Movement ecology of adfluvial bull trout (*Salvelinus confluentus*)

By

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Dedication

To Victoria, who has accompanied and encouraged me through all of my graduate studies. I also dedicate this thesis to my loving family and friends. Finally, in dedication to my earliest and most influential academic mentors, Mrs. Millar and Mr. Hudson.

Abstract

Organism movement can be explained by a combination of inter-related variables that are derived from an individual's internal state, environment, motion capacity, and navigation capacity. Movement ecology can be used as a framework under which to test ecological hypotheses across a variety of spatial and temporal scales. To reveal aspects of movement ecology of free-ranging adfluvial bull trout (*Salvelinus confluentus*), I used acoustic telemetry and tested hypotheses about thermal resource selection, diel vertical migration, and size and sex-related effects on movement. I tagged 187 adult fish and monitored these individuals for up to two years (2010-2012) in the ~ 425 km^2 Kinbasket Reservoir, BC. Correlates of movement included combinations of variables representing the internal state (e.g., phenotypic traits including sex and body size), the external environment (e.g., temperature and diel period), and the navigation capacity (e.g., the way in which an organism perceives and navigates its environment). Over the two-year period, temperature experience was similar for all body sizes (~ 400-800 mm total length). During summers, bull trout were predicted to experience temperatures that were within ~1°C of their lab-derived thermal optimum for metabolism and growth for juveniles. Bull trout occupied temperatures between approximately 11-15°C and selected higher temperatures as these temperatures became less available with the progression of summer and autumn. Diel vertical migration (DVM) was evident, with the largest individuals occupying the shallowest water. Significant DVM continued to occur during winter when the thermal profile was presumably isothermal. Winter DVM, and a significant effect of body size, indicated that multiple inter-related factors were responsible for vertical movements. Body size and season were significant predictors of home range size, with the largest home ranges predicted during autumn and spring in fish greater than 700 mm total length. A significant sex x body size interaction predicted horizontal movement such that in a given month, large females moved significantly farther than large males and small females, whereas there was no difference between large and small males. This work provides novel insight into thermal resource selection, diel vertical migration, and the correlates of horizontal movement. This research generates new information on the movement ecology of adfluvial bull trout in a hydropower reservoir which is relevant to understanding entrainment risk.

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Co-authorship

Chapter 2: Thermal Resource selection in bull trout: temperature experience and selection change with availability. Gutowsky, L. F. G, Harrison, P. M., Martins, E. G., Leake, A., Patterson, D. A., Zhu, D. Z., Power, M., Cooke, S. J.

While the work is my own, this research chapter is a collaborative effort among a number of researchers. I came up with the original idea, performed all of the analyses, and conducted all of the writing. Data were interpreted by LFGG, SJC, and MP. PMH, EGM, DAP, and SJC were involved with field work. AL, DAP, MP, DZZ, and SJC provided financial support. The manuscript is in the process of submission.

Chapter 3: Diel vertical migration hypotheses explain size-dependent behaviour in bull trout. Gutowsky, L. F. G., Harrison, P. M., Martins, E. G., Leake, A., Patterson, D. A., Power, M., Cooke S. J.

This study is my own yet there are a number of coauthors whose contributions were invaluable to its completion. PMH, MP, and I generated the original idea to examine diel vertical migration (DVM) in the context of DVM hypotheses. I performed all of the analyses and conducted all of the writing. EGM provided feedback on the statistics. PMH, EGM, DAP, and SJC were involved with the field work. AL, DAP, MP, and SJC provided financial support. All co-authors provided feedback on the manuscript which has been published with the following citation:

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Chapter 4: Sex and body size influence the spatial ecology of bull trout. Gutowsky, L. F. G, Harrison, P. M., Martins, E. G., Leake, A., Patterson, D. A., Power, M., Cooke, S. J.

Although the research is my own, this study could not have been completed without the help of a number of coauthors. I generated the original idea for this paper, performed all the analyses, and wrote the manuscript. PMH, EGM, DAP, and SJC were present during the field season. AL, DAP, MP, and SJC provided financial support. All of the authors provided valuable feedback on drafts of this manuscript which is currently in its second round of revisions.

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Chapter 1: General Introduction

"...most animals and plants keep to their proper homes, and do not needlessly wander about; we see this even with migratory birds, which almost always return to the same spot".- Charles Darwin

Individual-level movement is a change in the spatial location of a whole organism in time (Nathan et al. 2008; Schick et al. 2008). Taken collectively, the movement of many individuals can illustrate generalized patterns for whole aggregations, populations, communities, and meta-communities (Turchin 1998; Giuggioli and Bartumeus 2010; Morales et al. 2010). As such, organism movement is useful to test hypotheses about animal behaviour (Downes 2001; Busch and Mehner 2012), describe ecology (Bahr and Shrimpton 2004; Pade et al. 2009), and to direct management and conservation activities (Marshell et al. 2011; Barnett et al. 2013). In a recent review, Holyoak et al. (2008) found that an average of approximately 2 600 peer-reviewed articles/year were published on organism movement between 1997 and 2006. Given a growing recognition for its importance (Holyoak et al. 2008; Schick et al. 2008), today movement ecology has its own journal (*Movement Ecology*) and international symposium series (Symposium on Animal Movement and the Environment, 2014) to feature and encourage research on individual to meta-community movement.

The movement process can be broken into three basic states (internal, motion capacity, navigation capacity) and external factors represented by all abiotic and biotic elements in the environment (Nathan et al. 2008). The internal state accounts for the physiological and psychological conditions that drive an individual to move. For this state, organisms may move based on both proximate mechanisms and ultimate evolutionary factors that would likely change throughout the organism's lifetime, for example across life stages and body sizes (Haskell et al. 2002; Eckert et al. 2008). An individual's motion capacity refers to its ability to self-propel (biomechanical aspects of movement) or move with an external vector. Motion capacity asks the question "*how to move*?" and is most commonly linked with external factors or used to describe movement paths, e.g., seasonal variation in movement rate is observed but actual movement not measured (Holyoak et al. 2008). An individual's navigation capacity is the concept of *where and when* to move, and accounts for the ability to orient in space and/or time. Abiotic and biotic variables, which are stimulants that may influence whether an organism moves, interact with all other components and result in the movement path (changes in position over an individual's lifetime, Nathan et al. 2008). Importantly, these components are interrelated (Figure 1.1).

