

# Daily temperature experience and selection by adfluvial bull trout (*Salvelinus confluentus*)

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**Abstract** Bull trout (*Salvelinus confluentus*) are a thermally sensitive cold-water species with a threatened conservation status across much of North America. To improve our understanding of bull trout thermal ecology, we tagged more than 150 adults with temperature-sensing acoustic biotelemetry transmitters and monitored the animals in a British Columbia reservoir for two years. Thermal resource selection was estimated in open water from the summer to autumn as the system transitioned to isothermal conditions. On average, bull trout thermal history tracked seasonal changes and remained close to the optimum temperatures for growth

and metabolism. As summer progressed, bull trout increasingly selected temperatures of 11–15 °C as they became less available within the water column. Selection indicated the movement to shallower waters where 11–15 °C temperatures existed. The results show that bull trout mainly occupy a narrow range of temperatures which suggests the importance of cold-water refuge for the species.

**Keywords** Charr · Resource selection function · Habitat selection · Thermal history

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## Introduction

Temperature affects fish behaviour in that individuals select a thermal environment to regulate their body temperatures and obtain an optimum (Magnuson et al. 1979; Angilletta et al. 2002). However, habitat selection occurs as a result of trade-offs among proximate and ultimate factors such as bioenergetics optimization, predation risk, and prey availability (Mehner 2012). For instance, food consumption and metabolic requirements for maintenance is higher for small fish (Brett and Groves 1979; Storebakken and Austreng 1987; Elliott and Allonby 2013). Although small individuals should seek warmer temperatures to efficiently metabolize and convert food into body mass (Cuenco et al. 1985; Morita et al. 2010; Elliott and Allonby 2013), the habitat in which optimal temperatures occur may also pose, for example, a significant risk of predation (Gutowsky et al. 2013). While lab-based experiments are necessary to develop thresholds and other important metrics such as optimal temperatures for growth, field investigations provide much needed insights into the realized relationships between behaviour and temperature as populations are affected by changing environmental conditions and other natural co-occurring factors. Moreover, field-based investigations are especially critical for species with a threatened conservation status where actual thermal history may be useful in the development of management plans.

Bull trout (*Salvelinus confluentus*) are a temperature-sensitive charr that historically inhabited west of the North American Continental Divide from northern California north through Washington State, Idaho, parts of Montana, British Columbia, and the southeastern headwaters of the Yukon system (McPhail and Baxter 1996). Today the species' range has greatly contracted, leaving populations extirpated in several major tributaries. Although bull trout are recognized as important to recreational and aboriginal fisheries (Martins et al. 2014), the species remains listed as special concern or threatened in the USA and Canada (COSEWIC 2012; USFWS 2015). The threat of climate change has spurred an abundance of research projects aimed at identifying how this cold-water specialist responds to its thermal environment (Dunham et al. 2003; Rieman et al. 2007; Jones et al. 2014; Kovach et al. 2015). Radio and hydroacoustic telemetry have been particularly useful tools in the effort to understand bull trout spatial ecology including how animals distribute

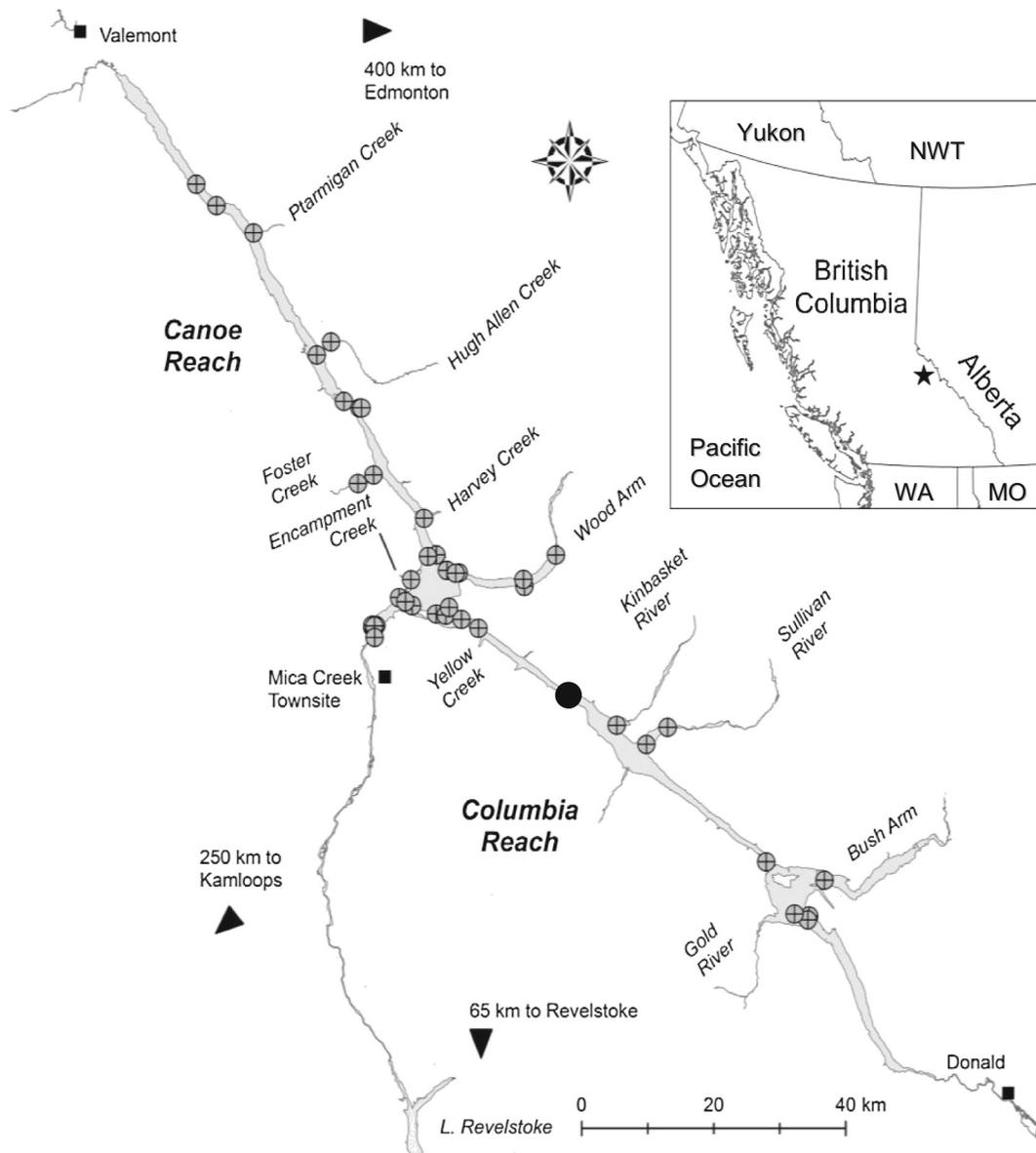
according to sex and body size (Gutowsky et al. 2013, 2015; Maret and Schultz 2014). With respect to water temperature and behaviour, most telemetry-based investigations have focused on fluvial populations (Swanberg 1997; Howell et al. 2010; Paragamian and Walters 2011; Benjamin et al. 2016), whereas less is known about adfluvial populations that exist where thermal regimes change more dramatically.

We tested hypotheses on how free-swimming adfluvial bull trout (*Salvelinus confluentus*) selected their thermal environment in Kinbasket Reservoir, British Columbia. Generalized additive mixed-models (GAMMs) and model selection were used to explore the effects of several putative covariates (sex, body size, and time of year) on thermal history. Daily temperature selection was calculated during the summer and autumn months when a thermal gradient existed. We expected the average thermal history and temperature selection of bull trout to range from 13 °C to 16 °C, which are the temperatures where standard metabolic rate is high and food consumption maximized (Mesa et al. 2013). We hypothesized that: (H<sub>1</sub>) bull trout thermal history is largely related to season and body size and, (H<sub>2</sub>) during the period of summer to autumn, selection will increase for temperatures between 13 °C and 16 °C as they become less available. The results generated here are intended to illustrate thermal habitat requirements that are based on the realized thermal history and selection of free-swimming adfluvial bull trout.

