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ARTICLE

Abiotic and biotic factors related to growth of nonnative Walleyes in Lake Pend Oreille, Idaho

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Abstract

Objective: Understanding factors influencing growth is vital to effective management of fish populations. This study investigated potential factors influencing growth of an established nonnative population of Walleyes *Sander vitreus* in the Lake Pend Oreille system in northern Idaho.

Methods: We used relative growth index to describe growth of Walleyes relative to populations across North America. Mixed-effects modeling was used to relate growth to abiotic (i.e., mean summer water temperature, river inflow) and biotic (i.e., kokanee *Oncorhynchus nerka* abundance and biomass; opossum shrimp *Mysis diluviana* density) variables. Models were ranked using Akaike's information criterion corrected for small sample size. Individual variability in growth was related to diet represented by stable isotopes (i.e., δ^{15}N, δ^{13}C) using linear regression for age-1, age-2, age-3, and age-5 individuals. Subsequently, for each age-class, we evaluated differences in δ^{15}N and δ^{13}C between fast-growing (i.e., 75th and higher percentiles of growth) and slow-growing (i.e., 25th and lower percentiles of growth) individuals.

Result: Walleyes grew fast relative to other populations. Growth of Walleyes was positively associated with temperature as well as abundance and biomass of kokanee; growth was unrelated to river inflow and opposum shrimp density. The top model indicated that growth of Walleyes was related to temperature and kokanee abundance. An equally plausible model explaining growth consisted of only temperature. Generally, fast-growing Walleyes exhibited higher δ^{15}N than slow-growing individuals. Similarly, δ^{13}C was more depleted in the fast-growing individuals for all ages except age 1. This suggests that fast-growing individuals likely consumed prey items at higher trophic positions and fast-growing Walleyes (except age 1) used higher proportions of pelagic prey items.

Conclusion: This study showed that kokanee abundance and temperature likely influenced growth of Walleyes in the Lake Pend Oreille system. Additionally, variability in growth was apparently related to variability in diet, particularly for age-1 Walleyes.

KEYWORDS

age and growth, ecology, lake and reservoir, stable isotopes

INTRODUCTION

Fish population dynamics are regulated by growth, mortality, and recruitment. Although an understanding of all three rate functions is critical for effectively managing fish populations, growth is particularly important given its implications for mortality and recruitment. Fast growth during juvenile stages is associated with increased survival at older ages in various fish populations (e.g., Cyterski and Spangler 1996; Mittelbach and Persson 1998; Ebersole et al. 2006; Evans et al. 2014). Individuals exhibiting fast growth are less vulnerable to predation (Fuiman 1993; Katzir and Camhi 1993; Belk 1998), and large individuals are often less susceptible to environmental stressors than smaller individuals (Miller et al. 1988). Similarly, fast-growing individuals typically mature at early ages and, as a result, can reproduce more frequently than individuals exhibiting slow growth (Wolfert 1969; Reed et al. 1992; Kraus et al. 2000). In addition to reproducing more frequently, fast-growing individuals are generally more fecund, resulting in higher reproductive output (Rideout and Morgan 2010). Given the importance of growth, identification of factors regulating growth is important for better understanding the ecology and management of fishes.

Various abiotic conditions can directly or indirectly influence growth of fishes. For example, thermal habitat (i.e., temperature, latitude, growing season) is one of the primary abiotic factors directly influencing growth of fishes (e.g., Fortin et al. 1996; King et al. 1999; Meise et al. 2003; Houston and Belk 2006; Siegel et al. 2017). Generally, populations at southern latitudes exhibit faster growth than populations at northern latitudes (Quist et al. 2003; Vinagre et al. 2009; Porter et al. 2014; Massie et al. 2018) due to increased duration of the growing season (Purchase et al. 2005; Dunlop and Shuter 2006; Nepal and Fabrizio 2020). Physical (or structural) habitat, such as woody material, vegetation, and substrate (e.g., Baltz et al. 1998; Quist and Guy 2001; Shervette and Gelwick 2006), can indirectly influence growth and may be influenced by factors including flow (Pedersen et al. 2004). River discharge (i.e., lake inflow) is one abiotic factor that may indirectly influence growth, particularly in regulated systems (e.g., Korman and Campana 2009; Grabowski et al. 2012; Jacquemin et al. 2015; Tonkin et al. 2017). However, the magnitude and direction of the effect may vary among systems. For example, growth of age-0 Rainbow Trout *Oncorhynchus mykiss* in Lees Ferry tailwater, Arizona, was negatively correlated with discharge from Glen Canyon Dam (Korman and Campana 2009). In contrast, Quist and Spiegel (2012) found that growth of catostomids was positively related to discharge. In both studies, the authors suggested a complex relationship between discharge and growth. Similar studies have argued that discharge influences abiotic (e.g., temperature) or biotic (e.g., prey availability) conditions, which then affect growth (Weisberg and Burton 1993; Bunn and Arthington 2002; Nilsson and Renöfält 2008).

Impact Statement

Growth of Walleyes has been extensively studied, yet few studies have evaluated growth of Walleyes in novel systems or assessed individual variability in growth. Our research adds to the understanding of individual variability in growth and factors influencing population dynamics of nonnative Walleyes.

Biotic conditions arguably have been more frequently associated with growth of fishes. Across multiple systems and species, prey availability is a contributing factor to variations in growth (e.g., Szendrey and Wahl 1996; Fincel et al. 2014; Kennedy et al. 2018). Prey availability is a function of prey abundance (e.g., biomass, density) and vulnerability (e.g., predator–prey size ratio; Sih 1980; Hoxmeier et al. 2009; Jacobson et al. 2018). Growth of White Crappie *Pomoxis annularis*, Black Crappie *Pomoxis nigromaculatus*, White Bass *Morone chrysops*, and Largemouth Bass *Micropterus nigricans* was positively related to biomass of age-0 Gizzard Shad *Dorosoma cepedianum* in five Missouri reservoirs (Michaletz 1998). Particularly when prey is limited, growth may be influenced by interspecific and intraspecific competition (Margenau et al. 1998; Weber and Brown 2013; McDougall et al. 2018). In Lawrence Lake, Michigan, competitive interactions between Bluegills *Lepomis macrochirus* and Pumpkinseeds *L. gibbosus* resulted in decreased growth of both species (Mittelbach 1988). Similarly, intraspecific competition was identified as a primary driver of growth in Rainbow Trout from 2012 to 2016 in the Colorado River, Arizona (Korman et al. 2021). Because of such interactions, considering both prey abundance and potential competitive interactions is important when evaluating factors related to growth.