Most movement research contains objectives and hypotheses that address specific components of the movement ecology framework (Holyoak et al. 2008; Nathan et al. 2008). By focusing on one or more components (e.g., the internal state and external factors) and tracking multiple study subjects, movement can be used both to test specific hypotheses and generalize movement (Morales et al. 2010). For example, external temperature is critically important for controlling all internal physiological processes in ectotherms (Bardach and Bjorklund 1957; Brett 1971; Angilletta et al. 2002). Thus, movement is considered a function of both changing internal and external temperatures. Hertz (1992) observed two sympatric lizard species (*Anolis spp.*) to test hypotheses about thermal resource partitioning which also allowed the author to make general comments about Anole movement ecology (e.g., shade-seeking behaviour). Ectotherms have also been shown to make behavioural modifications (i.e., movement) according to body size, light level, and the presence of predators and competitors (Pitt 1999; Hansson and Hylander 2009; Mehner 2012). In addition to finding evidence of size-structured zooplankton distribution, Hansson and Hylander (2009) clarified the mechanisms, including sensory (navigation capacity), driving diel vertical migration (DVM) in daphnids. These studies illustrate the interplay among multiple components in the movement ecology framework and show how movement can be used to address objectives, test hypotheses, and provide a general description of organism ecology.

For free-ranging animals, biotelemetry remains one of the best methods for assessing movement (Cooke et al. 2004; Rutz and Hays 2009). By remotely tagging and monitoring a number of focal individuals in their natural environments (passively or actively, Rogers and White 2007), data can be collected over long periods of time and, by using the appropriate analytical techniques, scaled-up to populations, communities, and meta-communities (Cagnacci et al. 2010; Hebblewhite and Haydon 2010). Although most studies focus on movement paths in relation to environmental factors (Holyoak et al. 2008), biotelemetry data can also be used to generate a response variable (e.g., rate of movement) and can be paired with any number of potential covariates representing the components of movement ecology. For example, telemetry data can be paired with data on body size and sex (Wearmouth and Sims 2008), or individual personalities (Chapman et al. 2011; Vardanis et al. 2011). Telemetry data can also be used to show alternative behavioural modes (e.g., time spent foraging, Brownscome et al. 2013; flying vs wading, Gutowsky et al. 2014; resident vs non-resident behaviour, Martins et al. 2014) and paired with biologically relevant spatial and temporal data (e.g., seasons, Owen-Smith et al. 2010; Harrison et al. 2013) to be used in analyses.

Recent advances in computing speed and open-source statistical software (e.g., the R statistical environment, R Development Core Team, 2012) make it relatively easy to apply appropriate statistical techniques, namely mixed-modelling, to analyse biotelemetry data (Fieberg et al. 2010; Frair et al. 2010). In the context of the movement ecology framework, mixed-modelling and biotelemetry are ideal for making generalized inferences about movement. Biotelemetry data (e.g., space, time, acceleration) from individually tagged animals can be spatially or temporally paired with any number of explanatory variables (e.g., environmental temperature, light). Individual-level random effects in mixed-models can be used to make generalized statements about a group of individuals (Zuur et al. 2009). For example, Bestley et al. (2010) found the most parsimonious model of southern bluefin tuna (*Thunnus maccoyii*) feeding success (generated from individually tagged fish) included sea surface temperature, sea surface colour anomaly, day of year, linearity index movement, and individual fish as a random effect. Indeed, recent research has taken advantage of mixed-modelling and biotelemetry to test hypotheses, illustrate complex ecological interactions, and generate novel insights into the movement process of animals that are otherwise difficult to study in the wild (e.g., Mandel et al. 2008; Harrison et al. 2013).

Bull trout

Within the genus *Salvelinus*, several species dominate the literature while others have received relatively little attention (Baxter et al. 1999; Selong et al. 2001; Dunham et al 2008; Kiser et al. 2010). Prior to 1978, government agencies in both Canada and the USA paid little attention to bull trout (*Salvelinus confluentus*, Suckley, 1859) as it was not considered a 'real' sport fish (McPhail and Baxter 1996). Over the past 30 years, many bull trout populations have been in decline as a result of barriers to migration (Rieman and McIntyre 1995; Schmetterling 2003), habitat degradation (Fraley and Shepard 1989), overfishing (Johnston et al. 2007), and poor water quality (Baxter et al. 1999; Kiser et al. 2010). Historically, bull trout were found west of the Continental Divide from northern California north through Washington State, Idaho, parts of Montana, British Columbia, and the southeastern headwaters of the Yukon system (McPhail and Baxter 1996). Today the species' range has greatly contracted, leaving populations extinct in several majour tributaries (Goetz 1989). In Canada, at least some populations appear to be recovering from historical threats while most are considered still in decline (COSEWIC 2012). Although bull trout are today recognized as important to recreational and aboriginal fisheries (Martins et al. 2014), the species remains listed as special concern or threatened in the USA and Canada (USFWS 1999; COSEWIC 2012).

Bull trout are a temperature-sensitive glacial relict charr that can exist in populations with one of several life history strategies including resident, fluvial, adfluvial, and anadromous (McPhail and Lindsey 1986; Dunham et al. 2008). Although typically associated with lotic environments, bull trout are increasingly found in reservoirs where rivers have been dammed to generate hydroelectricity (Mote et al. 2003). In reservoirs during autumn (AKA fall), mature adfluvial bull trout migrate from the lake environment to cold-water streams to spawn (Fraley and Shepard 1989). Rather than remain in stream habitat after spawning, adults return to the lake environment to forage for prey (Gutowsky et al. 2011). Bull trout can sprint up to 2.3 m/s (Sfakiotakis et al. 1999; Mesa et al. 2008) which allows them to capture energy-rich prey fishes including kokanee salmon (*Oncorhynchus nerka*) and smaller bull trout (Steinhart and Wurtsbaugh 1999; Beauchamp and Van Tassel 2001). The foraging strategy of bull trout in human-made lakes results in a wide range of sizes and some of the largest attained body sizes for the species (up to 100 cm total length, Goetz 1989; Pollard and Down 2001; Figure 1.2 a).

