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PRIMARY RESEARCH PAPER

Ontogenetic diet shifts with potential ramifications for 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. However, ontogenetic shifts are rarely placed into a population context due to the difficulty of incorporating the vagaries of size-mediated interactions. As such, we evaluated the role of ontogenetic shifts in diet as they relate to potential competitive interactions between kokanee *Oncorhynchus nerka* and Opossum Shrimp *Mysis diluviana* (hereafter Mysis) in Lake Pend Oreille, Idaho. Contemporary data were used to understand diet patterns of Mysis and kokanee. Historical data were evaluated within the context of ontogenetic shifts 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. When placed in a historical context, age-specific patterns in kokanee diet likely led to increases in adult growth following declines in Mysis abundance. Improved fitness of adult fish likely resulted in record high abundances of kokanee in Lake Pend Oreille thereby shifting the balance from inter- to intraspecific competition.

Keywords *Mysis diluviana* · Kokanee · Competition

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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 may be obscured by the confounding effects of ontogenetic shifts in diet that often occur in size-structured populations (Rose et al., 2001). Despite the challenges associated with identifying interspecific competition, understanding how species interact is important for explaining ecological processes and guiding management actions.

The importance of understanding the mechanisms underlying competition is typified in systems with co-occurring kokanee *Oncorhynchus nerka* (Walbaum, 1792) and Opossum Shrimp *Mysis diluviana* Audzijonyte & Väinölä, 2005 (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* (Suckley, 1859) and Rainbow Trout *Oncorhynchus mykiss* (Walbaum, 1792; Wydoski & Bennett, 1981; Paragamian & Bowles, 1995). In an effort to improve the size structure of kokanee (and other sport fish), Mysis were widely introduced in the mid-20th century throughout systems in North America and Europe (Nesler & Bergersen, 1991). Ironically, recipient fish populations exhibited inconsistent patterns in growth, and population declines of kokanee were widely reported following Mysis introductions (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 cladoceran zooplankton, the preferred prey of kokanee. In Lake Pend Oreille, Idaho *Daphnia* spp. and *Bosmina longirostris* (O.F. Müller, 1776) 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 & 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 & Goldman, 1980; Beattie & Clancey, 1991; Bowles et al., 1991). However, a direct link between Mysis' influence on zooplankton and potential effects on kokanee populations has remained difficult to identify.

One of the primary difficulties constraining our ability to understand Mysis–kokanee interactions in natural systems is the occurrence of numerous confounding factors. Kokanee populations are often subject to bottom-up (i.e., resource limitation) and top-down (i.e., predation) forces that are interrelated and co-occur. Bottom-up forces imposed by Mysis act over long temporal scales and may negatively influence growth, fitness, and population density (Hairston et al., 1960). Mysis also serve as an important prey resource for juvenile Lake Trout *Salvelinus namaycush* (Walbaum, 1792) thereby releasing the species from recruitment bottlenecks (Ellis et al., 2011; Schoen et al., 2015) resulting in reductions in kokanee densities via predation (Bowles et al., 1991; Martinez et al., 2009). Thus, systems with Lake Trout, kokanee, and Mysis often experience complex interactions that can confound understanding the role of any one agent. For instance, Lake Trout and Mysis were reported to negatively influence kokanee biomass and production in Lake Pend Oreille (Corsi et al., 2019). A collapse in Mysis abundance corresponded to an increase in kokanee production of 224–523 tonnes, whereas predation by Lake Trout combined with high Mysis densities negatively influenced kokanee biomass. Similarly, Mysis altered zooplankton composition and released Lake Trout from a recruitment bottleneck in Flathead Lake, Montana resulting in a widespread trophic cascade (Ellis et al., 2011). Identifying the influence of top-down and bottom-up forces in governing kokanee populations remains an important goal for natural resource agencies. Nevertheless, identifying the role of regulatory forces relies on a thorough understanding of how each mechanism acts on a population.

Mysis are typically considered to have a negative influence on kokanee populations by disproportionately affecting age-0 fish (Bowles et al., 1991; Clarke & Bennett, 2002; Caldwell et al., 2016). For instance, Mysis were implicated in the decline of kokanee in Lake Pend Oreille by competing with kokanee fry for cladocerans (Bowles et al., 1991). Although the presumption that age-0 fish are most susceptible to resource limitations has support (Hjort, 1914;

Cushing, 1969, 1990), previous research suggests age-0 kokanee may be less sensitive 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). If the dietary requirements of adult kokanee differ from juvenile fish, competition between kokanee and Mysis may exhibit age-specific patterns. Unfortunately, kokanee–Mysis interactions have rarely been framed in an age-specific context, thereby limiting our understanding of competitive interactions between species. We sought to evaluate age-specific patterns in abundance and growth of kokanee in Lake Pend Oreille before and after the decline of Mysis in 2011. We hypothesized that the decline of Mysis positively influenced kokanee abundance and growth in Lake Pend Oreille due to increases in available prey. However, previous research (e.g., Clarke et al., 2004) suggests kokanee may not respond to increased prey availability uniformly due to potential disparities in diet or energy requirements. As such, we also evaluated age-specific patterns in diet to better understand how diet potentially influenced competition between Mysis and kokanee. We hypothesized that competition for cladocerans disproportionally influenced adult kokanee resulting in distinct changes in abundance and growth following declines of Mysis in Lake Pend Oreille.

Methods

Study area

Lake Pend Oreille is a large (383 km^2), deep (mean depth = 164 m), meso-oligotrophic lake located in northern Idaho (Fig. 1). The northern basin of the lake is relatively shallow ($<$ 200 m maximum depth), whereas the majority of the southern basin is over 300 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 for sampling purposes (Fig. 1). In 1952, Cabinet Gorge (upstream) and Albeni Falls (downstream) dams began operation on Lake Pend Oreille. Mysis were introduced into Lake Pend Oreille from 1966 to 1970 and became established by 1974. Mysis establishment co-occurred with changes to dam operations (i.e., consistent, deep-water drawdowns) and likely influenced kokanee in Lake Pend Oreille. Following Mysis establishment and changes to dam operations, lake-wide kokanee abundance declined and remained at a depressed state until hatchery supplementation was initiated in the mid-1970s (Hoelscher et al., 1990). In 2011, Mysis exhibited an unexplained collapse and have averaged between 6 and 157 individuals m^{-3} annually from 2011 to 2017. In addition to kokanee, the fish assemblage of Lake Pend Oreille consists of 9 native and about 15 non-native species (Hoelshcer, 1993; Corsi et al., 2019). Of particular note was the establishment of Lake Trout in the mid-1990s that led to unsustainable predation and near collapse of kokanee (Hansen et al., 2010). However, a successful suppression program has reduced the effect of Lake Trout on kokanee (Dux et al., 2019). During the majority of the year, copepods [*Diacyclops thomasi* (S.A. Forbes, 1882), calanoid copepods] are the most abundant zooplankton in the system (Clarke & Bennett, 2002). However, cladocerans (*Daphnia* spp., *Bosmina longirostris*, *Diaphanosoma leuchtenbergianum* Fischer, 1854) 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 to 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 to 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 were randomly selected each year and were evenly distributed among lake transects (12 per section) to ensure complete spatial coverage throughout Lake Pend Oreille. Prior to sampling, the vertical distribution of kokanee was determined using a Furuno Model FCV-585 depth sounder with a 10° hull-mounted transducer (Furuno Electric Co, LTD, Washington). Each transect was