## Methods

### Study location

Kinbasket Reservoir is located in the Kootenay-Rocky Mountain Region of British Columbia, Canada (52° 8' N, 118° 28' W; Fig. 1). Kinbasket was created after the construction of Mica Dam in 1978. The system is the upper-most impoundment of the Columbia River, which flows southward through the state of Washington, USA, into the Pacific Ocean (Fig. 1). At high pool during summer and autumn, Kinbasket is one of the largest lakes in British Columbia, covering at least 425 km<sup>2</sup>. Dissolved oxygen is high (> 8 mg/L) throughout the reservoir over much of the year and only drops below 0.5 mg/L in the summer below 60 m (Bray 2012). Water turbidity and conductivity in the reservoir vary as a result of the many glacial and snowmelt streams that



**Fig. 1** Kinbasket Reservoir with telemetry receiver locations marked with an *open circle* and *cross*. The thermal logger chain with a telemetry receiver is illustrated by a *solid circle*

drain into the system. On average, turbidity is low and at times the system is relatively clear, e.g., 1% light penetration to 30 m in October (Bray 2012). The reservoir is characterized by steep, rocky shorelines, sand, rock, and mud substrates, and little vegetation. From August to mid-October, the reservoir develops a gradual thermal gradient that reduces to 4 °C at a depth of 60 to 90 m (Bray 2012). The system does not develop a clearly defined thermocline. Temperature in Kinbasket Reservoir is known to range from 2 to 15 °C from April to

May and in places has been recorded to reach 25 °C at the surface in August and September (Bray 2012). Maximum depth reaches approximately 190 m (Harrison et al. 2013) with an average depth of 57 m. Bull trout, rainbow trout (*Oncorhynchus mykiss*), northern pike-minnow (*Ptychocheilus oregonensis*) and burbot (*Lota lota*) are the confirmed piscivores in the system (Harrison et al. 2013). Kokanee salmon (*Oncorhynchus nerka*) is the predominant prey species for adfluvial bull trout (Gutowsky et al. 2013).

## Tagging

Bull trout were sampled from 11 April to 25 May, 2010 by trolling near the water surface ( $n = 122$ ; Gutowsky et al. 2011). In summer, bull trout were captured by angling at the mouths of tributaries (18 August to 9 September, 2010) where fish are known to congregate prior to spawning ( $n = 65$ ). Upon capture, fish were placed in a 100 L cooler filled with lake water that was regularly replaced. Bull trout were then moved into another 100 L cooler that contained anesthetic (40 mg/L; 1 part clove oil emulsified in 9 parts ethanol). Once anesthetized (characterized by a loss of equilibrium and no response to squeezing the caudal peduncle), bull trout were inverted and placed on a surgery table where a continuous supply of fresh water was pumped through the mouth and across the gills. Total length (nearest mm) was measured prior to surgery. Because age estimation would require lethal sampling (i.e., the collection of otoliths) and age varies widely with body size in this system (up to 400 mm fork length for a given age; Bray 2002), ages and growth increments were not estimated. For telemetry tag insertion and sex determination, a 3 cm long incision was made posterior to the pelvic girdle along the midline of the fish following the methods described by Wagner et al. (2011). Sex was determined by internal gonad examination (males: small clear to white gonads; females: yellowish gonads containing small to large eggs). A coded acoustic transmitter (model V13 TP-1 L; dimensions: 45 × 13 mm; weight in water: 6 g; weight in air: 12 g; temperature data transmissions every 2–6 min, accuracy  $\pm 0.5$  °C; expected battery life: 1028 d; VEMCO Division, AMIRIX Systems) was inserted into the body cavity. Incisions were closed with three simple interrupted stitches of 3/0 PDS-II absorbable suture material (Ethicon Inc., Somerville, New Jersey). Prior to release, post-surgery fish were allowed to fully recover for up to ~30 min in a bath of freshwater.

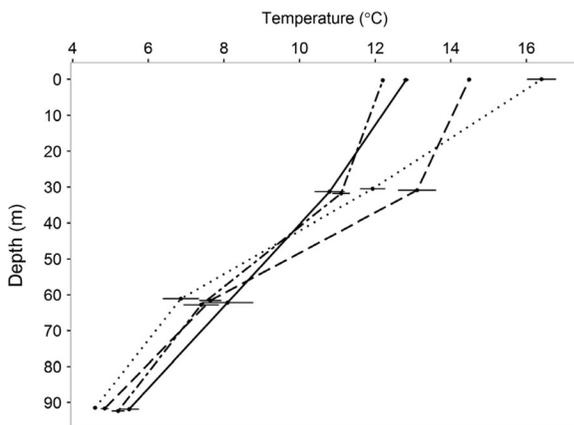
## Hydrophone deployment

To track bull trout, 42 omni-directional VR2W telemetry receivers (Vemco, Halifax, NS) were deployed in Kinbasket Reservoir at the beginning of May, 2010 (Fig. 1). In the current study, the detection radius for each receiver was assumed to be a conservative estimate of 500 m (Simpfendorfer et al. 2002; Shroyer and Logsdon 2009) which is the distance at which detection

efficiency is greater than 50% (Kessel et al. 2013). A 500 m detection radius would therefore result in an estimated maximum total receiver listening area of 33 km<sup>2</sup> (7.8% of the reservoir area). Although the listening area was lower than 10% of the total reservoir surface area at high pool, receivers were strategically placed in the littoral and limnetic zones of the confluence of the Canoe and Columbia Rivers (< 500 m from shore), at pinch-points where adjacent shorelines were separated by <500 m, and in the mouths of known spawning tributaries (Fig. 1). By placing receivers in these locations, we expected to detect bull trout more frequently than if receivers were randomly distributed across the system (Heupel et al. 2006). Additionally, the array listening area was expected to cover all of the temperatures available to bull trout within the lake habitat. In the spring of 2011, receivers were retrieved, downloaded onto a laptop using the program VUE (Vemco, Halifax, NS), and re-deployed at the original location. In the spring of 2012, receivers were once again retrieved and the data downloaded.

## Water temperature

Because the reservoir develops a thermal gradient for a short period of the year (i.e., summer and autumn) and maintains a steady surface elevation at the same time (Bray 2012), we focused the analysis of thermal habitat selection during this period which was found to occur between approximately 9 August and 24 October, 2010. During low pool in the spring of 2010, we deployed tidbit v2 thermister temperature loggers (Onset Hobo Data Loggers - UTBI-001, accuracy:  $\pm 0.2$  °C, maximum sustained temperature: 30 °C, temperature range (air): -20 °C to 70 °C, Bourne, MA) at a location near a hydrophone in the Columbia Reach where water temperatures were not affected by dam operations (Robertson et al. 2011). This location was chosen because it was both a pinch-point (i.e., to improve the likelihood of bull trout detection) and representative of the open-water habitat across the reservoir. In approximately 90 m of water, three thermister loggers were suspended at 30 m intervals on the receiver anchor rope that was anchored in pelagic habitat (> 500 m from shore, e.g., Figs. 1 and 2) with one additional logger secured on shore where high-pool water levels were projected to reach (during summer). The hourly data were collected from the thermal loggers varied little each day (Fig. 2b), thus we calculated water temperature



**Fig. 2** Thermal profiles ( $^{\circ}\text{C} \pm \text{SD}$ ) are taken 8 August (solid line), 10 September (dotted), 5 October (dashed), and 15 October (two-dash). Thermal profiles were taken from a thermal logger chain located in the Columbia Reach between 9 August and 24 October 2010

as daily averages, and paired with daily average temperature from fish collected from August to November, 2010. Loggers were retrieved the following spring when reservoir elevations facilitated their recovery.