Although growth is typically summarized across a population, understanding factors that affect individual variation in growth is important because the cumulative change among individuals influences populations. For example, at an individual level, growth efficiency increases with temperature until some threshold is exceeded (Kocovsky and Carline 2001; Neuheimer et al. 2011; Matthias et al. 2018; Martino et al. 2019). Fast growth may result in greater reproductive output and higher survival, thereby influencing population abundance. Individual differences in growth result from genetics (e.g., Overturf et al. 2003; Cleveland et al. 2017), physiological differences (e.g., Norin et al. 2016), phenotypic plasticity (e.g., Karjalainen et al. 2016), and complex interactions among genetics, biotic interactions, and environmental conditions (Goodrich and Clark 2023). Some evidence suggests that individual plasticity (e.g., behavioral differences, prey selection) may have a greater influence on the phenotypic response than genetic or physiological differences (Heath and Roff 1987; Karjalainen et al. 2016; Stamp and Hadfield 2020). Mayer and Wahl (1995) found that growth of large Walleye *Sander vitreus* larvae (i.e., 11–18 mm) was related to prey taxa consumed. Although a variety of mechanisms may be responsible, identifying individual variability in growth and factors related to growth can provide insight into population- and community-level dynamics, particularly of introduced species (Bolnick et al. 2003; Mittelbach et al. 2014; Svanbäck et al. 2015).

Walleyes are an ideal study species for examining growth dynamics because of their widespread distribution and plasticity in life history characteristics (e.g., food habits). Across various Walleye populations, growth has been shown to reflect large- and small-scale patterns in temperature (Staggs and Otis 1996; Craig 2000; Quist et al. 2003; Lavigne et al. 2010) and prey availability (Hartman and Margraf 1992; Johnson and Goettl 1999; Ward et al. 2007; VanDeValk et al. 2008). Although Walleyes have been extensively studied, few studies have evaluated growth of nonnative populations, particularly those in the western United States. Furthermore, relatively few studies have addressed individual variability in growth of Walleyes within either native or nonnative populations. In northern Idaho, a nonnative population of Walleyes was established in the early 2000s and the Idaho Department of Fish and Game (IDFG) has been monitoring their relative abundance since 2011 (Rust et al. 2022). Ryan et al. (2021) described population growth and life history characteristics (i.e., age structure, age at maturity, body condition) of Walleyes in the system. Those authors concluded that somatic growth of Walleyes in the system was near the physiological maximum, but they did not identify potential factors that might be influencing growth. As such, the goal of this research was to evaluate growth and factors that may be related to growth of Walleyes in the Lake Pend Oreille system of northern Idaho.

Lake Pend Oreille supports populations of littoral and pelagic species, particularly kokanee *O. nerka*, which have been consumed by Walleyes in the system (Frawley 2023). Since abundance and biomass of prey can be related to growth (e.g., VanDeValk et al. 2008; Fincel et al. 2014), we considered abundance and biomass of kokanee as potential factors positively influencing growth of Walleyes in the Lake Pend Oreille system. Additionally, opossum shrimp *Mysis diluviana* (hereafter, *Mysis*), which are prevalent in this system, have been shown to compete with kokanee for zooplankton resources (e.g., Lasenby et al. 1986; Schoen et al. 2015). As such, we expected that *Mysis* density may have a negative, indirect effect on growth of Walleyes. Because of the variability observed in Walleye diets in the Lake Pend Oreille system (Frawley 2023), we postulated that individual Walleyes would exhibit differences in growth because of selective use of pelagic prey resources. Anthony et al. (2000) found that schooling pelagic species that matured at smaller sizes were characterized by higher energy densities than littoral fishes. As such, we expected that individual Walleyes that consumed pelagic prey resources (i.e., kokanee) would grow faster than individuals that consumed littoral prey resources. In this study, we (1) broadly described growth of Walleyes, (2) evaluated select abiotic and biotic conditions (i.e., temperature, river inflow, kokanee abundance and biomass, *Mysis* density) that may be related to growth of Walleyes, and (3) evaluated the relationship between variation in individual growth and variation in the diets of Walleyes in the Lake Pend Oreille system.

METHODS

Study area

The Lake Pend Oreille system in northern Idaho includes Lake Pend Oreille, the Clark Fork River, and the Pend Oreille River (Figure 1). Lake Pend Oreille is an oligotrophic, coldwater lake. It is the largest lake in Idaho and the fifth deepest (average depth of 164 m; maximum depth of 357 m) natural lake in the United States (Woods 2004; Rust et al. 2020). The Clark Fork River is the primary inflow to the lake, and the Pend Oreille River is the only outflow. Daily fluctuations of the water level of Lake Pend Oreille are controlled by Cabinet Gorge Dam (operated by Avista) on the Clark Fork River, and seasonal fluctuations are regulated at Albeni Falls Dam (operated by the U.S. Army Corps of Engineers) on the Pend Oreille River. The bathymetry of the system, coupled with fluctuations in water level, results in a diversity of habitats throughout the system. In general, the southern portion of Lake Pend Oreille consists of steep shorelines and pelagic habitat and is characterized by coldwater species (e.g., Lake Trout *Salvelinus namaycush*, kokanee). The shorelines of both rivers and the northern portion of Lake Pend Oreille slope gradually, resulting in a higher proportion of littoral habitat, and are characterized by both coldwater and warmwater species (e.g., Smallmouth Bass *Micropterus dolomieu*, Black Crappie). The Lake Pend Oreille system supports robust populations of native and nonnative fishes partly because of diverse habitats.

