AN ABSTRACT OF THE THESIS OF

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Title: Bioenergetic Evaluation of Diel Vertical Migration by Bull Trout

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Jason B. Dunham

I evaluated hypotheses related to growth as a driver of depth use and diel vertical migration by bull trout (*Salvelinus confluentus*) in a thermally stratified reservoir. I applied a bioenergetic model to evaluate growth of bull trout in relation to potential patterns of diel depth use by bull trout in Ross Lake, Washington. Modeled patterns of growth were derived from observed vertical distributions of temperature and prey availability. I also observed bull trout depth (and corresponding temperature) use patterns to determine if observed behaviors corresponded with those predicted to maximize growth. Results of this work suggest that bull trout migrations beyond 25 m deep in Ross Lake cannot be explained exclusively by growth and survival alone, two common explanations for diel vertical migration. These deeper excursions may be explained by a third driver that has not been previously emphasized: the importance of colder water for gametogenesis. Further evaluation of this hypothesis as a means of explaining diel vertical migration for bull trout and other fish species in similar environments is warranted.

# Bioenergetic Evaluation of Diel Vertical Migration by Bull Trout

by

Madeleine Eckmann

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Madeleine Eckmann, Author

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# Bioenergetic Evaluation of Diel Vertical Migration by Bull Trout

## CHAPTER 1 – INTRODUCTION

Many species living in deeper lake and reservoir ecosystems exhibit daily movements that extend through much of the water column, generally referred to as diel vertical migration (DVM; Mehner 2012). DVM has been explained as a function of fitness, namely growth (Brett 1971) and survival (Eggers 1978, Clark and Levy 1988), both of which can be strongly tied to depth-related variation in temperature, light, prey availability (including foraging efficiency) and predation risk (Werner et al. 1983, Jobling 1997, Mehner 2014). These biotic and abiotic factors interact strongly and can vary with time of day, season, year, location, and among individuals. These complex interactions can be addressed through application of bioenergetic models to evaluate growth and consumption (e.g., Brandt et al. 2011). Bioenergetic models have been applied to model spatial and temporal variation in factors influencing growth potential in relation to DVM (Bevelhimer and Adams 1993, Busch et al. 2011, Plumb et al. 2014), and have demonstrated that DVM is a tactic that can maximize growth for animals that 1) follow a prey source exhibiting DVM (Hrabik et al. 2006), or 2) maximize bioenergetic efficiency moving between warmer prey-rich water and deeper, cooler water where metabolic costs are minimized (Brett 1971). Though growth is not the only factor that influences DVM, bioenergetic models allow evaluation of depth use patterns using growth as a common metric.

In this study, I employed a bioenergetic modeling approach to evaluate patterns of DVM in an apex predator (bull trout *Salvelinus confluentus*) living in a deep, seasonally stratified reservoir. The potential prey base for bull trout in this case was altered by an accidental introduction of redside shiners (*Richardsonius balteatus*) around the year 2000. Although diets of bull trout prior to the introduction are unknown, redside shiners are now believed to be the primary prey of bull trout. Whereas bull trout are among the most cold-adapted of freshwater fishes in North America (Selong et al. 2001, Dunham et al. 2003), redside shiners occupy warmer temperatures, often living in temperatures exceeding those required for survival of bull trout or other salmonids (Reeves et al. 1987). Consequently, when thermal stratification occurs during warmer months of the year, the optimal thermal habitat of these species may be spatially segregated. In this situation, if bull trout exclusively occupy warmer water for feeding metabolic costs may exceed energetic gains. Therefore, if redside shiners are the major prey and maximizing growth is the primary driver of behavior, it is reasonable to hypothesize that DVM by bull trout can maximize foraging opportunities while minimizing metabolic costs.

To compare the growth associated with DVM and alternative depth use patterns, I quantified bull trout diets, the distribution of fish prey, and patterns of thermal stratification in summer (July and August). With these data I parameterized foraging (Beauchamp et al. 1999, Mazur and Beauchamp 2006) and bioenergetics models (Mesa et al. 2013) to evaluate growth associated with constant depth use and DVM to various depths. These results were compared to observed behaviors exhibited by bull trout in the field to determine if individuals were behaving in a manner expected to maximize growth. Observed depth use patterns corresponding with maximum growth rates would support the hypothesis that maximum growth was the primary driver of bull trout behavior in Ross Lake. Alternatively, observed depth use patterns that fail to correspond with maximum growth would suggest alternative drivers of bull trout behavior.

# CHAPTER 2 – METHODS

## 2.1 Study Area**Error! Bookmark not defined.**

Ross Lake is the northern-most reservoir on the Skagit River in the North Cascades National Park, Washington (Fig. 1). At 489 m Ross Lake is surrounded by protected wilderness areas and steep alpine topography exceeding 2500 m. These wilderness areas are dominated by mixed mountain conifer and deciduous forest cover. Most of the perennial and ephemeral tributaries draining into the lake originate from glaciers and snowfields in the surrounding mountains. Ross Dam was constructed in 1950 and is operated by Seattle City Light for power generation. Lake levels fluctuate seasonally by up to 30 m rising from the lowest levels (90 m max depth) in April, to maximum depth (120 m max depth) in July. Summer water surface temperatures range from 14 ˚C in June to 22 ˚C in August (Fig. 3). A thermocline develops at a depth of approximately10 m deep in July. Throughout the summer, temperatures at 15 m remain below 16 ˚C dropping to approximately 10 ˚C by 50 m. Temperatures in the tributaries and the lake from October-May are less than 8 ˚C, and the lake remains isothermic around 5 ˚C for most of the winter. Ross Lake is oligotrophic and dissolved oxygen levels are near saturated from the surface to the bottom. The lake is a narrow (average width is approximately 2 km) 30 km long lake characterized by a steep rocky western shoreline and a more gradual littoral eastern shoreline. We focused this study on the southern end of the lake near the mouth of Big Beaver Creek (Fig. 1), where bull trout have been tagged by Seattle City Light since 2011.

Ross Lake harbors six species of fish including bull trout (the apex predator), nonnative brook trout (*Salvelinus fontinalis*), Dolly Varden (*Salvelinus malma*), rainbow trout (*Oncorhynchus mykiss*), cutthroat trout (*Oncorhynchus clarkii)* and nonnative redside shiner. The redside shiner was introduced to the lake around the year 2000. Since then, the redside shiner population has increased substantially. Observations of bull trout in the Skagit River above Ross Lake suggest a rapid increase in the size and number of bull trout following the introduction of redside shiners (Anaka and Scott 2011).

Bull trout emigrate from tributary streams to forage in Ross Lake during the winter and spring, with adults returning to spawn in tributaries in September through October. Given the cold temperatures in the lake and tributaries over the winter, thermal conditions are only amenable for rapid growth of bull trout during the summer (based on laboratory studies of temperature and bull trout growth rates; Selong et al. 2001, Mesa et al. 2013).