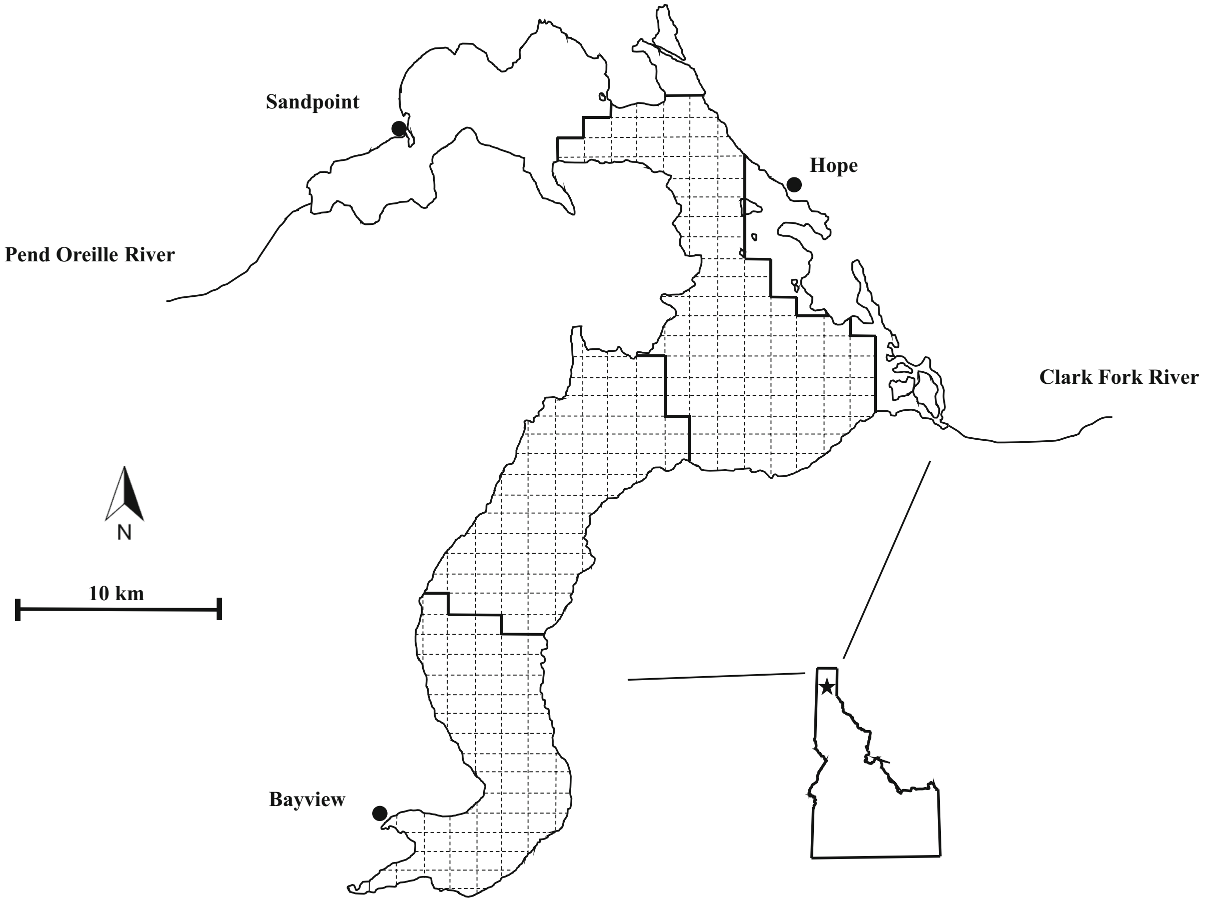

Fig. 1 Map of Lake Pend Oreille, Idaho with major tributaries included. Solid black lines represent boundaries between the south, middle, and north sections. Dotted lines represent 500 m^2 sampling quadrats. Areas of Lake Pend Oreille with an average depth < 25.0 m were excluded from sampling and do not have a sampling grid

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 to 2017, whereas weight and length data (nearest 1.0 mm) were collected from 2003 to 2017. Aging structures (e.g., scales, otoliths) were consistently removed from about 10 fish per 1-cm length bin from 1998 to 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 & 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 2 h of sunset (Rieman & 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 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 traveled 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 estimated 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 by multiplying the geometric mean density by the area of Lake Pend Oreille. Lake-wide abundance was 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. Abundance estimates of age-0 and adult (age 3–5) kokanee were used in analyses.

Mysis and zooplankton sampling

From 1998 to 2017, Mysis were sampled in June within 1 week of the new moon due to the negative phototaxis of Mysis (Rieman & 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 1000-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 & Falter, 1981). The net was rinsed, and all collected Mysis were preserved in 90% ethanol.

From 2015 to 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) to ensure complete spatial coverage throughout the system. 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} (Caldwell et al., 2016). Mysis and zooplankton samples were preserved in 90% ethanol.

Our analysis only focused on adult Mysis (> 10 mm) because Mysis less than 10 mm in length are primarily herbivorous and less likely to compete with kokanee for zooplankton prey (Branstrator et al., 2000). 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., 2016). 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 & 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 to 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

General patterns in the relationship between kokanee abundance and Mysis density were evaluated to understand the potential influence of Mysis on kokanee abundance. The abundance of juvenile kokanee (age 0), adult kokanee (age 3–5), and Mysis were summarized as lake-wide averages from 1998 to 2017. 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). Thus, the relationship between Mysis density and kokanee condition was evaluated as age-specific changes in mean weight of kokanee before and after the Mysis collapse in 2011. Potential changes in the average weight of kokanee following the collapse of Mysis were compared using *t* tests at an $\alpha = 0.05$ (Zar, 1996). Previous research has shown that mid-water trawls are size selective for small kokanee (Klein et al., 2019). As such, analysis of weight data focused on age-0 (mean length = 60 mm) through age-3 (221 mm) 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 (*calanoid copepods*, *Diacyclops thomasi, Bosmina longirostris*, *Diaphanosoma leuchtenbergianum,* and *Daphnia* spp.) were evaluated to understand the seasonal availability of zooplankton in Lake Pend Oreille. Zooplankton data were originally evaluated on an annual basis from 2015 to 2017. However, annual patterns in zooplankton densities were similar among years and were combined as a monthly average across years.

Age-specific diet patterns of kokanee were analyzed to evaluate potential ontogenetic shifts in diet. Ontogenetic diet shifts were assessed using mixed logistic regression (Agresti, 2007). The occurrence of a particular diet item (e.g., cladoceran, copepod) served as the dependent variable, whereas age (0–3) and sampling month were independent variables. The date of sampling was used as a random variable to account for the lack of independence among diet samples collected on the same date. Diet types included cladocerans (*Bosmina longirostris*, *Daphnia* spp., *Diaphanosoma leuchtenbergianum*), copepods (calanoid copepods, *Diacyclops thomasi*), and an "other" category. The other category included Aranea, Coleoptera, Collembola, Diptera, Ephemeroptera, Hymenoptera, Mysis, Odonata, and Ostracoda. Regressions were fit for each diet item and significant parameters were identified using a Wald Chi-square statistic ($P \leq 0.05$; Agresti, 2007). Regression analysis was conducted with R statistical software (R Development Core Team, 2018).

