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Spatio-temporal Movement Patterns of Sub-adult Adfluvial Bull Trout

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SPATIO-TEMPORAL MOVEMENT PATTERNS OF

SUB-ADULT ADFLUVIAL BULL TROUT

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by

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ABSTRACT

SPATIO-TEMPORAL MOVEMENT PATTERNS OF

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Bull Trout in the Yakima River basin of Washington are primarily adfluvial, often using managed lakes as habitat. Kachess Lake, composed of Big and Little Kachess Lakes, is managed by the Bureau of Reclamation (BOR) for water storage. BOR plans to build a structure that can withdraw an additional 200,000 acre-feet of water in drought years, which would disconnect the two basins for multiple years. This study examined the spatio-temporal movement of sub-adult Bull Trout in Kachess Lake to understand distribution patterns and the effects of environmental variables. We sought to answer 1) does time (week of the year), diel period, water surface elevation, precipitation, or surface temperature explain fish depth? and 2) Where are the home ranges and core use areas of individual fish? Yakama Nation biologists rescued Bull Trout fry from Kachess River, a tributary of Little Kachess that dewaters yearly, and reared them in captivity for about twelve months. Once fish attained a suitable weight, a subset were surgically implanted with Vemco V9 temperature pressure sensor tags. Then fish were transported and released into Kachess Lake, where a passive array of thirteen acoustic receivers were set. Eight fish had at least 500 detections and were detected 30+ days in the lake, fitting the criteria for analysis. A generalized linear mixed-model was used to model depth distribution and home ranges were calculated using Autocorrelated Kernel Density Estimation (AKDE). Results showed depth increases with higher surface temperature, and during the day. Fish depth was greatest during weeks in late Summer and Fall. Home range estimates were variable among individuals with a maximum 95% AKDE of 18.4 km^2 and a minimum of 1.69 km^2. Understanding the distribution of different life stages of Bull Trout allows managers to make conservation-driven decisions in the face of climate change and over-obligated water resources.

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CHAPTER I

INTRODUCTION

In the face of human population growth, limited natural resources, and the effects of climate change, we must understand how native species use their environments to protect and conserve them. Conservation depends heavily on regulating human resource use to minimize negative impacts on critical habitats of other organisms. On the East side of Washington state, water resources are limited and reconciling the needs of people and fish is a major topic of discussion. An important native fish, the Bull Trout, *Salvelinus confluentus*, is in decline in Washington and across their range (Goetz 1989). This research aims to advance ecological knowledge of Bull Trout, with the goal of reducing the adverse effects created by water resource allocation in an increasingly dry climate. The introductory chapter of this thesis will provide background and context for the species and the challenges they face, followed by the research problems, objectives, and questions.

Biology of Bull Trout

The Bull Trout, *Salvelinus confluentus*, was listed as “threatened” under the provisions of the United States Endangered Species Act in November of 1999 (USFWS 2015). Bull Trout are char of the genus *Salvelinus*, and a member of the Salmonidae family. The species is endemic to Western North America and range from northern Nevada (extirpated from California as of 1975), to the southern Yukon, and Northwest

Territories (Haas and McPhail 1991, 2001; Stewart et al. 2007). Bull Trout have special habitat requirements and play an important ecological role as the apex predator in cold water ecosystems of the Pacific Northwest (Goetz 1994). Ultimately, habitat degradation and land use management have been key factors in Bull Trout decline across their range (Rieman and Mclntyre 1993).

In comparison to other Pacific salmonids, Bull Trout have the most specific habitat requirements (Rieman and Mclntyre 1993). Cold, clean, complex, and connected habitats are essential for Bull Trout persistence (USFWS 2015). Cold water is necessary for spawning and incubation of the eggs, while clean substrate keeps them from being smothered in fine sediment (Fraley and Shepard 1989). Complex river habitat features like pools, undercut banks, and various substrate sizes are important for different life stages. Several Bull Trout life history forms are migratory, needing connected habitat for access to different spawning and foraging grounds (Goetz 1989).

The limiting factor in healthy Bull Trout populations is the finite amount of quality spawning and juvenile rearing habitat (Fraley and Shepard 1989). A loss of stream complexity, increased dams and diversions, invasive species introductions, and range contraction due to warming downstream temperatures has exacerbated habitat fragmentation and access to spawning and rearing habitat (Rieman and Mclntyre 1995). Dunham and colleagues (2014) found that Bull Trout in habitats with cold water during the summer, low flood disturbance during winter, and places with minimal human influence were most likely to persist into the future. Because of their specific habitat requirements, Bull Trout are sensitive to human-induced changes that affect any part of the aquatic environment. The species can thus be considered an important indicator of ecosystem health.

Having evolved to survive a dynamic landscape in the Pacific Northwest, Bull Trout exhibit three main life history strategies, depending on local environmental conditions. They can be fluvial, adfluvial, or stream residents (Goetz 1989). There is also evidence of occasional anadromy in Bull Trout, but those populations are less common because the range of the species is primarily inland (Dunham et al. 2008). Populations are considered resident if they spend their entire life in the river where they were spawned, and fluvial when they rear in their natal stream then migrate to a larger river to forage as an adult (Quinn 2018). Adfluvial populations rear as juveniles for two to three years in the stream, then migrate to a lake to grow into an adult prior to spawning at five to seven years old (Fraley and Shepard 1989). Behavior of adult adfluvial Bull Trout has been documented in several studies including movements associated with spawning (Fraley and Shepard 1989; Paragamian and Walters 2011; Barnett and Paige 2013; Al-Chokhachy et al. 2019), diel vertical migration (DVM) (Gutowsky et al. 2013, 2017; Eckmann et al. 2018), and lateral movements more generally (Gutowsky et al. 2016). Other studies have investigated the movement of juvenile and sub-adult Bull Trout while still present in the rivers (Muhlfeld and Marotz 2005; Downs et al. 2006; Bowerman and Budy 2012) but there is very little known about sub-adult adfluvial Bull Trout movements within a lake or reservoir.

Acoustic Telemetry

In the past, studying movement of freshwater fishes in lakes was difficult due to complex habitats, high mobility of organisms moving vertically and laterally, and low visibility (Cooke et al. 2016). Using passive acoustic telemetry to study the spatial ecology of aquatic animals is a tool to overcome some of those challenges. Using this technology allows a course position to be recorded as fish swim past acoustic receivers. At the same time, fine-scale temporal, depth, and temperature data can be documented (Cook et al. 2016). Understanding spatial ecology through acoustic telemetry has enabled scientists to provide information that aids in management and conservation of fish populations, including Bull Trout.

Study Area

Historically, most Bull Trout in the Columbia River system were fluvial, but with the addition of dams and other barriers to migration, many extant populations are now adfluvial and isolated in lakes and reservoirs above impassible dams (Goetz 1989). The Yakima River, a major tributary to the Columbia River, is one of the longest rivers in Washington state and historically held abundant populations of Bull Trout and other salmonids (Patten et al. 1970). Today, the Yakima River provides ecosystem services valued in billions of dollars including food-based agriculture, forest products, and outdoor recreation (Eco Northwest 2017). There are over 400,000 people living in the Yakima River Basin and the river supports 40% of the workforce (Ramboll Environmental 2017). This water-dependent economy has changed the natural condition of the river with the implementation of dams for water storage and hydropower, levees to protect inhabited flood plains, and diversions delivering water to farms. In 1992, Washington Department of Fish and Wildlife (WDFW) reported that populations of Bull Trout had been extirpated from the main-stem Yakima River below the city of Yakima (Mongillo 1992). As of 2017, there were 15 extant populations of Bull Trout in the Yakima River basin, primarily near the headwaters, in and above water storage reservoirs (Reiss et al. 2017). With most of the extant populations in the Yakima River basin exhibiting the adfluvial life history strategy, this system is a good model to study the movement ecology of sub-adult adfluvial Bull Trout within a lake. Moreover, new water management plans in the Yakima basin, and Kachess Lake specifically, are under development. Consequently, informing resource managers how sub-adult Bull Trout use lake habitat is important for conservation of local populations.

Kachess Lake is a glacially formed lake in the Cascade Mountain Range consisting of the southern “Big Kachess Lake,” and the northern “Little Kachess Lake” that were naturally connected by a one-mile long river channel (Miranda et al. 2003). Kachess Dam was constructed in 1912, inundating the river channel and connecting the two basins. Today they are still referred to as “Little Kachess” and “Big Kachess” lakes. The inundated section between the two main basins is now known as the “Kachess Narrows.” Damming of Kachess Lake, whose outflow contributes to the upper Yakima River, was to provide water storage for human use throughout the dry season (Baldwin 1913) and continues to fill that purpose. A history of land use in the Kachess Lake, and Kachess River basin includes timber logging, metal extraction, and road building (Meyer 2002). Due to their downstream migratory connection being lost, Kachess Lake Bull

Trout spawn in only two tributaries of the lake, Kachess River and Box Canyon Creek (Fig. 1).

Problems

Historic land use in the Kachess River basin has contributed to annual dewatering of the lower mile of the Kachess River (Meyer 2002). Logging of large trees that once surrounded the stream caused bank destabilization and a widened channel has formed. During high run-off events, stream bed material moves readily and deposits once the river meets the still water of the lake. During low flow conditions, the stream often redefines its channel into several braids (Meyer 2002). Once snowmelt run-off subsides, dewatering begins in the lower braided section of the river. Dropping water levels push juvenile Bull Trout into small, disconnected pools, where they occur in high densities and are vulnerable to avian and mammalian predators. Eventually, most of these pools dry up and the remaining juvenile Bull Trout die (Reiss et al. 2017). The dry river remains a passage barrier, isolating adult Bull Trout from reaching their spawning grounds until late fall when storm run-off brings a push of water. During low water years, Box Canyon Creek can also become disconnected from the reservoir in late summer. Flows across the alluvial fan become highly braided, resulting in shallow channels that may not be sufficient for Bull Trout passage. Redd counts in Kachess River and Box Canyon Creek have shown that the populations are critically depressed and are in danger of becoming extirpated (Reiss et al. 2017). With both spawning tributaries presenting challenging

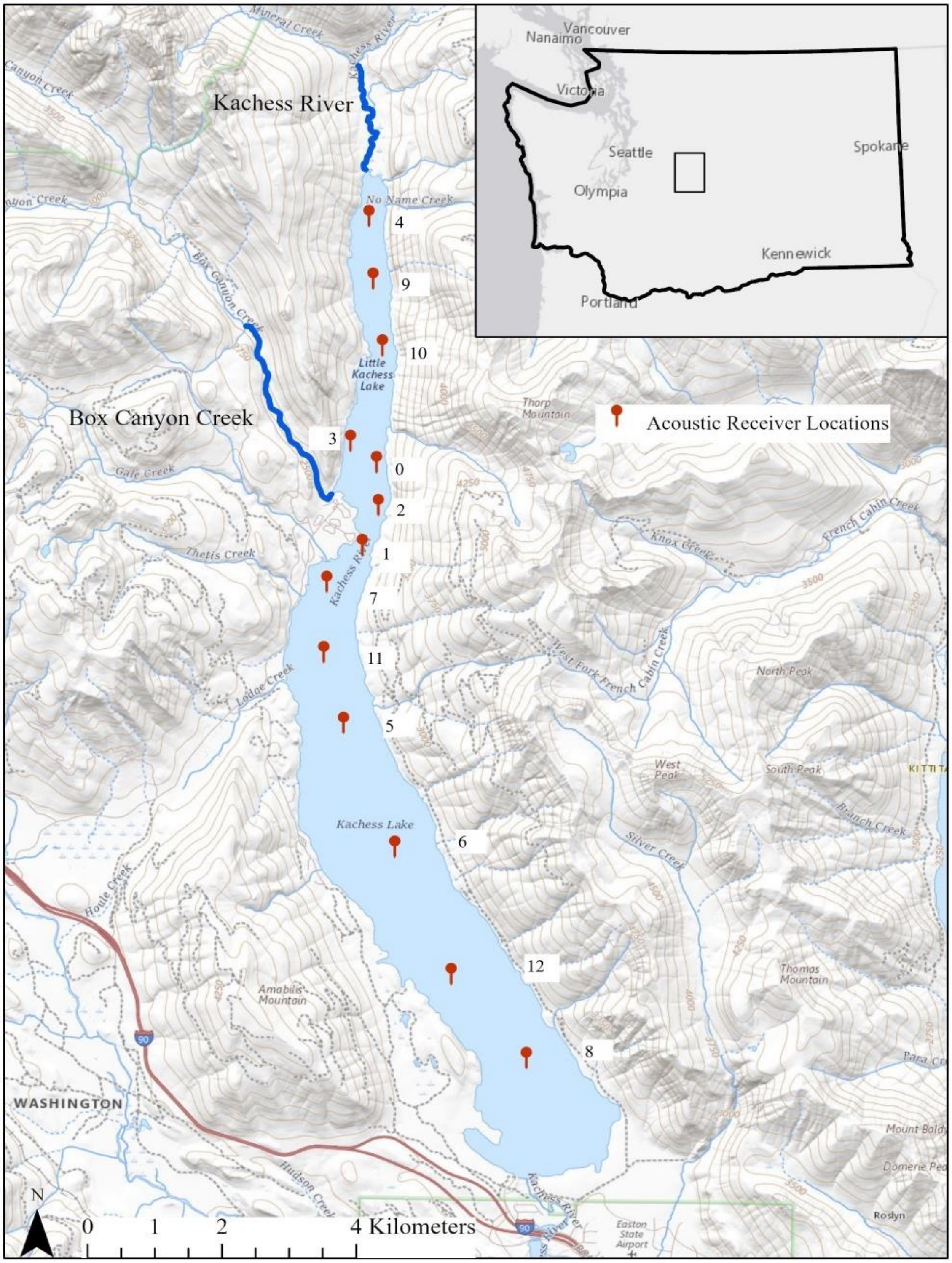

Figure 1 Study area: Kachess Lake, Washington, USA. Red pins denote locations of acoustic receivers. Spawning streams are marked in dark blue.

conditions during critical rearing and migration times, several agencies have had to implement strategies to protect the fish.