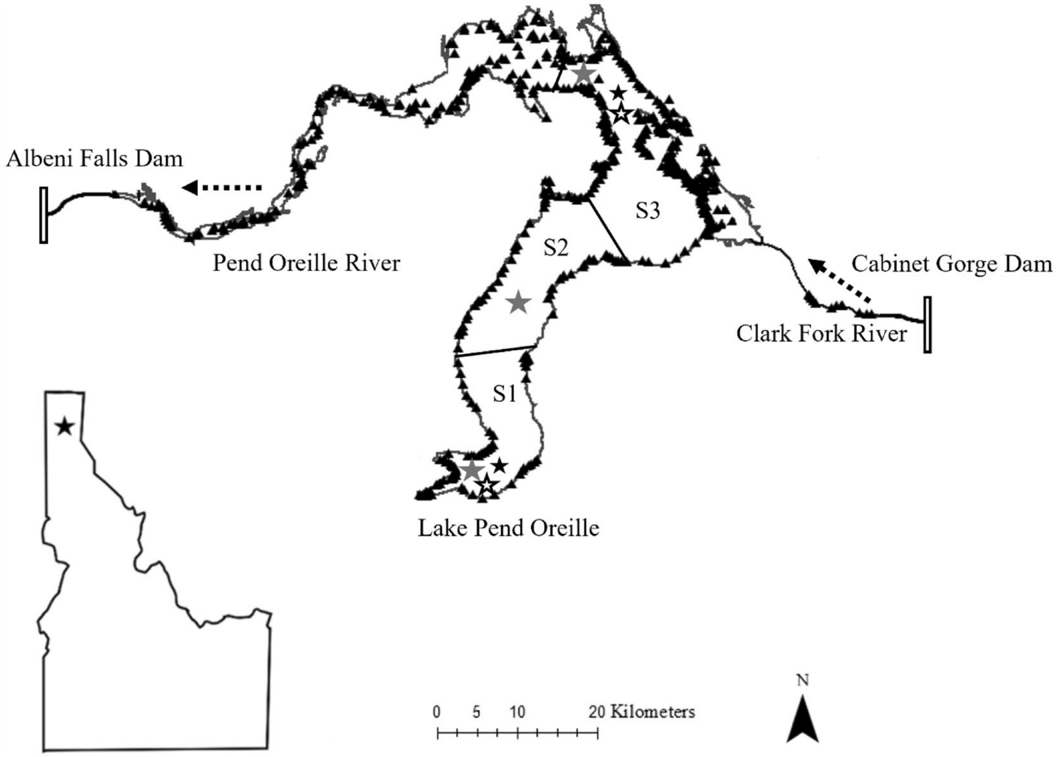

FIGURE 1 The Lake Pend Oreille system located in northern Idaho. This system includes Lake Pend Oreille, the Pend Oreille River, and the Clark Fork River. The white rectangles indicate the locations of hydropower facilities. Cabinet Gorge Dam is located on the border of Idaho–Montana, and Albeni Falls Dam is located on the border of Idaho–Washington. The black triangles represent sites sampled for Walleyes. The stars indicate sites for water quality or temperature monitoring. The gray stars represent sites surveyed by the Idaho Department of Environmental Quality; the white stars with a black outline indicate sites surveyed by the University of Idaho; and the black stars indicate the Idaho Department of Fish and Game sites for limnological profiles. The dashed arrows indicate the direction of flow for the rivers. The system was divided into three strata (S1, S2, S3) to sample kokanee and opossum shrimp. Inset map shows study system location (star) in the state of Idaho.

Native fishes include Bull Trout *Salvelinus confluentus*, Westslope Cutthroat Trout *O. lewisi*, Mountain Whitefish *Prosopium williamsoni*, Pygmy Whitefish *Prosopium coulterii*, Slimy Sculpin *Cottus cognatus*, Largescale Sucker *Catostomus macrocheilus*, Redside Shiner *Richardsonius balteatus*, Peamouth *Mylocheilus caurinus*, and Northern Pikeminnow *Ptychocheilus oregonensis*. Nonnative fishes include kokanee, Rainbow Trout, Lake Trout, Brown Trout *Salmo trutta*, Smallmouth Bass, Largemouth Bass, Tench *Tinca tinca*, Yellow Perch *Perca flavescens*, Northern Pike *Esox lucius*, and Walleyes (Maiolie et al. 2004; Rust et al. 2020).

Walleyes in the Lake Pend Oreille system were first sampled downstream of Cabinet Gorge Dam (Figure 1) in the early 2000s (Ryan et al. 2021). By 2006, Walleyes were identified in the main basin of Lake Pend Oreille (Schoby et al. 2007). From 2011 to 2017, IDFG observed a pattern of exponential population growth in which the Walleye population doubled approximately every 3 years (Ryan et al. 2021). In 2018, IDFG implemented an experimental suppression program to reduce Walleye abundance and recruitment in the system. In 2019, IDFG began an incentivized angler harvest program as an addition to the suppression program. Since its initiation, catch rates of Walleyes during the suppression efforts have decreased (Rust et al. 2022). Similarly, after the implementation of suppression, catch rates of Walleyes during standardized monitoring decreased until the 2023 survey (E. Geisthardt, IDFG, personal communication). Catch rates in the 2023 survey were the highest observed in standardized monitoring, but approximately 60% of the Walleyes sampled were age 0.

Fish sampling and processing

Walleyes were sampled every other week from May 2020 to May 2021 using standardized sinking gill nets following specifications from the fall Walleye index netting (FWIN) protocol (Morgan 2002). Nets were set across the system to sample Walleyes (Figure 1). Gill nets were 61.0 m long and 1.8 m in height. Each net consisted of eight panels, with gradually increasing stretched-mesh sizes (i.e., 25, 38, 51, 64, 76, 102, 127, and 152 mm). Gill nets were set perpendicular to shore; the mesh size (i.e., 25 or 152 mm) closest to shore was randomly assigned to each set. Six nets were set per evening. Nets were set 1–2 h before dusk and retrieved 1–3 h after dawn. Walleyes were also collected opportunistically from four other programs, including spring Walleye suppression netting conducted by a private entity and permitted by IDFG; FWIN monitoring conducted by IDFG; salmonid population monitoring conducted by Avista; and Lake Trout suppression conducted by a private entity and authorized by IDFG. During the spring Walleye suppression netting, sinking gill nets were 274.0 m long and contained three 91.4-m panels (Rust et al. 2020; Bouwens et al. 2021). Each panel consisted of a single mesh size (89-, 106-, or 114-mm stretched mesh). Ten gill nets (2740 m of net in total) were tied together and set parallel to shore. Nets were set prior to dawn and were allowed to soak for 4–6 h. In the FWIN sampling, sinking gill nets with the same specifications as the biweekly sampling were soaked for approximately 24 h. Sinking gill nets used during Lake Trout netting efforts consisted of 10 individual gill nets tied together. Each individual gill net was 274.0 m long and consisted of three 91.4-m panels, each with a single mesh size (i.e., 89-, 106-, 114-mm stretched mesh). During September and October, stretched-mesh sizes used for the Lake Trout suppression program were 127 and 140 mm. From December through March, mesh sizes were 38, 44, 51, 64, 76, 89, 102, 114, 127, and 140 mm. Walleyes were also captured during salmonid population monitoring with nighttime boat electrofishing using pulsed DC at 400 V, 60 Hz, and a 20% duty cycle (Ransom 2022).