Diet composition of Mysis and kokanee was evaluated to understand potential interactions between the species. Diet was expressed as proportion by weight. Identification and size estimation of individual diet items was impossible for most diet items due to varying degrees of digestion. In addition, Mysis rarely consume an entire prey item and instead focus on soft, easily digestible portions of zooplankton prey (Grossnickle, 1982; Smokorowski et al., 1998). As such, diet was expressed as simple taxonomic groupings that included cladocerans and copepods. Prey-specific weights were determined by multiplying the number of individuals in a given diet by the average dry weight of cladocerans and copepods that occur in Lake Pend Oreille (Rieman & Bowler, 1980). Although this approach ignores other diet items, length–weight relationships were not available for all diet items necessitating a simplified description of diet. Regardless, we were primarily interested in understanding use of common zooplankton by kokanee and Mysis in Lake Pend Oreille rather than a complete description of each predator's diet. 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 ($\geq$ 10 mm) and age-0–age-3 fish due to low catch of age-4 and age-5 kokanee in mid-water trawls.

Diet overlap between Mysis and kokanee was evaluated using the Schoener Index (Schoener, 1970). The Schoener Index of diet overlap (α) was estimated as

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

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. Prey items used to estimate diet overlap included cladocerans (*Bosmina longirostris*, *Daphnia* spp., *Diaphanosoma leuchtenbergianum*), copepods (calanoid copepods, *Diacyclops thomasi*), Aranea, Coleoptera, Collembola, Diptera, Ephemeroptera, Hymenoptera, Mysis, Odonata, Ostracoda, rotifers, and pollen. The Schoener Index varies from 0.0 to 1.0 with values over 0.60 denoting biologically significant diet overlap (Zaret & Rand, 1971; Mathur, 1977).

Results

Annual increases in kokanee abundance corresponded to reductions in Mysis density from 1998 to 2017 (Fig. 2). The inverse relationship between Mysis and kokanee density was most pronounced following declines of Mysis in 2011. After 2011, age-0 abundance reached a record high of over 16 million fish. Similarly, age-3 through age-5 kokanee neared two million fish in 2013 and 2014. The relationship between average weight of kokanee and the density of Mysis exhibited distinct, but alternative patterns by age class (Fig. 3). Following declines of Mysis, the mean weight of age-0 fish declined by about 42% and the average weight of age-1 fish decreased by about 16%. Declines in weight following the collapse of Mysis were significant for age-0 ($t = 7.14$, df = 51.66, $P < 0.001$) and age-1 ($t = 2.49$, df = 52.22, $P = 0.016$) fish. Conversely, the average weight of age-2 kokanee increased by approximately 5%, whereas the mean weight of age-3 fish increased by about 34% following Mysis collapse. However, significant increases in mean weight were only evident for age-3 kokanee ($t = -4.16$, df = 38.39, $P < 0.001$).

Zooplankton abundance and seasonal availability were variable and taxa-specific in Lake Pend Oreille (Fig. 4). Calanoid copepods were relatively abundant throughout the year (mean ± SD; $6.45 \pm 3.05\ \mathrm{l}^{-1}$), but exhibited a peak in abundance ($14.47 \pm 4.16\ \mathrm{l}^{-1}$) in May. *D. thomasi* occurred throughout the year in Lake Pend Oreille and exhibited a peak in abundance ($50.84 \pm 15.16\ \mathrm{l}^{-1}$) in July. Compared with

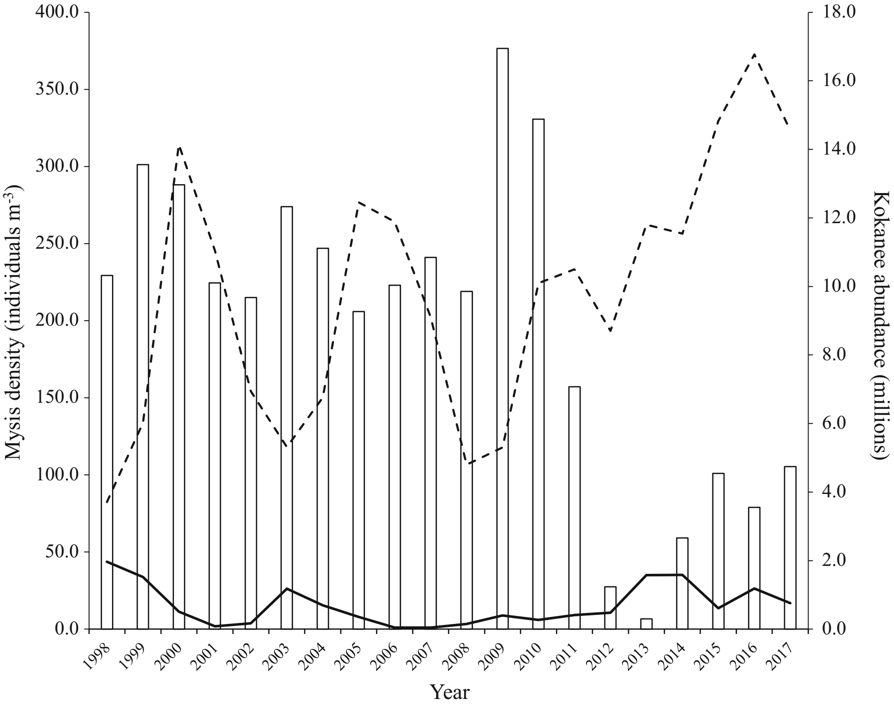

Fig. 2 Historical estimates of adult Mysis density (white bars) and kokanee abundance in Lake Pend Oreille, 1998–2017. Kokanee abundance is separated into age-0 (dashed line) and age-3–5 (solid line) fish

