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ORIGINAL ARTICLE

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Bioenergetic evaluation of diel vertical migration by bull trout (*Salvelinus confluentus*) in a thermally stratified reservoir

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Abstract

Many species living in deeper lentic ecosystems exhibit daily movements that cycle through the water column, generally referred to as diel vertical migration (DVM). In this study, we applied bioenergetics modelling to evaluate growth as a hypothesis to explain DVM by bull trout (*Salvelinus confluentus*) in a thermally stratified reservoir (Ross Lake, WA, USA) during the peak of thermal stratification in July and August. Bioenergetics model parameters were derived from observed vertical distributions of temperature, prey and bull trout. Field sampling confirmed that bull trout prey almost exclusively on recently introduced redside shiner (*Richardsonius balteatus*). Model predictions revealed that deeper (>25 m) DVMs commonly exhibited by bull trout during peak thermal stratification cannot be explained by maximising growth. Survival, another common explanation for DVM, may have influenced bull trout depth use, but observations suggest there may be additional drivers of DVM. We propose these deeper summertime excursions may be partly explained by an alternative hypothesis: the importance of colder water for gametogenesis. In Ross Lake, reliance of bull trout on warm water prey (redside shiner) for consumption and growth poses a potential trade-off with the need for colder water for gametogenesis.

KEYWORDS

temperature, foraging, behaviour, reservoir fisheries, telemetry

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 by cold-water predators has been explained as a function of fitness, namely growth (Brett, 1971) and survival (Clark & Levy, 1988; Eggers, 1978), both of which can be strongly tied to depth-related variation in biotic and abiotic factors, including temperature, light, prey availability and predation risk (Jobling, 1997; Mehner, 2014; Werner, Gilliam, Hall, & Mittelbach, 1983). These biotic and abiotic factors interact strongly and can vary with time of day, season, year, location, and among individuals. For example, a study of lake trout (*Salvelinus namaycush*) indicated individuals that exhibit DVM can maximise growth by moving to depths where foraging rates (related to prey densities and light levels) are optimal (Ahrenstorff, Hrabik, Stockwell, Yule, & Sass, 2011). In contrast, studies of bull trout (*Salvelinus confluentus*) have suggested smaller individuals dive deeper to avoid predators during the day (Gutowsky et al., 2013), whereas larger individuals can maximise growth by following prey that also exhibit DVM (Beauchamp & Van Tassell, 2001). Accordingly, the relative influences of growth and survival (i.e. predator avoidance) on depth use by fish in lakes can vary in relation to characteristics of lakes, species or life stages within species.

Whereas it can be challenging to concurrently assess the complex interactions driving depth use, the application of bioenergetics models allows an evaluation of factors related to growth as drivers of depth use (e.g. Brandt et al., 2011). Bioenergetics models have been applied to model spatial and temporal variation in factors influencing growth potential in relation to DVM (Bevelhimer & Adams, 1993; Busch, Johnson, Mehner, & Post, 2011; Plumb, Blanchfield, & Abrahams,

2014) and have demonstrated that DVM is a tactic that can maximise growth for animals that (i) follow a prey source exhibiting DVM (Hrabik, Jensen, Martell, Walters, & Kitchell, 2006), or (ii) maximise bioenergetic efficiency moving between warmer prey-rich water and deeper, cooler water where temperatures are most efficient for growth (Brett, 1971). Although bioenergetics models do not consider factors related to predator avoidance, these models allow an evaluation of various depth use patterns using growth as a common metric.

In this study, we employed a bioenergetics modelling approach to evaluate patterns of DVM in an apex predator (bull trout) living in a deep, seasonally stratified reservoir, Ross Lake, WA, USA. Bull trout commonly exhibit piscivory in lakes and reservoirs (Fraley & Shepard, 1989; Beauchamp & Van Tassell, 2001), as well as in the lower Skagit River below Ross Dam (Lowery & Beauchamp, 2015). Whereas previous work has emphasised the importance of cold-water prey fishes (e.g. salmonids and cottids), the prey base for bull trout in Ross Lake is believed to consist almost entirely of recently introduced redside shiners (*Richardsonius balteatus)*, which are known to congregate in warmer surface waters. Temperatures occupied by redside shiners often exceed those required for long-term survival of bull trout (Dunham, Rieman, & Chandler, 2003; Selong, McMahon, Zale, & Barrows, 2001) or other salmonids (Reeves, Everest, & Hall, 1987). Consequently, during the summer growth season, the optimal thermal habitat of these species may be spatially segregated. As such, Ross Lake offers a unique opportunity to investigate relationships between bull trout and a relatively novel prey species (redside shiner) with contrasting patterns of habitat use (shallow depths, warmer water). We hypothesised these biotic and abiotic factors (temperature, depth, prey availability) should strongly influence growth, and therefore behaviours of bull trout in this system. Data on individual growth and movement patterns are extremely limited in this system, so we applied a bioenergetics approach to evaluate growth potential associated with DVM and alternative depth use patterns. To this end, we quantified bull trout diets, the distribution of redside shiner prey, and patterns of thermal stratification in summer (July and August). With these data, we parameterised foraging (Beauchamp, Baldwin, Vogel, & Gubala, 1999; Mazur & Beauchamp, 2006) and bioenergetics models (Mesa, Weiland, Christiansen, Sauter, & Beauchamp, 2013) to evaluate growth associated with constant depth use and DVM to various depths.

1.1 | Study site

Ross Lake is the northern-most reservoir on the Skagit River in the North Cascades National Park, Washington State, USA (Figure 1) with a surface area of 4,700 hectares when full. The lake is oligotrophic and dissolved oxygen levels are near saturated from the surface to the bottom. The narrow lake (average width is approximately 2 km) is 30 km long and characterised by a steep rocky western shoreline and a more gradual littoral eastern shoreline. At 489 m in elevation, Ross Lake is surrounded by protected wilderness areas and steep alpine topography exceeding 2,500 m. These wilderness areas are dominated by mixed mountain conifer and deciduous forests. Most of the tributaries draining into the lake originate from glaciers and snowfields in the surrounding mountains. Construction of Ross Dam was completed in 1949, and the reservoir was filled in 1952. The reservoir is managed for hydropower generation, recreation and fisheries. 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. A thermocline develops at a depth of approximately 10 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 November to May are less than 8°C, and the lake remains isothermic at around 5°C for most of the winter. We focused this study on the southern end of the lake near the mouth of Big Beaver Creek (Figure 1), where we observed bull trout to concentrate.

