

MANAGEMENT BRIEF

Does Moon Phase Affect Indices of Kokanee Size and Abundance as Characterized by Gill-Net Catch?

Philip R. Branigan,*¹  Emily F. Washburne,² and Kevin A. Meyer 

Idaho Department of Fish and Game, 1414 East Locust Lane, Nampa, Idaho 83686, USA

Abstract

Many pelagic fish species such as kokanee *Oncorhynchus nerka* undertake diel vertical migration in response to dynamic interactions between ambient light, foraging opportunity, and predation risk. Consequently, kokanee populations are almost universally sampled during the dark phase of the moon (i.e., the new moon), presumably to optimize capture efficiency. However, it is unclear if this sampling precaution is necessary to avoid bias in kokanee catch data related to the moon phase. We used experimental gill nets to sample kokanee populations in two thermally stratified reservoirs during three distinct moon phases (i.e., new, first quarter, and full) to understand the relative effects of moon phase and other ambient light variables on total catch and average size of captured kokanee. The total catch of kokanee differed significantly between populations but was not significantly affected by moon phase, secchi depth, or net depth. The average size of kokanee sampled from both populations increased significantly with moon illuminance and likely reflects behavior associated with predator-prey dynamics. Results from this case study suggest that the effect of moon phase and other ambient light variables on gill-net catch composition of kokanee is likely population-specific and is governed in part by population parameters such as abundance, growth rate, and size-structure. As such, investigators should be cognizant of—or perhaps standardize gill-net samples to—ambient light variables when indexing populations of kokanee and other pelagic fishes that undertake diel vertical migrations, especially when size indices are examined.

Kokanee *Oncorhynchus nerka* are the nonanadromous form of Sockeye Salmon that serve as an important fishery resource throughout many oligotrophic freshwater systems in western North America. Like other species of Pacific salmon, kokanee achieve maximum ages of 3–4 years in

most populations and are capable of providing robust, harvest-oriented sport fisheries that generate high levels of angling effort. In addition, kokanee may also serve as an important forage base for other popular sport fishes that can achieve trophy size, such as Lake Trout *Salvelinus namaycush*, Bull Trout *S. confluentus*, and Rainbow Trout *O. mykiss* (Wydoski and Bennett 1981; Pate et al. 2014).

Due to their ecological and recreational value, many kokanee populations are actively managed to monitor and forecast recreational fisheries. For example, hatchery supplementation is often used to benefit trophy fisheries and (or) enhance fishing and harvest opportunities for kokanee angling. Most stocking programs follow a put-grow-take model, where age-0 fish are stocked as fry or fingerlings that are expected to achieve sizes exploitable by recreational anglers 1–4 years later. However, kokanee growth can be influenced by population density (Rieman and Myers 1992; Luecke et al. 1996), which may affect the size of exploited age-classes (Rieman and Maiolie 1995; Grover 2005). Many fisheries management agencies index kokanee populations to evaluate responses to environmental or management perturbations such as changes in reservoir operations, angling regulations, or stocking densities.

Kokanee typically congregate in the pelagic zone of lakes and reservoirs and are susceptible to capture with a variety of sampling gears. Active capture techniques such as hydroacoustic methods (e.g., Hardiman et al. 2004) and midwater trawling techniques (e.g., Rieman and Myers 1992; Paragamian and Bowles 1995) are often used to survey kokanee populations. Hydroacoustic surveys can effectively sample the entire pelagic zone and provide data

*Corresponding author: phil.branigan@idfg.idaho.gov

¹Present address: Idaho Department of Fish and Game, 15950 North Gate Boulevard, Nampa, Idaho 83687, USA.

²Present address: Idaho Department of Environmental Quality, 1445 North Orchard Street, Boise, Idaho 83706, USA.

Received December 2, 2021; accepted March 7, 2022

to estimate absolute population abundance, but acoustics data do not provide direct information on species composition or fish size. Midwater trawls are commonly used in conjunction with hydroacoustic surveys to determine species composition of acoustic targets and to obtain length data. Trawl data itself can also be used to calculate indices of population abundance or characterize size structure. However, midwater trawls tend to select the smallest kokanee that likely have not fully recruited to the recreational fishery (Klein et al. 2019), so size-structure metrics obtained through trawling may be biased low. Alternatively, gill-net surveys are a relatively inexpensive sampling method that can effectively index population abundance and characterize age and size structure of exploitable size-classes of kokanee (Klein et al. 2019). As a passive sampling gear, gill nets rely on movement of fishes to encounter the net and become entangled. Therefore, investigators must be cognizant of the ecology and behavior (e.g., migration patterns) of pelagic fish when conducting population surveys and drawing inferences used to manage and forecast recreational fisheries.

