PH.D. DISSERTATION PROPOSAL

Name: Rachelle Johnson **Faculty Adviser:** Julian Olden **Date:** 1/24/2023

This is to certify that this student's PhD Supervisory Committee had read and approved the Ph.D. Dissertation Proposal titled: Bioenergetics-based food web assessment of factors limiting production of native salmonids in Upper Skagit River reservoirs

Approval of Supervisory Committee:

POSITION	PRINTED NAME	SIGNATURE	DATE
CHAIR	Julian Olden	Julian Olden	1/24/2023
MEMBER	Dave Beauchamp		1/24/2023
MEMBER	Tom Quinn		
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Bioenergetics-based food web assessment of factors limiting production of native salmonids in Upper Skagit River reservoirs

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A proposal for the degree of

Doctor of Philosophy

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Introduction

Food web function drives ecosystem productivity and plays a critical role in ecosystem services and conservation of species of concern (McCann 2007). In lentic ecosystems, food web structure and function are influenced by a combination of biotic and abiotic factors, both natural and anthropogenic, including thermal structure, invasive species, climate change, and altered flow regimes. Increasing water demand and changing land use exacerbate impacts to native species through direct and indirect effects that propagate through food webs. Much progress has been made in studying how aquatic ecosystems are restructuring and adapting in response to both climatic and non-climatic stressors (McCann and Rooney 2009), but owing to complex interactions among stressors, the function of many ecosystems under future change remains highly uncertain (Staudinger et al. 2021). With increasing focus on managing for such ecosystem transformations (Lynch et al. 2021), additional research is needed to understand the complex dynamics that drive food web structure and adaptive capacity in lentic systems to best conserve ecosystem function, services, and species of concern under global change (McMeans et al. 2016).

Climate change alters thermal regimes and habitat accessibility in lakes and reservoirs worldwide (Woolway and Merchant 2019, Miranda et al. 2020). Seasonal thermal stratification in lakes is influenced by climatic factors such as regional air temperatures, timing, location, temperature, and magnitude of inflows, and wind-driven mixing. For ectotherms living in lakes or reservoirs (e.g., fish, invertebrates), temperature constrains habitat use by influencing metabolic rates, growth potential, and physiological stress (Magnuson et al. 1979). As climate change shifts the timing and increases the duration and magnitude of thermal stratification (O'Reilly et al. 2015, Richardson et al. 2017, Woolway et al. 2020, 2021), habitat availability for native cold-water species like trout and other salmonids will likely decrease (Ficke et al. 2007). Additionally, shifts in the timing of stratification can cause mismatches between predator and prey resources (Winder and Schindler 2004). In Germany's Bautzen reservoir, for example, shifts in thermal structure during a critical growing season caused decreased *Daphnia* densities due to overexploitation of phytoplankton and increased predation by small perch (Wagner and Benndorf 2007). Thermal stratification also affects fishes through prey availability and access when the majority of prey production occurs in the warmer, shallow depths of the offshore (pelagic) and nearshore or bottom-oriented (benthic) habitats (e.g., Tunney et al. 2012, Sorel et al. 2016a, Trottier et al. 2019). In cold water systems, increased surface temperatures coupled with increased duration of stratification could thermally exclude cold-water consumers from access to prey in the productive surface and littoral zones during critical periods of the growing season (Cyterski and Ney 2005, Dolson et al. 2009, Hansen et al. 2013, Plumb et al. 2014).

The effects of thermal exclusion and habitat limitations are further exacerbated by introductions of nonnative species (Cucherousset and Olden 2011). Species introductions in freshwater can alter food webs in a variety of ways, both by creating novel trophic links, or by otherwise disrupting or reducing existing links (Jackson et al. 2017). In temperate North American lakes and reservoirs, cold-water invasive species like lake trout *Salvelinus namaycush* and mysid shrimp have heavily disrupted native salmonid communities (Martinez 2009, Ellis et al. 2011). Because these invasive species share similar thermal ranges, they experience more direct interactions, and as suitable thermal habitat shrinks, they are concentrated together in high densities that can result in increased direct or indirect competitive or predation interactions, however the relative strength of these interactions is mediated by lake depth and temperature

(Schoen et al. 2015). But even when thermal requirements of the invader do not match that of the native species, competitive interactions could still exist depending on the food web and thermal structure. For example, lake trout are susceptible to direct resource competition for littoral prey fish following invasion of warm water predators (and associated decrease in growth rates) only when pelagic prey fish are not present in the lake (Vander Zanden et al. 2004). Thus, stratification patterns that restrict native species to deeper waters could favor production of invasive species due to higher habitat availability and access to prey.

To further amplify these issues, climate-induced drought can impose additional stressors on freshwater ecosystems confronted with a projected 20-30% increase in global water demands from the present to 2050 (Boretti and Rosa 2019) and an increased reliance on freshwater reservoirs to meet these demands. In these ecosystems, the effects of dam operations such as timing, magnitude, and depth of water withdrawals represent significant additional influences on food web structure through ecological impacts of de-watering (Carmignani and Roy 2017) and driving thermal structure (Duka et al. 2021). Extent of winter drawdown of reservoirs has been shown to be negatively associated with macroinvertbrate biomass (Trottier et al. 2019) and also implicated in trophic compression of the benthic energy pathway in fish food webs (Hansen et al. 2018). While lakes have an inherent adaptive capacity in their food web structure, large scale anthropogenic alterations (e.g., loss in benthic production due to drawdowns) could limit the ability of these ecosystems to adapt to other stressors (McMeans et al. 2016). Water management strategies can also play an important role in mitigating stressors on reservoir ecosystems. For example, reservoir drawdowns have been associated with decreased abundance in invasive species and release of native fish from predation pressure (Murphy et al. 2019b), and lake de-stratification has been posed as a method of eradicating warm-water invasive species in cold-water food webs (Gaeta et al. 2012). Water operations, climate change, and invasive species can interact in complex ways to shape lentic food webs, and we have limited understanding of how lake and reservoir ecosystems will respond to these complex dynamics and the associated impacts on native species of concern.

