

Trophic Ecology of Walleyes in the Lake Pend Oreille System, Idaho

A thesis

Presented in Partial Fulfillment of the Requirements for the

Degree of Master of Science

with a

Major in Natural Resources

in the

College of Graduate Studies

University of Idaho

by

Susan E. Frawley

Approved by:

Major Professor: Michael C. Quist, Ph.D.

Committee Members: Matthew P. Corsi Ph.D.; Timothy R. Johnson, Ph.D.;

Kerri Vierling, Ph.D.

Department Administrator: Janet L. Rachlow, Ph.D.

December 2023

Abstract

Walleyes *Sander vitreus* are ecologically and recreationally important. A non-native population of Walleyes has recently been established in the Lake Pend Oreille system in northern Idaho. Walleyes are piscivorous and the new population raises concerns regarding their potential effect on the system particularly regarding consumption of salmonids. The objective of my research was to evaluate the trophic ecology of Walleyes throughout the system, identify factors related to growth of Walleyes, and relate individual variability in growth to variability in isotopes (i.e., $\delta^{15}\text{N}$, $\delta^{13}\text{C}$). Food habits were diverse, and Walleyes consumed various fishes and macroinvertebrates. Kokanee *Oncorhynchus nerka* was the most frequently consumed prey item, and abundance of kokanee was related to growth of Walleyes in the system. Fast-growing individuals consumed prey items at higher trophic positions and from pelagic habitats. These results suggest that Walleyes will likely have negative effects on the kokanee population. This research provides valuable information regarding the direct and indirect effects of an established Walleye population in the Lake Pend Oreille system.

Acknowledgments

Many people provided unending support and encouragement throughout the duration of my research. First, I would like to thank my advisor, Dr. Michael Quist, for his patience, mentorship, and guidance throughout this process. He was constantly challenging me to become a better researcher through creative thinking and to develop a breadth of knowledge of fisheries management. I would also like to thank my committee member, Dr. Matthew Corsi, for his continued mentorship and encouragement. Matt continuously reminded me to think about how data can be used in different ways and contextualize my research in a management framework. Lastly, I would like to thank all the graduate students and biologists with whom I had the opportunity to collaborate. These individuals were a pleasure to work with, gave great advice, and were a joy to be around. In particular, I would like to mention two cohorts of graduate students in Dr. Quist's lab: Aaron Black, Courtnie Ghery, Megan Heller, Will Lubenau, Bryce Marciniak, Donovan Maude, Darcy McCarrick, Sage Unsworth, and Nick Voss as well as Molly Garrett, Marta Ulaski, and Bri Winkle for their invaluable friendship. During the best of times and the worst of times, we had many laughs that will forever be remembered.

Dedication

This work is dedicated to my family, Jim Frawley, Lilly Hammack, and Becky Mendoza, for their never-ending love and support. Additionally, this thesis was written in loving memory of my mother, Loretta Frawley, who always encouraged me to embrace challenges and live a life full of adventures.

Table of Contents

Abstract	ii
Acknowledgments	iii
Dedication	iv
List of Tables	vii
List of Figures	x
Chapter 1: General Information	1
Thesis Organization	2
References	4
Chapter 2: Food Habits and Seasonal Growth of Walleyes in the Lake Pend Oreille System, Idaho	9
Abstract	9
Introduction	10
Methods	12
Results	23
Discussion	27
References	35
Tables and Figures	51
Chapter 3: Factors related to growth and individual variability in an introduced piscivore population	70
Abstract	70
Introduction	70
Methods	74
Results	80
Discussion	81
References	86

Tables and Figures	101
Chapter 4: General Conclusions	109
Appendix A	112
Appendix B	113
Appendix C	115
Appendix D	117
Appendix E	120

List of Tables

- Table 2.1 Sample sizes for season, region, and cohort comparisons of diets collected from Walleyes in the Lake Pend Oreille system from May 2020 to May 2021. Seasons were defined as spring (March – May), summer (June – August), fall (September – November), and winter (December–February). Regions were defined as Pend Oreille River (POR), northern Lake Pend Oreille (LPO-N), central Lake Pend Oreille (LPO-C), Clark Fork River (CFR), and south Lake Pend Oreille (LPO-S). 51
- Table 2.2 Overall contribution of prey items to Walleye diets collected from the Lake Pend Oreille system from May 2020 to May 2021. Diet summarizations were frequency of occurrence (F), proportion by weight (W), and proportion of energy (calories) contributed (E). Taxa were denoted as Black Crappie (BCR), Gasterosteidae (GAS), Brook Trout (BKT), Bluegill (BLG), Brown Bullhead (BRB), kokanee (KOK), Largemouth Bass (LMB), Longnose Sucker (LNS), Largescale Sucker (LSS), Lake Whitefish (LWF), macroinvertebrates (MAC), Mountain Whitefish (MWF), *Mysis diluviana* (MYS), Northern Pikeminnow (NPM), other (OTH), Pumpkinseed (PKS), Peamouth Chub (PMC), Rainbow Trout (RBT), Cottidae (SCP), Smallmouth Bass (SMB), Tench (TNC), unknown fish (UNK), Walleye (WAE), Westslope Cutthroat Trout (WCT), and Yellow Perch (YEP). The symbol *a* indicates the proportional contribution was < 0.01 52
- Table 2.3 Proportional contribution to the differences in Walleye diets between regions collected from the Lake Pend Oreille system from May 2020 to May 2021. Proportions were estimated using the SIMPER analysis. Dashes indicate the species contributed < 0.05 to the differences in Walleye diets. Species abbreviations were Black Crappie (BCR), kokanee (KOK), macroinvertebrates (MAC), *Mysis diluviana* (MYS), Northern Pikeminnow (NPM), Peamouth Chub (PMC), and Yellow Perch (YEP). Regions were defined as Pend Oreille River (POR), northern Lake Pend Oreille (LPO-N), central Lake Pend Oreille (LPO-C), Clark Fork River (CFR), and south Lake Pend Oreille (LPO-S). 53
- Table 2.4 Proportional contribution to the differences in Walleye diets between seasons collected from the Lake Pend Oreille system from May 2020 to May 2021. Proportions were estimated using the SIMPER analysis. Dashes indicate the species contributed < 0.05 to the differences in Walleye diets. Species abbreviations were Black Crappie (BCR), kokanee (KOK), macroinvertebrates (MAC), *Mysis diluviana* (MYS), Northern

- Pikeminnow (NPM), Peamouth Chub (PMC), and Yellow Perch (YEP). Months were grouped into seasons as spring (March, April, May), summer (June, July, August), fall (September, October, November), and winter (December, January, February). 54
- Table 2.5 Proportional contribution to the differences in Walleye diets between cohorts collected from the Lake Pend Oreille system from May 2020 to May 2021. Proportions were estimated using the SIMPER analysis. Dashes indicate the species contributed < 0.05 to the differences in Walleye diets. Species abbreviations were Black Crappie (BCR), kokanee (KOK), macroinvertebrates (MAC), *Mysis diluviana* (MYS), Northern Pikeminnow (NPM), Peamouth Chub (PMC), and Yellow Perch (YEP). Cohort comparisons did not include the 2012 and older cohorts due to small sample size..... 55
- Table 2.6 . The $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and trophic positions of Walleyes sampled in the Lake Pend Oreille system from May 2020 to May 2021. Values were grouped by cohort. Minimum (Min), mean (Ave), and maximum (Max) values are shown for all three values as well as the associated standard error (SE) of each group. Differences (Diff) in maximum and minimum values of the trophic position are shown. Cells containing a indicate that the value was < 0.01. Dashes indicate a value was not available because only one sample was collected from the specific group..... 56
- Table 2.7 Mean (TP), minimum (Min), and maximum (Max) trophic position of taxa in the Lake Pend Oreille system. Trophic position was estimated from stable isotope signatures collected from May 2020 – June 2021. Zooplankton samples were collected in May 2022. Taxa abbreviations were Black Crappie (BCR), Brown Bullhead (BRB), crayfish (CRAY), kokanee (KOK), Lake Trout (LKT), Largemouth Bass (LMB), Longnose Sucker (LNS), Largescale Sucker (LSS), Lake Whitefish (LWF), macroinvertebrates (MAC), Mountain Whitefish (MWF), *Mysis diluviana* (MYS), Northern Pikeminnow (NPM), Pumpkinseed (PKS), Peamouth Chub (PMC), Rainbow Trout (RBT), Cottidae (SCP), Smallmouth Bass (SMB), Tench (TNC), Walleye (WAE), Westslope Cutthroat Trout (WCT), Yellow Perch (YEP), and zooplankton (ZOO). Species abbreviations with “-L” indicated values of large individuals (i.e., after an ontogenetic shift occurred) and “-S” indicated values of small individuals (i.e., before an ontogenetic shift occurred)...... 57
- Table 3.1 Back-calculated lengths (mm) at age and relative growth index (RGI) values of Walleyes sampled from 2020-2021 in the Lake Pend Oreille system. The mean (Mean),

- minimum (Min), and maximum (Max) values of each index are indicated in the corresponding columns. The numbers in parentheses indicate one standard error. 101
- Table 3.2 . Regression models evaluating factors related to growth of Walleyes collected from the Lake Pend Oreille system in 2020-2021. Akaike’s information criterion adjusted for small sample size (AIC_c) was used to rank candidate models. The number of model parameters (K), delta AIC_c (ΔAIC_c), model weight (w_i), and the multiple R^2 (R^2) are included. The direction of effect for each explanatory variable is indicated (positive [+] or negative[-]). An a indicates the value was < 0.01 . Variables are abbreviated as average water temperature from June through August ($^{\circ}C$; TEMP), kokanee abundance (millions; KOK_{abd}); kokanee biomass (tonnes; KOK_{bio}); inflow at Cabinet Gorge Dam (m^3/s ; INF); *Mysis diluviana* density (number/ m^2 ; MYS); and the null model (NULL). 102
- Table 3.3 Sum of Akaike’s Information Criteria 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 ($^{\circ}C$; TEMP), kokanee abundance (millions; KOK_{abd}); kokanee biomass (tonnes; KOK_{bio}); inflow at Cabinet Gorge Dam (m^3/s ; INF); and *Mysis diluviana* density (number/ m^2 ; MYS). 103
- Table 3.4 Average carbon ($\delta^{13}C$) and average nitrogen ($\delta^{15}N$) values for individuals of the 25th and 75th percentiles of growth for each age-class of Walleyes sampled in the Lake Pend Oreille system in 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 a test of differences between the percentile groups by age class. 104

List of Figures

- Figure 2.1 The Lake Pend Oreille system located in northern Idaho. This system included Lake Pend Oreille, the Pend Oreille River, and the Clark Fork River. The system was divided into five regions: the Pend Oreille River (POR), northwestern portion of Lake Pend Oreille (LPO-N), a transition zone between the shallow northern portion and the deep southern basin of the lake (LPO-C), the Clark Fork River and its delta (CFR), and the southern portion of the lake (LPO-S). Triangles indicate cities and diamonds represent a landmark on the lake used to separate regions. 58
- Figure 2.2 Mean catch per unit effort (CPUE = number of Walleyes [WAE] caught per net-night) in the Lake Pend Oreille system by season from May 2020 to May 2021. Bars represent one standard error. Months were grouped into seasons as spring (March, April, May), summer (June, July, August), fall (September, October, November), and winter (December, January, February). Regions were defined as Pend Oreille River (POR), northern Lake Pend Oreille (LPO-N), central Lake Pend Oreille (LPO-C), Clark Fork River and Delta (CFR), southern Lake Pend Oreille (LPO-S)..... 59
- Figure 2.3 . Length and age structure of sampled Walleyes in the Lake Pend Oreille system from May 2020 to May 2021. Individuals were grouped based on sampling method (i.e., standardized, mitigation, salmonid monitoring). The 2015, 2017, 2018, and 2019 cohorts represent approximately 75% of all individuals sampled. 60
- Figure 2.4 . Mean length and weight of Walleye cohorts collected from the Lake Pend Oreille system, May 2020 to May 2021. Bars represent one standard error. Months were grouped into seasons as spring (March, April, May), summer (June, July, August), fall (September, October, November), and winter (December, January, February). 61
- Figure 2.5 Overall prey-specific energy contribution of prey items observed in Walleye stomachs collected from the Lake Pend Oreille system during May 2020 to May 2021. Months were grouped into seasons as spring (March, April, May), summer (June, July, August), fall (September, October, November), and winter (December, January, February). Prey items were Black Crappie (BCR), Gasterosteidae (GAS), Brook Trout (BKT), Bluegill (BLG), Brown Bullhead (BRB), kokanee (KOK), Largemouth Bass (LMB), Longnose Sucker (LNS), Largescale Sucker (LSS), Lake Whitefish (LWF), macroinvertebrates (MAC), Mountain Whitefish (MWF), *Mysis diluviana* (MYS),

Northern Pikeminnow (NPM), other (OTH), Pumpkinseed (PKS), Peamouth Chub (PMC), Rainbow Trout (RBT), Cottidae (SCP), Smallmouth Bass (SMB), Tench (TNC), Walleye (WAE), Westslope Cutthroat Trout (WCT), and Yellow Perch (YEP)..... 62

Figure 2.6 . Frequency of occurrence of the six prey items most frequently consumed by Walleyes sampled from May 2020 to May 2021 in the Lake Pend Oreille system.

Frequency of occurrence was grouped by regions and seasons. Regions were defined as Pend Oreille River (POR), northern Lake Pend Oreille (LPO-N), central Lake Pend Oreille (LPO-C), Clark Fork River and Delta (CFR), southern Lake Pend Oreille (LPO-S). Months were grouped into seasons as spring (March, April, May), summer (June, July, August), fall (September, October, November), and winter (December, January, February). Prey items are Black Crappie (BCR), kokanee (KOK), macroinvertebrates (MAC), Northern Pikeminnow (NPM), Peamouth Chub (PMC), and Yellow Perch (YEP)..... 63

Figure 2.7 Seasonal frequency of occurrence of the six most frequently consumed prey items observed in Walleye stomachs collected from the Lake Pend Oreille system during May 2020 to May 2021. Months were grouped into seasons as spring (March, April, May), summer (June, July, August), fall (September, October, November), and winter (December, January, February). Prey items were Black Crappie (BCR), kokanee (KOK), macroinvertebrates (MAC), Northern Pikeminnow (NPM), Peamouth Chub (PMC), and Yellow Perch (YEP)..... 64

Figure 2.8 . Frequency of occurrence of the six prey items most frequently consumed by Walleyes sampled from May 2020 to May 2021 in the Lake Pend Oreille system. Frequency of occurrence was grouped by cohorts and seasons. Months were grouped into seasons as spring (March, April, May), summer (June, July, August), fall (September, October, November), and winter (December, January, February). Prey items in the figure were the six items most frequently consumed by Walleyes overall. Prey item abbreviations are as follows: Black Crappie (BCR), kokanee (KOK), macroinvertebrates (MAC), Northern Pikeminnow (NPM), Peamouth Chub (PMC), Yellow Perch (YEP).. 65

Figure 2.9 Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (mean \pm 1 standard error) for all species sampled in the Lake Pend Oreille system from May 2020 to May 2021. Taxa abbreviations are Black Crappie (BCR), Brown Bullhead (BRB), kokanee (KOK), Largemouth Bass (LMB),

Longnose Sucker (LNS), Largescale Sucker (LSS), Lake Whitefish (LWF), Mountain Whitefish (MWF), <i>Mysis diluviana</i> (MYS), Northern Pikeminnow (NPM), Pumpkinseed (PKS), Peamouth Chub (PMC), Rainbow Trout (RBT), sculpin (SCP), Smallmouth Bass (SMB), Tench (TNC), Walleye (WAE), Westslope Cutthroat Trout (WCT), Yellow Perch (YEP), and zooplankton (ZOO). Taxa abbreviations with “-L” indicated values of large individuals (i.e., after an ontogenetic shift occurred) and “-S” indicated values of small individuals (i.e., before an ontogenetic shift occurred).....	66
Figure 2.10 Mean \pm S.E. of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of Walleyes collected from the Lake Pend Oreille system from May 2020 to May 2021. Walleye were grouped by cohort. Individuals from the 2012-2020 were not shown due to low sample size ($n < 10$).	67
Figure 2.11 Estimated proportion of maximum consumption (P_c) from the bioenergetics model of Walleyes sampled from the Lake Pend Oreille system between May 2020 and May 2021. Walleyes were grouped by cohorts and estimates were made for each season. Months were grouped into seasons as spring (March, April, May), summer (June, July, August), fall (September, October, November), and winter (December, January, February). Individuals from the 2012 and older cohorts were grouped due to low sample sizes ($n < 10$).	68
Figure 2.12 Lengths of kokanee consumed by Walleyes collected from the Lake Pend Oreille system from May 2020 to May 2021. The top panel shows the length-frequency distribution of all kokanee that were consumed. The bottom panel shows the length of kokanee consumed relative to the length (KOK length) of the Walleye (WAE length); different ages are depicted by different symbols.	69
Figure 3.1 The Lake Pend Oreille system located in northern Idaho. This system included Lake Pend Oreille, the Pend Oreille River, and the Clark Fork River. The triangles indicated where hydroelectric facilities are located. Cabinet Gorge Dam is located on the border of Idaho-Montana, and Albeni Falls Dam is located on the border of Idaho-Washington. The stars indicate the water quality monitoring sites surveyed by the Department of Environmental Quality, and the plus signs indicate the Idaho Fish and Game sites for limnological profiles.	105
Figure 3.2 Estimated incremental growth from the mixed-effects regression model for Walleyes collected from the Lake Pend Oreille system in 2020-2021 compared to	

kokanee <i>Oncorhynchus nerka</i> abundance (millions), biomass of kokanee (tonnes), <i>Mysis diluviana</i> density (number/m ²), mean summer temperature (°C; June-August), and inflow (m ³ /s) from Cabinet Gorge Dam. Points represent the growth coefficient estimate for a given year and bars indicate one standard error.....	106
Figure 3.3 Age-specific regressions of $\delta^{15}\text{N}$ relative to length of Walleyes collected from the Lake Pend Oreille system in October, 2020.....	107
Figure 3.4 Age-specific regressions of $\delta^{13}\text{C}$ relative to length of Walleyes collected from the Lake Pend Oreille system in October, 2020.....	108

Chapter 1: General Information

Freshwater systems are among the most imperiled systems across the globe due to their susceptibility to natural and anthropogenic changes (Bednarek and Hart 2005; Pess et al. 2008; Carpenter et al. 2011). One of the foremost threats to the sustainability of freshwater systems is the negative effects of non-native species (Wilcove et al. 1998). Introductions of non-native fishes have consistently occurred throughout the history of North American fisheries management (Moyle 1986; Moyle and Light 1996). As a result, heterogeneity of fish assemblages among systems has and continues to decrease. For example, Rahel (2000) compared the similarity of fish species across the United States prior to and after European settlement and found that, on average, states now have 15.4 more species in common than before settlement. On a broad scale, decreased biodiversity affects ecosystem function (McGrady-Steed et al. 1997) and resilience to changing environmental conditions (Rebele 1994; Stachowicz et al. 2002). Non-native species negatively influence aquatic systems through indirect and direct mechanisms (Zaret and Paine 1973; Goldschmidt et al. 1993; Mooney and Cleland 2001; Cucherousset and Olden 2011). Indirectly, non-native species affect other species through habitat modification (Field-Dodgson 1987; Koehn 2004; Gutiérrez 2017), introduction of novel diseases and parasites (Blanc 1997; Prenter et al. 2004; Gozlan et al. 2005), and hybridization (Pierce and Van Den Avyle 1997; McKelvey et al. 2016; Blackwell et al. 2021). Direct mechanisms by which non-native species may negatively affect other species include predation (Ogutu-Ohwayo 1990; McIntosh and Townsend 1995; Pelicice and Agostinho 2009) and competition (McMillan 1984; Irons et al. 2007; Keller and Brown 2008).

Walleyes *Sander vitreus* are popular among anglers and have been widely introduced across the United States (Colby et al. 1979). Walleyes are generalists and exhibit ontogenetic shifts in diet from zooplankton as juveniles to fishes as adults (Mittelbach and Persson 1998). Across the native distribution of Walleye, Yellow Perch *Perca flavescens* are typically the predominant prey item. However, Walleye diets have been shown to vary based on prey availability. As a result, Walleyes also consume fishes from various families including cyprinids, clupeids, osmerids, and centrarchids (Colby et al. 1979). For example, Fincel et al. (2014) documented a shift in Walleye stomach contents from Gizzard Shad *Dorosoma*

cepedianum to Rainbow Smelt *Osmerus mordax* following a decrease in abundance and availability of Gizzard Shad in Lake Oahe, South Dakota. Such plasticity in diets results in robust populations of Walleyes under varying environmental conditions and in novel environments.

Walleyes have been introduced widely across the western United States (Colby et al. 1979; Fuller 2010; Barton 2011); however, the effects of these introductions remain largely undocumented. Partly due to the high prevalence of threatened and endangered species (i.e., anadromous salmonids), many of the published studies have documented the effects of non-native Walleyes in the Columbia River basin (e.g., Beamesderfer and Rieman 1988; Vigg et al. 1991; Murphy et al. 2021). Such studies typically have evaluated the relative abundance of Walleyes (e.g., Zimmerman and Parker 1995; Scarnecchia et al. 2014; Ryan et al. 2021) or described Walleye food habits and (or) evaluated the predatory demand of Walleyes on certain species of interest (e.g., Poe et al. 1991; Baldwin et al. 2003). Broadly, salmonids have been identified as important prey resources for non-native Walleye populations in western reservoirs (McMillan 1984; McMahon and Bennet 1996; Baldwin et al. 2003; Johnson et al. 2017). In the Lake Pend Oreille system, northern Idaho and western Montana, a self-sustaining Walleye population has recently established (Schoby et al. 2007; Rust et al. 2020; Ryan et al. 2021). The Lake Pend Oreille system supports ecologically and recreationally important salmonids including kokanee *Oncorhynchus nerka*, Rainbow Trout *O. mykiss*, Westslope Cutthroat Trout *O. clarkii lewisi*, and the federally threatened Bull Trout *Salvelinus confluentus*. Given the predation on salmonids observed in other western reservoirs, evaluation of the potential effects of non-native Walleyes on the existing fish assemblage is imperative to effectively manage this system in the future.

Thesis Organization

This thesis is divided into four chapters. Chapter two describes the food habits of Walleyes across the Lake Pend Oreille system. I identified changes in Walleye diets across spatial, temporal, and ontogenetic gradients. In addition, I evaluated consumption of prey items using a bioenergetics model. Furthermore, I described the overall trophic structure of the system using stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$). Chapter three describes growth of Walleyes in the system. Additionally, I evaluate a suite of abiotic and biotic factors potentially

influencing growth of Walleyes across the system using a linear mixed effects model. Finally, I evaluate variation in growth of individuals in relation to variations in stable isotopes. Chapters two and three will be submitted to as companion papers to *North American Journal of Fisheries Management*. Chapter four discusses general conclusions and management recommendations.

References

- Baldwin, C. M., J. G. McLellan, M. C. Polacek, and K. Underwood. 2003. Walleye predation on hatchery releases of kokanees and Rainbow Trout in Lake Roosevelt, Washington. *North American Journal of Fisheries Management* 23:660-667.
- Barton, B. A. 2011. *Biology, management, and culture of Walleye and Sauger*. American Fisheries Society, Bethesda, Maryland.
- Beamesderfer, R. C., and B. E. Rieman. 1988. Size selectivity and bias in estimates of population statistics of Smallmouth Bass, Walleye, and Northern Squawfish in a Columbia River Reservoir. *North American Journal of Fisheries Management* 8:505-510.
- Bednarek, A. T., and D. D. Hart. 2005. Modifying dam operations to restore rivers: ecological responses to Tennessee River dam mitigation. *Ecological Applications* 14:997-1008.
- Blackwell, T., A. G. P. Ford, A. G. Ciezarek, S. J. Bradbeer, C. A. Gracida Juarez, B. P. Ngatunga, A. H. Shechonge, R. Tamatamah, G. Etherington, W. Haerty, F. Di Palma, G. F. Turner, and M. J. Genner. 2020. Newly discovered cichlid fish biodiversity threatened by hybridization with non-native species. *Molecular Ecology* 30:895-911.
- Blanc, G. 1997. Introduced pathogens in European aquatic ecosystems: theoretical aspects and realities. *Bulletin Français de la Pêche et de la Pisciculture* 344:489-513.
- Carpenter, S. R., E. H. Stanley, and M. J. Vander Zanden. 2011. State of the world's freshwater ecosystems: physical, chemical, and biological changes. *Annual Review of Environment and Resources* 36:75-99.
- Colby, P. J., R. E. McNicol, and R. A. Ryder. 1979. Synopsis and biological data on the Walleye *Stizostedion v. vitreum* (Mitchill 1818). Food and Agriculture Organization of the United Nations Fisheries Synopsis 119.
- Cucherousset, J., and J. D. Olden. 2011. Ecological impacts of non-native freshwater fishes. *Fisheries* 36:215-230.
- Field-Dodgson, M. S. 1987. The effect of salmon redd excavation on stream substrate and benthic community of two salmon spawning streams in Canterbury, New Zealand. *Hydrobiologia* 154:3-11.

- Fincel, M. J., D. J. Dembkowski, and S. R. Chipps. 2014. Influence of variable Rainbow Smelt and Gizzard Shad abundance on Walleye growth. *Lakes and Reservoir Management* 30:258-267.
- Fuller, P. 2010. *Sander vitreus*. USGS nonindigenous aquatic species database. Gainesville, Florida. Available: nas.er.usgs.gov/queries/factsheet.aspx?SpeciesID=831. (March 2020).
- Goldschmidt, T., F. Witte, and J. Wanink. 1993. Cascading effects of the introduced Nile Perch on the detritivorous/phtoplanktivorous species in the sublittoral areas of Lake Victoria. *Conservation Biology* 7:686-700.
- Gozlan, R. E., S. St-Hilaire, S. W. Feist, P. Martin, and M. L. Kent. 2005. Biodiversity – disease threat to European fish. *Nature* 435:1046.
- Gutiérrez, J. L. 2017. Modification of habitat quality by non-native species. Pages 33-47 in M. Vila and P. Hulme, editors. *Impact of biological invasions on ecosystem services*. Springer, New York, New York.
- Irons, K. S., G. G. Sass, M. A. McClelland, and J. D. Stafford. 2007. Reduced condition factor of two native fish species coincident with invasion of non-native Asian carps in the Illinois River, U.S.A. Is this evidence for competition and reduced fitness? *Journal of Fish Biology* 71:258-273.
- Johnson, C. F., B. M. Johnson, T. E. Neebling, and J. C. Burckhardt. 2017. Walleye introduction eliminates predation refuge for adfluvial Cutthroat Trout and Rainbow Trout. *Transactions of the American Fisheries Society* 146:252-267.
- Keller, K., and C. Brown. 2008. Behavioural interactions between the introduced Plague Minnow *Gambusia holbrooki* and the vulnerable native Australian Ornate Rainbowfish *Rhadinocentrus ornatus*, under experimental conditions. *Journal of Fish Biology* 73:1714-1729.
- Koehn, J. D. 2004. Carp (*Cyprinus carpio*) as a powerful invader in Australian waterways. *Freshwater Biology* 49:882-894.
- McGrady-Steed, J., P. M. Harris, and P. J. Morin. 1997. Biodiversity regulates ecosystem predictability. *Nature* 390:162-165.

- McIntosh, A. R., and C. R. Townsend. 1996. Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish-induced changes to grazer behaviour. *Oecologia* 108:174-181.
- McKelvey, K. S., M. K. Young, T. M. Wilcox, D. M. Bingham, K. L. Pilgrim, and M. K. Schwartz. 2016. Patterns of hybridization among Cutthroat Trout and Rainbow Trout in northern Rocky Mountain streams. *Ecology and Evolution* 6:688-706.
- McMahon, T. E., and D. H. Bennet. 1996. Walleye and Northern Pike: boost or bane to northwest fisheries? *Fisheries* 21:6-13.
- McMillan, J. 1984. Evaluation and enhancement of the trout and Walleye fisheries in the North Platte River system of Wyoming with emphasis on Seminoe Reservoir. Final Report to Wyoming Game and Fish Department, Laramie.
- Mittlebach, G. G., and L. Persson. 1998. The ontogeny of piscivory and its ecological consequences. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1454-1465.
- Mooney, H. A., and E. E. Cleland. 2001. The evolutionary impact of invasive species. *Proceedings of the National Academy of Science* 98:5446-5451.
- Moyle, P. B. 1986. Fish introductions into North America: patterns and ecological impact. Pages 27-43 in H. A. Mooney and J. A. Drake, editors. *Ecology of biological invasion of North America and Hawaii*. Springer, New York.
- Moyle, P. B., and T. Light. 1996. Biological invasions of fresh water: empirical rules and assembly theory. *Biological Conservation* 78:149-161.
- Murphy, C. A., J. D. Romer, K. Stretz, I. Arismendi, R. Emig, F. Monzyk, and S. L. Johnson. 2021. Damming salmon fry: evidence for predation by non-native warmwater fishes in reservoirs. *Ecosphere* 12:1-17.
- Ogutu-Ohwayo, R. 1990. The reduction in fish species diversity in Lakes Victoria and Kyoga (East Africa) following human exploitation and introduction of non-native fishes. *Journal of Fish Biology* 37:207-208.
- Olden, J. D., N. L. Poff, M. R. Douglas, M. E. Douglas, and K. D. Fausch. 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution* 19:18-24.

- Pelicice, F. M., and A. A. Agostinho. 2009. Fish fauna destruction after the introduction of a non-native predator (*Cichla kelberi*) in a Neotropical reservoir. *Biological Invasions* 11:1789-1801.
- Pess, G. R., M. L. McHenry, T. J. Beechie, and J. Davies. 2008. Biological impacts of the Elwha River dams and potential salmonid responses to dam removal. *Northwest Science* 82:72-90.
- Pierce, P. C., and M. J. Van Den Avyle. 1997. Hybridization between introduced Spotted Bass and Smallmouth Bass in reservoirs. *Transactions of the American Fisheries Society* 126:939-947.
- Poe, T. P., H. C. Hansel, S. Vigg, D.E. Palmer and L.A. Prendergast. 1991. Feeding of predaceous fishes on out-migrating juvenile salmonids in John Day Reservoir, Colombia River. *Transactions of the American Fisheries Society* 120:405-420.
- Prenter, J. C., J. MacNeil, T. A. Dick, and A. M. Dunn. 2004. Roles of parasites in animal invasions. *Trends in Ecology and Evolution* 19:385-390.
- Rahel, F. J. 2000. Homogenization of fish faunas across the United States. *Science* 288:854-856.
- Rebele, F. 1994. Urban ecology and special features of urban ecosystems. *Global Ecology and Biogeography Letters* 4:173-187.
- Rust, P., N. G. Mucciarone, S. M. Wilson, M. P. Corsi, and W. H. Harryman. 2020. Lake Pend Oreille research, 2017 and 2018: Lake Pend Oreille fishery recovery project. Idaho Department of Fish and Game. Annual Report to Bonneville Power Administration, Project 1994-047-00. Portland, Oregon.
- Ryan, R. G., M. P. Corsi, and P. Rust. 2021. Characteristics of an introduced Walleye population with implications for suppression. *North American Journal of Fisheries Management* 41:1863-1877.
- Scarnecchia, D. L., Y. Lim, S. P. Moran, T. D. Tholl, J. M. Dos Santos, and K. Breidinger. 2014. Novel fish communities: native and non-native species trends in two run-of-the-river reservoirs, Clark Fork River, Montana. *Reviews in Fisheries Science and Aquaculture* 22:97-111.
- Schoby, G. P., T. P. Bassista, and M. A. Maiolie. 2007. Effects of higher winter water levels on the Pend Oreille River fish community: Lake Pen Oreille fishery recovery project.

- Annual report to Bonneville Power Administration, Project 1997-047-00. Portland, Oregon.
- Stachowicz, J. J., H. Fried, R. W. Osman, and R. B. Whitlatch. 2002. Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. *Ecology* 83:2575-2590.
- Wilcove, D., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. *BioScience* 48:607-615.
- Vigg, S., T. P. Poe, L. A. Prendergast, and H. C. Hansel. 1991. Rates of consumption of juvenile salmonids and alternative prey fish by Northern Squawfish, Walleyes, Smallmouth Bass, and Channel Catfish in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society* 120:421-438.
- Zaret, T. R., and R. T. Paine. 1973. Species introduction in a tropical lake: a newly introduced piscivore can produce population changes in a wide range of trophic levels. *Science* 182:449-455.
- Zimmerman, M. P., and R. M. Parker. 1995. Relative density and distribution of Smallmouth Bass, Channel Catfish, and Walleye in the Lower Columbia and Snake Rivers. *Northwest Science* 69:19-28.

Chapter 2: Food Habits and Seasonal Growth of Walleyes in the Lake Pend Oreille System, Idaho

Abstract

Walleye *Sander vitreus* is a recreationally and ecologically important species that has been widely introduced outside of its native distribution. The overall goal of this project was to assess the effects of a recently established Walleye population in the Lake Pend Oreille (LPO) system, Idaho. Specifically, I sought to describe Walleye food habits using stomach contents and stable isotopes, identify the food web structure of LPO using stable isotopes, and estimate the number of kokanee *Oncorhynchus nerka* consumed by Walleyes using a bioenergetics model. Overall, Walleyes consumed a diversity of prey items including eight macroinvertebrate orders and 22 fish species. Kokanee occurred in 23% of all Walleye stomachs, was the most frequently consumed prey item, and contributed approximately 79% of the total energy consumed by Walleyes. Combined, native cyprinid and catostomid species occurred in 31% of all Walleye stomachs. Walleye diets varied across seasons (i.e., spring, summer, fall, winter), regions in the system (Pend Oreille River, northern LPO, central LPO, Clark Fork River, and southern LPO), and cohorts. Kokanee, as well as native cyprinids and catostomids, were consumed by Walleyes in all seasons, regions, and by most cohorts. Occurrence of kokanee in Walleye diets increased with age, whereas occurrence of native cyprinids and catostomids generally remained consistent or decreased with age. Stable isotope ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$) analysis suggested that Walleyes occupied similar trophic positions as other top-level piscivores in the system such as Bull Trout *Salvelinus confluentus* and Lake Trout *S. namaycush*. As Walleye age increased, $\delta^{15}\text{N}$ increased and $\delta^{13}\text{C}$ decreased indicating increased consumption of pelagic prey resources. Proportion of maximum consumption estimated from the bioenergetics model varied from 0.21-0.77 across cohorts and seasons. Per-capita biomass ingestion varied by cohort from 473-6,101 g. Estimated Walleye abundance in the system was 22,971 individuals (95% confidence interval [CI] = 7,774-52,177). The estimated total biomass of kokanee consumed by Walleyes was 24,859 kg (95% CI = 8,413-56,465 kg) which represented approximately 725,654 individuals (95% = 245,581-1,648,271). This study revealed that Walleyes consumed kokanee and native fishes

at high rates across the Lake Pend Oreille system and contributes to our growing knowledge of the effects of non-native Walleyes in salmonid-dominated systems.

Introduction

Freshwater fisheries management in North America has a long history of non-native species introductions (Moyle 1986). Introductions of non-native species have occurred for a variety of reasons, from recreational purposes to biological control (Rahel 1997; Gozlan 2008; Rahel and Smith 2018). Prey species have been introduced to improve growth of consumers and ultimately enhance an existing fishery. For instance, *Mysis diluviana* (hereafter *Mysis*) has been introduced widely to lake systems to provide a prey resource for Lake Trout *Salvelinus namaycush* (Northcote 1973; Linn and Frantz 1965) and kokanee *Oncorhynchus nerka* (Lansenby et al. 1986; Spencer et al. 1991). Similarly, some non-native species have been introduced to purposefully alter system characteristics. Bighead Carp *Hypophthalmichthys nobilis* and Grass Carp *Ctenopharyngodon idella* were introduced to the United States in the 1970s to improve water quality and increase fish production in aquaculture facilities (Leslie et al. 1996; Conover et al. 2007; Fuller et al. 1999). Another common reason for the introduction of a non-native species is for recreation. Of the 17 most commonly introduced fish species in the United States, 13 (76%) were introduced as sport fishes (Rahel 2000). Non-native fishes were often deliberately introduced, but accidental introductions have also occurred (e.g., Courtenay et al. 1986; Gozlan et al. 2010). Whether deliberate or accidental, introductions of non-native fishes are either authorized or unauthorized. In general, authorized introductions of novel species by agencies have decreased, but unauthorized introductions still occur (Rahel 2004). In Wyoming, 62 unauthorized fish introductions occurred from 1973-2002, of which, half involved illegal introductions by the public. Unauthorized introductions may occur accidentally by improper cleaning of boats and equipment, but many are intentional (Rahel 2004; Johnson et al. 2009). Authorized or unauthorized introductions, combined with dispersal, lead to non-native species inhabiting new aquatic environments with a variety of positive and negative effects (e.g., Paul and Post 2001; Dunham et al. 2002).