Total length (nearest millimeter) and weight (nearest gram) were measured for all Walleyes. Tissue from the anterior dorsal musculature, sufficient to fill a 2-mL centrifuge tube, was collected from all Walleyes for stable isotope analysis. Muscle samples were immediately placed on ice in the field and stored at −20°C until further processing. Samples were dried at 60°C for 48 h, cooled in a desiccator for at least 30 min, and ground to a fine powder with either a mortar and pestle or a Wig-L-Bug automatic grinder (International Crystal Laboratories). Approximately 1 mg of each sample was encapsulated in a tin cup and processed for δ^{15}N and δ^{13}C. All isotope samples were sent to the Stable Isotope Core Laboratory at Washington State University for further processing. Samples were converted to N_2 and CO_2 with an elemental analyzer (ECS 4010; Costech Analytical) and analyzed with a continuous-flow isotope ratio mass spectrometer (Delta Plus XP, Thermo Finnigan; Brenna et al. 1997; Qi et al. 2003). Results were expressed as the difference between isotope ratios of the sample and a standard relative to the isotope ratio of the standard:

$$\delta = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \times 1000,$$

where δ (‰) is the difference, R_{standard} is the isotope ratio of the standard (Vienna Pee Dee belemnite for $^{13}C/^{12}C$; atmospheric N_2 for $^{15}N/^{14}N$), and R_{sample} is the isotope ratio of the sample. Three standards that were previously calibrated to internationally certified standards were used for calibration: acetanilide, corn *Zea mays*, and keratin. A mathematical correction using the C:N ratio was applied to all samples to account for bias caused by lipid depletion (Post et al. 2007).

Sagittal otoliths were collected from every Walleye for age and growth analysis. Otoliths were mounted in epoxy, sectioned along the transverse plane using an IsoMet low-speed saw (Buehler), and viewed under a dissecting microscope using transmitted light (Koch and Quist 2007). Annuli were enumerated to estimate age and marked to estimate back-calculated lengths at age (Erickson 1983). Back-calculated lengths at age were estimated using the Dahl–Lea method (Ricker 1992; Schramm et al. 1992). Growth patterns for individual Walleyes were described using the relative growth index (RGI; Quist et al. 2003) as

$$\text{RGI} = \left(L_t / L_s\right) \times 100,$$

where L_t is the back-calculated length at age t; and L_s is the predicted length at age s (i.e., the standard length). Values greater than 100 indicated that a fish grew faster than average, whereas a value below 100 indicated that a fish grew slower than average relative to Walleyes sampled across North America.

Factors influencing growth

A mixed-effects regression model was used to evaluate abiotic and biotic factors related to growth of Walleyes (Weisberg et al. 2010). The model was used to partition the observed growth into multiple sources of variation—an environmental effect (including both fixed and random effects), the within-fish effect, and residual variation—such that

$$y_{cka} = l_a + n_{ij} + h_{c+a-1} + f_{ck} + e_{cka},$$

where y_{cka} is the ath annular increment for the kth fish from year-class c; l_a is the annular increment for a fish in the ath year of life; n_{ij} represents the fixed effect of an environmental variable i for year $j = c + a - 1$ (i.e., the year in which a fish from year-class c was age a); h_{c+a-1} is the random environmental effect for year $c + a - 1$; f_{ck} is the random effect of fish k in the cth year-class; and e_{cka} is the error associated with the model. Incremental growth was modeled for ages 1–10. Because consumption of kokanee by Walleyes was observed after age 1 (Frawley 2023), the growth increment from age 0 to age 1 was not included in the model. Year and individual fish were treated as random effects, whereas age and environmental variables were treated as fixed effects. Environmental variables included abundance (millions) and biomass (metric tons) of kokanee, *Mysis* density (*Mysis*/m^2), average monthly water temperature (°C) from June to September, and inflow (m^3/s) from Cabinet Gorge Dam (Teichert et al. 2010; Sammons et al. 2021; Sinnickson et al. 2021). Kokanee abundance, kokanee biomass, and *Mysis* densities from 2009 to 2021 were obtained from standard monitoring efforts conducted by IDFG using midwater trawls (Wahl et al. 2011; Corsi et al. 2019). Kokanee were sampled using a stepwise (3.0 m in height), oblique tow (3–6 steps/tow; 3 min in duration) with a fixed-frame trawl consisting of a 3.0- × 2.2-m opening and a 10.5-m net (Corsi et al. 2019; Klein et al. 2019). In total, 36 trawl transects in three strata (i.e., 12 trawls/stratum; Figure 1) per sampling event were randomly selected across Lake Pend Oreille. Total length and weight were measured from all kokanee collected. Scales were collected from 10 to 15 individuals per 10-mm length-group for aging. Abundance and biomass of kokanee were evaluated with hydroacoustic surveys using a Simrad EK60 echosounder. Total lakewide abundance of kokanee was calculated by summing the estimated abundance across strata (Corsi et al. 2019). Abundance for each stratum was calculated by multiplying the mean density of all transects by the area of each stratum. Density was estimated with echo integration techniques using Echoview version 6.1.60.87483 (Echoview Software Pty Ltd; Parker-Stetter et al. 2009; Corsi et al. 2019). Biomass of kokanee was evaluated using age-specific abundance estimates. Age-specific abundances for each stratum were estimated by applying age proportions from the midwater trawl samples to abundance estimates for each stratum. Age-specific abundance estimates of all strata were then summed to estimate total lakewide, age-specific abundance. Biomass was calculated by multiplying the total age-specific abundance by the mean weight of an individual kokanee for each age-class. Lakewide biomass was then calculated by summing the age-specific biomass estimates across strata. Additional details for sampling kokanee and estimating abundance and biomass can be found in Wahl et al. (2011) and Corsi et al. (2019).

Mysis density was estimated in a manner similar to estimation of kokanee density. Vertical tows were conducted in the same strata that were sampled to evaluate abundance and biomass of kokanee. Eight sites per stratum were sampled using a 1-m conical net with a mesh size of 1000 μm and a collection bucket with a mesh size of 500 μm (Chipps and Bennet 1996). Density of *Mysis* for each site was estimated as the number of *Mysis* collected in each tow divided by the size of net opening. *Mysis* abundance for each stratum was estimated as the mean density of all tows per stratum multiplied by the area of each stratum (Corsi et al. 2019). The sum of estimated *Mysis* abundance for each stratum was then divided by the total lake surface area to estimate the lakewide density. Additional details regarding *Mysis* sampling and density calculation can be found in Wahl et al. (2011) and Corsi et al. (2019). Mean yearly inflow data (m^3/s) at Cabinet Gorge Dam were collected from the U.S. Geological Survey stream gauge (site 12391950) downstream of Cabinet Gorge Dam and accessed through the National Water Information System (U.S. Geological Survey 2023). Water temperature (°C) data from Lake Pend Oreille for 2009–2021 were collected by the Idaho Department of Environmental Quality, IDFG, and University of Idaho researchers. Data used in the regression model of growth represented the average monthly temperature of Lake Pend Oreille from June to September in each year. Water temperature was monitored once per month, and a measurement was collected at every 1 m at all sampling sites (Figure 1). For the mixed-effects model, we used temperature data for the epilimnion (i.e., 0–15 m) because approximately 95% of all Walleyes collected were sampled in water less than 15 m deep (Frawley 2023).