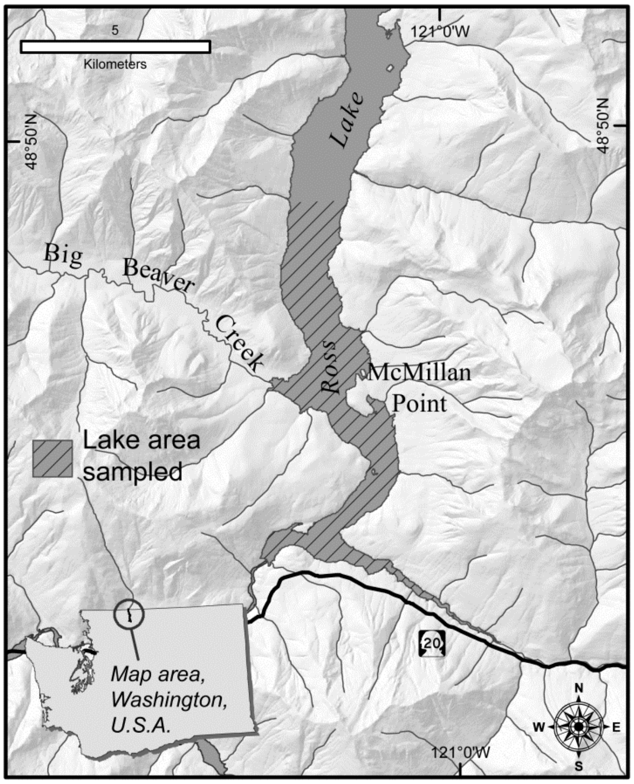

**Fig. 1**. Map of Ross Lake, North Cascades National Park, Washington. The map shows the entire lake and the crosshatched area depicts the specific area of the lake where this study took place. Big Beaver Creek is the location on the lake where all of the bull trout in this study were captured and tagged with acoustic tags. Across the lake, McMillan Point is the location where the vertical distribution of fish prey was assessed.

## 2.2 General approach

To determine growth associated with depth use by bull trout in Ross Lake I used a foraging model (Beauchamp et al. 1999, Mazur and Beauchamp 2006) and the Wisconsin bioenergetics model (Ney 1993, Hansen et al. 1997) with parameters modified for bull trout (Mesa et al. 2013; Fig. 2). The foraging model estimated consumption by bull trout based on prey density data collected in the field; estimates of predator swimming speed from previous studies; and reaction distances of bull trout calculated from modelled light intensity data. Estimated consumption values from the foraging model were input into the bioenergetics model to assess the growth of individuals. The bioenergetic model parameters are functions of temperature, prey energy density, and size of bull trout (Hansen et al. 1997). Temperature and prey vary as a function of depth, therefore, to model growth of bull trout in relation to depth use patterns it was necessary to identify 1) the primary prey types consumed by bull trout and 2) the vertical distribution of temperature and prey available in the lake, and 3) the depths and temperatures used by bull trout.

## 2.3 Field Sampling

### *2.3.1 Diet*

Twenty-nine bull trout were captured by angling during daylight hours, in July 2013. Each captured bull trout was anesthetized and submitted to gastric lavage following the procedures of Giles (1980). Stomach contents were evacuated into trays and identified. Whenever possible, food items identified included insects (identified to class) and fish (identified to family).

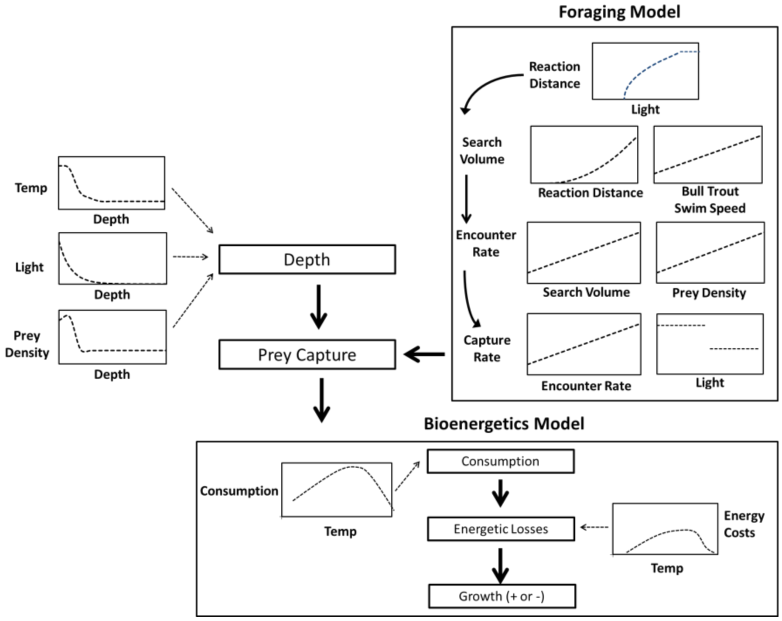

**Fig. 2.** A diagram of the data collection and modelling approach used in this study. Only general relationships among variables are depicted. In the foraging model the vertical axis for each row of figures is reaction distance, search volume, encounter rate and capture rate respectively.

### *2.3.2 Temperature*

Permanent temperature arrays (U22 Hobo © thermistors, Onset Computer Corporation, Bourne MA, USA) were located in two locations on Ross Lake within 3 km of Big Beaver Creek. These arrays collected hourly temperature data from the surface down to a maximum of 20 m depth at 2 m intervals. Additionally, vertical temperature profiles from the surface to 70 m were collected within 1 km of Big Beaver Creek once per month by the North Cascades National Park.

### *2.3.3 Prey Density*

I focused on quantifying abundance of redside shiners, as I initially suspected they were a major portion of the diet of bull trout in Ross Lake (H. Anthony, North Cascades National Park, unpublished data). Redside shiners were sampled using minnow trap arrays randomly distributed in a 70 X 30 m grid along the shoreline 2 km from the mouth of Big Beaver Creek (McMillan Point; Fig. 1). Preliminary minnow trap sets prior to the initiation of this study indicated that redside shiners were not located in depths below 25 m. Accordingly, minnow trap arrays were only placed in depths up to 25 m. Each minnow trap was 25 X 25 X 45 cm with a 6 cm diameter opening. On each array, unbaited minnow traps were placed from the surface to the bottom at 2 m intervals. The location of each array was selected from randomly generated sets of numbers corresponding with coordinates within the sampling grid. Catch per unit effort (CPUE) for redside shiners was calculated for each trap in each array by dividing the total number of redside shiners caught by the number of hours the trap was set for. Arrays (182 total) were set at all times of the day and night. Twenty-five arrays were set at night (between 20:01 and 06:00). Arrays set during the day (7:01-19:00) and twilight (6:01-7:00, 19:01-20:00) were never deployed for more than two hours. Due to safety concerns, arrays deployed at night were checked the following morning and consequently in place for up to 11 hours. The prey density data discussed are CPUE values calculated from minnow trap sets during the day and twilight hours (6:01-20:00; 157 arrays) because the foraging model (see chapter 2.4) indicated that consumption at night was limited by low light values, regardless of the prey densities. I opted to intensively sample a single location to determine fine-grained distributions of redside shiners with respect to depth and distance to shore. This location is unlikely to be representative of the entire shoreline of Ross Lake, but McMillan Point was adjacent to locations where we were tracking depth use by bull trout.

### *2.3.4 Depth and Temperature Use by Bull Trout*

Twelve bull trout were captured by Seattle City Light in October 2012 (E. Connor, Seattle City Light, personal communication) near the mouth of Big Beaver Creek via angling (Table 1). Each of these bull trout was anesthetized and surgically tagged with a Vemco © V13TP acoustic tag (Vemco Ltd., Halifax, Canada). The acoustic tags transmitted the depth and temperature occupied by each bull trout at random intervals between one and three minutes. Depth and temperature transmissions were recorded (along with date and time) by Vemco © VR2W acoustic receivers (Vemco Ltd., Halifax, Canada). Fourteen acoustic receivers were located within a 5 km radius of Big Beaver Creek, since all of the bull trout were captured and tagged at the mouth of Big Beaver Creek (Fig. 1). Range tests indicated that 75% of acoustic transmissions were detected by receivers within 500 m of a transmission, so receivers were located approximately 750 to 1000 m apart to maximize the area of the lake where bull trout could be detected.

