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MANAGEMENT BRIEF

Size Selectivity of Sampling Gears Used to Sample Kokanee

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Abstract

Kokanee *Oncorhynchus nerka* provide valued recreational fisheries and also serve as a prey resource for economically, socially, and ecologically important fishes. As such, management of kokanee is a major focus of natural resource agencies. Kokanee are typically monitored using midwater trawls, but the interpretation of data collected using midwater trawls is difficult due to the unknown size selectivity of the gear. We sought to assess the length selectivity of midwater trawls by comparing estimates obtained from midwater trawls with estimates obtained from gill nets adjusted for size selectivity. Experimental curtain gill nets and midwater trawls were used in conjunction to sample kokanee in seven lentic systems in Idaho. The size selectivity of gill nets was estimated by accounting for the probability of encounter and the probability of retention. Estimates of size selectivity were then used to adjust the length distribution of fish sampled in gill nets. The adjusted length distribution of fish sampled in gill nets was compared with estimates obtained from midwater trawls to identify potential size selectivity of midwater trawls. A pattern of size selectivity was apparent for both sampling techniques. The average length of kokanee sampled with midwater trawls was 111 mm; whereas, kokanee sampled with gill nets had a mean length of 235 mm. Our results suggest experimental gill nets are useful for common sampling of kokanee (e.g., trend monitoring) because the gear is less size selective than midwater trawls and is adjustable for size selectivity. However, midwater trawls are likely the best gear for addressing questions associated with early life history. Overall, our results provide a better understanding of gill-net and midwater trawl selectivity and ultimately improve the ability to sample and manage the species.

Kokanee *Oncorhynchus nerka* (lacustrine Sockeye Salmon) are culturally, ecologically, and economically important throughout their distribution and serve as a vital prey resource for various fishes including Bull Trout *Salvelinus confluentus* and Rainbow Trout *O. mykiss* (Wydoski and Bennett 1981; Paragamian and Bowles 1995). For instance, Lake Pend Oreille, Idaho, produced the previous world-record Rainbow Trout and the current world-record Bull Trout following the introduction of kokanee in the 1930s (Wydoski and Bennett 1981). Kokanee also support valued recreational fisheries. In 1998, kokanee was the fourth most harvested species in the Lake Roosevelt, Washington, fishery, which is valued at approximately US $8 million (Spotts et al. 2000). Due to their recreational and ecological importance, kokanee have been widely distributed and can now be found in North America, South America, Asia, Australia, and Europe (Nelson 1968; Burgner 1991). In North America, kokanee are common in lentic systems of the western United States and Canada (Nelson 1968) and are a major focus of natural resource management agencies.

Kokanee populations are typically monitored by using escapement estimates, hydroacoustic surveys, and midwater trawl surveys (Parkinson 1988; Rieman 1992; Askey 2016). In Idaho, the density of kokanee is monitored using hydroacoustic surveys and midwater trawl surveys (Rieman 1992). Unlike hydroacoustic surveys, midwater trawls can also be

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used to directly estimate the composition (e.g., age, maturity) of kokanee populations (Rieman 1992). However, inferences based on midwater trawl data (e.g., length structure) rely on the assumption that the composition of fish caught by the trawl is representative of the population (Hayes et al. 2012). The composition of fish caught in midwater trawls can vary depending on a number of factors, including trawl construction and fish density. For instance, trawls with cod ends constructed of 35-mm diamond mesh caught higher proportions of small (24–30 cm) Haddock *Melanogrammus aeglefinus* relative to trawls with cod ends having 87-mm mesh (Pope et al. 1975). Even when midwater trawling methods are standardized, questions remain regarding the size selectivity of the gear (Hayes et al. 2012). Midwater trawls targeting Sprat *Sprattus sprattus* and Atlantic Herring *Clupea harengus* in the Baltic Sea exhibited size selectivity unexplained by cod end selectivity (Bethke et al. 1999). Those authors suggested that the apparent size selectivity was due to escape from the front of the trawls, which, in turn, was related to fish size and swimming speed. Considering the importance of midwater trawls for drawing inference on the composition of fish populations, understanding the potential size selectivity of the gear is essential. Size selectivity is typically evaluated by using techniques such as mark–recapture studies (Millar and Fryer 1999). Unfortunately, high mortality rates of kokanee (i.e., ~100%) associated with midwater trawl sampling negates the use of direct measures of efficiency. Because the efficiency of midwater trawling cannot be directly evaluated, an indirect measure of efficiency is needed.

Gill nets provide a useful tool for understanding the potential size selectivity of midwater trawls. Gill nets are size selective, but their selectivity can be easily quantified relative to other sampling gears (Hamley 1975). Gill-net selectivity is most often estimated as retention selectivity, or the relative probability that a fish of a given length is captured assuming it contacts the net (Millar and Holst 1997; Millar and Fryer 1999). The retention selectivity of each mesh size can then be used to adjust the estimated length composition of the target fish population. For the adjusted length distribution of kokanee to represent the true length distribution of kokanee, all fish in a population must have an equal probability of contacting the net (Millar 2000). In practice, the probability of contacting a net is influenced by length-dependent factors (e.g., gear avoidance, behavior) that must be known to obtain an accurate estimate of population structure. Rudstam et al. (1984) argued that length-related encounter probability was the primary factor influencing capture of Cisco *Coregonus artedi* in gill nets and used estimates of encounter and retention probabilities to obtain a more accurate description of Cisco length frequency. Assuming that adjusted gill-net counts are a more accurate representation of kokanee length structure than unadjusted counts, we sought to compare the adjusted length distribution of kokanee sampled in gill nets with that of midwater trawls to identify the potential size selectivity of midwater trawls. In addition, we considered the strengths and limitations of each sampling gear for sampling a pelagic species.

