North American Journal of Aquaculture 81:169–177, 2019 © 2019 American Fisheries Society ISSN: 1522-2055 print / 1548-8454 online DOI: 10.1002/naaq.10084

ARTICLE

Growth Disparity in Sympatric Kokanee Breeding Groups

Zachary B. Klein*

Idaho Cooperative Fish and Wildlife Research Unit, Department of Fish and Wildlife Sciences, University of Idaho, 875 Perimeter Drive, Mail Stop 1141, Moscow, Idaho 83844, USA

Michael C. Quist

U.S. Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit, Department of Fish and Wildlife Sciences, University of Idaho, 875 Perimeter Drive, Mail Stop 1141, Moscow, Idaho 83844, USA

Andrew M. Dux and Matthew P. Corsi

Idaho Department of Fish and Game, 2885 West Kathleen Avenue, Coeur d'Alene, Idaho 83815, USA

Abstract

Growth is arguably the most important dynamic rate function due to its interaction with survival and recruitment. As such, understanding the mechanisms underlying growth is a primary focus of fisheries research. Kokanee Oncorhynchus nerka in Lake Pend Oreille, Idaho, provide an interesting case study for investigating the factors that influence growth. Early-run and late-run kokanee occur in Lake Pend Oreille, but early-run fish generally grow faster than late-run fish. The observed growth disparity between early- and late-run fish could be due to genetic differences between the two groups. Conversely, a common hatchery practice of slowing growth by reducing feed has been hypothesized to elicit a compensatory growth response in early-run fish and to explain the size difference between breeding groups. Using two different experiments, we tested the hypotheses that (1) early-run kokanee are genetically disposed to grow faster than late-run kokanee at identical water temperatures; and (2) feed restriction elicits a compensatory growth response in early-run kokanee that explains the observed size difference between breeding groups. Estimates of mean FL, weight, Fulton's condition factor (K), and specific growth rate (SGR) were not significantly different ($P \ge 0.05$) between early-run and late-run fish in the first experiment. However, water temperature was positively related to mean FL, weight, K, and SGR for both breeding groups. Fish that were subjected to food deprivation exhibited an increased growth rate and obtained weights similar to those of control fish. Overall, our results suggest that early- and late-run fish have similar growth potential, but certain hatchery practices likely provide early-run fish with an initial advantage in growth, size, or both.

Growth is arguably the most important dynamic rate function governing fish population dynamics. Growth is related to survival and recruitment through its effects on myriad factors, including size at maturity, size-mediated predator-prey interactions, and size-related mortality. For instance, the length and age of adult female Black Rockfish *Sebastes melanops* were positively related to growth of their progeny (Berkeley et al. 2004). Large larval Colorado Pikeminnow *Ptychocheilus lucius* (44 mm) exhibited a higher survival rate (100%) than small (30 mm; 3.3% survival) and intermediate-length (36 mm; 6.7%) fish subjected to starvation over a 210-d laboratory experiment (Thompson et al. 1991). The authors (Thompson et al. 1991) concluded that smaller individuals lacked the lipid reserves necessary to survive periods of low prey abundance. In addition, growth provides insight on the abiotic (e.g.,

^{*}Corresponding author: klei7686@vandals.uidaho.edu Received November 27, 2018; accepted February 20, 2019

water temperature) and biotic (e.g., habitat and prey resources) conditions of a fish's environment (Quist et al. 2012). For instance, the growth of Creek Chub *Semotilus tromaculatus*, Red Shiners *Cyprinella lutrensis*, and Green Sunfish *Lepomis cyanellus* was positively related to habitat quality (i.e., wood) in prairie streams within Fort Riley Military Reservation, Kansas (Quist and Guy 2001). Given the extent of the indirect and direct effects of growth on the ecology and life history of fishes, an understanding of the mechanisms underlying growth is critical.