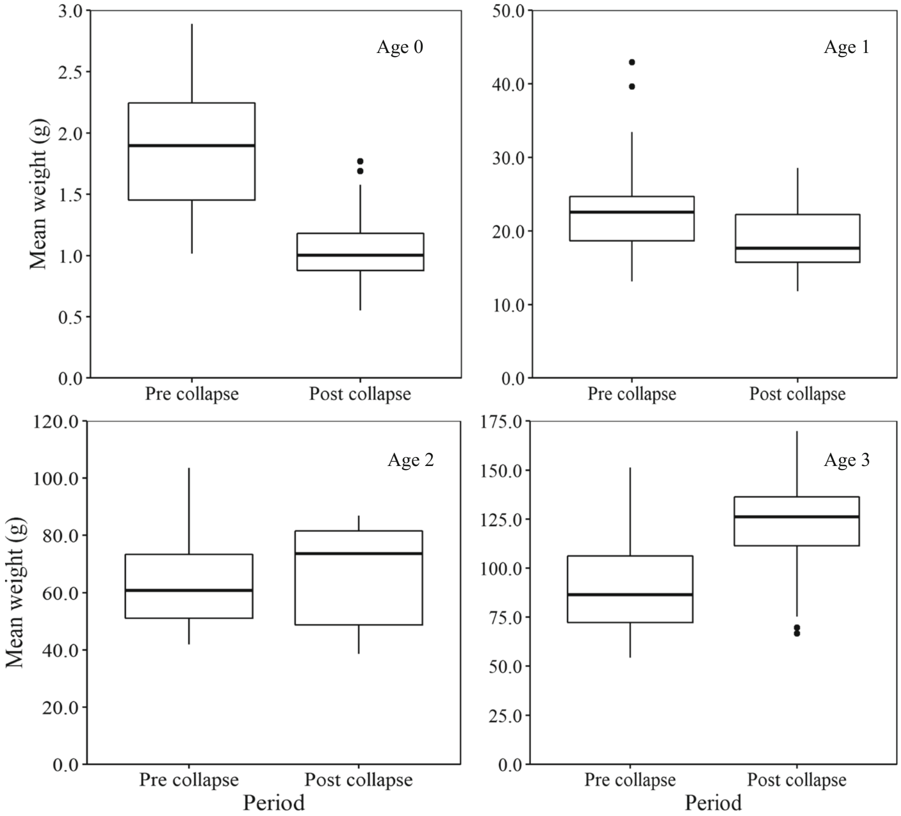

Fig. 3 Boxplots showing age-specific mean weights (g) for kokanee sampled from Lake Pend Oreille pre-Mysis collapse (1998–2010) and post-Mysis collapse (2011–2017). Note differing scale of y axis

copepods, cladocerans were less abundant and only available seasonally. *B. longirostris* were relatively rare in Lake Pend Oreille exhibiting 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 exhibited distinct patterns in consumption of zooplankton with age (Fig. 5). The probability of occurrence of cladocerans in the diet of kokanee increased from 0.80 for age-0 kokanee to 0.98 for age-3 fish. However, patterns in the probability of occurrence of particular diet items in the diet of kokanee differed by prey type. The predicted probability of the occurrence of copepods in kokanee diets exhibited little variability with fish age. Conversely, the probability of occurrence of "other" diet items in kokanee stomachs increased from 0.09 to 0.38 as fish age increased from 0 to 3. The probability of consuming cladocerans ($z = 3.14$, $P = 0.001$) and other diet items ($z = 2.40$, $P = 0.016$) was influenced by fish age. Age was not a significant predictor of the probability of occurrence of copepods in the diet of kokanee ($z = 1.52$, $P = 0.129$).

Kokanee and Mysis exhibited variable patterns in their use of zooplankton that largely reflected the seasonal availability of prey in Lake Pend Oreille (Fig. 6). In May, kokanee and Mysis consumed higher proportions of copepods than cladocerans. Cladocerans were more prevalent in the diets of kokanee and Mysis in August than May. However, copepods continued to outnumber cladocerans in the diet of Mysis. In November, Mysis consumed more cladocerans than in May and August. Kokanee continued to consume cladocerans in November, but they constituted a smaller proportion of kokanee diets when compared to August. In addition to seasonal variation among diets, age-specific patterns in diet were evident.

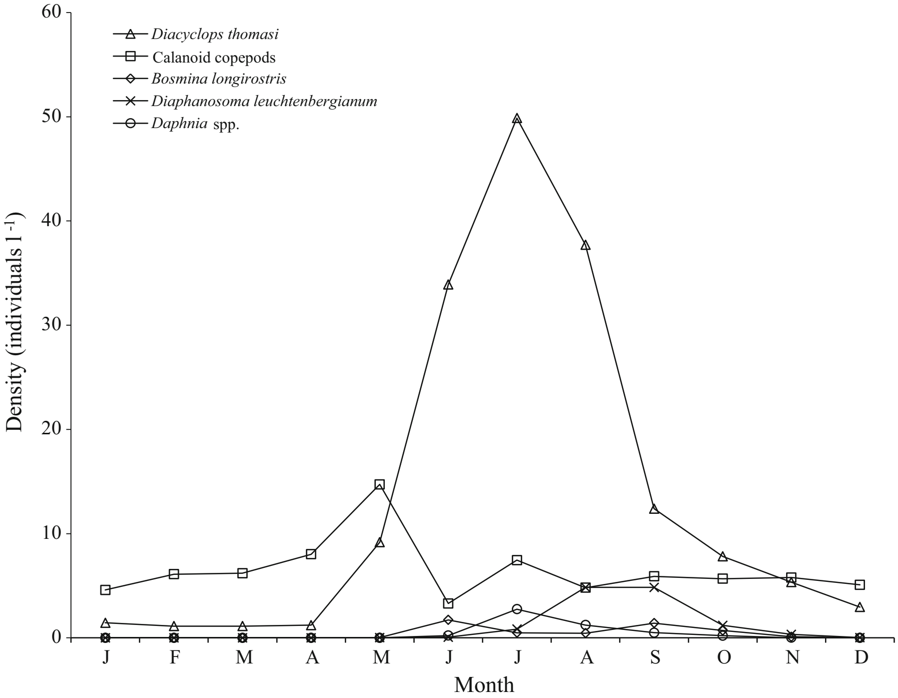

Fig. 4 Average density of zooplankton in Lake Pend Oreille, 2015–2017

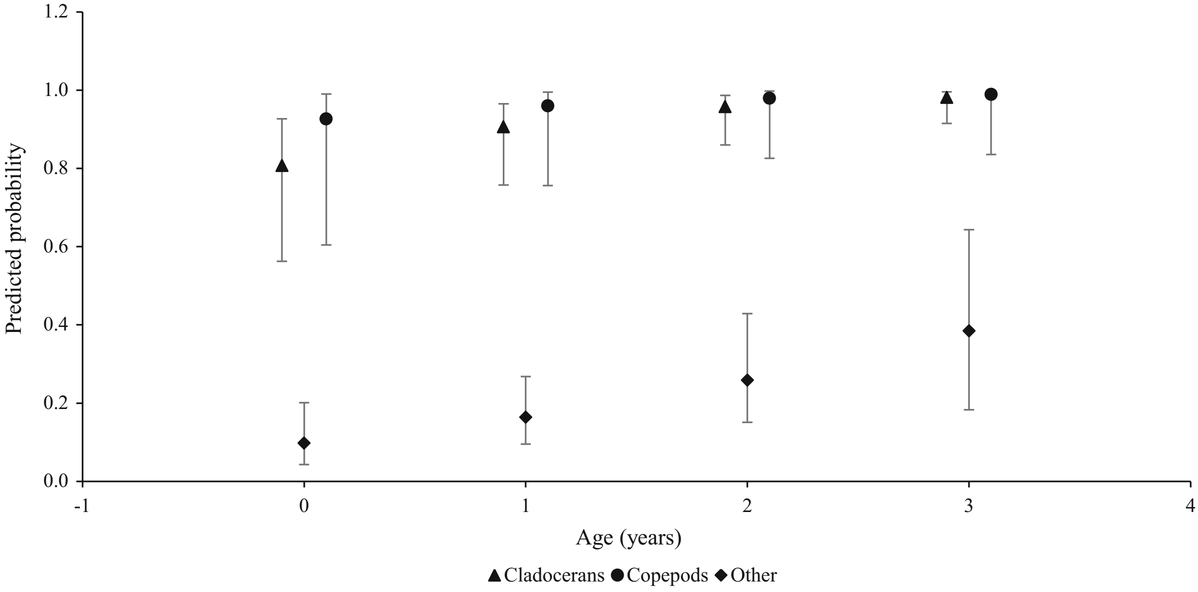

Fig. 5 Predicted probabilities of the occurrence of cladocerans, copepods, and other prey items in the diet of kokanee varying in age from 0 to 3 years. Bootstrapped 95% prediction intervals are included for each prey type. Note that the predicted cladoceran and copepod probabilities are offset to aid in interpretation

For instance, cladocerans accounted for 55–70% of the zooplankton consumed by age-2 and age-3 kokanee in August, whereas cladocerans represented smaller proportions of the zooplankton consumed by age-0 (0.19%) and age-1 (0.36%) kokanee.