I propose three areas of research in which to test hypotheses and improve on the current understanding of bull trout movement ecology. These areas of research are: 1) thermal resource selection and temperature use; 2) diel vertical migration and; 3) home range size and horizontal movement. 1) As apparently one of the most thermally-sensitive salmonids (Selong et al. 2001; Dunham et al. 2003; Rieman et al. 2007; Jones et al. 2013), adfluvial bull trout should be a good candidate for examining the relationship between internal temperature and a changing thermal environment, e.g., across seasons or as a thermocline shifts with the progression of summer into autumn. As temperature is an exploitable resource for fish (Magnuson et al. 1979), temperature selection could be examined as a function of its environmental availability (Arthur et al. 1996; Manly et al. 2002), which has not been well studied over short time series and in free-ranging fish. Current information on free-swimming adfluvial bull trout temperature experience is largely inconclusive due to low sample sizes (Howell et al. 2010). 2) Predation on vertically migrating prey (i.e., kokanee, Levy 1990, 1991; Bevelhimer and Adams 1993) and conspecifics (Wilhelm et al. 1999; Beauchamp and Van Tassell 2001) suggests that bull trout might exhibit diel vertical migration as a means to locate prey and avoid predation. Given the wide size range of individual bull trout found in reservoirs and the species' reputation for cannibalism, one could hypothesize size-related differences in diel vertical migration (Busch and Mehner 2012). Size-related differences in diel vertical migration have yet to be shown in piscivorous fish. In addition, it is not known whether bull trout perform diel vertical migration, and seasonal swimming depth may provide an explanation for seasonally-dependent entrainment risk (Martins et al. 2013; Martins et al. 2014). 3) Bull trout are sexually size-dimorphic (Nitychoruk et al. 2013) and given enough data from a wide range of body sizes, one could test hypotheses about the effects of yearly, seasonal, body size and sex-related differences in horizontal movement. Additionally, the relationships between phenotypic traits and movement have been investigated in riverine bull trout, e.g., home range size is not related to body size (Schoby and Keeley 2011), while to my knowledge this relationship has yet to be formally investigated in lacustrine populations.

Using adfluvial bull trout, biotelemetry, and mixed-modelling, my primary objective is to test hypotheses about thermal resource selection, diel vertical migration, and the internal factors related to horizontal movement and home range size. My secondary objective is to synthesize the results and generate information about the movement ecology of adfluvial bull trout. In my first research chapter, I focus on the relationship between the internal temperature of bull trout and external environmental temperature. I hypothesize that: i) bull trout thermal experience will be related to body size and the astronomical seasons, and; ii) during the period of weak stratification (i.e., summer to autumn), external temperature selection will occur as the availability of optimal external temperatures change. To date, I am not aware of biotelemetry-based models to predict daily thermal resource selection by fish that occur in thermally stratified systems. For my second research chapter, I explore internal and external factors that could drive diel vertical migration in adfluvial bull trout. As a cold-water piscivore that predates on vertically migrating prey and conspecifics, an interplay of factors including time of year (external factor and navigation capacity), diel period (external factors), and body size (phenotypic trait) are hypothesized to be important variables for explaining diel vertical migration in bull trout. It is currently unknown whether body size influences diel vertical migration in piscivores. For my final research chapter, I consider how phenotypic traits and external factors influence the distribution of individuals, home range size, and horizontal distance moved over two full years. Sex is not always considered as an internal factor of movement ecology, despite mounting evidence of sex-dependent movement (e.g., Hanson et al. 2008; Barnett et al. 2011). Here I hypothesize that biotic factors are important determinants of seasonal home range size and movement.

Although not central to the hypotheses being tested, the work emanating from this thesis also has the potential to contribute to bull trout management and conservation, particularly in the context of hydropower entrainment risk (Martins et al. 2013).

Study location

Kinbasket Reservoir is located in the Kootenay-Rocky Mountain Region of British Columbia, Canada (52° 8′ N, 118° 28′ W; Figures 1.3 and 1.4). Here the Mica dam was completed in 1978 as the first impoundment of the Columbia River which flows to its drainage basin in the Pacific Ocean in the state of Washington, USA (Figure 1.5). At high pool during summer and fall, Kinbasket is one of the largest lakes in British Columbia, covering at least 425 km^2. Dissolved oxygen in high (> 8 mg/L) throughout the reservoir over much of the year and only drops below 0.5 mg/L in the summer below 60 m (Bray 2011). Water turbidity and conductivity in the reservoir vary as a result of the many glacial and snowmelt streams that drain into the system. On average, turbidity is low and at times the system is remarkably clear, e.g., 1% light penetration to 30 m in October (Bray 2011). The reservoir is characterized by steep, rocky shorelines, sand, rock, and mud substrates, and little vegetation. 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 2011, 2012). Generally, no clearly defined surface mixed layer exists in the system (Bray 2011). Temperatures in Kinbasket Reservoir are known to range from 2-15°C from April to May and in places can reach 25°C at the surface in August and September (Bray

2012). Although maximum depths is approximately 190 m (Harrison et al. 2013), the average depth is approximately 57 m (RL and L 2001).

Although there are concerns about entrainment at the Mica hydro dam (Martins et al. 2013), Kinbasket Reservoir is considered a productive bull trout fishery (Gutowsky et al. 2011). As bull trout can be found in a number of deep cold water hydropower reservoirs such as Kinbasket (COSEWIC 2012), this is an ideal system in which to study the movement ecology of adfluvial bull trout. Kinbasket Reservoir also contains native populations of several species of piscivore including burbot (*Lota lota*), rainbow trout (*Oncorhynchus mykiss*), and northern pike minnow (*Ptychocheilus oregonensis*). Kokanee salmon were stocked in Kinbasket Reservoir (ca. 1980) with the intention of increasing fisheries productivity (RL and L 2001). When available as forage, kokanee salmon often become the principal prey for adfluvial bull trout (*O. nerka,* Steinhart and Wurtsbaugh 1999, Sebastian and Johner 2011). Acoustic sonar and trawl-net surveys for Kinbasket Reservoir kokanee are conducted over a short period in August when kokanee are found at a 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 and Johner 2011). Diatoms (mainly *Asterionella formosa*) are the dominant primary producers, whereas cladocerans and chironomids are the most abundant zooplankton and benthic organisms, respectively (RL and L 2001; Bray 2012). Cladocerans are considered the preferred prey for kokanee in Kinbasket (Bray 2012). The reservoir is oligotrophic, having low plankton biomass and low rates of primary productivity (RL and L 2001; Bray 2012).

Figures

Figure 1.1 - The general conceptual framework for movement ecology as adapted from Nathan et al. (2008).