Kokanee (lacustrine Sockeye Salmon Oncorhynchus nerka) provide an interesting subject for understanding the mechanisms influencing growth in fish. The kokanee is a widely distributed species and is often the focus of management agencies due to its ecological and recreational importance. Throughout their distribution, kokanee exhibit variable life history patterns ranging from stream spawning (Eiler et al. 1992) to shoreline spawning at depths greater than 20 m (Hassemer and Rieman 1981). However, naturally reproducing fish are generally categorized as shore-spawning or stream-spawning ecotypes. Management agencies often employ hatchery programs to supplement or maintain kokanee populations. The cooccurrence of hatchery propagation and naturally reproducing populations can create a complex mixture of wild and hatchery groups exhibiting different breeding strategies. The complex assortment of kokanee breeding groups is epitomized in Lake Pend Oreille (LPO), Idaho. Wild kokanee in LPO are categorized as either early- or laterun fish. Early-run kokanee spawn in tributaries from August to September, whereas late-run kokanee spawn in tributaries and along shorelines from November to December. Tributary-spawning fish (early run and late run) are also collected by the Idaho Department of Fish and Game (IDFG) for broodstock to support statewide kokanee needs. Progeny from LPO broodstock collections are stocked back into the lake; thus, kokanee in LPO represent wild-origin or hatchery-origin fish that exhibit early-run or late-run spawning behavior. In addition to disparate spawning times, growth differences exist among breeding groups (Whitlock et al. 2018). Based on trawl data collected from LPO during 2005-2015, early-run hatchery kokanee were on average about 20 mm longer than late-run hatchery kokanee and 20-30 mm longer than wild-origin (early-run and late-run) fish of the same age (0-3 years; IDFG, unpublished data). Although the disparity in average length between hatchery and wild fish is likely explained by hatchery rearing (e.g., consistent water temperatures and feeding), the difference in length between early-run and late-run hatchery fish is poorly understood. Understanding the mechanisms underlying the growth disparity between early- and late-run kokanee is important from a management perspective. Fast-growing kokanee require less time in hatcheries to reach "stockable" lengths and are more likely to avoid sizeselective predation than slow-growing fish once stocked (Miller et al. 1988). Furthermore, fast-growing fish have been shown to have higher catchability due to behavioral characteristics associated with fast growth (e.g., aggressiveness; Biro and Post 2008; Tsuboi et al. 2016). As such, identifying the factors that contribute to fast growth is an important management consideration for kokanee.

Identifying the primary factors that influence growth in kokanee is difficult. The observed growth difference among kokanee breeding groups could be influenced by a multitude of extrinsic (e.g., water temperature, dissolved oxygen levels, and food availability) and intrinsic (e.g., hormone secretion, age, and morphology) factors (Moyle and Cech 1982). However, we were primarily interested in addressing two hypotheses surrounding the growth disparity between early-run and late-run hatchery fish. Kokanee exhibited genetic differentiation based on breeding group (Whitlock et al. 2018), suggesting that early-run hatchery fish may be genetically predisposed (e.g., feed conversion efficiency) to grow faster than late-run hatchery fish (Huston and Deangelis 1987). Conversely, certain hatchery practices could explain the growth disparity between hatchery-reared kokanee. Due to disparate spawning times of wild fish, the development of early-run larvae reared in the hatchery precedes that of late-run progeny by about 2 months. In an effort to stock similar-size kokanee, hatchery managers may "hold back" early-run hatchery fish by reducing feed such that they are of similar size to late-run kokanee at the time of stocking (June; J. Rankin, IDFG, Cabinet Gorge Fish Hatchery, personal communication). Retarding the growth of early-run kokanee may result in a compensatory growth response whereby periods of depressed growth are followed by periods of accelerated growth (Ali et al. 2003; Dmitriew 2011). For instance, Yellow Perch *Perca flavescens* that were subjected to six cycles comprising 12 d of food deprivation (1.0% of body mass/d) followed by ad libitum feeding exhibited faster growth and achieved similar final weights as control fish (continuous ad libitum feeding) after 147 d (Hayward and Wang 2001). In an effort to determine the underlying cause of the observed growth differences between earlyrun and late-run kokanee, we experimentally tested the hypotheses that (1) early-run kokanee are genetically disposed to grow faster than late-run fish at identical water temperatures and (2) feed restriction elicits a compensatory growth response in early-run kokanee that explains the observed size difference between breeding groups.

METHODS

Experiment 1.—In January 2017, approximately 300 early-run kokanee (mean FL = 39.3 mm) were obtained

from the IDFG Cabinet Gorge Fish Hatchery and transported to the University of Idaho. A similar number of late-run kokanee (mean FL = 36.0 mm) was obtained from Cabinet Gorge Fish Hatchery and transported to the University of Idaho in February 2017. Prior to being transported to the University of Idaho for experimentation, both groups were approximately 125 d posthatch and had experienced the same hatchery conditions. Specifically, both breeding groups were reared at the same water temperatures (8.0–10.0°C) and were fed the same food at the same rate (3.8% of body weight). The two groups were used to evaluate potential growth differences between breeding groups.

Fish were allowed to acclimate for 48 h in a 950-L, flow-through tank at a water temperature of $10^{\circ}C$ ($\pm 1^{\circ}C$). During the acclimation period, fish were fed 3% of their body weight twice daily. After the acclimation period, fifteen 3.8-L, flow-through aquaria were stocked with 15 randomly selected early-run kokanee (n = 225). Fifteen additional aquaria were each stocked with 15 randomly selected late-run kokanee. Each aquarium was randomly assigned to one of three water temperature treatments (winter: $4 \pm 1^{\circ}$ C; spring: $10 \pm 1^{\circ}$ C; summer: $15 \pm 1^{\circ}$ C) such that five aquaria per breeding group were allocated to each treatment. Water temperatures used during the experiment were based on mean seasonal water temperatures of LPO. Kokanee were allowed to acclimate to their aquaria for 72 h before the experiment began. During the acclimation period, water temperatures were maintained at $10 \pm 1^{\circ}C$ for 24 h. After 24 h, water temperatures were increased or decreased to obtain the desired treatment temperature. After 72 h, kokanee were removed from their aquaria, anesthetized with tricaine methanesulfonate (MS-222; 75 mg/L; Western Chemical, Ferndale, Washington), measured for FL (nearest 1.0 mm), weighed (nearest 0.01 g), and returned to their respective aquaria. Fish were unfed for at least 15 h prior to collection of FL and weight data. In an effort to reduce handling stress, individual fish were removed from the anesthesia bath using a $5 - \times 5$ -cm aquarium net and placed directly onto a polyvinyl chloride measuring board. After length was recorded, the fish was transferred to a 5- \times 5-cm piece of nylon mesh that was set on a dry paper towel to absorb excess water. The fish was then transferred to a plastic weigh boat, weighed, and placed in an aerated recovery bath. Collection of length and weight data took about 10 s per fish.

