

Diel vertical migration hypotheses explain size-dependent behaviour in a freshwater piscivore



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In aquatic organisms, diel vertical migration (DVM) is typically characterized as ascent at dusk and descent at dawn. Often several hypotheses are required to explain the sensory-mechanisms and ultimate causes of DVM. Currently, most of the research focused at the individual level has identified DVM functions as a response to light, feeding opportunities, predator avoidance and bioenergetics in small planktivores. However, there are no studies examining whether DVM hypotheses can explain and predict individual behavioural characteristics in top-level predators. In this study, we test whether bull trout, *Salvelinus confluentus*, a cold-water pelagic-cruising piscivore, show size-dependent daily and seasonal patterns in DVM consistent with light levels (proximate trigger) and feeding opportunities, predator avoidance and bioenergetics hypotheses. To test these hypotheses, free-swimming bull trout ($N = 187$, 358–881 mm total length) in a large, temperate reservoir were implanted with depth-sensing acoustic transmitters for 1 year. We found that swimming depths of bull trout were shallowest at night, deepest during the day and showed clear patterns of DVM across all seasons. In line with the predator avoidance hypothesis, large and small bull trout occupied different depths in all seasons except the spring, while the likelihood of depth change for large and small fish varied depending on season and diel period. The greatest depth difference among large and small bull trout occurred in the summer and less so in autumn. In the summer, small bull trout remained at greater depths (~15 m) than larger fish (~7 m) regardless of diel period. Our results indicate that light is a proximate trigger, and since there is no clear temperature-related bioenergetic advantage to changing depths during winter, feeding opportunities and predator avoidance are the most parsimonious DVM hypotheses to explain body-size-dependent behaviour in this top-level predator.

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In fishes, diel vertical migration (DVM) is typically characterized as ascent at dusk and descent at dawn (Neilson & Perry 1990). Linked to a number of processes including thermoregulation (Brill et al. 1999; Cartamil & Lowe 2004; Sims et al. 2006), habitat selection (Pade et al. 2009; Plumb & Blanchfield 2009) and foraging (Sims et al. 2005; Fox & Bellwood 2011), the functional triggers and adaptive drivers of DVM currently explain patterns across daily and seasonal periods for planktivorous fish populations only (e.g.

Bevelhimer & Adams 1993; Gjelland et al. 2009; Quinn et al. 2012). Although piscivores have been hypothesized to show DVM in relation to prey species (Jensen et al. 2006; Kahilainen et al. 2009), investigations of depth and vertical movement in relation to the mechanisms (e.g. size-dependent behaviour) thought to be responsible for DVM remain scant, and we are aware of no studies on individual DVM patterns in piscivorous fish.

Recently DVM has been related to both proximate triggers (i.e. sensory-motor and genetic developmental mechanisms) and ultimate causes (i.e. behaviours shaped by natural selection) (Mehner 2012). Proximate triggers include changes in light intensity and, to a lesser extent, changes in hydrostatic pressure and responses to thermal gradients (Levy 1990; Mehner 2012). Ultimate causes of DVM are hypothesized to be related to bioenergetic efficiency,

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feeding opportunities and predator avoidance behaviour (Mehner 2012). Evidence to support these hypotheses, whether functional or adaptive, is often generated from observational studies, which are the most appropriate means of obtaining such information on migratory behaviour in free-living animals. For example, Levy (1990) used hydroacoustic sonar to infer that patterns of DVM in juvenile sockeye salmon, *Oncorhynchus nerka*, were related to changes in light and thermoregulation. In fishes, the most pervasive mechanism thought to reflect predator avoidance behaviour and prey detection is individual body size. Again using hydroacoustics, small planktivorous fish were shown to remain at greater depths (Levy 1991) or to ascend earlier and descend later (Busch & Mehner 2012) than larger conspecifics.

In this study we tested DVM hypotheses on adfluvial bull trout, *Salvelinus confluentus*, in a glacial-fed reservoir in British Columbia, Canada. Adfluvial bull trout are an excellent candidate species because they (1) possess a low thermal tolerance (Selong et al. 2001), (2) primarily feed on vertically migrating kokanee salmon, *Oncorhynchus nerka*, (3) show intra- and interspecific competitive behaviour (Beauchamp & Van Tassell 2001; Stewart et al. 2007) and (4) are similar to other cold-water pelagic-cruising predators (e.g. coaster brook charr, *Salvelinus fontinalis*; lake charr, *Salvelinus namaycush*). We used biotelemetry data to test hypotheses about DVM in bull trout across a wide size range (358–881 mm total length, TL) for 1 year. We hypothesized that putative factors related to DVM including diel period (proximate trigger), season (temperature-related bioenergetics efficiency) and body size (feeding opportunities and predator avoidance) would give rise to predictable patterns in depth distribution and vertical movement. Following the patterns observed in other salmonids (e.g. Levy 1990), we predicted that individuals' swimming depths would be shallowest at night. Since bull trout are a cold-water species (Selong et al. 2001) and the reservoir develops a thermal gradient (Bray 2012), swimming depths of bull trout were predicted to be deepest in the summer and shallowest in the winter and spring. While it was not possible to directly test individual interactions, any size-dependent depth distributions and vertical movements were predicted to result from competition and cannibalism risk among bull trout (Beauchamp & Van Tassell 2001).