Diel vertical migration (DVM) is a well-documented phenomenon observed across species and trophic levels in both freshwater and marine environments (Narver 1970; Hays 2003; Hansen and Beauchamp 2015). In general, kokanee and other pelagic species will ascend the water column at dusk and remain close to the surface until they descend to deeper water at dawn (Narver 1970; Clark and Levy 1988; Beauchamp et al. 1997). There are two major hypotheses associated with DVM: one suggests that DVM is driven primarily by foraging opportunity (e.g., Janssen and Brandt 1980), and the other is centered on predator avoidance (e.g., Eggers 1978; Clark and Levy 1988; Hrabik et al. 2005). As a model subject representing the lowest trophic level, zooplankton DVM patterns have been well described in freshwater and saltwater systems, and the magnitude (i.e., distance migrated) of the migrations are stronger when predators (e.g., kokanee) are present (e.g., Dodson 1990; Dawidowicz and Loose 1994; Dodson et al. 1997). In addition, the effect and overall magnitude of DVM in freshwater systems is seasonal and may be influenced by a variety of environmental conditions such as water temperature, latitude, photoperiod, and water clarity (Dodson 1990; Dawidowicz and Loose 1994; Stockwell and Johnson 1999; Hardiman et al. 2004; Hansen and Beauchamp 2015). Light intensity is another important driver of DVM and must fluctuate daily to induce migration, as DVM ceases for fish populations in arctic waters under the midnight sun (Bogorov 1946; Blachowiak-Samolyk et al. 2006). There are a number of potential reasons why a species may undertake DVM, but predator avoidance is thought to serve as a primary driver (Hays 2003). Just as kokanee exploit the DVM patterns of their prey, other piscivorous fishes in freshwater systems

may similarly exploit the DVM behavior of kokanee (Hardiman et al. 2004; Pate et al. 2014).

Kokanee populations are usually sampled overnight during the dark phase of the moon (i.e., the new moon), presumably to optimize capture efficiency (e.g., Rieman and Myers 1992; Paragamian and Bowles 1995; Stockwell and Johnson 1999; Hardiman et al. 2004; Klein et al. 2019). Despite the number of published studies documenting the causes and effects of DVM, it is unclear if moon phase and other ambient light variables (e.g., turbidity) significantly affect catch of kokanee sampled during gill-net surveys. Our objective was to sample kokanee populations with gill nets during three distinct moon phases (i.e., new, first quarter, and full) to understand the relative effects of ambient light variables on total catch and size structure.

METHODS

Study Sites

Kokanee were captured with monofilament, multi-panel gill nets at two reservoirs located in southern Idaho. Anderson Ranch Reservoir has a storage capacity of $5.86 \times 10^8 \text{ m}^3$ and surface area of 1,918 ha. It typically supports a harvest-oriented recreational kokanee fishery, self-sustaining populations of piscivores like Smallmouth Bass *Micropterus dolomieu* and Northern Pikeminnow *Ptychocheilus oregonensis*, and a hatchery-supported population of landlocked Chinook Salmon *Oncorhynchus tshawytscha* that may also exert predatory pressure on kokanee behavior. Kokanee have been stocked into Anderson Ranch Reservoir during the spring for decades, with releases varying from 50,000 to 200,000 individuals, but no kokanee were stocked in 2019. An unknown portion of the kokanee population stems from wild production.

Mackay Reservoir has a storage capacity of $5.55 \times 10^7 \text{ m}^3$ and surface area of 461 ha. Kokanee and Rainbow Trout comprise the sport fishery, and there are no notable predator populations. Some Rainbow Trout may grow large enough to exhibit piscivory, but their effect on the overall composition of the kokanee population is presumed to be negligible. The kokanee population is largely self-sustaining, but in 2019, 95,000 age-0 kokanee were stocked due to production surplus at a nearby hatchery, marking the first stocking event in 10 years.

Field Sampling

Surveys occurred in June and July of 2019, when both reservoirs were thermally stratified and before mature kokanee began spawning emigrations. The vertical distribution of kokanee and other pelagic fish in lentic systems is thought to be governed by complex interactions between fish size, thermal stratification, and predator-prey dynamics

(Luecke and Wurtsbaugh 1993; Stockwell and Johnson 1997, 1999; Hardiman et al. 2004). As such, we limited this evaluation to periods when both reservoirs were thermally stratified. Secchi depth (m) was measured at the beginning of each sampling event to quantify turbidity, which affects light attenuation (Kirk 1985). Both populations were sampled three times each month during each occurrence of the new, first quarter, and full moon phases (± 2 d).

Pairs of gill nets were positioned at unique depths and oriented in parallel (within 50 m) to sample a localized two-dimensional area. This approach afforded the opportunity to account for the progressive absorption of light through the water column while minimizing any differences in ambient light conditions experienced in other relative space. One net in each pair was positioned immediately beneath the water surface (hereafter, "surface net") and the other was suspended at a depth that intersected the thermocline (hereafter, "thermocline net"). Both reservoirs experience high levels of angling and boating traffic, so the float line of all surface nets was positioned 1.5 m below the surface of the water. We identified the depth of the thermocline by slowly lowering a thermometer (Vernier Software & Technology; Beaverton, Oregon, USA) in 0.5-m increments and observing changes in the temperature profile. Thermocline depth varied throughout the sampling period, and thermocline nets were positioned such that the horizontal center line of the net aligned with the depth of the thermocline.