Fish were fed 3% of their body weight twice daily using Rangen Trout and Salmon Starter Number 1 (Rangen, Buhl, Idaho) for the duration of the experiment. Feed rations of each aquarium were adjusted weekly to account for changes in weight and(or) fish density (i.e., mortalities). Aquaria were cleaned daily. Dissolved oxygen and water temperature were monitored weekly. All fish were exposed to a 12-h light : 12-h dark cycle. Every 7 d, kokanee were anesthetized with MS-222, measured for FL, and weighed via the procedure described above. On day 28 of the experiment, fish were euthanized with an overdose of MS-222 (200 mg/L), measured for FL, and weighed.

Experiment 2.- In February 2018, approximately 600 early-run kokanee (50.0 mm) were obtained from Cabinet Gorge Fish Hatchery and transported to the University of Idaho, where the potential for a compensatory growth response after starvation was evaluated. Fish were allowed to acclimate for 48 h in a 950-L, flow-through tank at a water temperature of 10°C (±1°C). During the acclimation period, fish were fed 3% of their body weight twice daily. After the acclimation period, thirty 3.8-L, flowthrough aquaria were each stocked with 15 randomly selected kokanee. Prior to stocking, fish were anesthetized with MS-222 (75 mg/L), measured for FL (nearest 1.0 mm), weighed (nearest 0.01 g), and placed in an aquarium. All fish were measured and weighed by using the procedure described for experiment 1. Five aquaria were randomly assigned to one of five food-deprivation treatments: 7, 14, 21, 28, or 35 d without feed (hereafter referred to as 7-, 14-, 21-, 28-, and 35-d groups, respectively). The remaining five aquaria served as controls. Control fish were fed for the duration of the experiment; treatment fish were fed after completion of their food deprivation period until the end of the experiment. Because compensatory growth most often occurs through hyperphagia (Ali et al. 2003), treatment and control fish were fed an excess ration (6% of mean body weight) of Rangen Trout and Salmon Starter Number 1 twice daily to allow for increased food intake. Feed rations of each aquarium were adjusted weekly to account for changes in weight, fish density (i.e., mortalities), or both. The experiment was run for 70 d to allow any growth compensation to manifest. Water temperatures of all aquaria were held at $10 \pm 1^{\circ}$ C to mimic spring water temperatures in LPO. All fish were exposed to a 12-h light : 12-h dark cycle. Every 7 d, kokanee were anesthetized with MS-222, measured for FL, and weighed. Aquaria were cleaned daily. Dissolved oxygen and water temperature were monitored weekly. On the final day of the experiment, fish were euthanized with an overdose of MS-222 (200 mg/L), measured for FL, and weighed.

Analysis.— For both experiments, average FL and weight were estimated for each measurement period and aquarium. The specific growth rate (SGR) was estimated for each measurement period and aquarium as

$$\mathrm{SGR} = \left(\frac{\log_e W_f - \log_e W_i}{t}\right) \times 100,$$

where W_f represents the average final weight of fish in an individual aquarium; W_i represents the average initial

weight of fish in an individual aquarium; and t represents the time between final and initial weight measurements (Shoup and Michaletz 2017).

Fulton's condition factor (K) was also estimated for each measurement period and aquarium as

$$K = \left(\frac{W_x}{L_x^3}\right) \times 100,000$$

where W_x is the final weight of fish x; and L_x is the final FL of fish x (see Nash et al. 2006; Neumann et al. 2012). Estimates of K were averaged for each aquarium and used for statistical comparisons.

For each experiment, potential differences in FL, weight, K, and SGR between breeding groups and among temperature treatments were evaluated using ANOVA or ANCOVA (Ott and Longnecker 2010). We were primarily interested in potential long-term growth patterns and thus focused our analysis on mean FLs, weights, K-values, and SGRs at the end of each experiment. Because starting weights and lengths differed between early- and late-run fish in experiment 1, ANCOVA was used to evaluate potential differences among final mean FLs, mean weights, and mean K-values between groups by treatment temperature. Breeding group (early run or late run) served as the main effect, and initial mean FL or initial mean weight was included as a covariate to control for initial differences in length and weight between early- and laterun kokanee. All other comparisons were evaluated using ANOVA. In experiment 2, mean FLs, weights, and SGRs of kokanee (treatment and control fish) were likely influenced by the time period after initial feeding (Ali et al. 2003). As such, ANOVA was used to compare final average FLs, weights, and SGRs based on the number of days since feeding commenced. For example, the SGRs of controls and 35-d fish were compared at the 35th day after initiation of feeding. If differences in indices occurred, Tukey's post hoc test was used to detect differences between treatments (Ott and Longnecker 2010). All analyses were conducted using R statistical software (R Development Core Team 2017) and were considered significant at $\alpha = 0.05$.