Ross Lake harbours six species of fish including bull trout (the apex predator), Dolly Varden (*Salvelinus malma*), rainbow trout (*Oncorhynchus mykiss*), non-native redside shiner, non-native brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Oncorhynchus clarkii)*. Brook trout and cutthroat trout are present in low numbers. The redside shiner was introduced to the lake around the year 2000. Since then, the redside shiner population has increased substantially. Prior to the introduction of the redside shiner, rainbow trout were the most abundant species. 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 & 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 growth of bull trout; Selong et al., 2001; Mesa et al., 2013).

2 | MATERIALS AND METHODS

2.1 | General approach

We focused our analysis on the months of July and August when Ross Lake is thermally stratified and before bull trout begin moving into tributaries to spawn. To determine the growth rates associated with depth use by bull trout in Ross Lake, we used a foraging model (Beauchamp et al., 1999; Mazur & Beauchamp, 2006) and the Wisconsin bioenergetics model (Ney 1993, Hansen, Johnson, Schindler, & Kitchell, 1997) with parameters modified for bull trout (Mesa et al., 2013). 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. These consumption inputs were capped based on the maximum consumption estimates (Cmax) in the bioenergetics model. The bioenergetics 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

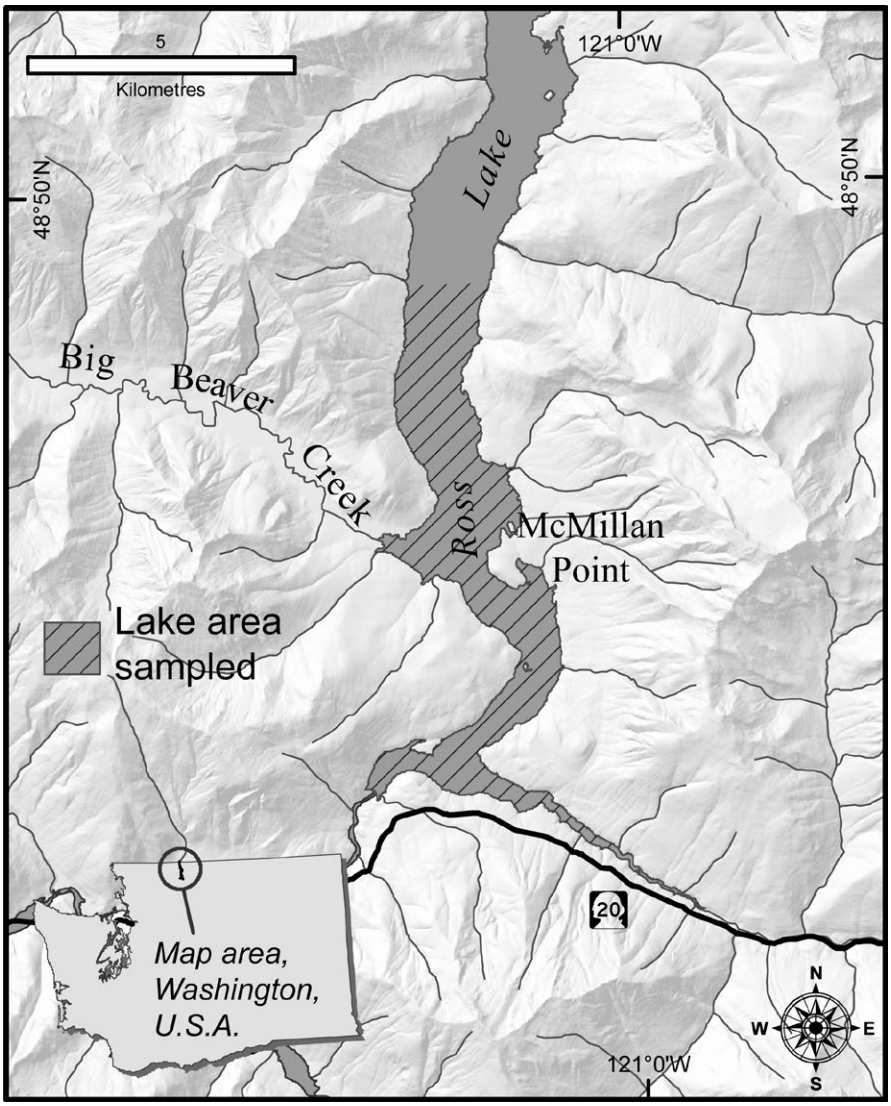

FIGURE 1 Map of Ross Lake, North Cascades National Park, Washington. The map shows the entire lake, within the United States border and the cross-hatched area depicts the specific area of the lake where this study took place. Big Beaver Creek is the location on the lake where all of the bull trout in 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

the growth of bull trout in relation to depth use patterns, it was necessary to identify (i) the vertical distribution of temperature and prey available in the lake, (ii) the primary prey types consumed by bull trout and (iii) the depths and temperatures used by bull trout.

2.2 | Temperature conditions

Temperature sensor arrays (U22 Hobo© thermistors, Onset Computer Corporation, Bourne, MA, USA) were deployed 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 25 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 | Bull trout diets

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

2.4 | Prey density and distribution

We focused on quantifying abundance of redside shiners, as we 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 × 30 m grid along the shoreline 2 km from the mouth of Big Beaver Creek (McMillan Point; Figure 1). This location is unlikely to be representative of the entire shoreline of Ross Lake, but based on local angler and our own captures it is a location where bull trout actively forage. Preliminary minnow trap sets prior to the initiation of this study indicated that redside shiners were not found in depths below 25 m. Accordingly, minnow trap arrays were only placed in depths up to 25 m. Each array

consisted of a series of traps connected to each other 2 m apart in the vertical dimension. 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 (total 182) were set at all times of the day and night. Based on the CPUE values, we conservatively approximated densities of redside shiners to input into the foraging model.