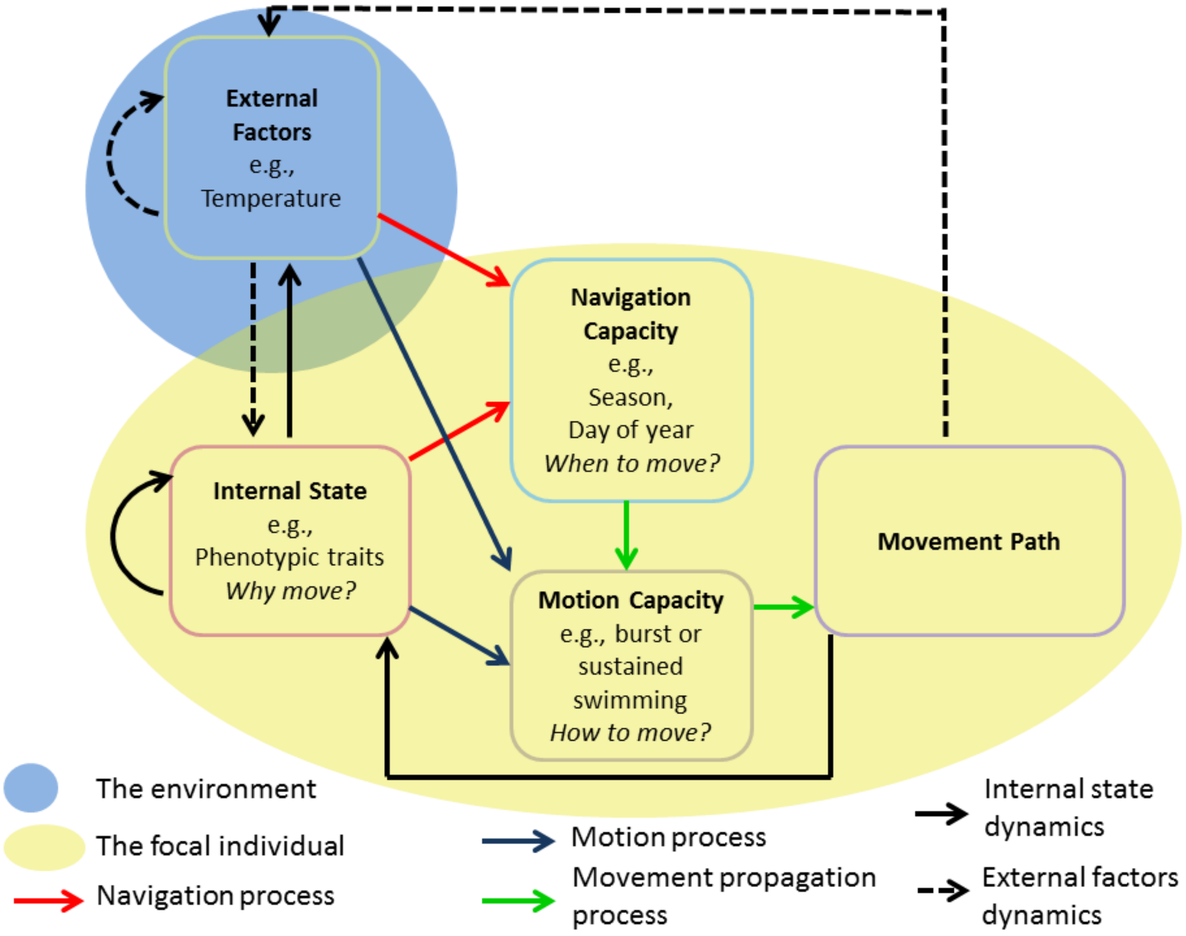


Figure 1.2 - An example of body-size extremes found in adfluvial bull trout angled from Kinbasket Reservoir, BC. The large individual (a) is 850 mm total length whereas the smaller individual (b) is 475 mm total length.
(Photo credit: Philip Harrison)

Figure 1.3 - Kinbasket Reservoir viewed in the Kootenay-Rocky-Mountain region of British Columbia. The photo is taken over pelagic habitat (approximate depth 60 m). The Mica Dam can be seen in the background (approximate distance 10 km).

Figure 1.4 - Kinbasket Reservoir with telemetry receiver and thermal logger locations. Circles represent telemetry receiver locations. Grey circles with crosshairs represent receivers that collected data for the two-year period. Black circles represent receivers that were lost in the second year of the study period. The thermal logger chain and associated receiver used in Chapter 2 are marked with a black star.

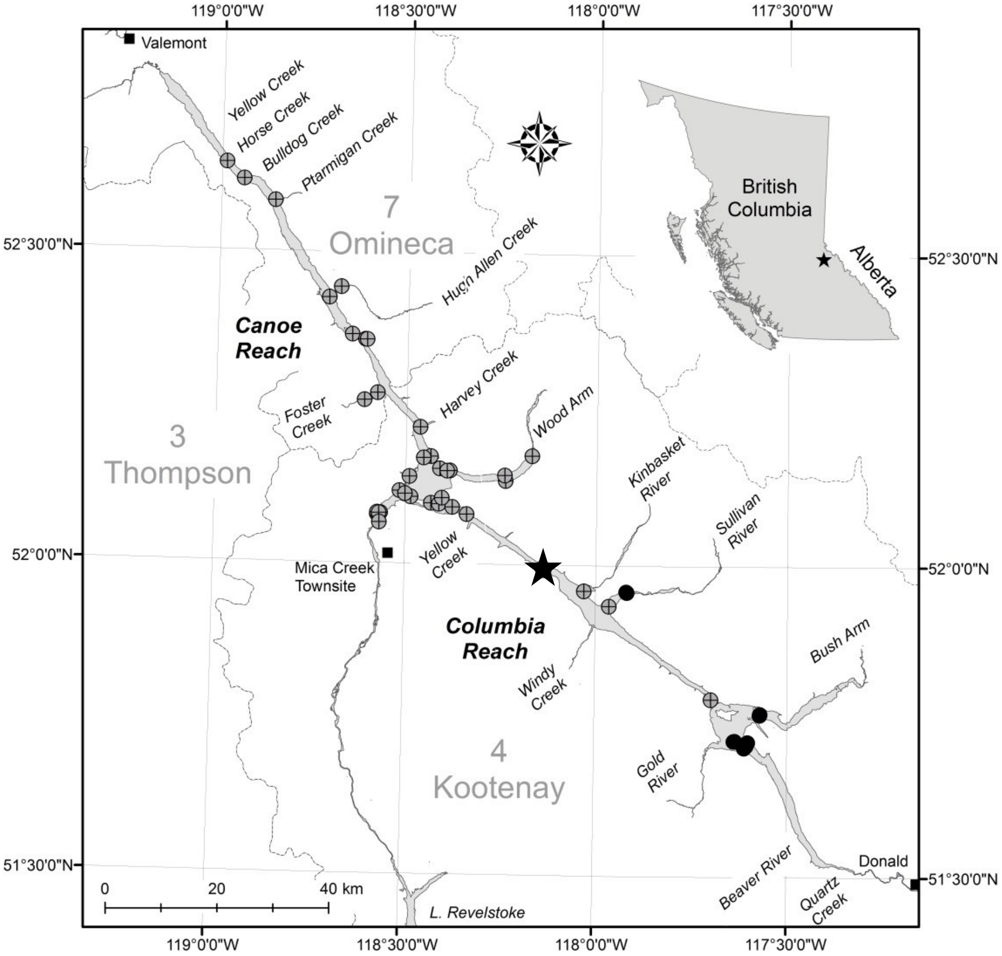


Figure 1.5 - The view from below the Mica Dam in the Kootenay-Rocky-Mountain region of British Columbia. Approximate distance to the dam is 1 km.