METHODS

Three lakes (Lake Coeur d'Alene, Hayden Lake, Lake Pend Oreille) and four reservoirs (Anderson Ranch Reservoir, Arrowrock Reservoir, Dworshak Reservoir, Lucky Peak Reservoir) throughout Idaho were selected for sampling. The systems varied in area and depth (Table 1), and were selected based on the presence of routinely monitored kokanee populations. Systems were also selected to represent a wide distribution of kokanee lengths and densities (Rieman and Myers 1992; Butts et al. 2013; Wahl et al. 2015).

Kokanee sampling was conducted from June to August in 2015–2017. Each system was sampled with midwater trawls and experimental gill nets. In an effort to maximize the catch of juvenile and adult kokanee, all sampling was conducted at night during thermal stratification within 5 d of the dark phase of the moon (Bowler et al. 1979; Rieman 1992; Rieman and Myers 1992). Before sampling, the vertical distribution of kokanee (hereafter, "kokanee layer") was determined using a Furuno model FCV-585 depth sounder with a 10° hull-mounted transducer (Furuno USA, Camas, Washington). Areas with high kokanee densities were targeted for sampling to maximize the catch by using gill nets and midwater trawls.

Each system was sampled using two standard trawls that were representative of those used for routine kokanee monitoring throughout western North America. The "large trawl" measured 10.5 m in length and was towed by an 8.5-m-long boat. The large trawl had a 3.0 × 2.2-m fixed-frame mouth and was constructed of graduated nylon mesh that was 32.0 mm in size starting at the mouth and then decreased to 25.0-, 19.0-, and 13.0-mm

TABLE 1. Surface area and maximum depth at full pool of seven lakes and reservoirs located throughout Idaho used to assess kokanee populations with gill nets and midwater trawls.

Water body	Surface area (km^2)	Maximum depth (m)
Lake Pend Oreille	380.0	351.0
Hayden Lake	15.4	58.0
Dworshak Reservoir	69.2	192.0
Lake Coeur d'Alene	129.0	67.0
Anderson Ranch Reservoir	20.3	97.5
Arrowrock Reservoir	31.5	54.9
Lucky Peak Reservoir	11.4	60.0

mesh in the body of the net. The cod end of the net was 6.0-mm mesh. The "small trawl" measured 11.9 m in length and was towed by a 7.3-m boat. The small trawl had a 2.4 × 1.8-m fixed-frame mouth and was constructed of graduated mesh in the same configuration as the large trawl. Both trawls were towed at approximately 1.5 m/s and sampled in a stepwise, oblique pattern (Rieman 1992). A step measured 3.0 m in height for the large trawl and 2.4 m in height for the small trawl. Trawl nets were towed for 3 min at each step. Following a 3-min tow at one step, the trawl was raised a single step and trawling continued for another 3 min. This process was repeated until the entire kokanee layer was sampled. A single trawl through the entire kokanee layer constituted a transect, and each trawler completed a total of six transects on each waterbody. All fish caught during a midwater trawl survey were measured for TL (nearest 1.0 mm).

Gill netting was conducted within 1 d of midwater trawl sampling. Depending on the vertical distribution of kokanee, one to four gill nets were used to sample the entire kokanee layer. Each gill net measured 48.8 m in length and 6.0 m in depth. Gill nets had 16 panels, each measuring 3.0 m in length. Nets consisted of eight different mesh sizes (12.7-, 19.0-, 25.4-, 38.1-, 50.8-, 63.5-, 76.2-, 101.6-mm stretch measure) with two panels of each mesh size randomly positioned throughout the net. Gill nets were set in the approximate midpoint of each trawl transect and were suspended horizontally within the kokanee layer. The deepest net was set at the bottom of the kokanee layer with subsequent nets placed in 6.0-m steps until the entire kokanee layer was sampled. Typically, three gill nets were set at each sampling site for a total of 18 nets set in each system. Gill nets were soaked overnight (approximately 12 h) and retrieved at dawn. Upon retrieval of each gill net, fish were enumerated by mesh size and information on the mode of capture (i.e., gilling, wedging, entangling) was recorded. A "gilled" kokanee was any fish that was caught in the mesh immediately posterior to the operculum (Millar and Fryer 1999). Fish that were caught on the body behind the operculum were considered "wedged." Fish that were wrapped in the netting or tangled by maxilla, preopercula, teeth, fins, and other projections were considered captured via "entanglement." In addition to capture information, fish were measured for TL and maximum girth (nearest 1.0 mm). Girth was measured directly anterior to the insertion of the dorsal fin.

Gill-net selectivity was modelled assuming two independent probabilities: the probability that a fish of length l encountered the net (encounter probability) and the probability that a fish of length l was retained in mesh m after encountering the net (retention probability; Hamley 1975; Rudstam et al. 1984). The encounter probability was considered proportional to the routine swimming speed of a fish. Swimming speed is related to fish length and can be approximated by a power function (Yates 1983). Therefore, encounter probability can be related to fish length as

$$P(E_l) = A \cdot l^z,$$

where A is a constant and z is the exponent expression for sustained swimming speed. Previous research suggests that a sustained swimming speed of a Sockeye Salmon is proportional to body length raised to a power between 0.42 and 0.50 (Brett and Glass 1973; Ware 1978). Therefore, the encounter probability of kokanee was estimated as fish length raised to the 0.50 power. The term A was unknown, but was scaled by assuming that the largest fish in a population had the highest probability of encountering a passive gear (e.g., $P[E_l]$ = 1.0; Rudstam et al. 1984; Spangler and Collins 1992).