All of the detections were imported into a Microsoft Access © (Microsoft, Seattle, WA, USA) database and filtered by removing all detections from any bull trout that met the following criteria: bull trout that died during the course of the summer (based on visual examination of movement patterns), and; bull trout that were not detected frequently enough to observe diel patterns of depth use (fewer than 100 detections in July and August). Single detections were filtered out by removing detections that met the following criteria: detections prior to July 1, 2013 and after August 31, 2013 (not within the studied timeframe); duplicate detections of bull trout recorded by a second receiver (detections less than 3 minutes apart in time from different receivers), and; any isolated detection within a given hour (ie., 10:00-11:00). After the dataset was filtered, detections from three bull trout remained. The filtered dataset was grouped by bull trout, date and hour. I followed the methods of Gutowsky et al (2013) to calculate average hourly depth (m) and temperature, (˚C) of each bull trout.

## 2.4 Foraging Model

Consumption inputs were based on observed diets of bull trout, prey abundance, and surface light intensity. These data were input into a foraging model (Beauchamp et al. 1999) to calculate encounter rates (ER= number of prey fish encountered per bull trout per hour at depth z and diel time period t) as a product of Search Volume (SV = $m^3 \cdot h^{-1}$) and Prey Density (PD = prey fish·$m^{-3}$; estimated from redside shiner CPUE).

(1) $ER_{z,t} = SV_{z,t} * PD_{z,t}$

Search volume was modeled as a function of reaction distance of predators to their prey (RD = m) and predator swimming speed (SS = $m \cdot s^{-1}$). Beauchamp et al. (1999) derived swimming speeds from laboratory data (Henderson and Northcote 1985) of Dolly Varden. Estimated daytime (7:01-19:00), twilight (6:01-7:00, 19:01-20:00) and nighttime (20:01-6:00) swimming speeds were 0.295, 0.235 and 0.040 ($m \cdot s^{-1}$) respectively.

(2) $SV_{z,t} = \pi * RD_{z,t}^2 * SS_t$

Beauchamp et al. (1999) modelled reaction distance as a function of light intensity (I = lux at depth z and time t) with a maximum reaction distance occurring at light intensities ≥ 17.8 lx (Vogel and Beauchamp 1999). The reaction distance equation was derived from experimental data on adult lake trout foraging on salmonid prey in varied light conditions (5.5–13.8 cm TL). The turbidity of Ross Lake is generally below the clear water threshold of this foraging model (0.3 NTU; C.A. Welch, North Cascades National Park, unpublished data) so this equation did not account for the influence of turbidity on reaction distance.

(3) $RD = 0.25490 * I_{z,t}^{0.4747}$ for $I_{z,t} \leq 17.8$ lx

$RD = RD_{max} = 1.012$ m for $I_{z,t} > 17.8$ lx

Daytime and twilight surface light intensities ($I_{0,t}$ = lux at surface at time t) were estimated at hourly intervals on August 1, 2013 (the middle of this study period). This was done using the Points Solar Radiation tool in the spatial analyst version toolbox for ArcGIS © version 10.0 (ESRI, Redlands, California, USA). A range of nighttime surface light intensities was modelled in order to account for lunar cycles. Values for starlight and moonlight were estimated to range from 0.002 – 0.25 lx. Light intensity at depth ($I_{z,t}$) was calculated as an exponential decay from surface light intensity ($I_0$).

$$I_{z,t} = I_{0,t} * e^{zk} \tag{4}$$

The light extinction coefficient (k) was calculated based on a 10 m Secchi disk depth (C.A. Welch, North Cascades National Park, unpublished data), assuming that light intensity at the Secchi disk depth was 10% of the light intensity at the surface (Wetzel 2001).

$$\mathrm{k} = \frac{\ln(10) - \ln(100)}{10} \tag{5}$$

Light dependent probability of capture to account for prey evasion at higher light levels (Mazur and Beauchamp 2006), was used to calculate consumption (C = number of prey fish consumed per bull trout per hour at depth z and diel time period t).

$$C = 0.49 * ER_{z,t} \qquad \text{for } I_{z,t} > 17.8 \text{ lx} \tag{6}$$

$$C = 1.0 * ER_{z,t} \qquad \text{for } I_{z,t} \leq 17.8 \text{ lx}$$

Consumption was converted into grams of prey by multiplying number of prey fish times 3.16 g (the average weight of a redside shiner in Ross Lake in the summer) (Welch 2012).

## 2.5 Bioenergetics Model

The Wisconsin bioenergetics model (Hansen et al. 1997, Hansen 2013, Mesa et al. 2013) calculates the growth of bull trout ($G = g \cdot g^{-1} \cdot d^{-1}$) as consumption ($C = g \cdot g^{-1} \cdot d^{-1}$ of prey, wet weight) minus respiration (R = resting/active metabolism + food assimilation costs), egestion ($F = g \cdot g^{-1} \cdot d^{-1}$), and excretion ($U = g \cdot g^{-1} \cdot d^{-1}$). The parameters for respiration (R), egestion (F) and excretion (U) depend on: the species and size of the fish; the water temperature occupied; and the type of prey consumed (Hansen et al. 1997, Hartman and Hayward 2006).

(7) $$G = C - (R + F + U)$$

To apply this model to bull trout specifically, model parameters derived by Mesa et al (2013) in a laboratory study with bull trout were used. For specific equations and parameter values used to calculate respiration, egestion and excretion see Hansen et al. (1997) and Mesa et al. (2013).

To assess the growth associated with DVM, where bull trout occupied two different depths (and corresponding temperatures) in a single day, the daily output from the bioenergetics model was divided by 2 in order to calculate growth in $g \cdot g^{-1} \cdot 12\ h^{-1}$. Three hypothetical bull trout depth use patterns were developed based on data collected in the field and corresponding growth hypotheses that may be driving such movement patterns. These growth hypothesis were: maximizing spatial overlap with prey (constant depth of 10 m); minimizing thermal metabolic expenditures (constant depth of 50 m, 8 ˚C); and bioenergetic efficiency (DVM between depths with the highest prey availability at night (5 m) and depths with cooler temperatures during the day (50 m, 8 ˚C)). For the DVM depth use pattern, I assumed that bull trout occupied each depth for 12 hours. For the constant depth use patterns, I assumed temperature at a given depth did not change over the course of a day. The growth of a bull trout exhibiting these hypothetical movement patterns was assessed using the foraging and bioenergetic models.

# CHAPTER 3 – RESULTS

## 3.1 Field Sampling

### *3.1.1 Diet*

During the month of July, 36 bull trout were captured by angling or in tangle nets. Capture depth ranged from 3 to 30 m deep, within 100 m of the shore. Capture times ranged from 06:00 to 18:00. Less than 10 hours of night fishing was conducted and no bull trout were captured during the night. Weights of bull trout captured ranged from 200 to 2075 g. Twenty-one of the 36 stomachs contained food items (non-empty stomachs). Redside shiner was the only observed fish prey item and the most common prey item observed. Only one insect was found from the stomach of a 450 g bull trout. One bull trout was captured (750 g) with 11 fish (29.4 g) in its stomach. Nine of these fish (27.2 g) were less than 20% digested and could be identified as redside shiners. This quantity of prey is more than can be digested by a 750 g bull trout in 12 hours, based on bioenergetic simulations.

### *3.1.2 Temperature*

Temperatures in Ross Lake ranged from 4.9 to 16.8 ˚C in July and 5.1 to 20.7 ˚C in August (Fig. 3). The thermocline was approximately 7 to 20 m deep (16 to 10 ˚C) in July. Comparatively, in August the thermocline was approximately 6 to 25 m deep (21 to 11 ˚C) Average daily temperature fluctuation at a given depth in the upper 17 m during August was 1.19 ˚C (Minimum = 0.17 ˚C, Maximum = 3.80 ˚C).