Despite the impetus and mechanism of introductions, non-native species can be detrimental to aquatic systems (Zaret and Paine 1973; Goldschmidt et al. 1993; Cucherousset

and Olden 2011). Many studies have documented the negative effects of established non-native fishes (e.g., Moyle and Light 1996; Mulhfeld et al. 2009; Jeschke et al. 2014). Non-native species indirectly effect native species through hybridization (Pierce and Van Den Avyle 1997; McKelvey et al. 2016; Blackwell et al. 2021), introduction of novel diseases and parasites (Blanc 1997; Prenter et al. 2004; Gozlan et al. 2005), and habitat modification (Field-Dodgson 1987; Koehn 2004; Gutiérrez 2017). More directly, non-native species have been shown to outcompete other species for resources which results in altered growth, survival, and reproduction (McMillan 1984; Irons et al. 2007; Keller and Brown 2008). Another common mechanism by which non-native species have influenced native fishes is through predation (Ogutu-Ohwayo 1990; McIntosh and Townsend 1995; Pelicice and Agostinho 2009). For example, after the introduction of Nile Perch *Lates niloticus* to Lake Victoria, abundance of native cichlid populations declined (Ogutu-Ohwayo 1990) and 60% of the endemic fishes were extirpated due to predation (Witte et al. 1992). Despite the recognized negative effects, non-native species have continued to appear in novel aquatic environments (Rahel and Smith 2018).

The Walleye *Sander vitreus* is an ecologically and recreationally important fish species that is widely distributed in cool, mesotrophic freshwater systems throughout North America (Colby et al. 1979; Hoagstrom and Berry 2010; Barton 2011). In the United States, its native distribution is the Mississippi River and Great Lakes drainage basins. Largely because of its popularity with anglers, Walleye has been widely introduced outside of its native distribution, particularly in the western United States (Colby et al. 1979; McMahon and Bennett 1996; Carlander 1997; Billington et al. 2011). Walleyes are highly piscivorous and often alter community structure through predation and competition (McMillan 1984; Lyons and Magnuson 1987; Scarnecchia et al. 2014). In systems across the western United States, Walleye consumption of kokanee and other important salmonid species has been documented (McMillan 1984; Poe et al. 1991; McMahon and Bennett 1996; Baldwin et al. 2003; Johnson et al. 2017; Murphy et al. 2021). In Lake Roosevelt, Washington, Baldwin et al. (2003) evaluated Walleye predation on kokanee and Rainbow Trout *O. mykiss*. From 1999-2000, Walleyes consumed ~7-15% of hatchery kokanee within 41 days of release. Similarly, in John Day Reservoir, Oregon-Washington, Poe et al. (1991) estimated that salmonids represented 10-39% of the Walleye diets by weight and were the most important

prey for Walleyes greater than 300 mm in length. Murphy et al. (2021) concluded that Walleyes were a primary threat to survival of juvenile Chinook Salmon *O. tshawytscha* in the Middle Fork Willamette River, Oregon.

Walleyes were first introduced to the Lake Pend Oreille (LPO) system in Noxon Rapids Reservoir, Montana, in the 1990s (Rust et al. 2020). By 2005, Walleyes were sampled in the Pend Oreille and Clark Fork rivers, Idaho, and then in LPO, Idaho, the following year (Schoby et al. 2007). Monitoring conducted by the Idaho Department of Fish and Game (IDFG) estimated that the Walleye population doubled approximately every three years from 2011 to 2017 (Ryan et al. 2021). The Lake Pend Oreille system supports robust populations of Westslope Cutthroat Trout *O. clarkii lewisi*, a species of conservation need in Idaho (IDFG 2017), and federally threatened Bull Trout *Salvelinus confluentus*. Additionally, Lake Pend Oreille is well known for its kokanee and trophy Rainbow Trout fisheries. Clarke et al. (2005) evaluated diet contents of piscivores in Lake Pend Oreille and found that kokanee was the dominant prey item (40-100% of the total biomass consumed) for large Bull Trout, Lake Trout, and Rainbow Trout. As such, the establishment of Walleyes will likely affect salmonid populations in the Lake Pend Oreille system; however, the extent to which is unknown.

This study aims to answer questions related to the food habits of Walleyes in the Lake Pend Oreille system. Specifically, the objectives of the study were to (1) describe the current distribution of Walleyes in the system, (2) evaluate spatial and temporal variation in Walleye diets, (3) describe the trophic structure of the fish assemblage, (4) identify trends in Walleye trophic ecology in relation to age, and (5) estimate consumption of kokanee by Walleyes.

Methods

Study system

The Lake Pend Oreille system is located in northern Idaho near the junction of the Cabinet, Selkirk, and Coeur d'Alene mountain ranges. The Lake Pend Oreille system encompasses 64,300 km² (Woods 2004) and consists of the Clark Fork River, Pend Oreille River, and Lake Pend Oreille (Figure 2.1). Lake Pend Oreille is Idaho's largest lake with a surface area of 36,400 ha, and the fifth deepest natural lake in the United States with an

average depth of 164 m and a maximum depth of 357 m (Woods 2004; Rust et al. 2020). The Clark Fork River, with headwaters in Montana, is the primary tributary to the lake. The Pend Oreille River, a tributary to the Columbia River, is the only outlet of Lake Pend Oreille.

Lake Pend Oreille supports a diversity of native and non-native fishes. Native fishes include Bull Trout, Westslope Cutthroat Trout, Mountain Whitefish *Prosopium williamsoni*, Pygmy Whitefish *P. coulterii*, Slimy Sculpin *Cottus cognatus*, Largescale Sucker *Castostomus macrocheilus*, Redside Shiner *Richardsonius balteatus*, Peamouth Chub *Mylocheilus caurinus*, and Northern Pikeminnow *Ptychocheilus oregonensis*. Non-native fishes include kokanee, Rainbow Trout, Lake Trout, Brown Trout *Salmo trutta*, Smallmouth Bass *Micropterus dolomieu*, Largemouth Bass *M. salmoides*, Tench *Tinca tinca*, Yellow Perch *Perca flavescens*, Northern Pike *Esox Lucius*, and Walleye (Maiolie et al. 2004; Rust et al. 2020).

The basin was divided into five regions to assess spatial variability in food habits (Figure 2.1). Regions were defined as (1) the Pend Oreille River to the train bridge in Sandpoint, Idaho (POR), (2) northern basin from the train bridge in Sandpoint to Hope, Idaho (LPO-N), (3) a transition zone in the northern basin from Hope to the Clark Fork Delta and south to Mineral Point (LPO-C), (4) the Clark Fork River and Delta (CFR), and (5) the southern basin of the lake from Mineral Point to Bayview, Idaho (LPO-S). Divisions were based on differences in habitat characteristics and were consistent with how IDFG defines the system. The POR and CFR regions are riverine habitats with seasonally abundant aquatic vegetation. The LPO-N and LPO-C regions are fairly shallow and warm with gradually sloping shorelines; whereas, LPO-S is deep, cold, and pelagic with steep, rocky shorelines. Regions were then stratified by depth to evaluate whether Walleye diets varied by depth. Depth categories were < 5 m, 5-15 m, and > 15 m as a modification of the Fall Walleye Index Netting protocol (FWIN; Morgan 2002).

Standardized sampling

Fish were sampled roughly every other week from May 25, 2020, to May 8, 2021 (approximately two weeks per month). Hazardous winter weather conditions, as well as exposure to COVID-19 limited sampling events in December 2020 when sampling only

occurred during the first week. Walleyes were sampled using standardized sinking gill nets. Gill nets were 1.8 m tall by 61.0 m long and consisted of eight panels of varying mesh sizes (i.e., 25-mm, 38-mm, 51-mm, 64-mm, 76-mm, 102-mm, 127-mm, and 152-mm stretched mesh) in accordance with FWIN specifications (Morgan 2002). Six nets were set per night. Nets were set perpendicular to shore and soaked overnight. Generally, nets were set 1-2 hours before dusk and pulled 1-3 hours after dawn.

Supplemental sampling

Walleyes were also collected from four other programs that occur consistently across the system. These programs include the spring Walleye mitigation netting conducted by Hickey Brothers Research (HBR) in conjunction with IDFG; FWIN conducted by IDFG; Lake Trout suppression, nursery, and assessment netting conducted by HBR and IDFG; and salmonid population monitoring in the Clark Fork River conducted by Avista Corporation. Five individuals per 10 mm length group were subsampled from the spring Walleye mitigation netting. Gill nets were 274.0 m long and consisted of three 91.4 m panels (Rust et al. 2020; Bouwens et al. 2021). Each panel consisted of a single mesh size (i.e., 89-mm, 106-mm, and 114-mm stretched mesh). Ten gill nets were joined together and fished at one location. Gill nets were set around dawn and retrieved 4-6 hours later. All incidentally captured Walleyes from the Lake Trout suppression, nursery, and assessment netting events were processed. Sinking gill nets for all Lake Trout netting efforts consisted of 10 gill nets. Gill nets had the same dimensions as the spring Walleye mitigation netting (i.e., length, number of panels) except that mesh sizes differed depending on the specific Lake Trout netting effort (Dux et al. 2019). Lake Trout suppression netting occurred in the fall for 10 weeks (September – November) and stretched mesh sizes were 127 mm and 140 mm. Nursery and assessment netting events occurred during the winter and spring for 14 weeks (December – March). Stretched mesh sizes were 51 mm and 64 mm for the Lake Trout nursery netting, whereas stretched mesh sizes were 38 mm, 44 mm, 51 mm, 64 mm, 76 mm, 89 mm, 102 mm, 114 mm, 127 mm, and 140 mm for the Lake Trout assessment netting. During all Lake Trout netting events, gill nets were set around dawn and retrieved 4-6 hours later (Rust et al. 2020; Bouwens et al. 2021). Samples were collected from all Walleyes

captured during the FWIN which occurred in October. Gill nets were 61.0 m long and 1.8 m tall with eight panels of increasing mesh sizes (i.e., 25-mm, 38-mm, 51-mm, 64-mm, 76-mm, 102-mm, 127-mm, and 152-mm stretched mesh; Morgan 2002). Gill nets soaked for approximately 24 hours (Ryan et al. 2021). Additionally, samples were collected from all Walleye encountered during the spring salmonid population monitoring on the Clark Fork River conducted by IDFG and Avista Corporation. Walleyes were collected by use of boat electrofishing conducted at night. Boats used pulsed DC at 400 volts, 60 hertz, and 20% duty cycle (Ransom 2022).

Zooplankton and *Mysis* were collected for stable isotope analysis (see below) using vertical tows. For *Mysis*, vertical tows occurred at night through *Mysis* layers that were identified with sonar (Caldwell and Wilhelm 2012). *Mysis* were collected using a Wisconsin-style zooplankton net with a 1-m diameter opening, 1-mm mesh, and a 500- μ m mesh collection bucket in June 2021. Zooplankton were sampled during May 2022 using a Wisconsin-style net with a 0.5-m diameter opening and an 80- μ m mesh size and collection bucket.

Fish processing

All fish sampled were measured to the nearest millimeter for total length and weighed to the nearest gram. Ageing structures, muscle samples, and stomach contents were collected from all sampled Walleyes. Sagittal otoliths were removed and placed into a centrifuge tube to prevent damage prior to laboratory analysis. Muscle tissue, sufficient to fill a 2 mL centrifuge tube, was collected from the anterior dorsal musculature for stable isotope analysis. Stomachs from the esophagus to the pyloric sphincter were removed in the field and preserved in 10% buffered formalin to assess food habits (Johnson et al. 2008). For all potential prey items collected from gill nets (i.e., fishes, Cambaridae), white muscle samples were collected from ~20 individuals in each region of the Lake Pend Oreille system during each season for stable isotope analysis. Muscle samples from all species were placed on ice and transported to the laboratory where they were stored at -20°C until further processing. For potential prey species that were known or expected to exhibit an ontogenetic diet shift (i.e., Bull Trout, Lake Trout, Largemouth Bass, Northern Pikeminnow, Smallmouth Bass),

muscle samples were collected from ~20 individuals less than and ~20 individuals greater than the length (Appendix A) at which a shift in diet was expected to occur (Carlander 1997; Olson and Young 2003; McIntyre et al. 2006; Yasuno et al. 2010; Lowery and Beauchamp 2015; Baranowska and Robinson 2017). Zooplankton and *Mysis* samples were immediately placed on ice and stored at -20°C until further processing. *Mysis* were analyzed separately from other zooplankton. Since *Mysis* diets often vary by length, *Mysis* were separated by length (small, < 1 cm; large > 1 cm). Individuals were combined until a 2-mL centrifuge tube was filled (~5 g wet weight). All other bulk zooplankton samples (~5 g) were grouped and analyzed by collection site. Copepods and cladocerans were the dominant zooplankters in the samples.

Laboratory processing

Otoliths were mounted in epoxy and sectioned along the transverse plane using an IsoMet Low Speed Saw (Buehler, Lake Bluff, Illinois; Koch and Quist 2007). Annuli were marked and enumerated to estimate growth. Stomach contents were rinsed with water prior to identification. Prey items were enumerated and identified to the lowest taxonomic classification possible using diagnostic keys (Scott and Crossman 1978; Frost 2000; Wydoski and Whitney 2003; Traynor and Greil 2010; Wallace and Zaroban 2013; Stroud and Scholz 2014). Macroinvertebrates were identified to order and fish to species when possible. Diagnostic bones (e.g., cleithra, dentaries, pharyngeal arches) were used to identify vertebrate prey items (Scott and Crossman 1978; Frost 2000; Traynor and Greil 2010; Stroud and Scholz 2014). When diagnostic bones were unavailable, vertebral counts were used to identify prey items to the lowest taxonomic classification (Scott and Crossman 1978; Wydoski and Whitney 2003; Wallace and Zaroban 2013). Lengths of prey items were measured using a caliper (Mitutoyo, Aurora, Illinois) to the nearest 0.01 mm and blotted-wet weight was collected for each prey item to the nearest 0.1 g (Chipps and Garvey 2008). Total length was measured for macroinvertebrate taxa. Total length, standard length, and fork length were measured for all intact fish taxa. If not intact, standard length, fork length, or vertebral counts were quantified (Johnson et al. 2008).

Muscle samples were dried at 60°C for 48 hours and ground to a fine powder with either a mortar and pestle or a Wig-I-Bug automatic grinder (International Crystal Laboratories, Garfield, New Jersey). All samples were sent to the Stable Isotope Core Laboratory at Washington State University. Samples were converted to N₂ and CO₂ with an elemental analyzer (ECS 4010, Costech Analytical, Valencia, California) and analyzed with a continuous flow isotope ratio mass spectrometer (Delta PlusXP, Thermofinnigan, Bremen; Brenna et al. 1997; Qi et al. 2003).

CPUE, age structure, and seasonal growth

Catch-per-unit-effort (CPUE) was described as the mean number of Walleyes caught per net-night in each region by season. Months were grouped into seasons: spring (March – May), summer (June – August), fall (September – November), and winter (December – February). The total number of Walleyes caught per net was averaged across all nets fished in each region during a particular season and across all depths. A Welch's *t*-test indicated that mean catch rates of Walleyes did not differ across depths ($\alpha = 0.05$). As such, CPUE was reported across regions by season. Estimates of CPUE only included Walleyes that were collected from the standardized sampling.

Age structure of Walleyes was described as the proportion of the sampled individuals assigned to each cohort. Seasonal growth was measured as the change in the average length and weight by cohort and season. Cohort summarizations were limited to the 2013 and younger cohorts due to low sample size ($n < 10$ individuals) of older cohorts.

Food habits

Walleye food habits were described using proportion by weight (W_i), frequency of occurrence (O_i), proportion energy contribution (E_i), and prey-specific energy contribution (Amundsen et al. 1996; Probst et al. 1984; Pope et al. 2001; Chipps and Garvey 2006; Walrath et al. 2015). Proportion by weight was estimated as:

$$W_i = \frac{X_i}{\sum_{i=1}^Q X_i},$$

where W_i is the proportion by weight of prey type i , X_i is the weight of prey type i , and Q is the number of prey types (Chipps and Garvey 2006). Frequency of occurrence was estimated as:

$$O_i = \frac{J_i}{P},$$

where O_i is the frequency of prey type i , J_i is the number of Walleye stomachs containing prey type i , and P is the number of non-empty stomachs. Percent energy contribution was estimated by multiplying the weight of a prey type by its energy density and dividing by the total energy contributed by all prey types (Probst et al. 1984). Energetic densities from the literature (Cummins and Wuycheck 1971; Wissing 1974; Kitchell et al. 1977; Minton and McLean 1982; Hanson 1997; Kamler and Tachowiak 1992; Yule and Luecke 1993; Liao et al. 2004; Antolos et al. 2005; Muhlfeld et al. 2008) were used to estimate energetic contributions. Prey-specific energy contribution of each prey type was estimated by dividing the energy contribution of a specific prey type by the total energy of all prey types for the stomachs that contained the specific prey type (Costello 1990; Amundsen et al. 1996). Macroinvertebrate prey types included species from the Amphipoda, Arthropoda, Diptera, Ephemeroptera, Isopoda, Odonata, Plecoptera, and Trichoptera orders as well as individuals from the Hirudinea and Oligochaeta subclasses of Annelida. Macroinvertebrate prey types were combined into one prey taxa. *Mysis* was grouped separately. Energy densities of all macroinvertebrate prey types were averaged and then used as the energy density of the macroinvertebrate group (Hartman and Brandt 1995). Additionally, the mean energy density of all fish species observed in Walleye diets was used to represent the energy density of unknown fish (Courtney et al. 2018).

Differences in diets across regions, seasons, and cohorts were assessed using the proportion by weight data. Prey types with $O_i < 5\%$ in all regions, seasons, and cohorts were removed to reduce the effects of rare species (Zar 1999; Smith et al. 2014). Prey types removed from the analysis due to low occurrence were Brook Trout, Bluegill, Largemouth Bass, Pumpkinseed, and Walleye. Differences in diet across regions, seasons, and cohorts were assessed using a permutational multivariate analysis of variation (PERMANOVA) with the Bray-Curtis dissimilarity matrix and 9,999 permutations (Rodger et al. 2021). A PERMANOVA was used because of its robust nature with unbalanced designs, various correlation structures, and heterogeneity of dispersions in comparison with traditional

multivariate analysis of variance, analysis of similarity, and Mantel test (Anderson 2001; Anderson and Walsh 2013). The PERMANOVA returns a pseudo- F statistic and P -value which were used to identify significant differences between groups ($P < 0.05$). For significant results, a similarity percentage (SIMPER) analysis was used to identify the species contributing to the differences between groups (Clarke 1993; Bonato et al. 2012). The PERMANOVA may be sensitive to heterogeneity in group dispersion. As such, heterogeneity of group dispersion was tested to evaluate differences existing between groups (i.e., seasons, regions, and cohorts). Analyses were completed using the `adonis2`, `simper`, and `betadisper` functions in the R package `vegan` (R Core Team 2022).

Trophic structure

Trophic structure of all species was described using ^{15}N and ^{13}C isotopes. Results were reported with respect to the Vienna Pee Dee belemnite and atmospheric nitrogen (air) in parts per thousand (‰; Coplen 2002). Results from the laboratory analysis were described as the relative difference of the isotopes from each sample and a standard such that,

$$\delta = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \times 1,000,$$

where δ (‰) is the difference, R_{sample} is the isotope ratio of the sample, and R_{standard} is the isotope ratio of the standard. Because lipids are typically depleted in $\delta^{13}\text{C}$ relative to proteins and carbohydrates (DeNiro and Epstein 1978), $\delta^{13}\text{C}$ values were normalized using a mathematical correction (Post et al. 2007). Trophic structure of the system was graphically assessed using bi-plots of the average $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for each species. Individuals from the same species were grouped unless the species was known to exhibit an ontogenetic shift in diets (e.g., Northern Pikeminnow), in which case individuals were classified as small and large by length (Appendix A). Limited sample size, particularly of piscivores, precluded statistical tests to assess differences within individual taxa among seasons. However, visual inspection suggested that variation in each taxon was consistent across seasons and no major differences occurred. As such, samples were pooled across seasons.

Trophic structure was further described by assessing the trophic position of all taxa in the system using converted $\delta^{15}\text{N}$ values. Zooplankton were assumed to be the primary

consumer and to feed at trophic position 2. The $\delta^{15}\text{N}$ values for individual taxa were converted to trophic position by:

$$TP_i = \frac{\delta^{15}\text{N}_i - \delta^{15}\text{N}_z}{3.4} + 2,$$

where TP_i is the trophic position of the i th taxon, $\delta^{15}\text{N}_i$ is the nitrogen signature of the i th taxon, and $\delta^{15}\text{N}_z$ is the nitrogen signature of zooplankton (Post 2002).

Isotope samples from Walleyes were subsequently assessed by cohort because of apparent ontogenetic shifts identified from the stomach content analysis. Differences in isotopic ratios between cohorts were visually evaluated by summarizing the mean and variance of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for each cohort. Since isotopic ratios incorporate long-term diet information (Post 2002; Boecklen et al. 2011), differences in the trends of the isotopic ratios would suggest that observed patterns in the stomach contents are not reflective of long-term food habits. In contrast, similarities in the trends would suggest that the observed patterns in stomach contents are an accurate reflection of diet shifts.

Bioenergetics modeling and per-capita consumption

Fish Bioenergetics 4.0 was used to estimate per-capita consumption of prey items (Ney 1993; Hanson et al. 1997; Deslauriers et al. 2017). The bioenergetics model is a mass balance equation that partitions energy consumed into physiological processes,

$$C = (R+S) + (F+U) + \Delta B,$$

where C is consumption, R is respiration, S is the specific dynamic action, F is fecal egestion, U is nitrogenous excretion, and ΔB is the change in growth (weight) per individual. The simulation was run with a daily timestep and divided into four periods (i.e., spring, summer, fall, winter) to better describe seasonal trends in consumption for each cohort. Bioenergetics models require information on water temperature, predator and prey energy densities, change in weight of the predator, and predator diet proportions (Kitchell et al. 1977; Hanson et al. 1997; Deslauriers et al. 2017). Water temperature was collected from HOBO Pendant temperature loggers (Onset Computer Corporation, Bourne, Massachusetts) placed on individual nets. Temperatures ($^{\circ}\text{C}$) were recorded every 15 minutes to estimate a mean daily temperature. Supplemental mean temperature estimates were obtained from IDFG for May – October. Ryan et al. (2021) estimated a 0.5 probability of maturity at 1.7 years for male and

3.6 years for female Walleyes in the Lake Pend Oreille system. Therefore, physiological parameters for juvenile Walleye were used for the 2020 and 2019 cohorts. Parameters for adult Walleyes were used for all other cohorts (2013-2018). Prey energy densities from the literature were used in the model (Cummins and Wuycheck 1971; Wissing 1974; Kitchell et al. 1977; Minton and McLean 1982; Hanson 1997; Kamler and Tachowiak 1992; Yule and Luecke 1993; Liao et al. 2004; Antolos et al. 2005; Muhlfeld et al. 2008). Seasonal weight change was estimated using the average weight of individuals in a cohort for each season. If the average weight of individuals in a cohort decreased between seasons, no growth was assumed to occur during that time period (Walrath et al. 2015). Proportion by weight for prey items was summarized by season and cohort, and then input into the model. Results of the bioenergetics modeling were reported as the per-capita biomass consumed across cohorts and seasons as well as proportion of maximum consumption (P_c). Proportion of maximum consumption was calculated as:

$$P_c = C \times \left(\frac{C_{max}}{r_c}\right),$$

where C is the estimated consumption, C_{max} is the maximum consumption of a specific ration at a given temperature, and r_c is a temperature-dependent proportional adjustment of consumption rate (Kitchell et al. 1977; Hanson et al. 1997). Bioenergetics modeling was conducted for all cohorts, but individuals from the 2012 and older cohorts were grouped together because of low sample size ($n < 10$ individuals per cohort).

Kokanee consumption

The bioenergetics model estimated the total per-capita biomass of all prey types consumed by Walleyes. Because of the importance of kokanee to Walleyes observed in this study and the importance of kokanee to the Lake Pend Oreille system, I estimated the total biomass of kokanee consumed by Walleyes in the system. The total biomass of kokanee consumed was estimated as:

$$T = \sum k_{ij},$$

where T is the total biomass (kg) of kokanee consumed by the Walleye population and k_{ij} is the biomass (kg) of kokanee consumed by the i th cohort and in the j th region. The biomass consumed in each region was calculated by:

$$k_{ij} = C_i \times W_{ij},$$

where C_i is the per-capita biomass (kg) of kokanee consumed by the i th cohort from the bioenergetics model and W_{ij} is the abundance of Walleye of the i th cohort in the j th region. Per-capita biomass of kokanee consumed by the i th cohort was estimated by multiplying the estimated total biomass of all prey items consumed (i.e., from the bioenergetics model) by the proportion of kokanee by weight from the food habits summarization (Schultz et al. 2017). The proportion of kokanee from the food habits summarization represented the average cohort-specific proportion of kokanee across the entire system. Abundance of Walleyes of each cohort in each region was estimated as:

$$W_{ij} = D_j \times S_j \times A_i,$$

where D_j is the density of Walleyes in the j th region (number/hectare) estimated using relationships provided in Giacomini et al. (2020), S_j represents the surface area of the j th region as defined by Ryan et al. (2021) for the FWIN conducted by IDFG, and A_i is the proportion of the Walleye population represented by the i th cohort (Loboschefskey et al. 2012; Cerino et al. 2013). Because age-0 individuals did not consume kokanee and were not fully recruited to the gear, age-0 individuals were excluded. After removing age-0 individuals, A_i was obtained using the observed age structure from the Walleyes collected. The 95% confidence interval for the population abundance (CI) was estimated following Giacomini et al. (2020). Although the biomass of kokanee consumed is informative, I also estimated the total number of kokanee consumed given its relevance to resource managers (Hansen 1993). The same method outlined above was used to estimate the total number of kokanee consumed where N_i represented the per-capita number of kokanee consumed per cohort. Since the bioenergetics model provides an estimate of the biomass consumed, I first estimated the average weight of an individual kokanee consumed by each cohort using the observed stomach contents. Because kokanee observed in Walleye stomachs were at varying stages of digestion, a standard length-total length regression from the kokanee observed in the stomach contents was used to estimate total length of partially digested kokanee. Subsequently, a total length-weight regression from all kokanee sampled during the

standardized sampling was used to estimate the weights of kokanee observed in Walleye stomachs prior to ingestion. For each cohort, the mean estimated weight prior to ingestion was used to represent the weight of an average kokanee consumed by a Walleye. The per-capita number of kokanee for each cohort was then estimated as:

$$N_i = \frac{(B_i \times P_i)}{F_i},$$

where B_i is the total per-capita biomass (kg) of all prey items consumed of the i th cohort, P_i is the mean proportion by weight of kokanee observed in stomach contents of Walleyes in the i th cohort, and F_i is the mean weight (kg) of an individual kokanee consumed by Walleyes in the i th cohort.

Results

In total, 1,157 Walleyes were caught across all sampling efforts with similar numbers caught during standardized sampling efforts ($n = 600$ Walleyes) and supplemental sampling ($n = 557$ Walleyes). Except for LPO-S, Walleyes were caught in all regions during all seasons (Table 2.1; Figure 2.2). During the spring and summer, catch rates were highest in CFR; whereas, in the fall and winter, catch rates were highest in POR. Catch rates of Walleyes were lowest in LPO-S during all seasons. The highest catch rates were observed in the fall in POR (mean \pm SE; 4.17 ± 0.50) and lowest in LPO-S during the spring and winter when no Walleyes were caught (Figure 2.2).

Walleyes varied in length from 175-822 mm and in age from 0-20 years (Figure 2.3). No individuals from the 2001-2005 cohorts were identified, and individuals from the 2006-2008 and 2000 cohorts represented $< 1\%$ of the sample. The 2015 and 2019 cohorts represented 53% of sampled Walleyes. Growth of Walleyes was fairly consistent throughout the year (Figure 2.4). The greatest changes in mean length and weight for the 2019 and 2020 cohorts occurred from the spring to summer and fall to winter, respectively (Figure 2.4). For the 2013-2018 cohorts, growth was typically fastest between summer to fall or winter to spring. However, the apparent fast growth between winter to spring is likely an artifact of low sample sizes. Fewer than 10 individuals in each cohort were sampled during the winter (Table 2.1).

Stomach contents of Walleyes included macroinvertebrates and fishes (Table 2.2). In total, 522 Walleye stomachs contained prey items. Generally, one prey type was observed in individual Walleye stomach samples (~70%). Approximately, 30% of all Walleyes stomachs contained more than one prey type. Unknown fish occurred in about 23% of all Walleye stomachs, which represented 2% of the total weight of all prey items consumed. Kokanee was the most frequently identified prey item in Walleye stomachs (23% of all Walleye stomachs) and accounted for approximately 79% of the total energy consumed. Macroinvertebrates were the second most common prey item (16%) followed by Black Crappie (13%), Peamouth Chub (13%), Northern Pikeminnow (9%), and Yellow Perch (9%). Collectively, these five taxa contributed 13% of the total energy. Other taxa that occurred in Walleye stomachs ($\leq 5\%$) included catostomids, salmonids (other than kokanee), centrarchids, ictalurids, and cottids. No predation on Bull Trout was observed and only one instance of cannibalism was documented. Visual observation of frequency of occurrence relative to prey-specific energy contribution indicated that select prey taxa were important to individual Walleyes (Figure 2.5). Few taxa were consumed at relatively high frequencies and contributed more than 50% of the total energy to individual Walleyes. For example, Peamouth Chub occurred in approximately 13% of all Walleye stomachs, but accounted for approximately 80% of the total energy consumed by Walleyes containing Peamouth Chub (i.e., prey-specific energy contribution). Similar patterns were evident for Black Crappie. Kokanee occurrence in Walleye diets was 23% and prey-specific energetic contribution was approximately 99%. Most other species occurred at $< 5\%$ and contributed $< 50\%$ prey-specific energy.

The PERMANOVA indicated that diets varied significantly across regions ($F_{4,385} = 7.04$, $P < 0.01$), seasons ($F_{3,385} = 5.83$, $P < 0.01$), and cohorts ($F_{13,385} = 3.51$, $P < 0.01$), but not across depths ($F_{3,385} = 1.078$, $P > 0.10$). Of the six most frequently observed prey items, all taxa were consumed in at least four regions (Figure 2.6). Kokanee and Northern Pikeminnow were consumed in all five regions. In general, diets of Walleyes from the southern basin of the lake (LPO-S) consisted of the lowest diversity of prey items, whereas Walleye stomachs collected from POR and LPO-N contained the highest diversity of prey items (Appendix B). Interestingly, rare prey items (i.e., Largemouth Bass, Walleye, Tench, Pumpkinseed, Bluegill) in Walleye diets were from Walleyes sampled in the POR. The POR

was the only region where kokanee occurred in < 10% of all Walleye stomachs and contributed < 50% of the total energy to Walleye diets. In all other regions, kokanee occurred in at least 20% of Walleye stomachs and represented 81%-100% of the total energy consumed. Although at low frequencies and energy contribution, Rainbow Trout, *Mysis*, and Westslope Cutthroat Trout were consumed consistently throughout the system. The SIMPER analysis indicated that differences in diets were largely driven by consumption of kokanee, Black Crappie, and Peamouth Chub (Table 2.3). Additionally, the proportion of macroinvertebrates consumed was an important difference among diets of the CFR compared to all other regions.

Similar to patterns observed across regions, Walleye diets varied among seasons (Appendix C). Except for the least commonly observed prey items (i.e., Tench, Largemouth Bass, Walleye, Gasterosteidae), all taxa identified in Walleye diets were consumed during at least three seasons. Kokanee and Black Crappie were the most frequently observed prey items across seasons, but other taxa were seasonally important (Figure 2.7). For example, *Mysis* was rare and contributed little (by weight) to Walleye diets during the spring, summer, and fall; however, *Mysis* was the third most frequently observed prey item in the winter (Appendix C). Similarly, Yellow Perch contributed 24% of the total energy consumed by Walleyes in the winter but contributed ~1% of the total energy in all other seasons. Kokanee occurred most frequently in all seasons except winter (Figure 2.7) but contributed the highest amount of energy to Walleye diets in all seasons. The SIMPER analysis indicated that consumption of kokanee and Black Crappie was the primary difference in diets across seasons (Table 2.4). However, consumption of Yellow Perch was important for summer and winter, as well as fall and winter comparisons. Similarly, macroinvertebrate consumption was important in the comparisons between spring and all other seasons.

Consistent with patterns across regions and seasons, Walleye diets varied by cohort (Appendix D). Fishes were consumed by all cohorts, but macroinvertebrates were only consumed by a few cohorts. Consumption of fishes by Walleyes increased with age, whereas consumption of macroinvertebrates generally decreased. The 2020 cohort consumed macroinvertebrates and *Mysis* more frequently than all other age classes (Figure 2.8). In general, consumption of catostomids and cyprinids remained consistent across all age classes whereas, consumption of centrarchids and percids decreased with age. In contrast,

consumption of salmonids, particularly kokanee, increased with age. Similarly, kokanee energy contribution to Walleye diets increased with age. In the 2017-2020 cohorts, kokanee represented 0-35% of the total energy consumed by Walleyes. Except the 2012 cohort, kokanee represented 80-100% of the total energy consumed by Walleyes for the 2016 and older cohorts. Similar to the comparisons across seasons and regions, the SIMPER analysis showed that consumption of Black Crappie and kokanee was the primary driver of differences between cohorts. Additionally, consumption of macroinvertebrates and Peamouth Chub was important in differences across cohorts (Table 2.5).

Taxa in the Lake Pend Oreille system had diverse isotopic ratios (Figure 2.9). On average, $\delta^{15}\text{N}$ varied from 7.0‰ to 12.5‰ and $\delta^{13}\text{C}$ varied from -34.1‰ to -23.4‰ for fishes. As expected, zooplankton represented the lowest $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values. Bull Trout generally had the highest $\delta^{15}\text{N}$ and Largemouth Bass had the highest $\delta^{13}\text{C}$. The $\delta^{15}\text{N}$ values of Walleyes (mean \pm SE; 11.7 ± 0.1 ‰) were similar to other piscivores in the system including Bull Trout (12.3 ± 0.2 ‰), Lake Trout (11.2 ± 0.2 ‰), and Smallmouth Bass (10.9 ± 0.1 ‰). Walleye isotopic ratios varied by age (Table 2.6; Figure 2.10). As Walleye age increased, $\delta^{13}\text{C}$ values decreased and $\delta^{15}\text{N}$ increased.

Trophic positions of taxa in the Lake Pend Oreille system varied from 2.0 to 4.2 (Table 2.7). Estimated trophic positions for Largemouth Bass represent juveniles as no adult individuals were sampled. In general, taxa associated with piscivory (e.g., Brown Trout, Bull Trout, Lake Trout, Northern Pikeminnow; Smallmouth Bass, Walleye) were identified at high trophic positions. As expected, estimated trophic positions for juvenile fishes were lower than their adult counterparts. Trophic position of Walleyes increased with age. The minimum trophic position of all Walleyes was 4.4 and the maximum was 6.4 (Table 2.6). For the 2020 cohort, the average trophic position was 4.9 ± 0.1 (mean \pm SE), whereas the average trophic position of the 2009 cohort (the oldest cohort with > 10 samples) was 5.8 ± 0.1 (mean \pm SE). Additionally, variability in trophic position generally decreased with age. The 2019 cohort had the greatest variation in trophic position (range = 1.4) which was approximately double the variation of the 2009 cohort.

Bioenergetics modeling revealed that P_c varied from 0.21 to 0.77 across seasons and cohorts. The 2019 and 2020 cohorts consumed prey items at the greatest proportion of maximum consumption (Figure 2.11). The P_c values of the 2017 and 2018 cohorts were

greatest in the winter. For all other cohorts, P_c values were generally lowest in the fall and highest in the summer. In general, per-capita biomass of prey consumed increased with age of Walleyes. Per-capita biomass of prey consumed by each cohort varied from 473 g to 6,101 g. Kokanee represented between 31% and 77% of the biomass consumed by Walleyes older than the 2019 cohort. The total estimated Walleye abundance was 22,971 individuals (95% CI = 7,774-52,177). Total biomass of kokanee consumed by Walleyes was approximately 24,859 kg (95% CI = 8,413-56,465 kg) which represented approximately 725,654 kokanee (95% CI = 245,581-1,648,271 individuals).