Retention selectivity was estimated using the SELECT (share each length's catch total) method (Millar and Holst 1997; Millar and Fryer 1999). The length–girth relationship was consistent among lakes; therefore, length and girth data were pooled across systems (Carol and García-Berthou 2007; Shoup and Ryswyk 2016) and summarized by 10-mm length groups for each mesh size. Five log-linear models (normal-skewed, normal, lognormal, gamma, binormal; Table 2) were fit to summarized length and girth data using maximum likelihood techniques (Millar and Holst 1997). Models were fit under the assumptions that the observed catches were Poisson random variables and effort was equal among mesh sizes (Millar and Holst 1997). Additionally, models were only fit to kokanee that were captured by gilling or wedging because entanglement is unrelated to fish girth and mesh size (Hamley 1975). The best model was selected based on the lowest model deviance (likelihood ratio goodness-of-fit statistic) and randomly distributed residuals (Millar and Holst 1997).

Selectivity was estimated as the retention probability and a combination of encounter and retention probabilities to understand the relative influence of both probabilities on the selectivity of kokanee in gill nets. The selectivity curves of the best-fit model were used to estimate the relative retention selectivity for gill nets. Relative retention selectivity was calculated as

$$S_l = \sum_j \left(\frac{s_j(l)}{\max_l} \right),$$

where $s_j(l)$ is the retention probability of length class l in mesh size j, and $\max_l$ is the maximum retention probability observed among all length classes (Hansen et al. 1997; Shoup and Ryswyk 2016). The estimated relative retention selectivity was then adjusted for encounter probability to

TABLE 2. Model equations and parameters for five selectivity models used to estimate the retention probability of kokanee sampled using experimental gill nets. Fish length is denoted as l, mesh of size j is m_j, and all other symbols are constants.

Model (parameters)	Selection curve equation [$s_j(l)$]
Normal scale (k_1, k_2)	$\exp\left(-\frac{\left(1-k_j\times m_j\right)^2}{2k_2^2\times m_j^2}\right)$
Normal location (k, σ)	$\exp\left(-\frac{\left(1-k_j\times m_j\right)^2}{2\sigma^2}\right)$
Lognormal (μ, σ)	$\frac{m_j}{l\times m_1}\exp\left(\mu-\frac{\sigma^2}{2}-\frac{\left(\log(l)-\mu-\log\left(\frac{m_j}{m_1}\right)\right)^2}{2\sigma^2}\right)$
Gamma (α, k)	$\left(\frac{l}{(\alpha-1)\times k\times m_j}\right)^{\alpha-1}\exp\left(\alpha-1-\frac{l}{k\times m_j}\right)$
Bimodal (k_1, k_2, k_3, k_4, c)	$\exp\left(-\frac{\left(l-k_1\times m_j\right)^2}{2k_2^2\times m_j^2}\right)+c\,\exp\left(-\frac{\left(l-k_3\times m_j\right)^2}{2k_4^2\times m_j^2}\right)$

estimate the overall relative selectivity of gill nets. The overall relative selectivity was estimated as

$$S_l = P(E_l)\sum_j\left(\frac{s_j(l)}{\max_l}\right),$$

where $P(E_l)$ is the encounter probability of length class l (Rudstam et al. 1984). Overall relative selectivity estimates were then used to adjust the observed count of each length bin by dividing the observed count for each 10-mm length bin by the estimated overall relative selectivity for that length bin. The adjusted length structure of kokanee sampled in gill nets was compared with the length structure of kokanee sampled in midwater trawls and observed gill net counts using a Kolmogorov–Smirnov test (Higgins 2004). All analysis was conducted using R statistical software (R Core Development Team 2017) and was considered significant at α = 0.05.

RESULTS

Bimodal models had the best fit regardless of the data type (i.e., TL, girth; Table 3), and the bimodal model using TL data had the lowest model deviance, indicating it was the best-fit model. Retention by individual mesh sizes increased with increasing kokanee length (Figure 1). For instance, 12.7-mm mesh primarily sampled fish varying in length from 50 to 80 mm; whereas, 50.8-mm mesh sampled kokanee varying in length from about 150 to 330 mm. Relative retention selectivity increased with increasing length and peaked for kokanee varying in length from 320 to 329 mm (Figure 1). However, relative retention selectivity was fairly high for most length classes (Table 4). Only six length classes had a retention probability less than 60%. Incorporation of encounter probability reduced the overall relative selectivity of small fish (≤330 mm). For instance, all fish less than 230 mm had an overall relative selectivity less than 60% following adjustment for encounter probability.

A pattern of size selectivity was apparent across gear types (Figure 2). Midwater trawls tended to sample small-length fish; whereas, gill nets sampled the larger fish in a population. Kokanee sampled with gill nets varied in length from 54 to 537 mm and had an average length of 235 mm (SD = 76.3). Kokanee sampled with the small trawl had an average length of 111 mm (64.6) and varied in length from 33 to 405 mm. The large trawl sampled kokanee that had an average length of 111 mm (SD = 80.8) and varied in length from 25 to 299 mm. Kokanee lengths from midwater trawl catches were centered around 40 and 110 mm; whereas, those from gill nets exhibited distinct modes around 90, 180, and 260 mm.

