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MANAGEMENT BRIEF

Influence of Population Density and Length Structure on Angler Catch Rate in Kokanee Fisheries

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Abstract

Management agencies are often charged with providing fisheries that lead to angler participation. Catch rate is one of the primary drivers of angler participation but can be influenced by a suite of factors, including population structure (e.g., density and size structure). The complexity of understanding how population structure influences angler catch rate is typified in kokanee *Oncorhynchus nerka* fisheries. Previous research suggests that angler catch rates of kokanee are positively influenced by fish density and total length. However, that research was based on data collected using size-selective midwater trawls. Due to the potential limitation of previous research, we sought to (1) understand the relative bias of midwater trawls and gill nets for describing the size structure of kokanee available to anglers and (2) re-evaluate the influence of fish density and fish length on angler catch rates in kokanee fisheries. Midwater trawl, gill-net, and creel data were collected on five prominent kokanee fisheries throughout Idaho in 2016 and 2017. Catch composition and percent overlap of midwater trawls, gill nets, and angler-caught fish were compared to understand the efficacy of midwater trawls and gill nets for representing the size structure of kokanee available to anglers. In addition, the influence of kokanee density and length on angler catch rates was evaluated. Midwater trawls primarily sampled small kokanee (<330 mm) and exhibited little overlap with angler-caught fish, whereas gill nets sampled more large fish (>330 mm) and exhibited higher overlap with angler-caught fish when compared to midwater trawls. Fish length was not positively associated with angler catch rates. However, fish density exhibited a positive relationship with angler catch rates. Our results highlight the importance of gear choice for understanding how kokanee populations function and elucidate the tradeoffs associated with population density, fish length, and resulting kokanee fisheries.

A primary goal of recreational fisheries management is to provide quality fisheries that result in fishing success and angler participation (Hunt and Grado 2010). Although angler participation is a function of various factors, including catch (e.g., high-yield fisheries and trophy fisheries) and noncatch (e.g., solitude and leisure time) motivations, catch rate is often cited as an important determinant of participation in consumption-oriented fisheries (Fedler and Ditton 1986; Aas and Kaltenborn

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1995; Beardmore et al. 2011). Due to the importance of catch rate for angler participation, understanding the mechanisms underlying angler catch rate has long been a focus of natural resource management agencies.

Catch rate is a function of abundance and catchability (Ricker 1975), but catch rate is most often associated with changes in fish density (Peterman and Steer 1981; Newby et al. 2000; VanDeValk et al. 2005). Angler catch rates of Walleye *Sander vitreus* were positively related to population density in 118 lakes in Wisconsin (Hansen et al. 2000). However, catchability can also effect catch rate and may be influenced by various characteristics, including turbidity (Drenner et al. 1997), fish behavior (Peterman and Steer 1981; Wilson et al. 2011), and population size structure (Isbell and Rawson 1989; Miranda and Dorr 2000). Of these, fish size is often positively associated with catchability due to the relationship between size, growth rate, and behavioral traits (e.g., aggression and boldness) that may increase capture vulnerability (Biro and Post 2008; Tsuboi et al. 2016). However, the influence of fish size and fish density on angler catch rate has not been clearly established.

