Parameter estimates used in population simulations of Burbot collected by anglers and using trammel nets in Fontenelle Reservoir and Flaming Gorge Reservoir, Wyoming, 2016 and 2017.

Variable	Description	Collection method			
		Angled	Netted	Angled	Netted
		Fontenelle Reservoir		Flaming Gorge Reservoir	
$b_{lw}$	Slope of regression: weight on length <sup>a</sup>	2.886	2.845	3.000	3.127
$a_{lw}$	Intercept of regression: weight on length <sup>a</sup>	-4.968	-4.831	-5.270	-5.636
$b_{fec}$	Slope of regression: fecundity on length <sup>a</sup>	2.693	2.693	3.287	3.287
$a_{fec}$	Intercept of regression: fecundity on length <sup>a</sup>	-1.760	-1.760	-3.405	-3.405
$L_{\infty}$	Theoretical mean maximum length (mm)	1178	1591	2100	2096
$k$	Growth coefficient	0.091	0.066	0.042	0.036
$t_0$	Theoretical time when length is zero (years)	-2.815	-1.818	-1.951	-2.771
Age <sub>max</sub>	Maximum age of sampled fish (years)	11	12	10	11

<sup>a</sup>Independent and dependent variables were  $\log_{10}$  transformed.

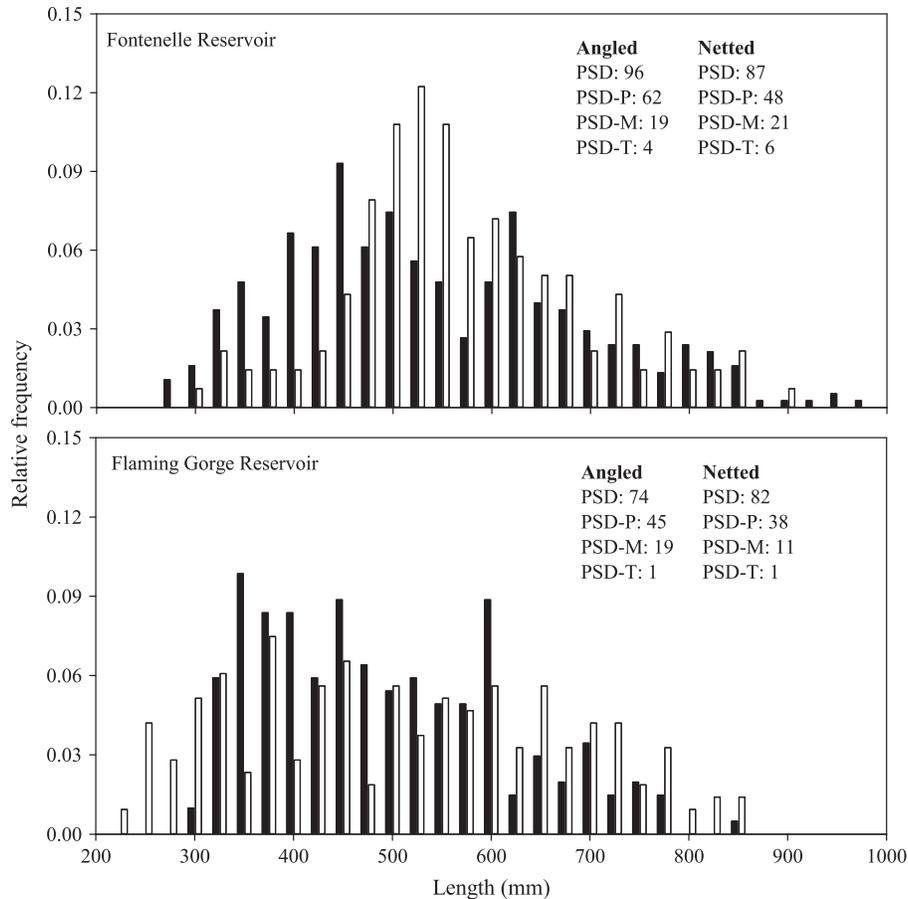


FIGURE 2. Length-frequency distributions of Burbot sampled by anglers (white bars) and trammel nets (black bars) in Fontenelle Reservoir and Flaming Gorge Reservoir, Wyoming, 2016 and 2017. Proportional size distribution index values are provided for stock (PSD), preferred (PSD-P), memorable (PSD-M), and trophy (PSD-T) size classifications.