TABLE 3. Model parameters, residual deviance, and degrees of freedom for five selectivity models estimated using maximum girth and TL of kokanee sampled using experimental gill nets. Top models are indicated in bold italic text. Model-specific parameters are defined in Table 2.

Model	Parameter 1	Parameter 2	Parameter 3	Parameter 4	Parameter 5	Deviance	df
			Girth				
Normal scale	3.34	1.09				2,327.64	166
Normal location	2.89	2.44				1,359.62	166
Log-normal	1.11	0.25				1,278.98	166
Gamma	14.69	0.17				1,453.59	166
Bimodal	***2.89***	***0.43***	***20.07***	***11.48***	***3.48***	***680.10***	***163***
			TL				
Normal scale	6.88	1.92				2,385.97	264
Normal location	5.85	4.40				1,469.05	264
Log-normal	1.85	0.21				1,232.66	264
Gamma	20.07	0.26				1,433.58	264
Bimodal	***6.05***	***0.69***	***13.42***	***10.20***	***4.04***	***452.24***	***261***

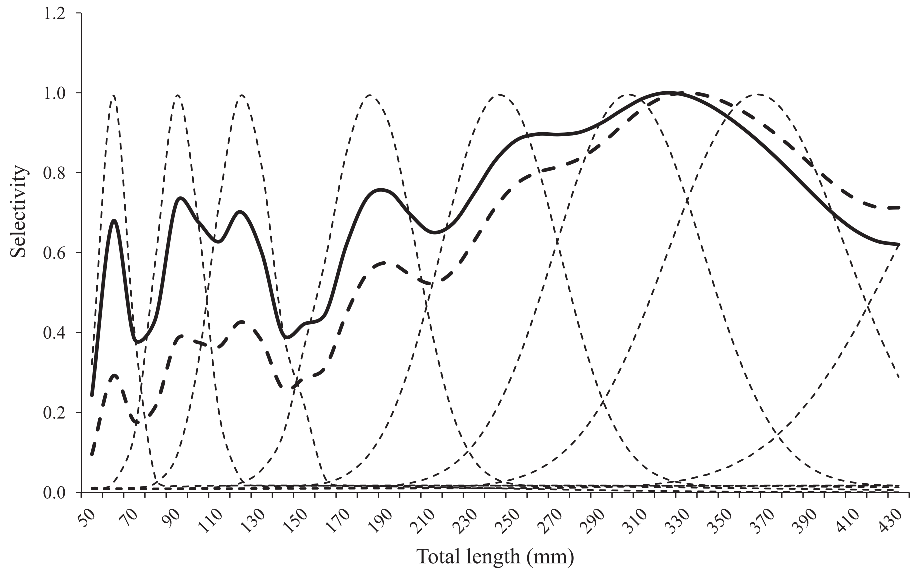

FIGURE 1. Relative retention selectivity (solid line) and overall relative selectivity (dashed line) by 10-mm length bin for kokanee sampled using experimental gill nets. The eight dotted lines represent selectivity curves for individual meshes (1.27-, 1.90-, 2.54-, 3.81-, 5.08-, 6.35-, 7.62-, and 10.16-cm stretch-measure mesh from left to right).

Accounting for overall relative selectivity in gill nets altered both the distribution and length-specific counts of kokanee sampled (Figure 2). The total number of fish increased from 3,159 to an estimated 5,378 fish. In addition, accounting for overall selectivity increased estimates of smaller-length fish (≤200 mm) and decreased estimates of kokanee greater than 200 mm. The adjusted length distributions of fish sampled in gill nets was not significantly different ($P = 0.42$) than the length distribution of the observed counts of fish sampled in gill nets. When gill-net catch was adjusted for overall selectivity, gill nets and midwater trawls exhibited similar catches for fish around 90 mm. However, gill nets and midwater trawls showed increasing discordance in catch as fish length increased. The adjusted length structure of fish sampled in gill nets was significantly different from that of fish sampled in both large and small midwater trawls ($P < 0.01$).

DISCUSSION

Midwater trawl data are commonly used to infer the length and(or) age structure of a target fish population. For instance, the Idaho Department of Fish and Game commonly uses midwater trawl data to apportion length and age distributions to data collected by using hydroacoustic surveys. However, our results suggest that

TABLE 4. The relative retention selectivity and overall relative selectivity by 10-mm length bin for kokanee sampled using experimental gill nets (defined above). The relative retention selectivity accounts for the retention probability; whereas, the overall relative selectivity accounts for the retention probability and the encounter probability.

Length class (mm)	Relative retention selectivity	Overall relative selectivity
50–59	0.243	0.095
60–69	0.679	0.291
70–79	0.384	0.178
80–89	0.435	0.216
90–99	0.727	0.382
100–109	0.678	0.375
110–119	0.628	0.365
120–129	0.702	0.426
130–139	0.600	0.379
140–149	0.396	0.259
150–159	0.421	0.286
160–169	0.447	0.313
170–179	0.621	0.448
180–189	0.740	0.550
190–199	0.753	0.575
200–209	0.695	0.545
210–219	0.651	0.523
220–229	0.673	0.553
230–239	0.748	0.629
240–249	0.830	0.713
250–259	0.882	0.772
260–269	0.897	0.801
270–279	0.896	0.815
280–289	0.902	0.836
290–299	0.925	0.872
300–309	0.958	0.919
310–319	0.987	0.962
320–329	1.000	0.991
330–339	0.994	1.000
340–349	0.971	0.992
350–359	0.938	0.972
360–369	0.897	0.943
370–379	0.850	0.905
380–389	0.798	0.862
390–399	0.745	0.814
400–409	0.694	0.769
410–419	0.654	0.734
420–429	0.629	0.714
430–439	0.620	0.712