2.5 | Bull trout tagging and telemetry analysis

Twelve bull trout (465–600 mm total length; TL) 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. Each of these bull trout was anesthetised and surgically implanted with a Vemco© V13TP acoustic tag (Vemco Ltd., Halifax, NS, 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.). Fourteen acoustic receivers were located within a 5 km radius of Big Beaver Creek, as all of the bull trout were captured and tagged at the mouth of Big Beaver Creek (Figure 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 1,000 m apart to maximise 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—one bull trout) 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 1 July 2013 and after 31 August 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 (i.e. 10:00–11:00). After the data set was filtered, detections from three bull trout remained. The filtered data set was grouped by bull trout, date and hour. We followed the methods of Gutowsky et al. (2013) to calculate average hourly depth (m) and temperature (°C) of each bull trout. We considered observed movement as DVM for any bull trout that exhibited a daily depth range ≥25 m and a minimum daily depth <25 m. We used this 25 m depth as a threshold for DVM based on the observation that shallow depths (<25 m) corresponded with the depths where redside shiners were observed.

2.6 | Foraging model

Consumption inputs were based on observed diets of bull trout, redside shiner capture rates and surface light intensity. For the model, we assumed bull trout consumed only redside shiners. Preliminary runs of the foraging model with vertical variations in redside shiner densities indicated that during the day and twilight even the lowest densities resulted in predation rates greater than the maximum consumption possible in the bioenergetics model (except at 25 m during twilight). At night, the vertical difference in predation rates from varying densities of redside shiners was negligible. Accordingly, for this study, we modelled a uniform distribution of redside shiners in the upper 25 m over the course of each day and throughout the entire study period. Further, we assumed there were no redside shiners below 25 m. We ran foraging model simulations using two different densities of redside shiners (0.01 and 0.1 redside shiner·m^{-3}). All of the parameters and values for this model are listed in Table A1. 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·hr^{-1}) and prey density (PD = prey fish·m^{-3}; estimated from redside shiner CPUE).

$$ER_{z,t} = SV_{z,t} \times PD_{z,t} \quad (1)$$

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

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

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 & Beauchamp, 1999). The reaction distance equation was derived from experimental data on adult lake trout foraging on salmonid prey (5.5–13.8 cm TL) in varied light conditions. 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.

$$\begin{aligned} RD &= 0.25490 \times I_{z,t}^{0.4747} \quad \text{for } I_{z,t} \le 17.8\,\text{lx} \\ RD &= RD_{max} = 1.012\,\text{m} \quad \text{for } I_{z,t} > 17.8\,\text{lx} \end{aligned} \quad (3)$$

Daytime and twilight surface light intensities ($I_{0,t}$ = lux at surface at time t) were estimated at hourly intervals on 1 August 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, CA, USA). A range of night-time surface light intensities was modelled to account for lunar cycles. Values for starlight and moonlight were estimated to range from 0.002 to 0.25 lx based on light intensity at depth ($I_{z,t}$), which was calculated as an exponential decay from surface light intensity (I_0).

$$I_{z,t} = I_{0,t} \times e^{zk} \quad (4)$$

The light extinction coefficient (k) was calculated based on a 10-m Secchi disc depth (C.A. Welch, unpublished data), assuming that light

intensity at the Secchi disc depth was 10% of the light intensity at the surface (Wetzel, 2001).

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

Light-dependent probability of capture to account for prey evasion at higher light levels (Mazur & 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).

$$\begin{aligned} C &= 0.49 \times \mathrm{ER}_{z,t} \quad \text{for } I_{z,t} > 17.8 \text{ lx} \\ C &= 1.0 \times \mathrm{ER}_{z,t} \quad \text{for } I_{z,t} \leq 17.8 \text{ lx} \end{aligned} \quad (6)$$

Consumption was converted into grams of prey by multiplying number of prey fish captured times 3.16 g (the average weight of a redside shiner in Ross Lake in the summer; Welch, Western Washington University M.Sc. Thesis, 2012).

2.7 | Bioenergetics model

The Wisconsin bioenergetics model (Hansen et al., 1997; Mesa et al., 2013) calculates the growth of bull trout (G = g·g^{-1}·d^{-1}) as consumption (C = g·g^{-1}·d^{-1} of prey, wet weight) minus respiration (R = resting/active metabolism + food assimilation costs), egestion (F = g·g^{-1}·d^{-1}) and excretion (U = g·g^{-1}·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 & Hayward 2007).

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

To apply this bioenergetics model to bull trout specifically, model parameters derived by Mesa et al. (2013) in a laboratory study with bull trout were used. This model was coded in R following 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, our model used a 12-hour timestep. To calculate growth during July and August using 12-hour timesteps, the daily (24 hr) output from the Wisconsin bioenergetics model was divided by 2 to calculate growth in g·g^{-1}·12 hr^{-1}. Four 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 (Table A2). These growth hypotheses were as follows: maximising spatial overlap with prey (constant depth of 10 m); minimising thermal metabolic expenditures (constant depth of 50 m, 8°C) and two DVM patterns (i) 5 m at night and 50 m during the day and (ii) 15 m at night and 45 m during the day. For the DVM depth use patterns, we assumed that bull trout occupied each depth for 12 hr. The fixed 12-hour depth use pattern was a simplification intended to provide clear insights into the consequences of alternative behaviours and not intended to precisely replicate the complexities of actual behaviours of bull trout. For the constant depth use patterns, we imposed an additional simplification by assuming temperature at a given depth did not change over the course of a day. The growth of a 1,500-g bull trout exhibiting these hypothetical movement patterns was assessed using the foraging and bioenergetics models.