The United States Fish and Wildlife Service (USFWS) and Yakama Klickitat Fisheries Program (YKFP) are evaluating new strategies to recover the Bull Trout in this system, including tracking adult Bull Trout to understand seasonal migration timing within the reservoir, and rescuing juvenile fish that are susceptible to dewatering in Kachess River. The Yakima Bull Trout Action Plan lists fish salvage and captive rearing as a priority in Bull Trout recovery in Kachess Lake (Reiss et al. 2017). Thus, starting in 2019, several partner agencies including YKFP, USFWS, WDFW, and Mid-Columbia Fisheries Enhancement Group have been working together to rescue Bull Trout fry from the Kachess River and transport a random subset of them to La Salle, a YKFP operated rearing facility in the city of Ahtanum, Washington. The young-of-year (YOY) Bull Trout are reared in tanks with constant water temperature, artificial habitat features, and a substantial food source for approximately 12 months. The goal is to optimize growth and survival during this critical life stage. The rescue-and-rear strategy is a novel approach for Bull Trout but has been implemented with limited success in a few other Salmonid species (Lopez Arriaza et al. 2017; Beebe et al. 2021).

Rescuing wild fish as juveniles and rearing for a short time before release (rescue-and-rear) has been studied in endangered populations of Southern California steelhead (*Oncorhynchus mykiss*) (Lopez Arraiza et al. 2017) and Coho Salmon (*Oncorhynchus kisutch*) (Beebe et al. 2021). A similar method, “smolt-to-adult captive-reared supplementation” has been implemented in Atlantic Salmon (*Salmo salar*) and a few

Pacific Salmon species. Fraser (2016) suggests that there are both risks and benefits to fish survival. A recent study on juvenile Coho Salmon showed strong evidence that maladaptive traits were acquired not through artificial selection over generations, but through rapid epigenetic changes within the lifetime of hatchery-propagated individuals (Le Luyer et al. 2017). Beebe et al. (2021) suggests there are population level benefits to rescue-and-rear only if humans continue efforts on a yearly basis. It remains clear that this strategy should only be used as temporary stock enhancement until habitat can be restored to better suit self-sufficient populations. Although there is minimal research on the fate of captive-reared wild fish, the technique presented me with a unique opportunity to study the behavior of these animals upon release and provide critical information to the United States Bureau of Reclamation (USBR) about how sub-adult Bull Trout use Kachess Lake.

As part of the Yakima Basin Integrated Plan there is a proposal dedicated to accessing the "dead storage" in Kachess Lake (USBR and WSDOE 2015). The proposed action is to construct the Kachess Reservoir Drought Relief Pumping Plant (KDRPP). KDRPP is a structure that would retrieve water deeper than the current dam intake. Operation of the plant would allow an additional 200,000 acre-feet of water to be withdrawn from Kachess Lake in drought years. This action could disconnect Little Kachess from Big Kachess, and it may take two to five years for the basins to reconnect after drought is over (USBR and WSDOE 2015). My research will help inform how Kachess Lake Bull Trout behave under pre-KDRPP conditions, allowing managers to make conservation driven decisions during the construction and operation of this plant.

Research Objectives

The goal of my research was to use acoustic telemetry to explore patterns in sub-adult Bull Trout movements within Kachess Lake and identify what factors influenced those movements. The study was conducted over a period of approximately one and half years, starting in June of 2020 and culminating in November of 2021. My objectives included gaining insight on which environmental variables drove sub-adult Bull Trout depth use and the timing of vertical and lateral movements. Specific research questions were: 1) does time (week) of the year, diel period, reservoir level, precipitation, or surface water temperature explain fish depth? and 2) do individual fish have core (home) areas, and if so, where are they? This research will contribute to the body of knowledge on Bull Trout ecology, filling in gaps about behavior of sub-adult sized fish in a lake environment. Additionally, the results of this study have direct implications in management of Kachess Lake water resources, especially in the face of climate change and over-obligated water resources.

CHAPTER II

METHODS

Bull Trout Captive Rearing

Yakama Nation Fisheries Program took the lead on rescuing and captive-rearing Bull Trout. Because Bull Trout fry are nocturnal, night rescue missions were held multiple nights during the same week in August. Keeping the rescue time-frame short reduced the coefficient of variation for growth. This protocol was followed to keep size differences and cannibalism-related mortalities at the rearing facility to a minimum. Fry were rescued from isolated pools and low water runs in the Kachess River using small aquarium dipnets. Once rescue for a given night ended, a random subset of fish was selected to be transported to La Salle Hatchery in Ahtanum, WA. The remaining Bull Trout fry were released in the river upstream of the dewatering section.

Fry in the hatchery were initially fed small frozen invertebrates, including *Daphnia* sp. and brine shrimp (*Artemia* sp.). Around October, the fish transitioned to larger frozen invertebrates, and in early March, Rainbow Trout fry were introduced as food for the Bull Trout. Once Bull Trout attained sufficient length to digest them, they were fed juvenile Spring Chinook Salmon (*Oncorhynchus tshawytscha*). All fry that were fed to Bull Trout were fed to satiation first, to ensure they were packed with nutrients. The Bull Trout were fed every hour during the workday, and a large portion at the end of the day. On the weekends the fish were fed twice daily.

The Bull Trout were reared in large tanks filled with de-gassed and oxygenated well-water. The water was held at a constant temperature of 12.2°C, year-round. Artificial habitat structure including cinder blocks and eight-inch-wide, one-foot-long PVC pipes and PVC elbows were placed throughout the tank. Tanks were cleaned as needed, about once per week. Mortalities were minimal.

Bull Trout were raised up to a minimum length of 250 millimeters (mm), the length at which Bull Trout should exceed a tag-to-body-weight ratio of 2%. The 2% threshold is commonly used in fish tagging studies and is assumed to be the least detrimental to swimming efficiency and natural behavior (Winter 1983). While rearing in the facility for 11 to 12 months, Bull Trout grew from roughly 50 mm to approximately 250 mm. Out of the reared population, only a small number were large enough to tag for this study.

Bull Trout Tagging and Transport

Two types of tags were used in this study. The majority of fish were tagged with Vemco V9TP-2x-69kHz coded transmitters with temperature and pressure sensors (TP sensors). A few fish were tagged with Vemco V9-2x-69kHz without temperature and pressure sensors (Fig. 2). Pressure was assumed to be accurate within 0.5 to 1 meter. Nominal delay was set at 90 seconds and tags transmitted randomly every 60 to 120 seconds. Tag life was estimated to be 445 days. Depth and temperature data are transmitted by the tag using different codes; thus, some detections have temperature and some have depth. All detections have a record of date, time, and the receiver where it was detected. Three out of 20 tags implanted were Vemco V9 transmitters without TP sensors.

Figure 2 Vemco V9TP-2x-69kHz coded transmitter (indicated by the red box).

Bull Trout were anesthetized with 100 mg/L MS-222 solution buffered with 200 mg/L sodium bicarbonate until they were unconscious (loss of equilibrium, slower opercular rate, no response to stimulus). Then, they were measured for total length and weight, and a passive integrated transponder (PIT) tag was injected into the dorsal sinus. PIT tags will be used to monitor individuals into the future, beyond this study. Fish were then placed ventral side up in a cradle and the gills were irrigated with MS-222 solution while surgery took place. A 15 to 20 mm incision was made just adjacent to the linea alba, and the acoustic tag was inserted into the coelomic cavity of the fish. The incision was closed with two interrupted sutures (Ethicon Z397H, absorbable). All surgical equipment and tags were sterilized with 99% isopropyl alcohol prior to each surgery. The time from complete anesthesia to being placed in the recovery tank was between three and four minutes per fish. After full recovery, Bull Trout were placed back into the tanks at the rearing facility.

Fish were left to recover from surgery for at least 24 hours in the rearing facility before transport to Kachess lake. Bull Trout were transported by truck in 150-quart Coleman coolers, with adequate aeration, about 90 miles to the Kachess Lake boat ramp. They were then moved from truck to boat and taken to Little Kachess Lake for release. Two different release locations were selected to avoid potential angling pressure. Fish were allowed to acclimate in a live well placed in the lake for 15 to 20 minutes before being released. Upon release, no Bull Trout that underwent surgery had died or shed a tag.

Acoustic Array

As part of an ongoing study, USFWS set up an array of six Vemco VR2W and seven Vemco VR2Wtx acoustic receivers spanning Kachess lake from North to South (Fig. 1). Receivers were setup with an assumed detection range of 500 meters (m) and estimated detection efficiency of 50% (Kessel et al. 2014). In addition to detecting tagged fish, acoustic receivers monitored water temperature and VR2Wtx units transmitted signals every 10 minutes. Receivers were assumed to detect tags across most of the lake's volume, but small gaps in detection were expected due to some level of environmental noise, and parts of Big Kachess Lake where receivers were over 500 m apart. Receivers were attached with cable ties to a rope that spanned between a 30-pound anchor on the bottom and an orange buoy at the surface of the water. A bullet float was placed between the receiver and the surface buoy to maintain the receiver's vertical orientation. The bullet float was placed on the line at the minimum pool depth for the location. Depth of receiver attachment was typically 20 to 30 meters (depending on lake level) below the surface with the receiver facing down. Station 1 receiver was within a meter of the surface, and station 2 receiver was attached at the anchor facing up, because the total depth in these locations was only ~ 3 to 4 meters, depending on lake level. Technical issues caused receivers 0 and 7 to not function for short periods of time during the study (20 to 30 days). There are no data from those receivers while they were sent in for repairs. Receiver data downloads and maintenance were done every one to two weeks during the warmer months, but snow and ice on the lake prevented access to the receiver array during the winter months.

Environmental Data Collection

Environmental data from Kachess Lake, such as precipitation and forebay elevation was taken from the USBR Hydromet tool, which provides 15-minute data for USBR managed reservoirs. Hydromet did not have surface water temperature, and unfortunately, I was not able to place an Onset HOBO temperature logger at Kachess Lake surface until October 2021. The surface water temperature (SWT) data used in the analysis was from the station 1 acoustic receiver (Fig. 1). This station was placed in the shallowest part of the lake and the receiver was within a meter of the surface. To justify use of station 1 as SWT, the temperatures were compared between the station 1 and the true SWT from the HOBO logger for the period that both were in the water (Fig. 3). On average, temperature collected by the receiver at station 1 was 1.5 degrees Celsius (°C) cooler than the real surface temperature logger.