Data management and filtering

*Thermal history*

Biotelemetry data from tagged bull trout were first filtered to remove false detections and incomplete tag-to-receiver transmissions. The minimum number of receiver detections per individual bull trout was set at two per receiver per 24-h period. We filtered the data to ensure that transmitter detections were tagged fish rather than code collisions or environmental noise (Niezgoda et al. 2002). Because surgical procedures were expected to affect behaviour for a short time following surgery (Rogers and White 2007), we eliminated the first seven days of data. Prior to filtering, 1.32 million temperature observations were contributed by 161 individuals. To facilitate modeling the large dataset, a minimum of  $\geq 20$  detections/receiver was arbitrarily selected to calculate the average temperature per diel period and individual. Post data filtering resulted in a data set comprised of 151 individuals (17.4 K observations). Average temperature was then calculated for each fish/receiver/diel period (i.e., day/night). Paired covariates included diel period (based on local sunset and sunrise times), body size (total length in mm), and

sex. Data filtering and exploration were performed using Microsoft Access and the R statistical environment (R Development Team 2016).

*Thermal habitat selection*

Available thermal habitat was assessed during summer and autumn by first fitting a 3rd-order polynomial through the daily average temperature collected by each thermal logger on the receiver rope in the Columbia Reach (Parker et al. 1975, Fig. 1; Suppl. A). Based on the coefficients from each fitted expression, the temperature (integers at  $1^{\circ}\text{C}$  intervals) at water depth was estimated by calculating the difference in water depths for  $2^{\circ}\text{C}$  intervals that were designated as categories (e.g.,  $>9\text{--}11^{\circ}\text{C}$  where  $>9$  was arbitrarily filtered as  $9.01^{\circ}\text{C}$  to  $11^{\circ}\text{C}$ ). Intervals were then converted into approximate percent of available thermal habitat (Supplement A). Categorizing thermal habitat into  $2^{\circ}\text{C}$  bins halved the number of levels for a predictor variable of temperature category, which was necessary to analyse a small dataset while providing what we considered an acceptably detailed profile of the available environmental temperatures. Vertical distribution of temperature was estimated between 9 August and 24 October, 2010. The telemetry dataset at the Columbia Reach receiver comprised of 15 individuals during this period.

To generate standardized resource selection indices (Arthur et al. 1996), the detection frequency ( $wf_{ijk}$ ) was calculated as a function of the time spent at each thermal habitat such that a count of one detection was equal to approximately two minutes (given the shortest possible tag transmission interval). Then, the proportion of time spent in a given thermal habitat relative to the total amount of time spent in that thermal habitat was calculated for the  $i^{\text{th}}$  day by the  $j^{\text{th}}$  individual for the  $k^{\text{th}}$  thermal habitat. Here we assumed that undetectable forays into warmer and colder water were minimal, particularly given that such forays would require exceptional vertical movements (e.g.,  $> 30\text{ m}$  to cover a range of  $5^{\circ}\text{C}$  during summer) over relatively short time spans ( $< 20\text{ min}$ ). Based on  $wf_{ijk}$ , standardized selection indices were generated for each individual per day and thermal habitat as:

$$B_{ijk} = wf_{ijk} / \sum_{i=1}^n wf_{ijk}$$

where  $B_{ijk}$  is the standardized selection index on the  $i^{\text{th}}$  day for the  $j^{\text{th}}$  individual for the  $k^{\text{th}}$  habitat. Values of  $B_{ijk}$  are constrained between zero and one where 1 represents complete selection by an animal ( $j$ ) for a given thermal habitat ( $k$ ) on the  $i^{\text{th}}$  day and values close to 0 represent selection against.

## Analyses

### *Thermal history*

Bull trout thermal histories were estimated across two years using a generalized additive mixed-effects model (GAMM). GAMM is a technique that fits a smoothing curve through the data. The Akaike Information Criteria was used to select the most parsimonious model from a set of candidate models (Burnham and Anderson 2004). The model for thermal history contained the number of days since 1 January, 2010 (Days since beginning study, DSBS) as a smoothing factor (Wood 2000, 2006) with fish ID as a random factor ( $n = 151$  individuals; detected across the array). Candidate models ( $n = 20$ ) contained one or more combinations of covariates, including: sex, body size, diel period (day or night, based on sunset and sunrise data), and a number of two-way interactions (Table 2). The response was assumed to follow a gamma distribution with a log link function to ensure fitted values were strictly positive. Parameters were estimated using restricted maximum likelihood and error terms were assumed to be normally distributed. The effective degrees of freedom (edf) for GAMM are taken from the influence/hat matrix, which yields the fitted value vector when post-multiplied by the data vector (Wood 2006). The amount of smoothing is determined by the edf, where an edf of 1 is a straight line and higher values indicate a more non-linear smoother (Zuur et al. 2014). Models were fitted using the R package “mgcv” (Wood 2000, 2006). GAMM from the package “mgcv” uses cross-validation which automatically determines the optimal amount of smoothing (Wood 2006; Zuur et al. 2009). Final models were validated by examining for patterns in the normalized residuals and by examining residual lag plots (Zuur et al. 2009). Despite the inclusion of random effects, the model validation process identified residual autocorrelation. Models were therefore further fitted with continuous autoregressive correlation structure on individual animals (Zuur et al. 2009). The correlation structure and random effect allowed us to model compound correlation between observations

from the same animal and the temporal correlation between all observations from the same animal and the irregularly spaced number of days between observations since beginning the study (Zuur et al. 2009). Further model validation showed no significant residual autocorrelation.

### *Thermal habitat selection*

The model describing thermal resource selection was based on several recommendations from the literature: (1) time must be included as the dimensional unit with which to quantify the thermal environment as a resource (Roughgarden et al. 1981; Tracy and Christian 1986; Dunham et al. 1989), (2) thermal availability is allowed to change with time (Arthur et al. 1996) and, (3) when individual is the level of replication, individual must be included as a random factor (Gillies et al. 2006). Similar to the analysis of thermal history, thermal resource selection was modelled using a GAMM with animal ID ( $n = 15$  individuals; detected at the Columbia Reach logger chain during summer/autumn) as a random factor. Given that initial data exploration indicated an abundance of zeros (87%, indicating no use of a given thermal habitat) for an analysis that included both selected and non-selected thermal resource, only selected thermal resources were analysed. In other words, a model of the standardized selection index ( $B_{ijk}$ ) shows selection over time within selected thermal habitats. Although selection indices should include the range of habitats available (Tracy and Christian 1986; Hertz 1992), we did not analyze habitat categories that were never observed to be selected. Limited by 32 observations (days), the model contained a smoother for day of the year (by each thermal resource) and thermal habitat as a categorical predictor (selection for 11–13 °C and 13–15 °C). The temperature category of 9–11 °C was removed from further analysis as only one telemetry observation was recorded in this range at the thermal logger chain. Body sizes and sexes were pooled. Given the distribution of the response variable, data were fit using a quasibinomial distribution and a logit link function. The model was estimated using restricted maximum likelihood. The model fit was assessed using the techniques described by (Zuur et al. 2009). Final model validation indicated no heterogeneity or serial autocorrelation in the residuals. To illustrate how bull trout may be selecting their thermal habitat within open water, we

examined the trend in mean depth distribution recorded for each individual detected at the Columbia Reach thermal logger between 9 August and 24 October, 2010.