The goal of my research is to quantify species interactions and identify limits to native salmonid growth and production within the context of an invasive species and potential introductions of anadromous salmonids in two impounded reservoirs in Washington State. The knowledge gained from this project can inform the management of native and introduced fish populations and future water management strategies given the emerging threat of climate change. Assessing the thermal and food web constraints to the growth and mortality potential for introduced salmonids will help managers decide if introducing salmonids into this system is justified and likely to succeed. Additionally, by understanding how thermal structure drives species interactions in these reservoirs, ecologically-based water management strategies can be employed to manipulate the thermal structure to support ecosystem balance and function in the reservoirs.

Ross and Diablo lakes are the upper two of three reservoirs impounded by hydroelectric projects in the Upper Skagit River, WA. While Gorge Lake is the lower reservoir in the project, it is smaller and more run-of-river than Ross or Diablo and does not thermally stratify, thus I will not be evaluating it in this project. Both Ross and Diablo lakes have simple fish communities characterized by native and nonnative species. Native species include rainbow trout *Oncorhynchus mykiss*, bull trout *S. confluentus*, and Dolly Varden *S. malma* and nonnative species include eastern brook trout *S. fontinalis* (introduced in early 1900s), cutthroat trout *O. clarkii* (introduced in early or mid-1900s), and redside shiner *Richardonius balteatus* (introduced ca. 2000). In addition, hybridization has been documented between rainbow trout and cutthroat trout, Dolly Varden and bull trout, and Dolly Varden and brook trout. Redside shiners spread to Diablo Lake after their introduction to Ross, but the population has not yet proliferated in Diablo as it has in Ross. Ross Lake is characterized by strong thermal stratification from around June to October when it deepens and begins to destratify, with peak summer surface temperatures between 19-22^{o}C. In addition, Ross Lake is drawn down between 16-25 m (50-75ft) every year during the winter, although drawdowns in recent years have reached 40 m (125 ft). Diablo on the other hand is colder, weakly stratified, and lake level fluctuates within ± 5 ft throughout the year.

Managers' concerns for the populations stem from historical trends in the population size and fish growth over the last 30 years, including recent trends of declining recruitment of juvenile salmonids, on top of additional stressors from climate change, invasive species, and hydropower management. Monitoring of the rainbow trout population in Ross Lake was first studied extensively for three years in the early 1970s, when data were collected on the physical environment, growth, diets, prey availability, spawning, population size, and mortality of rainbow trout in Ross Lake and the Upper Skagit River (Seattle City Light 1974). Additional monitoring has occurred periodically since the late 1980s, during which there was concern about the fishery negatively impacting the size and number of rainbow trout in the lake (Johnston 1989, Loof 1995). Contemporary monitoring found fluctuating trends in rainbow trout size and growth, decreasing from 2004 to 2006, but then maximum size, maximum age, and size at age for fish age-2 and older all increased between from 2006 to 2012 (Downen 2014; Hugh Anthony, unpublished data). Despite increases in age and growth, catch rates of rainbow trout continued to decline through 2012, mirroring similar trends observed in Ross Lake spawning surveys (Hugh Anthony, unpublished data) and snorkel surveys in the Canadian reaches of the Upper Skagit River (Foster 2020). These trends perhaps correspond to the adult rainbow trout accessing a new resource of redside shiner in the lake while the juveniles remain limited by competition with redside shiners. Unlike rainbow trout, the bull trout and Dolly Varden populations were not historically monitored in this system to the same extent. Thus, long-term trends in growth and abundance of the native char populations are unknown. However, snorkel surveys in the Canadian portion of the Skagit River conducted periodically since 1998 show a dramatic increase in the adult population peaking in 2011 and slowly decreasing in the following years.

While these monitoring data allow a glimpse of recent bull and rainbow trout population dynamics, food web data in Ross and Diablo lakes are necessary to understand the mechanisms driving changes in growth and production of native fish. For this system, however, these data are extremely limited or nonexistent. Seattle City Light conducted a study on the food web supporting rainbow trout in the lake from 1971-1974, but food web data in Diablo Lake do not exist. Climate warming and the invasion of redside shiner have shifted food web dynamics, underscoring a need for a contemporary study. Quantifying the species interactions in these lakes will identify limitations within the food web to growth and production of native fish populations and highlight vulnerabilities to mounting impacts of climate, invasive species, and dam operations.

Bioenergetics models provide a valuable tool in fisheries management as they allow for quantifying trophic interactions and evaluating biotic and abiotic limitations to fish growth

(Deslauriers et al. 2017). These models are based on simple energy-balance equations that partition total energy intake (i.e., food consumed) into three basic components: 1) waste losses, 2) metabolism, and 3) growth. As such, these models can be used to estimate growth from consumption or vice versa, while accounting for size- and temperature-dependent effects on these physiological processes. This provides insights into how bioenergetic requirements change as individuals grow, experience different thermal conditions (i.e., seasons), and have access to variable amounts and quality of food, allowing for the examination of key limiting factors during critical life stages (Beauchamp 2009). Applications of these models range widely (see Deslauriers et al. 2017 for review) but can include quantitative assessments of predation mortality (Lowery and Beauchamp 2015, Sorel et al. 2016b) or consumption demand and carrying capacity (Sorel et al. 2016a, Taylor et al. 2020), estimating habitat quantity/quality and growth potential (Weber et al. 2014, Carmichael et al. 2020), or evaluating possible distributional (Lawrence et al. 2015) or trophic shifts due to climate change (Breeggemann et al. 2016).