METHODS

Study Site

The study was conducted in the Kinbasket Reservoir, a 190 km long impoundment of the Columbia, Wood and Canoe Rivers in the north Kootenay Rocky Mountain region of British Columbia (52°8'N, 118°28'W; Fig. 1). Kinbasket is one of the largest reservoirs in BC, covering an area of 43 200 ha and containing approximately 14.8 km³ of water. The reservoir is fed by glacier melt-water streams and characterized by steep rocky shorelines, sand, rock and mud substrates, and little vegetation. Surface temperatures in the reservoir range from 2 to 15 °C in April–May, with summer surface temperatures typically in the 12–18 °C range (Bray 2012). In August through to mid-October, the reservoir typically has a gradual thermal gradient that reduces to 4 °C at a depth of 60 m (Bray 2012). The mean reservoir depth is 57 m, whereas the maximum depth is 160 m (RL&L Environmental Services Ltd 2001).

Kinbasket contains suitable habitat for native cold-water piscivores, including bull trout, rainbow trout, *Oncorhynchus mykiss*, burbot, *Lota lota*, and northern pike minnow, *Ptychocheilus oregonensis*. Kokanee salmon are a non-native planktivore that was stocked as a food source for bull trout and rainbow trout. Acoustic sonar and trawl-net surveys for kokanee salmon in the Kinbasket Reservoir are completed only during a brief period in August when kokanee are

found in uniform abundance (10–25 m depth) and a limited mix of size classes (29–70 mm fork length and 193–221 mm fork length; Sebastian & Johner 2011). Although not studied in Kinbasket Reservoir, it is well established that kokanee may perform DVM (e.g. Levy 1990, 1991; Bevelhimer & Adams 1993). Diatoms (mainly *Asterionella formosa*) are the dominant primary producers, whereas cladocerans and chironomids are the most abundant zooplankton and benthic organisms, respectively (RL&L Environmental Services Ltd 2001; Bray 2012). Cladocerans are considered the preferred prey for kokanee in Kinbasket (Bray 2012). As with kokanee, cladocerans are well known for DVM (e.g. Bevelhimer & Adams 1993; Ringleberg 1999). The reservoir is oligotrophic, having low plankton biomass and low rates of primary productivity (RL&L Environmental Services Ltd 2001; Bray 2012).

Biotelemetry Receiver Deployment and Retrieval

Forty-two VR2W telemetry receivers (Vemco, Halifax, NS) were deployed in Kinbasket Reservoir between 1 May and 5 May 2010 (Fig. 1). Assuming a conservative receiver detection radius of 500 m, spatial coverage by the telemetry array was approximately 33 km². Four receivers placed proximal to the dam face (within 400 m) were securely fixed to a 2 m length of 0.6 cm thick wire rope that was hung from a log boom and weighted with a 2 kg cannon ball. All other receivers were stationed 10–30 m from the substrate and attached to a 1.6 cm thick floating rope that was anchored with sandbags and suspended by a yellow buoy. In 2011, receivers were retrieved and the data downloaded onto a laptop using the program VUE (Vemco, Halifax, NS).

Tagging

Since bull trout are commonly targeted by recreational anglers in the spring, capture was accomplished by trolling between 11 April and 25 May 2010 (Gutowsky et al. 2011). In late summer, bull trout were captured by angling at the mouths of known spawning tributaries (18 August–9 September 2010) where they congregate prior to spawning. Once captured, fish were placed in a 100-litre cooler filled with lake water that was regularly replaced. Bull trout were then moved into another 100-litre cooler that contained anaesthetic (40 mg/litre; one part clove oil emulsified in nine parts ethanol). Once anaesthetized (assessed by 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 into the mouth and across the gills. Total length (to the nearest millimetre) and weight (to the nearest gram) were measured prior to surgery. A 3 cm long incision was made posterior to the pelvic girdle and a coded acoustic transmitter (model V13 TP; transmissions every 2–6 min, maximum depth 200 m, tag resolution 1.2 m) was inserted into the body cavity. Incisions were closed using three simple interrupted stitches. Postsurgery fish were placed in a recovery bath of fresh water, allowed to fully regain equilibrium, and released.

Our tagging procedures were approved by the Carleton University Animal Care Committee. Fish were obtained under scientific collection permits that were issued under the authority of the British Columbia Ministry of Environment (Permit No. CB-PG10-61414).

Database Management and Analysis

Biotelemetry data were sorted and stored in a Microsoft Access database. Bull trout detections were considered for analysis after the final receiver was deployed on 5 May 2010. Because the stress associated with tagging is believed to potentially affect fish