**Results**

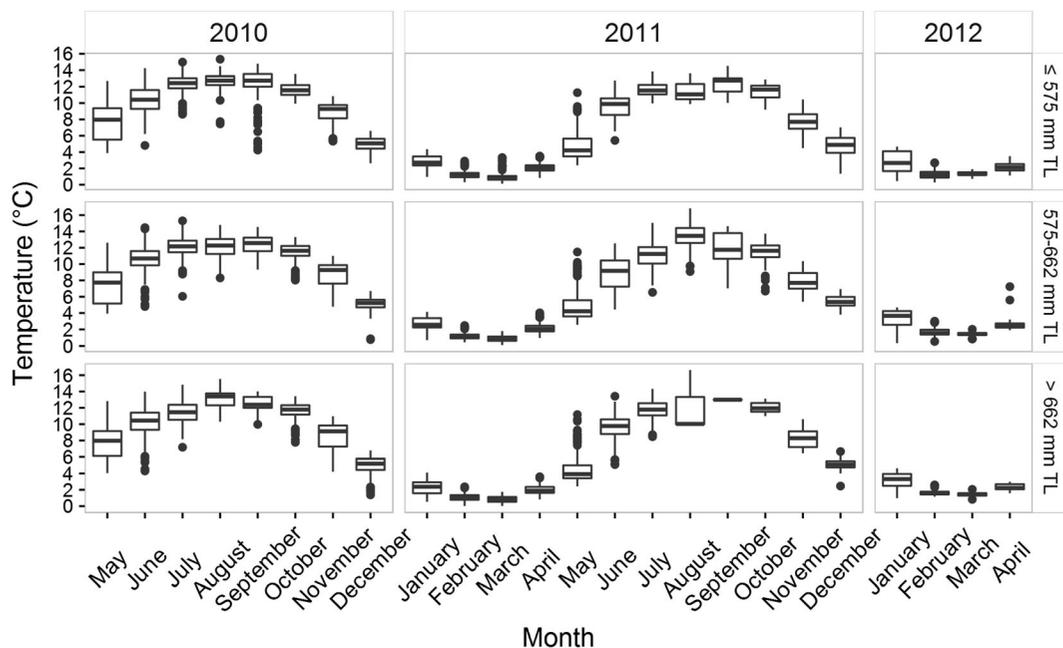
Raw data from the Columbia Reach thermal logger chain showed the expected thermal gradient that shifted toward isothermal from summer to autumn (Fig. 2). On 10 August, the surface temperature was 16.4 °C and gradually declined to 6.9 °C at a depth of 61.5 m. By 15 October, the thermal gradient shifted toward more isothermal conditions where temperatures of approximately 11.5 °C were recorded across the upper 30 m of water (Fig. 2). Daily water temperatures varied little across all measured depths (Fig. 2).

Thermal history appeared similar across body size quartiles except in the summer of 2011. For instance, in August 2011 the highest temperatures were recorded for large-sized bull trout (median: 13.04 °C, range: 8.5–16.5 °C), followed by medium-sized (median: 12.1 °C, range: 6.4–17.0 °C) and small-sized individuals (median: 11.1 °C, range: 8.8–15.1 °C; Fig. 3). The observed

average temperature ranges from the unfiltered data were 0.6–18.7 °C in 2010, 0.02–17.7 °C in 2011, and 0.2–7.2 °C in 2012 (Fig. 3). Temperature history was distinctly sinusoidal with relatively narrow temperature ranges observed during the winter months (Fig. 3). After filtering the raw data, 17,422 temperature observations were available to analyse the average thermal history from 151 individuals (81% of tagged bull trout). Males ( $n = 96$ ) outnumbered females ( $n = 55$ ) approximately 2:1 and the average size of males and females was similar at 612 mm TL  $\pm$  91 SD and 622 mm TL  $\pm$  66 SD (Fig. 4a). The frequency of body sizes roughly followed a normal distribution across the sample of tagged animals (Fig. 4a) and across the number of telemetry detections (Fig. 4b) used in the analysis of thermal history (range: 434–881 mm TL). Males contributed more data (55%) than females (45%; Fig. 4b).

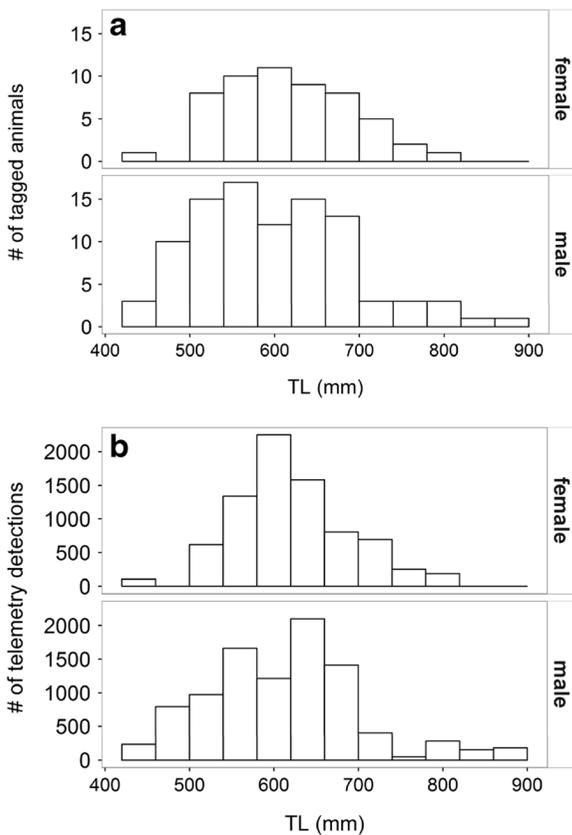
**Model of thermal history**

Based on AIC, the best model contained the smoothing function for day, total length, and total length \* day (M14, Tables 1 and 2). These terms explained 93.5% of the variation (adjusted  $R^2$ ) in the model of bull trout thermal history. The weak statistical interaction between total



**Fig. 3** Monthly average thermal history (°C) of three bull trout size classes (based on quartiles) detected by acoustic telemetry receivers in Kinbasket Reservoir (2010–2012). Data are

summarized by medians (dark horizontal lines), first and third quartiles (upper and lower box limits), whiskers (extending up to 1.5 times the interquartile range), and outliers (individual points)



**Fig. 4** Body length distributions for bull trout tagged in Kinbasket Reservoir. **a** The number of tagged male and female bull trout and **(b)** the number of telemetry detections by male and female bull trout **(b)**. Histogram bin width is 40 mm TL

length and day indicated an inter-annual difference in temperature history for smaller individuals (450 mm TL) whereas larger individuals (800 mm TL) experienced

similar temperatures across both years. For example, on 28 September 2011, an 800 mm TL bull trout would likely be found at an average temperature of 10.4 °C [9.8, 11.0, 95% confidence interval], whereas a 450 mm TL fish would have occupied on average a temperature of 9.8 °C [9.3, 10.2, 95% confidence interval, Fig. 5]. On 1 August 2010 and 9 July 2011, average sized bull trout were estimated to reach a maximum average temperature of 13.1 °C ± 0.16 SE and 12.4 °C ± 0.18 SE, respectively. During the summer in both years, bull trout occupied an average temperature > 12 °C and approximately ≤ 13 °C for 1.5 months (Fig. 5). Both summer periods were characterized by a peak, a gradual decline, and a sharp drop (5 October 2010 and 15 October 2011) that reached its low points during January and February of 2011 and 2012, respectively (Fig. 5).

