USING DIETARY DYNAMICS TO ASSESS THE EFFICACY OF BIOCONTROL AND TO PREDICT THE EFFECTS OF WARMING WATER TEMPERATURES ON SALMONIDS

by

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ABSTRACT

Salmonids are coldwater fishes with substantial ecological and economic importance, particularly in the northern Rocky Mountains in Montana, USA, where fisheries are valued over US$750M annually. Georgetown Lake (Montana, USA) is renowned for its salmonid fishery. Although many anglers target kokanee (*Oncorhynchus nerka*) in Georgetown Lake, the body length of kokanee has typically been considered unsatisfactory. To reduce the density of kokanee and increase the average size, Montana Fish, Wildlife & Parks (MFWP) began stocking piscivorous Gerrard strain of rainbow trout (*Oncorhynchus mykiss;* hereafter Gerrard) in 2015 to consume kokanee. To assess the efficacy of biocontrol through the introduction of a piscivore to improve the size structure of kokanee, I used diet composition to determine the amount of predation on kokanee and to understand the feeding ecology of all potential predators. There was extremely low prevalence of piscivory and no evidence of Gerrards consuming kokanee. Gerrards exhibited a generalist feeding strategy and there was dietary and niche overlap and no difference in trophic position among Gerrards and trout. These findings highlight the unpredictability of predator-prey dynamics and the importance of evaluating management interventions, such as biocontrols. Additionally, this popular fishery could be in jeopardy because air temperatures in the region have warmed at twice the global average, leading to warmer water temperatures that could affect the thermal suitability for salmonids. Increased water temperatures can have sub-lethal effects, influencing growth, metabolism, and feeding rates of fish. Bioenergetics models were used to simulate the effects of warming water temperature on food consumption and growth for rainbow trout and kokanee within Georgetown Lake. My findings indicate that kokanee are more sensitive to warming than rainbow trout. While both species experience growth challenges as water temperatures exceed their optimal ranges, kokanee are particularly vulnerable, requiring higher food consumption to meet basic metabolic needs under elevated water temperatures. Thus, kokanee are likely to experience greater declines in growth compared to rainbow trout. Climate change will pose challenges for freshwater fisheries management, thus understanding how projected warming water temperatures may affect popular recreational fisheries can provide managers with information to establish reasonable expectations for fish growth.

CHAPTER ONE

THESIS INTRODUCTION

Introduction

Recreational fishing is a popular global activity that effects economies, social interactions, and biota (Pitcher and Hollingworth 2008). In the United States, recreational angling generates an estimated US$99.4 billion annually (U.S. DOI and U.S. FWS 2022). One highly prized genera sought by anglers, with substantial ecological and socioeconomic importance, are salmonids (e.g., *Salmo* and *Oncorhynchus* spp.; Brown et al. 2019). The northern Rocky Mountains in Montana support some of North America's most popular trout fisheries, valued at more than US$750 million annually (Lewis 2018) and representing more than 20% of spending by tourism in the state (Grau 2019). Georgetown Lake (Montana, USA) is renowned for its popular salmonid fishery.

Georgetown Lake exemplifies the complexity and challenges of managing freshwater fisheries in the face of multifaceted ecological and environmental factors. Although many anglers target kokanee (*Oncorhynchus nerka*; hereafter kokanee) in Georgetown Lake, the body length of kokanee has typically been considered unsatisfactory. To reduce the density of kokanee and increase the average size, Montana Fish, Wildlife & Parks (MFWP) began stocking piscivorous Gerrard strain of rainbow trout (*Oncorhynchus mykiss;* hereafter Gerrard) in 2015 to consume kokanee. Two other strains of rainbow trout (i.e., Eagle Lake and Arlee) and brook trout (*Salvelinus fontinalis*) are also stocked annually to support this popular recreational fishery. Additionally, this popular fishery could be in jeopardy because air temperatures in the region have warmed at twice the global average (Pederson et al. 2010), leading to warmer water temperatures that could affect the thermal suitability for salmonid species (IPCC 2007; Christensen et al. 2007). Increased water temperatures can have sub-lethal effects, influencing growth, metabolism, and feeding rates of fish (Fry 1971; Kitchell et al. 1977; Shuter and Post 1990; Magnuson et al. 1997; Brandt et al. 2002; Casselman 2002). Thus, it is important to understand how increased water temperatures will affect popular fisheries.

This thesis investigates two central but distinct management challenges in this dynamic system: (1) the efficacy of biocontrol through the introduction of a piscivore to improve the size structure of kokanee, and (2) how salmonid growth will be affected by warming water temperature. Together, these investigations provide a more comprehensive understanding of both immediate and long-term factors shaping this popular fishery.

Evaluating the prevalence and extent of piscivory in an introduced population, as well as the feeding ecology and strategy of predators is necessary to understand the effect of the introduced piscivore on the fish assemblage. The objective of **Chapter 2** was to assess the efficacy of biocontrol through the introduction of a piscivore to improve the size structure of kokanee. I used diet composition to determine the amount of predation on kokanee and to understand the feeding ecology of all potential predators. By evaluating the dietary compositions of the three strains of rainbow trout and brook trout seasonally from 2021 through 2023, dietary overlap was quantified among the trout, both seasonally and cumulatively. Stable isotopes were additionally used to assess a more long-term resolution of dietary habits to quantify if the three strains of rainbow trout and brook trout occurred within the same trophic position and to quantify the degree in which overlap may exist among the trout.

The objective of **Chapter 3** was to understand how projected warming water temperatures may affect the popular rainbow trout and kokanee fisheries in Georgetown Lake. Using Bioenergetics 4.0 (Deslauriers et al. 2017), I simulated the effects of warming water temperature on food consumption and growth for rainbow trout and kokanee within Georgetown Lake. These models will improve our understanding of how projected warming water temperatures may affect popular recreational fisheries, which can provide managers with information to establish reasonable expectations for fish growth.

Finally, **Chapter 4** describes conclusions to the research conducted in **Chapters 2 and 3,** and addresses considerations for future research that could illicit a more thorough understanding of factors affecting salmonid growth in Georgetown Lake.

References

Brandt, S., D. Mason, M. McCormick, B. Lofgren, T. Hunter, and J. Tyler. 2002. Climate change: Implications for fish growth performance in the Great Lakes. Transactions of the American Fisheries Society 32(32):61–76.

Brown, J. C., K. H. Lokensgard, S. Snyder, and M. Draper. 2019. The cultural currents and social values of trout. Pages 65-93 *in* J. L. Kershner, J. E. Williams, R. E. Gresswell, and J. Lobón-Cerviá, editors. Trout and char of the world. American Fisheries Society, Bethesda, Maryland.

Casselman, J. M. 2002. Effects of temperature, global extremes, and climate change on year-class production of warmwater, coolwater, and coldwater fishes in the Great Lakes Basin. American Fisheries Society Symposium 2002:39–60.

Christensen, J. H., B. Hewitson, A. Busuioc, A. Chen, X. Gao, I. Held, R. Jones, R. K. Kolli, W. T. Kwon, R. Laprise, V. Magana Rueda, L. Mearns, C. G. Menendez, J. Raisanen, A. Rinke, A. Sarr, and P. Whetton. 2007. Regional climate projections. Chapter 11. Climate change 2007: the physical science basis. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

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(11):586–596.

Fry, F. E. J. 1971. The effect of environmental factors on the physiology of fish. Pages 1–98 *in* W. S. Hoar and D. J. Randall, editors. Fish physiology. Academic Press.

Grau, K. 2019. 2018 Economic contribution of nonresident travel spending in Montana travel regions and counties. Institute for Tourism and Recreation Research Publications, Missoula, Montana.

IPCC. 2007. Climate change 2007: Impacts, adaptation and vulnerability. Contribution of working group II to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, UK.

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 the Fisheries Research Board of Canada 34(10):1922–1935.

Lewis, M. 2018. Statewide estimates of resident and nonresident hunter & angler trip related expenditures in Montana. Human Dimensions Unit Research Summary. Montana Fish, Wildlife & Parks, Helena, Montana.

Magnuson, J. J., K. E. Webster, R. A. Assel, C. J. Bowser, P. J. Dillon, J. G. Eaton, H. E. Evans, E. J. Fee, R. I. Hall, L. R. Mortsch, D. W. Schindler, and F. H. Quinn. 1997. Potential effects of climate changes on aquatic systems: Laurentian Great Lakes and Precambrian Shield Region. Hydrological Processes 11(8):825–871.

Pederson, G. T., L. J. Graumlich, D. B. Fagre, T. Kipfer, and C. C. Muhlfeld. 2010. A century of climate and ecosystem change in western Montana: What do temperature trends portend? Climatic Change 98(1):133–154.

Pitcher, T. J., and C. Hollingworth. 2008. Recreational fisheries: Ecological, economic and social evaluation. John Blackwell Publishing, Osney Mead, Oxford, UK.

Shuter, B. J., and J. R. Post. 1990. Climate, population viability, and the zoogeography of temperate fishes. Transactions of the American Fisheries Society 119(2):314–336.

U.S. Department of the Interior and U.S. Fish and Wildlife Service. 2022. 2022 National survey of fishing, hunting, and wildlife-associated recreation, Washington, D.C.

CHAPTER TWO

GERRARD STRAIN RAINBOW TROUT ARE NOT PISCIVOROUS IN A SHALLOW, POLYMICTIC RESERVOIR

Contribution of Authors and Co-Authors

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Introduction

Biocontrol is the addition or removal of abiotic or biotic factors from an ecosystem to achieve a desired outcome in the environment, such as introducing a piscivore to improve fish growth. Introducing a piscivore to improve growth has been successful for several salmonid fisheries (Damsgård and Langeland 1994; Koenig et al. 2015). However, the effects of introduced piscivores on freshwater ecosystems can be difficult to predict (Eby et al. 2006; Martinez et al. 2009) and lead to unintended results such as competition with existing fishes and the alteration of food-web structure (Vander Zanden et al. 1999; Rahel 2000; Zanden et al. 2003; Eby et al. 2006; Walsworth et al. 2013; Reynolds 2017). Thus, it is necessary to not only evaluate the prevalence and extent of piscivory in an introduced population, but also the feeding ecology and strategy of predators to gain a better understanding of the effect of the introduced piscivore on the fish assemblage.

Kokanee salmon (non-anadromous *Oncorhynchus nerka*; hereafter kokanee) growth rates are often controlled by density dependence (Rieman and Myers 1992; Martinez and Wiltzius 1995; Grover 2006; Buktenica et al. 2007), which can regulate populations through negative physiological consequences, such as reduced growth and fecundity (Beverton and Holt 1957; Burrough and Kennedy 1979; Rask 1983; Rochet 1998; Jenkins et al. 1999; Post et al. 1999; Ylikarjula et al. 1999; Svedäng and Hornborg 2014). Kokanee are mid-trophic level planktivores that preferentially feed on large-bodied Cladocera (Rieman and Bowler 1980; Vinyard et al. 1982; Martinez and Bergersen 1991; Wilson et al. 2021), are prey for piscivores (Andrusak and Parkinson, 1984; Ashley et al., 1997, 1999; Rieman & Bowler, 1980; Vinyard et al., 1982; Wilson et al., 2021; Wydoski and Bennett, 1981), and provide important subsistence and recreational opportunities (Wydoski and Bennett 1981; Liermann 2013; Wallace and Zaroban 2013). Density dependent growth and survival is frequently observed in *O. nerka* (i.e., kokanee and sockeye salmon) when elevated abundance results in intraspecific competition for zooplankton (Burgner 1897; Beattie and Clancey 1991; Rieman and Myers 1992, 1992; Paragamian and Bowles 1995; McGurk 1999; Griswold et al. 2022).

Some successful efforts to improve kokanee growth have relied on bottom-up controls by nutrient additions to increase primary production, zooplankton production, and ultimately, kokanee growth (Budy et al. 1998; Arndt 2004; Wilson et al. 2018; Schindler et al. 2020). However, nutrient additions are not always successful in improving kokanee growth, as poor *O. nerka* growth can occur even under nutrient additions due to high juvenile densities that selectively predate on Cladocera (Mazumder and Edmundson 2002). An alternative management strategy to bottom-up methods for improving kokanee growth is the use of top-down controls, such as biocontrol through piscivore introduction. The increased predation by piscivores on kokanee may release a population from density-dependent competition, thus improving growth rates (Persson et al. 2007).

The use of biocontrol through the introduction of a piscivore to improve the size structure of kokanee is being used in Georgetown Lake (Montana, USA). To reduce the density of kokanee and increase the average size, Montana Fish, Wildlife & Parks (MFWP) began stocking Gerrard strain of rainbow trout (*Oncorhynchus mykiss;* hereafter Gerrard) in 2015 to consume kokanee. Gerrard, a genetically distinct population native to Kootenay Lake (B.C., Canada), represent a rare ecotype of highly piscivorous rainbow trout that prey on kokanee (Northcote 1973; Irvine 1978; Keeley et al. 2005). Gerrards are large-bodied (> 5 kg in weight), have rapid growth, and high metabolic rates (Northcote 1973; Irvine 1978; Behnke 2010; Grummer et al. 2021). When introduced outside of their native waters, Gerrards have consistently exhibited similar characteristics to those in their native habitats, including preying on kokanee when present. For example, Gerrards were introduced from Kootenay Lake into Lake Pend Oreille (Idaho, USA) to consume kokanee (Wydoski and Bennett 1981; Vidergar 2000; Clarke et al. 2005; Rust et al. 2022). The introduction enabled Gerrards in Lake Pend Oreille to reach trophy sizes (Vidergar 2000; Clarke et al. 2005; Rust et al. 2022), including the former-world-record rainbow trout that weighed 16.78 kg (Wydoski and Bennett 1981). Thus, MFWP introduced Gerrards into Georgetown Lake due to their reliance on kokanee and ability to attain trophy sizes (B. Liermann, MFWP, personal communication). Additionally, two strains of rainbow trout (i.e., Eagle Lake and Arlee) and brook trout (*Salvelinus fontinalis*) are stocked annually to support a popular recreational fishery. In 2020, preliminary evidence suggested that the average length of kokanee greater than 200 mm increased from 275 mm (± 0.87 SE) to 313 mm (± 1.46 SE), which may be a result of predation by Gerrards (Brad Liermann, MFWP, unpublished).

Concurrently with the stocking of Gerrards, Georgetown Lake was filled at least 0.15 meters higher than full pool in the 2017 – 2020 irrigation seasons (Brad Liermann, MFWP, unpublished). Thus, an alternative hypothesis to the increased growth in kokanee is the nutrient influx that occurred from riparian areas being flooded and increased littoral zone. Unfortunately, there was no historical or contemporary data to determine the effects of the elevated lake level on kokanee growth.

Given the multiple hypotheses for the observed increase in kokanee growth and the lack of nutrient data, I set out to determine the amount of predation on kokanee by Gerrards and whether the predation rate would be sufficient as a top-down biocontrol on kokanee. Additionally, I sought to understand the feeding ecology of all potential predators (i.e., the three rainbow trout strains and brook trout) by season in Georgetown Lake. In this research I specifically addressed the following questions: (1) are Gerrard, Eagle Lake, Arlee, or brook trout consuming kokanee; (2) what are the feeding strategies of Gerrard, Eagle Lake, Arlee, and brook trout; and (3) what is the dietary overlap and trophic relationship among Gerrard, Eagle Lake, Arlee, and brook trout? Among the salmonids in Georgetown Lake, I expected Gerrards to exhibit a more specialized piscivorous feeding strategy due to their reliance on kokanee. Thus, there would be minimal dietary overlap and Gerrards would be a trophic level above Eagle Lake, Arlee, and brook trout.

Methods

Study Area

Georgetown Lake is a relatively shallow, polymictic, high-elevation reservoir renowned for its salmonid fishery. It is located in southwestern Montana, about 100 km southwest of Helena, Montana (Figure 2.1). The watershed of Georgetown Lake is 137.3 km^2 (EPA 1977). The reservoir is the largest lentic water body in the upper Clark Fork River drainage (Liermann 2013), 1,690 m in elevation with a surface area of 1140 ha, mean depth of 4.9 m, and maximum depth of 10.7 m (Stafford 2013). The primary surface water outflow is at Flint Creek Dam, which discharges reservoir water to Flint Creek (Shaw et al. 2017). Georgetown Lake is a multipurpose reservoir that includes angling, recreation, irrigation, and hydropower uses. Dense macrophytes occur throughout the reservoir during ice-off (May-October), and evidence suggests macrophyte abundance has increased through time (Knight 1981; Stafford 2013).

The fish assemblage of Georgetown Lake includes rainbow trout (i.e., Gerrard, Eagle Lake, and Arlee), brook trout, kokanee, largescale suckers (*Catostomus macrocheilus*), longnose suckers (*Catostomus catostomus*), and redside shiners (*Richardsonius balteatus*; Liermann 2013). Rainbow trout and brook trout are stocked annually to provide a recreational opportunity by MFWP, with 565,000 rainbow trout and 214,000 brook trout stocked from 2021 through 2023 (Table A.1).

Fish Collection

Trout (i.e., rainbow trout and brook trout) were collected from Georgetown Lake using experimental sinking and floating gill nets. Experimental gill nets were 1.8-m deep and 38-m long with five 7.6-m panels. Mesh size for the panels were 1.9-cm, 2.5-cm, 3.2-cm, 3.8-cm, and 5.1-cm bar mesh. Gill nets were deployed in spring (mid-May – early-June), summer (July), and autumn (September) to account for potential temporal variation in prey availability. Locations of gill nets were set at standardized locations used by MFWP for their annual assessment netting (Figure 2.1). Gill nets were set in the evening and pulled the following morning. Total length (mm) and weight (g) were measured for rainbow trout and brook trout. This research was performed under the auspices of Institutional Animal Care and Use Protocol 2022-213-IA at Montana State University.

Strain Evaluation

Oxytetracycline marks on vertebrae were used to differentiate the three strains of rainbow trout (Figure 2.2). Fish were marked in the hatchery with oxytetracycline infused feed pellets. Arlee were not fed oxytetracycline. Gerrard were fed oxytetracycline feed for 10 days resulting in one mark. Eagle Lake were fed oxytetracycline feed for 10 days, no oxytetracycline feed for a minimum of 30 days, and again fed oxytetracycline feed for 10 days, resulting in two marks (Figure 2.2). Vertebrate samples were evaluated using a UV lamp (UVP Blak-Ray B-100A UV Lamp) to fluoresce the oxytetracycline mark and a microscope to count marks (Figure 2.2). A minimum of six vertebrae were read for each fish to determine the strain.

Diets

Rainbow trout sampled were euthanized with an overdose of Aqui-S 20E, and incidental mortalities of brook trout were sampled. I removed stomachs from trout in the field and stomachs were preserved in 70% ethanol. To avoid biasing diet composition by overestimating indigestible matter, only the portion of the stomach before the pyloric valve and caeca were sampled for diet contents (Sutela and Huusko 2000; Garvey and Chipps 2012). Stomachs were opened and rinsed with ethanol, and diet contents were poured into a container with ten equally sized units. To subsample the diets, a random number generator was used to select a number between 1 and 10, four times, to randomly select four grid units. Preliminary diet data were analyzed with and without subsampling to confirm that a 40% subsample was representative of the entire diet collected from the fish. Diet contents were identified to the lowest taxonomic level possible, generally species for fish and family for invertebrates. Prey items were separated by taxon and blotted wet weight (nearest 0.0001 g) was recorded for each prey category.

Frequency of occurrence O_i, proportion by weight W_i, and mean proportion by weight MW_i were calculated for each dietary item for trout using the following equations from Chipps and Garvey (2007):

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

$$W_i = \left(\frac{w_i}{\sum_{i=1}^{Q} w_i}\right),$$

$$MW_i = \frac{1}{P}\sum_{j=1}^{P}\left(\frac{w_{ij}}{\sum_{i=1}^{Q} w_{ij}}\right),$$

where J_i is the number of fish containing prey i, P is the number of fish containing food in their stomach, Q is the number of food types, and W_i is the weight of prey type i and j is for individual fish. To allow for comparisons, W_i is calculated for individual fish and averaged for each prey type to obtain MW_i (Chipps and Garvey 2007). Frequency of occurrence and mean proportion by weight were used to compare prey selection among trout.

Feeding patterns were assessed using the graphical technique proposed by Costello (1990) and modified by Amundsen et al. (1996), which evaluates the relationship between prey-specific abundance and percentage frequency of occurrence. Prey-specific abundance is the proportion that prey i comprises of all prey items in only the predators that contain prey i, and is calculated as:

$$P_i = \frac{\sum S_i}{\sum S_{ti}} \times 100,$$

where P_i is the prey-specific abundance of prey i, S_i is the stomach content weight comprised of prey i, and S_{ti} is the total stomach content weight in only those predators with prey i in their stomach (Amundsen et al. 1996). I used this graphical technique to analyze prey importance and feeding strategy. Summarized interpretation of the quadrant labels followed Amundsen (1996) and modified from (Costello 1990).

Diet overlap among species was analyzed using Schoener's index of niche overlap (D):

$$D = 1 - 0.5\left(\sum_{i=1}^{n} |p_{ij} - p_{ik}|\right),$$

where p_{ij} is the proportion resources i is of the total resources used by species j and p_{ik} is the proportion of resource i used by species k (Schoener 1968). A D value of 0.60 or higher is considered a noteworthy niche overlap (Wallace 1981).

Trophic Relationship

Stable isotope analysis was performed to estimate trophic position. Tissue plugs were collected below the dorsal fin and above the lateral line on the three strains of rainbow trout, brook trout, and kokanee. Samples were placed in a centrifuge tube and immediately stored on ice in the field, and frozen after leaving the field. Tissue plugs were freeze-dried for 18-36 hours using a Labconco Freezone 1 (Labconco Corporation, Kansas City, MO, USA) and ground to a powder using a mortar and pestle. The ground samples were analyzed by Wyoming Stable Isotope Facility using a Thermo Finnigan Delta Plus XP, Costech 4010 and Carlo Erba 1110 Elemental Analyzer, Costech Zero Blank Autosampler, and Finnigan Conflo III interface. Stable isotope ratios were calculated using the procedure outlined in Vander Zanden et al. (1999) and Hershey et al. (2017). Using the SIBER package (Stable Isotope Bayesian Ellipses) in R, standard ellipses were created for the three strains of rainbow trout, brook trout, and kokanee to represent the isotopic niche of a group (Jackson et al. 2011). The proportional overlap among ellipses was used to estimate niche overlap. Proportional overlaps greater than 60% are ecologically noteworthy (Guzzo et al. 2013; Pettitt-Wade et al. 2015).

Results

Diets were collected from 195 Gerrards (TL; 158-577 mm), 225 Eagle Lake (TL; 160-550 mm), 87 Arlee (total length TL; 165-525 mm), and 224 brook trout (TL; 165-512 mm).

Seventeen orders and 51 families were identified from the diets of the three strains of rainbow trout and brook trout (Table A.2).

Predation on Kokanee

No trout consumed kokanee (as indicated by species identification) in Georgetown Lake. Low rates of piscivory were observed among all strains and species among seasons (< 2% mean percent by weight; Table A.2). One Gerrard diet contained fish vertebrae, accounting for 0.04 mean percent by weight in autumn, and less than 0.001 mean percent by weight for all seasons combined. Piscivory accounted for 0.57 mean percent by weight for Eagle Lake throughout all seasons, 1.01 for Arlee, and 0.59 for brook trout.

Feeding Strategy

Overall, the three strains of rainbow trout and brook trout exhibited high dietary diversity, consuming a wide range of taxa (Figure 2.3). However, individual trout demonstrated a narrow diet breadth, consuming relatively few unique taxa (Figure 2.4). Eagle Lake fed on a slightly wider breadth of taxa across all seasons compared to Arlee and Gerrard (Figure 2.3). All strains of rainbow trout had considerably higher diet breadth than brook trout (Figure 2.3). The percent occurrence of unique taxa found in diet contents of individual trout was generally right skewed for Gerrard and brook trout for all seasons, suggesting that most individuals consumed few unique diet items, and only a few individuals consumed many diet items (Figure 2.4). For the three strains of rainbow trout and brook trout, at least 50% of individuals sampled consumed five or fewer unique diet taxa for all seasons, except for Eagle Lake sampled in the spring. The largest number of unique diet taxa found in an individual fish was 15 in a single Eagle Lake sampled in the spring.

When diets for all rainbow trout strains and seasons were pooled, the dietary habits of rainbow trout in Georgetown Lake exhibit a generalized feeding strategy (Figure 2.5). The most common diet items for rainbow trout were Amphipoda and Gastropoda, eaten by more than half of the fish, but their average contribution to the stomach contents of these fish was low. Annelida and Hymenoptera had the highest prey-specific abundance values but were consumed by the fewest rainbow trout (< 15%).

The three strains of rainbow trout and brook trout exhibited generalized feeding strategies (Figure 2.6). Although a diverse array of taxa was consumed by the three strains of rainbow trout and brook trout, only a limited number of taxa contributed at least 10% mean percent by weight (Figure 2.6; Table A.2). Among the rainbow trout strains across all seasons, Gerrards showed the largest individual variation in feeding strategy, where individual Gerrards had higher selectivity for certain diet taxa. That is, prey-specific abundance values were greater than 50 for certain taxa but were consumed by less than 50% of individual Gerrards. For example, in autumn, some individual Gerrards selectively consumed Hymenoptera, but less than 25% of Gerrards sampled consumed this prey (Figure 2.6). In brook trout, the highest individual variation was observed in summer, where some individuals selectively consumed Trichoptera and Amphipoda, yet these diet items were consumed by less than 30% of individuals. Overall, for Gerrards and brook trout, all diet taxa were classified as rare, being consumed by fewer than 50% of individuals, and their average contribution to the stomach contents of these fish was low. For Eagle Lake and Arlee overall, all diet taxa were classified as rare, except for Amphipoda and Gastropoda which were consumed by more than 50% of individuals, however the average contribution of these taxa to the stomach contents of these fish was low.

Seasonal shifts in frequency of occurrence and mean percent by weight were observed among the three strains of rainbow trout and brook trout (Figure 2.6; Table A.2). Seasonal shifts in the most often consumed taxa were observed for all trout (Figure 2.6). Amphipoda were most often consumed taxa in spring for all trout, Trichoptera in summer, and both Gastropoda and Amphipoda for autumn. However, the prey-specific abundance values for these taxa were less than 50%, except for Trichoptera consumed brook trout in summer.

Dietary Overlap and Trophic Positioning

Schoener's diet overlap values were between 0.42 and 0.81 among the three strains of rainbow trout and brook trout when seasons were analyzed individually and combined, with 15 combinations having significant overlap (Table 2.1). Significant overlap (i.e., > 0.60) was observed in all cross-strain pairings except between Gerrard and Arlee in spring. The highest levels of diet overlap occurred between Gerrard and Eagle Lake in summer (0.79), autumn (0.80), and all overall (0.81). In contrast, during summer, Arlee and brook trout exhibited the lowest degree of overlap (0.42). The combinations of rainbow trout strains and brook trout that had high diet overlap were with Eagle Lake in spring (0.63), Gerrard in autumn (0.62), and with Gerrard (0.65) and Eagle Lake (0.69) for overall.

All trout and kokanee were at a similar trophic level (Figure 2.7). The centroid value of $\delta^{15}N$ varied from 7.3 for Eagle Lake to 8.2 for kokanee. The centroid values for $\delta^{13}C$ varied from -22.2 for Arlee and brook trout to -24.2 for kokanee. Percentage overlap among ellipses for the three strains of rainbow trout and brook trout had two combinations with significant overlap, between Gerrard and Arlee (61%) and Eagle Lake and Arlee (63%; Table 2.2). The smallest percent overlap among ellipses of trout was between Eagle Lake and brook trout (26%).

Discussion

I predicted that Gerrards would exhibit a specialized piscivorous feeding strategy, minimal dietary overlap with Eagle Lake, Arlee, and brook trout, and thus occupy the highest trophic position among them. However, Gerrards exhibited a generalist feeding strategy, consuming a high variety of diet items, including Amphipoda, Annelida, Gastropoda, Trichoptera, Odonata, Isopoda, Dipteran, and Hymenoptera. Additionally, there was dietary and niche overlap and no difference in trophic position among Gerrards and Eagle Lake, Arlee, or brook trout.

I predicted Gerrards would exhibit a specialized piscivorous feeding strategy by relying on kokanee in Georgetown Lake; however, there was extremely low prevalence of piscivory and no evidence of Gerrards consuming kokanee. Thus, Gerrards not predating on kokanee nor exhibiting a high rate of piscivory in Georgetown Lake was unexpected. In several rainbow trout populations, larger individuals become increasingly piscivorous after reaching a length of about 250 – 300 mm (Jeppson and Platts 1959; Crossman 1959; Northcote 1973; Marrin and Erman 1982; Andrusak and Parkinson 1984; Parkinson 1988; Beauchamp 1990), and rainbow trout that have evolved in lakes with abundant forage fishes have developed the greatest degree of piscivory (Behnke 2010). Gerrards in Georgetown Lake reach lengths larger than 300 mm, which is the threshold for high rates of piscivory in Kootenay Lake and Lake Pend Oreille (Northcote 1973; Irvine 1978; Vidergar 2000; Clarke et al. 2005; Rust et al. 2022), yet they did not exhibit a piscivorous feed strategy. Additionally, kokanee, the preferred prey item for Gerrards (Northcote 1973; Irvine 1978; Vidergar 2000; Clarke et al. 2005; Rust et al. 2022), are thought to occur in high densities in Georgetown Lake. Thus, it is unlikely that predator size or the abundance of forage fishes is regulating piscivory of Gerrards in Georgetown Lake. However, forage fish abundance is not always a determinant for rainbow trout piscivory, exemplified by introduced rainbow trout in Lake DeSmet (Wyoming, USA) and in Flaming Gorge Reservoir (Utah-Idaho, USA), which did not exhibit the degree of piscivory seen elsewhere, even though forage fish were abundant (Hubert et al. 1994; Haddix and Budy 2005).

The prevalence and extent of piscivory in a population can be regulated by many factors, including ontogeny (Sánchez-Hernández et al. 2017), water temperature (Amundsen et al. 1999; Pereira et al. 2017), competition (Eloranta et al. 2015; Sánchez-Hernández et al. 2017), availability of vulnerable prey sizes (Sánchez-Hernández et al. 2017; Jacobson et al. 2019), presence of refuges for prey-fish (East and Magnan 1991), and fish assemblage structure or species richness (East and Magnan 1991; Eloranta et al. 2015; Sánchez-Hernández et al. 2017). The lack of piscivory by Gerrards in Georgetown Lake may be regulated by the presence of refuges for prey fish due to the high densities of macrophytes. Macrophytes provide refuge for small planktivorous fish, such as kokanee, against piscivorous fish, thus reducing the foraging efficiency of piscivores (Savino and Stein 1982; Gotceitas and Colgan 1989). Additionally, macrophytes provide important habitat for aquatic macroinvertebrates, increasing epiphytic macroinvertebrates abundance with increasing macrophyte density, which can increase fish biomass (Diehl and Kornijów 1998). Macrophytes increase the biomass of Gastropoda, Chironomidae, and Trichoptera (Kornijów and Gulati 1992), which I found to be important prey items for Gerrards. Thus, Gerrards may not switch to piscivory due to the high density of macrophytes in Georgetown Lake inhibiting predation on prey fish, providing sufficient macroinvertebrate forage, or both.

Additionally, diet plasticity and adaptive foraging strategies allow piscivores to rapidly respond to changes in food abundances or availability (Rooney et al. 2006; Hayden et al. 2014), as observed for lake trout (*Salvelinus namaycush*) switching from preying on Yellowstone cutthroat trout (*Oncorhynchus virginalis bouvieri*) to amphipods when Yellowstone cutthroat trout densities declined (Glassic et al. 2023). In Kootenay Lake, kokanee constituted over 50% of the volume of stomach contents of Gerrards greater than 300 mm, and kokanee represented over 30% of the diet by volume of Gerrards less than 300 mm (Andrusak and Parkinson 1984). Following the kokanee population collapse after lake trout introduction in Kootenay Lake, Gerrard diets shifted to being less piscivorous — illustrating their diet plasticity in relation to prey availability (Warnock et al. 2022).

My results indicate that predation of kokanee by trout is not regulating the abundance and size of kokanee in Georgetown Lake. Another potential cause for the increase in kokanee average length may be due to the over-filling of Georgetown Lake during the 2017 – 2020 irrigation seasons, when the reservoir was filled at least 0.15 meters higher than full crest (Brad Liermann, MFWP, unpublished). Thus, it is possible that a nutrient flux into Georgetown Lake has occurred from riparian areas being flooded and may have resulted in increased growth in kokanee. Nutrient additions have increased primary production, zooplankton production, and ultimately, kokanee growth in other systems (Budy et al. 1998; Arndt 2004; Wilson et al. 2018; Schindler et al. 2020).

As evident from gut content and stable isotope analyses, the three strains of rainbow trout and brook trout are insectivorous with similar trophic niches, wide dietary breadths, and opportunistic feeding strategies, characterizing them as generalist feeders. Although there was high niche overlap and a generalized feeding strategy among the three strains of rainbow trout, the resource use patterns of Gerrards were different. Gerrards and brook trout showed a moderately higher degree of individual selectivity and between-phenotype components of niche width, that is individuals have less dietary overlap (Amundsen et al. 1996), than Eagle Lake or Arlee. Niche overlap between Gerrards and brook trout was moderately high, higher than among combinations between Gerrards and brook trout, Eagle Lake, or Arlee. However, individual Gerrards generally fed selectively on different prey items than individual brook trout. The time required for individuals to learn to respond to new prey or under altered environmental conditions can result in within individual variation in feeding strategy (Mansueti 1962; Ware 1971; Curio 1976; Ringler 1979, 1983). Individual variation in feeding strategy can lead to differences in resource allocation and partitioning within a population, thereby minimizing competition (i.e., both inter- and intraspecific).