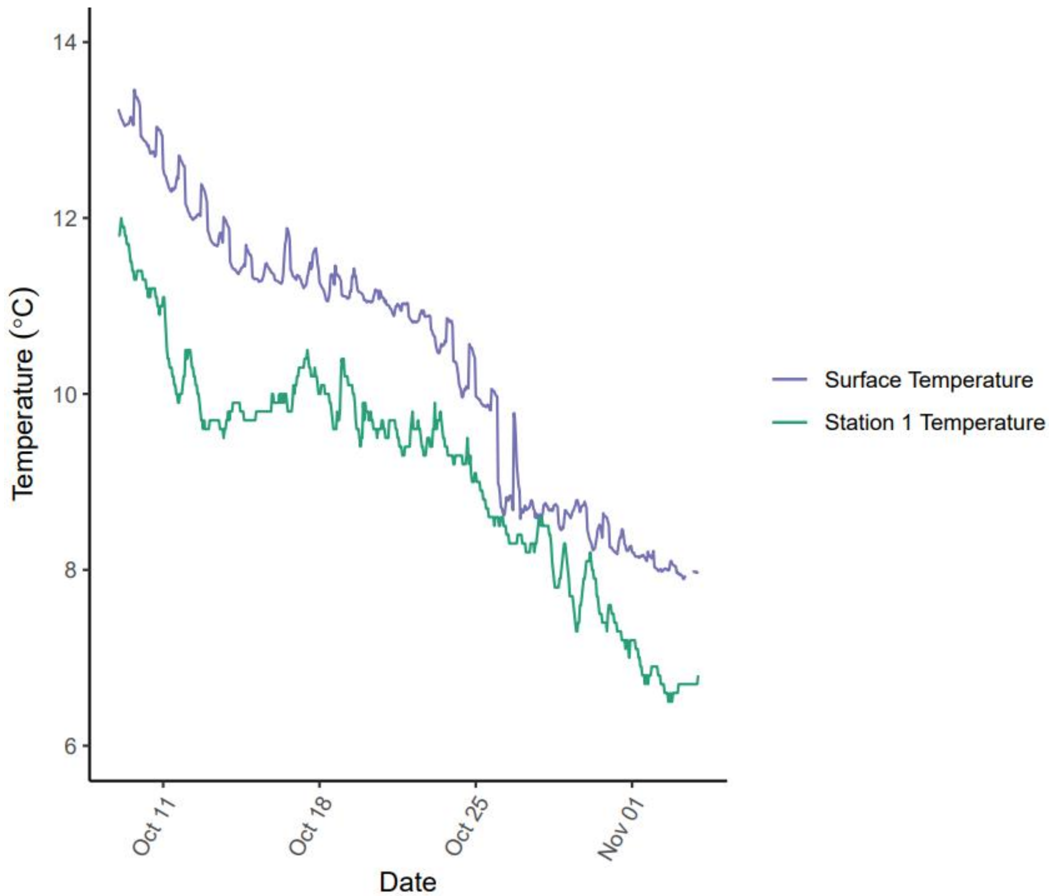

Figure 3 Comparison of surface water temperature and receiver temperature at station 1 for October 7 to November 3, 2021.

Range Test

A detection range test was performed using the VR2tx acoustic receivers to test the detection efficiency of the array. For a two-week period in fall of 2021, the built-in transmitters were set to "range test" mode and transmitted signals every 90 seconds. Detection data from all receivers were uploaded and the proportion of total transmissions received was plotted against the receiver's distance from the transmitter. Detection ranges were calculated from this relationship (Kessel et al. 2014).

Data Management

Unless otherwise noted, all data management and analyses were done using R Statistical Software (v4.0.2; R Core Team 2020). First, raw data were filtered to remove false detections. Detections were considered false if there was only a single detection within 45 minutes, the interval of maximum delay between tag transmissions (Pincock 2012). Code collisions that were recorded as unknown tag IDs were also removed. Second, all data from the first week after release of individuals was removed to avoid behavioral alterations due to the tagging or transport of fish from the rearing facility to the lake (Rogers and White 2007; Gutowsky et al. 2013). Third, to avoid interpreting data from under-represented individuals, only fish that had been in the lake at least 30 days and had at least 500 detections were retained in the analysis. Finally, any detection that was indicative of a dropped tag or mortality event, defined by no change in depth over multiple days, was removed from the dataset (Green et al. 2021).

As some Bull Trout were in the lake for different periods of time, the analysis of depth distribution data was constrained to the period between July 7 and November 21, the period where most individuals were actively being detected. July through November data for one individual was recorded in 2020 while data from the remainder of the individuals were recorded in 2021. Depth measurements were rounded to the nearest integer, as Gutowsky et al. 2013 suggested depth changes of less than 0.5 m were biologically insignificant. To facilitate more efficient modelling of depth distribution, depth data for each fish were averaged by date and hour. Surface temperature, and 15-minute precipitation data were also averaged by date and hour to stay consistent with depth observations.

The Stream Metabolism package in R was used to find local sunrise and sunset times (Sefick 2016). Diel periods were calculated from those times. The “day” period was considered to begin after sunrise and end at sunset, while “night” was considered to begin after sunset and end at sunrise. Week of the year was calculated using the Lubridate package and was implemented as a numerical covariate in the model (Grolemund and Wickham 2011).

To summarize detection data, individuals were given a detection index score following the formula: DI = DD/TP (Tracey et al. 2020). In the formula, detection index (DI) is equal to the number of days detected (DD) divided by the total period (TP) from release to disappearance, mortality, or the end of the study period. Other summary statistics on depth range, temperature use, and lateral movements were taken from the full dataset after false detections were removed, not the data that were averaged by hour.

Data Analysis

Depth Distribution: All Fish

A primary research question was: what timing and environmental factors are correlated with depth distribution? To answer this question and make population level inferences, the response variable, depth, was rounded to the nearest meter and modelled using a generalized linear mixed-effects model (GLMM) with individual fish as a random effect and Poisson distributed error terms (Gutowsky et al. 2013), implemented with the glmmPQL function from the MASS package (Venables and Ripley 2002). Diel period was included as a fixed factor in the model, and surface temperature, precipitation, week, and latitude were treated as numerical covariates. Water surface elevation (WSE) was removed from the model due to strong collinearity with week of the year. The decision to keep week in the model rather than WSE was made because timing of Bull Trout movements was deemed more important than the effect of WSE. For the period that depth distribution data were analyzed, the lake was under a typical "high water year" management schedule with most of the water release happening from August-November. Under drought-like conditions, WSE might decrease much sooner in the year and be less correlated with seasonal movements of Bull Trout, allowing it to be disentangled from week.

Data exploration was accomplished by fitting a general linear model to the data and plotting the residuals and estimated autocorrelation (Zuur 2009). Exploration showed non-normality and heteroscedasticity in the data. Autocorrelation plots showed temporal autocorrelation, which was to be expected given the nature of the tag transmission rate.

There was also strong evidence of non-normality and heteroscedasticity, which led to the decision to move forward with a GLMM. Modeling with a GLMM allowed implementation of a random effect to account for variation among different fish (Pinheiro and Bates 2000). Model selection was done by implementing the full model with all available predictor variables and interactions and, because glmmPQL does not produce AIC values, backward stepwise selection was based on which model contained the most factors with highly significant p-values ($P < 0.01$).

I attempted to address temporal autocorrelation by implementing and comparing several AR1 and corARMA autocorrelation structures, but this required more computational power than was readily available, given the size of the dataset. When comparing models with and without the autocorrelation structure within subsets of the data the results did not differ, so the structure was removed. Consequently, temporal autocorrelation in the data may have biased p-values downward.

Depth Distribution of Individual 8372

A single sub-adult Bull Trout was tracked for an entire year from July 2020 to July 2021. In addition to this individual being included in the July-November analysis, the depth data from this individual alone was analyzed to explore the effects of the same predictor variables on depth over the course of an entire year. A generalized linear model (GLM) with Gamma distribution was used to model the relationship between depth and the predictor variables described for the GLMM above. To reduce autocorrelation, depth data were averaged per diel period, per date. Averaging data lessened temporal autocorrelation, but not to a negligible level. I proceeded with the GLM despite the lack of total independence between depth observations. The best model was selected using the drop one method and comparing Akaike Information Criterion (AIC) between models (Zuur 2009). The final model included depth modelled as a response of week, precipitation, diel period, surface water temperature, and interactions between week and surface temperature, and diel period and surface temperature. For this individual, latitude and its interactions were dropped from the model during the model selection process.

Lateral Movements

Kernel density estimation (KDE) is a common non-parametric probability density estimator that can be used to determine the home range of an animal (Worton 1989). However, the only assumption of KDE is that observations are independent from one another, thus using standard KDE methods could underestimate the home range of an animal where autocorrelation is inherent (Fleming et al. 2015). The AKDE function from the ctmm package in R accounts for violation of independence in the data (Fleming and Calabrese 2021). The function is typically used for animals that are continuously tracked with radio or GPS tracking devices that are given a fixed detection location. The acoustic array for this study was passive, detecting fish anywhere within approximately 500 m of an acoustic receiver.

To define more fine scale locations of fish for use in this analysis, I simulated a correlated random walk (CRW) for each individual (R code written by Jason Romine, USFWS, personal communication). CRWs are useful when there is correlation between successive step orientations, also known as directional persistence (Patlak 1953). Because animals tend to move forward and not erratically, the locations of an animal can be modeled using a CRW (Codling et al. 2008). The CRW simulation used Bull Trout detection data to produce fine-scale point locations within a conservative detection buffer of 500 m from the receiver the fish was detected on. Once points were simulated, they were loaded into the ctmm package in R.

Simulated location data for each individual were examined for range residency, velocity autocorrelation, and positional autocorrelation and then classified into a “continuous-time stochastic process model” using the “ctmm.guess” function (Calabrese et al. 2016). Selected models included “independent identically distributed” (IID), and the “Ornstein-Uhlenbeck” (OU) model. The IID model assumes that positional autocorrelation is negligible, while the OU model combines a typical Brownian motion (BM) model of regular diffusion, with the tendency to stay in a certain area (Calabrese et al. 2016). The movement model with the lowest AIC value was selected and implemented into the AKDE function to find 50% and 95% Kernel Density Estimations. Analysis was done in R, but shapefiles were loaded into ArcGIS pro and the map visualization was created.

CHAPTER III

RESULTS

Range Test

The distance at which 50% of range test transmissions were detected varied from 375 to 1050 m with a mean 50% detection range of 609 m (± 261 m SD) (Fig. 4). Receivers within the Kachess Narrows had the smallest detection range, likely due to the bottleneck-like topography at that location. The narrows region of the lake is also nearest Kachess Lake campground, where boats are launched and frequently move within proximity to the receivers, possibly increasing ambient noise levels compared to other receivers. The overall average range of detection fell within the assumed 500 m radius.

Detection Summary

One individual Bull Trout tagged in 2020, and seven Bull Trout tagged in 2021 fit the criteria for analysis (n = 8). The mean total length (TL) for the eight individuals included in this analysis was 270.5 mm (± 16.6 mm SD) (Table 1). One individual that fit the analysis criteria, tag ID 54208, did not have a TP sensor tag, so only lateral movements were analyzed for this individual. There were 381,772 total detections after data were filtered for analysis. Detection index scores ranged from 0.42 to 1.00 with a mean detection index of 0.88 (± 0.19 SD) (Table 1), indicating Bull Trout were detected most of the time.

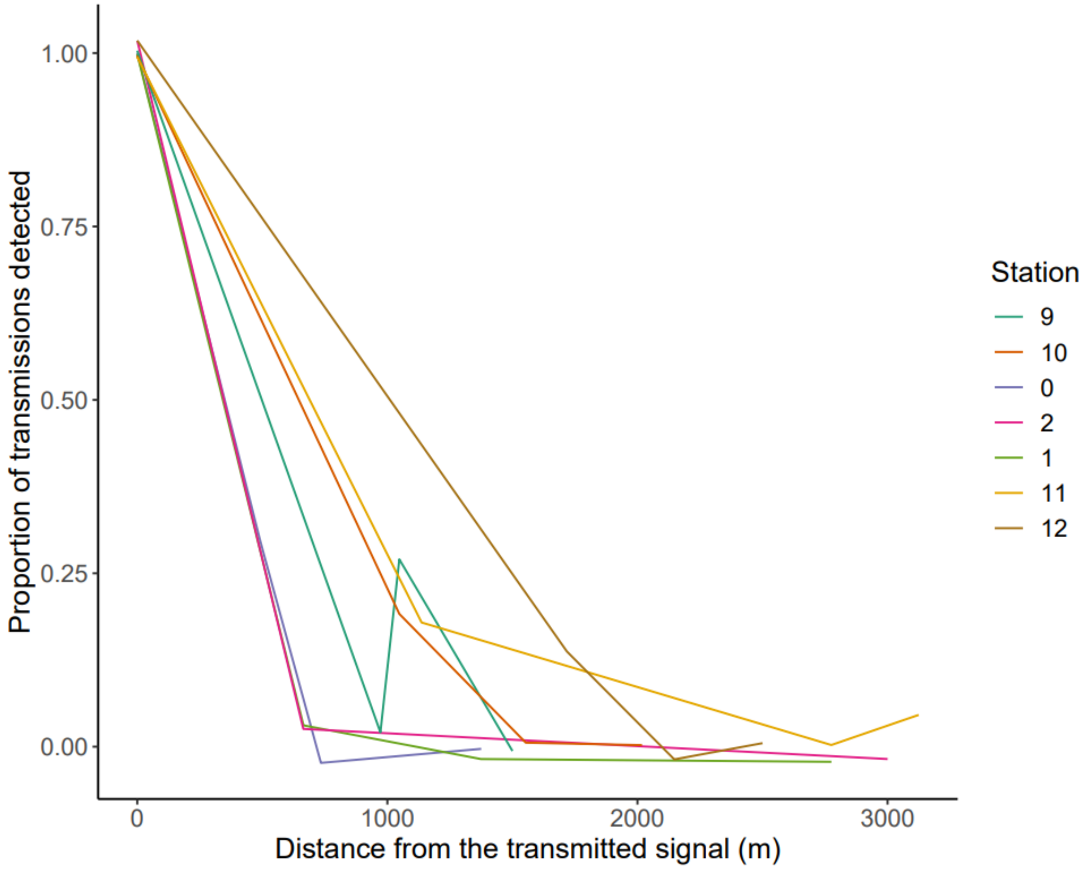

Figure 4 Detection efficiency of various stations. Stations in the legend are in order from North to South across Kachess Lake. Not all stations are reflected in this plot because some were out of range of a VR2Wtx transmitter.