#### Model of thermal habitat selection

The model of standardized selection indices ( $B_{ijk}$ ) contained a single significant smoother for the temperature category >11–13 °C ( $P < 0.001$ ; adjusted  $R^2 = 0.20$ ; Table 1; Fig. 6). Here, selection for >11–13 °C dropped sharply at approximately 9 September and increased again by 9 October (Fig. 6a). Standardized selection index, which included all temperature categories recorded during the period from 9 August to 24 October 2010 for all detected fish ( $n = 15$ ) over 32 days at the Columbia Reach receiver, indicated that temperatures between >11–13 °C were selected 1.6 times and 31 times more often than temperatures between >13–15 °C and >9–11 °C, respectively. Overtime, selection increased linearly for temperatures 13–15 °C

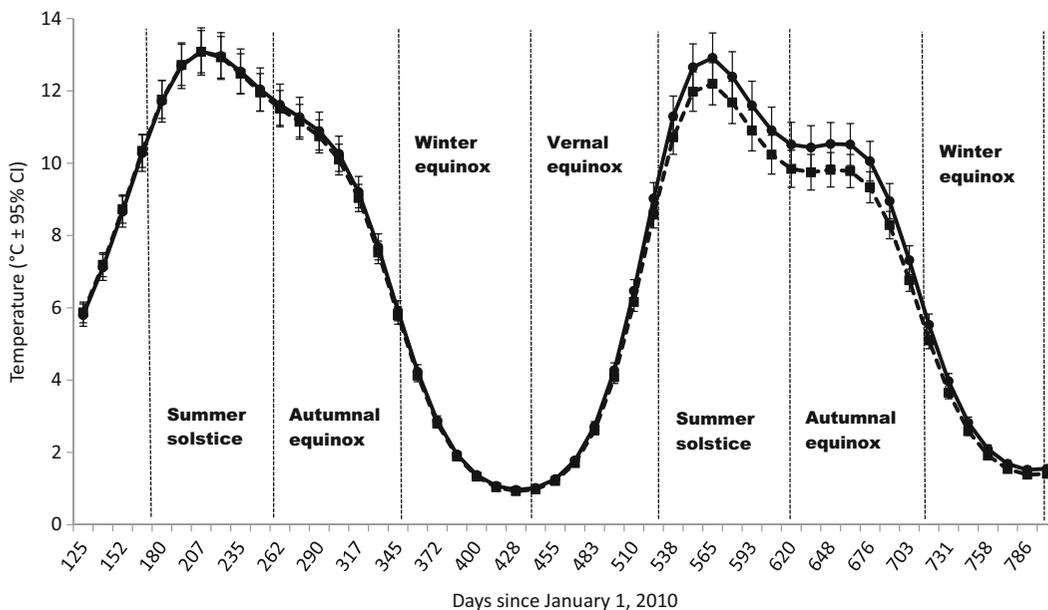
**Table 1** Model output for the generalized additive mixed models of (1) thermal history (Best model in the candidate set) and (2) thermal habitat selection. Test statistics are given from the  $F$ -distribution for the GAMM component and  $t$ -distribution for the linear

effects components of the model. Random intercept variance for models 1 and 2 was 0.21 and 0.18, respectively. Values of autocorrelation at lag 1 ( $\rho$ ) for model 1 was 0.914. The term “Days” is a continuous covariate numbered as Days since January 1, 2010

Model	Response	Model term	DF	Estimate	SE	Test statistic	$P$ -value
Thermal History (M14)	Temperature	s(Days)	9.0	—	—	F = 10,938	< 0.0001
		Intercept	17,269	19.51	0.0687	—	—
		TL	149	−0.0001	0.0001	$t = -0.68$	0.50
		TL: Days	17,269	2.946	0.0575	$t = 2.38$	0.02
Thermal Habitat Selection	$B_{ijk}$	s(Day of year): 13–15 °C	1.00	—	—	F = 1.7	0.20
		s(Day of year): 11–13 °C	6.15	—	—	F = 22.5	< 0.0001
		Intercept	—	−1.08	0.20	$t = -5.38$	< 0.001
		Temperature Category: 11–15 °C	—	1.31	0.40	$t = 3.27$	< 0.01

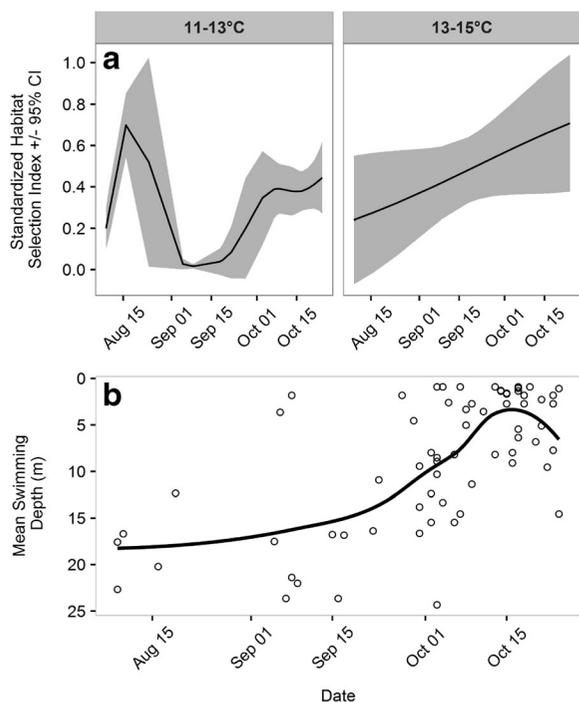
**Table 2** The set of candidate models used to test thermal history of adfluvial bull trout. DSBS is days since beginning study; TL is total length; K is the number of parameters; and AIC is Akaike Information Criterion. DNC are models that did not converge

Model	Model terms	K	AIC	ΔAIC	Weight	AIC Weight
M14	s(DSBS) + TL + TL:DSBS	8	16,906.6	0.0000	1.0000	0.6245
M17	s(DSBS) + TL + SEX + TL:DSBS	9	16,909.1	2.5436	0.2803	0.1751
M19	s(DSBS) + TL:DSBS	7	16,909.5	2.9463	0.2292	0.1431
M15	s(DSBS) + SEX + TL:DSBS	8	16,912.1	5.5827	0.0613	0.0383
M11	s(DSBS) + TL	7	16,914.9	8.3137	0.0157	0.0098
M18	s(DSBS)	6	16,916.5	9.9920	0.0068	0.0042
M7	s(DSBS) + SEX + TL	8	16,917.1	10.5847	0.0050	0.0031
M10	s(DSBS) + SEX	7	16,919.2	12.6951	0.0018	0.0011
M0	s(DSBS) + SEX + TL + DIEL + TL:DSBS + DSBS:SEX + TL:DIEL	12	16,921.2	14.6661	0.0007	0.0004
M2	s(DSBS) + SEX + TL + DIEL + TL:DSBS + TL:DIEL	11	16,924.1	17.5511	0.0002	0.0001
M13	s(DSBS) + SEX + TL + DIEL + TL:DSBS + TL:DIEL	11	16,924.1	17.5511	0.0002	0.0001
M1	s(DSBS) + SEX + TL + DIEL + TL:DSBS + DSBS:SEX	11	16,924.8	18.2170	0.0001	0.0001
M4	s(DSBS) + SEX + TL + DIEL + TL:DSBS	10	16,927.7	21.1279	<0.0001	<0.0001
M16	s(DSBS) + DIEL + TL:DSBS	8	16,928.1	21.5197	<0.0001	<0.0001
M5	s(DSBS) + SEX + TL + DIEL + TL:DIEL	10	16,932.7	26.1553	<0.0001	<0.0001
M9	s(DSBS) + TL+ DIEL	8	16,933.6	27.0697	<0.0001	<0.0001
M12	s(DSBS) + DIEL	7	16,935.3	28.7284	<0.0001	<0.0001
M8	s(DSBS) + SEX + DIEL	8	16,938.1	31.4947	<0.0001	<0.0001
M3	s(DSBS) + SEX + TL + DIEL + DSBS:SEX + TL:DIEL	NA	DNC	NA	NA	NA
M6	s(DSBS) + SEX + TL + DIEL + DSBS:SEX	NA	DNC	NA	NA	NA