Mean back-calculated lengths of Burbot in Fontenelle Reservoir were larger in angled fish than in netted fish up to age 5. After age 5, back-calculated lengths of netted fish were larger than those of angled fish. Conversely, back-calculated lengths of Burbot in Flaming Gorge Reservoir were similar between angled and netted fish until age 3; thereafter, growth of angled fish was faster than that of netted fish (Table 2). Parameter estimates from von Bertalanffy growth models differed between collection methods for both reservoirs, but differences were minor (Table 1).

Yield-per-recruit models produced similar estimates using data from angled and netted fish in each reservoir (Figure 4). Burbot sampled with trammel nets in Fontenelle Reservoir had higher potential yield than angled fish. The opposite pattern was observed in Flaming Gorge Reservoir where angled fish had higher potential yield than netted fish. Although estimates of yield differed between collection methods, differences in estimated yield varied from 1% to 21% and were generally under 15%.

Spawning potential ratio estimates remained consistent between collection methods (Figure 4). Using either data source, models without a minimum length limit indicated that recruitment overfishing would be achievable at an exploitation rate of 20% in both Fontenelle Reservoir and Flaming Gorge Reservoir.

## DISCUSSION

The results of this research support our hypothesis that fishery-dependent data would produce different estimates of growth compared with fishery-independent data. However, a clear pattern was not evident. Miranda et al. (1987) found that back-calculated lengths of angled Large-mouth Bass were greater than those collected using cove rotenone and electrofishing. Those authors also observed that growth rates converged as fish age increased, suggesting that angling selects for the fastest-growing members of younger age-classes. In our study, angled fish had larger back-calculated lengths at age than did netted fish in