Despite these valuable applications of bioenergetics models, their implementation is limited by the species of interest, as reliable model results are dependent upon accurate species-specific parameterizations (Ney 1993). For application in the Upper Skagit system, these models exist for the primary salmonids of interest (rainbow trout: Rand et al. 1993; eastern brook trout: Hartman and Cox 2008; bull trout/Dolly Varden: Mesa et al. 2013), but there is currently no model for redside shiner. Therefore, in Chapter 1 of my dissertation I aim to fill this knowledge gap using controlled laboratory experiments to develop and evaluate performance of a bioenergetics model for redside shiner. In Chapter 2 I will then apply this model in Ross and Diablo Lakes to quantify seasonal and annual food consumption by the invasive redside shiner to evaluate scope for competition with juvenile native rainbow trout. The focus of Chapter 3 will then shift towards the top of the reservoir food webs, to quantify consumption rates of piscivores and evaluate the impacts of predation mortality on the population dynamics of invasive redside shiner and native juvenile salmonids. Using the baseline food web data acquired in Chapters 2 and 3, I will then evaluate the feasibility of introducing anadromous salmonids above the dams in Chapter 4. This evaluation will include quantifying the carrying capacity of the reservoirs for reservoir-rearing species and quantifying predation mortality on juvenile salmonids rearing in and migrating through the reservoirs. The Upper Skagit River reservoirs are facing numerous emerging challenges that will affect food web dynamics and native fish populations, including persistence of a warm-water invasive species, possible introductions of anadromous salmonid populations, and climate change induced shifts to thermal structure and water operations. My PhD research will contribute valuable information on current food web dynamics as they relate to species introductions and thermal structure that can guide resource management and water operations in this specific system. These emerging challenges are not exclusive to the Upper Skagit River, and as such, this research will also provide important insights on the complex dynamics driving lentic food web structure that will help inform management and operations of these regulated ecosystems across the region to conserve key native species into the future.

Objectives

Chapter 1: Parameterize a species-specific bioenergetics model for the redside shiner and evaluate its predictive performance

Chapter 2: Quantify food and habitat use and availability among planktivorous fish in Ross and Diablo Lakes and evaluate the evidence for food limitation or resource competition with the non-native redside shiner

Chapter 3: Quantify food and habitat use among piscivores in Ross and Diablo Lakes, quantify predation on redside shiners and evaluate predation mortality risks to juvenile native salmonids rearing in the lakes

Chapter 4: Evaluate the role and capacity of Ross and Diablo Lakes for introduction of anadromous salmon, with particular attention to resource availability and predation threats depending on various life history strategies

Methods

Chapter 1: Parameterization of a redside shiner bioenergetics model

Status- Experiments are completed and the manuscript is submitted to TAFS

Redside Shiner (*Richardsonius balteatus*) have expanded from their native range in the Pacific Northwest region of North America to establish invasive populations in six other western states. This has fueled concerns regarding heightened competitive interactions between Redside Shiners and native salmonids both now, and as Redside Shiner distributions continue to grow. In this Chapter, I parameterized a bioenergetics model for this specie, thus providing a powerful tool to quantify the trophic role of this species in invaded ecosystems and evaluate their potential impacts on native species.

To parameterize a bioenergetics model for this species, I followed general methodology used for development of bioenergetics models for other species (Hartman and Sweka 2001, Moss 2001, Hartman and Cox 2008, Mesa et al. 2013, Hovel et al. 2015). Specifically, the objectives were to: 1) estimate the temperature-dependent and allometric relationships between daily maximum consumption (Cmax) and routine metabolic rate (RMR) of Redside Shiner using controlled laboratory experiments representing ecologically relevant ranges for temperature (5^{o}C to 30^{o}C, or their upper thermal limit) and fish sizes, 2) use the resulting data to parameterize a Wisconsin-type bioenergetics model for Redside Shiner, and 3) conduct controlled long-term growth studies to evaluate model performance and prediction error. Upon completion of the model evaluation studies, model prediction error was quantified, and an error correction equation developed to improve model predictions across a range of daily consumption rates (in terms of J·g-1·d-1). This model provides a method for attaining temperature- and size-dependent growth and consumption estimates for the Redside Shiner, which can be used to assess its trophic role across native or invaded ecosystems under variable environmental conditions.

1.1 Fish collection and holding

Fish were held in 120-L circular tanks supplied with filtered and UV-treated temperature-controlled water from Lake Washington at the U.S. Geological Survey, Western Fisheries Research Center. Temperatures up to 17^{o}C were controlled through the wet lab system, while higher temperatures required the use of submersible heaters. All fish were gradually introduced to new temperatures at a rate not exceeding 2^{o}C/day and were acclimated at the experimental temperature for at least 5 days prior to any experiments.

1.2 Temperature dependence of C_{max}

The effect of temperature on maximum consumption rates was determined using fish of the most commonly available size (55-65 mm FL, 1.3-4.5 g) at temperatures ranging from 5^{o}C to 32^{o}C. Pilot trials conducted in 2019 determined Cmax experiments needed to run for several days due to biases created by binge feeding on day 1. Additionally, fish appeared to feed normally when held individually in test arenas indicating that experiments can be conducted using one fish per test arena.

Maximum consumption experiments were conducted across 4 days – consumption rates were recorded for all days, but the first day was excluded and Cmax was computed across the final three days. For each temperature, 6 fish were deprived of food for at least 24-h and acclimated individually in small test arenas (Volume = 8-L containers filled with 5-L water). Fish were fed a pre-weighed ad libitum ration of 1-mm salmon sinking pellets (Skretting) offered 3-5 times over a 24-h period. Remaining food was collected after each 24-h period, dried in an oven for 48-h and weighed to maintain an accurate accounting for food eaten and food remaining each day. A subsample of pellets from each batch of food was weighed, dried for 48-h, and then weighed again to determine initial water content of the dry pellets. The percent dry mass for the dry pellets was used to convert the mass of dried leftover food to the initial pellet mass. The specific consumption per day (g/g/d) was calculated for each fish by dividing to total weight of food consumed each day by the initial mass of the fish at the beginning of the trials. Cmax was calculated for each fish as the mean specific daily consumption rate for days 2-4, and then a mean Cmax was calculated across all fish at each experimental temperature to determine the relationship between Cmax and temperature.

1.3 Mass dependence of C_{max}

The effect of body mass on Cmax was determined at the temperature associated with the maximum daily consumption rate for redside shiners. At the temperature associated with maximum consumption within the pilot size class, I repeated the Cmax experiments described above across a range of body masses of redside shiners ranging from 0.6 g to 27.3 g. An appropriate temperature-dependent function for consumption was selected based on the best fit for the data, and the applicable parameters for the chosen model based on the observed relationship between Cmax, temperature, and mass. A full description of the consumption models and parameters can be found in the User Guide to Fish Bioenergetics 4.0 (Deslauriers et al. 2017).