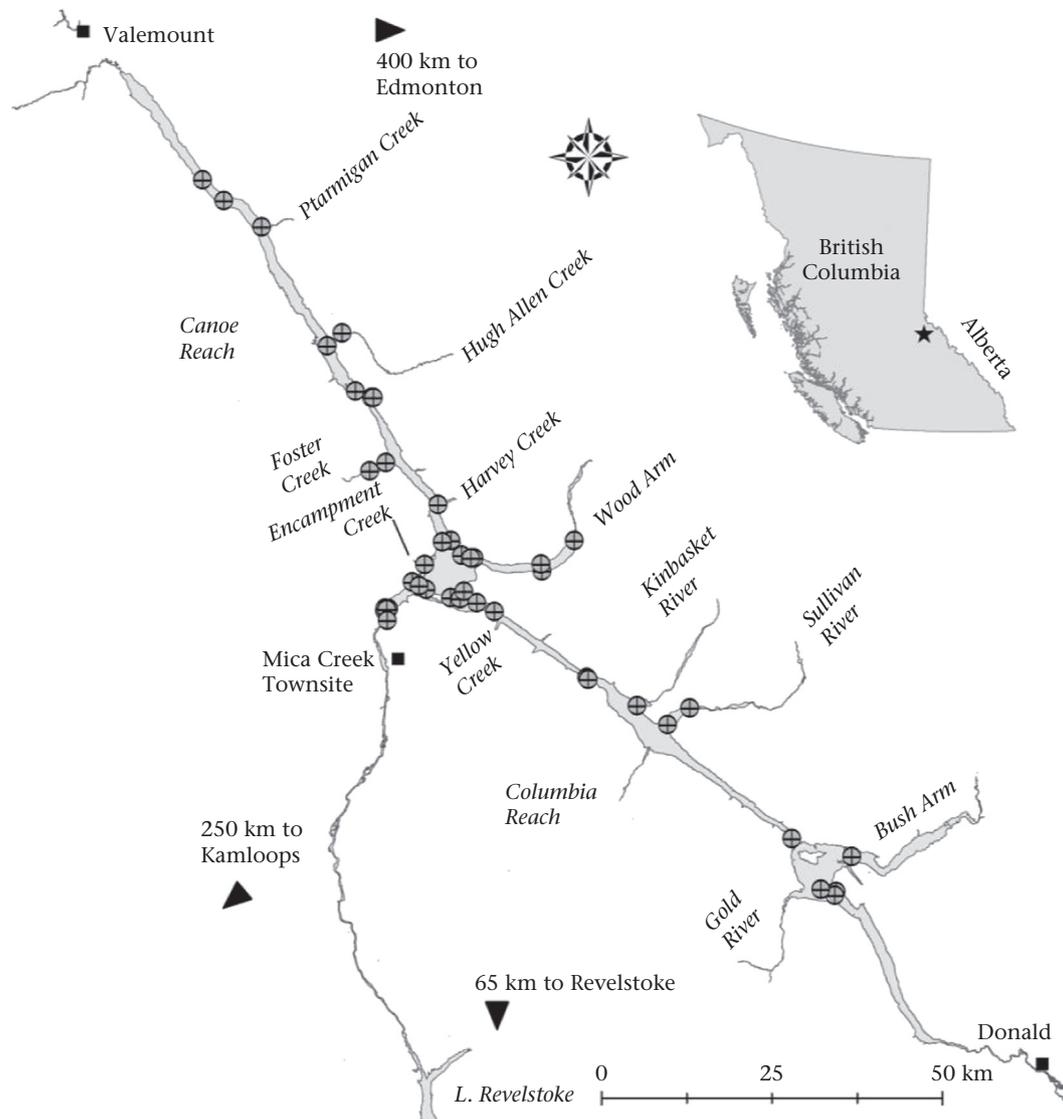


Figure 1. Kinbasket Reservoir in the Kootenay Rocky Mountain region of British Columbia. Shaded markers represent the location of biotelemetry receivers.

behaviour (Rogers & White 2007), we excluded detections that occurred within 1 week following tagging of a particular fish.

Seasons were delineated as winter (January–March), spring (April–June), summer (July–September) and autumn (October–December). The autumn represented the reproductive period between the first observation of bull trout traversing spawning tributary rapids (L. F. G. Gutowsky, personal observation) to the end of the postspawning period and beginning of the coldest few months of the year (i.e. winter). Diel period was calculated as day (>sunrise and <sunset) and night (>sunset and <sunrise) for a given 24 h period.

Patterns in DVM were assessed by examining the average depth and absolute maximum change in depth (hereafter referred to as 'vertical movement') by diel period, season and body size. For depth, detections were calculated as the average depth from a minimum of nine detections from each fish, per hour, and acoustic receiver ID (termed a detection event). Such filtering ensured that transmitter detections represented fish rather than code collisions or environmental noise (summarized in Niezgoda et al. 2002) while also decreasing the total number of data points to a manageable number for statistical modelling. In addition, filtering the data into

hourly periods restricted the maximum number of detections from each fish at each receiver to 19 (given the tag transmission rate). Thus, we used 9–19 detections to calculate depth and vertical movement for each filtered data point. Although behavioural consistency was not the focus of the current study, future studies may investigate personality in these animals (e.g. Dingemanse & Dochtermann 2012). Based on the time, date and body size measurement of each detection event, we categorized data into seasons, diel periods and hour of the day (for examining plots of the observed data). We calculated vertical movement as the detected absolute maximum change in depth during a detection event, rounded to the nearest integer. Since we considered only larger changes in depth biologically relevant, we also assigned vertical movement a score of "1" if movement was detected ($\Delta \text{depth} \geq 0.5 \text{ m}$) and a score of "0" if movement was minimal or not detected ($\Delta \text{depth} < 0.5 \text{ m}$). First, to check for continuous hourly patterns of vertical movement, we examined plots of depth and vertical movement from the filtered data and fitted them with smoothing functions of the class cyclic penalized cubic regression spline (Wood 2000, 2006). Outliers from the filtered database were identified by examining Cleveland dot plots and model residual

plots (Zuur et al. 2010). Although the accuracy of all detections could not be verified, outliers were documented as >60 m when depth was the response variable. The majority of recordings greater than 60 m were likely erroneous since this fish depth was often greater than the actual water depth (measured by known reservoir elevation and the receiver depth) at the time of detection. Therefore, we removed detections of >60 m deep ($N = 120$, <0.01%) from the analyses.

Model Type, Model Selection and Model Validation

Depth distribution was modelled using a generalized linear mixed effects model (GLMM) that treated the response variable, fish depth, as a count (rounded to the nearest integer), individual fish as a random factor (Pinheiro & Bates 2000), diel period and season as fixed factors, and total length as a continuous covariate. We used the model of depth distribution to examine correlations between putative factors and bull trout depth distribution. We modelled (GLMM) vertical activity to determine (1) whether putative factors were associated with the likelihood that bull trout would change depth, and (2) when bull trout changed depth, whether the putative factors were correlated with the magnitude of the depth change. To determine putative factors associated with the likelihood of depth change, we modelled (GLMM) a binary response variable (vertical movement = 1, no vertical movement = 0) as a function of predictor variables (season, diel period and body size), with individual fish as a random factor. To assess putative factors associated with the magnitude of the depth change, we estimated the magnitude of vertical activity by subsetting the data (Δ depth ≥ 0.5 m) and treating the response as a count variable (rounded to the nearest integer), individual fish as a random factor, diel period and season as fixed-predictor variables, total length as a continuous covariate, and an offset variable (log-elapsed time; Zuur et al. 2009) for the time between the shallowest and deepest detections. The parameters of all models were estimated using penalized quasi-likelihood, PQL (Bolker et al. 2009).