Chapter 2: Thermal resource selection in bull trout: temperature experience and selection change with availability

Abstract

Resource selection is widely recognized to change with its availability. While environmental temperature is accepted as an ecological resource for ectotherms, daily thermal habitat changes are seldom considered in resource selection studies. Given that ectotherms are known to change elevation (e.g., terrestrial organisms) or swimming-depth (e.g., aquatic organisms) to thermoregulate, I hypothesized that a bull trout would exhibit thermal resource selection as environmental temperature availability changes. Furthermore, by including body size as a covariate, I was able to test the prediction that larger fish would experience cooler temperatures than smaller conspecifics. To test the hypothesis and prediction, I surgically implanted temperature-sensing acoustic telemetry transmitters into 187 bull trout that swam freely for two years in Kinbasket Reservoir, British Columbia. Next, I compared environmental temperature profiles and bull trout temperature experience to generate resource selection indices from individual animals during a period when the system develops a thermal gradient (i.e., summer to fall). Using a generalized additive mixed model (GAMM) and an information theoretic approach, I found clear seasonality in bull trout temperature experience across two years. Despite a range of measured available temperatures (5-17°C), bull trout experienced remarkably narrow range of temperatures (adj. $R^2 = 93.5\%$) that were close to lab-derived optimal temperatures for growth in juveniles of this species (within 0.1°C in 2010 and within 0.8°C in 2011). Unlike the relationship between body size and temperature preference

often cited in laboratory and some field studies, I found a significant body size x day of the year interaction where large fish (800 mm TL) experienced slightly warmer temperatures than smaller conspecifics (450 mm TL, $\Delta < 1°C$). Using a GAMM to model thermal resource selection, I found selection for a narrow range of temperatures as availability for the highest temperature category (13-15°C) decreased with the progression of summer into fall. The results illustrate the importance of temperature as an ecological resource for bull trout and show how an ectotherm selects the thermal environment as it changes within and between seasons. Given the narrow window of temperatures in which bull trout thermoregulate, changing thermal regimes that result from climate change will likely have an impact on the behaviour of this and similar species. Through long-term monitoring programs, temperature and resource use in thermally sensitive species may be a useful indicator of the impacts of environmental temperature change as the climate continues to warm.

Introduction

Temperature strongly affects all aspects of ectotherm physiology and behaviour (Brett 1971; Huey and Kingsolver 1989) and in the past few decades, ecologists have recognized temperature as an ecological resource that can be accessed to maximize fitness (Magnuson et al. 1979; Huey 1991; Angilletta et al. 2002; Sims 2003). In this respect, rather than simply influencing behaviour and physiology, temperature is an exploitable resource across space and time (Roughgarden et al. 1981; Tracy and Christian 1986; Dunham et al. 1989). In competitive environments where temperatures are heterogeneous, thermal resource selection has physiological, ecological, and evolutionary consequences (Huey 1991; Hertz et al. 1992; Angilletta et al. 2002). As such, thermal experience, tolerance, and the concept of thermal habitat have been used to address a number of important issues such as how climate change may affect physiology and fitness (Pörtner and Farrell 2008; McCullough et al. 2009; Seebacher and Franklin 2012) and thus influence the distribution of organisms (McMahon and Hays 2006), or other ecological processes such as the outcome of competitive interactions under various thermal regimes (Taniguchi and Nakano 2000).

Given that environmental temperature changes (e.g., across diel periods or seasons) and temperature affect ectotherm behaviour and physiology, individuals should move to regulate their body temperatures and obtain an optimum, e.g., metabolic or behavioural (Magnuson et al. 1979; Angilleta et al. 2002). Where thermal gradients exist, for example in stratified aquatic ecosystems (Wetzel 2001), aquatic ectotherms may respond by changing their position in the water column (Cartamil et al. 2004; Sims et al. 2006). There are co-existing proximate and ultimate causes for such behaviour, including thermoregulation as an important mechanism for maximizing bioenergetics efficiency (Neverman and Wurtsbaugh 1994; Mehner 2012). For example, large pelagic salmonids tend to occupy cooler, deeper water, presumably to reach an optimum for growth while making trade-offs with a number of additional factors (Morita et al. 2010a; Jonsson and Jonsson 2011). By predictably changing position in the water column, aquatic organisms illustrate that depth offers a suite of habitat options (e.g., dissolved oxygen, prey, light intensity) including thermal resources that can be accessed to thermoregulate. Although temperature has been viewed as an ecological resource, few studies have addressed thermal resource selection as availability changes (except see Plumb and Blanchfield 2009, Goyer et al. 2014) and none have generated and analysed a resource selection index across daily changes in the thermal environment, such as those observed in stratified lakes and seas.

Resource selection occurs when organisms use a particular type of resource disproportionately in comparison to its availability (Johnson 1980). Generating inferences about resource selection can be challenging, particularly when data are taken from individuals with different numbers of observations over relatively short periods of time or at small spatial scales and as resource availability changes (Arthur et al 1996; Manly et al. 2002). The nature of such data will violate the assumption of independence, potentially producing biased parameter estimates, and increasing the chances of making type I errors (Legendre 1993; Lichstein et al. 2002; Zuur et al. 2009). Today, analytical techniques exist to minimize the bias associated with autocorrelated data (e.g., mixed-models, residual correlation structures, Markov-chain Monte Carlo simulations) without resorting to measures such as data thinning (McNay and Bunnell 1994; Frair et al. 2004; Gillies et al. 2006). These analytical techniques make it possible to draw inferences about resource selection when availability changes across fine spatial and temporal scales (Koper and Manseau 2009; Fieberg et al. 2010).

By using biotelemetry, temperature loggers and generalized mixed-models, I test hypotheses on how free-ranging adfluvial bull trout (*Salvelinus confluentus*), a thermally sensitive cold-water salmonid (Hillman and Essig 1998; Selong et al. 2001), selected their thermal environment in Kinbasket Reservoir over a two-year period beginning in 2010. I used generalized additive mixed-models (GAMM) and model selection to examine the effects of several putative covariates (sex, body size, and time of year) on the temperature experience of bull trout. I focused on a three-month period of the year when the system develops a thermal gradient and, by combining environmental temperature data and data from individual animals, generated resource selection indices to analyse using a GAMM. Specifically, I tested the hypotheses that: H_1) bull trout thermal experience will be related to body size and season resulting from size-specific temperature preference and seasonal changes in available temperature, and; H_2) during the period of weak stratification, bull trout will select a small range of thermal habitat as thermal habitat availability changes. For both hypotheses, I predict that when such temperatures are available during summer and fall, large adult bull trout thermal experience and selection will be markedly lower than the optimal temperature for growth and metabolism in juveniles (~13°C; Selong et al. 2001; Elliot and Allonby 2013).