Each net measured 54 m wide and 6 m deep and was constructed with 4.5-m-wide sections of monofilament mesh panels consisting of 20-, 25-, 32-, 38-, 51-, and 64-mm bar measure mesh (two panels per net). Monofilament diameter size was 0.15 mm for 20-, 25-, and 32-mm mesh and 0.28 mm for 38-, 51-, and 64-mm mesh. Sampling locations were randomly selected for each water body initially, and those same locations were repeated during each sampling event (i.e., moon phase). Two sets of net pairs (i.e., four total nets) were deployed at Anderson Ranch Reservoir, whereas one pair (two nets) was deployed at Mackay Reservoir due to elevated catch. Accordingly, 24 gill-net samples were collected at Anderson Ranch Reservoir and 12 samples were collected from Mackay Reservoir. All gill nets were positioned at respective depths in the evening and retrieved the following morning in the order that they were deployed. Fish captured from each net were identified and measured for total length to the nearest millimeter. Kokanee comprised the vast majority (~85%) of the catch, and all other species were removed from further analysis for this study.

Data Analysis

Catch and environmental data were summarized by moon phase, net depth, and fishery to describe patterns in

catch and evaluate differences among samples. Means were calculated to describe patterns in catch and inform regression models. Relative abundance (catch per unit effort [CPUE]) was estimated as the total number of fish caught in surface and thermocline nets divided by the total number of nets fished at each depth (i.e., fish-net night) during each lunar phase.

Negative binomial regression models were fit to evaluate the relative effects of ambient light variables on total catch of kokanee. A suite of candidate models was developed a priori using moon phase (i.e., light intensity), secchi depth (i.e., light penetration), and net depth (surface or thermocline) as predictor variables, whereby each gill net served as the sampling unit. Each candidate model included an offset term for gill-net fishing effort (measured to the nearest minute), as well as a fixed term for fishery to account for inherent differences between the populations (e.g., stocking regimes, angler harvest, reservoir operation). Although a mixed-effect modeling approach is typically applied to repeated measures data, our data set lacked the replication needed to incorporate a random effect structure. As such, inferences drawn from all models presented herein are specific to the time period (i.e., summer thermal stratification) and to the populations sampled and may not represent the patterns observed at all times across all kokanee populations. In addition, a null model that contained only an offset term for fishing effort was included in the candidate set to evaluate the relative effects of ambient light variables versus random chance. Moon phase and secchi depth could not be included as additive or interactive terms in any single model due to lack of replication between the range of secchi depths measured and lunar phases sampled. Instead, moon phase and secchi depth were isolated among models to determine the relative importance of light intensity versus light penetration on gill-net catch. Interactions between moon phase \times net depth and secchi depth \times net depth were included in the candidate suite to account for variation associated with the progressive attenuation of light that occurs through the water column.

Another suite of linear regression models was fit to evaluate the relative effects of ambient light variables on the average size of kokanee captured. Total length (mm) of each captured kokanee was used as the unit of observation, and candidate models were developed using the same a priori combinations of predictor terms that were included in the negative binomial suite, including a null model (described above). Moon phase and secchi depth remained segregated among candidate models, and each model in the candidate set included a fixed term for fishery (except the null).

Akaike's information criterion (AIC) was used to determine the relative likelihood of each model in the negative binomial and linear regression model suites. Any models

within 2.0 AIC units of that with the lowest AIC value (i.e., the top model) were selected as plausible alternates to explain patterns in gill-net catch (Burnham and Anderson 2002). Regression coefficients for the top negative binomial models were exponentiated to interpret the effect of each parameter on the odds scale. All regression coefficients were deemed statistically significant if their 95% confidence interval (CI) excluded one.

RESULTS

In total, 36 nets were fished overnight during the course of two lunar cycles (Table 1). Secchi depth differed between reservoirs throughout the sampling period, varying from 2.5 to 5.2 m (mean = 3.5 m; SD = 1.0) at Anderson Ranch Reservoir and from 1.5 to 2.7 m (mean = 2.2 m; SD = 0.4) at Mackay Reservoir. Thermocline depths ranged from 3.7 to 9.1 m (mean = 6.0; SD = 1.7) at Anderson Ranch Reservoir and from 3.7 to 7.9 m (mean = 5.6 m; SD = 1.6) at Mackay Reservoir. Net soak times varied from 11 h and 50 min to 15 h and 31 min.