Discussion

The food habits of Walleyes have been extensively studied to provide insight on their ecology and management (e.g., Jackson et al. 1993; Jones et al. 1994; Ward et al. 2007). Specifically, research has focused on potential overlap and competition among piscivores (Swenson and Smith 1976; Forney 1977; Wuellner et al. 2011), prey availability including novel or re-established prey species (Kershner et al. 1999; Fincel et al. 2014), and influence of abiotic conditions (Kocovsky and Carline 2001; Quist et al. 2002, 2003; Massie et al. 2021). As more non-native Walleye populations become established, understanding the direct and indirect effects of Walleyes is critical (Poe et al. 1991; Baldwin et al. 2003; Johnson et al. 2017; Murphy et al. 2021). Results of my research are consistent with other studies of Walleye diets. Not only have Walleye diets been shown to be diverse, but they vary spatially within a system (Bryan et al. 1995; Pothoven et al. 2017; Koenig et al. 2020), temporally (Knight et al. 1984; Liao et al. 2002; Herbst et al. 2016), and by length or age (Jackson et al. 1993; Slipke and Duffy 1997; Liao et al. 2002). Walleyes in the Lake Pend Oreille system exhibited similar variability in diet. Walleye stomachs contained a diversity of prey items, but differences in diets were largely driven by changes in the consumption of kokanee, Black Crappie, and Peamouth Chub. Kokanee was the most frequently consumed prey item, and consumption of kokanee increased with Walleye age. Stable isotopes revealed that Walleyes were at similar trophic levels as other piscivores in the system and an ontogenetic shift toward pelagic prey resources (i.e., kokanee) occurred.

Walleye is recognized as a generalist and can easily switch between prey resources when necessary (Forney 1974; Pothoven et al. 2017; Fincel et al. 2014). In the Lake Pend

Oreille system, Walleye food habits were highly variable among individuals. Typically, food habit studies identify general patterns in populations and variability within individuals is often overlooked. By assessing the energetic contribution of prey types relative to frequency of occurrence, inferring the relevance of a particular prey taxa to individuals is possible (Costello 1990). In the Lake Pend Oreille system, no prey items occurred in more than 50% of Walleye stomachs suggesting that no single prey item was dominant across all sampled individuals. However, the observed consumption of kokanee (23% occurrence, 99% prey-specific energy contribution) suggests that kokanee may become a dominant prey item. Multiple prey items contributed greater than 50% of the prey-specific energy. This pattern is indicative of a mixed-feeding strategy characterized by opportunistic feeding where individual Walleyes specialize on specific prey items (Colby et al. 1979; Schneider et al. 1991; Galarowicz et al 2006; Bozek et al. 2011). Bolnick et al (2003) and Svanbäck and Persson (2004) suggested that individual variation in diets helps to reduce intraspecific competition and results in faster growth and better condition of individuals. Overall, Walleyes in the Lake Pend Oreille system grew consistently throughout the sampling period suggesting that intraspecific competition was likely low. Additionally, plasticity in diets may also help Walleyes respond to shifts in prey availability. Bethke et al. (2012) documented a decrease in trophic position of Walleyes and increased diversity of prey items consumed after extirpation of Gizzard Shad *Dorosoma cepedianum* in two reservoirs in Lancaster County, Nebraska. Similarly, in Seminoe Reservoir, Wyoming, non-native Walleyes depleted populations of native cyprinids, catostomids, and percids (McMillan 1984). Subsequently, Walleye predation on Rainbow Trout increased. Walleyes in the Lake Pend Oreille system consumed greater proportions of Yellow Perch and centrarchids in regions where habitats were seemingly more favorable for these species (i.e., shallow, comparatively warm water temperatures). Similarly, the proportion by weight of kokanee was greatest in LPO-S where kokanee were generally more abundant relative to other regions of the system (Rust et al. 2020).

Walleye consumption varied seasonally. Proportion of maximum consumption was highest in the summer for most cohorts. Only the youngest cohort had a higher P_c in the spring. Higher P_c values are consistent with the period of greatest growth exhibited by Walleyes in the system. This likely reflects increased temperatures at which Walleyes are

more active and can optimize growth (Huh et al. 1976; Kitchell et al. 1977; Paragamian 1989; Struthers et al. 2017). Additionally, the periods of greatest growth and higher P_c values are consistent with the seasons in which kokanee were consumed by Walleyes at the greatest frequencies. Encounter rates between Walleyes and kokanee may simply have been higher in the summer. Kokanee typically inhabit areas near the thermocline and exhibit vertical diel movements (Finnell and Reed 1969; Bevelhimer and Adams 1990; Iida and Mukai 1995). Summer stratification of Lake Pend Oreille occurs between May and September, but a thermocline is typically established by June at a depth of 5-14 m (Caldwell et al. 2015). Most of the Walleyes collected during my research were sampled at depths < 10 m. Although encounter rates may have been higher as a result of abiotic conditions, Walleyes may be actively selecting kokanee as prey. In Lake Erie, temperature was not the underlying reason for seasonal movements of Walleye (Raby et al. 2017). Rather, individual Walleyes followed aggregations of soft-rayed prey fishes such as Rainbow Smelt *Osmerus mordax* and Emerald Shiner *Notropis atherinoides*. Previous research suggests that Walleyes prefer soft-rayed fishes over spiny-rayed fishes (Knight et al. 1984; Hartman and Margraf 1992). Despite the mechanism, research has shown non-native Walleyes negatively affect salmonid fisheries, particularly kokanee populations, via direct predation (McMahon and Bennett 1996). Poe et al. (1991) reported that salmonids were the most important prey item consumed by Walleyes in John Day Reservoir, Oregon. In Lake Roosevelt, Washington, approximately 200 kg of kokanee was consumed by 1,000 Walleyes (~0.2 kg per individual) from June through August (Baldwin et al. 2003). Using the estimated population abundance of Walleyes in the LPO system, my results suggest that Walleyes may consume approximately 24,859 kg (~1.1 kg per individual) of kokanee on an annual basis. In the Lake Pend Oreille system, standardized kokanee sampling showed that estimated kokanee biomass varied from 74-626 mt (mean \pm SE; 226 ± 124 mt) between 1995-2016 (Corsi et al. 2019). The estimated biomass of kokanee consumed by Walleyes represents approximately 10% of the mean annual biomass of kokanee from 1995-2016 and 7-11% of the total estimated biomass of kokanee in 2017 and 2018 (Rust et al. 2020).

Walleyes may have indirect effects on other piscivores in the Lake Pend Oreille system. Declines of salmonid populations after Walleye introductions have been documented in similar systems across the western United States (Scarnecchia et al. 2014; Bell and

Stevens 1984). In Seminoe Reservoir, Wyoming, McMillan (1984) observed decreased body condition of Brown Trout resulting from competition with Walleyes for prey resources. In the Lake Pend Oreille system, multiple studies have identified kokanee as the primary prey resource for piscivores including Bull Trout, Rainbow Trout, Northern Pikeminnow, and Lake Trout (Jeppson and Platts 1959; Wydoski and Bennett 1981; Videgar 2000). Clarke et al. (2005) found that kokanee comprised 50-100% by weight of the annual diet of large Northern Pikeminnow, Rainbow Trout, Lake Trout, and Bull Trout. Similarly, bioenergetics modeling revealed that P_c values were generally higher for Rainbow Trout ($P_c = 0.27-0.43$), Lake Trout ($P_c = 0.45-0.66$), and Bull Trout ($P_c = 0.29-0.46$; Videgar 2000) than the estimated P_c values for Walleyes from my study ($P_c = 0.27-0.34$). This suggests that consumption rates of prey items were slightly higher for other predators (i.e., not Walleyes) relative to their individual metabolic needs and that there is a high potential for competitive interactions among top-level predators. Interestingly, P_c values for Walleyes were most similar to P_c values of Rainbow Trout. Videgar (2000) found that Rainbow Trout consumed approximately 82% of the total number of kokanee consumed by piscivores in the Lake Pend Oreille system (approximately 3,412,465 kokanee). Comparatively, Walleyes consumed approximately 21% of the number of kokanee consumed by Rainbow Trout and 18% of the total estimated number of kokanee consumed by Rainbow Trout, Bull Trout, Lake Trout, and Northern Pikeminnow. This further supports the potential for interspecific competition between piscivores in the Lake Pend Oreille system.

Although the estimated consumption of kokanee by the Walleye population may be compelling, several assumptions were made when estimating the abundance of Walleyes and extrapolating the per-capita consumption to the population. As a result, uncertainty is embedded in the estimates. The first assumption underlying my estimates was that the relationship between density of Walleyes and the CPUE from FWIN (i.e., catchability) in Ontario and Quebec, Canada, waters (Giacomini et al. 2020) was representative of the Lake Pend Oreille system. Catchability varies among waters (e.g., Mogensen et al. 2013; Giacomini et al. 2020; Hansen et al 2023) and is influenced by a suite of abiotic and biotic conditions. For instance, when the catchability estimates from Giacomini et al. (2020) were applied to two Colorado reservoirs, abundance of Walleyes was underestimated by approximately 50% compared to mark-recapture estimates (Hansen et al. 2023). Regardless

of variation among waters, catchability of Walleyes in the Lake Pend Oreille system was likely different than the mean reported by Giacomini et al. (2020), particularly due to differences in lake morphology. For example, the mean depth of the sites in Canada varied from 3-9 m, whereas the mean depth in Lake Pend Oreille is approximately 164 m. Factors such as depth, bathymetry, or water clarity can affect catchability by influencing spatial distribution of fishes (Hamley 1975; Cook and Bergersen 1988; Hillborn and Walters 1992; Casselman 1996). In attempts to minimize the potential influence of differing catchability, I assumed that Walleyes used habitat (i.e., depth) in Lake Pend Oreille typical of other Walleye populations. Thus, I limited the surface area used to represent the area of suitable habitat (~10,000 ha) in concert with the selection of FWIN sampling sites (Ryan et al. 2021). The design used included sites ≤ 15 m deep and the resulting surface area was about one third of the total surface area of Lake Pend Oreille. Although Walleyes are typically associated with depths < 15 m, use of pelagic habitat (depths ≥ 15 m) has been shown to vary (Schlagenhaft and Murphy 1985; Gorman et al. 2019; Matley et al. 2020). Of the Walleyes captured during my research, approximately 5% were caught at depths > 15 m. The limited area used in my abundance estimates may have underestimated Walleye abundance. The second assumption I made related to size selectivity of the gear. Giacomini et al. (2020) used adult Walleyes ≥ 350 mm total length to minimize the effects of gear selectivity. However, I applied the relationship to Walleyes > 230 mm (i.e., age-1 and older individuals). Inherent to this decision is the assumption that selectivity on Walleyes < 350 mm is approximately equal to selectivity on individuals ≥ 350 mm. However, the opposite has been shown (Walker et al. 2013). As a result, the abundance of Walleyes in the Lake Pend Oreille system was likely underestimated.

The final assumptions concern the way in which age structure and diet proportions were summarized. Because of low sample sizes, I did not use region-specific age structure or diet proportions. Instead, I used age structure and diet proportions that were summarized for all individuals collected during the fall. However, the overall proportion of prey items by weight was not necessarily representative of each region (Appendix B). As a result, the number of kokanee consumed was likely overestimated for select regions (i.e., POR). Even if the estimated number of kokanee consumed by Walleyes is an overestimate, the potential effect of Walleyes on the kokanee population is particularly concerning when the length

structure of kokanee consumed is considered. Walleyes consumed kokanee that varied from 40 to 267 mm and length of kokanee consumed increased with Walleye length (Figure 2.12). In the Lake Pend Oreille system, kokanee mature and spawn between age 2 to 4 (i.e., > 170 mm; Whitlock et al. 2018; Rust et al. 2020). In 2018, the abundance of age-2 to age-4 kokanee was approximately 2.6 million fish (Rust et al. 2020). Approximately 40% (~ 290,262 individuals from my estimate) of the kokanee consumed by Walleyes during my study were > 170 mm which represents approximately 11% of the population of spawning kokanee estimated in 2018. Although my estimate contains uncertainty, the estimate illustrates the potential effect of Walleyes on kokanee throughout the system, particularly considering the potential population growth of Walleyes. Catch rates during the 2017 FWIN survey were approximately double those used to estimate Walleye abundance and consumption of kokanee (Ryan et al. 2021). Additionally, the authors concluded that somatic growth, body condition, and age at maturity were at the biological maxima for Walleyes despite increased catch rates from 2011-2017. This suggests that the estimated number of kokanee consumed from my study likely represents only a fraction of the consumption that has previously occurred or may occur in the future. Ultimately, this simulation illustrates the need for continued research to inform management actions.

The current management objectives of the Lake Pend Oreille system include maintaining the kokanee population to support a harvest fishery for kokanee and a trophy fishery for Rainbow Trout, maintain or enhance native Westslope Cutthroat Trout and Bull Trout populations, and provide diverse angling opportunities in Lake Pend Oreille (IDFG 2019). Results from my study suggest that an expanded Walleye population may directly conflict with management objectives because of predation by Walleyes on the kokanee population, as well as competitive interactions between Walleyes and important salmonids. As a method to mitigate the interactions between Walleyes and salmonids, IDFG implemented a tiered removal program using gill nets and incentivized angler harvest in 2017. Thus far, these efforts appear to have had some success in decreasing Walleye abundance in the system, at least in the main body of Lake Pend Oreille (Bouwens et al. 2021). Catch rates of Walleyes decreased in the 2020 FWIN assessment and in the targeted removal efforts since 2017. Although removing individuals from the Walleye population may aide in conserving native salmonid species and maintaining sustainable recreational fisheries,

implementation of suppression programs in large lakes or reservoirs comes with many challenges (Mueller 2005; Loppnow et al. 2013; Zelosko et al. 2016; Courtney 2018; Klein et al. 2022). For example, Kolar et al. (2010) described that the success of suppression programs can be confounded by compensatory changes in survival, recruitment, and growth. In Walleyes, these life history characteristics, particularly recruitment, can be highly variable in self-sustaining populations not subjected to removal efforts (Colby et al. 1979; Honsey et al. 2020). In Lake Pend Oreille, further research evaluating the cause of decreased catch rates (e.g., recruitment variability, decreased abundance) would likely be beneficial in evaluating management efforts. This likely would require increased frequency of FWIN surveys. Additionally, Dux et al. (2019) discussed the importance of understanding the distribution, spawning areas, and population characteristics of the target species to maximize efficiency and success of suppression efforts. In Lake Pend Oreille, some evidence (i.e., higher catch rates, telemetry detections) suggests increased use of LPO-S by Walleyes, particularly during the summer (E. Geisthardt, IDFG, personal communication). Continued monitoring of Walleye movements will likely inform future population estimates by identifying changes in distribution and habitat use. Additionally, my research suggests that catch rates of Walleyes remained high in the Pend Oreille River despite apparent reductions in overall abundance. This suggests that Walleyes may use the Pend Oreille River differently than expected. In particular, a portion of the population may spawn in the areas of the Pend Oreille River that are not targeted during removal efforts. Understanding the use of the Pend Oreille River by the Walleye population will likely provide information regarding additional removal opportunities. Because of the high catch rates in the Pend Oreille River, my estimates of Walleye abundance are highest in the Pend Oreille River, and therefore, influence the estimates of consumption of kokanee. Yet, in the diet analysis, kokanee represented a relatively small proportion of prey items raising questions about use of the Pend Oreille River by kokanee. As such, assessing the interactions between kokanee and Walleyes in the Pend Oreille River appears to be important to further understand the implications of the existing Walleye population.

This study adds to the growing body of literature documenting the effects of non-native Walleye populations in the western United States and has important implications for fisheries managers. Similar to other systems in the West (Poe et al. 1991; Baldwin et al.

2003; Johnson et al. 2017), salmonids, particularly kokanee, were important prey for Walleyes across various spatial and temporal scales in the Lake Pend Oreille system. As Walleye populations continue to expand throughout the West (e.g., colonization of the Columbia and Snake rivers), co-occurrence with vulnerable salmonids has exposed juveniles to higher predation risk and adults to increased competition (Murphy et al. 2021). Since many salmonid populations are supported through hatchery supplementation programs, increased abundances of established and novel non-native predators may inhibit the success of supplementation and reduce angling opportunities. This study provides evidence that introductions of non-native species continue to pose a challenge to fisheries management and emphasizes the importance of understanding how non-native species interact with their environment.

References

- Amundsen, P. A., H. M. Gabler, and F. J. Staldvik. 1996. A new approach to graphical analysis of feeding strategy from stomach contents data – modification of the Costello (1990) method. *Journal of Fish Biology* 48:607-614.
- Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32-46.
- Anderson, M. J., and D. C. I. Walsh. 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? *Ecological Monographs* 83:557-574.
- Antolos, M., D. D. Roby, and D. E. Lyons. 2005. Caspian Tern predation on juvenile salmonids in the mid-Columbia River. *Transactions of the American Fisheries Society* 134:466-480.
- Baldwin, C. M., J. G. McLellan, M. C. Polacek, and K. Underwood. 2003. Walleye predation on hatchery releases of kokanees and Rainbow Trout in Lake Roosevelt, Washington. *North American Journal of Fisheries Management* 23:660-667.
- Baranowska, K., and M. D. Robinson. 2017. Lake Koocanusa food web. Final report to the B.C. Ministry of Environment, Victoria, Canada.
- Barton, B. A. 2011. Biology, management, and culture of Walleye and Sauger. American Fisheries Society, Bethesda, Maryland.
- Bell, R. J., and J. Stevens. 1984. Salmon Falls Creek Reservoir and stream investigations. Idaho Department of Fish and Game, Federal Aid to Fish and Wildlife Restoration, Project F-53-R-11, Job Performance Report, Boise.
- Bethke, B. J., J. A. Vandehey, M. J. Fincel, B. D. S. Graeb, and M. T. Porath. 2012. Walleye trophic position before and after a Gizzard Shad extirpation. *The Prairie Naturalist* 44:72-78.
- Bevelhimer, M. S., and S. M. Adams. 1990. A bioenergetics analysis of diel vertical migration by kokanee salmon *Oncorhynchus nerka*. *Canadian Journal of Fisheries and Aquatic Sciences* 50:2336-2349.
- Billington, N., C. C. Wilson, and B. L. Sloss. 2011. Distribution and genetics of Walleye and Sauger. Pages 105-132 in B. A. Barton, editor. Biology, management, and culture of Walleye and Sauger. American Fisheries Society, Bethesda, Maryland.

- Blackwell, T., A. G. P. Ford, A. G. Ciezarek, S. J. Bradbeer, C. A. Gracida Juarez, B. P. Ngatunga, A. H. Shechonge, R. Tamatamah, G. Etherington, W. Haerty, F. Di Palma, G. F. Turner, and M. J. Genner. 2020. Newly discovered cichlid fish biodiversity threatened by hybridization with non-native species. *Molecular Ecology* 30:895-911.
- Blanc, G. 1997. Introduced pathogens in European aquatic ecosystems: theoretical aspects and realities. *Bulletin Français de la Pêche et de la Pisciculture* 344:489-513.
- Boecklen, W. J., C. T. Yarnes, B. A. Cook, and A. C. James. 2011. On the use of stable isotopes in trophic ecology. *Annual Review of Ecology, Evolution, and Systematics* 42:411-440.
- Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L. Forister. 2003. The ecology of individuals. Incidence and implications of individual specialization. *The American Naturalist* 161:1-28.
- Bonato, K. O., R. L. Delariva, and J. C. da Silva. 2012. Diet and trophic guilds of fish assemblages in two streams with different anthropic impacts in the northwest of Paraná, Brazil. *Zoologia* 29:27-38.
- Bouwens, K. A., J. Strait, P. Rust, R. Ryan, A. L. Ransom, and R. Jakubowski. 2021. 2020 Lake Pend Oreille predator management program annual project update. Annual Report to Avista, Noxon, Montana, and Idaho Department of Fish and Game, Boise.
- Bozek, M. A., D. A. Baccante, and N. P. Lester. 2011. Walleye and Sauger life history. Pages 223-301 in B. A. Barton, editor. *Biology, management, and culture of Walleye and Sauger*. American Fisheries Society, Bethesda, Maryland.
- Brenna, J. T., T. N. Corso, H. J. Tobias, and R. J. Caimi. 1997. High-precision continuous-flow isotope ratio mass spectrometry. *Mass Spectrometry Reviews* 16:227-258.
- Broughton, N. M., and A. M. Fisher. 1981. A comparison of three methods of pike *Esox lucius* removal from a lowland trout fishery. *North American Journal of Fisheries Management* 12:101-106.
- Bryan, S. D. 1995. Bioenergetics of Walleye in Lake Oahe, South Dakota. Master's thesis. South Dakota State University, Brookings.
- Caldwell, T. J., and F. M. Wilhelm. 2012. The life history characteristics, growth and density of *Mysis diluviana* in Lake Pend Oreille, Idaho, USA. *Journal of Great Lakes Research* 38:58-67.

- Caldwell, T. J., F. M. Wilhelm, and A. Dux. 2015. Non-native pelagic macro-invertebrate alters population dynamics of herbivorous zooplankton in a large deep lake. *Canadian Journal of Fisheries and Aquatic Sciences* 73:832-843.
- Carlander, K. D. 1997. *Handbook of Freshwater Fishery Biology*, Vol. 3: life history data on ichthyopercid and percid fishes of the United States and Canada. Iowa State University Press. Ames.
- Cerino, D., A. S. Overton, J. A. Rice, and J. A. Morris Jr. 2013. Bioenergetics and trophic impacts of the invasive Indo-Pacific Lionfish. *Transactions of the American Fisheries Society* 142:1522-1534.
- Chipps, S. R., and J. E. Garvey. 2006. Assessment of food habits and feeding patterns. Pages 473-514 in C. S. Guy, and M. L. Brown, editors. *Analysis and interpretation of freshwater fisheries data*. American Fisheries Society, Bethesda, Maryland.
- Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:117-143.
- Clarke, L. R., D. T. Videgar, and D. H. Bennett. 2005. Stable isotopes and gut content show diet overlap among native and introduced piscivores in a large oligotrophic lake. *Ecology of Freshwater Fish* 14:267-277.
- Colby, P. J., R. E. McNicol, and R. A. Ryder. 1979. Synopsis and biological data on the Walleye *Stizostedion v. vitreum* (Mitchill 1818). Food and Agriculture Organization of the United Nations Fisheries Synopsis 119.
- Conover, G., R. Simmonds, and M. Whalen, (editors). 2007. Management and control plan for Bighead, Black, Grass, and Silver carps in the United States. Report to the Aquatic Nuisance Species Task Force, Washington D. C.
- Coplen, T. B. 1994. Reporting of stable hydrogen, carbon, and oxygen isotopic abundances. *Pure and Applied Chemistry* 66:273-276.
- Costello, M. J. 1990. Predator feeding strategy and prey importance: a new graphical analysis. *Journal of Fish Biology* 36:261-263.
- Courtenay, W. R., Jr., D. A. Hensley, J. N. Taylor, and J. A. McCann. 1986. Distribution of exotic fishes in North America. Pages 675-689 in D. H. Hocutt and E. O. Wiley, editors. *The zoogeography of North American freshwater fishes*. John Wiley and Sons, New York.

- Courtney, M. B., E. R. Schoen, A. Wizik, P. A. H. Westley. 2018. Quantifying the net benefits of suppression: truncated size structure and consumption of native salmonids by invasive Northern Pike in an Alaska lake. *North American Journal of Fisheries Management* 38:1306-1315.
- Cummins, K. W., and J. C. Wuycheck, 1971. Caloric equivalents for investigations in ecological energetics. *Internationale Vereinigung fur Theoretische und Angewandte Limnologie*.
- Cucherousset, J., and J. D. Olden. 2011. Ecological impacts of non-native freshwater fishes. *Fisheries* 36:215-230.
- Deslauriers, D., S. R. Chipps, J. E. Breck, J. A. Rice, and C. P. Madenjian. 2017. Fish bioenergetics 4.0: an R – based modeling application. *Fisheries* 42:586-596.
- DeNiro, M. J., and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* 42:495-506.
- Dunham, J. B., S. B. Adams, R. E. Schroeter, and D. C. Novinger. 2002. Alien invasions in aquatic ecosystems: toward an understanding of Brook Trout invasions and potential impacts on inland Cutthroat Trout in western North America. *Reviews in Fish Biology and Fisheries* 12:373-391.
- Dux, A. M., M. J. Hansen, M. P. Corsi, N. H. Wahl, J. P. Fredericks, C. E. Corsi, D. J. Schill, and N. J. Horner. 2019. Effectiveness of Lake Trout (*Salvelinus namaycush*) suppression in Lake Pend Oreille, Idaho: 2006-2016. *Hydrobiologia* 840:319-333.
- Field-Dodgson, M. S. 1987. The effect of salmon redd excavation on stream substrate and benthic community of two salmon spawning streams in Canterbury, New Zealand. *Hydrobiologia* 154:3-11.
- Fincel, M. J., D. J. Dembkowski, and S. R. Chipps. 2014. Influence of variable Rainbow Smelt and Gizzard Shad abundance on Walleye growth. *Lakes and Reservoir Management* 30:258-267.
- Finnel, L. M., and E. B. Reed. 1969. The diel vertical movements of kokanee salmon *Oncorhynchus nerka*, in Granby Reservoir, Colorado. *Transactions of the American Fisheries Society* 2:245-252.

- Forney, J. L. 1974. Interactions between Yellow Perch abundance, Walleye predation, and survival of alternate prey in Oneida Lake, New York. *Transactions of the American Fisheries Society* 103:15-24.
- Forney, J. L. 1977. Evidence of inter- and intraspecific competition as factors regulating Walleye (*Stizostedion vitreum vitreum*) biomass in Oneida Lake, New York. *Journal of the Fisheries Board of Canada* 34:1812-1820.
- Frost, C. N. 2000. A key for identifying preyfish in the Columbia River based on diagnostic bones. Report to U.S. Geological Survey, Cook, Washington.
- Fuller, P. L., L. G. Nico, and J. D. Williams. 1999. Non-indigenous fishes introduced into inland water of the United States. American Fisheries Society, Special Publication 27, Bethesda, Maryland.
- Galarowicz, T. L., J. A. Adams, and D. H. Wahl. 2006. The influence of prey availability on ontogenetic diet shifts of a juvenile piscivore. *Canadian Journal of Fish and Aquatic Sciences* 63:1722-1733.
- Giacomini, H. C., N. P. Lester, P. Addison, S. Sandstrom, D. Nadeau, C. Chu, and D. R. De Kerckove. 2020. Gillnet catchability of Walleye (*Sander vitreus*): comparison of North American and provincial standards. *Fisheries Research* 224:105433.
- Goldschmidt, T., F. Witte, and J. Wanink. 1993. Cascading effects of the introduced Nile Perch on the detritivorous/phtoplanktivorous species in the sublittoral areas of Lake Victoria. *Conservation Biology* 7:686-700.
- Gorman, A. M., R. T. Kraus, L. F. G. Gutowsky, C. S. Vandergoot, Y. Zhao, C. T. Knight, M. D. Faust, T. A. Hayden, and C. C. Krueger. 2019. Vertical habitat use by adult Walleyes conflicts with expectations from fishery-independent surveys. *Transactions of the American Fisheries Society* 148:592-604.
- Gozlan, R. E., S. St-Hilaire, S. W. Feist, P. Martin, and M. L. Kent. 2005. Biodiversity – disease threat to European fish. *Nature* 435:1046.
- Gozlan, R. E. 2008. Introduction of non-native freshwater fish: is it all bad? *Fish and Fisheries* 9:106-115.
- Gozlan, R. E., J. R. Britton, I. Cowx, and G. H. Copp. 2010. Current knowledge on non-native freshwater fish introductions. *Journal of Fish Biology* 76:751-786.

- Gutiérrez, J. L. 2017. Modification of habitat quality by non-native species. Pages 33-47 in M. Vila and P. Hulme, editors. Impact of biological invasions on ecosystem services. Springer, New York.
- Hansen, A. G., M. W. Miller, E. T. Cristan, C. J. Farrell, P. Winkle, M. M. Brandt, K. D. Battige, and J. M. Lepak. 2023. Gill net catchability of Walleye (*Sander vitreus*): are provincial standards suitable for estimating adult density outside the region? Fisheries Research 266:article 106800. DOI: 10.1016/j.fishres.2023.106800.
- Hansen, M. J., D. Boisclair, S. P. Brandt, S. W. Hewett, J. F. Kitchell, M. C. Lucas, and J. L. Ney. 1993. Applications of bioenergetics models to fish ecology and management: where do we go from here? Transactions of the American Fisheries Society 122:1019-1030.
- Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish bioenergetics 3.0. University of Wisconsin Sea Grant Institute, Madison.
- Hartman, K. J., and S. B. Brandt. 1995. Predatory demand and impact of Striped Bass, Bluefish, and Weakfish in the Chesapeake Bay: applications of bioenergetics models. Canadian Journal of Fisheries and Aquatic Sciences 52:1667-1687.
- Herbst, S. J., B. M. Roth, D. B. Hayes, and J. D. Stockwell. 2016. Walleye foraging ecology in an interconnected chain of lakes influenced by nonnative species. Transactions of the American Fisheries Society 145:319-333.
- Hoagstrom, C. W., and C. R. Berry, Jr. 2010. The native range of Walleyes in the Missouri River drainage. North American Journal of Fisheries Management 30:642-654.
- Honsey, A. E., Z. S. Feiner, and G. J. A. Hansen. 2020. Drivers of Walleye recruitment in Minnesota's large lakes. Canadian Journal of Fisheries and Aquatic Sciences 77:1921-1933.
- Huh, H. T., H. E. Calbert, and D. A. Stuibler. 1976. Effect of temperature and light on growth of Yellow Perch and Walleye using formulated feed. Transactions of the American Fisheries Society 105:254-258.
- IDFG (Idaho Department of Fish and Game). 2017. Idaho State Wildlife Action Plan, 2015. Report to US Fish and Wildlife Service, Wildlife and Sport Fish Restoration Program, Portland, Oregon.

- IDFG (Idaho Department of Fish and Game). 2019. Fisheries Management Plan 2019 – 2024. Idaho Department of Fish and Game, Boise.
- Iida, K., and T. Mukai. 1995. Behavior of kokanee *Oncorhynchus nerka* in Lake Kuttara observed by echo sounder. *Fisheries Science* 61:641-646.
- Irons, K. S., G. G. Sass, M. A. McClelland, and J. D. Stafford. 2007. Reduced condition factor of two native fish species coincident with invasion of non-native Asian carps in the Illinois River, U.S.A. Is this evidence for competition and reduced fitness? *Journal of Fish Biology* 71:258-273.
- Jackson, J. J., D. W. Willis, and D. G. Fielder. 1993. Changes in Walleye food habits throughout Lake Oahe, South Dakota, in August 1991. *Journal of Freshwater Ecology* 25:331-340.
- Jeppson, P. W., and W. S. Platts. 1959. Ecology and control of the Columbia squawfish in northern Idaho lakes. *Transactions of the American Fisheries Society* 88:197-202.
- Jeschke, J. M., S. Bacher, T. M. Blackburn, J. T. A. Dick, F. Essl, T. Evans, M. Gaertner, P. E. Hulme, I. Kuhn, A. Mrugala, J. Pergl, P. Pyšek, W. Rabitsch, A. Ricciardi, D. M. Richardson, A. Sendek, M. Vilà, M. Winter, and S. Kumschick. 2014. Defining the impact of non-native species. *Conservation Biology* 5:1188-1194.
- Johnson, B. M., P. J. Martinez, J. A. Hawkins, and K. R. Bestgen. 2008. Ranking predatory threats by nonnative fishes in the Yampa River, Colorado, via bioenergetics modeling. *North American Journal of Fisheries Management* 58:1941-1953.
- Johnson, B. M., R. Arlinghaus, and P. J. Martinez. 2009. Are we doing all we can to stem the tide of illegal fish stocking? *Fisheries* 34:389-394.
- Johnson, C. F., B. M. Johnson, T. E. Neebling, and J. C. Burckhardt. 2017. Walleye introduction eliminates predation refuge for adfluvial Cutthroat Trout and Rainbow Trout. *Transactions of the American Fisheries Society* 146:252-267.
- Jones, M. S., J. P. Goettle Jr., and S. A. Flinckinger. 1994. Changes in Walleye food habits and growth following a Rainbow Smelt introduction. *North American Journal of Fisheries Management* 14:237-465.
- Kamler, E., and J. Stachowiak. 1992. Egg size and reproductive effort in Tench females from heated waters. *Polish Archives of Hydrobiology* 39:101-107.

- Keller, K., and C. Brown. 2008. Behavioural interactions between the introduced Plague Minnow *Gambusia holbrooki* and the vulnerable native Australian Ornate Rainbowfish *Rhadinocentrus ornatus*, under experimental conditions. *Journal of Fish Biology* 73:1714-1729.
- Kershner, M. W., D. M. Schael, R. L. Knight, R. A. Stein, and E. A. Marschall. 1999. Modeling sources of variation for growth and predatory demand of Lake Erie Walleye (*Stizostedion vitreum*), 1986-1995. *Canadian Journal of Fisheries and Aquatic Sciences* 56:527-538.
- Kitchell, J. F., D. J. Stewart, and D. Weininger. 1977. Applications of a bioenergetics model to Yellow Perch (*Perca flavescens*) and Walleye (*Stizostedion vitreum vitreum*). *Journal of Fisheries Research Board of Canada* 34:1922-1935.
- Klein, Z. B., M. C. Quist, and C. S. Guy. 2022. Suppression of invasive fish in the West: synthesis and suggestions for improvement. *North American Journal of Fisheries Management* 43:369-383.
- Knight, R. L., F. J. Margraf, and R. F. Carline. 1984. Piscivory by Walleyes and Yellow Perch in western Lake Erie. *Transactions of the American Fisheries Society* 113:677-693.
- Koch, J. D., and M. C. Quist. 2007. A technique for preparing fin rays and spines for age and growth analysis. *North American Journal of Fisheries Management* 27:782-784.
- Kocovsky, P. M., and R. F. Carline. 2001. Influence of extreme temperatures on consumption and condition of Walleyes in Pymatuning Sanctuary, Pennsylvania. *North American Journal of Fisheries Management* 21:198-207.
- Koehn, J. D. 2004. Carp (*Cyprinus carpio*) as a powerful invader in Australian waterways. *Freshwater Biology* 49:882-894.
- Koenig, L. 2020. Food web interactions among Walleye, Lake Whitefish, and Yellow Perch in Green Bay, Lake Michigan. M.S. Thesis, University of Wisconsin, Stevens Point.
- Kolar, C. S., W. R. Courtenay Jr., and L. G. Nico. 2010. Managing undesired and invading fishes. Pages 213-249 in W. A. Hubert and M. C. Quist, editors. *Inland fisheries management in North America*, 3rd edition. American Fisheries Society, Bethesda, Maryland.