Rainbow trout are typically opportunistic, generalist feeders with high feeding plasticity (Beauchamp 1990). Rainbow trout often prey on the most available organism at any given time and exhibit varying degrees of piscivory (Northcote 1973; Irvine 1978; Beauchamp 1990; Hubert et al. 1994; Haddix and Budy 2005). Rainbow trout diets are highly variable, corresponding to ontogenetic shifts (Landry et al. 1999), prey availability, and seasonal variability in prey availability and abundance (Beauchamp 1990). Common diet items for rainbow trout in Georgetown Lake included Isopoda, Amphipoda, Gastropoda, Dipteran, Trichoptera, Hymenoptera, Odonata, and Annelida, consistent with findings from previous studies (Burdick and Cooper 1956; Patten and Thompson 1957; Johannes and Larkin 1961; Koth 1980; Knapp 1981; Clodfelter 1982; Carmichael 1983; Beauchamp 1990; Hubert et al. 1994; Haddix and

Budy 2005). However, in most lentic systems, zooplankton are important prey items of rainbow trout (Galbraith 1967; Swift 1970; Brynildson and Kempinger 1973; Wiley and Varley 1978; Taylor and Gerking 1980; Schneidervin and Hubert 1987; Wang et al. 1996), which I did not observe based on low occurrences of *Daphnia* in the diets. However, the importance of zooplankton to rainbow trout increases in oligotrophic systems with low littoral or benthic productivity (Brynildson and Kempinger 1973; Wang et al. 1996; Black et al. 2003). Due to the dense macrophyte assemblage, Georgetown Lake likely has medium to high littoral and benthic productivity, thus potentially explaining the lack of zooplankton in rainbow trout diets.

Though it was believed the introduction of Gerrards, which typically have a piscivorous feeding strategy, would predate on kokanee, I instead found that Gerrards perform similarly to other strains of rainbow trout in Georgetown Lake. From a biological-control perspective, there is no benefit to continue stocking Gerrards to reduce kokanee densities in Georgetown Lake. Future research should explore other factors affecting kokanee growth because predation is not regulating the abundance and size of kokanee in Georgetown Lake. These findings underscore the challenge of predicting predator-prey relationships, as diet plasticity can lead to unexpected dynamics based on resource availability and habitat structure within aquatic ecosystems. My findings highlight the importance of assessing the efficacy of management actions, especially biocontrols, which may not perform as expected.

Tables

Table 2.1: Schoener's Index of Niche Overlap among Gerrard, Eagle Lake, Arlee, and brook trout by season and seasons pooled (overall). Values ≥ 0.60 are in bold. Niche overlap was calculated from lowest taxonomic identification, generally species for fishes and family for invertebrates. Fish were collected in Georgetown Lake, Montana, USA from 2021 through 2023.

		Strain or species		
Season	Strain or species	Eagle Lake	Arlee	Brook trout
Spring				
	Gerrard	**0.75**	0.51	0.58
	Eagle Lake		**0.61**	**0.63**
	Arlee			0.53
Summer				
	Gerrard	**0.79**	**0.74**	0.51
	Eagle Lake		**0.69**	0.58
	Arlee			0.42
Autumn				
	Gerrard	**0.80**	**0.69**	**0.62**
	Eagle Lake		**0.68**	0.59
	Arlee			0.57
Overall				
	Gerrard	**0.81**	**0.78**	**0.65**
	Eagle Lake		**0.71**	**0.69**
	Arlee			0.57

Table 2.2: Percentage overlap of 40% Bayesian ellipses from stable isotopes of Gerrard (N = 70), Eagle Lake (N = 70), Arlee (N = 41), and brook trout (N = 61). Fish were collected in Georgetown Lake, Montana, USA from 2021 through 2023.

	Strain or species		
Strain or species	Arlee	Eagle Lake	Brook trout
Gerrard	50	63	26
Eagle Lake	61		
Brook trout	58	37	

Figures

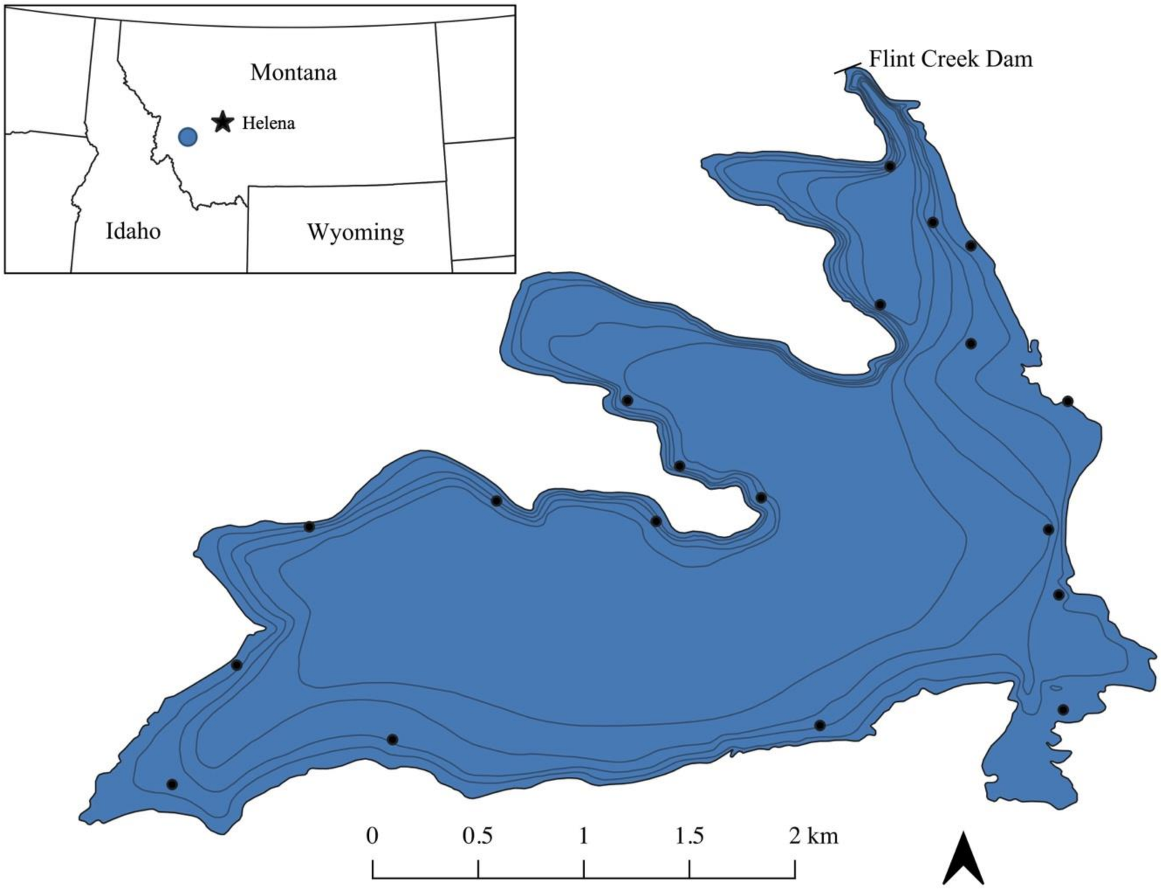

Figure 2.1: Map of Georgetown Lake, Montana, USA. Montana Fish, Wildlife & Parks standard gill net sampling locations are indicated with black circles. The bathymetric contour interval is 1.52 m and are indicated with black lines.

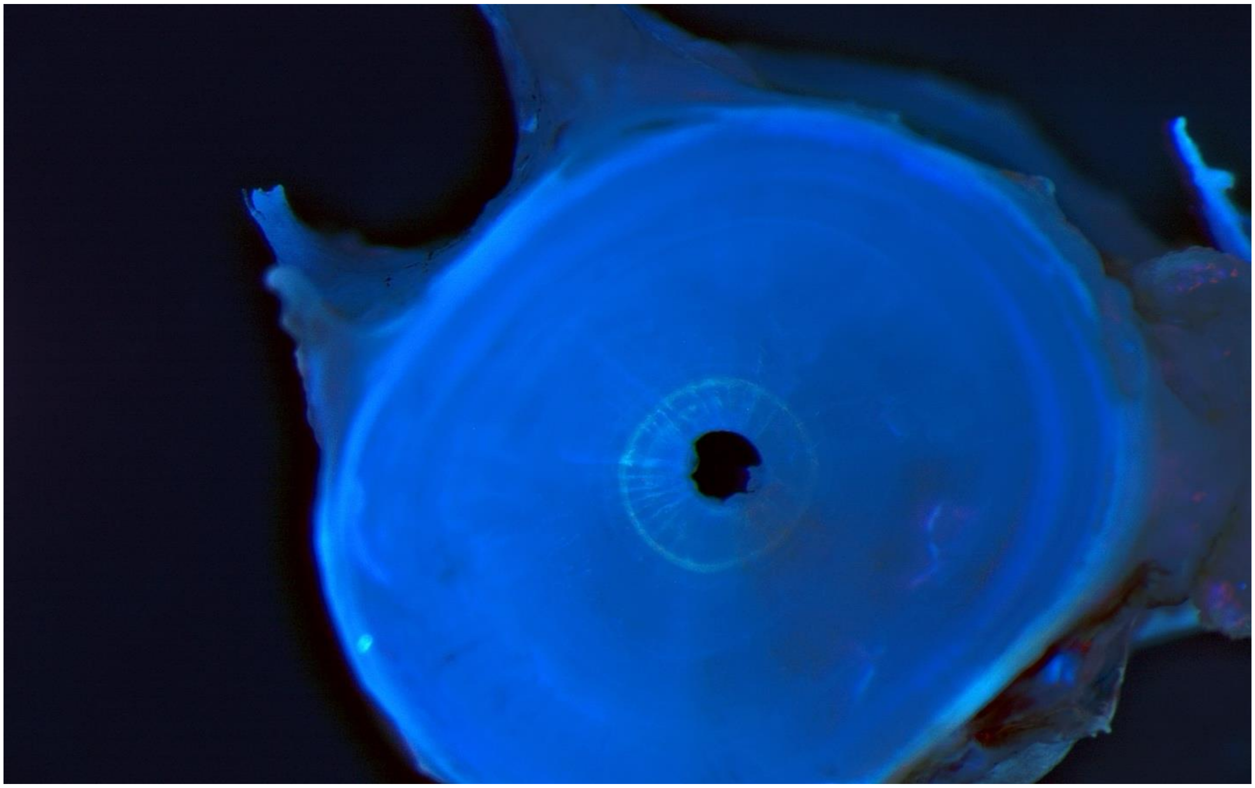

Figure 2.2: A vertebrate under UV light at 5x from a stocked Eagle Lake strain rainbow trout sampled in 2022 Georgetown Lake, Montana, USA. The fluoresced rings (see arrows) represent oxytetracycline marks from the hatchery. The Eagle Lake strain was marked with two oxytetracycline events.

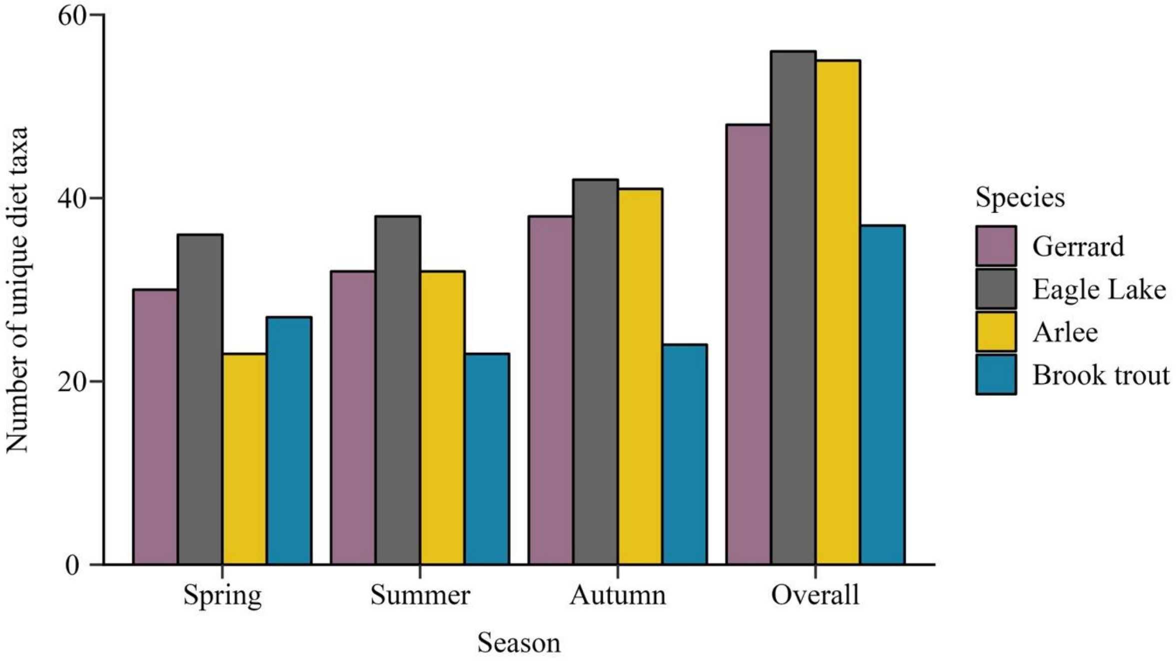

Figure 2.3: Number of unique taxa in the diets of Gerrard, Eagle Lake, Arlee, and brook trout by season in Georgetown Lake, Montana, USA from 2021 through 2023.

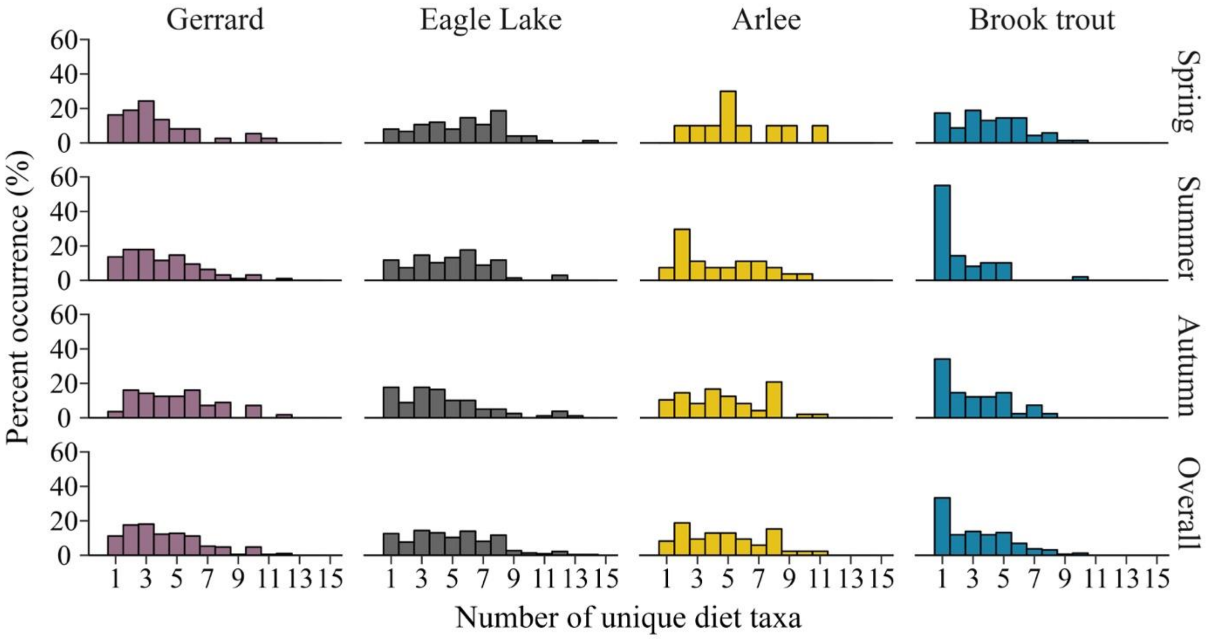

Figure 2.4: Percent occurrence of unique taxa found in diet contents of individual Gerrard, Arlee, Eagle Lake, brook trout by season and seasons pooled (overall) in Georgetown Lake, Montana, USA from 2021 through 2023.

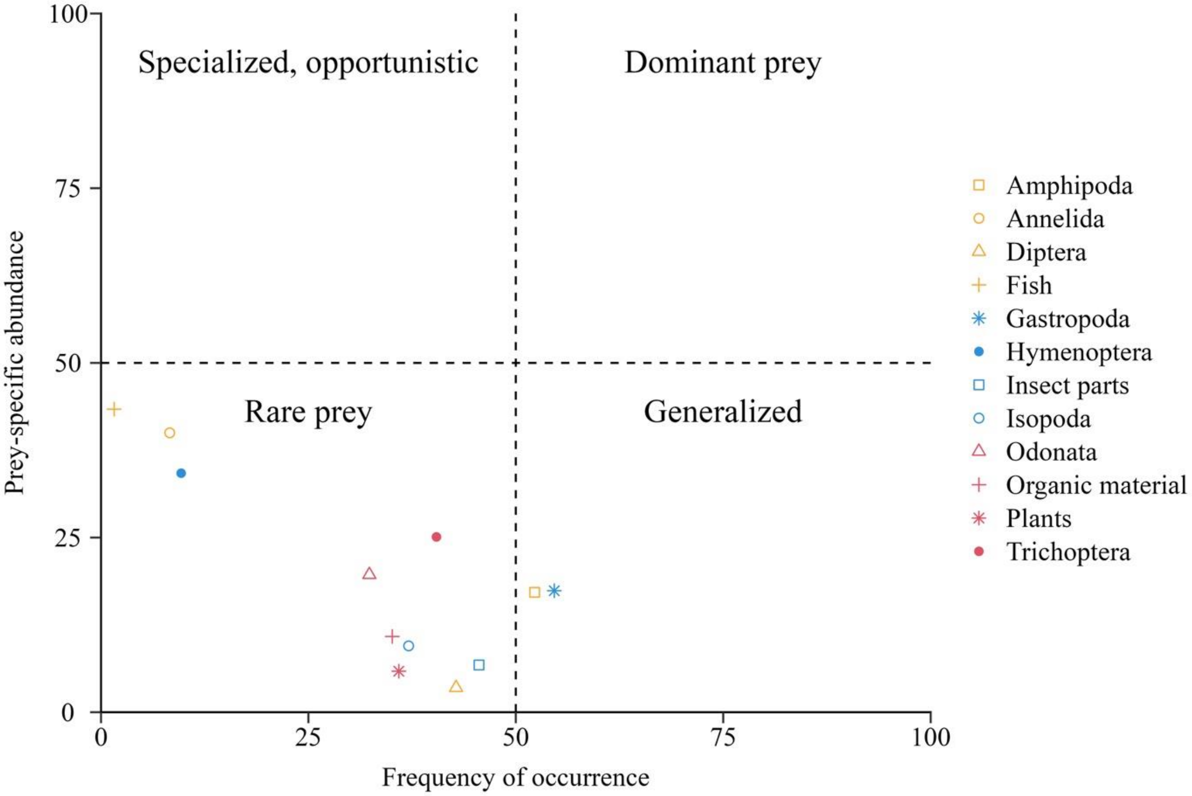

Figure 2.5: Prey-specific abundance - frequency of occurrence plot for all rainbow trout strains and seasons pooled. Prey-specific abundance is defined as the proportion a prey item constitutes of all prey items in only predators that contain prey i, and frequency of occurrence is how often a prey item is consumed. Diet taxa that represented a minimum of 10.0% by mean percent by weight for any combination of season and species were selected to be displayed, as well as fish, resulting in 12 diet taxon. Diets were collected from fish in Georgetown Lake, Montana, USA from 2021 through 2023.

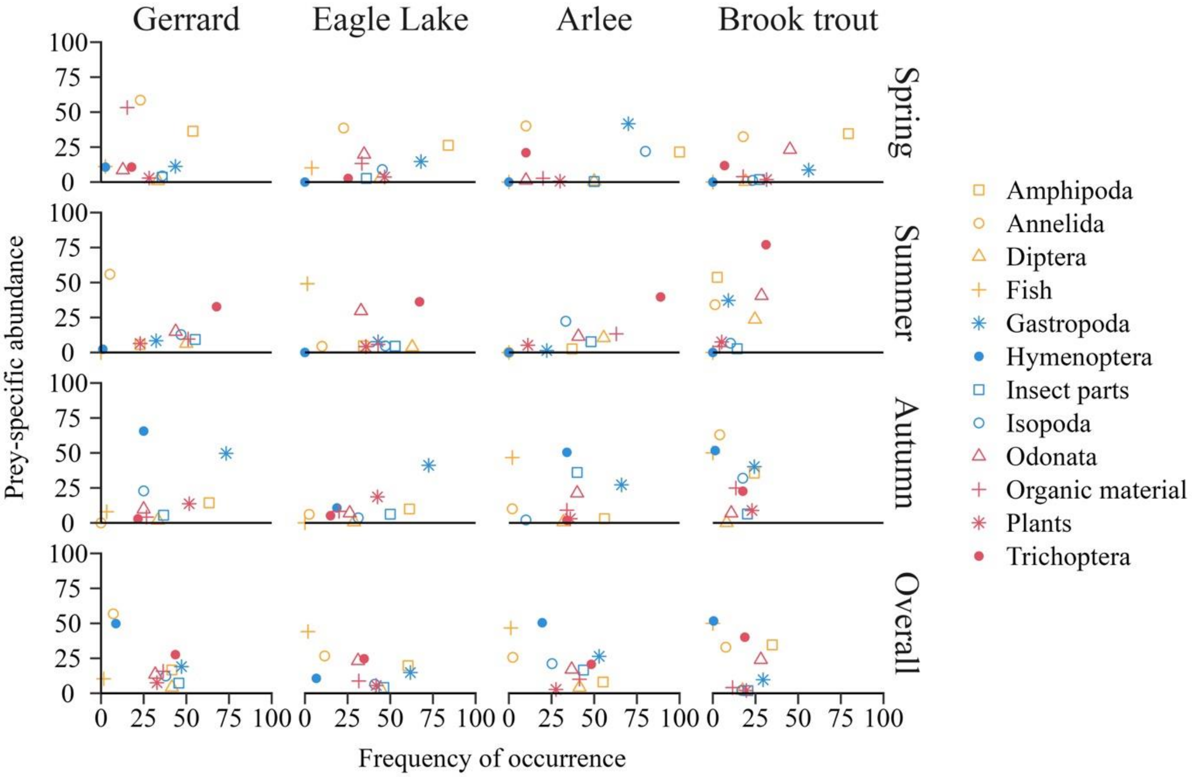

Figure 2.6: Prey-specific abundance - frequency of occurrence plot for Gerrard, Eagle Lake, Arlee, and brook trout by season and seasons pooled (overall). Prey-specific abundance is defined as the proportion a prey item constitutes of all prey items in only predators that contain prey *i*, and frequency of occurrence is how often a prey item is consumed. Diet taxa that represented a minimum of 10.0% by mean percent by weight for any combination of season and species were selected to be displayed, as well as fish, resulting in 12 diet taxon. Diets were collected from fish in Georgetown Lake, Montana, USA from 2021 through 2023.

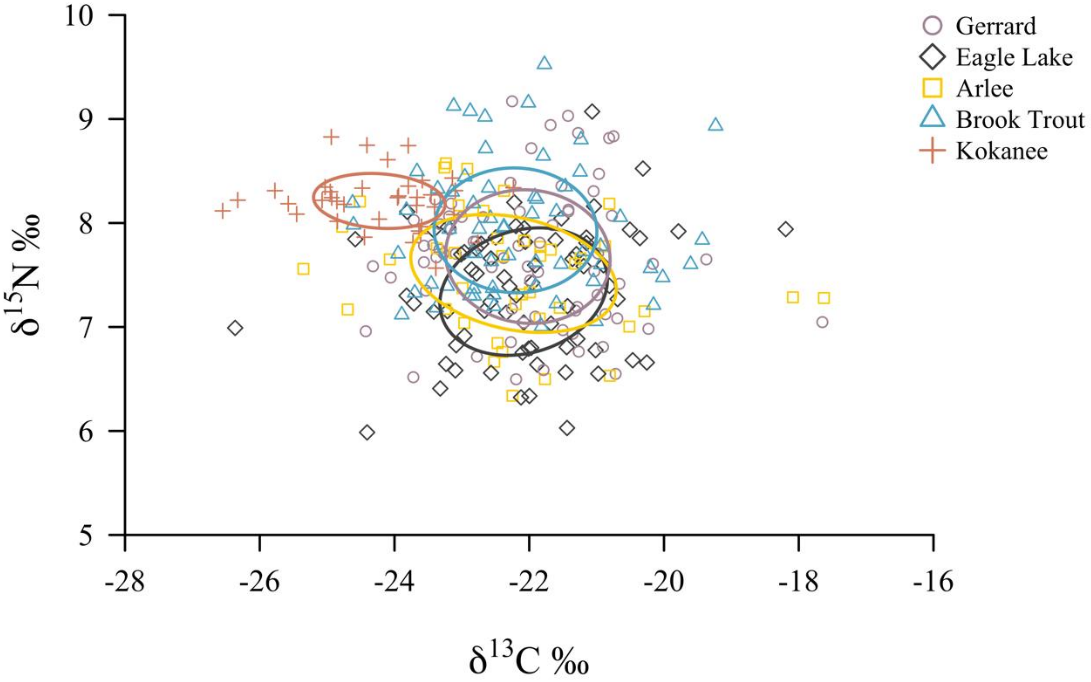

Figure 2.7: Stable isotope biplot of Arlee, Eagle Lake, Gerrard, brook trout, and kokanee sampled from Georgetown Lake, Montana, USA in 2022 and 2023. Ellipses represent 40% Bayesian standard ellipse areas for stable isotope signatures.

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(4):607–614.

Amundsen, P. A., M. A. Svenning, and S. I. Slikavuoplo. 1999. An experimental comparison of cannibalistic response in different Arctic charr (*Salvelinus alpinus* (L.)) stocks. Ecology of Freshwater Fish 8(1):43–48.

Andrusak, H., and E. A. Parkinson. 1984. Food habits of Gerrard stock rainbow trout in Kootenay Lake, British Columbia. British Columbia Fish and Wildlife Branch, Fisheries Technical Circular No. 60.

Arndt, S. 2004. Post-fertilization diet, condition, and growth of bull trout and rainbow trout in Arrow Lakes Reservoir. Columbia Basin Fish & Wildlife Compensation Program, Nelson, British Columbia.

Ashley, K., I. C. Thompson, D. Sebastian, D. Lasenby, K. E. Smokorowski, and H. Andrusak. 1999. Restoration of kokanee salmon in Kootenay Lake, a large intermontane lake, by controlled seasonal addition of limiting nutrients. Pages 127–169 *in* T. Murphy and M. Munawar, editors. Aquatic restoration in Canada. Backhuys Publisher, Leiden, Netherlands.

Ashley, K., L. C. Thompson, D. C. Lasenby, L. McEachern, K. E. Smokorowski, and D. Sebastian. 1997. Restoration of an interior lake ecosystem: The Kootenay Lake fertilization experiment. Water Quality Research Journal 32(2):295–324.

Beattie, W. D., and P. T. Clancey. 1991. Effects of *Mysis relicta* on the zooplankton community and kokanee population of Flathead Lake, Montana. Pages 39–48 *in* T. P. Nesler and E. P. Bergersen, editors. Mysids in fisheries; hard lessons from headlong introductions. American Fisheries Society, Bethesda, Maryland, USA.

Beauchamp, D. A. 1990. Seasonal and diel food habits of rainbow trout stocked as juveniles in Lake Washington. Transactions of the American Fisheries Society 119(3):475–482.

Behnke, R. J. 2010. Trout and salmon of North America. Simon and Schuster.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Great Britain Ministry of Agriculture, Fisheries and Food, London: HMSO.

Black, A. R., G. W. Barlow, and A. T. Scholz. 2003. Carbon and nitrogen stable isotope assessment of the Lake Roosevelt aquatic food web. Northwest Science 77(1):1–11.

Brynildson, O. M., and J. J. Kempinger. 1973. Production, food and harvest of trout in Nebish Lake, Wisconsin - UWDC - UW-Madison Libraries. Madison, Wisconsin: Wisconsin Department of Natural Resources, Technical bulletin.

Budy, P., C. Luecke, and W. A. Wurtsbaugh. 1998. Adding nutrients to enhance the growth of endangered sockeye salmon: Trophic transfer in an oligotrophic lake. Transactions of the American Fisheries Society 127(1):19–34.

Buktenica, M. W., S. F. Girdner, G. L. Larson, and C. D. McIntire. 2007. Variability of kokanee and rainbow trout food habits, distribution, and population dynamics, in an ultraoligotrophic lake with no manipulative management. Hydrobiologia 574(1):235–264.

Burdick, M. E., and E. L. Cooper. 1956. Growth rate, survival and harvest of fingerling rainbow trout planted in Weber Lake, Wisconsin. Journal of Wildlife Management 20(3):233–239.

Burgner, R. 1897. Factors influencing age and growth of juvenile sockeye salmon (*Oncorhynchus nerka*) in lakes. Pages 129–142. 96, Canadian Special Publication of Fisheries and Aquatic Sciences.

Burrough, R. J., and C. R. Kennedy. 1979. The occurrence and natural alleviation of stunting in a population of roach, *Rutilus rutilus* (L.). Journal of Fish Biology 15(1):93–109.

Carmichael, R. 1983. Feeding ecology and aspects of the biology of largemouth bass, rainbow trout, brown trout, and relict dace and the dietary overlap of largemouth bass and rainbow trout with canvasback and redhead ducks at Ruby Marsh, Nevada. Master's thesis, Oregon State University.

Chipps, S. R., and J. E. Garvey. 2007. Assessment of diets 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, USA.

Clarke, L. R., D. T. Vidergar, 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(3):267–277.

Clodfelter, K. C. 1982. Growth, food habits, and the relative effectiveness of stocking rainbow trout (*Salmo gairdneri*) in south-central South Dakota. Master's thesis, South Dakota State University.

Costello, M. J. 1990. Predator feeding strategy and prey importance: A new graphical analysis. Journal of Fish Biology 36(2):261–263.

Crossman, E. J. 1959. A predator–prey interaction in freshwater fish. Journal of the Fisheries Research Board of Canada 16(3):269–281.

Curio, E. 1976. The ethology of predation. Springer, Berlin, Heidelberg.

Damsgård, B., and A. Langeland. 1994. Effects of stocking of piscivorous brown trout, *Salmo trutta* L., on stunted Arctic charr, *Salvelinus alpinus* (L.). Ecology of Freshwater Fish 3(2):59–66.

Diehl, S., and R. Kornijów. 1998. Influence of submerged macrophytes on trophic interactions among fish and macroinvertebrates. Pages 24–46 *in* E. Jeppesen, M. Søndergaard, M. Søndergaard, and K. Christoffersen, editors. The structuring role of submerged macrophytes in lakes. Springer New York, New York, NY.

East, P., and P. Magnan. 1991. Some factors regulating piscivory of brook trout, *Salvelinus fontinalis*, in lakes of the Laurentian Shield. Canadian Journal of Fisheries and Aquatic Sciences 48(9):1735–1743.

Eby, L. A., W. J. Roach, L. B. Crowder, and J. A. Stanford. 2006. Effects of stocking-up freshwater food webs. Trends in Ecology & Evolution 21(10):576–584.

Eloranta, A. P., K. K. Kahilainen, P.A. Amundsen, R. Knudsen, C. Harrod, and R. I. Jones. 2015. Lake size and fish diversity determine resource use and trophic position of a top predator in high-latitude lakes. Ecology and Evolution 5(8):1664–1675.

EPA (U.S. Environmental Protection Agency). 1977. Report on Georgetown Lake, Deer Lodge and Granite Counties, Montana. USEPA Report Working Paper No. 793, Washington, D.C.

Galbraith, M. G. 1967. Size-selective predation on daphnia by rainbow trout and yellow perch. Transactions of the American Fisheries Society 96(1):1–10.

Garvey, J. E., and S. R. Chipps. 2012. Diets and energy flow. Pages 733–779 *in* A. Zale, D. L. Parrish, and T. M. Sutton, editors. Fisheries techniques, 3rd edition. American Fisheries Society, Bethesda, Maryland, USA.

Glassic, H. C., C. S. Guy, L. M. Tronstad, D. R. Lujan, M. A. Briggs, L. K. Albertson, and T. M. Koel. 2023. Invasive predator diet plasticity has implications for native fish conservation and invasive species suppression. PLoS ONE 18(2):e0279099.

Gotceitas, V., and P. Colgan. 1989. Predator foraging success and habitat complexity: Quantitative test of the threshold hypothesis. Oecologia 80(2):158–166.

Griswold, R. G., A. E. Kohler, K. A. Tardy, K. E. Griswold, and D. Taki. 2022. Density dependence in three Snake River sockeye salmon nursery lakes in Central Idaho. North American Journal of Fisheries Management 42(6):1477–1493.

Grover, M. C. 2006. Evaluation of a negative relationship between abundance during spawning and size at maturity in kokanee. Transactions of the American Fisheries Society 135(4):970–978.

Grummer, J. A., M. C. Whitlock, P. M. Schulte, and E. B. Taylor. 2021. Growth genes are implicated in the evolutionary divergence of sympatric piscivorous and insectivorous rainbow trout (*Oncorhynchus mykiss*). BMC Ecology and Evolution 21(1):63.

Guzzo, M. M., G. D. Haffner, N. D. Legler, S. A. Rush, and A. T. Fisk. 2013. Fifty years later: Trophic ecology and niche overlap of a native and non-indigenous fish species in the western basin of Lake Erie. Biological Invasions 15(8):1695–1711.

Haddix, T., and P. E. Budy. 2005. Factors that limit growth and abundance of rainbow trout across ecologically distinct areas of Flaming Gorge Reservoir, Utah–Wyoming. North American Journal of Fisheries Management 25(3):1082–1094.