The best model was selected based on the number of factors that were highly significant ($P < 0.01$) in the full models containing the available predictor variables and two-way interactions (Zuur et al. 2009). The selection method was appropriate since Akaike's Information Criterion (AIC) scores are not widely available for GLMMs with PQL estimation (Zuur et al. 2009) and because likelihood-based methods (e.g. AIC ranking) are generally discouraged when using PQL estimation (Bolker et al. 2009). We considered two-way interactions to be potentially biologically relevant. Although three-way interactions are relevant in some circumstances (Zuur et al. 2009), three-way interactions were not considered because they are often difficult to interpret, may add unnecessary complexity to

models and add little value to understanding the underlying ecological relationships (Bolker et al. 2009). Competitive interactions between individuals could not be directly modelled given the limitations of the statistical designs and biotelemetry equipment; however, strong size-dependent effects on depth and vertical movement were considered weak evidence for competitive interactions. Autocorrelation was addressed by adding an autocorrelation structure to all models (Pinheiro & Bates 2000). We used Q-Q plots and residual plots to evaluate normality, heteroscedasticity of residuals and overdispersion. Spatial autocorrelation was checked by plotting the size of the Pearson residuals at each receiver coordinate (Zuur et al. 2009). Residual size was randomly distributed across receivers. We used an autocorrelation function (ACF) to determine whether the moving-average correlation structure reduced autocorrelation (Pinheiro & Bates 2000). In all models the ACF plots showed the correlation structures to reduce autocorrelation. Models were graphically validated following Pinheiro & Bates (2000) and Zuur et al. (2009). Analyses and plots were done in R (v.2.15.1, R Development Core Team 2008) using the packages MASS (Venables & Ripley 2002), nlme (Pinheiro et al. 2012), and ggplot2 (Wickham 2009). Although we used highly significant P values to determine which model terms to retain, the large degrees of freedom also warranted use of effect sizes and a lack of confidence limit overlap to indicate significant differences between groups.

RESULTS

Filtering from the raw data set ($N = 1309115$ detections) resulted in 27372 depth detection events that were acquired from 171 fish (91% of tagged bull trout). Bull trout size ranged from 358 to 881 mm in total length (TL) and was well represented across diel periods and seasons (Table 1). The observed data showed typical DVM patterns where bull trout descended at dawn and ascended at dusk (Fig. 2). This pattern was least pronounced in the winter and spring and most pronounced in the summer and autumn (Fig. 2). Vertical activity appeared to increase at sunrise and decrease at sunset and was also observed to vary across seasons (Fig. 3).

To explain bull trout depth, the model containing all factors and two-way interactions contained the greatest number of highly significant terms (Supplementary Table S1, Fig. 4). Bull trout were at shallower depths during the night than during the day and depending on season, small bull trout were estimated to be deeper than large bull trout (Fig. 4). Results from the model predictions indicated that fish between 480 mm and 640 mm ($N = 72$) consistently showed significant differences in depth distribution between day and night periods across seasons (Fig. 4). During the winter, summer and autumn, larger bull trout tended to be at

Table 1
Summary of the observed data and number and size (mm total length, TL) of bull trout detected according to diel period and season

Season (diel period)	No. of bull trout	Mean size \pm SE (mm TL)	Size range (mm TL)	Mean observed depth \pm SE (m)	Mean binary response	Mean Δ depth (m)	Count
Winter							
Day	111	587.3 \pm 9.5	358–881	9.7 \pm 0.13	0.55	3.6 \pm 0.10	3604
Night	109	586.2 \pm 9.6	358–881	8.2 \pm 0.06	0.41	1.0 \pm 0.02	7814
Spring							
Day	116	604.1 \pm 8.8	434–881	6.1 \pm 0.10	0.57	4.3 \pm 0.12	3784
Night	99	605.1 \pm 9.4	434–881	5.4 \pm 0.08	0.34	0.74 \pm 0.04	2976
Summer							
Day	86	613.8 \pm 9.8	434–881	13.7 \pm 0.16	0.78	5.7 \pm 0.10	2969
Night	80	615.8 \pm 9.9	440–881	12.1 \pm 0.17	0.64	2.5 \pm 0.09	1863
Autumn							
Day	106	591.1 \pm 9.4	358–881	11.8 \pm 0.28	0.69	5.8 \pm 0.19	1637
Night	101	592.6 \pm 9.2	358–826	7.5 \pm 0.13	0.52	1.5 \pm 0.06	2725