- Lasenby, D. C., T. Northcote, and 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.
- Leslie Jr., A. J., J. R. Cassani, and R. J. Wattendorf. 1996. An introduction to Grass Carp biology and history in the United States. Pages 1-39 *in* J. R. Cassani, editor. *Managing aquatic vegetation with Grass Carp, a guide for water resource managers*. American Fisheries Society, Bethesda, Maryland.
- Liao, H., C. L. Pierce, and J. G. Larschedi. 2004. Consumption dynamics of the adult piscivorous fish community in Spirit Lake, Iowa. *North American Journal of Fisheries Management* 24:890-902.
- Linn, J. D., and T. C. Frantz. 1964. Introduction of the Opossum Shrimp (*Mysis relicta* Loven) into California and Nevada. *California Fish and Game* 51:48-51.
- Loboschefskey, E., G. Benigno, T. Sommer, K. Rose, T. Ginn, A. Massoudieh, and F. Loge. 2012. Individual-level and population-level historical prey demand of San Francisco estuary Striped Bass using a bioenergetics model. *San Francisco Estuary and Watershed Science* 10:1-23.
- Loppnow, G. L., K. Vaxcotto, and P. A. Venturelli. 2013. Invasive Smallmouth Bass (*Micropterus dolomieu*): history, impacts, and control. *Management of Biological Invasions* 4:191-206.
- Lowery, E. D., and D. A. Beauchamp. 2015. Trophic ontogeny of fluvial Bull Trout and seasonal predation on Pacific salmon in a riverine food web. *Transactions of the American Fisheries Society* 144:724-741.
- Maiolie, M. A., W. Harryman, and W. J. Ament. 2004. Lake Pend Oreille fishery recovery project. Annual progress report to Bonneville Power Administration, Report number 04-24, Idaho Department of Fish and Game, Boise.
- Massie, D. L., G. J. A. Hansen, Y. Li, G. G. Sass, and T. Wagner. 2021. Do lake-specific characteristics mediate the temporal relationship between Walleye growth and warming temperatures? *Canadian Journal of Fisheries and Aquatic Sciences* 78:913-923.
- Matley, J. K., M. D. Faust, G. D. Raby, Y. Zhao, J. Robinson, T. MacDougall, T. A. Hayden, A. T. Fisk, C. S. Vandergoot, and C. C. Kreuger. 2020. Seasonal habitat-use

- differences among Lake Erie's Walleye stocks. *Journal of Great Lakes Research* 46:609-621.
- McIntosh, A. R., and C. R. Townsend. 1996. Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish-induced changes to grazer behaviour. *Oecologia* 108:174-181.
- McIntyre, P. B., E. Michel, and M. Olsgard. 2006. Top-down and bottom-up controls on periphyton biomass and productivity in Lake Tanganyika. *Limnology and Oceanography* 51:1514-1523.
- McKelvey, K. S., M. K. Young, T. M. Wilcox, D. M. Bingham, K. L. Pilgrim, and M. K. Schwartz. 2016. Patterns of hybridization among Cutthroat Trout and Rainbow Trout in northern Rocky Mountain streams. *Ecology and Evolution* 6:688-706.
- McMahon, T. E., and D. H. Bennet. 1996. Walleye and Northern Pike: boost or bane to northwest fisheries? *Fisheries* 21:6-13.
- McMillan, J. 1984. Evaluation and enhancement of the trout and Walleye fisheries in the North Platte River system of Wyoming with emphasis on Seminoe Reservoir. Final Report to Wyoming Game and Fish Department, Laramie.
- Minton, J. W., and McLean, R. B. 1982. Measurements of growth and consumption of Sauger (*Stizostedion canadense*): implications for fish energetics studies. *Canadian Journal of Fisheries and Aquatic Sciences* 39:1396-1403.
- Morgan, G. E. 2002. Manual of instructions – fall Walleye index netting (FWIN). Ontario Ministry of Natural Resources, Peterborough.
- Moyle, P.B. 1986. Fish introductions into North America: patterns and ecological impact. Pages 27-43 in H. A. Mooney and J. A. Drake, editors. *Ecology of biological invasions of North America and Hawaii*. Ecological Studies, Volume 58, Springer, New York.
- Moyle, P. B., and T. Light. 1996. Biological invasions of fresh water: empirical rules and assembly theory. *Biological Conservation* 78:149-161.
- Mueller, G. A. 2005. Predatory fish removal and native fish recovery in the Colorado River mainstem: what have we learned? *Fisheries* 30:10-19.
- Muhlfeld, C. C., D. H. Bennett, R. K. Steinhorst, B. Marotz, and M. Boyer. 2008. Using bioenergetics modeling to estimate consumption of native juvenile salmonids by

- nonnative Northern Pike in the upper Flathead River system, Montana. *North American Journal of Fisheries Management* 28:636-648.
- Murphy, C. A., J. D. Romer, K. Stretz, I. Arismendi, R. Emig, F. Monzyk, and S. L. Johnson. 2021. Damming salmon fry: evidence for predation by non-native warmwater fishes in reservoirs. *Ecosphere* 12:1-17.
- Ney, J. J. 1993. Bioenergetics modeling today: growing pains on the cutting edge. *Transactions of the American Fisheries Society* 122:736-748.
- Northcote, T. G. 1973. Some impacts of man on Kootenay Lake and its salmonids. Report to Great Lakes Fishery Commission, Technical Report No. 25, Ann Arbor, Michigan.
- Ogutu-Ohwayo, R. 1990. The reduction in fish species diversity in Lakes Victoria and Kyoga (East Africa) following human exploitation and introduction of non-native fishes. *Journal of Fish Biology* 37:207-208.
- Olson, M. H., and B. P. Young. 2003. Patterns of diet and growth in co-occurring populations of Largemouth and Smallmouth Bass. *Transactions of the American Fisheries Society* 132:1207-1213.
- Paragamian, V. L. 1989. Seasonal habitat use by Walleye in a warmwater river system as determined by radio telemetry. *North American Journal of Fisheries Management* 9:392-401.
- Paul, A. J., and J. R. Post. 2001. Spatial distribution of native and nonnative salmonids in streams of the eastern slopes of the Canadian Rocky Mountains. *Transactions of the American Fisheries Society* 130:417-430.
- Pelicice, F. M., and A. A. Agostinho. 2009. Fish fauna destruction after the introduction of a non-native predator (*Cichla kelberi*) in a Neotropical reservoir. *Biological Invasions* 11:1789-1801.
- Pierce, P. C., and M. J. Van Den Avyle. 1997. Hybridization between introduced Spotted Bass and Smallmouth Bass in reservoirs. *Transactions of the American Fisheries Society* 126:939-947.
- Poe, T. P., H. C. Hansel, S. Vigg, D.E. Palmer and L.A. Prendergast. 1991. Feeding of predaceous fishes on out-migrating juvenile salmonids in John Day Reservoir, Colombia River. *Transactions of the American Fisheries Society* 120:405-420.

- Pope, K. L., M. L. Brown, W. G. Duffy, and P. H. Michaletz. 2001. A caloric-based evaluation of diet indices for Largemouth Bass. *Environmental Biology of Fishes* 61:329-339.
- Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83:703-718.
- Post, D. M., C. A. Layman, D. A. Arrington, G. Takimoto, J. Quattrochi, and C. G. Montaña. 2007. Getting to the fat of the matter: models, methods, and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* 152:179-189.
- Pothoven, S. A., C. P. Madenjian, and T. O. Höök. 2017. Feeding ecology of the Walleye (*Percidae*, *Sander vitreus*), a resurgent piscivore in Lake Huron (Laurentian Great Lakes) after shifts in the prey community. *Ecology of Freshwater Fish* 56:676-685.
- Prenter, J. C., J. MacNeil, T. A. Dick, and A. M. Dunn. 2004. Roles of parasites in animal invasions. *Trends in Ecology and Evolution* 19:385-390.
- Probst, W. E., C. F. Rabeni, W. G. Covington, and R. E. Marteney. 1984. Resource use by stream-dwelling Rock Bass and Smallmouth Bass. *Transactions of the American Fisheries Society* 113:283-294.
- Qi, H., T. B. Coplen, H. Geilmann, W. A. Brand, and J. K. Böhlke. 2003. Two new organic reference materials for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements and a new value for the $\delta^{13}\text{C}$ of NBS 22 oil. *Rapid Communications in Mass Spectrometry* 17:2483-2487
- Quist, M. C., C. S. Guy, R. J. Bernot, and J. L. Stephen. 2002. Seasonal variation in condition, growth, and food habits of Walleye in a Great Plains reservoir and simulated effects of an altered thermal regime. *Journal of Fish Biology* 61:1329-1344.
- Raby, G. D., C. S. Vandergoot, T. A. Hayden, M. D. Faust, R. T. Kraus, J. M. Dettmers, S. J. Cooke, Y. Zhao, A. T. Fisk, and C. C. Krueger. 2018. Does behavioural thermoregulation underlie seasonal movements in Lake Erie Walleye? *Canadian Journal of Fisheries and Aquatic Sciences* 75:488-496
- Rahel, F. J. 1997. From Johnny Appleseed to Dr. Frankenstein: changing values and the legacy of fisheries management. *Fisheries* 22:8-9.
- Rahel, F. J. 2000. Homogenization of fish faunas across the United States. *Science* 288:854-856.

- Rahel, F. J. 2004. Unauthorized fish introductions: fisheries management of the people, for the people, or by the people. *American Fisheries Society Symposium* 44:431-443.
- Rahel, F. J. and M. A. Smith. 2018. Pathways of unauthorized fish introductions and types of management responses. *Hydrobiologia* 817:41-56.
- Ransom, A. L. 2022. 2018 and 2021 Lower Clark Fork River salmonid abundance monitoring project annual project update. Annual report to Avista, Noxon, Montana, and Idaho Department of Fish and Game, Boise.
- R Core Team. 2022. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada*. Ottawa, Canada.
- Rodger, A. W., S. L. Wolf, T. A. Starks, J. P. Burroughs, and S. K. Brewer. 2021. Seasonal diet and habitat use of large, introduced Rainbow Trout in an Ozark highland stream. *North American Journal of Fisheries Management* 41:1764-1780.
- Rust, P., N. G. Mucciarone, S. M. Wilson, M. P. Corsi, and W. H. Harryman. 2020. Lake Pend Oreille research, 2017 and 2018: Lake Pend Oreille fishery recovery project. Idaho Department of Fish and Game. Annual Report to Bonneville Power Administration, Project 1994-047-00. Portland, Oregon.
- Ryan, R. G., M. P. Corsi, and P. Rust. 2021. Characteristics of an introduced Walleye population with implications for suppression. *North American Journal of Fisheries Management* 41:1863-1877.
- Scarnecchia, D. L., Y. Lim, S. P. Moran, T. D. Tholl, J. M. Dos Santos, and K. Breidinger. 2014. Novel fish communities: native and non-native species trends in two run-of-the-river reservoirs, Clark Fork River, Montana. *Reviews in Fisheries Science and Aquaculture* 22:97-111.
- Schlagenhaft, T. W., and B. R. Murphy. 1985. Habitat use and overlap between adult Largemouth Bass and Walleye in a west Texas reservoir. *North American Journal of Fisheries Management* 5:465-470.
- Schneider, J. C., T. J. Lychwick, E. J. Trimmerger, J. H. Peterson, R. O'Neal, and P. J. Schneeberger. 1991. Walleye rehabilitation in Lake Michigan, 1969-1989. Pages 23-61 in P. J. Colby, C. S. Lewis, and R. L. Eshenroder, editors. *Status of Walleye in the*

- Great Lakes: case studies prepared for the 1989 workshop. Great Lakes Fisheries Commission, Special Publication 91-1, Ann Arbor, Michigan
- Schoby, G. P., T. P. Bassista, and M. A. Maiolie. 2007. Effects of higher winter water levels on the Pend Oreille River fish community: Lake Pen Oreille fishery recovery project. Annual report to Bonneville Power Administration, Project 1997-047-00. Portland, Oregon.
- Schultz, L. D., M. P. Heck, B. M. Kowalski, C. A. Eagles-Smith, K. Coates, and J. B. Dunham. 2017. Bioenergetics models to estimate numbers of larval Lampreys consumed by Smallmouth Bass in Elk Creek, Oregon. *North American Journal of Fisheries Management* 37:714-723.
- Scott, W. B., and W. J. Crossman. 1973. *Freshwater fishes of Canada*. Fisheries Research Board of Canada, Ottawa.
- Simberloff, D. 2003. How much information on population biology is needed to manage introduced species? *Conservation Biology* 17:83-92.
- Slipke, J. W., and W. G. Duffy. 1997. Food habits of Walleye in Shadehill Reservoir, South Dakota. *Journal of Freshwater Ecology* 12:11-17.
- Smith, C. D., J. R. Fishcer, and M. C. Quist. 2014. Historical changes in Nebraska's lotic fish assemblages: implications of anthropogenic alterations. *American Midland Naturalist* 172:160-184.
- Spencer, C. N., B. R. McClelland, and J. A. Stanford. 1991. Shrimp stocking, salmon collapse, and eagle displacement. *Bioscience* 41:14-21.
- Stroud, A. G., and A. T. Scholz. 2014. A dichotomous key for the identification of nine salmonids of the inland northwest using six diagnostic skull bones: and associated equations to estimate total length and weight from bones ingested by piscivores or found in archeological sites. Biology Faculty Publications, Eastern Washington University, Cheney.
- Struthers, D. P., L. F. G. Gutowsky, E. C. Enders, K. E. Smokorowski, D. A. Watkinson, A. T. Silva, M. Cvetkovic, E. Bibeau, and S. J. Cooke. 2017. Factors influencing the spatial ecology of Lake Sturgeon and Walleye within an impounded reach of the Winnipeg River. *Environmental Biology of Fishes* 100:1085-1103.

- Svanbäck, R., and L. Persson. 2004. Individual diet specialization, niche width and population dynamics: implications for trophic polymorphisms. *Journal of Animal Ecology* 73:973-982.
- Swenson, W. A., and L. L. Smith, Jr. 1976. Influence of food competition, predation, and cannibalism on Walleye (*Stizostedion vitreum vitreum*) and Sauger (*S. canadense*) populations in Lake of the Woods, Minnesota. *Journal of the Fisheries Research Board of Canada* 33:1946-1954.
- Traynor, D., A. Moerke, and R. Greil. 2010. Identification of Michigan fishes using cleithra. Great Lakes Fishery Commission Miscellaneous Publication 2010-02.
- Vidregar, D. T. 2000. Population estimates, food habits and estimates of consumption of selected predatory fishes in Lake Pend Oreille, Idaho. Master's thesis. University of Idaho, Moscow.
- Wallace, R. L., and D. W. Zaroban. 2013. Native fishes of Idaho. American Fisheries Society. Bethesda, Maryland.
- Walrath, J. D., M. C., Quist, and J. A. Firehammer. 2015. Trophic ecology of nonnative Northern Pike and their effect on conservation of native Westslope Cutthroat Trout. *North American Journal of Fisheries Management* 35:158-177.
- Ward, M. C., D. W. Willis, B. R. Herwig, S. R. Chipps, B. G. Parsons, J. R. Reed, and M. A. Hanson. 2007. Consumption estimates of Walleye stocked as fry to suppress Fathead Minnow populations in west-central Minnesota wetlands. *Ecology of Freshwater Fish* 17:59-70.
- Whitlock, S. L., M. R. Campbell, M. C. Quist, and A. M. Dux. 2018. Using genetic and phenotypic comparisons to evaluate apparent segregation among kokanee spawning groups. *Transactions of the American Fisheries Society* 147:43-60.
- Wissing, T. E. 1974. Energy transformations by young-of-the-year White Bass *Morone chrysops* (Rafinesque) in Lake Mendota, Wisconsin. *Transaction of the American Fisheries Society* 103:32-37.
- Witte, F., T. Goldschmidt, P. C. Goudswaard, W. Ligtoet, M. J. P. van Oijen, and J. H. Wanink. 1992. Species extinction and concomitant ecological changes in Lake Victoria. *Netherlands Journal of Zoology* 42:214-232.

- Woods, P. F. 2004. Role of limnological processes in fate and transport of nitrogen and phosphorous loads delivered into Coeur d'Alene Lake and Lake Pend Oreille, Idaho, and Flathead Lake, Montana. U.S. Geological Survey Professional Paper 1682, Washington, D.C.
- Wuellner, M. R., D. W. Willis, B. G. Blackwell, and J. P. Lott. 2011. Empirical assessment of potential interactions between Walleye and Smallmouth Bass. *Journal of Applied Ichthyology* 27:1173-1180.
- Wydoski, R. S. and R. R. Whitney. 2003. *Inland fishes of Washington: second edition, revised and expanded*. University of Washington Press. Seattle.
- Yasuno, N., Y. Chiba, K. Shindo, Y. Fujimoto, T. Shimada, S. Shikano, and E. Kikuchi. 2012. Size-dependent ontogenetic shifts to piscivory documented from stable isotope analyses in an introduced population of Largemouth Bass. *Environmental Biology of Fishes* 93:255-266.
- Yule, D. L., and C. Luecke. 1993. Lake Trout consumption and recent changes in the fish assemblage of Flaming Gorge Reservoir. *Transactions of the American Fisheries Society*.
- Zar, J. H. 1999. *Biostatistical analysis*, 4th edition. Prentice-Hall and Pearson, Upper Saddle River, New Jersey.
- Zaret, T. R., and R. T. Paine. 1973. Species introduction in a tropical lake: a newly introduced piscivore can produce population changes in a wide range of trophic levels. *Science* 182:449-455.
- Zelosko, K. A., K. R. Bestgen, J. A. Hawkins, and G. C. White. 2016. Evaluation of a long-term predator removal program: abundance and population dynamics of invasive Northern Pike in the Yampa River, Colorado. *Transactions of the American Fisheries Society* 145:1153-1170.

Tables and Figures

Table 2.1 Sample sizes for season, region, and cohort comparisons of diets collected from Walleyes in the Lake Pend Oreille system from May 2020 to May 2021. Seasons were defined as spring (March – May), summer (June – August), fall (September – November), and winter (December–February). Regions were defined as Pend Oreille River (POR), northern Lake Pend Oreille (LPO-N), central Lake Pend Oreille (LPO-C), Clark Fork River (CFR), and south Lake Pend Oreille (LPO-S).

	Spring	Summer	Fall	Winter
	Overall			
	207	86	206	23
	Region			
POR	16	12	102	12
LPO-N	112	57	53	8
LPO-C	14	0	18	2
CFR	54	14	18	0
LPO-S	0	0	15	1
	Cohort			
2020	3	1	11	2
2019	38	21	98	9
2018	38	21	33	3
2017	24	8	10	2
2016	6	3	2	0
2015	54	22	33	5
2014	5	2	3	1
2013	15	4	4	1
2012	0	1	1	0
2010	1	1	0	0
2009	17	1	8	0
2007	1	0	1	0
2000	1	0	0	0

Table 2.2 Overall contribution of prey items to Walleye diets collected from the Lake Pend Oreille system from May 2020 to May 2021. Diet summarizations were frequency of occurrence (F), proportion by weight (W), and proportion of energy (calories) contributed (E). Taxa were denoted as Black Crappie (BCR), Gasterosteidae (GAS), Brook Trout (BKT), Bluegill (BLG), Brown Bullhead (BRB), kokanee (KOK), Largemouth Bass (LMB), Longnose Sucker (LNS), Largescale Sucker (LSS), Lake Whitefish (LWF), macroinvertebrates (MAC), Mountain Whitefish (MWF), *Mysis diluviana* (MYS), Northern Pikeminnow (NPM), other (OTH), Pumpkinseed (PKS), Peamouth Chub (PMC), Rainbow Trout (RBT), Cottidae (SCP), Smallmouth Bass (SMB), Tench (TNC), unknown fish (UNK), Walleye (WAE), Westslope Cutthroat Trout (WCT), and Yellow Perch (YEP). The symbol *a* indicates the proportional contribution was < 0.01.

Taxa	Summarization		
	F	W	E
UNK	0.23	0.02	0.01
KOK	0.23	0.67	0.79
MAC	0.16	<i>a</i>	<i>a</i>
PMC	0.13	0.09	0.06
BCR	0.13	0.05	0.03
NPM	0.09	0.03	0.02
YEP	0.09	0.03	0.01
LSS	0.05	0.02	0.01
RBT	0.04	0.03	0.02
OTH	0.04	<i>a</i>	<i>a</i>
WCT	0.04	0.02	0.02
LNS	0.04	<i>a</i>	<i>a</i>
BRB	0.03	0.01	<i>a</i>
SCP	0.03	<i>a</i>	<i>a</i>
MWF	0.02	0.01	0.01
MYS	0.02	<i>a</i>	<i>a</i>
SMB	0.02	<i>a</i>	<i>a</i>
LWF	0.02	0.01	<i>a</i>
TNC	0.01	<i>a</i>	<i>a</i>
LMB	0.01	<i>a</i>	<i>a</i>
GAS	0.01	<i>a</i>	<i>a</i>
BKT	<i>a</i>	<i>a</i>	<i>a</i>
BLG	<i>a</i>	<i>a</i>	<i>a</i>
PKS	<i>a</i>	<i>a</i>	<i>a</i>
WAE	<i>a</i>	<i>a</i>	<i>a</i>

Table 2.3 Proportional contribution to the differences in Walleye diets between regions collected from the Lake Pend Oreille system from May 2020 to May 2021. Proportions were estimated using the SIMPER analysis. Dashes indicate the species contributed < 0.05 to the differences in Walleye diets. Species abbreviations were Black Crappie (BCR), kokanee (KOK), macroinvertebrates (MAC), *Mysis diluviana* (MYS), Northern Pikeminnow (NPM), Peamouth Chub (PMC), and Yellow Perch (YEP). Regions were defined as Pend Oreille River (POR), northern Lake Pend Oreille (LPO-N), central Lake Pend Oreille (LPO-C), Clark Fork River (CFR), and south Lake Pend Oreille (LPO-S).

Region comparison	BCR	KOK	MAC	MYS	NPM	PMC	YEP
POR: LPO-N	0.18	0.19	0.11	--	--	0.14	0.10
POR: LPO-C	0.19	0.17	0.07	--	--	0.17	0.08
POR: CFR	0.16	0.19	0.13	--	0.12	0.15	--
POR: LPO-S	0.15	0.41	--	0.07	--	0.11	--
LPO-N: LPO-C	0.11	0.23	0.10	--	--	0.11	0.08
LPO-N: CFR	0.06	0.25	0.16	--	0.13	0.09	0.07
LPO-N: LPO-S	0.06	0.41	0.09	0.09	--	--	0.07
LPO-C: CFR	0.08	0.24	0.13	--	0.12	0.13	--
LPO-C: LPO-S	0.08	0.42	--	0.11	--	0.10	--
CFR: LPO-S	--	0.41	0.13	0.08	0.13	--	--

Table 2.4 Proportional contribution to the differences in Walleye diets between seasons collected from the Lake Pend Oreille system from May 2020 to May 2021. Proportions were estimated using the SIMPER analysis. Dashes indicate the species contributed < 0.05 to the differences in Walleye diets. Species abbreviations were Black Crappie (BCR), kokanee (KOK), macroinvertebrates (MAC), *Mysis diluviana* (MYS), Northern Pikeminnow (NPM), Peamouth Chub (PMC), and Yellow Perch (YEP). Months were grouped into seasons as spring (March, April, May), summer (June, July, August), fall (September, October, November), and winter (December, January, February).

Season comparison	BCR	KOK	MAC	MYS	NPM	PMC	YEP
Spring:Summer	0.12	0.26	0.15	--	0.07	0.09	0.07
Spring:Fall	0.12	0.20	0.13	--	0.09	0.13	0.07
Spring:Winter	0.14	0.17	0.13	0.10	--	0.07	0.12
Summer:Fall	0.19	0.26	0.06	--	--	0.13	0.10
Summer:Winter	0.21	0.24	--	0.10	--	0.08	0.14
Fall:Winter	0.20	0.16	--	0.10	--	0.12	0.14

Table 2.5 Proportional contribution to the differences in Walleye diets between cohorts collected from the Lake Pend Oreille system from May 2020 to May 2021. Proportions were estimated using the SIMPER analysis. Dashes indicate the species contributed < 0.05 to the differences in Walleye diets. Species abbreviations were Black Crappie (BCR), kokanee (KOK), macroinvertebrates (MAC), *Mysis diluviana* (MYS), Northern Pikeminnow (NPM), Peamouth Chub (PMC), and Yellow Perch (YEP). Cohort comparisons did not include the 2012 and older cohorts due to small sample size

Cohort comparison	BCR	KOK	MAC	MYS	NPM	PMC	YEP
2020-2019	0.21	--	0.12	0.10	0.10	0.13	0.12
2020-2018	0.17	0.08	0.12	0.09	0.10	0.11	0.10
2020-2017	0.14	0.13	0.12	0.08	--	0.15	0.09
2020-2016	0.15	0.37	0.13	0.08	--	--	--
2020-2015	0.13	0.28	0.10	--	--	0.10	0.08
2020-2014	0.13	0.33	0.10	--	0.09	--	0.09
2020-2013	0.12	0.23	0.10	0.08	--	0.13	0.064
2019-2018	0.18	0.10	0.12	--	0.10	0.10	0.11
2019-2017	0.15	0.14	0.13	--	0.07	0.13	0.09
2019-2016	0.16	0.37	0.14	--	--	--	0.07
2019-2015	0.14	0.29	0.10	--	--	0.09	0.09
2019-2014	0.14	0.33	0.10	--	0.09	--	0.09
2019-2013	0.13	0.24	0.10	--	--	0.12	0.07
2018-2017	0.10	0.18	0.14	--	0.07	0.13	0.08
2018-2016	0.12	0.38	0.16	--	0.06	--	--
2018-2015	0.10	0.30	0.11	--	0.08	0.08	0.08
2018-2014	0.09	0.34	0.12	--	0.10	--	0.09
2018-2013	0.08	0.29	0.11	--	0.06	0.12	--
2017-2016	0.09	0.38	0.18	--	--	0.11	--
2017-2015	--	0.32	0.13	--	--	0.13	0.06
2017-2014	--	0.35	0.13	--	0.07	0.10	0.07
2017-2013	--	0.28	0.13	--	--	0.16	--
2016-2015	0.11	0.41	0.20	--	--	--	--
2016-2014	0.11	0.42	0.23	--	--	--	--
2016-2013	0.07	0.39	0.18	--	--	0.11	--
2015-2014	--	0.38	0.13	--	0.10	--	0.09
2015-2013	--	0.35	0.11	--	--	0.13	--
2014-2013	--	0.37	0.11	--	0.07	0.11	--

Table 2.6 . The $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and trophic positions of Walleyes sampled in the Lake Pend Oreille system from May 2020 to May 2021. Values were grouped by cohort. Minimum (Min), mean (Ave), and maximum (Max) values are shown for all three values as well as the associated standard error (SE) of each group. Differences (Diff) in maximum and minimum values of the trophic position are shown. Cells containing a indicate that the value was < 0.01 . Dashes indicate a value was not available because only one sample was collected from the specific group.

Cohort	<i>n</i>	$\delta^{13}\text{C}$				$\delta^{15}\text{N}$				Trophic position				
		Min	Ave	Max	SE	Min	Ave	Max	SE	Min	Ave	Max	SE	Diff
2000	1	—	-26.28	—	—	—	12.84	—	—	—	5.78	—	—	—
2006	1	—	-26.51	—	—	—	14.16	—	—	—	6.16	—	—	—
2007	3	-26.77	-26.59	-26.48	0.05	13.03	13.27	13.60	0.10	5.83	5.90	6.00	0.03	0.17
2008	3	-27.48	-27.07	-26.74	0.13	12.79	13.41	14.08	0.22	5.76	5.94	6.14	0.06	0.38
2009	52	-29.80	-27.44	-24.49	0.02	11.89	13.05	14.37	0.01	5.50	5.84	6.23	<i>a</i>	0.73
2010	3	-28.20	-27.33	-26.81	0.25	12.53	13.10	13.66	0.19	5.69	5.85	6.02	0.06	0.33
2011	2	-28.70	-27.07	-25.43	1.16	12.50	12.85	13.19	0.24	5.68	5.78	5.88	0.07	0.20
2012	9	-28.46	-27.40	-26.01	0.09	12.24	12.92	13.74	0.06	5.60	5.80	6.04	0.02	0.44
2013	58	-31.37	-27.79	-25.68	0.02	11.47	12.73	13.93	0.01	5.37	5.74	6.10	<i>a</i>	0.72
2014	24	-29.64	-27.74	-25.70	0.05	11.30	12.46	13.74	0.02	5.32	5.66	6.04	0.01	0.72
2015	311	-30.76	-27.97	-24.80	<i>a</i>	10.58	12.63	15.02	<i>a</i>	5.11	5.71	6.42	<i>a</i>	1.31
2016	28	-29.91	-27.77	-25.08	0.05	10.32	12.19	14.89	0.03	5.04	5.58	6.38	0.01	1.34
2017	128	-31.08	-27.01	-23.69	0.01	9.52	11.49	14.08	0.01	4.80	5.38	6.14	<i>a</i>	1.34
2018	185	-28.84	-26.75	-22.83	0.01	8.74	10.96	13.22	<i>a</i>	4.57	5.22	5.89	<i>a</i>	1.32
2019	284	-28.88	-26.30	-21.97	<i>a</i>	8.34	10.59	13.17	<i>a</i>	4.45	5.11	5.87	<i>a</i>	1.42
2020	28	-27.23	-24.92	-20.37	0.07	8.95	9.99	11.51	0.03	4.63	4.94	5.39	0.01	0.75

Table 2.7 Mean (TP), minimum (Min), and maximum (Max) trophic position of taxa in the Lake Pend Oreille system. Trophic position was estimated from stable isotope signatures collected from May 2020 – June 2021. Zooplankton samples were collected in May 2022. Taxa abbreviations were Black Crappie (BCR), Brown Bullhead (BRB), crayfish (CRAY), kokanee (KOK), Lake Trout (LKT), Largemouth Bass (LMB), Longnose Sucker (LNS), Largescale Sucker (LSS), Lake Whitefish (LWF), macroinvertebrates (MAC), Mountain Whitefish (MWF), *Mysis diluviana* (MYS), Northern Pikeminnow (NPM), Pumpkinseed (PKS), Peamouth Chub (PMC), Rainbow Trout (RBT), Cottidae (SCP), Smallmouth Bass (SMB), Tench (TNC), Walleye (WAE), Westslope Cutthroat Trout (WCT), Yellow Perch (YEP), and zooplankton (ZOO). Species abbreviations with “-L” indicated values of large individuals (i.e., after an ontogenetic shift occurred) and “-S” indicated values of small individuals (i.e., before an ontogenetic shift occurred).

Taxa	<i>n</i>	TP	Min	Max
BCR-A	65	3.6	2.2	4.0
BCR-J	27	2.8	2.4	3.1
BLT-A	39	4.2	3.4	4.6
BNT	27	3.8	3.0	4.3
BRB	38	2.9	2.2	3.4
CRAY	30	3.1	2.7	3.4
KOK	72	3.4	3.1	4.0
LKT	66	3.8	3.0	4.5
LMB-J	13	2.6	2.1	3.3
LNS	103	3.2	2.1	3.9
LSS	130	3.1	2.0	3.8
LWF	434	3.6	2.9	4.3
MAC	13	2.0	1.3	2.7
MWF	68	3.4	2.5	4.3
MYS-A	32	2.7	2.5	2.9
MYS-J	13	2.2	2.1	2.4
NPK	36	3.6	2.7	4.0
NPM-A	233	3.8	2.7	4.3
NPM-J	81	3.3	2.5	4.2
PKS	32	3.1	2.2	3.6
PMC	236	3.2	2.7	4.0
RBT	9	3.4	3.1	3.8
SCP	4	3.9	3.6	4.2
SMB-A	129	3.7	3.0	4.3
SMB-J	6	3.2	2.4	3.9
TNC	42	2.7	2.1	3.1
WAE	1147	3.9	3.0	4.9
WCT	32	2.8	2.3	3.4
YEP	209	3.3	2.2	4.0
ZOO	13	2.1	1.4	2.5

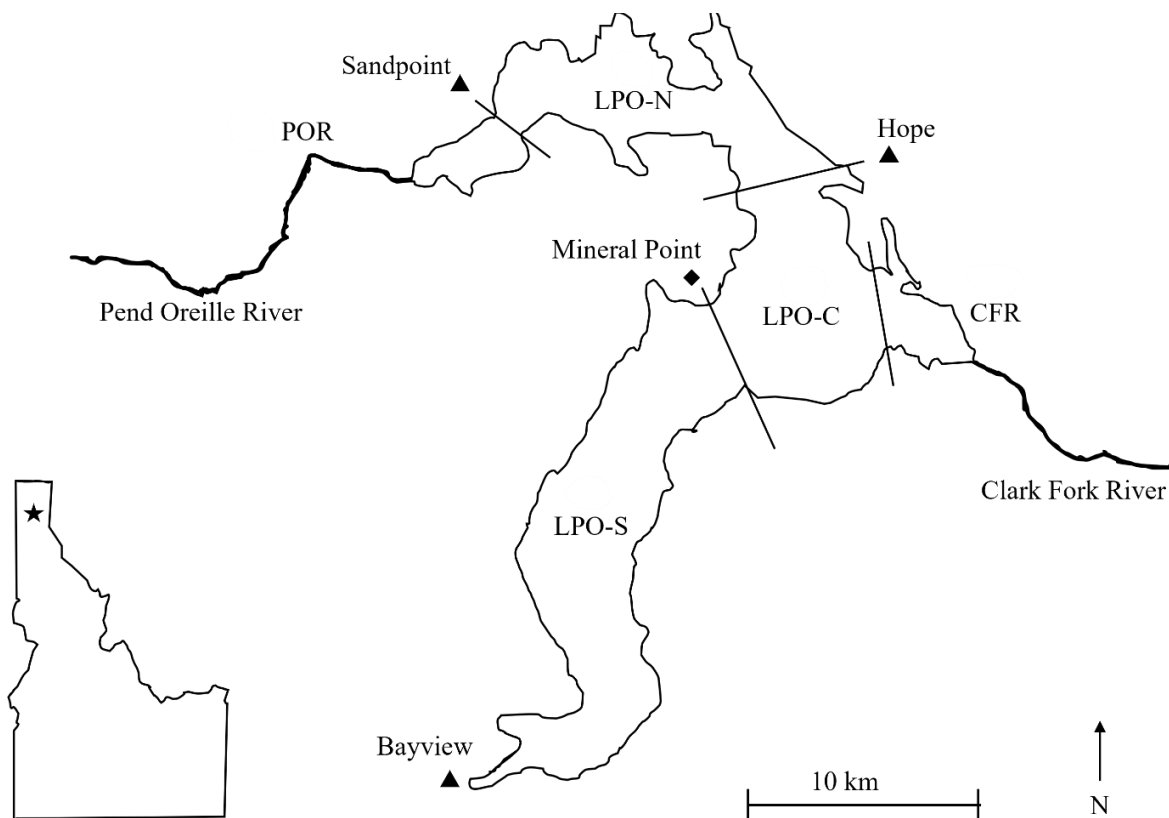


Figure 2.1 The Lake Pend Oreille system located in northern Idaho. This system included Lake Pend Oreille, the Pend Oreille River, and the Clark Fork River. The system was divided into five regions: the Pend Oreille River (POR), northwestern portion of Lake Pend Oreille (LPO-N), a transition zone between the shallow northern portion and the deep southern basin of the lake (LPO-C), the Clark Fork River and its delta (CFR), and the southern portion of the lake (LPO-S). Triangles indicate cities and diamonds represent a landmark on the lake used to separate regions.

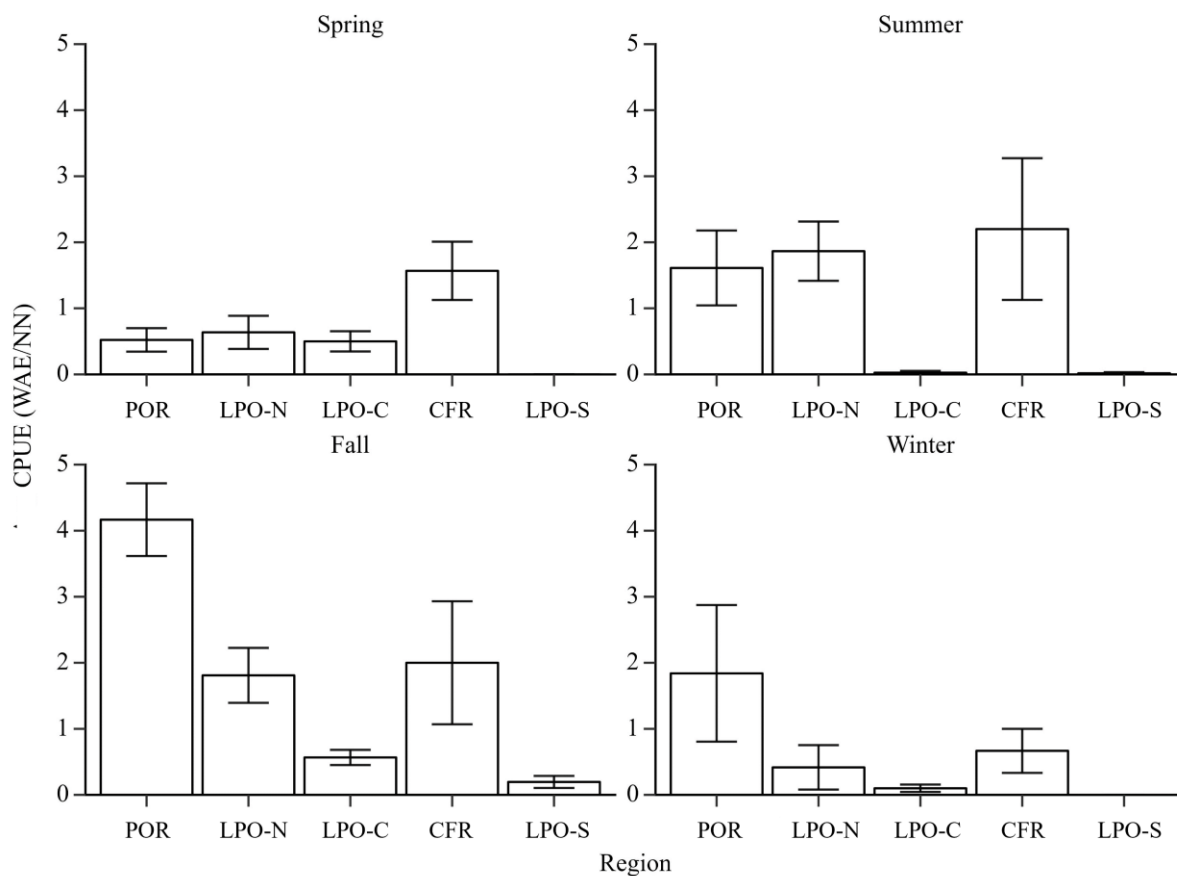


Figure 2.2 Mean catch per unit effort (CPUE = number of Walleyes [WAE] caught per net-night) in the Lake Pend Oreille system by season from May 2020 to May 2021. Bars represent one standard error. Months were grouped into seasons as spring (March, April, May), summer (June, July, August), fall (September, October, November), and winter (December, January, February). Regions were defined as Pend Oreille River (POR), northern Lake Pend Oreille (LPO-N), central Lake Pend Oreille (LPO-C), Clark Fork River and Delta (CFR), southern Lake Pend Oreille (LPO-S).