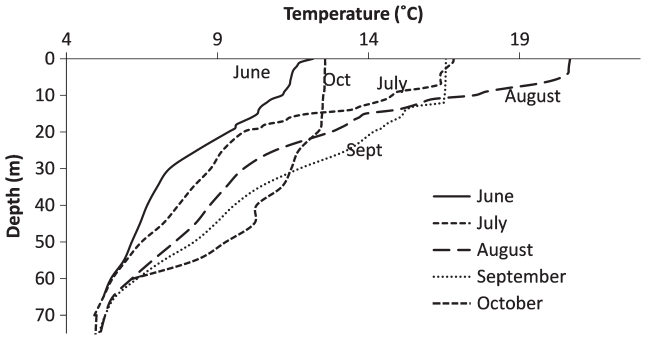

FIGURE 2 Temperature profiles of Ross Lake collected in the middle of Ross Lake, between Big Beaver Creek and McMillan Point in 2013. Profiles were collected in the middle of each month (13th, 14th, or 15th) except for September and October which were collected on the 23rd and 21st respectively. All profiles were collected within 1 hr of 12:00

3 | RESULTS

3.1 | Temperature conditions

Temperatures in Ross Lake ranged vertically from 4.9 to 16.8°C in July and 5.1 to 20.7°C in August (Figure 2). 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).

3.2 | Bull trout diets

During the month of July, 29 bull trout were captured by angling or in tangle nets. Capture depth ranged from 3 to 30 m, within 100 m of the shore. Capture times ranged from 06:00 to 18:00. Less than 10 hr of night fishing was conducted, and no bull trout were captured at night. Weights of bull trout captured ranged from 200 to 2,075 g. Twenty-one of the 36 stomachs contained food items (nonempty stomachs). Redside shiner was the only observed fish prey item and the most common prey item observed.[1] 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 the maximum amount that a 750-g bull trout can consume in 24 hr indicating the bull trout was feeding to satiation.

3.3 | Prey density and distribution

The prey density data presented in the results and input into the models (Figures 3 and 4) are based on CPUE values calculated from minnow trap sets during all times of the day and night. The CPUE at each

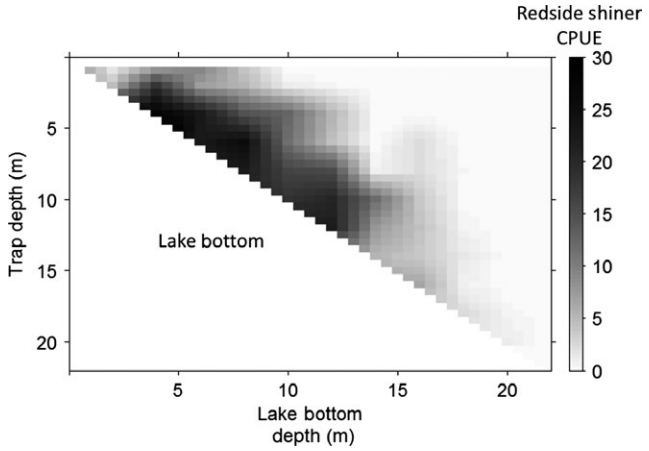

FIGURE 3 The average number of redside shiners captured per hour (CPUE) in minnow traps set during day and twilight hours (6:01–20:00; 157 arrays) at McMillan point on Ross Lake (Figure 1). Traps on each array were set at 2-m depth intervals, and linear interpolation was used to smooth this graphic

depth varied depending on the maximum depth of the array. These CPUE values between 5 and 15 m were never less than 5 redside shiners·hr^{-1} and usually closer to 20. Accordingly, we felt that using densities of 0.01 and 0.1 redside shiners·m^{-3} in the foraging model was appropriate. Minnow trap arrays set down to 25 m depth captured redside shiners congregated primarily along the bottom (Figure 3).

3.4 | Bull trout tagging and telemetry analysis

After filtering the raw telemetry data set, detections from only three bull trout remained (Figures 5 and 6). Consequently, we used observations of these individuals as points of reference for alternative behaviours (including DVM) considered in modelled scenarios. The scenarios included, but were not limited to behaviours exhibited by these fish because we know that even a very large number (>100) of tracked individuals may fail to describe the full range of movement behaviours exhibited in the wild (Monnot, Dunham, Hoem, & Koetsier, 2008). Detection depths ranged from 2.1 to 59.8 m. Detection temperatures ranged from 6.1 to 18.9°C (Table 1). DVM below 20 m was apparent in all bull trout on some days of the study. Two of the bull trout were detected only in shallow water (<20 m) on some of the days of the study.

3.5 | Foraging model

Modelled predation rates of redside shiners by bull trout were greatest during the daytime due to high light intensities and bull trout swimming speeds (Table 2). All surface light intensities above 5,630 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 1 hr than could be digested in 12 hr (35 g of prey for a 1,500 g bull trout). Predation rates estimated from the visual foraging model indicated that bull trout could consume maximum stomach capacity over relatively short periods of feeding on redside