The complexity of understanding the factors influencing angler catch rates is typified in many kokanee *Oncorhynchus nerka* fisheries. Kokanee are highly valued sport fish and also serve as important prey for numerous fishes (Wydoski and Bennett 1981). As such, managers are often charged with maintaining kokanee densities to satisfy piscivorous sport fishes while limiting density-dependent reductions in growth that may negatively influence kokanee fisheries (Martinez and Wiltzius 1995; Rieman and Maiolie 1995). Unfortunately, the relationships among kokanee density, fish size, and resulting fisheries are poorly understood. Rieman and Maiolie (1995) evaluated the influence of fish length and density on seven kokanee fisheries in Oregon and Idaho. The authors noted a positive relationship between kokanee density and angler catch rate, yield, and effort. In addition, catchability of kokanee was reported to be positively associated with fish length (Rieman and Maiolie 1995). As such, some managers have operated under the premise that an increase in either total density or mean length of kokanee would positively influence angler catch rates (Koenig 2011). However, the results of Rieman and Maiolie (1995) were based on data collected using midwater trawls, which have recently been shown to provide biased estimates of kokanee length structure (Klein et al. 2019). Because of the potential limitation of the Rieman and Maiolie (1995) study, we sought to (1) understand the relative bias of midwater trawls and gill nets for describing the size structure of kokanee available to anglers and (2) re-evaluate the influence of fish density and fish length on angler catch rates in kokanee fisheries by using gill-net data.

METHODS

Lake Pend Oreille, Anderson Ranch Reservoir, Arrowrock Reservoir, Lucky Peak Reservoir, and Dworshak Reservoir, Idaho, were selected for sampling. The systems vary in surface area and depth (Table 1) and were selected based on the presence of prominent kokanee fisheries. Each system has exhibited fluctuations in fish density and growth due to changes in productivity (Rieman and Myers 1992). For instance, kokanee in Anderson Ranch, Arrowrock, Lucky Peak, and Dworshak reservoirs mature at age 2, whereas kokanee in Lake Pend Oreille tend to mature later (age 3 or 4; Rieman and Myers 1992; Butts et al. 2013; Wahl et al. 2015). Nevertheless, populations of kokanee in Anderson Ranch, Arrowrock, and Lucky Peak reservoirs have been characterized by low densities of large fish (>330 mm) in recent history. Conversely, Lake Pend Oreille and Dworshak Reservoir tend to support high densities of small kokanee (<330 mm).

Kokanee were sampled using midwater trawls and experimental gill nets during June–August in 2016 and 2017. All sampling was conducted at night within 5 d of the new moon during thermal stratification (Bowler et al. 1979; Rieman and Myers 1992). On the night prior to sampling, the vertical distribution of kokanee ("kokanee layer") was identified using a depth sounder (Furuno Model FCV-585; Furuno USA, Camas, Washington).

Each system was sampled concurrently with two midwater trawls used by the Idaho Department of Fish and Game that are representative of those used for routine kokanee monitoring throughout much of North America (Klein et al. 2019). The "large trawl" measured 10.5 m in length and had a 3.0- × 2.2-m fixed-frame mouth. The "small trawl" was 12.0 m in length and had a 2.4- × 1.8-m fixed-frame mouth. Each trawl was constructed of graduated nylon mesh that decreased in size from 32.0 mm at the mouth to 6.0 mm at the cod end. Both trawls were towed at approximately 1.5 m/s, and the entire kokanee layer was sampled in a stepwise, oblique pattern (Rieman and Myers 1992; Klein et al. 2019). "Steps" measured 3.0 m for the large trawl and 2.4 m for the small trawl. A step

TABLE 1. Surface area and maximum depth at full pool for the five study systems in Idaho.

System	Surface area (km^2)	Maximum depth (m)
Anderson Ranch Reservoir	20.3	97.5
Arrowrock Reservoir	31.5	54.9
Dworshak Reservoir	69.2	192.0
Lake Pend Oreille	380.0	351.0
Lucky Peak Reservoir	11.4	60.0

was towed for 3 min, the net was then raised to the next step, and towed for an additional 3 min. The step pattern was repeated until the entire kokanee layer had been sampled. In general, four to eight steps sampled the entire kokanee layer and constituted a single transect. Each trawler completed six transects per system. All collected fish were measured for total length (nearest 1.0 mm), and the total towing time (min) was recorded.