midwater trawls are size selective for small fish and may underestimate the larger or older components of a population. For instance, fish greater than 300 mm were rarely (one occasion) sampled using midwater trawls even though they comprised about 7% of the fish sampled using gill nets. Similar patterns of size selectivity for midwater trawls have been reported in the literature. Beam trawls underestimated the density of kokanee by 46–79% compared with estimates from otter trawls in Lake Coeur d'Alene (Parkinson et al. 1994). Those authors noted a discordance between density estimates derived from beam and otter trawls as fish age increased, suggesting there is a pattern of size selectivity for one or both gear types. Midwater trawls failed to sample fishes greater than 215 mm in Stechlin and Breiter lakes, Germany, although they represented 2.3% of all single echo detections in concurrent hydroacoustic surveys (Emmrich et al. 2010). The smallest and largest fishes in Lakes Huron and Michigan were consistently underrepresented in the catch of midwater trawls (Warner et al. 2012). The authors suggested that the apparent size selectivity of midwater trawls was most likely attributable to net avoidance.

In addition to net avoidance, the catch of midwater trawls can be influenced by a myriad of factors including trawl construction (Pearcy 1980; Hayes et al. 2012), towing speed (Parkinson et al. 1994), escape (McClatchie et al. 2000; Emmrich et al. 2010), availability of the target species to the gear (Beauchamp et al. 1997), and environmental factors (Robinson and Barraclough 1978; Thorne and Thomas 1984). Each of the aforementioned factors likely influenced the catch of kokanee in midwater trawls in the current study, but unpublished observations suggest escape is an important factor influencing the catch of large fish. Using underwater cameras, we witnessed large kokanee swimming in and out of actively towed midwater trawls. Although anecdotal, these observations suggest that kokanee reach a length threshold at which point swimming speed exceeds towing speed and escape is possible. Yanase et al. (2007) reported that Sand Flathead *Platycephalus bassensis* exhibited swimming speeds faster than typical trawl-towing speeds (1.5 m/s) but were captured due to the herding aspect of the trawl design. Regardless of the exact mechanism underlying size selectivity of midwater trawls, the fact remains that midwater trawls are selective for smaller fishes, and compositional data from midwater trawls should be used with caution.

Gill nets are also size selective, but select for larger kokanee than do midwater trawls. For instance, the length of fish observed in the gill-net catch peaked at 260 mm in our study; whereas, the modal length from the midwater trawl catch was around 30 mm. Fish less than 50 mm comprised 51% of the total trawl catch in Lake Hiidenvesi, Finland; whereas, only 1% of fish caught in gill nets were less than 50 mm (Olin and Malinen 2003). The gill-net catch of Arctic Char *Salvelinus alpinus* (regionally, lake char *S. umbla*) in Lake Vättern, Sweden, underrepresented small fish (<350 mm) and overrepresented large fish (>350 mm: Jonsson et al.