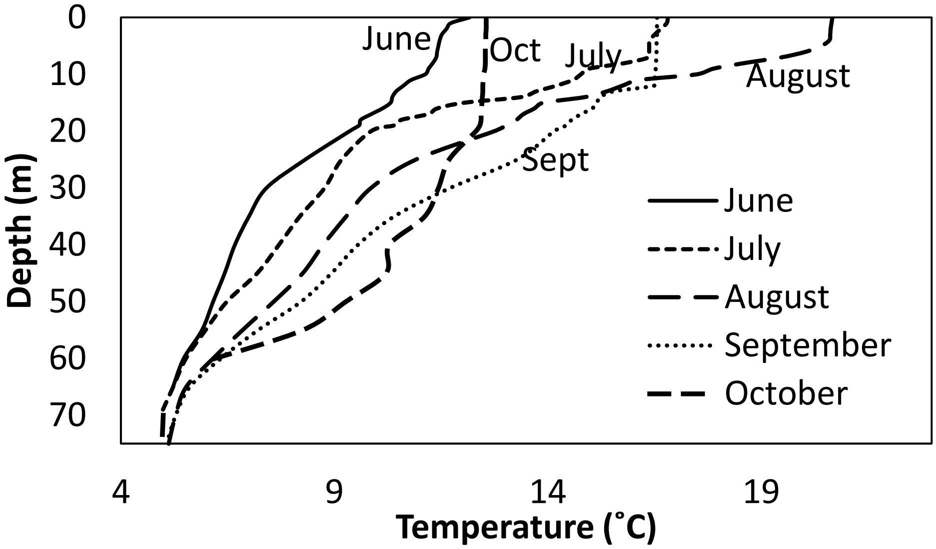

**Fig 3.** Temperature profiles of Ross Lake collected in the middle of Ross Lake, between Big Beaver Creek and McMillan Point in 2013. Profiles were collected in the middle of each month (13th, 14th, or 15th) except for September and October which were collected on the 23rd and 21st respectively. All profiles were collected within one hour of 12:00.

### *3.1.3 Prey Density*

Consumption at night was limited by low light values, regardless of the prey densities (See results from foraging model, chapter 2.4). Accordingly, the prey density data presented in the results and input into the models (Fig. 4; Fig. 5) are CPUE values calculated from minnow trap sets during the day and twilight hours.

The CPUE at each depth varied depending on the maximum depth of the array. Minnow trap arrays set down to 20 m depth captured redside shiners congregated primarily along the bottom (Fig. 4).

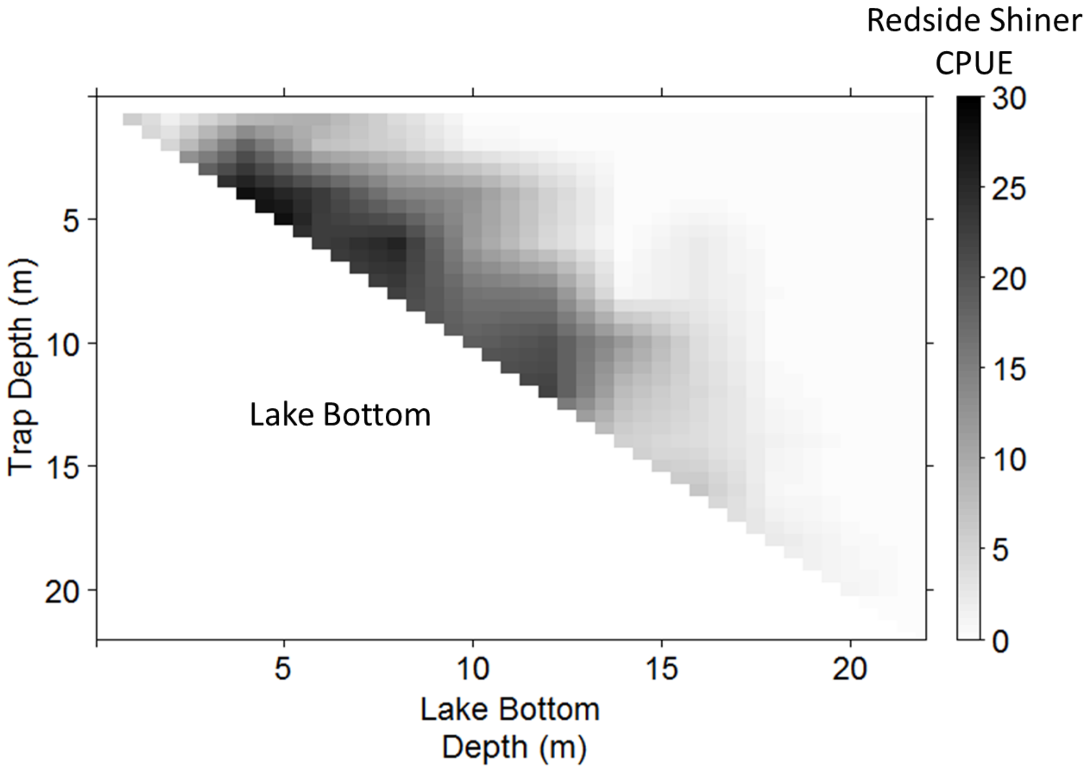

**Fig. 4.** The average number of redside shiners captured per hour (CPUE) in minnow traps set during day and twilight hours (6:01-20:00; 157 arrays) at McMillan point on Ross Lake (Fig. 1). Traps on each array were set at 2 m depth intervals and linear interpolation was used to smooth this graphic.

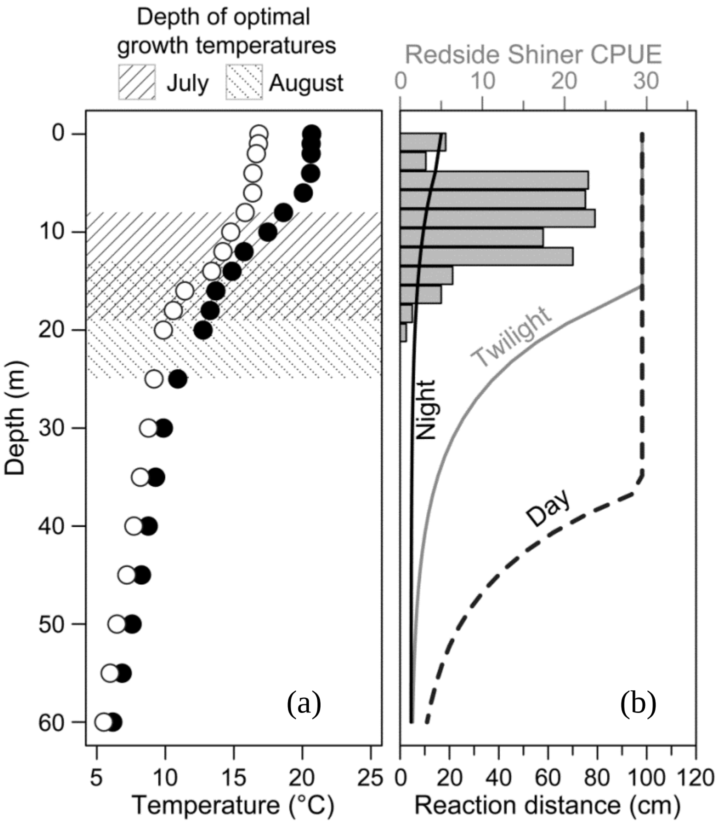

**Fig. 5** (a) Temperature profiles for Ross Lake from July 15 (open dots) and August 15 (solid dots). Diagonal horizontal lines indicate the depth range corresponding to optimal bull trout growth temperatures (10.9-15.4 ˚C) in July and August. (b) Distribution of redside shiner CPUE (number of redside shiners captured in a minnow trap per hour) in relation to depth along the bottom 2 m (standard deviations are listed in table A1). CPUE values depicted are from trap arrays set during twilight and daytime hours (6:01-20:00).Reaction distances of bull trout (solid lines) during the night, twilight and daytime hours were caluclated in the foraging model and are overlaid in this figure. All reaction distances in this figure are based on light values predicted for August 1st. The specific times of the day when light was calculated were: 13:00 (day); the average of dusk (6:00) and dawn (19:00; twilight). Nighttime light levels were low and values for a full moon are displayed, which represents maximum light available at night.