1.4 Estimating routine metabolic rate (RMR)

I conducted respirometry experiments to determine routine metabolic rates as a function of fish size and water temperature, following standard methods for the design and setup of an intermittent-flow respirometry system (Clark et al. 2013, Svendsen et al. 2016) using fiber-optic oxygen probe sensors (FireSting O_2, PyroScience, www.pyroscience.com). Pilot trials ran for at least 24 hours to identify the presence of any diel cycles in respiration rates and determine the acclimation time required for respiration rates to stabilize following handling stress upon entry. Respiration trials ran for 24 h due to diel cycles and variation in activity observed during pilot trials. Fish were placed in small groups, in appropriately sized respirometers to encourage the typical swimming behavior observed for this species under natural conditions to most closely estimate routine metabolic demand. Timing of measurement and flush periods of the respirometers were determined by a pilot trial at each temperature, targeting a drop of 5-10% O_2, and never allowing respirometers to drop below 80% saturation. I accounted for background respiration rates using methodology detailed in Rodgers et al. 2016. Oxygen measurement data from the respirometers was processed by 1) filtering O_2 data from the measurement periods, 2) performing linear regressions and diagnostics of O_2 vs. time for each measurement period, and 3) calculating MO_2 for each measurement period using Eq 2 in Svendsen et al. 2016. I visually inspected the MO_2 data for each fish and calculated individual RMRs by taking a mean of all MO_2 rates across the entire 24 h period.

I choose an appropriate temperature- and activity-dependent function and applicable parameters for metabolism based on the best fit for the data. Estimates of routine metabolic rates (RMR; g O^2/g/d) from each fish were used in multiple regression analysis of RMR against temperature and fish mass to estimate the model coefficients.

1.5 Waste losses, SDA, and energy densities

The bioenergetics model also requires estimates of waste losses (egestion and excretion) and specific dynamic action (SDA). Waste losses are often reported as a constant proportion to consumption (Kitchell et al. 1977) and are relatively insensitive in bioenergetics simulations (Bartell et al. 1986; Ney 1993). Experiments with the common minnow also found SDA and excretion parameters to be equally insensitive to bioenergetics simulation predictions (Cui & Wootton 1988). Thus, values for these parameters were borrowed from closely related species in the literature (i.e., small-bodied Cyprinids).

Bomb calorimetry was performed on a range of sizes of Redside Shiners to determine energy density (ED, J/g wet weight) as a function of body mass and proportion dry weight (pDW). Energy densities for the consumer can be input as values assigned on specific simulation days with linear interpolation between entries; this option was used because the energy density data did not conform well to linear functions of body mass.

1.6 Model corroboration

After parameterization of the bioenergetics model, I conducted a long-term growth experiment in the laboratory to evaluate the accuracy of the model estimates. Fish of a commonly available size were held in individual aquaria with temperature loggers, fed known rations of prey for a minimum of 8 weeks (up to 6 months) and measured for growth in order to evaluate performance of the model. The parameterized model was used to 1) estimate consumption from measured growth, and 2) estimate growth from measured consumption. Observed estimates were compared to predicted estimates of both consumption and growth in order to evaluate the fit of the model. The long-term growth experiments included variable feeding rates and temperatures to evaluate model performance across a range of conditions

Chapter 2: Food web dynamics and competitive interactions between the juvenile salmonids and the redside shiner in Ross and Diablo Lakes

In this chapter I will explore the potential for competition between the redside shiner and juvenile salmonids rearing in Ross and Diablo Lakes using a bioenergetics-based approach to quantify food web interactions. This approach will utilize seasonal data on fish populations related to reservoir habitats, growth, distribution of fish species and key prey species, and environmental data. The biological data collected will be combined with environmental data as inputs to bioenergetics simulations to estimate seasonal consumption demand of primary prey resources (Beauchamp et al. 2007) by planktivorous fish in this system, which include both native salmonids and the invasive redside shiner.

2.1 Data collection

Over three years (2019-2021), fish were collected seasonally (spring, summer, fall) using sinking multi-mesh gill nets set in three distinct depth strata corresponding to the epilimnion, metalimnion, and hypolimnion. Limitations to fish sampling in 2019 and 2020 due to concerns about incidental lethal take of bull trout resulted in low or missing sample sizes for some species/size class/season bins, so data might be pooled for those years as necessary. Catch per unit effort (CPUE) by depth, season and region from the gill nets will be examined for each species and size class to estimate seasonal distribution patterns and thermal experience as an input for bioenergetics modeling. Fish were measured for fork length (mm) and weight (0.1 g), in addition to collection of diet, fin tissue (for genetics and stable isotopes), and scale samples (plus otoliths from mortalities). Other invertebrate herbivores and omnivores will be collected for stable isotope analysis to provide representative end-members for primary pelagic and benthic consumers in the food web. Vertical temperature profiles will be conducted monthly to measure the thermal structure of the lake from spring through fall, which will be supplemented by Seattle City Light temperature loggers in the forebays for winter and early spring temperatures. Redside shiner abundance and spatial distribution will be estimated using hydroacoustic surveys that were conducted in October 2022.

Hydroacoustic surveys were conducted to estimate redside shiner density and abundance in Diablo and Ross Lakes in September and October 2022, respectively. Pilot surveys indicated redside shiner did not move offshore until after dusk, therefore all surveys were conducted at night. The entire shoreline of Diablo Lake was surveyed in a single night, and some daytime surveys were conducted as well. Due to the size of Ross Lake, transects were determined by dividing the shoreline into 500 m segments and randomly sampling these segments within region (north, mid, south), shore (east or west), and slope (steep or shallow) blocking groups. We targeted six transects within each blocking group (n=59), in addition to transects within 500 m of each tributary mouth (4th order or higher, n=28). We sampled each tributary mouth as we anticipated higher densities of redside shiner and wanted to ensure adequate survey coverage. Ground truthing of targets was accomplished by deploying a sinking multi-mesh gillnet (36-m by 1.8-m; stretched mesh panel sizes (mm): 20, 25, 37, 50, 66, 76) during one of the surveys where we identified fish targets. Minnow trap collection data from 2019 were additionally used to determine redside shiner size structure. Due to the schooling nature of the redside shiner in Ross Lake, echo integration was used and all data processing, filtering, and acoustics analysis was conducted in EchoView (version ?). Target strength (dB) for redside shiner across their size distribution was estimated using total length (mm) according to Love's equation (Love 1977). Density estimates were computed for individual depth bins: 2-7, 7-12, and 12-17 m (the top 2 meters were excluded due to positioning of the transducer and acoustic noise). Density estimates from the hydroacoustics transects will be expanded to the remainder of the Ross Lake shoreline to estimate total biomass and abundance of redside shiner.