RESULTS

Experiment 1

Over the course of experiment 1, five fish (3 early run; 2 late run) died. At the beginning of the experiment, average FLs differed between breeding groups (Figure 1). Early-run kokanee averaged 39.28 mm FL (SD = 0.98), and late-run fish averaged 36.07 mm FL (SD = 1.21). As the experiment progressed, average lengths of all

treatment groups increased and were positively influenced by water temperature. Fish reared at 4°C were the shortest (P < 0.001) among the treatment groups. Early-run fish raised in 4°C water had a final mean length of 46.09 mm (SD = 0.61), and late-run fish in the same treatment averaged 43.58 mm (SD = 0.98) at the end of the experiment. Both early- and late-run fish reared in 15°C water obtained the longest mean FLs of any treatment group (early run: 47.75 mm FL, SD = 1.12; late run: 48.10 mm FL, SD = 0.79) by the conclusion of the experiment. At the end of the experiment, mean FLs of early- and laterun fish were not statistically different for the 4°C $(F_{1, 9} = 0.41, P = 0.54)$ and 10°C $(F_{1, 9} = 2.07, P = 0.19)$ treatments. However, early- and late-run fish reared in 15°C water exhibited a significant difference in mean FL at the end of the experiment ($F_{1, 9} = 17.69, P = 0.0001$).

At the beginning of the experiment, average weights differed between breeding groups (Figure 1). Early-run kokanee averaged 0.39 g (SD = 0.02), whereas late-run fish exhibited a mean weight of 0.28 g (SD = 0.01). As the experiment progressed, average weights were variable and primarily influenced by water temperatures. Both breeding groups obtained the lowest final mean weight in 4°C water (P < 0.001) at the conclusion of the experiment. At the termination of the experiment, early-run fish raised in 4°C water averaged 0.64 g (SD = 0.19) in



FIGURE 1. Average FL (top panel) and weight (bottom panel) of earlyrun (solid lines; solid symbols) and late-run (dashed lines; open symbols) kokanee reared at 4° C (triangles), 10° C (squares), or 15° C (circles).

weight, and late-run fish in the same treatment had a mean weight of 0.51 g (SD = 0.14). Early-run fish raised in 10°C water were the heaviest among treatments (0.73 g; SD = 0.25) at the end of the experiment, whereas late-run kokanee obtained the heaviest mean weight in 15°C water (0.71 g; SD = 0.15) over the same time period. At the end of the experiment, mean weights were not statistically different between early- and late-run fish in the 4°C ($F_{1, 9} = 2.32$, P = 0.18), 10°C ($F_{1, 9} = 0.85$, P = 0.39), or 15°C ($F_{1, 9} = 2.22$, P = 0.19) treatment.

Early-run kokanee exhibited better body condition than late-run fish at comparable time frames (Figure 2). After 14 d, early-run fish had an average K between 0.66 (SD = 0.06) and 0.69 (SD = 0.09), and late-run fish had an average K between 0.61 (SD = 0.05) and 0.64 (SD = 0.05) over the same time frame. Similar patterns in condition were apparent at the end of the experiment. For instance, estimates of K for all early-run fish were about 0.64 at 28 d, whereas the K of late-run fish was between 0.59 (SD = 0.05) and 0.65 (SD = 0.05) over the same time period. Average K was influenced by water temperature, but the effects were variable. Fish reared at 10°C and 15°C tended to have better condition than fish reared at 4°C. At the end of the experiment, K was not statistically different between early- and late-run fish at any temperature treatment (4°C: $F_{1, 9} = 4.45$, P = 0.08; 10°C: $F_{1, 9} = 1.08$, P = 0.34; 15°C: $F_{1, 9} = 1.88$, P = 0.22).

The SGRs were variable between kokanee breeding groups through time and among treatments (Figure 3). Late-run fish in the 10° C treatment exhibited the fastest growth rate among all treatments. For instance, late-run kokanee in the 10° C treatment averaged 4.58%



(SD = 0.62) growth each day in the first week of experimentation, whereas all other treatments had SGRs of 3.62% or less. Overall, SGRs declined through time and converged on relatively similar values by the end of the experiment. No difference in growth between breeding groups was apparent at the conclusion of the experiment ($F_{1, 29} = 0.33$, P = 0.57). However, water temperature influenced the growth rates of both groups ($F_{2, 29} = 28.12$, P < 0.001). The final SGR of fish held at 4°C was significantly less than that of fish held at 10°C and 15°C (P < 0.001), but there was no difference in mean SGR between fish in the 10°C and 15°C treatments (P = 0.86).