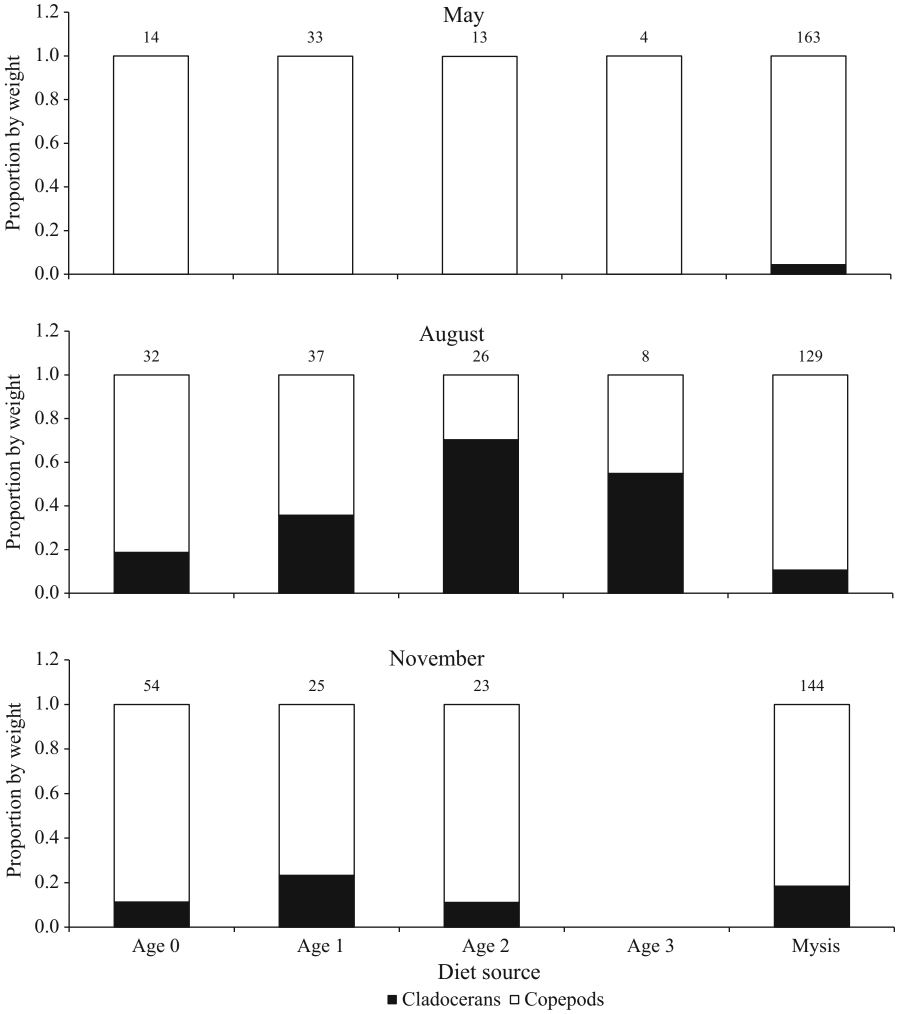

Fig. 6 Average proportion by weight in the diets of age-0 through age-3 kokanee and Mysis for May, August, and November in Lake Pend Oreille. Diet categories include cladocerans (*Bosmina longirostris*, *Daphnia* spp., *Diaphanosoma leuchtenbergianum*) and copepods (calanoid copepods, *Diacyclops thomasi*). Sample sizes are included above each column

Schoener Index values largely reflected season-specific diet habits (Table 1). For instance, Schoener Index values increased from 0.11 in May to 0.58 in November. In addition, patterns in diet overlap were fairly consistent between kokanee age classes and Mysis. Diet overlap was estimated as 0.11 in May regardless of the kokanee age class under consideration. Diet overlap increased to near significant levels in November, but continued to exhibited little variability with kokanee age classes.

Table 1 Schoener Index values of diet overlap between kokanee and Mysis sampled in the May, August, and November of 2017

	Age (years)				
Season	0	1	2	3	Overall
Spring	0.10	0.10	0.11	0.10	0.11
Summer	0.49	0.49	0.31	0.49	0.50
Autumn	0.57	0.58	0.53	0.58	0.58

Indices were calculated using percent by number for each prey type

Discussion

Our results suggest kokanee exhibit consistent ontogenetic shifts in diet. Cladocerans composed between 70 and 55% of age-2 and age-3 kokanee diets in August, whereas age-0 and age-1 fish contained between 19 and 36% over the same period. Although our results highlight apparent ontogenetic shifts in diet of kokanee, the majority of literature focused on kokanee food habits suggest kokanee diets vary little with age (Bevelhimer & Adams, 1993; Stockwell & Johnson, 1997; Stockwell & Johnson, 1999) and are largely related to seasonal zooplankton availability (Northcote & 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 in the summer and copepods dominated diets for the remainder of the year (Martinez & Bergersen, 1991). Optimal foraging theory suggests fish should maximize their net rate of energy intake by consuming energetically profitable (e.g., larger prey) items that require short handling times (Townsend & 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 influenced by myriad factors including prey availability, habitat, and biotic interactions (e.g., competition, predation; Morin, 1999). However, previous research suggests that predator avoidance is a predominant factor influencing the behavior and diet of kokanee (Townsend & Winfield, 1985; Levy, 1991). For instance, age-0 kokanee exhibited large diel vertical migrations in Blue Mesa Reservoir, Colorado despite decreased daytime foraging opportunities (Hardiman et al., 2004). The authors suggested the observed migration patterns were largely associated with increased predation risk from Lake Trout. Similarly, juvenile *Oncorhynchus 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 by Lake Trout is a principal concern in Lake Pend Oreille (Hansen et al., 2008, 2010; Corsi et al., 2019) and has the potential to influence the behavior of kokanee. As immature fish are most susceptible to predation in Lake Pend Oreille (Vidergar, 2000), juvenile kokanee may avoid limnetic zones until light attenuation reduces predation risk (Beauchamp et al., 1999; Mazur & Beauchamp, 2006). Cladocerans are typically distributed in the upper epilimnion; therefore, predator avoidance behavior by juvenile kokanee may constrain fish to deeper habitats that are dominated by copepods (Rieman & 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.