Gillnetting was conducted within 1 d of midwater trawl sampling. Depending on the thickness of the kokanee layer, one to four gill nets were used to encompass the vertical distribution of kokanee. Gill nets measured 48.8 × 6.0 m and were constructed of sixteen 3.0-m-long panels (Klein et al. 2019). Each gill net consisted of eight different mesh sizes (12.7-, 19.0-, 25.4-, 38.1-, 50.8-, 63.5-, 76.2-, and 101.6-mm stretch measure), with two panels of each mesh size randomly positioned throughout the net. Gill nets were set at the approximate midpoint of each trawl transect and were soaked overnight (about 12 h). All sampled fish were measured for total length, enumerated by mesh size, and the mode of capture (i.e., gilling, wedging, or entangling) was recorded.

Access-point creel surveys were conducted within the same year as midwater trawl and gill-net sampling (Jones and Pollock 2012). Arrowrock Reservoir, Lucky Peak Reservoir, Anderson Ranch Reservoir, and Lake Pend Oreille were sampled throughout the fishing season in 2016. Dworshak Reservoir was sampled during the fishing season of 2017. Surveys were stratified by month and day type (i.e., weekday or weekend–holiday). Creel clerks interviewed kokanee anglers following trip completion. Creel clerks collected data on the number of anglers in a party, time fishing, and number of kokanee that were harvested or released. In addition, clerks generally collected data on total length from all harvested kokanee. Due to logistical constraints, 25 harvested fish per week were randomly selected for measurement in Dworshak Reservoir. Although not available for all systems, creel data indicated that less than 10% of angler-caught fish were released. As such, the length composition of a given kokanee population was estimated by multiplying the length proportion of harvested fish sampled by the total number of angled kokanee. Only creel data collected within 1 month of gill-net and midwater trawl sampling were used for analysis to avoid the confounding effect of changes in fish size with time.

Analysis.— The efficacy of gill nets and midwater trawls for representing the length structure of kokanee available to anglers was evaluated by visually comparing the length structure of kokanee sampled with each gear to the length structure of angler-caught fish. Because gill nets are size selective for large kokanee, gill-net catch was adjusted for length-specific patterns in encounter and retention probabilities as described by Klein et al. (2019). Length-specific encounter and retention probabilities could only be estimated for fish up to 440 mm; thus, fish larger than 440 mm were excluded from gill-net adjustments. However, fish greater than 440 mm only represented 1.2% of the total angler-caught fish, suggesting that exclusion of larger fish (≥440 mm) was not important to the overall analysis. A similar adjustment was not available for midwater trawls, so observed counts were used for comparisons. In addition, the percent overlap in length distribution between each gear and angler-caught fish was estimated to better understand which gear best represented the length distribution of angler-caught fish. Percent overlap was estimated for gill nets and midwater trawls as the sum of the minimum percent catch for each 1-cm length category between angler-caught kokanee and fish sampled by a given gear. Percent overlap was only calculated for fish greater than or equal to the minimum size observed in the creel of each system to avoid the influence of high catches of fish (in midwater trawls and gill nets) that were unavailable to anglers.

The influence of fish length on catchability was evaluated by estimating the relative catchability of kokanee in each fishery. Midwater trawls are size selective for small fish (Klein et al. 2019), whereas angling tends to capture larger, adult kokanee (Martinez and Wiltzius 1995; Rieman and Maiolie 1995; Cassinelli et al. 2018). Adjusted gill-net catch was used to calculate relative catchability because gill nets have been shown to provide a better representation of the larger, adult portion of a population (Klein et al. 2019). Relative catchability was estimated as the proportion of angler-caught kokanee in a length-class divided by the proportion of gill-net sampled kokanee in the same length-class (Rieman and Maiolie 1995). Catch proportions were truncated at the minimum size of fish observed in the creel in each system (Rieman and Maiolie 1995). Relative catchability values greater than 1.0 indicate that anglers caught kokanee in a higher proportion than was available in the environment.