Experiment 2

A single fish died during experiment 2. The mean FL of study fish varied little over the course of the experiment (Figure 4). At the beginning of the experiment, the mean FL of all groups was 50.53 mm (SD = 1.37), and there was no significant difference between groups ($F_{5, 29} = 0.65$, P = 0.66). Control fish obtained the longest average FL of all fish after 70 d (74.29 mm; SD = 7.35). However, control fish exhibited similar average FLs as treatment fish for a given time period. For example, the average FL of treatment and control fish 35 d after initiation of feeding varied from 61.37 mm (35-d group) to 65.70 mm (14-d group). No significant differences in average FL were observed between control fish and treatment groups regardless of the time period ($P \ge 0.05$).

Treatment fish exhibited fairly consistent weight gain regardless of their treatment (Figure 4). The mean weight of study fish was 0.86 g (SD = 0.03) at the beginning of the experiment, and there was no significant difference between groups ($F_{5, 29} = 2.04$, P = 0.11). Control fish obtained the largest maximum weight of all fish and achieved an average weight of 3.22 g (SD = 0.96) after 70 d. In general, food-deprived fish exhibited mean



FIGURE 2. Average Fulton's condition factor for early-run (solid lines; solid symbols) and late-run (dashed lines; open symbols) kokanee reared at 4° C (triangles), 10° C (squares), or 15° C (circles).

FIGURE 3. Mean specific growth rate (% per day) of early-run (solid lines; solid symbols) and late-run (dashed lines; open symbols) kokanee reared at 4°C (triangles), 10°C (squares), or 15°C (circles).



FIGURE 4. Average FL (top panel) and weight (bottom panel) after initial feeding for early-run kokanee that were starved for 7 d (x-symbols), 14 d (open triangles), 21 d (open diamonds), 28 d (open circles), or 35 d (open squares). Average values for control fish are indicated by the solid squares.

weights similar to controls for a given time period (P > 0.05). The 14-d group was the only treatment that showed a significant difference in mean weight at the end of the experiment when compared to controls (P = 0.03). Fish in the 14-d treatment group averaged 2.99 g (SD = 0.78) after 56 d of excess feeding, whereas controls had a mean weight of 2.64 g (SD = 0.77) after 56 d.

Average K of study fish was fairly consistent throughout the experiment (Figure 5). Control fish tended to exhibit the highest K-values regardless of the time period. Average K decreased with increasing food deprivation time but quickly achieved values similar to those of controls once feeding resumed. However, the time required to reach K-values similar to those of controls was related to the amount of time for which fish were deprived of food. For instance, 7-d fish obtained an average K similar to that of control fish after 7 d of feeding, whereas 28-d fish required 42 d of feeding to obtain a mean K similar to that of control fish. Excluding 35-d fish, all fish achieved a mean K similar to that of control fish by the end of the experiment (P > 0.05). Fish that were deprived of food for 35 d had the lowest mean K (0.73; SD = 0.01) and were the only group to exhibit a mean K that was statistically different from that of controls (P = 0.01).

The SGRs of treatment fish tended to be positively related to the food deprivation period (Figure 6). For



FIGURE 5. Average Fulton's condition factor for early-run kokanee that were starved for 7 d (x-symbols), 14 d (open triangles), 21 d (open diamonds), 28 d (open circles), or 35 d (open squares), after which feeding was resumed. Average values for control fish are indicated by the solid squares.



FIGURE 6. Average specific growth rate (% per day) after initial feeding for early-run kokanee that were starved for 7 d (x-symbols), 14 d (open triangles), 21 d (open diamonds), 28 d (open circles), or 35 d (open squares). Average values for control fish are indicated by the solid squares.

instance, 7-d fish obtained a maximum average SGR of 3.13% (SD = 0.19) after feeding resumed, whereas 28-d fish had a maximum mean SGR of 3.42% (SD = 0.40) after the resumption of feeding. However, the longer fish

were deprived of food, the longer it took those fish to obtain their maximum SGR. Fish that were deprived of food for 14 d achieved their maximum SGR (3.05%; SD = 0.22) after 7 d of feeding, whereas 35-d fish obtained their maximum SGR (3.25%; SD = 0.09) after 28 d of feeding. All fish that were deprived of food for more than 7 d exhibited a higher SGR than controls for the duration of the experiment. After 70 d, the 35-d group (2.43%; SD = 0.32) and 28-d group (2.41%; SD = 0.13)had the highest SGRs, followed by 21-d fish (1.80%; SD = 0.18), 14-d fish (1.60%; SD = 0.08), controls (1.40%; SD = 0.15), and 7-d fish (1.32%; SD = 0.07). Fish that were starved for 14 and 28 d were the only groups to exhibit SGRs statistically higher than those of controls (14 d: P = 0.00; 28 d: P < 0.001) at comparable time frames. All other treatments were not statistically different from controls at similar time periods (P > 0.05).