A total of 3,242 fish was captured during the study period, with kokanee comprising the vast majority of the catch at both reservoirs ($n = 2,729$). In general, kokanee CPUE varied between nets (i.e., surface or thermocline nets) and fishery (Figure 1). Mean length (\pm SD) of kokanee sampled from Anderson Ranch Reservoir was 367 mm (\pm 111), whereas the mean length in Mackay Reservoir was 233 mm (\pm 51).

The most plausible negative binomial regression models explaining variation in kokanee gill-net catch contained factors associated with ambient light variables. The top negative binomial model associated with kokanee CPUE included secchi depth and net depth, which represented 49% of the AIC weight (i.e., relative likelihood) of all models in the candidate suite (Table 2). An alternate model included moon phase and net depth, and accounted for 36% of the relative AIC weight in the negative binomial suite. However, the 95% CIs associated with parameters in both models indicated that fishery was the only

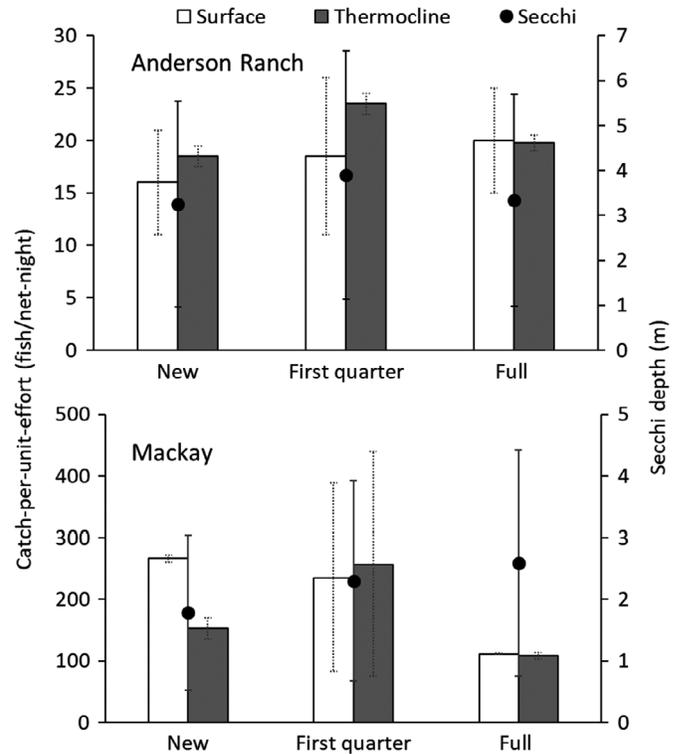


FIGURE 1. Mean catch per unit effort (\pm SE) of kokanee and mean Secchi depth sampled from Anderson Ranch and Mackay reservoirs in June and July 2019 during the new, first quarter, and full moon phases. Nets were positioned at 1.5 m below the water’s surface (i.e., white bars) or at the depth of the thermocline (i.e., gray bars) and fished overnight.

significant variable associated with total catch of kokanee during this study (Table 3).

Length-frequency distributions were similar among moon phases in both populations, but an appreciable decline in catch was observed for the largest mode during the full moon at Mackay Reservoir (Figure 2). The top linear regression model explaining variation in mean size of kokanee in the gill-net catch accounted for 80% of AIC weight and included moon phase, net depth, and fishery

TABLE 1. Data type and means (\pm SD) for variables measured during three distinct moon phases in June and July 2019 at Anderson Ranch and Mackay reservoirs. Data informed negative binomial and linear models developed to describe patterns in total catch and average size of kokanee sampled during gill-net surveys.

Variable	Data type	Anderson Ranch Reservoir			Mackay Reservoir		
		New	First quarter	Full	New	First quarter	Full
Surface net depth (m)	Categorical	1.5 (\pm 0.0)	1.5 (\pm 0.0)	1.5 (\pm 0.0)	1.5 (\pm 0.0)	1.5 (\pm 0.0)	1.5 (\pm 0.0)
Thermocline net depth (m)	Categorical	6.4 (\pm 2.9)	5.6 (\pm 0.5)	6.1 (\pm 0.0)	5.8 (\pm 0.4)	5.8 (\pm 2.5)	5.2 (\pm 1.8)
Secchi depth (m)	Continuous	3.3 (\pm 0.8)	3.9 (\pm 1.4)	3.3 (\pm 0.7)	2.6 (\pm 0.1)	1.8 (\pm 0.4)	2.3 (\pm 0.3)
Effort (h)	Continuous	13.4 (\pm 1.1)	14.5 (\pm 0.5)	14.7 (\pm 0.5)	12.9 (\pm 0.6)	14.3 (\pm 1.4)	13.2 (\pm 0.8)

TABLE 2. Comparison of negative binomial models used to assess the relative effects of ambient light variables on total catch of kokanee sampled with gill nets. Number of parameters (k), Akaike's information criterion (AIC), change in AIC value (Δ AIC), and relative model weight (w_i) was used to select top models from the candidate set.