### *3.1.4 Depth and Temperature Use by Bull Trout*

Twelve (465-600 mm TL) were tagged with acoustic tags (Table 1). After filtering the raw telemetry dataset, detections from three bull trout remained (Fig. 6; Fig. 7). Detection depths ranged from 2.1 to 59.8 m. Detection temperatures ranged from 6.1 to 18.9 ˚C (Table 2). We summarized observed DVM for any bull trout that exhibited a daily depth range ≥ 20 m and a minimum daily depth <20 m. The shallow depths (<20 m) corresponded with optimal foraging habitat, and depths below 20 m corresponded with cooler temperatures where metabolic expenditures were minimized. Based on this threshold, DVM was apparent in all bull trout on some days of the study. Shallow depth use (daily maximum <20 m where prey was most abundant) was observed for two of the bull trout on some of the days of the study.

Table 1. Specifications of bull trout tagged with acoustic telemetry tags in this study. All bull trout were captured and measured on October 24, 2012. Each bull trout was assigned a unique fish identification number (FID). These FID numbers correspond with the FID numbers in Table 2, Figure 6 and Figure 7.

| Bull trout FID | Sex | Fork Length (mm) | Weight (g) |
|---|---|---|---|
| [a]1 | f | 465 | 1150 |
| [a]2 | m | 465 | 1045 |
| [a]3 | m | 565 | 1800 |
| 4 | m | 600 | 2050 |
| 5 | m | 580 | 2100 |
| 6 | m | 565 | 1750 |
| 7 | f | 590 | 1895 |
| 8 | m | 538 | 1445 |
| 9 | f | 585 | 2000 |
| 10 | m | 575 | 1750 |
| 11 | m | 545 | 1600 |
| 12 | f | 535 | 1770 |

[a] Individual bull trout that were detected frequently enough to analyze the telemetry results in this study.

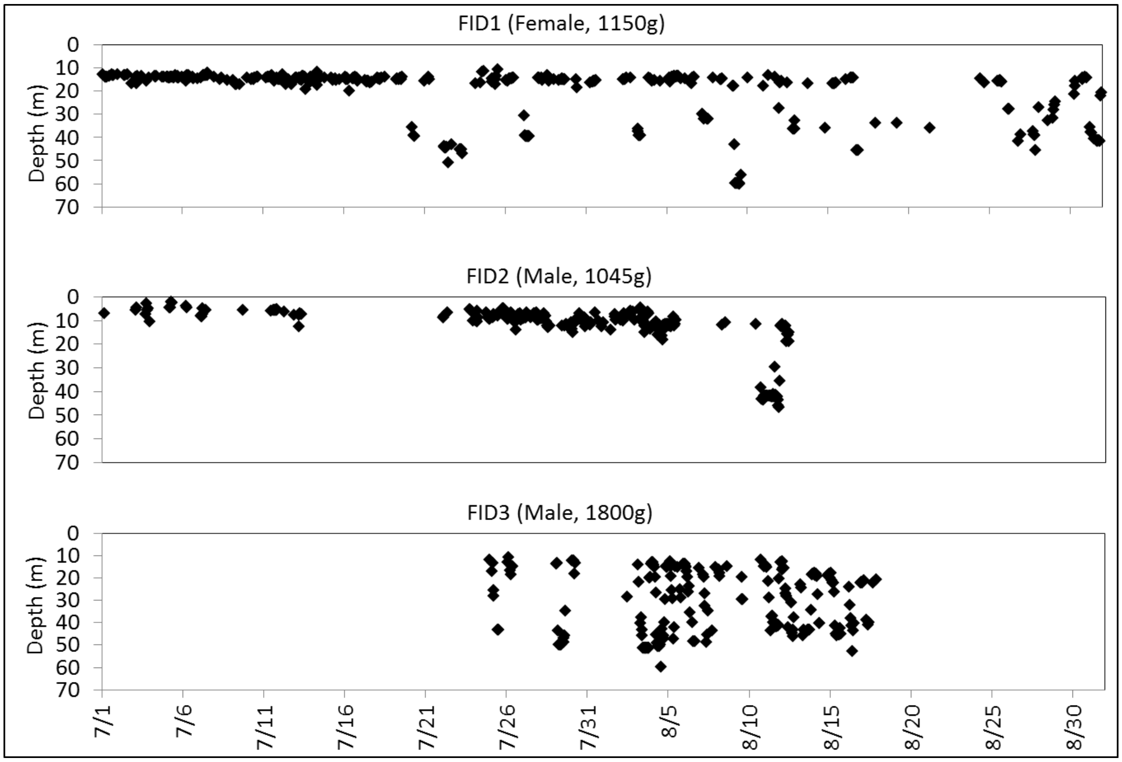

**Fig. 6.** Average hourly depths (m) of bull trout tagged with acoustic tags during the months of July and August, 2013. The sizes of each bull trout were measured at the time of tagging (October 2012) nearly nine months before the dates shown. Acoustic receivers that detected these bull trout were located within a 5km radius of Big Beaver Creek, their capture location, on Ross Lake, WA.

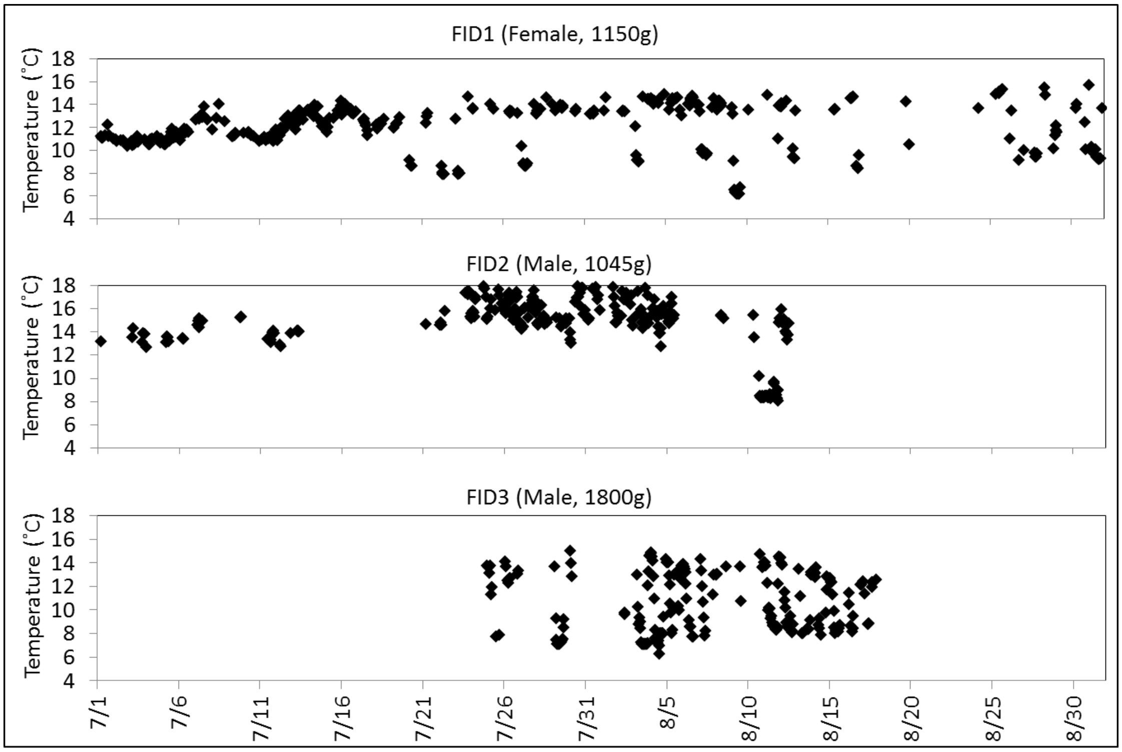

**Fig. 7.** Average hourly temperatures (˚C) of bull trout tagged with acoustic tags during the months of July and August, 2013. The sizes of each bull trout were measured at the time of tagging (October 2012) nearly nine months before the dates shown in this figure. Acoustic receivers that detected these bull trout were located within a 5km radius of Big Beaver Creek, their capture location, on Ross Lake, WA.