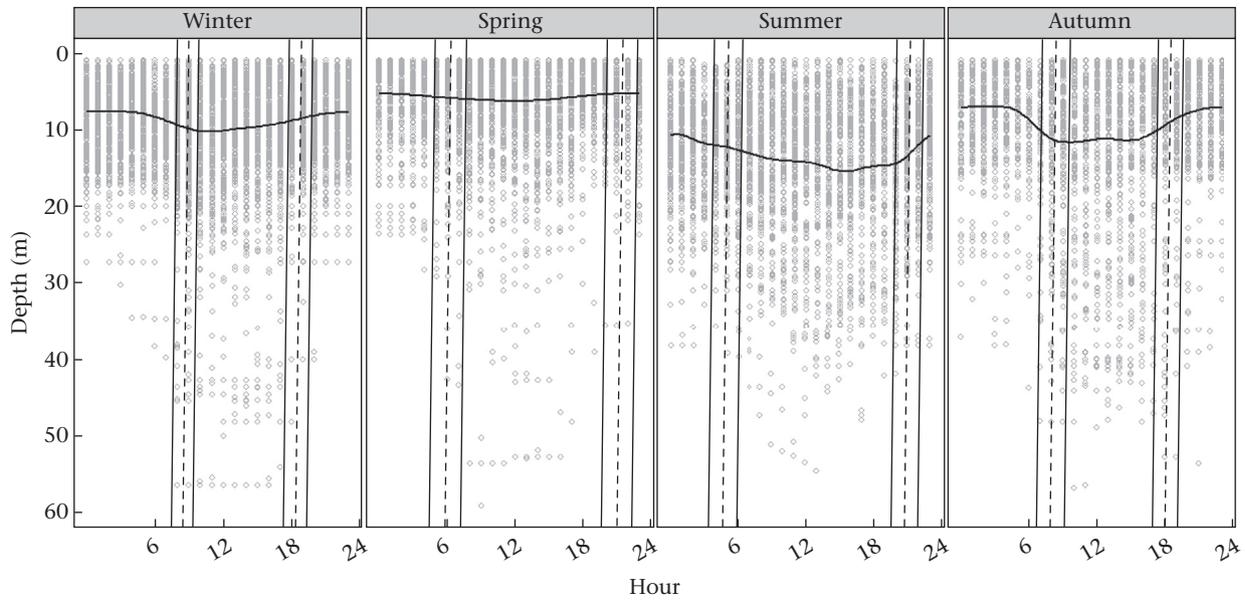


Figure 2. Observed data (depth (m)) by hour and season. Dashed vertical lines represent the average sunrise or sunset; solid vertical lines represent the minimum and maximum sunrise and sunset for a given period. Smoothing functions are modelled from the expression $y = s(\text{hour, by season})$, where s is the smoothing term of the form cyclic penalized cubic regression spline.

shallower depths than smaller conspecifics. For example, a 400 mm bull trout detected on a summer day was estimated to be at a depth of 15.3 m (12.9, 18.1, 95% confidence interval), whereas the estimated depth of a bull trout that was twice as long and detected during the same period was almost twice as shallow at 7.8 m (6.4, 9.4, 95% confidence interval). Overall, the depth of a typical bull trout (average TL = 590 mm) was deepest during a summer day and shallowest during a winter or spring night (Fig. 4).

To evaluate the probability that a bull trout changed depth during a detection period, the most highly significant model contained all main effects and two-way interactions (Supplementary

Table S1). The model indicated that bull trout were more likely to move vertically during the day in any given season (Fig. 5). For instance, an average size bull trout detected during a spring day was 26% more likely to change depth than the same size bull trout detected on a spring night. A 400 mm bull trout detected during a summer night was 43% more likely to change depth than the same size fish detected on a spring night. However, the probability that a bull trout changed depth was largely dependent on all two-way interactions (Supplementary Table S1). For example, the probability that a bull trout of average size would change depth was 0.492 (0.478, 0.506, 95% confidence interval) on a spring night, but

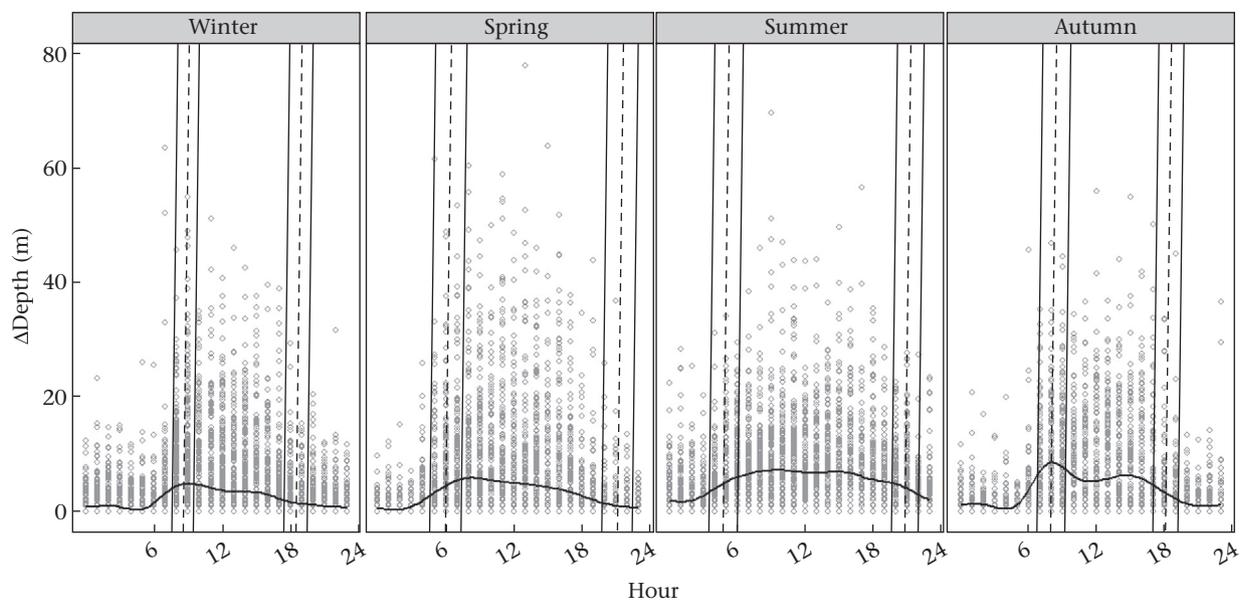


Figure 3. Observed data (Δ depth (m/detection period)) by hour and season. Dashed vertical lines represent the average sunrise or sunset; solid vertical lines represent the minimum and maximum sunrise and sunset for a given period. Smoothing functions are modelled from the expression $y = s(\text{hour, by season})$, where s is the smoothing term of the form cyclic penalized cubic regression spline.