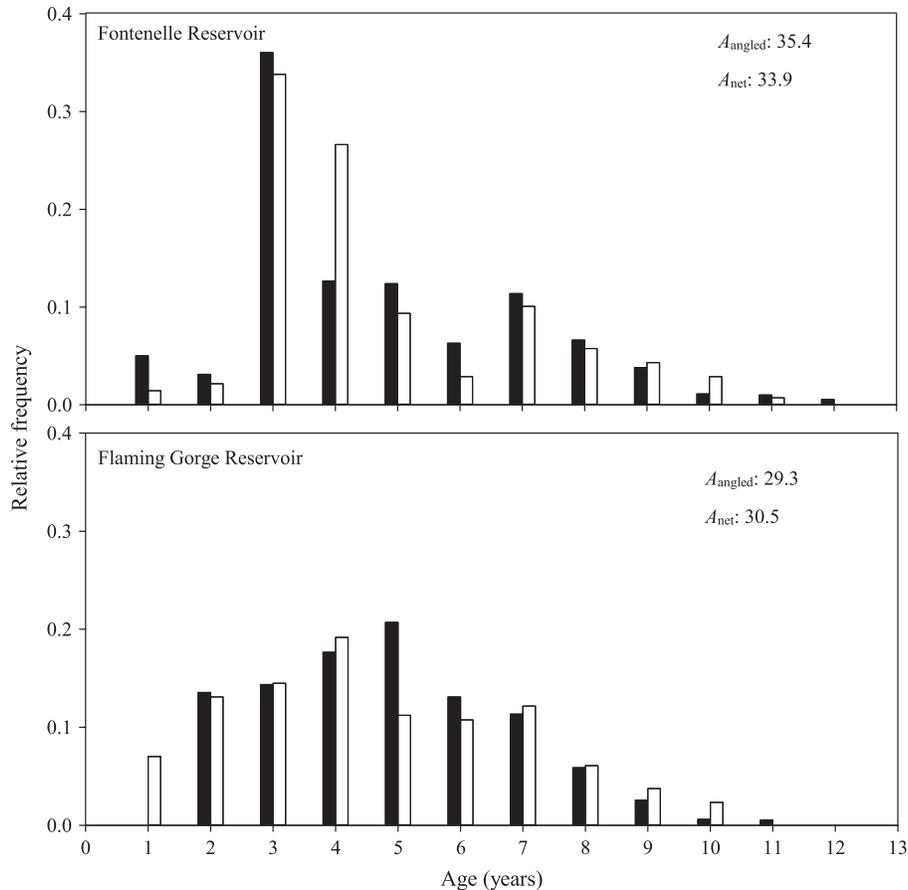


FIGURE 3. Age-frequency distributions of Burbot sampled by anglers (white bars) and trammel nets (black bars) in Fontenelle Reservoir and Flaming Gorge Reservoir, Wyoming, 2016 and 2017. Variable  $A$  represents total annual mortality rate by collection method.

Flaming Gorge Reservoir, and the opposite pattern was observed in Fontenelle Reservoir. Contrary to our initial hypothesis, the disparity in mean back-calculated lengths between collection methods was large enough to be statistically significant, but yield-per-recruit models resulted in minor differences in potential yield and SPR estimates between data sources in both reservoirs.

Like many collection methods, angling is size selective. Angling data can also be biased by differences in angling technique, gear type, and species. Miranda and Dorr (2000) found that angler exploitation was highest in intermediate length classes of crappies throughout five Mississippi reservoirs due to factors such as fish behavior and gear type. Schultz (2004) stated that exploitation rates of White Bass *Morone chrysops* were highest in large length classes in Kansas reservoirs. Similarly, Isermann et al. (2005) detected a selective harvest of large Yellow Perch *Perca flavescens* by anglers compared with trap-net samples. Although length-frequency distributions differed significantly between collection methods in our study, PSD values were similar between collection methods.

Similarities in PSDs may be an artifact of the manner in which the Burbot were collected. Many angling tournaments have prize payouts based on size and total weight (Wilde et al. 1998), and competitive anglers often target large numbers of smaller, scoring-size fish in order to maximize total weight instead of targeting larger, warier fish (Holbrook 1975). This phenomenon was documented by Gabelhouse and Willis (1986) where the size and number of Largemouth Bass caught and reported by tournament anglers relied on the angler's intentions and values during that tournament. The authors found that nontournament anglers caught size-classes that were proportional to those sampled by electrofishing. However, tournament angler catch underestimated the PSDs of small size-classes and overestimated those of larger size-classes. It is important to consider that anglers in our study were required by law to harvest all captured Burbot. Anglers were also required to present all captured fish to tournament officials as prizes were based on concurrent size and total catch categories. Such regulations allowed for the collection of small and large size-classes and reduced the

TABLE 2. Mean back-calculated lengths at age for Burbot collected by angling (angled) and using trammel nets (netted) from Fontenelle Reservoir and Flaming Gorge Reservoir, Wyoming, 2016 and 2017. Standard errors for estimates are included;  $n$  = number.

Age (years)	$n$ (angled)	$n$ (netted)	Mean back-calculated length at age (mm)			
			Angled	SE	Netted	SE
<b>Fontenelle Reservoir</b>						
1	2	2	251.5	10.2	200.1	12.7
2	3	5	356.7	13.3	317.5	10.1
3	47	55	393.3	3.8	408.2	3.9
4	37	17	512.8	4.5	504.3	6.6
5	13	18	570.8	6.7	568.5	8.9
6	4	9	611.7	18.4	624.8	14.5
7	14	15	659.6	9.3	682.2	10.3
8	8	8	714.8	11.5	761.3	6.6
9	6	5	770.9	13.8	802.1	7.5
10	4	2	818.9	16.5	852.6	4.8
11	1	2	880.5	0.0	878.9	2.1
12	0	1			911.6	0.0
<b>Flaming Gorge Reservoir</b>						
1	15	0	189.9	3.0		
2	28	18	282.3	4.7	289.5	8.7
3	31	19	367.2	5.3	362.9	11.9
4	41	24	448.7	4.6	427.3	12.4
5	24	33	516.9	6.1	490.7	10.2
6	23	24	585.6	6.1	553.6	10.6
7	26	21	645.9	5.4	613.2	9.6
8	13	10	695.8	7.5	665.2	13.7
9	8	4	745.5	9.3	717.8	21.5
10	5	1	803.9	0.0	786.6	40.5
11	0	1			838.5	0.0

