Management of Kokanee in Idaho Lakes: Sampling Techniques, Growth Disparities, and Mysis-Kokanee Interactions

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by

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Authorization to Submit Dissertation

This dissertation of Zachary B. Klein, submitted for the degree of Doctor of Philosophy with a Major in Natural Resources and titled "Management of Kokanee in Idaho Lakes: Sampling Techniques, Growth Disparities, and Mysis-Kokanee Interactions," has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

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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. Despite considerable research over the last 60 years, several questions remain regarding the management of kokanee in Idaho. Specifically, uncertainty surrounding common sampling techniques for kokanee undermine confidence in population assessments for the species. Additionally, observed growth differences between kokanee breeding groups (e.g., early-run, late-run) raise questions about the potential influence of genetics and hatchery practices on the population structure of the species. Finally, the potential mechanisms underlying competitive interactions between kokanee and Opossum Shrimp *Mysis diluviana* (hereafter Mysis) are largely unresolved. In an effort to improve the understanding of the ecology and management of kokanee, we sought to 1) evaluate the size selectivity of different sampling techniques for kokanee, 2) evaluate the potential causes of growth disparities among kokanee breeding groups (early-run, late-run) in Idaho, and 3) investigate how ontogenetic shifts in diet in kokanee potentially influence competitive interactions with Mysis.

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Dedication

This work is dedicated to my wife, Helen S. Westbrook. Helen is my best friend and I remain convinced I would not have succeeded in this endeavor had it not been for her love and support.

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Statement of Contribution

Chapters 2, 3, and 4 were coauthored by M.C. Quist, A.M. Dux, and M.P. Corsi. Z.B. Klein was the primary author on all chapters. However, each coauthor contributed to the development and design of the research underlying the chapters. In addition, all coauthor assisted in the final preparation of each manuscript.

Chapter 1: Introduction

Oncorhynchus nerka is native to the northern Pacific Ocean and occurs as both anadromous Sockeye Salmon and non-anadromous kokanee (Burgner 1991). Sockeye Salmon spend 1–2 years in freshwater and migrate to the ocean; whereas, kokanee live their entire lives in freshwater (Burgner 1991). Kokanee are generally smaller and mature at an earlier age than Sockeye Salmon (Wood and Foote 1996). Both forms are semelparous. Sockeye Salmon and kokanee bury their eggs in gravel depressions in lotic and lentic systems (Hassemer 1984), but may also broadcast spawn over large substrates (Hassemer and Rieman 1981). After hatching, kokanee alevins remain in the gravel and absorb their yolk before emerging and migrating to pelagic habitats (Burgner 1991).

Kokanee and Sockeye Salmon are sympatric throughout much of their distribution (Burgner 1991; Wood and Foote 1996). Kokanee are thought to have derived from Sockeye Salmon populations on several independent occasions (Nelson 1968; Behnke 1972). Examination of the distribution of both forms and the fact that kokanee populations have appeared following the introduction of Sockeye Salmon supports this assertion (Nelson 1968; Foote et al. 1989). Kokanee are now distributed in North America, South America, Asia, Russia, 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).

In Idaho, kokanee established in Lake Pend Oreille (LPO) in the 1930s after emigrating from Flathead Lake, Montana (Wydoski and Bennet 1981). Kokanee flourished in LPO and supported a successful fishery while also serving as prey for sport fishes (Wydoski and Bennett 1981). Following the success of kokanee in LPO, kokanee were stocked into Priest Lake, Idaho in the early 1940s. Kokanee thrived and are largely believed

to have contributed to the substantial increase in size of Bull Trout *Salvelinus confluentus* and Lake Trout *S. namaycush* in Priest Lake (Wydoski and Bennett 1981). Due to the success of kokanee in LPO and Priest Lake, kokanee were introduced throughout Idaho and are now considered one of the most important fish species in the state (Wydoski and Bennett 1981; Rieman and Myers 1992; Rieman and Maiolie 1995).

Despite considerable research over the last 60 years, several questions remain regarding the management of kokanee in Idaho. For instance, kokanee experienced significant declines in the late 1960s in LPO. Similar population declines have been described throughout the western United States and Canada (Rieman and Bowler 1980; Rieman and Falter 1981; Nesler and Bergersen 1991). Factors such as water development, the introduction of Opossum Shrimp *Mysis diluviana* (hereafter Mysis), predation, and exploitation have been hypothesized as causing kokanee declines in Idaho and western North America (Rieman and Myers 1992; Rieman and Maiolie 1995). However, the cause(s) of kokanee declines throughout western North America have not been identified. In an effort to maintain kokanee populations in Idaho, the Idaho Department of Fish and Game has instituted large-scale hatchery supplementation of the species. Unfortunately, the variable success of hatchery supplementation in Idaho necessitates a better understanding of the comparative success of different breeding groups (early-run, late-run) and stocking strategies (size at stocking, timing). Underlying research questions associated with the management of kokanee in western North America is the ability to effectively sample kokanee populations. Therefore, the goals of the proposed research are to 1) evaluate the size selectivity of different sampling techniques for kokanee, 2) evaluate the potential causes of growth disparities among kokanee breeding groups (early-run, late-run) in Idaho, and 3) investigate

how ontogenetic shifts in diet and behavior in kokanee influence competitive interactions with Mysis.

Dissertation Organization

This dissertation is composed of four chapters. Chapter 2 focuses on evaluating the size selectivity of mid-water trawls and has been accepted for publication in the *North American Journal of Fisheries Management*. Chapter 3 tests the hypotheses that growth differences between early- and late-run fish are influenced by 1) genetic differences between groups or 2) the hatchery practice of retarding growth of early-run fish. Chapter 3 has been accepted for publication in the *North American Journal of Aquaculture*. Chapter 4 evaluates how ontogenetic changes in diet potentially influence competition between kokanee and Mysis. The fourth chapter will be submitted to the *Canadian Journal of Fisheries and Aquatic Sciences*. The final chapter provides general conclusions and future directions.

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Chapter 2: Size Selectivity of Sampling Gears Used to Sample Kokanee

A manuscript that is forthcoming in the *North American Journal of Fisheries Management*

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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 mid-water trawls, but the interpretation of data collected using mid-water trawls is difficult due to the unknown size selectivity of the gear. We sought to assess the length selectivity of mid-water trawls by comparing estimates obtained from mid-water trawls to estimates obtained from gill nets adjusted for size selectivity. Experimental curtain gill nets and mid-water 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 to estimates obtained from mid-water trawls to identify potential size selectivity of mid-water trawls. A pattern of size selectivity was apparent for both sampling techniques. The average length of kokanee sampled with mid-water 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 kokanee sampling (e.g., trend monitoring) because the gear is less size selective than mid-water trawls and is adjustable for size selectivity. However, mid-water 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 mid-water trawl selectivity and ultimately improve the ability to sample and manage the species.

Introduction

Kokanee *Oncorhynchus nerka* 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 were the fourth most harvested species in the Lake Roosevelt, Washington fishery 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 using escapement estimates, hydroacoustic surveys, and mid-water trawl surveys (Parkinson 1988; Rieman 1992; Askey 2016). In Idaho, the density of kokanee is monitored using hydroacoustic surveys and mid-water trawl surveys (Rieman 1992). Unlike hydroacoustic surveys, mid-water trawls can also be used to directly estimate the composition (e.g., age, maturity) of kokanee populations (Rieman 1992). However, inferences based on mid-water 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 mid-water 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

87 mm mesh cod ends (Pope et al. 1975). Even when mid-water trawling methods are

standardized, questions remain regarding the size selectivity of the gear (Hayes et al. 2012).

Mid-water trawls targeting Sprat *Sprattus sprattus* and Herring *Clupea harengus* in the Baltic

Sea exhibited size selectivity unexplained by cod end selectivity (Bethke et al. 1999). The

authors suggested that the apparent size selectivity was due to escape out of the front of the

trawls which, in turn, was related to fish size and swimming speed. Considering the

importance of mid-water 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 using techniques such as mark-recapture studies (Millar and Fryer 1999).

Unfortunately, high mortality rates (e.g., ~100%) associated with mid-water trawl sampling

negates the use of direct measures of efficiency measures. Because the efficiency of mid-

water 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 mid-

water 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 artedii* 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 to that of mid-water trawls to identify potential size selectivity of mid-water trawls. In addition, we consider the strengths and limitations of each sampling gear for sampling a pelagic species.

Methods

Three lakes (Coeur d'Alene Lake, 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 2.1), 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 mid-water trawls and experimental gill nets. In an effort to maximize catch of juvenile and adult kokanee, all sampling was conducted at night during thermal stratification within five days of the dark phase of the moon (Bowler et al. 1979; Rieman 1992; Rieman and Myers 1992). Prior to sampling, the vertical distribution of kokanee (hereafter "kokanee layer") was determined using a Furuno Model FCV-585 depth sounder with a 10º hull-mounted transducer (Furuno USA, Camas, Washington). Areas with high

kokanee densities were targeted for sampling to maximize catch using gill nets and mid-water 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" was towed by a 8.5 m boat and measured 10.5 m in length. The large trawl had a 3.0 m $\times$ 2.2 m fixed-frame mouth and was constructed of graduated nylon mesh starting at 32.0 mm at the mouth decreasing to 25.0, 19.0, and 13.0 mm mesh in the body of the net. The cod end of the net was 6.0 mm mesh. The "small trawl" was towed by a 7.3 m boat and measured 11.9 m in length. The small trawl had a 2.4 m $\times$ 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 three minutes at each step. Following a three-minute tow at one step, the trawl was raised a single step and trawling continued for another three minutes. 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 mid-water trawl survey were measured for total length (nearest 1.0 mm).

Gillnetting was conducted within one day of mid-water 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 (i.e., 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 hours) 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 total length 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 sustained swimming speed of Sockeye Salmon *Oncorhynchus nerka* (anadromous form of kokanee) is proportional to body length raised to a power between 0.42–0.50 (Brett and Glass 1973; Ware 1978). Therefore, the encounter probability of kokanee was estimated as fish length raised to the 0.50 power. *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 et al. 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 2.2) 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 catch 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 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 to the length structure of kokanee sampled in mid-water 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 $\alpha = 0.05$.

Results

Bimodal models had the best fit regardless of the data type (i.e., total length, girth; Table 2.3), and the bimodal model using total length data had the lowest model deviance, indicating it was the best fit model. Retention by individual meshes increased with

increasing kokanee length (Figure 2.1). For instance, 12.7-mm mesh primarily sampled fish

varying in length from 50–80 mm; whereas, 50.8-mm mesh sampled kokanee varying in

length from about 150–330 mm. Relative retention selectivity increased with increasing

length and peaked for kokanee varying in length from 320–329 mm (Figure 2.1). However,

relative retention selectivity was fairly high for most length classes (Table 2.4). Only six

length classes had a retention probability less than 60%. Incorporation of encounter

probability reduced the overall relative selectivity of small fish ($\leq$ 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 gears (Figure 2.2). Mid-water 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 54–537 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 33–405 mm. The large trawl sampled kokanee with an

average length of 111 mm (80.8) and varied in length from 25–299 mm. Mid-water trawl

catches were centered around 40 mm and 110 mm; whereas, gill nets exhibited distinct

modes around 90 mm, 180 mm, and 260 mm.

Accounting for overall relative selectivity in gill nets altered both the distribution and

length-specific counts of kokanee sampled (Figure 2.2). 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 ($\leq$ 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 mid-water trawls exhibited similar catches for fishes around 90 mm. However, gill nets and mid-water 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 mid-water trawls ($P < 0.01$).

Discussion

Mid-water 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 mid-water trawl data to apportion length and age distributions to data collected using hydroacoustic surveys. However, our results suggest that mid-water 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 mid-water trawls even though they comprised about 7% of the fish sampled using gill nets. Similar patterns of size selectivity for mid-water trawls have been reported in the literature. Beam trawls underestimated density of kokanee by 46%–79% when compared to otter trawls in Coeur d'Alene Lake, Idaho (Parkinson et al. 1994). The authors noted a discordance between density estimates derived from beam and otter trawls with increasing fish age, suggesting a pattern of size selectivity for one or both gear types. Mid-water 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 mid-water trawls (Warner et al. 2012). The authors

suggested that the apparent size selectivity of mid-water trawls was most likely attributable to net avoidance.

In addition to net avoidance, catch of mid-water trawls can be influenced by myriad factors including trawl construction (Pearcy 1980; Hayes et al. 2012), towing speed (Parkinson et al. 1994), escape (McClatchie et al. 2000; Emmich 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 catch of kokanee in mid-water trawls in the current study, but unpublished observations suggest escape is an important factor influencing catch of large fish. Using underwater cameras, we witnessed large kokanee swimming in and out of actively towed mid-water 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 mid-water trawls, the fact remains that mid-water trawls are selective for smaller fishes and compositional data from mid-water trawls should be used with caution.

Gill nets are also size selective, but select for larger kokanee than mid-water trawls. For instance, observed gill net catch peaked at 260 mm in our study; whereas, the mode of mid-water trawl catch was around 30 mm. Fishes 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). Gill net catch of Arctic Char *Salvelinus umbla* in Lake Vättern, Sweden underrepresented small fish (< 350 mm) and overrepresented

large fish (> 350 mm; Jonson et al. 2013). Catch of gill nets considerably overestimated the

number of large Roach *Rutilus rutilus* relative to small Roach (Borgström 1989). Much like

mid-water trawls, gill nets catch can be influenced by myriad 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 survival of age–9 to age–11 Lake Trout

Salvelinus 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 kokanee (7.3 body lengths/s).

However, the authors noted that the difference in critical swimming speed between Sockeye

Salmon and kokanee decreased following one 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 that may influence catch such as gear

avoidance, availability, and(or) the mechanism of capture (e.g., low momentum of small fish;

Hamley 1975). 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 140–160 mm were

rarely sampled among systems by both gill nets and mid-water trawls. The low catch of

140–160 mm fish resulted in declines in estimated retention probabilities of 17%–20% when

compared to 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.

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 mid-water trawls and gill nets would provide disparate representation 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 entering the fishery. Additionally, the adjustments provided herein should provide more accurate estimates of catch rate and population structure than mid-water trawl data. Biologists using gill nets with the same configuration as described above need only divide their observed catch by the relative selectivity estimates (Table 2.4) to achieve an adjusted count (Shoup and Ryswyk 2016). Mid-water trawls are size selective for small fish and likely provide poor estimates of kokanee length and(or) age structure. As such, mid-water trawl data should be used with caution when making inferences on older and larger fish. However, mid-water 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. Mid-water 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 mid-water trawl selectivity should simplify identifying an appropriate gear and ultimately improve management of kokanee.

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Table 2.1. Surface area and maximum depth at full pool of seven lakes and reservoirs located throughout Idaho.

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

Table 2.2. 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)	$exp\left(-\dfrac{\left(1 - k_j \times m_j\right)^2}{2k_2^2 \times m_j^2}\right)$
Normal location (k, σ)	$exp\left(-\dfrac{\left(1 - k_j \times m_j\right)^2}{2\sigma^2}\right)$
Lognormal (μ, σ)	$\dfrac{m_j}{l \times m_1}\, exp\left(\mu - \dfrac{\sigma^2}{2} - \dfrac{\left(\log(l) - \mu - \log\left(\frac{m_j}{m_1}\right)\right)^2}{2\sigma^2}\right)$
Gamma (α, k)	$\left(\dfrac{l}{(\alpha - 1) \times k \times m_j}\right)^{\alpha - 1} exp\left(\alpha - 1 - \dfrac{l}{k \times m_j}\right)$
Bimodal (k_1, k_2, k_3, k_4, c)	$exp\left(-\dfrac{\left(l - k_1 \times m_j\right)^2}{2k_2^2 \times m_j^2}\right) + c\, exp\left(-\dfrac{\left(l - k_3 \times m_j\right)^2}{2k_4^2 \times m_j^2}\right)$

Table 2.3. Model parameters, residual deviance, and degrees of freedom (df) for five selectivity models estimated using maximum girth and total length of kokanee sampled using experimental gill nets. Top models are indicated in bold text. Model-specific parameters are defined in table 2.2.