Multicollinearity among independent variables was evaluated using Spearman's correlation coefficient (r). Variables were considered correlated if $|r|$ was 0.70 or greater (Sokal and Rohlf 2001); no variables were identified as correlated. Abundance and biomass of kokanee were not included in the same models given their relatedness. Candidate models included all combinations of kokanee abundance, kokanee biomass, water temperature, *Mysis* density, and inflow. Competing models were ranked and evaluated for goodness of fit using Akaike's information criterion corrected for small sample size (AIC$_c$; Burnham and Anderson 2002). The model with the lowest AIC$_c$ score was considered the top model. Additional models were considered plausible if they were within 2 AIC$_c$ units of the top model. Akaike weights (w_i) were used to evaluate the relative likelihood of each model. The w_i values were then summed across all models containing each of the explanatory variables to evaluate the relative importance of a specific explanatory variable (Marchetti et al. 2004; Quist et al. 2005; Katsanevakis and Maravelias 2008). Model fit was further evaluated using the coefficient of determination (R^2; Sokal and Rohlf 2001), specifically the marginal R^2 and conditional R^2 values. The marginal R^2 indicates the proportion of the variance in the model explained by the fixed effects, whereas the conditional R^2 indicates the proportion of variance explained by both the fixed and random effects (Nakagawa and Schielzeth 2013).

Individual growth

The relationship between $\delta^{15}N$, $\delta^{13}C$, and growth was assessed using two approaches. Because growth of fishes varies seasonally, including the growth of Walleyes in the Lake Pend Oreille system (Frawley 2023), we used only individuals sampled in October to eliminate growth variation due to time of sampling. Additionally, the greatest number of individuals, by month, was sampled in October. The first approach evaluated the age-specific relationship between growth (i.e., length at age at capture) and $\delta^{15}N$ or $\delta^{13}C$ using linear regression. The response variable was length at age at capture, and the explanatory variable was $\delta^{15}N$ or $\delta^{13}C$. Relationships were evaluated for age-1, age-2, age-3, and age-5 individuals because fewer than 10 individuals were sampled during October for all other age-classes. The second approach evaluated differences in growth as a function of $\delta^{15}N$ and $\delta^{13}C$ by classifying individuals as either fast or slow growing (Ng et al. 2017). Length at age at capture was used to identify fast- and slow-growing individuals in each age-class. Individuals in the 75th or higher percentiles (hereafter, "75th percentile") of growth were considered fast-growing Walleyes, and those in the 25th or lower percentiles (hereafter, "25th percentile") were categorized as slow-growing Walleyes. Only age-classes with sufficient sample sizes ($n > 3$ individuals in the percentile group) were included in this analysis (i.e., ages 1, 2, 3, and 5). Differences in $\delta^{15}N$ and $\delta^{13}C$ between fast- and slow-growing Walleyes by age-class were evaluated using a nonparametric Wilcoxon test (Conover 1980). All analyses were conducted in R (R Core Team 2022) with a type I error rate of 0.05.

RESULTS

In total, 1157 Walleyes were collected from the Lake Pend Oreille system. Total length varied from 175 to 822 mm, and age varied from 0 to 20 years. The RGI values varied from 45 to 165 among individuals (Table 1). Mean RGI was over 100 for all ages and was greatest for age 1. Minimum

TABLE 1 Back-calculated total length (mm) at age and relative growth index (RGI) values of Walleyes sampled from 2020 to 2021 in the Lake Pend Oreille system. The mean, minimum (Min), and maximum (Max) values of each index are indicated in the corresponding columns. The numbers in parentheses indicate one standard error.

		Back-calculated length			RGI		
Age	*n*	Mean	Min	Max	Mean	Min	Max
1	1081	225 (1)	108	293	127 (1)	61	165
2	856	333 (2)	132	432	115 (1)	46	149
3	657	418 (2)	167	521	112 (1)	45	140
4	507	483 (3)	276	587	111 (1)	64	135
5	458	538 (3)	321	658	112 (1)	67	137
6	232	570 (5)	353	690	111 (1)	69	134
7	135	588 (7)	387	747	109 (1)	72	139
8	91	598 (7)	408	790	107 (1)	73	142
9	68	617 (8)	426	769	108 (1)	75	135
10	65	650 (8)	449	750	112 (1)	77	129
11	61	681 (9)	472	784	115 (2)	80	133
12	21	690 (19)	501	822	116 (3)	84	138
13	7	656 (35)	521	791	110 (6)	87	132
14	2	631 (75)	556	707	105 (13)	93	118
15	1	582	582	582	97	97	97
16	1	621	621	621	103	103	103
17	1	652	652	652	108	108	108
18	1	680	680	680	112	112	112
19	1	710	710	710	117	117	117
20	1	729	729	729	120	120	120

RGI values generally increased with age, whereas maximum RGI decreased.

Walleye growth was related to environmental characteristics (Table 2). Growth of Walleyes was positively related with average summer water temperature, abundance of kokanee, and biomass of kokanee, whereas inflow from Cabinet Gorge Dam and *Mysis* density appeared to be unrelated to growth. Models containing kokanee abundance generally ranked higher than models containing kokanee biomass. The two exceptions were the model with kokanee abundance, inflow, and *Mysis* density as well as the model with kokanee abundance, inflow, *Mysis* density, and temperature. The top model contained kokanee abundance and temperature. The model containing only temperature was equally plausible (i.e., within 2 AIC_c units). All other models were not within 2 AIC_c units of the top model. The model with only kokanee abundance as the explanatory variable was the third highest ranked model ($\Delta\mathrm{AIC}_c = 2.20$); however, the marginal R^2 and conditional R^2 values were equal to those of the model with kokanee abundance and temperature (i.e., the top-ranked model). The sum of w_i provided additional evidence of the importance of temperature ($\Sigma w_i = 0.80$) and kokanee abundance ($\Sigma w_i = 0.75$) for Walleye growth (Table 3).

Growth (i.e., length at age at capture) varied among individual Walleyes for each age-class. Length at age at capture of Walleyes was related to δ^{15}N and δ^{13}C for certain age-classes (Figures 2 and 3). For age-1, age-2, and age-3 individuals, length was positively related to δ^{15}N, whereas length was negatively associated with δ^{15}N for age-5 Walleyes (Figure 2). However, the relationships

TABLE 2 Mixed-effect models evaluating factors related to growth of Walleyes collected from the Lake Pend Oreille system in 2020–2021. Model parameters include only the environmental variables that were used in each model. All models contained a fixed effect for age. Akaike's information criterion corrected for small sample size (AIC_c) was used to rank candidate models. The number of model parameters (K), delta AIC_c ($\Delta\mathrm{AIC}_c$), Akaike weight (w_i), conditional R^2 (R^2_c), and marginal R^2 (R^2_m) are included. The direction of effect for each explanatory variable is indicated (positive [+] or negative [−]). An "a" indicates that the value was less than 0.01. Variables are abbreviated as average water temperature from June through August (°C; TEMP), kokanee abundance (millions; $\mathrm{KOK_{abd}}$), kokanee biomass (metric tons; $\mathrm{KOK_{bio}}$), inflow at Cabinet Gorge Dam ($\mathrm{m^3/s}$; INF), and opossum shrimp density (number/$\mathrm{m^2}$; MYS). The model with no environmental variables is indicated as "NULL."