Table 1 Detection Summary of the Eight Individuals that fit the Criteria for Analysis.

Tag ID	Tot. Length (mm)	First Detection	Last Detection	Days Detected	Total Period	Detection Index
8372	262	7/2/2020	7/9/2021	345	367	0.94
12024	294	7/5/2021	11/22/2021	138	138	1
54208	266	7/27/2021	11/22/2021	112	112	1
12820	261	7/27/2021	11/22/2021	110	112	0.98
12834	263	7/27/2021	11/22/2021	104	112	0.93
12824	279	7/27/2021	11/22/2021	102	112	0.91
12046	294	7/3/2021	11/3/2021	48	54	0.88
12026	252	7/2/2021	9/26/2021	31	73	0.42

Summary Statistics – Depth and Temperature Usage

Sub-adult Bull Trout exhibited a wide range of depth and temperature use. Depths ranged from 0 to 104.7 m. Most individuals were detected at depths less than 50 m, while individual 12820 was primarily detected at depths greater than 50 m (Fig. 5). Bull Trout were rarely detected near the surface in the months between July and October. For the entire study duration, the average depth for all fish, not including individual 12820 was 11.7 m. The overall average depth of individual 12820 was 92 m. The average depth for all fish combined was 38.8 m.

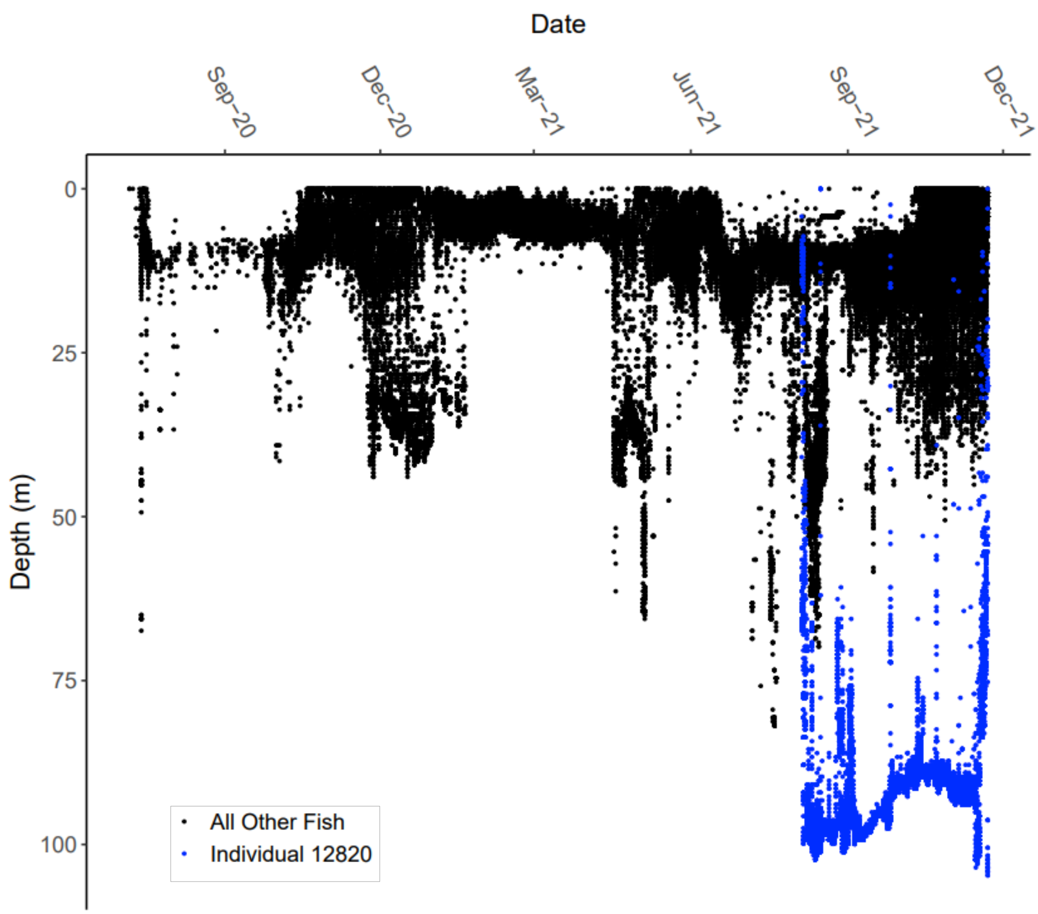

Figure 5 Depth detections over the course of the study.

Diel vertical migrations (DVMs) became consistent in most of the individuals starting around October (Fig. 6). During July, August and September, there were no consistent vertical movement patterns across individuals, but in early to mid-October, a pattern emerged where fish were seen diving to depths between 25 and 50 m during the daytime and approaching the surface at night (Fig. 7). Two individuals had stopped being detected by this time in 2021, and individual 12820 continued to make only occasional movements toward the surface. Around October 20th, thermal stratification broke down and the lake began mixing (Fig. 8). Around this time, sub-adult Bull Trout began making DVMs with wider ranges. Surface water temperatures dropped from approximately 14 °C on October 9th to roughly 9 °C on October 26th, consistent with when fish started incorporating movements all the way to the surface into their DVMs (Fig. 6).

Fish generally utilized areas with water temperature less than 10 °C (91% of detections). The known optimal growth temperature range for Bull Trout is from 10.9-15.4 °C (Selong et al. 2001), however only 6% of temperature detections fell within this range. The average weekly fish temperature ranged from 2.6 °C to 11.8 °C, with only four weeks where average fish temperature was 10 °C or higher. During the weeks between June 7 and June 20, and July 12 and July 25, the average fish temperature was between 10.8 °C and 11.8 °C. Just 0.5% of detections exceeded 15 °C, despite surface water temperature and the entire water column in Kachess Narrows exceeding 15 °C for most of July to October (Fig. 9). The overall average temperature that fish experienced was 5.7 °C.

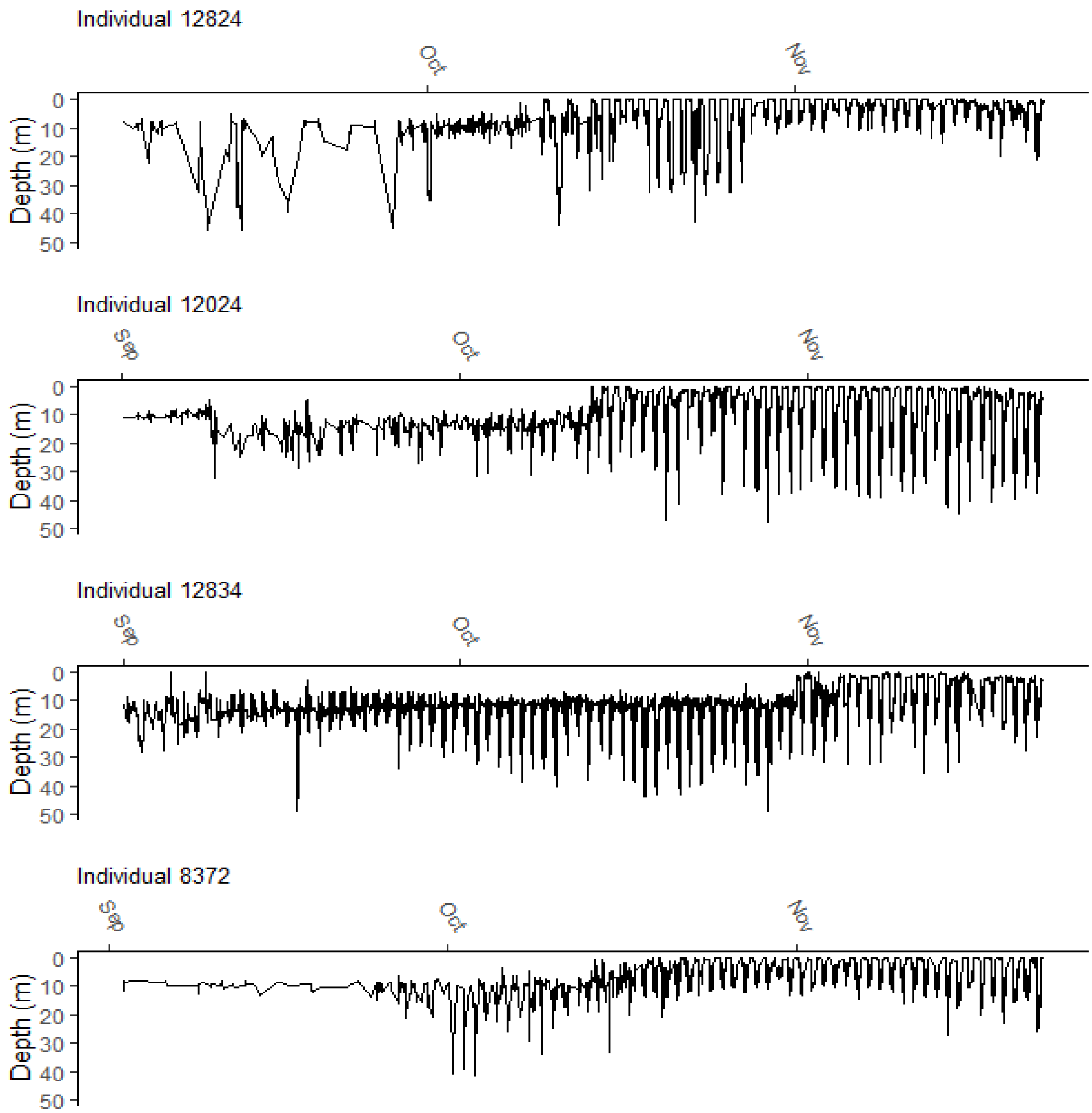

Figure 6 Depth profiles for four individuals from September 1st to November 22nd. The data from individual 8372 was from 2020, data for other individuals was from 2021.

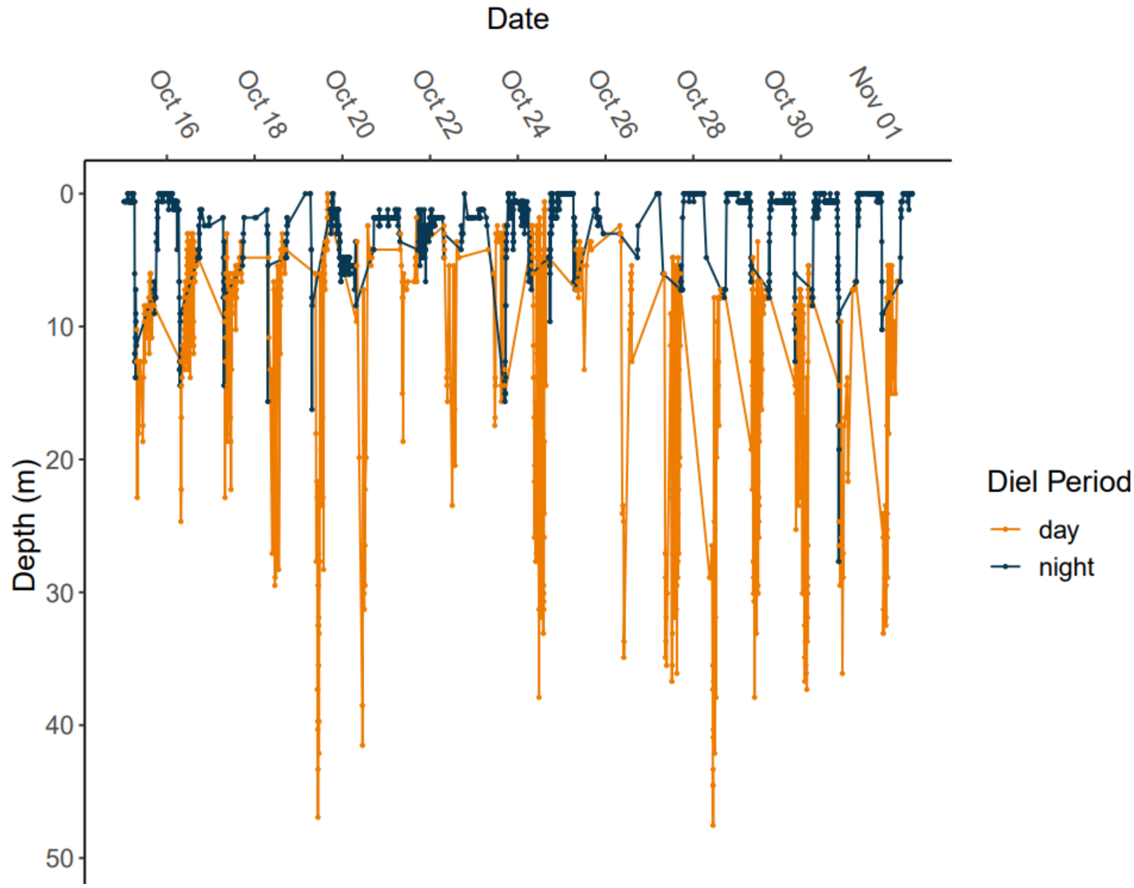

Figure 7 DVMs of individual 12024 over a two-week period in October 2021.