Model	Parameters 1	2	3	4	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**
Total length							
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**

Table 2.4. 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
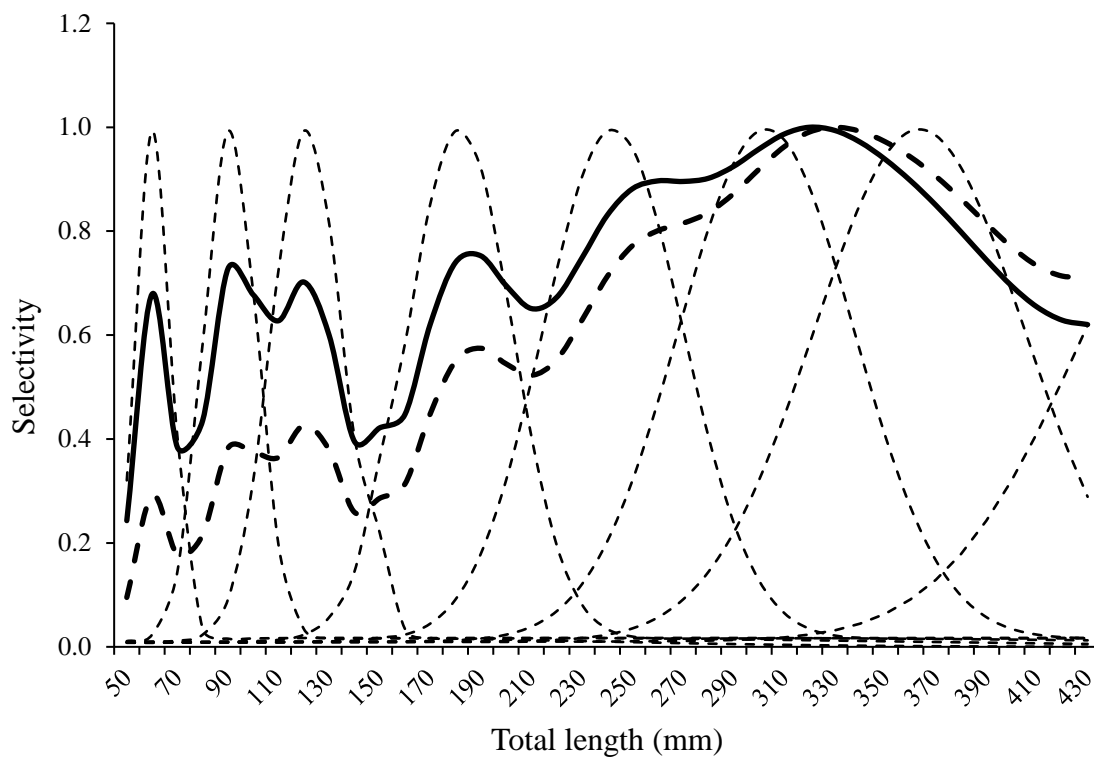
Figure 2.1. Relative retention selectivity (solid line) and overall relative selectivity (dashed line) by 10-mm length bin for kokanee sampled using experimental gill nets. The eight dotted lines represent selectivity curves for individual meshes (1.27-, 1.90-, 2.54-, 3.81-, 5.08-, 6.35-, 7.62-, and 10.16-cm stretch measure mesh from left to right).
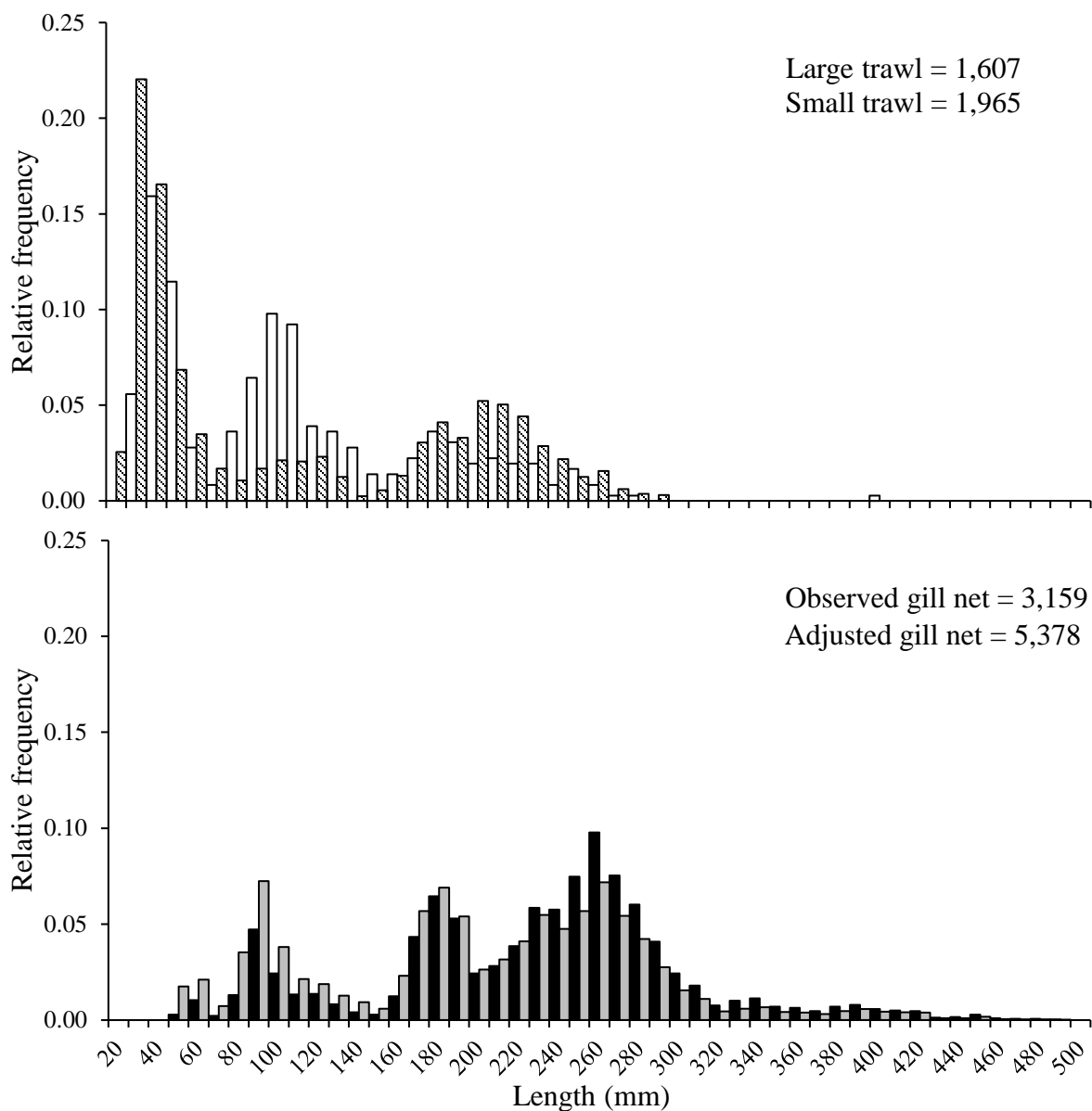
Figure 2.2. Relative length frequency of kokanee sampled from 2015–2017 using trawls (top panel) and gill nets (bottom panel). Mid-water trawling data are shown for the large trawl (white bars) and small trawl (hashed bars). Gill netting data are separated into observed (black bars) and adjusted (gray bars) counts. Sample sizes are provided for all gear types.

Chapter 3: Growth Disparity in Sympatric Kokanee Breeding Groups

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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 each group. 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 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 or 2) feed restriction elicits a compensatory growth response in early-run kokanee that explains the observed size difference between breeding groups. Estimates of mean lengths, weights, Fulton's condition factor, and specific growth rate were not statistically different ($P \geq 0.05$) between early-run and late-run fish in the first experiment. However, water temperature was positively related to mean lengths, weights, Fulton's condition factor, and specific growth rate for both breeding groups. Fish subjected to food deprivation exhibited an increased growth rate and obtained weights similar to control fish. Overall, our results suggest early- and late-run fish have similar growth potential, but certain hatchery practices likely provide early-run fish with an initial growth and(or) size advantage.

Introduction

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 (Berkely 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 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., water temperature) and biotic (e.g., habitat, prey resources) conditions of a fish's environment (Quist et al. 2012). For instance, growth of Creek Chubs *Semotilus atromaculatus*, Red Shiners *Cyprinella lutrensis*, and Green Sunfish *Lepomis cyanellus* was positively related to habitat quality (i.e., wood) in prairie streams in 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, understanding the mechanisms underlying growth is critical.

Kokanee *Oncorhynchus nerka* provide an interesting subject for understanding the mechanisms influencing growth in fish. Kokanee is a widely distributed species and is often the focus of management agencies due to its ecological and recreational importance. Throughout its distribution, kokanee exhibit variable life-history patterns varying 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. In LPO, wild kokanee are categorized as either early- or late-run 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 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 from 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 y; Idaho Department of Fish and Game, 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 size-selective 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, food availability) and intrinsic (e.g., hormone secretion, age, 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., food-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 two 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 stocking (June; J. Rankin, personal communication). Retarding 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* subjected to six cycles of 12 d of food deprivation (1.0% body mass day $^{-1}$) followed by *ad libitum* feeding exhibited faster growth and achieved similar final weights as

control fish (continuous *ad libitum* feeding) after 147 d (Hayward et al. 2001). In an effort to

determine the underlying cause of the observed growth differences between early-run and

late-run fish, we experimentally tested the hypotheses that 1) early-run kokanee are

genetically disposed to grow faster than late-run kokanee at identical water temperatures or

2) feed restriction elicits a compensatory growth response in early-run kokanee that explains

the observed size difference between breeding groups.

Methods

Experiment one

In January 2017, approximately 300 early-run kokanee (mean length = 39.3 mm)

were obtained from the Idaho Department of Fish and Game Cabinet Gorge Hatchery and

transported to the University of Idaho. A similar number of late-run kokanee (mean length =

36.0 mm) were obtained from Cabinet Gorge 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 post hatch and experienced the same

hatchery conditions. Specifically, both breeding groups were reared at the same water

temperatures (8.0°C–10.0°C) and were fed the same food at the same rate (3.8% body

weight). Both 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 water

temperature of 10°C (± 1°C). During the acclimation period, fish were fed 3% of their body

weight twice daily. Following the acclimation period, 15 3.8 l flow-through aquaria were

stocked with 15 randomly selected early-run kokanee ($n = 225$). Each aquarium was

randomly assigned to one of three water-temperature treatments (winter [4°C (± 1°C)], spring

[10ºC (± 1°C)], and summer [15ºC (± 1°C)]) such that five aquaria 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 beginning the experiment. During the acclimation period, water temperatures were maintained at 10ºC (± 1°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 MS-222 (75 mg/l; tricaine methanesulfonate, Western Chemical, Ferndale, WA), measured for fork length (nearest 1.0 mm), weighed (nearest 0.01 g), and returned to their respective aquaria. Fish were not fed at least 15 h prior to collection of length and weight data. In an effort to reduce handling stress, individual fish were removed from the anesthesia bath using a 5 cm × 5 cm aquarium net and placed directly onto a polyvinyl chloride measuring board. After a length was recorded, the fish was transferred to a 5 cm × 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 #1 (Rangen, Buhl, ID) 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 fork length, and weighed following the procedure described above. On the 28th d of the experiment, fish were euthanized with an overdose of MS-222 (200 mg/l), measured for fork length, and weighed.

Experiment two

In February 2018, approximately 600 early-run kokanee (50.0 mm) were obtained from Cabinet Gorge Hatchery and transported to the University of Idaho to evaluate the potential for a compensatory growth response following starvation. Fish were allowed to acclimate for 48 h in a 950 l flow-through tank at water temperature of 10°C (± 1°C). During the acclimation period, fish were fed 3% of their body weight twice daily. Following the acclimation period, 30 3.8 l flow-through aquaria were each stocked with 15 randomly selected kokanee. Prior to stocking, fish were anesthetized with MS-222 (75 mg/l), measured for fork length (nearest 1.0 mm), weighed (nearest 0.01 g), and placed in an aquarium. All fish were measured and weighed following the procedure described for experiment one. Five aquaria were randomly assigned to one of five food-deprivation treatments: 7 d without feed (7 d), 14 d without feed (14 d), 21 d without feed (21 d), 28 d without feed (28 d), and 35 d without feed (35 d). The remaining five aquaria served as controls. Control fish were fed for the duration of the experiment and treatment fish were fed following completion of their food deprivation period until the end of the experiment. Because compensatory growth most often occurs through hyperphagia (Ali et al. 2008), treatment and control fish were fed an excess ration (6% mean body weight) of Rangen Trout and Salmon Starter # 1 twice daily to allow for increased food intake. Feed rations of each aquarium were adjusted weekly to account for changes in weight and(or) fish density (i.e., mortalities). The experiment was run for 70 d to allow any growth compensation to manifest. Water temperatures of all aquaria were held at 10°C (± 1°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 fork length, and weighed. Aquaria were cleaned daily. Dissolved oxygen and water

temperature was monitored weekly. On the final day of the experiment, fish were euthanized with an overdose of MS-222 (200 mg/L), measured for fork length, and weighed.

Analysis

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

$$\left(\frac{ln\ W_f - ln\ W_i}{t}\right) \times 100$$

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:

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

where W is the final weight of fish x and L is the final length 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 length, weight, K, and SGRs between breeding groups and temperature treatments were evaluated using an analysis of variance (ANOVA) or analysis of covariance (ANCOVA; Ott and Longnecker 2010). We were primarily interested in potential long-term growth patterns and thus focused our analysis on mean lengths, weights, Ks, and SGRs at the end of each experiment. Because starting

weights and lengths differed between early- and late-run fish in experiment one, an

ANCOVA was used to evaluate potential differences among final mean length, mean

weights, and mean *K* between groups by treatment temperature. Breeding group (early-run,

late-run) served as the main effect and initial mean length or initial mean weight was

included as a covariate to control for initial differences in length and weight between early-

and late-run kokanee. All other comparisons were evaluated using ANOVA. In experiment

two, mean lengths, weights, and SGRs of kokanee (treatments, controls) were likely

influenced by the time period following initial feeding (Ali et al. 2008). As such, final

average lengths, weights, and SGRs were compared by the number of days since feeding

commenced using an ANOVA. For example, SGR of controls and 35-d fish were compared

at the 35th day following initiation of feeding. If differences in indices occurred, a Tukey

post-hoc test was used to detect differences between treatments (Ott and Longnecker 2010).

All analyses were conducted using R statistical software (R Core Development Team 2017)

and were considered significant at $\alpha = 0.05$.

Results

Experiment one

Over the course of the experiment, five fish (3 early-run; 2 late-run) died. At the

beginning of the experiment, average lengths differed between breeding groups (Figure 3.1).

Early-run kokanee averaged 39.28 mm (SD = 0.98) in length and late-run fish were 36.07

mm (1.21) in length. As the experiment progressed, average lengths of all treatment groups

increased and were positively influenced by water temperature. Fish reared in 4°C water

were the shortest ($P < 0.001$) among treatment groups. Early-run fish raised in 4°C water

had a final mean length of 46.09 mm (0.61) and late-run fish in the same treatment averaged

43.58 mm (0.98) in length at the end of the experiment. Both early- and late-run fish reared

in 15°C water obtained the longest mean length of any treatment group (early-run = 47.75

mm [1.12], late-run = 48.10 mm [0.79]) by the conclusion of the experiment. At the end of

the experiment, mean lengths of early- and late-run 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 length 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 3.1). Early-run kokanee averaged 0.39 g (0.02); whereas, late-run fish

exhibited a mean weight of 0.28 g (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 weight and late-run fish in the same treatment had a mean

weight of 0.51 g (0.14). Early-run fish raised in 10°C water were the heaviest among

treatments (0.73 g, 0.25) at the end of the experiment; whereas, late-run kokanee obtained the

heaviest mean weight in 15°C water (0.71 g, 0.15) over the same time period. At the end of

the experiment, mean weights between early- and late-run fish were not statistically different

for 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) treatments.

Early-run kokanee exhibited better body condition than late-run fish at comparable

time frames (Figure 3.2). After 14 d, early-run fish had an average K between 0.66 (0.06)

and 0.69 (0.09) and late-run fish had an average K between 0.61 (0.05) and 0.64 (0.05) over the same time frame. Similar patterns in condition were apparent at the end of the experiment. For instance, estimates of K of all early-run fish were about 0.64 at 28 d; whereas, K of late-run fish were between 0.59 (0.05) and 0.65 (0.05) over the same time period. Average K was influenced by water temperature, but the effects were variable. Fish reared in 10°C and 15°C water tended to have better condition than fish raised in 4°C water. 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 [$F_{1,9} = 1.88$, $P = 0.22$]).

Specific growth rates between kokanee breeding groups were variable through time and among treatments (Figure 3.3). Late-run fish in 10°C treatment exhibited the fastest growth rate of all treatments. For instance, late-run kokanee in the 10°C treatment averaged 4.58% (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 at the end of the experiment. No difference in growth between breeding group was apparent at the end of the experiment ($F_{1,29} = 0.33$, $P = 0.57$). However, water temperature influenced the growth rate of both groups ($F_{2,29} = 28.12$, $P < 0.001$). The final SGR of fish held in 4°C water was significantly less than that of fish held in 10°C and 15°C water ($P < 0.001$), but there was no difference in mean SGR between fish in the 10°C and 15°C treatments ($P = 0.86$).

