ECOLOGICAL INTERACTIONS AND ENVIRONMENTAL STRESSORS: ASSESSING DIETARY DYNAMICS AND POPULATION STABILITY OF BURBOT AMID NON-NATIVE TROUT AND WARMING WINTER TEMPERATURES

by

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ABSTRACT

Burbot *Lota lota* are a cold-water specialist that have a circumpolar distribution. Though historically widespread, many populations are experiencing declines, including the burbot population in the Torrey Creek drainage, Wyoming, which occurs at the southwest most extent of their native range. One hypothesis for the decline observed in burbot abundance within the drainage is the presence of non-native piscivorous predators (i.e., brown trout *Salmo trutta* and lake trout *Salvelinus namaycush*). Using diet composition, bioenergetics, and population modeling, I evaluated the effects non-native trout are having on burbot. There was little dietary overlap among all species combinations. Predation of burbot was not observed by lake trout and was minimal by brown trout, estimated at 7.9 – 37.6 kg annual for the drainage. Nevertheless, I modified a previously developed model to investigate how much predation would be necessary to negatively influence the burbot population. Both the observed and increased predation scenarios yielded positive population growth rates. However, when demographic stochasticity and parameter uncertainty were introduced, every simulation carried a risk of extirpation for burbot within a century, primarily attributed to the high uncertainty associated with the adult mortality estimate. In addition to predation effects, I investigated water temperature induced recruitment failure using a model where egg survival decreased from 86.7% at 2ºC to 47.9% at 4ºC. This critical water temperature, 4ºC, was observed to occur during the putative embryogenesis period of 2022 – 2023 for burbot in the Torrey Creek drainage. The addition of the recruitment penalty to the population models decreased the probability of persistence for all simulation and reduced mean population growth. However, the reduction in recruitment even when occurring annually resulted in higher lambda estimates than the increased predation simulation without the occurrence of a recruitment penalty, indicating that juvenile survival has a greater proportional effect on the population growth rate than the reduction in recruitment as modeled by the recruitment penalty. With the findings from the bioenergetics modeling coupled with the population modeling, direct predations and intraguild predation from brown trout and lake trout are currently not a key factor contributing to the decline of burbot within the drainage.

CHAPTER ONE

DISSERTATION INTRODUCTION

Recreational angling is a popular global activity with economic, social, and biological effects (Pitcher and Hollington 2009). In the United States, recreational angling generates an estimated US$99.4 billion in expenditures and provided 595 thousand jobs, with freshwater anglers numbering 35.1 million (USDOI and USFWS 2022; National Marine Fisheries Service 2023). The revenue sources associated with angling can be an important contribution to local economies (Martin 1987), leading to management decisions that benefit the resource and the public (Fedler and Ditton 1984).

Predatory fishes are often favored by anglers and commonly introduced into novel systems due to aggressive feeding behaviors and large body size (Dextrase and Coscarelli 1999). Brown trout *Salmo trutta* are one such species that are extremely popular as a sportfish but are one of the most pervasive and successful non-native species in North America (Budy and Gaeta 2018) — species occurs on the *100 of The World's Worst Invasive Alien Species* list (Lowe et al. 2000). Prey species are often vulnerable and naïve to the introduced predator (Moyle and Light 1996), which can lead to decreasing adundance, or even extirpation, of native species. Systems that already have a native apex piscivorous species can suffer exacerbated negative influences associated with direct competition and predation from the novel species (Lorenzoni et al. 2002; Bacheler et al. 2004; Saylor et al. 2012). Invasive species may displace native apex predators by directly competing for the same limited food source if both species occupy the same ecological niche.

Multiple predators may also interact in an intraguild predation relationship where predation and competition intertwine, leading to scenarios where predatory actions serve to mitigate potential competition among the species (Polis 1988). Interactions among intraguild predators becomes complicated with symmetrical and reciprocal intraguild predation where species can be mutual predators based on length or age (Werner and Gilliam 1984; Taniguchi et al. 2002; van der Hammen et al. 2010; Henkanaththegedara and Stockwell 2014).

The Torrey Creek drainage in the Wind River basin of Wyoming offers an opportunity to investigate the interactions of three apex predators (i.e., burbot *Lota lota*, brown trout, and lake trout *Salvelinus namaycush*) in a single system. Burbot, the sole freshwater representative of the cod family (Gadidae), are the native apex piscivore and are classified as a species of greatest conservation need within Wyoming, with a declining population within the Wind River drainage (Hubert et al. 2008; Wyoming Game & Fish Department 2017). The Torrey Creek drainage, a smaller drainage within the Wind River drainage, represents the most southwest extent of the native range of burbot within the United States (Fuller 2024). Declines of burbot within the Wind River basin were hypothesized to be associated with fluctuations and alterations of natural flows and water levels, entrapment in irrigation canals, emigration, and angler harvest (Hubert et al. 2008). The hypotheses for burbot decline within the Wind River basin have been investigated within the Torrey Creek drainage specifically, and evidence does not support the hypotheses because the drainage is free flowing (Lewandoski et al. 2017), entrapment in irrigation canals was limited (Hooley-Underwood et al. 2018), emigration rates into the Wind River were low (Underwood et al. 2016), and angler exploitation was low (Lewandoski et al. 2017). The drainage is isolated from the Wind River by a series of steep cascades (Underwood et al. 2016).

Thus, more contemporary hypotheses for the decline in burbot in the Torrey Creek drainage have focused on negative interactions with two non-native predators, brown trout and lake trout, and recruitment decline associated with warming winter water temperatures. Average water temperatures, including winter months, are projected to increase for the major rivers and streams within the Greater Yellowstone Ecosystem, which includes the Torrey Creek drainage (Hostetler et al. 2021).

Declines in burbot catch rates from annual monitoring of the Torrey Creek drainage by Wyoming Game & Fish Department have led biologists to be concerned with declines in burbot since the 1990s. Burbot catch rates in trammel nets declined from 0.22/hour in 1995 – 1996 to 0.02/hour in 2018 (Krueger 1996). The objective of **Chapter 2** was to obtain baseline information on population structure of burbot, brown trout, and lake trout within the Torrey Creek drainage to create a more complete understanding and representation of the system. These data were necessary to inform models to address research questions in subsequent chapters.

Examining the diet composition, diet overlap, and trophic position of native and non-native fishes is critical for determining the effects of introduced species. The objective of **Chapter 3** was to address if the piscivorous species were interacting in an intraguild relationship (potential competitors that prey on each other; Polis et al. 1989). By evaluating the dietary compositions of burbot, brown trout, and lake trout seasonally from 2020 through 2022, dietary overlap was quantified among the species, both seasonally and cumulatively. Stable isotopes were additionally used to assess a more long-term response to quantify if burbot, brown trout, and lake trout occurred within the same trophic position and to quantify the degree in which overlap may exist among the species.

Despite the extensive research conducted in the Torrey Creek drainage to identify declines in burbot abundance, the direct effect of non-native predators and the negative influence of warming winter water temperatures as a source of recruitment failure had not been evaluated. The objective of **Chapter 4** was to evaluate the dynamics of burbot population growth within the Torrey Creek drainage, focusing on the influence of non-native trout predation on juvenile burbot and warming winter temperatures on embryo survival. Using Bioenergetics 4.0 (Deslauriers et al. 2017), I quantified the number of burbot being consumed annually by non-native trout. The burbot annual population growth rate and probability of the population persisting for 100-years was then evaluated with reduced juvenile survival (i.e., increased non-native trout predation) combined with burbot recruitment failure influenced by warming winter water temperatures. These models will improve our understanding of how interactions between non-native species and climate affect the persistence of cold-adapted species.

Finally, **Chapter 5** describes conclusions to the research conducted in **Chapters 2**, **3**, and **4** and addressing considerations for future management implications and research that could illicit a more thorough understanding of burbot population dynamics within the Torrey Creek drainage.

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CHAPTER TWO

POPULATON CHARACTERISTICS OF PISCIVOROUS FISHES IN THE TORREY CREEK DRAINAGE

Introduction

In ecology, conservation science is one of the fastest growing disciplines (Anderson et al. 2021), largely due to the increasing demands that a growing human population places on our ecosystems (Kareiva and Marvier 2012). Consequently, ecologists have become more reliant on modeling to describe and evaluate ecologic systems and disturbances (Pielou 1981; Jackson et al. 2010; DeAngelis and Grimm 2014). However, models in general are highly sensitive to the accuracy and precision of estimated parameters they use (Ludwig 1999; Fieberg and Ellner 2000; Münzbergova and Ehrlén 2005).

Descriptive population demographic data is primarily collected to derive parameter estimates to parameterize predictive models and to provide a mechanistic understanding of demographic processes (Caswell 2001; Eacker et al. 2017). Repeat sampling of these demographic parameters further enhances the statistical inference, allowing for more robust conclusions and predictions (Dennis et al. 2010). The repeated data collection is crucial to capture temporal variations and improve reliability of models in general. Descriptive population demographic data enable scientists to identify trends and patterns in population dynamics, which are fundamental for assessing the viability of species (Münzbergova and Ehrlén 2005).

A practical application of this methodology is observed in the Torrey Creek drainage in Wyoming. This system is routinely sampled, leading to the suspicion of a declining native species. The Torrey Creek drainage has three apex piscivorous sport fishes in a single system. Burbot *Lota lota* are the native apex piscivorous fish and are classified as a species of greatest conservation need within Wyoming that occupies the southwest extent of their native range (Hubert et al. 2008; Glaid et al. 2021; Fuller 2024). Lake trout *Salvelinus namaycush* were first stocked in 1937 and brown trout *Salmo trutta* are suspected of entering the drainage in the late 1940s or early 1950s, likely immigrating from the Wind River because no stocking records exist (Connell 1977, 1978).

Burbot conservation and research within the Torrey Creek drainage is needed as burbot are the native apex predator, have cultural significance for the Eastern Shoshone and Northern Arapahoe (Hubert et al. 2008), and have complicated life-history strategies. Adfluvial and lacustrine life-history strategies exist within the Torrey Creek drainage (Bjorn 1940; Hagan 1952; Williams 1959; Miller 1970; Glaid et al. 2021). Additionally, genetic evidence supports a homogenous burbot breeding population that differs from other systems within the Wind River range, likely due to movement barriers isolating Torrey Creek drainage from the Wind River (Underwood et al. 2016; Glaid et al. 2021). Putting this population of burbot at higher risk of sensitivity to disturbances due to the limitation for recolonization from the Wind River.

Monitoring and establishing baseline information is crucial for the management and understanding of changes within populations. In this chapter we establish baseline demographics to inform population models in subsequent chapters and providing metrics that are useful for Wyoming Game & Fish Department. The objective of this chapter is to describe the population demographics of burbot, brown trout, and lake trout within the Torrey Creek drainage. More specifically, we aim to (1) describe the size structure and condition of burbot, brown trout, and lake trout, (2) estimate abundance for brown trout and lake trout and describe abundance estimation for burbot from a previous study, and (3) develop growth models for burbot, brown trout, and lake trout within the Torrey Creek drainage. Size structure and condition will be used in **Chapter 4** to inform population projection models, specifically the weight-length relationship for burbot. Additionally, the abundance estimates for brown trout and lake trout will be used in **Chapter 4** to determine population level predation of burbot by non-native trout species. Bioenergetic growth models for brown trout in **Chapter 4** will be calibrated to annual growth as predicted from growth models in this chapter.

Materials and Methods

The Torrey Creek drainage is located south of the Wind River and near Dubois, Wyoming (Figure 2.1) encompassing Torrey Lake, Ring Lake, Trail Lake, and Torrey Creek. Of these, Torrey Lake is the largest and most downstream lake (93 ha), Ring Lake is directly upstream (40 ha), and a section of Torrey Creek (0.9 km) connects Ring Lake and Trail Lake (51 ha). The Torrey Creek drainage was created from glacial moraines and is fed by snow melt and glacier melt from the Continental Glacier located in the Wind River Range (Vandeberg and VanLooy 2016). The headwaters of Torrey Creek flow through the Shoshone National Forest before entering Wyoming Game & Fish Department Whiskey Basin Wildlife Management Area 4.5 km upstream of Trail Lake. Torrey and Ring lakes are largely encircled by private ranches but offer access through public boat ramps. Movement of fish from the Wind River is unlikely as a series of steep cascades exist downstream of Torrey Lake (Hubert et al. 2008).

Native fishes include burbot, mountain whitefish *Prosopium williamsoni*, Yellowstone cutthroat trout *Oncorhynchus virginalis bouvieri*, mountain sucker *Catostomus platyrhynchus*, longnose sucker *Catostomus catostomus*, white sucker *Catostomus commersonii*, lake chub *Couesius plumbeus*, and longnose dace *Rhinichthys cataractae*. Nonnative sport fishes include brown trout, lake trout, and rainbow trout *Oncorhynchus mykiss*. Rainbow trout are stocked annually in the system as a recreational opportunity by Wyoming Game & Fish Department. Much of the angling for trout is catch and release whereas burbot are typically harvested. Wyoming Game & Fish regulates the fishery with a creel limit that allows for six trout among rainbow trout, brown trout, and Yellowstone cutthroat trout; six lake trout of which only one can exceed 610 mm; and three burbot.

Fish Sampling

Burbot, brown trout, and lake trout were sampled from Torrey, Ring, and Trail lakes using short duration gill nets and electrofishing. Gill nets were set for a maximum of three hours but typically for a period less than two hours. Short duration was used to reduce mortality and minimize regurgitation of dietary contents (Lester et al. 2009; Garvey and Chipps 2012). Two types of gill nets, an experimental gill net and a standard gill net, were used to collect fish. The experiment gillnet was 48.8 m by 1.8 m with eight 6.1-m panels. Mesh size for the panels were 1.91-cm, 2.54-cm, 3.18-cm, 3.8-cm, 4.45-cm, 5.08-cm, 6.72-cm, and 6.35-cm bar mesh. The standard gillnet was 61 m by 2.44 m with 4.45-cm bar mesh throughout. Electrofishing was conducted at night using an ETS MBS box shocking at 500 volts to achieve 2-3 amps. All fish sampled were immediately transferred to a live well located on the boat. The live well was filled with local lake water and changed between samples. Backpack, throwable anode, and towable cataraft shocking were conducted in Torrey Creek above Trail Lake and in the section that connects Ring and Trail lakes. Fish captured in Torrey Creek were placed in live cars located in the creek. Burbot, brown trout, and lake trout were collected by gillnetting annually in spring (late March – May) and autumn (September – November). Night electrofishing occurred annually in spring, summer (June-August), and autumn in 2020, 2021, and 2022; creek shocking occurred in autumn of 2020 and spring, summer, and autumn of 2021. Total length (mm) and weight (g) were measured for all target species.

Size Structure and Body Condition

To evaluate the size structure of burbot, brown trout, and lake trout in the Torrey Creek drainage, we used proportional size distribution (PSD) and length-frequency histograms (Anderson 1976; Neumann et al. 2012).

Weight-length relationships were developed for burbot, brown trout, and lake trout. To expand the sample size, data from Wyoming Game & Fish Department was included into the collection of recorded lengths and weights. Data from Wyoming Game & Fish Department spanned from 1957 to 2019. Due to high variance in weights on small fish, all fish below the minimal total length used for standard weight calculations (i.e., burbot < 120 mm, brown trout < 140 mm, and lake trout < 280) were excluded from the analysis (Neuman et al. 2012). Outliers were excluded and identified as having an absolute value greater than three from a standard residual cutoff on the $\log_e$ weight-$\log_e$ length linear relationship, which was repeated twice (Osborne and Overbay 2004; Eckelbecker et al. 2023). Weight-length relationships were created from the following equation:

$$\log_{10}(W) = a' + b \text{ x} \log_{10}(L),$$

where W is weight, L is length, a' is the y-intercept, and b is the slope.

Body condition of burbot, brown trout, and lake trout was evaluated using relative weight ($W_r = (W/W_s) * 100$), where W represents the observed weight of an individual fish and W_s is the length-specific standard weighted predicted from the species-specific weight-length regression (Wege and Anderson 1978). Standard weight equation parameters were obtained from the literature (Piccolo and Whaley 1993; Fisher et al. 1996; Hyatt and Hubert 2001).

Abundance and Biomass

Burbot abundance was previously estimated in Torrey Lake using program Mark that grouped data by year and constrained abundance to be equal among years (Lewandoski et al. 2017). Burbot greater than 389 mm were marked using a Carlin tag and were sampled using a bottom-set trammel net that fished for 24 hours (Lewandoski et al. 2017). No abundance estimates were obtained for burbot in Ring and Trail lakes because of low recapture rates (Lewandoski et al. 2017).

Brown trout greater than 280 mm in Torrey, Ring, and Trail lakes were sampled using night electrofishing and tagged with individually numbered FD-94 Floy T-bar anchor tags during autumn of 2022. Torrey, Ring, and Trail lakes were sampled by shocking the entire perimeter of the shoreline for four nights. On the first night, all brown trout were marked and on nights two and three, unmarked brown trout were marked, and the number of recaptures were recorded. For the fourth night, no new fish were marked, and the total number of new fish and previously marked fish were recorded. Abundance of brown trout was estimated individually for Torrey, Ring, and Trail lakes using the Schnabel method (Schnabel 1938):

$$\widehat{N} = \frac{\sum_t (C_t M_t)}{\sum_t R_t},$$

where $\hat{N}$ is the total estimate of abundance, M_t is the number of previously marked fish at time t, C_t is the number of fish caught at time t, and R_t is the number of marked fish at time t. Variance of the estimate was calculated using the reciprocal of $\hat{N}$ (Krebs 2014):

$$Variance\ \left(\frac{1}{\hat{N}}\right) = \frac{\sum R_t}{(\sum C_t M_t)^2}.$$

Biomass of brown trout was estimated in the lakes as (Hayes et al. 2007):

$$\hat{B} = \sum \hat{N}_i\ x\ \overline{w}_i,$$

where $\hat{B}$is the estimated biomass (g), $\hat{N}_i$is the estimated abundance for age *i* and $\overline{w_\iota}$ is the mean weight of fish for age *i* (g). Variance (*V*) of the biomass estimate was calculated as (Hayes et al. 2007):

$$V(\hat{B}) = \sum \left[\overline{w}_i{}^2 V(\hat{N}_i) + (\hat{N}_i{}^2 V(\overline{w}_i)\right].$$

We attempted to estimate brown trout abundance in Torrey Creek using a three-pass depletion. To ensure a closed population during the estimate, a block net was deployed above and below the reach while the depletion occurred. After each pass, all captured trout were placed downstream of the block net to remove sampled fish from the reach. Depletion estimates were conducted at two sites, a 200-m middle reach located between Ring and Trail lakes and a 400-m reach upstream of Trail Lake. Unfortunately, abundance estimates were not obtained because the upstream reach had no captures and the middle reach had relatively few brown trout, which mostly consisted of previously marked individuals (i.e., from the lake marking runs).

The lake trout population in the Torrey Creek drainage was predicted to be too low for a reliable estimate to be obtained from mark-recapture methods. Therefore, a hydroacoustic survey was conducted by Wyoming Game & Fish Department to estimate the lake trout abundance in Torrey and Trail lakes during summer of 2023. The survey used a Hydroacoustic Technology

Incorporated (HTI) Model 241 portable, split-beam echo sounder, a 15° 200 kHz transducer, and a 6° 200 kHz transducer. Using a 6-m boat, transects were conducted at a speed of 5-6 km/hour to “ping” fish within the water column that are processed using Digital Echo Processor software. Mid-water curtain nets and SPIN, Summer Profundal Index Netting, nets were used to partition hydroacoustic targets by species (Sandstrom and Lester 2009). Mid-water curtain nets were 48.77 m by 6.1 m with eight 6.1-m panels varying in size from 19 mm to 63.5 mm bar mesh in consecutive order (i.e., 19 mm, 25.4, 31.8 mm, 38.1, 44.5 mm, 50.8 mm, 57.2 mm, 63.5 mm; Neebling 2014).

Age and Growth

Incidental mortalities of burbot, brown trout, and lake trout during sampling had sagittal otoliths removed for aging. Additional otoliths were collected from brown trout after the final mark-recapture sampling to obtain three brown trout per total length centimeter group. Brown trout were euthanized with an overdose of Aqui-S20E for otolith collection. Otoliths were embedded using epoxy, West System 105 Epoxy Resin and West System 207 Special Clear Hardener, and sectioned transversely along the dorsoventral plane using a low speed IsoMet saw. Cross-sections were mounted to microscope slides using crystalbond mounting adhesive. Cross-sections were aged by counting the number of annuli present by two independent readings using a dissection microscope, Leica M 165C. Discrepancies were resolved by a consensus reading. To increase sample size, an age-length key was created using a probability matrix, allowing for all sampled brown trout and lake trout to be aged (Isermann and Knight 2005). Brown trout and lake trout length-at-age were derived from von Bertalanffy growth function (von Bertalanffy 1938):

$$l_t = L_\infty(1 - e^{-K(t-t_0)}),$$

where l_t is the length at time t, L_∞ is the asymptotic length, K is the growth coefficient, and t_0 is a fitting parameter that theoretically represents the length at time 0. Using maximum likelihood, estimates of L_∞, K, and t_0 were calculated using R (R Core Team 2022). A von Bertalanffy growth curve was unable to be developed for burbot due to an inadequate sample size of otoliths.

Results

Size Structure and Weight-Length Relationship

A total of 153 burbot were sampled between spring 2020 and autumn 2022, with total lengths varying from 93 to 800 mm (Figure 2.2). Burbot between 200 and 250 mm were the most frequently sampled, representing 24% of the sampled population. Larger individuals (> 400 mm) were less commonly encountered, and no burbot exceeding 800 mm were observed (PSD-T). Within the Torrey Creek drainage, the PSD values indicated a size structure skewed towards larger individuals, with more observations of smaller individuals (Figure 2.2). From the weight-length relationship, burbot had slope of 3.12 (N = 535; Figure 2.3).

Brown trout, the most abundant piscivorous fish sampled (N = 666), varied from 60 to 844 mm (Figure 2.2). Brown trout above 175 mm exhibited a more uniform length-frequency distribution compared to burbot. A peak in sampling occurred around 400 mm and left skewed (Figure 2.2). Nearly all brown trout sampled were greater than quality size (> 300 mm) with more than half of the sampled brown trout being even greater than preferred size (> 400 mm). From the weight-length relationship, brown trout had a slope of 3.05 (N = 965; Figure 2.3),

Lake trout were the least frequently encountered piscivorous fish (N = 58) and exhibited a size distribution skewed towards smaller lengths, varying from 311 to 1021 mm (Figure 2.2). Similar to brown trout, the majority of lake trout sampled were greater than quality size (> 500 mm) with more than half of the sampled lake trout being even greater than preferred size (> 650 mm). Lake trout had the highest slope from the weight-length relationship compared to burbot and brown trout (N = 161; Figure 2.3).

Body Condition

Relative weight, W_r, for burbot, brown trout, and lake trout for all incremental PSD categories was less than 100, indicating weights less than that of a fish representing the 75th percentile of the geographic range (Table 2.1). Burbot had the lowest W_r in the stock (200 mm) to quality (380 mm) length category. As burbot length increased, average W_r also increased, with M-T having the highest W_r value (Table 2.1). In contrast, brown trout exhibited a decreasing trend in W_r as length increased (Table 2.1). Brown trout had the highest W_r in the S-Q length category, 86, decreasing to 80 for the T length category. Lake trout relative weight was relatively consistent among length categories (76 – 84), except for lake trout in the P-M length category where W_r peaked at 90.

Age and Growth

Otoliths were removed and aged from 142 brown trout varying from 72 to 844 mm representing ages from 1 to 14 years of age. The two oldest brown trout (14 years) were 506 mm and 664 mm in total length. Brown trout within the drainage had an L_{inf} of 616 mm (550 – 690 ± 95% CI; Figure 2.4). Twenty-four otoliths were removed and aged from lake trout. Lake trout ages varied from 3 to 24 years (Figure 2.4). The oldest observed lake trout, 24 years, was 955 mm, and the youngest lake trout, 3 years, was 311 mm. Lake trout had an L_{∞} of 885 mm (790 – 1187 ± 95% CI; Figure 2.4). Brown trout and lake trout had the same point estimate for K (0.17) but lake trout had more uncertainty around the estimate (0.06 – 0.35 ± 95% CI) compared to brown trout (0.12 – 0.24 ± 95% CI).

Abundance and Biomass

Burbot abundance was only estimated for Torrey Lake in 2013 and was estimated to be 966 (616 – 1558 ± 95% CI; Table 2.2; Lewandoski 2015). Total abundance in Torrey, Ring, and Trail lakes for brown trout > 280 mm was 893 (535 – 1652 ± 95% CI). Brown trout abundance was similar among all lakes but had the highest point estimate and upper confidence interval in Ring (337; 172 – 719 ± 95% CI) compared to Torrey (330; 220 – 515 ± 95% CI) and Trail (226; 143 – 418 ± 95% CI). Younger individuals contributed most to the abundance brown trout abundance estimate within the drainage, with age 1 representing 15% of the total abundance and age 2 representing 13% (Figure 2.5)

Density of brown trout within the lakes of the drainage was 4.9 (2.9 – 9.0 ± 95% CI) fish/ha. Biomass for brown trout was estimated at 563.8 (213.3 – 1651.7 ± 95% CI) kg or 3.0 (1.1 – 8.9 ± 95% CI) kg/ha within the Torrey Creek drainage.

Hydroacoustic surveys were ineffective in Torrey and Trail lakes for estimating lake trout abundance. Only a single lake trout was captured during the netting events that were used to partition hydroacoustic targets, making estimation of lake trout abundance unreliable. Instead, an abundance estimate of pelagic swimming fishes was conducted, largely dominated by longnose sucker. In Torrey Lake an abundance of 1500 (942 – 2091 ± 95% CI; Table 2.2) pelagic swimming fishes was estimated accounting for 1103.6 (668.6 – 1592.8 ± 95% CI) kg of biomass and in Trail Lake the abundance estimate was 3131 (1813 – 4449 ± 95% CI; Table 2.2) pelagic swimming fishes accounting for 2303.6 (1286.8 – 3388.9 ± 95% CI) kg of biomass.

Discussion

Torrey Creek drainage supports a unique ecosystem hosting two non-native trophy trout fisheries, with a noteworthy abundance of trophy-sized brown trout (TL > 600). We were able to describe the population size structure and body condition of burbot, brown trout, and lake trout within the drainage. Weight-length relationships were developed for each species, allowing for updated recruitment indices to be developed for burbot in **Chapter 4** and allowing Wyoming Game & Fish Department to make comparisons of fish condition in regards to the average piscivorous predator found within the Torrey Creek drainage.

We observed relatively low body condition indices for all species within the Torrey Creek drainage. However, the geographic distribution and sample size that creates the W_s equation can bias condition indices (Brown and Murphy 1996), which is observed in burbot populations differing between lentic and lotic habitats (Fisher et al. 1996). Within the Torrey Creek drainage, the discrepancy could be more closely related to the environmental conditions that allow for poor growth in weight compared to length such as seen in Lake Superior cisco *Coregonus artedi*, which generally have a lower condition compared to other North American populations (Fisher and Fielder 1998).

The available age data for lake trout in our study were limited, contributing to uncertainties in estimating growth parameters. Although our observed *K* values align with those reported in other studies (Ruzycki et al. 2003; He and Bence 2007; Hansen et al. 2012), caution is warranted in interpreting growth estimates for lake trout within the Torrey Creek drainage, due to the small sample size and large 95% CI around *K* estimates. In contrast, brown trout had adequate sample size to infer growth. Brown trout, which can thrive in diverse habitats and exhibit anadromous behaviors, have large variability in L_{inf} and growth (K) parameters (Cucherousset et al. 2005; Östergren and Nilsson 2012; Sánchez-Hernández et al. 2016). The growth coefficient for brown trout in the Torrey drainage is within the range reported for other brown trout populations. For example, growth coefficients for brown trout in the River Tomes varied from 0.12 to 0.63, averaging at 0.2 (Lobon-Cervia et al. 1986; Sánchez-Hernández et al. 2016) compared to 0.17 reported here.