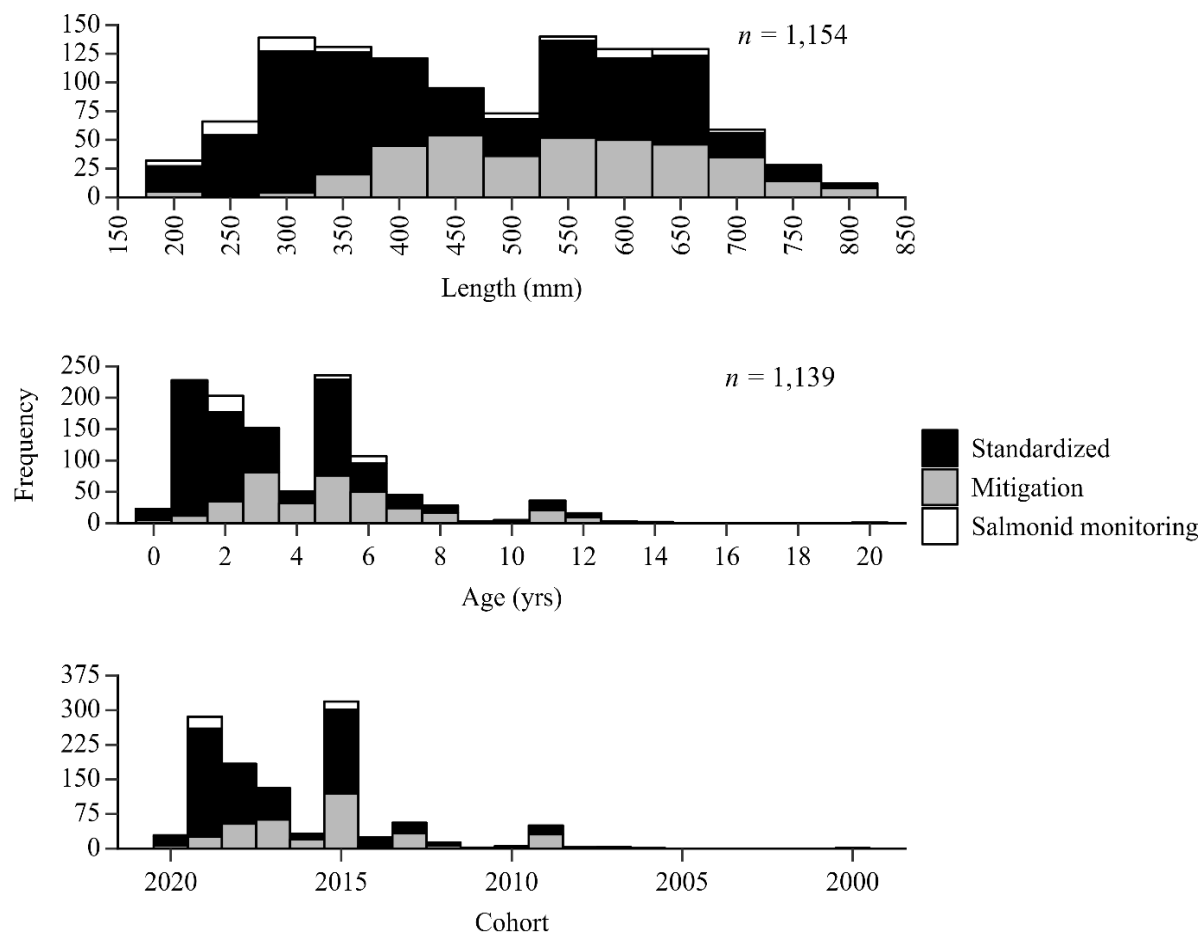


Figure 2.3 . Length and age structure of sampled Walleyes in the Lake Pend Oreille system from May 2020 to May 2021. Individuals were grouped based on sampling method (i.e., standardized, mitigation, salmonid monitoring). The 2015, 2017, 2018, and 2019 cohorts represent approximately 75% of all individuals sampled.

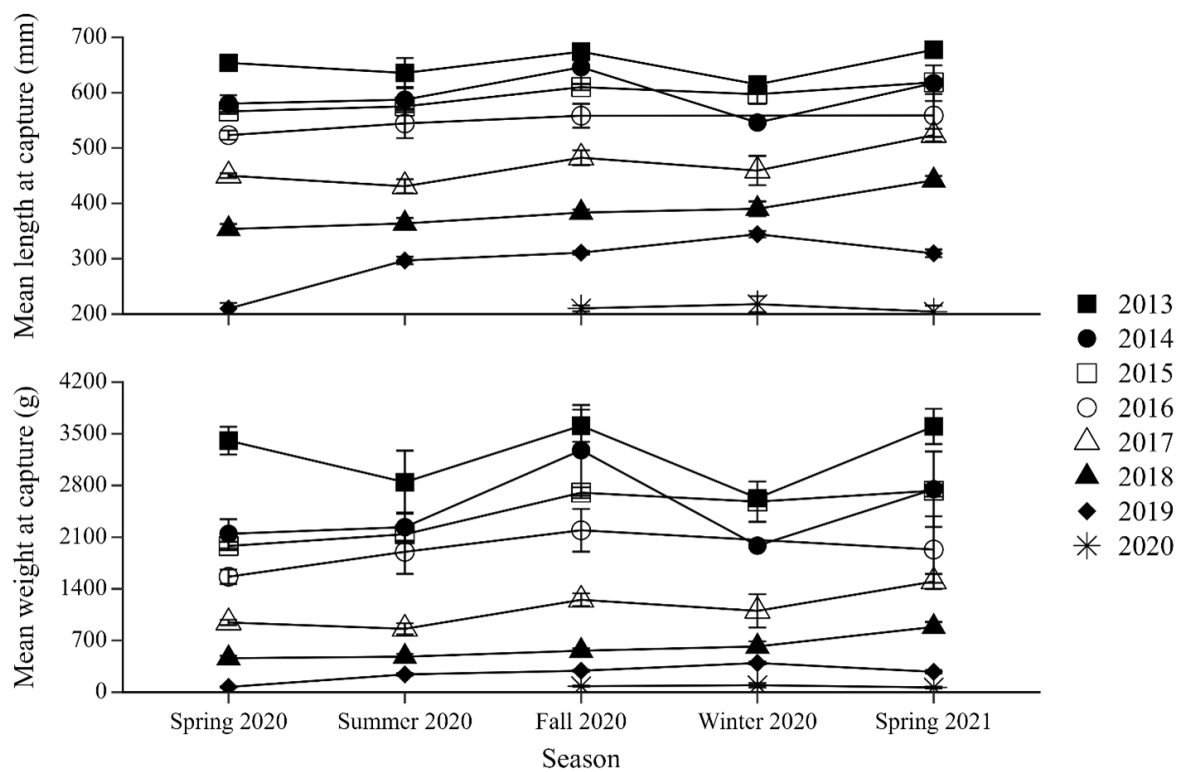


Figure 2.4 . Mean length and weight of Walleye cohorts collected from the Lake Pend Oreille system, May 2020 to May 2021. Bars represent one standard error. Months were grouped into seasons as spring (March, April, May), summer (June, July, August), fall (September, October, November), and winter (December, January, February).

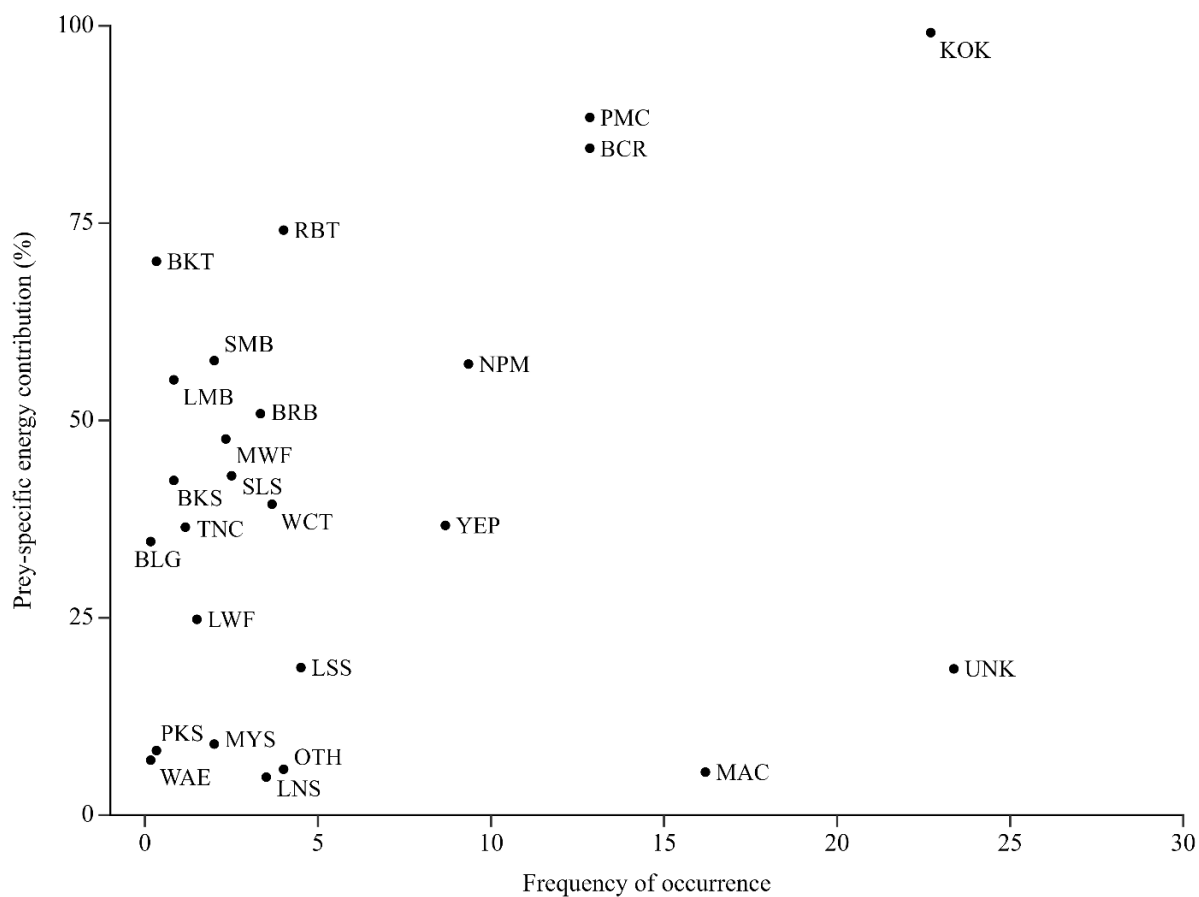


Figure 2.5 Overall prey-specific energy contribution of prey items observed in Walleye stomachs collected from the Lake Pend Oreille system during May 2020 to May 2021. Months were grouped into seasons as spring (March, April, May), summer (June, July, August), fall (September, October, November), and winter (December, January, February). Prey items were Black Crappie (BCR), Gasterosteidae (GAS), Brook Trout (BKT), Bluegill (BLG), Brown Bullhead (BRB), kokanee (KOK), Largemouth Bass (LMB), Longnose Sucker (LNS), Largescale Sucker (LSS), Lake Whitefish (LWF), macroinvertebrates (MAC), Mountain Whitefish (MWF), *Mysis diluviana* (MYS), Northern Pikeminnow (NPM), other (OTH), Pumpkinseed (PKS), Peamouth Chub (PMC), Rainbow Trout (RBT), Cottidae (SCP), Smallmouth Bass (SMB), Tench (TNC), Walleye (WAE), Westslope Cutthroat Trout (WCT), and Yellow Perch (YEP).

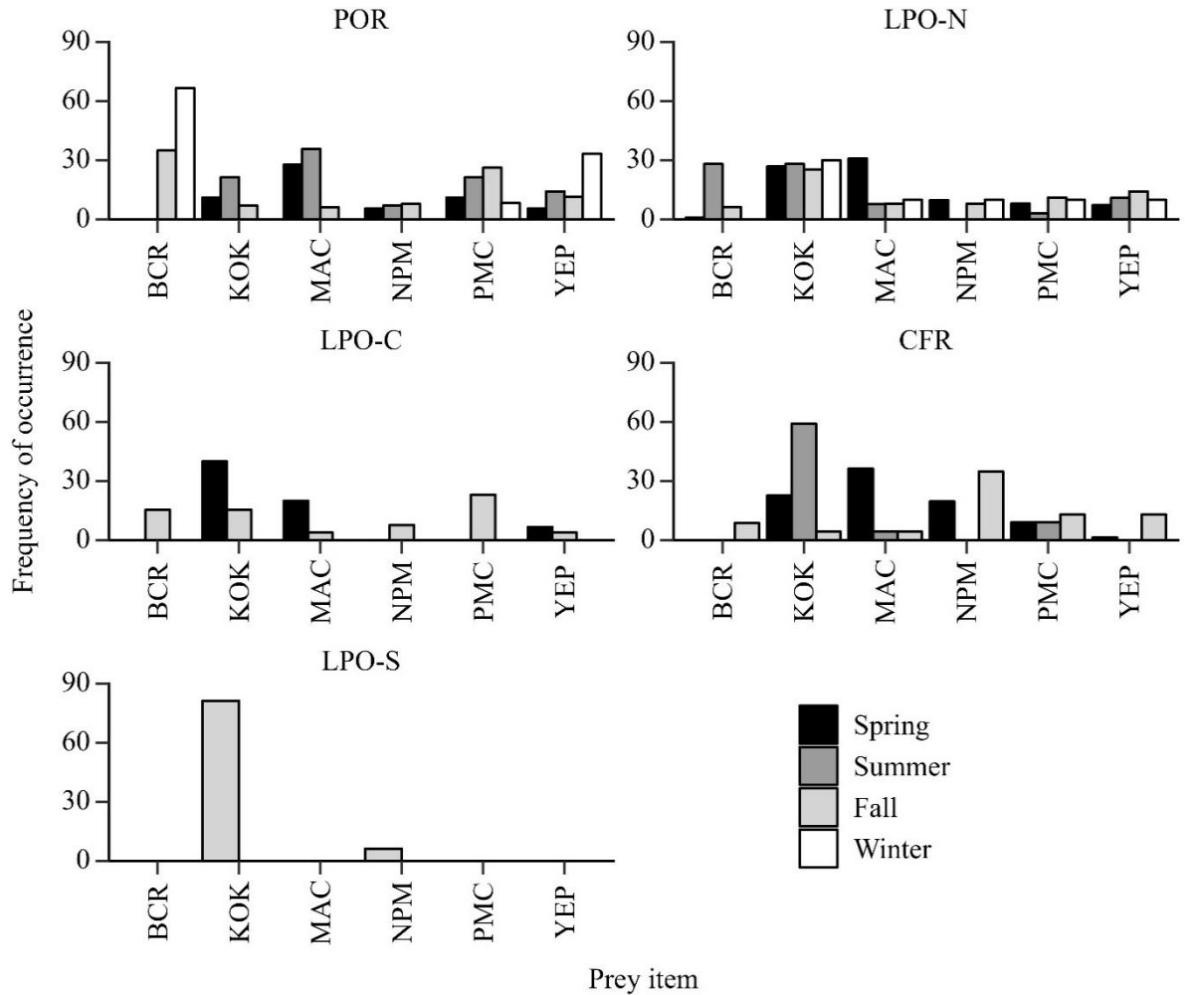


Figure 2.6 . Frequency of occurrence of the six prey items most frequently consumed by Walleyes sampled from May 2020 to May 2021 in the Lake Pend Oreille system. Frequency of occurrence was grouped by regions and seasons. Regions were defined as Pend Oreille River (POR), northern Lake Pend Oreille (LPO-N), central Lake Pend Oreille (LPO-C), Clark Fork River and Delta (CFR), southern Lake Pend Oreille (LPO-S). Months were grouped into seasons as spring (March, April, May), summer (June, July, August), fall (September, October, November), and winter (December, January, February). Prey items are Black Crappie (BCR), kokanee (KOK), macroinvertebrates (MAC), Northern Pikeminnow (NPM), Peamouth Chub (PMC), and Yellow Perch (YEP).

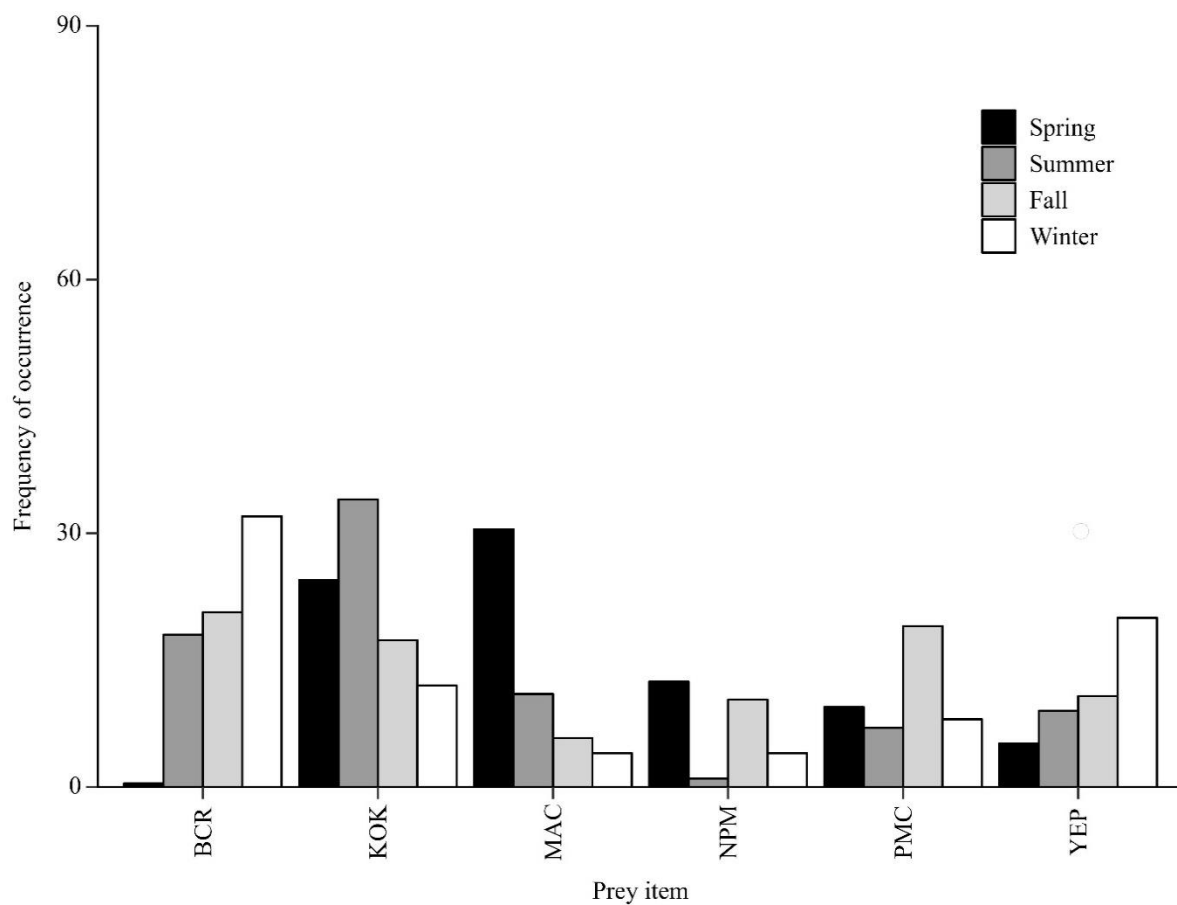


Figure 2.7 Seasonal frequency of occurrence of the six most frequently consumed prey items observed in Walleye stomachs collected from the Lake Pend Oreille system during May 2020 to May 2021. Months were grouped into seasons as spring (March, April, May), summer (June, July, August), fall (September, October, November), and winter (December, January, February). Prey items were Black Crappie (BCR), kokanee (KOK), macroinvertebrates (MAC), Northern Pikeminnow (NPM), Peamouth Chub (PMC), and Yellow Perch (YEP).

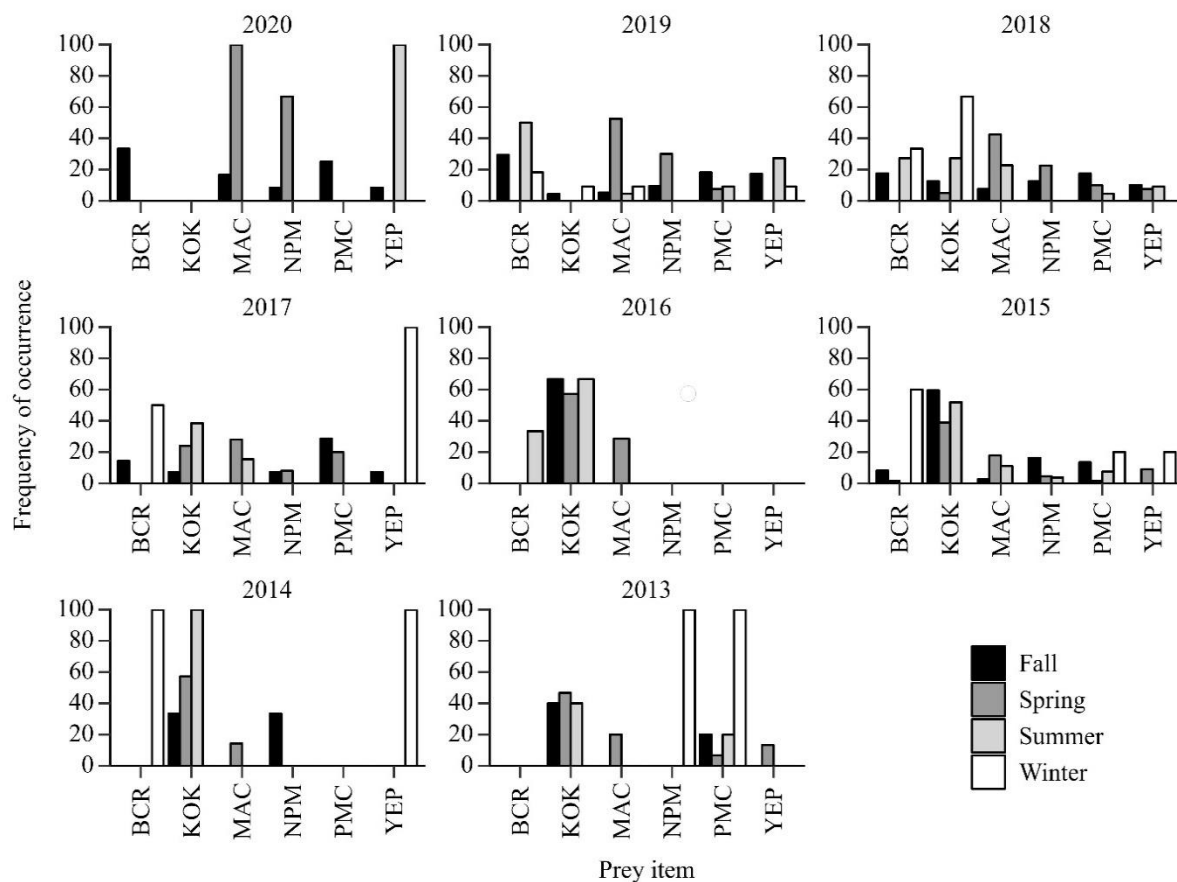


Figure 2.8 . Frequency of occurrence of the six prey items most frequently consumed by Walleyes sampled from May 2020 to May 2021 in the Lake Pend Oreille system. Frequency of occurrence was grouped by cohorts and seasons. Months were grouped into seasons as spring (March, April, May), summer (June, July, August), fall (September, October, November), and winter (December, January, February). Prey items in the figure were the six items most frequently consumed by Walleyes overall. Prey item abbreviations are as follows: Black Crappie (BCR), kokanee (KOK), macroinvertebrates (MAC), Northern Pikeminnow (NPM), Peamouth Chub (PMC), Yellow Perch (YEP).

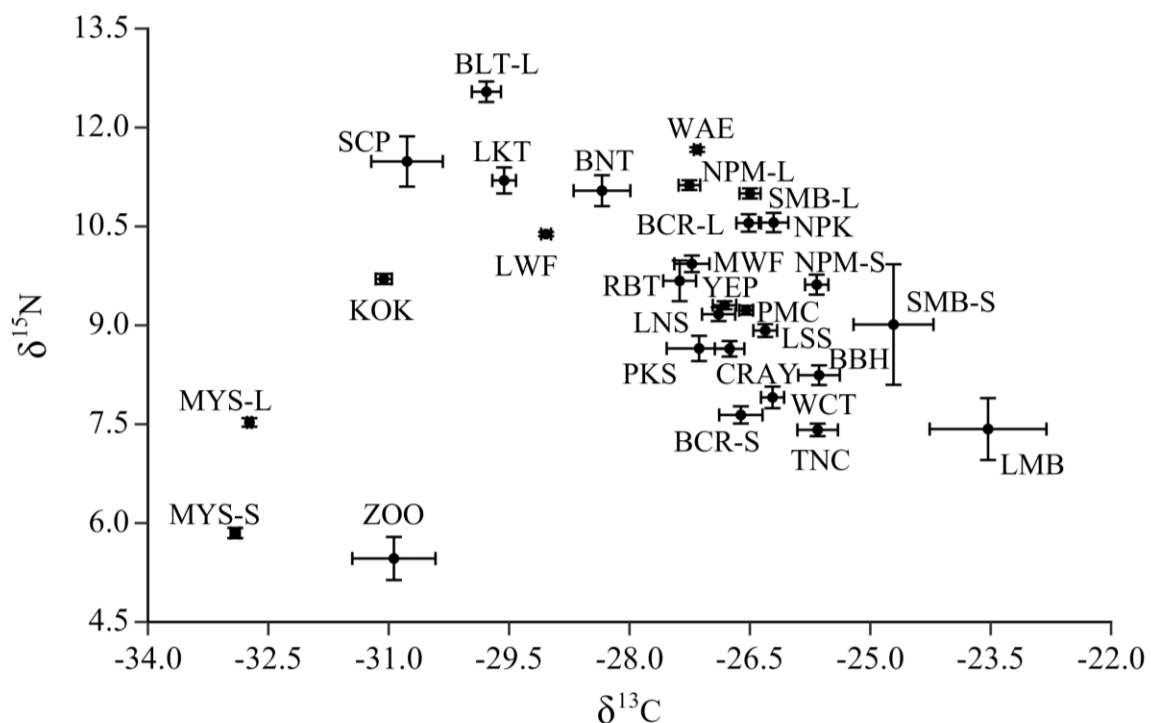


Figure 2.9 Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (mean ± 1 standard error) for all species sampled in the Lake Pend Oreille system from May 2020 to May 2021. Taxa abbreviations are Black Crappie (BCR), Brown Bullhead (BRB), kokanee (KOK), Largemouth Bass (LMB), Longnose Sucker (LNS), Largescale Sucker (LSS), Lake Whitefish (LWF), Mountain Whitefish (MWF), *Mysis diluviana* (MYS), Northern Pikeminnow (NPM), Pumpkinseed (PKS), Peamouth Chub (PMC), Rainbow Trout (RBT), sculpin (SCP), Smallmouth Bass (SMB), Tench (TNC), Walleye (WAE), Westslope Cutthroat Trout (WCT), Yellow Perch (YEP), and zooplankton (ZOO). Taxa abbreviations with “-L” indicated values of large individuals (i.e., after an ontogenetic shift occurred) and “-S” indicated values of small individuals (i.e., before an ontogenetic shift occurred).

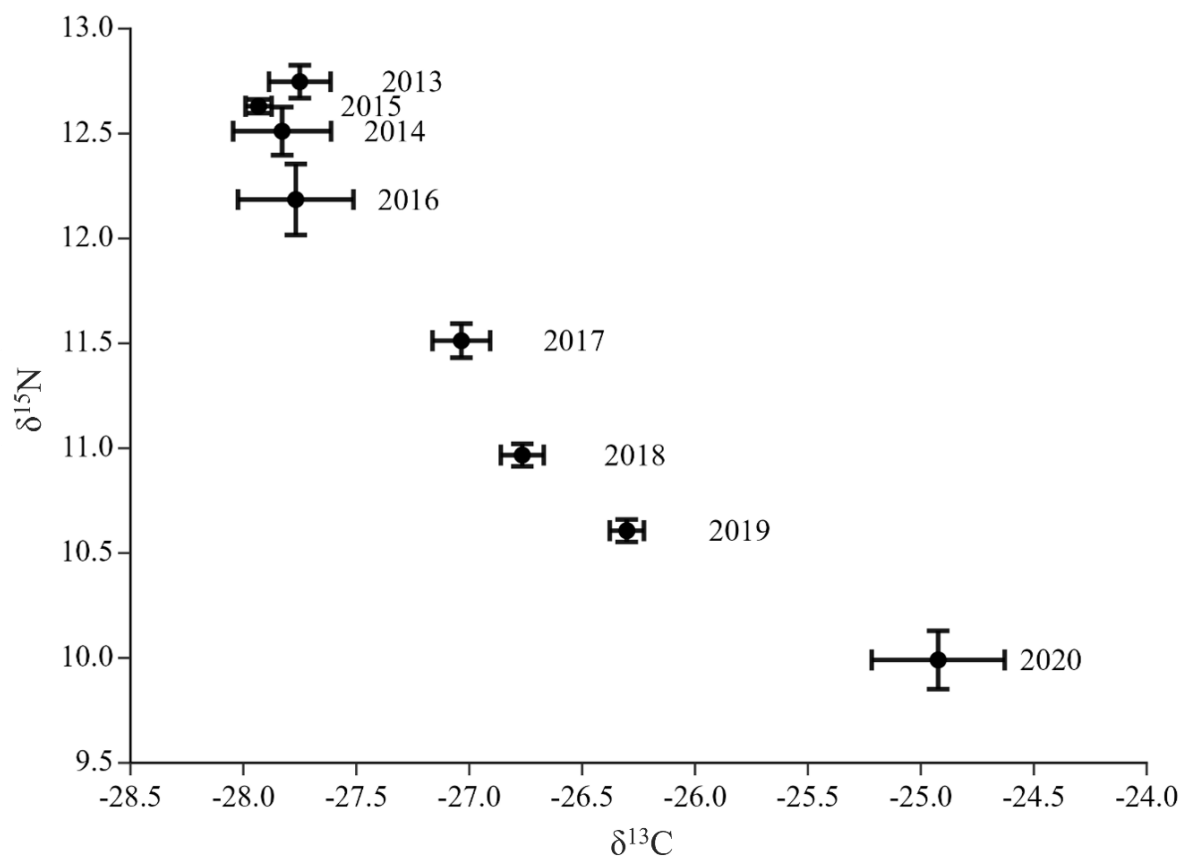


Figure 2.10 Mean \pm S.E. of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of Walleyes collected from the Lake Pend Oreille system from May 2020 to May 2021. Walleye were grouped by cohort. Individuals from the 2012-2020 were not shown due to low sample size ($n < 10$).

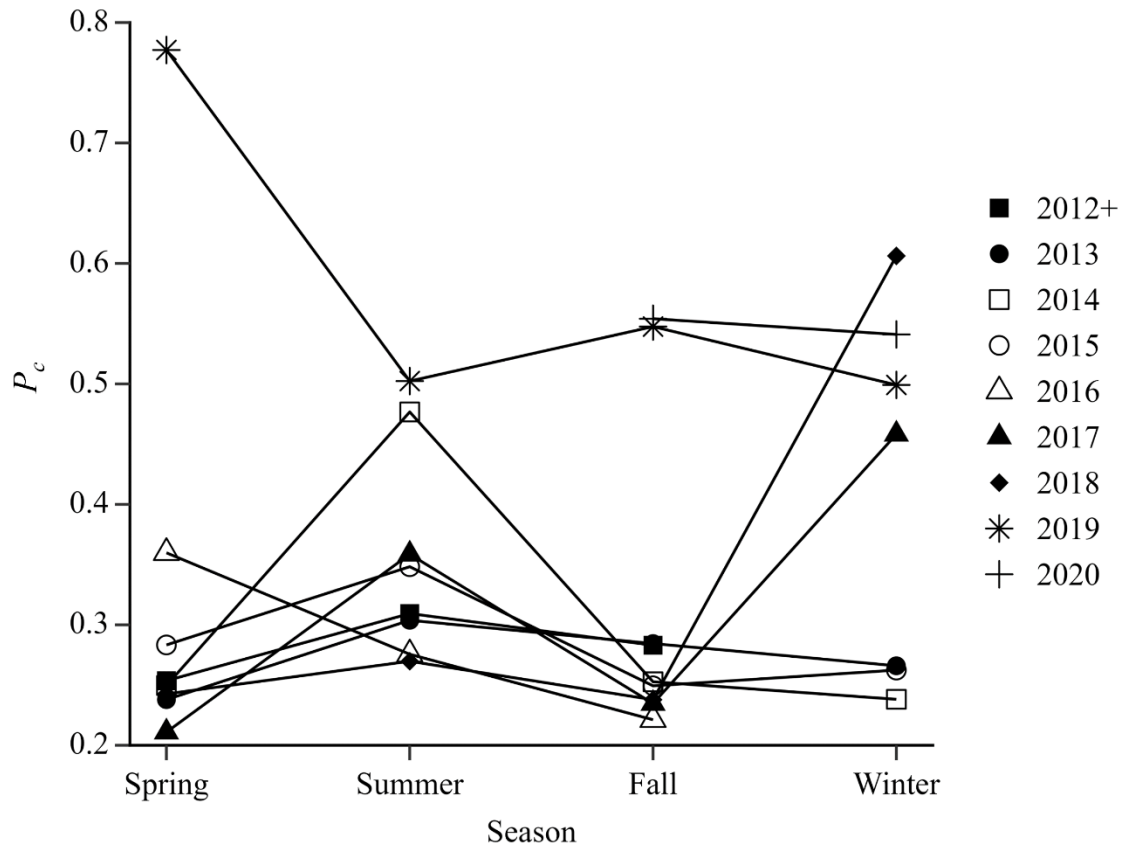


Figure 2.11 Estimated proportion of maximum consumption (P_c) from the bioenergetics model of Walleyes sampled from the Lake Pend Oreille system between May 2020 and May 2021. Walleyes were grouped by cohorts and estimates were made for each season. Months were grouped into seasons as spring (March, April, May), summer (June, July, August), fall (September, October, November), and winter (December, January, February). Individuals from the 2012 and older cohorts were grouped due to low sample sizes ($n < 10$).