Experiment two

A single fish died over the course of the experiment. The mean length of study fish varied little over the course of the experiment (Figure 3.4). At the beginning of the experiment, the mean length of all groups was 50.53 mm (1.37) and there was no significant difference between groups ($F_{5,29} = 0.65$, $P = 0.66$). Control fish obtained the longest average length of all fish after 70 d (74.29 mm [7.35]). However, control fish exhibited similar average lengths as treatment fish for a given time period. For example, average lengths of treatment and control fish varied from 61.37 mm (35 d) to 65.70 mm (14 d) 35 d after initiation of feeding. No significant differences in average length was observed between control fish and treatment groups regardless of the time period ($P \geq 0.05$).

Treatment fish exhibited fairly consistent weight gain regardless of their treatment (Figure 3.4). The mean weight of study fish was 0.86 g (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 (0.96) after 70 d. In general, food-deprived fish exhibited mean weights similar to controls for a given time period ($P > 0.05$). The 14-d treatment 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 (0.78) after 56 d of excess feeding; whereas, controls had a mean weight of 2.64 (0.77).

Average K of study fish was fairly consistent throughout the experiment (Figure 3.5). Control fish tended to exhibit the highest K regardless of the time period. Average K decreased with increasing food deprivation time, but quickly achieved condition values similar to controls once feeding resumed. However, the time required to reach K values

similar to controls was related to the amount of time fish were deprived of food. For instance, 7-d fish obtained an average K similar to control fish after 7 d of feeding; whereas, 28-d fish obtained a mean K similar to control fish after 42 d of feeding. Excluding 35-d fish, all fish achieved a mean K similar to control fish by the end of the experiment ($P >$ 0.05). Fish deprived of food for 35 d had the lowest mean K (0.73 [0.01]) and were the only group to exhibit a mean K that was statistically different from that of controls ($P = 0.01$).

Specific growth rates of treatment fish tended to be positively related to food deprivation period (Figure 3.6). For instance, 7-d fish obtained a maximum average SGR of 3.13% (0.19) following feeding; whereas, 28-d fish had a maximum mean SGR of 3.42% (0.40) following refeeding. However, the longer fish were deprived of food the longer it took those fish to obtain their maximum SGR. Fish deprived of food for 14 d achieved a SGR (3.05% [0.22]) after 7 d of feeding; whereas, 35-d fish obtained a maximum growth rate (3.25% [0.09]) after 28 d of feeding. All fish deprived of food for more than 7 d exhibited a higher SGR than controls for the duration of the experiment. After 70 d, 35-d (2.43% [0.32]) and 28-d (2.41% [0.13]) fish had the highest specific growth rates followed by 21-d (1.80% [0.18]), 14-d (1.60% [0.08]), controls (1.40% [0.15]), and 7-d (1.32% [0.07]) fish. Fish starved for 14 d and 28 d were the only groups to exhibit growth rates that were statistically higher than 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 fishes' 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 in 10°C and 15°C water 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% d^{-1} 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, 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 was 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 length, 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 Charr *Salvelinus alpinus* morphs exhibited incongruent growth patterns in Lake Fjellfrøsvatn, Norway (Knudeson et al. 2015). The authors suggested that 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 mid-water 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 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 growth rate of control fish was 2.38 d^{-1} (SD = 0.44) during their first week of feeding; whereas, fish deprived of food exhibited growth rates varying from 2.28 d^{-1} (0.24; 35 d) to 3.13 d^{-1} (0.19; 7 d) during the first week of re-feeding. Similar patterns of increased growth rate following 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 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 two, none of the treatment groups obtained final mean weights similar to control fish. However, when weights were compared by post-feeding time, all treatment groups equaled or exceeded the mean weight of controls. Six weeks following feeding of excess rations, 7-d, 14-d, 21-d, and 28-d treatments had average weights between 1.88 g (SD = 0.54) and 2.04 g (0.53); whereas, controls had a mean weight of 1.88 g (0.56). Fish starved for 14 d were the only treatment group to achieve an average weight that was significantly heavier than that of controls. Although 14-d fish were the only group to surpass the mean weight of controls, these results suggest kokanee possess the capacity to overcompensate for lost growth and obtain heavier mean weights than controls. Notwithstanding, it is unclear if 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. (2008), 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 *Lepomis cyanellus* × *L. macrochirus* to repeated cycles of no feeding and refeeding that varied in length from 2 d–14 d. Sunfish subjected to the 2-d treatment outgrew controls by two times and fish from the 14-d treatment exceeded growth of controls by about one and a half times 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 if the growth trajectories of treatment fish would persist if they were fed similar to controls. Age-1 Arctic Charr fed a restricted diet for 8 weeks and then fed *ad libitum* for 8 weeks showed an initial increase in growth that then decreased to levels similar to that of control fish (*ad libitum* feeding; Miglavs and Jobling 1989). In the current study, kokanee generally resumed growth rates commensurate with 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 late-run 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 late-run fish by about 13 mm in a given year (J. Rankin, Idaho Department of Fish and Game, personal communication). The initial disparity in size between early- and late-run fish could persist assuming the growth rate of early-run fish

never declined below that of late-run fish. Bimodal size distributions can be perpetuated through time assuming 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 rates. 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, reproductive success) in adult cichlids *Simochromis pleurospilus* (Taborsky 2006). The author reported that juvenile growth rate (and size) influenced adult size, but noted that growth rates were highly flexible and could be altered through feeding regimes. Previously food deprived Atlantic Salmon displayed full compensation in autumn, but exhibited slower growth rates and lipid reserves than control fish the following spring (Morgan and Metcalfe 2001). Presumably, early-run fish would be able to maintain a size advantage over late-run fish, but without long-term data on growth-manipulated 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 observed growth differences are due to factors other than those related to the genetics of each breeding group. The growth rate 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, habitat use) for a growth difference to manifest. In light of the results of the first experiment, we hypothesized that the hatchery practice of retarding growth of early-run fish would result in a compensatory growth response and the observed differences in length between breeding groups. Our results suggest kokanee possess the ability to overcompensate for lost growth following 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 fish. In addition, our results provide valuable insight for kokanee management. Controlled feed restriction in hatcheries could be used to positively influence the growth rate 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 avoid size-selective mortality (e.g., predation, 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. 2008; 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.