The effect of fish density on angler catch rate was evaluated by plotting the relative abundance of kokanee sampled in gill nets by the catch rate of fish caught by anglers. Due to the influence of small kokanee on gill-net catch rates, gill-net catch was truncated to only include fish that were vulnerable to anglers. Fish were assumed to have recruited to a fishery at the smallest length-class observed in the creel of a given system.

RESULTS

Kokanee that were sampled with gill nets, midwater trawls, and by anglers exhibited clear differences in length structure (Figure 1). Midwater trawls tended to sample small fish and only sampled one fish greater than 300 mm. Conversely, angler-caught fish varied in length from 192

to 590 mm, with the majority of fish having lengths greater than 250 mm. Gill nets sampled the greatest breadth of kokanee lengths, with fish varying in length from 54 to 537 mm. Gill-net and midwater trawl length distributions exhibited variable overlap with the length distribution of angler-caught fish (Table 2). However, gill nets tended to have a higher overlap with angler catch when compared to midwater trawls. Percent overlap in lengths between fish captured in midwater trawls and angler-caught fish varied from 0.0% to 64.2% among systems, whereas fish sampled in gill nets exhibited 22.8–90.4% overlap with angler-caught fish.

The relationship between length and catchability was inconsistent among systems (Figure 2). Relative catchability peaked between 240 and 290 mm in systems with relatively small fish (i.e., Dworshak Reservoir and Lake Pend Oreille). In systems with large fish (i.e., Lucky Peak, Anderson Ranch, and Arrowrock reservoirs), relative catchability peaked between 360 and 430 mm. Relative catchability also exhibited variability in magnitude among systems. For instance, in Lake Pend Oreille the rate at which 240-mm kokanee were caught by anglers was three times the rate at which they were sampled by gill nets. Conversely, in Lucky Peak Reservoir 350-mm kokanee were caught by anglers nearly 17 times more frequently than they were sampled in gill nets.

In general, the relative abundance of kokanee was positively associated with angler catch rate among systems (Figure 3). However, the relationship between angler and gill-net catch rates was variable among systems. Systems

TABLE 2. Percent overlap in length distributions between angler catch of kokanee and catch of kokanee in midwater trawls or gill nets.

System	Percent overlap with angler catch	
	Midwater trawls	Gill nets
Anderson Ranch Reservoir	8.0	54.3
Arrowrock Reservoir	0.0	22.8
Dworshak Reservoir	38.9	49.4
Lake Pend Oreille	64.2	90.4
Lucky Peak Reservoir	7.5	51.1