Methods

Telemetry receiver deployment

To track bull trout, 42 omni-directional VR2W telemetry receivers (Vemco, Halifax, NS) were deployed in Kinbasket Reservoir between 1 May and 5 May, 2010 (Figure 1.4). In the current study, the detection radius for each receiver was assumed to be a conservative estimate of 500 m (Simpfendorfer et al. 2002; Shroyer and Logsdon 2009) which is the distance at which detection efficiency is greater than 50% (Kessel et al. 2013). A 500 m detection radius would therefore result in an estimated maximum total receiver listening area of 33 km^2 (7.8% of the reservoir area). Although the listening area was lower than 10% of the total reservoir surface area at high pool, receivers were placed in locations where bull trout were expected to inhabit, such as the littoral and limnetic zones of the confluence (< 500 m from shore), pinch-points (i.e., adjacent shorelines separated by < 500m), and the mouths of known spawning tributaries (Figure 1.4). By placing receivers in such locations, I expected to detect bull trout more frequently than if receivers were randomly distributed across the system (Heupel et al. 2006). In the spring of 2011, receivers were retrieved, downloaded onto a laptop using the program VUE (Vemco, Halifax, NS), and re-deployed at the original location. In the spring of 2012, receivers were once again retrieved and the data downloaded. In year one, no receivers were lost. In year two, five of the 42 receivers were lost, likely due to unusually low water levels and spring-time ice movement.

Water temperature

Because the reservoir develops a thermal gradient for a short period of the year (i.e., summer and fall) and maintains a steady surface elevation at the same time (Bray 2012), I focused the analysis of thermal habitat selection during this period which was found to occur between approximately 9 August and 24 October, 2010. During low pool in the spring of 2010, I deployed tidbit v2 thermister temperature loggers (Onset Hobo Data Loggers - UTBI-001, accuracy ± 0.2°C, Bourne, MA) at two locations where water temperatures were not affected by dam operations (Robertson et al. 2011), including in the Columbia Reach and Canoe Reach. Three thermister loggers were suspended at approximately 30 m intervals on each of the two receiver anchor ropes that were placed in pelagic habitat (> 500 m from shore, e.g., Figure 1.3) with one additional logger secured on shore where high pool water levels were projected to reach (during summer). Data were collected at 1 hour intervals and converted into daily averages from August to November, 2010. Loggers were retrieved the following spring when reservoir elevations facilitated their recovery. Several thermal loggers failed to collect data from the Canoe Reach, thus only temperature data from the Columbia Reach were used for the analysis of thermal habitat selection (Figure 1.4).

Tagging

Adfluvial bull trout were sampled from 11 April to 25 May, 2010 by trolling near the water surface (n = 122, Gutowsky et al. 2011). In summer, bull trout were captured by angling at the mouths of known spawning tributaries (18 August to 9 September, 2010) where fish congregate prior to spawning (n = 65). Upon capture, fish were placed in a 100 L cooler filled with lake water that was regularly replaced. Prior to surgery, individual bull trout were then moved into another 100 L cooler that contained anesthetic (40 mg/L; 1 part clove oil emulsified in 9 parts ethanol). Once anesthetized (characterized by a loss of equilibrium and no response to squeezing the caudal peduncle), bull trout were inverted and placed on a surgery table where a continuous supply of fresh water was pumped through the mouth and across the gills. Total length (nearest mm) was measured prior to surgery. For telemetry tag insertion and sex determination, a 3 cm long incision was made posterior to the pelvic girdle along the midline of the fish following the methods described by Wagner et al. (2011). Sex was determined by internal gonad examination (males: small clear to white gonads; females: yellowish gonads containing small to large eggs). A coded acoustic transmitter (model V13 TP; temperature data transmissions every 2-6 minutes, accuracy ± 0.5°C) was inserted into the body cavity. Incisions were closed using three simple interrupted stitches using 3/0 PDS-II absorbable suture material (Ethicon Inc., Somerville, New Jersey). Prior to release, post-surgery fish were allowed to fully recover in a bath of fresh water for ~30 minutes.

Tag temperature does not instantaneously reach equilibrium with the external temperature (Negus and Bergstedt 2012). There is a latency time before the deep tissues of fish reach thermal equilibrium with the ambient temperature, e.g., it can take 20 minutes for internal temperature to reach within 2°C of ambient temperature when fish are exposed to a 15°C temperature change (Negus and Bergstedt 2012). Although bull trout could swim between cooler and warmer temperatures without a detectable change in core temperature, data in the current study were examined at a relatively course scale (i.e., diel period) and therefore assumed representative of the average temperature experience or selection for a given individual.

Data management and filtering

Temperature experience

Biotelemetry data from tagged bull trout were first filtered to remove false detections and incomplete tag-to-receiver transmissions. The minimum number of receiver detections per individual bull trout was set at two per receiver per 24 hour period. Because surgical procedures were expected to affect behaviour for a short time following surgery (Rogers and White 2007), analyses were only carried out on data collected 7 days after tagging. The analysis only included detections that were recorded after the final receiver was deployed in May, 2010. For the analysis of temperature experience across two years, I calculated the average temperature recorded for each fish/receiver/diel period (i.e., day/night). I arbitrarily selected a minimum of ≥ 20 detections/receiver to calculate the average temperature per diel period and individual. Filtering ensured that transmitter detections were fish rather than code collisions or environmental noise (summarized in Niezgoda et al. 2002) and decreased the total number of observations, gathered across two years, to a reasonable number for statistical analysis. Paired covariates included diel period (based on local sunset and sunrise times), size (total length in mm), and sex. Data filtering and exploration were performed using Microsoft Access and the R statistical environment (R Development Core Team 2012).

Thermal resource selection

Available thermal habitat was assessed during summer and fall by first generating a line of best fit (3rd-order polynomial, Parker et al. 1975) through the daily average temperature collected by each thermal logger on the receiver rope in the Columbia Reach (Figure 1.4). Based on the coefficients from each line of best fit, I estimated the temperature (integers at 1°C intervals) at water depth , calculated the difference in water depths for 2°C intervals, and converted these intervals into approximate percent of available thermal habitat (see Appendix). Since there were only four thermal loggers for a large volume of water, not all temperature profiles could be fitted with a 3rd-order polynomial. Nevertheless, I was able to estimate the vertical distribution of temperature for 32 days between 9 August and 24 October, 2010.