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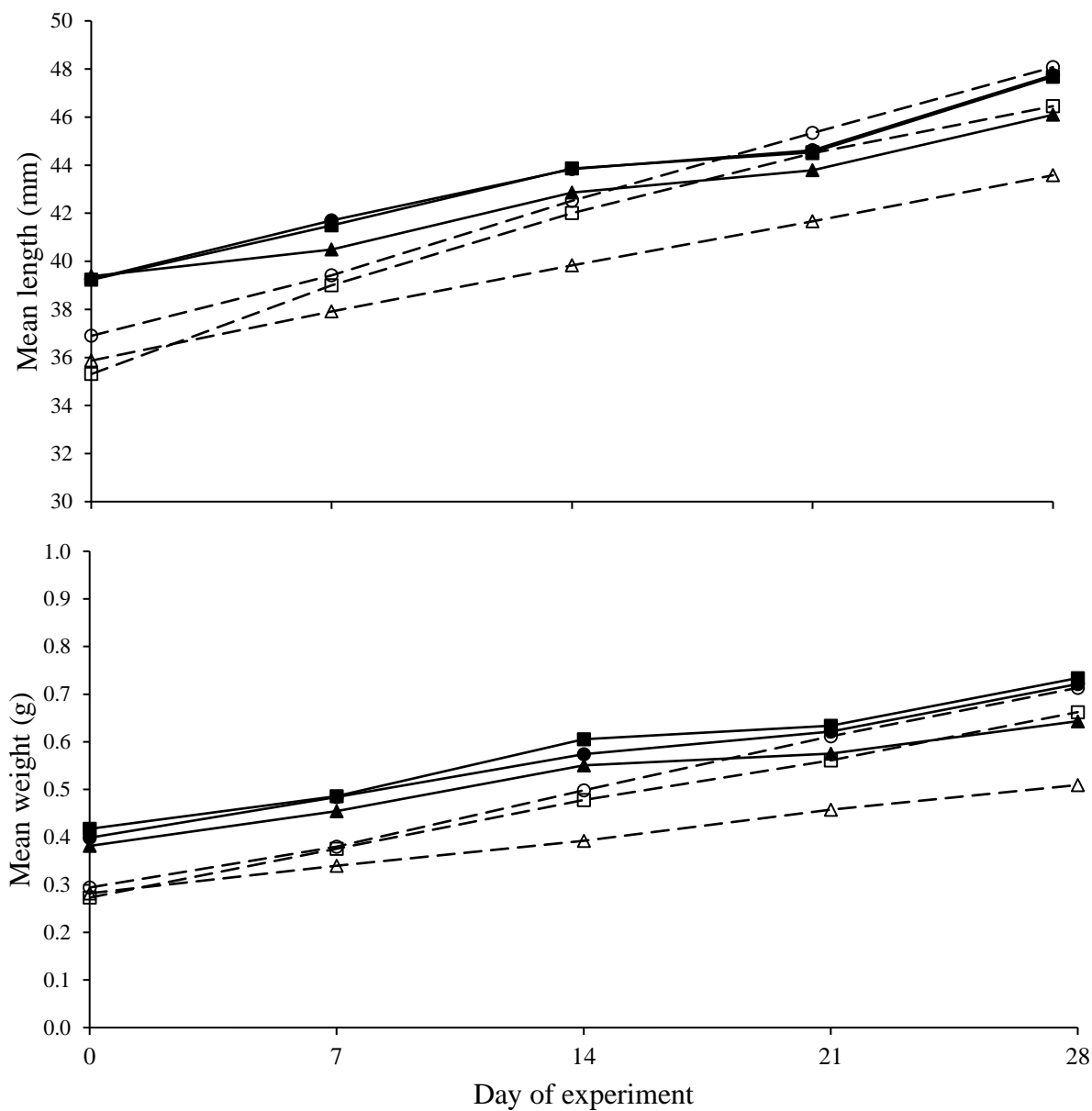
Figure 3.1. Average fork length (top panel) and weight (bottom panel) for early-
(solid line; solid symbols) and late-run (dashed line; open symbols) kokanee
raised in 4°C (triangle), 10°C (square), and 15°C (circle) water.
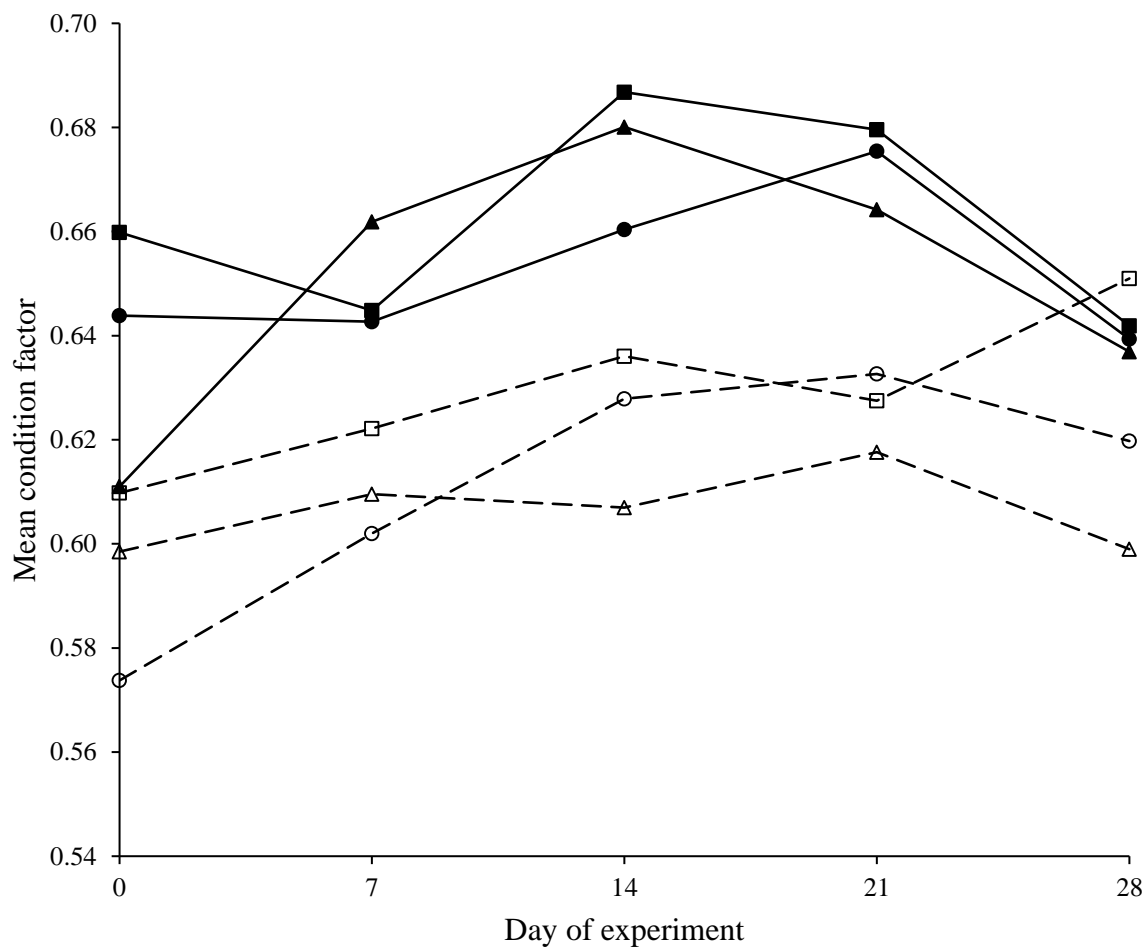
Figure 3.2. Average Fulton condition factor for early- (solid line; solid symbols) and late-run (dashed line; open symbols) kokanee raised in 4°C (triangle), 10°C (square), and 15°C (circle) water.
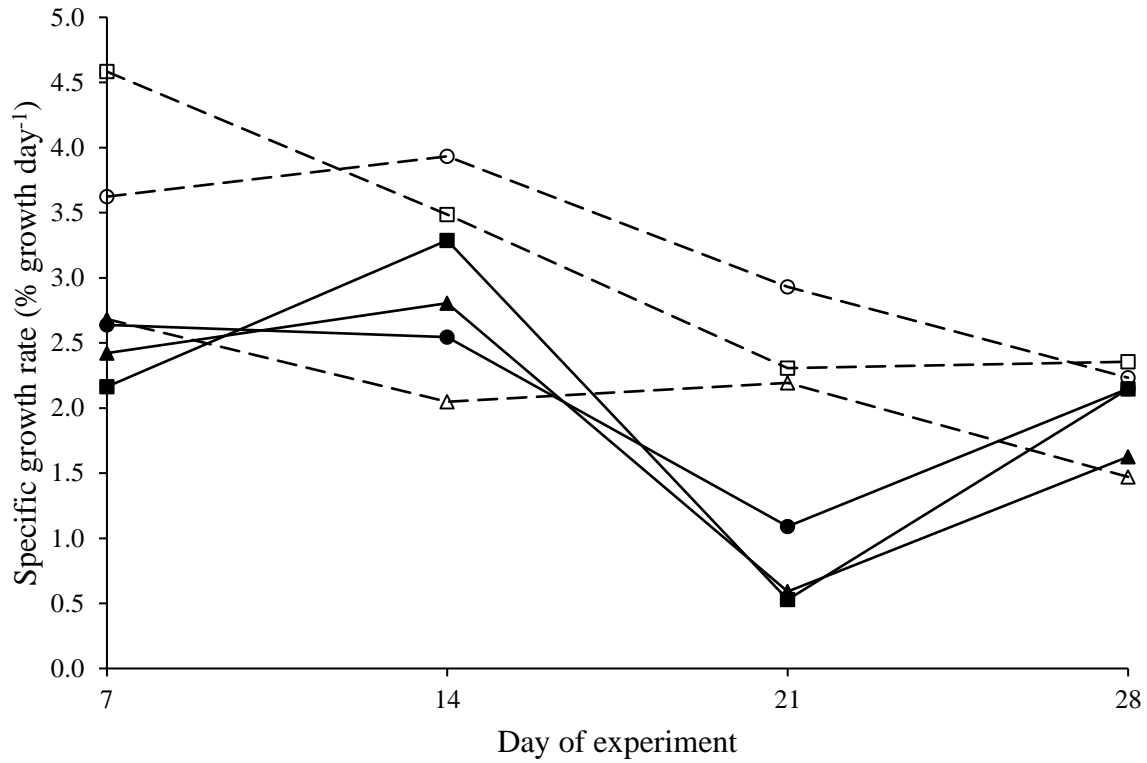
Figure 3.3. Mean specific growth rate for early- (solid line; solid symbols) and late-run (dashed line; open symbols) kokanee raised in 4°C (triangle), 10°C (square), and 15°C (circle) water.
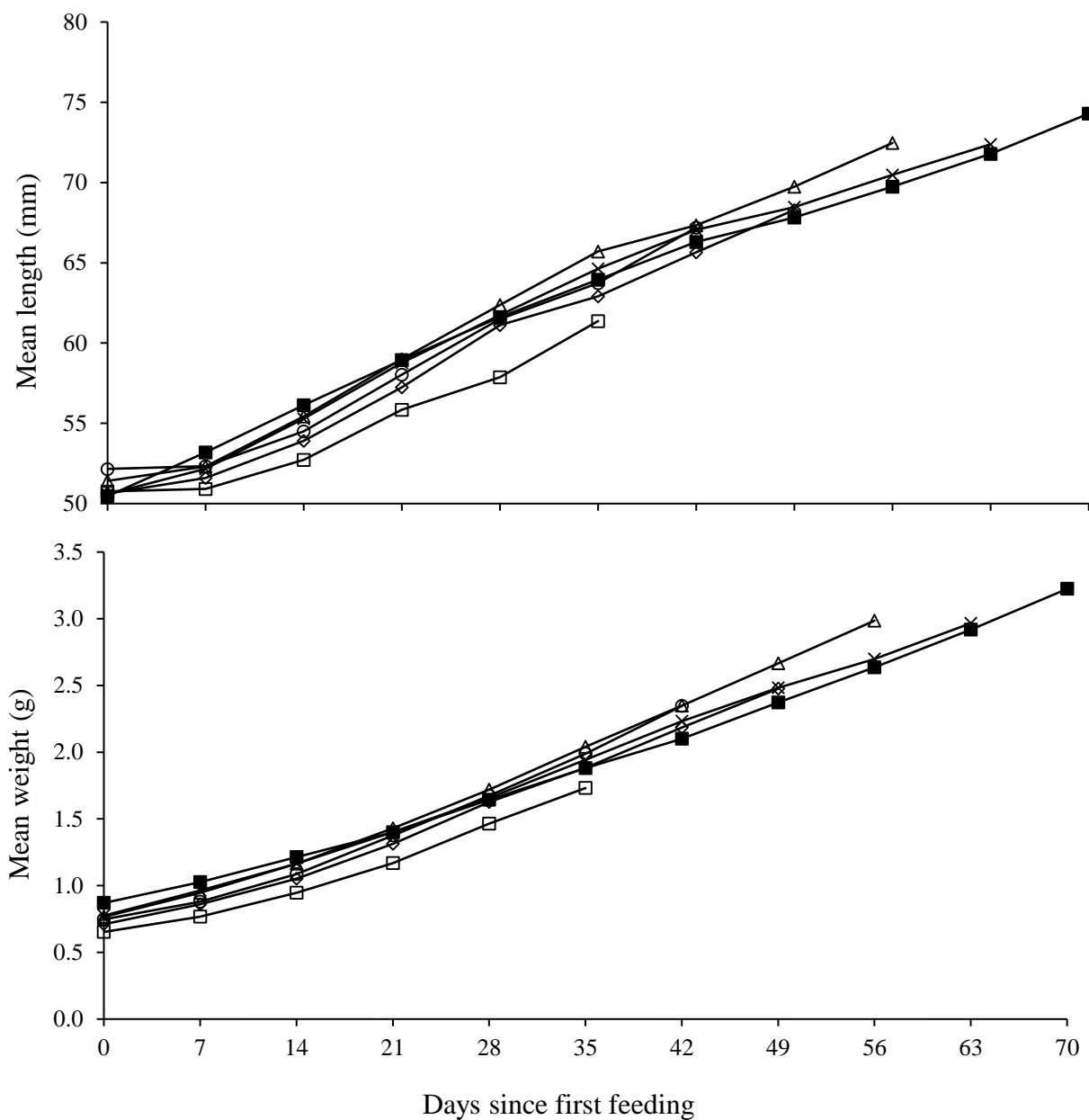
Figure 3.4. Average fork length (top panel) and weight (bottom panel) following initial feeding for early-run kokanee starved for 7 d (solid ×), 14 d (open triangle), 21 d (open diamond), 28 d (open circle), and 35 d (open square). Control fish are indicated by solid squares.
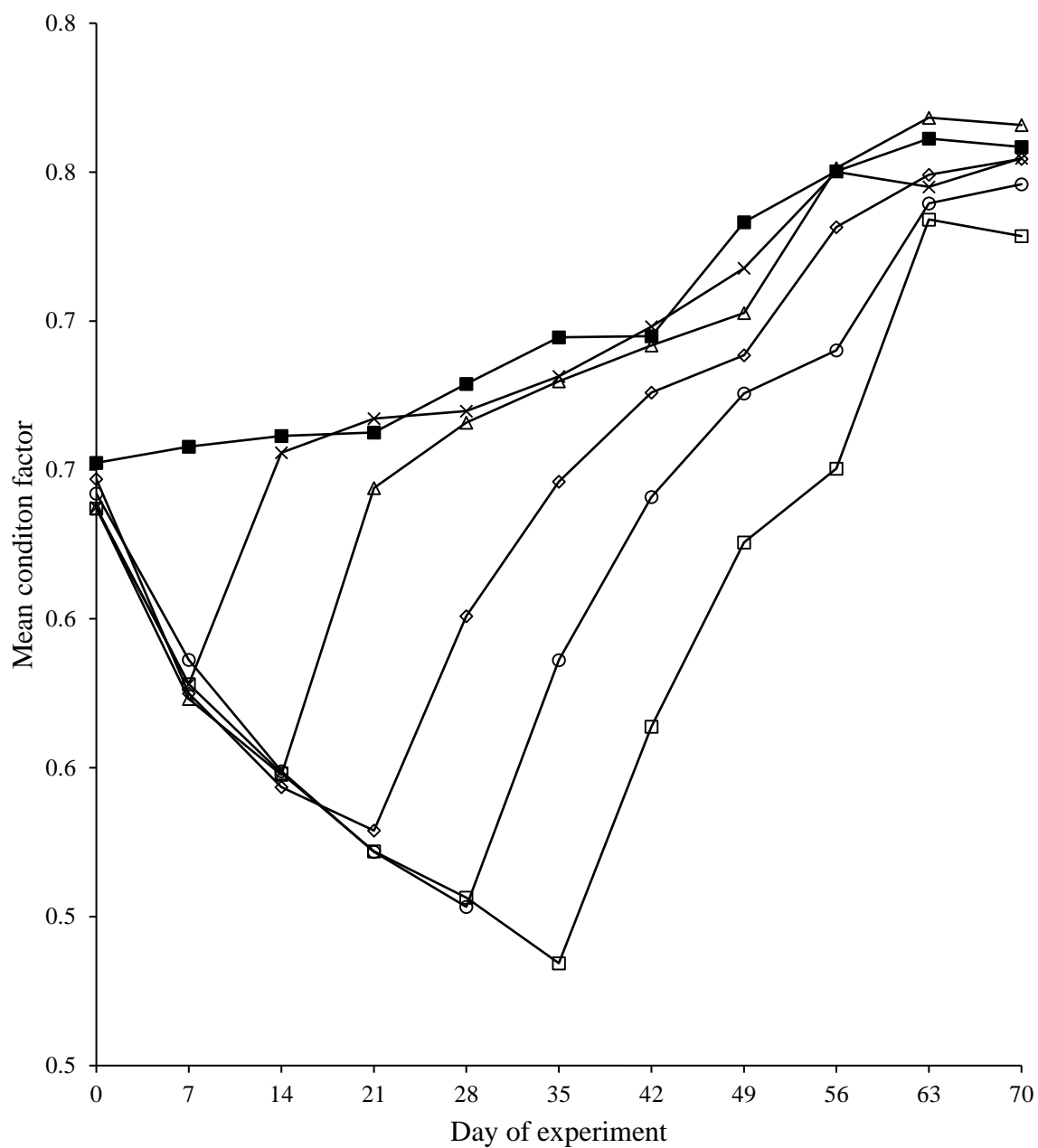
Figure 3.5. Average Fulton condition factor for early-run kokanee starved for 7 d (solid ×), 14 d (open triangle), 21 d (open diamond), 28 d (open circle), and 35 d (open square). Control fish are indicated by solid squares.
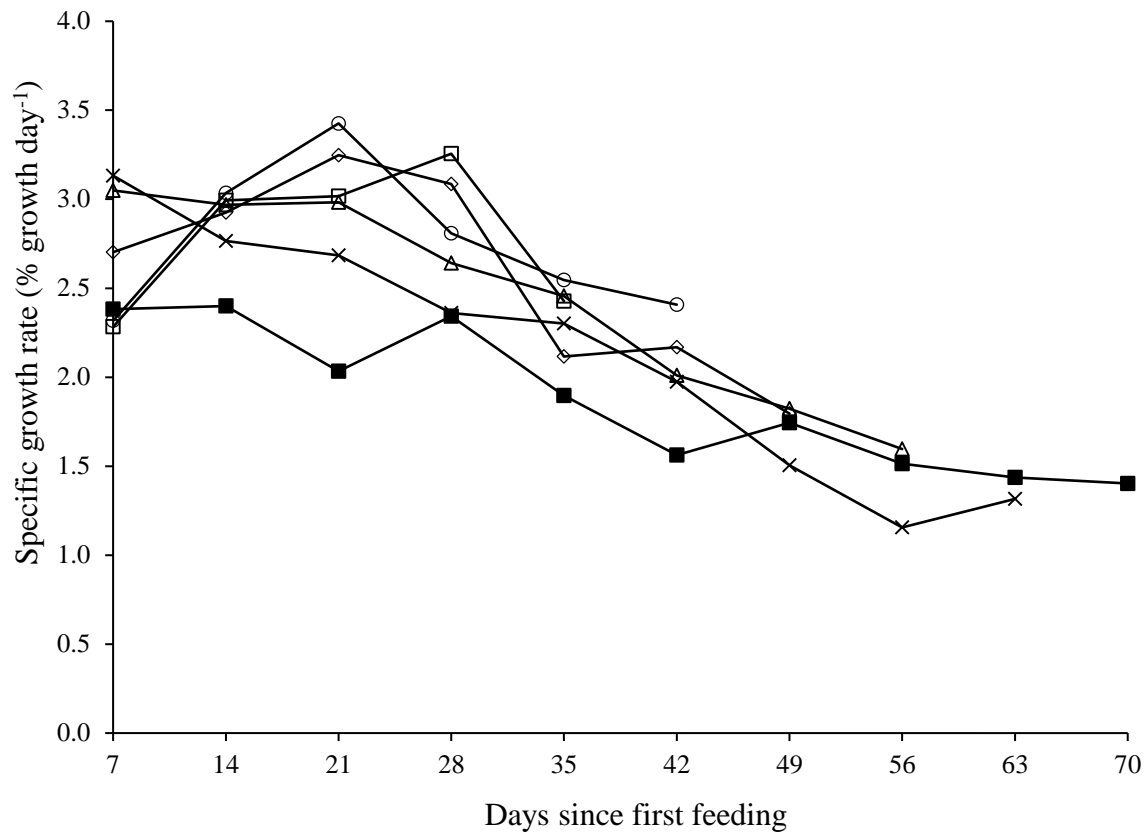
Figure 3.6. Average specific growth rate following initial feeding for early-run kokanee starved for 7 d (solid ×), 14 d (open triangle), 21 d (open diamond), 28 d (open circle), and 35 d (open square). Control fish are indicated by solid squares.

Chapter 4: Ontogenetic-Mediated Resource Competition in a Kokanee-*Mysis diluviana* System

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Abstract

Ontogenetic shifts represent important transitions that can influence how fish interact with their environment and other organisms. However, ontogenetic shifts are rarely placed into a population context due to the difficulty of incorporating the vagaries of size-mediated interactions. In an effort to better understand how kokanee *Oncorhynchus nerka* and Opossum Shrimp *Mysis diluviana* (hereafter Mysis) potentially compete for zooplankton prey, we investigated the role of ontogenetic shifts in diet as they relate to interactions between species in Lake Pend Oreille, Idaho. Contemporary data were used to understand the short-term, spatiotemporal overlap in diet and distribution between Mysis and kokanee. Historical data were evaluated within the context of ontogenetic shits to better understand the long-term, population-level ramifications of interactions between Mysis and kokanee. Diet analysis revealed age-specific divergences in diet whereby juvenile kokanee primarily consumed copepods and adult kokanee preferentially consumed cladocerans. Our results also suggest kokanee and Mysis exhibit diet overlap that peaks in the autumn. Age-specific diets coupled with seasonal diet overlap suggest Mysis primarily compete with adult fish and have the potential to influence kokanee population structure. Following declines in Mysis density, cladoceran densities increased and adult kokanee experienced pronounced increases in growth. Concurrently, age-0 kokanee exhibited a distinct increase in abundance and a subsequent decrease in growth. Collectively, our results highlight the role ontogenetic diet shifts play in influencing competitive interactions and provide managers with an improved understanding of the mechanism by which Mysis influence kokanee growth and abundance.

Introduction

Competitive interactions are characterized by spatiotemporal overlap in the use of a limited resource and theoretically result in declines in the fitness and density of inferior competitors (Morin 1999). As such, interspecific competition and its effects have long been a major focus of ecologists. However, clear patterns surrounding competitive interactions have remained elusive due to the confounding effects of ontogenetic shifts in diet and behavior that often occur in size-structured populations (Rose et al. 2001). Competing species can also mitigate interactions by using alternative resources, further obscuring competitive relationships (Morin 1999). Despite the challenges associated with identifying interspecific competition, understanding how species interact is incredibly important for explaining ecological processes and guiding management actions.

The importance of understanding the mechanisms underlying competition is typified in systems with cooccurring kokanee *Oncorhynchus nerka* and Opossum Shrimp *Mysis diluviana* (hereafter Mysis) populations. Kokanee is a zooplanktivore that provides valued recreational fisheries and represents an important prey resource for economically, socially, and ecologically important species such as Bull Trout *Salvelinus confluentus* and Rainbow Trout *O. mykiss* (Wydoski and Bennett 1981; Paragamian and Bowles 1995). In an effort to improve the size structure of kokanee (and other sport fish), Mysis where widely introduced in the mid-20th century throughout systems in North American and Europe (Nesler and Bergersen 1991). Ironically, recipient fish populations exhibited inconsistent patterns in growth, and population declines of kokanee were widely reported following introductions of Mysis (Lasenby et al. 1986; Bowles et al. 1991; Northcote 1991). Mysis were later identified as a poor prey resource for kokanee due to opposing diel vertical migrations (Beeton 1960; Johnston 1990; Levy 1991) and proved to be an effective consumer of the preferred prey of

kokanee (i.e., cladoceran zooplankton). In Lake Pend Oreille, Idaho *Daphnia* spp. and *B. longirostris* were generally available from April to December prior to the introduction of Mysis, but were restricted to July and August following establishment of Mysis (Rieman and Falter 1981). The negative effect of Mysis on the composition and distribution of zooplankton led to the hypothesis that Mysis negatively influence kokanee through resource competition (Cooper and Goldman 1980; Rieman and Falter 1981; Beattie and Clancey 1991; Bowles et al. 1991; Chipps and Bennett 2000). However, a direct link between Mysis' influence on zooplankton and potential effects on kokanee populations has remained difficult to identify.

Intuitively, age-0 fish should be more susceptible to competitive interactions than older fish due to their low energy reserves and limited prey options (Hjort 1914; Cushing 1969, 1990). However, previous research suggest age-0 kokanee are less susceptible to competitive interactions with Mysis than adult fish. Age-0 kokanee exhibited no difference in lipid content or stomach fullness in lakes with and without Mysis; whereas, age-1 fish exhibited decreasing lipid content in systems with Mysis when compared to systems without Mysis (Clarke et al. 2004). As competition between Mysis and kokanee is largely postulated on the ability of Mysis to regulate the density of seasonally available cladocerans (Rieman and Falter 1981), age-specific patterns in resource use become important considerations for understanding kokanee-Mysis interactions. Assuming the dietary requirements of adult kokanee differ from juvenile fish, kokanee-Mysis interactions may exhibit age-specific patterns whereby adult fish are disproportionately influenced by Mysis. However, competitive interactions between Mysis and kokanee may be complicated by mitigatory behavior of one or both species. For instance, juvenile fish may seek alternative prey

resources to limit competitive interactions with Mysis. Similarly, adult kokanee may partition resources in space and time to avoid competing with Mysis. Notwithstanding, the ability to evaluate predictions associated with age-specific patterns in competition between Mysis and kokanee are limited by a general paucity of data. As such, we sought to evaluate Mysis-kokanee interactions from an age-specific context with a focus on dietary and spatial overlap. In addition, we leverage data surrounding a system-wide collapse of Mysis to better understand the population-level effects of resource overlap between Mysis and kokanee in Lake Pend Oreille, Idaho.