Model parameters	K	AIC_c	$\Delta\mathrm{AIC}_c$	w_i	R^2_c	R^2_m
$\mathrm{KOK_{abd}}$ (+), TEMP (+)	14	25,199.59	0.00	0.53	0.85	0.67
TEMP (+)	13	25,201.44	1.85	0.21	0.85	0.64
$\mathrm{KOK_{abd}}$ (+)	13	25,201.79	2.20	0.18	0.85	0.67
$\mathrm{KOK_{abd}}$ (+), TEMP (+), MYS (−)	15	25,206.10	6.51	0.02	0.85	0.67
$\mathrm{KOK_{abd}}$ (+), TEMP (+), INF (−)	15	25,206.28	6.69	0.02	0.84	0.66
TEMP (+), INF (−)	14	25,206.32	6.72	0.02	0.84	0.64
INF (−)	13	25,207.98	8.39	0.01	0.84	0.64
$\mathrm{KOK_{abd}}$ (+), INF (−)	14	25,208.19	8.60	0.01	0.84	0.65
$\mathrm{KOK_{abd}}$ (+), MYS (−)	14	25,208.31	8.72	0.01	0.85	0.66
$\mathrm{KOK_{bio}}$ (+), TEMP (−)	14	25,209.00	9.40	a	0.84	0.64
MYS (−)	13	25,209.74	10.15	a	0.85	0.64
$\mathrm{KOK_{bio}}$ (+)	13	25,210.71	11.11	a	0.84	0.64
NULL	12	25,211.41	11.82	a	0.84	0.64
$\mathrm{KOK_{abd}}$ (+), MYS (−), TEMP (+), INF (−)	16	25,212.82	13.23	a	0.85	0.65
MYS (−), TEMP (+), INF (−)	15	25,212.89	13.30	a	0.84	0.64
$\mathrm{KOK_{bio}}$ (+), TEMP (+), INF (−)	15	25,214.11	14.52	a	0.84	0.64
MYS (−), INF (−)	14	25,214.61	15.02	a	0.84	0.64
$\mathrm{KOK_{abd}}$ (+), INF (−), MYS (−)	15	25,214.77	15.18	a	0.84	0.65
$\mathrm{KOK_{bio}}$ (+), MYS (−), TEMP (+)	15	21,214.93	15.34	a	0.85	0.63
$\mathrm{KOK_{bio}}$ (+), INF (−)	14	25,216.03	16.44	a	0.84	0.64
$\mathrm{KOK_{bio}}$ (+), MYS (−)	14	25,216.67	17.08	a	0.84	0.64
$\mathrm{KOK_{bio}}$ (+), MYS (−), TEMP (+), INF (−)	16	25,220.28	20.69	a	0.84	0.63
$\mathrm{KOK_{bio}}$ (+), TEMP (+), INF (−)	15	25,222.29	22.70	a	0.84	0.63

for ages 3 and 5 were not compelling ($r^2 < 0.15$). A similar trend existed for $\delta^{13}C$, as length of Walleyes and $\delta^{13}C$ were positively associated for individuals of ages 1, 2, and 3 and were negatively associated for age-5 individuals (Figure 3). Similar to $\delta^{15}N$, the relationships for ages 2, 3, and 5 were not strong ($r^2 < 0.10$). Apparent differences in $\delta^{15}N$ and $\delta^{13}C$ existed between slow- and fast-growing Walleyes (Table 4). For age-1 to age-3 individuals, $\delta^{15}N$ was higher for fast-growing Walleyes than for slow-growing Walleyes. Carbon isotopes did not exhibit the same pattern. Except for age-1 fish, fast-growing individuals had more depleted $\delta^{13}C$.

TABLE 3 Sum of Akaike weights (w_i) of the relationship for each environmental variable used in the mixed-effects regression models to evaluate factors related to growth of Walleyes in the Lake Pend Oreille system. The direction of effect for each explanatory variable is indicated (positive [+] or negative [−]). Variables are abbreviated as average water temperature from June through August (°C; TEMP), kokanee abundance (millions; KOK_{abd}), kokanee biomass (metric tons; KOK_{bio}), inflow at Cabinet Gorge Dam (m^3/s; INF), and opossum shrimp density ($number/m^2$; MYS).

Variable	Σw_i
TEMP (+)	0.80
KOK_{abd} (+)	0.75
INF (−)	0.05
MYS (−)	0.04
KOK_{bio} (+)	0.01

DISCUSSION

Walleyes have been established in the Lake Pend Oreille system for about 20 years, yet little is known about factors regulating their population dynamics. The objectives of our research were to describe factors influencing growth and to evaluate variability in individual growth. Walleyes in the Lake Pend Oreille system grew quickly, and growth remained high as Walleyes aged. Values of RGI were consistently greater than 100 for all age-classes, suggesting that Walleyes in this system exhibited faster growth than other populations across North America. For instance, in Lake Winnipeg, Manitoba, mean length at age 2 was approximately 250 mm (Sheppard et al. 2018), whereas mean back-calculated length at age 2 for Walleyes in Lake Pend Oreille was 333 mm. Generally, Walleyes in the northern latitudes grow slower than their southern counterparts (Quist et al. 2003). However, the observed RGI values in the Lake Pend Oreille system were greater than those observed from populations at similar latitudes and were most similar to populations at the southern extent of the species' distribution (Colby et al. 1979; Wolf et al. 1994; Carlander 1997). For example, mean RGI for age-1 Walleyes from the Lake Pend Oreille system was 127; RGI for age-1 Walleyes in Kansas reservoirs varied from 133 to 162 (Quist et al. 2003). This pattern suggests that environmental conditions (e.g., temperature) and resource availability (e.g., prey availability) in the Lake Pend Oreille system are likely contributing to the faster growth than would be expected for Walleyes at northern latitudes.