Hayden, B., C. Harrod, and K. K. Kahilainen. 2014. Dual fuels: Intra-annual variation in the relative importance of benthic and pelagic resources to maintenance, growth and reproduction in a generalist salmonid fish. Journal of Animal Ecology 83(6):1501–1512.

Hershey, A. E., R. M. Northington, J. C. Finlay, and B. J. Peterson. 2017. Stable isotopes in stream food webs. Pages 3–20 *in* G. A. Lamberti and F. R. Hauer, editors. Methods in Stream Ecology, 2nd edition. Academic Press, San Diego.

Hubert, W. A., R. D. Gipson, R. A. McDowell, and A. C. Stewart. 1994. Diet of Eagle Lake rainbow trout in Lake DeSmet, Wyoming. North American Journal of Fisheries Management 14(2):457–459.

Irvine, J. R. 1978. The Gerrard rainbow trout of Kootenay Lake, British Columbia: A discussion of their life history with management, research and enhancement recommendations. Fish and Wildlife Branch.

Jackson, J. R., R. Inger, A. C. Parnell, and S. Bearhop. 2011. Comparing isotopic niche widths among and within communities: SIBER-stable isotope Bayesian ellipses in R. Journal of Animal Ecology 80(3):595–602.

Jacobson, P., U. Bergström, and J. Eklöf. 2019. Size-dependent diet composition and feeding of Eurasian perch (*Perca fluviatilis*) and northern pike (*Esox lucius*) in the Baltic Sea. Boreal Environmental Research 24:137–153.

Jenkins, T. M., S. Diehl, K. W. Kratz, and S. D. Cooper. 1999. Effects of population density on individual growth of brown trout in streams. Ecology 80(3):941–956.

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(3):197–202.

Johannes, R. E., and P. A. Larkin. 1961. Competition for food between redside shiners (*Richardsonius balteatus*) and rainbow trout (*Salmo gairdneri*) in two British Columbia lakes. Journal of the Fisheries Research Board of Canada 18(2):203–220.

Keeley, E. R., E. A. Parkinson, and E. B. Taylor. 2005. Ecotypic differentiation of native rainbow trout (*Oncorhynchus mykiss*) populations from British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 62(7):1523–1539.

Knapp, S. M. 1981. The fisheries potential of Medical Lake, Washington, after a whole-lake alum treatment, with emphasis on food and food habits of rainbow trout (*Salmo gairdneri*). Master's thesis, Eastern Washington University.

Knight, J. C. 1981. An investigation of the general limnology of Georgetown Lake, Montana. Doctoral dissertation, Montana State University, Bozeman, Montana.

Koenig, M. K., K. A. Meyer, J. R. Kozfkay, J. M. DuPont, and E. B. Schriever. 2015. Evaluating the ability of tiger muskellunge to eradicate brook trout in Idaho alpine lakes. North American Journal of Fisheries Management 35(4):659–670.

Kornijów, R., and R. D. Gulati. 1992. Macrofauna and its ecology in Lake Zwemlust, after biomanipulation II. Fauna inhabiting hydrophytes. Archiv für Hydrobiologie 123(3):349–359.

Koth, R. M. 1980. Food habits and growth of rainbow trout in a prairie pond. Master's thesis, South Dakota State University.

Landry, F., J. R. Post, and E. A. Parkinson. 1999. Spatial ontogeny of lentic age-0 rainbow trout, *Oncorhynchus mykiss*: Whole-lake manipulations of population size structure. Canadian Journal of Fisheries and Aquatic Sciences 56(10):1916–1928.

Liermann, B. 2013. Analysis and management implications of multiple decades of fisheries data for Georgetown Lake, MT. Montana Fish, Wildlife & Parks, Missoula, Montana.

Mansueti, R. 1962. Review of experimental ecology of the feeding of fishes; Rate of metabolism and food requirements of fishes. Chesapeake Science 3(1):56–58.

Marrin, D. L., and D. C. Erman. 1982. Evidence against competition between trout and nongame fishes in Stampede Reservoir, California. North American Journal of Fisheries Management 2(3):262–269.

Martinez, P. J., and E. P. Bergersen. 1991. Interactions of zooplankton, *Mysis relicta*, and kokanees in Lake Granby, Colorado. Pages 49–64.

Martinez, P. J., P. E. Bigelow, M. A. Deleray, W. A. Fredenberg, B. S. Hansen, N. J. Horner, S. K. Lehr, R. W. Schneidervin, S. A. Tolentino, and A. E. Viola. 2009. Western lake trout woes. Fisheries 34(9):424–442.

Martinez, P. J., and W. J. Wiltzius. 1995. Some factors affecting a hatchery-sustained kokanee population in a fluctuating Colorado reservoir. North American Journal of Fisheries Management 15(1):220–228.

Mazumder, A., and J. A. Edmundson. 2002. Impact of fertilization and stocking on trophic interactions and growth of juvenile sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 59(8):1361–1373.

McGurk, M. D. 1999. Size dependence of natural mortality rate of sockeye salmon and kokanee in freshwater. North American Journal of Fisheries Management 19(2):376–396.

Northcote, T. G. 1973. Some impacts of man on Kootenay Lake and its salmonids. Great Lakes Fishery Commission, Technical Report No. 25, Ann Arbor, Michigan.

Paragamian, V. L., and E. C. Bowles. 1995. Factors affecting survival of kokanees stocked in Lake Pend Oreille, Idaho. North American Journal of Fisheries Management 15(1):208–219.

Parkinson, E. A. 1988. Long term data collection on kokanee from large lakes: Does it make sense? British Columbia Fisheries Branch, Fisheries Technical Circulation No. 83.

Patten, B. G., and R. B. Thompson. 1957. Food studies of a small sample of rainbow trout (*Salmo gairdneri*) and kokanee salmon (*Oncorhynchus nerka*) from Crater Lake, Oregon. Page 14. National Park Service, Unpublished report, Crater Lake, Oregon.

Pereira, L. S., F. W. Keppeler, A. A. Agostinho, and K. O. Winemiller. 2017. Is there a relationship between fish cannibalism and latitude or species richness? PLoS ONE 12(1):e0169813.

Persson, L., P. A. Amundsen, A. M. De Roos, A. Klemetsen, R. Knudsen, and R. Primicerio. 2007. Culling prey promotes predator recovery - Alternative states in a whole-lake experiment. Science 316(5832):1743–1746.

Pettitt-Wade, H., K. W. Wellband, D. D. Heath, and A. T. Fisk. 2015. Niche plasticity in invasive fishes in the Great Lakes. Biological Invasions 17(9):2565–2580.

Post, J. R., E. A. Parkinson, and N. T. Johnston. 1999. Density-dependent processes in structured fish populations: Interaction strengths in whole-lake experiments. Ecological Monographs 69(2):155–175.

Rahel, F. J. 2000. Homogenization of fish faunas across the United States. Science 288(5467):854–856.

Rask, M. 1983. Differences in growth of perch (*Perca fluviatilis* L.) in two small forest lakes. Hydrobiologia 101(1):139–143.

Reynolds, J. 2017. Predicting the impact of a northern pike (*Esox lucius*) invasion on endangered June sucker (*Chasmistes liorus*) and sport fishes in Utah Lake, UT. Master's thesis, Utah State University.

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

Rieman, B. E., and D. L. Myers. 1992. Influence of fish density and relative productivity on growth of kokanee in ten oligotrophic lakes and reservoirs in Idaho. Transactions of the American Fisheries Society 121(2):178–191.

Ringler, N. H. 1979. Selective predation by drift-feeding brown trout (*Salmo trutta*). Journal of the Fisheries Research Board of Canada 36(4):392–403.

Ringler, N. H. 1983. Variation in foraging tactics of fishes. Pages 159–171 *in* D. L. G. Noakes, D. G. Lindquist, G. S. Helfman, and J. A. Ward, editors. Predators and prey in fishes: Proceedings of the 3rd biennial conference on the ethology and behavioral ecology of fishes, held at Normal, Illinois, U.S.A., May 19–22, 1981. Springer Netherlands, Dordrecht.

Rochet, M. 1998. Short-term effects of fishing on life history traits of fishes. ICES Journal of Marine Science 55(3):371–391.

Rooney, N., K. McCann, G. Gellner, and J. C. Moore. 2006. Structural asymmetry and the stability of diverse food webs. Nature 442(7100):265–269.

Rust, P., S. M. Wilson, N. G. Mucciarone, R. Hardy, M. P. Corsi, and J. Strait. 2022. Lake Pend Oreille research, 2019 Lake Pend Oreille fishery recovery project. Idaho Department of Fish and Game, Annual progress report IDFG Report Number 22-04, Boise, Idaho.

Sánchez-Hernández, J., A. P. Eloranta, A. G. Finstad, and P. A. Amundsen. 2017. Community structure affects trophic ontogeny in a predatory fish. Ecology and Evolution 7(1):358–367.

Savino, J. F., and R. A. Stein. 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. Transactions of the American Fisheries Society 111(3):255–266.

Schindler, E. U., B. Shafii, P. J. Anders, W. J. Price, C. Holderman, K. I. Ashley, and M. Bassett. 2020. Characterizing the phytoplankton and zooplankton communities in Kootenay Lake: A time series analysis of 24 years of nutrient addition. Canadian Journal of Fisheries and Aquatic Sciences 77(5):904–916.

Schneidervin, R. W., and W. A. Hubert. 1987. Diet overlap among zooplanktophagous fishes in Flaming Gorge Reservoir, Wyoming-Utah. North American Journal of Fisheries Management 7(3):379–385.

Schoener, T. W. 1968. The anoles lizards of Bimini: Resource partitioning in a complex fauna. Ecology 49(4):704–726.

Shaw, G. D., K. L. Mitchell, and C. H. Gammons. 2017. Estimating groundwater inflow and leakage outflow for an intermontane lake with a structurally complex geology: Georgetown Lake in Montana, USA. Hydrogeology Journal 25:135–149.

Stafford, C. 2013. Long-term trends in the water quality of Georgetown Lake, Montana - Georgetown State of the lake project report to Montana Department of Justice and Montana Department of Environmental Quality. Missoula, Montana.

Sutela, T., and A. Huusko. 2000. Varying resistance of zooplankton prey to digestion: Implications for quantifying larval fish diets. Transactions of the American Fisheries Society 129(2):545–551.

Svedäng, H., and S. Hornborg. 2014. Selective fishing induces density-dependent growth. Nature Communications 5(1):4152.

Swift, M. C. 1970. A qualitative and quantitative study of trout food in Castle Lake, California. Pages 109–120. California Fish and Game.

Taylor, W. W., and S. D. Gerking. 1980. Population dynamics of *Daphnia pulex* and utilization by the rainbow trout (*Salmo gairdneri*). Hydrobiologia 71(3):277–287.

Vander Zanden, M. J., B. J. Shuter, N. Lester, and J. B. Rasmussen. 1999. Patterns of food chain length in lakes: A stable isotope study. The American Naturalist 54(4): 406-416.

Vidergar, D. 2000. Population estimates, food habits and estimates of consumption of selected predatory fishes in Lake Pend Oreille, Idaho. Master's thesis, University of Idaho.

Vinyard, G. L., R. W. Drenner, and D. A. Hanzel. 1982. Feeding success of hatchery-reared kokanee salmon when presented with zooplankton prey. The Progressive Fish-Culturist 44(1):37–39.

Wallace, R. K. 1981. An assessment of diet-overlap indexes. Transactions of the American Fisheries Society 110(1):72–76.

Wallace, R. K., and D. Zaroban. 2013. Native fishes of Idaho. American Fisheries Society, Bethesda, Maryland, USA.

Walsworth, T. E., P. Budy, and G. P. Thiede. 2013. Longer food chains and crowded niche space: Effects of multiple invaders on desert stream food web structure. Ecology of Freshwater Fish 22(3):439–452.

Wang, L., K. Zimmer, P. Diedrich, and S. Williams. 1996. The two-story rainbow trout fishery and its effect on the zooplankton community in a Minnesota lake. Journal of Freshwater Ecology 11(1):67–80.

Ware, D. M. 1971. Predation by rainbow trout (*Salmo gairdneri*): The effect of experience. Journal of the Fisheries Research Board of Canada 28(12):1847–1852.

Warnock, W. G., J. L. Thorley, S. K. Arndt, T. J. Weir, M. D. Neufeld, J. A. Burrows, and G. F. Andrusak. 2022. Kootenay Lake kokanee (*Oncorhynchus nerka*) collapse into a predator pit. Canadian Journal of Fisheries and Aquatic Sciences 79(2):234–248.

Wiley, R. W., and J. D. Varley. 1978. The diets of rainbow and brown trout from Flaming Gorge Reservoir, 1964 through 1969. Wyoming Game and Fish Department, Cheyenne.

Wilson, S. M., D. H. Brandt, M. P. Corsi, and A. M. Dux. 2018. Early trophic responses to nutrient addition in Dworshak Reservoir, Idaho. Lake and Reservoir Management 34(1):58–73.

Wilson, S. M., M. P. Corsi, D. H. Brandt, and E. J. Stark. 2021. The response of *Daphnia* to nutrient additions and kokanee abundance in Dworshak Reservoir, Idaho. Canadian Journal of Fisheries and Aquatic Sciences 78(11):1677–1688.

Wydoski, R. S., and D. H. Bennett. 1981. Forage species in lakes and reservoirs of the western United States. Transactions of the American Fisheries Society 110(6):764–771.

Ylikarjula, J., M. Heino, and U. Dieckmann. 1999. Ecology and adaptation of stunted growth in fish. Evolutionary Ecology 13(5):433–453.

Zanden, M. J. V., S. Chandra, B. C. Allen, J. E. Reuter, and C. R. Goldman. 2003. Historical food web structure and restoration of native aquatic communities in the Lake Tahoe (California-Nevada) basin. Ecosystems 6(3):274–288.

CHAPTER THREE

A CHANGING CLIMATE NEGATIVELY INFLUENCES GROWTH FOR SALMONIDS IN GEORGETOWN LAKE

Contribution of Authors and Co-Authors

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Introduction

Freshwater fisheries (e.g., commercial, subsistence, and recreational) have considerable social, ecological, and economic importance (Pitcher and Hollingworth 2008; Cowx et al. 2010; Lynch et al. 2016; Arlinghaus et al. 2019) and are exposed to rapidly changing conditions by a changing climate (Millennium Ecosystem Assessment (Program) 2005). Global average air temperatures have increased over the last two centuries (Hartmann et al. 2014), with air temperatures in the northern Rocky Mountains, USA increasing at twice the global average over the past century (Pederson et al. 2010). Increasing air temperatures contributes to warmer water temperatures, thus altering the thermal suitability of waters for freshwater species (IPCC 2007; Christensen et al. 2007). The warming of water disproportionally effects coldwater fishes, which have a lower temperature tolerance than that of cool and warmwater species (Shuter and Post 1990; Magnuson et al. 1997). Due to the physiological responses of fishes, climate change is predicted to adversely affect coldwater fisheries, and thus detrimentally affect recreational fishing, commercial fishing, and tourism for coldwater fishes (Jones et al. 2013). Thus, it is important to understand how increased water temperatures will affect popular fisheries.

Recreational fishing is a popular global activity that effects economies, social interactions, and biota (Pitcher and Hollingworth 2008). In the United States, recreational angling generates an estimated US$99.4 billion annually (U.S. DOI and U.S. FWS 2022). One highly prized genera sought by anglers, with substantial ecological and socioeconomic importance, are salmonids (e.g., *Salmo* and *Oncorhynchus* spp.; Brown et al. 2019). The northern Rocky Mountains in Montana support some of North America’s most popular trout fisheries, valued at more than US$750 million annually (Lewis 2018) and representing more than 20% of spending by tourism in the state (Grau 2019).

Georgetown Lake, in Montana, is a multipurpose reservoir that provides angling, recreation, irrigation, and hydropower uses. Georgetown Lake ranks as the 12th highest for angling pressure among all water bodies, 4th highest among lentic water bodies, and 1st in terms of angling pressure per acre among reservoirs in Montana in 2019 (MFWP 2022). Georgetown Lake is popular for the salmonid fishery present (i.e., rainbow trout *Oncorhynchus mykiss*, book trout *Salvelinus fontinalis*, and kokanee *Oncorhynchus nerka*). Montana Fish, Wildlife & Parks (MFWP) annually stock rainbow trout and brook trout to support the popular recreational fishery, and kokanee are a self-sustaining population. Georgetown Lake is a relatively shallow (mean depth = 4.7 m), polymictic, high-elevation reservoir, and thus will respond quicker to fluctuating air temperatures than deeper lentic systems (Murdoch and Power 2013).

Reservoir ecosystems are artificial but can provide critical water storage and coldwater habit for coldwater fishes, however, reservoir ecosystems are particularly vulnerable to effects of climate change (Miranda et al. 2020). Climate warming effects on reservoirs include higher water temperatures and shifts in hydrology that can result in reduced water levels in summer and autumn, altered water residence cycles, eutrophication, and anoxia (Yasarer and Sturm 2016; Miranda et al. 2020), which can result in fish kills. Increased drought frequencies, intensities, and durations particularly in summer are expected to intensify annual water-level fluctuations, particularly in Montana (Whitlock et al. 2017). The largest negative influence of warming on coldwater fish habitat is projected to occur in medium-depth lakes (13 m max depth; Stefan et al. 2001), such as Georgetown Lake. Water temperature is the main factor directly governing the physiology of fish and ultimately determines their growth and survival (Fry 1971; Christie and Regier 1988; Magnuson et al. 1990; Sharma et al. 2007; Busch et al. 2012).

Increased water temperatures can have sub-lethal effects, influencing fish through a variety of pathways including growth, metabolism, feeding rates, reproductive timing, and recruitment (Fry 1971; Kitchell et al. 1977; Shuter and Post 1990; Magnuson et al. 1997; Brandt et al. 2002; Casselman 2002). Metabolic responses to different water temperatures determines what proportion of the energy budget of a fish is required for basal and active metabolism versus somatic growth, reproduction, or high-energy lipid storage (Beauchamp et al. 2007). Increased water temperatures can affect fish metabolism by elevating metabolic demand to maintain cardiac function and respiration (Brown et al. 2004). Increased metabolism can lead to increased consumption rates that directly affect individual growth and survival rates (Christie and Regier 1988). Growth integrates the combined effects of feeding rate, food quality, water temperature, and metabolic costs associated with activity level and environmental stress (Beauchamp et al. 2007). Growth is an important process in fish population dynamics, affecting production, mortality, fecundity, and egg quality (Audzijonyte et al. 2013; Hixon et al. 2014; Lorenzen 2016; Denechaud et al. 2020). Changes in fish growth have been linked to climate change and evaluated through the use of bioenergetics modeling (Brandt and Hartman 1993; Ney 1993; Breeggemann et al. 2016).

Bioenergetics modeling offers a flexible framework to evaluate factors (e.g., diet composition and environmental conditions) that affect fish growth (Bevelhimer and Adams 1993; Breeggemann et al. 2016). Bioenergetic models are based on mass balance equations, and provide a sound, theoretical approach for estimating energy allocation in animals by partitioning consumed energy into three basic components: metabolism, wastes, and growth (Winberg 1956; Ney 1993). Using a bioenergetics approach is advantageous because bioenergetics modelling is readily available, well-documented, widely used, inexpensive, and relatively simple to use (Ney 1993; Hanson et al. 1997; Deslauriers et al. 2017). In this study, I used bioenergetics models to simulate the effects of warming water temperature on food consumption and growth for rainbow trout and kokanee in Georgetown Lake. I addressed how salmonid growth in Georgetown Lake will be affected by warming water temperature through the following inquiries: (1) how does food consumption change with increased water temperatures for rainbow trout and kokanee; and (2) how does growth change from baseline water temperatures to increased summer water temperatures for rainbow trout and kokanee? Climate change will pose challenges for freshwater fisheries management in the future, thus understanding how projected warming water temperatures may affect popular recreational fisheries can provide managers with information to anticipate population-level responses.

Methods

Study Area

Georgetown Lake is a relatively shallow (mean depth = 4.9 m), high-elevation reservoir located in southwestern Montana, about 13 km south of Philipsburg, Montana and approximately 37 km west of Anaconda, Montana (Figure 3.1). The watershed of Georgetown Lake is 137.3 km^2, and the reservoir is the largest lentic water body in the upper Clark Fork River drainage (EPA (U.S. Environmental Protection Agency) 1977; Liermann 2013). The reservoir is at 1,690 m in elevation with a surface area of 1,140 ha, and maximum depth of 10.7 m (Stafford 2013).

The primary surface water outflow is at Flint Creek Dam, which discharges reservoir water to Flint Creek (Shaw et al. 2017).

The fish assemblage of Georgetown Lake includes rainbow trout, brook trout, kokanee, largescale suckers (*Catostomus macrocheilus*), longnose suckers (*Catostomus catostomus*), and redside shiners (*Richardsonius balteatus*; Liermann 2013). Rainbow trout and brook trout are stocked annually in Georgetown Lake to provide a recreational opportunity by MFWP, with 565,000 total rainbow trout and 214,000 brook trout stocked from 2021 through 2023 (Table B.1).

Fish Collection

Gill nets 1.8-m deep and 38-m long were used to sample fish (standard MFWP experimental gill net array set at standardized locations). Experimental gill nets were constructed of monofilament and consist of five panels of varying mesh sizes including 1.9-cm, 2.5-cm, 3.2-cm, 3.8-cm, and 5.1-cm bar mesh panels. Sinking and floating gill nets were used to sample varying depth strata — three or four gill nets were set each day. Gill nets were set in the evening and pulled the following morning. Gill nets were deployed in spring (mid-May – early-June), summer (July), and autumn (September) to account for potential temporal variation in prey availability (Figure 3.1). This research was performed under the auspices of Institutional Animal Care and Use Protocol 2022-213-IA at Montana State University.

Weight-at-Age

Length (mm), weight (g), and otoliths were collected from all targeted fish sampled (i.e., rainbow trout and kokanee). Rainbow trout and kokanee were euthanized with an overdose of Aqui-S 20E. At least five otoliths per 50-mm length group were aged. Otoliths were embedded in an epoxy mold and sectioned transversely along the dorsoventral plane using a low speed Isomet saw. Cross-sections were mounted to microscope slides using Crystalbond mounting adhesive. Age was estimated by counting the number of annuli present by two independent readers using a dissecting microscope (Leica M165C). Discrepancies were resolved by a consensus reading. Rainbow trout weight-at-age estimates were derived from the von Bertalanffy growth function (von Bertalanffy 1938), and predicted weight-at-age for kokanee was estimated using a linear weight at age model (Figure B.1). For each species, ages with less than two individuals were omitted from the bioenergetics models.

Bioenergetics

Bioenergetics modeling was used to project rainbow trout and kokanee growth for observed and simulated warming water temperature regimes in Georgetown Lake following methods similar to Breeggemann et al. (2016). Analyses were conducted using Fish Bioenergetics 4.0, an open-access software that uses an R-based application (Deslauriers et al. 2017). Input parameters of water temperature, diet proportions, prey energy density (Table B.2), predator energy density (i.e., rainbow trout and kokanee), and proportion of indigestible prey were required to run species-specific bioenergetic models. The bioenergetics models were run from 1 May 2023 to 31 October 2023 to represent the ice-free portion of the calendar for Georgetown Lake (i.e., the putative growing season).

Water Temperature Water temperature was measured in Georgetown Lake using a handheld YSI unit two meters below the surface and obtained at least once monthly from May 2023 through September 2023. Mean water temperature was used when more than one water temperature was recorded for a month. Monthly water temperatures recorded by Stafford (2013) were averaged from two locations to estimate water temperatures for October (Table 3.1). The lower and upper projected air temperatures (+ 2.5 °C and + 5.4 °C) from the Montana Climate Assessment (Whitlock et al. 2017) were selected to simulate water temperatures. A 2.5 °C increase in air temperature is predicted to occur in mid-century (2040-2069), and a 5.4 °C in air temperature is predicted to occur in end-of-century (2070-2099; Whitlock et al. 2017). Water temperature was adjusted to account for corresponding changes in air temperature (Pine III and Allen 2001; Wuellner et al. 2010; Pease and Paukert 2014; Breeggemann et al. 2016); thus, for a 1 °C degree change in air temperature, water temperature was correspondingly changed by 1 °C change in water temperature, therefore mean ice-off (May-October) water temperatures were increased by 2.5 °C and 5.4 °C.

Diet Proportions Diet proportions and proportions of indigestible prey were obtained from stomach samples of fish sampled from Georgetown Lake (see Chapter 2). Diet proportions were summarized by taxon and season. Diet taxa that appeared infrequently, accounted for less than 5.0% mean percent by weight for all seasons (Eckelbecker 2024), or that were unable to be identified to a taxon were summarized as “other.” The “other” category was largely comprised of insect parts. To estimate the proportions of indigestible prey, a value of 100% was selected for organic material and plants, and a value of 10% was selected for all other prey items (Stewart et al. 1983; Yule and Luecke 1993; Neebling and Moan 2013). Seasons for diet proportions were defined as spring (1 May – 10 June), summer (11 June – 10 August), and autumn (11 August – 30 October).

Prey and Predator Energy Densities Prey energy densities and predator energy densities (i.e., rainbow trout and kokanee) were obtained from the literature. Prey energy densities were converted to J/g of wet weight (Cumminns and Wuycheck 1971; Hanson et al. 1997; Table B.2). The energy density of the “other” category was obtained by averaging the energy density estimates of all prey categories. Rainbow trout predator energy density was set to 5648 J/g (Johnson et al. 2017) and kokanee energy density was 9736 J/g (Johnson et al. 2017).

Bioenergetics Modeling Bioenergetics modeling was used to simulate the effects of increasing water temperature on food consumption and growth for rainbow trout and kokanee in Georgetown Lake. Bioenergetics modeling was used to evaluate two scenarios for each species; food consumption scenario based on maintenance consumption (i.e., starting weight = final weight) and a growth scenario based on empirical growth data (Table 3.2) from Georgetown Lake for each species. Starting weights for each age class were obtained from weight-at-age point estimates (Table 3.2). Both scenarios were conducted for three temperature models, observed ice-off water temperatures in 2023 (i.e., observed temperature), + 2.5 °C, and + 5.4 °C water temperatures during the ice-off season (Table 3.3). Daily consumption and cumulative food consumption were assessed for the food consumption scenarios, and final weights at the end of the growing season were estimated for the growth scenarios (Table 3.3).

Food Consumption Scenario To examine changes in consumption related to increased water temperatures, results from the observed temperature food consumption scenario were compared to consumption at the + 2.5 °C and + 5.4 °C water temperatures (Table 3.3). The proportion of maximum consumption (C_{max}) for one growing season was quantified using the P value (proportion of C_{max}) for rainbow trout and kokanee. Mean percent change in daily consumption by month and percent change in cumulative consumption among models were calculated for rainbow trout and kokanee throughout the growing season (May-October).

Growth Scenario Observed ice-off water temperatures in 2023 and growth for rainbow trout and kokanee from 2022 and 2023 in Georgetown Lake were used to develop an observed consumption model for each species (Table 3.3). The proportion of C_{max} (P value) generated from the baseline consumption model (i.e., 2022 and 2023 consumption) was held constant for rainbow trout and kokanee for the + 2.5 °C and + 5.4 °C water temperatures representing that fish continued to eat at the same rate as the baseline consumption model. Effects of increasing water temperature on the growth of rainbow trout and kokanee were assessed by comparing the percent change in final weight between the baseline consumption model and those predicted from the + 2.5 °C and + 5.4 °C water temperatures (Table 3.3).

Results

Weight-at-Age

Otoliths were removed and aged from 157 rainbow trout varying from 158 to 597 mm and 35 to 1990 g representing ages from 0 to 10 years of age (Figures B.1 and B.2). However, age classes 7 to 10 had insufficient samples size ($n \leq 3$) to include in the bioenergetics modelling (Figure B.2). Thirty-six otoliths were removed and aged from kokanee varying from 193 mm to 320 mm and 40 to 265 g (Table 3.2; Figures B.1 and B.2). Kokanee ages varied from 1 to 4 years (Figure B.2).

Bioenergetics

Food Consumption Scenario The pattern in percent change in daily consumption throughout the growing season was similar for rainbow trout and kokanee (Figure 3.2). Percent change in daily consumption was highest at the beginning and end of the growing season (Figure

3.2). The highest percent increase in daily consumption was for kokanee (205%) in May for the + 5.4 °C water temperature model (Figure 3.2). Only in July for the + 5.4 °C water temperature model, did rainbow trout and kokanee have a percent decrease in consumption — 94% for rainbow trout and by 20% for kokanee (Figure 3.2).

Despite the percent decrease in mean daily consumption during July, cumulative consumption for rainbow trout and kokanee increased for both increased water temperatures compared to observed water temperature (Figure 3.3; Table 3.4). The mean percent change in cumulative consumption was higher for + 5.4 °C water temperature compared to + 2.5 °C water temperature for rainbow trout and kokanee (Figure 3.3), and cumulative consumption was higher and more variable for kokanee than rainbow trout at both increased water temperatures. For all ages and species, the *P* value increased for the + 2.5 °C and + 5.4 °C water temperatures compared to the observed water temperatures for the consumption scenario (Table 3.4). For kokanee, the *P* value exceeded 1.00 for age 3 for the + 2.5 °C and for all ages for the food consumption scenario with + 5.4 °C water temperature (Table 3.4).

<u>Growth Scenario</u> Mean percent change, from point estimates, in final weight declined for both increased water temperature models for rainbow trout and kokanee; however, confidence intervals overlapped zero for rainbow trout in the 2.5 °C increase in water temperature (Figure 3.4). Kokanee growth declined by 37% with a 2.5 °C increase in water temperature and declined by 64% with a 5.4 °C increase (Figure 3.4).

Daily weight estimates for rainbow trout were similar for the + 2.5 °C water temperature scenario compared to the observed water temperature (Figure 3.5). In contrast, the + 5.4 °C water temperature scenario showed a decrease in rainbow trout weights in July (corresponds to peak water temperatures in the observed data) then increases during the autumn; however final weight were below the start weight (Figure 3.5). Kokanee weight declined from June through August for the observed temperature, however the final weight exceeded the start weight for all ages (Figure 3.6). For both increased water temperatures, kokanee weight decreased compared to the observed water temperatures across all ages, except for age 1 kokanee, where final weight slightly increased (< 4 g) from the start weight in the + 2.5 °C water temperature model (Figure 3.6). By the end of the growing season kokanee lose up to 68% of their body weight with a 5.4 °C increase in water temperature.

Discussion

Climate change is projected to increase water temperatures beyond the thermal optimum for salmonids in Georgetown Lake, and in response salmonids may allocate a higher proportion of energy to support basal and active metabolism instead of somatic growth, reproduction, and lipid storage. Our findings indicate that climate-driven increases in water temperature may not affect salmonid species equally in Georgetown Lake, with kokanee exhibiting greater sensitivity to water temperature increases compared to rainbow trout.

As water temperature increases, metabolic rates increase until an optimum temperature is reached, above that metabolic efficiency declines. Within this thermal optimum, metabolism and activity function at maximum efficiency (Brett 1971; Ficke et al. 2007); outside this optimum, organismal performance declines (Ficke et al. 2007; Schulte et al. 2011). The optimum growth temperature range for rainbow trout occurs from 15 °C to 18.6 °C (Grabowski 1973; Wurtsbaugh and Davis 1977; Hokanson 1977; Railsback and Rose 1999; Jiang et al. 2020), whereas for kokanee it is slightly narrower at 15 °C to 17 °C (Brett 1971; Marine and Cech 2004). The slight difference in thermal preference explains the greater sensitivity of kokanee to increased water temperatures. Notably, observed water temperatures in Georgetown Lake during July and August already exceed the optimum growth temperature range for both species, adversely affecting kokanee weight, which declines during July and August across all temperature models. Kokanee weights are expected to decline farther with increased water temperatures. In contrast, rainbow trout weight only decreases for all ages in the + 5.4 °C water temperature scenario, suggesting a higher resilience to predicted climate-induced water temperature increases.

Both species must increase food consumption to meet basic metabolic needs (i.e., start weight = final weight) under elevated water temperatures; however, kokanee require nearly double the increase in food consumption compared to rainbow trout. For kokanee, the proportion of max consumption exceeded the theoretical maximum for age 3 in + 2.5 °C and for all ages in the + 5.4 °C water temperature model, indicating that they would need to exceed their maximum theoretical food consumption to meet minimum metabolic demands. This suggests that kokanee may be unable to meet their basic metabolic needs without losing weight as water temperatures increases in Georgetown Lake. This is consistent with previous studies that show kokanee food consumption and conversion efficiency decrease above 17 °C, with growth suppression at 23 °C, and complete appetite loss at 24 °C (Brett and Higgs 1970; Brett 1971; Marine and Cech 2004). Even at observed water temperatures, kokanee are suboptimal in food consumption and growth during June and July, as water temperatures exceed 17 °C.

The increased metabolic costs observed in our study are generally consistent with findings from other bioenergetics assessments examining the effects of warming water temperatures. For example, in the lower Quinault River, Washington, juvenile salmon experience reduced growth from April to September, while juvenile steelhead (anadromous rainbow trout) experience positive growth due to their higher thermal tolerances (Spanjer et al. 2022). Similar to my findings, rainbow trout are predicted to decrease in size as water temperatures increase in Methow River, Washington (Benjamin et al. 2013). Juvenile sockeye in Black Lake, Alaska are expected to exhibit a 15% reduction in growth under future predicted warming water temperatures (Griffiths and Schindler 2012). However, unlike our findings, growth differences were minimal in simulations where the *P* value was held constant (Griffiths and Schindler 2012). This difference is likely due to differences in thermal regimes, as future water temperatures in Georgetown Lake are expected to exceed 25 °C, whereas in Black Lake future water temperatures are not predicted to exceed 19 °C.