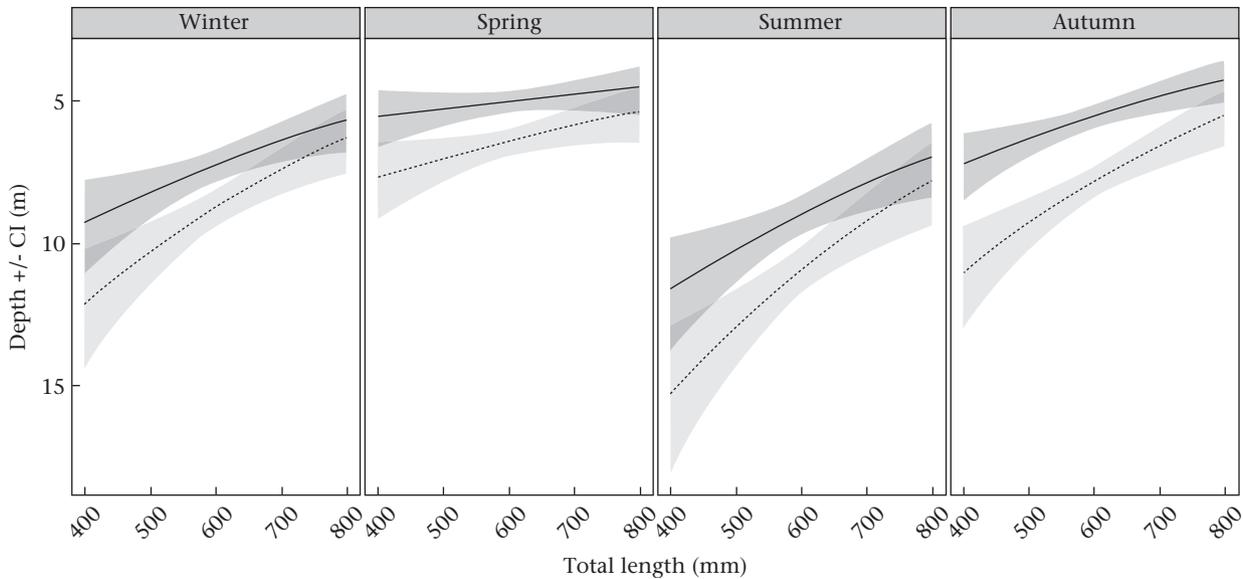


Figure 4. Model estimates of bull trout depth (m) by season, diel period (solid line: night; dotted line: day) and body size (total length (mm)). Shaded regions represent 95% confidence limits for the day (light grey) and night (medium grey). Regions of confidence limit overlap between day and night periods are emphasized in dark grey.

0.860 (0.840, 0.880, 95% confidence interval) on a summer day. A 700 mm bull trout detected on a spring night was more likely to change depth than a 500 mm bull trout detected during the same period (700 mm: $0.558 \geq 0.532 \geq 0.507$, 95% CI; 500 mm: $0.494 \geq 0.457 \geq 0.424$), whereas the relationship was reversed on a summer night (700 mm: $0.682 \geq 0.652 \geq 0.624$, 95% CI; 500 mm: $0.839 \geq 0.804 \geq 0.770$; Fig. 5).

When bull trout changed depth during a detection period, the model containing all factors and two-way interactions contained the most significant terms (Supplementary Table S1). When bull trout were detected to change depth, highly significant two-way interactions between predictor variables explained the magnitude of the depth change (Fig. 6). Changes in depth were most pronounced during the day in all seasons and were greater during the day for all but the smallest individuals during the summer.

The magnitude of depth change was greatest on a spring day (Fig. 6). During the spring, and compared with small conspecifics, large bull trout also showed the greatest change in depth. For instance, changes in depth on a spring day were twice as great for an 800 mm bull trout than they were for 400 mm bull trout ($6.56 \geq 5.25 \geq 4.20$, 95% CI; 800 mm: $12.10 \geq 9.79 \geq 7.91$, 95% CI; Fig. 6). In contrast, large fish made fewer drastic depth changes than smaller conspecifics during the night in autumn (e.g. 400 mm: $5.67 \geq 4.56 \geq 3.68$, 95% CI; 800 mm: $2.90 \geq 2.30 \geq 1.83$, 95% CI; Fig. 6).

DISCUSSION

Depth distribution and vertical movement of piscivorous bull trout are related to diel, seasonal and size-related factors, which is