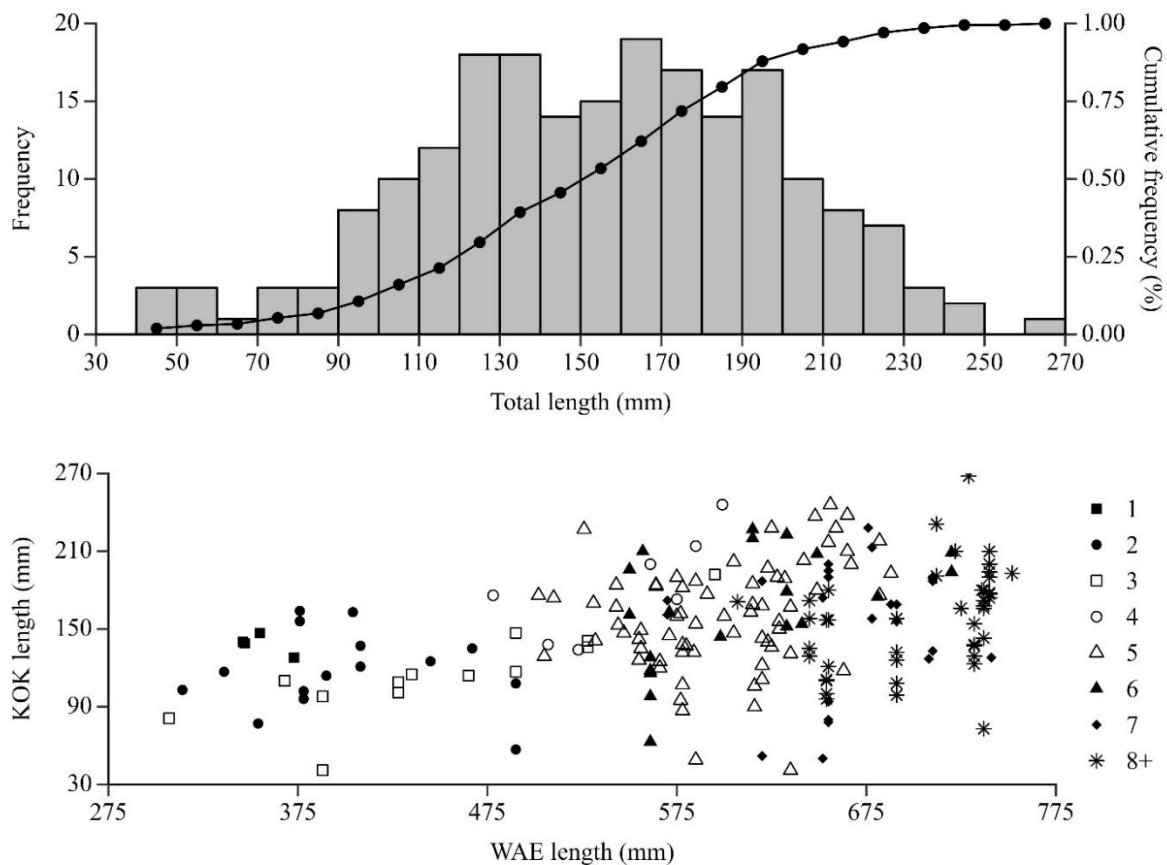


Figure 2.12 Lengths of kokanee consumed by Walleyes collected from the Lake Pend Oreille system from May 2020 to May 2021. The top panel shows the length-frequency distribution of all kokanee that were consumed. The bottom panel shows the length of kokanee consumed relative to the length (KOK length) of the Walleye (WAE length); different ages are depicted by different symbols.

Chapter 3: Factors related to growth and individual variability in an introduced piscivore population

Abstract

Growth is one of the primary drivers of fish population dynamics and understanding factors influencing growth is vital to effective management of fish populations. This study investigated potential factors influencing growth of a recently established, non-native population of Walleyes *Sander vitreus* in the Lake Pend Oreille system of northern Idaho. Relative growth index was used to describe growth of Walleyes relative to other populations across North America. Linear mixed-effects regression modeling was used to estimate yearly growth increments from back-calculated lengths at age and relate growth increments to abiotic and biotic variables (i.e., average summer water temperature, inflow, kokanee *Oncorhynchus nerka* abundance and biomass, *Mysis diluviana* density). Models were ranked using Akaike's Information Criterion (AIC_c) corrected for small sample size. Individual variability in growth (i.e., 75th and higher, 25th and lower percentiles of growth) was related to variability in diet using stable isotopes (i.e., $\delta^{15}N$, $\delta^{13}C$). The relative growth index suggested that Walleyes grew fast relative to other populations, particularly those at similar latitudes to the Lake Pend Oreille system. Regression modeling indicated that growth of Walleyes was positively associated with temperature, as well as abundance and biomass of kokanee; growth was negatively associated with inflow and *Mysis diluviana* density. Growth of Walleyes varied among individuals. In general, fast-growing Walleyes (i.e., 75th percentile of growth) had higher $\delta^{15}N$ than slow-growing Walleyes (i.e., 25th percentile of growth). Similarly, $\delta^{13}C$ was more depleted in the fast-growing individuals for all age classes except age 1. This suggests that age-1, fast-growing individuals used higher proportions of littoral prey items. This research adds to our understanding of individual variability in growth of fishes and the factors influencing population dynamics of non-native Walleyes.

Introduction

Growth, mortality, and recruitment govern fish population dynamics. Although an understanding of all three rate functions is critical for effectively managing fish populations,

growth is particularly important given its interactions with 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 less susceptible to environmental stressors than individuals growing slowly (Miller et al. 1988). Fast-growing individuals typically mature at early ages compared to individuals exhibiting slow growth (Wolfert et al. 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). Because annual growth increments are recorded in calcified structures of fishes, changes in growth can be related to environmental characteristics over the lifetime of an individual. Identifying environmental conditions related to growth provides insight on factors influencing the ecology of fishes and characteristics regulating fish population dynamics.

A variety of abiotic conditions can directly or indirectly influence growth of fishes. 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, growth increases with temperature until an optimum temperature is exceeded (Kocovsky and Carline 2001; Neuheimer et al. 2011; Matthias et al. 2018; Martino et al. 2019). As a result, growth varies across thermal gradients such as latitude. At a large-scale, populations in southern latitudes exhibit faster growth than populations in northern latitudes (Quist et al. 2003; Vinagre et al. 2008; Porter et al. 2014; Massie et al. 2018) due to duration of the growing season (Purchase et al. 2005; Dunlop and Shuter 2006; Nepal and Fabrizio 2020). In addition to thermal habitat, structural habitat (i.e., woody material, vegetation, substrate) can indirectly influence growth of fishes (Baltz et al. 1998; Quist and Guy 2001; Shervette and Gelwick 2006). For example, in Chancellor Lake, Michigan, growth of age-0 Largemouth Bass *Micropterus salmoides* increased with macrophyte cover despite consistent zooplankton and macroinvertebrate densities (Nohner et al. 2018). Similarly, growth of fishes may be indirectly influenced by discharge, particularly in regulated riverine systems (e.g., Korman and Campana 2009; Grabowski et al. 2012; Jacquemin et al. 2014; 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). On the contrary, 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 suggest that discharge influences abiotic (e.g., temperature) or biotic (e.g., prey availability) conditions which then affects growth of fishes (Weisberg and Burton 1993; Bunn and Arthington 2002; Nilsson and Renöfält 2008).

Biotic conditions have frequently been associated with growth. 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 *P. nigromaculatus*, White Bass *Morone chrysops*, and Largemouth Bass was positively related to biomass of age-0 Gizzard Shad *Dorosoma cepedianum* in five Missouri reservoirs (Michaletz 1998a). However, in the same systems, fast growth (i.e., reduced vulnerability) of Gizzard Shad was negatively related to growth of piscivores. When prey is limited, interspecific and intraspecific competition may be a primary factor related to growth of fishes (Margenau et al. 1998; Weber and Brown 2013; McDougall et al. 2018). In Lawrence Lake, Michigan, competitive interactions between Bluegills and Pumpkinseeds *L. gibossus* resulted in decreased growth of both species (Mittelbach 1988). Similarly, intraspecific competition was identified as a primary driver of growth in Rainbow Trout from 2012-2016 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 of fishes.

Growth is typically summarized across individuals in a population, but understanding factors that affect individual variation in growth is also important. Individual differences in growth result from genetics, phenotypic plasticity, and complex interactions between genetics, biotic interactions, and environmental conditions (Goodrich and Clark 2023). For example, differences in growth of various genetic strains of Rainbow Trout have been well documented (Reinitz et al. 1979; Overtuf et al. 2003; Cleveland et al. 2017). Similarly,

physiological differences between individuals (e.g., resting metabolic rate, energy cost of digestion) have been shown to influence growth. In Barramundi *Lates calcarifer*, individuals with a higher standard metabolic rate grew faster than individuals with a low standard metabolic rate (Norin et al. 2016). However, some evidence suggests individual plasticity (e.g., behavioral differences) 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). For instance, foraging behaviors of Coho Salmon *O. kisutch* were related to growth in Huckleberry Creek, Washington (Nielsen 1992). Individuals that staged at feeding stations exhibited higher growth rates than individuals that patrolled larger areas. Environmental and social stressors can alter behaviors such as migration and aggression (Gilmour et al. 2005). In the presence of predators, migration and growth rates were positively correlated in individual Jumping Guabine *Rivulus hartii* (Fraser et al. 2001). Similarly, the social hierarchy of Burton's Mouthbrooder *Haplochromis burtoni* influenced growth rates (Hofmann et al. 1999). Non-dominant (i.e., subordinate) individuals did not allocate energy to reproduction resulting in higher growth rates than territorial individuals. Although a variety of mechanisms may be responsible, identifying individual variability in growth and factors related to growth can provide further insight into the population- and community-level dynamics, particularly of introduced species (Bolnick et al. 2011; Mittelbach et al. 2014; Svanbäck et al. 2015).

Walleye *Sander vitreus* is an ideal study species for examining growth dynamics because of its ecological and social value, widespread distribution, and plasticity in life history characteristics (e.g., food habits). Growth of Walleyes 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), prey availability (Hartman and Margraf 1992; Johnson and Goettl 1999; Ward et al. 2007; VanDeValk et al. 2008), and intraspecific competition (Sass et al. 2004). Although Walleyes have been extensively studied, few studies have evaluated growth of Walleyes in novel systems, particularly in the western United States. Additionally, relatively few studies have addressed individual variability in growth of fishes, including Walleyes. The non-native Walleye population in the Lake Pend Oreille system, Idaho, was recently established. Ryan et al. (2021) described length and age structure of Walleyes in the system but did not assess factors influencing growth. As such, the goal of this research was to

identify factors related to growth of Walleyes. I hypothesized that temperature, abundance of kokanee, and discharge would be important factors related to growth of Walleyes in the Lake Pend Oreille system. Additionally, because of the variability observed in Walleye diets (Chapter 2), I postulated that Walleyes would exhibit differences in growth rates because of selective use of soft-rayed prey resources. I expected that individuals that consumed pelagic prey resources (e.g., kokanee *O. nerka*) would grow faster than individuals that consumed littoral prey resources. As such, the specific objectives of this study were to (1) describe growth of Walleyes, (2) evaluate abiotic and biotic conditions related to growth of Walleyes, and (3) evaluate variation in individual growth related to variation in diet of Walleyes in the Lake Pend Oreille system.

Methods

Study site

The Lake Pend Oreille system is located in northern Idaho and contains Lake Pend Oreille, the Clark Fork River, and the Pend Oreille River (Figure 3.1). Lake Pend Oreille is an oligotrophic, cold-water lake with an average depth of 164 m and a maximum depth of 351 m. The Clark Fork River is the main inflow to the lake and the Pend Oreille River is the only outflow. Daily and seasonal fluctuations of the water level of Lake Pend Oreille are controlled by Cabinet Gorge Dam on the Clark Fork River and Albeni Falls Dam on the Pend Oreille River. Lake Pend Oreille supports robust populations of native and non-native fishes. Native fishes include Bull Trout *Salvelinus confluentus*, Westslope Cutthroat Trout *O. clarkii lewisi*, Mountain Whitefish *Prosopium willimsoni*, Pygmy Whitefish *P. coulterii*, Slimy Sculpin *Cottus cognatus*, Largescale Sucker *Castostomus macrocheilus*, Redside Shiner, Peamouth Chub *Mylocheilus caurinus*, and Northern Pikeminnow *Ptychocheilus oregonensis*. Non-native fish include kokanee, Rainbow Trout, Lake Trout *S. namaycush*, Brown Trout *Salmo trutta*, Smallmouth Bass *M. dolomieu*, Largemouth Bass, Tench *Tinca tinca*, Yellow Perch *Perca flavescens*, Northern Pike *Esox lucius*, and Walleye (Maiolie et al. 2004; Rust et al. 2020).

Walleyes in the Lake Pend Oreille system were first sampled below Cabinet Gorge Dam (Figure 3.1) 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). Since 2011, the Idaho Department of Fish and Game (IDFG) has monitored the population and observed patterns of exponential population growth in which the population doubled approximately every three years. In 2018, IDFG implemented a mitigation program to reduce Walleye recruitment in the system (Rust et al. 2020; Ryan et al. 2021). Since its initiation, catch rates of Walleyes during the mitigation efforts have decreased, as have catch rates during standardized monitoring.

Field sampling and processing

Fishes were sampled every other week from May 2020–May 2021 using standardized sinking gill nets following specifications from the Fall Walleye Index Netting (FWIN) protocol (Morgan 2002). 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 mm, 38 mm, 51 mm, 64 mm, 76 mm, 102 mm, 127 mm, and 152 mm). Typically, nets were set 1-2 hours before dusk and retrieved 1-3 hours after dawn. Walleyes were also collected opportunistically from four other programs including spring Walleye mitigation netting conducted by the Hickey Brothers Research (HBR) and IDFG; FWIN monitoring conducted by IDFG; salmonid population monitoring conducted by Avista Corporation; and Lake Trout suppression, nursery, and assessment netting conducted by HBR and IDFG. Sinking gill nets used in the spring Walleye mitigation netting were 274 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-mm, 106-mm, or 114-mm stretched mesh). Ten gill nets were joined together. Nets were set around dawn and allowed to soak for 4–6 hours. In the FWIN sampling, sinking gill nets with the same specifications as the bi-weekly sampling were soaked for approximately 24 hours. Walleyes were also captured during salmonid population monitoring with nighttime boat electrofishing using pulsed DC at 400 volts, 60 hertz, and 20% duty cycle (Ransom 2022). Sinking gill nets used during all the Lake Trout netting efforts consisted of 10 individual gill nets tied together. Each individual gill net was 274 m long and consisted of three 91.4 m panels each with a single mesh size. Stretched mesh sizes for the suppression program (September–November) were 127 mm and 140 mm. Mesh sizes for the nursery program targeting juvenile Lake Trout (December–March) were 51 mm and 64 mm; and mesh sizes

used for the assessment program (December–March) were 38 mm, 44 mm, 51 mm, 64 mm, 76 mm, 89 mm, 102 mm, 114 mm, 127 mm, and 140 mm.

Zooplankton were sampled in May 2022 and *Mysis diluviana* (hereafter, *Mysis*) were sampled in June 2021. Both taxa were sampled via vertical tows. Zooplankton were sampled using a zooplankton net with a 0.5-m diameter opening, 80- μ m mesh, and 80- μ m collection bucket. *Mysis* were sampled using a zooplankton net with 1-m diameter opening 1-mm mesh, and 500- μ m collection bucket.

Total length to the nearest millimeter and weight to the nearest gram was measured for all collected fishes. Tissue from the anterior dorsal musculature, sufficient to fill a 2 mL centrifuge tube, was collected from all Walleyes and a subset of all bycatch for stable isotope analysis. If a substantial ontogenetic shift in diet was expected to occur for bycatch (i.e., Bull Trout, Lake Trout, Northern Pikeminnow, Smallmouth Bass), muscle samples were collected from 20 individuals less than and 20 individuals greater than the length at which the shift was expected to occur (Appendix A). Because *Mysis* diets can vary by size (Chipps and Bennett 2000), individuals were grouped based on size (< 1 cm, small; > 1 cm, large). A single *Mysis* sample for isotope analysis consisted of ~5 g of large or small individuals. Bulk zooplankton samples were grouped by site and one sample consisted of up to 5 g. Muscle, zooplankton, and *Mysis* 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 hours, cooled in a desiccator for at least 30 minutes, and ground to a fine powder with either a mortar and pestle or a Wig-I-bug automatic grinder (International Crystal Laboratories, Garfield, New Jersey). Approximately 1 mg of each sample was encapsulated in a tin cup and processed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. All isotope samples were processed at the Washington State University Stable Isotope Core Laboratory. Samples were converted to N_2 and CO_2 with an elemental analyzer (ECS 4010, Costech Analytical, Valencia, CA) and analyzed with a continuous flow isotope ratio mass spectrometer (Delta PlusXP, Thermofinnigan, Bremen; 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 standard:

$$\delta = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \times 1,000,$$

where δ (‰) is the difference, R_{standard} is the isotope ratio of the standard (Vienna Pee Dee Belmnite for $^{13}\text{C}/^{12}\text{C}$ and atmospheric N_2 for $^{15}\text{N}/^{14}\text{N}$), and R_{sample} is the isotope ratio of the

sample. Three 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, Lake Bluff, Illinois) 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. Back-calculated lengths at age were estimated using the Dahl-Lea method (Ricker 1992). Growth patterns for individual Walleye were described using the relative growth index (Quist et al. 2003) as:

$$RGI = (L_t/L_s) \times 100,$$

where RGI is the relative growth index, 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 a fish grew faster than average, whereas a value below 100 indicated a fish grew slower than average relative to Walleyes sampled across North America.

Factors influencing growth

A mixed-effects regression model was used to assess the effects of age and year on growth of Walleyes in the Lake Pend Oreille system (Weisberg et al. 2010). The effects of age and year were evaluated as:

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

where y_{cka} is the a th annular increment for the k th fish from year class c ; l_a is the annular increment for a fish in the a th year of life; h_{c+a-1} is the environmental effect for the year that a fish in year-class c was age a ; f_{ck} is the random effect of fish k in the c th year-class, and e_{cka} is the error associated with the model. Age was treated as a fixed effect; whereas, year and individual fish were treated as random effects. Incremental growth was modeled for ages 1–14. Because consumption of kokanee by Walleyes was observed after an apparent shift to piscivory (i.e., age 1; Chapter 2), the growth increment from age 0 to age 1 was not included in the model. Estimates of the year effects from the model were then used as the response variable in linear regression to evaluate the relationship between growth and environmental

conditions among years (Watkins et al. 2017; McCarrick et al. 2021). Independent variables included abundance (millions) and biomass (tonnes) of kokanee, *Mysis* density ($Mysis/m^2$), average monthly water temperature ($^{\circ}C$) from June–September, and discharge (i.e., inflow [m^3/s] from Cabinet Gorge Dam, Teichert et al. 2010; Sammons et al. 2021; Sinnickson et al. 2001). Kokanee abundance, kokanee biomass, and *Mysis* densities from 2009–2021 were obtained from standard monitoring efforts conducted by IDFG. Mid-water trawls were used to collect morphometric data (i.e., length, weight) and evaluate age structure of kokanee (Corsi et al. 2019). Prior to trawling, the vertical distribution of kokanee was identified using a depth sounder. Kokanee were sampled using a stepwise (3.0 m in height), oblique tow (3–6 steps per tow, 3 min in duration) with 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 per stratum) were randomly selected across Lake Pend Oreille. Total length and weight were measured from all kokanee collected. Scales were collected from 10–15 individuals per 10 mm length group for ageing. Abundance and biomass of kokanee were evaluated with hydroacoustic surveys using a Simrad EK60 echosounder. Total lake-wide 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 software version 6.1.60.87483 (Echoview Software Pty Ltd, Hobart, Tasmania; 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 mid-water trawls to abundance estimates for each stratum. Age-specific abundance estimates of all strata were then summed to estimate total lake-wide, 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. Lake-wide biomass was then calculated by summing the age-specific biomass estimates across strata.

Mysis were collected using vertical tows in the same strata sampled to evaluate abundance and biomass of kokanee. Eight sites per strata were sampled using a 1 m conical net with a mesh size of 1000 μm and a collection bucket with a 500 μm mesh size (Chippis and Bennett 1996). Density 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 lake-wide density. Mean yearly inflow data (m^3/s) at Cabinet Gorge Dam were collected from the U.S. Geological Survey Stream Gage (site 12391950 below Cabinet Gorge Dam) and accessed through the National Water Information System (USGS 2001). Water temperature ($^{\circ}\text{C}$) data from Lake Pend Oreille were collected by the Idaho Department of Environmental Quality and IDFG from 2011–2021. Data used in the regression model of growth represented the average monthly temperature of Lake Pend Oreille from June to July in each year. Water temperature was monitored once per month and a measurement was collected at every 1 m increment through the epilimnion (i.e., 0–15 m) at all sampling sites (Figure 3.1). The mixed-effects regression model included year effects for 2009 and 2010, but water temperature data were not available for these years. Because of the necessity of complete cases in information theoretic processes (Nakagawa and Freckleton 2011), I predicted water temperature for 2009 and 2010 from a regression relating observed air temperature and observed water temperature (Appendix E). Air temperature data were collected from the National Oceanic and Atmospheric Administration weather station in Sandpoint, Idaho (station US1IDBR0004). Mean monthly air temperature data were retrieved from Climate Data Online maintained by the National Climatic Data Center (NOAA 2006).

Multicollinearity among independent variables was evaluated using Spearman's correlation coefficient (r). Variables were considered correlated if $|r| \geq 0.70$ (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 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 within two AIC_c of the top model. Akaike's weights (w_i) were used to evaluate the relative likelihood of each model. The w_i was then summed across all models containing each of the explanatory variables (Marchetti et al. 2004; Quist et al. 2005; Katsanevakis and Maravelias 2008). The summation of w_i was used to evaluate the relative

importance of a specific explanatory variable. Model fit was further evaluated using the coefficient of determination (R^2 ; Sokal and Rohlf 2001).

Individual growth

The relationship between $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, and growth was assessed using two approaches. Because growth of fishes varies seasonally, including Walleyes in the Lake Pend Oreille system (Chapter 2), only individuals sampled in October were used to eliminate variation in growth due to time of sampling. Additionally, the greatest number of individuals, by month, were sampled in October. The first approach evaluated the age-specific relationship between growth (i.e., length-at-age-at-capture) and $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ using linear regression. The response variable was length-at-age-at-capture and the explanatory variable was $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$. Relationships were evaluated for age-1, age-2, age-3, and age-5 individuals because all other age classes had fewer than 10 individuals. The second approach evaluated differences in growth as a function $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were further evaluated 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., age 1, age 2, age 3, age 5). Differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ between fast- and slow-growing Walleyes were evaluated using a non-parametric Wilcoxon test stratified by age class (Conover 1980). All analyses were conducted in R (R Core Team 2022) with a type-I error rate of 0.05.

Results

In total, 1,157 Walleyes were collected from the Lake Pend Oreille system. Total length varied from 175 mm to 822 mm and ages varied from 0 to 20 years. Relative growth index values varied from 45-165 among individuals (Table 3.1). Mean RGI was >100 for all ages and was greatest for age 1. Generally minimum RGI values increased with age, whereas maximum RGI decreased.

Walleye growth was variable across years and was generally fastest in recent years (Figure 3.2). Walleye growth was related to environmental characteristics (Table 3.2). 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 were negatively associated with growth (Table 3.2; Figure 3.2). In all instances, models containing kokanee abundance ranked higher than models containing kokanee biomass (Table 3.2). The top model explaining growth only contained kokanee abundance. The three highest-ranked models included kokanee abundance. The sum of Akaike weights provided additional evidence of the importance of kokanee abundance to Walleye growth (Table 3.3).

Growth varied among individual Walleyes. Length-at-age-at-capture of Walleyes was related to $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for certain age classes (Figure 3.3). Length at age 1, age 2, and age 3 was positively related to $\delta^{15}\text{N}$, but negatively associated with age 5 (Figure 3.3). However, the relationships for age 3 and age 5 were not compelling ($r^2 < 0.15$). A similar trend existed for $\delta^{13}\text{C}$ where length of Walleyes and $\delta^{13}\text{C}$ were positively associated for age 1, age 2, and age 3, and negatively associated for age-5 individuals (Figure 3.4). Similar to $\delta^{15}\text{N}$, the relationships for age 2, age 3, and age 5 were not strong ($r^2 < 0.10$). Apparent differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ existed between the 25th and 75th percentiles of growth (Table 3.4). For age-1 to age-3 individuals, $\delta^{15}\text{N}$ was higher for walleye in the 75th percentile of growth than those in the 25th percentile. Carbon isotopes did not exhibit the same pattern. Individuals in the 75th percentile of growth had more depleted $\delta^{13}\text{C}$ except for age-1 individuals.

Discussion

Walleyes are newly established in the Lake Pend Oreille system, and as a result, little is known about factors regulating their population dynamics. The objectives of my research were to describe factors influencing growth and evaluate variability in individual growth. Walleyes in the Lake Pend Oreille system grew quickly, and growth remained high as Walleyes aged. Relative growth index values were consistently >100 for all age classes suggesting that Walleyes exhibited faster growth than other populations across North America. Generally, Walleyes in the northern latitudes grow slower compared to their southern counterparts (Quist et al. 2003). However, the observed RGI values in the Lake

Pend Oreille systems were greater than those observed from populations at similar latitudes and most similar to populations at the southern extent of their 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, whereas RGI for age-1 Walleyes in Kansas reservoirs varied from 133-162 (Quist et al. 2003). This pattern suggests that environmental conditions and resource availability in the Lake Pend Oreille system are not likely limiting growth of Walleyes. Additionally, the Walleye population density may be low enough that intraspecific competition is not likely an important factor limiting growth.

At a smaller spatial scale, growth of Walleyes did not appear to be related to temperature. Temperature has been identified as one of the most important abiotic conditions influencing growth of Walleye across its distribution (e.g., Hokanson 1977; Colby et al. 1979; Quist et al. 2003; Pedersen et al. 2018). As such, I expected water temperature to be an important predictor of Walleye growth in the Lake Pend Oreille system, but that hypothesis was not supported. 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). However, the Lake Pend Oreille system supports diverse habitats which likely provide a wide range of water temperatures. For example, temperature profiles in August 2011 on Lake Pend Oreille indicated that surface temperatures approached to 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.

The use of predicted water temperature in the mixed-effects regression models may have obscured the relationship between growth and water temperature. The relationship between air temperature and water temperature can be complex (Benyahya et al. 2007; Sharma et al. 2008; Laanaya et al. 2016). However, a high correlation between air temperature and water temperature has been well documented (e.g., Edinger et al. 1968; Livingstone and Lotter 1998; Piccolroaz et al. 2013; Honsey et al. 2019), including for lacustrine systems (Jacobson et al. 2010; Chezik et al. 2014; Walrath et al. 2015; Christianson et al. 2020). In an effort to assess whether the use of predicted water temperature affected my results, I used a subset of the data (i.e., not including the years with missing water temperature data) to assess the relationships between growth increments and

environmental variables. Temperature was not included in any of the top models, thereby suggesting that other factors (e.g., kokanee abundance) were more important for Walleye growth.

Similar to other systems (e.g., Hartman and Margraf 1992; Michaletz 1998b; Porath and Peters 1997; Hoxmeier et al. 2004; Graeb et al. 2008), prey abundance, in particular kokanee abundance, appeared to be the most important factor influencing growth of Walleyes in the Lake Pend Oreille system. Kokanee is an important prey species for many piscivores, particularly in cool- or cold-water systems (e.g. Clarke et al. 2005; Schoen et al 2012; Pate et al. 2014; Walrath et al. 2015; Warnock et al. 2021). For systems in the western United States, both native and non-native fishes consume kokanee at high rates. For example, in Lake Ozette, Washington, kokanee represented 20-60% of prey items consumed (by weight) of native Cutthroat Trout and 40-100% of prey items consumed by non-native Northern Pikeminnow (Beauchamp et al. 1995). Similarly, estimated consumption of kokanee by non-native Lake Trout represented 53-73% of the total kokanee production and biomass in Lake Chelan, Washington, during 2005 (Schoen et al. 2012). In Lake Pend Oreille, kokanee is the primary prey resource for piscivores (Vidergar 2000; Clarke et al. 2005). In total, Northern Pikeminnow, Rainbow Trout, Lake Trout, and Bull Trout consumed approximately 65% of the kokanee biomass in Lake Pend Oreille during 1998 (Vidergar 2000). As with other western systems (e.g., Baldwin et al 2003; High et al 2015), my results suggested that kokanee is an important prey resource for Walleyes. Kokanee abundance explained most of the variation in growth of Walleyes in the Lake Pend Oreille system. Analysis of Walleye food habits in Lake Pend Oreille further supported this finding (Chapter 2). On average, kokanee comprised 20-100% (by weight) of diets sampled from age-3 and older Walleye diets in the Lake Pend Oreille system. Arguably, kokanee abundance could be a surrogate for other factors influencing growth of Walleyes, but it is unclear what these factors may be.

Growth is a function of energy intake and expenditure (Hewett and Johnson 1987; Brandt and Hartman 1993; Jørgensen and Mangel 2016). Energy intake and expenditure varies across individuals and depends on factors such as temperature, prey availability, and handling time of prey (Werner 1974; Brown et al. 2004; Wright et al. 2014). As such, populations are composed of slow- and fast-growing individuals. My results indicated that

differences in growth of individuals may be 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 $\delta^{15}\text{N}$ values than slow-growing individuals. This pattern suggests that fast-growing individuals capitalized on fish rather than invertebrates and (or) fishes characteristic of higher trophic positions. Ontogenetic shifts to fishes as prey have been shown to influence growth and survival of juvenile fishes (e.g., Buijase and Houthujzen 1992; Olson 1996; Graeb et al. 2006). For instance, piscivorous age-0 Walleyes were longer than non-piscivorous age-0 Walleyes in Harlan County Reservoir, Nebraska (Uphoff et al. 2019). Additionally, in the Lake Pend Oreille system, the disparity in $\delta^{15}\text{N}$ values declined with age. This suggests that older individuals likely consumed similar prey items and (or) prey items at similar trophic positions. In nearby Priest Lake, little difference in $\delta^{15}\text{N}$ values was observed between fast- and slow-growing Lake Trout (Ng et al. 2017). The authors attributed the lack of variation to homogeneity in the diet. Similar patterns have been observed in Lake Pend Oreille piscivores (i.e., Bull Trout, Lake Trout, Northern Pikeminnow, Rainbow Trout; Clarke et al. 2005). Kokanee represented 88-100% of prey items observed in stomach contents by weight of Bull Trout and Lake Trout, and $\delta^{15}\text{N}$ values varied little with length for individuals ≥ 400 mm for both predators. Examination of stomach contents showed that kokanee was the dominant prey items of age-3 and older Walleyes (Chapter 2).

Evaluation of $\delta^{13}\text{C}$ provided additional insight into the factors related to growth of Walleyes. Given the importance of kokanee to Walleyes in the Lake Pend Oreille system, I expected fast-growing individuals to have more depleted $\delta^{13}\text{C}$. As with $\delta^{15}\text{N}$, the relationship between $\delta^{13}\text{C}$ and growth was not particularly strong, and $\delta^{13}\text{C}$ 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 individuals. However, fast-growing age-1 individuals had more enriched $\delta^{13}\text{C}$ 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 artedii* generally grew faster than Walleyes that consumed invertebrates and Yellow Perch

(Kaufman et al. 2009). However, in Lake Massey which contained no Ciscoes, female Walleyes that consumed Yellow Perch grew faster until maturity than Walleyes that consumed 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 (Chapter 2). This region contains an abundance of spiny-rayed fishes that may have been more available than soft-rayed fishes to age-1 Walleyes. Individual 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 (Chapter 2). In general, the main body of Lake Pend Oreille supports an abundance of soft-rayed fishes, in particular kokanee. Age-2 and older Walleyes likely benefitted from the high abundance of preferred prey types resulting in similar $\delta^{13}\text{C}$ among fast- and slow-growing individuals.

Walleyes in the Lake Pend Oreille system grew quickly relative to other populations across their distribution, particularly populations at similar latitudes. On a population level, kokanee abundance explained a majority of the variation in growth of Walleyes. Variation in individual growth appeared to reflect differences in diet particularly in age-1 Walleyes. My research adds to the body of literature describing factors that influence growth of Walleyes across their distribution. Although factors influencing the growth of Walleyes have been widely studied, my research is unique in that it describes growth of a recently established non-native population. Additionally, to my knowledge, no other study has explicitly identified a relationship between kokanee abundance and growth of Walleyes in western reservoirs. My study is one of few that has attempted to relate individual variability in growth to variability in stable isotopes. Understanding the factors influencing growth provide managers with valuable information on how Walleye growth might change under varying conditions and will inform management decisions.

References

- Baldwin, C. M., J. G. McLellan, M. C. Polacek, and K. Underwood. 2003. Walleye predation on hatchery releases of kokanees and Rainbow Trout in Lake Roosevelt, Washington. *North American Journal of Fisheries Management* 23:660-667.
- Baltz, D. M., J. W. Fleeger, C. F. Rakocinski, and J. N. McCall. 1998. Food, density, and microhabitat: factors affecting growth and recruitment potential of juvenile saltmarsh fishes. *Environmental Biology of Fishes* 53:89-103.
- Beauchamp, D. A., M. G. Lariviere, and G. L. Thomas. 1995. Evaluation of competition and predation as limits to juvenile kokanee and Sockeye Salmon production in Lake Ozette, Washington. *North American Journal of Fisheries Management* 15:193-207.
- Belk, M. C. 1998. Predator-induced delayed maturity in Bluegill sunfish (*Lepomis macrochirus*): variation among populations. *Oecologia* 113:203-209.
- Benyahya, L., D. Caissie, A. St-Hilarie, T. B. M. J. Ouarda, and B. Bobée. 2007. A review of statistical water temperature models. *Canadian Water Resources Journal* 32:179-192.
- Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulse, and M. L. Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist* 161:1-28.
- Bouwens, K. A., J. Strait, P. Rust, R. Ryan, A. L. Ransom, and R. Jakubowski. 2021. 2020 Lake Pend Oreille predator management program annual project update. Annual Report to Avista, Noxon, Montana, and Idaho Department of Fish and Game, Boise.
- Brandt, S. B., and K. J. Hartman. 1993. Innovative approaches with bioenergetics models: future applications to fish ecology and management. *Transactions of the American Fisheries Society* 122:731-735.
- Brenna, J. T., T. N. Corso, H. J. Tobias, and R. J. Caimi. 1998. High-precision continuous-flow isotope ratio mass spectrometry. *Mass Spectrometry Review* 16:337-258.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* 85:1771-1789.
- Buijse, A. D., and R. P. Houthuijzen. 1992. Piscivory, growth, and size-selective mortality of age-0 Pikeperch (*Stizostedion lucioperca*). *Canadian Journal of Fisheries and Aquatic Sciences* 19:894-902.

- Bunn, S. E., and A. H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30:492-507.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information theoretic approach, 2nd edition. Springer, New York.
- Carlander, K. D. 1997. Handbook of freshwater fishery biology: volume three. Iowa State University Press, Ames.
- Chezik, K. A., N. P. Lester, and P. A. Venturelli. 2014. Fish growth and degree-days II: selecting a base temperature for an among-population study. *Canadian Journal of Fisheries and Aquatic Sciences* 71:1303-1311.
- Chipps, S. R., and D. H. Bennet. 2000. Zooplanktivory and nutrient regeneration by invertebrate (*Mysis relicta*) and vertebrate (*Oncorhynchus nerka*) planktivores: implications for trophic interactions in oligotrophic lakes. *Transactions of the American Fisheries Society* 129:569-583.
- Chipps, S. R., and D. H. Bennet. 2006. Comparison of net mesh sizes for estimating abundance of the opossum shrimp *Mysis relicta* from vertical hauls. *North American Journal of Fisheries Management* 16:689-692.
- Christianson, K. R., B. M. Johnson, and M. B. Hooten. 2020. Compound effects of water clarity, inflow, wind and climate warming on mountain lake thermal regimes. *Aquatic Sciences* [online serial] 82:article 6. DOI: 10.1007/s00027-019-0676.6.
- Christie, G. C., and H. A. Regier. 1988. Measures of optimal thermal habitat and their relationship to yields for four commercial fish species. *Canadian Journal of Fisheries and Aquatic Sciences* 45:301-314.
- Clarke, L. R., D. T. Videgar, and D. H. Bennett. 2005. Stable isotopes and gut content show diet overlap among native and introduced piscivores in a large oligotrophic lake. *Ecology of Freshwater Fish* 14:267-277.
- Cleveland, B. M., T. D. Leeds, and C. E. Rexroad, III, S. T. Summerfelt, C. M. Good, J. W. Davidson, T. May, C. Crouse, W. R. Wolters, B. Plemmons, and P. B. Kenney. 2017. Genetic line by environment interaction on Rainbow Trout growth and processing traits. *North American Journal of Aquaculture* 79:140-154.