Model	k	AIC	Δ AIC	w_i
Catch ~ Secchi depth + Net depth + Fishery	3	326.8	0.0	0.49
Catch ~ Moon phase + Net depth + Fishery	3	327.4	0.6	0.36
Catch ~ Secchi depth \times Net depth + Fishery	4	329.5	2.7	0.13
Catch ~ Moon phase \times Net depth + Fishery	4	332.9	6.1	0.02
Intercept only	0	389.3	62.5	0.00

TABLE 3. Coefficient estimates (i.e., odds) and 95% CIs for the most highly supported negative binomial regression models used to estimate total catch of kokanee sampled with experimental gill nets from Anderson Ranch and Mackay reservoirs. Nets were positioned 1.5 m below the surface or at the depth of the thermocline and fished overnight during three distinct moon phases. Thermocline net, new moon, and Anderson Ranch Reservoir serve as the reference categories for net depth, moon phase, and fishery.

Coefficient	Estimate	95% CI
Catch ~ Secchi depth + Net depth + Fishery		
Intercept	1.35	0.66–2.79
Secchi depth	1.01	0.83–1.22
Surface net	0.95	0.68–1.33
Mackay Reservoir	10.62	6.81–16.59
Catch ~ Moon phase + Net depth + Fishery		
Intercept	1.42	1.01–2.03
First quarter moon	1.12	0.76–1.66
Full moon	0.82	0.55–1.22
Surface net	0.97	0.70–1.33
Mackay Reservoir	10.14	7.30–14.22

for predictive factors (Table 4). The 95% CIs associated with the parameter estimates indicated that average length of kokanee was significantly greater in nets set during the first quarter and full moon than during the new moon but did not differ significantly between the surface and thermocline nets (Table 5). In addition, the average length of kokanee sampled from Mackay Reservoir was significantly smaller than those sampled from Anderson Ranch Reservoir. There was virtually no support for any other model in the candidate suite.

DISCUSSION

Anderson Ranch and Mackay reservoirs support kokanee populations that differ in relative abundance, but

overnight gill-net catch used to characterize abundance at these waters was apparently unaffected by nighttime ambient light. Although the results of the negative binomial model selection process suggest that secchi depth, net depth, and moon phase served as better predictors of total catch than random chance, the only parameter that was considered significant in any of the most plausible models was the fishery being sampled. The lack of evidence that moon phase affected kokanee gill-net catch contrasts results from the commercial gill-net fishery of Lake Huron, where average CPUE of Lake Whitefish *Coregonus clupeaformis* declined appreciably during the full moon (Collins 1979). As noted earlier, kokanee fisheries are generally monitored overnight during the new moon due to a perceived moon phase influence on catch (e.g., Rieman and Myers 1992; Paragamian and Bowles 1995; Stockwell and Johnson 1999; Hardiman et al. 2004; Klein et al. 2019). Such a sampling scheme greatly restricts when kokanee population monitoring can be conducted on a monthly basis, and our results suggest that perhaps the practice of restricting kokanee gill-net sampling to the new moon phase can be relaxed with respect to indices of abundance. However, our inference related to kokanee CPUE is admittedly not robust with respect to sample size (i.e., gill-net sets and populations), and we caution against such relaxation until future research can be conducted to qualify the current findings.

In contrast to indices of kokanee abundance, indices of kokanee size structure were influenced by moon phase, whereby the average size of kokanee sampled increased with moon illuminance. This is congruent with DVM theory that (1) smaller kokanee were likely less active at higher light levels in response to increased predation risk and (2) larger individuals were more active due to increased feeding efficiency on zooplankton. Indeed, an appreciable reduction in 190–220-mm kokanee (presumably age-1 fish) was evident with increased moon illuminance, especially during the full moon phase (see Figure 2). *Oncorhynchus nerka* DVM patterns are well linked to the dynamics between predator–prey interactions and ambient light conditions (Narver 1970; Levy 1990; Beauchamp et al. 1995; Scheuerell and Schindler 2003; Hardiman et al. 2004). As such, indices of size structure in kokanee populations gleaned through gill-net catch may be disparate if samples are not standardized by moon phase. Despite this finding, the effect size of Mackay Reservoir in the top linear regression model was an order of magnitude larger than moon phase and net depth, indicating that moon phase and net depth had a much smaller effect on fish size than the effect of water body.