Hydroacoustic methods provided insights into pelagic fish populations but were ineffective in estimating lake trout abundance within the drainage. As the sonar is unable to infer targets on the bottom (Neebling 2014), we can only quantify the fish that were in the water column. Notably, longnose sucker are expected to represent the majority of the abundance of pelagic fishes, as they were the most frequently caught species in the midwater curtain nets (Neebling 2022).

Overall, this study provided the necessary information to inform the models used in subsequent chapters and provide summarized capture occasion data to Wyoming Game & Fish Department. Additionally, it provided population structure in a single location for burbot, brown trout, and lake trout for the Torrey Creek drainage, allowing for clear identification of knowledge gaps (i.e., lake trout abundance and burbot age and growth) to be easily identified as further research needs for the drainage.

Tables

Table 2.1: Relative weight (W_r) by incremental proportional size distribution (PSD) categories for burbot, brown trout, and lake trout. Burbot PSD length categories are 200 mm for stock, 380 mm quality, 430 mm preferred, 670 mm memorable, and 820 mm for trophy. Brown trout (lentic) PSD length categories are 200 mm for stock, 300 mm quality, 400 preferred, 500 memorable, and 600 mm for trophy. Lake trout PSD length categories are 300 mm for stock, 500 mm for quality, 650 mm for preferred, 800 for memorable, and 1000 mm for trophy. Fish were captured in the Torrey Creek drainage in Dubois, Wyoming, USA during spring, summer, and autumn of 2020-2022.

	Relative weight				
Species	S-Q	Q-P	P-M	M-T	T
Burbot	71	84	86	91	
Brown trout	86	79	75	72	80
Lake trout	78	76	90	84	84

Table 2.2: Abundance estimates for burbot, brown trout greater than 280 mm, and pelagic fishes in the Torrey Creek drainage, Dubois Wyoming, USA. Burbot abundance was obtained from Lewandoski (2015) with estimation occurring in 2013. Brown trout abundance was estimated in autumn of 2021 and the abundance of pelagic fishes was estimated in summer of 2022. Numbers in parenthesis represent ± 95% confidence interval of abundance estimate.

	Waterbody		
Species	Torrey	Ring	Trail
Burbot	966 (616 –1558)		
Brown trout	330 (220 – 515)	337 (172 – 719)	226 (143 – 418)
Pelagic fishes	1500 (942 – 2091)		3131 (1813 – 4449)

Figures

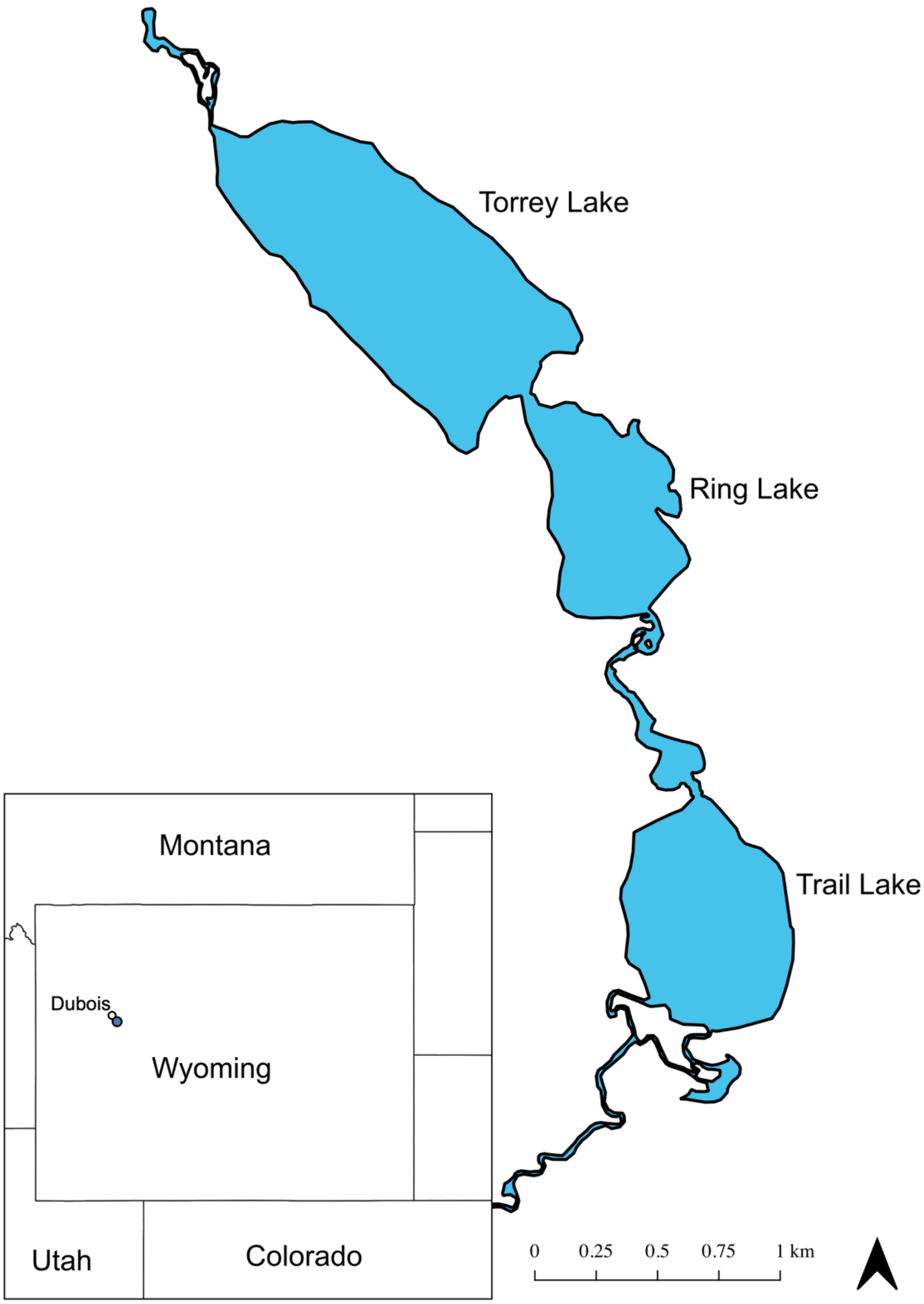

Figure 2.1: Map of a section of the Torrey Creek drainage near Dubois, Wyoming, USA. The area delineated in the map represents the extent of the sampling locations.

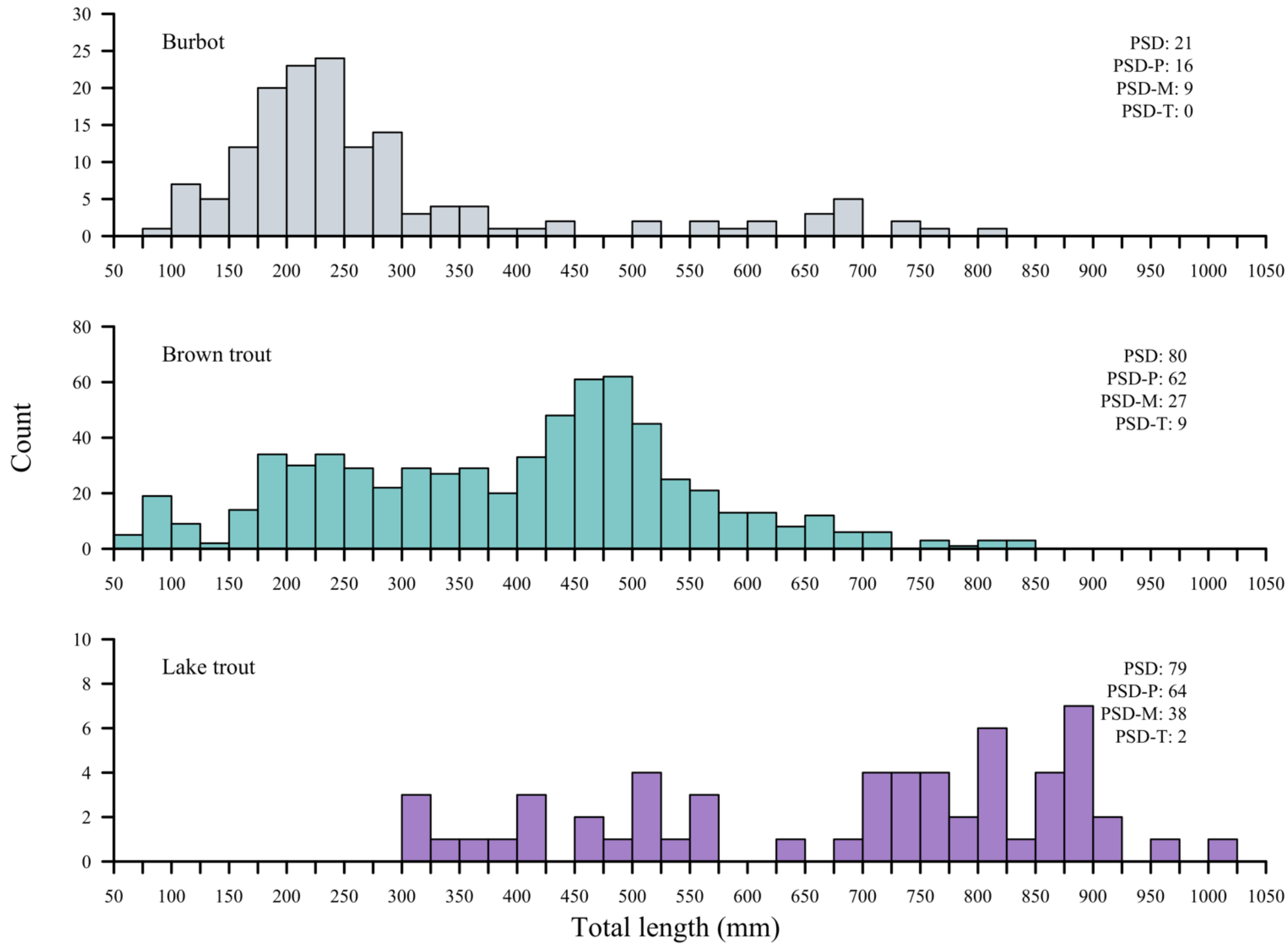

Figure 2.2: Length frequency for burbot (grey), brown trout (green), and lake trout (purple) captured within the Torrey Creek drainage in Dubois, Wyoming, USA. Fish were collected in spring, summer, and autumn using gill nets, trammel nets, boat electrofishing, cord and reel electrofishing, and barge electrofishing during 2020-2022.

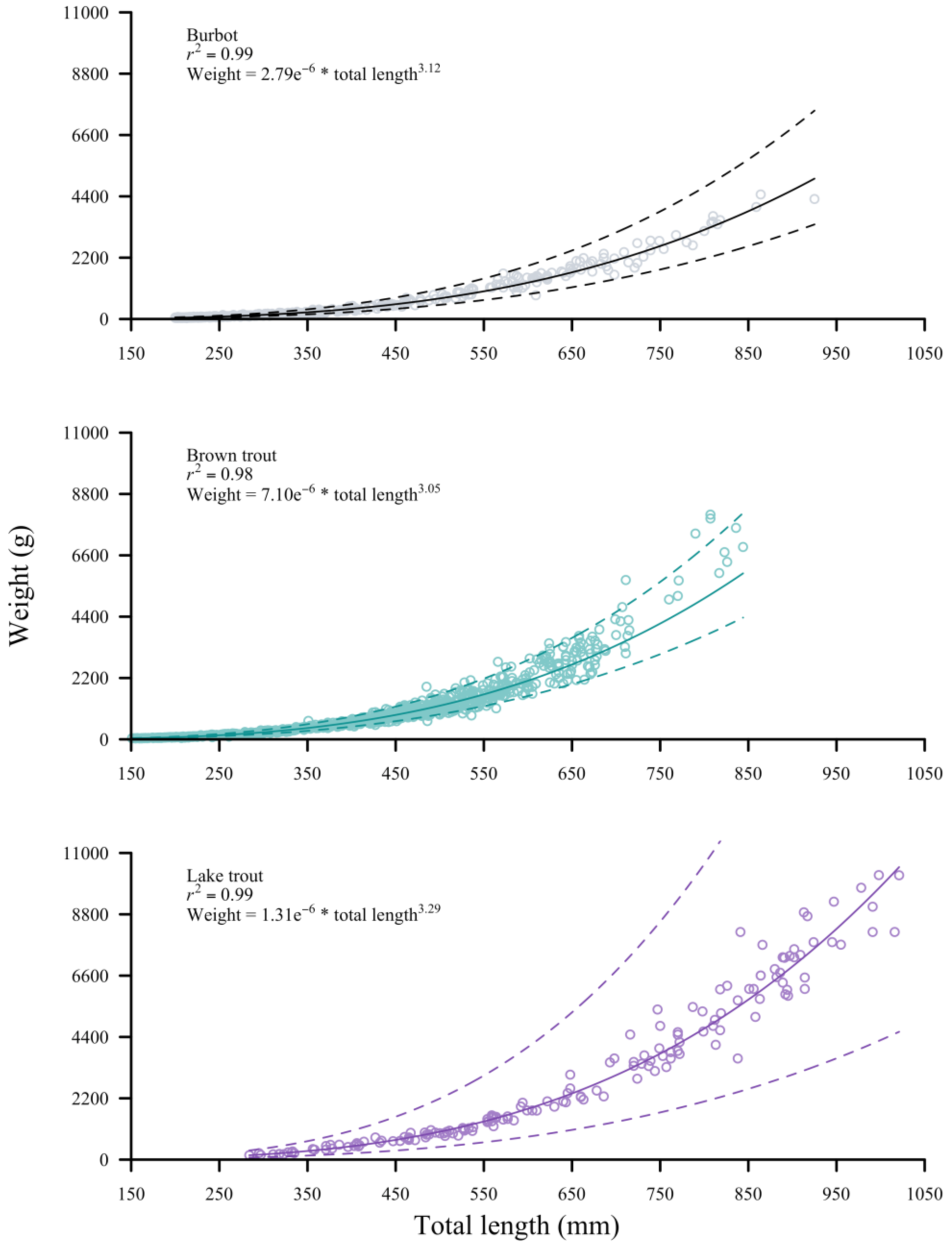

Figure 2.3: Weight-length relationships for burbot (grey), brown trout (green), and lake trout (purple) captured within the Torrey Creek drainage in Dubois Wyoming, USA. The solid line represents the average fish as predicted from weight-length relationship and the dashed lines are the 95% confidence intervals. USA. Fish were collected from 1957 to 2022 during spring, summer, and autumn.

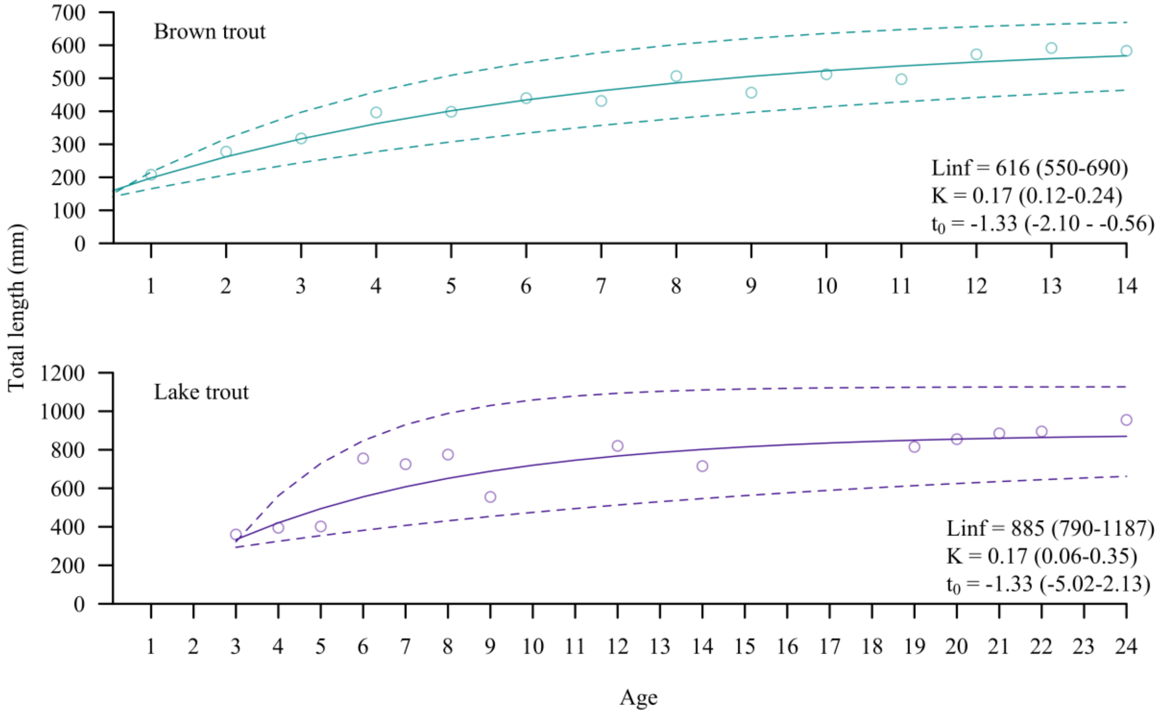

Figure 2.4: Growth curves for brown trout and lake trout sampled from the Torrey Creek drainage, Dubois, Wyoming, USA during 2020 – 2022. Points represent the mean total length at age for each individual year. Most brown trout were sampled in autumn of 2021 and lake trout were sampled spring and autumn of all three years.

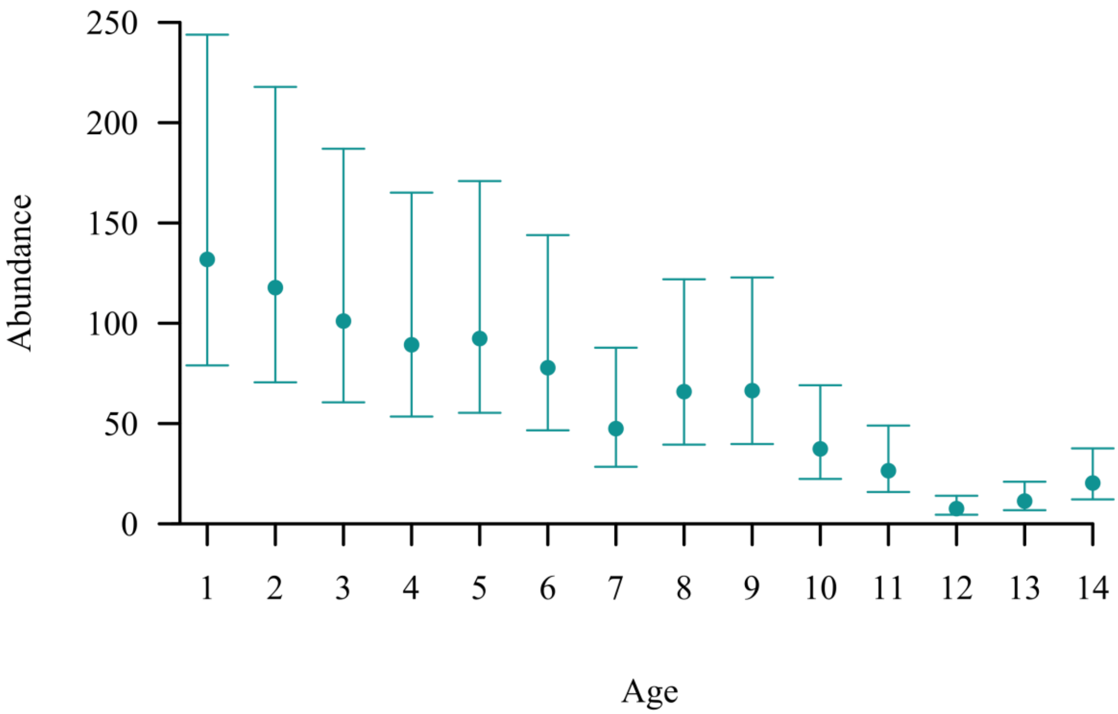

Figure 2.5: Abundance by age for brown trout captured within the Torrey Creek drainage, Dubois, Wyoming, USA during autumn of 2021. Error bars represent 95% confidence intervals of abundance estimates for brown trout within the drainage.

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CHAPTER THREE

NICHE PARTITIONING AMONG THREE APEX PISCIVOROUS FISHES: EVIDENCE OF LIMITED INTRAGUILD PREDATION

Introduction

Invasive species are among the greatest threats to biodiversity, costing governments billions of dollars annually and potentially resulting in collapse of sensitive habitats and extirpation of native species (Pimentel et al. 2005; Dudgeon et al. 2006; Bonebrake et al. 2019; Shabani et al. 2020; Morelli et al. 2021). Invasive species are defined as non-native species that result in negative economic or ecological consequences (NOAA 2024). Economic effects of invasive species include reduced agriculture output, damage to infrastructure, or negative consequences to human well-being (Drake and Bossenbroek 2004; Nentwig et al. 2010; Kumschick et al. 2012). For example, invasive zebra mussels *Dreissena polymorpha* were first observed in North American in 1988 (Hebert et al. 1989) and have caused $267 million in damages over fifteen years by fouling pipes and equipment in power plants and drinking water facilities (Connelly et al. 2007) as they spread across the eastern and central United States. Invasive species may alter ecological relationships at multiple levels of the ecological hierarchy (i.e., individual, population, community, or ecosystem; Strayer 2012) through competitive exclusion, niche displacement, hybridization, predation, and the introduction of novel parasites and pathogens (Rahel 2000; Mooney and Cleland 2001). For example, invasive brown trout *Salmo trutta* were introduced into New Zealand and caused population declines and habitat displacement of native common river galaxias *Galaxias vulgaris* via predation and habitat exclusion (McIntosh et al. 1992; Townsend 1996; Jones and Closs 2017).

Introduction of aquatic invasive species occur globally via multiple introduction pathways such as aquaculture (Nico and Fuller 1999; Forneck et al. 2021), aquaria trade (Liang et al. 2006), vessel transportation and ballast water dumping (Bailey 2015), and recreational angling (Fuller et al. 1999; Carpio et al. 2019). Introductions are often illegal or unintentional (Hickley and Chare 2004; Canonico et al. 2005; Fernández et al. 2019). However, in some cases natural resource agencies have introduced non-native organisms into freshwater ecosystems to provide novel recreational opportunities (Jones et al. 1994; Rahel 2000), enhance existing fisheries (Jones et al. 1994), or as biologic controls (Gozlan et al. 2010).

Predatory fishes are favored by anglers and commonly introduced into novel systems due to aggressive feeding behaviors and large body size that support desirable recreational opportunities (Dextrase and Coscarelli 1999). These traits often allow piscivorous fishes to establish as invasive species and can cause negative ecological effects on native species (Moyle and Light 1996a, 1996b). Prey species are often vulnerable and naïve to the introduced predator (Moyle and Light 1996b). For example, the intentional introduction of smallmouth bass *Micropterus dolomieu* in the Pacific Northwest for sportfishing (Carey et al. 2011) caused a decrease in native fish populations because smallmouth bass consumed up to 40% of out-migrating juvenile salmon in the Columbia River Basin (Sanderson et al. 2009) and up to 3% of annual production of Chinook salmon *Oncorhynchus tshawytscha* in the lower Yakima River (Fritts and Pearsons 2004).

In addition to decreasing the abundance of native species, invasive apex predators can cause top-down trophic cascade effects by altering food-web complexity (Eby et al. 2006; Tronstad et al. 2010; Ellis et al. 2011). A classic example of trophic cascade occurred in Yellowstone Lake with the invasion of lake trout *Salvelinus namaycush*. Lake trout caused a reduction in native Yellowstone cutthroat trout *Oncorhynchus virginalis bouvieri*, which allowed zooplankton to increase and led to a decrease in phytoplankton (Tronstad et al. 2010; Koel et al. 2019). The introduction of lake trout altered the number of terrestrial predators that relied on Yellowstone cutthroat trout as a food resource (Koel et al. 2019). Additionally, lake trout within Yellowstone Lake exhibited diet plasticity, switching from Yellowstone cutthroat trout to amphipods when abundance of Yellowstone cutthroat trout declined (Syslo et al. 2016). The ability of predators to exhibit diet plasticity, alternating prey selection with variation in abundance of prey species (Syslo et al. 2016; Creel et al. 2018; Robinson et al. 2019; Glassic et al. 2024), allows predators to use either specialized or generalized feeding strategies dependent on prey abundance (Ringler 1979; Jensen et al. 2008; Syslo et al. 2016; Glassic et al. 2024). Diet plasticity over multiple trophic levels allows for predators to maintain fitness and population densities even as preferred prey species decline (McMahon and Bennett 1996; Roseman et al. 2014), which contributes to the success of invasive apex predators (Sinclair et al. 2003; Vejřík et al. 2017).

Direct competition and predation can result when piscivorous fishes are introduced into systems where a native apex piscivorous species already exist (Lorenzoni et al. 2002; Bacheler et al. 2004; Saylor et al. 2012). Invasive species may displace native apex predators by directly competing for the same limited food source if both species occupy the same ecological niche.

For example, invasive lake trout were able to reduce native bull trout *Salvelinus confluentus* populations though niche overlap and competition (Donald and Alger 1993). Multiple predators may also interact in an intraguild predation relationship where predation and competition intertwine, leading to scenarios where predatory actions serve to mitigate potential exploitation competition among intraguild predators (Polis 1988). Interactions among intraguild predators becomes complicated with symmetrical and reciprocal intraguild predation where species can be mutual predators based on length or age (Werner and Gilliam 1984; Taniguchi et al. 2002; van der Hammen et al. 2010; Henkanaththegedara and Stockwell 2014).

The Torrey Creek drainage in the Wind River basin of Wyoming offers an opportunity to investigate the interactions of three apex predators in a single system. Burbot *Lota lota* are the native apex piscivorous fish. Lake trout were first stocked in 1937, and it is assumed that brown trout entered the drainage in the late 1940s or early 1950s (Connell 1977, 1978). In Wyoming, burbot are listed as a species of greatest conservation need, with a declining population within the Wind River drainage (Hubert et al. 2008; Wyoming Game & Fish Department 2018). The Torrey Creek drainage represents the southwestern extent of the native range of burbot (Glaid et al. 2021). Hypotheses for the declining burbot population in the Wind River drainage included angler harvest, emigration, entrapment in irrigation canals, and fluctuations in water levels (Hubert et al. 2008). However, within the Torrey Creek drainage, burbot are at a low risk of overexploitation (Lewandoski et al. 2017), have low emigration rates (Hooley-Underwood et al. 2018), limited instances of entrapment in irrigation canals (Hooley-Underwood et al. 2018), and the Torrey Creek drainage has an unaltered flow regime (Hubert et al. 2008). As a result, the declines in burbot abundance are now hypothesized to be a result of alterations in the food web.

The presence of multiple apex predators exhibiting predation causes the food web to become more complex and can result in a decrease of diversity and biomass at higher trophic levels when prey is limited (Wang et al. 2019). Thus, intraguild predation among burbot, brown trout, and lake trout in this system may be contributing to the decline in burbot abundance over the past two decades (Hubert et al. 2008).

In this study, we investigate whether burbot, brown trout, and lake trout are in a reciprocal intraguild predation relationship where adults of all three species consume juveniles of all three guild species while also competing for the same prey species (Figure 3.1). Predation on burbot by brown trout was confirmed by Wyoming Game & Fish Department in the autumn of 2017 in the Torrey Creek drainage (Wyoming Game & Fish Department 2017) and burbot have been observed feeding on juvenile lake trout in Lake Michigan (Van Oosten and Deason 1938; Jacobs et al. 2010). We aim to address how these piscivorous species are interacting in an intraguild predation relationship through the following inquiries: (1) what are the dietary compositions of burbot, brown trout, and lake trout, (2) to what extent does dietary overlap occur among burbot, brown trout, and lake trout, and (3) do burbot, brown trout, and lake trout occupy different trophic levels? Additionally, we are interested in investigating if intraguild predation remains constant among seasons when thermal preferences may restrict species to occupy similar habitat.