DISCUSSION

Growth in fishes is influenced by numerous intrinsic and extrinsic factors that often interact and change with a fish's age (Moyle and Cech 1982). Our results confirm the positive effect of water temperature on the growth rate of fish. Early-run and late-run kokanee reared at 10°C and 15°C exhibited significantly faster growth rates than fish raised in 4°C water. In controlled experiments, the growth rate of Sockeye Salmon was maximized at 2.60% per day at 15°C (Brett et al. 1969). Juvenile Atlantic Salmon Salmo salar and Rainbow Trout O. mykiss increased their growth rate by as much as nine times as water temperature increased from 4°C to 16°C (Austreng et al. 1987). However, early- and late-run fish were similarly influenced by increasing water temperature in the current study, suggesting that sympatric fish would have to exhibit divergent behavior (e.g., habitat use and diet) for differences in growth to manifest. Whitlock et al. (2018) suggested that the observed differences in growth between adult (age-2-4) early-run and late-run wild kokanee in LPO were due to differences in behavior and(or) physiology related to genetic differentiation between groups. Despite the findings of Whitlock et al. (2018), we did not observe meaningful differences in FL, weight, or SGR between early-run and late-run kokanee. However, the current study focused on age-0 fish and did not allow for potential differences in behavior or physiology that may manifest in wild adult fish. The offspring of two sympatric Arctic Char Salvelinus *alpinus* morphs exhibited incongruent growth patterns in Lake Fjellfrøsvatn, Norway (Knudeson et al. 2015). Knudeson et al. (2015) suggested that the divergent growth patterns were due to differences in habitat use whereby one morph occupied the profundal zone and exhibited consistent growth rates and the other morph occurred in the littoral zone and exhibited seasonal fluctuations in growth. Early- and late-run hatchery kokanee are stocked in the same locations in LPO and are thought to occupy the same habitat type (limnetic zone) based on standard midwater trawl surveys. Furthermore, the observed growth disparity likely occurs early in life, as evidenced by the consistent size difference among all age-classes of early- and late-run kokanee in LPO. As such, our results suggest that the observed growth difference between early- and late-run kokanee is due to extrinsic rather than intrinsic factors.

The response of kokanee to periods of food deprivation may partially explain the difference in mean length observed in LPO. The average SGR of control fish in experiment 2 was 2.38% per day (SD = 0.44) during their first week of feeding, whereas fish that were deprived of food exhibited SGRs varying from 2.28% per day (SD = 0.24; 35-d group) to 3.13% per day (SD = 0.19;7-d group) during the first week of resumed feeding. Similar patterns of increased growth rate after periods of food deprivation have been reported for various fishes. Atlantic Salmon receiving restricted rations for 37 d attained the same body size as control fish after 215 d of feeding (Nicieza and Metcalfe 1997). Sockeye Salmon that were starved for 1-3 weeks achieved the mean weight of control fish after 8 weeks of feeding (Bilton and Robins 1973). Despite the accelerated growth rate of kokanee in experiment 2, none of the treatment groups obtained final mean weights similar to those of control fish. However, when weights were compared based on post-feeding time, all treatment groups equaled or exceeded the mean weight of controls. After 6 weeks of receiving excess rations, the 7-, 14-, 21-, and 28-d treatments had average weights between 1.88 g (SD = 0.54) and 2.04 g (SD = 0.53), whereas controls had a mean weight of 1.88 g (SD = 0.56). Fish that were starved for 14 d were the only treatment group to achieve an average weight significantly heavier than that of controls. Although the 14-d treatment was the only group to surpass the mean weight of controls, these results suggest that kokanee possess the capacity to overcompensate for lost growth and obtain heavier mean weights than controls. Nevertheless, it is unclear whether an accelerated growth at age 0 would manifest as appreciable size differences in adult fish.

If compensatory growth causes long-term size differences between early- and late-run kokanee, the growth rate of early-run fish would have to equal or exceed that of late-run fish over long time frames. However, previous research suggests that prolonged periods of accelerated growth are rare. Of the 50 growth compensation studies reviewed by Ali et al. (2003), only one (Hayward et al. 1997) reported changes in final size that would likely perpetuate to later life stages. Hayward et al. (1997) subjected hybrid sunfish (Green Sunfish × Bluegill *L. macrochirus*)

to repeated cycles of no feeding and refeeding that varied from 2 to 14 d in length. Sunfish that were subjected to the 2-d treatment outgrew controls by 2x, and those from the 14-d treatment exceeded the growth of controls by about 1.5× at the end of the 105-d experiment. The growth rate of food-deprived sunfish never declined to that of control fish. However, Hayward et al. (1997) continually subjected treatment fish to feed-no feed cycles, so it is unclear whether the growth trajectories of treatment fish would have persisted if they were fed similar to controls. Age-1 Arctic Char that were given a restricted diet for 8 weeks and then were fed an ad libitum ration for 8 weeks showed an initial increase in growth, which then decreased to levels similar to those of control fish (ad libitum feeding; Miglavs and Jobling 1989). In the current study, kokanee generally resumed growth rates commensurate with those of controls once a "normal" growth trajectory was achieved. If early- and late-run kokanee exhibit similar growth patterns in LPO, early-run fish would have to achieve and maintain an initial size advantage over late-run fish for long-term growth disparities to manifest.