Trade-offs between foraging opportunities and predation risk likely drive a species' propensity to undertake DVM, and although the proximate causes and mechanisms of DVM may be unknown, vertical migration

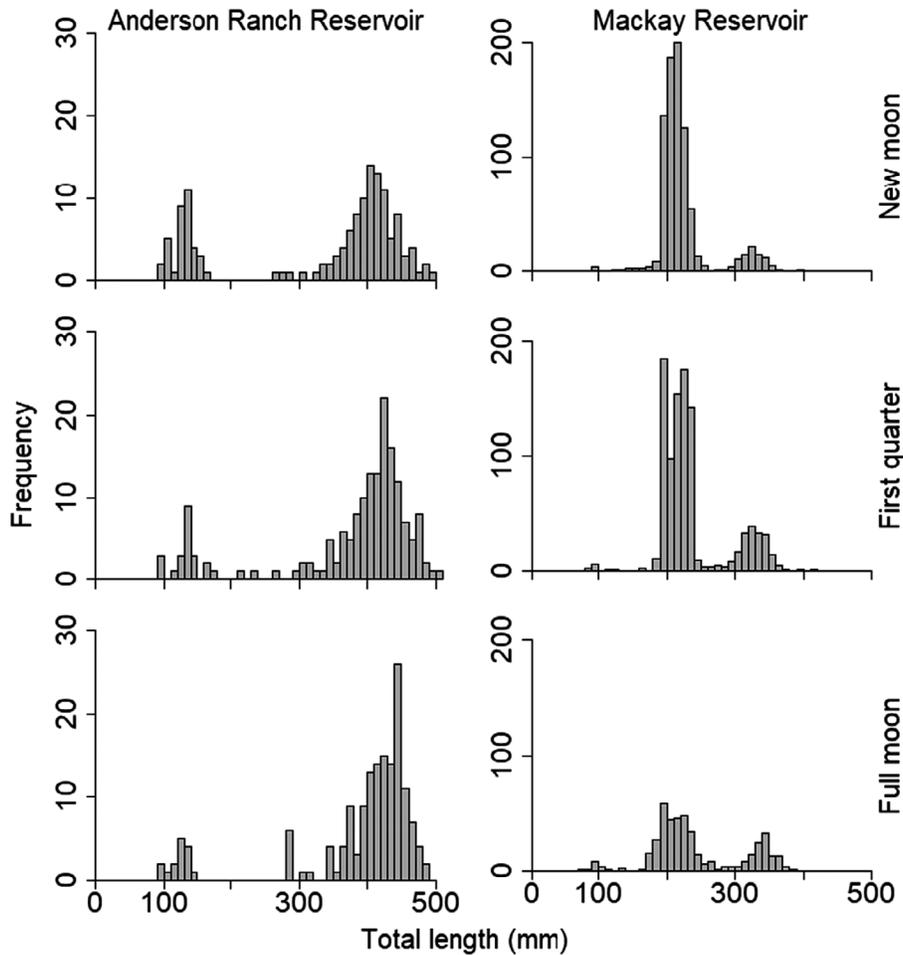


FIGURE 2. Length-frequency histograms for kokanee sampled from Anderson Ranch and Mackay reservoirs using experimental gill nets in June and July 2019 during the new, first quarter, and full moon phases.

TABLE 4. Comparison of linear regression models used to assess the relative effects of ambient light variables on average length of kokanee sampled with gill nets. Number of parameters (k), Akaike’s information criterion (AIC), change in AIC value (ΔAIC), and relative model weight (w_i) was used to select top models from the candidate set.

Model	k	AIC	ΔAIC	w_i
Length ~ Moon phase + Net depth + Fishery	3	30,466.2	0.0	0.80
Length ~ Moon phase \times Net depth + Fishery	4	30,469.1	2.8	0.20
Length ~ Secchi depth + Net depth + Fishery	3	30,532.0	65.76	0.00
Length ~ Secchi depth \times Net depth + Fishery	4	30,533.8	67.57	0.00
Intercept only	0	31,817.1	1,350.8	0.00

TABLE 5. Coefficient estimates and 95% CIs for a linear model used to evaluate the effect of moon phase (new, first quarter, and full) and net depth on average length of kokanee sampled from Anderson Ranch and Mackay reservoirs, Idaho. Experimental gill nets were positioned 1.5 m below the surface or at the depth of the thermocline and fished overnight during three distinct moon phases. New moon, thermocline net, and Anderson Ranch Reservoir serve as the reference categories for moon phase, net depth, and fishery.

Coefficient	Estimate	95% CI
Total length ~ Moon phase + Net depth + Fishery		
Intercept	350.25	342.88–357.61
First quarter moon	17.55	12.04–23.07
Full moon	27.35	20.75–33.94
Surface net	2.14	–2.73–7.01
Mackay Reservoir	–131.50	–137.97 to –125.02

unquestionably influences the visual environment. Feeding rates of planktivorous fish are substantially higher in well-lit conditions than in the dark (Ryer and Olla 1999), but feeding efficiency is reduced in turbid environments (De Robertis et al. 2003). Turbidity has a light-scattering effect that impairs visual clarity and is associated with increases in the magnitude and duration of DVM in freshwater systems (Hansen and Beauchamp 2015). The lack of replication among secchi depths measured and moon phases sampled precluded our ability to include both variables in the same model and evaluate their interactive effects. For instance, the interaction between moon light intensity and secchi depth can account for up to 84% of the variation in DVM amplitude for zooplankton in freshwater systems (Dodson 1990). Diel patterns of kokanee and Bonneville Cisco *Prosopium gemmifer* populations in Bear Lake, Utah–Idaho border have demonstrated that DVM and other foraging movements (e.g., schooling) are minimized in response to increased moon illuminance (Luecke and Wurtsbaugh 1993). Interestingly, angler catch of high-profile piscivores like Northern Pike *Esox lucius* and Muskellunge *E. masquinongy* is maximized during the full moon as well as the new moon (Kuparinen et al. 2010; Vinson and Angradi 2014), suggesting that predator populations will capitalize on the overall effects of the entire lunar cycle as it relates to foraging opportunity.