2.2 Stable isotope analysis and niche overlap

Stable isotope analysis of nitrogen (N) and carbon (C) is a valuable tool commonly used to evaluate the trophic position and basal resources supplying consumers within a food web (Layman et al. 2012). The ratio of $^{15}N{:}^{14}N$ ($\delta^{15}N$) is used to estimate trophic position of a consumer, as their tissues become enriched in ^{15}N relative to their food by an average of 3.4 ‰ (Post 2002). Ratios of carbon isotopes ($\delta^{13}C$) however, change little with trophic transfer but can vary greatly depending on the basal carbon source of the primary producer (e.g., pelagic phytoplankton vs benthic algae in lakes), and can thus be used to evaluate the primary energy pathway supplying the consumer (France 1995). Due to the sensitivity and cost-effectiveness of this tool, stable isotopes have been used extensively to study and gain new insights into the ecological effects of non-native species (Cucherousset et al. 2012).

Stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) will be used to quantify resource niche overlap between redside shiners and planktivorous life stages of salmonids in Ross and Diablo lakes using Bayesian ellipse and probabilistic methods (Jackson et al. 2011, Swanson et al. 2015). I will also fit stable isotope mixing models using the MixSIAR package in R to estimate diet proportions for redside shiners and to verify or modify diet proportions from salmonid stomach content analysis.

2.3 Quantification of key prey resources

Densities and biomass of key zooplankton species (Daphnia, Leptodora) will be estimated from monthly zooplankton tows collected at 0-10m depth and 10-20m depth. Daphnia egg counts will be used with the egg-ratio method to estimate population production (see Sorel et al. 2016a).

2.4 Bioenergetics Simulations

Bioenergetics simulations for redside shiner consumption will use the newly parameterized bioenergetics model (see Chapter 1 above).

Field data will be used as the following inputs to bioenergetics simulations: thermal experience, seasonal or annual growth of each species/age class, seasonal diet proportions, energy content of prey items. Thermal experience will be calculated using a combination of lake temperature data and seasonal depth distributions inferred from relative catch rates in the three depth-stratified gillnet sets (supplemented with telemetry data for Bull Trout; Eckmann et al. 2018). Fish growth will be estimated from scale back-calculations and size at age data (from otoliths), depending on the species and size of fish. Annual growth measures will be the default for many species and size-classes, however seasonal growth will be partitioned where possible with scale analysis (e.g., rainbow trout). Seasonal prey proportions will come from averages across species/size-class grouping from diet analysis. Prey energy densities (J/g wet mass) will be taken from the literature or measured directly from bomb calorimetry when appropriate values cannot be found in the literature. I will use data from spawner surveys conducted in 2002-2004 in Ross Lake to determine the age(s) at partial to full maturation (Downen 2014) and I will estimate percent energy investment in spawning losses from the literature, or measured using direct bomb calorimetry where adequate samples exist.

Operating on a daily timestep, these simulations estimate 1) the feeding rate of consumers as a percentage of their maximum consumption rate (%Cmax), and 2) daily consumption rates for each prey category (g/day) necessary to reach growth rates observed in the field, given the consumer's body size, thermal experience, and diet. Estimates of %Cmax will be used as an indicator of food availability for various consumers after accounting for the effects of temperature and body size of the consumer on their consumption capability. For these simulations, I will use species-specific bioenergetics models parameterized for Bull Trout(Mesa et al. 2013), Rainbow Trout(Rand et al. 1993), and Brook Trout(Hartman and Sweka 2001, Hartman and Cox 2008). Dolly Varden would be modeled using Bull Trout.

Each age class of each forage species will be simulated separately to account for their variation in growth and consumption capacity, seasonal diet composition, and thermal experience. These age-specific seasonal consumption rates for each species will be expanded to standardized populations of consumers by multiplying per capita consumption for each age by the relative proportional abundance of each age class in the population, fitted to the observed size and age structure for that species(Beauchamp et al. 2007). Population age structure for each salmonid species has been estimated using gillnet catch data from the NPS surveys (every 3 years, 2006-2019), and redside shiner age structure will be taken from Welch (2012). These population-level estimates of seasonal and annual consumption demand (g/day) of key prey will be used to empirically assess the potential for interspecific resource competition.

2.5 Results and interpretation

Status: Data collection is complete, data analysis is wrapping up and writing is in progress

- Hydroacoustics survey: Surveys are complete and data has been filtered, pre-processed, and analyzed. We have mean areal density estimates for each transect. Preliminary GIS analysis of total lake area of occupancy and expansion of transect estimates to get a whole-lake estimate of redside shiner biomass and abundance has been completed, however still needs to be refined.
- Stable isotopes: lab analysis complete.

- Zooplankton: monthly depth-stratified samples have been completed for density estimates, size distributions, egg counts, and production estimates.
- Age and growth: Scales and otoliths have been analyzed for all fish in Ross and Diablo Lakes. Annual growth estimates for each age-class of each species have been computed.
- Diets: all diets have been analyzed. Diets will be compared to results from mixing models.
- Energy density: bomb calorimetry on select fish samples is complete.
- Population age structure: complete

Resource niche overlap between salmonids and redside shiner will be evaluated using stable isotope analysis and used alongside bioenergetics modeling and prey resource production estimates to evaluate scope for and possible drivers of competition. Resource niche size will be compared among relevant life stages in each species (using the SIBER package), and resource niche overlap will be evaluated by the estimated probability that an individual from one species is found in the niche region of another species (using the nicheROVER package). Importantly, resource niche overlap alone provides limited information on competitive interactions between species. For example, significant overlap in diet would only indicate competition if those resources are in limiting supply. Alternatively, a lack of diet overlap could indicate a natural resource partitioning between species which helps buffer competition potential, or it could indicate one species is being competitively excluded from their preferred prey/habitat, with consequences on their growth/survival. Therefore, patterns in overlap will be evaluated alongside bioenergetics analysis and prey resource availability data to provide a fuller view of competition potential between these two species.