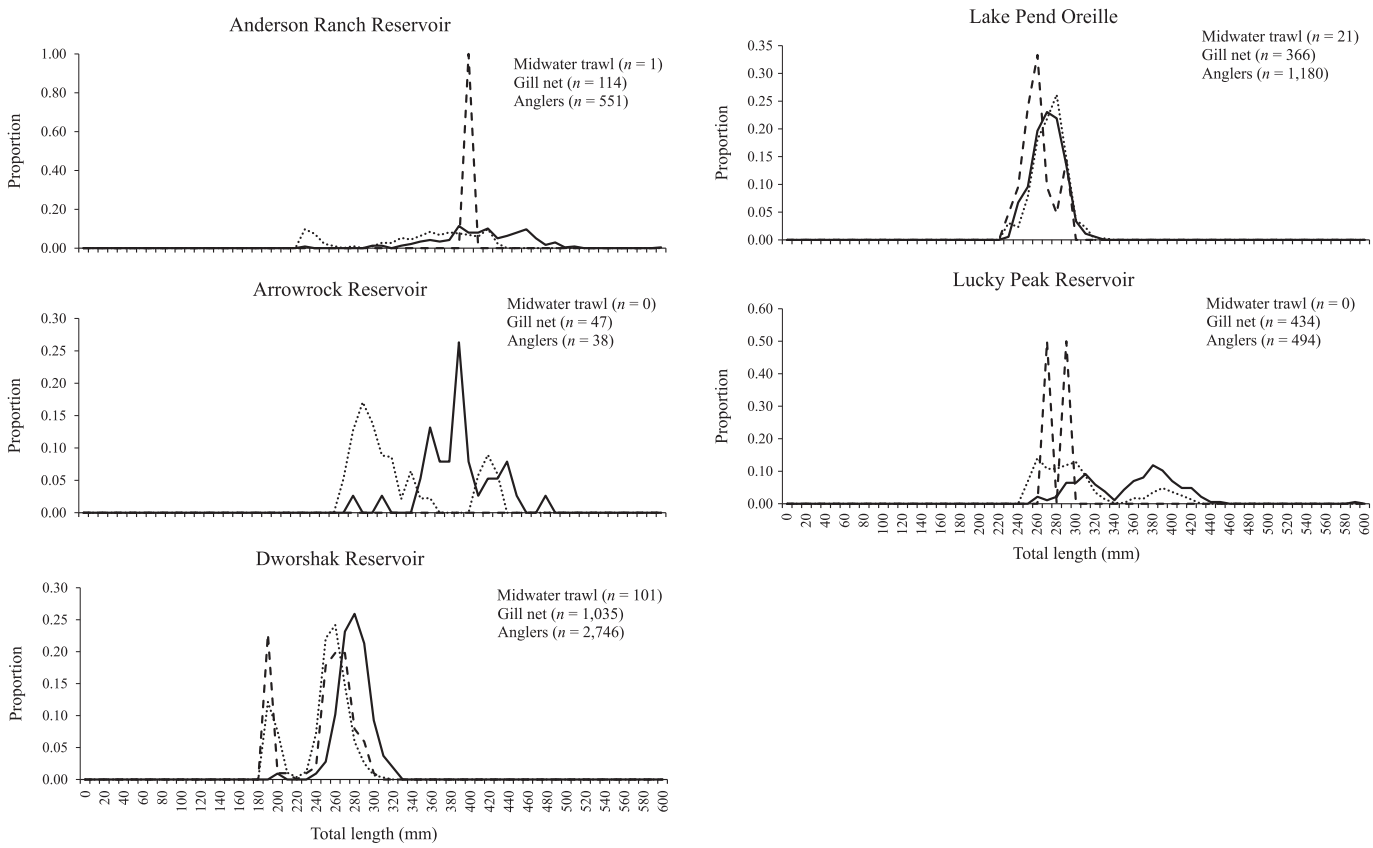

FIGURE 1. Length proportions of kokanee caught with midwater trawls (dashed line), with gill nets (dotted line), and by anglers (solid line) in Anderson Ranch Reservoir, Arrowrock Reservoir, Dworshak Reservoir, Lake Pend Oreille, and Lucky Peak Reservoir, Idaho. Gear-specific sample sizes are included on each plot. Note that *y*-axes vary in scale.