**Table 2.** Summary of patterns of depth use by bull trout, patterns including daily vertical migrations and constant use of shallow depths.

| Month (FID) | Num. of days with a detection | [a] Num. of days with DVM | [a] Avg. minimum detection depth (m) of DVM | [a]Avg. maximum detection depth (m) of DVM | Num. of days with a detection ≥40 m | Num. of days with a detection ≤10 m | [b] Num. of shallow days | [b]Avg. detection depth (m) on a shallow day |
|---|---|---|---|---|---|---|---|---|
| **July** | | | | | | | | |
| 1 | 31 | 0 | -- | -- | 5 | 3 | 25 | 14.6 |
| 2 | 19 | 0 | -- | -- | 0 | 19 | 19 | 8.3 |
| 3 | 5 | 2 | 13.5 | 44.6 | 2 | 1 | 2 | 14.5 |
| **August** | | | | | | | | |
| 1 | 26 | 3 | 15.4 | 44.6 | 5 | 0 | 10 | 16.6 |
| 2 | 9 | 2 | 11.5 | 45.2 | 2 | 9 | 5 | 11.2 |
| 3 | 16 | 12 | 16.3 | 47.5 | 13 | 3 | 2 | 15.8 |

[a] DVM defined as follows: difference in daily minimum and maximum detection is ≥20m

[b] Shallow day defined as follows: all daily detections < 20m

### 3.2 Foraging Model

Modelled capture rates of redside shiners by bull trout were greatest during the daytime due to high light intensities and bull trout swimming speeds (Table 3). All surface light intensities above 5630 lx (less than daytime surface light intensities at any date within the study) resulted in maximum bull trout reaction distances in depths less than 25 m. During the daytime in less than 25 m of water, bull trout could capture more redside shiners in one hour than could be digested in 12 hours (35 g of prey for a 1500 g bull trout). These high capture rates in shallow water during the day indicate that bull trout were feeding to satiation. In contrast, capture rates of redside shiners by bull trout during the night were much lower than digestion rates, except for at the highest modelled prey density in 5 m depth.

### 3.3 Bioenergetics Model

The depth use pattern that corresponded with the highest modeled growth was a constant depth of 12 and 15 m ("maximum spatial overlap with prey;" Fig. 8) in July and August, respectively. In contrast, bull trout occupying only deep water (>50 m; "minimizing metabolic expenditures") lost weight due to a lack of prey and cold temperatures below 8 ˚C. For bull trout exhibiting DVM corresponding with maximum spatial overlap with prey and metabolic efficiency ("bioenergetic efficiency"), growth was 44% and 62% lower (July and August, respectively). Growth associated with the observed DVM patterns (Table 2; Fig. 6; Fig. 7) were 44% and 27% lower (July and August, respectively) relative to that observed for constant depth use of 12-15m (Fig. 8).

**Table 3.** Parameters in the foraging model (surface light intensity, predator swimming speed and redside shiner density) and corresponding redside shiner capture rates (g prey·h$^{-1}$) at 5, 15 and 25 m depths. Twilight surface light intensity (434 lx) was the average surface light intensity at dusk and dawn on August 1, 2013. A range of nighttime surface light intensities were examined to account for variations in the lunar cycle. Redside shiner densities were conservative estimates based on the average capture rates from the minnow trap arrays (Fig. 4, Fig. 5).

| | | **Parameters in foraging model** | | |
|---|---|---|---|---|
| | | | Redside shiner density (fish·m$^{-3}$) 0.01 | Redside shiner density (fish·m$^{-3}$) 0.1 |
| Time of day | Light at depth (lx) | Swimming speed (m·s$^{-1}$) | Capture rates (g·prey·hr$^{-1}$) | Capture rates (g·prey·hr$^{-1}$) |
| **5-m depth** | | | | |
| [a]Day | ≥1780 | 0.295 | 52.9 | 529 |
| [b]Twilight | 137.5 | 0.235 | 42.10 | 421.0 |
| [c]Night | 0.00063 – 0.079 | 0.040 | 0.000853 – 0.0835 | 0.00853 – 0.835 |
| **15-m depth** | | | | |
| [a]Day | ≥178.0 | 0.295 | 52.9 | 529 |
| [b]Twilight | 13.75 | 0.235 | 36.8 | 368 |
| [c]Night | 0.000063 – 0.0079 | 0.040 | 0.0000958 – 0.00938 | 0.000958 – 0.0938 |
| **25-m depth** | | | | |
| [a]Day | ≥17.80 | 0.295 | 52.9 | 529 |
| [b]Twilight | 13.75 | 0.235 | 3.62 | 36.2 |
| [c]Night | 0.0000063 – 0.00079 | 0.040 | 0.0000107 – 0.0000105 | 0.000107 – 0.000105 |

[a] Day = 7:01 - 19:00

[b] Twilight = 6:01 - 7:00, 19:01 - 20:00

[c] Night = 20:01- 6:00; the range of values represents possible illumination scenarios ranging from starlight alone (lowest light levels) to full moonlight (highest light levels).