Methods

Study area

Lake Pend Oreille is a large (383.0 km^2), deep (mean depth = 164.0 m), meso-oligotrophic lake located in northern Idaho (Figure 4.1). The northern basin of the lake is relatively shallow (<200.0 m maximum depth), while the majority of the southern basin is over 300.0 m deep. Due to the variable bathymetry of the system, the Idaho Department of Fish and Game divides the lake into northern, middle, and southern sections (Figure 4.1). Mysis were introduced into Lake Pend Oreille between 1966 and 1970, became established by 1974, and annual densities averaged between 200–400 individuals m^{-3}. Concurrently, lake-wide kokanee abundance declined and remained at a depressed state until hatchery supplementation was initiated in the mid-1970s (Hoelscher et al. 1990). Mysis and kokanee abundance remained relatively unchanged until 2011. In 2011, Mysis exhibited an unexplained collapse and have averaged between 6 and 157 individuals m^{-3} annually from 2011–2017. In addition to kokanee, the fish assemblage of Lake Pend Oreille consists of Largescale Sucker *Catostomus macrocheilus*, Longnose Sucker *C. catostomus*, Northern

Pikeminnow *Ptychocheilus oregonensis*, Mountain Whitefish *Prosopium williamsoni*, Pygmy

Whitefish *P. coultreii*, Slimy Sculpin *Cottus cognatus*, Peamouth *Mylocheilus caurinus*, Bull

Trout, Westslope Cutthroat Trout *Oncohynchus clarki lewisi*, Rainbow Trout, Lake

Whitefish *Coregonus culpeaformis*, Brook Trout *S. fontinalis*, Brown Trout *Salmo trutta*,

Lake Trout *S. namaycush*, Yellow Perch *Perca flavescens*, Black Crappie *Pomoxis*

nigromaculatus, Largemouth Bass *Micropterus salmoides*, Brown Bullhead *Ictalurus*

nebulosus, Pumpkinseed *Lepomis gibbosus*, Northern Pike *Esox lucius*, Walleye *Sander*

vitreus, and Tench *Tinca tinca* (Hoelshcer 1993). During the majority of the year, copepods

(*Cyclops bicuspidatus*, *Calanoida* spp.) are the most abundant zooplankton in the system

(Clarke and Bennett 2002). However, cladocerans (*Daphnia* spp., *Bosmina longirostris*,

Diaphanasoma leuchtenbergianum) are relatively abundant during summer.

Trawling

Since 1998, kokanee population composition (e.g., length structure, age distribution)

has been evaluated using annual mid-water trawling surveys. Mid-water trawling was

conducted at night during the new moon in August or September. From 1998–2002, kokanee

were sampled using an otter trawl that measured 13.7 m in length and had a 3.0 m × 3.0 m

mouth. From 2003–2017, kokanee were sampled with a fixed-frame trawl that had a 3.0 m ×

2.2 m opening and measured approximately 10.5 m in length. Both trawls were constructed

of graduated mesh starting at 32.0 mm at the mouth decreasing to 6.0 mm mesh at the cod

end. Thirty-six transects (12 per section) were randomly selected each year. Prior to

sampling, the vertical distribution of kokanee was determined using a Furuno Model FCV-

585 depth sounder with a 10º hull-mounted transducer (Furuno Electric Co, LTD,

Washington). Each transect was sampled in a stepwise-oblique pattern to sample the entire

kokanee layer (Rieman 1992). Each step was defined by the net height and was towed for

three minutes at a consistent speed (~1.6 m s^{-1}). Due to changes in sampling protocols,

weight data (nearest 0.1 g) were collected from 1998–2017; whereas, weight and length data

(nearest 1.0 mm) were collected from 2003–2017. Ageing structures (e.g., scales, otoliths)

were consistently removed from about 10 fish per 1-cm length bin from 1998–2017.

Kokanee age was independently estimated by two readers and age-length keys were applied

to the corrected length distribution of kokanee to represent the ages and lengths of all

kokanee sampled (Isley and Grabowski 2007; Quist et al. 2012).

In 2017, juvenile and adult kokanee were sampled with mid-water trawls three times

per year (i.e., May, August, November) to evaluate age-specific food habits. Mid-water

trawling was conducted as described previously. However, trawl sampling opportunistically

focused on areas of high kokanee density to ensure adequate catch. Following each tow, the

net was retrieved, and five kokanee from each 1-cm length group were preserved with 90%

ethanol for diet analysis. Kokanee less than 150 mm in length were preserved whole after

the body cavity was opened to aid in preservation of gut contents. The stomachs of kokanee

larger than 150 mm were removed and preserved whole. In an effort to avoid digestion of

gut contents, trawl sampling only occurred within two hours of sunset (Rieman and Bowler

1980). The diet of individual kokanee was assessed by removing the digestive tract from

esophagus to pyloric caeca. The stomach was opened and its contents were rinsed into a

graduated cylinder. Stomach contents were then subsampled until at least 200 individuals of

the most abundant taxa were identified and enumerated (Hyslop 1980; Bunnell et al. 2011).

Due to varying degrees of digestion, zooplankton and macroinvertebrates were only

identified to order (e.g., Cladocera, Hymenoptera).

Hydroacoustics

Since 1998, hydroacoustic surveys occurred immediately before or after annual mid-

water trawl sampling to provide abundance estimates. Surveys consisted of six to eight

transects varying in length from 3.6 to 7.7 km. Each transect travelled from shore to shore at

a boat speed of approximately 1.3 m s^{-1}. All surveys were conducted using a Simrad EK60

echo-sounder equipped with a 120.0 kHz split-beam transducer (Kongsberg Maritime,

Horten, Norway). Kokanee density was estimated with Echoview software (Echoview

Software, Hobart, Tasmania) using the echo-integration technique (Parker-Stetter et al.

2009). The density of kokanee along each transect was estimate as:

$$\rho = \left(\frac{NASC}{4\pi 10^{\frac{TS}{10}}} \right) 0.00292$$

where ρ is density (number of fish per ha), *NASC* is the total backscattering (m^2/nautical

mile^2), and *TS* is the mean target strength (decibels) in the sampling area. Kokanee

abundance was estimated for each section by multiplying the geometric mean density by the

area within a section. Lake-wide and section-specific abundances were apportioned to age-

specific abundances by first separating age-0 kokanee (<100 mm) from older age classes

based on a frequency histogram of target strengths. Older age-classes (1–5 years) were

further separated based on the age frequency identified from mid-water trawling data. Age-

specific estimates of abundance were used in analyses.

From 2015–2017, the spatiotemporal distribution of kokanee was sampled with

hydroacoustic surveys. Contemporary sampling was largely conducted using the methods

described above; however, the frequency was changed to elucidate monthly patterns in kokanee distribution. Three to four transects per lake section (11 total transects) were sampled from April 2015 to December 2017. All other facets of hydroacoustic surveys remained unchanged.

Mysis and zooplankton sampling

From 1998–2017, Mysis were sampled in June within one week of the new moon due to the negative phototaxis of Mysis (Rieman and Bowler 1980). Mysis sampling intensity varied through time, but between eight and fifteen samples were annually collected from each lake section. Mysis were collected with vertical hauls using a 1-m diameter net with a 1,000 µm mesh body and a 500 µm mesh collection bucket. The net was lowered to a depth of 45.7 m and raised to the surface at about 0.5 m s^{-1} (Rieman and Falter 1981). The net was rinsed and all collected Mysis were preserved in 90% ethanol.

From 2015–2017, Mysis and zooplankton were sampled monthly to evaluate their distribution, species composition (zooplankton), and the diet of Mysis. All sampling was conducted at night within five days of the new moon. From April 2015 to December 2017, Mysis and zooplankton were sampled at 10–12 randomly selected sites per lake section (34 total sites). Sites were randomly selected using a geographic information system based on 500.0 m^2 quadrats of the lake surface and were re-selected on a monthly basis. Mysis were sampled once at each site following the sampling methods described above. Zooplankton were sampled once at each site using a 0.5-m-diameter Wisconsin-style plankton net (80.0-µm-mesh). Zooplankton were sampled from a depth of 20.0 m to the surface at a speed of

0.4 m s^{-1} (Paragamian and Bowles 1995). Mysis and zooplankton samples were preserved in 90% ethanol.

Mysis less than 10 mm in length are primarily herbivorous and less likely to compete with kokanee for zooplankton prey (Branstrator et al. 2000). As such, our analysis focused on adult Mysis (>10 mm). Adult Mysis density was estimated for each site and month by dividing the total number of adult Mysis sampled by the volume of water sampled. In May, August, and November of 2017, five Mysis from each site were sampled for diet analysis. The gastric mill (i.e., foregut) of each individual was removed and transferred to a glass slide with melted glycerol jelly (Caldwell et al. 2015). The contents were distributed throughout the melted glycerol jelly, covered with a coverslip, and analyzed under a compound microscope. Contents in Mysis guts were identified to the lowest possible taxonomic level and enumerated. Zooplankton prey were identified to order (e.g., Cladocera) based on diagnostic structures (e.g., caudal rami, mandibles; Chess and Stanford 1998; Johannsson et al. 1994).

Zooplankton composition and density were estimated for each site and month. Zooplankton were identified and enumerated from 1.0–2.0 ml subsamples until 200–400 zooplankton of the most abundant taxa were identified (Barbiero et al. 2009; Bunnell et al. 2011). Zooplankton were identified to the lowest possible taxonomic level. Zooplankton density was estimated for each site and month by dividing the total number of zooplankton sampled by the volume of water sampled.

Analysis

The potential influence of Mysis on kokanee was evaluated using data collected from 1998–2017. General patterns in the relationship between kokanee abundance and Mysis density was summarized as lake-wide averages for each year. The analysis focused on age-0 and adult fish (ages 3-5) to understand patterns in recruitment and abundance of kokanee. Although competition may ultimately result in changes in abundance, competitive interactions likely manifest as changes in fitness-related measures (e.g., growth, survival) prior to observable changes in density (Morin 1999). As such, the relationship between Mysis density and kokanee condition was evaluated as age-specific changes in mean length and weight of kokanee before and after the Mysis collapse in 2011. Because lake-wide averages likely obfuscate smaller-scale changes in kokanee length and weight, length and weight data were described by lake section. Previous research has shown that mid-water trawls are size selective for small kokanee (Klein et al. *in press*). As such, analysis of length and weight data focused on age-0 through age-3 kokanee to avoid erroneous conclusions based on small sample sizes of large, old fish (age-4 and age-5 kokanee).

The temporal dynamics of common zooplankton (*Calanoida* spp., *Cyclops bicuspidatus, Bosmina longirostris*, *Diaphanosoma leuchtenbergianum,* and *Daphnia* spp.) were originally evaluated on an annual basis. However, annual patterns in zooplankton densities were similar among years and were combined as a monthly average from 2015–2017 to aid in interpretation. Patterns in the distribution of kokanee, Mysis, and zooplankton were evaluated by month and section to describe the temporal distribution of each species. Spatiotemporal patterns among kokanee, Mysis, and zooplankton were further analyzed to understand resource use and spatial overlap across taxa. Biotic interactions among taxa were

evaluated by stratification period (stratified, unstratified), lake section, and year using linear regression. Kokanee and Mysis density served as dependent variables and taxa-specific density of zooplankton were independent variables. Kokanee and Mysis densities were also included as independent variables to evaluate spatial overlap between species. Kokanee density could only be partitioned as age-0 and age-1 and older fish because monthly mid-water trawling data were unavailable.

Distribution models were fit using R statistical software (R Development Core Team, 2018). Candidate models were constructed using the dredge function in the MuMin package. Akaike's information criterion adjusted for small sample size (AICc) was used to compare candidate models and select the best model (i.e., lowest AICc value; Burnham and Anderson 2002). Models with a delta AICc (ΔAICc) less than or equal to two were considered plausible. Models were further evaluated using the coefficient of determination (R^2).

In 2017, seasonal diet overlap was evaluated to understand potential interactions between kokanee and Mysis. Diet was described as percent by number for cladocerans (*Bosmina longirostris*, *Daphnia* spp., *Diaphanosoma leuchtenbergianum*), copepods (*Calanoida* spp., *Cyclops bicuspidatus*), and an "other" category. The other category for kokanee included Aranea, Coleoptera, Collembola, Diptera, Emphemoptera, Hymenoptera, Mysis, Odonata, and Ostracoda. The other category for Mysis included rotifers and pollen. Mysis rarely consume an entire prey item and instead focus on soft, easily digestible portions of zooplankton prey (Grossnickle 1982; Smokorowski et al. 1982). Thus, the total number of items consumed by Mysis is likely underestimated (Caldwell et al. 2015). Notwithstanding, we were primarily interested in describing temporal patterns in diet and assume estimates of diet composition were consistent through time. Due to the difficulty of sampling large

numbers of fish, Mysis and kokanee diets were summarized as lake-wide averages for each

month (May, August, November) and age class (kokanee only). Diet analysis focused on

adult Mysis ($\geq$ 10mm) and age-0–age-3 fish due to low catch of age-4 and age-5 kokanee in

mid-water trawls.

Diet overlap was described using the Schoener Index of diet overlap (α; Schoener

1970):

$$\alpha = 1 - 0.5\left(\sum_{i=1}^{n}|p_{xi} - p_{yi}|\right)$$

where n denotes the number of food categories, p_{xi} represents the proportion of prey item i in

the diet of species x, and p_{yi} represents the proportion of prey item i in the diet of species y.

Proportions were based on the number of individual prey items. The Schoener Index varies

from 0.0 to 1.0 with values over 0.60 denoting biologically significant diet overlap (Zaret and

Rand 1971; Mathur 1977).

Results

The annual abundance of kokanee was negatively related to Mysis density from

1998–2017 (Figure 4.2). Following declines of Mysis in 2011, age-0 abundance peaked at

over 16 million fish. Similarly, age-3 through age-5 kokanee neared two million fish in 2013

and 2014. The relationship between average length of kokanee and the density of Mysis

exhibited distinct, but alternative patterns by age class (Figure 4.3). Age-0 and age-1 fish

exhibited decreases in mean length following declines in Mysis; whereas, age-2 and age-3

fish generally increased in average length after Mysis collapsed. Patterns in mean weight

were similar to those observed for mean length (Figure 4.4). Age-0 and age-1 fish exhibited

a decrease in mean weight following declines in Mysis density. However, declines in mean

weight were most apparent in age-0 fish. Age-2 and age-3 kokanee exhibited increases in mean weight following Mysis collapse, but the pattern was more distinct in age-3 fish. In general, age-0 fish were the only group to exhibit spatial patterns in growth whereby fish were typically larger in the northern portion of Lake Pend Oreille (Figures 4.3 and 4.4).

Zooplankton abundance and seasonal availability were variable and taxa specific in Lake Pend Oreille (Figure 4.5). *Calanoida* spp. were relatively abundant throughout the year (mean $\pm$ SD; 6.45 ± 3.05 L^{-1}), but exhibited a slight peak in abundance (14.47 ± 4.16 L^{-1}) in May. *C. bicuspidatus* occurred throughout the year in Lake Pend Oreille, but exhibited a peak in abundance (50.84 ± 15.16 L^{-1}) in July. Compared with copepods, cladocerans were less abundant and only available seasonally. *B. longirostris* were relatively rare in Lake Pend Oreille, but exhibited two minor peaks in abundance in June (1.71 ± 0.14 L^{-1}) and September (1.39 ± 0.47 L^{-1}). *Daphnia* spp. were generally absent from samples until May and then peaked in abundance in July and August (1.98 ± 0.90 L^{-1}). *D. leuchtenbergianum* were the most abundant cladoceran in Lake Pend Oreille. *D. leuchtenbergianum* appeared in samples in May and exhibited peak densities in August and September (4.80 ± 0.71 L^{-1}).

Kokanee and Mysis had similar temporal distributions in Lake Pend Oreille (Figure 4.6). Average Mysis densities tended to be similar throughout Lake Pend Oreille and exhibited peaks in density in July among all lake sections. Age-0 kokanee were most abundant in the southern portion of Lake Pend Oreille throughout the year and exhibited peak abundance in May and July. Age-1 and older fish were also most abundant in the southern portion of Lake Pend Oreille and were most abundant in March. Zooplankton composition was similar among sections in Lake Pend Oreille.

Kokanee and Mysis exhibited similar patterns in spatial use and overlap with zooplankton in Lake Pend Oreille (Table 4.1). Mysis were positively associated with *C. bicuspidatus*, and *D. leuchtenbergianum* densities and negatively associated with *Calanoida* spp. densities. Age-0 fish densities were predominately associated with stratification period and lake section; whereas, age-1 and older fish densities were positively related to the density of *C. bicuspidatus*, and *D. leuchtenbergianum* and negatively associated with copepod densities. In general, Mysis and kokanee densities were positively associated regardless of the time period or lake section.