Differences in sizes at stocking could potentially influence the size disparity observed between early- and laterun fish in LPO. Hatchery staff attempt to produce similarly sized early- and late-run fish at the time of stocking; however, early-run kokanee may exceed the length of laterun fish by about 13 mm in a given year (Rankin, personal communication). The initial disparity in size between early- and late-run fish could persist, assuming the growth rate of early-run fish never declines below that of late-run fish. Bimodal size distributions can be perpetuated through time given an initial size disparity and constant growth rates (Huston and Deangelis 1987). Furthermore, differences in growth rates between sympatric groups would be amplified in relation to divergences in growth rate. As such, a compensatory growth response of early-run fish coupled with an initial size advantage would magnify the disparity in size between early- and late-run fish. Nonetheless, it remains unclear how size and growth rate at age 0 influence long-term growth trajectories. Juvenile size and growth rate have been shown to influence a suite of life history traits (e.g., adult growth rates and reproductive success) in adult cichlids Simochromis pleurospilus (Taborsky 2006). Taborsky (2006) reported that juvenile cichlid growth rate (and size) influenced adult size, but the author noted that growth rates were highly flexible and could be altered through feeding regimes. Previously fooddeprived Atlantic Salmon displayed full compensation in autumn but exhibited slower growth rates and lipid reserves than control fish during the following spring (Morgan and Metcalfe 2001). Presumably, early-run kokanee would be able to maintain a size advantage over late-run fish, but without long-term data on growthmanipulated kokanee, it is difficult to know how accelerated growth in juvenile fish would influence the growth of kokanee at later life stages.

The primary goal of this research was to identify the cause of divergent growth in sympatric breeding groups of kokanee. We hypothesized that the observed growth difference between early- and late-run fish was due to each group's respective genetics. However, early- and late-run kokanee did not exhibit divergent growth patterns under experimental conditions, suggesting that the observed growth differences are due to factors other than those related to the genetics of each breeding group. The growth rates of both groups responded similarly to changes in water temperature, implying that early- and late-run fish would have to exhibit different behavior (e.g., diet and habitat use) for a growth difference to manifest. In light of the results from experiment 1, we hypothesized that the hatchery practice of retarding the growth of early-run fish would result in a compensatory growth response and lead to the observed differences in length between breeding groups. Our results suggest that kokanee possess the ability to overcompensate for lost growth after periods of food deprivation and support the hypothesis that growth retardation of hatchery fish may partially explain the observed growth difference between early- and late-run kokanee. In addition, our results provide valuable insight for kokanee management. Controlled feed restriction in hatcheries could be used to positively influence the growth rates of age-0 kokanee. Increased growth rates would likely reduce the amount of time fish spend in the hatchery, and even small increases in size may help juvenile fish to avoid size-selective mortality (e.g., predation and starvation; Miller et al. 1988). However, growth compensation has been associated with considerable costs, including hyperphagia-related predation, growth abnormalities, and decreased longevity (Ali et al. 2003; Inness and Metcalfe 2008). As such, large-scale growth manipulations should be used with caution. Although disentangling the factors that influence growth in fishes is difficult, an improved understanding of growth will help advance the management and conservation of economically and ecologically important species.

ACKNOWLEDGMENTS

We greatly appreciate the IDFG, J. Rankin, and the Cabinet Gorge Fish Hatchery staff for providing fish and helpful insight on kokanee growth and husbandry. We thank T. Bruce, J. Evavold, and University of Idaho wet lab staff for assistance in setting up the experimentation facilities. We are also grateful for the continued assistance provided by J. Best. We appreciate D. Schill, C. Conway, T. Johnson, S. Whitlock, and three anonymous reviewers for providing helpful comments on previous versions of the manuscript. Funding for this project was provided by the IDFG and the Bonneville Power Administration. Additional support was provided by the U.S. Geological Survey and the Idaho Cooperative Fish and Wildlife Research Unit. The Unit is jointly sponsored by the U.S. Geological Survey, University of Idaho, IDFG, and Wildlife Management Institute. The use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. There is no conflict of interest declared in this article.