Salmonid growth and thermal tolerances are further restricted if food quality and quantity decline (Eggers 1978; Beauchamp et al. 2007). The quantity and quality of prey can vary spatially and temporally in response to climate-driven increased water temperature (Fisher and Pearcy 2005; Zamon and Welch 2005; Coyle and Pinchuk 2005; Aydin et al. 2005). Climate change may reduce the density and size of macroinvertebrates such as Gastropoda, Ephemeroptera, Coleoptera, Trichoptera, and Diptera (Burgmer et al. 2007; Forster et al. 2012; Horne et al. 2015), which are important food items for rainbow trout in Georgetown Lake (see Chapter 1). Additionally, higher water temperatures lead to earlier insect emergence, altering the temporal availability of common prey species, including Odonata, Ephemeroptera, Plecoptera, Trichoptera, and Diptera (Nebeker 1971; Dingemanse and Kalkman 2008; Richter et al. 2008; Hassall and Thompson 2008; Čmrlec et al. 2013; Dickson and Walker 2015; Chacón et al. 2016; Cheney et al. 2019; Nyquist et al. 2020). The detrimental effects of climate change on macroinvertebrates are likely more severe in shallow, gently sloping reservoirs, such as Georgetown Lake, than in deep, steep-sided reservoirs (Miranda et al. 2020). Increased water temperatures are likely to affect prey quantity, quality, and temporal availability and thus, salmonid growth.

Climate-driven water temperature increases could render Georgetown Lake uninhabitable for salmonids by the end-of-century in the + 5.4 °C water temperature scenario. The estimated upper lethal temperature limit for kokanee is 24.4 °C, and for all *Oncorhynchus* species at 25.1 °C (Brett 1952). Predicted July temperatures in the + 5.4 °C scenario exceed these limits for *Oncorhynchus* species, and August water temperatures also surpass the lethal limit for kokanee. Georgetown Lake is polymictic, so it does not thermally stratify during the summer, thus there is no cold thermal refuge available for salmonids.

However, climate-induced increased water temperatures may benefit the salmonid fishery in Georgetown Lake by decreasing the period of ice-cover. Climate change is predicted to decrease the period of ice cover on lakes and reservoirs (Gao and Stefan 2004; Gebre et al. 2014; Hamilton et al. 2018). Georgetown Lake is susceptible to low dissolved oxygen (DO) in the winter due to a combination of factors including ice and snow cover and macrophyte decomposition, which has resulted in multiple fish kills (Stafford 2013). By reducing the duration of ice-cover, salmonids would experience shorter periods of low DO, which would minimize stress and mortality. Additionally, the reduction in duration of ice-cover may increase the length of time of optimal growing temperatures in the spring and autumn, potentially offsetting growth reductions that occur in the warmest summer months.

This study provides valuable insights into the potential effects of climate-driven increases in water temperature on salmonids in Georgetown Lake; however, there are limitations that should be considered when interpreting the results. One limitation is the certainty of the water temperatures used in my analyses. The Montana Climate Assessment found high model agreement and low uncertainty that temperatures will increase by mid-century and end-of-century, however the magnitude of warming depends future emission rates and estimates are more uncertain when modeled further in time (Whitlock et al. 2017). Additionally, water temperature data were collected only once per month, which likely does not capture the variability of thermal conditions in Georgetown Lake. Water temperature fluctuations occur on a much shorter timescale than monthly intervals, and daily variation in water temperatures were missed. More frequent water temperature monitoring will provide a more detailed and accurate assessment of thermal conditions and the resulting effects on salmonids in Georgetown Lake. Future research should address these gaps to develop more accurate models. Another limitation is the assumption that the diets of rainbow trout and kokanee remained constant despite changes in water temperature. Increased water temperatures will likely alter the availability, abundance, and quality of prey species, requiring fish to adapt their feeding habits. Changes in diet composition could affect growth, but this study did not account for such potential shifts. Future research should consider dynamic diet models that reflect the potential for altered prey availability under varying temperature models.

My findings indicate that climate-driven increases in water temperature may differentially affect salmonid species in Georgetown Lake, with kokanee being more sensitive to rising water temperatures than rainbow trout. While both species experience growth challenges as water temperatures exceed their optimal ranges, kokanee are particularly vulnerable, requiring higher food consumption to meet basic metabolic needs under elevated water temperatures. As a result, kokanee are likely to experience more severe declines in growth compared to rainbow trout. Climate change will pose challenges for freshwater fisheries management, thus understanding how projected warming water temperatures may affect popular recreational fisheries can provide managers with information to establish reasonable expectations for fish growth.

Tables

Table 3.1: Water temperature (°C) by month used in the bioenergetics models. Observed water temperature values are empirical water temperature measurements from Georgetown Lake, Montana, USA. The + 2.5 °C and + 5.4 °C water temperature values are predicted increases in air temperature from the Montana Climate Assessment (Whitlock et al. 2017).

Month	Observed water temperature	+ 2.5 °C	+ 5.4 °C
May	10.4	12.9	15.8
June	12.7	15.2	18.1
July	19.8	22.3	25.2
August	19.2	21.7	24.6
September	15.5	18.0	20.9
October[a]	8.3	10.8	13.7

[a] Water temperature data obtained from Stafford (2012).

Table 3.2: Predicted weight (g) and 95% confidence intervals (in parentheses) by age for rainbow trout and kokanee sampled in 2022 and 2023 in Georgetown Lake, Montana, USA. Age 0, age 5, and age 6 kokanee were not sampled.

	Species	
Age	Rainbow trout	Kokanee
0	136.6 (69.4 – 189.7)	
1	310.5 (266.2 – 359.8)	26.6 (4.7 – 48.5)
2	668.5 (624.8 – 725.2)	95.5 (82.8 – 108.1)
3	938.4 (879.7 – 997.6)	164.3 (148.4 – 182.2)
4	1142.0 (1061.8 – 1212.5)	233.2 (202.2 – 264.1)
5	1295.5 (1198.3 – 1399.5)	
6	1411.2 (1286.5 – 1551.7)	

Table 3.3: Two scenarios were used for bioenergetics modeling for rainbow trout and kokanee; a food consumption scenario based on maintenance consumption (i.e., start weight = final weight) and a growth scenario based on empirical growth data for each species. The growth scenario was fit to the observed water temperature and empirical growth to estimate the proportion of maximum consumption (*P* value). The estimated *P* value was held constant for the increased water temperature models for the growth scenario. Both scenarios were conducted using observed ice-off water temperatures, + 2.5 °C water temperatures, and + 5.4 °C water temperatures during the growing season (May-October). The + 2.5 °C and + 5.4 °C water temperature values are predicted increases in water temperature from the Montana Climate Assessment (Whitlock et al. 2017).

Scenario	Water temperature	Variable manipulated	Response metric
Food consumption			
	Observed	Final weight	Daily consumption, cumulative consumption
	+ 2.5 °C		
	+ 5.4 °C		
Growth			
	Observed	*P* value	Final weight
	+ 2.5 °C		
	+ 5.4 °C		

Table 3.4: Proportion of maximum consumption (*P* value) and cumulative consumption (g; in parenthesis) for rainbow trout and kokanee estimated by bioenergetics model for one season of growth by age class and scenarios (see methods of scenario definitions). Data for models was obtained from Georgetown Lake, Montana, USA.

		Scenario					
		Food consumption			Growth		
Species	Age	Observed	+2.5	+5.4	Observed	+2.5	+5.4
Rainbow trout		0.41	0.43	0.55	0.68	0.68	0.68
	0	(1116)	(1278)	(1316)	(2521)	(2893)	(1882)
		0.44	0.46	0.59	0.78	0.78	0.78
	1	(2118)	(2428)	(2520)	(5041)	(5736)	(3891)
		0.47	0.49	0.63	0.66	0.66	0.66
	2	(3853)	(4421)	(4622)	(6113)	(6839)	(4913)
		0.49	0.50	0.65	0.61	0.61	0.61
	3	(5021)	(5763)	(6045)	(6774)	(7541)	(5541)
		0.50	0.51	0.66	0.58	0.58	0.58
	4	(5853)	(6720)	(7062)	(7205)	(7985)	(5940)
		0.50	0.51	0.67	0.56	0.56	0.56
	5	(6458)	(7416)	(7804)	(7497)	(8278)	(6206)
Kokanee		0.56	0.76	1.25	0.81	0.81	0.81
	1	(317)	(432)	(591)	(804)	(449)	(265)
		0.69	0.97	1.74	0.93	0.93	0.93
	2	(985)	(1373)	(2054)	(1547)	(1291)	(757)
		0.77	1.08	2.20	0.92	0.92	0.92
	3	(1607)	(2280)	(3754)	(2090)	(1773)	(1085)

Figures

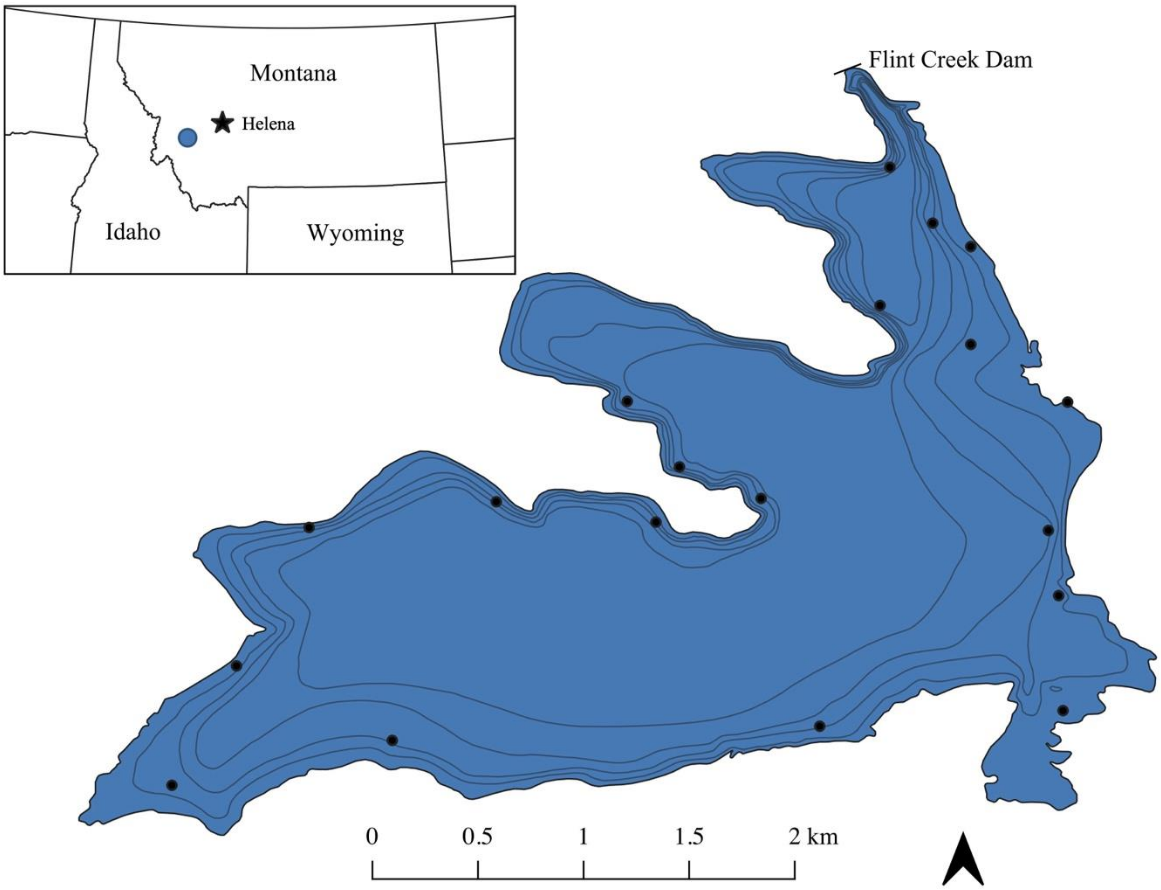

Figure 3.1: Map of Georgetown Lake, Montana, USA. Montana Fish, Wildlife & Parks standard gill net sampling locations are indicated with black circles. The bathymetric contour interval is 1.52 m and are indicated with black lines.

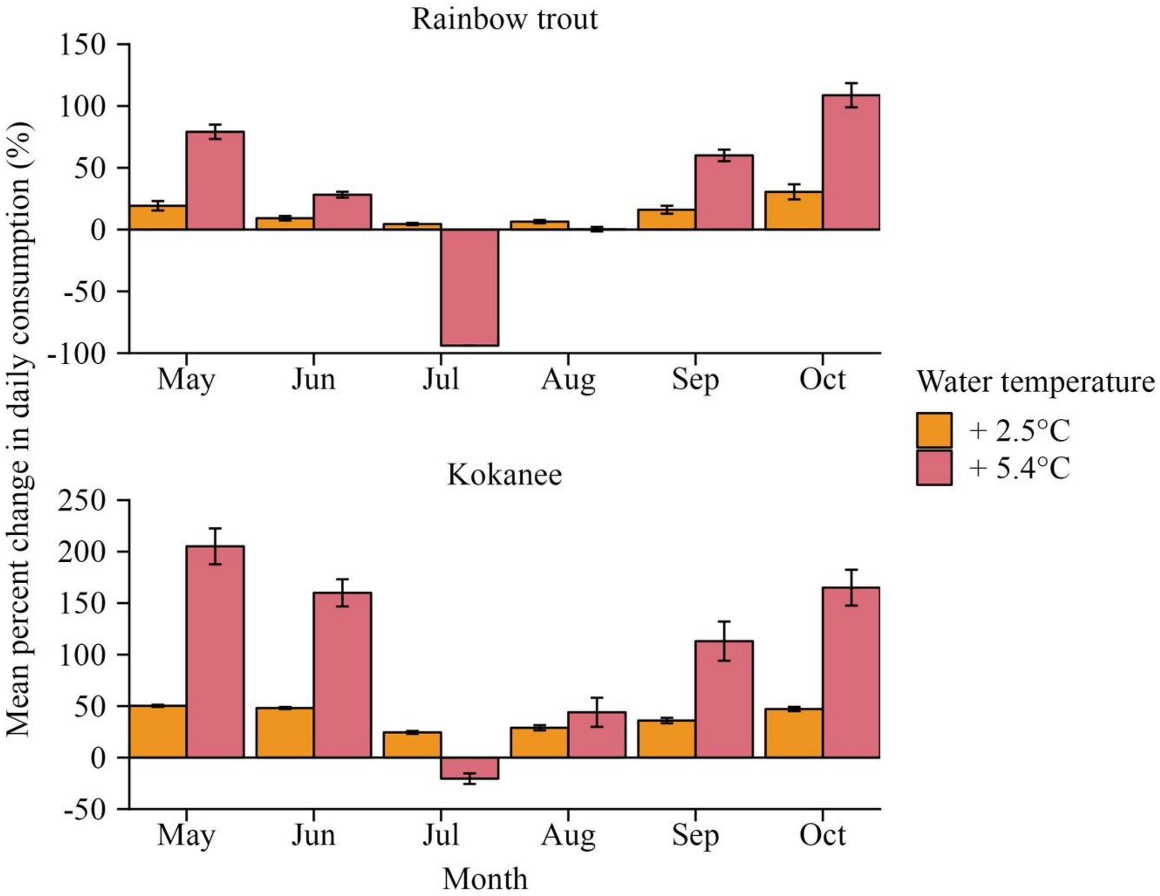

Figure 3.2: Mean percent change in daily consumption by month from bioenergetic models for rainbow trout and kokanee in Georgetown Lake, Montana, USA. A baseline model was constructed using observed ice-off temperatures in 2023. The baseline food consumption scenario was used to compare percent changes in daily consumption averaged for each month for the + 2.5 °C and + 5.4 °C water temperatures models during the growing season (May-October). Error bars represent standard error of the mean.

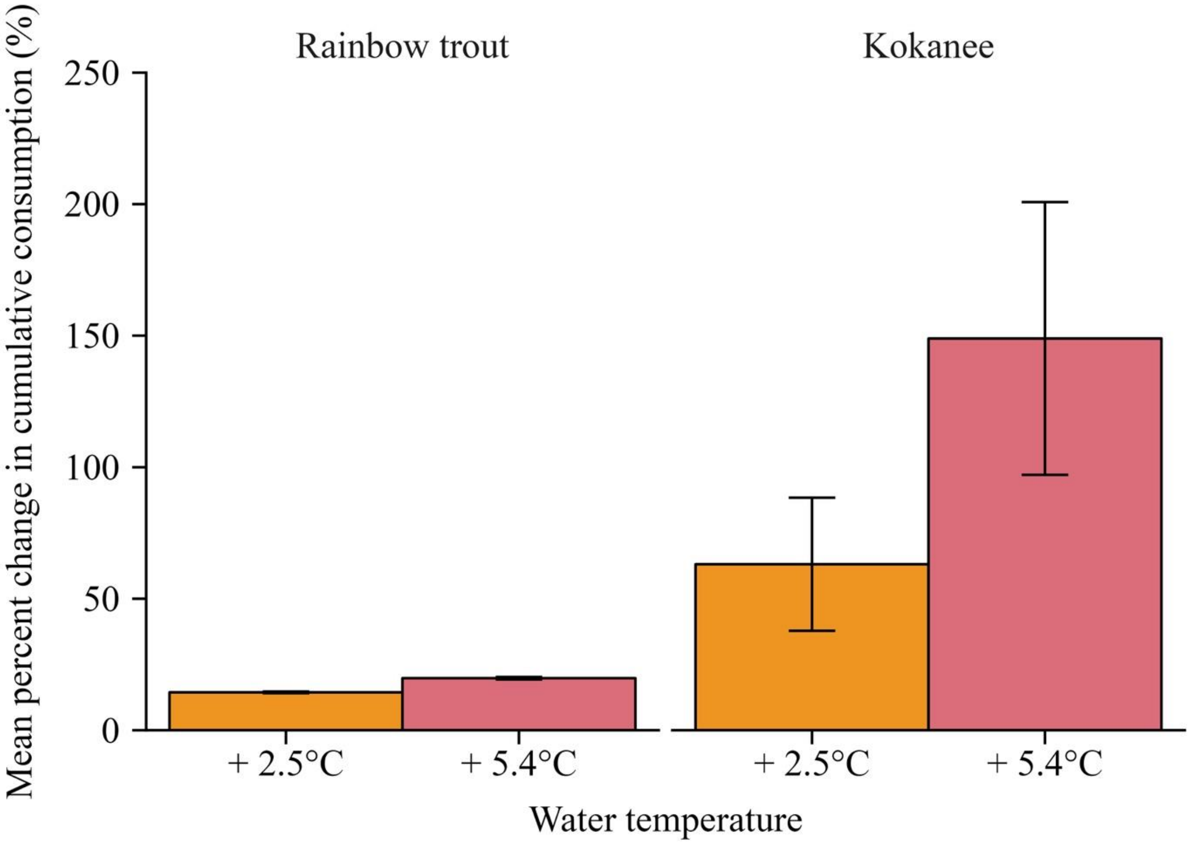

Figure 3.3: Mean percent change in cumulative consumption from bioenergetic models for rainbow trout and kokanee in Georgetown Lake, Montana, USA. Percent change in cumulative consumption was averaged across all ages for each species. A baseline model was constructed using observed ice-off temperatures in 2023. The baseline food consumption scenario was used to compare percent changes in cumulative consumption for the + 2.5 °C and + 5.4 °C water temperatures models during the growing season (May-October). Error bars represent standard error of the mean.

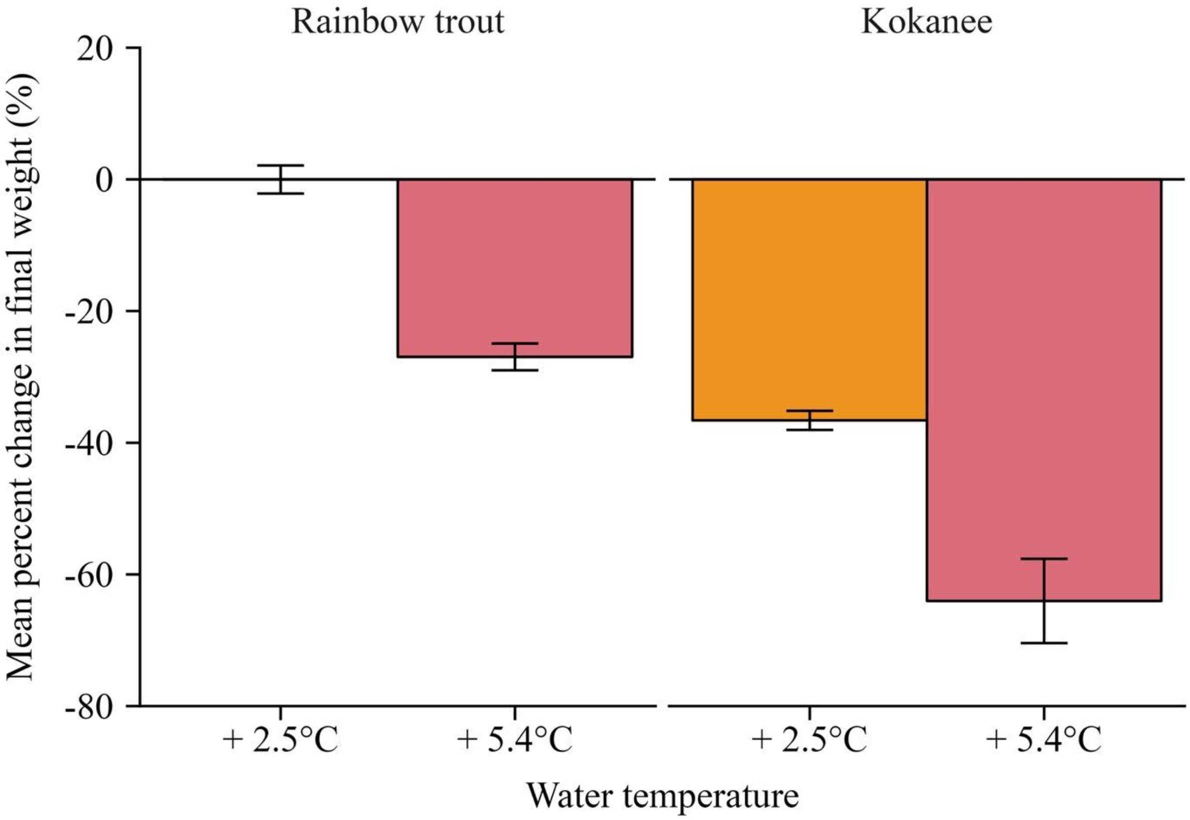

Figure 3.4: Mean percent change in final weight from bioenergetic models for one growing season for rainbow trout and kokanee in Georgetown Lake, Montana, USA. Percent change in final weight was averaged for all ages for each species. Observed water temperatures in 2023 and observed growth for rainbow trout and kokanee from 2022 and 2023 in Georgetown Lake were used to develop a baseline consumption scenario. The P values generated from the baseline consumption model (i.e., 2022 and 2023 consumption) were held constant for the + 2.5 °C and + 5.4 °C water temperature models. The percent change in final weight from the baseline consumption model was compared to those predicted from the + 2.5 °C and + 5.4 °C water temperatures models. Error bars represent standard error of the mean.

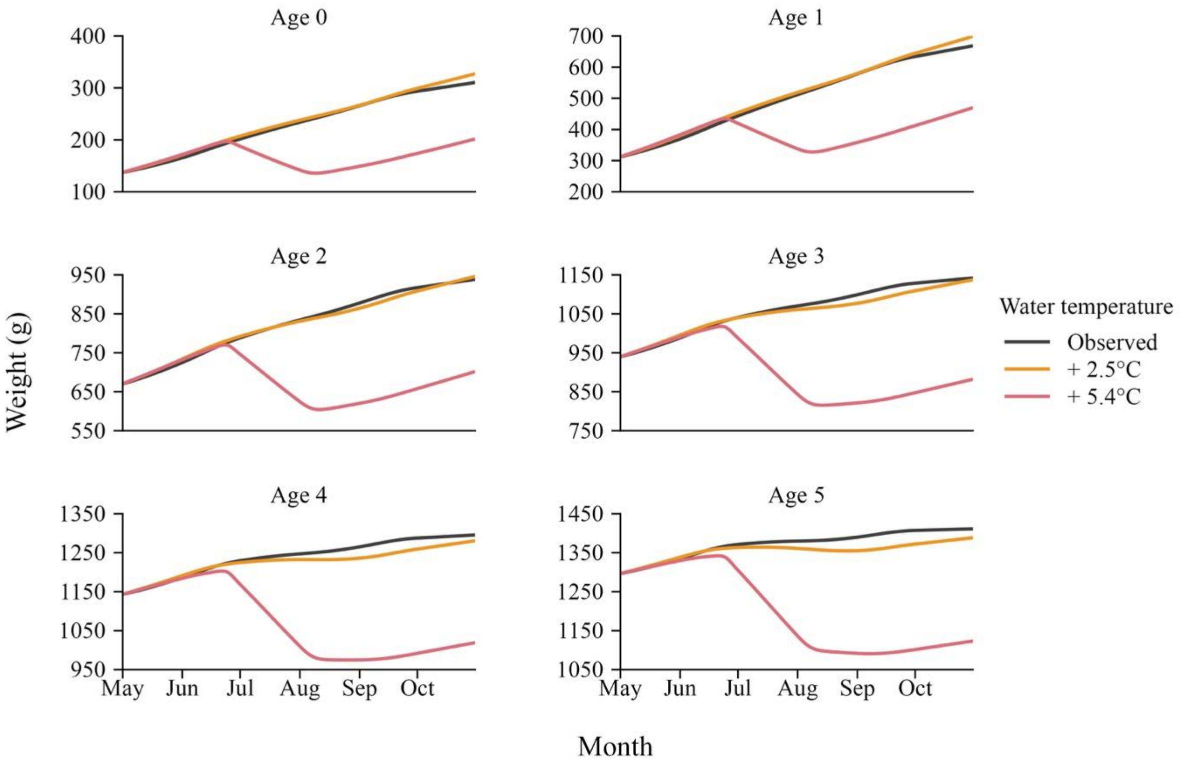

Figure 3.5: Daily weight (g) estimates from bioenergetic models for one growing season for rainbow trout in Georgetown Lake, Montana, USA. Observed growth simulations were conducted using observed ice-off water temperatures in 2023 (i.e., baseline model), + 2.5 °C, and + 5.4 °C water temperatures during the growing season (May-October).

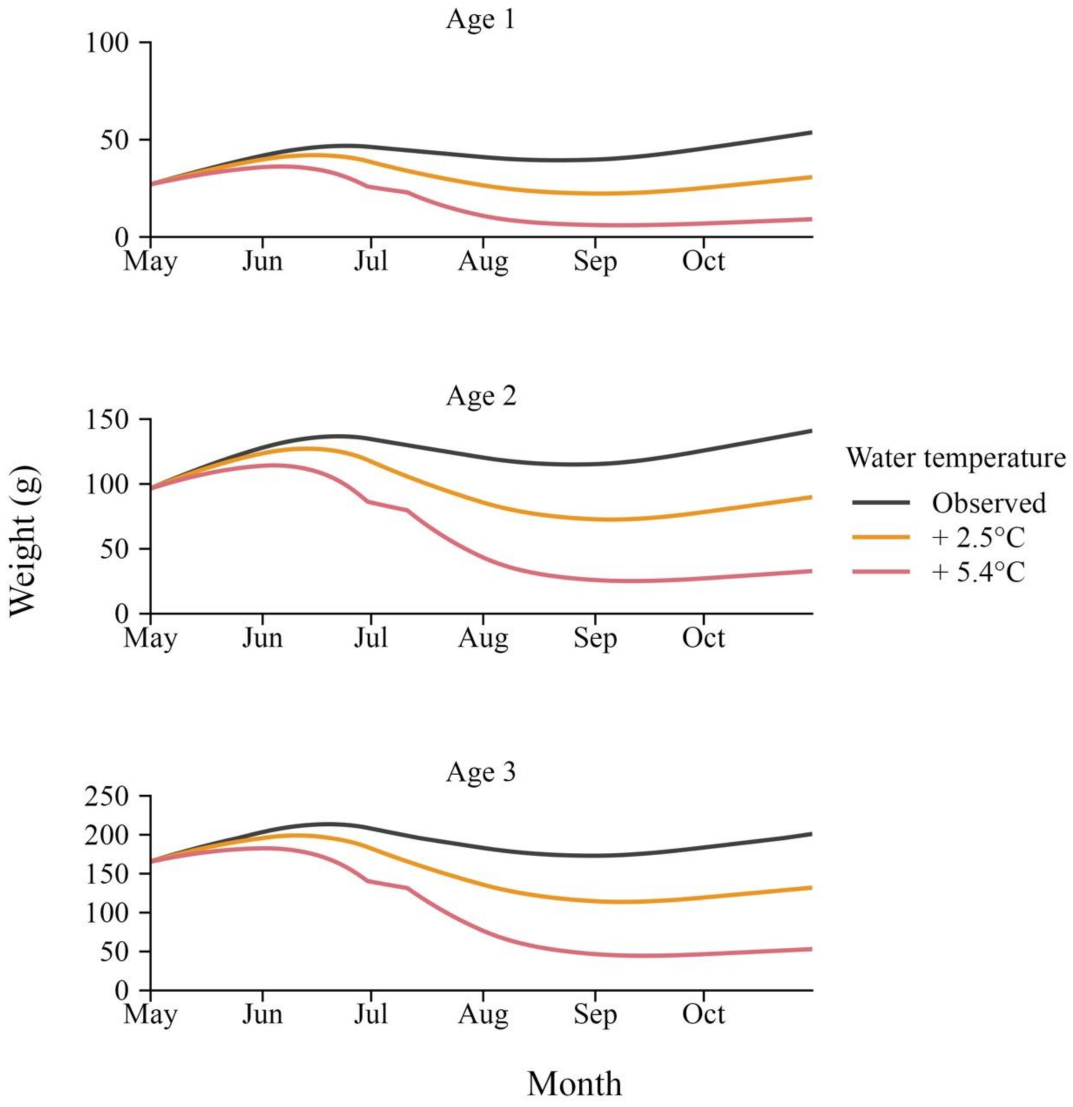

Figure 3.6: Daily weight (g) estimates from bioenergetic models for one growing season for kokanee in Georgetown Lake, Montana, USA. Observed growth simulations were conducted using observed ice-off water temperatures in 2023 (i.e., baseline model), + 2.5 °C, and + 5.4 °C water temperatures during the growing season (May-October).

References

Arlinghaus, R., J. K. Abbott, E. P. Fenichel, S. R. Carpenter, L. M. Hunt, J. Alós, T. Klefoth, S. J. Cooke, R. Hilborn, O. P. Jensen, M. J. Wilberg, J. R. Post, and M. J. Manfredo. 2019. Governing the recreational dimension of global fisheries. Proceedings of the National Academy of Sciences 116(12):5209–5213.

Audzijonyte, A., A. Kuparinen, R. Gorton, and E. A. Fulton. 2013. Ecological consequences of body size decline in harvested fish species: Positive feedback loops in trophic interactions amplify human impact. Biology Letters 9(2):20121103.

Aydin, K. Y., G. A. McFarlane, J. R. King, B. A. Megrey, and K. W. Myers. 2005. Linking oceanic food webs to coastal production and growth rates of Pacific salmon (*Oncorhynchus* spp.), using models on three scales. Deep Sea Research Part II: Topical Studies in Oceanography 52(5):757–780.

Beauchamp, D. A., A. D. Cross, J. L. Armstrong, K. W. Myers, J. H. Moss, J. L. Boldt, and L. J. Haldorson. 2007. Bioenergetic responses by Pacific salmon to climate and ecosystem variation. The North Pacific Anadromous Fish Commission 4:257–269.

Benjamin, J. R., P. J. Connolly, J. G. Romine, and R. W. Perry. 2013. Potential effects of changes in temperature and food resources on life history trajectories of juvenile *Oncorhynchus mykiss*. Transactions of the American Fisheries Society 142(1):208–220.

von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws II). Human Biology 10(2):181–213.

Bevelhimer, M. S., and S. M. Adams. 1993. A bioenergetics analysis of diel vertical migration by kokanee salmon, *Oncorhynchus nerka*. Canadian Journal of Fisheries and Aquatic Sciences 50(11):2336–2349.

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(5):731–735.

Brandt, S., D. Mason, M. McCormick, B. Lofgren, T. Hunter, and J. Tyler. 2002. Climate change: Implications for fish growth performance in the Great Lakes. Transactions of the American Fisheries Society 32(32):61–76.

Breeggemann, J. J., M. A. Kaemingk, T. J. DeBates, C. P. Paukert, J. R. Krause, A. P. Letvin, T. M. Stevens, D. W. Willis, and S. R. Chipps. 2016. Potential direct and indirect effects of climate change on a shallow natural lake fish assemblage. Ecology of Freshwater Fish 25(3):487–499.

Brett, J. R. 1952. Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. Journal of the Fisheries Research Board of Canada 9(6):265–323.

Brett, J. R. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). American Zoologist 11(1):99–113.

Brett, J. R., and D. A. Higgs. 1970. Effect of temperature on the rate of gastric digestion in fingerling sockeye salmon, *Oncorhynchus nerka*. Journal of the Fisheries Research Board of Canada 27(10):1767–1779.

Brown, J. C., K. H. Lokensgard, S. Snyder, and M. Draper. 2019. The cultural currents and social values of trout. Pages 65-93 *in* J. L. Kershner, J. E. Williams, R. E. Gresswell, and J. Lobón-Cerviá, editors. Trout and char of the world. American Fisheries Society, Bethesda, Maryland.

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(7):1771–1789.

Burgmer, T., H. Hillebrand, and M. Pfenninger. 2007. Effects of climate-driven temperature changes on the diversity of freshwater macroinvertebrates. Oecologia 151(1):93–103.