likelihood of common, bias-inducing, angler practices (i.e., culling small fish). However, a potential source of bias remains as anglers generally target Burbot in spawning aggregations during tournaments and have a higher chance of catching large, mature fish. Given the similarity in age distributions between data types, this did not seem to be occurring.

Angler data present the opportunity to estimate other population vital statistics such as mortality rates that require reliable age-frequency data. Ebbers (1987) concluded that estimates of total annual mortality for Largemouth Bass in Minnesota were consistent between electrofishing data and data supplied by tournament anglers. The mortality rates in our study were not estimated from total angler catch due to either logistical limitations (e.g., too many fish were caught to process in a timely manner) or angler value limitations (e.g., unwillingness of anglers to donate fish). Therefore, we could not properly estimate age structure for the entire tournament

catch. Despite this shortcoming, age-frequency distributions of Burbot were similar between collection methods in each reservoir in our study. Due to the similarities in age frequencies, estimates of total annual mortality were nearly identical between angled and netted fish. In the future, collecting length data from the entire tournament catch, in addition to collecting otoliths, may provide better insight into the concordance of age structure and mortality estimates derived from angling and netting.

Angling tournaments provide a cost-effective option for monitoring fish populations as well as a removal tool that provides angler opportunity. A black bass tournament monitoring program has been in place in Kansas since 1977 and has successfully used angling-tournament data to monitor Largemouth Bass populations and assess management actions (Willis and Hartmann 1986). Similar programs that use angling data as a monitoring tool have existed in Texas (Dolman 1991), Nova Scotia (Macmillan et al. 2002), and Australia (Park 2007). Successful use of angling data in previous research coupled with the results of this research are promising to fishery managers. Data collected from tournaments produced estimates of PSD, age structure, and total annual mortality that were similar to data collected using trammel nets. Estimates of growth varied between collection methods, but yield-per-recruit models fit using both data sources showed minimal difference in their model output. Thus, management decisions (e.g., exploitation targets) would not likely differ based on either data source. Collecting data from tournaments also required substantially less effort than standard survey methods. Trammel netting surveys required approximately 1 week of intensive netting in each reservoir during which a crew of over 10 people using various boats and other equipment (e.g., nets) to collect data. Obtaining angling data required 1 d of collection in Fontenelle Reservoir and 2 d of collection in Flaming Gorge Reservoir. At tournaments, data collection required minimal equipment and three people to process fish.

We acknowledge that the small sample of tournaments from which we collected data may be a source of bias due to factors such as annual variations in fish abundance and angler behavior. Despite this concern, we argue that the lack of research evaluating angler-supplied data makes the results of our study extremely important to fishery managers. Additionally, the few studies that have compared data sources have focused on a single system; whereas, our study compared data from two dissimilar reservoirs. Given these caveats, occasional comparison with fishery-independent data seems prudent if angler-supplied data are used to monitor populations in the future. Additionally, developing specific benchmarks for acceptable differences between fishery-dependent and fishery-independent data will be important for fishery managers using angler-supplied data.