- Colby, P. J., R. E. McNicol, and R. A. Ryder. 1979. Synopsis of biological data on the Walleye, *Stizostedion v. vitreum* (Mitchill 1818). FAO Fisheries Synopsis 119.
- Conover, W. J. 1980. Practical nonparametric statistics, second edition. Wiley, New York.
- Corsi, M. P., M. J. Hansen, M. C. Quist, D. J. Schill, and 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.
- Craig, J. F. 2000. Percid fishes: systematics, ecology and exploitation. Blackwell Scientific Publications, Oxford.
- Cyterski, M. J., and G. R. Spangler. 1996. Development and utilization of a population growth history of Red Lake Walleye, *Stizostedion vitreum*. *Environmental Biology of Fishes* 46:45-59.
- Dunlop, E. S., and B. J. Shuter. 2006. Native and introduced populations of Smallmouth Bass differ in concordance between climate and somatic growth. *Transactions of the American Fisheries Society* 135:1175-1190.
- Ebersole, J. L., P. J. Wigington, Jr., J. P. Baker, M. A. Cairns, M. R. Church, B. P. Hansens, B. A. Miller, H. R. LaVigne, J. E. Compton, and S. G. Leibowitz. 2006. Juvenile Coho Salmon growth and survival across stream network seasonal habitats. *Transactions of the American Fisheries Society* 135:1681-1697.
- Edinger, J. E., D. W. Duttweiler, J. C. Geyer. 1968. The response of water temperatures to meteorological conditions. *Water Resources Research* 4:1137-1143.
- Einfalt, L. M., and D. H. Wahl. 1997. Prey selection by juvenile Walleye as influenced by prey morphology and behavior. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2618-2626.
- Evans, A. F., N. J. Hostetter, K. Collis, D. D. Roby, and F. J. Loge. 2014. Relationship between juvenile fish condition and survival to adulthood in Steelhead. *Transactions of the American Fisheries Society* 143:899-909.
- Fincel, M. J., D. J. Dembkowski, and S. R. Chipps. 2014. Influence of variable Rainbow Smelt and Gizzard Shad abundance on Walleye diets and growth. *Lake and Reservoir Management* 30:258-267.

- Fortin, R., P. Dumont, and S. Gu nette. 1996. Determinants of growth and body condition of Lake Sturgeon (*Acipenser fulvescens*). Populations from the St. Lawrence and Ottawa River system, Quebec. *Canadian Journal of Zoology* 71:638-650.
- Fraser, D. F., J. F. Gillam, M. J. Daley, A. N. Le, and G. T. Skalski. 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *The American Naturalist* 158:124-135.
- Fuiman, L. A. 1993. Development of predator evasion in Atlantic Herring *Clupea harangus*. *Animal Behavior* 45:1101-1116.
- Gilmour, K. M., J. D. DiBattista, and J. B. Thomas. 2005. Physiological causes and consequences of social status in salmonid fish. *Integrative and Comparative Biology* 45:263-273.
- Goodrich, H. R., and T. D. Clark. 2023. Why do some fish grow faster than others? *Fish and Fisheries* 24:796-811.
- Grabowski, T. B., S. P. Young, J. J. Isley, and P. C. Ely. 2012. Age, growth, and reproductive biology of three catostomids from the Apalachicola River, Florida. *Journal of Fish and Wildlife Management* 3:223-237.
- Graeb, B. D. S., M. T. Mangan., J. C. Jolly, D. H. Wahl, and J. M. Dettmers. 2006. Ontogenetic changes in prey preference and foraging ability of Yellow Perch: insights based on relative energetic return of prey. *Transactions of the American Fisheries Society* 135:1433-1742.
- Graeb, B. D. S., S. R. Chipps, D. W. Willis, J. P. Lott, R. P. Hanten, W. Nelson-Stastny, and J. W. Erickson. 2008. Walleye response to Rainbow Smelt population decline and liberalized angling regulations in a Missouri River reservoir. Pages 275-291 in M. S. Allen, S. Sammons, and M. J. Maceina, editors. *Balancing fisheries management and water uses for impounded river systems*. American Fisheries Society, 4th International Reservoir Symposium, Bethesda, Maryland.
- Hansen, M. J., D. Schill, J. Fredericks, and A. Dux. 2010. Salmonid predator-prey dynamics in Lake Pend Oreille, Idaho, USA. *Hydrobiologia* 650:85-100.
- Hartman, K. J., and F. J. Margraf. 1992. Effects of prey and predator abundances on prey consumption and growth of Walleyes in western Lake Erie. *Transactions of the American Fisheries Society* 121:245-260.

- Heath, D., and D. A. Roff. 1987. Test of genetic differentiation in growth of stunted and nonstunted populations of Yellow Perch and Pumpkinseed. *Transactions of the American Fisheries Society* 116:98-102.
- Hewett, S. W., and B. L. Johnson. 1987. A generalized bioenergetics model of fish growth for microcomputers. University of Wisconsin, Sea Grant Institute, Technical Report WIS-SG-87-24, Madison.
- High, B., D. Garren, G. Schoby, and J. Buelow. 2015. 2013 Upper Snake region annual fisheries management report. Annual Report to Idaho Department of Fish and Game, Boise.
- Hofmann, H. A., M. E. Benson, and R. D. Fernald. 1999. Social status regulates growth rate: consequences for life-history strategies. *Proceedings of the National Academy of Sciences* 96:14171-14176.
- Hokanson, K. E. F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. *Journal of Fisheries Research Board of Canada* 34:1524-1550.
- Honsey, A. E., P. A. Venturelli, and N. P. Lester. 2018. Bioenergetic and limnological foundations for using degree-days derived from air temperatures to describe fish growth. *Canadian Journal of Fisheries and Aquatic Sciences* 76:657-669.
- Houston, D. D., and M. C. Belk. 2006. Geographic variation in somatic growth of Redside Shiner. *Transactions of the American Fisheries Society* 135:801-810.
- Hoxmeier, R. J. H., D. H. Wahl, M. L. Hooe, and C. L. Pierce. 2004. Growth and survival of larval Walleyes in response to prey availability. *Transactions of the American Fisheries Society* 133:45-54.
- Hoxmeier, R. J. H., D. D. Aday, and D. H. Wahl. 2009. Examining interpopulation variation in Bluegill growth rates and size structure: effects of harvest, maturation, and environmental variables. *Transactions of the American Fisheries Society* 9:423-432.
- Jacobson, P., A. Gårdmark, J. Östergren, M. Casini, and M. Huss. 2018. Size-dependent prey availability affects diet and performance of predatory fish at sea: a case study of Atlantic Salmon. *Ecosphere* [online serial] 9:article e02081. DOI: 10.1002/ecs2.2081.

- Jacobson, P. C., H. G., Stefan, and D. L. Pereira. 2010. Coldwater fish oxythermal habitat in Minnesota lakes: influence of total phosphorus, July air temperature, and relative depth. *Canadian Journal of Fisheries and Aquatic Sciences* 67:2002-2013.
- Jacquemin, S. J., J. C. Doll, M. Pyron, M. Allen, and D. A. S. Owen. 2015. Effects of flow regime on growth rate in Freshwater Drum, *Aplodinotus grunniens*. *Environmental Biology of Fishes* 98:993-1003.
- Johnson, B. M., and J. P. Goettl, Jr. 1999. Food web changes over fourteen years following introduction of Rainbow Smelt into a Colorado reservoir. *North American Journal of Fisheries Management* 19:629-642.
- Jørgensen, C., K. Enberg, and M. Mangel. 2016. Modelling and interpreting fish bioenergetics: a role for behaviour, life-history traits and survival trade-offs. *Journal of Fish Biology* 88:389-402.
- Karjalainen, J., O. Urpanen, T. Keskinen, H. Huuskonen, J. Sarvala, P. Valkeajärvi, and T. J. Marjomäki. 2016. Phenotypic plasticity in growth and fecundity induced by strong population fluctuations affects reproductive traits of female fish. *Ecology and Evolution* 6:779-790.
- Katsanevakis, S., and C. D. Maravelias. 2008. Modelling fish growth: multi-model inference as a better alternative to *a priori* using von Bertalanffy equation. *Fish and Fisheries* 9:178-187.
- Katzir, G., and J. M. Camhi. 1993. Escape response of Black Mollies (*Poecilia sphenops*) to predatory dives of a Pied Kingfisher (*Ceryle rudis*). *Copeia* 1993:549-53.
- Kaufman, S. D., G. E. Morgan, and J. M. Gunn. 2009. The role of Ciscoes as prey in the trophy growth potential of Walleyes. *North American Journal of Fisheries Management* 29:468-477.
- Kennedy, P. J., T. J. Bartley, D. M. Gillis, K. S. McCann, and M. D. Rennie. 2018. Offshore prey densities facilitate similar life history and behavioral patterns in two distinct aquatic apex predators, Northern Pike and Lake Trout. *Transactions of the American Fisheries Society* 147:972-995.
- King, J. R., B. J. Shuter, and A. P. Zimmerman. 1999. Empirical links between thermal habitat, fish growth, and climate change. *Transactions of the American Fisheries Society* 128:656-665.

- Klein, Z. B., M. C. Quist, A. M. Dux, and M. P. Corsi. 2019. Size selectivity of sampling gears used to sample kokanee. *North American Journal of Fisheries Management* 39:343-352.
- Koch, J. D., and M. C. Quist. 2007. A technique for preparing fin rays and spines for age and growth analysis. *North American Journal of Fisheries Management* 27:782-784.
- Kocovsky, P. M., and R. F. Carline. 2001. Influence of extreme temperatures on consumption and condition of Walleyes in Pymatuning Sanctuary, Pennsylvania. *North American Journal of Fisheries Management* 21:198-207.
- Korman, J., and S. E. Campana. 2009. Effects of hydropeaking on nearshore habitat use and growth of age-0 Rainbow Trout in a large regulated river. *Transactions of the American Fisheries Society* 138:76-87.
- Korman, J., M. D. Yard, M. C. Dzul, C. B. Yackulic, M. J. Dodrill, B. R. Deemer, and T. A. Kennedy. 2021. Changes in prey, turbidity, and competition reduce somatic growth and cause the collapse of a fish population. *Ecological Monographs* [online serial] 91:article e01427. DOI: 10.1002/ecm.1427.
- Kraus, G., A. Müller, K. Trella, and F. W. Köster. 2000. Fecundity of Baltic cod: temporal and spatial variation. *Journal of Fish Biology* 56:1327-1341.
- Laanaya, F., A. St-Hilaire, and E. Gloaguen. 2017. Water temperature modelling: comparison between the generalized additive model, logistic, residuals regression and linear regression models. *Hydrological Sciences Journal* 62:1078-1093.
- Lavigne, M., M. Lucotte, and S. Paquet. 2010. Relationship between mercury concentration and growth rates for Walleyes, Northern Pike, and Lake Trout from Quebec lakes. *North American Journal of Fisheries Management* 30:1221-1237.
- Lee, D. S., C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister, and J. R. Stauffer. 1980. Atlas of North American fishes. North Carolina State Museum of Natural History, Raleigh.
- Livingstone, D. M., and A. F. Lotter. 1998. The relationship between air and water temperature in lakes of the Swiss Plateau: a case study with palaeolimnological implications. *Journal of Paleolimnology* 19:181-198.

- Maiolie, M. A., W. Harryman, and W. J. Ament. 2004. Lake Pend Oreille fishery recovery project. Idaho Department of Fish and Game. Annual Report to Bonneville Power Administration, Project 0002204. Portland, Oregon.
- Marchetti, M. P., P. B. Moyel, and R. Levine. 2004. Alien fishes in California watersheds: characteristic of successful and failed invaders. *Ecological Applications* 14:587-596.
- Margenau, T. L., P. W. Rasmussen, and J. M. Kampa. 1998. Factors affecting growth of Northern Pike in small northern Wisconsin lakes. *North American Journal of Fisheries Management* 18:625-639.
- Martino, J. C., A. J. Fowler, Z. A. Doubleday, G. L. Grammer, and B. M. Gillanders. 2019. Using otolith chronologies to understand long-term trends and extrinsic drivers of growth in fisheries. *Ecosphere* [online serial] 10. DOI: 10.1002/ecs2.2553.
- Massie, D. L., G. D. Smith, T. F. Bonvechio, A. J. Bunch, D. O. Lucchesi, and T. Wagner. 2018. Spatial variability and macro-scale drivers of growth for native and introduced Flathead Catfish populations. *Transactions of the American Fisheries Society* 147:554-565.
- Matthias, B. G., R. N. M. Ahrens, M. S. Allen, T. Tuten, Z. A. Siders, and K. L. Wilson. 2018. Understanding the effects of density and environmental variability on the process of fish growth. *Fisheries Research* 198:209-219.
- McCarrick, D. K., J. C. Dillon, B. High, and M. C. Quist. 2021. Population dynamics of Yellowstone Cutthroat Trout in Henrys Lake, Idaho. *Journal of Fish and Wildlife Management* 13:169-181.
- McDougall, C. A., P. A. Nelson, and C. C. Barth. 2018. Extrinsic factors influencing somatic growth of Lake Sturgeon. *Transactions of the American Fisheries Society* 147:459-479.
- Meise, C. J., D. L. Johnson, L. L. Stehlik, J. Manderson, and P. Shaheen. 2003. Growth rates of juvenile Winter Flounder under varying environmental conditions. *Transactions of the American Fisheries Society* 132:335-345.
- Michaletz, P. H. 1998a. Effects on sport fish growth of spatial and temporal variation in age-0 Gizzard Shad availability. *North American Journal of Fisheries Management* 18:616-624.

- Michaletz, P. H. 1998b. Population characteristics of Gizzard Shad in Missouri reservoirs and their relation to reservoir productivity, mean depth, and sportfish growth. *North American Journal of Fisheries Management* 18:114-123.
- Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marshall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences* 45:1657-1670.
- Mittelbach, G. G. 1988. Competition among refuging sunfishes and effects of fish density on littoral zone invertebrates. *Ecology* 69:614-623.
- Mittelbach, G. G., and L. T. Persson. 1998. The ontogeny of piscivory and its ecological consequences. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1454-1465.
- Mittelbach, G., G., N. G. Ballew, and M. K. Kjelson. 2014. Fish behavioral types and their ecological consequences. *Canadian Journal of Fisheries and Aquatic Sciences* 71:927-944.
- Morgan, G. E. 2002. Manual of Instructions – fall Walleye index netting (FWIN). Ontario Ministry of Natural Resources, Peterborough.
- Nakagawa, S., and R. P. Freckleton. 2011. Model averaging, missing data and multiple imputation: a case study for behavioural ecology. *Behavioral Ecology and Sociobiology* 65:103-116.
- Nepal, V., and M. C. Fabrizio. 2020. Density-dependence mediates the effects of temperature on growth of juvenile Blue Catfish in nonnative habitats. *Transactions of the American Fisheries Society* 149:108-120.
- Neuheimer, A. B., R. E. Thresher, J. M. Lyle, and J. M. Semmens. 2011. Tolerance limit for fish growth exceeded by warming waters. *Nature Climate Change* 1:110-113.
- Ng, E. L., J. P. Fredericks, and M. C. Quist. 2017. Stable isotope evaluation of population- and individual-level diet variability in a large, oligotrophic lake with non-native Lake Trout. *Ecology of Freshwater Fish* 26:271-279.
- Nielsen, J. L. 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile Coho Salmon. *Transactions of the American Fisheries Society* 121:617-634.
- Nilsson, C., and B. M. Renöfält. 2008. Linking flow regime and water quality in rivers: a challenge to adaptive catchment management. *Ecology and Society* [online serial] 13:article 18.

- NOAA (National Oceanic and Atmospheric Administration). 2006. Climate Data Online. Available: <https://www.ncei.noaa.gov/cdo-web/search?datasetid=GHCND>. (October 2023).
- Nohner, J. K., W. W. Taylor, D. B. Hayes, and B. M. Roth. 2018. Influence of aquatic macrophytes on age-0 Largemouth Bass growth and diets. *Transactions of the American Fisheries Society* 147:758-769.
- Norin, T., H. Malte, and T. D. Clark. 2016. Differential plasticity of metabolic rate phenotypes in a tropical fish facing environmental change. *Functional Ecology* 30:369-378.
- Olson, M. H. 1996. Predator-prey interactions in size-structured fish communities: implications of prey growth. *Oecologia* 108:757-763.
- Overtuf, K., M. T. Casten, S. L. LaPatra, C. Rexroad III, and R. W. Hardy. 2003. Comparison of growth performance, immunological response and genetic diversity of five strains of Rainbow Trout (*Oncorhynchus mykiss*). *Aquaculture* 217:93-106.
- Parker-Stetter, S. L., L. G. Rudstam, P. J. Sullivan, and D. M. Warner. 2009. Standard operating procedures for fisheries acoustic surveys in the Great Lakes. Great Lakes Fishery Commission, Special Publication 09-01. Ann Arbor, Michigan.
- Pate, W. M., B. M. Johnson, J. M. Lepak, and D. Brauch. 2013. Managing for coexistence of kokanee and trophy Lake Trout in a montane reservoir. *North American Journal of Fisheries Management* 34:908-922.
- Pedersen, E. J., D. Goto, J. W. Gaeta, G. J. A. Hansen, G. G. Sass, M. J. Vander Zanden, T. A. Cichosz, and A. L. Rypel. 2018. Long-term growth trends in northern Wisconsin Walleye populations under changing biotic and abiotic conditions. *Canadian Journal of Fisheries and Aquatic Sciences* 75:733-745.
- Piccolraoz, S., M. Toffolon, and B. Majone. 2013. A simple lumped model to convert air temperature into surface water temperature in lakes. *Hydrology and Earth System Sciences* 17:3323-3338.
- Porath, M. T., and E. J. Peters. 1997. Use of Walleye relative weights (W_r) to assess prey availability. *North American Journal of Fisheries Management* 17:628-637.
- Porter, N. J., T. F. Bonvechio, J. L. McCormick, and M. C. Quist. 2014. Population dynamics of Bowfin in a south Georgia reservoir: latitudinal comparisons of population

- structure, growth, and mortality. *Journal of the Southeastern Association of Fish and Wildlife Agencies* 1:103-109.
- Post, D. M., C. A. Layman, D. A. Arrington, G. Takimoto, J. Quattrochi, and C. G. Montaña. 2007. Getting to the fat of the matter: models, methods, and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* 152:179-189.
- Purchase, C. F., N. C. Collins, G. E. Morgan, and B. J. Shuter. 2005. Predicting life history traits of Yellow Perch from environmental characteristics of lakes. *Transactions of the American Fisheries Society* 134:1369-1381.
- Qi, H., T. B. Coplen, H. Geilmann, W. A. Brand, and J. K. Böhlke. 2003. Two new organic reference materials for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements and a new value for the $\delta^{13}\text{C}$ of NBS 22 oil. *Rapid communications in Mass Spectrometry* 17:2483-2487.
- Quist, M. C., and C. S. Guy. 2001. Growth and mortality of prairie stream fishes: relations with fish community and instream habitat characteristics. *Ecology of Freshwater Fish* 10:88-96.
- Quist, M. C., C. S. Guy, R. D. Schultz, and J. L. Stephen. 2003. Latitudinal comparisons of Walleye growth in North America and factors influencing growth of Walleyes in Kansas reservoirs. *North American Journal of Fisheries Management* 23:677-692.
- Quist, M. C., Rahel, J., and W. A. Hubert. 2005. Hierarchical faunal filters: an approach to assessing effects of habitat and nonnative species on native fishes. *Ecology of Freshwater Fish* 14:24-39.
- Quist, M. C., and J. R. Spiegel. 2012. Population demographics of catostomids in large river ecosystems: effects of discharge and temperature on recruitment dynamics and growth. *River Research and Applications* 28:1567-1586.
- R Core Team. 2022. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Ransom, A. L. 2022. 2018 and 2021 Lower Clark Fork River salmonid abundance monitoring project annual project update. Annual Report to Avista, Noxon, Montana, and Idaho Department of Fish and Game, Boise.
- Reed, B. C., W. E. Kelso, and D. A. Rutherford. 1992. Growth, fecundity, and mortality of Paddlefish in Louisiana. *Transactions of the American Fisheries Society* 121:378-384.

- Reinitz, G. L., L. E. Orme, and F. N. Hitzel. 1979. Variations of body composition and growth among strains of Rainbow Trout. *Transactions of the American Fisheries Society* 108:204-207.
- Ricker, W. E. 1992. Back-calculation of fish lengths based on proportionality between scale and length increments. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1018-1026.
- Rideout, R. M., and M. J. Morgan. 2010. Relationships between maternal body size, condition, and potential fecundity of four north-west Atlantic demersal fishes. *Journal of Fish Biology* 76:1379-1395.
- Rust, P., N. G. Mucciarone, S. M. Wilson, M. P. Corsi, and W. H. Harryman. 2020. Lake Pend Oreille research, 2017 and 2018: Lake Pend Oreille fishery recovery project. Idaho Department of Fish and Game. Annual Report to Bonneville Power Administration, Project 1994-047-00. Portland, Oregon.
- Ryan, R. G., M. P. Corsi, and P. Rust. 2021. Characteristics of an introduced Walleye population with implications for suppression. *North American Journal of Fisheries Management* 41:1863-1877.
- Sammons, S. M., L. Earley, and M. Goclowski. 2021. Effect of discharge on hatching and growth of age-0 black bass in two southeastern U.S. rivers. *Journal of Fish and Wildlife Management* 12:434-452.
- Sass, G. G., S. W. Hewett, D. Beard Jr., A. H. Fayram, and J. F. Kitchell. 2004. The role of density dependence in growth patterns of ceded territory Walleye populations of Northern Wisconsin: effects of changing management regimes. *North American Journal of Fisheries Management* 24:1262-1278.
- Schoby, G. P., T. P. Bassista, and M. A. Maiolie. 2007. Effects of higher winter water levels on the Pend Oreille River fish community: Lake Pen Oreille fishery recovery project. Annual report to Bonneville Power Administration, Project 1997-047-00. Portland, Oregon.
- Schoen, E. R., D. A. Beauchamp, and N. C. Overman. 2012. Quantifying latent impacts of an introduced piscivore: pulsed predatory inertia of Lake Trout and decline of kokanee. *Transactions of the American Fisheries Society* 141:1191-1206.

- Shervette, V. R., and F. Gelwick. 2006. Habitat-specific growth in juvenile Pinfish. *Transactions of the American Fisheries Society* 136:445-451.
- Siegel, J. E., M. V. McPhee, M. D. Adkison. 2017. Evidence that marine temperatures influence growth and maturation of western Alaskan Chinook Salmon. *Marine and Coastal Fisheries* 9:441-456.
- Sih, A. 1980. Optimal foraging: partial consumption of prey. *The American Naturalist* 116:281-290.
- Sinnickson, D., D. Chegaris, and M. Allen. 2021. Exploring impacts of river discharge on forage fish and predators using ecopath with ecosim. *Frontiers in Marine Science* 8:article 689950. DOI:10.3389/fmars.2021.689950.
- Sokal, R. R., and F. J. Rohlf. 2001. *Biometry: the principles and practice of statistics in biological research* 3rd edition. W. H. Freeman and Company, New York.
- Staggs, M. D., and K. J. Otis. 1996. Factors affecting first-year growth of fishes in Lake Winnebago, Wisconsin. *North American Journal of Fisheries Management* 16:608-618.
- Stamp, M. A., and J. D. Hadfield. 2020. The relative importance of plasticity versus genetic differentiation in explaining between population differences; a meta-analysis. *Ecology Letters* 23:1432-1441.
- Svanbäck, R., M. Quevedo, J. Olsson, and P. Eklöv. 2015. Individuals in food webs: the relationships between trophic position and omnivory and among-individual diet variation. *Oecologia* 177:1-2.
- Szendrey, T. A., and D. H. Wahl. 1996. Size-specific survival and growth of stocked Muskellunge: effects of predation and prey availability. *North American Journal of Fisheries Management* 16:395-402.
- Teichert, M. A. K., E. Kvingedal, T. Forseth, O. Ugedal, and A. G. Finstad. 2010. Effects of discharge and local density on the growth of juvenile Atlantic Salmon *Salmon salar*. *Journal of Fish Biology* 76:1751-1769.
- Tonkin, Z., A. Kitchingman, J. Lyon, J. Kearns, G. Hackett, J. O'Mahony, P. D. Moloney, K. Krusic-Golub, and T. Bird. 2017. Flow magnitude and variability influence growth of two freshwater fish species in a large regulated floodplain river. *Hydrobiologia* 797:289-301.

- USGS (U.S. Geological Survey). 2001. National Water Information System. Available: <https://waterdata.usgs.gov/monitoring-location/12391950/>. (February 2023).
- Uphoff, C. S., C. W. Schoenebeck, K. D. Koupal, K. L. Pope, and W. W. Hoback. 2019. Age-0 Walleye *Sander vitreus* display length-dependent diet shift to piscivory. *Journal of Freshwater Ecology* 34:27-36.
- VanDeValk, A. J., J. L. Forney, and J. R. Jackson. 2008. Relationships between relative weight, prey availability, and growth of Walleyes in Oneida Lake, New York. *North American Journal of Fisheries Management* 28:1868-1875.
- Vidregar, D. T. 2000. Population estimates, food habits and estimates of consumption of selected predatory fishes in Lake Pend Oreille, Idaho. Master's thesis. University of Idaho, Moscow.
- Vinagre, C., T. Ferreira, L. Matos, M. J. Costa, and H. N. Cabral. 2009. Latitudinal gradients in growth and spawning of Sea Bass, *Dicentrarchus labrax*, and their relationship with temperature and photoperiod. *Estuarine, Coastal, and Shelf Science* 81:375-380.
- Walrath, J. D., M. C. Quist, and J. A. Firehammer. 2015. Trophic ecology of nonnative Northern Pike and their effect on conservation of native Westslope Cutthroat Trout. *North American Journal of Fisheries Management* 35:158-177.
- Ward, M. J., D. W. Willis, B. H. Miller, and S. R. Chipps. 2007. Walleye consumption and long-term population trends following Gizzard Shad introduction into a western South Dakota reservoir. *Journal of Freshwater Ecology* 22:339-345.
- Warnock, W. G., J. L. Thorley, S. K. Arndt, T. J. Weir, M. D. Neufeld, J. A. Burrows, and G. F. Andrusak. 2021. Kootenay Lake kokanee (*Oncorhynchus nerka*) collapse into a predator pit. *Canadian Journal of Fisheries and Aquatic Sciences* 79:234-248.
- Watkins, C. J., T. J. Ross, M. C. Quist, and R. S. Hardy. 2017. Response of fish population dynamics to mitigation activities in a large regulated river. *Transactions of the American Fisheries Society* 146:703-715.
- Weber, M. J., and M. L. Brown. 2013. Density-dependence and environmental conditions regulate recruitment and first-year growth of Common Carp in shallow lakes. *Transactions of the American Fisheries Society* 142:471-482.

- Weisberg, S. B., and W. H. Burton. 1993. Enhancement of fish feeding and growth after an increase in minimum flow below the Conowingo Dam. *North American Journal of Fisheries Management* 13:103-109.
- Weisberg, S., G. Spangler, and L. S. Richmond. 2010. Mixed effects models for fish growth. *Canadian Journal of Fisheries and Aquatic Sciences* 67:269-277.
- Werner, E. E. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. *Journal of the Fisheries Research Board of Canada* 31:1531-1536.
- Wolf, A. E., M. J. Hubers, B. A. Johnson, T. R. St. Sauver, and D. W. Willis. 1994. Growth of Walleyes in South Dakota waters. *Prairie Naturalist* 26:217-220.
- Wolfert, D. R. 1969. Maturity and fecundity of Walleyes from the eastern and western basins of Lake Erie. *Journal of the Fisheries Board of Canada* 26:1877-1888.

Tables and Figures

Table 3.1 Back-calculated lengths (mm) at age and relative growth index (RGI) values of Walleyes sampled from 2020-2021 in the Lake Pend Oreille system. The mean (Mean), minimum (Min), and maximum (Max) values of each index are indicated in the corresponding columns. The numbers in parentheses indicate one standard error.

Age	<i>n</i>	Back-calculated length			RGI		
		Mean	Min	Max	Mean	Min	Max
1	1081	225 (1)	108	293	127 (0.6)	60.5	165
2	856	333 (2)	132	432	115 (0.6)	45.7	149
3	657	418 (2)	167	521	112 (0.5)	44.8	140
4	507	483 (3)	276	587	111 (0.6)	63.6	135
5	458	538 (3)	321	658	112 (0.6)	66.9	137
6	232	570 (5)	353	690	111 (0.9)	68.7	134
7	135	588 (7)	387	747	109 (1.2)	71.8	139
8	91	598 (7)	408	790	107 (1.3)	73.2	142
9	68	617 (8)	426	769	108 (1.4)	74.7	135
10	65	650 (8)	449	750	112 (1.4)	77.3	129
11	61	681 (9)	472	784	115 (1.5)	80.2	133
12	21	690 (19)	501	822	116 (3.1)	84.3	138
13	7	656 (35)	521	791	110 (5.9)	87.0	132
14	2	631 (75)	556	707	105 (12.5)	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

Table 3.2 . Regression models evaluating factors related to growth of Walleyes collected from the Lake Pend Oreille system in 2020-2021. Akaike's information criterion adjusted for small sample size (AIC_c) was used to rank candidate models. The number of model parameters (K), delta AIC_c (ΔAIC_c), model weight (w_i), and the multiple R^2 (R^2) are included. The direction of effect for each explanatory variable is indicated (positive [+] or negative[-]). An a indicates the value was < 0.01 . Variables are abbreviated as average water temperature from June through August ($^{\circ}C$; TEMP), kokanee abundance (millions; KOK_{abd}); kokanee biomass (tonnes; KOK_{bio}); inflow at Cabinet Gorge Dam (m^3/s ; INF); *Mysis diluviana* density (number/ m^2 ; MYS); and the null model (NULL).

Model parameters	K	AIC_c	ΔAIC_c	w_i	R^2
KOK_{abd} (+)	3	94.43	0.00	0.42	0.51
KOK_{abd} (+), TEMP (+)	4	96.80	2.37	0.13	0.58
KOK_{abd} (+), MYS (-)	4	97.31	2.87	0.10	0.57
MYS (-)	3	98.41	3.98	0.06	0.34
KOK_{abd} (+), INF (-)	4	98.74	4.31	0.05	0.41
MYS (-), TEMP (+)	4	98.93	4.50	0.04	0.51
KOK_{bio} (+)	3	99.35	4.91	0.04	0.29
TEMP (+)	3	99.56	5.13	0.03	0.28
MYS (-), INF (-)	4	100.21	5.78	0.02	0.46
NULL	2	100.34	5.90	0.02	--
KOK_{abd} (+), MYS (-), TEMP (+)	5	100.65	6.22	0.02	0.63
KOK_{bio} (+), MYS (-)	4	101.46	7.02	0.01	0.40
KOK_{bio} (+), TEMP (+)	4	101.75	7.32	0.01	0.39
KOK_{abd} (+), MYS (-), INF (-)	5	102.11	7.68	0.01	0.59
KOK_{abd} (+), TEMP (+), INF (-)	5	102.37	7.93	0.01	0.58
MYS (-), TEMP (+), INF (-)	5	103.03	8.59	0.01	0.56
INF (-)	3	103.51	9.08	a	0.02
KOK_{bio} (+), INF (-)	4	103.65	9.22	a	0.29
TEMP (+), INF (-)	4	103.87	9.44	a	0.28
KOK_{bio} (+), MYS, TEMP (+)	5	104.32	9.89	a	0.51
KOK_{bio} (+), INF (-), MYS (-)	5	105.76	11.33	a	0.46
KOK_{bio} (+), INF (-), TEMP (+)	5	107.25	12.82	a	0.39
KOK_{abd} (+), MYS (-), TEMP (+), INF (-)	6	107.62	13.19	a	0.65
KOK_{bio} (+), MYS (-), TEMP (+), INF (-)	6	110.29	15.86	a	0.57

Table 3.3 Sum of Akaike's Information Criteria 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 ($^{\circ}\text{C}$; TEMP), kokanee abundance (millions; KOK_{abd}); kokanee biomass (tonnes; KOK_{bio}); inflow at Cabinet Gorge Dam (m^3/s ; INF); and *Mysis diluviana* density (number/ m^2 ; MYS).

Variable	$\sum w_i$
KOK_{abd} (+)	0.74
MYS (-)	0.27
TEMP (+)	0.25
INF (-)	0.10
KOK_{bio} (+)	0.06

Table 3.4 Average carbon ($\delta^{13}\text{C}$) and average nitrogen ($\delta^{15}\text{N}$) values for individuals of the 25th and 75th percentiles of growth for each age-class of Walleyes sampled in the Lake Pend Oreille system in 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 a test of differences between the percentile groups by age class.

Percentile	n	Length	$\delta^{15}\text{N}$	P	$\delta^{13}\text{C}$	P
Age 1						
25	16	271 (4)	9.71 (0.10)	< 0.01	-27.25 (0.17)	0.01
75	16	375 (8)	10.67 (0.16)		-26.10 (0.34)	
Age 2						
25	8	347 (7)	10.59 (0.10)	< 0.01	-27.17 (0.19)	0.95
75	9	448 (9)	11.64 (0.22)		-27.20 (0.24)	
Age 3						
25	4	444 (1)	11.53 (0.24)	0.44	-28.14 (0.29)	0.60
75	4	529 (5)	11.96 (0.47)		-27.84 (0.46)	
Age 5						
25	10	526 (12)	12.90 (0.12)	0.28	-27.48 (0.47)	0.12
75	10	668 (4)	12.72 (0.10)		-28.33 (0.21)	

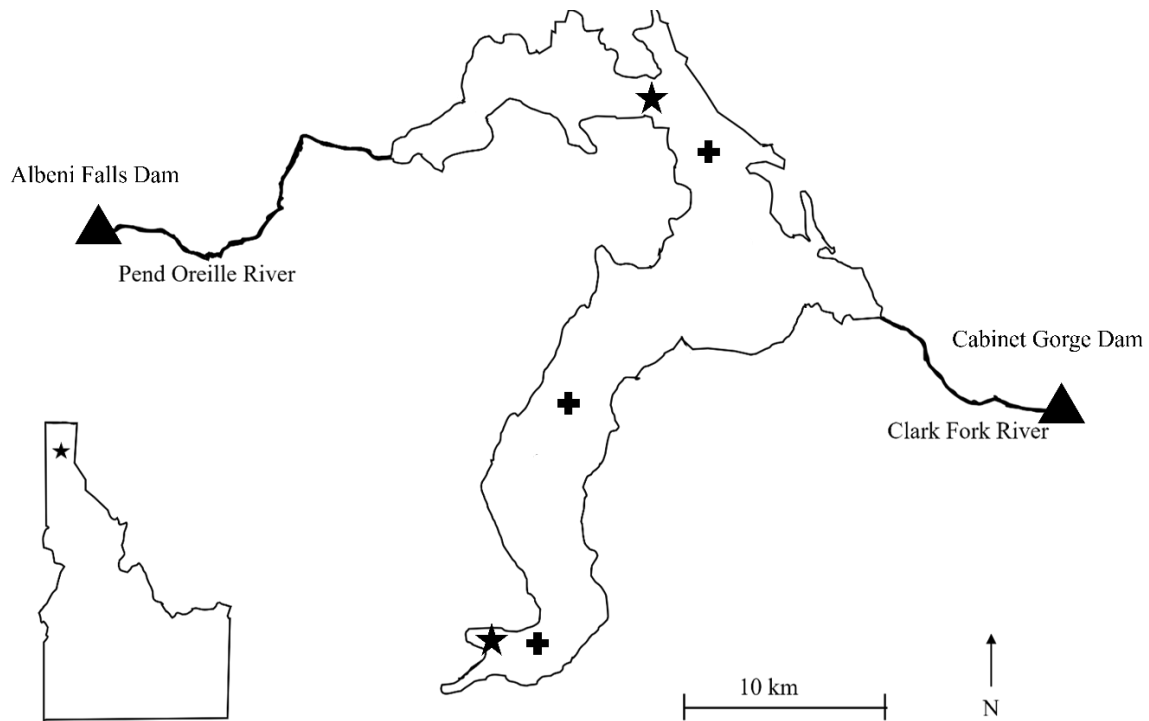


Figure 3.1 The Lake Pend Oreille system located in northern Idaho. This system included Lake Pend Oreille, the Pend Oreille River, and the Clark Fork River. The triangles indicated where hydroelectric facilities are located. Cabinet Gorge Dam is located on the border of Idaho-Montana, and Albeni Falls Dam is located on the border of Idaho-Washington. The stars indicate the water quality monitoring sites surveyed by the Department of Environmental Quality, and the plus signs indicate the Idaho Fish and Game sites for limnological profiles.