Materials and Methods

Study Site

The Torrey Creek drainage is located south of the Wind River and near Dubois, Wyoming (Figure 3.2) encompassing Torrey Lake, Ring Lake, Trail Lake, and Torrey Creek. Of these, Torrey Lake is the largest and most downstream lake (93 ha), Ring Lake is directly upstream (40 ha), and a section of Torrey Creek (0.9 km) connects Ring Lake and Trail Lake (51 ha). The Torrey Creek drainage was created from glacial moraines and is fed by snow melt and glacier melt from the Continental Glacier located in the Wind River Range (Vandeberg and VanLooy 2016). The headwaters of Torrey Creek flow through the Shoshone National Forest before entering Wyoming Game & Fish Department Whiskey Basin Wildlife Management Area 4.5 km upstream of Trail Lake. Torrey and Ring lakes are largely encircled by private ranches but offer access through public boat ramps. Movement of fish upstream from the Wind River into Torrey Lake is unlikely because a series of steep cascades exist downstream of Torrey Lake (Hubert et al. 2008). We treated the Torrey, Ring, and Trail lakes along with Torrey Creek as a single system in all analysis due to movement of tagged fishes being observed.

Native fishes in the Torrey Creek drainage include burbot, mountain whitefish *Prosopium williamsoni*, Yellowstone cutthroat trout, mountain sucker *Catostomus platyrhynchus*, longnose sucker *Catostomus catostomus*, white sucker *Catostomus commersonii*, lake chub *Couesius plumbeus*, and longnose dace *Rhinichthys cataractae*. Nonnative sportfish include brown trout, lake trout, and rainbow trout *Oncorhynchus mykiss*. Rainbow trout are stocked annually in the system as a recreational opportunity by Wyoming Game & Fish Department, with 150,800 total rainbow trout being stocked from 2020 through 2023 (Table 3.1). Much of the angling for trout is catch and release whereas burbot are typically harvested. Wyoming Game & Fish regulate the fishery with a creel limit that allows for six trout among rainbow trout, brown trout, and Yellowstone cutthroat trout; six lake trout of which only one can exceed 610 mm; and three burbot.

Fish Collection

Burbot, brown trout, and lake trout were collected from Torrey, Ring, and Trail lakes using short duration gill nets and electrofishing. Gill nets were set for a maximum of three hours but typically for a period less than two hours. The short duration was to reduce mortality and minimize regurgitation of dietary contents (Lester et al. 2009; Garvey and Chipps 2012). Two types of gill nets, an experimental gill net and a standard gill net, were used to collect fish. The experiment gill net was 48.8 m by 1.8 m with eight 6.1-m panels. Mesh size for the panels were 1.91-cm, 2.54-cm, 3.18-cm, 3.8-cm, 4.45-cm, 5.08-cm, 6.72-cm, and 6.35-cm bar mesh. The standard gill net was 61 m by 2.44 m with 4.45-cm bar mesh throughout. Electrofishing was conducted at night using an ETS MBS shocking at 500 volts to achieve 2-3 amps. All fish captured were immediately transferred to a live well located on the boat. The live well was filled with lake water and changed between samples. Backpack, throwable anode, and towable cataraft shocking were conducted in Torrey Creek above Trail Lake and in the section that connects Ring and Trail lakes. Fish captured in Torrey Creek were placed in live cars located in the creek. Burbot, brown trout, and lake trout were collected by gillnetting annually in spring (late March – May) and autumn (September – November). Night electrofishing occurred annually in spring, summer (June-August), and autumn in 2020, 2021, and 2022; and electrofishing in the creek occurred in autumn of 2020 and spring, summer, and autumn of 2021. Total length (mm) and weight (g) were measured for all burbot, brown trout, and lake trout.

Dietary Overlap and Trophic Positioning

Diets were obtained from live fish using a gastric lavage technique (Light et al. 1983; Hakala and Johnson 2004). Using a 12-volt 4160 liters/hour bilge pump, various flexible tubing with outer dimensions varying from 8 to 24 mm (depending on size of esophageal opening) were attached to a garden hose nozzle to pump water into the esophagus of the fish. Once the tube was inserted, residential drinking water was pumped into the inverted fish to flush out stomach contents while applying forward pressure externally to the stomach. Discharged contents were strained through a 500-µm sieve and then stored in 70% ethanol. We removed stomachs from incidental mortalities of burbot, brown trout, and lake trout for diet collection and stored them in 70% ethanol.

Count, wet mass (g), and dry mass (g) were recorded for all items in the diets. Samples were identified to lowest taxon possible, generally species for fish and family for invertebrates. Fish diet items that were not able to be identified to species were classified as fish parts. Frequency of occurrence O_i, proportion by weight W_i, and mean proportion by weight MW_i were calculated for each dietary item for burbot, brown trout < 300 mm, brown trout ≥ 300 mm, and lake 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 was 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 selected to inform relative prey importance and used to quantify differences in prey selection among burbot, brown trout < 300 mm, brown trout ≥ 300 mm, and lake trout. We separated brown trout into two categories (i.e., < 300 mm and ≥ 300 mm) because 300 mm has been identified as the point where brown trout become more piscivorous (Næsje et al. 1998; Jensen et al. 2012). Unfortunately, due to small sample sizes for burbot and lake trout we were unable to separate these species by ontogenetic shifts in diet.

Diet overlap was analyzed using Schoener's index of niche overlap (D; Schoener 1970):

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

where p_{ij} is the proportion resource i is of the total resources used by species j and p_{ik} is the proportion of resource i used by species k. The decision to use Schoener's index of niche overlap was made to mitigate bias associated with total weight or count overlap analyses while also being limited in the data regarding the availability of prey resources within the Torrey Creek drainage (Wallace 1981). A D value of 0.6 or higher is considered a noteworthy niche overlap (Wallace 1981).

Stable isotope analyses were performed to estimate trophic position. As fish consume higher trophic level prey, nitrogen isotope ratios increase, and carbon isotope ratios are used to identify where energy originated from (Minagawa and Wada 1984). The addition of stable isotope analyses helps identify any long-term dietary overlaps among the species when compared to the short-term diet compositions from the gastric-lavage samples. Tissue plugs were collected below the dorsal fin and above the lateral line on burbot, brown trout < 300 mm, brown trout ≥ 300 mm, and lake trout with a 4-mm biopsy punch (Biopunch 4). 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 Zanden and Rasmussen (1999) and Hershey et al. (2017). Using the SIBER package (Stable Isotope Bayesian Ellipses) in R, standard ellipses were created for each species to represent the isotopic niche of a group (Jackson et al. 2011). The proportional overlap between ellipses was used to quantify an estimate of niche overlap. Proportional overlaps greater than 60% are ecologically noteworthy, similarly to Schoener's index of niche overlap (Guzzo et al. 2013; Pettitt-Wade et al. 2015).

Results

We collected diets from 108 brown trout (total length TL; 89-299 mm), 372 brown trout (TL; 300-836 mm), 56 burbot (TL; 164–800 mm), and 22 lake trout (TL; 356-1021 mm). Twenty orders and 77 families were identified from the diets (Table A.1). Brown trout ≥ 300 mm fed on a wider breadth of taxa across all seasons (number of taxa — spring 68; summer 70; autumn 67) and consumed more unique taxa overall (101) compared to brown trout < 300 mm (number of taxa — spring 28; summer 17; autumn 43; overall 49), burbot (number of taxa — spring 18; summer 15; autumn 26; overall 39), and lake trout (number of taxa — spring 12; autumn 4; overall 14; Figure 3.3). Brown trout ≥ 300 mm had the largest breadth of diet taxa consumed in summer, where a single individual had 20 different taxa identified in their diet (Figure 3.4). Though a single brown trout ≥ 300 mm had 20 diet taxa, the most abundant number of different diet taxa was one in spring (relative frequency = 0.20), six in summer (relative frequency =

0.17), and one in autumn (relative frequency = 0.20; Figure 3.4). Brown trout < 300 mm followed the same trend with the most abundant number of unique diet taxa occurring in summer (six; relative frequency 0.33), and one for spring (relative frequency 0.21) and summer (relative frequency 0.24). In contrast, burbot and lake trout had one diet item as the most abundant occurring in individual fish across all seasons (Figure 3.4).

Frequency of Occurrence and Mean Proportion by Weight

Shifts in frequency of occurrence and mean proportion by weight were observed among all species during spring, summer, and autumn. Brown trout, burbot, and lake trout consumed multiple taxa, only a limited number of taxa contributed more than 0.1 mean proportion by weight (Figure 3.5).

Brown Trout < 300 mm: *Daphnia*, Chironomidae, and Leptoceridae were important prey resources for brown trout < 300 mm among all seasons (Figure 3.5). Leptoceridae were the prominent diet items in spring (64% *O*; 0.21 *MW*) and *Daphnia* were the prominent forage for summer (67% *O*; 0.26 *MW*) and autumn (49% *O*; 0.27 *MW*). Additionally, Gammaridae was seasonally important during spring (36% *O*; 0.09 *MW*) and autumn (49% *O*; 0.19 *MW*) but noticeably absent in the diets during summer.

Brown Trout ≥ 300 mm: Overall, brown trout ≥ 300 mm exhibited a broader dietary breadth compared to burbot and lake trout (Figure 3.5). In spring, seven different diet items were present in more than 15% of diets. Gammaridae was the most frequently occurring (42%) and contributed the most to mean proportion by weight (0.12). In summer, brown trout ≥ 300 mm continued to exhibit a diverse diet, with eight diet categories occurring in more than 10% of the diets. Formicidae had the highest frequency of occurrence (55%) and mean proportion by weight

(0.19) in summer. Chironomidae followed as the next most frequently occurring diet item (42%), albeit contributing minimally to the mean proportion by weight (0.03). For autumn, Gammaridae occurred in 50% of diets constituting 0.15 mean proportion by weight and Phyrganeidae occurred in 43% of diets and 0.21 mean proportion by weight, thus representing the dominant prey taxa by mean proportion by weight.

Burbot: During spring, Gammaridae dominated the dietary composition, accounting for the highest mean proportion by weight (0.22) and frequency of occurrence (35%; Figure 3.5). In summer, unidentifiable insect part were the predominant dietary component, occurring in 50% of diets and the highest mean proportion by weight (0.23). Moreover, lake chub (0.22 *MW*; 22% *O*) and unidentifiable fish parts (0.15 *MW*; 28% *O*) constituted notable components compared to other taxa. For autumn, trichopteran parts occurred most frequently (47%) but only represented 0.12 mean proportion by weight. However, two families of Trichoptera, Phryganeidae and Limnephilidae, occurred in 13% of autumn diets each and contributed 0.11 and 0.02 mean percent by weight, respectively. Furthermore, fish eggs were also an important diet item in the autumn, occurring in 20% of diets and representing 0.16 mean proportion by weight. Despite *Daphnia* being present in 27% of diets and unidentifiable fish parts being present in 20%, they made minimal contributions to the mean proportion by weight, 0.05 and 0.00, respectively.

Lake Trout: During spring, lake trout had a concentrated dietary preference in comparison to brown trout and burbot, with rainbow trout constituting a substantial portion of their diet. Specifically, rainbow trout accounted for 0.59 mean proportion by weight and occurred in 65% of lake trout diets (Figure 3.5). In autumn, lake trout diets were characterized by a near-even split between rainbow trout (0.19) and unidentified insect parts (0.21), representing the largest mean proportions by weight; however, unidentified insect parts occurred more frequently than rainbow trout.

Piscivory

Piscivory accounted for 0.82 mean proportion by weight for lake trout for all seasons combined, compared to 0.36 for burbot, 0.17 for brown trout ≥ 300 mm, and 0.03 for brown trout < 300 mm (Table 3.2). Burbot rarely consumed brown trout, with an overall mean proportion by weight and frequency of occurrence of 0.02, and lake trout consumed brown trout infrequently, with an overall mean proportion by weight and frequency of occurrence of 0.09 (Table 3.2). Brown trout consumed burbot minimally, representing 0.01 overall mean proportion by weight and frequency of occurrence (Table 3.2). Burbot and brown trout did not consume lake trout, and lake trout did not consume burbot within the Torrey Creek drainage. Cannibalism was documented in brown trout and burbot, albeit minimal. Brown trout cannibalism occurred in 0.01 of brown trout diets and burbot cannibalism was only observed during spring and occurred in 0.09 burbot and represented 0.08 of mean proportion by weight.

Dietary Overlap and Trophic Positioning

Diet overlap values were less than 0.6 for all seasonal species combinations (Table 3.3). The highest levels of diet overlap between burbot and both brown trout groups were observed in autumn, with overlap values of 0.44 (Table 3.3). In contrast, during spring, lake trout exhibited the highest degree of overlap with all other species combinations, having values of 0.13 with brown trout < 300 mm, 0.20 with brown trout ≥ 300 mm, and 0.28 with burbot. Notably, intraspecific diet overlap between brown trout < 300 mm and brown trout ≥ 300 mm was the highest overlap of all comparisons (Table 3.3).

All species were at a similar trophic level in relation to $\delta^{15}N$ from stable isotope signatures. The center point for 40% Bayesian ellipses of $\delta^{15}N$ varied from 7.8 for juvenile brown trout to 10.2 for lake trout (Figure 3.6). In terms of carbon assimilation, using $\delta^{13}C$, burbot had the most positive value, -19.1, in comparison to brown trout < 300 mm, -21.7, brown trout ≥ 300 mm, -20.3, and lake trout, -22.6 (Figure 3.6). Isotopic niche overlap was low for the 40% standard Bayesian ellipses among all pairings (Figure 3.6). Burbot and brown trout ≥ 300 mm had the highest overlap of 40% ellipses (39%), burbot and lake trout had a 1% overlap, and brown trout and lake trout had a 13% overlap. Juvenile brown trout shared no overlap with any other species grouping.

Discussion

We predicted burbot, brown trout, and lake trout would have been highly piscivorous in the Torrey Creek system; however, there was a low prevalence of fish in the diets of brown trout and burbot. Lake trout exhibited the highest level of piscivory, which was mostly a function of lake trout consuming stocked rainbow trout. These stocked rainbow trout appeared in the diets of all three piscivorous predators; however, this selective pressure is not observed for native salmonid species within the drainage (i.e., mountain whitefish and Yellowstone cutthroat trout). For example, mountain whitefish were rarely consumed by brown trout (N = 2) and did not occur within the diets of lake trout and burbot. Reciprocal predation of piscivorous fishes (i.e., among brown trout, burbot, and lake trout) was minimal except for lake trout predation on brown trout, thus reciprocal intraguild predation is not currently occurring in the Torrey Creek drainage. However, unidentifiable fish parts were observed in 12% of brown trout ≥ 300 mm and 20% of burbot. Thus, some predation estimates may have been slightly underestimated. Though lake trout predated on brown trout, the minimal dietary overlap between lake trout and brown trout does not suggest competition is occurring between these species; therefore, the lake trout and brown trout ecological interaction could be described as simple intraguild predation (van der Hammen et al. 2010). This was similarly observed in Arctic char *Salvelinus alpinus* and brown trout, where intraguild predation was present but had limited evidence of interspecific competition (Persson et al. 2013).

Surprisingly, we did not document any predation occurring between burbot and lake trout within the Torrey Creek drainage. Burbot and lake trout overlap in their native range and demonstrate reciprocal intraguild predation in other systems (Martin 1970; Jacobs et al. 2010; Gorman and Sitar 2013). Our lack of observed predation on lake trout by burbot could be related to the hypothesized limited recruitment of lake trout within the Torrey Creek drainage; however, burbot and lake trout have been documented cooccurring without negative interactions in other systems (Van Oosten and Deason 1938). The frequent stocking of rainbow trout within the Torrey Creek drainage, occurring up to six times per year, could serve as a buffer to protect burbot from lake trout predation. Lake trout took advantage of the repetitively stocked rainbow trout, potentially decreasing the demand for other prey species as stocked fishes are generally naïve to predators (Warner et al. 1968; Hoxmeier and Wahl 2002; Freedman et al. 2012; Becher et al. 2021).

Cannibalism was documented in brown trout and burbot within the Torrey Creek drainage. Our study revealed that instances of cannibalism among brown trout were relatively infrequent, occurring in 0.01 of all brown trout diets, which is congruent with other research

(L'Abée-Lund et al. 1992; Vik et al. 2001; Montori et al. 2006). Conversely, our estimate of the frequency of burbot cannibalism (3%) is lower than reported in the literature where burbot cannibalism varies from 16% to 93% (Jacobs et al. 2010; Knudsen et al. 2010; Gallagher and Dick 2015). Several hypotheses exist for why burbot may cannibalize including accumulating energy for growth or reproduction (Gallagher and Dick 2015), when competition for shared resources exist (Polis 1988), or a lack of refuge (Smith and Reay 1991). However, not all populations of burbot exhibit cannibalism (Clemens 1951; Hewson 1955; Beeton 1956; Lawler 1963; Bailey 1972; Fratt et al. 1997; Tolonen et al. 1999; Knudsen et al. 2010).

Diet overlap values among burbot, brown trout, and lake trout was minimal by season but increased when compared with all seasons combined, especially for burbot and brown trout ≥ 300 mm. For example, in spring, Limnephilidae accounts for a mean proportion by weight of 0.11 in brown trout ≥ 300mm and 0 in burbot, while in autumn, Limnephilidae is 0 for brown trout ≥ 300 mm and 0.02 in burbot (Table A.1). Among the cross-species pairings, burbot and brown trout had the highest dietary overlap, primarily due to the shared importance of Gammaridae in the diets of both species. Though burbot in the Torrey Creek drainage consumed less fish than in other systems, we report comparable values of Schoener's index of niche overlap between burbot and lake trout (0.32) to that reported for northern Lake Michigan (0.39; Jacobs et al. 2010). Likely, the separation in diets among burbot, brown trout, and lake trout in the Torrey Creek drainage is a response to reduce interspecific competition among these species (Putman and Wratten 1984; Gabler and Amundsen 2010).

Lake trout had the highest trophic position, largely due their degree of piscivory, as indicated by δ^{15}N. However, they shared a similar trophic level with burbot and brown trout ≥

300 mm, with a trophic level difference in lakes being represented as a difference of 3.40‰ ± 1.1 in $\delta^{15}N$ (Wada et al. 1991; Zanden and Rasmussen 1999). Notably, some individual brown trout ≥ 300 mm exhibited the highest $\delta^{15}N$ values, comparable to those of lake trout. This is likely because larger brown trout had a more piscivorous diet similar to those of lake trout. Based on $\delta^{13}C$ values, burbot and lake trout appear to specialize in obtaining their diet from different zones of the lakes (i.e., pelagic and littoral; France 1995). Lake trout had the lowest $\delta^{13}C$ values, indicating a more pelagic origin of carbon, particularly compared to burbot, which had the highest $\delta^{13}C$ values. This is likely due to lake trout predominantly feeding on rainbow trout in comparison to burbot consuming larger proportions of macroinvertebrates and fish such as lake chub. Brown trout, both < 300 mm and ≥ 300 mm, had $\delta^{13}C$ values between those of burbot and lake trout, suggesting they feed less exclusively from a single zone. Despite burbot, brown trout ≥ 300 mm, and lake trout sharing a similar trophic level, there was no major overlap in isotopic niches according to the stable isotope data. These findings align with the low dietary overlap observed among the species, indicating that both short- and long-term overlaps are likely minimal among these piscivorous predators.

Our results indicate that brown trout or lake trout are not the mechanism for the decline in burbot within the Torrey Creek drainage. However, our finding of limited competition and predation represent ecological interactions among burbot, brown trout, and lake trout for the years 2020 – 2023. Historically, burbot were in higher abundances in the Torrey Creek drainage with biologist being concerned of declines since 1990s, with catch rates in fyke nets decreasing from 0.22/hour in 1995-1996 to 0.02/hour in 2018 (Krueger 1996). In 2018, burbot were found in two of six brown trout stomach sampled (WGFD 2018), suggesting a predatory interaction between the species. It is plausible that brown trout and lake trout predation on burbot in the past has driven the burbot population to such a low abundance that burbot are currently rarely encountered by their intraguild members and thus not frequently consumed. This scenario parallels the situation observed with lake trout and Yellowstone cutthroat trout after lake trout introduction to Yellowstone Lake, where the decline in Yellowstone cutthroat trout populations led to lake trout exhibiting prey plasticity (Syslo et al. 2016; Glassic et al. 2024).

The coexistence dynamics among burbot, brown trout, and lake trout within the Torrey Creek drainage are intricately tied to the interplay of competition and predation dynamics among these apex predators. The coexistences hinges on the absence of significant competitive pressures and predation intensity within the ecosystem. The presence of ample resources and productivity in the Torrey Creek system fosters the potential for alternative stable states to emerge among these predators. Particularly, the phenomenon of prey switching, where predators adjust their foraging preferences based on the relative abundance of prey species, plays a pivotal role in sustaining this coexistence framework, especially in regard to an intraguild predation interaction (Holt and Huxel 2007, 2007; Nishijima et al. 2014). Intricate ecological interactions, such as those presented here, underscore the complexity of predator-prey relationships, and highlight the importance of resource availability in shaping community dynamics within aquatic ecosystems.

Tables

Table 3.1: Number and mean length (mm; in parenthesis) of rainbow trout stocked into the Torrey Creek drainage, Wyoming, USA by season and year from 2020 through 2023.

	Year and Season											
	2020			2021			2022			2023		
Waterbody	Spring	Summer	Autumn	Spring	Summer	Autumn	Spring	Summer	Autumn	Spring	Summer	Autumn
Torrey Lake	11,099 (231)		5,502 (229)	14,999 (226)			16,450 (226)			16,512 (216)		10,260 (152)
Ring Lake			1,976 (221)			1,801 (221)			2,111 (241)			1998 (224)
Trail Lake	10,010 (236)		3,298 (229)			11,739 (224)			13,515 (211)		12,320 (90)	13,068 (226)
Torrey Creek		1,004 (226)			980 (244)			1,053 (244)			1,105 (241)	

Table 3.2: Mean proportion by weight and frequency of occurrence (in parenthesis) of fish prey consumed by brown trout < 300 mm, brown trout ≥ 300 mm, burbot, and lake trout sampled from the Torrey Creek drainage, Wyoming, USA for all seasons combined for years 2020 – 2022.

Prey	Predator			
	Brown trout < 300 mm	Brown trout ≥ 300 mm	Burbot	Lake trout
Brown trout	0.00 (0.00)	0.00 (0.01)	0.02 (0.02)	0.09 (0.09)
Burbot	0.00 (0.00)	0.01 (0.01)	0.03 (0.04)	0.00 (0.00)
Fish parts	0.02 (0.05)	0.03 (0.12)	0.09 (0.20)	0.07 (0.09)
Lake chub	0.00 (0.00)	0.01 (0.02)	0.09 (0.09)	0.00 (0.00)
Longnose dace	0.01 (0.01)	0.02 (0.06)	0.03 (0.04)	0.00 (0.00)
Longnose sucker	0.00 (0.01)	0.03 (0.04)	0.05 (0.05)	0.07 (0.09)
Mountain whitefish	0.00 (0.00)	0.00 (0.01)	0.00 (0.00)	0.00 (0.00)
Rainbow trout	0.00 (0.00)	0.05 (0.06)	0.04 (0.04)	0.50 (0.55)
White sucker	0.00 (0.00)	0.02 (0.03)	0.01 (0.04)	0.09 (0.09)

Table 3.3: Schoener's Index of Niche Overlap among burbot, brown trout < 300 mm, brown trout ≥ 300 mm, and lake trout. Niche overlap was calculated from lowest taxonomic identification, species for fishes and family for invertebrates. Fish were collected from the Torrey Creek, Wyoming drainage in 2020-2022. No lake trout were sampled in summer across all years.

Season	Species	Species: Brown trout < 300 mm	Brown trout ≥ 300 mm	Lake trout
Spring				
	Burbot	0.32	0.05	0.28
	Brown trout < 300 mm		0.52	0.13
	Brown trout ≥ 300 mm			0.20
Summer				
	Burbot	0.20	0.37	
	Brown trout < 300 mm		0.31	
	Brown trout ≥ 300 mm			
Autumn				
	Burbot	0.44	0.44	0.10
	Brown trout < 300 mm		0.57	0.05
	Brown trout ≥ 300 mm			0.14
Overall				
	Burbot	0.45	0.55	0.32
	Brown trout < 300 mm		0.60	0.14
	Brown trout ≥ 300 mm			0.26

Figures

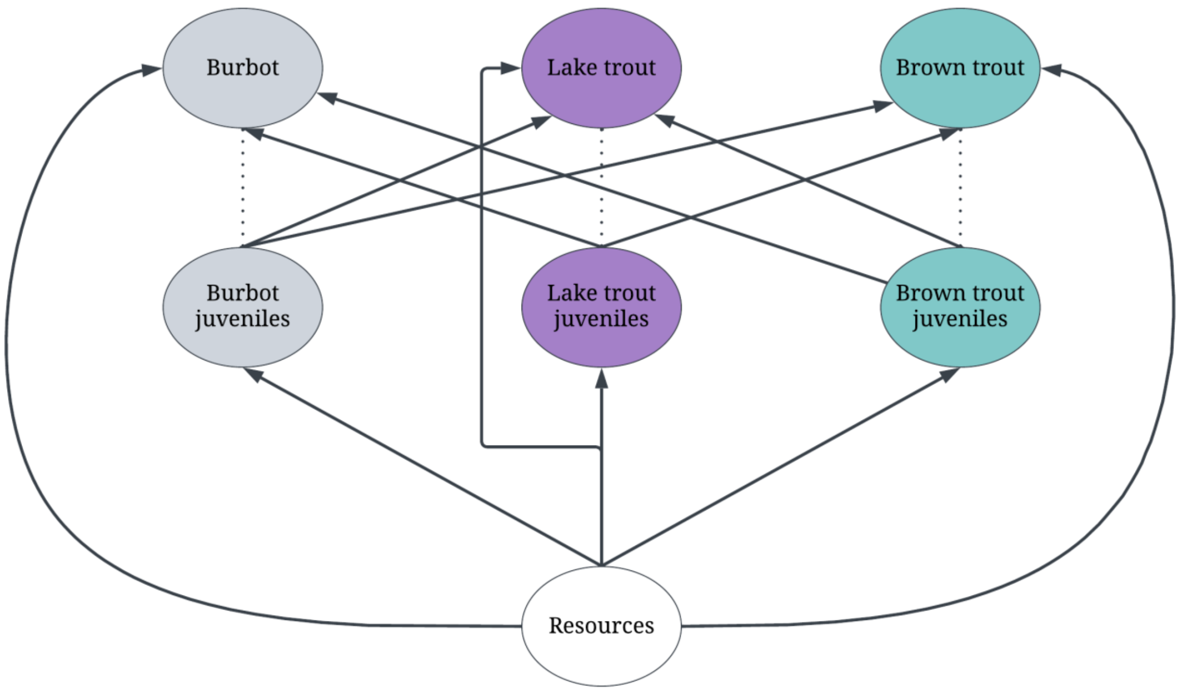

Figure 3.1: Conceptual model of hypothesized reciprocal intraguild predation with life-history structure occurring within the Torrey Creek drainage modified from van der Hammen et al. (2010) to include a third predator. In this model, consumers (i.e., burbot, brown trout, and lake trout) feed on juveniles of allospecific species while also competing for the same resource. Dotted lines represent growth from juveniles to adult and solid lines represent consumption.