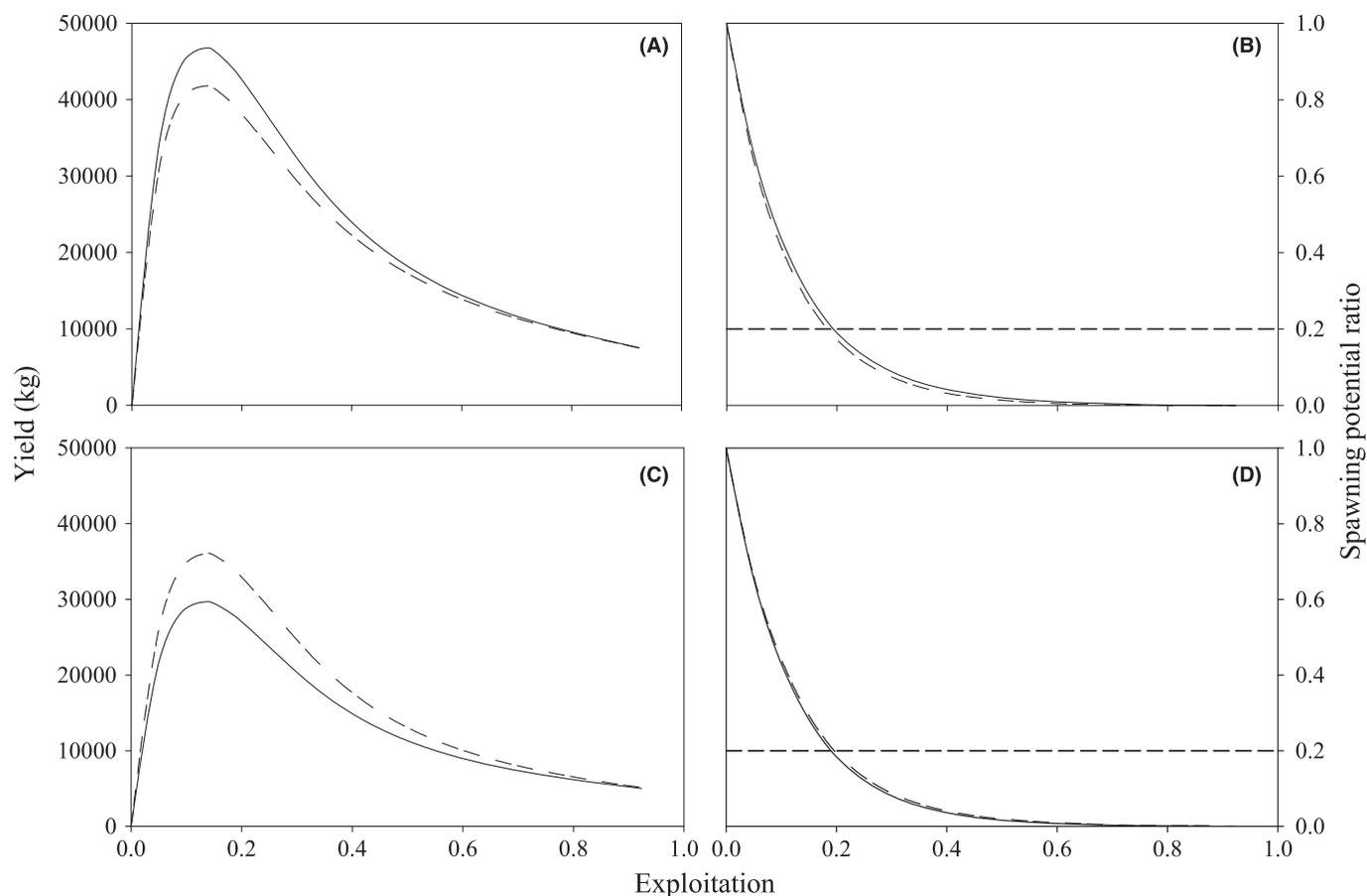


FIGURE 4. Yield-per-recruit models and spawning potential ratios using data collected by anglers and trammel nets. Models included data from Burbot caught by anglers and assuming no minimum length limit on harvest (dashed line), and Burbot caught using trammel nets assuming no minimum length limit on harvest (solid line). Panels (A) and (B) correspond to fish collected in Fontenelle Reservoir, and panels (C) and (D) correspond to fish collected from Flaming Gorge Reservoir. Horizontal dashed lines represent the theoretical point where a fishery starts to experience recruitment overfishing.

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