**Fig. 5** The fitted values ( $\pm$  95% confidence limits) for bull trout thermal history in Kinbasket Reservoir from 21 June 2010 to 10 March 2012. The x-axis is days since January 1, 2010. The thermal history of large fish (800 mm TL) is shown as a solid line demarcated by circles whereas small fish (450 mm TL) are shown

with a dashed line demarcated by squares. Bull trout used to build the model ranged in size from approximately 350 mm to 880 mm TL ( $n = 151$ ). The approximate timing of astronomical seasons is illustrated with vertical dashed lines



**Fig. 6** **a** Smoothers and 95% point-wise confidence limits from the model to predict bull trout thermal habitat selection, illustrating changes in thermal habitat selection from 9 August to 24 October, 2010. Selection moderately increases then decreases for temperatures between 11 and 13 °C until mid-September before again increasing in early October ( $F = 22.5$ ,  $P < 0.0001$ ). The effective degrees of freedom ( $\text{edf}_{1-13^{\circ}\text{C}} = 6.15$ ;  $\text{edf}_{3-15^{\circ}\text{C}} = 1.00$ ) are taken from the model hat matrix. **b** Mean swimming depth of individual bull trout detected at the thermal logger chain. Data are fitted with a LOESS smoother

as they became less available (Figs. 6a and 2). Despite their availability during the summer to autumn period, temperature categories below 9 °C and despite the temperature range experienced by bull trout across the reservoir (Fig. 3), those above 15 °C were not selected at the Columbia Reach receiver on any of the days when thermal habitat availability data were calculated

(Table 3). Over this period bull trout increasingly moved into shallower waters, shifting from relatively deep in the August (mean: 16 m  $\pm$  7.8 SD) to shallow by late October (mean: 5.4 m  $\pm$  5.2 SD, Fig. 6b).

## Discussion

Across this large Reservoir in British Columbia, adult bull trout exhibited a narrow average thermal history and selected summer water temperatures that were within the expected optimal range for the species' metabolism and growth. When the greatest range of thermal habitats were available during summer (e.g., 17 °C or greater surface temperature; Fig. 2), bull trout moved between warm and cold water while maintaining average temperatures where food consumption is maximized for fish up to 1 kg (13–16 °C; Mesa et al. 2013). Importantly, the model indicates that a typical bull trout would occupy a daily range between approximately 12 °C and 14 °C from August to October (1.5 months) when warmer temperatures were available. From mid-September to mid-October as relatively warm waters became limited, bull trout showed increasing selection for temperatures between 13 °C and 15 °C. Our results suggest that adult adfluvial bull trout select, on average, 11 °C to 15 °C in a lake environment that is typical east of the BC Coast Mountains (McPhail and Baxter 1996).

The raw data and a weak statistical interaction between body size and day of the year in our model indicated an inter-annual difference in thermal history for small fish only. In the summer of 2011, large adfluvial bull trout thermal history was slightly warmer than that of conspecifics roughly half the size (Figs. 4 and 5,  $H_1$ ). However, the lack of an effect of body size in 2010 makes it difficult to conclude that a relationship exists between body size and thermal habitat use among

**Table 3** Standardized selection index ( $B_{ijk}$ ) and average available thermal habitat (%) in each temperature category.  $B_{ijk}$  was calculated for individual fish ( $i$ ) per day ( $j$ ) per thermal habitat ( $k$ ) and taken simply as the mean during the study period from 9 August 24 October, 2010

Temp Category (°C)	Mean $B_{ijk}$	SD $B_{ijk}$	- 95% CI	+ 95% CI	% Avail	SD
>5–7	0	0	NA	NA	30.7	5.37
>7–9	0	0	NA	NA	12.8	7.73
>9–11	0.008	0.088	NA	NA	12.8	7.12
>11–13	0.501	0.456	0.415	0.588	26.0	14.2
>13–15	0.316	0.410	0.169	0.463	15.7	15.0
>15–17	0	0	NA	NA	2.13	5.46

adult adfluvial bull trout. Theoretically, ectotherms should select temperatures that deliver physiologically optimal conditions (Tracy and Christian 1986; Wildhaber and Crowder 1990; Sims et al. 2004) whereas thermal preference may be further conditional on availability or the presence of prey, predators, and competitors (Mysterud and Ims 1998; Downes 2001; Godvik et al. 2009). In this system, the difference in body sizes may not be sufficient to show a difference in metabolic optimum expressed in the thermal history of small to large individuals. Optimal temperatures during summer may not be limiting, as the gradual thermal gradient covers the range of optimal temperatures over considerable depths (Bray 2012; Fig. 2). Additionally, optimal temperatures and adequate dissolved oxygen concentrations (>8 mg/L) are apparently not limiting (Bray 2012). Small adfluvial bull trout (400 mm TL) are known to occupy greater depths than larger conspecifics (> 800 mm TL), presumably resulting from a trade-off between locating kokanee salmon prey in the upper portion of the water column and avoiding predators under high population densities, i.e., other bull trout (Wilhelm et al. 1999; Beauchamp and Van Tassell 2001; Gutowsky et al. 2013). Compared to potentially cannibalistic conspecifics, smaller individuals can maintain similar temperatures while occupying greater depths. It remains likely that both large and small bull trout remain within the window of temperatures that maximize metabolism, consumption and growth while also occupying habitat where they can gorge on available kokanee salmon prey (Gutowsky et al. 2013; Furey et al. 2016). The thermal history of adfluvial bull trout lends further support to the notion that size-dependent diel vertical migration is largely related to factors other than bioenergetics (Beauchamp and Van Tassell 2001; Gutowsky et al. 2013).

Bull trout occupied a narrow range of temperatures that changed with availability ( $H_2$ , Figs. 2 and 6). Behavioural thermoregulation occurs when animals actively maintain their body temperature close to a defined target range where performance is maximized (Hertz et al. 1993; Díaz and Cabezas-Díaz 2004) and has important consequences for resource selection in fish and other ectotherms (Magnuson et al. 1979; Huey 1991). In pelagic habitats, fish are known to exhibit behavioural thermoregulation across depth gradients (Brett 1971; Cartamil and Lowe 2004; Jensen et al. 2006; Sims et al. 2006). Although thermal resource availability along a vertical gradient is certainly not the

only factor to consider when assessing habitat selection (Plumb and Blanchfield 2009), two biologically reasonable outcomes are evident from the results of the current study. First, excluding the single detection between >9–11 °C, bull trout occupied only a relatively narrow window of average temperatures between 11 and 15 °C that accounted for 41.7% (Table 3) of the available temperature range at the thermal logger chain from August to October. Second, bull trout increasingly selected these temperatures by changing their average swimming depth from relatively deep in the August to shallow by late October (Fig. 6b). Selection for temperatures between 11 and 15 °C was achieved by moving into shallow waters where this range of temperatures was becoming scarce as autumn progressed and the system turned over. In a recent study, Eckmann et al. (2016) suggested that free-swimming bull trout, preying on an invasive and relatively warm-water cyprinid species (reidside shiner, *Richardsonius balteatus*), would achieve 80–100% growth potential by occupying depths where mean daily temperature was between approximately 11.5 and 18.5 °C. In this system, bull trout primarily remained at a depth and temperature range where growth could be maximized (Eckmann et al. 2016). Taken together, in stratifying environments thermal habitat selection is largely driven by shifting thermal regimes and prey availability to maximize growth potential. Large conspecifics and possibly avian predators would affect habitat selection for relatively small bull trout.