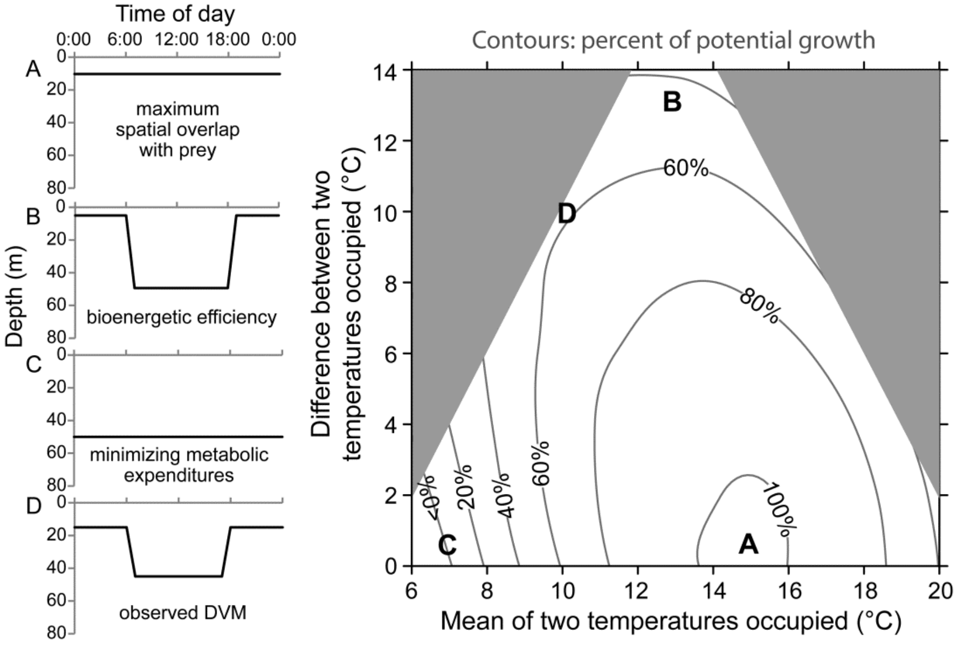

**Fig. 8.** Relative growth associated with observed and potential depth use patterns for bull trout in Ross Lake. Contrasting depth use patterns are depicted on the left panel (A, B, C, D). Growth contours on the plot to the right are relative to depth use pattern A, which corresponded to maximum growth (100%). The axes of this graph (difference between occupied temperatures and mean of two occupied temperatures) represent variation in potential depth use patterns (e.g., A, B, C, D), ranging from constant depth use (no difference between two temperatures occupied) to utilization of depths corresponding to a daily range of temperatures of up to 14 ˚C. Relative daily growth associated with each depth use pattern is marked (A, B, C, D) on the contour plot. The contour plot shows relative daily growth of a 1500 g bull trout exhibiting DVM and constant depth use patterns. The shaded grey regions of the contour plot cover depth-temperature combinations not likely to occur in Ross Lake. The area of the graphic to the left of the 0% contour indicates weight loss.

# CHAPTER 4 – DISCUSSION

Growth is often considered a primary driver of fish behavior due to the strong connection between growth and fitness (Brett 1971). In many lentic systems (lakes and reservoirs) temperature and prey vary with depth, and depth use patterns can strongly influence growth. It is unlikely that growth is the only explanation driving depth use, however, because constraints vary among systems and among species due to different environments and life history requirements (Beauchamp et al. 1999). Under some circumstances, for example, survival can strongly influence fitness and therefore can also be a driver of depth use (Clark and Levy 1988). In this study, I found that bull trout frequently engaged in behaviors that resulted in reduced growth, relative to the maximum potential attainable in Ross Lake. In light of this, it is reasonable to infer that other constraints are operating to limit growth of bull trout in this system. Here, I discuss the configuration of constraints in Ross Lake and alternative hypotheses that could explain observed patterns of depth use by bull trout.

One of the most important drivers of growth in any predator is availability of prey. Bull trout in Ross Lake were highly piscivorous, preying nearly exclusively on redside shiners, which were more prevalent in warmer surface layers (Fig. 4, Fig. 5). Our results mirror those from sampling of bull trout diets in other surveys of Ross Lake (H. Anthony, North Cascades National Park, unpublished data). Such results are not surprising as bull trout commonly exhibit piscivory in lakes and reservoirs (Fraley and Shepard 1989, Vidergar 2000, Beauchamp and Van Tassell 2001), as well as in the lower Skagit River below Ross Dam (Lowery 2009). In these studies warm water prey (ie., redside shiners or other cyprinids) were available, but bull trout consumed primarily cold-water prey species (ie., kokanee and cottids in Lake Billy Chinook; Beauchamp and Van Tassell 2001). In contrast, redside shiner are the primary summer prey item for bull trout in Ross Lake due to a lack of cold-water prey fish alternatives, or because it is more efficient to forage on redside shiner due to their high abundance.

In surface waters average capture rates of redside shiners were high, but extremely variable (Table A.1), suggesting patchy distributions. Accordingly, in the foraging model I examined a range of redside shiner densities (1 - 10 redside shiners per 100 $m^3$) that were conservative estimates relative to the high average capture rates I observed (> 20 redside shiners per hour). Using these conservative estimates of prey density, foraging models indicated that bull trout could easily capture maximum stomach capacity (more redside shiners than could be digested in 12 hours) during the daytime near the surface (Table 3). This suggests that daytime consumption near the surface is limited by the time required to digest prey, ie., maximum consumption (Elliott and Persson 1978, Amundsen and Klemetsen 1988, He and Wurtsbaugh 1993). Furthermore, since maximum stomach capacity could be captured in less than one hour near the surface during twilight, consumption at night, regardless of low reaction distances and prey capture rates, can also be limited by digestion rates. This same logic holds for bull trout exhibiting DVM, occupying shallow water during the twilight immediately before a deep water migration (into depths with no prey) during the day.

In previous studies, DVM corresponding with maximum growth occurred under two different scenarios: 1) maximizing consumption by following prey exhibiting DVM (lake trout, *Salvelinus namaycush siscowet*; Hrabik et al. 2006), and 2) minimizing metabolic expenditures in deeper, cooler water during the day and maximizing foraging opportunities near the surface at night (Brett 1971, Biette and Geen 1980). A third scenario where DVM is observed in the presence of predation is referred to as the “anti-predation window,” where fish avoid predation risks in the well-lit surface water during the day and maximize foraging benefits at night (Clark and Levy 1988, Scheuerell and Schindler 2003, Mehner 2012). In each of these scenarios, diverse biotic and abiotic conditions can result in similar depth use patterns that maximize growth. For adult bull trout in Ross Lake in July and August, maximum growth occurs at a constant depth of 15 to 25 m where prey is most abundant and metabolic efficiency is maximized (Fig. 5). Our hypothesis was that bull trout behavior was driven primarily by opportunities for growth, therefore, I did not expect to see adult bull trout exhibit DVM in Ross Lake.

Despite the higher growth rates modelled on the surface, the three bull trout observed in this study exhibited DVM to depths greater than 40 m on some days (Fig. 6). Dives below 40 m corresponded with temperatures less than 9 ˚C and limited prey- conditions resulting in at least 44% lower modelled growth rates than bull trout occupying constant depths less than 25 m deep. Although bull trout frequently occupied shallow depths corresponding with optimal growth, migrations to deeper water were not infrequent and occasionally repeated on a daily basis. It is reasonable to conclude these migrations appear must be motivated by an additional constraint unrelated to growth in Ross Lake.

Predation is another commonly invoked driver of DVM, but was not examined directly in this study. Several pieces of evidence suggest, however, predation was an unlikely driver. First, the only potential predators of large (>400 mm) bull trout in Ross Lake are other bull trout and birds such as Osprey (*Pandion haliaetus*) or mammals such as North American river otters (*Lontra canadensis*). Depths commonly used by bull trout (> 25 m) are well beyond the diving range of these avian or mammalian predators. Similarly, the bull trout observed in this study were all large enough that the threat of cannibalism should have been non-existent, and instances of cannibalism were not observed. Our findings with limited cannibalism were supported by Lowery (2009) who examined bull trout diets below Ross Lake, WA in the Skagit river. He found bull trout cannibalism was infrequent, and that the bull trout cannibalized had a mean length less than 15 cm. These observations suggest that predation and cannibalism are not constraints driving DVM behavior for adult bull trout in Ross Lake.

A constraint not previously considered with respect to DVM is temperature suitable for gametogenesis (egg and sperm development) prior to spawning (Van Der Kraak and Pankhurst 1997, Pankhurst and King 2010). I studied bull trout in July and August prior to spawning in mid-October, so gametogenesis may have been an important influence on behavior. It has been well established that temperature strongly influences the reproductive development of female fish, ultimately influencing the viability (fertilization and survival of eggs to the eyed stage) of the eggs (Jobling 1997, Pankhurst and King 2010). Specific influences of temperature on reproduction include: 1) timing of ovulation (Jobling et al. 1995), and 2) provisioning of vitellogenin to eggs (Pankhurst et al. 1996, King et al. 2003). Ovulation of Arctic char held in temperatures from 4-20 ˚C four months prior to spawning was examined by Jobling et al (1995). Despite being returned to ambient water temperatures one month prior to spawning, ovulation was progressively later (up to 4 weeks delayed) for fish held in warmer temperatures and delayed ovulation has been shown to be detrimental for egg survival (Gillet 1991, King and Pankhurst 2000). Provisioning of vitellogenin to eggs is also important for survival (Campbell 1994) and vitellogenin synthesis has been shown to be inhibited by warmer temperatures (rainbow trout, Pankhurst et al. 1996; Atlantic salmon (*Salmo salar*), King et al. 2003). Much less research has been conducted examining the influence of temperature on male reproductive development, but temperature may influence spermatogenesis (sperm development) as well (Hokanson et al. 1973, Taranger et al. 2003). Temperature, however, is not the only variable influencing reproductive development. Gametogenesis is an energetically demanding process dependent on growth. If there is a vertical segregation between depths suitable for growth and gametogenesis, DVM may be a behavior driven by growth and gametogenesis.