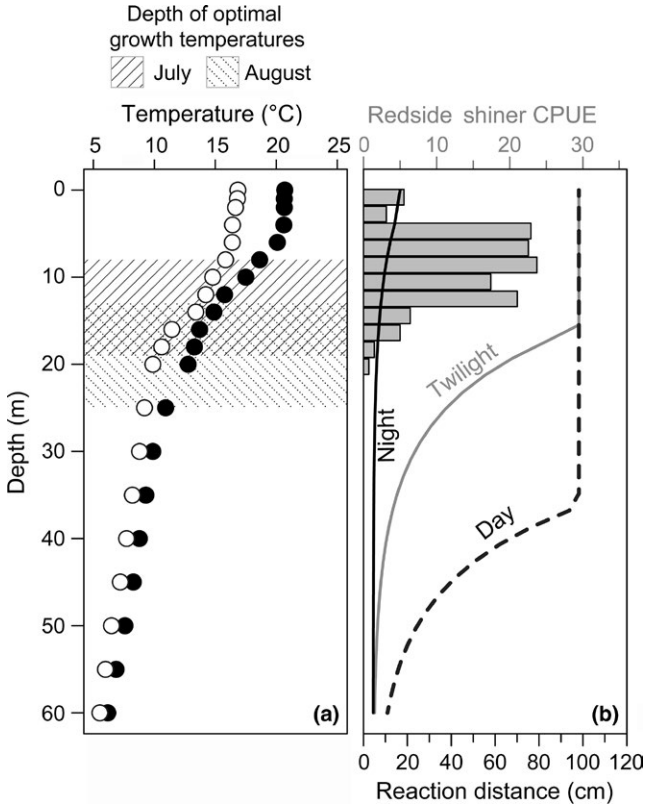

FIGURE 4 (a) Temperature profiles for Ross Lake from 15 July (open dots) and 15 August (solid dots). Diagonal horizontal lines indicate the depth range corresponding to optimal bull trout growth temperatures (10.9–15.4°C) in July and August. (b) Distribution of redside shiner CPUE (number of redside shiners captured in a minnow trap per hour) in relation to depth along the bottom 2 m (SDs are listed in Table A3). 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 calculated in the foraging model and are overlaid in this figure. All reaction distances in this figure are based on light values predicted for 1st August. The specific times of the day when light was calculated were as follows: 13:00 (day); the average of dusk (19:00) and dawn (6:00; twilight). Night-time light levels were low and values for a full moon are displayed, which represents maximum light possible at night

shiners in warm surface water. In contrast, predation 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.

3.6 | Bioenergetics model

The depth use pattern that corresponded with the highest modelled growth was a constant depth of 12 and 15 m (Figure 7) in July and August respectively. This constant shallow depth use strategy corresponded with a gain of 16 g·d^{-1}. In contrast, bull trout occupying only deep water (>50 m) lost weight due to a lack of prey and cold temperatures below 8°C. For bull trout exhibiting the two pictured DVM scenarios (Table A2), growth was 27%–62% lower than the maximum possible growth.

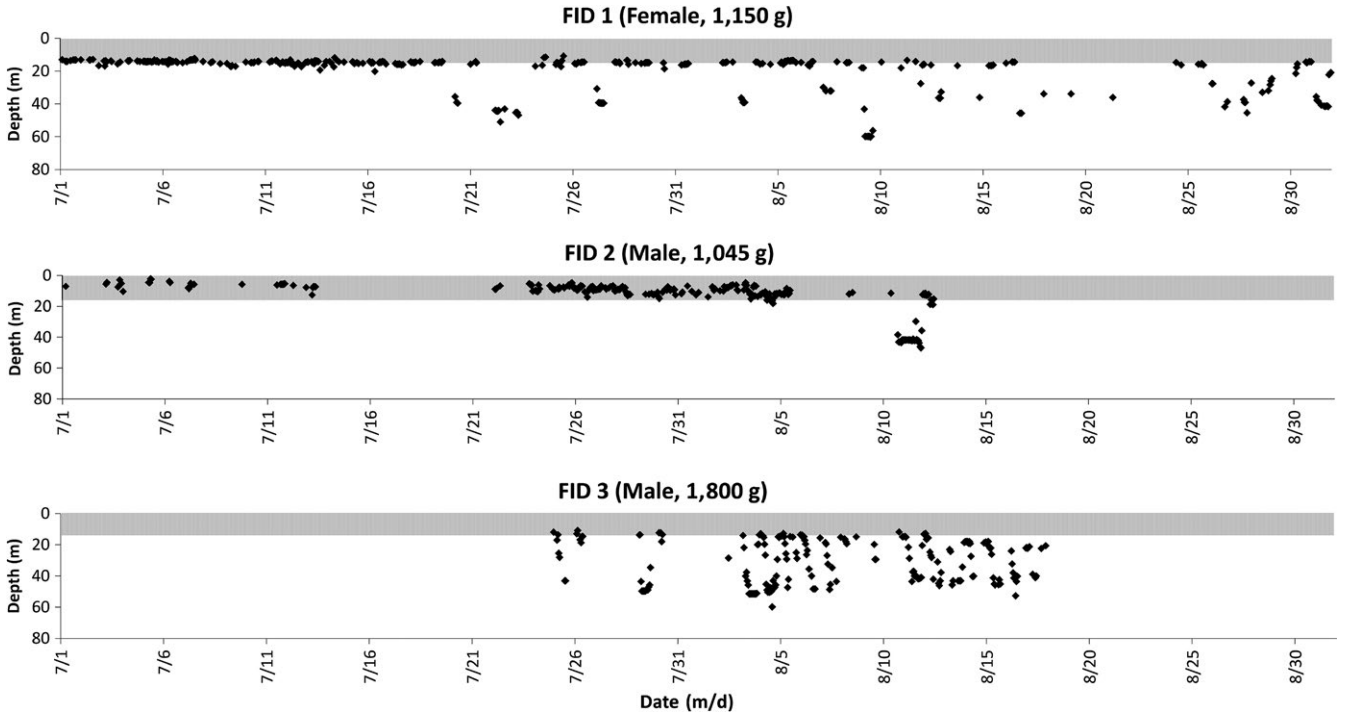

FIGURE 5 Average hourly depths (m) of bull trout tagged with acoustic tags during the months of July and August 2013. The sizes of each bull trout were measured at the time of tagging (October 2012). Acoustic receivers that detected these bull trout were located within a 5-km radius of Big Beaver Creek, their capture location, on Ross Lake, WA, USA. Shaded gray boxes correspond with the depth range of the greatest prey availability based on prey density and light

4 | DISCUSSION

Growth is often considered a primary driver of fish behaviour due to the strong connections between growth and fitness (Brett, 1971). In many lentic systems (lakes and reservoirs), temperature and prey availability vary with depth, and thus, 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 & Levy, 1988). Whereas the seasonal scope of this study is limited to the thermally stratified months of July and August, we found that bull trout frequently engaged in behaviours that resulted in reduced growth relative to the maximum potential attainable in Ross Lake. In the light of this, it is reasonable to infer that during July and August in Ross Lake other constraints are operating to limit growth of bull trout in this system. Here, we discuss the configuration of constraints that may be operating to influence bull trout in Ross Lake and explore alternative hypotheses that could explain observed patterns of depth use.