As a passive sampling technique, the catchability of kokanee in gill nets is directly related to their movement and eventual entanglement. Fisheries managers must be cognizant of foundational sampling considerations such as survey design (e.g., random or stratified sampling) and gill-net effort needed to accurately characterize kokanee population structure. In light of the current study and previous empirical evaluations, it seems prudent to measure ambient light variables such as moon phase, net depth, and secchi depth when indexing pelagic fish populations with gill nets to account for factors that may affect their movement and associated capture. Accounting for these ambient light variables may explain differences in catch composition among sampling events. Considering the significant effect of fishery (i.e., water body) related to total catch and average size of kokanee sampled, gill-net catch metrics for some populations may respond differently to ambient light variables due to inherent population-specific differences in abundance, growth rate, size-structure, and predator assemblages. In addition, system-specific processes such as reservoir inputs (i.e., precipitation, sediments) and outputs (i.e., water withdrawal) had a considerable effect on thermocline depth and secchi depth among sampling events during this study. As such, we encourage future studies to sample several kokanee populations (i.e., more than three) across multiple years to (1) increase the sample size needed to model the interaction between moon phase and secchi depth and (2) provide an

improved modeling framework (i.e., a random effect structure) to assist in controlling for unobserved variation among populations (e.g., predation, angler exploitation, reservoir operations). Such a design would expand the scope of inference provided by the current case study and further elucidate factors associated with the precision of annual kokanee population indices that are used to forecast recreational fisheries or measure changes in management strategies.

ACKNOWLEDGMENTS

A special thanks to B. Marciniak, J. Besson, J. Unsworth, J. Valdez, H. Reynolds, K. Ballinger, and others who assisted with field sampling. We thank J. McCormick and L. Chiaramonte for providing assistance with the development of our analytical approach. We also thank the efforts of three anonymous reviewers, whose comments improved the clarity of this article. Funding for this project was provided by anglers and boaters through their purchase of Idaho fishing licenses, tags, and permits from federal excise taxes on fishing equipment and boat fuel through the Federal Aid in Sport Fish Restoration Program. There is no conflict of interest declared in this article.

ORCID

Philip R. Branigan  <https://orcid.org/0000-0003-3799-0573>

Kevin A. Meyer  <https://orcid.org/0000-0002-1192-3906>

REFERENCES

- Beauchamp, D. A., M. G. LaRiviere, and G. L. Thomas. 1995. Evaluation of competition and predation as limits to juvenile kokanee and Sockeye Salmon production in Lake Ozette, Washington. *North American Journal of Fisheries Management* 15:193–207.
- 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.
- Blachowiak-Samolyk, K., S. Kwasniewski, K. Richardson, K. Dmoch, E. Hansen, H. Hop, S. Falk-Petersen, and L. T. Mouritsen. 2006. Arctic zooplankton do not perform diel vertical migration (DVM) during periods of midnight sun. *Marine Ecology Progress Series* 308:101–116.
- Bogorov, B. G. 1946. Peculiarities of diurnal vertical migrations of zooplankton in polar seas. *Journal of Marine Research* 6:25–32.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multi-model inference: a practical information-theoretic approach*. Springer-Verlag, New York.
- Clark, C. W., and D. A. Levy. 1988. Diel vertical migrations by juvenile Sockeye Salmon and the antipredation window. *American Naturalist* 131:271–290.
- Collins, J. J. 1979. Relative efficiency of multifilament and monofilament nylon gill net towards Lake Whitefish (*Coregonus clupeaformis*) in Lake Huron. *Journal of the Fisheries Research Board of Canada* 36:1180–1185.