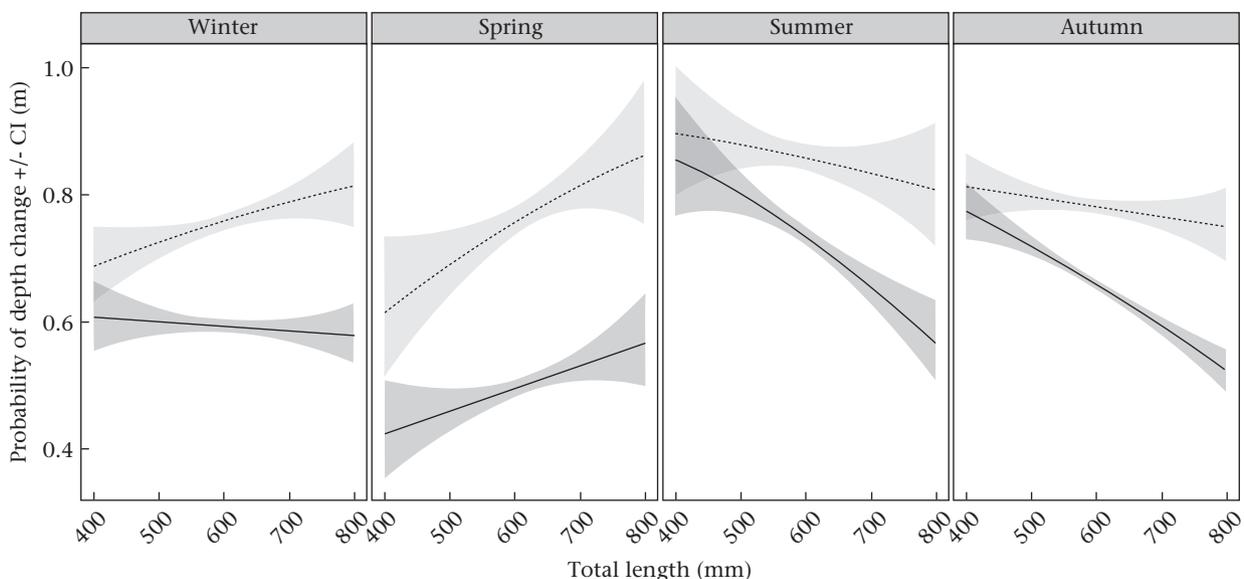


Figure 5. Model estimates of the probability that bull trout change depth by season, diel period (solid line: night; dotted line: day) and body size (total length (mm)). Shaded regions represent 95% confidence limits for the day (light grey) and night (medium grey). Regions of confidence limit overlap between day and night periods are emphasized in dark grey.

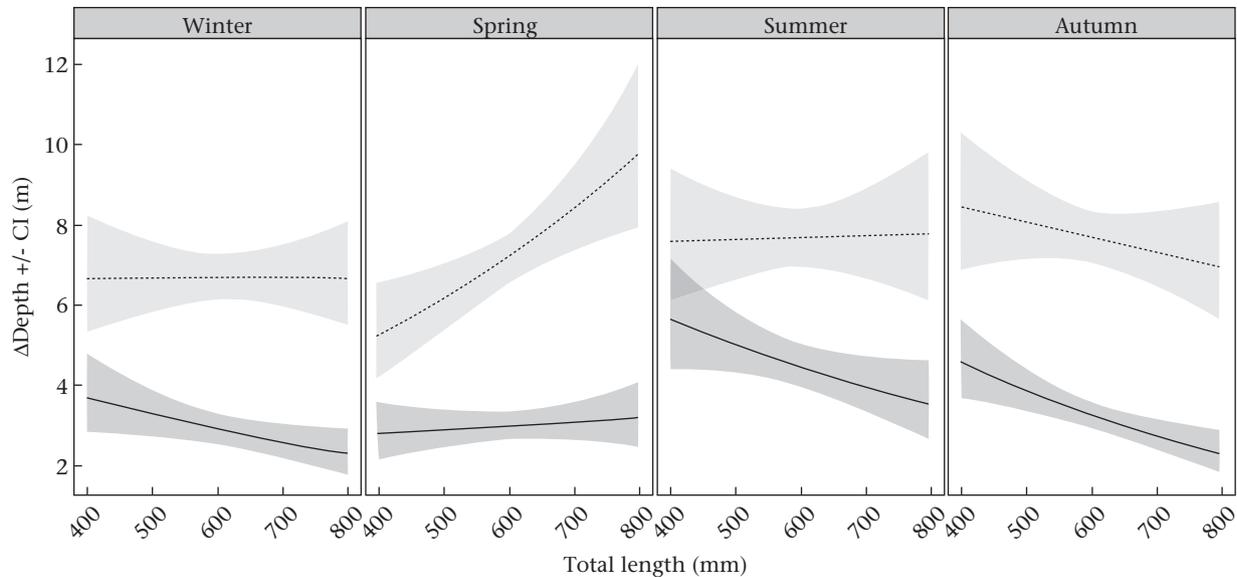


Figure 6. Model estimates of change in depth for bull trout by season, diel period (solid line: night; dotted line: day) and body size (total length (mm)). Shaded regions represent 95% confidence limits for the day (light grey) and night (medium grey). Regions of confidence limit overlap between day and night periods are emphasized in dark grey.

consistent with the original predictions (i.e. individuals' depths were shallowest at night and deepest during summer). In addition, DVM continued to occur during winter. According to our results, depth and vertical movement correspond with DVM hypotheses related to light sensitivity, feeding opportunities and predator avoidance behaviour, and less so with the bioenergetics efficiency hypothesis.