Busch, S., G. Kirillin, and T. Mehner. 2012. Plasticity in habitat use determines metabolic response of fish to global warming in stratified lakes. Oecologia 170(1):275–287.

Casselman, J. M. 2002. Effects of temperature, global extremes, and climate change on year-class production of warmwater, coolwater, and coldwater fishes in the Great Lakes Basin. American Fisheries Society Symposium 2002:39–60.

Chacón, M. M., S. Segnini, and D. Briceño. 2016. Temperatura y emergencia diaria de siete géneros de Ephemeroptera (Insecta) en un río de la Selva Nublada de los Andes Tropicales. Revista de Biología Tropical 64(1):117–130.

Cheney, K. N., A. H. Roy, R. F. Smith, and R. E. Dewalt. 2019. Effects of stream temperature and substrate type on emergence patterns of Plecoptera and Trichoptera from Northeastern United States headwater streams. Environmental Entomology 48(6):1349–1359.

Christensen, J. H., B. Hewitson, A. Busuioc, A. Chen, X. Gao, I. Held, R. Jones, R. K. Kolli, W. T. Kwon, R. Laprise, V. Magana Rueda, L. Mearns, C. G. Menendez, J. Raisanen, A. Rinke, A. Sarr, and P. Whetton. 2007. Regional climate projections. Chapter 11. Climate change 2007: the physical science basis. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

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(2):301–314.

Čmrlec, K., M. Ivković, P. Šemnički, and Z. Mihaljević. 2013. Emergence phenology and microhabitat distribution of aquatic Diptera community at the outlets of barrage lakes: Effect of temperature, substrate and current velocity. Polish Journal of Ecology 61(1):135–144.

Cowx, I. G., R. Arlinghaus, and S. J. Cooke. 2010. Harmonizing recreational fisheries and conservation objectives for aquatic biodiversity in inland waters. Journal of Fish Biology 76(9):2194–2215.

Coyle, K. O., and A. I. Pinchuk. 2005. Seasonal cross-shelf distribution of major zooplankton taxa on the northern Gulf of Alaska shelf relative to water mass properties, species depth preferences and vertical migration behavior. Deep Sea Research Part II: Topical Studies in Oceanography 52(1):217–245.

Cumminns, K. W., and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Internationale Vereinigung für Theoretische und Angewandte Limnologie: Mitteilungen 18(1):1–158.

Denechaud, C., S. Smoliński, A. J. Geffen, J. A. Godiksen, and S. E. Campana. 2020. A century of fish growth in relation to climate change, population dynamics and exploitation. Global Change Biology 26(10):5661–5678.

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(11):586–596.

Dickson, T. R., and I. R. Walker. 2015. Midge (Diptera: Chironomidae and Ceratopogonidae) emergence responses to temperature: Experiments to assess midges' capacity as paleotemperature indicators. Journal of Paleolimnology 53(2):165–176.

Dingemanse, N. J., and V. J. Kalkman. 2008. Changing temperature regimes have advanced the phenology of Odonata in the Netherlands. Ecological Entomology 33(3):394–402.

Eckelbecker, R. W. 2024. Ecological interactions and environmental stressors: Assessing dietary dynamics and population stability of burbot amid non-native trout and warming winter temperatures. Doctoral dissertation, Montana State University, Bozeman, Montana.

Eggers, D. M. 1978. Limnetic feeding behavior of juvenile sockeye salmon in Lake Washington and predator avoidance. Limnology and Oceanography 23(6):1114–1125.

EPA (U.S. Environmental Protection Agency). 1977. Report on Georgetown Lake, Deer Lodge and Granite Counties, Montana. USEPA Report Working Paper No. 793, Washington, D.C.

Ficke, A. D., C. A. Myrick, and L. J. Hansen. 2007. Potential impacts of global climate change on freshwater fisheries. Reviews in Fish Biology and Fisheries 17(4):581–613.

Fisher, J. P., and W. G. Pearcy. 2005. Seasonal changes in growth of coho salmon (*Oncorhynchus kisutch*) off Oregon and Washington and concurrent changes in the spacing of scale circuli. Fishery Bulletin 103(1):34–51.

Forster, J., A. G. Hirst, and D. Atkinson. 2012. Warming-induced reductions in body size are greater in aquatic than terrestrial species. Proceedings of the National Academy of Sciences 109(47):19310–19314.

Fry, F. E. J. 1971. The effect of environmental factors on the physiology of fish. Pages 1–98 *in* W. S. Hoar and D. J. Randall, editors. Fish physiology. Academic Press.

Gao, S., and H. G. Stefan. 2004. Potential climate change effects on ice covers of five freshwater lakes. Journal of Hydrologic Engineering 9(3):226–234.

Gebre, S., T. Boissy, and K. Alfredsen. 2014. Sensitivity to climate change of the thermal structure and ice cover regime of three hydropower reservoirs. Journal of Hydrology 510:208–227.

Grabowski, S. J. 1973. Effects of fluctuating and constant temperatures on some hematological characteristics, tissue glycogen levels, and growth of steelhead trout (*Salmo Gairdneri*). Doctoral dissertation, University of Idaho, Moscow, Idaho.

Grau, K. 2019. 2018 Economic contribution of nonresident travel spending in Montana travel regions and counties. Institute for Tourism and Recreation Research Publications, Missoula, Montana.

Griffiths, J. R., and D. E. Schindler. 2012. Consequences of changing climate and geomorphology for bioenergetics of juvenile sockeye salmon in a shallow Alaskan lake. Ecology of Freshwater Fish 21(3):349–362.

Hamilton, D. P., M. R. Magee, C. H. Wu, and T. K. Kratz. 2018. Ice cover and thermal regime in a dimictic seepage lake under climate change. Inland Waters 8(3):381–398.

Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish Bioenergetics 3.0 for Windows. University of Wisconsin-Madison Center for Limnology and University of Wisconsin Sea Grant Institute, Technical Report WISCU-T-97-001, Madison, Wisconsin.

Hartmann, D. L., A. M. G. K. Tank, M. Rusticucci, L. V. Alexander, S. Brönnimann, Y. A. R. Charabi, F. J. Dentener, E. J. Dlugokencky, D. R. Easterling, A. Kaplan, B. J. Soden, P. W. Thorne, M. Wild, and P. Zhai. 2014. Observations: Atmosphere and surface. Pages 159–254 *in* Climate change 2013: The physical science basis. Cambridge University Press, Cambridge.

Hassall, C., and D. J. Thompson. 2008. The effects of environmental warming on Odonata: a review. International Journal of Odonatology 11(2):131–153.

Hixon, M. A., D. W. Johnson, and S. M. Sogard. 2014. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. ICES Journal of Marine Science 71(8):2171–2185.

Hokanson, K. E. F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. Journal of the Fisheries Research Board of Canada 34(10):1524–1550.

Horne, C. R., Andrew. G. Hirst, and D. Atkinson. 2015. Temperature-size responses match latitudinal-size clines in arthropods, revealing critical differences between aquatic and terrestrial species. Ecology Letters 18(4):327–335.

IPCC. 2007. Climate change 2007: Impacts, adaptation and vulnerability. Contribution of working group II to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, UK.

Jiang, X., S. Dong, Y. Zhou, Q. Gao, and Z. Pan. 2020. An effective method of prompting juvenile rainbow trout (*Oncorhynchus mykiss*) to cope with heat stress. Journal of Ocean University of China 19(1):216–224.

Johnson, B. M., W. M. Pate, and A. G. Hansen. 2017. Energy density and dry matter content in fish: new observations and an evaluation of some empirical models. Transactions of the American Fisheries Society 146(6):1262–1278.

Jones, R., C. Travers, C. Rodgers, B. Lazar, E. English, J. Lipton, J. Vogel, K. Strzepek, and J. Martinich. 2013. Climate change impacts on freshwater recreational fishing in the United States. Mitigation and Adaptation Strategies for Global Change 18(6):731–758.

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 the Fisheries Research Board of Canada 34(10):1922–1935.

Lewis, M. 2018. Statewide estimates of resident and nonresident hunter & angler trip related expenditures in Montana. Human Dimensions Unit Research Summary. Montana Fish, Wildlife & Parks, Helena, Montana.

Liermann, B. 2013. Analysis and management implications of multiple decades of fisheries data for Georgetown Lake, MT. Montana Fish, Wildlife & Parks, Missoula, Montana.

Lorenzen, K. 2016. Toward a new paradigm for growth modeling in fisheries stock assessments: Embracing plasticity and its consequences. Fisheries Research 180:4–22.

Lynch, A. J., S. J. Cooke, A. M. Deines, S. D. Bower, D. B. Bunnell, I. G. Cowx, V. M. Nguyen, J. Nohner, K. Phouthavong, B. Riley, M. W. Rogers, W. W. Taylor, W. Woelmer, S.-J. Youn, and B. T. D. Jr. 2016. The social, economic, and environmental importance of inland fish and fisheries. Environmental Reviews 24(2):115–121.

Magnuson, J. J., J. D. Meisner, and D. K. Hill. 1990. Potential changes in the thermal habitat of Great Lakes fish after global climate warming. Transactions of the American Fisheries Society 119(2):254–264.

Magnuson, J. J., K. E. Webster, R. A. Assel, C. J. Bowser, P. J. Dillon, J. G. Eaton, H. E. Evans, E. J. Fee, R. I. Hall, L. R. Mortsch, D. W. Schindler, and F. H. Quinn. 1997. Potential effects of climate changes on aquatic systems: Laurentian Great Lakes and Precambrian Shield Region. Hydrological Processes 11(8):825–871.

Marine, K. R., and J. J. Cech. 2004. Effects of high water temperature on growth, smoltification, and predator avoidance in juvenile Sacramento River chinook salmon. North American Journal of Fisheries Management 24(1):198–210.

MFWP. 2022. Appendix A - Annual pressure by waterbody 2020. Montana Fish, Wildlife & Parks, Report, Helena, Montana.

Millennium Ecosystem Assessment (Program), editor. 2005. Ecosystems and human well-being: Wetlands and water synthesis: A report of the Millennium Ecosystem Assessment. World Resources Institute, Washington, DC.

Miranda, L. E., G. Coppola, and J. Boxrucker. 2020. Reservoir fish habitats: A perspective on coping with climate change. Reviews in Fisheries Science & Aquaculture 28(4):478–498.

Murdoch, A., and M. Power. 2013. The effect of lake morphometry on thermal habitat use and growth in Arctic charr populations: Implications for understanding climate-change impacts. Ecology of Freshwater Fish 22(3):453–466.

Nebeker, A. V. 1971. Effect of high winter water temperatures on adult emergence of aquatic insects. Water Research 5(9):777–783.

Neebling, T., and C. Moan. 2013. A bioenergetics assessment of the kokanee and lake trout populations in Boulder Lake. Wyoming Game and Fish Department, Fish Division, Administrative Report, Casper, Wyoming.

Ney, J. J. 1993. Bioenergetics modeling today: Growing pains on the cutting edge. Transactions of the American Fisheries Society 122(5):736–748.

Nyquist, C., B. Vondracek, and L. Ferrington. 2020. The influence of an in-stream thermal gradient on chironomid emergence during winter. Hydrobiologia 847(15):3153–3167.

Pease, A. A., and C. P. Paukert. 2014. Potential impacts of climate change on growth and prey consumption of stream-dwelling smallmouth bass in the central United States. Ecology of Freshwater Fish 23(3):336–346.

Pederson, G. T., L. J. Graumlich, D. B. Fagre, T. Kipfer, and C. C. Muhlfeld. 2010. A century of climate and ecosystem change in western Montana: What do temperature trends portend? Climatic Change 98(1):133–154.

Pine III, W. E., and M. S. Allen. 2001. Differential growth and survival of weekly age-0 black crappie cohorts in a Florida lake. Transactions of the American Fisheries Society 130(1):80–91.

Pitcher, T. J., and C. Hollingworth. 2008. Recreational fisheries: Ecological, economic and social evaluation. John Blackwell Publishing, Osney Mead, Oxford, UK.

Railsback, S. F., and K. A. Rose. 1999. Bioenergetics modeling of stream trout growth: Temperature and food consumption effects. Transactions of the American Fisheries Society 128(2):241–256.

Richter, O., F. Suhling, O. Müller, and D. Kern. 2008. A model for predicting the emergence of dragonflies in a changing climate. Freshwater Biology 53(9):1868–1880.

Schulte, P. M., T. M. Healy, and N. A. Fangue. 2011. Thermal performance curves, phenotypic plasticity, and the time scales of temperature exposure. Integrative and Comparative Biology 51(5):691–702.

Sharma, S., D. A. Jackson, C. K. Minns, and B. J. Shuter. 2007. Will northern fish populations be in hot water because of climate change? Global Change Biology 13(10):2052–2064.

Shaw, G. D., K. L. Mitchell, and C. H. Gammons. 2017. Estimating groundwater inflow and leakage outflow for an intermontane lake with a structurally complex geology: Georgetown Lake in Montana, USA. Hydrogeology Journal 25:135–149.

Shuter, B. J., and J. R. Post. 1990. Climate, population viability, and the zoogeography of temperate fishes. Transactions of the American Fisheries Society 119(2):314–336.

Spanjer, A. R., A. S. Gendaszek, E. J. Wulfkuhle, R. W. Black, and K. L. Jaeger. 2022. Assessing climate change impacts on Pacific salmon and trout using bioenergetics and spatiotemporal explicit river temperature predictions under varying riparian conditions. PLOS ONE 17(5):e0266871.

Stafford, C. 2013. Long-term trends in the water quality of Georgetown Lake, Montana - Georgetown State of the lake project report to Montana Department of Justice and Montana Department of Environmental Quality. Missoula, Montana.

Stefan, H. G., X. Fang, and J. G. Eaton. 2001. Simulated fish habitat changes in North American lakes in response to projected climate warming. Transactions of the American Fisheries Society 130(3):459–477.

Stewart, D. J., D. Weininger, D. V. Rottiers, and T. A. Edsall. 1983. An energetics model for Lake Trout, *Salvelinus namaycush*: Application to the Lake Michigan population. Canadian Journal of Fisheries and Aquatic Sciences 40(6):681–698.

U.S. Department of the Interior and U.S. Fish and Wildlife Service. 2022. 2022 National survey of fishing, hunting, and wildlife-associated recreation, Washington, D.C.

Whitlock, C., W. F. Cross, B. D. Maxwell, N. Silverman, and A. A. Wade. 2017. 2017 Montana Climate Assessment: Stakeholder driven, science informed. Montana Institute on Ecosystems, Bozeman, Montana.

Winberg, G. G. Rate of metabolism and food requirements of fishes. Fisheries Research Board of Canada, Translation Series 194, Nanaimo, British Columbia, Canada.

Wuellner, M. R., S. R. Chipps, D. W. Willis, and W. E. Adams Jr. 2010. Interactions between walleyes and smallmouth bass in a Missouri River reservoir with consideration of the influence of temperature and prey. North American Journal of Fisheries Management 30(2):445–463.

Wurtsbaugh, W. A., and G. E. Davis. 1977. Effects of temperature and ration level on the growth and food conversion efficiency of *Salmo gairdneri* Richardson. Journal of Fish Biology 11(2):87–98.

Yasarer, L. M. W., and B. S. M. Sturm. 2016. Potential impacts of climate change on reservoir services and management approaches. Lake and Reservoir Management 32(1):13–26.

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 122(6):1058–1069.

Zamon, J. E., and D. W. Welch. 2005. Rapid shift in zooplankton community composition on the northeast Pacific shelf during the 1998–1999 El Niño – La Niña event. Canadian Journal of Fisheries and Aquatic Sciences 62(1):133–144.

CHAPTER FOUR

THESIS CONCLUSION

The findings presented in this thesis underscore the complexity of ecological and environmental factors affecting the salmonid fishery in Georgetown Lake. Together, the studies in **Chapters 2 and 3** provide valuable insights into the challenges and opportunities for managing salmonid fisheries in a dynamic aquatic ecosystem.

Though it was believed the introduction of Gerrards, which typically have a piscivorous feeding strategy, would predate on kokanee, the results from **Chapter 2** instead found that Gerrards perform similarly to other strains of rainbow trout in Georgetown Lake. There was extremely low prevalence of piscivory and no evidence of Gerrards consuming kokanee. Gerrards exhibited a generalist feeding strategy and there was dietary and niche overlap and no difference in trophic position among Gerrards, Eagle Lake, Arlee, or brook trout. Diet proportions and proportions of indigestible prey were obtained from **Chapter 2** were used in bioenergetic models in **Chapter 3**. These findings highlight the unpredictability of predator-prey dynamics and the importance of evaluating management interventions, such as biocontrols.

In **Chapter 3**, bioenergetics models were used to simulate the effects of warming water temperature on food consumption and growth for rainbow trout and kokanee within Georgetown Lake. Climate change is projected to increase water temperatures beyond the thermal optimum for salmonids in Georgetown Lake, and in response salmonids may allocate a higher proportion of energy to support basal and active metabolism instead of somatic growth, reproduction, and lipid storage. Our findings indicate that climate-driven increases in water temperature may not affect salmonid species equally in Georgetown Lake, with kokanee exhibiting greater sensitivity to water temperature increases compared to rainbow trout. While both species experience growth challenges as water temperatures exceed their optimal ranges, kokanee are particularly vulnerable, requiring higher food consumption to meet basic metabolic needs under elevated water temperatures. Thus, kokanee are likely to experience greater declines in growth compared to rainbow trout. Climate change will pose challenges for freshwater fisheries management, thus understanding how projected warming water temperatures may affect popular recreational fisheries can provide managers with information to establish reasonable expectations for fish growth.

This work also highlights several key areas that warrant future research. More frequent and detailed monitoring of water temperature would improve predictions of climate effects. Additionally, exploring dynamic diet models that incorporate shifts in prey availability and quality under changing environmental conditions would provide a more comprehensive understanding of salmonid growth and survival in Georgetown Lake.

The findings presented in this thesis underscore the importance of integrating short-term management strategies with long-term ecological modeling. Together, the approaches used in **Chapters 2 and 3** contribute to a more comprehensive understanding of the challenges and opportunities for managing the popular salmonid fishery in Georgetown Lake. This research not only informs local management decisions but also offers broader lessons for the sustainable management of freshwater fisheries in a changing world.

REFERENCES CITED

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(4):607–614.

Amundsen, P. A., M. A. Svenning, and S. I. Slikavuoplo. 1999. An experimental comparison of cannibalistic response in different Arctic charr (*Salvelinus alpinus* (L.)) stocks. Ecology of Freshwater Fish 8(1):43–48.

Andrusak, H., and E. A. Parkinson. 1984. Food habits of Gerrard stock rainbow trout in Kootenay Lake, British Columbia. British Columbia Fish and Wildlife Branch, Fisheries Technical Circular No. 60.

Arlinghaus, R., J. K. Abbott, E. P. Fenichel, S. R. Carpenter, L. M. Hunt, J. Alós, T. Klefoth, S. J. Cooke, R. Hilborn, O. P. Jensen, M. J. Wilberg, J. R. Post, and M. J. Manfredo. 2019. Governing the recreational dimension of global fisheries. Proceedings of the National Academy of Sciences 116(12):5209–5213.

Arndt, S. 2004. Post-fertilization diet, condition, and growth of bull trout and rainbow trout in Arrow Lakes Reservoir. Columbia Basin Fish & Wildlife Compensation Program, Nelson, British Columbia.

Ashley, K., I. C. Thompson, D. Sebastian, D. Lasenby, K. E. Smokorowski, and H. Andrusak. 1999. Restoration of kokanee salmon in Kootenay Lake, a large intermontane lake, by controlled seasonal addition of limiting nutrients. Pages 127–169 *in* T. Murphy and M. Munawar, editors. Aquatic restoration in Canada. Backhuys Publisher, Leiden, Netherlands.

Ashley, K., L. C. Thompson, D. C. Lasenby, L. McEachern, K. E. Smokorowski, and D. Sebastian. 1997. Restoration of an interior lake ecosystem: The Kootenay Lake fertilization experiment. Water Quality Research Journal 32(2):295–324.

Audzijonyte, A., A. Kuparinen, R. Gorton, and E. A. Fulton. 2013. Ecological consequences of body size decline in harvested fish species: Positive feedback loops in trophic interactions amplify human impact. Biology Letters 9(2):20121103.

Aydin, K. Y., G. A. McFarlane, J. R. King, B. A. Megrey, and K. W. Myers. 2005. Linking oceanic food webs to coastal production and growth rates of Pacific salmon (*Oncorhynchus* spp.), using models on three scales. Deep Sea Research Part II: Topical Studies in Oceanography 52(5):757–780.

Beattie, W. D., and P. T. Clancey. 1991. Effects of *Mysis relicta* on the zooplankton community and kokanee population of Flathead Lake, Montana. Pages 39–48 *in* T. P. Nesler and E. P. Bergersen, editors. Mysids in fisheries; hard lessons from headlong introductions. American Fisheries Society, Bethesda, Maryland, USA.

Beauchamp, D. A. 1990. Seasonal and diel food habits of rainbow trout stocked as juveniles in Lake Washington. Transactions of the American Fisheries Society 119(3):475–482.

Beauchamp, D. A., A. D. Cross, J. L. Armstrong, K. W. Myers, J. H. Moss, J. L. Boldt, and L. J. Haldorson. 2007. Bioenergetic responses by Pacific salmon to climate and ecosystem variation. The North Pacific Anadromous Fish Commission 4:257–269.

Behnke, R. J. 2010. Trout and salmon of North America. Simon and Schuster.

Benjamin, J. R., P. J. Connolly, J. G. Romine, and R. W. Perry. 2013. Potential effects of changes in temperature and food resources on life history trajectories of juvenile *Oncorhynchus mykiss*. Transactions of the American Fisheries Society 142(1):208–220.

von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws II). Human Biology 10(2):181–213.

Bevelhimer, M. S., and S. M. Adams. 1993. A bioenergetics analysis of diel vertical migration by kokanee salmon, *Oncorhynchus nerka*. Canadian Journal of Fisheries and Aquatic Sciences 50(11):2336–2349.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Great Britain Ministry of Agriculture, Fisheries and Food, London: HMSO.

Black, A. R., G. W. Barlow, and A. T. Scholz. 2003. Carbon and nitrogen stable isotope assessment of the Lake Roosevelt aquatic food web. Northwest Science 77(1):1–11.

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(5):731–735.

Brandt, S., D. Mason, M. McCormick, B. Lofgren, T. Hunter, and J. Tyler. 2002. Climate change: Implications for fish growth performance in the Great Lakes. Transactions of the American Fisheries Society 32(32):61–76.

Breeggemann, J. J., M. A. Kaemingk, T. J. DeBates, C. P. Paukert, J. R. Krause, A. P. Letvin, T. M. Stevens, D. W. Willis, and S. R. Chipps. 2016. Potential direct and indirect effects of climate change on a shallow natural lake fish assemblage. Ecology of Freshwater Fish 25(3):487–499.

Brett, J. R. 1952. Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. Journal of the Fisheries Research Board of Canada 9(6):265–323.

Brett, J. R. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). American Zoologist 11(1):99–113.

Brett, J. R., and D. A. Higgs. 1970. Effect of temperature on the rate of gastric digestion in fingerling sockeye salmon, *Oncorhynchus nerka*. Journal of the Fisheries Research Board of Canada 27(10):1767–1779.

Brown, J. C., K. H. Lokensgard, S. Snyder, and M. Draper. 2019. The cultural currents and social values of trout. Pages 65-93 *in* J. L. Kershner, J. E. Williams, R. E. Gresswell, and J. Lobón-Cerviá, editors. Trout and char of the world. American Fisheries Society, Bethesda, Maryland.

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(7):1771–1789.

Brynildson, O. M., and J. J. Kempinger. 1973. Production, food and harvest of trout in Nebish Lake, Wisconsin - UWDC - UW-Madison Libraries. Madison, Wisconsin: Wisconsin Department of Natural Resources, Technical bulletin.

Budy, P., C. Luecke, and W. A. Wurtsbaugh. 1998. Adding nutrients to enhance the growth of endangered sockeye salmon: Trophic transfer in an oligotrophic lake. Transactions of the American Fisheries Society 127(1):19–34.

Buktenica, M. W., S. F. Girdner, G. L. Larson, and C. D. McIntire. 2007. Variability of kokanee and rainbow trout food habits, distribution, and population dynamics, in an ultraoligotrophic lake with no manipulative management. Hydrobiologia 574(1):235–264.

Burdick, M. E., and E. L. Cooper. 1956. Growth rate, survival and harvest of fingerling rainbow trout planted in Weber Lake, Wisconsin. Journal of Wildlife Management 20(3):233–239.

Burgmer, T., H. Hillebrand, and M. Pfenninger. 2007. Effects of climate-driven temperature changes on the diversity of freshwater macroinvertebrates. Oecologia 151(1):93–103.

Burgner, R. 1897. Factors influencing age and growth of juvenile sockeye salmon (*Oncorhynchus nerka*) in lakes. Pages 129–142. 96, Canadian Special Publication of Fisheries and Aquatic Sciences.

Burrough, R. J., and C. R. Kennedy. 1979. The occurrence and natural alleviation of stunting in a population of roach, *Rutilus rutilus* (L.). Journal of Fish Biology 15(1):93–109.

Busch, S., G. Kirillin, and T. Mehner. 2012. Plasticity in habitat use determines metabolic response of fish to global warming in stratified lakes. Oecologia 170(1):275–287.

Carmichael, R. 1983. Feeding ecology and aspects of the biology of largemouth bass, rainbow trout, brown trout, and relict dace and the dietary overlap of largemouth bass and rainbow trout with canvasback and redhead ducks at Ruby Marsh, Nevada. Master’s thesis, Oregon State University.

Casselman, J. M. 2002. Effects of temperature, global extremes, and climate change on year-class production of warmwater, coolwater, and coldwater fishes in the Great Lakes Basin. American Fisheries Society Symposium 2002:39–60.

Chacón, M. M., S. Segnini, and D. Briceño. 2016. Temperatura y emergencia diaria de siete géneros de Ephemeroptera (Insecta) en un río de la Selva Nublada de los Andes Tropicales. Revista de Biología Tropical 64(1):117–130.

Cheney, K. N., A. H. Roy, R. F. Smith, and R. E. Dewalt. 2019. Effects of stream temperature and substrate type on emergence patterns of Plecoptera and Trichoptera from Northeastern United States headwater streams. Environmental Entomology 48(6):1349–1359.

Chipps, S. R., and J. E. Garvey. 2007. Assessment of diets 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, USA.

Christensen, J. H., B. Hewitson, A. Busuioc, A. Chen, X. Gao, I. Held, R. Jones, R. K. Kolli, W. T. Kwon, R. Laprise, V. Magana Rueda, L. Mearns, C. G. Menendez, J. Raisanen, A. Rinke, A. Sarr, and P. Whetton. 2007. Regional climate projections. Chapter 11. Climate change 2007: the physical science basis. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

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(2):301–314.

Clarke, L. R., D. T. Vidergar, 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(3):267–277.

Clodfelter, K. C. 1982. Growth, food habits, and the relative effectiveness of stocking rainbow trout (*Salmo gairdneri*) in south-central South Dakota. Master’s thesis, South Dakota State University.

Čmrlec, K., M. Ivković, P. Šemnički, and Z. Mihaljević. 2013. Emergence phenology and microhabitat distribution of aquatic Diptera community at the outlets of barrage lakes: Effect of temperature, substrate and current velocity. Polish Journal of Ecology 61:135–144.

Costello, M. J. 1990. Predator feeding strategy and prey importance: A new graphical analysis. Journal of Fish Biology 36(2):261–263.

Cowx, I. G., R. Arlinghaus, and S. J. Cooke. 2010. Harmonizing recreational fisheries and conservation objectives for aquatic biodiversity in inland waters. Journal of Fish Biology 76(9):2194–2215.

Coyle, K. O., and A. I. Pinchuk. 2005. Seasonal cross-shelf distribution of major zooplankton taxa on the northern Gulf of Alaska shelf relative to water mass properties, species depth preferences and vertical migration behavior. Deep Sea Research Part II: Topical Studies in Oceanography 52(1):217–245.

Crossman, E. J. 1959. A predator–prey interaction in freshwater fish. Journal of the Fisheries Research Board of Canada 16(3):269–281.

Cumminns, K. W., and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Internationale Vereinigung für Theoretische und Angewandte Limnologie: Mitteilungen 18(1):1–158.

Curio, E. 1976. The ethology of predation. Springer, Berlin, Heidelberg.

Damsgård, B., and A. Langeland. 1994. Effects of stocking of piscivorous brown trout, Salmo trutta L., on stunted Arctic charr, *Salvelinus alpinus* (L.). Ecology of Freshwater Fish 3(2):59–66.

Denechaud, C., S. Smoliński, A. J. Geffen, J. A. Godiksen, and S. E. Campana. 2020. A century of fish growth in relation to climate change, population dynamics and exploitation. Global Change Biology 26(10):5661–5678.

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(11):586–596.

Dickson, T. R., and I. R. Walker. 2015. Midge (Diptera: Chironomidae and Ceratopogonidae) emergence responses to temperature: Experiments to assess midges' capacity as paleotemperature indicators. Journal of Paleolimnology 53(2):165–176.

Diehl, S., and R. Kornijów. 1998. Influence of submerged macrophytes on trophic interactions among fish and macroinvertebrates. Pages 24–46 *in* E. Jeppesen, M. Søndergaard, M. Søndergaard, and K. Christoffersen, editors. The structuring role of submerged macrophytes in lakes. Springer New York, New York, NY.

Dingemanse, N. J., and V. J. Kalkman. 2008. Changing temperature regimes have advanced the phenology of Odonata in the Netherlands. Ecological Entomology 33(3):394–402.

East, P., and P. Magnan. 1991. Some factors regulating piscivory of brook trout, *Salvelinus fontinalis*, in lakes of the Laurentian Shield. Canadian Journal of Fisheries and Aquatic Sciences 48(9):1735–1743.

Eby, L. A., W. J. Roach, L. B. Crowder, and J. A. Stanford. 2006. Effects of stocking-up freshwater food webs. Trends in Ecology & Evolution 21(10):576–584.

Eckelbecker, R. W. 2024. Ecological interactions and environmental stressors: Assessing dietary dynamics and population stability of burbot amid non-native trout and warming winter temperatures. Doctoral dissertation, Montana State University, Bozeman, Montana.

Eggers, D. M. 1978. Limnetic feeding behavior of juvenile sockeye salmon in Lake Washington and predator avoidance. Limnology and Oceanography 23(6):1114–1125.

Eloranta, A. P., K. K. Kahilainen, P.A. Amundsen, R. Knudsen, C. Harrod, and R. I. Jones. 2015. Lake size and fish diversity determine resource use and trophic position of a top predator in high-latitude lakes. Ecology and Evolution 5(8):1664–1675.

EPA (U.S. Environmental Protection Agency). 1977. Report on Georgetown Lake, Deer Lodge and Granite Counties, Montana. USEPA Report Working Paper No. 793, Washington, D.C.

Ficke, A. D., C. A. Myrick, and L. J. Hansen. 2007. Potential impacts of global climate change on freshwater fisheries. Reviews in Fish Biology and Fisheries 17(4):581–613.

Fisher, J. P., and W. G. Pearcy. 2005. Seasonal changes in growth of coho salmon (*Oncorhynchus kisutch*) off Oregon and Washington and concurrent changes in the spacing of scale circuli. Fishery Bulletin 103(1):34–51.

Forster, J., A. G. Hirst, and D. Atkinson. 2012. Warming-induced reductions in body size are greater in aquatic than terrestrial species. Proceedings of the National Academy of Sciences 109(47):19310–19314.

Fry, F. E. J. 1971. The effect of environmental factors on the physiology of fish. Pages 1–98 *in* W. S. Hoar and D. J. Randall, editors. Fish Physiology. Academic Press.

Galbraith, M. G. 1967. Size-selective predation on daphnia by rainbow trout and yellow perch. Transactions of the American Fisheries Society 96(1):1–10.

Gao, S., and H. G. Stefan. 2004. Potential climate change effects on ice covers of five freshwater lakes. Journal of Hydrologic Engineering 9(3):226–234.

Garvey, J. E., and S. R. Chipps. 2012. Diets and energy flow. Pages 733–779 *in* A. Zale, D. L. Parrish, and T. M. Sutton, editors. Fisheries techniques, 3rd edition. American Fisheries Society, Bethesda, Maryland, USA.

Gebre, S., T. Boissy, and K. Alfredsen. 2014. Sensitivity to climate change of the thermal structure and ice cover regime of three hydropower reservoirs. Journal of Hydrology 510:208–227.

Glassic, H. C., C. S. Guy, L. M. Tronstad, D. R. Lujan, M. A. Briggs, L. K. Albertson, and T. M. Koel. 2023. Invasive predator diet plasticity has implications for native fish conservation and invasive species suppression. PLoS ONE 18(2):e0279099.

Gotceitas, V., and P. Colgan. 1989. Predator foraging success and habitat complexity: Quantitative test of the threshold hypothesis. Oecologia 80(2):158–166.

Grabowski, S. J. 1973. Effects of fluctuating and constant temperatures on some hematological characteristics, tissue glycogen levels, and growth of steelhead trout (*Salmo Gairdneri*). Doctoral dissertation, University of Idaho, Moscow, Idaho.

Grau, K. 2019. 2018 Economic contribution of nonresident travel spending in Montana travel regions and counties. Institute for Tourism and Recreation Research Publications.

Griffiths, J. R., and D. E. Schindler. 2012. Consequences of changing climate and geomorphology for bioenergetics of juvenile sockeye salmon in a shallow Alaskan lake. Ecology of Freshwater Fish 21(3):349–362.

Griswold, R. G., A. E. Kohler, K. A. Tardy, K. E. Griswold, and D. Taki. 2022. Density dependence in three Snake River sockeye salmon nursery lakes in Central Idaho. North American Journal of Fisheries Management 42(6):1477–1493.