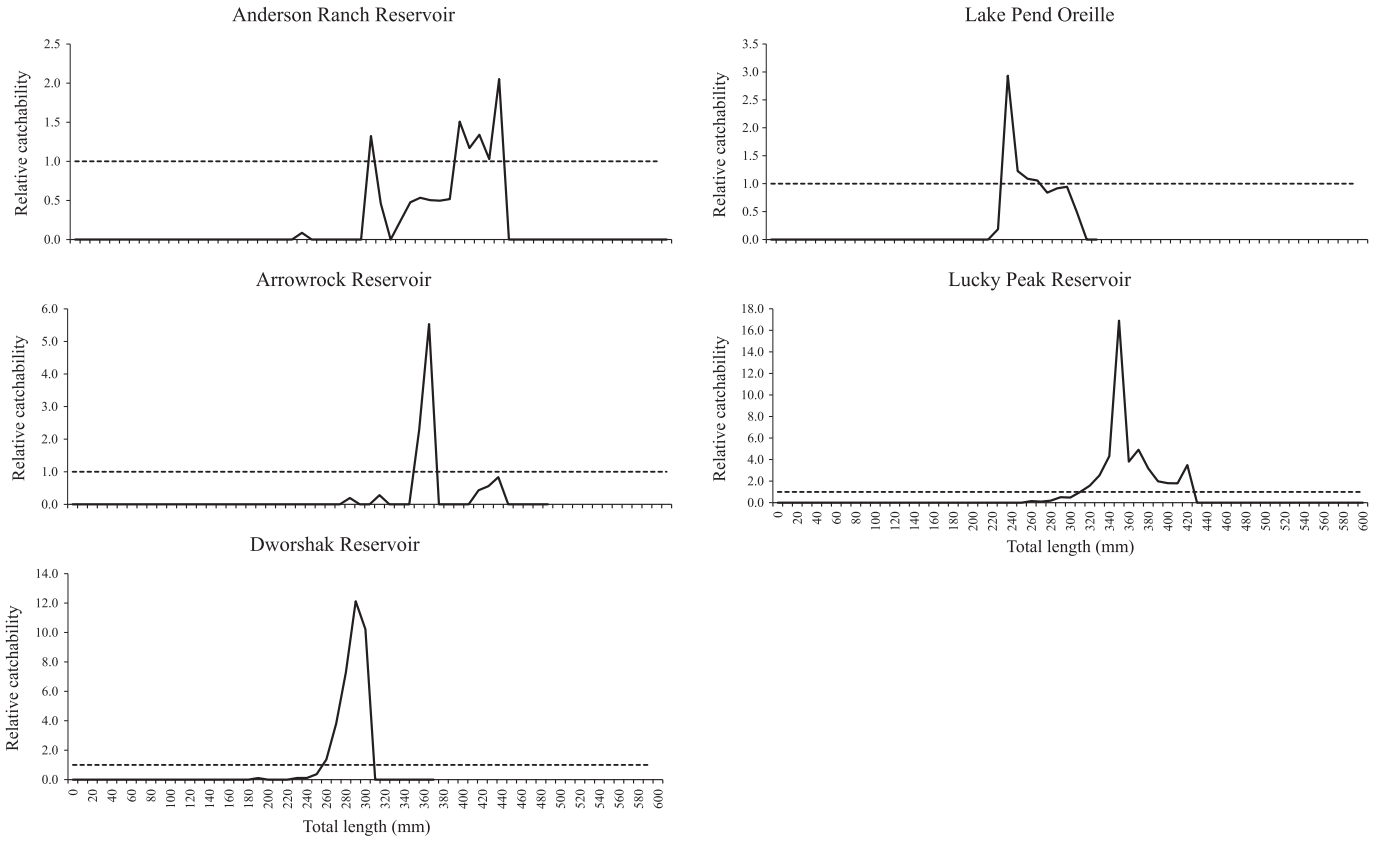

FIGURE 2. Relative catchability (solid line) by total length for kokanee sampled from Anderson Ranch Reservoir, Arrowrock Reservoir, Dworshak Reservoir, Lake Pend Oreille, and Lucky Peak Reservoir, Idaho. The dashed line (at relative catchability = 1.0) represents angler catch rates in proportion to the availability of kokanee in the environment. Note that *y*-axes vary in scale.

with small kokanee (Lake Pend Oreille and Dworshak Reservoir) exhibited much higher angler catch rates than systems with large kokanee (Arrowrock, Lucky Peak, and Anderson Ranch reservoirs). Although an increase in fish density was positively associated with angler catch rates among systems, patterns between catch rate and density were less apparent for systems with similarly sized kokanee. For instance, Lake Pend Oreille and Dworshak Reservoir exhibited an inverse relationship between angler catch rates and relative abundance.