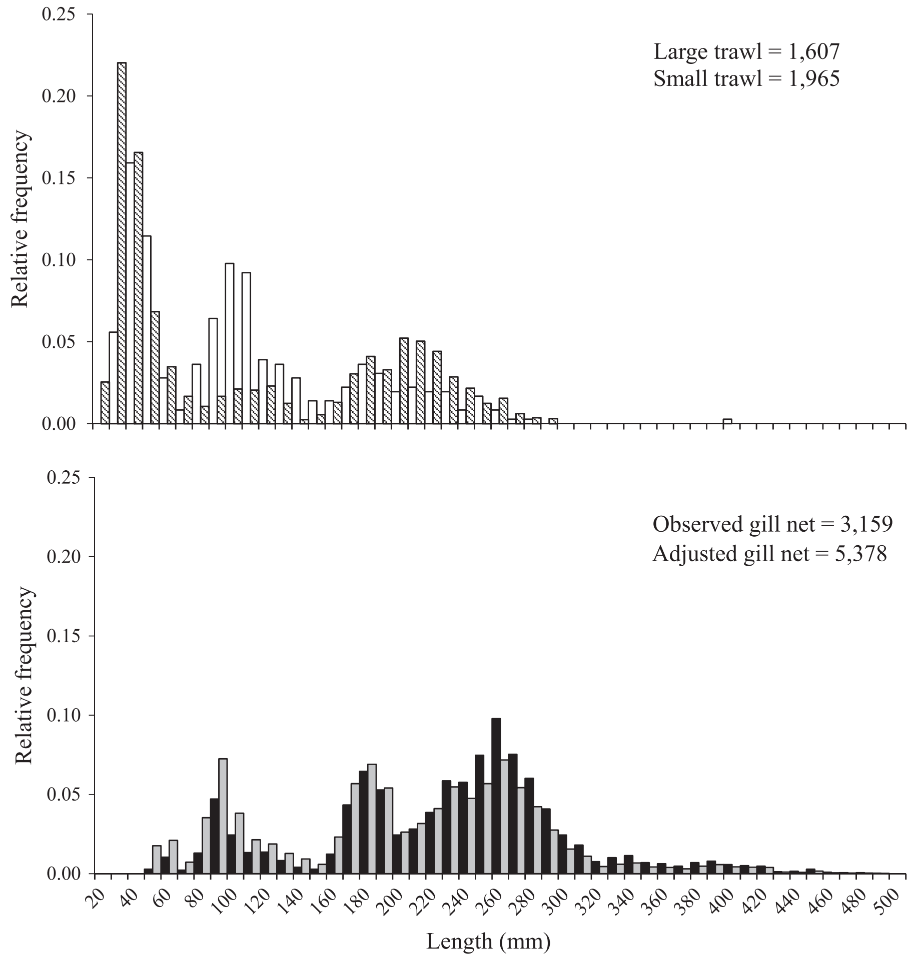

FIGURE 2. Relative length frequency of kokanee sampled from 2015 to 2017 using trawls (top panel) and gill nets (bottom panel). Midwater trawling data are shown for the large trawl (white bars) and small trawl (hashed bars). Gill-netting data are separated into observed (black bars) and adjusted (gray bars) counts. Sample sizes are provided for all gear types.

2013). Catch with gill nets considerably overestimated the number of large Roach *Rutilus rutilus* relative to small Roach (Borgström 1989). Much like midwater trawls, gill-nets catches can be influenced by a myriad of factors including net construction, fish behavior, and environmental characteristics (Hamley 1975; McClatchie et al. 2000; Hayes et al. 2012). However, the disparity in encounter probability between small and large fish likely accounts for much of the selectivity pattern exhibited by gill nets (Rudstam et al. 1984; McClatchie et al. 2000). Small fish are less likely to encounter a passive gear (slow swimming speed) and once they encounter a gear, may lack the momentum needed to penetrate the mesh (McClatchie et al. 2000; Hayes et al. 2012). Overall, the tendency of gill nets to select large fish may also lead to questionable length-structure data and uncertain inferences if left unadjusted.

Accounting for gill-net selectivity is valuable for improving estimates of incidental mortality and length or age distributions (Millar and Fryer 1999). In freshwater fisheries, the primary objective of selectivity modeling focuses on adjusting length or age distributions derived from gill nets. For instance, Shoup and Ryswyk (2016) estimated gill-net selectivity for six recreationally important species and provided selectivity adjustments for the North American standard gill net. The authors reported estimates of proportional size distribution between adjusted and unadjusted gill-net data changed by as much as 15 units. Length data unadjusted for gill-net selectivity would have underestimated the peak length of Channel Catfish *Ictalurus punctatus* by 80 mm (Smith et al. 2017). Survival estimates derived from unadjusted gill-net data likely underestimated the survival of age-9 to age-11 Lake Trout *S. namaycush* in Lake Superior by about 20% (Hansen et al. 1997). The estimated number of 90–99-mm kokanee more than doubled following adjustment for gill-net selectivity in our study. The estimated increase in 90–99-mm fish shifted the modal length from 260–269 mm (observed data) to 90–99 mm (adjusted data) and provided a more realistic representation of the true population structure of kokanee (assuming a type-3 survivorship curve). However, the adjusted length structure of fish sampled in gill nets may still not accurately reflect the true population structure. The encounter probability estimates were based on the sustained swimming speed of Sockeye Salmon and may not reflect the swimming speed of kokanee. Taylor and Foote (1991) compared critical swimming velocities of juvenile Sockeye Salmon and kokanee and found that Sockeye Salmon had a greater mean critical swimming speed (8.3 body lengths/s) than did kokanee (7.3 body lengths/s). However, the authors noted that the difference in critical swimming speed between Sockeye Salmon and kokanee decreased after 1 month of growth. The encounter probabilities used in our study also only account for the relationship between swimming speed and fish length and do not address other length-specific factors, such as gear avoidance, availability, and(or) the mechanism of capture (e.g., low momentum of small fish; Hamley 1975), that may influence catch. Even if retention and encounter probability are the primary factors influencing selectivity of gill nets, estimates of relative retention selectivity are sensitive to initial sample size. For instance, kokanee varying in length from about 140 to 160 mm were rarely sampled among systems by both gill nets and midwater trawls. The low catch of 140–160-mm fish resulted in declines in estimated retention probabilities of 17–20% compared with that of adjacent length classes (e.g., 130–139 mm, 170–179 mm). However, the relatively low estimated retention probability of 140–160-mm kokanee is a reflection of their low occurrence in the sample rather than a length-related reduction in retention probability. Although estimates of encounter and retention probabilities do not account for all the factors that influence fish capture in gill nets, they likely provide a more accurate representation of population structure than unadjusted estimates.

Management Implications

Identifying appropriate sampling gears remains a challenge in fisheries (Bonar and Hubert 2002). In fact, the difficulty with selecting gears is one of the reasons standardized sampling techniques were developed (Bonar et al. 2009). Our results suggest midwater trawls and gill nets would provide disparate representations of kokanee populations due to the size selectivity of each gear. Ideally, data collected from both gears could be combined to account for the limitations of each gear. However, the ability to combine data collected using different gears is limited for many routine population assessments due to feasibility and analytical techniques (e.g., catch-curve analysis; Quist et al. 2012). As such, biologists will most likely attempt to identify a single sampling technique that is most effective for their given study objectives. One of the most common objectives associated with kokanee management is the ability to monitor trends in abundance and forecast the fishery. Gill nets are likely the most effective gear for general trend monitoring as the gear samples kokanee that are in or are entering the fishery. Additionally, the adjustments provided herein should provide more accurate estimates of catch rate and population structure than midwater trawl data. Biologists using gill nets with the same configuration as described above need only to divide their observed catch by the relative selectivity estimates (Table 4) to achieve an adjusted count (Shoup and Ryswyk 2016). Midwater trawls are size selective for small fish and likely provide poor estimates of kokanee length and(or) age structure. As such, midwater trawl data should be used with caution when making inferences about older and larger fish. However, midwater trawls may be effective at addressing specific questions associated with kokanee management. For instance, understanding recruitment dynamics of kokanee in Lake Pend Oreille is of interest to managers of the region. Midwater trawls are likely the best gear to use in this instance because of their selectivity for small fish. No single gear will be able to address all of the questions associated with kokanee management, but an improved understanding of gill-net and midwater trawl selectivity should simplify identifying an appropriate gear and ultimately improve the management of kokanee.