Kokanee and Mysis diets reflected the seasonal availability of zooplankton in Lake Pend Oreille (Figure 4.7). In May, kokanee diets were dominated by copepods; whereas, Mysis primarily consumed pollen and rotifers over the same period. Cladocerans were more prevalent in the diets of kokanee and Mysis in August when compared to May. However, cladocerans were a relatively minor component of Mysis diets. In November, Mysis consumed more cladocerans when compared to May and August. Kokanee continued to consume cladocerans in November, but they constituted a smaller proportion of overall kokanee diets. Schoener Index values largely reflected season-specific diet habits and increased from 0.11 in May to 0.58 in August (Table 4.2). In addition to seasonal food habits, kokanee exhibited distinct age-specific patterns in consumption of zooplankton (Figure 4.7). When cladocerans were available, age-2 and age-3 kokanee consumed higher proportions of cladocerans when compared to younger age classes. For example, cladocerans composed about 36% of the diet of age-3 kokanee in November; whereas, cladocerans constituted about 12% of the diet of age-0 fish in the same month.

Discussion

Our results suggest kokanee exhibit age-specific patterns in diet that influence how

the species interacts with Mysis. Cladocerans comprised between 75% and 57% of age-2

and age-3 kokanee diets in August; whereas, age-0 and age-1 fish contained between 15%

and 39% over the same time frame. Although our results highlight apparent ontogenetic

shifts in diet of kokanee, the majority of literature surrounding kokanee food habits suggest

kokanee diets vary little with age (Bevelhimer and Adams 1993; Stockwell and Johnson

1997; Stockwell and Johnson 1999) and are largely related to seasonal zooplankton

availability (Northcote and Lorz 1966; Scheuerell et al. 2005). For instance, age-0 through

age-2 kokanee consumed seasonally abundant zooplankton in Lake Granby, Colorado,

whereby cladocerans were the dominant prey item of kokanee in the summer and copepods

dominated diets for the remainder of the year (Martinez and Bergersen 1991). Optimal

foraging theory suggests fish should maximize their energy intake by consuming

energetically profitable (e.g., larger prey) items that require short handling times (Townsend

and Winfield 1985). As such, the use of energetically costly prey items (e.g., evasive

behavior; O'Brien 1979; Drenner et al. 1980) by juvenile kokanee raises questions as to the

constraints imposed on kokanee that lead to age-specific patterns in resource use.

Diet can be influence by myriad factors including prey availability, habitat, and biotic

interactions (e.g., competition, predation; Morin 1999). However, considerable research

suggest predation is a predominant factor influencing the behavior and diet of kokanee

(Townsend and Winfield 1985). For instance, age-0 kokanee exhibited large diel vertical

migrations in Blue Mesa Reservoir despite decreased daytime foraging opportunities

(Hardiman et al. 2004). The authors suggested the observed migration patterns were largely

associated with increased predation risk by Lake Trout. Similarly, juvenile *O. nerka*

(kokanee, Sockeye Salmon) in lakes in the Stanley Basin, Idaho, exhibited increasing avoidance of limnetic zones as predator densities increased and zooplankton densities decreased (Beauchamp et al. 1997). Although direct comparisons between systems are difficult, predation of kokanee is a principal concern in Lake Pend Oreille (Hansen et al. 2008; Hansen et al. 2010; Corsi et al. *in press*) and is principally focused on juvenile fish (Vidergar 2000). As such, juvenile kokanee in Lake Pend Oreille may avoid limnetic zones until light attenuation reduces predation risk (Beauchamp et al. 1997). As cladocerans are typically distributed in the upper epilimnion, predator avoidance behavior by juvenile kokanee may constrain fish to deeper habitats that are dominated by copepods (Rieman and Falter 1981). Adult fish are not subject to the same constraints and can more readily feed on cladocerans thereby increasing their competitive interactions with Mysis.

Adult kokanee could mitigate competitive interactions with Mysis by partitioning habitat use to avoid areas of high Mysis density (Morin 1999). For instance, Bluegill *Lepomis macrochirus* and Pumpkinseed transitioned from littoral habitats to energetically sub-optimal open water habitats to avoid interactions with a superior competitor (i.e., Green Sunfish *L. cyanellus*) in experimental ponds (Werner and Hall 1979). Mysis and kokanee densities were positively related in Lake Pend Oreille resulting in consistent overlap in the areal distribution of both species. However, adult kokanee and Mysis were positively associated with the most abundant cladoceran in the system (i.e., *D. leuchtenbergianum*); whereas, juvenile kokanee and Mysis did not exhibit similar patterns in resource use. Concurrent patterns in resource use between Mysis and adult kokanee suggest an increased potential for competitive interactions that likely have population-level effects when cladocerans are limited in Lake Pend Oreille.

Theoretically, competition for limited resources should result in declines in density related to emigration, increased mortality, or decreases in fitness components (e.g., body size; Morin 1999). Bluegill and Pumpkinseed growth declined linearly as Bluegill density and competition for littoral invertebrates increased (Mittelbach 1988). Mysis' consumption of zooplankton has been estimated to account for 70%–100% of the daily standing stock of cladocerans in Lake Pend Oreille (Chipps and Bennett 2000; Caldwell et al. 2015) during the period of highest dietary overlap between Mysis and kokanee (e.g., autumn). Thus, reductions in Mysis in Lake Pend Oreille should result in overall increases in cladoceran abundance and positively influence the growth and survival of adult fish (Rieman and Myers 1992). In Lake Pend Oreille, cladoceran densities more than doubled following the collapse of Mysis (see Hoelscher et al. 1990) while age-3 kokanee exhibited an average increase of about 10 mm in length (pre-Mysis collapse vs. post-Mysis Collapse; 225.8 ± 24.4 mm vs. 236.3 ± 15.1 mm) and 30.0 g in weight (90.3 ± 24.5 g vs. 121.32 ± 28.1 g). Body size is positively related to nearly every aspect of a fish's life including survival (Sogard 1997) and reproduction (e.g., fecundity, egg size; McGurk 2000; Whitlock et al. 2018a). Therefore, increases in kokanee body size can confer improvements in overall fitness and likely explain population-level patterns observed in Lake Pend Oreille. For instance, the number of mature adults increased from an average of about 570,000 to over 900,000 following declines in Mysis densities in Lake Pend Oreille. Similarly, natural recruitment increased from a mean of 6.6 million to about 10.4 million over the same time period. Although declines in Mysis and concurrent increases in cladocerans have positively influenced kokanee in Lake Pend Oreille, a reduction in interspecific competition may exacerbate interactions between conspecifics.

O. nerka are well known for exhibiting density-dependent reductions in growth (Ricker 1937; Goodlad et al. 1974; Peterman 1984; Rieman and Myers 1992). Age-1–3 kokanee displayed a clear inverse relationship between fish density and length-at-age in ten lakes and reservoirs throughout Idaho (Rieman and Myers 1992). In the current study, age-0 kokanee exhibited similar density-dependent effects. Following increases in natural recruitment in Lake Pend Oreille in 2011, age-0 kokanee lost an average of 10 mm in length (60.95 mm $\pm$ 4.99 vs. 50.76 mm $\pm$ 6.45) and 0.8 g in weight (1.86 g $\pm$ 0.47 vs. 1.07 g $\pm$ 0.35). Although reduced growth in age-0 kokanee implies increased intraspecific competition, identifying competitive interactions among kokanee is difficult. Increases in kokanee abundance should confer decreases in zooplankton density; however, average zooplankton density nearly doubled following the collapse of Mysis in Lake Pend Oreille (see Hoelscher et al. 1990). Despite increases in overall zooplankton abundance, reductions in growth of age-0 fish could be associated with more complex changes in the food web of Lake Pend Oreille. The vertical distribution of pelagic zooplankton can be "squeezed" between planktivorous fish from above and predatory invertebrates from below (Zaret and Suffern 1976; Bowers and Vanderploeg 1982; Hays et al. 2003; Peacor et al. 2005). In the absence of high Mysis densities, zooplankton may be released from invertebrate predation and able to exhibit more extensive avoidance of kokanee. Regardless of the exact mechanism governing density-dependent processes in Lake Pend Oreille, the observed patterns in growth of age-0 kokanee brings into question common kokanee management practices in the system.

Hatchery supplementation was initiated in Lake Pend Oreille to rebuild the declining kokanee population in the 1970s. Between 500,000 and 17 million age-0 fish are annually stocked into Lake Pend Oreille following years of low adults returns or when abundant

spawning adults create "surplus" juveniles (Whitlock et al. 2018b). However, each stocking scenario can create abnormally high numbers of age-0 fish that likely intensifies density-dependent processes. Additions of hatchery fish following years of low adult returns likely compounds density-dependent processes due to compensatory stock-recruitment relationships typical of wild kokanee in Lake Pend Oreille (Whitlock et al. 2018b). Similarly, high returns of mature kokanee are positively correlated with the number of hatchery and wild age-0 fish leading to concordant increases in natural recruitment and stocking rates of juveniles. Declines in Mysis have only acted to intensify existing density-dependent processes due to increases in adult fitness and survival. For instance, the total number of kokanee in Lake Pend Oreille has increased by 62% following the collapse of Mysis in 2011. Hatchery supplementation is an undeniably valuable tool for kokanee management, but declines in Mysis abundance have further altered the dynamics of Lake Pend Oreille necessitating a reevaluation of current hatchery practices.

Admittedly, the ability to completely untangle the complex relationships occurring between Mysis and kokanee is challenging. However, our results suggest kokanee exhibit spatiotemporally variable patterns in resource use that change with age and ultimately influence how the species interacts with Mysis. Competitive interactions between species have the potential to alter the population structure of kokanee and may necessitate large-scale mitigation measures. Mysis-kokanee interactions can presumably be mitigated through habitat manipulations (e.g., lake-wide fertilization; Northcote 1991; Thompson 1999), biological agents (e.g., parasites, disease, predators; Leathe 1984; Martinez and Bergersen 1989), mechanical removals (Northcote 1991; Ashley et al. 1997), and hatchery supplementation. Although each mitigation measure has merit, hatchery supplementation is

proven and has consistently controlled kokanee declines in Lake Pend Oreille. However, recent declines in Mysis densities have again altered the dynamics of Lake Pend Oreille and shifted the balance between interspecific and intraspecific competition. Collectively, our results highlight the need to fully consider the age-specific dynamics of biotic interactions to more completely understand how fish interact with competitors thereby influencing large-scale patterns in population structure.

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Table 4.1. Candidate models used to evaluate the influence of covariates on the section-specific density of Mysis, juvenile kokanee, and adult kokanee in Lake Pend Oreille, 2015–2017. Akaike's Information Criterion (AIC$_c$) adjusted for small sample size was used to rank models. Models with a delta AIC rank (ΔAICc) less than 2 were considered plausible and are shown. Model weight (w_i), total number of parameters (K), log likelihood (LL), and coefficient of determination (R^2) are also included. Directionality of effects are indicated with a negative or positive sign. Covariates include *Mysis* (Mys.), *Bosmina longirostris* (Bos.) *Calanoida* (Cal.), *Cyclops bicuspidatus* (Cyc.), *Daphnia* spp. (Dap.), *Diaphanosoma leuchtenbergianum* (Dia.), Period (Per.), and Section (Sec.), and Year.

Candidate models by group	K	AICc	ΔAICc	W_i	LL	R^2
Mysis						
⁻Cal. + ⁺Cyc. + ⁺Dia. + Sec. + Year	9	131.50	0.00	0.07	-55.56	0.44
⁺Kok. + ⁻Cal. + ⁺Cyc. + ⁺Dia. + Sec. + Year	10	132.00	0.49	0.06	-54.52	0.45
⁻Cal. + ⁺Cyc. + ⁺Dia. + Per. + Sec. + Year	10	132.50	1.03	0.04	-54.79	0.45
⁺Dia. + Per. + Sec. + Year	8	132.80	1.29	0.04	-57.45	0.41
⁺Cyc. + ⁺Dia. + Per. + Sec. + Year	9	132.80	1.31	0.04	-56.22	0.43
⁻Cal. + ⁺Dia. + Per. + Sec. + Year	9	133.20	1.74	0.03	-56.43	0.43
⁺Kok. + ⁻Cal. + ⁺Cyc. + ⁺Dia. + Per. + Sec. + Year	11	133.30	1.80	0.03	-53.86	0.46
Age-0 fish						
Per. + Sec.	5	179.60	0.00	0.04	-84.44	0.19
⁻Cal. + Per. + Sec.	6	179.70	0.12	0.04	-83.34	0.21
⁻Cal. + ⁺Dia. + Per. + Sec.	7	179.90	0.27	0.03	-82.23	0.23
⁺Dia. + Per. + Sec.	6	180.30	0.65	0.03	-83.61	0.21
⁻Cal. + ⁺Dia. + Sec.	6	180.30	0.67	0.03	-83.62	0.21
⁻Bos. + ⁻Cal. + ⁺Dia. + Per. + Sec.	8	180.30	0.70	0.03	-81.27	0.25
⁺Mys. + Per. + Sec.	6	180.70	1.12	0.02	-83.84	0.21
⁻Bos. + ⁻Cal. + Per. + Sec.	7	180.80	1.21	0.02	-82.70	0.23
⁻Bos. + Per. + Sec.	6	180.90	1.23	0.02	-83.90	0.20
⁻Bos. + ⁻Dia. + Per. + Sec.	7	181.00	1.41	0.02	-82.80	0.22
⁺Mys. + ⁻Cal. + Per. + Sec.	7	181.00	1.42	0.02	-82.81	0.22
⁻Cyc. + Per. + Sec.	6	181.60	1.95	0.02	-84.26	0.20
Age-1 and older fish						
⁻Bos. + ⁻Cal. + ⁻Cyc. + ⁺Dia. + Per. + Sec.	9	211.40	0.00	0.05	-95.52	0.31
⁻Bos. + ⁻Cal. + ⁺Dia. + Per. + Sec.	8	211.90	0.52	0.04	-97.02	0.28
⁻Bos. + ⁻Cyc. + ⁺Dia. + Per. + Sec.	8	211.90	0.53	0.03	-97.03	0.28
⁻Bos. + ⁻Cyc. + Per. + Sec.	7	212.10	0.65	0.03	-98.31	0.26
⁺Mys. + ⁻Bos. + ⁻Cyc. + Per. + Sec.	8	212.20	0.84	0.03	-97.18	0.28
⁺Mys. + ⁻Cyc. + Per. + Sec.	7	212.30	0.87	0.03	-98.42	0.26
⁻Cyc. + Per. + Sec.	6	212.30	0.93	0.03	-99.63	0.24
⁻Bos. + ⁻Cal. + ⁻Cyc. + Per. + Sec.	8	212.30	0.93	0.03	-97.23	0.28
⁺Mys. + ⁻Bos. + ⁻Cal. + ⁻Cyc. + Per. + Sec.	9	212.90	1.49	0.02	-96.26	0.30
⁻Cal. + ⁻Cyc. + Per. + Sec.	7	212.90	1.49	0.02	-98.73	0.25
⁻Cyc. + ⁺Dia. + Per. + Sec.	7	213.00	1.64	0.02	-98.80	0.25
⁻Cal. + ⁻Cyc. + ⁺Dia. + Per. + Sec.	8	213.10	1.71	0.02	-97.62	0.27
⁺Mys. + ⁻Cal. + ⁻Cyc. + Per. + Sec.	8	213.20	1.79	0.02	-97.66	0.27
⁻Bos. + ⁻Cal. + ⁻Cyc. + ⁺Dap. + ⁺Dia. + Per. + Sec.	10	213.30	1.90	0.31	-95.18	0.31
⁻Bos. + ⁻Cal. + ⁻Cyc. + ⁺Dap. + Per. + Sec.	9	213.30	1.91	0.29	-96.47	0.29

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Table 4.2. Schoener index values of diet overlap between kokanee and Mysis sampled in the May, August, and November of 2017. Indices were calculated using percent by number for each prey type.