Predictable variations in depth use by bull trout may be influenced by size, sex, and reproductive status. Size is directly related to predation risk because smaller bull trout are more susceptible to predation. If predation risk is a primary driver of depth use, we may expect smaller bull trout to dive to deeper depths to avoid predators (Gutowsky et al. 2013). Sex may be an important factor as egg and sperm development may be differentially influenced by temperature and growth. Sperm development occurs over a shorter time period before reproduction and is much less energetically demanding than egg development. Somatic growth, however, is important for males competing for access to females during reproduction (Quinn 2005). Reproductive status may also result in predictable differences in depth use by bull trout. For immature individuals or mature individuals that forgo spawning in a given year (Johnston and Post 2009, Rideout and Tomkiewicz 2011) constraints related to gametogenesis may not be important, and if true, such individuals may be less likely to exhibit DVM. Differences in the depth use by spawning and non-spawning adults may not arise however if gametogenesis proceeds throughout the summer and the decision to spawn or skip spawning does not occur until early in the fall (Rideout and Tomkiewicz 2011). In this study, males and females across a range of sizes (465 - 565 mm TL) were observed exhibiting DVM deeper than 40 m, suggesting the constraint driving males and females to deep, cool water is similar. The reproductive status of these bull trout was unknown. Further research is warranted to evaluate thermal requirements for egg and sperm development in bull trout, which I offer as a new hypothesis to explain DVM in species that require cold water for gametogenesis.

# CHAPTER 5 – CONCLUSION

Ross Lake was established less than 60 years ago when Ross Dam was constructed. Since then, changes to Ross Lake have occurred at a rapid pace especially with the introduction of redside shiners around 2000. Results of this work show that redside shiners are now the dominant prey of bull trout in the system. Furthermore, spawner surveys of bull trout in the upper Skagit River (above Ross Lake) suggest a rapid increase in the size and number of fish following the introduction (Anaka and Scott 2011). In this study, I was able to apply bioenergetic simulations to show how bull trout could maximize growth opportunities by utilizing a novel prey base (redside shiners) in the context of constraints imposed by depth-related variability in temperature, light, and prey availability. Despite the potential for high growth rates near the surface, bull trout exhibit migrations to colder, deeper water indicating maximizing growth is not the only constraint in Ross Lake. If this is true, future bull trout population assessments cannot be predicted based on growth opportunities alone. Further, I could reasonably eliminate common explanations for DVM related to avoidance of predators, leading me to develop a relatively novel explanation for DVM: the need to utilize cold (and deeper) water for gametogenesis. Little is known about this for bull trout and thus future studies of gametogenesis under daily temperature fluctuations may be particularly helpful.

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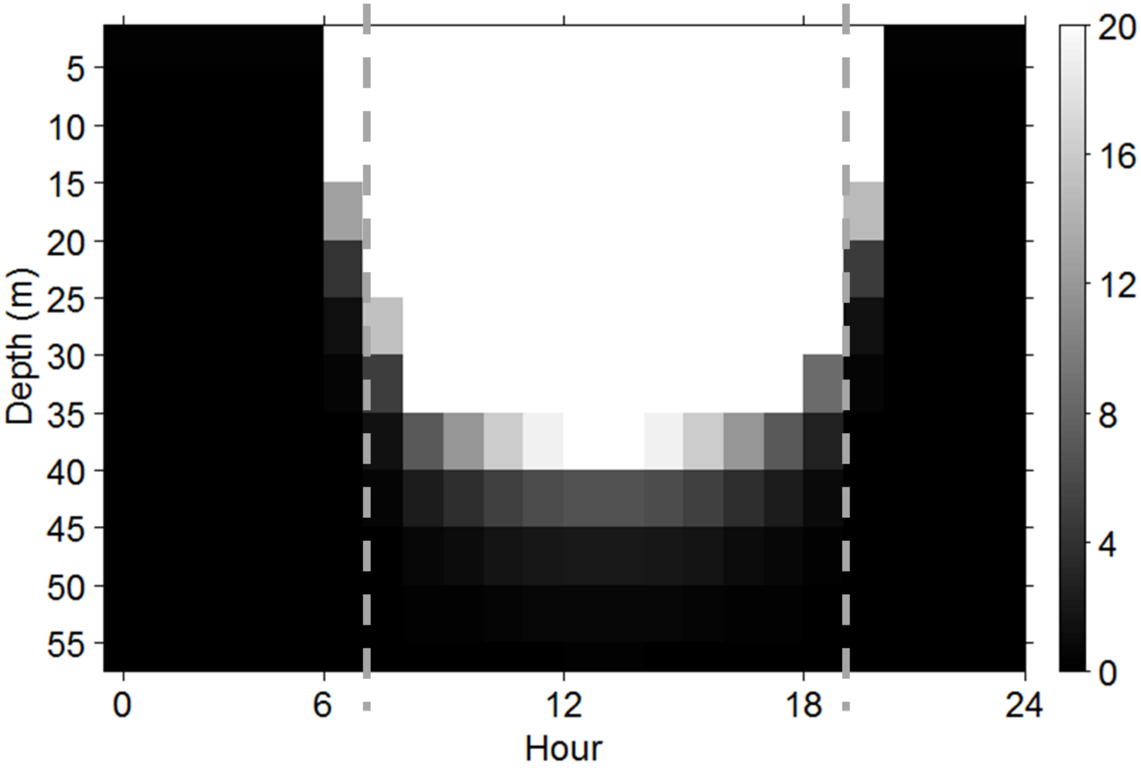
# APPENDICES

**A.1.** Average (and standard deviation) redside shiner CPUE (number of redside shiners captured in a minnow trap per hour) from the bottom two meters of Ross Lake (ie., for all minnow trap arrays set in a maximum depth of 8 m, the average CPUE of all traps at 6 and 8 m depth was calculated).

| Bottom Depth (m) | Average | Standard Deviation |
|---:|---:|---:|
| 0 | 5.09 | 6.74 |
| 2 | 3.17 | 3.81 |
| 4 | 23.13 | 42.53 |
| 6 | 22.76 | 32.60 |
| 8 | 23.95 | 29.24 |
| 10 | 17.58 | 23.96 |
| 12 | 21.23 | 26.80 |
| 14 | 6.45 | 12.09 |
| 16 | 5.05 | 12.11 |
| 18 | 1.50 | 3.53 |
| 20 | 0.75 | 1.39 |



**A.2.** A vertical light profile over the course of 24 hours on August 1, 2013 from the middle of Ross Lake, across from Big Beaver Creek. All values in white are ≥17.8 lx, which correspond with the maximum bull trout reaction distance in the foraging model. Horizontal gray lines indicate the time threshold for daytime (7:01-19:00) and nighttime (including twilight) (19:01-7:00) periods used in the bioenergetic model. Surface light values were obtained from the spatial analyst version toolbox for ArcGIS © version 10.0 (ESRI, Redlands, California, USA) and this graph was developed using a light extinction coefficient (eq. 4, 5) to estimate light at depth.