One of the most important drivers of growth for 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 (Figures 5 and 6). Such results are not surprising as bull trout commonly exhibit piscivory in lakes and reservoirs (Fraley & Shepard, 1989; Beauchamp & Van Tassell, 2001), as well as in the lower Skagit River below Ross Dam (Lowery & Beauchamp, 2015). In these studies, warm water prey (i.e. redside shiners or other cyprinids) were available, but bull trout consumed primarily cold-water prey species (i.e. kokanee and cottids in Lake Billy Chinook; Beauchamp & 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. Although bull trout in this system evolved in a fluvial ecosystem without access to novel prey items now available in Ross Lake, it appears they are capable of rapid shifts in selection of prey and in foraging tactics (e.g. lentic versus lotic; see also Beauchamp & Van Tassell, 2001).

In surface waters, average CPUE of redside shiners was high, but extremely variable (Table A1), suggesting patchy distributions. Accordingly, in the foraging model we examined a range of redside shiner densities (1–10 redside shiners per 100 m^3) that were conservative estimates relative to the high average CPUE we observed (>20 redside shiners·hr^{-1}). Using these conservative estimates of prey density, foraging models indicated that bull trout could nonetheless easily consume enough prey to reach maximum stomach capacity (more redside shiners than could be digested in 12 hr) during the daytime near the surface (Table 2). This suggests that daytime consumption near the surface is limited by the time required to digest prey (i.e. maximum consumption; Elliott & Persson, 1978; Amundsen & Klemetsen, 1988; He & Wurtsbaugh, 1993). Furthermore, as maximum stomach capacity

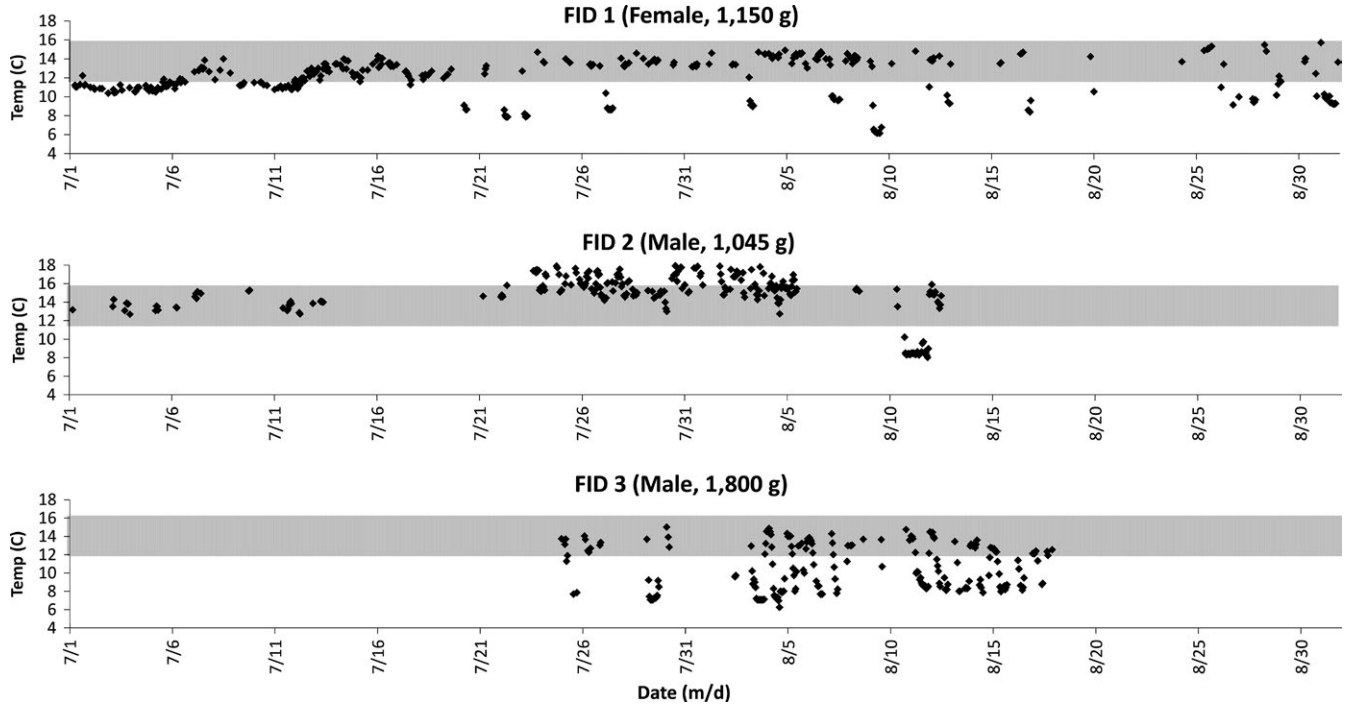

FIGURE 6 Average hourly temperatures (°C) of bull trout tagged with acoustic tags during the months of July and August 2013. The sizes of each bull trout were measured at the time of tagging (October 2012) nearly 9 months before the dates shown in this figure. Acoustic receivers that detected these bull trout were located within a 5-km radius of Big Beaver Creek, their capture location, on Ross Lake, WA. Shaded gray boxes represent the depth range with the most efficient temperatures for growth

TABLE 1 Summary of patterns of depth use by bull trout, patterns including daily vertical migrations and constant use of shallow depths

Month (FID)	Number of days with a detection	Number of days with DVM[a]	Number of days with a detection ≥40 m	Number of days with a detection ≤10 m
July				
1	31	0	5	3
2	19	0	0	19
3	5	2	2	1
August				
1	26	3	5	0
2	9	2	2	9
3	16	12	13	3

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

could be captured in less than 1 hr near the surface during twilight, consumption at night, regardless of low reaction distances and predation 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: (i) maximising consumption by following prey exhibiting DVM (lake trout, *Salvelinus namaycush siscowet*; Hrabik et al., 2006) and (ii) minimising metabolic expenditures in deeper, cooler water during the day and maximising foraging opportunities near the surface at night (Biette & Geen, 1980; Brett, 1971). A third scenario where DVM is observed in the presence of predation is referred to as the "antipredation window," where fish avoid predation risks in the well-lit surface water during the day and maximise foraging benefits at night (Clark & Levy, 1988; Mehner, 2012; Scheuerell & Schindler, 2003). In each of these scenarios, diverse biotic and abiotic conditions can result in similar depth use patterns that maximise growth or survival. 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 temperatures are most efficient for growth (Figure 4). Our hypothesis was that bull trout behaviour was