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REFERENCES

Askey, P. J. 2016. Managing dynamic fisheries with static regulations: an assessment of size-graded bag limits for recreation kokanee fisheries. North American Journal of Fisheries Management 36:241–253.

Beauchamp, D. A., C. Luecke, W. A. Wurtsbaugh, H. G. Gross, P. E. Budy, S. Spaulding, R. Dillenger, and C. P. Gubala. 1997. Hydroacoustic assessment of abundance and diel distribution of Sockeye Salmon and kokanee in the Sawtooth Valley lakes, Idaho. North American Journal of Fisheries Management 17:253–267.

Bethke, E., F. Arrhenius, M. Cardinale, and N. Håkansson. 1999. Comparison of the selectivity of three pelagic sampling trawls in a hydroacoustic survey. Fisheries Research 44:15–23.

Bonar, S. A., and W. A. Hubert. 2002. Standard sampling of inland fish: benefits, challenges, and a call for action. Fisheries 27(3):10–16.

Bonar, S. A., W. A. Hubert, and D. W. Willis, editors. 2009. Standard methods for sampling North American freshwater fishes. American Fisheries Society, Bethesda, Maryland.

Borgström, R. 1989. Direct estimation of gill-net selectivity for Roach (*Rutilus rutilus* (L.)) in a small lake. Fisheries Research 7:289–298.

Bowler, B., B. E. Rieman, and V. L. Ellis. 1979. Pend Oreille Lake fisheries investigations. Idaho Department of Fish and Game, Federal Aid in Fish Restoration, Project F-73-R-1, Job Performance Report, Boise.

Brett, J. R., and N. R. Glass. 1973. Metabolic rates and critical swimming speeds of Sockeye Salmon, *Oncorhynchus nerka*, in relation to size and temperature. Journal of the Fisheries Research Board of Canada 30:379–387.

Burgner, R. L. 1991. Life history of Sockeye Salmon. Pages 1–117 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. UBC (University of British Columbia) Press, Vancouver.

Butts, A. E., M. Koenig, J. R. Kozfkay, P. Gardner, and R. Gillingham. 2013. Southwest region (Nampa) fisheries management report, 2012. Idaho Department of Fish and Game, Fisheries Management Report Number 13-122, Boise.

Carol, J., and E. García-Berthou. 2007. Gillnet selectivity and its relationship with body shape for eight freshwater fish species. Journal of Applied Ichthyology 23:654–660.

Emmrich, M., I. P. Helland, S. Busch, S. Schiller, and T. Mehner. 2010. Hydroacoustic estimates of fish densities in comparison with stratified pelagic trawl sampling in two deep, coregonid-dominated lakes. Fisheries Research 105:178–186.

Hamley, J. M. 1975. Review of gillnet selectivity. Journal of the Fisheries Research Board of Canada 32:1943–1969.

Hansen, M. J., C. P. Madenjian, J. H. Selgeby, and T. E. Helser. 1997. Gillnet selectivity for Lake Trout (*Salvelinus namaycush*) in Lake Superior. Canadian Journal of Fisheries and Aquatic Sciences 54:2483–2490.

Hayes, D. B., C. Paola-Ferreri, and W. W. Taylor. 2012. Active fish capture methods. Pages 267–304 *in* A. V. Zale, D. L. Parrish, and T. M. Sutton, editors. Fisheries techniques, 3rd edition. American Fisheries Society, Bethesda, Maryland.

Higgins, J. J. 2004. An introduction to modern nonparametric statistics. Thomson, Brooks, and Cole, Pacific Grove, California.

Jonsson, T., M. Setzer, J. G. Pope, and A. Sandström. 2013. Addressing catch mechanisms in gillnets improves modelling of selectivity and estimate of mortality rates: a case study using survey data on an endangered stock of Arctic Char. Canadian Journal of Fisheries and Aquatic Sciences 70:1477–1487.

McClatchie, S., R. E. Thorne, P. Grimes, and S. Hanchet. 2000. Ground truth and target identification for fisheries acoustics. Fisheries Research 47:173–191.

Millar, R. B. 2000. Untangling the confusion surrounding the estimation of gillnet selectivity. Canadian Journal of Fisheries and Aquatic Sciences 57:507–511.

Millar, R. B., and R. J. Fryer. 1999. Estimating the size-selection curves of towed gears, traps, nets and hooks. Reviews in Fish Biology and Fisheries 9:89–116.

Millar, R. B., and R. Holst. 1997. Estimation of gillnet and hook selectivity using log-linear models. ICES (International Council for the Exploration of the Sea) Journal of Marine Science 54:471–477.