Grover, M. C. 2006. Evaluation of a negative relationship between abundance during spawning and size at maturity in kokanee. Transactions of the American Fisheries Society 135(4):970–978.

Grummer, J. A., M. C. Whitlock, P. M. Schulte, and E. B. Taylor. 2021. Growth genes are implicated in the evolutionary divergence of sympatric piscivorous and insectivorous rainbow trout (*Oncorhynchus mykiss*). BMC Ecology and Evolution 21(1):63.

Guzzo, M. M., G. D. Haffner, N. D. Legler, S. A. Rush, and A. T. Fisk. 2013. Fifty years later: Trophic ecology and niche overlap of a native and non-indigenous fish species in the western basin of Lake Erie. Biological Invasions 15(8):1695–1711.

Haddix, T., and P. E. Budy. 2005. Factors that limit growth and abundance of rainbow trout across ecologically distinct areas of Flaming Gorge Reservoir, Utah–Wyoming. North American Journal of Fisheries Management 25(3):1082–1094.

Hamilton, D. P., M. R. Magee, C. H. Wu, and T. K. Kratz. 2018. Ice cover and thermal regime in a dimictic seepage lake under climate change. Inland Waters 8(3):381–398.

Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish Bioenergetics 3.0 for Windows. University of Wisconsin-Madison Center for Limnology and University of Wisconsin Sea Grant Institute, Technical Report WISCU-T-97-001, Madison, Wisconsin.

Hartmann, D. L., A. M. G. K. Tank, M. Rusticucci, L. V. Alexander, S. Brönnimann, Y. A. R. Charabi, F. J. Dentener, E. J. Dlugokencky, D. R. Easterling, A. Kaplan, B. J. Soden, P. W. Thorne, M. Wild, and P. Zhai. 2014. Observations: Atmosphere and surface. Pages 159–254 *in* Climate Change 2013: The Physical Science Basis. Cambridge University Press, Cambridge.

Hassall, C., and D. J. Thompson. 2008. The effects of environmental warming on Odonata: a review. International Journal of Odonatology 11(2):131–153.

Hayden, B., C. Harrod, and K. K. Kahilainen. 2014. Dual fuels: Intra-annual variation in the relative importance of benthic and pelagic resources to maintenance, growth and reproduction in a generalist salmonid fish. Journal of Animal Ecology 83(6):1501–1512.

Hershey, A. E., R. M. Northington, J. C. Finlay, and B. J. Peterson. 2017. Stable isotopes in stream food webs. Pages 3–20 *in* G. A. Lamberti and F. R. Hauer, editors. Methods in Stream Ecology, 2nd edition. Academic Press, San Diego.

Hixon, M. A., D. W. Johnson, and S. M. Sogard. 2014. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. ICES Journal of Marine Science 71(8):2171–2185.

Hokanson, K. E. F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. Journal of the Fisheries Research Board of Canada 34(10):1524–1550.

Horne, C. R., Andrew. G. Hirst, and D. Atkinson. 2015. Temperature-size responses match latitudinal-size clines in arthropods, revealing critical differences between aquatic and terrestrial species. Ecology Letters 18(4):327–335.

Hubert, W. A., R. D. Gipson, R. A. McDowell, and A. C. Stewart. 1994. Diet of Eagle Lake rainbow trout in Lake DeSmet, Wyoming. North American Journal of Fisheries Management 14(2):457–459.

IPCC. 2007. Climate change 2007: Impacts, adaptation and vulnerability. Contribution of working group II to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, UK.

Irvine, J. R. 1978. The Gerrard rainbow trout of Kootenay Lake, British Columbia: A discussion of their life history with management, research and enhancement recommendations. Fish and Wildlife Branch.

Jackson, J. R., R. Inger, A. C. Parnell, and S. Bearhop. 2011. Comparing isotopic niche widths among and within communities: SIBER-stable isotope Bayesian ellipses in R. Journal of Animal Ecology 80:595–602.

Jacobson, P., U. Bergström, and J. Eklöf. 2019. Size-dependent diet composition and feeding of Eurasian perch (*Perca fluviatilis*) and northern pike (*Esox lucius*) in the Baltic Sea. Boreal Environmental Research 24:137–153.

Jenkins, T. M., S. Diehl, K. W. Kratz, and S. D. Cooper. 1999. Effects of population density on individual growth of brown trout in streams. Ecology 80(3):941–956.

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(3):197–202.

Jiang, X., S. Dong, Y. Zhou, Q. Gao, and Z. Pan. 2020. An effective method of prompting juvenile rainbow trout (*Oncorhynchus mykiss*) to cope with heat stress. Journal of Ocean University of China 19(1):216–224.

Johannes, R. E., and P. A. Larkin. 1961. Competition for food between redside shiners (*Richardsonius balteatus*) and rainbow trout (*Salmo gairdneri*) in two British Columbia lakes. Journal of the Fisheries Research Board of Canada 18(2):203–220.

Johnson, B. M., W. M. Pate, and A. G. Hansen. 2017. Energy density and dry matter content in fish: new observations and an evaluation of some empirical models. Transactions of the American Fisheries Society 146(6):1262–1278.

Jones, R., C. Travers, C. Rodgers, B. Lazar, E. English, J. Lipton, J. Vogel, K. Strzepek, and J. Martinich. 2013. Climate change impacts on freshwater recreational fishing in the United States. Mitigation and Adaptation Strategies for Global Change 18(6):731–758.

Keeley, E. R., E. A. Parkinson, and E. B. Taylor. 2005. Ecotypic differentiation of native rainbow trout (*Oncorhynchus mykiss*) populations from British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 62(7):1523–1539.

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 the Fisheries Research Board of Canada 34(10):1922–1935.

Knapp, S. M. 1981. The fisheries potential of Medical Lake, Washington, after a whole-lake alum treatment, with emphasis on food and food habits of rainbow trout (*Salmo gairdneri*). Master's thesis, Eastern Washington University.

Knight, J. C. 1981. An investigation of the general limnology of Georgetown Lake, Montana. Doctoral dissertation, Montana State University, Bozeman, Montana.

Koenig, M. K., K. A. Meyer, J. R. Kozfkay, J. M. DuPont, and E. B. Schriever. 2015. Evaluating the ability of tiger muskellunge to eradicate brook trout in Idaho alpine lakes. North American Journal of Fisheries Management 35(4):659–670.

Kornijów, R., and R. D. Gulati. 1992. Macrofauna and its ecology in Lake Zwemlust, after biomanipulation II. Fauna inhabiting hydrophytes. Archiv für Hydrobiologie:349–359.

Koth, R. M. 1980. Food habits and growth of rainbow trout in a prairie pond. Master's thesis, South Dakota State University.

Landry, F., J. R. Post, and E. A. Parkinson. 1999. Spatial ontogeny of lentic age-0 rainbow trout, *Oncorhynchus mykiss*: Whole-lake manipulations of population size structure. Canadian Journal of Fisheries and Aquatic Sciences 56(10):1916–1928.

Lewis, M. 2018. Statewide estimates of resident and nonresident hunter and angler trip related expenditures in Montana. Human Dimensions Unit Research Summary. Montana Fish, Wildlife & Parks, Helena, Montana.

Liermann, B. 2013. Analysis and management implications of multiple decades of fisheries data for Georgetown Lake, MT. Montana Fish, Wildlife & Parks, Missoula, Montana.

Lorenzen, K. 2016. Toward a new paradigm for growth modeling in fisheries stock assessments: Embracing plasticity and its consequences. Fisheries Research 180:4–22.

Lynch, A. J., S. J. Cooke, A. M. Deines, S. D. Bower, D. B. Bunnell, I. G. Cowx, V. M. Nguyen, J. Nohner, K. Phouthavong, B. Riley, M. W. Rogers, W. W. Taylor, W. Woelmer, S.-J. Youn, and B. T. D. Jr. 2016. The social, economic, and environmental importance of inland fish and fisheries. Environmental Reviews 24(2):115–121.

Magnuson, J. J., J. D. Meisner, and D. K. Hill. 1990. Potential changes in the thermal habitat of Great Lakes fish after global climate warming. Transactions of the American Fisheries Society 119(2):254–264.

Magnuson, J. J., K. E. Webster, R. A. Assel, C. J. Bowser, P. J. Dillon, J. G. Eaton, H. E. Evans, E. J. Fee, R. I. Hall, L. R. Mortsch, D. W. Schindler, and F. H. Quinn. 1997. Potential effects of climate changes on aquatic systems: Laurentian Great Lakes and Precambrian Shield Region. Hydrological Processes 11(8):825–871.

Mansueti, R. 1962. Review of experimental ecology of the feeding of fishes; Rate of metabolism and food requirements of fishes. Chesapeake Science 3(1):56–58.

Marine, K. R., and J. J. Cech. 2004. Effects of high water temperature on growth, smoltification, and predator avoidance in juvenile Sacramento River chinook salmon. North American Journal of Fisheries Management 24(1):198–210.

Marrin, D. L., and D. C. Erman. 1982. Evidence against competition between trout and nongame fishes in Stampede Reservoir, California. North American Journal of Fisheries Management 2:262–269.

Martinez, P. J., and E. P. Bergersen. 1991. Interactions of zooplankton, *Mysis relicta,* and kokanees in Lake Granby, Colorado. Pages 49–64.

Martinez, P. J., P. E. Bigelow, M. A. Deleray, W. A. Fredenberg, B. S. Hansen, N. J. Horner, S. K. Lehr, R. W. Schneidervin, S. A. Tolentino, and A. E. Viola. 2009. Western lake trout woes. Fisheries 34(9):424–442.

Martinez, P. J., and W. J. Wiltzius. 1995. Some factors affecting a hatchery-sustained kokanee population in a fluctuating Colorado reservoir. North American Journal of Fisheries Management 15(1):220–228.

Mazumder, A., and J. A. Edmundson. 2002. Impact of fertilization and stocking on trophic interactions and growth of juvenile sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 59(8):1361–1373.

McGurk, M. D. 1999. Size dependence of natural mortality rate of sockeye salmon and kokanee in freshwater. North American Journal of Fisheries Management 19(2):376–396.

MFWP. 2022. Appendix A - Annual pressure by waterbody 2020. Montana Fish, Wildlife & Parks, Report, Helena, Montana.

Millennium Ecosystem Assessment (Program), editor. 2005. Ecosystems and human well-being: Wetlands and water synthesis: A report of the Millennium Ecosystem Assessment. World Resources Institute, Washington, DC.

Miranda, L. E., G. Coppola, and J. Boxrucker. 2020. Reservoir fish habitats: A perspective on coping with climate change. Reviews in Fisheries Science & Aquaculture 28(4):478–498.

Murdoch, A., and M. Power. 2013. The effect of lake morphometry on thermal habitat use and growth in Arctic charr populations: Implications for understanding climate-change impacts. Ecology of Freshwater Fish 22(3):453–466.

Nebeker, A. V. 1971. Effect of high winter water temperatures on adult emergence of aquatic insects. Water Research 5(9):777–783.

Neebling, T., and C. Moan. 2013. A bioenergetics assessment of the kokanee and lake trout populations in Boulder Lake. Wyoming Game and Fish Department, Fish Division, Administrative Report, Casper, Wyoming.

Ney, J. J. 1993. Bioenergetics modeling today: Growing pains on the cutting edge. Transactions of the American Fisheries Society 122(5):736–748.

Northcote, T. G. 1973. Some impacts of man on Kootenay Lake and its salmonids. Great Lakes Fishery Commission, Technical Report No. 25, Ann Arbor, Michigan.

Nyquist, C., B. Vondracek, and L. Ferrington. 2020. The influence of an in-stream thermal gradient on chironomid emergence during winter. Hydrobiologia 847(15):3153–3167.

Paragamian, V. L., and E. C. Bowles. 1995. Factors affecting survival of kokanees stocked in Lake Pend Oreille, Idaho. North American Journal of Fisheries Management 15(1):208–219.

Parkinson, E. A. 1988. Long term data collection on kokanee from large lakes: Does it make sense? British Columbia Fisheries Branch, Fisheries Technical Circulation No. 83.

Patten, B. G., and R. B. Thompson. 1957. Food studies of a small sample of rainbow trout (*Salmo gairdneri*) and kokanee salmon (*Oncorhynchus nerka*) from Crater Lake, Oregon. Page 14. National Park Service, Unpublished report, Crater Lake, Oregon.

Pease, A. A., and C. P. Paukert. 2014. Potential impacts of climate change on growth and prey consumption of stream-dwelling smallmouth bass in the central United States. Ecology of Freshwater Fish 23(3):336–346.

Pederson, G. T., L. J. Graumlich, D. B. Fagre, T. Kipfer, and C. C. Muhlfeld. 2010. A century of climate and ecosystem change in Western Montana: What do temperature trends portend? Climatic Change 98(1):133–154.

Pereira, L. S., F. W. Keppeler, A. A. Agostinho, and K. O. Winemiller. 2017. Is there a relationship between fish cannibalism and latitude or species richness? PLoS ONE 12(1):e0169813.

Persson, L., P. A. Amundsen, A. M. De Roos, A. Klemetsen, R. Knudsen, and R. Primicerio. 2007. Culling prey promotes predator recovery - Alternative states in a whole-lake experiment. Science 316(5832):1743–1746.

Pettitt-Wade, H., K. W. Wellband, D. D. Heath, and A. T. Fisk. 2015. Niche plasticity in invasive fishes in the Great Lakes. Biological Invasions 17(9):2565–2580.

Pine III, W. E., and M. S. Allen. 2001. Differential growth and survival of weekly age-0 black crappie cohorts in a Florida lake. Transactions of the American Fisheries Society 130(1):80–91.

Pitcher, T. J., and C. Hollingworth. 2008. Recreational fisheries: Ecological, economic and social evaluation. John Blackwell Publishing, Osney Mead, Oxford, UK.

Post, J. R., E. A. Parkinson, and N. T. Johnston. 1999. Density-dependent processes in structured fish populations: Interaction strengths in whole-lake experiments. Ecological Monographs 69(2):155–175.

Rahel, F. J. 2000. Homogenization of fish faunas across the United States. Science 288(5467):854–856.

Railsback, S. F., and K. A. Rose. 1999. Bioenergetics modeling of stream trout growth: Temperature and food consumption effects. Transactions of the American Fisheries Society 128(2):241–256.

Rask, M. 1983. Differences in growth of perch (*Perca fluviatilis* L.) in two small forest lakes. Hydrobiologia 101(1):139–143.

Reynolds, J. 2017. Predicting the impact of a northern pike (*Esox lucius*) invasion on endangered June sucker (*Chasmistes liorus*) and sport fishes in Utah Lake, UT. Master's thesis, Utah State University.

Richter, O., F. Suhling, O. Müller, and D. Kern. 2008. A model for predicting the emergence of dragonflies in a changing climate. Freshwater Biology 53(9):1868–1880.

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

Rieman, B. E., and D. L. Myers. 1992. Influence of fish density and relative productivity on growth of kokanee in ten oligotrophic lakes and reservoirs in Idaho. Transactions of the American Fisheries Society 121(2):178–191.

Ringler, N. H. 1979. Selective predation by drift-feeding brown trout (*Salmo trutta*). Journal of the Fisheries Research Board of Canada 36(4):392–403.

Ringler, N. H. 1983. Variation in foraging tactics of fishes. Pages 159–171 *in* D. L. G. Noakes, D. G. Lindquist, G. S. Helfman, and J. A. Ward, editors. Predators and prey in fishes: Proceedings of the 3rd biennial conference on the ethology and behavioral ecology of fishes, held at Normal, Illinois, U.S.A., May 19–22, 1981. Springer Netherlands, Dordrecht.

Rochet, M. 1998. Short-term effects of fishing on life history traits of fishes. ICES Journal of Marine Science 55(3):371–391.

Rooney, N., K. McCann, G. Gellner, and J. C. Moore. 2006. Structural asymmetry and the stability of diverse food webs. Nature 442(7100):265–269.

Rust, P., S. M. Wilson, N. G. Mucciarone, R. Hardy, M. P. Corsi, and J. Strait. 2022. Lake Pend Oreille research, 2019 Lake Pend Oreille fishery recovery project. Idaho Department of Fish and Game, Annual progress report IDFG Report Number 22-04, Boise, Idaho.

Sánchez-Hernández, J., A. P. Eloranta, A. G. Finstad, and P. A. Amundsen. 2017. Community structure affects trophic ontogeny in a predatory fish. Ecology and Evolution 7(1):358–367.

Savino, J. F., and R. A. Stein. 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. Transactions of the American Fisheries Society 111(3):255–266.

Schindler, E. U., B. Shafii, P. J. Anders, W. J. Price, C. Holderman, K. I. Ashley, and M. Bassett. 2020. Characterizing the phytoplankton and zooplankton communities in Kootenay Lake: A time series analysis of 24 years of nutrient addition. Canadian Journal of Fisheries and Aquatic Sciences 77(5):904–916.

Schneidervin, R. W., and W. A. Hubert. 1987. Diet overlap among zooplanktophagous fishes in Flaming Gorge Reservoir, Wyoming-Utah. North American Journal of Fisheries Management 7(3):379–385.

Schoener, T. W. 1968. The anoles lizards of Bimini: Resource partitioning in a complex fauna. Ecology 49:704–726.

Schulte, P. M., T. M. Healy, and N. A. Fangue. 2011. Thermal performance curves, phenotypic plasticity, and the time scales of temperature exposure. Integrative and Comparative Biology 51(5):691–702.

Sharma, S., D. A. Jackson, C. K. Minns, and B. J. Shuter. 2007. Will northern fish populations be in hot water because of climate change? Global Change Biology 13(10):2052–2064.

Shaw, G. D., K. L. Mitchell, and C. H. Gammons. 2017. Estimating groundwater inflow and leakage outflow for an intermontane lake with a structurally complex geology: Georgetown Lake in Montana, USA. Hydrogeology Journal 25:135–149.

Shuter, B. J., and J. R. Post. 1990. Climate, population viability, and the zoogeography of temperate fishes. Transactions of the American Fisheries Society 119(2):314–336.

Spanjer, A. R., A. S. Gendaszek, E. J. Wulfkuhle, R. W. Black, and K. L. Jaeger. 2022. Assessing climate change impacts on Pacific salmon and trout using bioenergetics and spatiotemporal explicit river temperature predictions under varying riparian conditions. PLOS ONE 17(5):e0266871.

Stafford, C. 2013. Long-term trends in the water quality of Georgetown Lake, Montana - Georgetown State of the lake project report to Montana Department of Justice and Montana Department of Environmental Quality. Missoula, Montana.

Stefan, H. G., X. Fang, and J. G. Eaton. 2001. Simulated fish habitat changes in North American lakes in response to projected climate warming. Transactions of the American Fisheries Society 130(3):459–477.

Stewart, D. J., D. Weininger, D. V. Rottiers, and T. A. Edsall. 1983. An energetics model for Lake Trout, *Salvelinus namaycush*: Application to the Lake Michigan population. Canadian Journal of Fisheries and Aquatic Sciences 40(6):681–698.

Sutela, T., and A. Huusko. 2000. Varying resistance of zooplankton prey to digestion: Implications for quantifying larval fish diets. Transactions of the American Fisheries Society 129:545–551.

Svedäng, H., and S. Hornborg. 2014. Selective fishing induces density-dependent growth. Nature Communications 5(1):4152.

Swift, M. C. 1970. A qualitative and quantitative study of trout food in Castle Lake, California. Pages 109–120. California Fish and Game.

Taylor, W. W., and S. D. Gerking. 1980. Population dynamics of *Daphnia pulex* and utilization by the rainbow trout (*salmo gairdneri*). Hydrobiologia 71(3):277–287.

U.S. Department of the Interior and U.S. Fish and Wildlife Service. 2022. 2022 National survey of fishing, hunting, and wildlife-associated recreation, Washington, D.C.

Vander Zanden, M. J., B. J. Shuter, N. Lester, and J. B. Rasmussen. 1999. Patterns of food chain length in lakes: A stable isotope study. The American Naturalist 54(4): 406-416.

Vidergar, D. 2000. Population estimates, food habits and estimates of consumption of selected predatory fishes in Lake Pend Oreille, Idaho. Master's thesis, University of Idaho.

Vinyard, G. L., R. W. Drenner, and D. A. Hanzel. 1982. Feeding success of hatchery-reared kokanee salmon when presented with zooplankton prey. The Progressive Fish-Culturist 44(1):37–39.

Wallace, R. K. 1981. An assessment of diet-overlap indexes. Transactions of the American Fisheries Society 110(1):72–76.

Wallace, R. K., and D. Zaroban. 2013. Native fishes of Idaho. American Fisheries Society, Bethesda, Maryland, USA.

Walsworth, T. E., P. Budy, and G. P. Thiede. 2013. Longer food chains and crowded niche space: Effects of multiple invaders on desert stream food web structure. Ecology of Freshwater Fish 22(3):439–452.

Wang, L., K. Zimmer, P. Diedrich, and S. Williams. 1996. The two-story rainbow trout fishery and its effect on the zooplankton community in a Minnesota lake. Journal of Freshwater Ecology 11(1):67–80.

Ware, D. M. 1971. Predation by rainbow trout (*Salmo gairdneri*): The effect of experience. Journal of the Fisheries Research Board of Canada 28(12):1847–1852.

Warnock, W. G., J. L. Thorley, S. K. Arndt, T. J. Weir, M. D. Neufeld, J. A. Burrows, and G. F. Andrusak. 2022. Kootenay Lake kokanee (*Oncorhynchus nerka*) collapse into a predator pit. Canadian Journal of Fisheries and Aquatic Sciences 79(2):234–248.

Whitlock, C., W. F. Cross, B. D. Maxwell, N. Silverman, and A. A. Wade. 2017. 2017 Montana Climate Assessment: Stakeholder driven, science informed. Montana Institute on Ecosystems, Bozeman, Montana.

Wiley, R. W., and J. D. Varley. 1978. The diets of rainbow and brown trout from Flaming Gorge Reservoir, 1964 through 1969. Wyoming Game and Fish Department, Cheyenne.

Wilson, S. M., D. H. Brandt, M. P. Corsi, and A. M. Dux. 2018. Early trophic responses to nutrient addition in Dworshak Reservoir, Idaho. Lake and Reservoir Management 34(1):58–73.

Wilson, S. M., M. P. Corsi, D. H. Brandt, and E. J. Stark. 2021. The response of *Daphnia* to nutrient additions and kokanee abundance in Dworshak Reservoir, Idaho. Canadian Journal of Fisheries and Aquatic Sciences 78(11):1677–1688.

Winberg, G. G. Rate of metabolism and food requirements of fishes. Fisheries Research Board of Canada, Translation Series 194, Nanaimo, British Columbia, Canada.

Wuellner, M. R., S. R. Chipps, D. W. Willis, and W. E. Adams Jr. 2010. Interactions between walleyes and smallmouth bass in a Missouri River reservoir with consideration of the influence of temperature and prey. North American Journal of Fisheries Management 30(2):445–463.

Wurtsbaugh, W. A., and G. E. Davis. 1977. Effects of temperature and ration level on the growth and food conversion efficiency of *Salmo gairdneri*, Richardson. Journal of Fish Biology 11(2):87–98.

Wydoski, R. S., and D. H. Bennett. 1981. Forage species in lakes and reservoirs of the western United States. Transactions of the American Fisheries Society 110(6):764–771.

Yasarer, L. M. W., and B. S. M. Sturm. 2016. Potential impacts of climate change on reservoir services and management approaches. Lake and Reservoir Management 32(1):13–26.

Ylikarjula, J., M. Heino, and U. Dieckmann. 1999. Ecology and adaptation of stunted growth in fish. Evolutionary Ecology 13(5):433–453.

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 122(6):1058–1069.

Zamon, J. E., and D. W. Welch. 2005. Rapid shift in zooplankton community composition on the northeast Pacific shelf during the 1998–1999 El Niño – La Niña event. Canadian Journal of Fisheries & Aquatic Sciences 62(1):133–144.

Zanden, M. J. V., S. Chandra, B. C. Allen, J. E. Reuter, and C. R. Goldman. 2003. Historical food web structure and restoration of native aquatic communities in the Lake Tahoe (California-Nevada) basin. Ecosystems 6(3):274–288.

APPENDICES

APPENDIX A

CHAPTER 2 SUPPLEMENTAL TABLES

Tables

Table A.1: Number and mean total length (mm; TL) of stocked trout by species and strain in Georgetown Lake, Montana, USA from 2004 through 2023.

Year	Species	Strain	Number stocked	TL (mm)
2004	Rainbow trout	Arlee	70,208	160.88
2004	Rainbow trout	Eagle Lake	116,183	129.56
2004	Rainbow trout	Kamloops	39,186	155.85
2004	Brook trout		10,360	121.16
2005	Rainbow trout	Arlee	194,681	127.25
2005	Rainbow trout	Eagle Lake	10,215	108.20
2005	Rainbow trout	Kamloops	35,077	124.46
2005	Brook trout		52,954	89.62
2006	Rainbow trout	Arlee	76,274	125.94
2006	Rainbow trout	Eagle Lake	80,100	113.42
2006	Rainbow trout	Kamloops	36,955	105.41
2007	Rainbow trout	Arlee	67,796	117.14
2007	Rainbow trout	Eagle Lake	80,035	123.50
2007	Rainbow trout	Kamloops	32,580	118.36
2007	Brook trout		59,290	101.81
2008	Rainbow trout	Arlee	104,779	136.15
2008	Rainbow trout	Eagle Lake	131,670	135.40
2008	Rainbow trout	Kamloops	24,244	90.42
2008	Brook trout		47,520	104.14
2009	Rainbow trout	Arlee	74,397	127.00
2009	Rainbow trout	Eagle Lake	108,598	113.09
2009	Brook trout		40,339	101.60
2010	Rainbow trout	Arlee	66,875	130.68
2010	Rainbow trout	Eagle Lake	93,696	128.21
2010	Brook trout		48,488	101.60
2011	Rainbow trout	Arlee	75,455	123.28
2011	Rainbow trout	Eagle Lake	100,680	121.22
2011	Brook trout		58,643	101.60
2012	Rainbow trout	Arlee	68,366	142.18
2012	Rainbow trout	Eagle Lake	106,652	123.18
2012	Brook trout		64,835	119.38
2013	Rainbow trout	Arlee	72,986	135.72

Table A.1: Continued.

Year	Species	Strain	Number stocked	TL (mm)
2013	Rainbow trout	Eagle Lake	100,630	108.39
2013	Brook trout		49.328	109.22
2014	Rainbow trout	Arlee	83,136	119.07
2014	Rainbow trout	Eagle Lake	109,674	122.92
2014	Brook trout		50,000	108.20
2015	Rainbow trout	Arlee	82,521	130.15
2015	Rainbow trout	Eagle Lake	88,990	99.56
2015	Rainbow trout	Gerrard	24,949	128.52
2015	Brook trout		50,543	102.11
2016	Rainbow trout	Arlee	53,247	130.55
2016	Rainbow trout	Eagle Lake	82,416	122.37
2016	Rainbow trout	Gerrard	24,724	117.86
2016	Brook trout		14,379	94.23
2017	Rainbow trout	Arlee	80,894	116.29
2017	Rainbow trout	Eagle Lake	78,412	121.20
2017	Rainbow trout	Gerrard	20,974	126.22
2017	Brook trout		42,302	124.46
2018	Rainbow trout	Arlee	50,717	122.41
2018	Rainbow trout	Eagle Lake	80,336	117.49
2018	Rainbow trout	Gerrard	22.992	112.52
2018	Brook trout		51,164	123.95
2019	Rainbow trout	Arlee	53,487	118.43
2019	Rainbow trout	Eagle Lake	86,132	117.09
2019	Rainbow trout	Gerrard	38,256	140.21
2019	Brook trout		54,950	122.17
2020	Rainbow trout	Arlee	50,199	130.24
2020	Rainbow trout	Eagle Lake	84,000	131.89
2020	Rainbow trout	Gerrard	31,541	111.76
2021	Rainbow trout	Arlee	52,831	119.11
2021	Rainbow trout	Eagle Lake	59,525	123.64
2021	Rainbow trout	Gerrard	37,789	122.68
2021	Brook trout		41,135	78.74
2022	Rainbow trout	Arlee	107,357	52.07
2022	Rainbow trout	Eagle Lake	98,175	88.31
2022	Rainbow trout	Gerrard	54,825	65.53
2022	Brook trout		43,000	65.53
2023	Rainbow trout	Arlee	53,384	100.37

Table A.1: Continued.

Year	Species	Strain	Number stocked	TL (mm)
2023	Rainbow trout	Eagle Lake	73,123	117.35
2023	Rainbow trout	Gerrard	28,000	141.22
2023	Brook trout		22,880	65.53

Table A.2: Mean percent by weight and frequency of occurrence (in parenthesis) of diet items for rainbow trout strains (Arlee, ARB; Eagle Lake, ERB; Gerrard, GRB) and brook trout (EB), by season and seasons combined (Overall; data are pooled for years 2021 – 2023) sampled from Georgetown Lake, Montana, USA. Diet taxa are generally grouped by order; however, some taxa could only be classified to phylum or class (e.g., Arachnida and Bivalvia). Sample size of diets with contents (in parenthesis) are displayed under each species by season. Mean percent by weight values ≥ 10.00% are indicated in bold.

	Spring				Summer				Autumn				Overall			
Diet item	ARB (10)	ERB (75)	GRB (39)	EB (73)	ARB (27)	ERB (70)	GRB (96)	EB (77)	ARB (50)	ERB (80)	GRB (60)	EB (74)	ARB (87)	ERB (225)	GRB (195)	EB (224)
Amphipoda																
Amphipoda parts	9.70	**10.53**	8.66	**21.96**	1.77	2.48	2.53	0.16	2.43	4.83	2.66	0.00	3.06	6.00	3.80	9.22
	(70.00)	(46.67)	(28.21)	(46.58)	(22.22)	(21.43)	(14.58)	(1.30)	(16.00)	(27.50)	(11.67)	(0.00)	(24.14)	(32.00)	(16.41)	(15.62)
Gammaridae	**19.95**	**17.19**	**13.24**	**27.25**	3.51	1.09	1.57	1.85	2.43	2.95	4.44	3.57	4.78	7.12	4.79	**12.91**
	(60.00)	(50.67)	(25.64)	(49.32)	(14.81)	(8.57)	(6.25)	(1.30)	(18.00)	(22.50)	(26.67)	(13.51)	(21.84)	(27.56)	(16.41)	(20.98)
Hyalellidae	1.31	1.24	2.61	0.54	0.07	0.72	0.28	0.00	4.94	6.14	4.73	**16.64**	3.01	2.82	2.11	4.63
	(50.00)	(40.00)	(12.82)	(23.29)	(7.41)	(10.00)	(5.21)	(0.00)	(36.00)	(30.00)	(40.00)	(22.97)	(28.74)	(27.11)	(17.44)	(15.19)
Annelida																
Hirudinea	4.01	8.52	**14.13**	5.95	0.00	0.79	1.56	0.63	0.20	0.40	0.00	4.63	0.58	3.23	3.59	3.91
	(10.00)	(18.67)	(23.08)	(16.44)	(0.00)	(5.71)	(4.17)	(1.30)	(2.00)	(2.50)	(0.00)	(4.05)	(2.30)	(8.89)	(6.67)	(7.14)
Oligochaeta	0.00	0.21	0.00	0.20	0.00	0.14	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.01	0.08
	(0.00)	(4.00)	(0.00)	(2.74)	(0.00)	(4.29)	(1.04)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(2.67)	(0.51)	(0.89)
Anomopoda																
Daphniidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.45	0.05	0.00	0.00	0.14	0.01
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(2.50)	(3.33)	(1.35)	(0.00)	(0.89)	(1.03)	(0.45)
Arachnida																
Arachnida	0.18	0.00	0.90	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.06	0.03	0.00	0.02	0.02
	(10.00)	(0.00)	(2.56)	(0.00)	(0.00)	(1.43)	(0.00)	(0.00)	(2.00)	(1.25)	(0.00)	(1.35)	(2.30)	(0.89)	(0.51)	(0.45)
Bivalvia																
Bivalvia parts	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.01	0.00	0.01	0.02	0.14	0.01	0.00	0.01	0.04
	(0.00)	(1.33)	(0.00)	(0.00)	(3.70)	(0.00)	(0.00)	(1.30)	(2.00)	(1.25)	(6.67)	(1.35)	(2.30)	(0.89)	(2.05)	(0.89)
Coleoptera																
Amphizoidae	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00
	(0.00)	(0.00)	(2.56)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.51)	(0.00)

Table A.2: Continued.