Season	Age (years)				Overall
	0	**1**	**2**	**3**	
Spring	0.11	0.11	0.11	0.11	0.11
Summer	0.50	0.50	0.50	0.49	0.50
Autumn	0.57	0.58	0.53	0.58	0.58
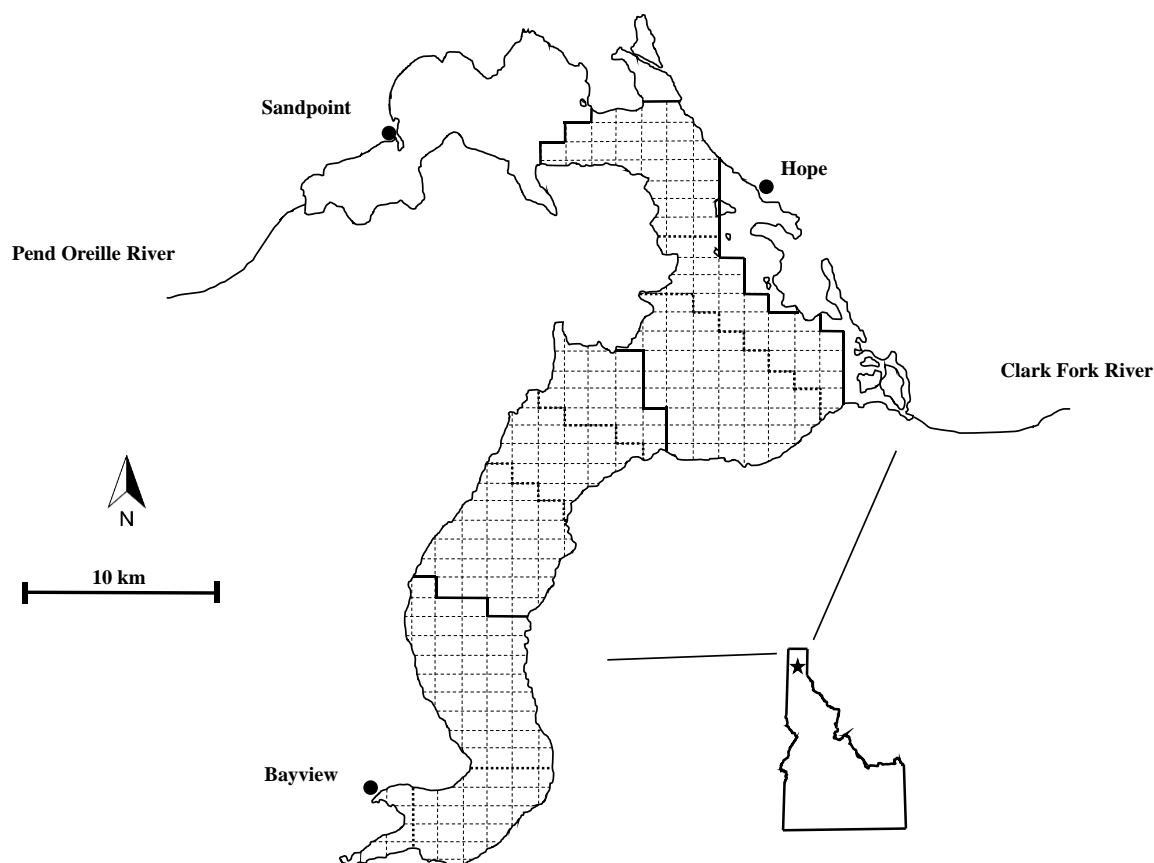
**Figure 4.1.** Map of Lake Pend Oreille, Idaho with major tributaries included. Solid black lines represent boundaries between the south, middle, and north sections. Dashed black lines represent boundaries between zones within each section. Dotted lines represent 500 m^2 sampling quadrats. Areas of Lake Pend Oreille with an average depth < 25.0 m were excluded from sampling and do not have a sampling grid.
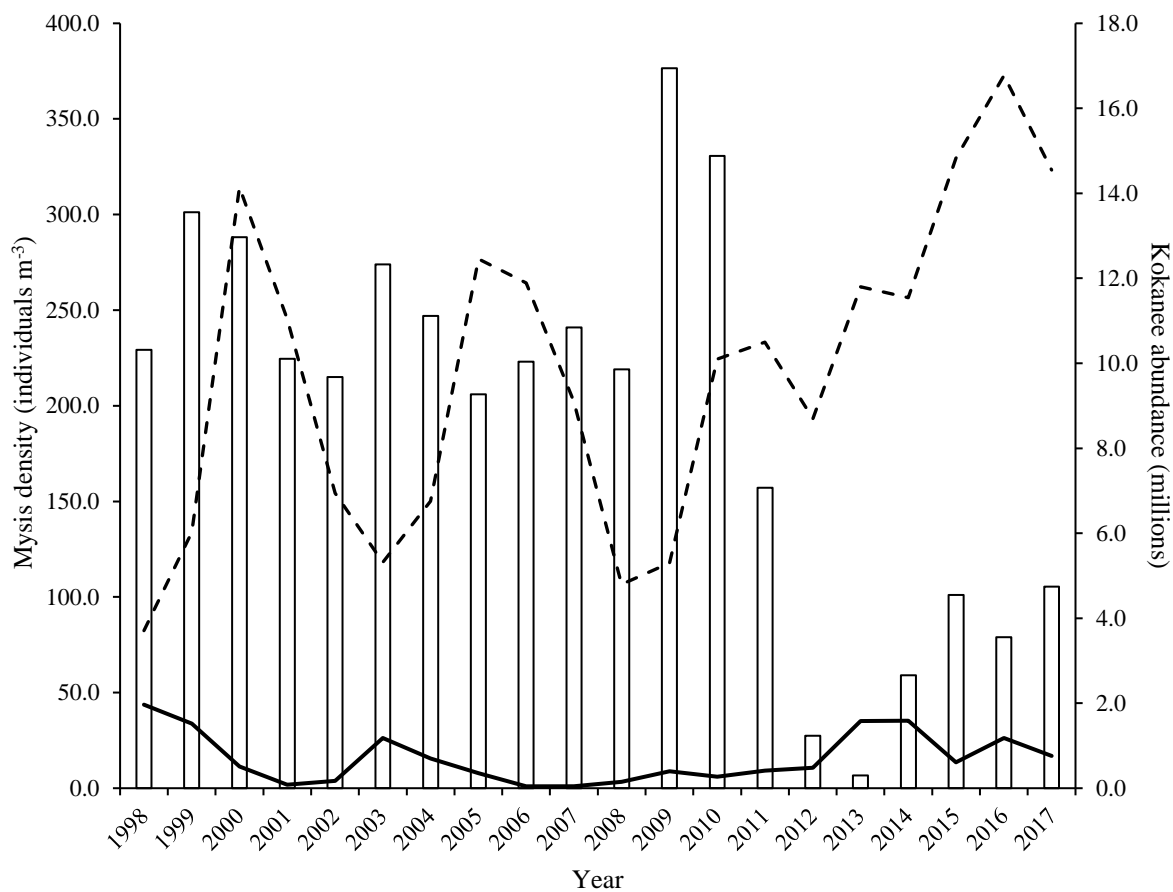
Figure 4.2. Historic estimates of adult Mysis density (white bars) and kokanee abundance in Lake Pend Oreille, 1998–2017. Kokanee abundance is separated into age-0 (dashed line) and age 3-5 (solid line) fish.
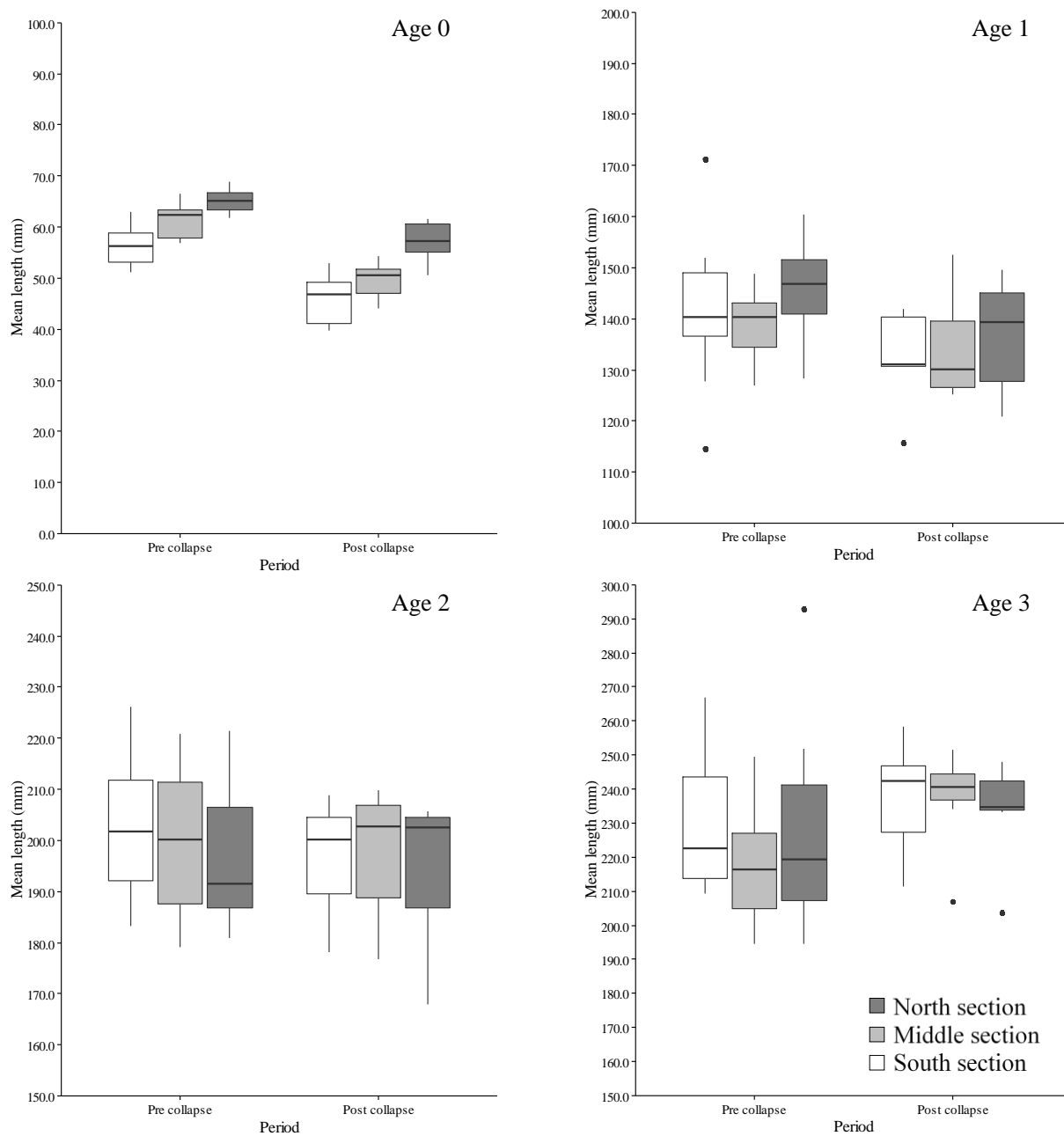
Figure 4.3. Boxplots showing age-specific mean length (mm) for kokanee sampled from Lake Pend Oreille pre-Mysis collapse (1998–2010) and post-Mysis collapse (2011–2017).
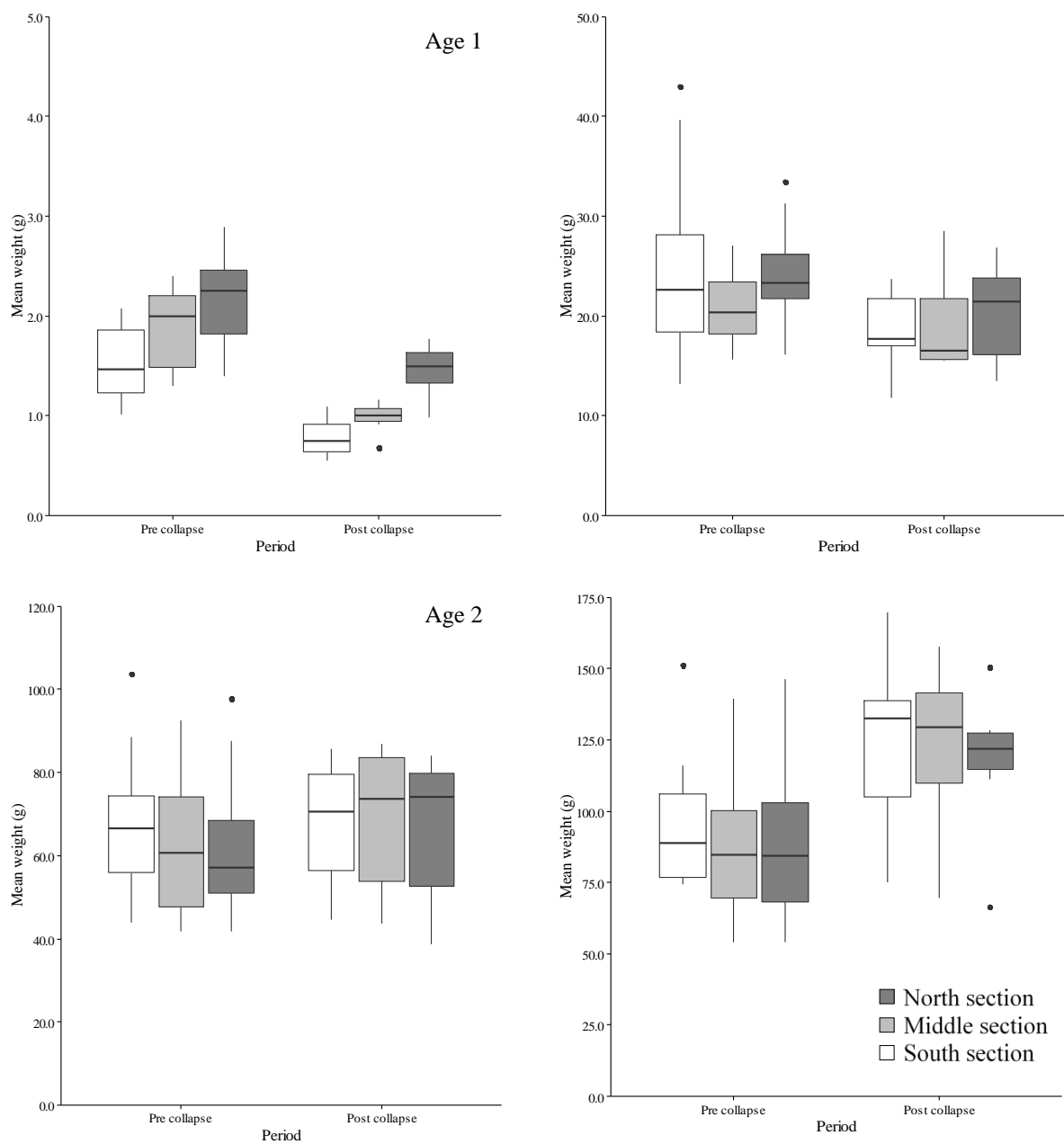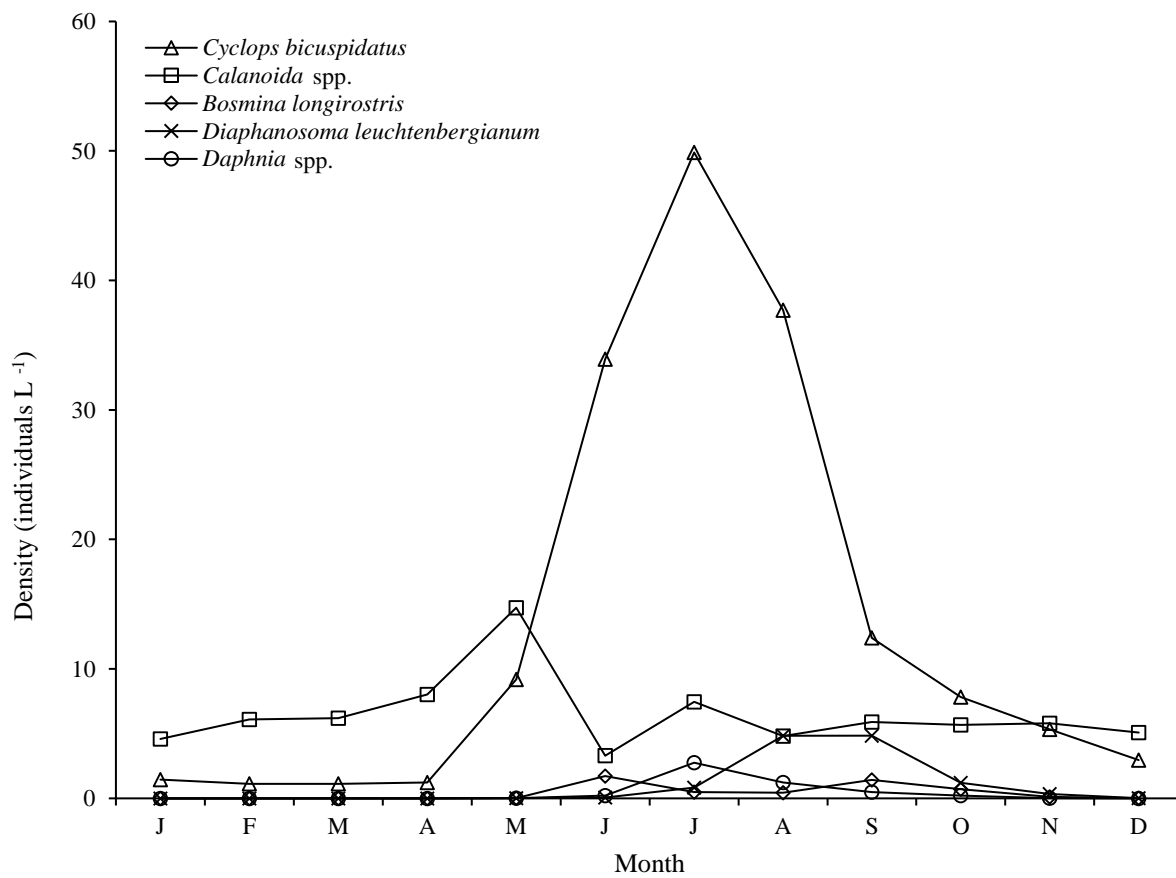
Figure 4.4. Boxplots showing age-specific mean weight (g) for kokanee sampled from Lake Pend Oreille pre-Mysis collapse (2003–2010) and post-Mysis collapse (2011–2017).