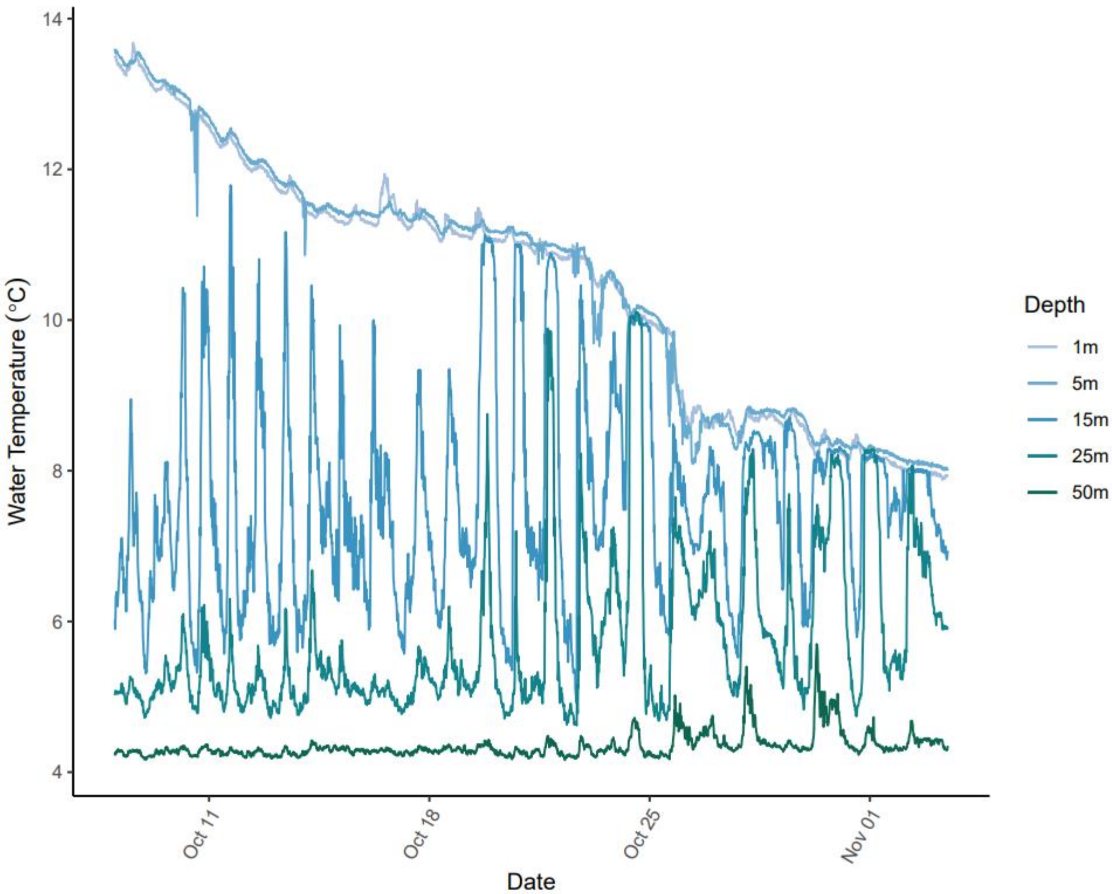

Figure 8 Kachess Lake temperature profile for October 2021.

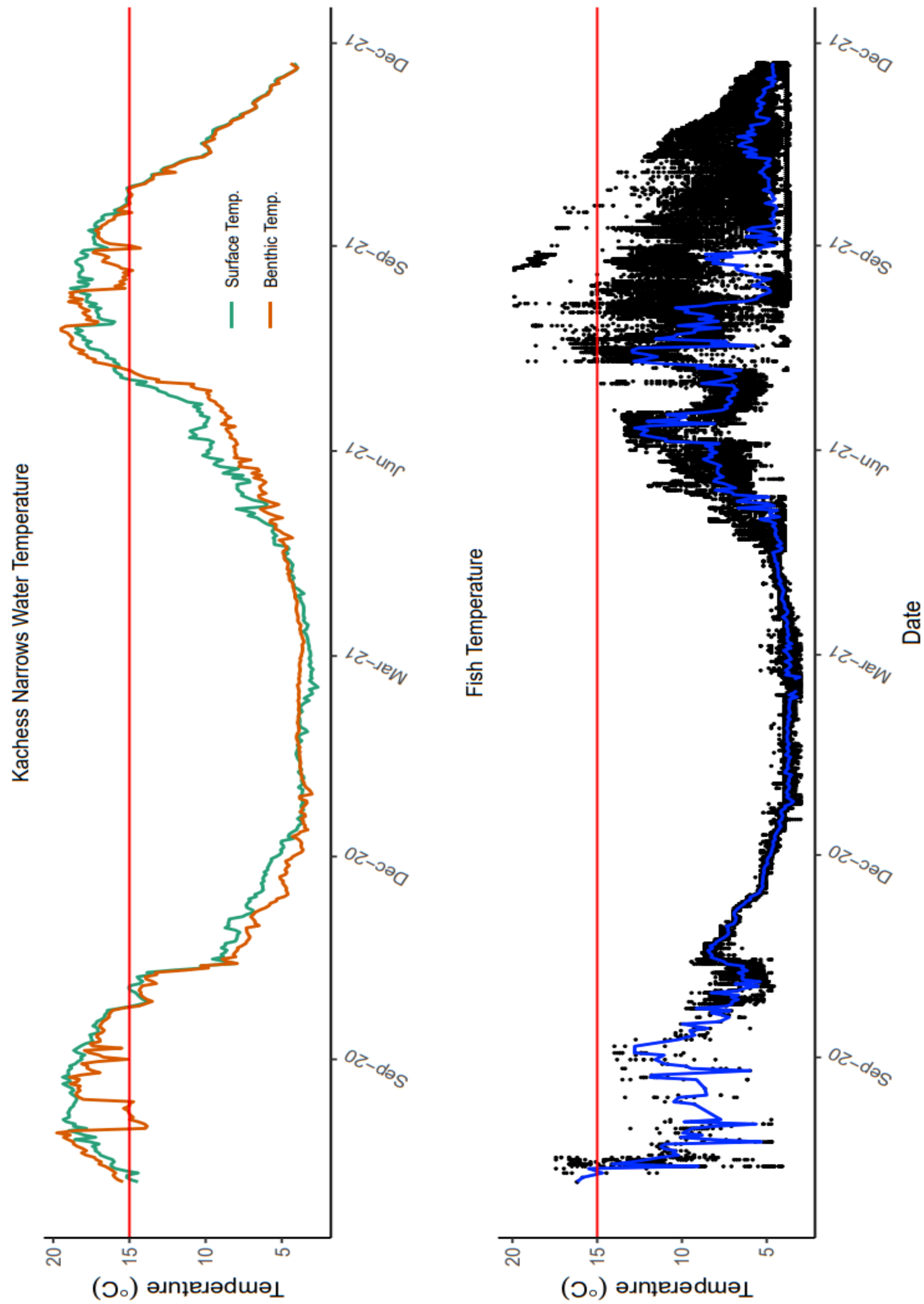

Figure 9 Water and fish temperatures over the course of the study. Top: water temperatures for Kachess Narrows surface and benthic temperatures (red line at 15°C). Bottom: all fish temperature detections represented as black dots; blue line represents average daily fish temperature.

Depth Distribution

All fish

The GLMM of best fit included surface water temperature (SWT), week, diel period, latitude, precipitation, and two-way interactions between SWT and diel period, SWT and week, SWT and latitude, and week and latitude (Table 2). The model predicted all explanatory variables and interactions to have a significant effect on depth (significance level of $P < 0.05$).

Table 2 Results of Generalized Linear Mixed Effects Model with PQL Estimation.

Estimate	Value	Std. Error	t-value	p-value
(Intercept)	-1818.3597	207.6902	-8.7551	< 0.0001
Week	49.1090	4.0593	12.0977	< 0.0001
SWT	-16.4418	4.2306	-3.8633	0.0001
Precipitation	0.0157	0.0049	3.2153	0.0013
Diel Period (night)	-0.3209	0.0209	-15.3637	< 0.0001
Latitude	38.4844	4.3848	8.7767	< 0.0001
SWT:Latitude	0.3464	0.0893	3.8795	0.0001
SWT:Week	0.0012	0.0002	4.9319	< 0.0001
SWT:Diel Period	0.0161	0.0015	10.8846	< 0.0001
Week:Latitude	-1.0378	0.0857	-12.1094	< 0.0001

Bull Trout were predicted to move deeper in the water column as SWT increased ($P < 0.0001$) (Fig. 10A; Fig. 11). Additionally, week of the year was a significant predictor of depth without any interactions, but also in combination with SWT, and latitude ($P < 0.0001$; $P < 0.0001$; $P = 0.0001$, respectively) (Fig. 10B; Fig. 12). Depth distribution was also predicted to differ by diel period ($P < 0.0001$). Sub-adult Bull Trout were predicted to be closer to the surface at night and deeper in the water column during the day (Fig. 10C). For precipitation, depth was predicted to increase from an average of 16.5 m at 0 cm of precipitation to ~18 m at ~5 cm of hourly precipitation (Fig. 10E).

Depth Distribution of Individual 8372

GLM results from individual 8372 over a period of one year showed similar patterns in depth distribution to the GLMM results for all fish from July through November (Table 3). Latitude was removed from the model during model selection, likely because this individual showed site fidelity and was detected primarily in a small range within Little Kachess Lake. Depth distribution predictions from the GLM showed that as weeks progressed through the year, depth decreased ($P < .0001$) (Fig. 13A). Individual 8372 tended to swim deeper as SWT increased ($P < .0001$) (Fig. 13B), consistent with the results of the GLMM with all other individuals. However, individual 8372 had more pronounced diel depth differences, and preferred to stay much deeper during the day compared to night ($P < .0001$) (Fig. 13C). Precipitation was not a significant predictor of depth distribution for the individual with a year-long dataset ($P = 0.08$).