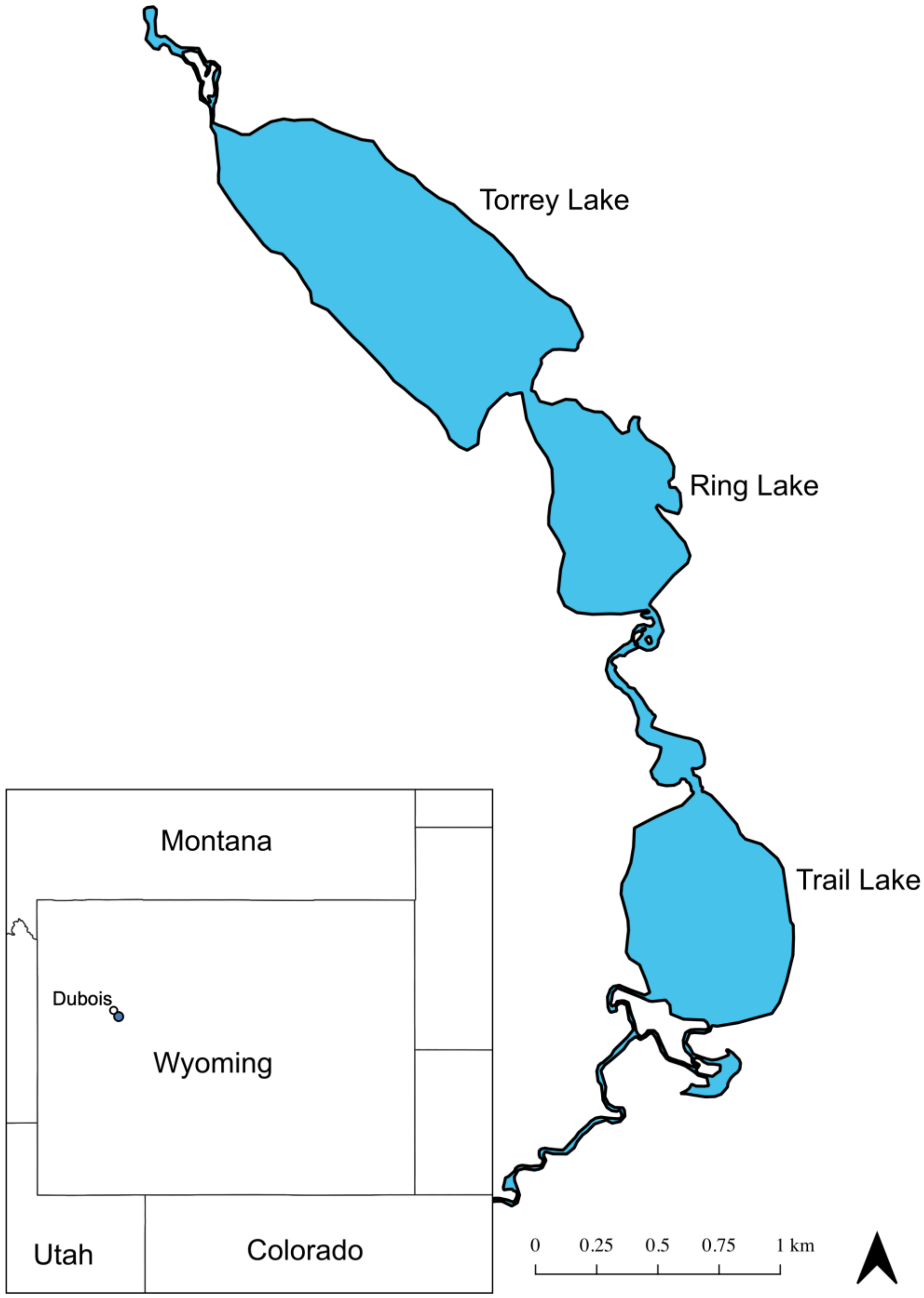

Figure 3.2: Map of a section of the Torrey Creek drainage near Dubois, Wyoming, USA. The area delineated in the map represents the extent of the sampling locations.

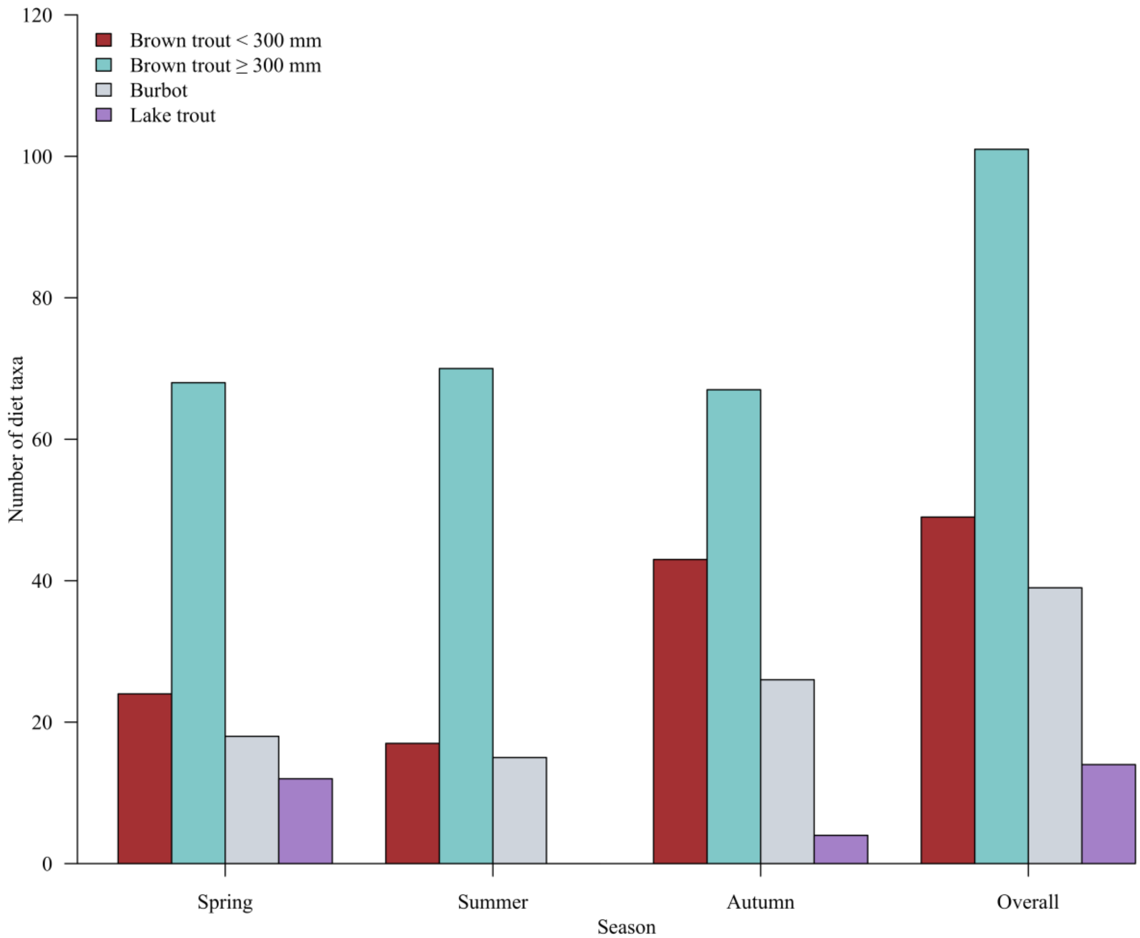

Figure 3.3: The number of unique taxa found in diet contents of juvenile brown trout < 300 mm, brown trout ≥ 300 mm, burbot, and lake trout by season within the Torrey Creek drainage, Wyoming, USA for the years 2020-2022.

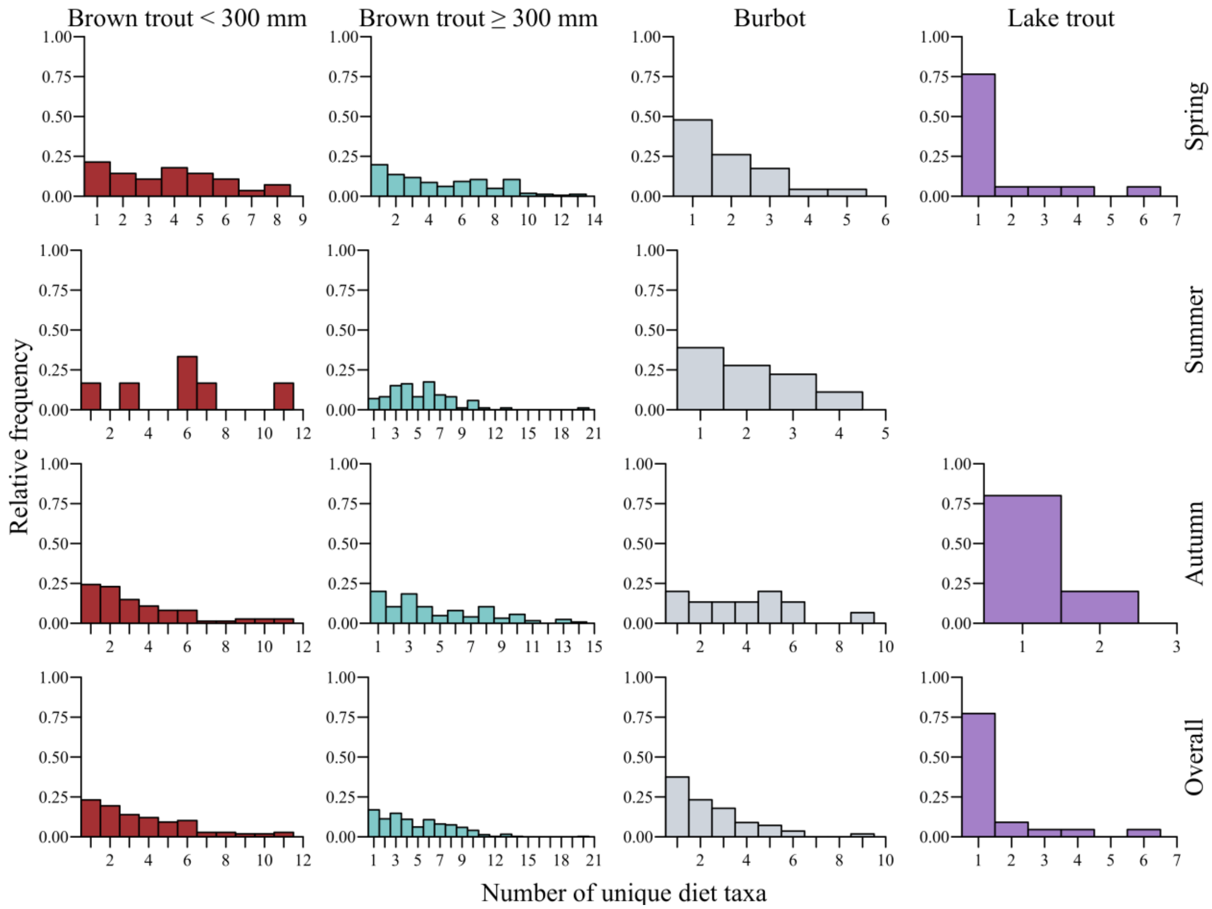

Figure 3.4: Relative frequency of taxa found in diet contents of individual brown trout < 300 mm, brown trout ≥ 300 mm, burbot, and lake trout by season within the Torrey Creek drainage, Wyoming, USA from 2020 through 2022.

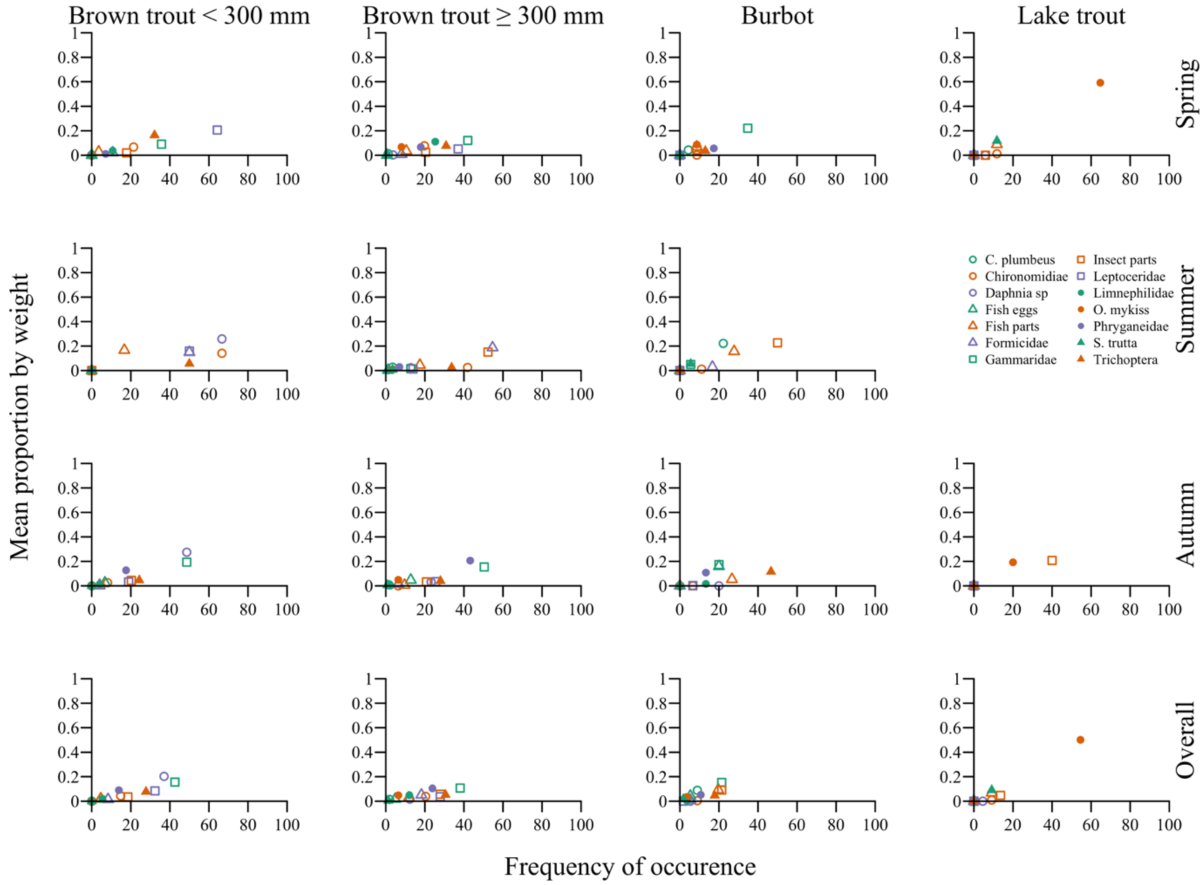

Figure 3.5: Mean proportion by weight–frequency of occurrence plot for brown trout < 300 mm, brown trout ≥ 300 mm, burbot, and lake trout by season and overall. Diet taxa that represented a minimum of 0.1 by mean proportion by weight for any combination of season and species were selected to be displayed resulting in 14 diet taxon categories. Diets were collected from the Torrey Creek drainage, Wyoming, USA for the years 2020 through 2022.

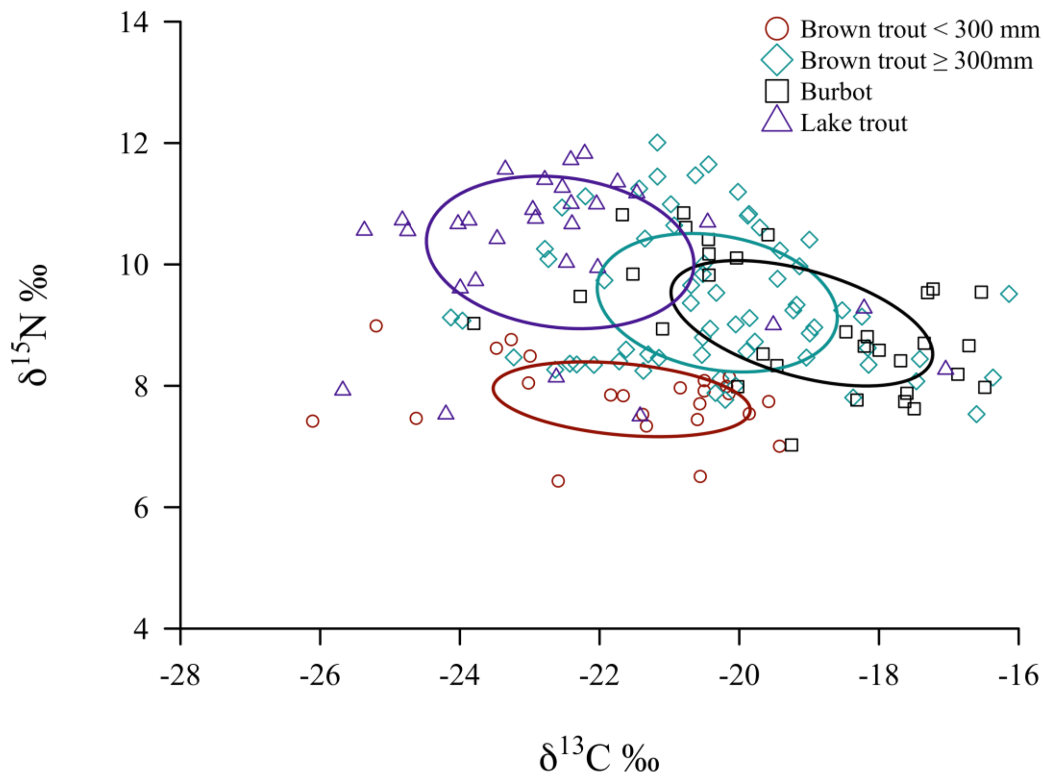

Figure 3.6: Stable isotope biplot of brown trout < 300 mm, brown trout ≥ 300 mm, burbot, and lake trout tissue samples collected from Torrey Creek drainage, Wyoming, USA in 2020 and 2021. Ellipses represent 40% Bayesian standard ellipse areas for stable isotope signatures.

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CHAPTER FOUR

CLIMATIC AND BIOTIC CHALLENGES: UNDERSTANDING BURBOT RESILIENCE IN A CHANGING ENVIRONMENT

Introduction

Freshwater species have an elevated risk of extinction compared to forest, grasslands, and coastal species (Rosen 2000). Within North America, the extinction rate of freshwater fauna mirrors that of species loss in tropical rainforest (Ricciardi and Rasmussen 1999), surpassing the terrestrial fauna extinction rate by a factor of five (Rosen 2000). The threats to freshwater biodiversity are predominantly attributed to overexploitation, water pollution, alteration of natural flow patterns, habitat destruction, and the incursion of exotic species (Dudgeon et al. 2006). These anthropogenic threats have led to an extinction crisis for aquatic biodiversity (Ceballos et al. 2015; Gangloff et al. 2016), which is further exacerbated by a publication bias for relatively few imperiled fishes (Guy et al. 2021).

Burbot *Lota lota*, the sole representative of the cod family (Gadidae) adapted to freshwater habitats, are imperiled or extirpated from portions of their native range, particularly the southern regions, such as the United Kingdom, Belgium, and the Tongue River in Wyoming USA (Eiserman 1964; Dillen et al. 2008; Pinnegar and Engelhard 2008; Stapanian et al. 2010). Pollution and the introduction of non-native species are the primary drivers of diminishing abundances of burbot in lentic systems (Stapanian et al. 2010). Conversely, habitat alteration, particularly the impoundment of rivers and streams, are the primary drivers of burbot decline in lotic systems (Stapanian et al. 2010).

In addition to the factors listed above, warming water temperatures may influence burbot recruitment, especially for the southernmost populations. Burbot, which are adapted to cold-water, exhibit the capacity to endure a broad spectrum of water temperatures (Hofmann and Fischer 2002), however, burbot embryos exhibit a more constrained thermal tolerance (Jäger et al. 1981; Hofmann and Fischer 2002; Lahnsteiner et al. 2012; Ashton et al. 2019). Adult burbot have an upper thermal limit at 32°C (Hofmann and Fischer 2002), prefer a water temperature between 10°C and 14°C (Cooper and Fuller 1945; Hackney 1973; Hofmann and Fischer 2002), and avoid habitats where average water temperature exceeds 18°C (Robins and Deubbler 1955; Hofmann and Fischer 2002). Optimal survival rates for embryogenesis are observed at water temperatures below 4°C, with temperatures below 2°C having the highest survival rates (Jäger et al. 1981; Lahnsteiner et al. 2012; Żarski et al. 2014; Ashton et al. 2019). Conversely, water temperatures of 4°C and greater are lethal for burbot embryos (Vught et al. 2008; Żarski et al. 2014; Ashton et al. 2019). Elevated winter spawning temperatures exceeding 4°C could lead to recruitment bottlenecks for burbot, particularly when access to cold-water spawning habitats are limited due to factors including impoundments or warming water conditions (Ashton et al. 2019).

In Wyoming, burbot are designated as a Species of Greatest Conservation Need (Wyoming Game & Fish Department 2018) and there have been concerns of declining burbot abundance within the Wind River basin. The Torrey Creek drainage, a smaller drainage within the Wind River basin, represents the most southwest extent of the native range of burbot within the United States (Fuller 2024), and burbot within the drainage are declining concurrently with others in the Wind River basin (Hubert et al. 2008).

Declines of burbot within the Wind River basin were hypothesized to be associated with fluctuations and alterations of natural flows and water levels, entrapment in irrigation canals, emigration, and angler harvest (Hubert et al. 2008). The hypotheses for burbot decline within the Wind River basin have been investigated within the Torrey Creek drainage specifically, and evidence does not support the hypotheses. Burbot had limited instances of entrapment in irrigation canals (Hooley-Underwood et al. 2018), had low emigration rates into the Wind River (Underwood et al. 2016), low risk of angler exploitation (Lewandoski et al. 2017), and the Torrey Creek drainage is free flowing (Lewandoski 2015). Thus, more contemporary hypotheses for the decline in burbot in the Torrey Creek drainage have focused on negative interactions with two non-native predators, brown trout *Salmo trutta* and lake trout *Salvelinus namaycush*. However, diet overlap among burbot, brown trout, and lake trout was recently found to be minimal (see **Chapter 3**). Specifically, predation on burbot by brown trout was minimal and lake trout did not consume burbot (see **Chapter 3**). Nevertheless, the limited occurrence of predation of burbot by brown trout could have population level effects when extrapolated to the entire population. In addition, the negative influence of warming winter water temperature as a source of recruitment failure has not been evaluated. Average water temperatures, including winter months, are projected to increase for the major rivers within the Greater Yellowstone Ecosystem (Hostetler et al. 2021), which includes the Wind River drainage. Therefore, this study addresses the dynamics of burbot population growth within the Torrey Creek drainage, focusing on the influence of non-native brown trout and declining embryo survival. Our research seeks to address these through the following inquiries: (1) how many burbot are being consumed annually by non-native brown trout, (2) what is the annual individual growth of burbot based on water temperature and consumption by brown trout, and (3) how do non-native brown trout and warming winter water temperature affect annual population growth rate of burbot and persistence of a population within the Torrey Creek drainage? The results of this study improve our understanding of how interactions between non-native species and climate, especially for species living on the edge of their native range where requirements may be at their tolerance thresholds, affect the persistence of a cold-adapted native fish species.

Methods

Study Site

The Torrey Creek drainage is located south of the Wind River and near Dubois, Wyoming (Figure 4.1) encompassing Torrey Lake, Ring Lake, Trail Lake, and Torrey Creek. Of these, Torrey Lake is the largest and most downstream lake (93 ha), Ring Lake is directly upstream (40 ha), and a section of Torrey Creek (0.9 km) connects Ring Lake and Trail Lake (51 ha). The Torrey Creek drainage was created from glacial moraines and is fed by snow melt and glacier melt from the Continental Glacier located in the Wind River Range (Vandeberg and VanLooy 2016). The headwaters of Torrey Creek flow through the Shoshone National Forest before entering Wyoming Game & Fish Department Whiskey Basin Wildlife Management Area 4.5 km upstream of Trail Lake. Torrey and Ring lakes are largely encircled by private ranches but access through public boat ramps. Movement of fish from the Wind River is unlikely as a series of steep cascades exist downstream of Torrey Lake (Hubert et al. 2008).

Native fishes include burbot, mountain whitefish *Prosopium williamsoni*, Yellowstone cutthroat trout *Oncorhynchus virginalis bouvieri*, mountain sucker *Catostomus platyrhynchus*, longnose sucker *Catostomus catostomus*, white sucker *Catostomus commersonii*, lake chub

Couesius plumbeus, and longnose dace *Rhinichthys cataractae*. Nonnative sportfish include brown trout, lake trout, and rainbow trout *Oncorhynchus mykiss*. Rainbow trout are stocked annually in the system to provide recreational opportunity by Wyoming Game & Fish Department.

Bioenergetics

Bioenergetics modeling was used to estimate total consumption of burbot by brown trout. 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, predator-energy density, and proportion of indigestible prey were required to run species specific bioenergetic models. Bioenergetic models were run twice, representing a single year of 1 October 2021 – 30 September 2022 and 1 October 2022 – 30 September 2023. These dates were because they had the fewest days of missing daily mean water temperature data. Missing data resulted from the loss of water temperature loggers and battery failure. Winter water temperatures were not collected from Ring Lake due to the loss of water temperature loggers.

Water temperature was measured in Torrey, Ring, and Trail lakes using HOBO pendant MX220 loggers. Loggers were deployed in May 2020 and removed August 2023. A cement weight was attached to a bullet float with three pendant loggers attached to measure water temperatures at different depths (i.e., 0.3-m above substrate [hereafter referred to as benthic], half of maximum depth, and 1.8-m below the surface). Water temperature was recorded every 30 minutes and daily average water temperature was calculated for each depth by lake. The minimum and maximum mean daily water temperature were used to inform the bioenergetic models, representing the extremes that brown trout and burbot experience in the Torrey Creek drainage (Table B.1).

Diet proportions and proportions of indigestible prey were obtained from gastric lavage and stomach samples within the Torrey Creek drainage (see **Chapter 3**). Diet proportions were summarized by taxon order and season. Diet taxa that appeared infrequently, accounted for less than 0.05 mean proportion by weight for all seasons, or that were unable to be identified to order were summarized as “other.” The “other” category was largely comprised of insect parts. Seasons were described as spring (1 March – 31 May), summer (1 June – 31 August), autumn (1 September – 30 November), and winter (1 December – 28 February). No sampling occurred during winter; therefore, winter diet proportions were calculated as the mean proportion by weight of autumn and spring samples.

Prey energy densities and predator energy densities (i.e., burbot and brown trout) were obtained from estimates in the literature. Prey energy densities were converted to joules (J)/g of wet weight (Table B.2; Cumminns and Wuycheck 1971). The energy density of the “other” category was obtained by averaging the energy density estimates of all prey categories. Brown trout predator energy density was set to 5,502 J/g (Johnson et al. 2017) and burbot predator energy density was 5,135 J/g (Johnson et al. 1999).

Predation of burbot by brown trout was estimated by modeling brown trout consumption over the minimum and maximum mean daily temperature during 2022 and 2023. The model was tailored to brown trout in the Torrey Creek drainage by leveraging growth estimates derived from a von Bertalanffy growth curve, followed by calculating estimated weights using length-weight relationship established for the drainage (see **Chapter 2**). The annual consumption of burbot was estimated as the annual consumption of burbot by a single brown trout multiplied by the abundance estimate of brown trout within the Torrey Creek drainage (see **Chapter 2**).