Diet item	Spring				Summer				Autumn				Overall			
	ARB (10)	ERB (75)	GRB (39)	EB (73)	ARB (27)	ERB (70)	GRB (96)	EB (77)	ARB (50)	ERB (80)	GRB (60)	EB (74)	ARB (87)	ERB (225)	GRB (195)	EB (224)
Buprestidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.08	0.00	0.00	0.00	0.02	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(1.25)	(1.67)	(0.00)	(0.00)	(0.44)	(0.51)	(0.00)
Byturidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(1.25)	(0.00)	(0.00)	(0.00)	(0.44)	(0.00)	(0.00)
Coleoptera parts	0.00	0.02	0.43	0.00	0.10	0.38	0.00	0.00	0.25	0.06	0.58	0.00	0.18	0.14	0.27	0.00
	(0.00)	(1.33)	(7.69)	(0.00)	(3.70)	(4.29)	(1.04)	(0.00)	(14.00)	(2.50)	(6.67)	(0.00)	(9.20)	(2.67)	(4.10)	(0.00)
Curculionidae	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.16	0.00	0.01	0.00	0.05	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(3.70)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(1.67)	(0.00)	(1.15)	(0.00)	(0.51)	(0.00)
Dysticidae	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00
	(0.00)	(1.33)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.44)	(0.00)	(0.00)
Elateridae	0.00	0.00	0.00	0.00	0.02	0.02	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.05	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(3.70)	(2.86)	(0.00)	(0.00)	(0.00)	(1.25)	(0.00)	(0.00)	(1.15)	(1.33)	(0.00)	(0.00)
Halipilidae	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.30	0.01	0.00	0.00
	(0.00)	(1.33)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(4.00)	(0.00)	(0.00)	(0.00)	(2.30)	(0.44)	(0.00)	(0.00)
Hydrophilidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.02	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(2.00)	(0.00)	(0.00)	(0.00)	(1.15)	(0.00)	(0.00)	(0.00)
Meloidae	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(1.43)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.44)	(0.00)	(0.00)
Staphylinidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.08	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(2.00)	(0.00)	(0.00)	(0.00)	(1.15)	(0.00)	(0.00)	(0.00)
Scarabaeidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.41	0.01	0.00	0.00	1.39	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(8.00)	(1.25)	(0.00)	(0.00)	(4.60)	(0.44)	(0.00)	(0.00)
Cypriniformes																
C. catostomus	0.00	0.00	0.00	0.00	0.00	1.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.43	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(1.43)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.44)	(0.00)	(0.00)
C. macrocheilus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.75	0.00	0.00	0.00	1.01	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(2.00)	(0.00)	(0.00)	(0.00)	(1.15)	(0.00)	(0.00)	(0.00)
Decapoda																
Decapoda parts	0.00	1.05	4.04	1.15	0.00	1.42	1.80	2.50	1.20	2.16	2.53	3.37	0.69	1.56	2.47	2.17
	(0.00)	(1.33)	(7.69)	(4.11)	(0.00)	(1.43)	(2.08)	(3.90)	(2.00)	(5.00)	(5.00)	(4.05)	(1.15)	(2.67)	(4.10)	(4.02)
Diptera																

Table A.2: Continued.

	Spring				Summer				Autumn				Overall			
Diet item	ARB	ERB	GRB	EB	ARB	ERB	GRB	EB	ARB	ERB	GRB	EB	ARB	ERB	GRB	EB
	(10)	(75)	(39)	(73)	(27)	(70)	(96)	(77)	(50)	(80)	(60)	(74)	(87)	(225)	(195)	(224)
Ceratopogonidae	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00
	(0.00)	(1.33)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.44)	(0.00)	(0.00)
Chaoboridae	0.00	0.00	0.00	0.00	0.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(3.70)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(1.15)	(0.00)	(0.00)	(0.00)
Chironomidae	0.36	3.31	4.66	0.05	7.56	7.69	5.68	0.27	0.11	0.43	0.02	0.01	2.45	3.65	3.73	0.11
	(40.00)	(38.67)	(30.77)	(9.59)	(48.15)	(52.86)	(40.62)	(5.19)	(14.00)	(17.50)	(8.33)	(2.70)	(27.59)	(35.56)	(28.72)	(5.80)
Culicidae	0.00	0.09	0.00	0.00	0.73	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.23	0.03	0.00	0.00
	(0.00)	(1.33)	(0.00)	(0.00)	(3.70)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(1.15)	(4.44)	(0.00)	(0.00)
Diptera parts	0.00	0.22	0.20	0.57	3.13	2.80	1.85	**10.54**	0.15	1.31	0.44	0.02	1.06	1.41	1.09	3.59
	(10.00)	(8.00)	(10.26)	(9.59)	(14.81)	(15.71)	(12.50)	(23.38)	(16.00)	(15.00)	(21.67)	(1.35)	(14.94)	(12.89)	(14.87)	(11.61)
Muscidae	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.37	0.00	0.30	0.00	0.21	0.00	0.10	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(1.04)	(0.00)	(6.00)	(0.00)	(3.33)	(0.00)	(3.45)	(0.00)	(1.54)	(0.00)
Simuliidae	0.00	0.00	0.00	0.00	0.01	0.16	0.13	2.15	0.00	0.01	0.09	0.01	0.00	0.05	0.09	0.68
	(0.00)	(0.00)	(0.00)	(0.00)	(3.70)	(2.86)	(1.04)	(2.60)	(2.00)	(5.00)	(11.67)	(4.05)	(2.30)	(2.67)	(4.10)	(2.23)
Tipuloidae	0.00	0.00	0.00	0.00	0.37	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.02	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(3.70)	(1.43)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(1.15)	(0.44)	(0.00)	(0.00)
Ephemeroptera																
Baetidae	0.02	0.08	0.00	0.09	0.02	0.60	0.71	0.00	3.84	6.99	1.72	0.99	2.21	2.70	0.88	0.30
	(10.00)	(2.67)	(0.00)	(2.74)	(3.70)	(5.71)	(4.17)	(1.30)	(22.00)	(23.75)	(20.00)	(10.81)	(14.94)	(11.11)	(8.21)	(4.91)
Caenidae	0.00	0.00	0.00	0.00	2.75	0.57	0.26	0.01	0.00	0.00	0.00	0.00	0.85	0.18	0.13	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(25.93)	(12.86)	(11.46)	(0.00)	(0.00)	(1.25)	(1.67)	(0.00)	(8.05)	(4.44)	(6.15)	(0.45)
Ephemerellidae	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(7.41)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(2.30)	(0.00)	(0.00)	(0.00)
Ephemeroptera parts	0.08	0.61	0.24	0.18	1.91	2.11	4.20	0.80	0.06	0.05	0.09	0.00	0.64	0.88	2.14	0.33
	(10.00)	(28.00)	(12.82)	(5.48)	(18.52)	(17.14)	(29.17)	(5.19)	(8.00)	(3.75)	(10.00)	(0.00)	(11.49)	(16.00)	(20.00)	(3.57)
Siphlonuridae	0.00	0.00	0.00	0.00	0.43	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(3.70)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(1.15)	(0.00)	(0.00)	(0.00)
Gastropoda																
Basommatophora	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(1.43)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.44)	(0.00)	(0.00)
Bithyniidae	**11.98**	2.83	3.23	5.27	0.00	4.64	1.47	2.64	7.71	5.00	4.12	3.88	5.81	4.18	2.64	4.05
	(30.00)	(13.33)	(10.26)	(20.55)	(0.00)	(10.00)	(6.25)	(2.60)	(14.00)	(8.75)	(11.67)	(4.05)	(11.49)	(10.67)	(8.72)	(8.93)

Table A.2: Continued.

	Spring				Summer				Autumn				Overall			
Diet item	ARB (10)	ERB (75)	GRB (39)	EB (73)	ARB (27)	ERB (70)	GRB (96)	EB (77)	ARB (50)	ERB (80)	GRB (60)	EB (74)	ARB (87)	ERB (225)	GRB (195)	EB (224)
Gastropoda parts	1.61	0.06	0.65	0.04	0.01	0.75	0.03	2.21	0.00	1.61	0.00	0.00	0.19	0.82	0.14	0.72
	(20.00)	(4.00)	(5.13)	(2.74)	(3.70)	(7.14)	(2.08)	(2.60)	(0.00)	(3.75)	(0.00)	(0.00)	(3.45)	(4.89)	(2.05)	(1.79)
Hydrobiidae	8.17	9.74	8.54	6.56	1.84	2.52	4.23	0.92	**17.45**	**26.23**	**24.80**	**14.60**	**11.54**	**13.36**	**11.42**	6.90
	(60.00)	(61.33)	(30.77)	(49.32)	(22.22)	(34.29)	(22.92)	(5.19)	(50.00)	(63.75)	(68.33)	(21.62)	(42.53)	(53.78)	(38.46)	(25.00)
Lymnaeidae	1.12	1.89	0.11	0.00	0.00	0.09	0.00	0.00	0.00	0.28	0.00	0.00	0.13	0.76	0.02	0.00
	(10.00)	(5.33)	(2.56)	(0.00)	(0.00)	(1.43)	(0.00)	(0.00)	(0.00)	(1.25)	(0.00)	(0.00)	(1.15)	(2.67)	(0.51)	(0.00)
Physidae	0.00	0.66	0.16	0.00	0.00	1.03	0.00	0.00	0.92	0.00	1.04	0.00	0.53	0.54	0.35	0.00
	(0.00)	(2.67)	(2.56)	(0.00)	(0.00)	(1.43)	(0.00)	(0.00)	(2.00)	(0.00)	(1.67)	(0.00)	(1.15)	(1.33)	(1.03)	(0.00)
Planorbidae	0.00	0.01	0.00	0.00	0.00	0.22	0.13	0.00	0.00	0.11	0.00	0.08	0.00	0.11	0.07	0.02
	(0.00)	(2.67)	(0.00)	(0.00)	(0.00)	(2.86)	(3.12)	(0.00)	(0.00)	(1.25)	(1.67)	(1.35)	(0.00)	(2.22)	(2.05)	(0.45)
Thiaridae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.03	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(1.67)	(0.00)	(0.00)	(0.00)	(0.51)	(0.00)
Valvatidae	2.24	3.18	0.43	0.62	0.00	0.25	0.14	0.00	0.71	4.49	6.53	0.73	0.67	2.73	2.16	0.45
	(30.00)	(34.67)	(15.38)	(21.92)	(0.00)	(8.57)	(7.29)	(0.00)	(12.00)	(16.25)	(16.67)	(4.05)	(10.34)	(20.00)	(11.79)	(8.48)
Hemiptera																
Coreidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.12	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(2.00)	(0.00)	(0.00)	(0.00)	(1.15)	(0.00)	(0.00)	(0.00)
Corixidae	0.00	0.00	0.19	0.00	0.00	0.00	0.00	0.01	0.19	0.23	0.17	0.00	0.11	0.08	0.09	0.00
	(0.00)	(0.00)	(2.56)	(0.00)	(0.00)	(0.00)	(0.00)	(2.60)	(14.00)	(10.00)	(10.00)	(0.00)	(8.05)	(3.56)	(3.59)	(0.89)
Hemiptera parts	0.00	0.00	0.10	0.00	0.00	0.02	0.00	0.00	0.63	0.14	0.04	0.00	0.36	0.05	0.03	0.00
	(0.00)	(0.00)	(2.56)	(0.00)	(0.00)	(1.43)	(0.00)	(0.00)	(22.00)	(10.00)	(10.00)	(0.00)	(12.64)	(4.00)	(3.59)	(0.00)
Notonectidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.28	0.00	0.00	0.05	0.10	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(2.00)	(3.75)	(0.00)	(0.00)	(1.15)	(1.33)	(0.00)	(0.00)
Rhopalidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.01	0.00	0.00	0.01	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(2.50)	(1.67)	(0.00)	(0.00)	(0.89)	(0.51)	(0.00)
Hymenoptera																
Formicidae	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	**12.15**	4.03	**10.21**	1.15	6.98	1.43	3.15	0.30
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(1.04)	(0.00)	(32.00)	(18.75)	(25.00)	(1.35)	(18.39)	(6.67)	(8.20)	(0.45)
Hymenoptera parts	0.00	0.00	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.04	0.00
	(0.00)	(0.00)	(2.56)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(1.25)	(1.67)	(0.00)	(0.00)	(0.44)	(1.03)	(0.00)
Ichneumonidae	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.02	0.00
	(0.00)	(0.00)	(2.56)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(2.00)	(0.00)	(0.00)	(0.00)	(1.15)	(0.00)	(0.51)	(0.00)

Table A.2: Continued.

	Spring				Summer				Autumn				Overall			
Diet item	ARB	ERB	GRB	EB	ARB	ERB	GRB	EB	ARB	ERB	GRB	EB	ARB	ERB	GRB	EB
	(10)	(75)	(39)	(73)	(27)	(70)	(96)	(77)	(50)	(80)	(60)	(74)	(87)	(225)	(195)	(224)
Vespidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.43	0.04	0.00	0.00	0.25	0.01	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(2.00)	(2.50)	(0.00)	(0.00)	(1.15)	(0.89)	(0.00)	(0.00)
Isopoda																
Asellidae	0.22	0.00	0.00	0.34	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.03	0.18	0.00	0.14
	(10.00)	(0.00)	(0.00)	(1.37)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(3.75)	(0.00)	(0.00)	(1.15)	(1.33)	(0.00)	(0.45)
Isopoda parts	**32.83**	8.01	4.39	1.59	6.93	**10.42**	**12.90**	2.49	0.42	2.63	2.74	4.81	6.17	6.85	8.07	2.73
	(70.00)	(45.33)	(35.90)	(21.92)	(33.33)	(47.14)	(46.88)	(10.39)	(10.00)	(27.50)	(25.00)	(17.57)	(24.14)	(39.56)	(37.95)	(16.52)
Lepidoptera																
Lepidoptera parts	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(3.70)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(1.15)	(0.00)	(0.00)	(0.00)
Odonata																
Coenagrionidae	0.00	4.13	5.55	**11.76**	**13.06**	**12.58**	**15.60**	**25.91**	6.00	4.58	3.36	3.05	7.50	6.92	9.82	**13.95**
	(0.00)	(26.67)	(12.82)	(38.36)	(40.74)	(32.86)	(41.67)	(28.57)	(36.00)	(25.00)	(25.00)	(10.81)	(3.33)	(28.00)	(30.77)	(25.89)
Lestidae	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
	(0.00)	(0.00)	(0.00)	(1.37)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.45)
Libellulidae	0.00	3.54	0.00	2.67	0.00	0.00	0.00	0.24	4.04	1.53	0.00	0.00	2.32	1.72	0.00	1.19
	(0.00)	(5.33)	(0.00)	(4.11)	(0.00)	(0.00)	(0.00)	(1.30)	(10.00)	(3.75)	(0.00)	(0.00)	(5.75)	(3.11)	(0.00)	(1.79)
Odonata parts	0.19	1.03	0.00	2.20	0.00	0.00	1.28	0.00	2.03	0.00	0.00	0.00	1.19	0.34	0.63	0.92
	(10.00)	(2.67)	(0.00)	(5.48)	(0.00)	(1.43)	(2.08)	(0.00)	(4.00)	(0.00)	(0.00)	(0.00)	(3.45)	(1.33)	(1.03)	(1.79)
Plecoptera																
Plecoptera parts	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.04	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(2.08)	(0.00)	(0.00)	(0.00)	(1.67)	(0.00)	(0.00)	(0.00)	(1.54)	(0.00)
Salmoniformes																
O. mykiss	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.22	0.00	0.00	0.00	0.59
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(1.35)	(0.00)	(0.00)	(0.00)	(0.45)
O. nerka	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Sphaeriida																
Sphaeriidae	0.28	0.53	0.56	0.14	0.06	0.09	0.01	0.00	0.00	0.00	0.00	0.00	0.05	0.21	0.12	0.06
	(10.00)	(22.67)	(7.69)	(8.22)	(3.70)	(5.71)	(2.08)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(2.30)	(9.33)	(2.56)	(2.68)

Table A.2: Continued.

Diet item	Spring				Summer				Autumn				Overall			
	ARB (10)	ERB (75)	GRB (39)	EB (73)	ARB (27)	ERB (70)	GRB (96)	EB (77)	ARB (50)	ERB (80)	GRB (60)	EB (74)	ARB (87)	ERB (225)	GRB (195)	EB (224)
Trichoptera																
Hydroptilidae	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.02	0.01	0.01	0.00	0.01	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(3.70)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(1.67)	(1.35)	(1.15)	(0.00)	(0.51)	(0.45)
Leptoceridae	0.00	0.02	0.00	0.00	3.33	1.97	1.91	0.06	0.00	0.00	0.09	0.00	1.04	0.62	0.97	0.02
	(0.00)	(5.33)	(0.00)	(0.00)	(48.15)	(31.43)	(32.29)	(2.60)	(2.00)	(0.00)	(5.00)	(0.00)	(16.09)	(11.56)	(17.44)	(0.89)
Limnephilidae	0.00	0.03	0.22	0.16	3.63	**14.71**	6.09	**28.46**	0.89	0.27	0.32	5.82	1.64	4.68	3.14	**10.65**
	(0.00)	(1.33)	(2.56)	(1.37)	(11.11)	(28.57)	(16.67)	(23.38)	(12.00)	(3.75)	(8.33)	(14.86)	(10.34)	(10.67)	(11.28)	(13.39)
Phryganeidae	2.09	1.83	2.93	0.34	3.47	1.28	3.93	0.00	0.08	0.10	0.00	0.00	1.36	1.04	2.52	0.14
	(10.00)	(18.67)	(12.82)	(2.74)	(11.11)	(10.00)	(15.62)	(0.00)	(4.00)	(3.75)	(0.00)	(0.00)	(6.90)	(10.67)	(10.26)	(0.89)
Trichoptera parts	0.01	0.02	0.00	0.76	**22.55**	7.40	**10.68**	4.05	0.50	0.96	1.10	0.15	7.28	2.65	5.60	1.64
	(10.00)	(4.00)	(10.26)	(2.74)	(48.15)	(34.29)	(33.33)	(7.79)	(16.00)	(7.50)	(13.33)	(1.35)	(25.29)	(14.67)	(22.56)	(4.02)
Trombidiformes																
Trombidiformes parts	0.02	0.26	0.17	0.00	0.00	0.19	0.05	0.00	0.10	0.04	1.27	0.00	0.06	0.16	0.45	0.00
	(10.00)	(10.67)	(5.13)	(1.37)	(3.70)	(7.14)	(6.25)	(0.00)	(2.00)	(7.50)	(5.00)	(0.00)	(3.45)	(8.44)	(5.64)	(0.45)
Other																
Fish eggs	0.00	0.29	0.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.31	0.00	0.00	0.10	0.15	0.00
	(0.00)	(4.00)	(2.56)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(1.67)	(0.00)	(0.00)	(1.33)	(1.03)	(0.00)
Fish parts	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.40	0.00	0.00	0.04	0.01	0.00
	(0.00)	(2.67)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(1.67)	(0.00)	(0.00)	(0.89)	(0.51)	(0.00)
Fishing tackle	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00	1.55	1.67	0.00	0.13	0.55	0.57	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(1.04)	(0.00)	(2.00)	(2.50)	(1.67)	(0.00)	(1.15)	(0.89)	(1.03)	(0.00)
Insecta parts	0.64	2.03	7.54	4.87	**10.86**	8.54	**10.63**	9.60	9.27	**10.02**	9.96	**14.69**	8.77	6.90	9.81	8.98
	(50.00)	(36.00)	(35.90)	(27.40)	(48.15)	(52.86)	(55.21)	(14.29)	(40.00)	(50.00)	(36.67)	(20.27)	(43.68)	(46.22)	(45.64)	(20.54)
Organic matter	2.68	**12.16**	8.69	2.56	9.93	7.27	7.34	0.53	8.01	2.65	1.98	7.80	7.99	7.26	5.95	3.30
	(20.00)	(33.33)	(15.38)	(17.81)	(62.96)	(42.86)	(51.04)	(3.90)	(34.00)	(20.00)	(26.67)	(13.51)	(41.38)	(31.56)	(36.41)	(11.61)
Plants	0.33	4.38	7.57	2.19	1.16	3.51	2.75	3.92	5.5	7.23	**11.76**	**11.46**	3.56	5.12	6.48	5.19
	(30.00)	(46.67)	(28.21)	(31.51)	(11.11)	(35.71)	(22.92)	(5.19)	(36.00)	(42.50)	(51.67)	(22.97)	(27.59)	(41.78)	(32.82)	(19.64)
Plastic	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	(0.00)	(2.67)	(0.00)	(0.00)	(0.00)	(0.00)	(1.04)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.89)	(0.51)	(0.00)
Unidentified	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.03	2.07	0.00	0.00	0.07	1.19	0.00	0.00	0.03
	(0.00)	(1.33)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(1.30)	(6.00)	(0.00)	(0.00)	(1.35)	(3.45)	(0.44)	(0.00)	(0.89)

APPENDIX B

CHAPTER 3 SUPPLEMENTAL TABLES AND FIGURES

Tables

Table B.1: Number and mean total length (mm; TL) of stocked trout by species and strain in Georgetown Lake, Montana, USA from 2004 through 2023.

Year	Species	Strain	Number stocked	TL (mm)
2004	Rainbow trout	Arlee	70,208	160.88
2004	Rainbow trout	Eagle Lake	116,183	129.56
2004	Rainbow trout	Kamloops	39,186	155.85
2004	Brook trout		10,360	121.16
2005	Rainbow trout	Arlee	194,681	127.25
2005	Rainbow trout	Eagle Lake	10,215	108.20
2005	Rainbow trout	Kamloops	35,077	124.46
2005	Brook trout		52,954	89.62
2006	Rainbow trout	Arlee	76,274	125.94
2006	Rainbow trout	Eagle Lake	80,100	113.42
2006	Rainbow trout	Kamloops	36,955	105.41
2007	Rainbow trout	Arlee	67,796	117.14
2007	Rainbow trout	Eagle Lake	80,035	123.50
2007	Rainbow trout	Kamloops	32,580	118.36
2007	Brook trout		59,290	101.81
2008	Rainbow trout	Arlee	104,779	136.15
2008	Rainbow trout	Eagle Lake	131,670	135.40
2008	Rainbow trout	Kamloops	24,244	90.42
2008	Brook trout		47,520	104.14
2009	Rainbow trout	Arlee	74,397	127.00
2009	Rainbow trout	Eagle Lake	108,598	113.09
2009	Brook trout		40,339	101.60
2010	Rainbow trout	Arlee	66,875	130.68
2010	Rainbow trout	Eagle Lake	93,696	128.21
2010	Brook trout		48,488	101.60
2011	Rainbow trout	Arlee	75,455	123.28
2011	Rainbow trout	Eagle Lake	100,680	121.22
2011	Brook trout		58,643	101.60
2012	Rainbow trout	Arlee	68,366	142.18
2012	Rainbow trout	Eagle Lake	106,652	123.18
2012	Brook trout		64,835	119.38
2013	Rainbow trout	Arlee	72,986	135.72
2013	Rainbow trout	Eagle Lake	100,630	108.39

Table B.1: Continued.

Year	Species	Strain	Number stocked	TL (mm)
2013	Brook trout		49.328	109.22
2014	Rainbow trout	Arlee	83,136	119.07
2014	Rainbow trout	Eagle Lake	109,674	122.92
2014	Brook trout		50,000	108.20
2015	Rainbow trout	Arlee	82,521	130.15
2015	Rainbow trout	Eagle Lake	88,990	99.56
2015	Rainbow trout	Gerrard	24,949	128.52
2015	Brook trout		50,543	102.11
2016	Rainbow trout	Arlee	53,247	130.55
2016	Rainbow trout	Eagle Lake	82,416	122.37
2016	Rainbow trout	Gerrard	24,724	117.86
2016	Brook trout		14,379	94.23
2017	Rainbow trout	Arlee	80,894	116.29
2017	Rainbow trout	Eagle Lake	78,412	121.20
2017	Rainbow trout	Gerrard	20,974	126.22
2017	Brook trout		42,302	124.46
2018	Rainbow trout	Arlee	50,717	122.41
2018	Rainbow trout	Eagle Lake	80,336	117.49
2018	Rainbow trout	Gerrard	22.992	112.52
2018	Brook trout		51,164	123.95
2019	Rainbow trout	Arlee	53,487	118.43
2019	Rainbow trout	Eagle Lake	86,132	117.09
2019	Rainbow trout	Gerrard	38,256	140.21
2019	Brook trout		54,950	122.17
2020	Rainbow trout	Arlee	50,199	130.24
2020	Rainbow trout	Eagle Lake	84,000	131.89
2020	Rainbow trout	Gerrard	31,541	111.76
2021	Rainbow trout	Arlee	52,831	119.11
2021	Rainbow trout	Eagle Lake	59,525	123.64
2021	Rainbow trout	Gerrard	37,789	122.68
2021	Brook trout		41,135	78.74
2022	Rainbow trout	Arlee	107,357	52.07
2022	Rainbow trout	Eagle Lake	98,175	88.31
2022	Rainbow trout	Gerrard	54,825	65.53
2022	Brook trout		43,000	65.53
2023	Rainbow trout	Arlee	53,384	100.37
2023	Rainbow trout	Eagle Lake	73,123	117.35

Table B.1: Continued.

Year	Species	Strain	Number stocked	TL (mm)
2023	Rainbow trout	Gerrard	28,000	141.22
2023	Brook trout		22,880	65.53

Table B.2: Caloric values of dietary taxa parameters used in bioenergetics models for Georgetown Lake, Montana, USA. Surrogates were used for taxa that did not have specific energy density estimates. Energy densities were converted from calories/g of wet weight to J/g of wet weight to be used for Bioenergetics 4.0.

Prey item	Surrogate	J/g of wet weight	Source
Amphipoda		3908	Cumminns & Wuycheck (1971)
Annelida		2699	Cumminns & Wuycheck (1971)
Ceriodaphnia	Daphnidae	1314	Cumminns & Wuycheck (1971)
Cyclopidae	Copepod	2942	Hanson et al. (1997)
Daphniidae		1314	Cumminns & Wuycheck (1971)
Diptera		2565	Cumminns & Wuycheck (1971)
Ephemeroptera	Baetidae	4703	Cumminns & Wuycheck (1971)
Gastropoda		1800	Cumminns & Wuycheck (1971)
Hymenoptera	Insecta	3176	Cumminns & Wuycheck (1971)
Isopoda	Insecta	3176	Cumminns & Wuycheck (1971)
Odonata	Insecta	3176	Cumminns & Wuycheck (1971)
Trichoptera	Insecta	3176	Cumminns & Wuycheck (1971)
Other – rainbow trout		2960	See Methods
Other - kokanee		2697	See Methods

Figures

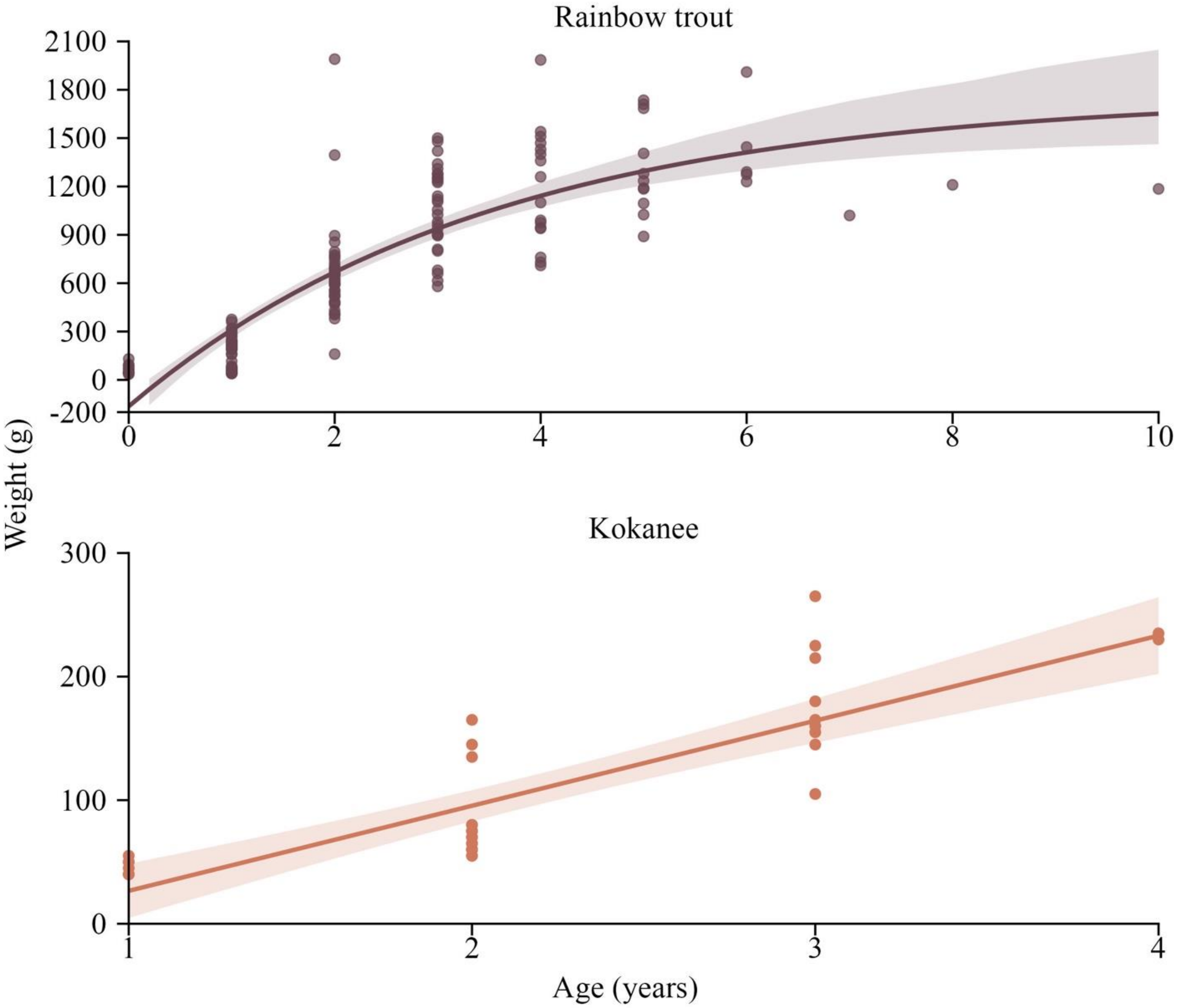

Figure B.1: Growth models for rainbow trout (von Bertalanffy model) and kokanee (linear model) sampled from Georgetown Lake, Montana, USA during 2022 – 2023. Points represent the weight (g) of individual aged fish. For rainbow trout, weight (g) at age (years*)* was estimated from the equation $W_{age} = 1505.91\text{g}\ (1 - e^{-0.20(\text{age}-0.11)})$. For kokanee, weight (g) at age (years) was estimated from the equation $W_{age} = -42.21\text{g} + 68.84\text{g} \times \text{age}$.

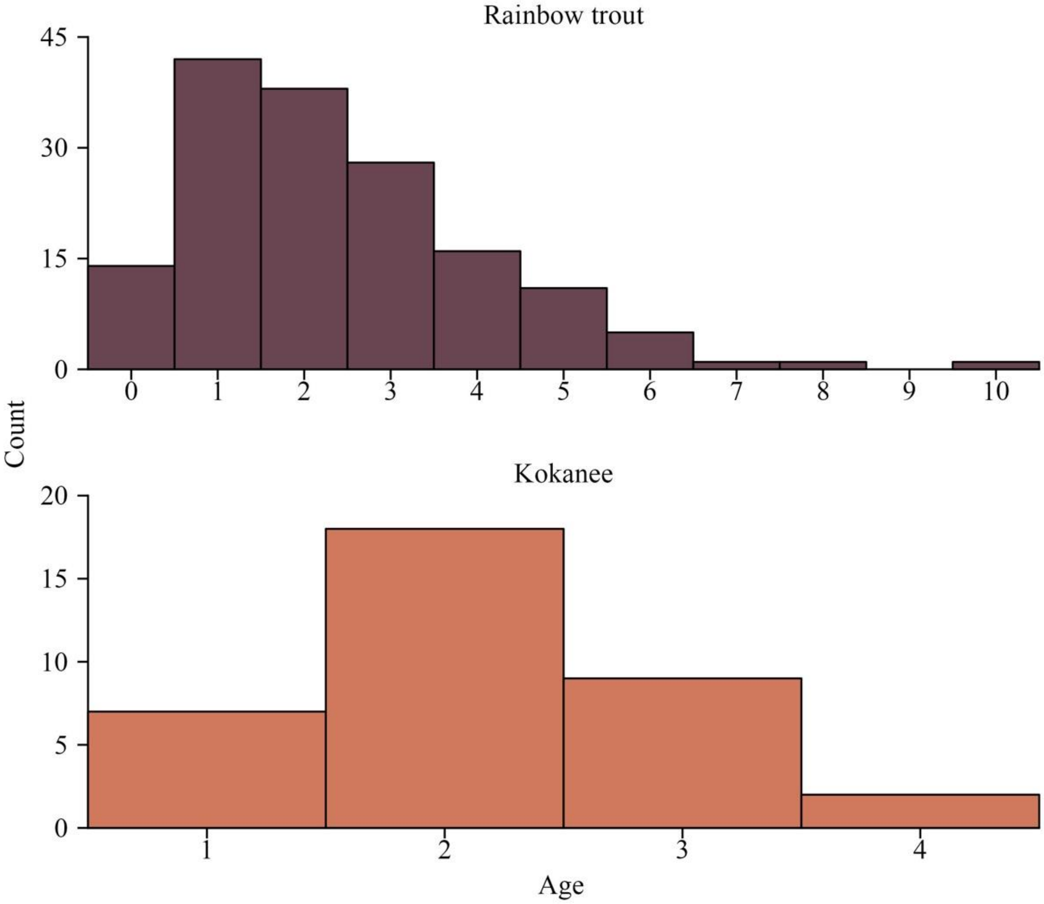

Figure B.2: Age frequency for rainbow trout and kokanee sampled from Georgetown Lake, Montana, USA during 2022 – 2023.

APPENDIX C

SUPPLEMENTAL MATERIAL

Tables

Table C.1: Mean percent by weight and frequency of occurrence (in parenthesis) for kokanee by season and all seasons combined in 2023 (overall) sampled in Georgetown Lake, Montana, USA. Diet taxa are generally grouped by order; however, some taxa could only be classified to class (i.e., Hirudinea). Sample size of diets with contents (in parenthesis) are displayed under each season. Mean percent by weight values ≥ 10.00% are indicated in bold.