Temperature is among the factors limiting bull trout populations in both lotic and lentic environments across North America (McPhail and Baxter 1996; Poole et al. 2001; Kovach et al. 2015). To date much of the work on bull trout temperature preference has been performed on small fish within a lab environment, or used telemetry on sub-adults and adults in lotic environments. Under laboratory conditions, growth and metabolism for small bull trout is maximized at approximately 13–16 °C (Selong et al. 2001; Mesa et al. 2013) and the tolerable upper limit is considered 16 °C (Poole et al. 2001). Although adult bull trout have been recorded in rivers where temperatures reach 18 to 25 °C (Lostine River, Oregon; Howell et al. 2010), the species is uncommon where temperatures exceed 15 °C for extended periods (McPhail and Baxter 1996). In the Arrowrock Reservoir, acoustic-tagged adult and potentially sub-adult bull trout were found suspended off bottom in temperatures ranging from 4.4 to 11.6 °C with surface temperatures of

6 to 16.2 °C (Maret and Schultz 2013). However, suspended bull trout apparently moved upriver as the reservoir was drawn down and suitable thermal habitat became scarce during the warm summer months. These movements coincided with a warming of the reservoir, which suggest that bull trout were either making early spawning migrations or seeking thermal refuge in colder tributaries (Maret and Schultz 2013). Unlike in Arrowrock Reservoir, the Kinbasket lake environment provided cold-water habitat throughout the summer (Fig. 2). In a recent review of factors affecting bull trout population dynamics, Kovach et al. (2016) showed that lake populations free of invasive salmonids typically had high abundances, relatively low variability, and stable or increasing trajectories. The opposite pattern was evident for lifelong riverine populations (Kovach et al. 2016). Given that bull trout in Kinbasket Reservoir are relatively abundant and currently exist without invasive salmonid competitors, e.g., lake trout, (*Salvelinus namaycush*), it follows that the existence of cold water refuge and optimal temperatures during the summer months are necessary conditions that enable this species' success and persistence in lake environments.

Free-swimming adult bull trout select temperatures that approximate those found to optimize growth and metabolism under laboratory conditions. By moving into ever diminishing thermal habitat, bull trout are able to inhabit a thermal environment that offers optimal temperatures before the lake became isothermal. In future work, telemetry and thermal logging devices with a higher sampling rate should be considered for determining fine-scale thermal habitat selection as a function of additional covariates (e.g., body size, predators and prey) in systems where preferred thermal habitat changes or has become limited. Deep cold-water lake environments may be the last refuge for this cold-water specialist, making information on thermal habitat availability and thermal habitat use essential for managing these systems to ensure that adfluvial populations persist.

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## References

- Angilletta MJ, Niewiarowski PH, Navas CA (2002) The evolution of thermal physiology in ectotherms. *J Therm Biol* 27:249–268
- Arthur SM, Manly BFF, McDonald LL, Garner GW (1996) Assessing habitat selection when availability changes. *Ecology* 77:215. doi:10.2307/2265671
- Beauchamp DA, Van Tassell JJ (2001) Modeling seasonal trophic interactions of adfluvial bull trout in Lake Billy Chinook, Oregon. *Trans Am Fish Soc* 130:204–216
- Benjamin JR, Heltzel JM, Dunham JB et al (2016) Thermal regimes, nonnative trout, and their influences on native bull trout in the upper Klamath River basin, Oregon. *Trans Am Fish Soc* 145: 1318–1330. doi:10.1080/00028487.2016.1219677
- Bray KE (2002) Fish derby summary: Shelter Bay, Nakusp, and Mica 1997–2001. British Columbia, Revelstoke
- Bray K (2012) Kinbasket and Revelstoke reservoirs ecological productivity monitoring. Progress report year 2 (2010), CLBMON-3. BC Hydro: Burnaby
- Brett JR (1971) Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *Am Zool* 11:99–113
- Brett JR, Groves TDD (1979) Physiological energetics. In: Hoar WS, Randall DJ, Brett JR (eds) *Fish physiology*. Academic Press, New York, pp 279–352
- Burnham K, Anderson D (2004) Multimodel inference understanding AIC and BIC in model selection. *Sociol Methods Res* 33:261–304
- Cartamil DP, Lowe CG (2004) Diel movement patterns of ocean sunfish *Mola mola* off southern California. *Mar Ecol Prog Ser* 266:245–253
- COSEWIC (2012) COSEWIC assessment and status report on the bull trout *Salvelinus confluentus* in Canada. Ottawa
- Cuenca ML, Stickney RR, Grant WE (1985) Fish bioenergetics and growth in aquaculture ponds: II. Effects of interactions among, size, temperature, dissolved oxygen, unionized ammonia and food on growth of individual fish. *Ecol Model* 27: 191–206. doi:10.1016/0304-3800(85)90002-X
- Díaz JA, Cabezas-Díaz S (2004) Seasonal variation in the contribution of different behavioural mechanisms to lizard thermoregulation. *Funct Ecol* 18:867–875
- Downes S (2001) Trading heat and food for safety: costs of predator avoidance in a lizard. *Ecology* 82:2870. doi:10.2307/2679967