Deterministic Models

A stage-based matrix model was created to estimate population growth rates of burbot within the Torrey Creek drainage (Figure 4.2; Lefkovitch 1965). The model was adapted from Lewandoski (2015) and the matrix model, **A**, was constructed as:

$$\mathbf{A} = \begin{bmatrix} S_j * (1-\varphi_{i,j}) & f_j m_j a & f_j m_j a & f_j m_j a \\ S_j * \varphi_{i,j} & S_j * (1-\varphi_{i,j}) & 0 & 0 \\ 0 & S_j * \varphi_{i,j} & S_j * (1-\varphi_{i,j}) & 0 \\ 0 & 0 & S_j * \varphi_{i,j} & S_j \end{bmatrix},$$

where S_j is the survival at stage j, $\varphi_{i,j}$ is the transition probability from stage i to j after 1-year of growth, f_j is the mean weight (kg) of burbot in stage j, m_j is the probability of maturity in stage j, a is the number of age-1 recruits per kg of spawning burbot.

Two scenarios (i.e., observed [empirical predation rate measured in Torrey Creek drainage, see **Chapter 3**] and increased predation) were created using the matrix model, **A**, to analyze the effects of population growth with different estimates of S_1 and S_2. The observed scenario represents burbot population growth with minimal predation effects on juvenile size classes whereas the increased-predation scenario represents lower rates of survival for juvenile size classes — caused by predation. An estimate of survival of burbot < 390 mm was not available for burbot within the Torrey Creek drainage; therefore, estimates of survival for S_1 and S_2 were obtained from Klein et al. (2016) where burbot survival was estimated in a system with no predators and one with predators in an aquaculture setting (Vught et al. 2008; Paragamian and Laude 2010). Estimates of adult survival (S_a), number of age-1 recruits per kg of spawning burbot (*a*), and length classes for each stage were obtained from Lewandoski (2015; Table 4.1). Stages were based on four size classes of < 200 mm, 200–389 mm, 390–529 mm, and 530–955 mm. Probability of maturity was determined based on aged burbot from Fontanelle and Flaming Gorge reservoirs, Wyoming (Brauer et al. 2019). Average length of each stage for burbot from the Torrey Creek drainage was matched to the closest length of each age as calculated from the von Bertalanffy growth model created from burbot within Fontanelle and Flaming Gorge reservoirs (Brauer et al. 2019). Mean weight of burbot for each stage (f_j) was calculated using a linear model with $\log_{10}$ length and $\log_{10}$ weight of burbot sampled (see **Chapter 2**) and Wyoming Game & Fish Department data. A deterministic model was first developed to evaluate annual population growth (λ) and elasticity using the R package "popbio" (R Core Team 2022; Stubben et al. 2024).

Elasticity offers insights into predicting the anticipated changes in λ as demographic rates undergo variation (Caswell 2000, 2001). Elasticity measures the relative change in λ with proportionate changes to the demographic rates allowing us to evaluate the individual influence of each demographic rate to population dynamics (Schaub and Kéry 2022).

Stochastic Models

Stochastic models were built using MCMC algorithm in JAGS (R package "jagsUI; Kellner and Meredith 2024) and the R package IPMbook (Schaub et al. 2023). Stochastic models allowed us to expand on the deterministic stage-structured model, **A**, by including parameter uncertainty and demographic stochasticity. Parameter uncertainty was included to allow error associated with the derivation of estimates of the demographic rates to be carried forward in the projection models (Schaub and Kéry 2022). Survival (S_j) and probability of maturity (*m*) estimates were selected from a beta distribution using R package IPMbook to obtain beta shape parameters from reported mean and standard error (Table 4.1; Lewandoski 2015; Klein et al. 2016; Brauer et al. 2019; Schaub et al. 2023). The number of age-1 recruits per kg of spawning burbot (*a*) was obtained from a lognormal distribution using the mean and standard deviation of *a* (Lewandoski 2015). Average weight per size class (f_j) was obtained from a normal distribution using the mean weight of predicted weights of burbot in a size class and the precision variable tau (inverse of the variance).

Demographic stochasticity was included because it can have strong effects on population growth (Sæther et al. 2007) especially when populations are small (Lande 1993). Demographic stochasticity was incorporated in our simulations by using a Poisson distribution for recruitment processes and a binomial distribution for survival processes at each time step.

To investigate the effects of warming water temperatures on recruitment, we introduced a recruitment penalty into a subset of our simulation models. The penalty was created due to the decline in survival of embryos at 4°C (Ashton et al. 2019). Burbot embryos incubated at 2°C had a survival of 86.7% in contrast to 47.9% at 4°C (Ashton et al. 2019). Our recruitment penalty was created by setting the upper bounds of a beta distribution, with both shape parameters of 3, at 0.39, the difference observed in survival percentages at 2°C and 4°C, and a lower bound at 0.05. The upper bound represents the decline in embryo survival as additive to the recruitment of S_1 individuals, while the lower bound represents the embryo mortality observed at higher water temperatures is partially compensatory. One minus the recruitment penalty was multiplied by the number of S_1 recruits. We used the recruitment penalty to model varying scenarios where water temperature in the Torrey Creek system during embryogenesis exceeded 4°C at varying frequencies. We modeled the frequency of the recruitment penalty by setting a threshold probability (i.e., 0.25, 0.50, and 1.0) and for each year of the simulation determined if the iteration exceeded the water temperature threshold by using a binomial likelihood function.

Population growth, lambda (λ), and the probability of persistence were calculated from the simulations. Burbot populations were projected for 100 years and iterated 10,000 times. Population growth was calculated as the arithmetic mean of the annual growth rates on the log scale (*r*) and then reported on the natural scale for lambda (Schaub and Kerry 2022). Annual growth rate was calculated for each time, *t*, step using the following formula:

$$r_t = log\left(N_{1,t+1} + N_{2,t+1} + N_{3,t+1} + N_{4,t+1}\right) - log\left(N_{1,t} + N_{2,t} + N_{3,t} + N_{4,t}\right),$$

where *N* is the number of individuals for each stage in the population at time *t*. Probability of persistence was calculated as the number of iterations where abundance was greater than zero at the final time step (t = 100) divided by the total number of iterations (10,000). Additionally, for the observed and increased predation scenarios, where the recruitment penalty occurred annually, parameter estimates were evaluated for iterations in which in λ equaled one.

Results

Water Temperature

Water temperature varied from 0.8°C to 19.2°C (Figure 4.3) with the highest average daily maximum water temperature observed in August 2022 (19.2°C), and the warmest average daily minimum water temperature in August 2023 (14.0°C). Conversely, the coldest average daily maximum water temperature was in December 2021 (1.2°C), with the coldest average daily minimum water temperature occurred in November 2021 (0.8°C; Figure 4.3). Maximum daily water temperatures peaked in August for both years (Figure 4.3), whereas the smallest difference between maximum and minimum water temperature was in December for both years (Figure 4.3). Minimal variation in average seasonal water temperatures was observed between the two years (i.e., Oct 2021-Sep 2022 and Oct 2022-Sep 2023; Figures 4.4 and 4.5).

Seasonal average daily water temperatures exhibited a broad range across seasons, except for winter (Figures 4.4 and 4.5). Autumn had the widest range in minimum and maximum average daily water temperatures for both years (Figures 4.4 and 4.5). Specifically, autumn average water temperatures varied from 2.0 to 17.9ºC, with an average of 10.4 ºC (0.37; SE). Conversely, winter daily average water temperatures varied from 1.2 to 5.1ºC averaging at 3.8ºC (0.08; SE). Spring and summer average daily water temperature had a range of 8.9 and 9.9ºC, respectively.

During the putative burbot embryogenesis period, early February through early April, the average daily benthic water temperature was 4.0°C (0.04; SE) for 2022 in Torrey and Trail lakes (Figure 4.6). Average daily benthic water temperature of Torrey Lake exceeded 4°C for 27 days (39%) during embryogenesis in 2022 and for 31 days (46%) for Trail Lake (Figure 4.6). In 2023, average benthic daily water temperature for Torrey Lake was 4.9°C (0.01; SE) and 4.5°C (0.01) for Trail Lake during embryogenesis with average daily water temperatures for Torrey and Trail lakes in the hypolimnion exceeding 4°C for the entire period of embryogenesis (Figure 4.6).

Bioenergetics Brown Trout

The proportion of maximum consumption (C_{max}) modeled by brown trout bioenergetics for one year of growth, as predicted from the von Bertalanffy growth curve and average weight at length, was quantified using the p-value (proportion of C_{max}). For year 2021, at maximum and minimum temperatures, the p-value was 0.42 and 0.34, respectively. Similarly, the p-values for 2022 were 0.38 at maximum temperature and 0.36 for the minimum temperature.

A single brown trout (> 299 mm) was estimated to consume between 15 and 23 g of burbot annually. Based on estimated brown trout abundance within the drainage (893; 544 –1652 95% CI; see **Chapter 2**), during the maximum temperatures of 2022, brown trout consumed approximately 20.30 kg (12.14 – 37.55) of burbot, decreasing to 13.86 kg (7.88 – 24.38) during the minimum temperatures. Similarly, in 2023, consumption remained consistent, with estimated consumption during maximum temperatures at 20.04 kg (11.98 – 37.07) and at minimum temperatures 13.86 kg (8.29 – 25.64) of burbot.

Deterministic Models

Annual population growth rate (λ) for burbot was 1.12 for the deterministic observed model and 1.02 for the increased predation model. Both models indicated population growth, with the observed model having the population double ever 6 years, compared to every 35 years in the increased predation model.

Survival across all stage classes exhibited the most proportional effect on burbot population dynamics given the elasticity values from both the observed and increased predation models (Figure 4.7). Specifically, survival of adults (0.28 observed, 0.33 increased predation), survival of stage 1 (0.25 observed, 0.23 increased predation), survival of stage 2 (0.23 observed, 0.22 increased predation), and the transition probability from stage 1 to stage 2 (0.21 observed, 0.20) all had elasticity values exceeding 0.2, highlighting their critical roles as drivers of population dynamics within the models (Figure 4.7).

Stochastic Models

In stochastic simulation models without a recruitment penalty, burbot persisted in 82% of iterations in the observed model and 69% in the increased predation model (Figure 4.8). Similar to the deterministic models, the average λ was 1.15 (0.73-1.72; 95% CI) in the observed model, resulting in a population doubling time in 5 years, whereas λ was 1.04 (0.67-1.51; 95% CI) in the increased predation model with a doubling time of 18 years.

When a recruitment penalty was added to each model, all models demonstrated a greater than 0.5 probability of burbot persistence over 100 years (Figure 4.9). Specifically, with an annual recruitment penalty, burbot persisted in 74% of the observed model iterations and 59% of the increased predation model iterations (Figure 4.9). The addition of the recruitment penalty resulted in a decrease of 0.14 – 0.16 in the probability of persistence in the increased predation scenario compared to the observed scenario under the same recruitment penalty frequency.

Mean λ was greater than 1 in all models except when a recruitment penalty occurred annually with the increased predation model (λ = 0.98; Figure 4.9). The recruitment penalty decreased lambda by 0.1 – 0.2 for every 25% increase in frequency of the recruitment penalty, observed across both increased predation and observed models. Although mean λ was greater than 1 in most simulations, the lower 95% confidence interval of mean λ was below 1 for all simulations. When λ was one for the observed and increased predation scenarios in which the recruitment penalty occurred annually, we observed a weak positive relationship between the recruitment penalty and survival of adults (Figure 4.10).

Discussion

Brown trout are not a primary driver of the current status of burbot in the Torrey Creek drainage. The population of brown trout in the Torrey Creek drainage consumes a relatively modest 12 – 28 kg of burbot annually, which is equivalent to 3 – 14 adult burbot (S_4) or 50 – 238 juvenile burbot (S_2). Notably, the adult burbot population in Torrey Lake alone was estimated to be 966 (616–1558 95% CI; Lewandoski 2015) in 2013, so the rate of brown trout predation is low in comparison to the abundance (0.3 – 1.4 % mortality from predation). Furthermore, elasticity values from the deterministic matrix population model underscore that adult burbot survival exerts the most influence on the population growth rate, notably in the increased predation model, and brown trout predation predominantly affects juvenile fish.

Deterministic modeling further corroborates our findings by excluding brown trout predation as a current factor contributing to the decline of burbot within the Torrey Creek drainage. Both observed and increased predation scenarios yielded positive population growth rates, suggesting that even if the observed scenario represents an underestimation of true predation in the system, the resulting decreased survival rate of juveniles in the increased predation model would not hinder overall population growth. However, when demographic stochasticity and parameter uncertainty were introduced, every simulation carried a risk extirpation for burbot within a century, primarily attributed to high uncertainty associated with the adult mortality estimate (0.2 – 0.7; 95% CI; Lewandoski 2015).

The observed estimate of mortality for burbot in the Torrey Creek drainage (0.43; 0.2 – 0.7 95% CI; Lewandoski 2015), only includes natural mortality, because exploitation rates were estimated to be low (Lewandoski et al. 2017). Despite the exclusion of exploitation from the estimate of mortality for burbot in the Torrey Creek drainage, the mortality estimate is higher than in many other systems, including those that have exploitation included in the annual mortality estimate, such as Lake Erie (40%; Clemens 1951) and Lake Superior (39%; Bailey 1972). Other systems, such as Lake of the Woods (64%; Muth and Smith 1974) and Kootenai River (63%; Paragamian et al. 2008), have higher reported mortality estimates due to angling harvest, but the point estimates associated with total mortality are within the 95% confidence interval used to model burbot mortality within the Torrey Creek drainage (Lewandoski 2015). Other studies in Wyoming have found that burbot populations could be suppressed when total annual mortality was 0.57 and greater (Klein et al. 2016; Brauer et al. 2019). Thus, the high mortality rate for adult burbot in the Torrey Creek drainage is a key driver of the observed risk of local extinction in the population.

Our models improved upon the previously developed Torrey Creek drainage population growth models by incorporating uncertainty around parameter estimates. Incorporating this variability is crucial to prevent overreliance on point estimates that can oversimplify stable stage distributions, potentially leading to significant disparities in demographic interpretations (Ezard et al. 2010; Nelson et al. 2010). By integrating uncertainty from the confidence intervals into our stochastic simulations without recruitment penalties, we observed notable differences compared to our static models (i.e., mean λ being below 1 in 95% confidence intervals and a chance of extirpation), underscoring the importance of accounting for uncertainty in demographic analysis.

Though incorporating uncertainty is important, it contributed to a major limitation in our modeling framework. Adult burbot survival estimates from Lewandoski (2015) were summarized across multiple systems within the Wind River range with low recapture rates and tag returns (Lewandoski 2015). Reducing the error associated with survival estimation, as current estimates were nearly as broad as 0.0 to 1.0, likely leading to higher probabilities of persistence and mean λ values. However, by evaluating the iterations from the observed scenario in which the recruitment penalty occurred annually where λ was equal to one, we believe that adult survival is likely close to the point estimate (0.57). This is supported by the observation that the burbot population within the drainage is not doubling every 9 years, as would be expected with a λ of 1.08, which is predicted from the observed scenario with the recruitment penalty occurring annually.

Although we anticipated warming winter water temperatures, as modeled by the recruitment penalty occurrence, will have a substantial effect on burbot survival and persistence within the Torrey Creek drainage, our simulations showed evidence that juvenile burbot survival was more influential on persistence than reduced embryo survival during warm winter water temperatures. The addition of a recruitment penalty to our population projection models decreased the probability of persistence of all simulations and reduced the mean λ. Notably, the probability of persistence decreased from 0.82 to 0.74 when our recruitment penalty was added annually to our observed model. Additionally, λ of the simulation of the observed model with an annual recruitment penalty is a more optimistic scenario for burbot persistence than the increased predation simulation without the occurrence of a recruitment penalty, representing that juvenile survival has a larger effect on λ than a reduction in recruitment.

The recruitment penalty and increased predation were modeled as additive effects of mortality and recruitment on the simulated burbot population, which may not be entirely realistic. Though predation can be “super-additive” as observed with Caspian Terns

Hydroprogne caspia predating on out migrating juvenile salmonids (Payton et al. 2020), it is likely that for brown trout and burbot within the Torrey Creek drainage that some level of mortality would be compensatory between reduction in embryo survival from warming winter water temperatures and predation. The mortality associated with S_1 and S_2 from the increased predation simulations would probably be partially compensatory with increasing winter water temperatures as burbot incubated at 4ºC suffer from higher rates of deformities, reducing their natural survival probability (Ashton et al. 2021). Thus, predation might primarily remove individuals that are already at higher risk of not surviving due to these deformities. Similar to the “doomed surplus” where ducks harvested by hunters often exhibit lower body conditions compared to the general population (Errington and Hamerstrom Jr. 1935; Hepp et al. 1986; Payton et al. 2020). These weaker or poorer-condition ducks are less likely to survive, making their removal from the population a compensatory mortality mechanism.

Additionally, we did observe winter water temperatures above 4ºC for the entirety of the burbot embryogenesis period in 2023 and partially in 2022. This indicates that the observed simulations with a recruitment penalty are the most informatic and realistic models for current environmental conditions. Burbot are not the only fish to experience reduced recruitment due to warming conditions during embryogenesis. Walleye *Sander vitreus*, a cool-water species, also exhibit this trend (Hansen et al. 2017A, Hansen et al. 2017B). Yellow perch *Perca flavescens* and North Sea herring *Clupea harengus* similarly show reduced recruitment with warming water temperatures, though this trend is associated with alterations in plankton production during critical larvae feeding periods (Payne et al. 2009; Kaemingk et al. 2014). We recognize the negative effects of elevated water temperatures during embryogenesis; however, the potential mismatch in timing between fry emergence and altered plankton production has not been evaluated in burbot and could also lead to recruitment failure. Additionally, the recruitment penalty was created from burbot originating from Kootenai River (Ashton et al. 2021), which may have different thermal tolerances than other burbot populations. Local adaptations likely occur for burbot; for example, burbot embryos from brood stock originating from the Albe River, France have been successfully incubated up to 6ºC (Vught et al. 2008). Burbot embryos from the Torrey Creek drainage have not been reared in captivity; therefore, the thermal tolerance of embryos and local adaptation is unknown.

Though we modeled different simulations to represent a range of conditions in the Torrey Creek drainage, we have no evidence to currently support that the increased predation simulations are more likely than the observed simulations. This could be refuted if brown trout were found to have increased predation rates on burbot during the winter season, when we did not sample. However, brown trout food consumption rate has been documented in other systems to decrease substantially during the ice-covered period in comparison to ice-off (Amundsen and Knudsen 2009), which mirrors consumption rate output from our bioenergetics simulations for consumption rate during the winter.

In our analysis, burbot were modeled to spawn annually, however, certain populations exhibit skip spawning, which reduces population growth rates and decreases the likelihood of persistence (Evenson 1991; Pulliainen and Korhonen 1993). However, unique life history strategies or plasticity in life-history traits could potentially counteract the reduction in population growth if skip spawning were to occur. Burbot within Torrey Creek are smaller and more likely to mature at a younger age compared to burbot within Torrey Lake (Glaid et al.

2021). Movement and genetic evidence support a homogenous breeding population (Underwood et al. 2016; Glaid et al. 2021), with the existence of both adfluvial and lacustrine burbot life-history strategies within the Torrey Creek drainage (Bjorn 1940; Hagan 1952; Williams 1959; Miller 1970; Glaid et al. 2021). The early size and age of maturity of adfluvial burbot were not accounted for in our models, because the proportion of the population exhibiting an adfluvial life history is unknown, and fecundity has not been quantified for adfluvial burbot in the system.

Our models incorporated adfluvial morphological measurements that affected the recruitment rate function. Contrary to the previous population model developed for burbot within the Torrey Creek drainage (Lewandoski 2015), which used a length-weight regression from a burbot population in British Columbia (Neufeld et al. 2011), the current model used a length-weight regression specific to burbot within Torrey Creek (see **Chapter 1**). The average weight of burbot for each state was greatly reduced in our model as compared to the previous modeling efforts, resulting in a decrease in biomass per spawner (i.e., a 34% reduction in S_4 and 25% reduction in S_3) and a reduction in fecundity.

In this study there was a lack of evidence to support the hypothesis that non-native trout predation was negatively affecting burbot persistence within the Torrey Creek drainage, supporting coexistence of both piscivorous predators. Furthermore, even with winter water temperatures exceeding 4ºC and reducing embryo survival, we did not predict a catastrophic decline of burbot abundance and persistence. Only when modeling a recruitment penalty annually coupled with increased predation (i.e., reduced juvenile survival) did we predict a declining population based on point estimates. Incorporating additional empirical data specific to the Torrey Creek drainage led to a revision of previous λ predictions. Refinement and optimization of the models could be achieved by better understanding the frequency of winter water temperatures exceeding 4ºC during burbot embryogenesis and minimizing errors associated with vital rate estimates. Nevertheless, despite these uncertainties, burbot persistence appears likely, albeit potentially in an altered state compared to what has been historically observed within the drainage.

Our research indicates that burbot in the Torrey Creek drainage can coexist with other apex predators and that the burbot population is likely to persist with contemporary water temperatures despite water temperature exceeding the optimal water temperature for embryo development. Current climate predictions indicate that water temperature in the Torrey Creek drainage will continue to warm, but the severity of warming is unknown, emphasizing the need for system-specific water temperature monitoring. This research underscores the importance of examining multiple population stressors simultaneously, such as non-native species and climate change, as they influence population dynamics and persistence.

Tables

Table 4.1: Parameter estimates and standard errors used for parameterization of population matrix models. Standard errors and point estimates were used to allow for parameter uncertainty in population projections.

Parameters	Estimate	Standard error	Source
Survival (yr^{-1})			
Observed			
S_1	0.188	0.04	Klein et al. (2016)
S_2	0.335	0.07	Klein et al. (2016)
S_a	0.57	0.13	Lewandoski (2015)
Increased predation			
S_1	0.146	0.006	Klein et al. (2016)
S_2	0.289	0.011	Klein et al. (2016)
S_a	0.57	0.13	Lewandoski (2015)
Transition probability			
$\varphi_{1,2}$	0.62		Lewandoski (2015)
$\varphi_{2,3}$	0.21		Lewandoski (2015)
$\varphi_{3,4}$	0.17		Lewandoski (2015)
Mean weight (kg)			
f_2	0.158	0.03	See methods
f_3	0.582	0.11	See methods
f_4	2.767	0.57	See methods
Probability of maturity			
m_2	0.330	0.086	Brauer et al. (2019)
m_3	0.790	0.049	Brauer et al. (2019)
m_4	1		Lewandoski (2015)
Recruitment rate (age 1 * kg)			
a	50.78	7.83	Lewandoski (2015)
Recruitment penalty			
rp	0.22		See methods

Figures

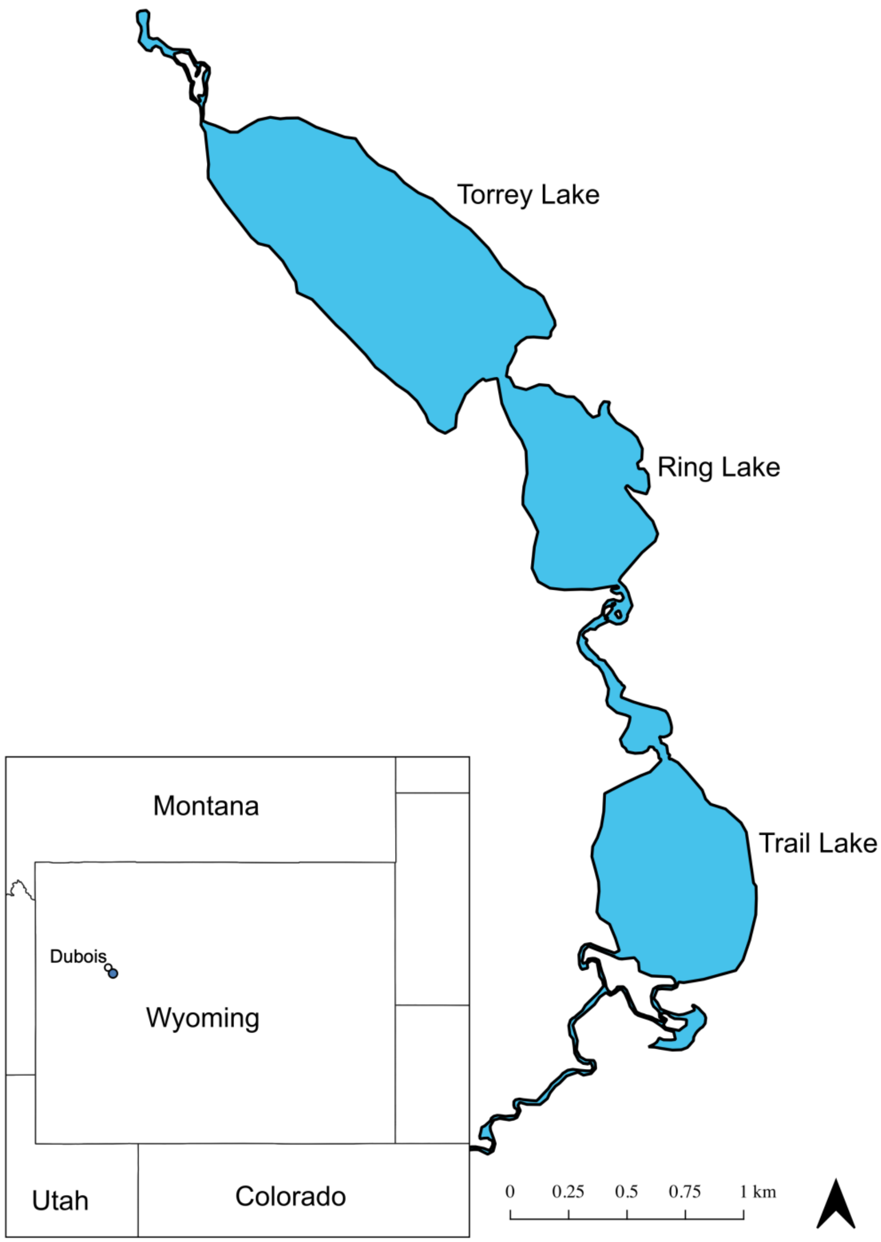

Figure 4.1: Map of a section of Torrey Creek drainage near Dubois, Wyoming, USA. The area delineated in the map represents the extent of the sampling locations.

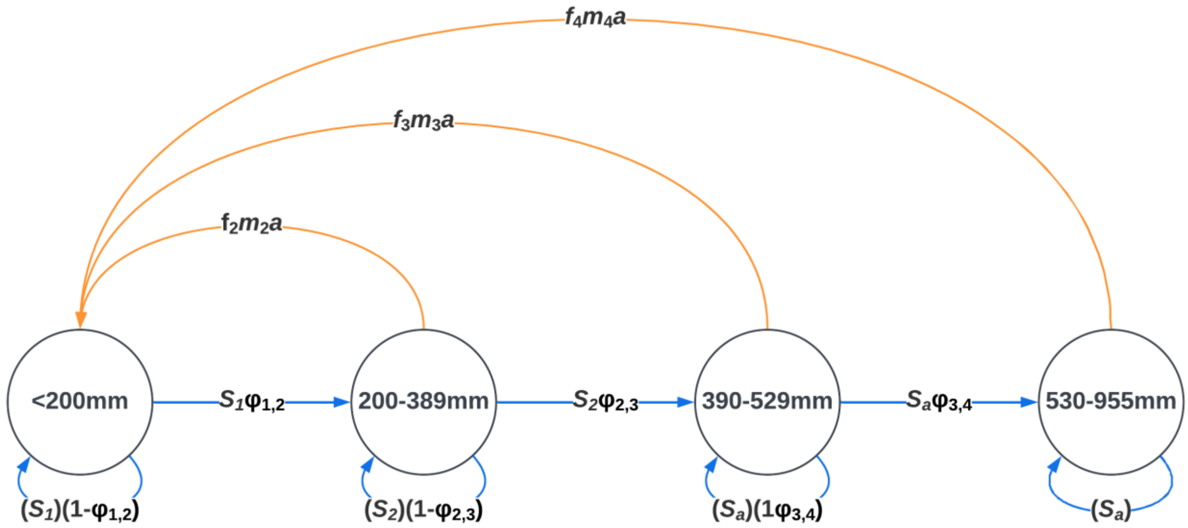

Figure 4.2: Simplified life-cycle graph for stage-structured model of burbot within the Torrey Creek drainage, Dubois, Wyoming, US, adapted from Lewandoski (2015). Orange lines represent recruitment processes and blue lines represent survival processes.