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 *Lepomis macrochirus* (Rafinesque, 1819) and Pumpkinseed *Lepomis gibbosus* (Linnaeus, 1758) growth declined linearly as Bluegill density and competition for littoral invertebrates increased (Mittelbach, 1988). Diet overlap between Mysis and kokanee approached significant levels in August and November suggesting the potential for competitive interactions between species. Furthermore, Mysis' ability to regulate zooplankton abundance has been well documented. Prior to the collapse of Mysis, Mysis were estimated to consume 70%–100% of the daily standing stock of cladocerans in Lake Pend Oreille (Chipps & Bennett, 2000; Caldwell et al., 2016). Additionally, Mysis consumed over four times as many cladocerans as kokanee in a given year in Lake Pend Oreille (Chipps & Bennett, 2000). Thus, reductions of Mysis in Lake Pend Oreille should result in overall increases in cladoceran abundance and positively influence the growth of adult fish (Rieman & Myers, 1992) assuming contemporary age-specific diet patterns are reflective of historical food habits. In Lake Pend Oreille, summer (July–September) cladoceran (*Daphnia* spp., *Diaphanosoma leuchtenbergianum*) densities increased from an average of 2,270 individuals m^3 in 2009 (Caldwell et al., 2016) to 3,479 individuals m^3 in 2015–2017. The decline of Mysis and increase in cladocerans was associated with an average increase in weight of 30.0 g in age-3 kokanee (pre-Mysis collapse vs. post-Mysis collapse; 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 frame. Although declines in Mysis and concurrent increases in cladocerans have likely positively influenced kokanee in Lake Pend Oreille, a reduction in interspecific competition may exacerbate interactions between conspecifics.

Oncorhynchus nerka are well known for exhibiting density-dependent reductions in growth (Ricker, 1937; Goodlad et al., 1974; Peterman, 1984). Age-1–3 kokanee displayed a clear inverse relationship between fish density and length-at-age in ten lakes and reservoirs throughout Idaho (Rieman & 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, the average weight of age-0 kokanee declined by nearly 50%. Increases in kokanee abundance should correspond to decreases in zooplankton density; however, average zooplankton density increased following the collapse of Mysis in Lake Pend Oreille (Caldwell et al., 2016). 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 & Suffern, 1976; Bowers & Vanderploeg, 1982; Peacor et al., 2005). In the absence of high Mysis densities, zooplankton may be released from invertebrate predation and 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 resulting in the annual stocking of between 500,000 and 17 million age-0 fish. Oftentimes, higher rates of stocking in Lake Pend Oreille have followed years of low adult returns or when abundant adults create surplus eggs (Whitlock et al., 2018b). 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 compound 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, survival, and recruitment. 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.

Despite the often-reported negative effects of Mysis on kokanee populations (Cooper & Goldman, 1980; Beattie & Clancey, 1991; Bowles et al., 1991), the presence of piscivorous Lake Trout in the system complicates identifying clear patterns in kokanee abundance. Lake Trout negatively influence the abundance of kokanee in systems where the species co-occur (Martinez et al., 2009; Ellis et al., 2011). Increases in Lake Trout abundance coincided with declines in kokanee abundance in Lake Pend Oreille (Corsi et al., 2019). However, the negative influence of Lake Trout could not be decoupled from the negative effects of competition between Mysis and kokanee. Thus, Corsi et al. (2019) concluded that Mysis were just as important as Lake Trout in regulating the kokanee population in Lake Pend Oreille. Although Mysis and Lake Trout likely both act to regulate kokanee in Lake Pend Oreille, management resources have been directed at Lake Trout suppression in the system due to lack of feasible suppression techniques for Mysis. Following the inception of Lake Trout suppression in Lake Pend Oreille, age-8 and older Lake Trout have been reduced by about 64% (Dux et al., 2019). The continued suppression of Lake Trout in Lake Pend Oreille may have shifted kokanee regulation from top-down to bottom-up controls as evidenced by the precipitous increases in kokanee following the collapse of Mysis in 2011. In addition, declines in the weight of kokanee most susceptible to Lake Trout predation (e.g., juvenile kokanee) suggest an increase in density-dependent processes rather than a reduction in density-dependent processes that would be expected under top-down regulation (Rose et al., 2001). Nevertheless, the influence of Lake Trout cannot be discounted. Rather, Mysis and Lake Trout impose complimentary regulatory forces on kokanee (Ellis et al., 2011; Schoen et al., 2015; Corsi et al., 2019) thereby necessitating consideration of both top-down and bottom-up processes and their ability to structure kokanee populations.

Admittedly, the ability to completely untangle the complex relationships occurring between Mysis and kokanee is challenging given the variable factors influencing the Lake Pend Oreille ecosystem. Predation, competition, and hatchery supplementation have continually altered population abundance of kokanee in Lake Pend Oreille. Notwithstanding, our results suggest kokanee exhibit age-specific patterns in resource use that ultimately influence how the species interacts with Mysis. Adult kokanee exhibited significant increases in weight and abundance following the collapse of Mysis. Simultaneously, juvenile kokanee abundance increased but corresponded to a significant decline in the average weight of age-0 and age-1 fish. Concordant declines in weight and increases in juvenile kokanee abundance suggest density-dependent processes are negatively influencing juvenile fish. Such density-dependent processes are exacerbated by ongoing stocking that acts to magnify intraspecific competition among juvenile fish. Hatchery supplementation has mitigated kokanee declines in the face of predation and competition. However, the continued suppression of Lake Trout and decline of Mysis may have intensified intraspecific competition necessitating a reconsideration of traditional stocking practices. The concurrent influence of various factors on kokanee in Lake Pend Oreille poses an interesting challenge for managers. However, the continued sustainability of kokanee in Lake Pend Oreille requires a comprehensive consideration of the age-specific dynamics of biotic interactions to more fully understand how fish interact with potential competitors and ultimately influence large-scale patterns in population structure.

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References

Agresti, A., 2007. An introduction to categorical data analysis, 2nd ed. Wiley, Hoboken, NJ.

Barbiero, R. P., M. Balcer, D. C. Rockwell & M. L. Tuchman, 2009. Recent shifts in the crustacean zooplankton community of Lake Huron. Canadian Journal of Fisheries and Aquatic Sciences 66: 816–828.

Beattie, W.D. & P.T. Clancey, 1991. Effects of *Mysis relicta* on the zooplankton community and kokanee population of Flathead Lake, Montana. In: Nesler, T.P. & Bergersen, E.P. (eds) Mysids in fisheries: Hard lessons from headlong introductions. American Fisheries Society, Symposium 9, Bethesda, MD. pp. 39–48.

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

Beauchamp, D. A., C. M. Baldwin, J. L. Vogel & C. P. Gubala, 1999. Estimating diel, depth-specific foraging with a visual encounter rate model for pelagic piscivores. Canadian Journal of Fisheries and Aquatic Sciences 56: 128–139.

Beeton, A. M., 1960. The vertical migration of *Mysis relicta* in Lakes Huron and Michigan. Journal of the Fisheries Research Board of Canada 17: 517–540.

Bevelhimer, M. S. & S. M. Adams, 1993. A bioenergetics analysis of diel vertical migration by kokanee salmon, *Oncorhynchus nerka*. Canadian Journal of Fisheries and Aquatic Sciences 50: 2336–2349.