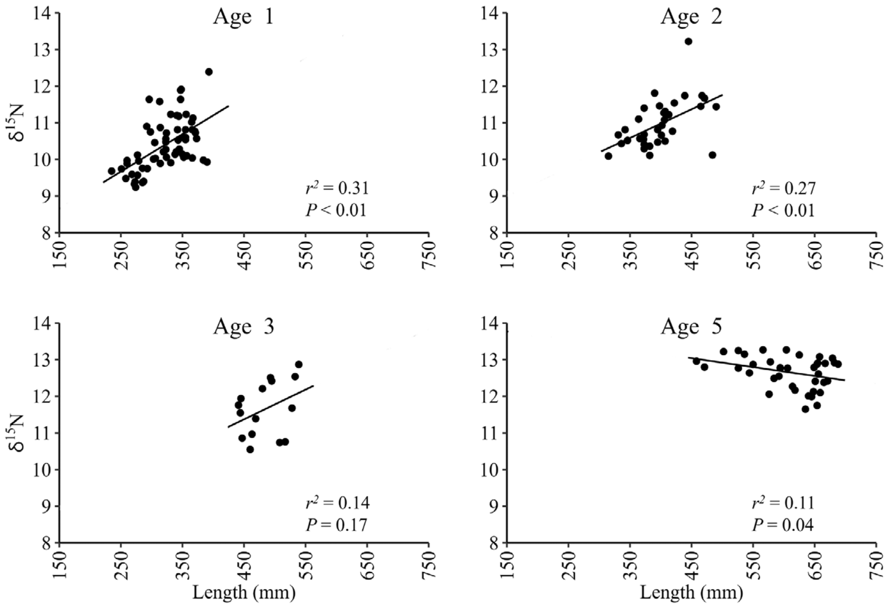

FIGURE 2 Age-specific regressions of $\delta^{15}N$ relative to total length of Walleyes collected from the Lake Pend Oreille system in October 2020.

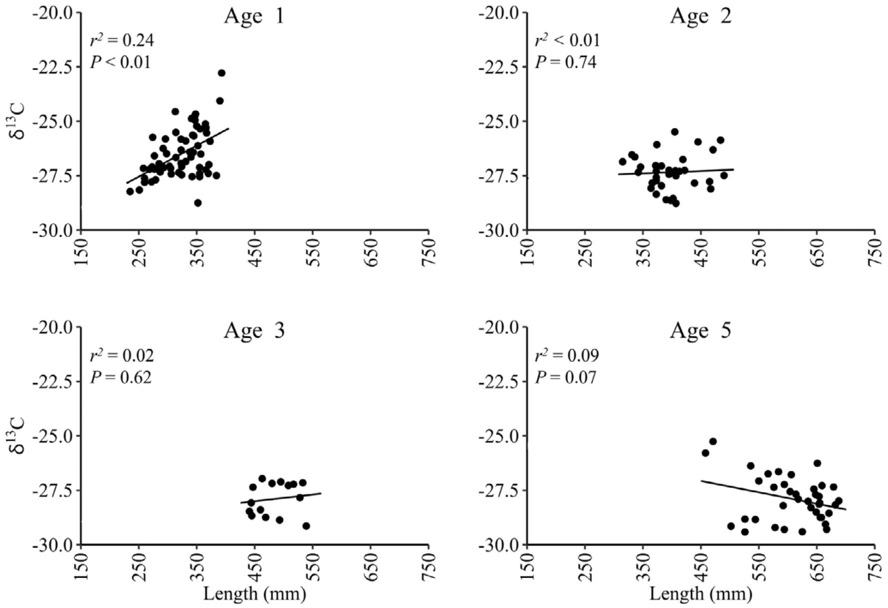

FIGURE 3 Age-specific regressions of $\delta^{13}C$ relative to total length of Walleyes collected from the Lake Pend Oreille system in October 2020.

TABLE 4 Average carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope values for slow-growing (i.e., 25th and lower percentiles of growth) and fast-growing (i.e., 75th and greater percentiles of growth) individuals for each age-class of Walleyes sampled in the Lake Pend Oreille system during October 2020. Length represents the average total length (mm) of individuals for the indicated percentile and age-group. Numbers in parentheses indicate one standard error. The *p*-values indicate results of a test of differences between the percentile groups for each age-class.

Group	*n*	Length	$\delta^{15}N$	*p*	$\delta^{13}C$	*p*
Age 1						
Slow	16	270.81 (3.74)	9.71 (0.10)	<0.01	−27.25 (0.17)	0.01
Fast	16	375.44 (7.84)	10.67 (0.16)		−26.10 (0.34)	
Age 2						
Slow	8	346.50 (6.94)	10.59 (0.10)	<0.01	−27.17 (0.19)	0.95
Fast	9	447.89 (8.96)	11.64 (0.22)		−27.20 (0.24)	
Age 3						
Slow	4	444.25 (1.25)	11.53 (0.24)	0.44	−28.14 (0.29)	0.60
Fast	4	529.25 (4.66)	11.96 (0.47)		−27.84 (0.46)	
Age 5						
Slow	10	525.50 (12.17)	12.90 (0.12)	0.28	−27.48 (0.47)	0.12
Fast	10	668.00 (3.40)	12.72 (0.10)		−28.33 (0.21)	

Temperature has been identified as one of the most important abiotic conditions influencing growth of Walleyes across their distribution (e.g., Hokanson 1977; Colby et al. 1979; Quist et al. 2003; Pedersen et al. 2018). As such, we expected water temperature to be an important predictor of Walleye growth in the Lake Pend Oreille system. Although average temperatures in the epilimnion (15–19°C) during the summer were slightly lower than the thermal optimum for growth of Walleyes (18–22°C; Hokanson 1977; Christie and Regier 1988), temperature apparently influenced Walleye growth, particularly in combination with kokanee abundance. If water temperatures increase in the future, Walleyes in the Lake Pend Oreille system could exhibit faster growth. This system supports diverse habitats that likely provided a wide range of water temperatures available to Walleyes, particularly in the north end of Lake Pend Oreille and in the Pend Oreille and Clark Fork rivers. For example, temperature profiles from Lake Pend Oreille in August 2011 indicated that surface temperatures approached 22°C, whereas water temperature at the thermocline was 12°C (IDFG, unpublished data). As such, Walleyes may have consistently occupied habitats with sufficiently high temperatures to promote fast growth.