Data were categorized into temperature bins of 2°C and counted as the number of detections in a given bin per day (i) per individual (j) per habitat (k). Resource selection was first assessed by examining whether an animal was found to use (1 = used, 0 = not used) a given thermal habitat per day:

$$w_{ijk} = \frac{o_{ijk}}{l_{ijk}}$$

Where w_{ijk} is the selection index on the i^{th} day for the j^{th} individual for the k^{th} habitat, o_{ijk} is habitat use (1, 0), and l_{ij} is the proportion of available thermal habitat on the i^{th} day. Indices can theoretically range between 0 and ∞.

To generate standardized resource selection indices, I first calculated wf_{ijk} as a function of time spent at each thermal habitat such that a count of one detection was equal to approximately two minutes (given the shortest possible tag transmission interval). This allowed me to estimate the proportion of time spent in a given habitat relevant to the total amount of time spent in that habitat on the i^{th} day by the j^{th} individual for the k^{th} habitat. Based on the detection frequency (wf_{ijk}), I generated a standardized selection index for each individual per day as:

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

Where B_{ijk} is the standardized selection index on the i^{th} day for the j^{th} individual for the k^{th} habitat. Values of B_{ijk} are constrained between zero and one where 1 represent complete selection for a given temperature category on the i^{th} day and values close to 0 represent no selection.

Analyses

Temperature experience

Temperature experience of the bull trout population was modelled across two years using a generalized additive mixed-effects model (GAMM, Zuur et al. 2014). I used Akaike Information Criteria to select the most parsimonious model from a set of candidate models (Akaike 1974). The model for temperature experience contained the number of days since beginning the study (continuous variable: day of the year since January 1, 2010, abbreviate as “day”) as a smoother (Wood 2006, 2011) and fish ID as a random factor. Candidate models (n = 18) contained one or more combinations of covariates, including: sex, body size, diel period (day or night, based on sunset and sunrise data), and a number of two-way interactions (Table 2.2). Models were estimated using restricted maximum likelihood and error terms were assumed to follow a gamma distribution to ensure fitted values were strictly positive. Models were fitted to the data using the R packages “nlme” (Pinheiro et al. 2013) and “mgcv” (Wood 2006, 2011). I validated the final models by examining for patterns in the normalized residuals and by examining residual lag plots (Zuur et al. 2009). Despite the inclusion of random effects, the model validation process identified residual autocorrelation. Models were therefore further fitted with continuous autoregressive correlation structure on individual animals (Zuur et al. 2009). Including a correlation structure and random effect allowed me to model compound correlation between observations from the same animal and the temporal correlation between all observations from the same animal and the irregularly spaced number of days between observations since beginning the study (Zuur et al. 2009). Further model validation showed no significant residual autocorrelation. Finally, plotting the Pearson residuals at each receiver coordinate indicated a random distribution and therefore no clear evidence for spatial autocorrelation (Zuur et al. 2009).

Thermal resource selection

I based the model of thermal resource selection on several recommendations from the literature: 1) time must be included as the dimensional unit with which to quantify the thermal environment as a resource (Roughgarden et al. 1981; Tracy and Christian 1986; Dunham et al. 1989); 2) thermal availability is allowed to change with time (Arthur et al. 1996) and; 3) when individual is the level of replication, individual must be included as a random factor (Gillies et al. 2006). Similar to the analysis of thermal experience, thermal resource selection was modelled using a GAMM with animal ID as a random factor. Given that initial data exploration indicated an abundance of zeros (87%, indicating no use of a given thermal resource) for an analysis that included both selected and non-selected thermal resource, I instead only analysed selection for thermal resources that were experienced by bull trout. Although selection should be based on the range of thermal habitats that were available (Tracy and Christian 1986; Bakken 1989: from Hertz 1992), models would not converge with such zero-inflation. Only unstandardized selection indices (w_{ijk}) were examined across all available thermal habitats. Since there was a small number of data available (n = 32), I only ran a simple model that included a smoother for day of the year (by each thermal resource) and thermal habitat as a categorical predictor. No model selection was performed. The intercept was allowed to randomly vary for each individual fish. The response variable used was w_{ijk}. Although w_{ijk} can theoretically vary between 0 and ∞, values of w_{ijk} during the current study varied between 1.81 and 16.91. Due to serial autocorrelation, I included a CAR1 correlation structure to model the dependency between residuals at different time points (Zuur et al.

2009). The model was estimated using restricted maximum likelihood and the error term was assumed to follow a Gaussian distribution. The model of habitat selection was assessed using the techniques described by Zuur et al. (2009). No serial autocorrelation was observed after incorporating the correlation structure.

Results

After filtering the raw data, 17 422 temperature observations were available to analyse the average temperature experience from 151 individuals (81% of tagged bull trout). Males outnumbered females approximately 2:1 and the average size of males and females was similar at 612 mm TL ± 91 SD and 622 mm TL ± 66 SD. Males contributed only slightly more data (~55%) than females (~45%). For the analysis of thermal resource selection, there was a high degree of variation within temperature categories and availability of the upper most categories decreased with time (Figure 2.1). From 9 August to 24 October 2010, bull trout experienced temperatures between 9°C and 15°C. However, only one individual was detected in the temperature category of 9-11°C (once in September) and was therefore removed from the analysis. The model of thermal habitat selection therefore contained only two temperature categories (11-13°C and 13-15°C) for which to examine how bull trout selected their thermal environment over time.

Temperature experience

Based on AIC, the top model contained the smoothing function for day, total length, and total length x day (M13, Tables 2.1 and 2.2). These factors were capable of explaining 93.5% of the variation in bull trout thermal experience. The interaction between total length and day resulted from larger individuals experiencing the warmest temperatures during periods when water temperature was also warmest, i.e., across summers. During the summer in both years, bull trout experienced an average temperature >12°C for 1.5 months. Thermal experience for these animals followed a distinct and sinusoidal pattern that repeated across years (Figure 2.2) with the interaction between body size and day occurring between the summer periods of each study year (Figure 2.3). Specifically, there were no body size-related differences in temperature experience in the summer of 2010 whereas marginal differences were apparent during the summer of 2011 (Figure 2.3). For example on 28 September 2011, an 800 mm TL bull trout was predicted to experience an average temperature of 10.4°C [9.8, 11.0, 95% confidence interval] whereas a 450 mm TL fish would have experienced on average a temperature of 9.8°C [9.3, 10.2, 95% confidence interval, Figure 2.3]. The predicted yearly range of temperatures experienced by average sized bull trout (mean = 617 mm TL) in 2010 and 2011 spanned 12.2°C and 11.5°C, respectively. On 1 August 2010 and 9 July 2011, average sized bull trout reached a maximum (predicted) temperature of 13.1°C ± 0.16 SE and 12.4°C ± 0.18 SE, respectively. Thermal experiences for both summer periods were characterized by a peak, a gradual decline, and a sharp drop (5 October 2010 and 15 October 2011) that reached its low points during January and February of 2011 and 2012, respectively (Figures 2.2 and 2.3). Bull trout experienced minimum temperatures between 1°C and 2°C from January to April in 2010 and slightly warmer minimum temperatures from January to April in 2011.