Nelson, J. S. 1968. Distribution and nomenclature of North American kokanee, *Oncorhynchus nerka*. Journal of Fisheries Research Board of Canada 25:409–414.

Olin, M., and T. Malinen. 2003. Comparison of gillnet and trawl in diurnal fish community sampling. Hydrobiologia 506–509:443–449.

Paragamian, V. L., and E. C. Bowles. 1995. Factors affecting survival of kokanees stocked in Lake Pend Oreille, Idaho. North American Journal of Fisheries Management 15:208–219.

Parkinson, E. A. 1988. Long term data collection on kokanee from large lakes: does it make sense? British Columbia Ministry of Environment Fisheries Technical Circular 83.

Parkinson, E. A., B. E. Rieman, and L. G. Rudstam. 1994. Comparison of acoustic and trawl methods for estimating density and age composition of kokanee. Transactions of the American Fisheries Society 123:841–854.

Pearcy, W. G. 1980. A large opening closing midwater trawl for sampling oceanic nekton, and comparison of catches with an Isaacs–Kidd midwater trawl. U.S. National Marine Fisheries Service Fishery Bulletin 78:529–534.

Pope, J. A., A. R. Margetts, J. M. Hamley, and E. Akyuz. 1975. Manual of methods for fish stock assessment, part III selectivity of fish gear. FAO (Food and Drug Organization of the United Nations) Fisheries Technical Paper 41.

Quist, M. C., M. A. Pegg, and D. R. Devries. 2012. Age and growth. Pages 677–731 *in* A. V. Zale, D. L. Parrish, and T. M. Sutton, editors. Fisheries techniques, 3rd edition. American Fisheries Society, Bethesda, Maryland.

R Core Development Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rieman, B. E. 1992. Status and analysis of salmonid fisheries. Idaho Department of Fish and Game, Federal Aid in Fish and Wildlife Restoration, Project F-73-R-14, Job Performance Report, Boise.

Rieman, B. E., and D. L. Myers. 1992. Influence of fish density and relative productivity on growth of kokanee in ten oligotrophic lake and reservoirs in Idaho. Transaction of the American Fisheries Society 121:178–191.

Robinson, D. G., and W. F. Barraclough. 1978. Population estimates of Sockeye Salmon in a fertilized oligotrophic lake. Journal of the Fisheries Research Board of Canada 35:851–860.

Rudstam, L. G., J. J. Magnuson, and W. M. Tonn. 1984. Size selectivity of passive fishing gear: a correction for encounter probability applied to gill nets. Canadian Journal of Fisheries and Aquatic Sciences 41:1252–1255.

Shoup, D. E., and R. G. Ryswyk. 2016. Length selectivity and size-bias correction for the North American standard gill net. North American Journal of Fisheries Management 36:485–496.

Smith, B. J., B. G. Blackwell, M. R. Wuellner, B. D. S. Graeb, and D. W. Willis. 2017. Contact selectivity for four fish species sampling with North American standard gill nets. North American Journal of Fisheries Management 37:149–161.

Spangler, G. R., and J. J. Collins. 1992. Lake Huron fish community structure based on gill-net catches corrected for selectivity and encounter probability. North American Journal of Fisheries Management 12:585–597.

Spotts, J. V., J. P. Shield, K. D. Underwood, and T. C. Cichosz. 2000. Lake Roosevelt fisheries evaluation program, creel survey, and population status analysis, 1998. Spokane Tribe of Indians, Department of Natural Resources, prepared for the Bonneville Power Administration, Division of Fish and Wildlife, Portland, Oregon.

Taylor, E. B., and C. J. Foote. 1991. Critical swimming velocities of juvenile Sockeye Salmon and kokanee, the anadromous and non-anadromous forms of *Oncorhynchus nerka* (Walbaum). Journal of Fish Biology 38:407–419.

Thorne, R. E., and G. L. Thomas. 1984. Recent applications of hydroacoustics to assessment of limnetic fish abundance and behavior. Pages 305–309 *in* Proceedings of the NALMS (North American Lake Management Society) 1983 International Symposium on Lake and Reservoir Management, Knoxville, Tennessee.

Wahl, N. C., A. M. Dux, M. R. Campbell, W. J. Ament, and W. Harryman. 2015. Lake Pend Oreille research, 2012. Annual Report to the Bonneville Power Administration, Project 15-04, Portland, Oregon.

Ware, D. M. 1978. Bioenergetics of pelagic fish: theoretical change in swimming speed and ration with body size. Journal of the Fisheries Research Board of Canada 35:220–228.

Warner, D. M., R. M. Claramunt, J. S. Schaeffer, D. L. Yule, T. R. Hrabik, B. Pientka, L. G. Rudstam, J. D. Holuszko, and T. P. O'Brien. 2012. Relationship between mid-water trawling effort and catch compostion uncertainty in two large lakes (Huron and Michigan) dominated by alosines, osmerids, and coregonines. Fisheries Research 123–124:62–69.

Wydoski, R. S., and D. H. Bennett. 1981. Forage species in lakes and reservoirs of the western United States. Transactions of the American Fisheries Society 110:764–771.

Yanase, K., S. Eayrs, and T. Arimoto. 2007. Influence of water temperature and fish length on the maximum swimming speed of Sand Flathead *Platycephalus bassensis*: implications for trawl selectivity. Fisheries Research 84:180–188.

Yates, G. T. 1983. Hydromechanics of body and caudal fin propulsion. Pages 177–213 *in* P. W. Webb and D. Weihs, editors. Fish biomechanics. Praeger, New York.