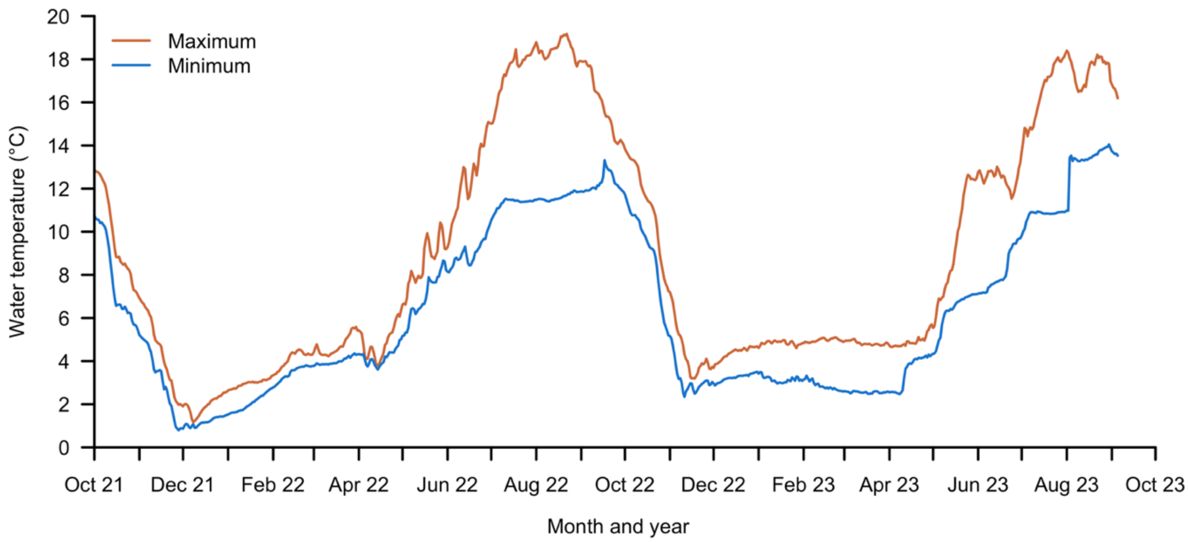

Figure 4.3: Minimum and maximum mean daily water temperature (ºC) observed for Torrey, Ring, and Trail lakes pooled, Wyoming, USA. Minimum mean daily water temperature represents the lake and depth location (i.e., 0.3-meters below surface, half of max depth, and max depth) that had the lowest average temperature for that given day. Conversely, maximum mean daily water temperature represents the lake and depth location with the highest average temperature for a given day.

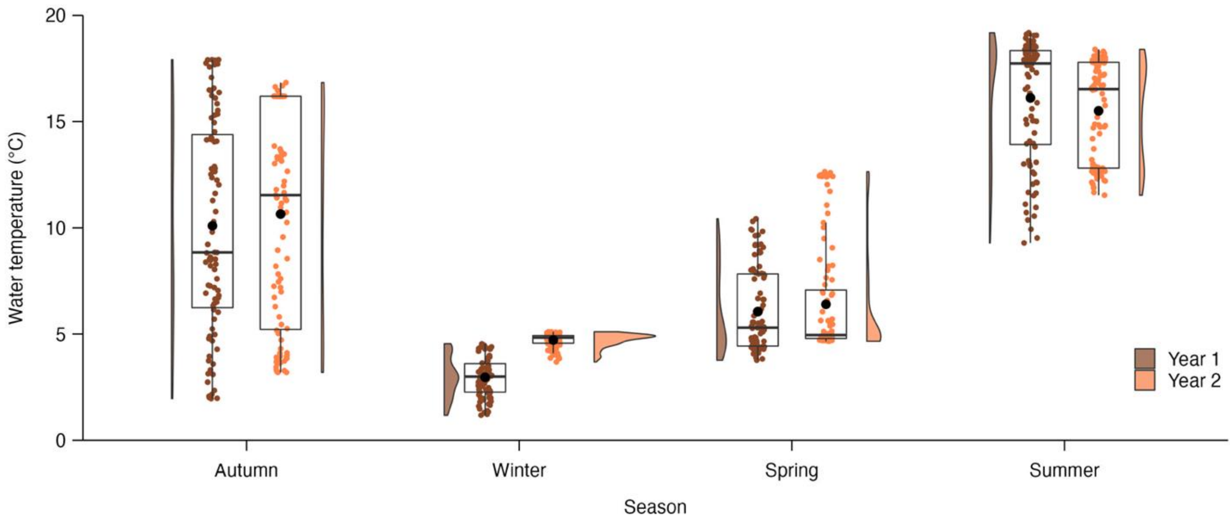

Figure 4.4: Maximum mean daily water temperature (ºC) observed for Torrey, Ring, and Trail lakes pooled, Wyoming, USA. Maximum mean daily water temperature represents the lake and depth location (i.e., 0.3-meters below surface, half of max depth, and max depth) that had the highest average temperature for that given day. Year 1 occurs from 1 Oct 2021 to 30 Sep 2022 and year 2 occurs from 1 Oct 2022 to 30 Sep 2023. Each point represents a single day that was used for the bioenergetics models at maximum water temperatures.

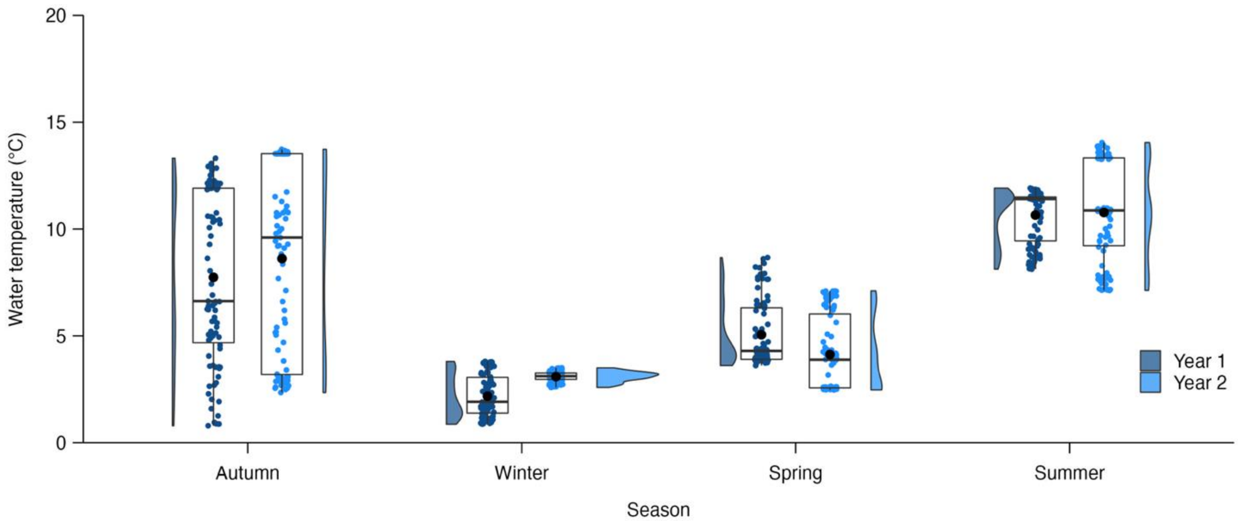

Figure 4.5: Minimum mean daily water temperature (ºC) observed for Torrey, Ring, and Trail lakes pooled, Wyoming, USA. Minimum mean daily water temperature represents the lake and depth location (i.e., 0.3-meters below surface, half of max depth, and max depth) that had the lowest average temperature for that given day. Each point represents a single day that was used for the bioenergetics models at minimum water temperatures.

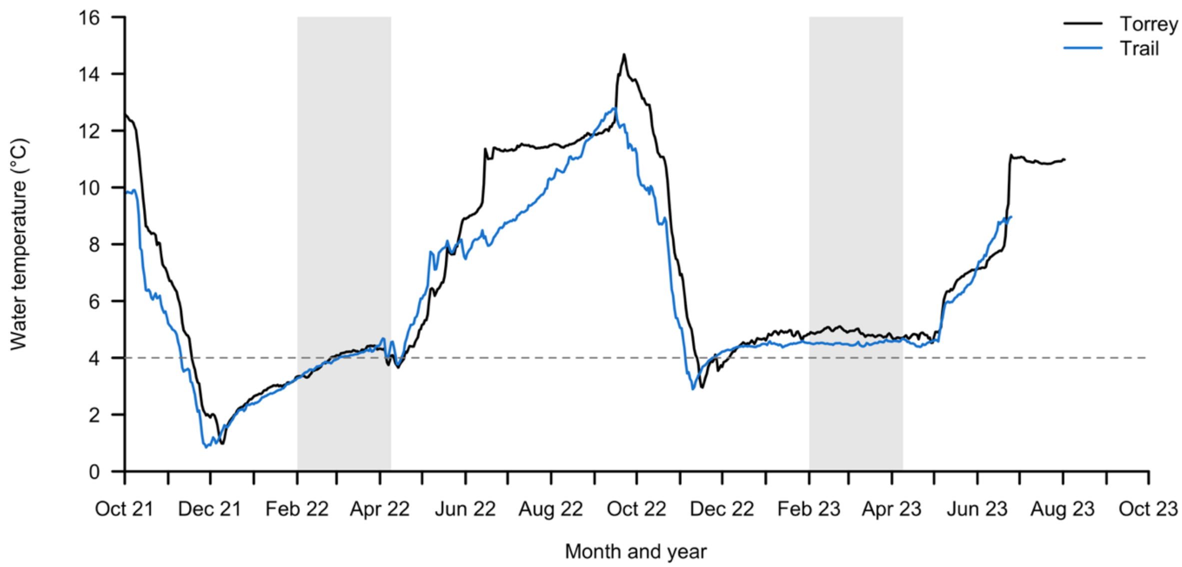

Figure 4.6: Mean daily benthic water temperatures for Torrey Lake (18 m) and Trail Lake (11 m) in the Torrey Creek drainage, Wyoming. Grey dashed line at 4°C indicates a threshold for burbot embryo survival (see Methods). Grey vertical rectangles represent the putative embryogenesis period for burbot in the Torrey Creek drainage.

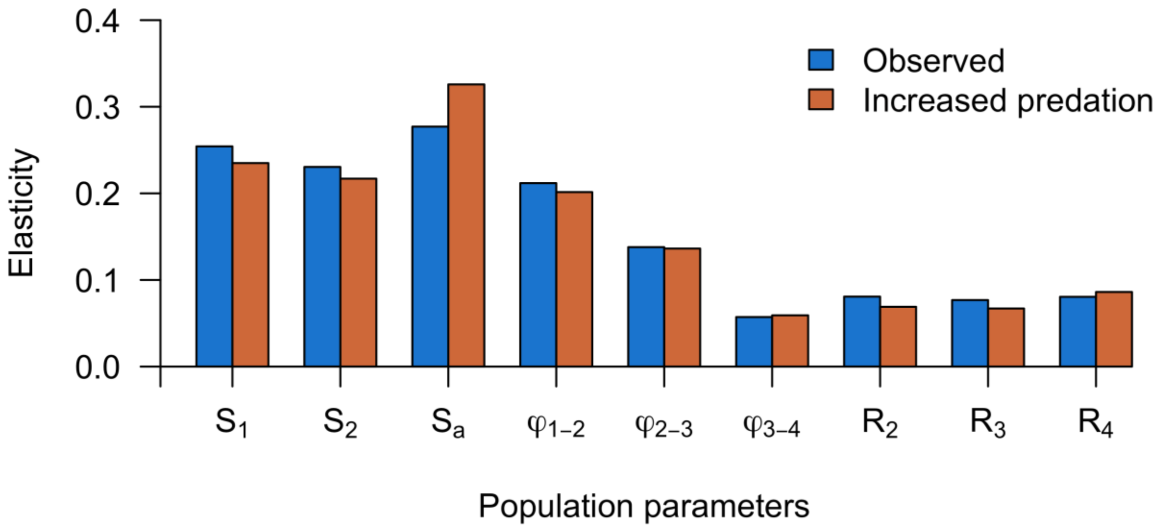

Figure 4.7: Elasticity values for population parameters estimates used in the burbot projection models (i.e., observed model in blue and increased predation model in orange). Elasticity of parameters were calculated from the deterministic model containing no parameter uncertainty or recruitment penalty due to embryo failure (see Methods for definitions of population parameters). R represents recruitment for each size class that reproduces.

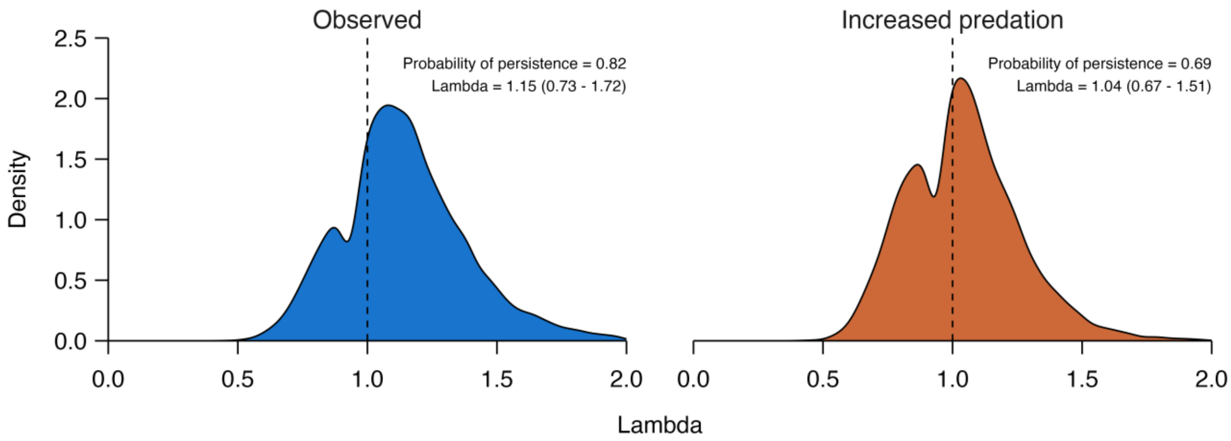

Figure 4.8: Density distributions of lambda for observed (blue) and increased predation (orange) model simulations of burbot within the Torrey Creek drainage, Wyoming, USA. Dashed line represents a lambda of 1.

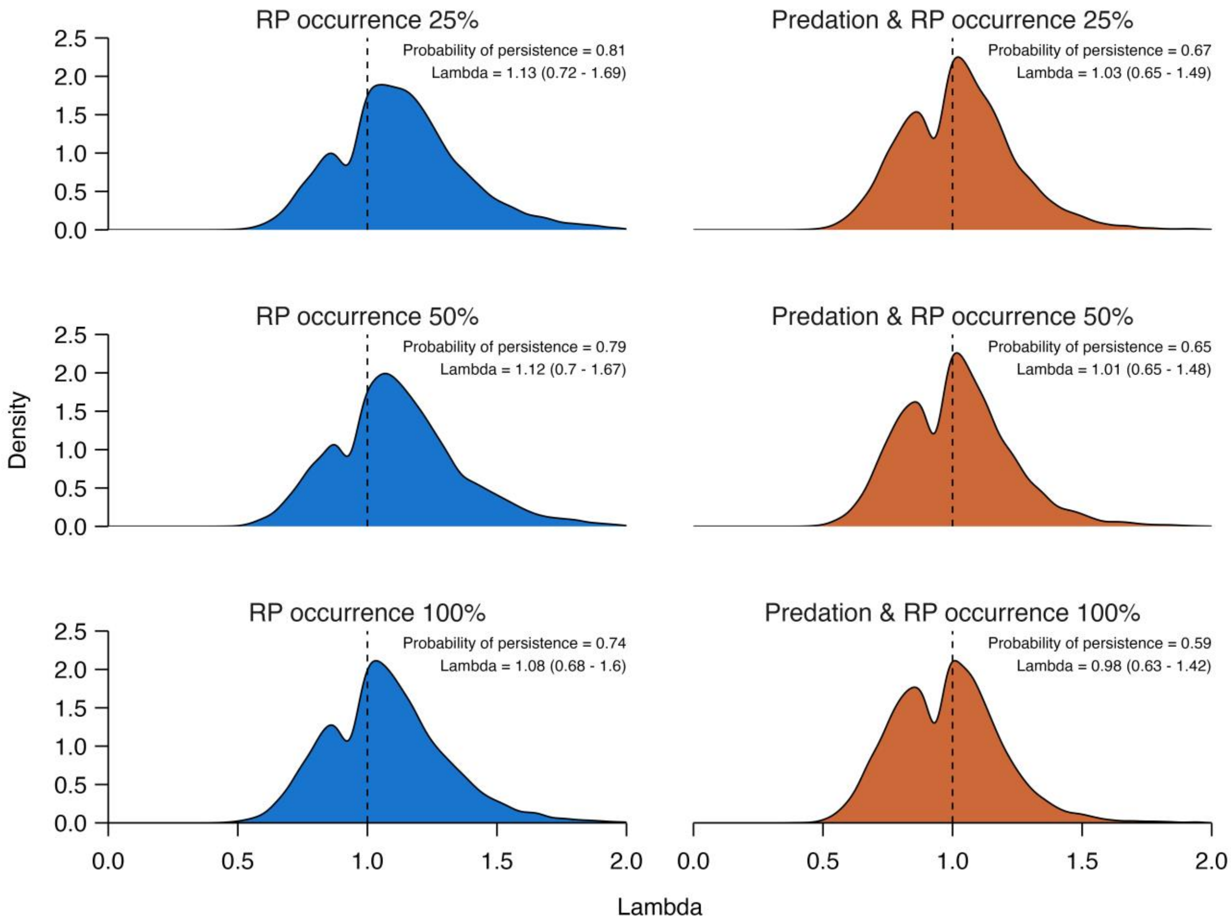

Figure 4.9: Density distributions of lambda for observed (blue) and increased predation (orange) model simulations of burbot within the Torrey Creek drainage, Wyoming, USA with recruitment penalty (RP) occurrence. Dashed line represents a lambda of 1.

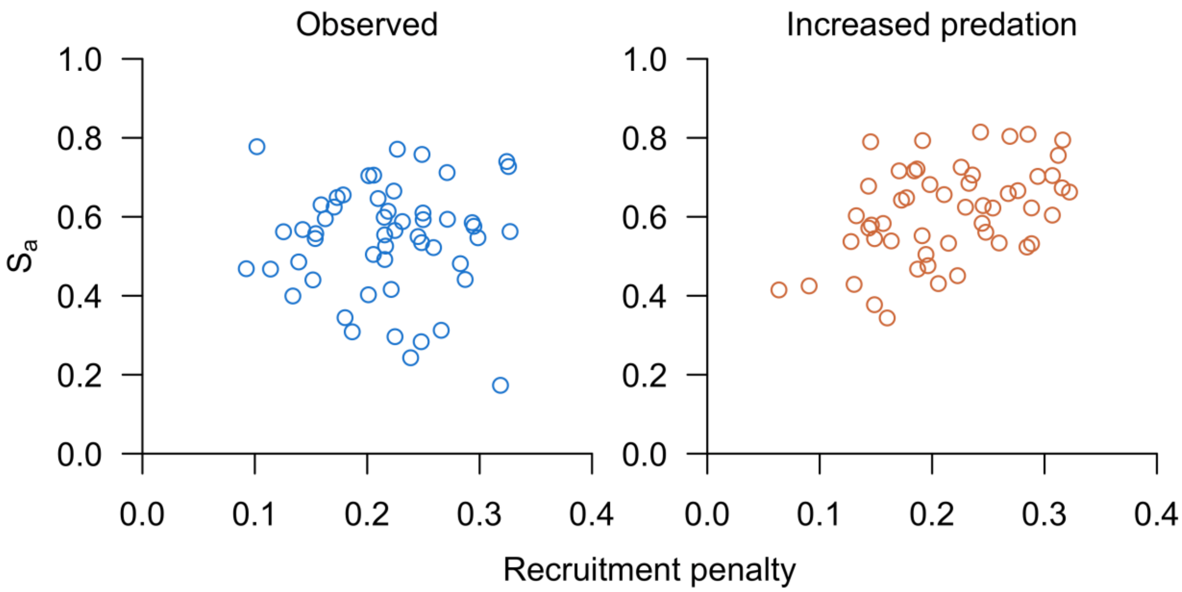

Figure 4.10: Scatterplot of survival of adults (S_a) and recruitment penalty for observed (blue) and increased predation (orange) scenario in which the recruitment penalty occurred annually and λ was equal to 1.

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CHAPTER FIVE

DISSERTATION CONCLUSION

The Torrey Creek drainage has experienced a decline in catch rates of burbot *Lota lota* as observed by catch per unit effort from annual sampling (Krueger 1996), and Wyoming Game & Fish Department documented predation of burbot by brown trout *Salmo trutta* during the autumn of 2017 (Wyoming Game & Fish Department 2018). From this sampling event, burbot occurred in 33% of brown trout samples, although sample size was small (n = 6; Wyoming Game & Fish Department 2018). This alone provided compelling evidence to investigate any detrimental effects non-native trout may be having on burbot, especially given the potential situation in which suppression of a trophy fishery is considered for conservation of a native species.

Baseline demographic parameters were necessary for research questions used **in Chapter 3** and **Chapter 4**. **Chapter 2** established baseline information regarding size structure, condition, and growth within the Torrey Creek drainage for the years 2020-2022. An abundance estimate and growth model was developed for brown trout within the drainage. Additionally, a growth model was also developed for lake trout, but this model had higher confidence intervals due to low sample size of aged individuals. A burbot growth model has yet to be developed for the Torrey Creek drainage. Additionally, I used proportional size distribution and relative weight to quantify the size distribution and describe the overall plumpness of burbot, brown trout, and lake trout within the drainage. The abundance estimate and growth model established in **Chapter 2** for brown trout were used in analytical approaches for research questions in **Chapter 3 and 4**.

Burbot, brown trout, and lake trout overlap in many ecosystems, but little to no research has investigated the deleterious effects of trout on burbot. Instead, it is more common for burbot to have antagonistic relationships with juvenile lake trout (Martin 1970; Jacobs et al. 2010; Gorman and Sitar 2013). **Chapter 3** describes the diets of burbot, brown trout, and lake trout while quantifying the dietary overlap among the species. Burbot did not occur in the diets of lake trout and were infrequent in brown trout diets within the Torrey Creek drainage. Additionally, diet overlap among burbot, brown trout, and lake trout was minimal, likely as a response to reduce interspecific competition. Though diets were diverse, I did document similar trophic positioning among the burbot, brown trout ≥ 300 mm, and lake trout. The consumption data of burbot from **Chapter 3** was used to estimate burbot consumption of the entire Torrey Creek drainage in **Chapter 4**.

Despite the extensive research into burbot declines within the Torrey Creek drainage, the response of burbot population growth has not been evaluated for decreased survival of juvenile size classes or the effect of recruitment failure caused by warming winter water temperatures. In **Chapter 4**, using Bioenergetics 4.0, the annual consumption estimate of burbot by brown trout was relatively modest. Largely signifying that the current level of predation is not responsible for the decline observed in burbot abundance. Although the population-level effect of predation was minimal, a previously developed stage-based population was updated for burbot to analyze population growth rate and probability of persistence at a varying levels of mortality and warming water temperature inducing a recruitment failure. The model developed in **Chapter 4** further improved the previous model by including parameter uncertainty and demographic stochasticity while also providing scenarios that could be occurring within the Torrey Creek drainage. Only in the most drastic scenario (i.e., recruitment penalty occurring annually and increased predation on juvenile burbot) is there a case of a declining burbot population within the

Torrey Creek drainage, based on point estimates of lambda. Though the model used in this chapter provides an optimistic scenario in which burbot persistence in the Torrey Creek drainage is likely, the model could be refined with more drainage specific metrics.

Further research should investigate the frequency of winter water temperatures exceeding 4ºC during embryogenesis. Winter water temperatures were only recorded for two years in this study. In 2022, temperatures exceeded 4ºC during part of the embryogenesis period, while in 2023, this temperature was sustained through the embryogenesis period. Understanding the frequency of this threshold could elicit differences in year-class strengths. Additionally, a harsher threshold at 6ºC, where 99% of embryos die (Ashton et al. 2021), is only two degrees away from current temperatures, warranting attention.

Improved survival estimates are necessary to better inform the models in **Chapter 4**. Current estimates vary from 0.3 to 0.8, which is nearly as broad as 0.0 to 1.0. Reducing error in survival estimates would substantially update population projection scenarios regarding the likelihood of burbot persistence within the Torrey Creek drainage.

Regarding management implications, there is no evidence that non-native trout currently negatively affect burbot persistence within the Torrey Creek drainage. Therefore, the coexistence of the trophy trout fisheries and burbot appears plausible. Without more detailed historical samples for comparison, burbot may now be in an altered state, dominated by smaller and younger spawning individuals rather than larger burbot.

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APPENDICES

APPENDIX A

CHAPTER 3 SUPPLEMENTAL TABLES

Table A.1: Mean proportion by weight and frequency of occurrence (in parenthesis) for brown trout < 300 mm (BNT-J), brown trout ≥ 300 mm (BNT), burbot (BBT), and lake trout (LKT) by season and all seasons combined (data are pooled for years 2020 – 2022). Diet taxa are generally grouped by order; however, some taxa could only be classified to phylum or class (i.e., Annelida and Arachnida). No lake trout were sampled during summer across all years; therefore, no diet statistics were calculated for summer lake trout. Sample size of diets with contents (in parenthesis) are displayed under each species by season.

	Spring				Summer			Autumn				Overall			
Diet item	BNT-J (28)	BNT (162)	BBT (23)	LKT (17)	BNT-J (6)	BNT (86)	BBT (18)	BNT-J (74)	BNT (124)	BBT (15)	LKT (5)	BNT-J (108)	BNT (372)	BBT (56)	LKT (22)
Amphipoda															
Amphipoda parts	0.01	0.04	0.02	0.00	0.00	0.01	0.00	0.01	0.02	0.00	0.00	0.01	0.03	0.01	0.00
	(0.18)	(0.32)	(0.09)	(0.00)	(0.00)	(0.03)	(0.01)	(0.05)	(0.18)	(0.13)	(0.00)	(0.08)	(0.21)	(0.07)	(0.00)
Gammaridae	0.09	0.12	0.22	0.00	0.00	0.02	0.05	0.19	0.15	017	0.00	0.16	0.11	0.15	0.00
	(0.36)	(0.42)	(0.35)	(0.00)	(0.00)	(0.13)	(0.06)	(0.49)	(0.50)	(0.20)	(0.00)	(0.43)	(0.38)	(0.21)	(0.00)
Hyalellidae	0.02	0.01	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.02	0.00
	(0.32)	(0.17)	(0.13)	(0.00)	(0.00)	(0.13)	(0.00)	(0.14)	(0.17)	(0.13)	(0.00)	(0.18)	(0.16)	(0.09)	(0.00)
Annelida															
Annelida	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.01	0.00	0.00	0.02	0.00	0.00	0.00
	(0.04)	(0.00)	(0.00)	(0.06)	(0.00)	(0.01)	(0.00)	(0.07)	(0.02)	(0.00)	(0.00)	(0.06)	(0.01)	(0.00)	(0.05)
Hirudinea	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)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.02)	(0.00)
Oligochaeta	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	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)	(0.01)	(0.02)	(0.00)	(0.00)	(0.01)	(0.01)	(0.00)	(0.00)
Anomopoda															
Bosminidae	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)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Daphniidae	0.00	0.00	0.00	0.00	0.26	0.02	0.00	0.27	0.03	0.00	0.00	0.20	0.02	0.00	0.00
	(0.00)	(0.04)	(0.00)	(0.06)	(0.67)	(0.13)	(0.00)	(0.49)	(0.23)	(0.20)	(0.00)	(0.37)	(0.12)	(0.05)	(0.05)
Arachnida															
Arachnida	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
	(0.04)	(0.00)	(0.00)	(0.00)	(0.00)	(0.03)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)	(0.01)	(0.01)	(0.00)	(0.00)

Table A.1: Continued.