Similar to other systems, prey abundance—in particular, kokanee abundance—appeared to be an important factor influencing growth of Walleyes in the Lake Pend Oreille system. Kokanee serve as important prey for many piscivores in coolwater or coldwater systems in the western United States (e.g., Clarke et al. 2005; Schoen et al. 2012; Pate et al. 2014; Walrath et al. 2015; Warnock et al. 2021). In Lake Ozette, Washington, kokanee represented 20–60% of prey items (by weight) consumed by native Coastal Cutthroat Trout *O. clarkii* and 40–100% of prey items consumed by nonnative Northern Pikeminnow (Beauchamp et al. 1995). Similarly, estimated consumption of kokanee by nonnative Lake Trout represented 53–73% of the total production and biomass of kokanee in Lake Chelan, Washington (Schoen et al. 2012). In Lake Pend Oreille, kokanee constitute the primary prey resource for piscivores (Vidergar 2000; Clarke et al. 2005). Kokanee represented approximately 50–100% of the prey items (by weight) consumed by Northern Pikeminnow, Rainbow Trout, Lake Trout, and Bull Trout (Clarke et al. 2005). For Walleyes, abundance of kokanee combined with temperature explained about 67% of the variation in growth in the Lake Pend Oreille system due to environmental conditions. Analysis of Walleye food habits in Lake Pend Oreille further supported this finding (Frawley 2023). On average, kokanee composed 20–100% (by weight) of diets sampled from age-3 and older Walleyes in the Lake Pend Oreille system.

Growth is a function of energy intake and expenditure (Hewett and Johnson 1987; Brandt and Hartman 1993; Jørgensen et al. 2016). Energy intake and expenditure vary across individuals and depend on factors such as temperature, prey availability, and handling time of prey (e.g., Werner 1974; Brown et al. 2004; Hoxmeier et al. 2004; Jacobson et al. 2018). As such, populations are composed of slow- and fast-growing individuals. Our results indicated that differences in growth of individuals may have been related to differences in diet, especially for young age-classes of Walleyes. As hypothesized, fast-growing individuals, particularly from age 1 to age 3, had greater δ^{15}N values than slow-growing individuals. This pattern suggests that fast-growing individuals capitalized on fish rather than invertebrates and (or) fish characterized by higher trophic positions. Additionally, the disparity in δ^{15}N values declined with age, suggesting that older individuals likely consumed similar prey items and (or) prey items at similar trophic positions. In nearby Priest Lake, little difference in δ^{15}N values was observed between fast- and slow-growing Lake Trout (Ng et al. 2017). The authors of that study attributed the lack of variation to homogeneity in the diet. Similarly, previous studies in Lake Pend Oreille showed that δ^{15}N values varied little with length for 400-mm and larger Bull Trout and Lake Trout, and stomach content analysis revealed that kokanee were the dominant prey item for the predators (Clarke et al. 2005).

Evaluation of δ^{13}C provided additional insight into the factors related to growth of Walleyes. Given the importance of kokanee for Walleyes in the Lake Pend Oreille system, we expected fast-growing individuals to have more depleted δ^{13}C. As with δ^{15}N, the relationship between δ^{13}C and growth was not particularly strong, and δ^{13}C values were similar between fast- and slow-growing individuals. This suggests only slight differences in use of pelagic prey resources between fast- and slow-growing Walleyes. However, fast-growing age-1 individuals had more enriched δ^{13}C values compared to slow-growing individuals. The apparent discrepancy could be a result of the trade-off between prey quantity and prey quality. In some instances, deficits from consuming less beneficial (e.g., smaller) prey could be offset by consuming greater quantities of the less beneficial prey, at least prior to sexual maturity. For example, in Ontario lakes, Walleyes that consumed Ciscoes *Coregonus artedi* generally grew faster than Walleyes that consumed invertebrates and Yellow Perch (Kaufman et al. 2009). However, in systems with no Ciscoes and an abundant Yellow Perch population, female Walleyes grew faster until maturity compared to systems with Ciscoes. During the first year of growth, habitat overlap with spiny-rayed fishes (i.e., increased prey abundance; Lee et al. 1980) resulted in fast growth of Walleyes despite low availability of preferred prey types (i.e., soft-rayed fishes; Goddard and Redmond 1978; Knight et al. 1984; Einfalt and Wahl 1997). In the Lake Pend Oreille system, catch rates of age-1 Walleyes were highest in the Pend Oreille River (Frawley 2023). This region contains an abundance of spiny-rayed fishes (IDFG, unpublished data) that may have been more available than soft-rayed fishes to age-1 Walleyes. Individual age-1 Walleyes likely capitalized on high availability of spiny-rayed fishes. Comparatively, catch rates of age-2 and older Walleyes were highest in the main body of Lake Pend Oreille (Frawley 2023). In general, the main body of Lake Pend Oreille supports an abundance of kokanee. Age-2 and older Walleyes likely benefited from the high abundance of preferred prey types (i.e., kokanee), resulting in similar δ^{13}C among fast- and slow-growing individuals.

Walleyes in the Lake Pend Oreille system grew fast relative to other populations across their distribution, particularly populations at similar latitudes. On a broad scale, growth of Walleyes in large, natural lakes has been extensively studied. Our findings are consistent in that temperature and prey abundance were among the most important factors associated with growth (e.g., Knight et al. 1984; Pedersen et al. 2018; Sheppard et al. 2018).

However, the assessment of Walleye growth in Lake Pend Oreille is somewhat unique given the implementation of suppression efforts. Although Walleyes are established throughout the western United States, Lake Pend Oreille may be the only system where Walleyes are actively suppressed. Removal of individuals may have implications for growth. For example, Smith et al. (2022) found that Walleye growth and abundance were inversely related in several West Virginia systems. In Lake Pend Oreille, RGI values were consistently high across age-classes even though estimates of relative abundance (i.e., catch rates) increased from 2011 to 2017 (Ryan et al. 2021). Similarly, RGI values for ages 1 and 2 suggested that Walleyes continued to grow fast after the implementation of suppression in 2018. As suppression continues, Walleyes will likely continue to exhibit fast growth rates, which could have implications within a bioenergetic framework, particularly concerning the consumption of important prey items. From 2020 to 2021, Walleyes consumed about 13% of the abundance of adult kokanee in the Lake Pend Oreille system (Frawley 2023). Considering that the proportion of maximum consumption exhibited was generally less than 0.5, this suggests that Walleyes have the potential to consume more prey items than previously estimated. In systems where Walleyes are nonnative, managers may need to monitor growth rates and food habits to help guide management strategies that minimize the negative effects of Walleyes.

Our research adds to the body of literature describing factors that influence growth of Walleyes across their distribution. To our knowledge, no other study has explicitly identified a relationship between kokanee abundance and growth of Walleyes in western systems. Furthermore, our work is one of few studies that have attempted to relate individual variability in growth to variability in stable isotopes. Although factors influencing the growth of Walleyes have been widely studied, our study is unique in that it describes growth of nonnative Walleyes at varying scales. Understanding the factors influencing growth provides managers with valuable information on how Walleye growth and population dynamics might change under varying conditions and will inform management decisions.

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CONFLICT OF INTEREST STATEMENT

There is no conflict of interest declared in this article.

DATA AVAILABILITY STATEMENT

Data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

This project was conducted under Protocol 2019-88 approved by the University of Idaho's Institutional Animal Care and Use Committee.

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