Population consumption of zooplankton by redside shiner and planktivorous salmonids estimated from bioenergetics modeling will be compared to total zooplankton biomass and production on a monthly basis to determine how resource demand compares to resource availability and to identify any possible temporal bottlenecks in prey supply to evaluate whether prey availability may be limiting for these species (e.g., Sorel et al. 2016, Taylor et al. 2020). Depth-stratified zooplankton availability will be assessed as it relates to the depth distribution of fish during stratification, which will be inferred from hydroacoustics surveys for redside shiner and gillnet catch data for salmonids. Growth rates, energy densities, pCmax values and growth efficiency (g growth/g consumed) from bioenergetics simulations will be compared to populations in the literature to determine if there is evidence for depressed feeding rates in the salmonids. Collectively, these results will be used to evaluate the existence and relative magnitude of resource competition with redside shiner. This will be discussed in the context of the current environment as well as possible mechanisms that might change this trophic relationship in the future (e.g., population dynamics, changes in thermal structure due to dam operations and/or climate change).

Chapter 3: Food web dynamics of piscivores in Ross and Diablo Lakes

In this chapter I will explore the role an invasive species (redside shiner) plays in structuring the trophic interactions of top-level piscivores in two high-elevation hydropower reservoirs (Ross and Diablo Lakes) using a bioenergetics-based approach to quantify food web interactions. This approach will utilize seasonal data on fish populations related to reservoir habitats, growth, distribution of fish species and key prey species, and environmental data. The biological data will be combined with environmental data as inputs to bioenergetics simulations to estimate seasonal consumption demand of primary prey resources by piscivores in this system, which include both native and nonnative salmonids (Beauchamp et al. 2007).

In this chapter, I am specifically interested in addressing the following questions: 1) how does piscivore niche-space (e.g., overlap or segregation) compare between Ross and Diablo lakes and across thermal structure, 2) how important are redside shiner to the annual energy budget of each species, 3) does the importance of redside shiner vary seasonally or by predator or prey size, 4) what is the seasonal and annual consumption rate of redside shiner by each predator species, and 5) what is the seasonal and annual consumption rate of juvenile salmonids by each predator species? Answers to these questions will shed light on the role that the invasive redside shiner plays as a forage fish in the reservoirs, and the impact of predation on juvenile salmonids due to an increased predator population (i.e., apparent competition). This chapter will provide managers with important information on the food web status to guide management actions and monitoring plans aimed at conserving native species in the reservoirs.

3.1 Data collection

Data collection followed that of Chapter 2 above.

3.2 Stable isotope analysis and niche overlap

Stable isotopes (d13C and d15N) will be used to quantify resource niche overlap between piscivorous life stages of salmonids in Ross and Diablo lakes using Bayesian ellipse and probabilistic methods (Jackson et al. 2011, Swanson et al. 2015) I will also fit stable isotope mixing models using the MixSIAR package in R to verify or modify diet proportions from salmonid stomach content analysis. CPUE by depth, region, and season will be evaluated and related to reservoir thermal structure to estimate depth and temperature experience for piscivorous life stages of all salmonids and evaluate season habitat segregation or overlap between predator species and prey (i.e., redside shiner) availability.

3.3 Bioenergetics Simulations

Bioenergetics simulations will follow as described in the methods for Chapter 2.

Each age class of each predator species will be simulated separately to account for their variation in growth and consumption capacity, seasonal diet composition, and thermal experience. These age-specific seasonal consumption rates for each species will be expanded to standardized populations of consumers by multiplying per capita consumption for each age by the relative proportional abundance of each age class in the population, fitted to the observed size and age structure for that species (Beauchamp et al. 2007). These population-level estimates of seasonal and annual consumption demand (g/day) of key prey will be used to empirically assess the impact of predation mortality on redside shiners and juvenile salmonids.

3.4 Results and Interpretation

Status: Data collection is complete, data analysis is wrapping up and writing is in progress

- Hydroacoustics survey: Surveys are complete and data has been filtered, pre-processed, and analyzed. We have mean areal density estimates for each transect. Preliminary GIS analysis of total lake area of occupancy and expansion of transect estimates to get a whole-lake estimate of redside shiner biomass and abundance has been completed, however still needs to be refined.
- Stable isotopes: lab analysis complete.
- Age and growth: Scales and otoliths have been analyzed for all fish in Ross and Diablo Lakes. Annual growth estimates for each age-class of each species have been computed.
- Diets: all diets have been analyzed. Diets will be compared to results from mixing models.
- Energy density: bomb calorimetry on select fish samples is complete.
- Population age structure: complete

Niche overlap will be compared among piscivore species in Ross and Diablo lakes using stable isotope analysis and diet analysis (resource niche) as well as seasonal vertical distribution data from gillnet sets (habitat niche). Resource niche size will be compared among relevant life stages in each species (using the SIBER package), and resource niche overlap will be evaluated by the estimated probability that an individual from one species is found in the niche region of another species (using the nicheROVER package). Levels of niche segregation/overlap among species will be compared between Ross and Diablo Lakes to evaluate if differences in thermal structure and prey availability/density (i.e., redside shiner abundance/density) differences between the two reservoirs shape the overall impact of the species introduction on food web structure. Depth-specific abundance and density of the primary prey fish (redside shiner) will be estimated and compared to vertical distribution of the predators. Bioenergetics simulations will estimate seasonal consumption of fish prey for each predator species and size class. Estimates of redside shiner consumption will be compared to their population abundance (from hydroacoustic surveys detailed in Chapter 2) to assess the availability of this primary food supply. Estimates of predation mortality of juvenile native salmonids will be compared to estimates of their age-specific abundance to infer whether predation mortality could be limiting population growth.