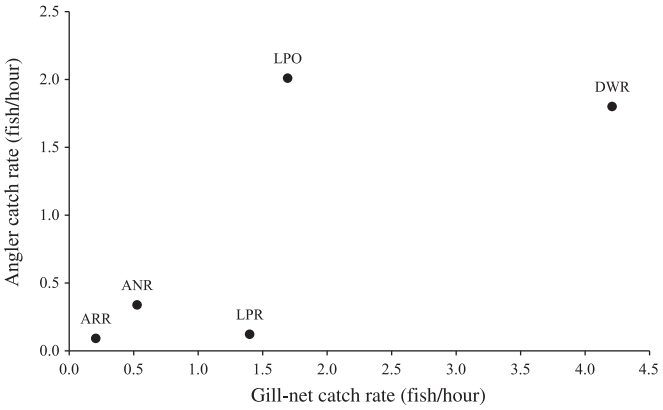

FIGURE 3. Relationship between angler catch rate and gill-net catch rate (fish/h) for kokanee sampled from Anderson Ranch Reservoir (ANR), Arrowrock Reservoir (ARR), Dworshak Reservoir (DWR), Lake Pend Oreille (LPO), or Lucky Peak Reservoir (LPR), Idaho.

DISCUSSION

Our research highlights the importance of gear selection in addressing questions associated with population size structure. Midwater trawls exhibited less than 10% overlap with angler-caught fish in three of the five systems sampled in the current study. Similar size-selective biases of midwater trawls have been reported elsewhere (Pope et al. 1975; Bethke et al. 1999; McClatchie et al. 2000). Although present, fish greater than 215 mm were not sampled by midwater trawls in Stechlin and Breiter lakes, Germany (Emmrich et al. 2010). The abundance of large Bloater *Coregonus hoyi* was suggested to be underestimated by trawls in Lakes Huron and Michigan (Warner et al. 2012). Estimates of kokanee density were 1.8–3.3

times lower for three trawling methods in comparison with hydroacoustic surveys in Lake Coeur d'Alene (Parkinson et al. 1994). Klein et al. (2019) suggested that midwater trawls were only effective for sampling juvenile kokanee due to the consistent size selectivity of the gear. Gill nets provide a more accurate representation of population size structure (Klein et al. 2019), resulting in higher overlap with angler-caught fish when compared to midwater trawls. Despite the relatively high overlap between gill-net sampled fish and angler-caught fish, gill nets do not effectively sample the largest individuals in some populations. Gill-net data were truncated at 440 mm because fish greater than 440 mm were not effectively retained in the mesh sizes used during the current study. Therefore, managers may want to consider using larger mesh sizes or alternative size selectivity adjustments when monitoring kokanee populations that contain individuals larger than 440 mm. For instance, Hansen (2019) extended size selectivity adjustments of kokanee up to 500 mm by incorporating a "tangling" parameter to account for fish whose girth exceeded that of the available mesh. Conversely, managers may wish to consider the applicability of fisheries-dependent data for characterizing kokanee populations. Although gill nets are likely not effective in all situations, our results suggest that this gear better represents the size structure of kokanee available to anglers when compared with midwater trawls and should be an effective sampling technique under most circumstances.

Contrary to previous research, our results suggest that kokanee length does not confer increases in catchability. Relative catchability of gill nets generally peaked at intermediate length-classes in each system. In Lucky Peak Reservoir, catchability of 350-mm kokanee was nearly four times higher than that of 420-mm fish. However, relative catchability may be an ineffective index for understanding the true catchability of any species due to its reliance on the use of an unbiased sampling technique. In fact, the limitation of relative catchability is a major drawback of the findings of Rieman and Maiolie (1995). The authors reported that relative catchability increased exponentially with kokanee length; a 40-mm increase in length was predicted to increase angler catch rates by 20 times. However, the positive relationship between fish length and catchability reported by Rieman and Maiolie (1995) was likely an artifact of the size selectivity of midwater trawls. The authors estimated relative catchability as the proportion of angler-caught kokanee in a length-class divided by the proportion of kokanee in the same length-class sampled with midwater trawls. Because midwater trawls are size selective for small fish and anglers primarily catch large, adult kokanee, the relative catchability estimates used by Rieman and Maiolie (1995) were predisposed to increase with fish length. Although gill nets sample a large breadth of kokanee lengths (Klein et al. 2019), they may suffer from similar limitations with regard to estimates of relative catchability. For instance, gill nets sampled one 350-mm fish in Lucky Peak Reservoir, whereas anglers caught 21 fish in the 350-mm length-group. The disparity between the gill-net catch and angler catch resulted in an unreasonably high estimate of relative catchability. Although the magnitude of relative catchability likely does not represent true catchability in a fishery, the general lack of increasing catchability with fish length in the current study suggests that other factors influence angler catch rates in kokanee fisheries.