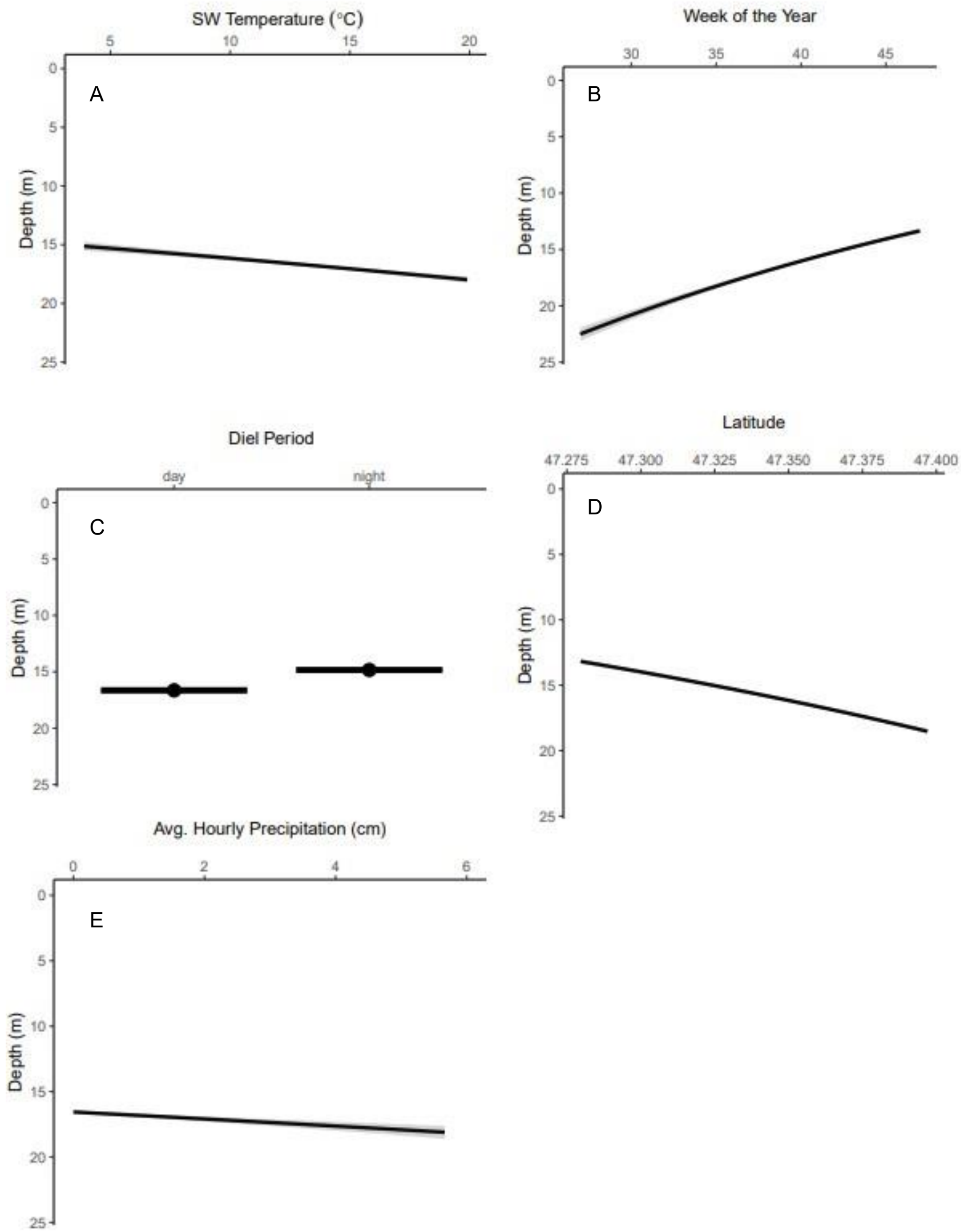

Figure 10 GLMM predictions of sub-adult Bull Trout depth for each significant explanatory variable (all other variables held at their mean). The shaded gray area represents 95% confidence intervals. A) Depth vs. Surface Water Temperature, B) Depth vs. Week of the Year, C) Depth vs. Diel Period, D) Depth vs. Latitude, E) Depth vs. Average Hourly Precipitation.

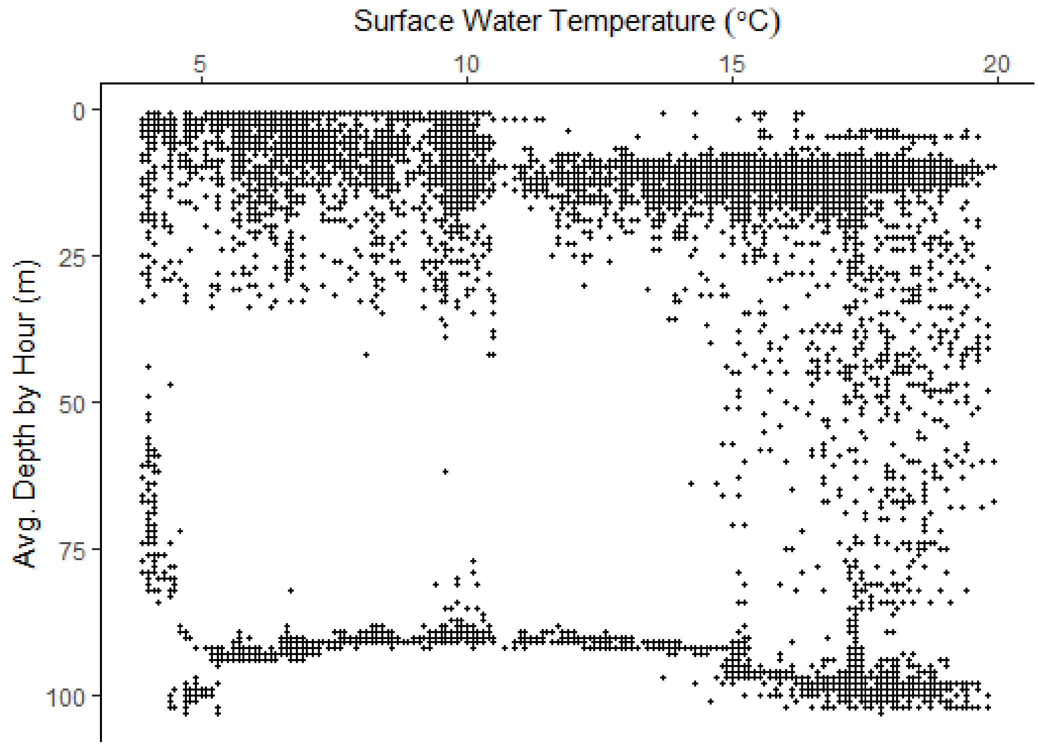

Figure 11 Raw data from the duration of the study showing the association of depth distribution with surface water temperature.

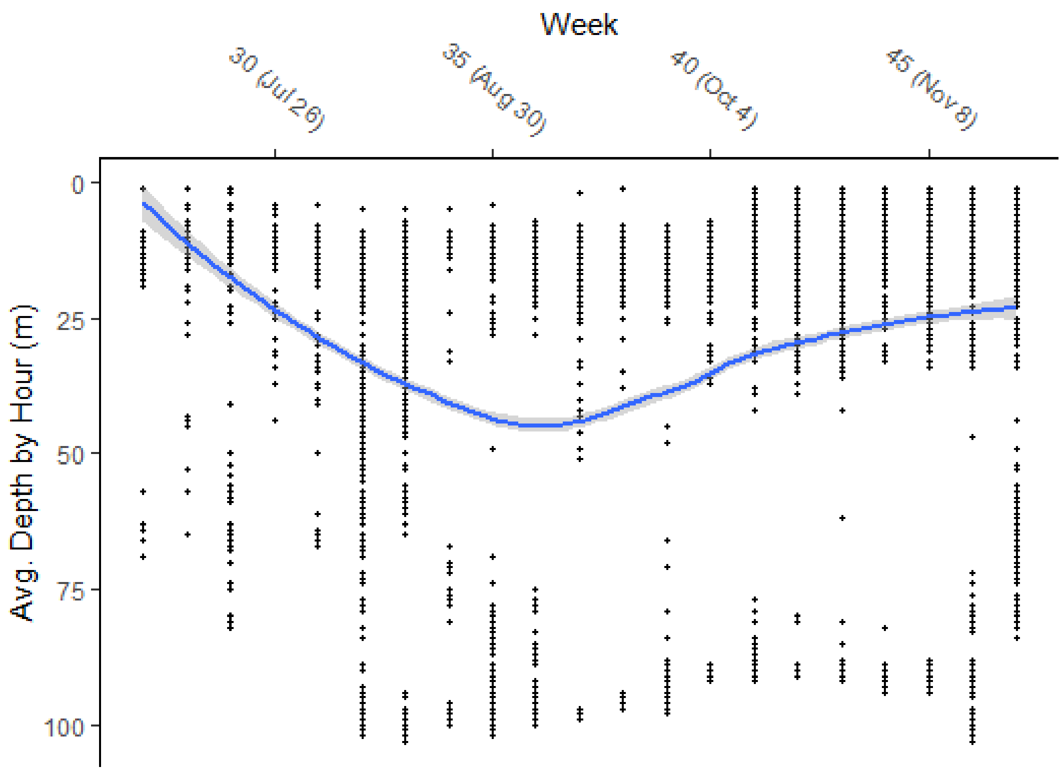

Figure 12 Raw data with average hourly depth detections plotted by week of the year from July 7, 2021, to November 21, 2021. The blue line represents a LOESS smoother.

Table 3 Results of Generalized Linear Model for individual 8372.

Term	Estimate	Std.error	Statistic	P.value
(Intercept)	0.145562	0.012362	11.77514	< 0.0001
Week	-0.00249	0.000365	-6.81963	< 0.0001
Precipitation	0.006815	0.003921	1.738236	0.0826
Diel period (night)	0.175272	0.013293	13.18517	< 0.0001
SWT	-0.01052	0.002111	-4.98544	< 0.0001
Week:SWT	0.000354	6.73E-05	5.264021	< 0.0001
Diel period:SWT	-0.00969	0.00112	-8.64677	< 0.0001

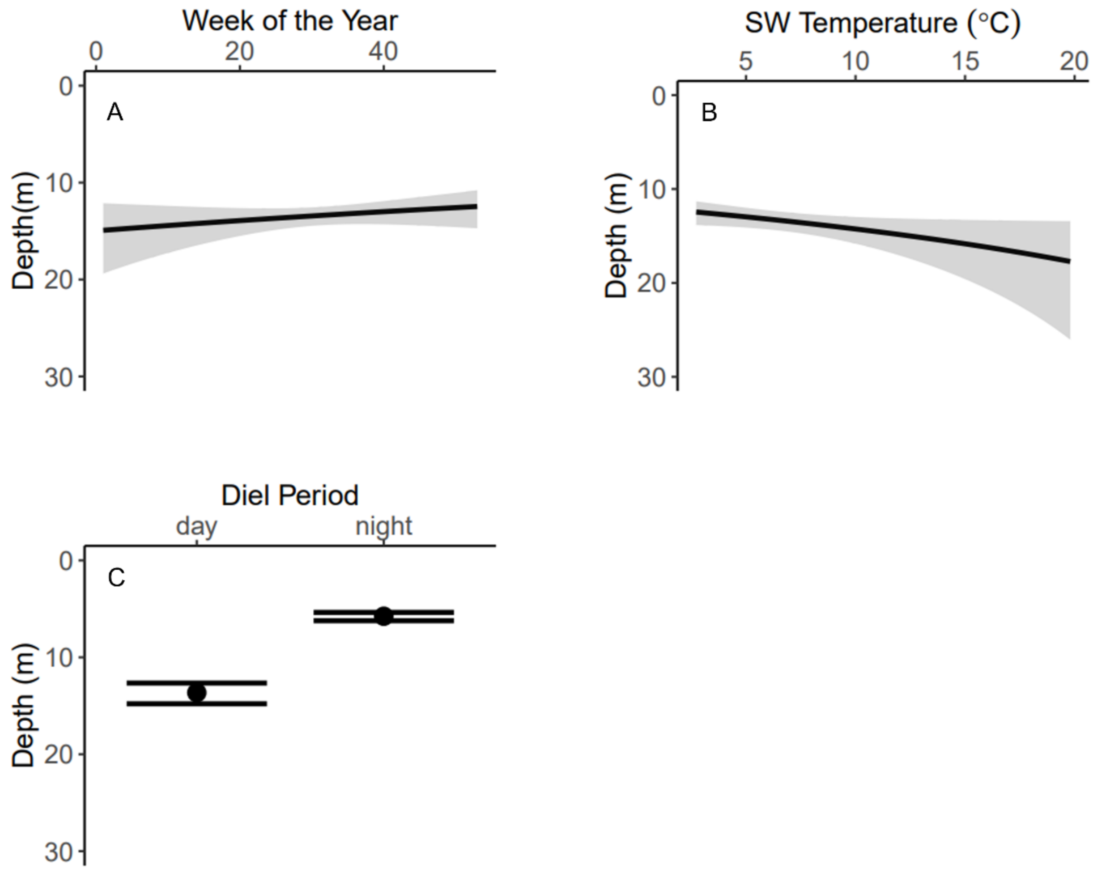

Figure 13 Depth predictions from GLM for individual 8372. Shaded gray represents 95% confidence intervals. A) Depth vs. Week, B) Depth vs. Surface Water Temperature, C) Depth vs. Diel Period

Lateral Movements

Movement models including the independent identically distributed process (IID), and the Ornstein-Ohlenbeck process (OU) were chosen as best fit models of continuous time movement (Table 4). Individuals that did not exhibit lateral movements from receiver to receiver very often were assigned to an IID model, because despite simulation of individual point locations via correlated random walk, the data showed no evidence of correlated movements between receivers. Other individuals were assigned to the OU movement model because there was some evidence of restricted space use in addition to positional autocorrelation.

Table 4 Results of Autocorrelated Kernel Density Estimation (AKDE) of 95% Home Range. “Low” and “High” represent 95% confidence intervals of the estimate. The asterisks denote that the AKDE was estimated as larger than the area of the lake, and home range was cut off at the boundaries of Kachess Lake.

Individual	Model	Low km2	Estimated km2	High km2
12834	IID	1.65	1.69	1.72
54208	IID	2.37	2.39	2.42
12820	OU	3.34	3.36	3.38
12824	IID	3.65	3.68	3.72
8372	IID	5.56	5.59	5.62
12046	IID	6.02	6.11	6.2
12026	OU	18.37*	18.37*	18.37*
12024	IID	18.37*	18.37*	18.37*

Using the best fit model for each fish, the AKDE estimated home ranges (95% utilization distribution) varied from a low of 1.69 km^2 to a high of 18.37 km^2, which is the total surface area of the lake (Table 4). Although CRW locations within 500m of each receiver were used in the model to predict home range, this function does not have an option to incorporate land as a barrier to fish movement. Thus, some home ranges were estimated beyond what is physically possible. For the two individuals that had a larger estimated home range than possible, the AKDE estimates were cut off at the boundary of land. Core use areas (50% utilization distribution) were also estimated and mapped. The core areas for four individuals were confined to Little Kachess, while three individuals, 12026, 12024, and 12046 had 50% core area habitat in both basins (Fig. 14). Individual 12820's core area was confined to the Big Kachess basin.