Bowers, J. A. & H. A. Vanderploeg, 1982. *In situ* predatory behavior of *Mysis relicta* in Lake Michigan. Hydrobiologia 93: 121–131.

Bowles, E.D., R.E. Rieman, G.R. Mauser, & D.H. Bennett, 1991. Effects of introductions of *Mysis relicta* on fisheries in northern Idaho. In: Nesler T.P. & Bergersen, E.P. (eds) Mysids in fisheries: Hard lessons from headlong introductions. American Fisheries Society, Symposium 9, Bethesda, MD. pp. 65–74.

Branstrator, D. K., G. Cabana, A. Mazumder & J. B. Rasmussen, 2000. Measuring life-history omnivory in the opossum shrimp, *Mysis relicta*, with stable nitrogen isotopes. Limnology and Oceanography 45: 463–467.

Bunnell, D. B., B. M. Davis, D. M. Warner, M. A. Chriscinske & E. F. Roseman, 2011. Planktivory in the changing Lake Huron zooplankton community: *Bythotrephes* consumption exceeds that of *Mysis* and fish. Freshwater Biology 56: 1281–1296.

Caldwell, T. J., F. M. Wilhelm & A. Dux, 2016. Non-native pelagic macroinvertebrate alters population dynamics of herbivorous zooplankton in a large deep lake. Canadian Journal of Fisheries and Aquatic Sciences 73: 832–843.

Chess, D. W. & J. A. Stanford, 1998. Comparative energetics and life cycle of the Opossum Shrimp (*Mysis relicta*) in native and non-native environments. Freshwater Biology 40: 783–794.

Chipps, S. R. & D. H. Bennett, 2000. Zooplanktivory and nutrient regeneration by invertebrate (*Mysis relicta*) and vertebrate (*Oncorhychus nerka*) planktivores: implications for trophic interactions in oligotrophic lakes. Transactions of the American Fisheries Society 129: 569–583.

Clarke, L. R. & D. H. Bennett, 2002. Newly emerged kokanee growth and survival in an oligotrophic lake with *Mysis relicta*. Transactions of the American Fisheries Society 131: 176–185.

Clarke, L. R., P. S. Letizia & D. H. Bennett, 2004. Autumn-to-spring energetic and diet changes among kokanee from north Idaho lakes with and without *Mysis relicta*. North American Journal of Fisheries Management 24: 597–608.

Cooper, S. D. & C. R. Goldman, 1980. Oppossum shrimp (*Mysis relicta*) predation on zooplankton. Canadian Journal of Fisheries and Aquatic Sciences 37: 909–919.

Corsi, P. M., M. J. Hansen, M. C. Quist, D. J. Schill & A. M. Dux, 2019. Influences of Lake Trout (*Salvelinus namaycush*) and *Mysis diluviana* on Kokanee (*Oncorhynchus nerka*) in Lake Pend Oreille, Idaho. Hydrobiologia 840: 351–362.

Cushing, D. H., 1969. The regularity of the spawning season of some fishes. Journal of Marine Science 33: 81–92.

Cushing, D. H., 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Advances in Marine Biology 26: 249–293.

Drenner, R. W. & S. R. McComas, 1980. The roles of zooplankton escape ability and fish size selectivity in the selective feeding and impact of planktivorous fish. In Kerfoot, W. C. (ed.), Evolution and ecology of zooplankton communities. University Press of New England, Hanover, Connecticut: 87–593.

Dux, A. M., M. J. Hansen, M. P. Corsi, N. C. Wahl, J. P. Fredericks, C. E. Corsi, D. J. Schill & N. J. Horner, 2019. Effectiveness of Lake Trout (*Salvelinus namaycush*) suppression in Lake Pend Oreille, Idaho: 2006–2016. Hydrobiologia 840: 319–333.

Ellis, B. K., J. A. Stanford, D. Goodman, C. P. Stafford, D. L. Gustafson, D. A. Beauchamp, D. W. Chess, J. A. Craft, M. A. Deleray & B. S. Hansen, 2011. Long-term effects of a trophic cascade in a large lake ecosystem. PNAS 108: 1070–1075.

Goodlad, J. C., T. W. Gjernes & E. L. Brannon, 1974. Factors affecting Sockeye Salmon (*Oncorhychus nerka*) growth in four lakes of the Fraser River system. Journal of the Fisheries Research Board of Canada 31: 871–892.

Grossnickle, N. E., 1982. Feeding habits of *Mysis relicta* – an overview. Hydrobiologia 93: 101–107.

Hairston, N. G., F. E. Smith & L. B. Slobodkin, 1960. Community structure, population control, and competition. American Naturalist 94: 421–425.

Hansen, M. J., N. J. Horner, M. Liter, M. P. Peterson & M. A. Maiolie, 2008. Dynamics of an increasing Lake Trout population in Lake Pend Oreille, Idaho. North American Journal of Fisheries Management 28: 1160–1171.

Hansen, M. J., D. Schill, J. Fredericks & A. Dux, 2010. Salmonid predator–prey dynamics in Lake Pend Oreille, Idaho, USA. Hydrobiologia 650: 85–100.

Hardiman, J. M., B. M. Johnson & P. J. Martinez, 2004. Do predators influence the distribution of age-0 kokanee in a Colorado reservoir? Transactions of the American Fisheries Society 133: 1366–1378.

Hjort, J., 1914. Fluctuations in the great fisheries of northern Europe, viewed in the light of biological research. Rapports et Procès-Verbaux Conseil Permanent International Pour L'Exploration de la Mer 20: 1–228.

Hoelscher, B., E.C. Bowles, & V.L. Ellis, 1990. Kokanee stock status and contribution of Cabinet Gorge Hatchery, Lake Pend Oreille, Idaho. Annual report to the Bonneville Power Administration, Project 85-339, Idaho Department of Fish and Game, Boise, Idaho.

Hoelshcer, B., 1993. Pend Oreille Lake fishery assessment Bonner and Kootenai counties. Idaho 1951–1989. Water Quality Summary Report No. 102, Idaho Division of Environmental Quality, Boise, Idaho.

Hyslop, E. J., 1980. Stomach contents analysis—a review of methods and their application. Journal of Fish Biology 17: 411–429.

Isley, J. J. & T. B. Grabowski, 2007. Age and growth. In Guy, C. S. & M. L. Brown (eds.), Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, MD: 187–228.

Johannsson, O. E., L. G. Rudstam & D. C. Lasenby, 1994. *Mysis relicta*: assessment of metalimnetic feeding and implication for competition with fish in Lakes Ontario and Michigan. Canadian Journal of Fisheries and Aquatic Sciences 51: 2591–2602.

Johnston, N. T., 1990. A comparison of the growth of vertically-migrating and nonmigrating kokanee (*Oncorhynchus nerka*) fry. Canadian Journal of Fisheries and Aquatic Sciences 47: 486–491.

Klein, Z. B., M. C. Quist, A. M. Dux & M. P. Corsi, 2019. Size selectivity of sampling gears used to sample kokanee. North American Journal of Fisheries Management 39: 343–352.

Lasenby, D. C., T. G. Northcote & M. Furst, 1986. Theory, practice, and effects of *Mysis relicta* introductions to North American and Scandinavian lakes. Canadian Journal of Fisheries and Aquatic Sciences 43: 1277–1284.