- Dawidowicz, P., and C. J. Loose. 1994. Trade-offs in diel vertical migrations by zooplankton: the costs of predator avoidance. *Ecology* 75:2255–2263.
- De Robertis, A., C. H. Ryer, A. Veloza, and R. D. Brodeur. 2003. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1517–1526.
- Dodson, S. 1990. Predicting diel vertical migration of zooplankton. *Limnology and Oceanography* 35:1995–2000.
- Dodson, S. I., R. Tollrian, and W. Lampert. 1997. *Daphnia* swimming behavior during vertical migration. *Journal of Plankton Research* 19:969–978.
- Eggers, D. M. 1978. Limnetic feeding behavior of juvenile Sockeye Salmon in Lake Washington and predator avoidance. *Limnology and Oceanography* 23:1114–1125.
- Grover, M. C. 2005. Changes in size and age at maturity in a population of kokanee *Oncorhynchus nerka* during a period of declining growth conditions. *Journal of Fish Biology* 66:122–134.
- Hansen, A. G., and D. A. Beauchamp. 2015. Latitudinal and photic effects on diel foraging and predation risk in freshwater pelagic ecosystems. *Journal of Animal Ecology* 84:532–544.
- Hardiman, J. M., B. M. Johnson, and P. J. Martinez. 2004. Do predators influence the distribution of age-0 kokanee in a Colorado reservoir? *Transactions of the American Fisheries Society* 133:1366–1378.
- Hays, G. C. 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia* 503:163–170.
- Hrabik, T. R., O. P. Jensen, S. J. Mertell, C. Walters, and J. Kitchell. 2005. Diel vertical migration in the Lake Superior pelagic community, 1. Changes in vertical migration of coregonids in response to varying predation risk. *Canadian Journal of Fisheries and Aquatic Sciences* 63:2286–2295.
- Janssen, J. and S. B. Brandt. 1980. Feeding ecology and vertical migration of adult Alewives (*Alosa pseudoharengus*) in Lake Michigan. *Canadian Journal of Fisheries and Aquatic Sciences* 37:177–184.
- Kirk, J. T. O. 1985. Effects of suspensoids (turbidity) on penetration of solar radiation in aquatic ecosystems. *Hydrobiologia* 125:195–208.
- Klein, Z. B., M. C. Quist, A. M. Dux, and M. P. Corsi. 2019. Size selectivity of sampling gears used to sample kokanee. *North American Journal of Fisheries Management* 39:343–352.
- Kuparinen, A., T. Klefoth, and R. Arlinghaus. 2010. Abiotic and fishing-related correlates of angling catch rates in pike (*Esox Lucius*). *Fisheries Research* 105:111–117.
- Levy, D. A. 1990. Sensory mechanism and selective advantage for diel vertical migration in juvenile Sockeye Salmon *Oncorhynchus nerka*. *Canadian Journal of Fisheries and Aquatic Sciences* 47:1796–1802.
- Luecke, C., and W. A. Wurtsbaugh. 1993. Effects of moonlight and daylight on hydroacoustic estimates of pelagic fish abundance. *Transactions of the American Fisheries Society* 122:112–120.
- Luecke, C., W. A. Wurtsbaugh, P. Budy, H. P. Gross, and G. Steinhart. 1996. Simulated growth and production of endangered Snake River Sockeye Salmon: assessing management strategies for the nursery lakes. *Fisheries* 21(6):18–25.
- Narver, D. W. 1970. Diel vertical movement and feeding of underyearling Sockeye Salmon and limnetic zooplankton in Babine Lake, British Columbia. *Journal of the Fisheries Research Board of Canada* 27:281–316.
- Paragamian, V. L., and E. C. Bowles. 1995. Factors affecting survival of kokanees stocking in Lake Pend Oreille, Idaho. *North American Journal of Fisheries Management* 15:208–219.
- Pate, W. M., B. M. Johnson, J. M. Lepak, and D. Brauch. 2014. Managing for coexistence of kokanee and trophy Lake Trout in a montane reservoir. *North American Journal of Fisheries Management* 34:908–922.
- Rieman, B. E., and M. A. Maiolie. 1995. Kokanee population density and resulting fisheries. *North American Journal of Fisheries Management* 15:229–237.
- Rieman, B. E., and D. L. Myers. 1992. Influence of fish density and relative productivity on growth of kokanee in ten oligotrophic lakes and reservoirs in Idaho. *Transactions of the American Fisheries Society* 121:178–191.
- Ryer, C. H., and B. L. Olla. 1999. Light-induced changes in the prey consumption and behavior of two juvenile planktivorous fish. *Marine Ecology Progress Series* 181:41–51.
- Scheuerell, M. D., and D. E. Schindler. 2003. Diel vertical migration by juvenile Sockeye Salmon: empirical evidence for the antipredation window. *Ecology* 84:1713–1720.
- Stockwell, J. D., and B. M. Johnson. 1997. Refinement and calibration of a bioenergetics-based foraging model for kokanee (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* 54:2659–2676.
- Stockwell, J. D., and B. M. Johnson. 1999. Field evaluation of a bioenergetics-based foraging model for kokanee (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* 56(Supplement 1):140–151.
- Vinson, M. R., and T. R. Angradi. 2014. Muskie lunacy: does the lunar cycle influence angler catch of Muskellunge (*Esox masquinongy*)? *PLOS (Public Library of Science) ONE [online serial]* 9(5):e98046.
- 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.