For the individuals that moved between basins, timing of these movements showed no patterns (Fig. 15a). Individual 12024, moved South across the Kachess Narrows sometime within the first week after release (this data was filtered out), back North to Little Kachess in mid-July, and back South to Big Kachess in early-September. This fish remained in Big Kachess between early-September and late November at the last download. Individual 12024 did not remain within the Kachess Narrows for any duration of time, only passed through. Individual 12026 had the lowest detection index of all fish, and evaded detection about 60% of the time. This individual also moved to Big Kachess within the first week after release, moved to Little Kachess in mid-July, and back to Big Kachess just days later. Individual 12026 remained in Big Kachess until September 26, when it was last detected (Table 1). Finally, the last fish that had 50% core area in both basins was individual 12046, who was detected moving from Little Kachess into Kachess Narrows in early-July and remained within detection range of the Kachess Narrows receivers until late July, then moved back North to Little Kachess. Individual 12046 was last detected in early-November (Table 1).

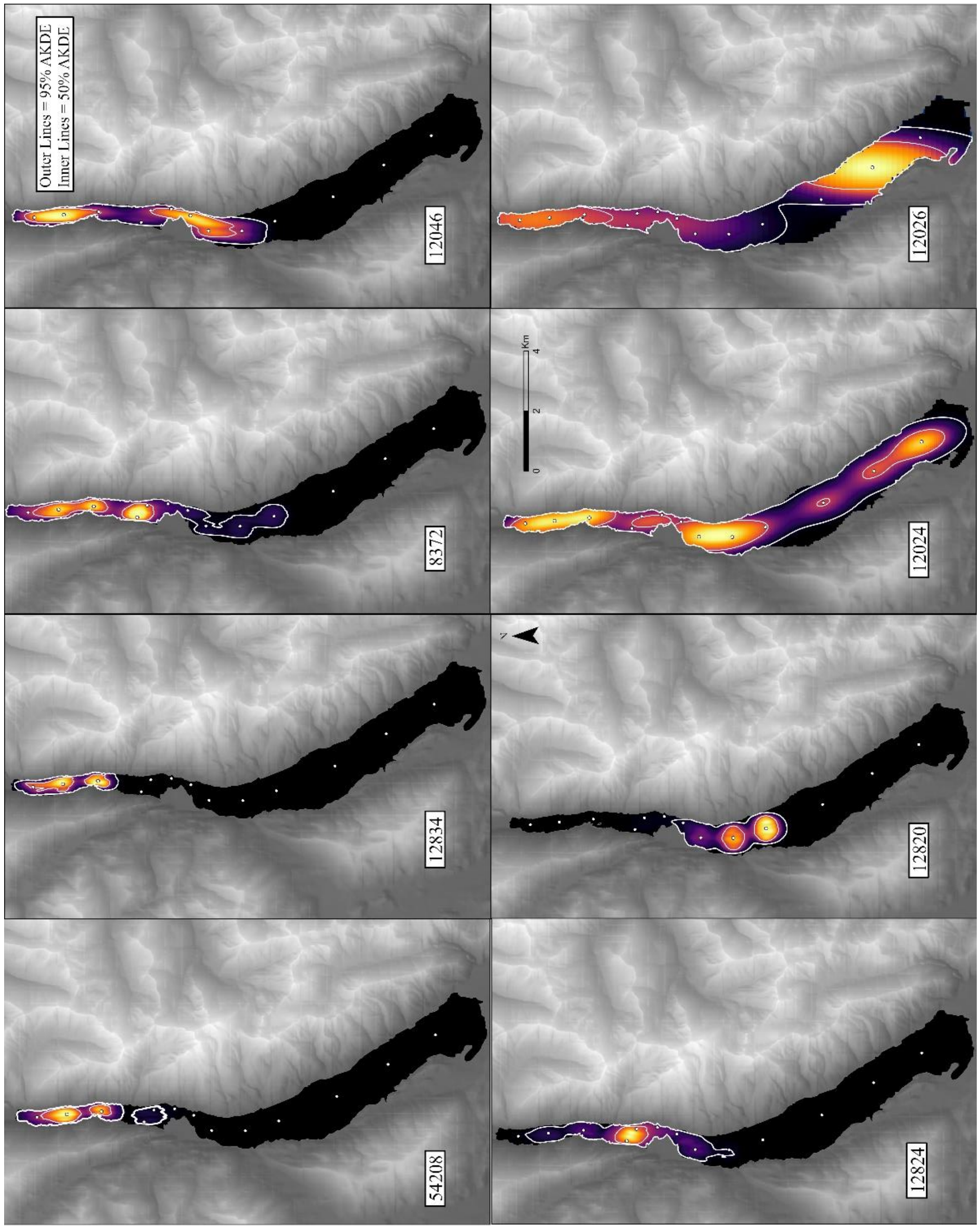

Figure 14 Home-range and core use areas. Bold white lines represent 95% Kernel utilization distributions while thin white lines represent 50% Kernel utilization distributions. Yellow = hot spots of detections, black = zero or very few detections. White points represent acoustic receiver locations.

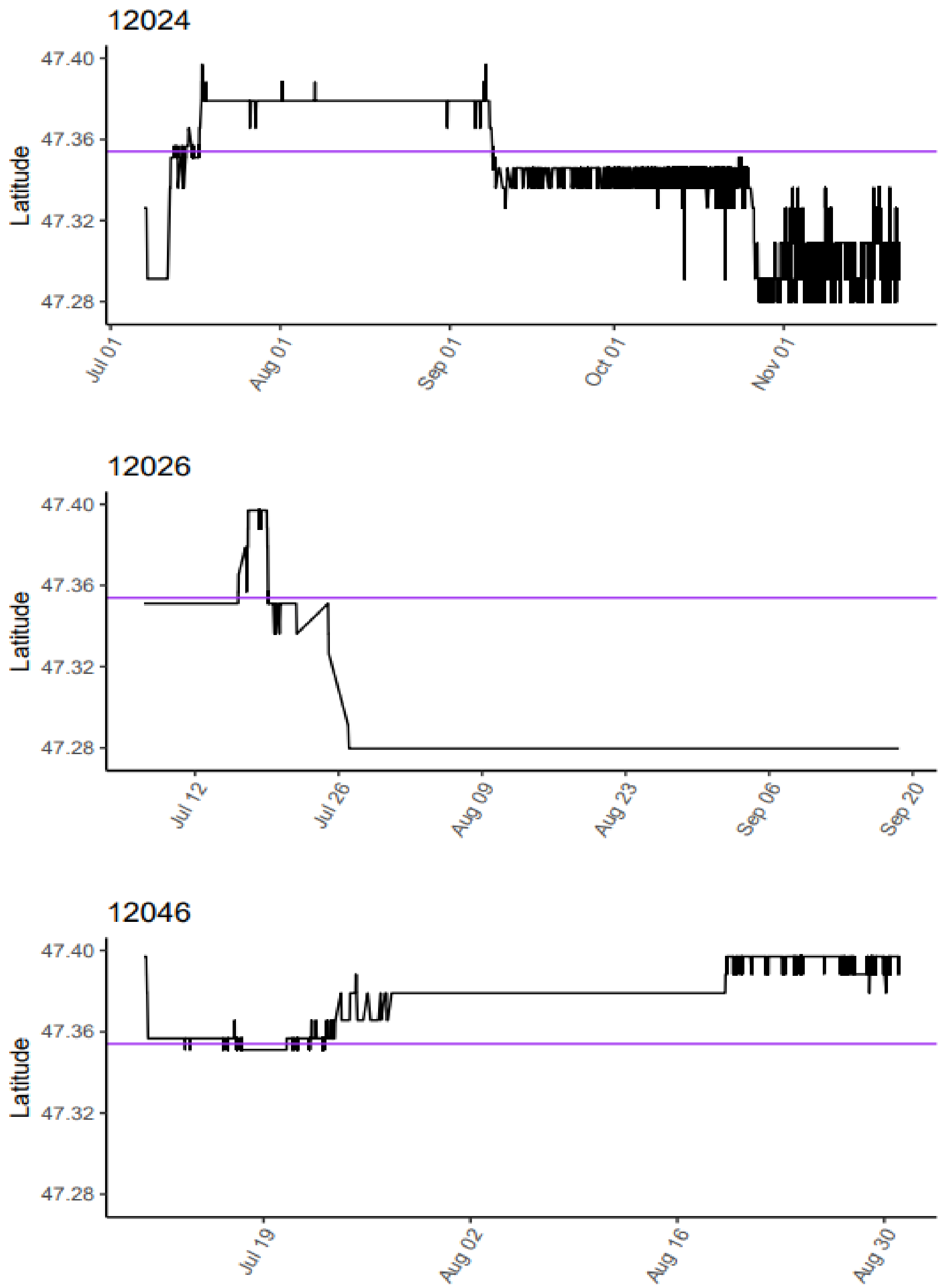

Figure 15a Lateral positions over time for the three individuals that had 50% core area in both basins. The Y-axis shows latitude with 47.40 being the northernmost receiver in Little Kachess, and 47.28 being the southernmost receiver in Big Kachess. The purple line represents the narrowest part between the basins (Fig. 15b). Note that X-axis dates differ due to amount of time each fish was detected in the lake.

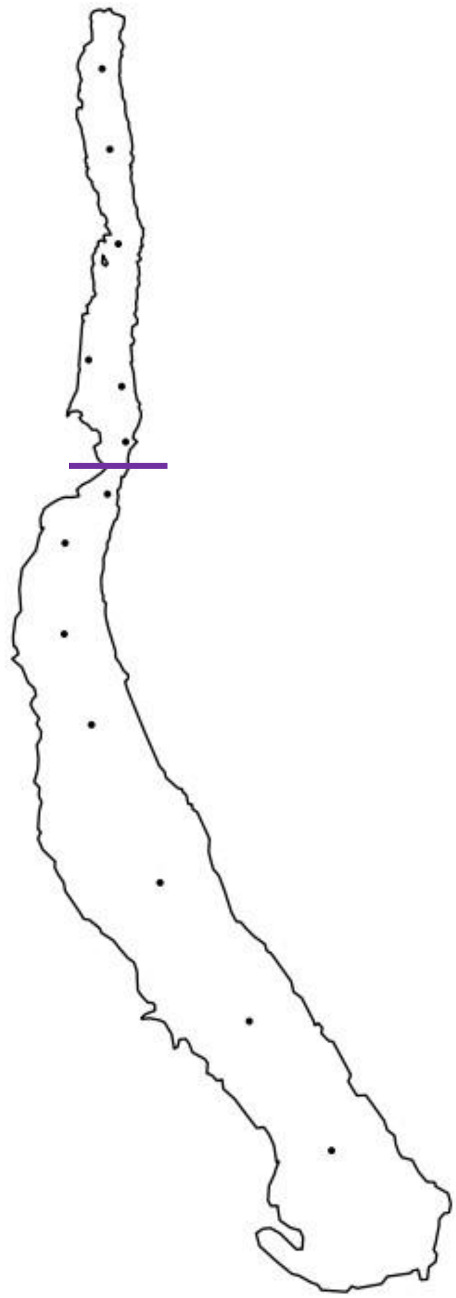

Figure 15b Kachess Lake with purple line representing the pinch point at Kachess Narrows that was visualized in figure 15a. Black points are locations of acoustic receivers.

CHAPTER IV

DISCUSSION

Summary

In an acoustic telemetry dataset of over 380,000 detections of sub-adult Bull Trout, there was wide variation between individual fish in vertical and lateral habitat use. However, water temperature was a primary driver of depth distribution for all individuals. Sub-adult Bull Trout exhibited a tendency to utilize water temperatures less than 10°C. Vertical movements were variable, but depth distribution can be predicted by environmental conditions and week of the year. Additionally, the data show no clear patterns in DVMs emerging until late-fall. My sample of Bull Trout dispersed from one another after release, showing differences in lateral space use almost immediately. Some individuals were highly mobile, and others showed site fidelity. In the discussion to follow, I mention some contrasts between the sub-adults I studied and adult Bull Trout in other systems and discuss other potential explanations for sub-adult Bull Trout habitat use.