Levy, D. A., 1991. Acoustic analysis of diel vertical migration behavior of *Mysis relicta* and kokanee (*Oncorhynchus nerka*) within Okanagan Lake, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 48: 67–72.

Martinez, P.J. & E.P. Bergersen, 1991. Interactions of zooplankton, *Mysis relicta*, and kokanees in Lake Granby, Colorado. In: Nesler, T.P. & Bergersen, E.P. (eds) Mysids in fisheries: hard lessons from headlong introductions. American Fisheries Society, Symposium 9, Bethesda, MD. pp. 49–64.

Martinez, P. J., P. E. Bigelow, M. A. Deleray, W. A. Fredenberg, B. S. Hansen, N. J. Horner, S. K. Lehr, R. W. Schneidervin, S. A. Tolentino & A. E. Viola, 2009. Western lake trout woes. Fisheries 34: 424–442.

Mathur, D., 1977. Food habits and competitive relationships of the Bandfin Shiner in Halawakee Creek, Alabama. American Midland Naturalist 97: 89–100.

Mazur, M. M. & D. A. Beauchamp, 2006. Linking piscivory to spatial-temporal distributions of pelagic prey fish with a visual foraging model. Journal of Fish Biology 69: 151–175.

McGurk, M. D., 2000. Comparison of fecundity-length-latitude relationships between nonanadromous (kokanee) and anadromous Sockeye Salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 78: 1791–1805.

Mittelbach, G. G., 1988. Competition among refuging sunfishes and effects of fish density of littoral zone invertebrates. Ecology 69: 614–623.

Morin, P., 1999. Community Ecology. Blackwell Science, Oxford.

Nesler, T.P. & E.P. Bergersen, 1991. Mysids and their impacts on fisheries: an introduction to the 1988 Mysid–fisheries symposium. In: Nesler, T.P., & Bergersen, E.P. (eds) Mysids in fisheries: hard lessons from headlong introductions. American Fisheries Society, Symposium 9, Bethesda, MD. pp. 1–4.

Northcote, T. G. & H. W. Lorz, 1966. Seasonal and diel changes in food of adult kokanee (*Oncorhynchus nerka*) in Nicola Lake, British Columbia. Journal of the Fisheries Research Board of Canada 23: 1259–1263.

Northcote, T.G., 1991. Success, problems, and control of introduced Mysid populations in lakes and reservoirs. In: Nesler, T.P. & Bergersen, E.P. (eds) Mysids in fisheries: hard lessons from headlong introductions. American Fisheries Society, Symposium 9, Bethesda, MD. pp. 5–16.

O'Brien, J. W., 1979. The predator-prey interaction of planktivorous fish and zooplankton: recent research with planktivorous fish and their zooplankton prey shows the evolutionary thrust and parry of the predator-prey relationship. American Scientist 67: 572–581.

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

Parker-Stetter, S.L., L.G. Rudstam, P.J. Sullivan, & D.M. Warner, 2009. Standard operating procedures for fisheries acoustic surveys in the Great Lakes. Special Publication 09-01, Great Lakes Fishery Commission, Ann Arbor, Michigan.

Peacor, S. D., K. L. Pangle & H. A. Vanderploeg, 2005. Behavioral response of Lake Michigan *Daphnia mendotae* to *Mysis relicta*. Journal of Great Lakes Research 31: 144–154.

Peterman, R. M., 1984. Density-dependent growth in early ocean life of Sockeye Salmon (*Oncorhychus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 41: 1825–1829.

Quist, M. C., M. A. Pegg & D. R. Devries, 2012. Age and growth. In Zale, A. V., D. L. Parrish & T. M. Sutton (eds.), Fisheries techniques, 3rd ed. American Fisheries Society, Bethesda, MA: 677–731.

R Development Core Team, 2018. R: a language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria.

Ricker, W. E., 1937. The food and the food supply of Sockeye Salmon (*Oncorhynchus nerka*) in Cultus Lake, British Columbia. Journal of the Biological Board of Canada. 3: 450–468.

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

Rieman, B.E. & B. Bowler, 1980. Kokanee trophic ecology and limnology in Pend Oreille Lake, Idaho. Idaho Department of Fish and Game, Fisheries Bulletin 1, Boise, Idaho.

Rieman, B. E. & C. M. Falter, 1981. Effects of the establishment of *Mysis relicta* on the macrozooplankton of a large lake. Transaction of the American Fisheries Society 110: 613–620.

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

Rose, K. A., J. H. Cowan, K. O. Winemiller, R. A. Myers & R. Hilborn, 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. Fish and Fisheries 2: 293–327.

Scheuerell, J. M., D. E. Schindler, M. D. Scheuerell, K. L. Fresh, T. H. Sibley, A. H. Litt & J. H. Shepard, 2005. Temporal dynamics in foraging behavior of a pelagic predator. Canadian Journal of Fisheries and Aquatic Sciences 62: 2494–2501.

Schoen, E. R., D. A. Beauchamp, A. R. Buettner & N. C. Overman, 2015. Temperature and depth mediate resource competition and apparent competition between *Mysis diluviana* and kokanee. Ecological Applications 25: 1962–1975.

Schoener, T. W., 1970. Non-synchronous spatial overlap of lizards in patchy habitats. Ecology 51: 408–418.

Smokorowski, K. E., D. C. Lasenby & R. D. Evans, 1998. Quantifying the uptake and release of cadmium and copper by the Oppossum Shrimp *Mysis relicta* preying upon the cladoceran *Daphnia magna* using stable isotope tracers. Canadian Journal of Fisheries and Aquatic Sciences 55: 909–916.

Sogard, S. M., 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Sciences 60: 1129–1157.

Stockwell, J. D. & B. M. Johnson, 1997. Refinement and calibration of a bioenergetics-based foraging model for kokanee (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 54: 2659–2676.

Stockwell, J. D. & B. M. Johnson, 1999. Field evaluation of a bioenergetics-based foraging model for kokanee (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 56: 140–151.

Townsend, C. R. & I. J. Winfield, 1985. The application of optimal foraging theory to feeding behavior in fish. In Tytler, P. & P. Calow (eds.), Fish Energetics. Croom Helm, London: 67–98.

Vidergar, D.T., 2000. Population estimates, food habits and estimates of consumption of selected predatory fishes in Lake Pend Oreille, Idaho. M.Sc. thesis. The University of Idaho, Moscow, Idaho.

Whitlock, S. L., M. R. Campbell, M. C. Quist & A. M. Dux, 2018a. Using genetic and phenotypic comparisons to evaluate apparent segregation among kokanee spawning groups. Transactions of the American Fisheries Society 147: 43–60.

Whitlock, S. L., M. C. Quist & A. M. Dux, 2018b. Effects of water-level management and hatchery supplementation on kokanee recruitment in Lake Pend Oreille, Idaho. Northwest Science 92: 136–148.

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

Zar, J. H., 1996. Biostatistical analysis, 3rd ed. Prentice-Hall, Upper Saddle River, NJ.

Zaret, T. M. & A. S. Rand, 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 25: 336–342.

Zaret, T. M. & J. S. Suffern, 1976. Vertical migration in zooplankton as a predator avoidance mechanism. Limnology and Oceanography 21: 804–813.