- Dunham AE, Grant BW, Overall KL (1989) Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. *Physiol Zool* 62:335–355
- Dunham J, Rieman B, Chandler G (2003) Influences of temperature and environmental variables on the distribution of bull trout within streams at the southern margin of its range margin of its range. *North Am J Fish Manag* 23:894–904. doi:10.1577/M02-028
- Eckmann M, Dunham J, Connor EJ & Welch CA (2016) Bioenergetic evaluation of diel vertical migration by bull trout (*Salvelinus confluentus*) in a thermally stratified reservoir. *Ecol Freshw Fish*. doi:10.1111/eff.12321
- Elliot J, Allonby J (2013) An experimental study of ontogenetic and seasonal changes in the temperature preference of unfed and fed brown trout, *Salmo trutta*. *Freshw Biol* 58:1840–1848
- Furey NB, Hinch SG, Mesa MG, Beauchamp DA (2016) Piscivorous fish exhibit temperature-influenced binge feeding during an annual prey pulse. *J Anim Ecol* 85:1307–1317. doi:10.1111/1365-2656.12565
- Gillies CS, Hebblewhite M, Nielsen SE et al (2006) Application of random effects to the study of resource selection by animals: random effects in resource selection. *J Anim Ecol* 75:887–898. doi:10.1111/j.1365-2656.2006.01106.x
- Godvik IMR, Loe LE, Vik JO et al (2009) Temporal scales, trade-offs, and functional responses in red deer habitat selection. *Ecology* 90:699–710
- Gutowky LFG, Harrison PM, Guimaraes Martins EE et al (2015) Interactive effects of sex and body size on Adfluvial bull trout (*Salvelinus confluentus*) movement ecology. *Can J Zool*. doi:10.1139/cjz-2015-0104
- Gutowky LFG, Harrison PM, Landsman SJ et al (2011) Injury and immediate mortality associated with recreational troll capture of bull trout (*Salvelinus confluentus*) in a reservoir in the Kootenay-Rocky Mountain region of British Columbia. *Fish Res* 109:379–383. doi:10.1016/j.fishres.2011.02.022
- Gutowky LFG, Harrison PM, Martins EG et al (2013) Diel vertical migration hypotheses explain size-dependent behavior in a freshwater piscivore. *Anim Behav* 86:365–373. doi:10.1016/j.anbehav.2013.05.027
- Harrison PM, Gutowky LFG, Martins EG et al (2013) Diel vertical migration of adult burbot: a dynamic trade-off between feeding opportunity, predator avoidance, and bioenergetic gain. *Can J Fish Aquat Sci* 70:1765–1774
- Hertz PE (1992) Evaluating thermal resource partitioning. *Oecologia* 90:127–136
- Hertz PE, Huey RB, Stevenson RD (1993) Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *Am Nat* 142:796–818
- Heupel MR, Semmens JM, Hobday AJ (2006) Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. *Mar Freshw Res* 57:1–13
- Howell PJ, Dunham JB, Sankovich PM (2010) Relationships between water temperatures and upstream migration, cold water refuge use, and spawning of adult bull trout from the Lostine River, Oregon, USA. *Ecol Freshw Fish* 19:96–106. doi:10.1111/j.1600-0633.2009.00393.x
- Huey RB (1991) Physiological consequences of habitat selection. *Am Nat* 137:S91–S115
- Jensen OP, Hrabik TR, Martell SJ et al (2006) Diel vertical migration in the Lake superior pelagic community. II. Modeling trade-offs at an intermediate trophic level. *Can J Fish Aquat Sci* 63:2296–2307
- Jones LA, Muhlfeld CC, Marshall LA et al (2014) Estimating thermal regimes of bull trout and assessing the potential effects of climate warming on critical habitats. *River Res Appl* 30:204–216. doi:10.1002/rra.2638
- Kessel ST, Cooke SJ, Heupel MR et al (2013) A review of detection range testing in aquatic passive acoustic telemetry studies. *Rev Fish Biol Fish* 24:199–218. doi:10.1007/s11160-013-9328-4
- Kovach RP, Muhlfeld CC, Wade AA et al (2015) Genetic diversity is related to climatic variation and vulnerability in threatened bull trout. *Glob Chang Biol* 21:2510–2524. doi:10.1111/gcb.12850
- Kovach RP, Muhlfeld CC, Al-Chokhachy R, Dunham JB, Letcher BH, Kershner JL (2016) Impacts of climatic variation on trout: a global synthesis and path forward. *Rev Fish Biol Fish* 26(2):135–151
- Magnuson JJ, Crowder LB, Medvick PA (1979) Temperature as an ecological resource. *Am Zool* 19:331–343
- Maret TR, Schultz JE (2013) Bull trout (*Salvelinus confluentus*) movement in relation to water temperature, season, and habitat features in Arrowrock Reservoir, Idaho, 2012 (No. 2013-5158). US Geological Survey
- Maret TE, Schultz JE (2014) Bull trout (*Salvelinus confluentus*) movement in relation to water temperature, season, and habitat features in Arrowrock reservoir, Idaho, 2012
- Martins EG, Gutowky LFG, Harrison PM et al (2014) Behavioral attributes of turbine entrainment risk for adult resident fish revealed by acoustic telemetry and state-space modeling. *Anim Biotelemetry* 2:13
- McPhail JD, Baxter JS (1996) A review of bull trout (*Salvelinus confluentus*) life-history and habitat use in relation to compensation and improvement opportunities. Fisheries Management Report No. 104. Department of Zoology, University of British Columbia, Vancouver
- Mehner T (2012) Diel vertical migration of freshwater fishes - proximate triggers, ultimate causes and research perspectives: diel vertical migration in freshwater fishes. *Freshw Biol* 57:1342–1359. doi:10.1111/j.1365-2427.2012.02811.x
- Mesa MG, Weiland LK, Christiansen HE et al (2013) Development and evaluation of a bioenergetics model for bull trout. *Trans Am Fish Soc* 142:41–49. doi:10.1080/00028487.2012.720628
- Morita K, Fukawaka M, Tanimata N Yamamura O (2010) Size-dependent thermal preference in a pelagic fish. *Oikos* 119(8): 1265–1272
- Mysterud A, Ims RA (1998) Functional responses in habitat use: availability influences relative use in trade-off situations. *Ecology* 79:1435–1441
- Niezgoda G, Benfield MC, Sisak M, Anson P (2002) Tracking acoustic transmitters by code division multiple access (CDMA)-based telemetry. *Hydrobiologia* 483:275–286
- Paragamian VL, Walters JP (2011) Bull trout (*Salvelinus confluentus*) movement in a transboundary river. *J Freshw Ecol* 26:65–76. doi:10.1080/02705060.2011.553854
- Parker FL, Benedict BA, Tsai C (1975) Evaluation of mathematical models for temperature prediction in deep reservoirs. EPA 660/3-75-038. U.S. Environmental Protection Agency, Corvallis

- Plumb JM, Blanchfield PJ (2009) Performance of temperature and dissolved oxygen criteria to predict habitat use by lake trout (*Salvelinus namaycush*). *Can J Fish Aquat Sci* 66:2011–2023. doi:10.1139/F09-129
- Poole G, Dunham J, Hicks M, et al (2001) Technical synthesis: scientific issues relating to temperature criteria for Salmon, Trout, and Char Native to the Pacific Northwest. EPA 910-R-01-007. U.S. Environmental Protection Agency, Seattle
- R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/>
- Rieman BE, Isaak D, Adams S et al (2007) Anticipated climate warming effects on bull trout habitats and populations across the interior Columbia River basin. *Trans Am Fish Soc* 136: 1552–1565. doi:10.1577/T07-028.1
- Robertson CB, Langford MT, Zhu DZ, Leake A (2011) Reservoir thermal structure and its effect on hydropower operation induced fish entrainment. In *World Environmental and Water Resources Congress 2011: Bearing Knowledge for Sustainability*, pp. 2449–2458
- Rogers KB, White GC (2007) Analysis of movement and habitat use from telemetry data. In: Guy CS, Brown ML (eds) *Analysis and interpretation of freshwater fisheries data*. Bethesda, American Fisheries Society, pp 625–676
- Roughgarden J, Porter W, Heckel D (1981) Resource partitioning of space and its relationship to body temperature in *Anolis* lizard populations. *Oecologia* 50:256–264
- Selong JH, McMahon TE, Zale AV, Barrows FT (2001) Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerance in fishes. *Trans Am Fish Soc* 130:1026–1037
- Shroyer SM, Logsdon DE (2009) Detection distances of selected radio and acoustic tags in Minnesota lakes and rivers. *North Am J Fish Manag* 29:876–884
- Simpfendorfer CA, Heupel MR, Hueter RE (2002) Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. *Can J Fish Aquat Sci* 59:23–32. doi:10.1139/f01-191
- Sims DW, Wearmouth VJ, Genner MJ et al (2004) Low-temperature driven early spawning migration of a temperate marine fish. *J Anim Ecol* 73:333–341
- Sims DW, Wearmouth VJ, Southall EJ et al (2006) Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. *J Anim Ecol* 75:176–190. doi:10.1111/j.1365-2656.2005.01033.x
- Storebakken T, Austreng E (1987) Ration level for salmonids: II. Growth, feed intake, protein digestibility, body composition, and feed conversion in rainbow trout weighing 0.5–1.0 kg. *Aquaculture* 60:207–221. doi:10.1016/0044-8486(87)90288-2
- Swanberg TR (1997) Movements of and habitat use by fluvial bull trout in the Blackfoot River, Montana. *Trans Am Fish Soc* 126:735–746. doi:10.1577/1548-8659(1997)126<0735
- Tracy CR, Christian KA (1986) Ecological relations among space, time, and thermal niche axes. *Ecology* 67:609. doi:10.2307/1937684
- USFWS (2015) Recovery plan for the coterminous United States population of bull trout (*Salvelinus confluentus*). US Fish and Wildlife Service, Portland, Oregon
- Wagner GN, Cooke SJ, Brown RS, Deters KA (2011) Surgical implantation techniques for electronic tags in fish. *Rev Fish Biol Fish* 21:71–81
- Wildhaber ML, Crowder LB (1990) Testing a bioenergetics-based habitat choice model: bluegill (*Lepomis macrochirus*) responses to food availability and temperature. *Can J Fish Aquat Sci* 47:1664–1671
- Wilhelm FM, Parker BR, Schindler DW, Donald DB (1999) Seasonal food habits of bull trout from a small alpine lake in the Canadian Rocky Mountains. *Trans Am Fish Soc* 128: 1176–1192. doi:10.1577/1548-8659(1999)128<1176 :SFHOBT>2.0.CO;2
- Wood SN (2000) Modelling and smoothing parameter estimation with multiple quadratic penalties. *J R Stat Soc Ser B Stat Methodol* 62:413–428
- Wood S (2006) *Generalized additive models: an introduction with R*. CRC Press, Boca Raton
- Zuur AF, Ieno EN, Walker N et al (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York
- Zuur AF, Saveliev AA, Ieno EN (2014) *A beginner's guide to generalised additive mixed models with R*. Highland Statistics Ltd, Newburgh