Chapter 4: Feasibility of anadromous salmonid introductions into Ross and Diablo Lakes

Species reintroductions are becoming an increasingly popular and important tool to conserve biodiversity in light of ongoing rapid ecological change (Seddon et al. 2007). As a conservation tool, the goal of reintroduction is to re-establish viable populations of at-risk species throughout their native range. Despite the wild popularity, decades of failed reintroductions prompted researchers and the IUCN to develop guidelines for reintroduction programs to help mitigate risk, increase chance of success, and improve our understanding of factors driving reintroduction success (Armstrong and Seddon 2008, IUCN 2013). Reintroduction can play an important role in conservation of freshwater fish in particular, as many species are facing extreme range contraction (He et al. 2019), however many of these programs have been historically unsuccessful (Cochran-Biederman et al. 2015). Two key factors correlated with reintroduction success for freshwater fishes are 1) adequately addressing the initial cause for decline and 2) thoroughly assessing habitat availability and quality in the reintroduction area (Cochran-Biederman et al. 2015), and this is reflected in the various guidelines provided for managing reintroduction programs (e.g., Dunham et al. 2011, IUCN 2013, Anderson et al. 2014).

Introducing anadromous salmonids above impassable dams is gaining traction as a method of restoring populations restricted from historical spawning and rearing habitat (Anderson et al. 2014) or as conservation introductions into new habitats. Trap and haul programs are one of the only methods available to reintroduce anadromous salmonids to historic spawning habitat upstream of high head dams, and are currently being used and proposed in regulated systems throughout the Pacific Northwest (reviewed in Kock et al. 2021). Many of these programs are in their infancy and/or have limited monitoring data that has been reported, limiting our ability to evaluate factors driving success of reintroduction efforts into reservoir habitats. Kock et al. 2021 reported considerable variation in the effectiveness of the programs reviewed, but also noted that success is context dependent and defined by different management objectives of stakeholders. Limitations to success of reintroduction into reservoirs are also reviewed in Kock et al. (2021) and can include collection efficiency of the traps, handling stress, prespawn mortality, high mortality rates and migration difficulty associated with downstream passage of dams (Flagg and Ruehle 2000, Keefer et al. 2012), high fry mortality rates associated with predation in the reservoirs (Kock et al. 2019), differential fitness of hatchery fish and impacts of interbreeding (Sard et al. 2015, Evans et al. 2016), or differenced in stock-specific production rates of the donor population(s) (Matala et al. 2019). While reservoir habitats can be limiting to survival of juvenile salmonids due to predation, they can also provide better growing conditions that may confer higher survival through downstream migration and ocean residency (Monzyk et al. 2014, Bourret et al. 2014, Murphy et al. 2019a). Additionally, cold water available in deep thermally stratified reservoirs could provide important thermal refuge for adult fish on their spawning migration (Naughton et al. 2018). It is important to note that evaluating success of reintroduction programs upstream of dams is further complicated by uncertainty in post-migration survival rates (e.g., in downstream migration, estuary, and ocean residence). Production could be high in the reintroduced habitat, but high mortality rates in other parts of the life history could be masking this if success is being monitored by rates of adult returns alone. Continued monitoring of these reintroduction programs and evaluation of stage-specific survival rates will be critical to evaluate factors driving success and inform future reintroduction efforts.

In the Skagit River, local stakeholders and resource managers have proposed introducing anadromous salmonids above the three Upper Skagit reservoirs to increase salmon runs in the basin. However, the feasibility and success of anadromous introductions will depend on a number of physical and ecological risks and constraints (Anderson et al. 2014, Kock et al. 2021). A critical piece of this is understanding the food web constraints of the recipient habitat, to ensure that the rearing capacity of the reservoirs is not exceeded (Koenings and Kyle 1997, Sorel et al. 2016a) and evaluate the potential of the reservoir habitat for increased growth rates (e.g., Chinook salmon *O. tshawytscha*: Monzyk et al. 2013, Bourret et al. 2014) or predation losses (Beauchamp et al. 1995, Sorel et al. 2016b). Building on the analyses completed in Chapters 2 and 3, Chapter 4 will evaluate the Ross Lake food web in the context of anadromous salmonid introductions. The primary objective will be to estimate rearing capacity in Ross Lake for each proposed species introduction (i.e., every anadromous salmon species in the Skagit River). Additionally, for species that would only be utilizing reservoir habitat as a migration corridor, constraints of this habitat – such as predation mortality during out-migration (e.g., Furey and Hinch 2017) or mismatch between migration timing and reservoir drawdown (Keefer et al. 2012) – will be evaluated in terms of impacts on successful reintroduction.

4.1 Bioenergetics simulations

The preliminary list of candidate species considered for introductions include steelhead *O. mykiss*, Chinook salmon, coho salmon *O. kisutch*, and sockeye salmon *O. nerka*. Simulations will be run for each species depending on their likely life history and usage of the reservoir (Arostegui and Quinn 2019). Existing literature and data will be reviewed to determine appropriate bioenergetic model inputs for potential anadromous salmonid species to be introduced. These inputs include growth information (rates, size-at-age, length-weight regression) of juveniles, seasonal diet composition, energy density, and seasonal depth distribution. Thermal experience will be estimated using seasonal depth distribution and reservoir temperature profiles based on data reported for other populations in similar habitats.

4.2 Results and interpretation

Simulations will be used to estimate consumption demand on reservoir zooplankton to determine how many lake rearing salmon the Upper Skagit reservoirs can support, based on estimates of current consumption rates and *Daphnia* production in Ross Lake (determined in Chapter 2). Preliminary simulations for sockeye salmon potential consumption and rearing capacity in Ross Lake have been completed and results presented at the American Fisheries Society Annual Conference in August 2022. These simulations need to be refined using an updated surrogate for growth rate (ideally Baker Lake sockeye if the data can be obtained, otherwise I will use growth rates from Lake Wenatchee sockeye which is data we have on hand). Consumption rates from piscivores (determined in Chapter 3) will be used to estimate predation potential on lake rearing juveniles as well as smolts using the reservoir as a migration corridor. An additional component to this paper will be an explicit acknowledgement of uncertainty in the key influential parameters/inputs (e.g., population size, diet proportions, fish growth, and *Daphnia* density), for example by using Monte Carlo simulations to model uncertainty for our estimates of population consumption, carrying capacity, and predation rates.