Diet item	Spring BNT-J (28)	Spring BNT (162)	Spring BBT (23)	Spring LKT (17)	Summer BNT-J (6)	Summer BNT (86)	Summer BBT (18)	Autumn BNT-J (74)	Autumn BNT (124)	Autumn BBT (15)	Autumn LKT (5)	Overall BNT-J (108)	Overall BNT (372)	Overall BBT (56)	Overall LKT (22)
Coleoptera															
Amphizoidae	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)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.02)	(0.00)	().00)	(0.00)	(0.01)	(0.00)	(0.00)
Anthicidae	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)	(0.01)	(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)
Carabidae	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)	(0.03)	(0.00)	(0.01)	(0.01)	(0.00)	(0.00)	(0.01)	(0.01)	(0.00)	(0.00)
Chrysomelidae	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)	(0.01)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)
Coleoptera parts	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)	(0.01)	(0.00)	(0.00)	(0.00)	(0.02)	(0.06)	(0.05)	(0.08)	(0.07)	(0.00)	(0.04)	(0.04)	(0.04)	(0.00)
Curculionidae	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)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Dryopidae	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)	(0.01)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)
Dysticidae	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)	(0.01)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)	(0.02)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)
Gyrinidae	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)	(0.04)	(0.00)	(0.00)	(0.17)	(0.09)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)	(0.01)	(0.04)	(0.00)	(0.00)
Halipilidae	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
	(0.04)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)	(0.00)	(0.02)	(0.00)	(0.00)	(0.00)
Histeridae	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.00
	(0.04)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)	(0.00)	(0.02)	(0.00)	(0.00)	(0.00)
Hydraenidae	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)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Scarabaeidae	0.00	0.01	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.02)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)
Tenebrionidae	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)	(0.02)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)
Copepoda															
Copepoda	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)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Cypriniformes															

Table A.1: Continued.

Diet item	Spring				Summer			Autumn				Overall			
	BNT-J (28)	BNT (162)	BBT (23)	LKT (17)	BNT-J (6)	BNT (86)	BBT (18)	BNT-J (74)	BNT (124)	BBT (15)	LKT (5)	BNT-J (108)	BNT (372)	BBT (56)	LKT (22)
C. catostomus	0.00	0.02	0.09	0.08	0.00	0.04	0.06	0.00	0.02	0.00	0.00	0.00	0.03	0.05	0.07
	(0.00)	(0.04)	(0.09)	(0.12)	(0.00)	(0.06)	(0.06)	(0.01)	(0.02)	(0.00)	(0.00)	(0.01)	(0.04)	(0.05)	(0.09)
C. commersonii	0.00	0.01	0.03	0.00	0.00	0.03	0.00	0.00	0.01	0.00	0.04	0.00	0.02	0.01	0.09
	(0.00)	(0.02)	(0.09)	(0.00)	(0.00)	(0.06)	(0.00)	(0.00)	(0.02)	(0.00)	(0.04)	(0.00)	(0.03)	(0.04)	(0.09)
C. plumbeus	0.00	0.01	0.04	0.00	0.00	0.03	0.22	0.00	0.01	0.00	0.00	0.00	0.01	0.09	0.00
	(0.00)	(0.01)	(0.04)	(0.00)	(0.00)	(0.03)	(0.22)	(0.00)	(0.02)	(0.00)	(0.00)	(0.00)	(0.02)	(0.09)	(0.00)
R. cataractae	0.00	0.01	0.04	0.00	0.00	0.02	0.03	0.01	0.03	0.00	0.00	0.01	0.02	0.03	0.00
	(0.00)	(0.04)	(0.04)	(0.00)	(0.00)	(0.07)	(0.06)	(0.01)	(0.06)	(0.00)	(0.00)	(0.01)	(0.06)	(0.04)	(0.00)
Diptera															
Ceratopogonidae	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)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Chironomidae	0.07	0.08	0.00	0.01	0.14	0.03	0.01	0.03	0.00	0.00	0.00	0.04	0.04	0.00	0.01
	(0.21)	(0.20)	(0.09)	(0.12)	(0.67)	(0.42)	(0.11)	(0.08)	(0.06)	(0.07)	(0.00)	(0.15)	(0.20)	(0.09)	(0.09)
Culicidae	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)	(0.01)	(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)
Diptera parts	0.05	0.03	0.00	0.05	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.01	0.02	0.00	0.04
	(0.07)	(0.09)	(0.00)	(0.18)	(0.33)	(0.21)	(0.00)	(0.08)	(0.06)	(0.00)	(0.00)	(0.09)	(0.11)	(0.00)	(0.14)
Ephydridae	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)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Phoridae	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)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Sciomyzidae	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)	(0.01)	(0.00)	(0.01)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)	(0.00)
Simuliidae	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)	(0.01)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)
Ephemeroptera															
Baetidae	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)	(0.04)	(0.00)	(0.00)	(0.00)	(0.02)	(0.00)	(0.00)	(0.06)	(0.07)	(0.00)	(0.00)	(0.05)	(0.02)	(0.00)
Caenidae	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	(0.04)	(0.01)	(0.00)	(0.00)	(0.50)	(0.30)	(0.00)	(0.01)	(0.02)	(0.07)	(0.00)	(0.05)	(0.08)	(0.02)	(0.00)
Ephemerella	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.02)	(0.04)	(0.00)	(0.17)	(0.00)	(0.00)	(0.01)	(0.03)	(0.00)	(0.00)	(0.02)	(0.02)	(0.02)	(0.00)
Ephemeroptera	0.06	0.03	0.08	0.04	0.01	0.01	0.07	0.03	0.00	0.04	0.00	0.04	0.01	0.06	0.03
parts	(0.43)	(0.03)	(0.22)	(0.06)	(0.33)	(0.16)	(0.22)	(0.15)	(0.13)	(0.27)	(0.00)	(0.23)	(0.21)	(0.21)	(0.05)

Table A.1: Continued.

Diet item	Spring				Summer			Autumn				Overall			
	BNT-J (28)	BNT (162)	BBT (23)	LKT (17)	BNT-J (6)	BNT (86)	BBT (18)	BNT-J (74)	BNT (124)	BBT (15)	LKT (5)	BNT-J (108)	BNT (372)	BBT (56)	LKT (22)
Heptageniidae	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	0.01	0.00
	(0.00)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.07)	(0.00)	(0.00)	(0.01)	(0.02)	(0.00)
Isonchia	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)	(0.17)	(0.01)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)	(0.01)	(0.01)	(0.00)	().00)
Letophyphidae	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)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Neoephemeridae	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)	().00)	(0.00)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Oligoneuriidae	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)	(0.17)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)	(0.00)
Gadiformes															
L. lota	0.00	0.01	0.08	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.03	0.00
	(0.00)	(0.01)	(0.09)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)	(0.00)	(0.01)	(0.04)	(0.00)
Gastropoda															
Gastropoda parts	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.02	0.01	0.00	0.00	0.01	0.01	0.00	0.00
	(0.00)	(0.07)	(0.00)	(0.00)	(0.00)	(0.03)	(0.06)	(0.07)	(0.07)	(0.00)	(0.00)	(0.05)	(0.06)	(0.02)	(0.00)
Lymnaeidae	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.02	0.00	0.02	0.05	0.00	0.00
	(0.00)	(0.02)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.04)	(0.02)	(0.13)	(0.00)	(0.06)	(0.12)	(0.04)	(0.00)
Physidae	0.00	0.02	0.00	0.00	0.00	0.04	0.00	0.02	0.08	0.00	0.00	0.02	0.05	0.00	0.00
	(0.04)	(0.13)	(0.00)	(0.00)	(0.17)	(0.14)	(0.00)	(0.05)	(0.21)	(0.00)	(0.00)	(0.06)	(0.16)	(0.00)	(0.00)
Planorbidae	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)	(0.01)	(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)
Hemiptera															
Corixidae	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.01	0.01	0.00	0.00	0.00	0.01	0.00
	(0.00)	(0.15)	(0.00)	(0.06)	(0.00)	(0.07)	(0.11)	(0.09)	(0.24)	(0.13)	(0.00)	(0.06)	(0.16)	(0.07)	(0.05)
Gerridae	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)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)
Hemiptera parts	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.00
	(0.00)	(0.01)	(0.00)	(0.00)	(0.00)	(0.03)	(0.00)	(0.04)	(0.02)	(0.00)	(0.00)	(0.03)	(0.02)	(0.00)	(0.00)
Homoptera	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)	(0.03)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)
Lygaeidae	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)	(0.02)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)

Table A.1: Continued.

Diet item	Spring BNT-J (28)	Spring BNT (162)	Spring BBT (23)	Spring LKT (17)	Summer BNT-J (6)	Summer BNT (86)	Summer BBT (18)	Autumn BNT-J (74)	Autumn BNT (124)	Autumn BBT (15)	Autumn LKT (5)	Overall BNT-J (108)	Overall BNT (372)	Overall BBT (56)	Overall LKT (22)
Saldidae	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)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.02)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)
Hymenoptera															
Anthophila	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)	(0.01)	(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)
Apidae	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)	(0.01)	(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)
Braconidae	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)	(0.08)	(0.00)	(0.01)	(0.03)	(0.00)	(0.00)	(0.01)	(0.03)	(0.00)	(0.00)
Diapriidae	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)	(0.01)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)	(0.00)
Formicidae	0.02	0.01	0.00	0.00	0.15	0.19	0.03	0.00	0.02	0.00	0.00	0.01	0.05	0.01	0.00
	(0.11)	(0.08)	(0.00)	(0.00)	(0.50)	(0.55)	(0.17)	(0.04)	(0.06)	(0.00)	(0.00)	(0.08)	(0.18)	(0.05)	(0.00)
Hymenoptera parts	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)	(0.01)	(0.00)	(0.00)	(0.02)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)
Ichneumonidae	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)	(0.01)	(0.00)	(0.00)	(0.00)	(0.02)	(0.00)	(0.00)	(0.02)	(0.00)	(0.00)	(0.00)	(0.02)	(0.00)	(0.00)
Pompilidae	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)	(0.02)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)
Lepidoptera															
Lepidoptera parts	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)	(0.17)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)	(0.00)
Odonata															
Coenagrionidae	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00
	(0.04)	(0.02)	(0.00)	(0.00)	(0.00)	(0.05)	(0.06)	(0.01)	(0.02)	(0.00)	(0.00)	(0.02)	(0.02)	(0.02)	(0.00)
Odonata parts	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)	(0.03)	(0.02)	(0.00)	(0.00)	(0.02)	(0.01)	(0.00)	(0.00)
Petaluridae	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)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Orthoptera															
Caelifera	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)	(0.01)	(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)
Turbellaria															

Table A.1: Continued.

Diet item	Spring				Summer			Autumn				Overall			
	BNT-J (28)	BNT (162)	BBT (23)	LKT (17)	BNT-J (6)	BNT (86)	BBT (18)	BNT-J (74)	BNT (124)	BBT (15)	LKT (5)	BNT-J (108)	BNT (372)	BBT (56)	LKT (22)
Turbellaria	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)	(0.01)	(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)
Plecoptera															
Capniidae	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.01
	(0.00)	(0.01)	(0.00)	(0.06)	(0.00)	(0.01)	(0.00)	(0.00)	(0.02)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.05)
Peltoperlidae	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)	(0.01)	(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)
Perlidae	0.01	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.02	0.01	0.00
	(0.04)	(0.10)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.01)	(0.01)	(0.13)	(0.00)	(0.02)	(0.05)	(0.04)	(0.00)
Perlodidae	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)	(0.10)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.04)	(0.07)	(0.00)	(0.00)	(0.06)	(0.02)	(0.00)
Plecoptera parts	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00
	(0.04)	(0.12)	(0.00)	(0.00)	(0.00)	(0.08)	(0.00)	(0.07)	(0.04)	(0.13)	(0.00)	(0.06)	(0.09)	(0.04)	(0.00)
Rodentia															
Muridae	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)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Salmoniformes															
O. mykiss	0.00	0.07	0.09	0.59	0.00	0.01	0.00	0.00	0.05	0.00	0.19	0.00	0.05	0.04	0.50
	(0.00)	(0.08)	(0.09)	(0.65)	(0.00)	(0.03)	(0.00)	(0.00)	(0.06)	(0.00)	(0.20)	(0.00)	(0.06)	(0.04)	(0.55)
P. williamsoni	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)	(0.01)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)
S. trutta	0.00	0.00	0.00	0.12	0.00	0.01	0.05	0.00	0.01	0.00	0.00	0.00	0.00	0.02	0.09
	(0.00)	(0.01)	(0.00)	(0.12)	(0.00)	(0.03)	(0.06)	(0.00)	(0.01)	(0.00)	(0.00)	(0.00)	(0.01)	(0.02)	(0.09)
Sphaeriida															
Sphaerridae	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	0.01	0.00
	(0.00)	(0.02)	(0.04)	(0.00)	(0.00)	(0.01)	(0.00)	(0.03)	(0.04)	(0.00)	(0.00)	(0.02)	(0.02)	(0.02)	(0.00)
Trichoptera															
Brachycentridae	0.08	0.01	0.00	0.00	0.00	0.01	0.00	0.01	0.03	0.00	0.00	0.03	0.02	0.00	0.00
	(0.21)	(0.19)	(0.00)	(0.00)	(0.00)	(0.05)	(0.00)	(0.11)	(0.19)	(0.07)	(0.00)	(0.13)	(0.16)	(0.02)	(0.00)
Glossomatidae	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)	(0.01)	(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)
Helicopsychidae	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

Table A.1: Continued.

Diet item	Spring BNT-J (28)	Spring BNT (162)	Spring BBT (23)	Spring LKT (17)	Summer BNT-J (6)	Summer BNT (86)	Summer BBT (18)	Autumn BNT-J (74)	Autumn BNT (124)	Autumn BBT (15)	Autumn LKT (5)	Overall BNT-J (108)	Overall BNT (372)	Overall BBT (56)	Overall LKT (22)
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.03)	(0.00)	(0.07)	(0.01)	(0.00)	(0.00)	(0.05)	(0.01)	(0.00)	(0.00)
Hydropsychidae	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.01	0.01	0.09	0.00	0.00	0.01	0.02	0.00
	(0.00)	(0.01)	(0.00)	(0.00)	(0.00)	(0.08)	(0.00)	(0.08)	(0.06)	(0.40)	(0.00)	(0.06)	(0.04)	(0.11)	(0.00)
Hydroptilidae	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)	(0.01)	(0.00)	(0.00)	(0.33)	(0.03)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.02)	(0.01)	(0.00)	(0.00)
Lepidostomatidae	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)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.01)	(0.03)	(0.00)	(0.00)	(0.01)	(0.01)	(0.00)	(0.00)
Leptoceridae	0.21	0.05	0.00	0.00	0.16	0.01	0.00	0.03	0.03	0.00	0.00	0.08	0.04	0.00	0.00
	(0.64)	(0.37)	(0.00)	(0.00)	(0.50)	(0.14)	(0.00)	(0.19)	(0.26)	(0.07)	(0.00)	(0.32)	(0.28)	(0.02)	(0.00)
Molannidae	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)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Philopotamidae	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)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Phryganeidae	0.01	0.07	0.06	0.00	0.00	0.03	0.00	0.13	0.21	0.11	0.00	0.09	0.10	0.05	0.00
	(0.07)	(0.18)	(0.17)	(0.00)	(0.00)	(0.07)	(0.00)	(0.18)	(0.43)	(0.13)	(0.00)	(0.14)	(0.24)	(0.11)	(0.00)
Polycentropodidae	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)	(0.01)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Psychomyiidae	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)	(0.03)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)
Rhyacophilidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	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)	(0.07)	(0.00)	(0.00)	(0.00)	(0.02)	(0.00)
Trichopteran parts	0.16	0.08	0.04	0.00	0.06	0.02	0.00	0.05	0.04	0.12	0.00	0.08	0.05	0.05	0.00
	(0.32)	(0.31)	(0.13)	(0.00)	(0.50)	(0.34)	(0.00)	(0.24)	(0.28)	(0.47)	(0.00)	(0.28)	(0.31)	(0.18)	(0.00)
Uenoidae	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)	(0.02)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)
Trombidiformes															
Hydrachnidia	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)	(0.01)	(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)
Other															
Exuviae	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00
	(0.00)	(0.05)	(0.00)	(0.00)	(0.00)	(0.09)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.04)	(0.00)	(0.00)
Fish eggs	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.05	0.16	0.00	0.02	0.02	0.04	0.00

Table A.1: Continued.

Diet item	Spring				Summer			Autumn				Overall			
	BNT-J (28)	BNT (162)	BBT (23)	LKT (17)	BNT-J (6)	BNT (86)	BBT (18)	BNT-J (74)	BNT (124)	BBT (15)	LKT (5)	BNT-J (108)	BNT (372)	BBT (56)	LKT (22)
	(0.00)	(0.01)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.07)	(0.13)	(0.20)	(0.00)	(0.05)	(0.05)	(0.05)	(0.00)
Fish parts	0.03	0.04	0.07	0.09	0.17	0.04	0.16	0.01	0.01	0.05	0.00	0.02	0.03	0.09	0.07
	(0.04)	(0.01)	(0.09)	(0.12)	(0.17)	(0.17)	(0.24)	(0.04)	(0.10)	(0.27)	(0.00)	(0.05)	(0.12)	(0.20)	(0.09)
Insecta parts	0.02	0.02	0.04	0.00	0.00	0.15	0.23	0.04	0.03	0.00	0.21	0.04	0.06	0.09	0.05
	(0.18)	(0.20)	(0.09)	(0.06)	(0.00)	(0.52)	(0.00)	(0.20)	(0.21)	(0.07)	(0.40)	(0.19)	(0.28)	(0.21)	(0.14)
Organic matter	0.11	0.04	0.04	0.00	0.00	0.08	0.00	0.00	0.04	0.10	0.20	0.03	0.05	0.04	0.05
	(0.14)	(0.07)	(0.04)	(0.00)	(0.00)	(0.14)	(0.00)	(0.04)	(0.11)	(0.13)	(0.20)	(0.06)	(0.10)	(0.05)	(0.05)
Seeds	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00
	(0.00)	(0.01)	(0.00)	(0.00)	(0.17)	(0.08)	(0.00)	(0.03)	(0.00)	(0.00)	(0.00)	(0.03)	(0.02)	(0.00)	(0.00)
Zooplankton parts	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)	(0.02)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	(0.00)

APPENDIX B

CHAPTER 4 SUPPLEMENTAL TABLES AND FIGURES

Table B.1: Maximum and minimum mean daily water temperature (ºC) observed for Torrey, Ring, and Trail lakes pooled, Wyoming, USA. Maximum mean daily water temperature represents the lake and depth location (i.e., 0.3-meters below surface, half of max depth, and max depth) that had the highest average temperature for that given day. Conversely, minimum mean daily water temperature represents the lake and depth location with the lowest average temperature for a given day. Average daily water temperatures were used to simulate consumption in bioenergetic modeling.

Date	Maximum average daily temperature (ºC)	Minimum average daily temperature (ºC)	Simulation Day	Simulation Year
10/1/21	12.89	10.76	1	1
10/2/21	12.79	10.60	2	1
10/3/21	12.78	10.57	3	1
10/4/21	12.73	10.54	4	1
10/5/21	12.65	10.41	5	1
10/6/21	12.52	10.44	6	1
10/7/21	12.36	10.33	7	1
10/8/21	12.24	10.25	8	1
10/9/21	12.02	10.07	9	1
10/10/21	11.62	9.68	10	1
10/11/21	11.28	9.28	11	1
10/12/21	10.76	8.63	12	1
10/13/21	10.29	8.04	13	1
10/14/21	9.80	7.43	14	1
10/15/21	9.22	6.91	15	1
10/16/21	8.83	6.57	16	1
10/17/21	8.82	6.61	17	1
10/18/21	8.84	6.63	18	1
10/19/21	8.61	6.61	19	1
10/20/21	8.53	6.43	20	1
10/21/21	8.47	6.42	21	1
10/22/21	8.52	6.53	22	1
10/23/21	8.38	6.39	23	1
10/24/21	8.29	6.23	24	1
10/25/21	8.21	6.25	25	1
10/26/21	8.04	6.20	26	1
10/27/21	7.60	5.86	27	1
10/28/21	7.30	5.69	28	1
10/29/21	7.26	5.68	29	1

Table B.1: Continued.

Date	Maximum average daily temperature (ºC)	Minimum average daily temperature (ºC)	Simulation Day	Simulation Year
10/30/21	7.19	5.60	30	1
10/31/21	7.05	5.41	31	1
11/1/21	6.92	5.21	32	1
11/2/21	6.81	5.13	33	1
11/3/21	6.71	5.06	34	1
11/4/21	6.64	5.00	35	1
11/5/21	6.50	4.94	36	1
11/6/21	6.42	4.89	37	1
11/7/21	6.33	4.79	38	1
11/8/21	6.14	4.57	39	1
11/9/21	6.03	4.41	40	1
11/10/21	5.70	4.06	41	1
11/11/21	5.24	3.62	42	1
11/12/21	4.97	3.48	43	1
11/13/21	4.89	3.53	44	1
11/14/21	4.82	3.55	45	1
11/15/21	4.78	3.58	46	1
11/16/21	4.68	3.53	47	1
11/17/21	4.28	3.08	48	1
11/18/21	3.95	2.69	49	1
11/19/21	3.74	2.80	50	1
11/20/21	3.59	2.64	51	1
11/21/21	3.30	2.29	52	1
11/22/21	3.13	2.03	53	1
11/23/21	3.09	1.92	54	1
11/24/21	2.73	1.59	55	1
11/25/21	2.34	1.25	56	1
11/26/21	2.16	0.95	57	1
11/27/21	2.07	0.88	58	1
11/28/21	1.97	0.79	59	1
11/29/21	2.01	0.88	60	1
11/30/21	1.96	0.88	61	1
12/1/21	1.90	0.87	62	1

Table B.1: Continued.

Date	Maximum average daily temperature (ºC)	Minimum average daily temperature (ºC)	Simulation Day	Simulation Year
12/2/21	2.00	1.01	63	1
12/3/21	2.01	1.09	64	1
12/4/21	1.97	1.07	65	1
12/5/21	1.83	0.95	66	1
12/6/21	1.65	0.89	67	1
12/7/21	1.34	0.98	68	1
12/8/21	1.18	1.08	69	1
12/9/21	1.22	0.91	70	1
12/10/21	1.30	0.92	71	1
12/11/21	1.39	0.99	72	1
12/12/21	1.47	1.05	73	1
12/13/21	1.60	1.11	74	1
12/14/21	1.70	1.15	75	1
12/15/21	1.79	1.14	76	1
12/16/21	1.86	1.16	77	1
12/17/21	1.91	1.16	78	1
12/18/21	1.99	1.17	79	1
12/19/21	2.02	1.19	80	1
12/20/21	2.14	1.24	81	1
12/21/21	2.20	1.30	82	1
12/22/21	2.24	1.36	83	1
12/23/21	2.27	1.38	84	1
12/24/21	2.26	1.41	85	1
12/25/21	2.33	1.40	86	1
12/26/21	2.38	1.43	87	1
12/27/21	2.39	1.43	88	1
12/28/21	2.47	1.43	89	1
12/29/21	2.54	1.44	90	1
12/30/21	2.54	1.48	91	1
12/31/21	2.58	1.50	92	1
1/1/22	2.64	1.53	93	1
1/2/22	2.67	1.56	94	1
1/3/22	2.68	1.59	95	1
1/4/22	2.71	1.62	96	1

Table B.1: Continued.

Date	Maximum average daily temperature (ºC)	Minimum average daily temperature (ºC)	Simulation Day	Simulation Year
1/5/22	2.74	1.61	97	1
1/6/22	2.73	1.63	98	1
1/7/22	2.76	1.64	99	1
1/8/22	2.84	1.69	100	1
1/9/22	2.86	1.70	101	1
1/10/22	2.86	1.73	102	1
1/11/22	2.93	1.73	103	1
1/12/22	2.95	1.79	104	1
1/13/22	2.97	1.83	105	1
1/14/22	2.99	1.90	106	1
1/15/22	3.03	1.93	107	1
1/16/22	3.03	1.98	108	1
1/17/22	3.02	2.03	109	1
1/18/22	3.05	2.10	110	1
1/19/22	3.00	2.11	111	1
1/20/22	3.03	2.19	112	1
1/21/22	3.00	2.23	113	1
1/22/22	3.03	2.30	114	1
1/23/22	3.05	2.34	115	1
1/24/22	3.06	2.40	116	1
1/25/22	3.13	2.40	117	1
1/26/22	3.14	2.48	118	1
1/27/22	3.12	2.54	119	1
1/28/22	3.14	2.60	120	1
1/29/22	3.18	2.65	121	1
1/30/22	3.22	2.71	122	1
1/31/22	3.31	2.74	123	1
2/1/22	3.34	2.78	124	1
2/2/22	3.38	2.81	125	1
2/3/22	3.41	2.89	126	1
2/4/22	3.50	2.94	127	1
2/5/22	3.53	3.01	128	1
2/6/22	3.63	3.07	129	1
2/7/22	3.74	3.18	130	1

Table B.1: Continued.

Date	Maximum average daily temperature (ºC)	Minimum average daily temperature (ºC)	Simulation Day	Simulation Year
2/8/22	3.77	3.22	131	1
2/9/22	3.86	3.28	132	1
2/10/22	3.92	3.30	133	1
2/11/22	3.99	3.28	134	1
2/12/22	4.19	3.33	135	1
2/13/22	4.32	3.52	136	1
2/14/22	4.40	3.58	137	1
2/15/22	4.39	3.58	138	1
2/16/22	4.34	3.59	139	1
2/17/22	4.45	3.65	140	1
2/18/22	4.51	3.69	141	1
2/19/22	4.54	3.71	142	1
2/20/22	4.51	3.73	143	1
2/21/22	4.45	3.75	144	1
2/22/22	4.34	3.74	145	1
2/23/22	4.29	3.78	146	1
2/24/22	4.30	3.80	147	1
2/25/22	4.35	3.77	148	1
2/26/22	4.31	3.76	149	1
2/27/22	4.29	3.75	150	1
2/28/22	4.30	3.78	151	1
3/1/22	4.42	3.77	152	1
3/2/22	4.61	3.83	153	1
3/3/22	4.78	3.90	154	1
3/4/22	4.56	3.86	155	1
3/5/22	4.37	3.83	156	1
3/6/22	4.30	3.84	157	1
3/7/22	4.29	3.86	158	1
3/8/22	4.29	3.85	159	1
3/9/22	4.29	3.86	160	1
3/10/22	4.27	3.86	161	1
3/11/22	4.23	3.84	162	1
3/12/22	4.28	3.88	163	1
3/13/22	4.35	3.88	164	1

Table B.1: Continued.