In general, our results corroborate the commonly cited positive relationship between fish density and angler catch rates. Gill-net catch rates explained 85–97% of the variability in angler catch rates of Walleye in Lake Erie (Isbell and Rawson 1989). Population abundance estimates served as accurate predictors of angler catch rates for 11 Walleye fisheries in Wisconsin (Beard et al. 1997). Angler catch rate more than doubled following increases in stocking density of Rainbow Trout *O. mykiss* in six Texas lakes (Miko et al. 1995). However, our research also highlights the nuanced interplay among population density, fish length, and resulting kokanee fisheries.

Kokanee often exhibit density-dependent reductions in growth (Goodlad et al. 1974; Peterman 1984; Rieman and Myers 1992) that have the potential to influence resulting fisheries. High-density kokanee populations tend to exhibit reduction in growth, resulting in low average lengths. Conversely, low-density populations can exhibit fast growth, resulting in larger adults. At either end of the density–size spectrum, angler catch rates can decline precipitously due to extremely low fish densities or insufficient maximum sizes of kokanee. For instance, numerous authors have warned against trophy kokanee fisheries due to the potential for fishery collapse resulting from low population density (Bowles et al. 1991; Rieman and Maiolie 1995; Hanzel et al. 1998). Similarly, 99% of the fish caught by anglers in the current study were 230 mm or larger. Thus, populations that fall below a similar minimum threshold may be highly abundant but would not recruit to the fishery. Assuming that a population falls somewhere in the middle of the density–size spectrum, increases in density may not necessarily equate to an increase in angler catch rates. For instance, Lucky Peak Reservoir and Lake Pend Oreille exhibited similar densities of kokanee, but the angler catch rate in Lake Pend Oreille was nearly twice that in Lucky Peak Reservoir. Numerous factors, such as prey density (VanDeValk et al. 2005), fish behavior (Peterman and Steer 1981; Wilson et al. 2011), or angler experience (Sampson 1991), may explain the variability in angler catch rate observed among systems in the current study. However, the paucity of additional data (e.g., zooplankton densities) limits our ability to identify the influence of external factors on angler catch rates.

Notwithstanding, our data suggest that increases in adult kokanee density generally confer increases in angler catch rates.

Collectively, our results highlight the importance of understanding gear selectivity for managing kokanee. Gill nets and midwater trawls are both size selective. As such, a complete understanding of the biases of gill nets and midwater trawls is impossible without knowing the true selectivity of both gears. Nevertheless, our results suggest that the size selectivity of midwater trawls limits their use as indicators of the size structure of kokanee available to anglers. Gill nets also exhibited size selectivity, but they sampled a wide breadth of kokanee lengths and are beneficial for understanding how kokanee fisheries function. When gill-net data were coupled with creel survey data, our results indicated that fish density (rather than fish length) was the primary factor influencing angler catch rates among study systems. However, fish length is also an important consideration for kokanee managers due to the interrelationship between fish size and population density. Overall, our results suggest that gill nets are a preferable gear for monitoring adult kokanee and can provide valuable insight into kokanee populations and resulting fisheries.

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