Depth Distribution

Depth use by sub-adult Bull Trout in Kachess Lake is driven by water temperature, week of the year, and time of day. The data showed avoidance of depths between 0 m and 15 m during times when surface water was 15 °C or higher. The Kachess Narrows surface and benthic temperature exceeded 15 °C for most of July through September, and at times climbed to 20 °C. Only 5.9% of all the detections from

July through September occurred within detection range of the Kachess Narrows receivers, and from those the majority were on receiver 2, which was in proximity to deeper, cooler water. Given the results, it is possible that the Kachess Narrows act as a thermal barrier for sub-adult Bull Trout to pass between Big and Little Kachess basins during the warmest weeks of the year. In addition, when DVMs started becoming more apparent in the fall, the data showed Bull Trout ascending at night only to the depth of temperature stratification (roughly 15 to 20 m), until that stratification broke down in mid-October. With results showing depth distribution as highly dependent on temperature, it is important to consider what leads Bull Trout to seek out cooler temperatures.

In a lab – based study, peak growth rate for satiated juvenile Bull Trout was found to be in water of 13.2 °C, with predicted upper and lower limits for growth at 20.7 °C and 5.2 °C (Selong et al. 2001). My results showed sub-adult Bull Trout spent time near this optimal growth temperature (average between 10.8 °C and 11.8 °C) for only four weeks throughout the entire study. In contrast, adult Bull Trout in Kinbasket Reservoir, British Columbia, generally favored temperatures in this range (Gutowsky et al. 2016). Between August and October adult Bull Trout selected for an average temperature range between 11 and 15 °C, despite that range accounting for only 41.7% of the total available temperature range in the reservoir. Adult Bull Trout were found to move shallower in pursuit of these temperatures as they became less available in the late summer and fall (Gutowsky et. al 2016). The sub-adult individuals in my study did not remain in this temperature range, despite warm temperatures being available for longer than four weeks.

Eckmann et al. (2018) found that adult Bull Trout in Ross Lake, WA made frequent DVMs in cold water that could not be explained by optimizing growth. Their hypothesis was that colder temperatures may support gametogenesis. Sub-adult Bull Trout are sexually immature, so the gametogenesis hypothesis does not hold in this case. One potential explanation for sub-adults not staying in optimal growth temperatures is to decrease the energy consumption that would occur under warmer temperature conditions (Javaid and Anderson 1967).

Studies on other species including walleye and juvenile Salmonids including Brook Trout (*Salvelinus frontalis*), Rainbow Trout, and Atlantic Salmon showed fish choosing colder temperatures when deprived of food (Javaid and Anderson 1967; Sogard and Olla 1996). Choosing a lower temperature has been hypothesized as a way for ectotherms to reduce metabolic energy consumption, and diving to deeper areas could be a behavioral mechanism to delay or reduce the effects of reduced prey consumption. The duration of time when sub-adult Bull Trout did spend time in water near the suggested peak growth temperature coincided with when WDFW stocked ~312,000 Kokanee Salmon (*Oncorhynchus nerka*) fry into Kachess Lake in early-June 2021. It is possible that Kokanee were an easy and plentiful prey target for Bull Trout in the first few weeks they were in the lake. After July, sub-adult Bull Trout generally stayed out of temperatures greater than 10°C.

An alternative hypothesis to explain why sub-adult Bull Trout were not always found within the optimal temperature range for growth designated by Selong et al. (2001) could be that temperature is not actually the primary driver of growth. A bioenergetics study by Railsback (2022) suggests that at relatively high food consumption rates in salmonids, substantial growth can occur even at low temperatures. The author's argument is that lab-based studies on optimal temperature, like Selong et al. 2001, typically occur under ad-libitum feeding, and growth is limited by digestion rate because feed is readily available and rich in energy. This effect could have been seen in the weeks following the Kokanee stocking event at Kachess Lake. But under more natural conditions, salmonid fishes growth may be limited by food capture rate (Railsback 2022). It is unlikely that in the wild, a fish can feed at a higher rate than digestion can occur. A 2017 report by Hansen et. al claims that food resources for Bull Trout in Kachess Lake are not limited, and thus it is possible sub-adult Bull Trout in this system are in fact capturing enough prey but not to the point where they are waiting for digestion to occur between feedings. A 2020 study by Mulder et al. suggested that Arctic Char (*Salvelinus alpinus*), a closely related species to Bull Trout, utilize deeper, colder water for feeding and shallower warmer water to potentially aid in digestion. My temperature data suggest that Bull Trout may have used warmer temperatures directly post-stocking of Kokanee to aid in digestion, but the general trend to spend time in cooler water after June does not necessarily mean they were lacking in food. Cooler temperature use could be explained by Bull Trout hunting and consuming prey under natural environmental conditions.

The 2017 Hansen et al. food web study at Kachess Lake was conducted during the summer season and showed that adult Bull Trout primarily consumed other salmonids. Kokanee Salmon fry were identified in the stomachs of all large piscivorous fish in the study. Because sub-adult Bull Trout around 250 mm are gape limited, they would feed on small salmonids, which may include Pygmy Whitefish (*Prosopium coilterii*). Both Kokanee Salmon and Pygmy Whitefish are known to make diel movements from deeper to shallower water and have low thermal tolerances (Levy 1990; Bevelhimer and Adams 1993; Hallock and Mongillo 1998; Zemlak and McPhail 2006). A study done in a Utah reservoir looking at predator prey interactions between Lake Trout (*Salvelinus namaycush*) and Kokanee found that during summer when the reservoir was lowest and temperature stratification was occurring, cold-water prey was concentrated and easily accessed by predators (Klobucar and Budy 2016). Once lake mixing occurred, they found prey to be more dispersed and predator efficiency and growth was reduced. This could help explain the start of consistent DVMs in the fall in sub-adult Bull Trout. As kokanee began to disperse during lake mixing, Bull Trout likely increased vertical search activity in pursuit of prey. The depth distribution and DVM patterns displayed in the data by most of the individual Bull Trout are consistent with the idea that Bull Trout are following prey and eating at a natural rate, rather than being limited by digestion or altering behavior to reduce energy consumption at low temperatures.

Although latitude and precipitation were considered “significant” predictors of depth distribution, it is possible there are indirect effects at play for these variables. For latitude, there were a very small number of observations at the southernmost receivers when compared to northern latitudes. One shallow swimming may have skewed the model to predict shallower depth distribution in Big Kachess. Additionally, bathymetry likely played a role in the connection between depth and latitude. As the lake was drawn down in the summer, shallow water habitats in Little Kachess like the Box Canyon Creek alluvial fan and the Kachess River delta became unavailable to fish. In terms of precipitation, it is unlikely that rain at the surface of the lake would cause disturbance deeper than a meter or so. It is possible, however, that Bull Trout are responding to a drop in barometric pressure, which has been significantly correlated with depth distribution in other species like largemouth bass (*Micropterus salmoides*) (Hanson et al. 2008).

Lateral Movements

Within a sample of eight individual sub-adult Bull Trout, there was considerable variation in lateral space use within Big Kachess and Little Kachess basins. Five individuals showed strong site fidelity and rarely moved laterally once they settled into an area after release (12820, 54208, 12824, 12834, 8372). Shortly after release in July 2020, individual 8372 moved from Little to Big Kachess, and then back to Little Kachess within a week. Individual 8372 remained in Little Kachess until July 2021 when the last detection was recorded. One individual, 12046, included Kachess Narrows within its 50% core area, but was only detected for a total of 48 days, giving the two weeks this fish spent around Kachess Narrows extensive weight in the home range analysis (Fig. 14). Two individuals were highly mobile, making multiple movements between Little and Big Kachess basins and having 50% core habitat in both locations (12024 and 12026) (Fig. 14; Fig. 15).

Given the wide range of lateral habitat use, and no specific patterns in timing of lateral movements, it seems likely that there is suitable habitat and prey in both Big and Little Kachess basins. Despite a lack of patterns in timing related to lateral movements, data showed no Bull Trout in this study spent considerable time in the Kachess Narrows when the temperature exceeded 15°C. Even with individual 12046 spending time around Kachess Narrows in mid-July, the mean temperature this individual experienced during that timeframe was 13.1°C, indicating use of a potential thermal refuge in the vicinity of the Narrows when lake levels were the highest.

Under a KDRPP Scenario

With the Kachess Reservoir Drought Relief Pumping Plant (KDRPP) installed and operating, an additional 200,000 acre-feet of water would be removed from the lake during drought years (USBR and WSDOE 2015). Decreasing the current low-water elevation an additional 80 feet would dewater the Kachess Narrows and much of the productive littoral zone around the lake.

Keechelus Lake, an adjacent reservoir, has substantial water draw down earlier in the season to provide water for agriculture in the Yakima Valley and appropriate flows for Spring Chinook spawning in the upper Yakima River. The food web of Keechelus Lake relies on pelagic basal energy production rather than littoral and benthic energy production due to the early draw down and degradation of the littoral zone (Hansen et al. 2017). The authors of this report suggest that if USBR were to draw down an additional 80 feet in Kachess Lake, a similar change could happen, putting more reliance on the pelagic food web. Given the range of lateral, depth, and temperature use in my study, sub-adult Bull Trout may not be directly impacted by a loss of littoral habitat. However, losing littoral production of aquatic macrophytes, algae and benthic invertebrates could induce a trophic change where insectivorous fishes switch to forage on pelagic zooplankton, thus reducing food supply for Kokanee, and indirectly the Bull Trout (Hansen et al. 2017). Sogard and Olla (1996) showed that the response of Walleye (*Sander vitreus*) to intermediate food rations was to increase vertical activity as a search response to find more food. Rising competition among planktivorous fishes, and subsequently piscivorous fishes may increase vertical and lateral movements for Bull Trout that are searching for food, potentially exacerbating the need for fish to access both basins.

Under KDRPP the volume of available habitat would be reduced. The glacially carved bathymetry would still provide adequate depths for Bull Trout to not be threatened by warm surface temperatures in the top 15-20 m of the water column, but lateral space use in Big Kachess would be diminished. In moderate to low precipitation years, Kachess watershed does not produce enough yearly run-off to refill the lake (USBR and WSDOE 2015). After full withdrawal from KDRPP, the lake may take 2-5 years to refill after drought has ended. A primary concern is that a passage barrier at the Kachess Narrows would eliminate access to spawning habitat for migrating adult Bull Trout that forage in Big Kachess. However, my data show that sub-adult Bull Trout are also using habitat in both basins. A passage barrier would eliminate the ability for Bull Trout of all sizes to access a variety of foraging grounds, which I predict to be very important if littoral production is lost. The results of this study show the importance of having plans for two-way fish passage during years when KDRPP is operating.

Limitations of This Study

The limitations of this research are important to address, given the implications. The final sample size after applying criteria for analysis, was eight Bull Trout. Of the eight fish, seven fish had tags that conveyed temperature and pressure information, but one fish had a tag that only conveyed date and time of detection. Furthermore, of those eight fish, there was considerable variability in the detection periods – e.g individual 8372 was detected for 345 days, and individual 12026 was detected for only 31 days. Due to fish size requirements, most of the Bull Trout were not tagged and released until July 2021, when the last data download of the year was in November 2021 (after which winter conditions prevented access to the lake). Despite some level of unbalanced data, the flexibility of a GLMM allowed me to effectively analyze the data I did collect.

Regarding the GLMM statistical analysis some limitations stem from the assumptions of linear regression. An assumption of linear regression is that each sample is random and independent of one another. In the depth observations, temporal autocorrelation was present, which may result in biased parameter estimates and p-values. In terms of individual fish being independently chosen from one another, all the Bull Trout fry were rescued from isolated pools in the lower Kachess River. In this tributary, Bull Trout redd counts were relatively low, with 23 redds counted in 2019, and only two redds reported in 2020 (personal communication with WDFW). It is possible that captive-reared fish, especially from brood year 2020, could be siblings and may behave similarly in the lake. Additionally, time constraints obliged me to tag the biggest and fastest growing of the captive-reared fish for my study, not a completely random sample from the captive-reared population. Given the small sample size, and other modelling limitations, results may be statistically significant, but may not be biologically significant.

It is important to note that growth was extremely fast compared to those in the wild. Although I released study fish when they were approximately one-and-a-half years old, which would be considered a juvenile in nature, I chose to consider these fish “sub-adults” given their large size and placement in the lake rather than river.

Conclusion

The number one recovery action for Bull Trout to be de-listed from the endangered species act is to “protect, restore, and maintain suitable habitat” (USFWS 2015). With a future of impending climate change, uneven precipitation years, drought, and humans need for water resources, my research following the behaviors of sub-adult fish helps to define the “suitable habitat” for this Bull Trout population. As a long-lived species, typically not reaching sexual maturity until 5-7 years old, the growth and survival of the sub-adult life-stage is critical (Fraley and Shepard 1989, Goetz 1989, Rieman and McIntyre 1993). My research discovered key environmental influences on Bull Trout distribution across Kachess lake, which allows managers to make decisions that maintain suitable habitat while also preparing for a warmer and dryer future.

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