TABLE 2 Parameters in the foraging model (surface light intensity, predator swimming speed and redside shiner density) and corresponding redside shiner predation rates (g prey·hr^{-1}) at 5, 15 and 25 m depths. Twilight surface light intensity was the average surface light intensity at dusk and dawn on 1 August 2013. A range of night-time surface light intensities were examined to account for variations in the lunar cycle. At all depths examined, daytime light levels on all days of the study exceeded the light intensity threshold (17.8 lx) where maximum bull trout reaction distance occurs. Redside shiner densities were conservative estimates based on the average capture rates from the minnow trap arrays (Figures 3 and 6)

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

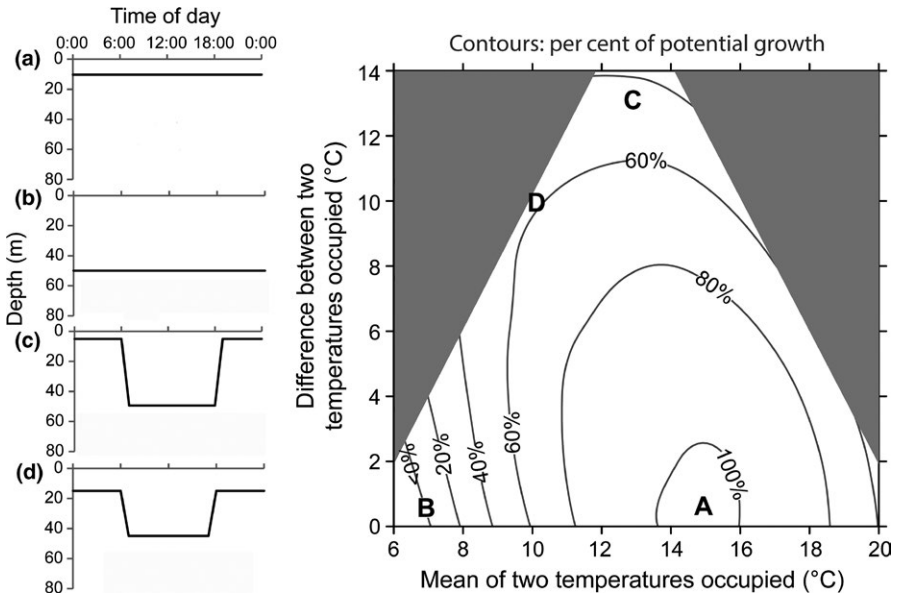

FIGURE 7 Relative growth associated with potential depth use patterns for a 1,500-g bull trout in Ross Lake. Contrasting depth use patterns are depicted on the left panel (a–d). Growth contours on the plot to the right are relative to depth use pattern (a), which corresponded to maximum growth (100%). 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–d), ranging from constant depth use (no difference between two temperatures occupied) to utilisation 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–d) on the contour plot. 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

driven primarily by opportunities for growth, and therefore, we 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 exhibited substantial variation in depth use patterns including DVM to depths greater than 40 m on some days (Figure 5). Dives below 40 m corresponded with temperatures less than 9°C (Figure 6) 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 occasionally repeated on a daily basis. It is reasonable to conclude these migrations in July and August 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. We cannot rule out predation as a cause of DVM, but several observations suggest it may not be the only 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 (>40 m) are well beyond the diving range (~25 m) of these avian or mammalian predators and deeper than necessary to minimise visibility in low light levels (Figure A1). If avian predation was the primary predation threat, we expected bull trout would dive only deep enough to avoid diving birds, while capitalising on growth advantages closer to the surface (e.g. Power, 1984). Finally, the bull trout observed in this study were all large enough that the threat of cannibalism should have been limited, and instances of cannibalism were not observed: a result supported by studies of bull trout diets in habitats directly downstream of our study system (Lowery & Beauchamp, 2015). Although the evidence for a direct threat of predation appears weak, we cannot rule out the possibility that bull trout in Ross Lake are more influenced by the perceived, rather than actual risk of predation. Perceived risks may be a strong influence on bull trout, but such responses can be extremely difficult to quantify (Stankowich & Blumstein, 2005).

A plausible constraint not previously considered with respect to DVM is temperature suitable for gametogenesis (egg and sperm development) prior to spawning (Pankhurst & King, 2010; Van Der Kraak & Pankhurst, 1997). We studied bull trout in July and August prior to spawning in mid-October, so gametogenesis may have been an important influence on behaviour. It has been well established that temperature strongly influences the reproductive development of female fish, ultimately influencing the viability (fertilisation and survival of eggs to the eyed stage) of the eggs (Jobling, 1997; Pankhurst & King, 2010). Specific influences of temperature on reproduction include: (i) timing of ovulation (Jobling, Johnsen, Pettersen, & Henderson, 1995) and (ii) provisioning of vitellogenin to eggs (King, Pankhurst, Watts, & Pankhurst, 2003; Pankhurst, Purser, Van Der Kraak, Thomas, & Forteath, 1996). Ovulation of Arctic char held in temperatures from 4 to 20°C four months prior to spawning was examined by Jobling et al. (1995). Despite being returned to ambient water temperatures 1 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 & 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, McCormick, Jones, & Tucker, 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 behaviour driven by growth and gametogenesis.

We have framed our hypotheses for depth use by bull trout in the general context of fitness-related drivers, such as growth, survival and reproduction, but the importance of these can be modified by a host of state-dependent factors, including size, sex and reproductive status. We were not able to consider these in this study, but their influences merit some discussion in the light of direction for future studies. 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, can be 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 & Post, 2009; Rideout & Tomkiewicz, 2011), constraints related to gametogenesis may not be important, and if true, such individuals may be less likely to exhibit DVM as hypothesised herein. Differences in the depth use by spawning and nonspawning 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 & Tomkiewicz, 2011).