Date	Maximum average daily temperature (ºC)	Minimum average daily temperature (ºC)	Simulation Day	Simulation Year
3/14/22	4.37	3.90	165	1
3/15/22	4.42	3.90	166	1
3/16/22	4.45	3.90	167	1
3/17/22	4.50	3.92	168	1
3/18/22	4.57	3.98	169	1
3/19/22	4.66	3.99	170	1
3/20/22	4.68	3.99	171	1
3/21/22	4.67	4.04	172	1
3/22/22	4.86	4.12	173	1
3/23/22	5.02	4.12	174	1
3/24/22	5.09	4.18	175	1
3/25/22	5.19	4.24	176	1
3/26/22	5.30	4.16	177	1
3/27/22	5.51	4.24	178	1
3/28/22	5.55	4.30	179	1
3/29/22	5.51	4.35	180	1
3/30/22	5.59	4.29	181	1
3/31/22	5.42	4.31	182	1
4/1/22	5.42	4.32	183	1
4/2/22	5.37	4.31	184	1
4/3/22	5.27	4.29	185	1
4/4/22	4.82	4.33	186	1
4/5/22	4.24	4.10	187	1
4/6/22	4.10	3.84	188	1
4/7/22	4.12	3.75	189	1
4/8/22	4.39	3.89	190	1
4/9/22	4.66	4.08	191	1
4/10/22	4.66	4.09	192	1
4/11/22	4.44	3.98	193	1
4/12/22	4.15	3.80	194	1
4/13/22	3.77	3.70	195	1
4/14/22	3.83	3.61	196	1
4/15/22	3.88	3.73	197	1
4/16/22	4.07	3.84	198	1

Table B.1: Continued.

Date	Maximum average daily temperature (ºC)	Minimum average daily temperature (ºC)	Simulation Day	Simulation Year
4/17/22	4.21	3.90	199	1
4/18/22	4.40	3.96	200	1
4/19/22	4.76	4.21	201	1
4/20/22	4.83	4.18	202	1
4/21/22	5.10	4.28	203	1
4/22/22	5.24	4.41	204	1
4/23/22	5.30	4.41	205	1
4/24/22	5.33	4.40	206	1
4/25/22	5.55	4.40	207	1
4/26/22	5.85	4.55	208	1
4/27/22	6.06	4.65	209	1
4/28/22	6.18	4.72	210	1
4/29/22	6.07	4.97	211	1
4/30/22	6.36	5.01	212	1
5/1/22	6.62	5.17	213	1
5/2/22	6.67	5.19	214	1
5/3/22	6.62	5.32	215	1
5/4/22	6.92	5.32	216	1
5/5/22	7.59	5.54	217	1
5/6/22	7.76	6.03	218	1
5/7/22	8.18	6.41	219	1
5/8/22	8.00	6.45	220	1
5/9/22	7.83	6.40	221	1
5/10/22	7.64	6.18	222	1
5/11/22	7.83	6.29	223	1
5/12/22	7.96	6.41	224	1
5/13/22	7.85	6.45	225	1
5/14/22	7.88	6.54	226	1
5/15/22	8.06	6.65	227	1
5/16/22	9.22	6.65	228	1
5/17/22	9.63	6.87	229	1
5/18/22	9.93	7.26	230	1
5/19/22	9.66	7.89	231	1
5/20/22	9.17	7.75	232	1

Table B.1: Continued.

Date	Maximum average daily temperature (ºC)	Minimum average daily temperature (ºC)	Simulation Day	Simulation Year
5/21/22	8.84	7.68	233	1
5/22/22	8.82	7.64	234	1
5/23/22	8.74	7.65	235	1
5/24/22	8.91	7.65	236	1
5/25/22	9.08	7.90	237	1
5/26/22	9.89	7.92	238	1
5/27/22	10.42	8.19	239	1
5/28/22	10.30	8.40	240	1
5/29/22	9.83	8.67	241	1
5/30/22	9.21	8.61	242	1
5/31/22	9.20	8.22	243	1
6/1/22	9.29	8.14	244	1
6/2/22	9.52	8.12	245	1
6/3/22	9.93	8.25	246	1
6/4/22	10.36	8.33	247	1
6/5/22	10.55	8.46	248	1
6/6/22	10.72	8.74	249	1
6/7/22	10.96	8.80	250	1
6/8/22	11.11	8.70	251	1
6/9/22	11.67	8.71	252	1
6/10/22	12.12	8.79	253	1
6/11/22	12.54	9.01	254	1
6/12/22	12.99	9.13	255	1
6/13/22	12.91	9.31	256	1
6/14/22	12.13	8.93	257	1
6/15/22	11.52	8.55	258	1
6/16/22	11.63	8.44	259	1
6/17/22	12.05	8.46	260	1
6/18/22	12.62	8.61	261	1
6/19/22	13.15	8.75	262	1
6/20/22	13.00	9.06	263	1
6/21/22	12.61	9.08	264	1
6/22/22	13.08	9.20	265	1
6/23/22	13.81	9.29	266	1

Table B.1: Continued.

Date	Maximum average daily temperature (ºC)	Minimum average daily temperature (ºC)	Simulation Day	Simulation Year
6/24/22	14.08	9.49	267	1
6/25/22	13.96	9.59	268	1
6/26/22	13.97	9.67	269	1
6/27/22	14.46	9.66	270	1
6/28/22	14.88	9.97	271	1
6/29/22	15.09	10.15	272	1
6/30/22	15.04	10.32	273	1
7/1/22	15.01	10.53	274	1
7/2/22	15.04	10.66	275	1
7/3/22	15.25	10.80	276	1
7/4/22	15.60	10.91	277	1
7/5/22	15.88	11.08	278	1
7/6/22	16.33	11.08	279	1
7/7/22	16.52	11.16	280	1
7/8/22	16.62	11.31	281	1
7/9/22	17.10	11.35	282	1
7/10/22	17.30	11.46	283	1
7/11/22	17.22	11.53	284	1
7/12/22	17.45	11.50	285	1
7/13/22	17.65	11.48	286	1
7/14/22	17.81	11.49	287	1
7/15/22	17.85	11.47	288	1
7/16/22	17.91	11.49	289	1
7/17/22	18.10	11.44	290	1
7/18/22	18.46	11.44	291	1
7/19/22	17.76	11.44	292	1
7/20/22	17.65	11.42	293	1
7/21/22	17.72	11.38	294	1
7/22/22	17.82	11.38	295	1
7/23/22	17.98	11.39	296	1
7/24/22	17.98	11.39	297	1
7/25/22	18.12	11.40	298	1
7/26/22	18.17	11.40	299	1
7/27/22	18.17	11.42	300	1

Table B.1: Continued.

Date	Maximum average daily temperature (ºC)	Minimum average daily temperature (ºC)	Simulation Day	Simulation Year
7/28/22	18.20	11.43	301	1
7/29/22	18.33	11.41	302	1
7/30/22	18.49	11.43	303	1
7/31/22	18.63	11.48	304	1
8/1/22	18.79	11.48	305	1
8/2/22	18.57	11.51	306	1
8/3/22	18.28	11.52	307	1
8/4/22	18.39	11.52	308	1
8/5/22	18.38	11.51	309	1
8/6/22	18.14	11.50	310	1
8/7/22	18.00	11.47	311	1
8/8/22	18.05	11.43	312	1
8/9/22	18.10	11.42	313	1
8/10/22	18.25	11.40	314	1
8/11/22	18.45	11.45	315	1
8/12/22	18.47	11.48	316	1
8/13/22	18.48	11.47	317	1
8/14/22	18.52	11.52	318	1
8/15/22	18.51	11.51	319	1
8/16/22	18.61	11.53	320	1
8/17/22	18.81	11.55	321	1
8/18/22	19.06	11.57	322	1
8/19/22	19.05	11.61	323	1
8/20/22	19.13	11.66	324	1
8/21/22	19.11	11.67	325	1
8/22/22	19.18	11.70	326	1
8/23/22	18.93	11.75	327	1
8/24/22	18.80	11.75	328	1
8/25/22	18.57	11.83	329	1
8/26/22	18.48	11.83	330	1
8/27/22	18.22	11.91	331	1
8/28/22	17.84	11.89	332	1
8/29/22	17.67	11.84	333	1
8/30/22	17.86	11.85	334	1

Table B.1: Continued.

Date	Maximum average daily temperature (ºC)	Minimum average daily temperature (ºC)	Simulation Day	Simulation Year
8/31/22	17.92	11.85	335	1
9/1/22	17.91	11.87	336	1
9/2/22	17.88	11.85	337	1
9/3/22	17.90	11.87	338	1
9/4/22	17.91	11.92	339	1
9/5/22	17.75	11.91	340	1
9/6/22	17.67	11.91	341	1
9/7/22	17.71	11.94	342	1
9/8/22	17.57	12.01	343	1
9/9/22	17.07	12.04	344	1
9/10/22	16.57	12.04	345	1
9/11/22	16.48	11.99	346	1
9/12/22	16.45	12.14	347	1
9/13/22	16.37	12.13	348	1
9/14/22	16.22	12.26	349	1
9/15/22	16.11	12.29	350	1
9/16/22	15.84	12.54	351	1
9/17/22	15.52	13.32	352	1
9/18/22	15.34	13.07	353	1
9/19/22	15.35	12.93	354	1
9/20/22	15.30	12.85	355	1
9/21/22	15.18	12.84	356	1
9/22/22	14.95	12.75	357	1
9/23/22	14.52	12.52	358	1
9/24/22	14.21	12.25	359	1
9/25/22	14.14	12.20	360	1
9/26/22	14.07	12.15	361	1
9/27/22	14.16	12.05	362	1
9/28/22	14.26	11.99	363	1
9/29/22	14.16	11.91	364	1
9/30/22	14.05	11.85	365	1
10/1/22	13.85	11.73	1	2
10/2/22	13.71	11.51	2	2
10/3/22	13.60	11.29	3	2

Table B.1: Continued.

Date	Maximum average daily temperature (ºC)	Minimum average daily temperature (ºC)	Simulation Day	Simulation Year
10/4/22	13.47	11.07	4	2
10/5/22	13.38	10.87	5	2
10/6/22	13.34	10.76	6	2
10/7/22	13.32	10.77	7	2
10/8/22	13.25	10.78	8	2
10/9/22	13.14	10.66	9	2
10/10/22	13.02	10.59	10	2
10/11/22	12.66	10.48	11	2
10/12/22	12.18	10.15	12	2
10/13/22	11.98	10.01	13	2
10/14/22	11.79	9.89	14	2
10/15/22	11.66	9.79	15	2
10/16/22	11.54	9.60	16	2
10/17/22	11.41	9.44	17	2
10/18/22	11.37	9.29	18	2
10/19/22	11.29	9.23	19	2
10/20/22	11.15	9.20	20	2
10/21/22	10.95	9.11	21	2
10/22/22	10.73	8.84	22	2
10/23/22	10.25	8.36	23	2
10/24/22	9.56	7.68	24	2
10/25/22	8.95	7.12	25	2
10/26/22	8.55	6.61	26	2
10/27/22	8.19	6.19	27	2
10/28/22	7.82	5.78	28	2
10/29/22	7.60	5.60	29	2
10/30/22	7.46	5.40	30	2
10/31/22	7.25	5.19	31	2
11/1/22	7.19	5.16	32	2
11/2/22	6.99	5.04	33	2
11/3/22	6.72	4.70	34	2
11/4/22	6.29	4.33	35	2
11/5/22	5.81	3.83	36	2
11/6/22	5.45	3.40	37	2

Table B.1: Continued.

Date	Maximum average daily temperature (ºC)	Minimum average daily temperature (ºC)	Simulation Day	Simulation Year
11/7/22	5.25	3.18	38	2
11/8/22	5.18	3.21	39	2
11/9/22	5.02	3.03	40	2
11/10/22	4.72	2.55	41	2
11/11/22	4.31	2.35	42	2
11/12/22	4.10	2.60	43	2
11/13/22	4.00	2.70	44	2
11/14/22	3.76	2.83	45	2
11/15/22	3.27	2.97	46	2
11/16/22	3.19	2.96	47	2
11/17/22	3.21	2.67	48	2
11/18/22	3.20	2.49	49	2
11/19/22	3.30	2.55	50	2
11/20/22	3.44	2.68	51	2
11/21/22	3.69	2.81	52	2
11/22/22	3.78	2.87	53	2
11/23/22	3.90	2.94	54	2
11/24/22	3.85	2.99	55	2
11/25/22	3.93	3.06	56	2
11/26/22	4.11	3.10	57	2
11/27/22	3.95	3.09	58	2
11/28/22	3.66	2.89	59	2
11/29/22	3.63	2.91	60	2
11/30/22	3.73	3.03	61	2
12/1/22	3.68	2.97	62	2
12/2/22	3.85	2.87	63	2
12/3/22	3.87	2.94	64	2
12/4/22	3.90	2.99	65	2
12/5/22	3.96	2.99	66	2
12/6/22	4.01	3.03	67	2
12/7/22	4.10	3.08	68	2
12/8/22	4.18	3.15	69	2
12/9/22	4.22	3.17	70	2
12/10/22	4.23	3.19	71	2

Table B.1: Continued.

Date	Maximum average daily temperature (ºC)	Minimum average daily temperature (ºC)	Simulation Day	Simulation Year
12/11/22	4.32	3.21	72	2
12/12/22	4.36	3.22	73	2
12/13/22	4.41	3.22	74	2
12/14/22	4.45	3.21	75	2
12/15/22	4.50	3.24	76	2
12/16/22	4.54	3.22	77	2
12/17/22	4.51	3.27	78	2
12/18/22	4.48	3.31	79	2
12/19/22	4.51	3.32	80	2
12/20/22	4.49	3.33	81	2
12/21/22	4.54	3.31	82	2
12/22/22	4.61	3.34	83	2
12/23/22	4.55	3.34	84	2
12/24/22	4.49	3.36	85	2
12/25/22	4.59	3.31	86	2
12/26/22	4.69	3.41	87	2
12/27/22	4.67	3.42	88	2
12/28/22	4.66	3.44	89	2
12/29/22	4.65	3.46	90	2
12/30/22	4.66	3.49	91	2
12/31/22	4.68	3.50	92	2
1/1/23	4.61	3.42	93	2
1/2/23	4.71	3.49	94	2
1/3/23	4.84	3.48	95	2
1/4/23	4.81	3.26	96	2
1/5/23	4.79	3.22	97	2
1/6/23	4.86	3.24	98	2
1/7/23	4.92	3.27	99	2
1/8/23	4.94	3.27	100	2
1/9/23	4.89	3.23	101	2
1/10/23	4.82	3.08	102	2
1/11/23	4.90	3.09	103	2
1/12/23	4.96	3.10	104	2
1/13/23	4.92	3.02	105	2

Table B.1: Continued.

Date	Maximum average daily temperature (ºC)	Minimum average daily temperature (ºC)	Simulation Day	Simulation Year
1/14/23	4.89	2.96	106	2
1/15/23	4.91	3.01	107	2
1/16/23	4.90	3.00	108	2
1/17/23	4.93	2.98	109	2
1/18/23	4.97	2.98	110	2
1/19/23	4.97	3.02	111	2
1/20/23	4.80	3.01	112	2
1/21/23	4.76	3.13	113	2
1/22/23	4.79	3.10	114	2
1/23/23	4.91	3.07	115	2
1/24/23	4.93	3.24	116	2
1/25/23	4.83	3.18	117	2
1/26/23	4.70	3.10	118	2
1/27/23	4.60	3.28	119	2
1/28/23	4.75	3.27	120	2
1/29/23	4.77	3.10	121	2
1/30/23	4.78	3.14	122	2
1/31/23	4.83	3.09	123	2
2/1/23	4.83	3.15	124	2
2/2/23	4.90	3.17	125	2
2/3/23	4.88	3.32	126	2
2/4/23	4.86	3.19	127	2
2/5/23	4.84	3.06	128	2
2/6/23	4.88	3.15	129	2
2/7/23	4.90	3.19	130	2
2/8/23	4.90	2.99	131	2
2/9/23	4.90	2.89	132	2
2/10/23	4.94	2.94	133	2
2/11/23	4.98	2.95	134	2
2/12/23	5.03	2.82	135	2
2/13/23	5.04	2.82	136	2
2/14/23	5.08	2.82	137	2
2/15/23	5.07	2.78	138	2
2/16/23	5.02	2.74	139	2

Table B.1: Continued.

Date	Maximum average daily temperature (ºC)	Minimum average daily temperature (ºC)	Simulation Day	Simulation Year
2/17/23	4.95	2.78	140	2
2/18/23	4.95	2.73	141	2
2/19/23	5.00	2.78	142	2
2/20/23	5.05	2.75	143	2
2/21/23	5.05	2.70	144	2
2/22/23	5.09	2.75	145	2
2/23/23	5.10	2.70	146	2
2/24/23	5.06	2.66	147	2
2/25/23	5.00	2.63	148	2
2/26/23	4.96	2.62	149	2
2/27/23	4.94	2.62	150	2
2/28/23	4.89	2.59	151	2
3/1/23	4.92	2.61	152	2
3/2/23	4.95	2.59	153	2
3/3/23	4.95	2.58	154	2
3/4/23	4.96	2.57	155	2
3/5/23	4.95	2.51	156	2
3/6/23	4.99	2.53	157	2
3/7/23	5.02	2.61	158	2
3/8/23	5.02	2.62	159	2
3/9/23	4.90	2.59	160	2
3/10/23	4.85	2.60	161	2
3/11/23	4.86	2.57	162	2
3/12/23	4.81	2.54	163	2
3/13/23	4.74	2.53	164	2
3/14/23	4.78	2.54	165	2
3/15/23	4.80	2.55	166	2
3/16/23	4.79	2.57	167	2
3/17/23	4.78	2.50	168	2
3/18/23	4.80	2.48	169	2
3/19/23	4.77	2.51	170	2
3/20/23	4.73	2.49	171	2
3/21/23	4.75	2.58	172	2
3/22/23	4.79	2.60	173	2

Table B.1: Continued.

Date	Maximum average daily temperature (ºC)	Minimum average daily temperature (ºC)	Simulation Day	Simulation Year
3/23/23	4.80	2.61	174	2
3/24/23	4.79	2.58	175	2
3/25/23	4.76	2.52	176	2
3/26/23	4.72	2.52	177	2
3/27/23	4.75	2.51	178	2
3/28/23	4.74	2.56	179	2
3/29/23	4.82	2.54	180	2
3/30/23	4.86	2.57	181	2
3/31/23	4.81	2.58	182	2
4/1/23	4.72	2.55	183	2
4/2/23	4.66	2.57	184	2
4/3/23	4.66	2.57	185	2
4/4/23	4.69	2.56	186	2
4/5/23	4.72	2.55	187	2
4/6/23	4.70	2.52	188	2
4/7/23	4.69	2.50	189	2
4/8/23	4.70	2.47	190	2
4/9/23	4.70	2.54	191	2
4/10/23	4.75	2.64	192	2
4/11/23	4.79	3.17	193	2
4/12/23	4.71	3.64	194	2
4/13/23	4.91	3.73	195	2
4/14/23	4.92	3.86	196	2
4/15/23	4.84	3.90	197	2
4/16/23	4.83	3.87	198	2
4/17/23	4.84	3.95	199	2
4/18/23	4.82	4.07	200	2
4/19/23	4.80	4.11	201	2
4/20/23	4.93	4.08	202	2
4/21/23	5.12	4.15	203	2
4/22/23	4.97	4.15	204	2
4/23/23	4.98	4.14	205	2
4/24/23	5.04	4.17	206	2
4/25/23	4.95	4.19	207	2

Table B.1: Continued.

Date	Maximum average daily temperature (ºC)	Minimum average daily temperature (ºC)	Simulation Day	Simulation Year
4/26/23	5.13	4.25	208	2
4/27/23	5.38	4.17	209	2
4/28/23	5.45	4.30	210	2
4/29/23	5.63	4.23	211	2
4/30/23	5.70	4.30	212	2
5/1/23	5.54	4.34	213	2
5/2/23	5.63	4.36	214	2
5/3/23	6.05	4.46	215	2
5/4/23	6.58	4.72	216	2
5/5/23	6.90	4.97	217	2
5/6/23	6.83	5.08	218	2
5/7/23	6.93	5.63	219	2
5/8/23	6.99	5.96	220	2
5/9/23	7.32	6.21	221	2
5/10/23	7.55	6.33	222	2
5/11/23	7.65	6.34	223	2
5/12/23	8.00	6.33	224	2
5/13/23	8.19	6.42	225	2
5/14/23	8.23	6.39	226	2
5/15/23	8.50	6.46	227	2
5/16/23	9.06	6.59	228	2
5/17/23	9.49	6.69	229	2
5/18/23	10.01	6.75	230	2
5/19/23	10.24	6.78	231	2
5/20/23	10.68	6.83	232	2
5/21/23	11.07	6.87	233	2
5/22/23	11.71	6.87	234	2
5/23/23	12.03	6.95	235	2
5/24/23	12.42	6.97	236	2
5/25/23	12.64	7.00	237	2
5/26/23	12.59	7.03	238	2
5/27/23	12.44	7.05	239	2
5/28/23	12.46	7.10	240	2
5/29/23	12.42	7.09	241	2

Table B.1: Continued.

Date	Maximum average daily temperature (ºC)	Minimum average daily temperature (ºC)	Simulation Day	Simulation Year
5/30/23	12.40	7.10	242	2
5/31/23	12.49	7.10	243	2
6/1/23	12.77	7.13	244	2
6/2/23	12.84	7.15	245	2
6/3/23	12.66	7.14	246	2
6/4/23	12.44	7.17	247	2
6/5/23	12.24	7.18	248	2
6/6/23	12.41	7.17	249	2
6/7/23	12.58	7.20	250	2
6/8/23	12.81	7.42	251	2
6/9/23	12.79	7.45	252	2
6/10/23	12.84	7.54	253	2
6/11/23	12.76	7.57	254	2
6/12/23	12.57	7.61	255	2
6/13/23	12.66	7.65	256	2
6/14/23	13.02	7.69	257	2
6/15/23	12.88	7.71	258	2
6/16/23	12.68	7.75	259	2
6/17/23	12.51	7.78	260	2
6/18/23	12.60	7.76	261	2
6/19/23	12.55	7.84	262	2
6/20/23	12.30	7.94	263	2
6/21/23	12.14	8.28	264	2
6/22/23	12.04	8.98	265	2
6/23/23	11.89	9.16	266	2
6/24/23	11.53	9.24	267	2
6/25/23	11.66	9.42	268	2
6/26/23	11.88	9.45	269	2
6/27/23	12.20	9.46	270	2
6/28/23	12.50	9.62	271	2
6/29/23	12.95	9.68	272	2
6/30/23	13.20	9.69	273	2
7/1/23	13.71	9.82	274	2
7/2/23	14.19	10.01	275	2

Table B.1: Continued.

Date	Maximum average daily temperature (ºC)	Minimum average daily temperature (ºC)	Simulation Day	Simulation Year
7/3/23	14.81	10.13	276	2
7/4/23	14.75	10.45	277	2
7/5/23	14.43	10.60	278	2
7/6/23	14.70	10.79	279	2
7/7/23	14.84	10.90	280	2
7/8/23	14.74	10.91	281	2
7/9/23	14.87	10.90	282	2
7/10/23	15.20	10.88	283	2
7/11/23	15.46	10.88	284	2
7/12/23	15.76	10.94	285	2
7/13/23	16.03	10.92	286	2
7/14/23	16.31	10.91	287	2
7/15/23	16.59	10.87	288	2
7/16/23	16.82	10.85	289	2
7/17/23	17.04	10.83	290	2
7/18/23	16.98	10.85	291	2
7/19/23	17.19	10.84	292	2
7/20/23	17.19	10.83	293	2
7/21/23	17.22	10.83	294	2
7/22/23	17.37	10.84	295	2
7/23/23	17.77	10.83	296	2
7/24/23	17.87	10.85	297	2
7/25/23	17.98	10.87	298	2
7/26/23	18.09	10.90	299	2
7/27/23	17.91	10.91	300	2
7/28/23	17.88	10.92	301	2
7/29/23	18.02	10.92	302	2
7/30/23	18.09	10.92	303	2
7/31/23	18.25	10.93	304	2
8/1/23	18.40	10.99	305	2
8/2/23	18.30	10.98	306	2
8/3/23	18.04	13.44	307	2
8/4/23	17.88	13.53	308	2
8/5/23	17.59	13.28	309	2

Table B.1: Continued.

Date	Maximum average daily temperature (ºC)	Minimum average daily temperature (ºC)	Simulation Day	Simulation Year
8/6/23	17.36	13.41	310	2
8/7/23	16.95	13.38	311	2
8/8/23	16.68	13.32	312	2
8/9/23	16.48	13.27	313	2
8/10/23	16.55	13.27	314	2
8/11/23	16.51	13.33	315	2
8/12/23	16.66	13.33	316	2
8/13/23	16.81	13.30	317	2
8/14/23	16.71	13.35	318	2
8/15/23	17.18	13.33	319	2
8/16/23	17.51	13.38	320	2
8/17/23	17.79	13.43	321	2
8/18/23	17.89	13.44	322	2
8/19/23	17.84	13.52	323	2
8/20/23	17.74	13.54	324	2
8/21/23	18.00	13.59	325	2
8/22/23	18.21	13.59	326	2
8/23/23	18.06	13.72	327	2
8/24/23	18.13	13.79	328	2
8/25/23	18.10	13.79	329	2
8/26/23	17.85	13.84	330	2
8/27/23	17.90	13.88	331	2
8/28/23	17.78	13.92	332	2
8/29/23	17.84	13.93	333	2
8/30/23	17.79	14.05	334	2
8/31/23	16.99	13.88	335	2
9/1/23	16.83	13.73	336	2
9/2/23	16.68	13.67	337	2
9/3/23	16.64	13.61	338	2
9/4/23	16.46	13.62	339	2
9/5/23	16.19	13.53	340	2
9/6/23	16.19	13.53	341	2
9/7/23	16.19	13.53	342	2
9/8/23	16.19	13.53	343	2

Table B.1: Continued.

Date	Maximum average daily temperature (ºC)	Minimum average daily temperature (ºC)	Simulation Day	Simulation Year
9/9/23	16.19	13.53	344	2
9/10/23	16.19	13.53	345	2
9/11/23	16.19	13.53	346	2
9/12/23	16.19	13.53	347	2
9/13/23	16.19	13.53	348	2
9/14/23	16.19	13.53	349	2
9/15/23	16.19	13.53	350	2
9/16/23	16.19	13.53	351	2
9/17/23	16.19	13.53	352	2
9/18/23	16.19	13.53	353	2
9/19/23	16.19	13.53	354	2
9/20/23	16.19	13.53	355	2
9/21/23	16.19	13.53	356	2
9/22/23	16.19	13.53	357	2
9/23/23	16.19	13.53	358	2
9/24/23	16.19	13.53	359	2
9/25/23	16.19	13.53	360	2
9/26/23	16.19	13.53	361	2
9/27/23	16.19	13.53	362	2
9/28/23	16.19	13.53	363	2
9/29/23	16.19	13.53	364	2
9/30/23	16.19	13.53	365	2

Table B.2: Caloric values of dietary taxa parameters used in bioenergetics models. 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 for use in Bioenergetics 4.0.

Prey item	Surrogate	J/g of wet weight	Source
Amphipoda		3908	Cummins & Wuycheck (1971)
Annelida		3272	Cummins & Wuycheck (1971)
Coleoptera	Insecta	3176	Cummins & Wuycheck (1971)
Diptera		2565	Cummins & Wuycheck (1971)
Ephemeroptera	Baetidae	4703	Cummins & Wuycheck (1971)
Gastropoda	Mollusca	2008	Cummins & Wuycheck (1971)
Hemiptera	Insecta	3176	Cummins & Wuycheck (1971)
Hymenoptera	Insecta	3176	Cummins & Wuycheck (1971)
Burbot	Osteichthyes	6247	Cummins & Wuycheck (1971)
Odonata	Insecta	3176	Cummins & Wuycheck (1971)
Osteichthyes		6247	Cummins & Wuycheck (1971)
Plecoptera	Insecta	3176	Cummins & Wuycheck (1971)
Trichoptera	Insecta	3176	Cummins & Wuycheck (1971)
Zooplankton	Daphnidae	1314	Cummins & Wuycheck (1971)
Other		3523	See Methods