Figure 4.5. Average density of zooplankton in Lake Pend Oreille, 2015–2017.
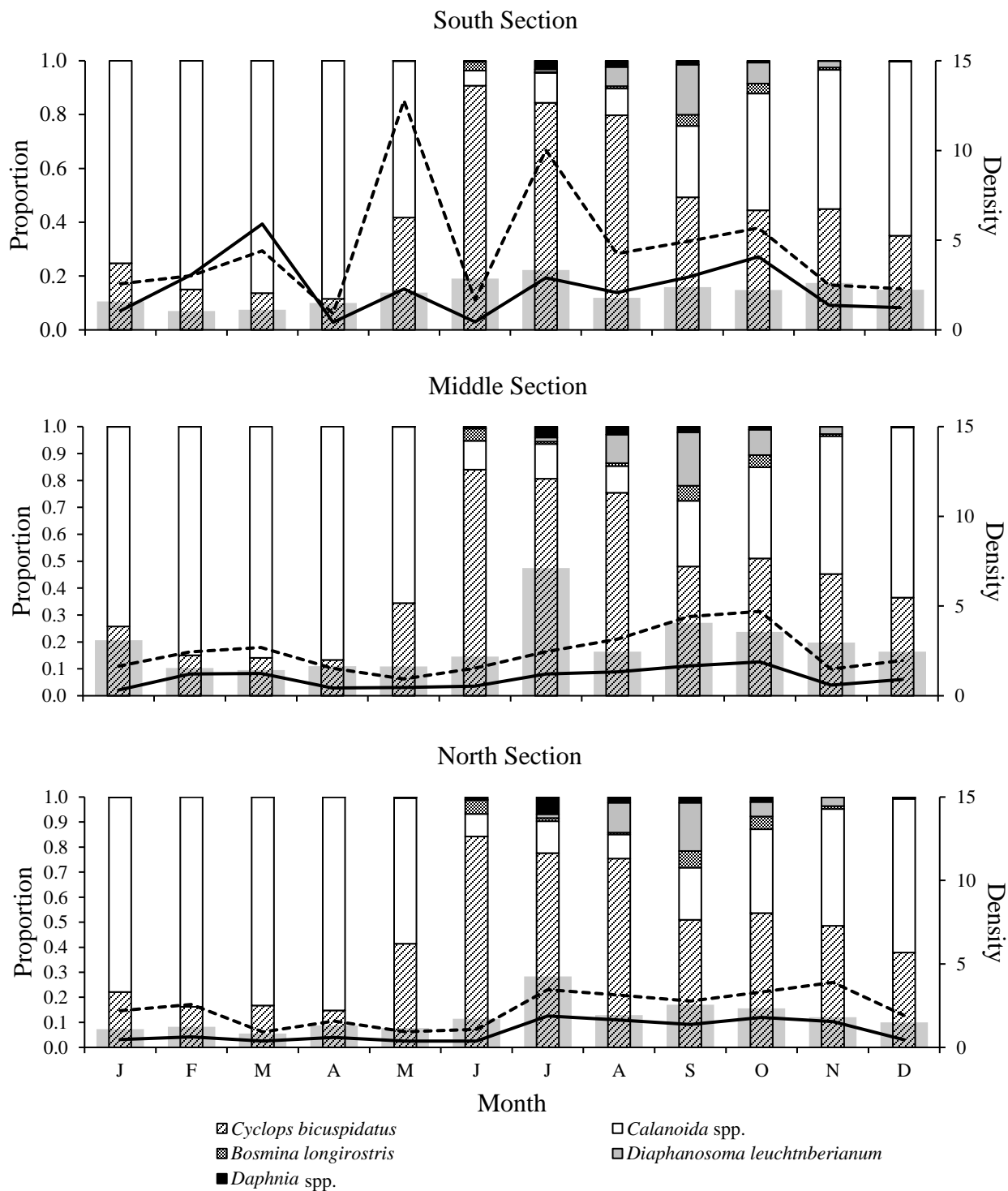
Figure 4.6. Average monthly composition (proportional density) of common zooplankton and mean density of Mysis (transparent gray bars), age-0 (dashed line), and age-1 and older (solid line) kokanee by section for Lake Pend Oreille, 2015–2017. Kokanee abundance is represented as individuals hectare^{-1} ($\times$ 1,000) and Mysis densities are represented as individuals m^{-3}.
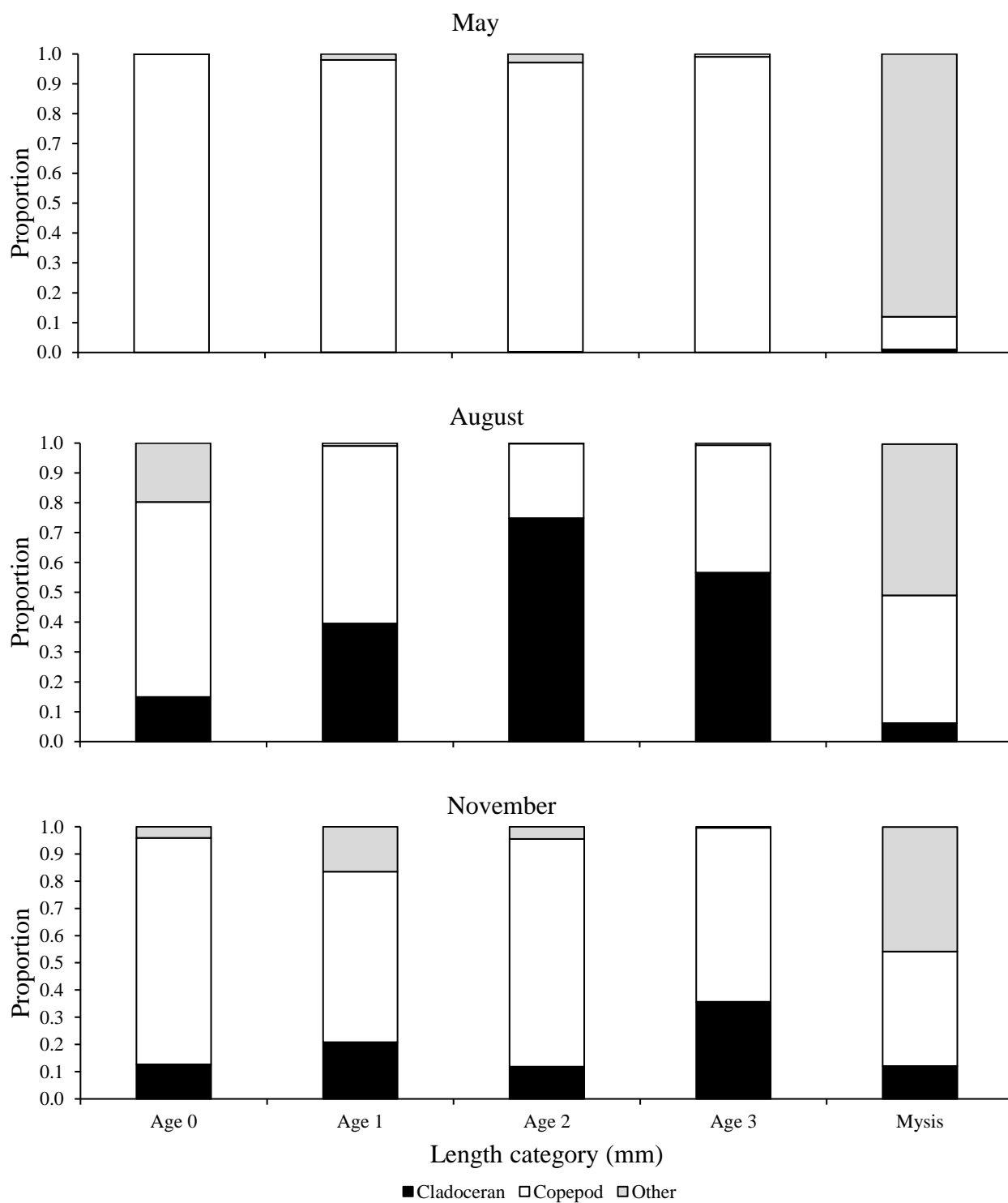
Figure 4.7. Average proportion by number in the diets of age-0 through age-3 kokanee and Mysis for May, August, and November in Lake Pend Oreille. Diet categories include cladocerans (*Bosmina longirostris*, *Daphnia* spp., *Diaphanosoma leuchtenbergianum*), copepods (*Calanoida* spp., *Cyclops bicuspidatus*), and other (see text for details).

Chapter 5: Conclusion

Kokanee *Oncorhynchus nerka* are arguably one of the most important cold-water fish due to their value as a recreational species and prey resource for ecologically, economically, and culturally significant fishes. As such, the effective management of kokanee is a central concern for biologists and was the primary goal of this dissertation. Specifically, this work addressed uncertainty surrounding common kokanee sampling techniques, evaluated the potential causes of growth disparities between different breeding groups of kokanee, and investigated age-specific patterns in competition between kokanee and Mysis.

Each chapter of this dissertation focused on a specific question surrounding the management and(or) ecology of kokanee that was ultimately limiting management of the species. The results of Chapter 2 suggest that mid-water trawls are size selective for small kokanee; whereas, gill nets are size-selective for large fish. Although these results are largely corroborated in the literature, managers now have empirical data supporting their gear choice as it relates to their sampling objectives. Chapter 3 identified that small changes in hatchery practices can have large, long-term ramifications for the growth trajectory of kokanee. The results of Chapter 3 not only provide a mechanism explaining observed growth patterns between early- and late-run kokanee, but also suggest periodic growth retardation could be used to increase the overall growth rate of juvenile fish. Finally, the results of Chapter 4 clarify the mechanism by which Mysis and kokanee compete and suggest large, adult fish are likely most susceptible to resource competition. Chapter 4 highlights the need to fully consider how ontogenetic shifts influence biotic interactions and provide managers with a better understanding of the population-level effects of resource competition between Mysis and kokanee.

Although each chapter revolves around a different aspect of kokanee management and ecology, our results improve the understanding of the species. For instance, the results of Chapter 3 suggest age-0 kokanee are fairly robust to starvation and possess the ability to rebound from period of food deprivation. As such, age-0 fish are likely resistant to the negative effects of competitive interactions with Mysis. However, the resiliency of age-0 kokanee necessitates comprehensive consideration of hatchery supplementation to avoid negatively influencing kokanee through density dependent processes. Collectively, our results highlight the complexity of managing kokanee, but aid the ability to provide a valued recreational species and important prey resource into perpetuity.

Future Directions

Chapters 2–4 provide valuable information regarding the management of kokanee in Idaho and North America. However, each chapter raises interesting questions as to the future of kokanee management and research that are addressed below.

Chapter 2

- All sampling in Chapter 2 was conducted within five days of the new moon to circumvent gear avoidance by kokanee. However, this sampling scheme is largely based on speculation necessitating corroboration with empirical data. As such, future research should address the influence of light intensity on the efficacy of gill nets and mid-water trawls.

- The results of Chapter 2 identify gill nets as an effective tool for sampling most kokanee populations. However, our results suggest relative selectivity adjustments for gill nets do not effectively represent the "true" population structure. As such, future research should address the efficacy of gill nets at characterizing "true" population structure by estimating selectivity using traditional techniques (e.g., mark-recapture).

Chapter 3

- The results of Chapter 3 suggest the observed growth differences between early-run and late-run kokanee in Lake Pend Oreille is largely due to hatchery practices, but the long-term ramifications of altered growth trajectories are not addressed. For instance, what do growth disparities mean for the respective survival of early- and late-run fish? Similarly, how do increased growth rates of age-0 fish influence their future fitness? Future research should address the influence of slowing growth of fish in the hatchery on the long-term growth and survival of kokanee in Lake Pend Oreille.

- Chapter 3 suggests that retardation of growth in the hatchery could result in increased growth rates of hatchery fish in the wild. As such, periodic starvation could be used to increase the growth rate of hatchery fish. However, the ability to (and influence of) improve growth rates through starvation cycles in kokanee is largely untested and necessitates future research.

Chapter 4

- Chapter 4 shows that ontogenetic shifts in diet and behavior influence biotic interactions between Mysis and kokanee and can result in large-scale, population-level changes. However, our results are largely correlative and may be confounded by biotic or abiotic characteristics that were unidentified in the current study. As such, future investigations surrounding Mysis-kokanee interactions should address age-specific patterns in competitive interactions using controlled experiments.

- The results of Chapter 4 highlight the difficulty of managing kokanee in a dynamic system such as Lake Pend Oreille. For instance, hatchery supplementation was invaluable for rebuilding kokanee stocks following population declines in the 1970s. However, the collapse of Mysis has altered the dynamics of Lake Pend Oreille thereby shifting the balance from competition between species to competition among conspecifics. As such, future research should evaluate alternative hatchery supplementation strategies to account for apparent increases in competition among kokanee in Lake Pend Oreille.

Appendix A.1. Average monthly densities (individuals L^{-1}) of *Calanoida* spp., *Cyclops bicuspidatus, Bosmina longirostris*, *Daphnia* spp., and *Diaphanosoma leuchtenbergianum* sampled from Lake Pend Oreille, 2015–2017. Standard deviations are provided in parenthesis.

Month	*Calanoida* spp.	*Cyclops bicuspidatus*	*Bosmina longirostris*	*Daphnia* spp.	*Diaphanosoma leuchtenbergianum*
			2015		
April	5.7 (4.5)	0.5 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
May	15.3 (9.0)	9.6 (6.9)	0.0 (0.1)	0.0 (0.0)	0.0 (0.0)
June	1.6 (1.0)	41.9 (27.3)	4.7 (2.3)	0.6 (0.5)	0.1 (0.1)
July	8.9 (4.1)	60.7 (26.4)	0.8 (0.7)	7.7 (3.4)	1.8 (0.9)
August	6.4 (2.9)	30.0 (10.4)	0.5 (0.5)	0.4 (0.2)	6.6 (4.1)
September	7.7 (2.1)	10.1 (3.0)	1.5 (0.8)	0.3 (0.2)	2.7 (1.3)
October	7.9 (2.1)	5.0 (1.6)	1.3 (0.6)	0.2 (0.1)	1.7 (0.7)
November	5.7 (1.8)	5.0 (1.3)	0.2 (0.2)	0.0 (0.0)	0.5 (0.2)
December	5.2 (3.0)	1.9 (0.9)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
			2016		
January	4.1 (1.5)	1.3 (0.4)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
February	7.2 (2.9)	1.1 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
March	6.2 (3.0)	1.0 (0.6)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
April	9.9 (5.3)	1.5 (0.9)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
May	19.5 (8.5)	7.7 (4.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
June	3.3 (1.8)	35.5 (10.5)	0.4 (0.4)	0.0 (0.1)	0.1 (0.2)
July	6.0 (2.0)	57.6 (20.5)	0.4 (0.5)	0.6 (0.6)	0.3 (0.3)
August	5.4 (2.4)	53.6 (15.1)	0.8 (0.6)	3.2 (1.8)	7.0 (3.0)
September	7.6 (1.3)	14.1 (3.8)	2.7 (1.3)	1.2 (0.5)	8.1 (3.2)
October	4.4 (1.3)	9.3 (2.7)	0.2 (0.2)	0.4 (0.3)	1.0 (0.6)
November	4.5 (1.0)	6.0 (1.3)	0.0 (0.0)	0.0 (0.0)	0.3 (0.2)
December	5.2 (0.9)	4.7 (0.9)	0.0 (0.0)	0.0 (0.0)	0.1 (0.0)
			2017		
January	5.1 (2.9)	1.6 (0.7)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
February	5.0 (1.8)	1.1 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
March	6.2 (2.9)	1.3 (0.8)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
April	8.7 (5.4)	1.7 (1.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
May	9.5 (7.2)	10.3 (5.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
June	4.9 (3.0)	24.3 (9.2)	0.1 (0.2)	0.0 (0.0)	0.0 (0.1)
July	7.5 (1.8)	31.6 (11.5)	0.2 (0.2)	0.1 (0.1)	0.5 (0.4)
August	2.4 (1.1)	28.8 (8.0)	0.0 (0.0)	0.0 (0.0)	0.6 (0.4)
September	2.4 (1.0)	12.9 (4.8)	0.1 (0.1)	0.0 (0.0)	3.7 (1.4)
October	4.7 (1.4)	9.2 (2.1)	0.6 (0.4)	0.0 (0.0)	0.9 (0.4)
November	7.3 (2.8)	5.0 (1.8)	0.0 (0.0)	0.0 (0.0)	0.2 (0.1)
December	4.9 (1.2)	2.2 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)