One direction I could take this chapter would be using the Upper Skagit River as a case-study, and have the chapter serve as a guide for evaluating reservoir food web constraints on salmonid re-introductions. This could include a review of reservoir usage by anadromous salmon and any research relating to anadromous reintroductions above barriers. This could be a valuable food web focused companion to recent reviews on efficacy of trap and haul programs supporting anadromous (re)-introductions (e.g., Lusardi and Moyle 2017, Kock et al. 2021).

Another valuable contribution could be predicting prey selection of piscivorous fish between redside shiner and different salmonids. Bull trout in other thermally stratified reservoirs tend to consume primarily cool- and coldwater pelagic species when they are available (e.g., Beauchamp and Van Tassell 2001, Benjamin et al. 2020, Hansen et al. 2021). In Ross Lake, redside shiner are the primary prey item for bull trout (Eckmann et al. 2018), however the availability of cold-water pelagic fish prey in Ross Lake is limited to juvenile rainbow trout that likely do no exist in high densities. If anadromous salmonids are introduced above the dams, will bull trout (and other piscivorous salmonid) consumption shift from littoral redside shiner to pelagic cold-water salmonids? What would drive/control this shift (e.g., pelagic salmonid density, littoral temperatures, seasonal migration pulse)? If some predation shifted, what impact would decreased predation mortality on redside shiner have on the food web? A similar phenomenon was observed with lake trout where home ranges decreased dramatically and foraging in the littoral (on warm-water cyprinids) appeared to cease following the introduction of the pelagic cool-water yellow perch, although corresponding trophic cascades were not evaluated (Wall and Blanchfield 2012). This evaluation would feed into the analysis of predation potential on introduced salmonids in the reservoirs and could be accomplished using some combination of Optimal Foraging Theory and Visual Foraging Theory/Functional Response Curves.

Timeline

	2019	2020				2021				2022				2023	
	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp
Form MSc Committee	■														
MSc proposal submission					■										
MSc coursework	■	■	■	■	■	■	■								
Ch. 1 data collection	■	■	■	■	■	■	■	■	■						
Ch. 1 analysis						■	■	■	■						
Ch. 1 manuscript and submission								■	■	■					
Ch. 2 and 3 data collection	■	■	■	■	■	■	■	■	■						
Submit bypass application											■				
Form PhD committee											■				
PhD final proposal submission														■	
Ch. 2 and 3 analysis								■	■	■	■	■	■		
Written qualifying exam													■		
General exam														■	
Ch 2 and 3 manuscript and submission												■	■	■	
Ch. 4 analysis											■	■	■	■	
Ch. 4 manuscript and submission														■	■
Dissertation submission and defense															■

Funding: Full time employment as a “Pathways” position with the USGS – Western Fisheries Research Center throughout the remainder of my dissertation

Significance

Results from this project will add to the growing body of literature looking at food web interactions in the context of water-use, thermal structure, and invasive species (e.g., Negus 1995, Vigliano et al. 2009, Juncos et al. 2013, Plumb et al. 2014). The information gained from this study, paired with similar studies will help fill the knowledge gap of how reservoir ecosystem structure is impacted by thermal structure, how this is mediated by water-management strategies, and the role that invasive species play in the face of climate change and growing water demands. This is particularly important to understand in the Upper Skagit River reservoirs to ensure persistence of the ESA-listed bull trout population and the native rainbow trout fishery in the face of continued climate change. To protect these native species, it will be critical to understand how these species interactions are mediated by the reservoir thermal structure and how this might change under increased warming or alternative dam operation strategies.

Results from Chapter 1 will add to the bioenergetics literature and fill an important data gap in our understanding of the bioenergetics of the invasive redside shiner. This parameterized model will provide the necessary first step for studies to quantify trophic impacts in sensitive ecosystems where redside shiner have invaded or in ecosystems where anadromous salmonid re-introductions are being considered. For example, this model could be used by managers to guide/assess eradication efforts in waterbodies where redside shiner invasion poses a serious risk to native fish (Gaeta et al. 2012, Smith et al. 2021). This model could also be used to understand habitat-specific risk for population expansion and evaluate how that might change with climate-change-induced warming (e.g., Lawrence et al. 2015). And even in systems where this species is native, habitat changes associated with water operations (e.g., irrigation withdrawals, hydropower) and climate change have the potential to alter trophic structure in a way that may be disadvantageous to cold- and cool-water salmonids, so this model may be critical in understanding future changes to the role the redside shiner plays as a forage fish in these systems.

By quantifying food web interactions in the Upper Skagit reservoirs, Chapters 2 and 3 will increase our understanding of how a species invasion can structure a simple high-elevation reservoir food web. Understanding these food web dynamics will be critical to managing the Upper Skagit population of ESA-listed bull trout. By tying these food web dynamics to the reservoir thermal structure, we can begin to understand how food web interactions might change given climate-induced alterations to reservoir thermal structure. Similarly, as water operations can also impact thermal structure, understanding these dynamics will help inform water management strategies to protect the native species of concern under future habitat changes.

By building on the baseline food web assessment in Chapters 2 and 3, Chapter 4 will be integral in determining the feasibility and implications of introducing anadromous salmonids into the Ross Lake food web. As anadromous salmon continue to decline throughout the region, re-introductions above dams will increasingly be used to bolster existing populations. Understanding the reservoir food web constraints on the dynamics of these populations will be critical to assessing the feasibility of success. Therefore, this chapter will provide an important resource to guide reservoir food web considerations of anadromous salmon that can be applied to other ecosystems as well.

Having a better understanding of and capability to predict ecosystem responses to altered thermal structure in lakes will help managers determine optimal water-use strategies to minimize detrimental impacts to aquatic communities within and downstream of dams and lakes. Results from this project will pave the way for future analyses coupling food web patterns with hydrodynamic models predicting climate change alterations to lake thermal structure (e.g., see Winslow et al. 2017) in order to identify how water management strategies could mitigate climate change stressors on lake ecosystems. For example, in systems where stratification is restricting native fish production and favoring the spread of invasive species, reservoirs could be de-stratified by altering the timing, depth and rate at which water is drawn. These water management strategies directly impact local communities that rely on hydropower, flood control, agricultural irrigation, potable and other water needs.

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