While the averaged population-wide trends in bull trout depth and vertical movement may mask the more extreme behaviours of some individuals (e.g. Mehner & Kasprzak 2011; Busch & Mehner 2012), there was an overall shift in depth and vertical movement in relation to light (Figs 1, 2). Bull trout behaviour is consistent with several empirical investigations that have linked DVM to light sensitivity, predator avoidance and foraging efficiency (Levy 1990; Sims et al. 2005; Hrabik et al. 2006; Stockwell et al. 2010). DVM in bull trout has not been documented but probably has important consequences for prey behaviour. For instance, the pursuit of coregonids by siscowet (*Salvelinus namaycush*) in Lake Superior has been shown to alter coregonid vertical distribution and is suggested as the leading cause of DVM in these fishes (Hrabik et al. 2006; Jensen et al. 2006). Kokanee salmon, a species that is well documented for DVM (Levy 1990, 1991; Bevelhimer & Adams 1993; Scheuerell & Schindler 2003), are found in numerous reservoirs (Crawford & Muir 2008) and considered the principal prey for bull trout (up to 77% of diet; Steinhart & Wurtsbaugh 1999; RL&L Environmental Services Ltd 2001). Rather than being strictly related to light levels, water temperature and prey detection efficiency (i.e. zooplankton), it is possible that kokanee DVM, which continues to occur during winter (Steinhart & Wurtsbaugh 1999), partly results from predator avoidance (Hrabik et al. 2006). Scheuerell & Schindler (2003) found empirical evidence to suggest that juvenile sockeye salmon (anadromous *Oncorhynchus nerka*) vertically migrated to exploit an antipredation window whereby light levels allowed sockeye to forage while minimizing predator detection efficiency. Here juvenile sockeye inhabit depths where light levels are below the minimum irradiance that maximizes a predator's reactive distance while also maintaining spatial overlap with zooplankton prey (Scheuerell & Schindler 2003; Busch & Mehner 2012). Unfortunately, there is little available information on kokanee prey behaviour and kokanee depth distribution by size,

diel period and season in Kinbasket Reservoir. Despite the lack of information in this system, diel shifts in depth and vertical movement indicate a proximate response to light levels while the presence of vertically migrating prey may provide the motivation (i.e. the feeding opportunities hypothesis) for these behavioural patterns during crepuscular periods (Figs 2, 3).

In most seasons, smaller individuals remained deeper than larger conspecifics (Fig. 3). In addition, there was no difference in depth among sizes in the spring, and while the maximum change in depth did not differ across size classes of fish during the summer and autumn, during day and night, small-bodied fish were more likely to be active than larger fish (Fig. 5). Individual differences in DVM have not been previously identified across body sizes in a piscivore. However, planktivorous fishes are known to show body-size-related differences in behaviour that are linked to competitive interactions (Levy 1990; Mehner & Kasprzak 2011). Busch & Mehner (2012) found that the timing of ascent or descent in coregonid species depends on both the time of day and the body size of the individual. Specifically, smaller coregonids migrated earlier than larger conspecifics, which was hypothesized to be an adaptive response to balance increased feeding opportunities with increased risk of predation. Although not specifically linked to DVM, some piscivores have shown alternative diel foraging strategies across sizes (Alanärä et al. 2001; Harwood et al. 2002). For example, individuals (either Arctic charr, *Salvelinus alpinus*, or rainbow trout) with a low social status have been predicted to attain adequate growth by feeding at night (Alanärä & Brännäs 1997), or may be forced into deeper water by dominant (larger) individuals (McCauley et al. 1977). Such competitive interactions are widely regarded as important for regulating population structure and density in charr (Langeland et al. 1991; Nakano et al. 1998; Helland et al. 2011). Rainbow trout and bull trout (Bray 2002; Westslope Fisheries Ltd & CCRIFC 2005) show optimal growth at the same temperature (13.1 °C; Bear et al. 2007) and may occupy similar lake habitat. In addition, adfluvial rainbow trout migrate into spawning tributaries during the spring. The absence of rainbow trout in the spring could relieve competitive pressure and allow small-bodied individual bull trout to inhabit shallow water (Fig. 3). Bull trout are widely considered aggressive and cannibalistic to the point where cannibalism has been regarded to be an important limiting

factor of population size (Wilhelm et al. 1999; Beauchamp & Van Tassell 2001). Although anecdotal, we observed a larger individual attack and handle a bull trout that we were angling (591 mm TL; L. F. G. Gutowsky & P. M. Harrison, personal observations). We surmise that during most seasons, the presence of both rainbow trout and large-bodied cannibalistic bull trout near the surface forces small-bodied individuals into deep water refuge (i.e. into an antipredation window). Although we do not have depth data for rainbow trout, or the capacity to directly test competitive interactions, size-dependent DVM and the ecology of these animals provide indirect support for the predator avoidance hypothesis of DVM.

The deeper average depths recorded during the summer and autumn (i.e. when a thermal gradient is present) are consistent with the prediction that cold-water fishes with a narrow thermal tolerance seek deeper water, on average, during the warmest periods of the year. However, the average change in depth during a summer day is only 2 m greater than that during a winter day (Table 1), and the moderate temperatures in the reservoir (Bray 2012) do not pose any direct thermal threat to bull trout survival (Selong et al. 2001). Diel differences in depth use and vertical movement when the reservoir shows no thermal gradient (i.e. winter and spring, Bray 2012) indicate that bioenergetic requirements alone cannot explain DVM across seasons, as there is no bioenergetic advantage to moving between deep and shallow water. While knowing the thermal profile at each telemetry receiver would further explain the effect of temperature on behaviour, such data were unavailable. Despite the lack of receiver-specific temperature data in the reservoir, the persistence of DVM behaviour in the winter and spring, modest differences in vertical movements during the warmer summer months and the presence of bull trout at the surface throughout the diel period and across all seasons (Fig. 2) suggest that processes other than thermal bioenergetic constraints, namely proximate cues from light, feeding opportunities and predator avoidance, are the primary drivers of DVM in this system.

In studies of DVM there is typically no single unifying hypothesis to describe patterns in behaviour (Kahilainen et al. 2009; Jensen et al. 2011; Mehner 2012). In the present study, several putative factors and their interactions indicated light as a proximate trigger in bull trout, a cold-water piscivore, while behaviour among body sizes and seasons provided support for the ultimate causes of DVM. In addition, our results highlight the need to consider animal behaviour hypotheses at the individual level.

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Supplementary data

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