Diet item	Spring (53)	Summer (25)	Autumn (23)	Overall (101)
Amphipoda				
Amphipoda parts	5.63	0.00	6.25	4.24
	(11.32)	(0.00)	(8.70)	(7.92)
Gammaridae	0.49	1.64	0.00	0.71
	(9.43)	(8.00)	(0.00)	(6.93)
Hyalellidae	4.39	0.00	0.00	2.40
	(16.98)	(4.00)	(4.35)	(11.34)
Annelida				
*Hirudine*a	2.05	0.00	0.00	1.12
	(3.77)	(0.00)	(0.00)	(1.98)
Anomopoda				
Bosmina	0.00	0.00	0.00	0.00
	(0.00)	(8.00)	(0.00)	(1.98)
Daphniidae	0.32	**51.84**	**87.47**	**30.31**
	(18.87)	(48.00)	(60.87)	(35.64)
Cyclopoida				
Cyclopidae	**48.62**	0.33	0.03	**26.67**
	(43.40)	(20.00)	(21.74)	(32.67)
Diptera				
Chironomidae	9.80	0.00	0.00	5.35
	(49.06)	(8.00)	(0.00)	(27.72)
Culicidae	0.00	0.00	0.00	0.00
	(1.89)	(0.00)	(0.00)	(0.99)
Diptera parts	0.00	**19.82**	6.25	6.46
	(0.00)	(32.00)	(21.74)	(12.87)
Simuliidae	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(13.04)	(2.97)
Ephemeroptera				
Baetidae	0.32	0.00	0.00	0.17
	(5.66)	(0.00)	(0.00)	(2.97)
Caenidae	0.71	0.00	0.00	0.39
	(1.89)	(4.00)	(0.00)	(1.98)

Table C.1: Continued.

Diet item	Spring (53)	Summer (25)	Autumn (23)	Overall (101)
Ephemeroptera parts	0.00	0.25	0.00	0.07
	(0.00)	(4.00)	(0.00)	(0.99)
Gastropoda				
Bithyniidae	0.00	0.00	0.00	0.00
	(0.00)	(4.00)	(0.00)	(0.99)
Hydrobiidae	6.33	0.00	0.00	3.46
	(7.55)	(0.00)	(8.79)	(5.94)
Hymenoptera				
Formicidae	0.23	0.00	0.00	0.13
	(1.89)	(0.00)	(0.00)	(0.99)
Isopoda				
Isopoda parts	0.00	0.00	0.00	0.00
	(1.89)	(4.00)	(0.00)	(1.98)
Odonata				
Coenagrionidae	0.00	**21.76**	0.00	5.82
	(1.89)	(52.00)	(0.00)	(13.86)
Trombidiformes				
Trombidiformes parts	0.00	0.00	0.00	0.00
	(1.89)	(4.00)	(17.39)	(5.94)
Other				
Insecta parts	**21.11**	4.35	0.00	**12.70**
	(35.85)	(4.00)	(0.00)	(19.80)
Plants	0.00	0.00	0.00	0.02
	(0.00)	(0.00)	(0.00)	(0.00)
Unidentified	0.00	0.00	0.00	0.00
	(0.00)	(4.00)	(0.00)	(0.99)

Table C.2: Total number and percentage (in parentheses) of each strain (Gerrard, Eagle Lake, and Arlee) of rainbow trout sampled in Georgetown Lake, Montana, USA from 2021 through 2023 by 100-mm length class, and the proportion of each strain stocked (averaged from the last five years).

Length class	Gerrard	Eagle Lake	Arlee
100	56 (73)	14 (18)	7 (9)
200	58 (27)	116 (55)	38 (18)
300	118 (29)	262 (65)	22 (6)
400	130 (47)	122 (44)	26 (9)
500	37 (52)	26 (36)	9 (12)
Total	399 (38)	540 (52)	102 (10)
Proportion stocked (%)	20	45	35

Table C.3: Mean relative weight (W_r) and standard error (in parenthesis) by incremental proportional size distribution (PSD) length categories for the three rainbow trout strains, brook trout, and kokanee. Rainbow trout PSD length categories are 250 mm for stock, 400 mm for quality, 500 mm for preferred, 650 mm for memorable, and 800 for trophy. Brook trout PSD length categories are 200 mm for stock, 300 mm for quality, 400 mm for preferred, 500 mm for memorable, and 600 mm for trophy. Kokanee PSD length categories are 120 mm for stock, 250 mm for quality, 300 mm for preferred, 400 mm for memorable, and 500 mm for trophy. Fish were sampled in Georgetown Lake, Montana, USA during spring, summer, and autumn of 2021 – 2023.

	Mean relative weight				
Species	S-Q	Q-P	P-M	M-T	T
Arlee	90	87	82	0	0
	(1.6)	(2.3)	(6.3)		
Gerrard	85	84	80	0	0
	(0.6)	(0.7)	(2.7)		
Eagle Lake	85	86	83	0	0
	(0.5)	(1.0)	(3.3)		
Brook trout	94	98	96	117	0
	(0.8)	(1.1)	(1.0)		
Kokanee	83	83	79	0	0
	(0.6)	(0.6)	(1.4)		

Table C.4: Number and percent in parenthesis by sex for each species and strain sampled in Georgetown Lake, Montana, USA during spring, summer, and autumn of 2021 – 2023.

Sex	Brook trout	Kokanee	Rainbow trout	Arlee	Gerrard	Eagle Lake
Female	147 (0.59)	79 (0.30)	520 (0.54)	17 (0.28)	101 (0.40)	131 (0.34)
Male	108 (0.41)	186 (0.70)	446 (0.46)	44 (0.72)	152 (0.60)	251 (0.66)

Figures

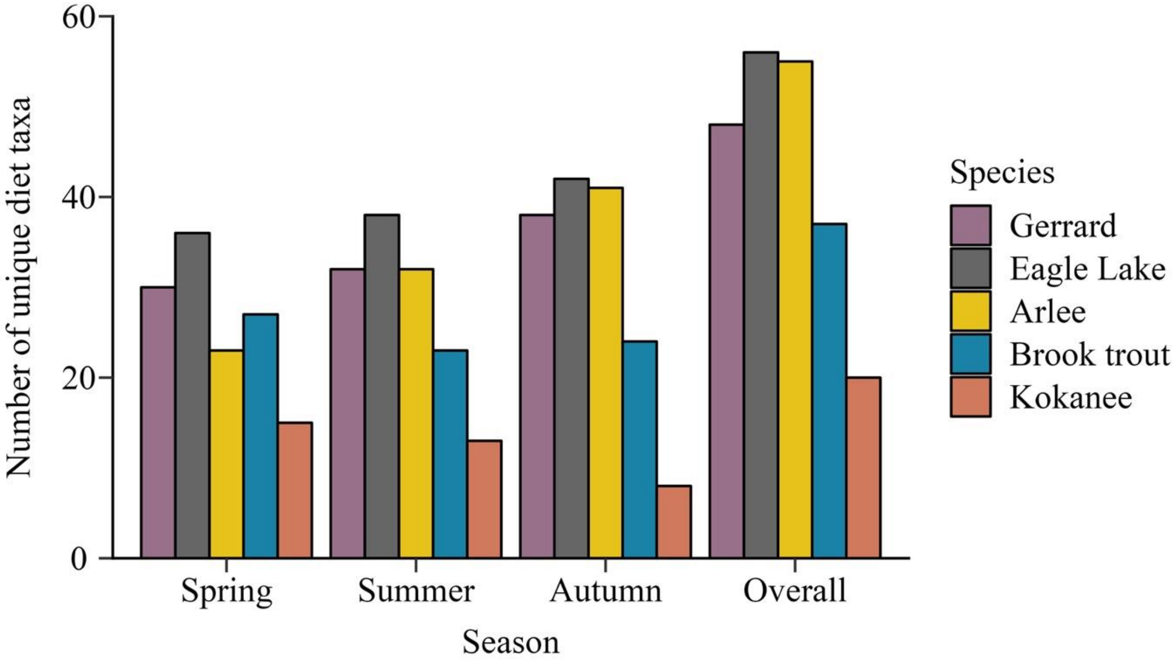

Figure C.1: Number of unique taxa in the diets of brook trout, Arlee, Eagle Lake, Gerrard, and kokanee by season in Georgetown Lake, Montana, USA from 2021 through 2023.

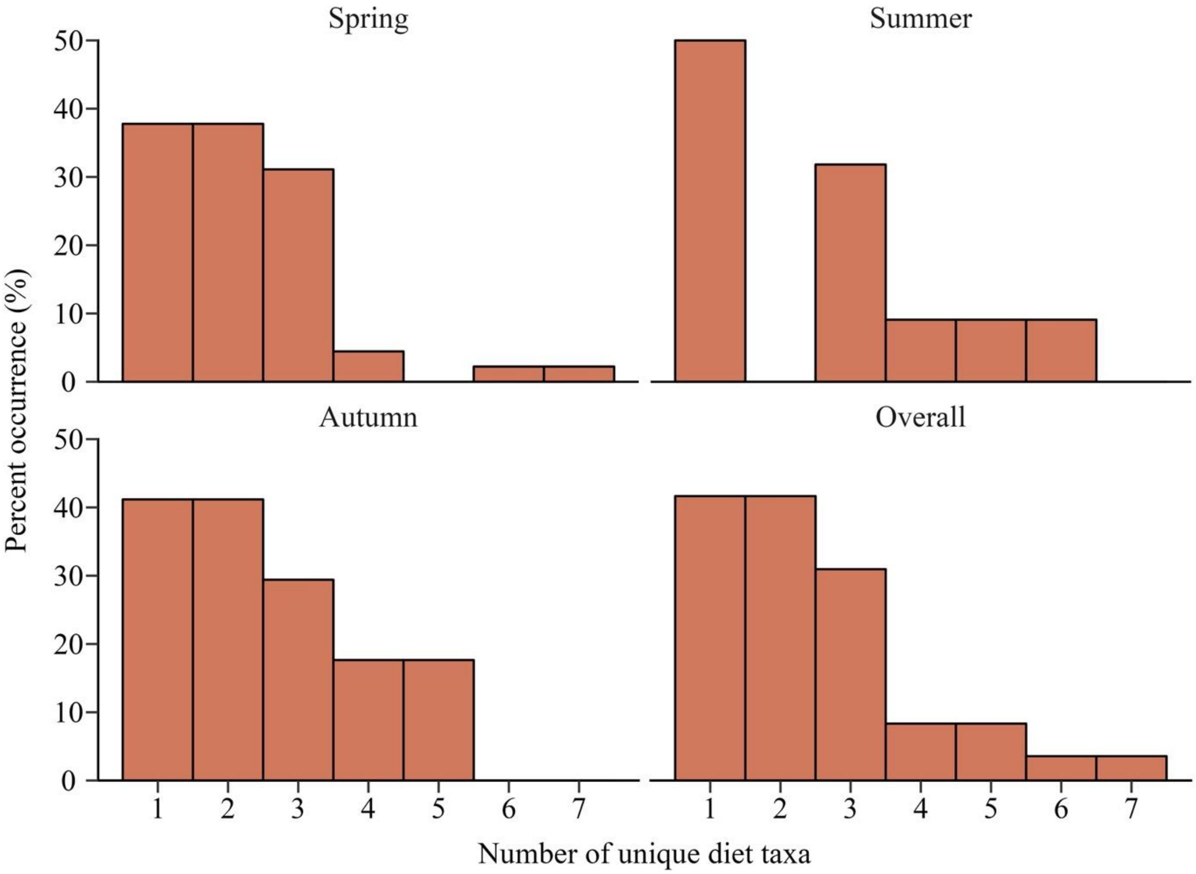

Figure C.2: Percent occurrence of taxa found in diet contents of individual kokanee across seasons within Georgetown Lake, Montana, USA from 2023.

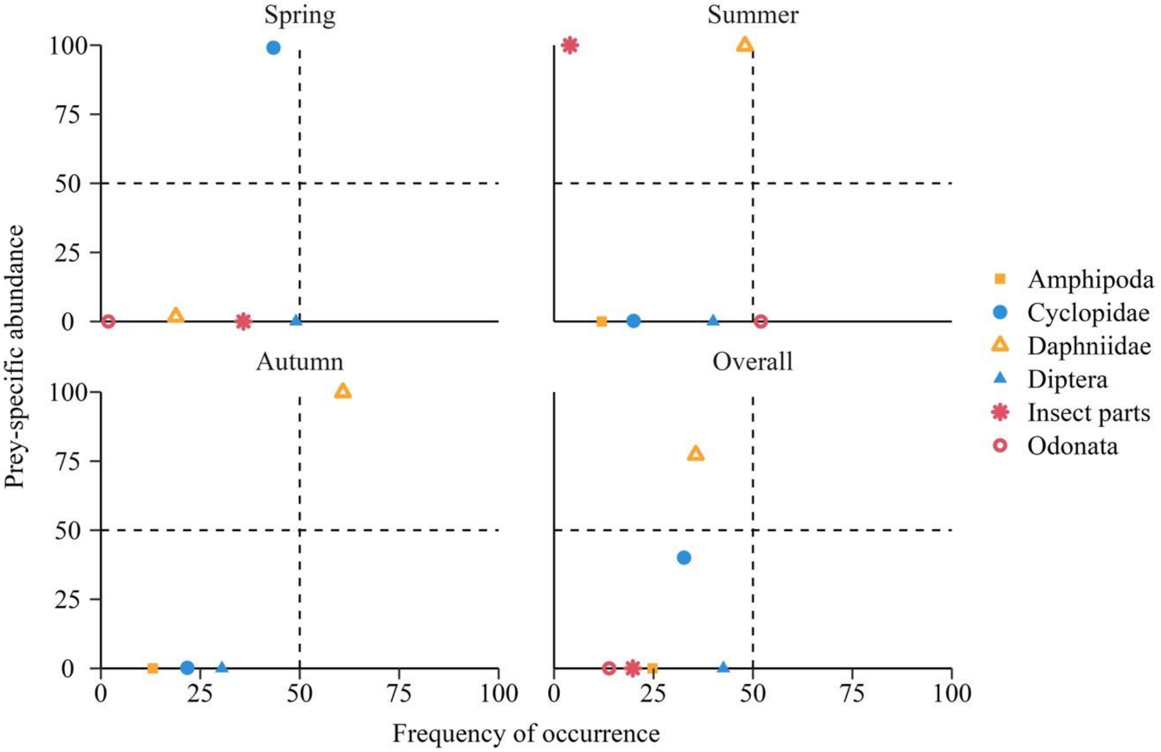

Figure C.3: Prey-specific abundance –frequency of occurrence plot for kokanee by season and overall. Diet taxa that represented at least 10.0% by mean percent by weight for any combination of season and species were selected to be displayed resulting in six diet taxon categories. Diets were sampled from Georgetown Lake, Montana, USA in 2023.

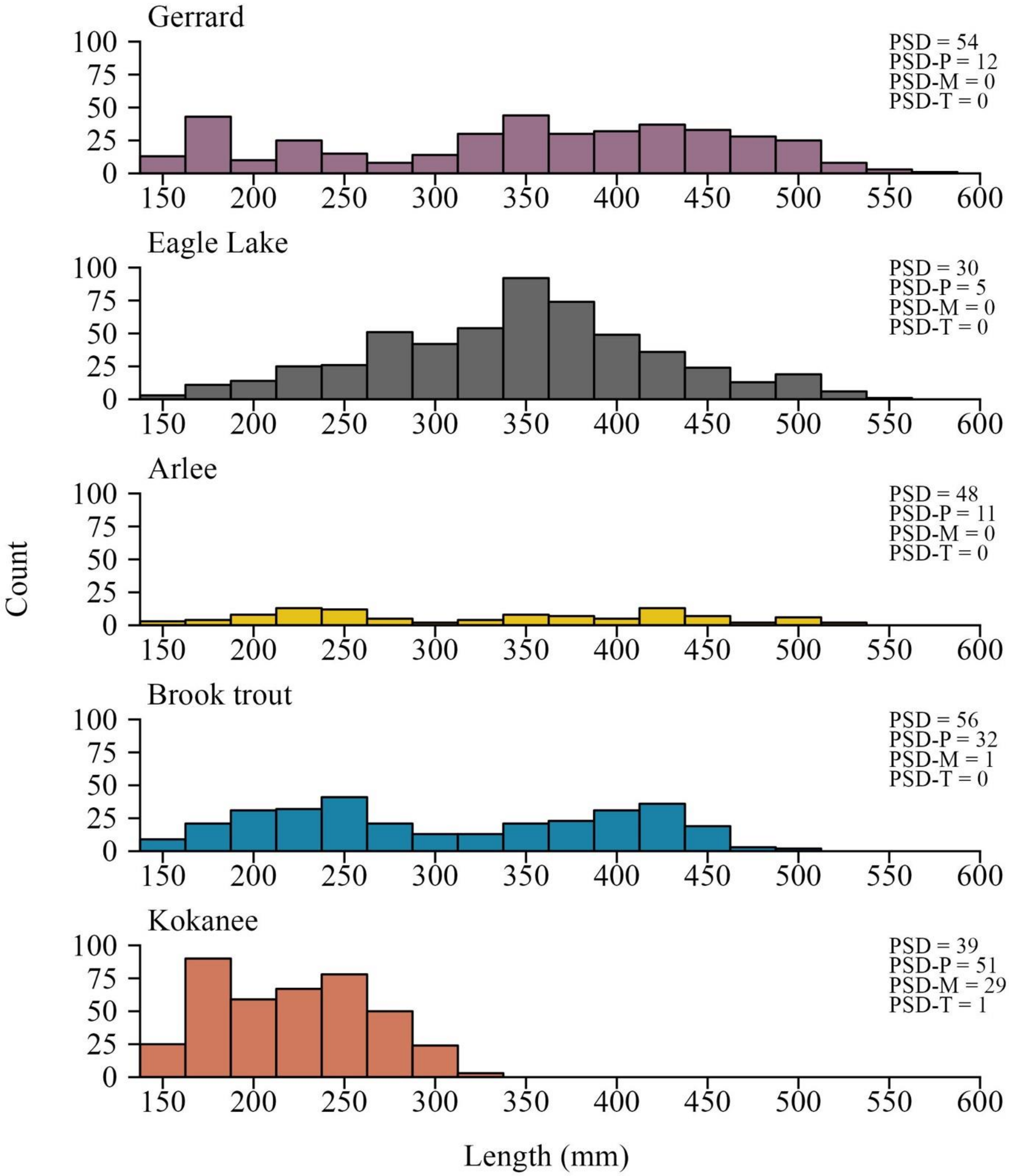

Figure C.4: Length frequency for Arlee, Gerrard, Eagle Lake, brook trout, and kokanee sampled in Georgetown Lake, Montana, USA. Fish were collected in spring, summer, and autumn during 2021 – 2023.

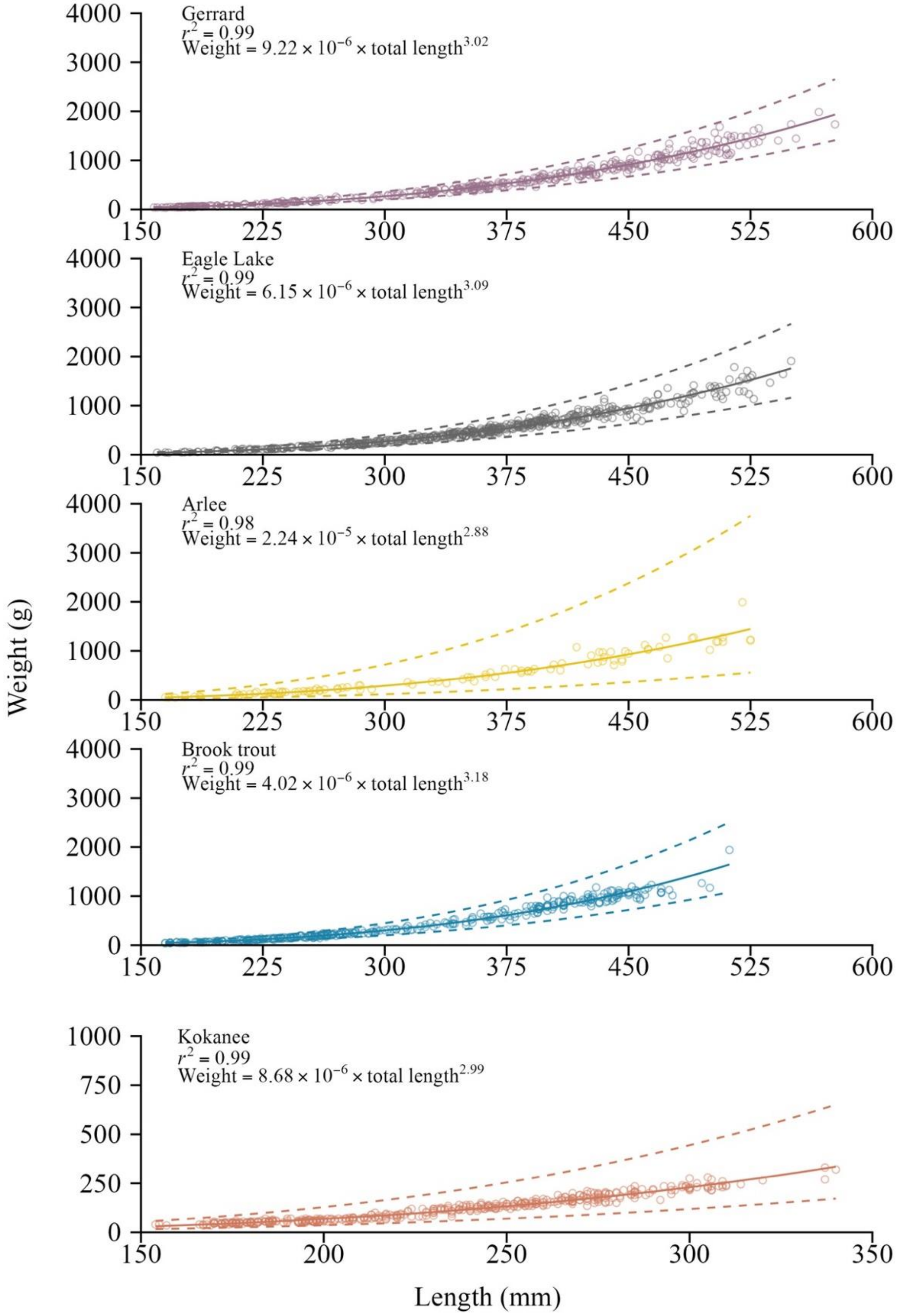

Figure C.5: Weight-length relationships for Arlee, Gerrard, Eagle Lake, brook trout, and kokanee captured in Georgetown Lake, Montana, USA. The solid line represents the average fish as predicted from weight-length relationship and the dashed lines are the 95% confidence intervals. Fish were collected from 2021 through 2023 during spring, summer, and autumn.

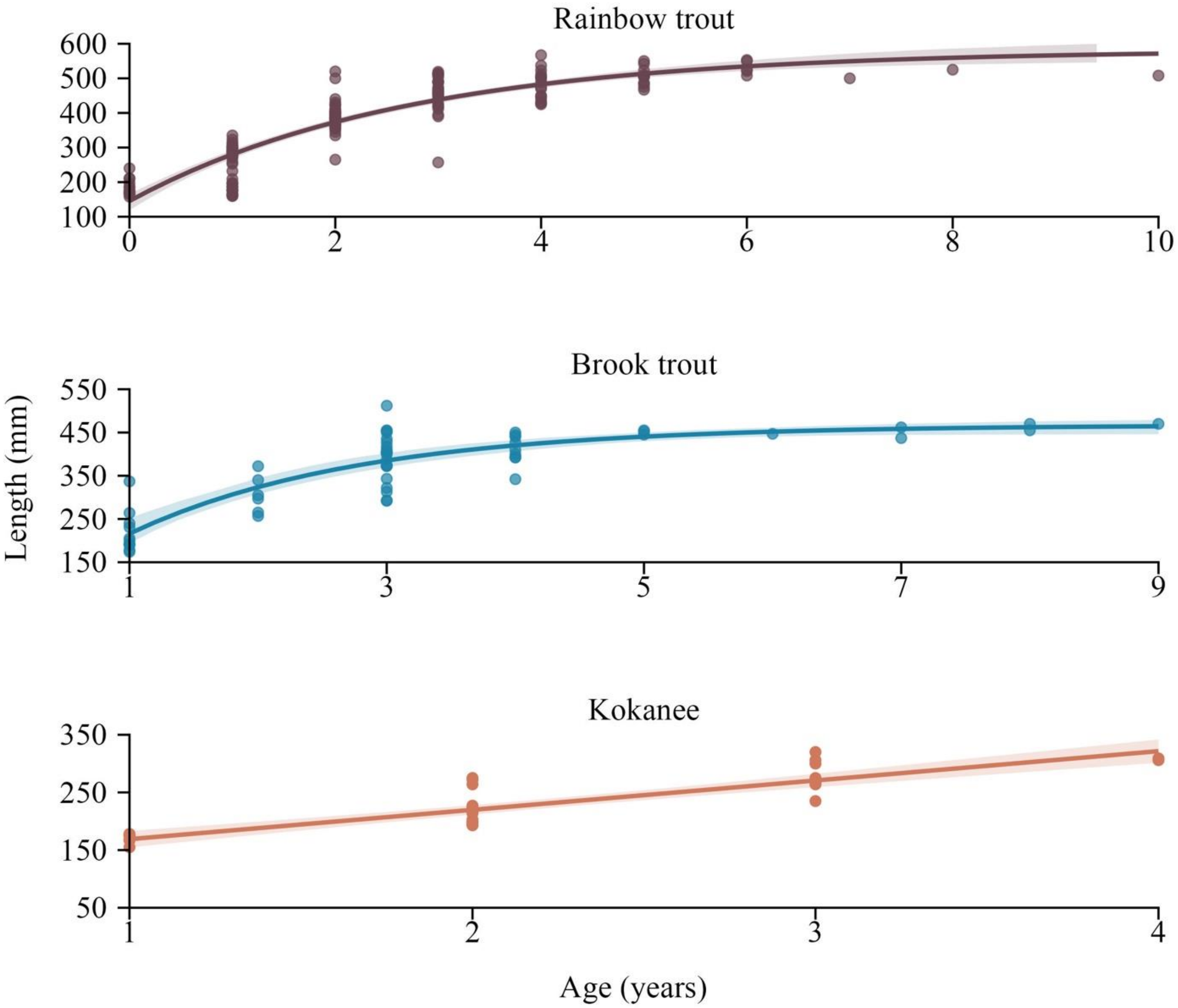

Figure C.6: Growth models for rainbow trout, brook trout (von Bertalanffy model), and kokanee (linear model) sampled from Georgetown Lake, Montana, USA during 2022 – 2023. Points represent the length (mm) of individual aged fish. For rainbow trout, length (mm) at age (years) was estimated from the equation Lage = 582.20 mm (1 – $e^{-0.37(\text{age}-0.78)}$). For brook trout, length (mm) at age (years) was estimated from the equation Lage = 467.25 mm (1 – $e^{-0.56(\text{age}-0.11)}$). For kokanee, length (mm) at age (years) was estimated from the equation Lage = 118.07 mm + 50.88 mm × age.

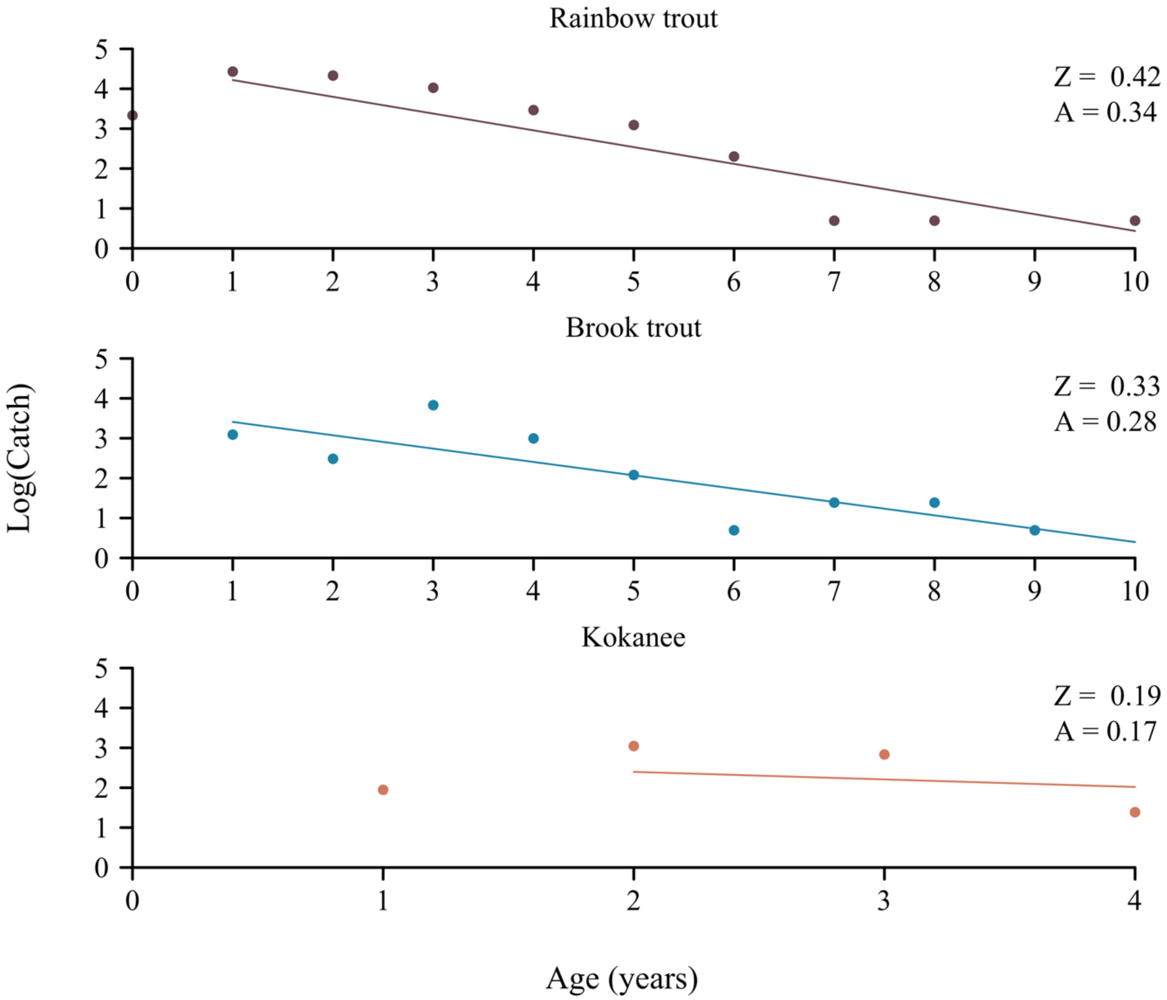

Figure C.7: Catch curves for rainbow trout, brook trout, and kokanee sampled in Georgetown Lake, Montana, USA in 2022 and 2023.

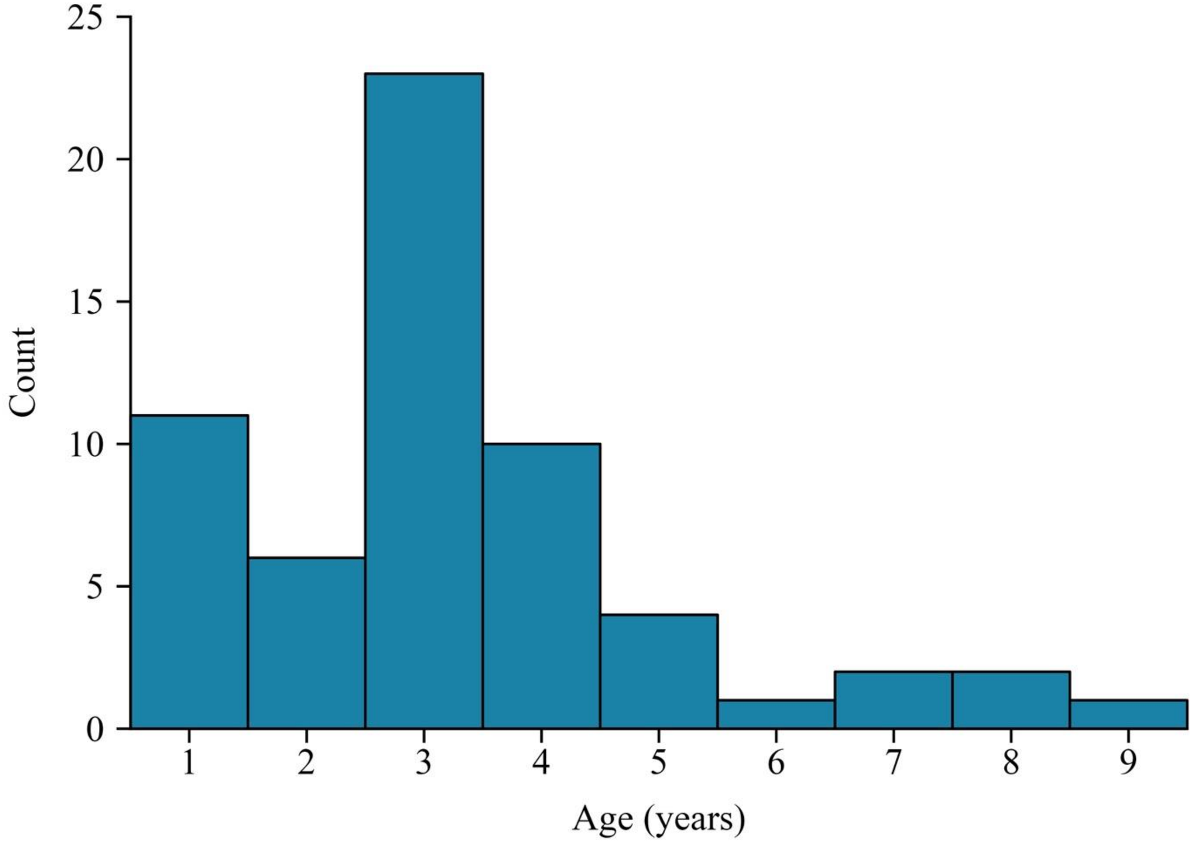

Figure C.8: Age frequency for brook trout sampled in Georgetown Lake, Montana, USA in 2022 and 2023.