In conclusion, we found that a bioenergetics approach provided a useful, mechanistic assessment of alternative patterns of depth use by bull trout. Certainly, more information on individual movements would allow us to better understand how bull trout actually use the lake environment, but the scenarios we simulated allowed us to explore the potential fitness consequences of adopting a range of observed behaviours and how they contrasted with alternative suites of behaviours. In other words, simulating behaviours that are not exhibited by fish in nature can help us to understand why we observe only a subset of possible patterns. Ultimately, when resources and logistics permit, approaches that combine evaluations of individual movement with mechanistic (i.e. bioenergetics) models will provide more detailed insights (e.g. Hanson, Beauchamp, & Baldwin, 2013). In

our experience, studies of *how* fish move (e.g. Gowan, Young, Fausch, & Riley, 1994) are much more prevalent that studies of *why* fish move, and model-based approaches to evaluating fish movements (e.g. Hughes & Grand, 2000; Railsback & Harvey, 2002) can provide a stronger process-based foundation for understanding depth use and other movement behaviours.

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ENDNOTE

[1] See video of Ross Lake bull trout foraging on redside shiners in supplementary materials.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX Contains tables of model parameters; potential energetic influences to movement patterns; and average/standard deviation values for redside shiners captured in minnow traps. Appendix also contains a figure of a vertical light profile in Ross Lake.

TABLE A1 Parameters used in the bioenergetics and foraging models. The bioenergetics model input parameters and their values are described in detail in Mesa et al. (2013)

Symbol	Description	Range of input values	Unit
Foraging model input parameters			
$PD_{z,t}$	Prey density (density of redside shiners). Conservative estimate from minnow trapping efforts	0.01–0.1	prey fish·m^{-3}
SS_t	Swimming speeds of bull trout at hour *t* (Henderson & Northcote, 1985)	144–1,062	m·hr^{-1}
$I_{0,t}$	Light intensity at the lake surface and hour *t* (modelled in ArcGIS)	0.25–70,000	lux
k	The rate of light extinction at depth calculated based on Secchi disc depth in Ross Lake	−0.2932	unitless
Foraging model outputs			
$ER_{z,t}$	Encounter rate depth *z* and hour *t* (bull trout encountering redside shiners)		redside shiners·hr^{-1}
$SV_{z,t}$	Search volume (area of water a bull trout swim through and could encounter a redside shiner)		m^3·hr^{-1}
$RD^2_{z,t}$	Reaction distance at depth *z* and hour *t* (the distance a bull trout can see redside shiners and react)		m
$I_{z,t}$	Light intensity at depth *z* and hour *t*		lux
C	Redside shiners consumed per bull trout per hour at depth *z* and hour *t*		number of redside shiners·hr^{-1}
Bioenergetic model outputs			
G	Growth of a bull trout in 12 hr		g·g^{-1}·12 hr^{-1}
C	Consumption of a bull trout in 12 hr, wet weight		g·g^{-1}·12 hr^{-1}
R	Resting/active metabolism + Food assimilation costs		g·g^{-1}·12 hr^{-1}
F	Egestion		g·g^{-1}·12 hr^{-1}
U	Excretion		g·g^{-1}·12 hr^{-1}

TABLE A2 Hypothetical depth use scenarios and energetic influences that may be driving such a pattern

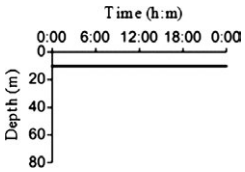
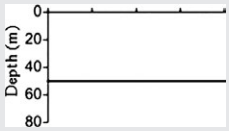
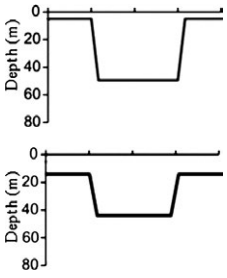
Movement pattern	Possible drivers of movement pattern in a thermally stratified lake
	When prey availability is not limited by any biotic or abiotic factors and prey is located in temperatures corresponding to a predators optimal growth temperature, predator growth is maximized by maintaining a constant depth overlapping prey.
	When prey availability is limited, predators maximize growth by maintaining a constant depth in cooler, deeper water to prevent metabolic costs from exceeding energetic gains and thus maximizing growth (Brett, 1971).
	When prey availability is limited and spatially segregated from temperatures conducive to predator growth, predators can maximize growth by foraging where prey is the most abundant and then moving to cooler, deeper waters where metabolic expenditures are minimized (Biette & Geen, 1980; Brett, 1971). In contrast, this diel vertical migration (DVM) scenario has also been observed to benefit growth when fish are following a prey source exhibiting DVM (Hrabik et al., 2006).

TABLE A3 Average (and SD) redside shiner CPUE (number of redside shiners captured in a minnow trap per hour) from the bottom 2 m of Ross Lake (i.e. 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	SD
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

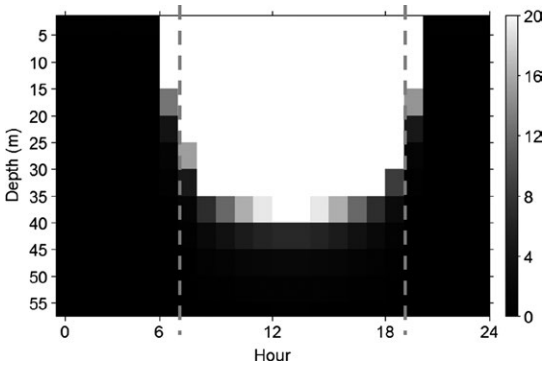


FIGURE A1 A vertical light profile over the course of 24 hr on 1 August 2013 from the middle of Ross Lake, across from Big Beaver Creek. All values in white are ≥17.8 lx, which correspond with the maximum bull trout reaction distance in the foraging model. Horizontal grey lines indicate the time threshold for daytime (7:01–19:00) and night-time (including twilight) (19:01–7:00) periods used in the bioenergetics model. Surface light values were obtained from the spatial analyst version toolbox for ArcGIS© version 10.0 (ESRI, Redlands, CA, USA) and this graph was developed using a light extinction coefficient (Equations 4 and 5) to estimate light at depth