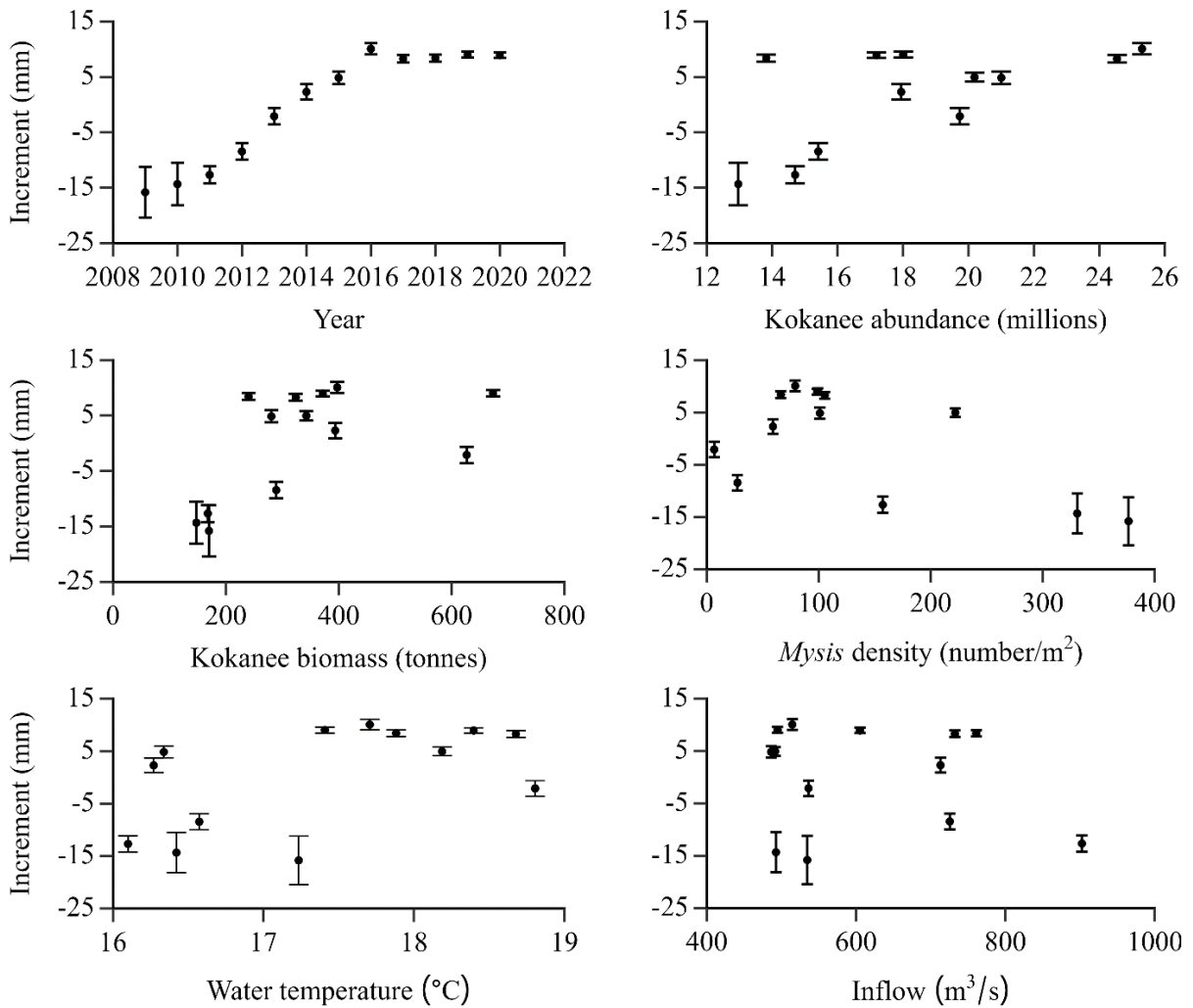


Figure 3.2 Estimated incremental growth from the mixed-effects regression model for Walleyes collected from the Lake Pend Oreille system in 2020-2021 compared to kokanee *Oncorhynchus nerka* abundance (millions), biomass of kokanee (tonnes), *Mysis diluviana* density (number/m²), mean summer temperature (°C; June-August), and inflow (m³/s) from Cabinet Gorge Dam. Points represent the growth coefficient estimate for a given year and bars indicate one standard error.

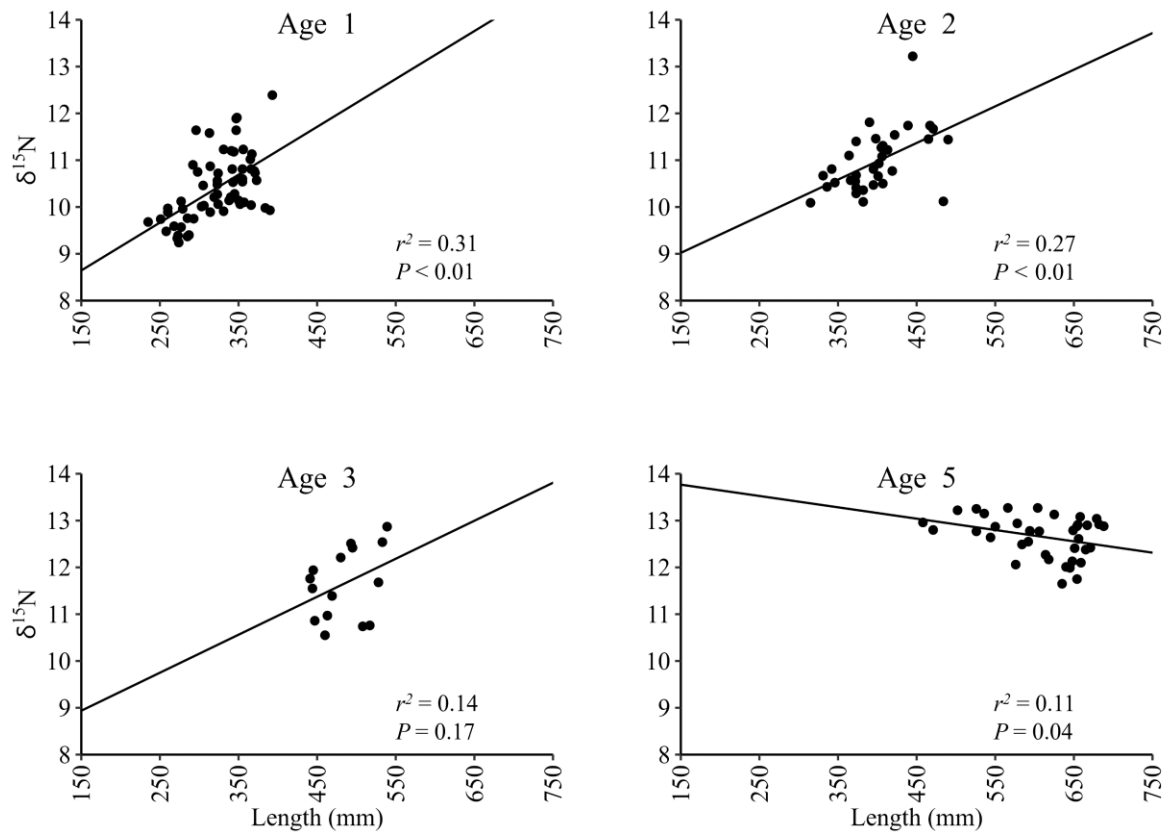


Figure 3.3 Age-specific regressions of $\delta^{15}\text{N}$ relative to length of Walleyes collected from the Lake Pend Oreille system in October, 2020.

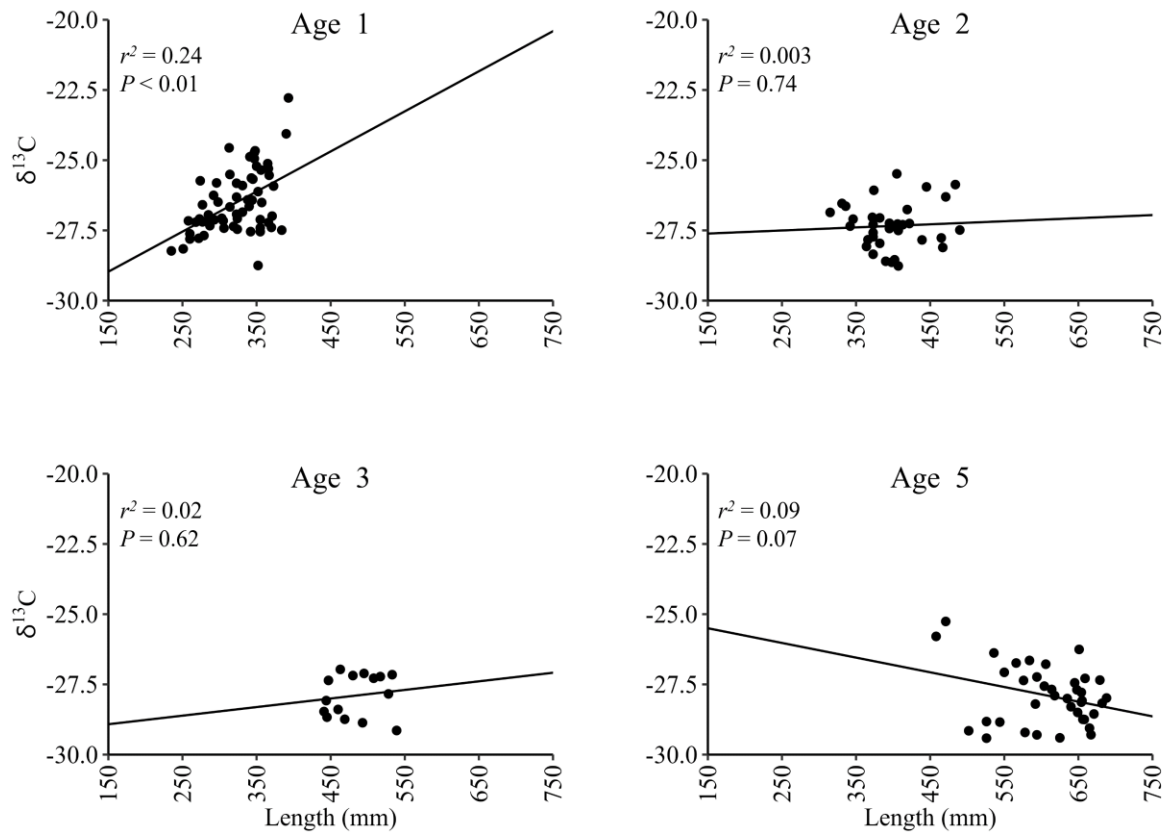


Figure 3.4 Age-specific regressions of $\delta^{13}\text{C}$ relative to length of Walleyes collected from the Lake Pend Oreille system in October, 2020.

Chapter 4: General Conclusions

Walleyes *Sander vitreus* are important for their recreation and ecological value particularly in their native distribution. However, Walleyes have been introduced widely throughout North America and many populations currently exist in the western United States. Because of their highly predatory nature, non-native Walleyes have the capacity to negatively effect prey populations. The goal of this research was to evaluate the trophic ecology and factors influencing growth of a recently established, non-native Walleye population in the Lake Pend Oreille system located in northern Idaho. This thesis provides valuable information regarding the consumption of various prey resources by Walleyes. Additionally, this thesis contains information regarding factors influencing growth of Walleyes and assessed individual variability as it relates to variability in diets.

Overall, consumption of prey resources by Walleyes is reminiscent of other systems across the United States. Walleyes consumed multiple prey types including fishes and macroinvertebrates. Kokanee *Oncorhynchus nerka* was identified as an important prey item in Walleye stomachs and was the most frequently consumed prey item. Other important prey items included native cyprinids and catostomids, as well as non-native centrarchids and percids. Consumption of prey types varied by age and across spatial and temporal gradients. Although most prey types were consumed consistently by Walleyes, consumption of kokanee increased with Walleye age. Bioenergetics modeling revealed that, for most cohorts, Walleyes were not consuming prey items at the maximum rates given the observed temperatures. However, Walleyes grew continuously through the year and generally grew faster than populations across North America, particularly those at similar latitudes. Growth of Walleyes in the Lake Pend Oreille system was likely related to diet. Abundance of kokanee was an important factor related to Walleye growth in the system. Fast-growing individuals had more enriched $\delta^{15}\text{N}$ and more depleted $\delta^{13}\text{C}$ values suggesting consumption of prey types at higher trophic positions and from pelagic habitats.

My thesis provides insight into the food habits of Walleyes and factors influencing growth of the population in the Lake Pend Oreille system. Although kokanee is an important resource for Walleyes, the extent of direct predation is still relatively unknown due to little information regarding encounter rates between Walleyes and kokanee, suitability of habitat

throughout the system, and the current density of Walleyes in the system. Despite uncertainty in the predatory demand of Walleyes, this research shows that Walleyes use similar prey resources as other piscivores in the system (i.e., Rainbow Trout *O. mykiss*, Bull Trout *Salvelinus confluentus*, Lake Trout *S. namaycush*, Northern Pikeminnow *Ptychocheilus oregonensis*). The current management objectives of the Lake Pend Oreille system are to provide a harvest fishery for kokanee and a trophy fishery for Rainbow Trout, maintain or enhance Westslope Cuthroat Trout *O. clarkii lewisi* and Bull Trout populations, and provide diverse angling opportunities in Lake Pend Oreille. Meeting these goals will likely be difficult especially if the Walleye population continues to grow in the system. Consistent monitoring of the Walleye population will aid in identifying changes in relative abundance and provide insight into factors regulating Walleye abundance. Given the management goals, continued removal of Walleyes from the Lake Pend Oreille system appears to be necessary particularly if environmental conditions become more favorable for Walleyes.

Although this thesis provides critical information about Walleyes in the Lake Pend Oreille system, much remains unknown. During my sampling, few Walleyes were captured during the winter. Assessing Walleye movements and habitat use (i.e., location, depth) may provide important information regarding habitat overlap or encounter rates with kokanee and other piscivores. Although kokanee was identified as an important prey resource, native catostomids and cyprinids were consistently consumed by Walleyes. Monitoring the relative abundance of these taxa may aid in further identifying the predatory demand of Walleyes. Additionally, little information is known about Walleye recruitment and associated variation that may occur. Since Walleye populations typically exhibit substantial variation in recruitment, changes in relative abundance observed in this system may be a function of recruitment variation rather than a result of management actions. Identifying factors related to or limiting recruitment will likely provide insight regarding management actions to maintain the Walleye population at a low abundance. Current management actions remove large, spawning females from the system. Removing these individuals likely influences size structure of the population and may influence age at maturity. Size selectivity of the gear used to remove Walleyes could potentially leave a portion of the spawning population unaffected by removal efforts. Additionally, changes to the size structure caused by gear selectivity may influence total predatory demand particularly since I observed differences in

food habits across age (i.e., length). Thus, it may be necessary to reevaluate food habits of Walleyes in the future.

Appendix A

Appendix A.1. Length (mm) thresholds for species in the Lake Pend Oreille system. Individuals larger than the threshold values were considered adults, and individuals smaller than the threshold values were classified as juveniles.

Species	Threshold length (mm)	Reference
Black Crappie	140	Tuten et al. 2008
Bull Trout	300	Lowery and Beauchamp 2015
Northern Pikeminnow	300	McIntyre et al. 2011
Lake Trout	430	Zimmerman et al. 2009
Smallmouth Bass	150	Olson and Young 2003

Appendix B

Appendix B.1. Regional contribution of prey items to Walleye diets collected from the Lake Pend Oreille system from May 2020 to May 2021. Summarizations were proportion by weight (W), frequency of occurrence (F), and proportion of energy (calories) contributed (E). Blank cells indicate the species did not occur in the given region, and *a* indicates the proportional contribution was < 0.01. Taxa abbreviations were Black Crappie (BCR), Brook Trout (BKT), Bluegill (BLG), Brown Bullhead (BRB), Gasterosteidae spp. (GAS), kokanee (KOK), Largemouth Bass (LMB), Longnose Sucker (LNS), Largescale Sucker (LSS), Lake Whitefish (LWF), macroinvertebrates (MAC), Mountain Whitefish (MWF), *Mysis diluviana* (MYS), Northern Pikeminnow (NPM), other (OTH), Pumpkinseed (PKS), Peamouth Chub (PMC), Rainbow Trout (RBT), Cottidae spp. (SCP), Smallmouth Bass (SMB), Tench (TNC), unknown fish (UNK), Walleye (WAE), Westslope Cutthroat Trout (WCT), and Yellow Perch (YEP). Regions were defined as Pend Oreille River (POR), northern Lake Pend Oreille (LPO-N), central Lake Pend Oreille (LPO-C)

Taxa	Region														
	POR			LPO-N			LPO-C			CFR			LPO-S		
	F	W	E	F	W	E	F	W	E	F	W	E	F	W	E
UNK	0.25	0.13	0.02	0.23	0.13	0.01	0.33	0.24	0.04	0.23	0.18	0.01	0.12	0.06	<i>a</i>
KOK	0.08	0.08	0.46	0.27	0.26	0.84	0.23	0.21	0.83	0.26	0.26	0.81	0.76	0.76	1.00
MAC	0.11	0.06	<i>a</i>	0.19	0.11	<i>a</i>	0.09	0.04	<i>a</i>	0.23	0.13	<i>a</i>			
PMC	0.23	0.18	0.24	0.08	0.05	0.02	0.14	0.11	0.04	0.10	0.08	0.08			
BCR	0.30	0.24	0.13	0.09	0.08	0.03	0.09	0.09	0.01	0.02	0.01	<i>a</i>			
NPM	0.07	0.05	0.04	0.07	0.04	0.01	0.05	0.01	<i>a</i>	0.19	0.15	0.03	0.06	<i>a</i>	<i>a</i>
YEP	0.13	0.08	0.04	0.10	0.09	0.01	0.05	0.05	0.04	0.04	0.02	<i>a</i>			
LSS	0.06	0.05	0.04	0.05	0.03	0.01	0.00	0.00	0.00	0.03	0.01	<i>a</i>			
RBT	<i>a</i>	<i>a</i>	<i>a</i>	0.06	0.04	0.03	0.07	0.04	0.01	0.04	0.02	0.03			
OTH	0.05	0.01	<i>a</i>	0.03	0.01	<i>a</i>	0.02	0.00	<i>a</i>	0.07	0.03	<i>a</i>			
WCT	0.01	<i>a</i>	<i>a</i>	0.05	0.03	0.02	0.05	0.02	0.01	0.05	0.03	0.02			
LNS	0.04	0.01	<i>a</i>	0.04	0.01	<i>a</i>				0.02	<i>a</i>	<i>a</i>			
BRB	0.02	0.01	<i>a</i>	0.06	0.05	0.01	0.02	0.02	<i>a</i>						
SCP	0.02	0.01	<i>a</i>	0.04	0.03	<i>a</i>	0.05	0.05	<i>a</i>						
MWF	0.00	0.00	0.00	0.03	0.01	0.01	0.02	0.02	0.01	0.05	0.04	0.02			
MYS	0.02	0.01	<i>a</i>	0.02	0.01	<i>a</i>	0.05	0.05	<i>a</i>	0.01	<i>a</i>	<i>a</i>	0.12	0.12	<i>a</i>
SMB	0.04	0.03	<i>a</i>	0.02	0.01	<i>a</i>							0.06	0.06	<i>a</i>
LWF				0.03	0.01	0.01				0.02	0.01	<i>a</i>			
TNC	0.04	0.02	0.01	<i>a</i>	<i>a</i>	<i>a</i>									
LMB	0.03	0.01	<i>a</i>							0.01	0.01	<i>a</i>			
GAS				<i>a</i>	<i>a</i>	<i>a</i>	0.05	0.03	0.00	0.02	0.01	<i>a</i>			
BKT				<i>a</i>	<i>a</i>	<i>a</i>	0.02	<i>a</i>	<i>a</i>						

continued

Appendix C

Appendix C.1. Seasonal contribution of prey items to Walleye diets collected from the Lake Pend Oreille system from May 2020 to May 2021. Summarizations were proportion by weight (W), frequency of occurrence (F), and proportion of energy (calories) contributed (E). Blank cells indicate the species did not occur in the given region, and *a* indicates the proportional contribution was < 0.01. Months were categorized as spring (March, April, May), summer (June, July, August), fall (September, October, November), and winter (December, January, February). Taxa abbreviations were Black Crappie (BCR), Brook Trout (BKT), Bluegill (BLG), Brown Bullhead (BRB), Gasterosteidae (GAS), kokanee (KOK), Largemouth Bass (LMB), Longnose Sucker (LNS), Largescale Sucker (LSS), Lake Whitefish (LWF), macroinvertebrates (MAC), Mountain Whitefish (MWF), *Mysis diluviana* (MYS), Northern Pikeminnow (NPM), other (OTH), Pumpkinseed (PKS), Peamouth Chub (PMC), Rainbow Trout (RBT), Cottidae (SCP), Smallmouth Bass (SMB), Tench (TNC), unknown fish (UNK), Walleye (WAE), Westslope Cutthroat Trout (WCT), and Yellow Perch (YEP).

Taxa	Season											
	Spring			Summer			Fall			Winter		
	F	W	E	F	W	E	F	W	E	F	W	E
UNK	0.15	0.10	<i>a</i>	0.29	0.17	0.01	0.29	0.17	0.01	0.20	0.13	0.07
KOK	0.24	0.23	0.86	0.34	0.34	0.79	0.17	0.17	0.71	0.12	0.10	0.09
MAC	0.30	0.18	<i>a</i>	0.11	0.05	<i>a</i>	0.06	0.02	<i>a</i>	0.04	0.04	<i>a</i>
PMC	0.09	0.08	0.03	0.07	0.07	0.04	0.19	0.14	0.12	0.08	0.06	0.06
BCR	<i>a</i>	<i>a</i>	<i>a</i>	0.18	0.17	0.07	0.21	0.18	0.06	0.32	0.21	0.37
NPM	0.12	0.10	0.02	0.01	0.01	0.01	0.10	0.06	0.03	0.04	0.01	0.01
YEP	0.05	0.04	<i>a</i>	0.09	0.07	<i>a</i>	0.11	0.08	0.01	0.20	0.18	0.24
LSS	0.04	0.02	<i>a</i>	0.05	0.02	<i>a</i>	0.05	0.04	0.02	0.04	0.03	0.02
RBT	0.04	0.03	0.02	0.04	0.03	0.05	0.05	0.02	0.01			
OTH	0.05	0.02	<i>a</i>	0.04	0.01	<i>a</i>	0.03	<i>a</i>	<i>a</i>			
WCT	0.05	0.03	0.02	0.02	<i>a</i>	<i>a</i>	0.03	0.01	<i>a</i>			
LNS	0.03	<i>a</i>	<i>a</i>	0.04	<i>a</i>	<i>a</i>	0.03	0.01	<i>a</i>	0.04	0.01	<i>a</i>
BRB	0.06	0.06	<i>a</i>	0.02	<i>a</i>	<i>a</i>	0.01	<i>a</i>	<i>a</i>			
SCP	0.05	0.04	<i>a</i>				0.01	<i>a</i>	<i>a</i>	0.04	0.04	<i>a</i>
MWF	0.03	0.02	<i>a</i>	0.01	<i>a</i>	<i>a</i>	0.02	0.02	<i>a</i>			
MYS	0.02	0.01	<i>a</i>	0.01	<i>a</i>	<i>a</i>	0.01	<i>a</i>	<i>a</i>	0.16	0.16	<i>a</i>
SMB	<i>a</i>	<i>a</i>	<i>a</i>	0.02	0.02	<i>a</i>	0.03	0.02	<i>a</i>			
LMB	<i>a</i>	<i>a</i>	<i>a</i>				0.02	<i>a</i>	<i>a</i>			
LWF	0.02	<i>a</i>	<i>a</i>	0.03	0.02	<i>a</i>	<i>a</i>	<i>a</i>	<i>a</i>			
TNC							0.02	0.01	<i>a</i>	0.04	0.02	0.11
LMB	<i>a</i>	<i>a</i>	<i>a</i>				0.02	<i>a</i>	<i>a</i>			
GAS	0.02	0.01	<i>a</i>							0.04	<i>a</i>	<i>a</i>

continued

Appendix C.1. continued

	Season											
	Spring			Summer			Fall			Winter		
	F	W	E	F	W	E	F	W	E	F	W	E
BKT	<i>a</i>	<i>a</i>	<i>a</i>	0.01	0.01	<i>a</i>						
BLG				0.01	<i>a</i>	<i>a</i>						
PKS	<i>a</i>	<i>a</i>	<i>a</i>							0.04	<i>a</i>	<i>a</i>
WAE							<i>a</i>	<i>a</i>	<i>a</i>			

Appendix D

Appendix D.1. Cohort-specific contribution of prey items to Walleye diets collected from the Lake Pend Oreille system from May 2020 to May 2021. Summarizations (SUM) were proportion by weight (W), frequency of occurrence (F), and proportion of energy (calories) contributed (E). Blank cells indicate the species did not occur in the given region and *a* indicates the proportional contribution was < 0.01. Taxa abbreviations were Black Crappie (BCR), Brook Trout (BKT), Bluegill (BLG), Brown Bullhead (BRB), Gasterosteidae (GAS), kokanee (KOK), Largemouth Bass (LMB), Longnose Sucker (LNS), Largescale Sucker (LSS), Lake Whitefish (LWF), macroinvertebrates (MAC), Mountain Whitefish (MWF), *Mysis diluviana* (MYS), Northern Pikeminnow (NPM), other (OTH), Pumpkinseed (PKS), Peamouth Chub (PMC), Rainbow Trout (RBT), Cottidae (SCP), Smallmouth Bass (SMB), Tench (TNC), unknown fish (UNK), Walleye (WAE), Westslope Cutthroat Trout (WCT), and Yellow Perch (YEP).

SUM	UNK	KOK	MAC	PMC	BCR	NPM	YEP	LSS	RBT	OTH	WCT	LNS	BRB	SCP	MWF	MYS	SMB	LWF	TNC	LMB	GAS	BKT	BLG	PKS	WAE
2000																									
F	—	1.00	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
W	—	1.00	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
E	—	1.00	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2007																									
F	—	1.00	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
W	—	1.00	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
E	—	1.00	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2009																									
F	0.11	0.33	0.15	0.41	—	—	—	—	—	0.04	0.04	—	0.04	0.04	0.04	—	0.04	0.04	—	—	—	—	—	—	—
W	0.05	0.31	0.12	0.36	—	—	—	—	—	<i>a</i>	0.04	—	0.04	0.02	0.02	—	0.04	<i>a</i>	—	—	—	—	—	—	—
E	<i>a</i>	0.86	<i>a</i>	0.11	—	—	—	—	—	<i>a</i>	<i>a</i>	—	<i>a</i>	<i>a</i>	0.01	—	<i>a</i>	<i>a</i>	—	—	—	—	—	—	—
2010																									
F	—	0.50	—	—	—	—	—	—	—	—	0.50	—	—	—	—	—	—	—	—	—	—	—	—	—	—
W	—	0.50	—	—	—	—	—	—	—	—	0.50	—	—	—	—	—	—	—	—	—	—	—	—	—	—
E	—	0.91	—	—	—	—	—	—	—	—	0.09	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2012																									
F	0.50	0.17	—	0.17	—	—	—	—	—	0.17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
W	0.50	0.17	—	0.17	—	—	—	—	—	0.17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

continued

Appendix D.1. continued

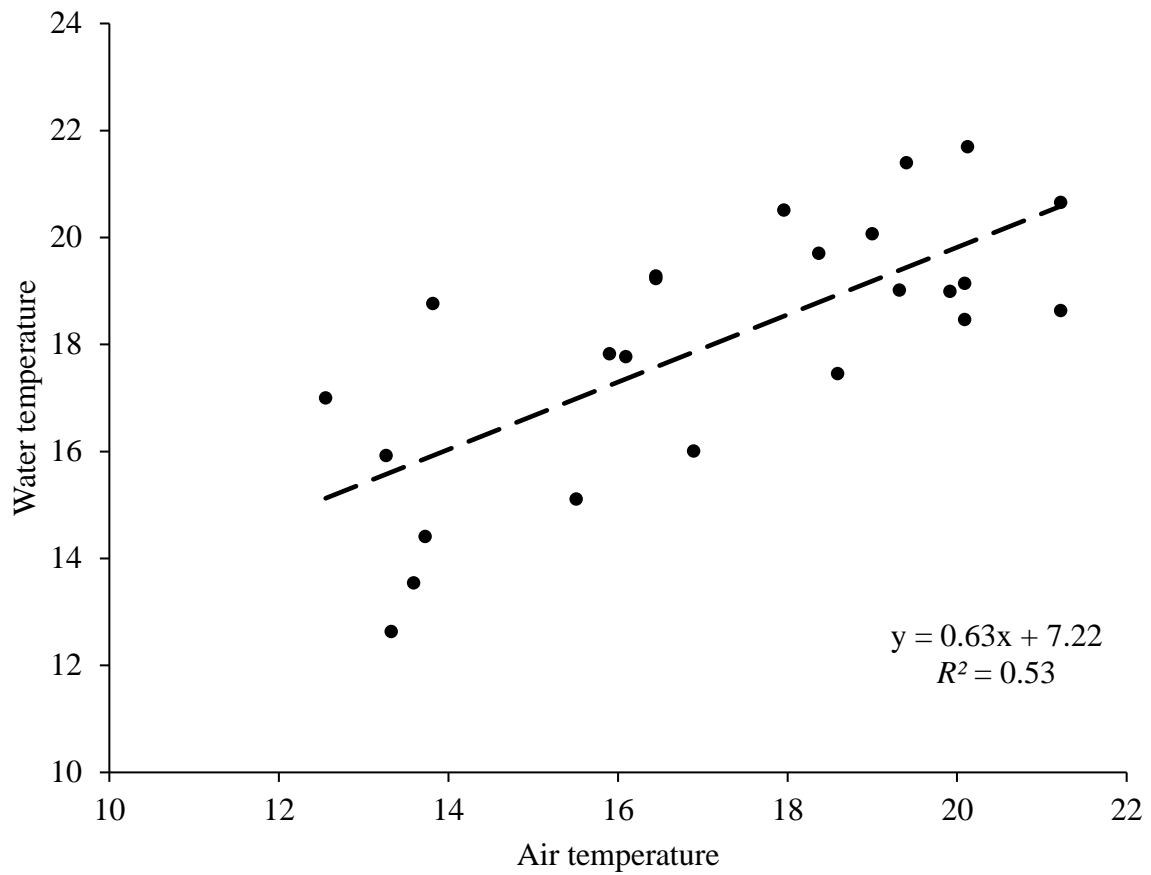
SUM	UNK	KOK	MAC	PMC	BCR	NPM	YEP	LSS	RBT	OTH	WCT	LSS	BRB	SCP	MWF	MYS	SMB	LWF	TNC	LMB	GAS	BKT	BLG	PKS	WAE	
2012																										
E	0.58	0.21	—	0.21	—	—	—	—	—	<i>a</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2013																										
F	0.12	0.42	0.12	0.15	—	0.04	0.08	0.12	0.12	—	0.12	0.08	0.08	—	—	—	—	—	—	—	0.04	—	—	—	—	—
W	0.08	0.41	0.08	0.14	—	0.01	<i>a</i>	0.07	0.08	—	0.04	0.01	0.08	—	—	—	—	—	—	—	<i>a</i>	—	—	—	—	—
E	<i>a</i>	0.9	<i>a</i>	0.03	—	<i>a</i>	<i>a</i>	0.04	<i>a</i>	—	<i>a</i>	<i>a</i>	<i>a</i>	—	—	—	—	—	—	—	<i>a</i>	—	—	—	—	—
2014																										
F	0.15	0.54	0.08	—	0.08	0.08	0.08	0.08	—	0.08	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
W	0.13	0.54	0.08	—	0.02	0.08	0.06	0.06	—	0.03	—	0.02	—	—	—	—	—	—	—	—	—	—	—	—	—	—
E	<i>a</i>	0.92	<i>a</i>	—	0.01	0.05	0.01	<i>a</i>	—	<i>a</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2015																										
F	0.24	0.46	0.12	0.07	0.05	0.07	0.05	<i>a</i>	0.04	0.02	0.04	0.01	0.04	0.02	—	—	<i>a</i>	—	0.01	<i>a</i>	—	—	—	—	0.01	—
W	0.17	0.45	0.05	0.06	0.03	0.04	0.04	<i>a</i>	0.03	0.01	0.03	<i>a</i>	0.04	0.01	—	—	<i>a</i>	—	<i>a</i>	<i>a</i>	—	—	—	—	<i>a</i>	—
E	0.01	0.86	<i>a</i>	0.04	0.02	0.01	<i>a</i>	<i>a</i>	0.02	<i>a</i>	0.02	<i>a</i>	<i>a</i>	<i>a</i>	—	—	<i>a</i>	—	<i>a</i>	<i>a</i>	—	—	—	—	<i>a</i>	—
2016																										
F	0.15	0.62	0.15	—	0.08	—	—	—	—	0.15	—	—	0.08	—	0.08	—	—	0.08	—	—	—	—	—	—	—	—
W	0.08	0.6	0.15	—	0.08	—	—	—	—	0.08	—	—	<i>a</i>	—	<i>a</i>	—	—	<i>a</i>	—	—	—	—	—	—	—	—
E	<i>a</i>	0.97	<i>a</i>	—	0.02	—	—	—	—	<i>a</i>	—	—	<i>a</i>	—	<i>a</i>	—	—	<i>a</i>	—	—	—	—	—	—	—	—
2017																										
F	0.30	0.22	0.17	0.17	0.06	0.06	0.06	0.02	0.07	0.06	0.06	0.02	0.04	—	0.02	—	0.02	—	—	—	0.04	0.04	—	—	—	—
W	0.20	0.20	0.11	0.14	0.04	0.03	0.04	0.01	0.06	<i>a</i>	0.03	<i>a</i>	0.04	—	0.02	—	0.01	—	—	—	0.03	0.02	—	—	—	—
E	0.02	0.54	<i>a</i>	0.14	0.05	0.01	0.02	<i>a</i>	0.13	<i>a</i>	0.06	<i>a</i>	<i>a</i>	—	0.01	—	<i>a</i>	—	—	—	<i>a</i>	<i>a</i>	—	—	—	—
2018																										
F	0.22	0.14	0.24	0.11	0.13	0.13	0.09	0.06	0.04	0.04	0.04	0.05	0.06	0.08	0.04	0.02	—	0.06	—	—	—	—	—	—	—	—
W	0.11	0.13	0.13	0.08	0.12	0.09	0.08	0.04	0.02	<i>a</i>	0.02	0.02	0.05	0.06	0.02	<i>a</i>	—	0.03	—	—	—	—	—	—	—	—
E	0.02	0.35	<i>a</i>	0.15	0.12	0.10	0.05	0.03	0.03	<i>a</i>	0.01	0.02	0.02	0.02	0.03	<i>a</i>	—	0.04	—	—	—	—	—	—	—	—
2019																										
F	0.26	0.03	0.15	0.14	0.25	0.12	0.14	0.08	0.04	0.04	0.02	0.05	0.02	0.02	0.04	0.04	0.04	<i>a</i>	0.02	0.02	<i>a</i>	—	<i>a</i>	—	<i>a</i>	—
W	0.15	0.03	0.09	0.10	0.22	0.09	0.10	0.05	0.02	<i>a</i>	<i>a</i>	0.02	<i>a</i>	0.02	0.03	0.03	0.03	<i>a</i>	<i>a</i>	0.01	<i>a</i>	—	<i>a</i>	—	<i>a</i>	—

continued

Appendix D.1. continued

SUM	UNK	KOK	MAC	PMC	BCR	NPM	YEP	LSS	RBT	OTH	WCT	LSS	BRB	SCP	MWF	MYS	SMB	LWF	TNC	LMB	GAS	BKT	BLG	PKS	WAE
2019																									
E	0.04	0.15	<i>a</i>	0.13	0.31	0.09	0.06	0.06	0.03	<i>a</i>	0.01	0.01	<i>a</i>	0.01	0.06	<i>a</i>	0.02	<i>a</i>	<i>a</i>	0.01	<i>a</i>	—	<i>a</i>	—	<i>a</i>
2020																									
F	0.28	—	0.28	0.17	0.22	0.17	0.11	—	0.06	—	—	—	—	—	—	0.17	0.06	—	0.06	—	—	—	—	—	—
W	0.12	—	0.11	0.11	0.21	0.10	0.09	—	<i>a</i>	—	—	—	—	—	—	0.15	0.06	—	0.04	—	—	—	—	—	—
E	0.11	—	0.02	0.23	0.34	0.10	0.05	—	<i>a</i>	—	—	—	—	—	—	0.01	0.11	—	0.02	—	—	—	—	—	—

Appendix E



Appendix E.1. Relationship between air temperature (°C) and water temperature (°C) during the summer months (June-August) 2011-2021 in Lake Pend Oreille.