REFERENCES

- Ali, M., A. Nicieza, and R. J. Wootton. 2003. Compensatory growth in fishes: a response to growth depression. Fish and Fisheries 4:147–190.
- Austreng, E., T. Storebakken, and T. Åsgård. 1987. Growth rate estimates for cultured Atlantic Salmon and Rainbow Trout. Aquaculture 60:157–160.
- Berkeley, S. A., C. Chapman, and S. M. Sogard. 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. Ecology 58:1258–1264.
- Bilton, H. T., and G. L. Robins. 1973. The effects of starvation and subsequent feeding on survival and growth of Fulton Channel Sockeye Salmon fry (*Oncorhynchus nerka*). Journal of the Fisheries Research Board of Canada 30:1–5.
- Biro, P. A., and J. R. Post. 2008. Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. Proceedings of the National Academy of Sciences of the United States of America 105:2919–2922.
- Brett, J. R., J. E. Shelbourn, and C. T. Shoop. 1969. Growth rate and body composition of fingerling Sockeye Salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. Journal of the Fisheries Research Board of Canada 26:2363–2394.
- Dmitriew, C. M. 2011. The evolution of growth trajectories: what limits growth rate? Biological Reviews 86:97–116.
- Eiler, J. H., B. D. Nelson, and R. F. Bradshaw. 1992. Riverine spawning by Sockeye Salmon in the Taku River, Alaska and British Columbia. Transactions of the American Fisheries Society 121:701–708.
- Hassemer, P. F., and B. F. Rieman. 1981. Observation of deep-spawning kokanee on artificially created spawning habitat. North American Journal of Fisheries Management 1:173–176.
- Hayward, R. S., D. B. Noltie, and N. Wang. 1997. Use of compensatory growth to double sunfish growth rates. Transactions of the American Fisheries Society 126:316–322.
- Hayward, R. S., and N. Wang. 2001. Failure to induce over-compensation of growth in maturing Yellow Perch. Journal of Fish Biology 59:126–140.
- Huston, M. A., and D. L. Deangelis. 1987. Size bimodality in monospecific populations: a critical review of potential mechanisms. American Naturalist 129:678–707.
- Inness, C. L. W., and N. B. Metcalfe. 2008. The impact of dietary restriction, intermittent feeding and compensatory growth on reproductive and lifespan in a short-lived fish. Proceedings of the Royal Society B: Biological Sciences 275:1703–1708.

- Knudeson, R., H. Johnsen, B. S. Sæther, and S. I. Siikavuopio. 2015. Divergent growth patterns between juveniles of two sympatric Arctic Charr morphs with contrasting depth gradient niche preferences. Aquatic Ecology 49:33–42.
- Miglavs, I., and M. Jobling. 1989. Effects of feeding regime on food consumption, growth rates and tissue nucleic acids in juvenile Arctic Charr, *Salvelinus alpinus*, with particular respect to compensatory growth. Journal of Fish Biology 34:947–957.
- Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Canadian Journal of Fisheries and Aquatic Sciences 45:1657–1670.
- Morgan, I. J., and N. B. Metcalfe. 2001. Deferred cost of compensatory growth after autumnal food shortage in juvenile salmon. Proceedings of the Royal Society B: Biological Sciences 268:295–301.
- Moyle, P. B., and J. J. Cech. 1982. Fishes: an introduction to ichthyology. Prentice-Hall, Englewood Cliffs, New Jersey.
- Nash, R. D. M., A. H. Valencia, and A. J. Geffen. 2006. The origin of Fulton's condition factor—setting the record straight. Fisheries 31:236–238.
- Neumann, R. M., C. S. Guy, and D. W. Willis. 2012. Length, weight, and associated indices. Pages 637–676 in A. V. Zale, D. L. Parrish, and T. M. Sutton, editors. Fisheries techniques, 3rd edition. American Fisheries Society, Bethesda, Maryland.
- Nicieza, A. G., and N. B. Metcalfe. 1997. Growth compensation in juvenile Atlantic Salmon: responses to depressed temperature and food availability. Ecology 78:2385–2400.
- Ott, L. R., and M. Longnecker. 2010. An introduction to statistical methods and data analysis. Brooks-Cole, Belmont, California.
- Quist, M. C., and C. S. Guy. 2001. Growth and mortality of prairie stream fishes: relations with fish community and instream habitat characteristics. Ecology of Freshwater Fish 10:88–96.
- 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 Development Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Shoup, D. E., and P. H. Michaletz. 2017. Growth estimation: summarization. Pages 233–264 in M. C. Quist and D. A. Isermann, editors. Age and growth of fishes: principles and techniques. American Fisheries Society, Bethesda, Maryland.
- Taborsky, B. 2006. The influence of juvenile and adult environments on life-history trajectories. Proceedings of the Royal Society B: Biological Sciences 273:741–750.
- Thompson, J. T., E. P. Bergersen, C. A. Carlson, and L. R. Kaeding. 1991. Role of size, condition, and lipid content in the overwinter survival of age-0 Colorado Squawfish. Transactions of the American Fisheries Society 120:346–353.
- Tsuboi, J., K. Morita, T. Klefoth, S. Endou, and R. Arlinghaus. 2016. Behaviour-mediated alteration of positively size-dependent vulnerability to angling in response to historical fishing pressure in a freshwater salmonid. Canadian Journal of Fisheries and Aquatic Sciences 73:461–468.
- Whitlock, S. L., M. R. Campbell, M. C. Quist, and A. M. Dux. 2018. Using genetic and phenotypic comparisons to evaluate apparent segregation among kokanee spawning groups. Transactions of the American Fisheries Society 147:43–60.