Thermal resource selection

In the model of thermal resource selection, smoothers for both 11-13°C and 13-15°C were highly significant (Table 1). Smoothers explained 60.5% of the variation in w_{ij} (adjusted R^2). Bull trout selected temperatures between 11°C and 13°C as availability first decreased and later increased in late September and October (Figure 2.3). Simultaneously, availability of warmer temperatures (13-15°C) decreased as bull trout continued to select for these temperatures (Figures 2.1 and 2.3). The standardized selection index (B_{ij}), which included all temperature categories recorded during the period from 9 August to 24 October 2010 ($n = 505$) and is here calculated as an average across all fish and days, indicated that temperatures between 11-13°C were selected 1.6 times and 31 times more often than temperatures between 13-15°C and 9-11°C, respectively. Despite their availability during the summer to fall period, temperature categories below 9°C and those above 15°C were never selected on any of the days where thermal resource availability data were calculated (Figures 2.3 and 2.4; Table 2.3).

Discussion

In addition to experiencing a narrow range of temperatures that were clearly related to season (H_1, Figure 2.2), adfluvial bull trout selected a small range of temperature (11 to 15°C) during the period of weak thermal stratification and when additional ambient temperatures are available in the water column. Although this species has been shown to occupy a range of temperatures (Howell et al. 2010) and I do not suggest bull trout never venture into warmer or cooler water, in Kinbasket Reservoir a large number individuals showed a remarkably narrow thermal experience across two full years (Figure 2.2). The average temperature experience was between 12°C and 13°C for 1.5 months in both years when warmer and cooler temperatures were available, perhaps indicating temperature preference in wild bull trout. Maximum temperatures were experienced during the peak of summer and minimums during a period when much of system is covered in ice (Figure 2.3). Notably, thermal experience remained within a narrow window during the period of weak stratification (when the greatest range of temperatures would be available) and outside this period when temperatures would be isothermal (Bray 2012). Indeed, confidence limit width may reflect the variability of thermal habitat whereas mean estimates and the temperature selection analysis indicates temperature preference as these animal swam freely in the system (Figure 2.3).

Theoretically, ectotherms should select temperatures that deliver physiologically optimal conditions (Tracy and Christian 1986, Wildhaber and Crowder 1990, Sims et al. 2004). Adfluvial bull trout were expected to show a relationship between body size and temperature such that larger individuals should experience, on average, colder temperatures than smaller conspecifics (Morita et al. 2010a; Jonsson and Jonsson 2011; Elliot and Allonby 2013). Laboratory experiments have rather consistently demonstrated this relationship in young fish (e.g., age 0+ - 3+; Coutant 1997; Mccauley and Huggins 1979; Morita et al. 2010b; Elliot and Allonby 2013). However, for larger (i.e., adult) specimens examined in the field, the relationship is not always as clear. Spigarelli et al. (1983) found that while the upper preferred temperature for large wild riverine brown trout was 1.5°C lower than the reported final preferendum for juveniles, body size was not a significant covariate to explain central tendency of temperature experience. In the current study, the average temperature for a large adfluvial bull trout remained below the optimal temperature for juveniles and slightly above the average temperature experienced by a conspecific of roughly half the size (Figure 2.3). Despite laboratory findings and some field-based research, according to Jonsson and Jonsson (2011), there may be no direct relationship between either the optimum temperature for growth or the temperature for maximum growth efficiency and habitat selection by wild salmonids. In nature, resource selection involves a complex suite of factors that may weight differently according to a number of variables (e.g., phenotypic traits, environmental conditions) as it does with diel vertical migration (Busch and Mehner et al. 2012). In Kinbasket Reservoir, preferred temperatures may not be limiting, as the gradual thermocline covers a wide range of temperatures across a range of depths (Bray 2011, 2012). Thus, smaller individuals can maintain their preferred temperatures while remaining at deeper depths than larger cannibalistic conspecifics (Beauchamp and Van Tessel 2001; In Chapter 3). Again, in nature the relationships between temperature preference and body size may not be as straightforward as in the laboratory (Jonsson and Jonsson 2011).

Bull trout occupied a narrow range of temperatures that changed with availability when the reservoir contained a thermal gradient (H_2, Figure 2.4). Behavioral thermoregulation, which occurs when ectothermic animals actively maintain their body temperature close to a defined target range where performance is maximized (Huey 1982; Hertz et al. 1993; Diaz and Cabezas-Diaz 2004), is an important component of resource selection in ectotherms (Cowles and Bogert 1944; Magnuson and Crowder 1979; Huey 1991; Reinert 1993). Analogous to terrestrial lizards that thermoregulate by moving across different elevations (Hertz and Huey 1981; Adolph 1990), fishes exhibit behavioural thermoregulation across depth gradients in pelagic habitat (Brett 1971; Cartamil and Lowe; Jensen et al. 2006; Sims et al. 2006). Although thermal resource availability along a vertical gradient is certainly not the only factor to consider when assessing habitat selection (Plumb and Blanchfield 2009), two biologically reasonable outcomes remain evident from the results of the current study. First, excluding the single detection between 9-11°C, bull trout occupied only a relatively narrow window of temperatures between 11 and 15°C that accounted for 41.6% of the available temperature range from August to October, 2010 (H_2, Table 2.3). Second, bull trout selected these temperatures as availability fluctuated for the coolest temperature category (11-13°C) and significantly decreased for the warmest category 13-15°C ($H_{2,}$ Figure 2.4). Given that fish can detect relatively fine-scale changes in temperature (Brett 1971) and variables such as wind, cloud cover, and rain will alter thermal resource availability on a daily basis (Wetzel 2001), aquatic ectotherms ought to respond to daily changes in available thermal resources while simultaneously accounting for additional abiotic and biotic factors. As metabolically optimal water temperatures decrease in availability with the progression of autumn, bull trout continue to select for these diminishing thermal resources (Figure 2.4).

While there may be a bioenergetic advantage to selecting a small range of temperatures within a changing volume of thermal habitat, there are also costs associated with selection, for example a trade-off with the likelihood of encountering prey (Scheuerell and Schindler 2003). Behaviour is expected to vary spatially and temporally as a result of trade-offs, e.g., thermal preference may be conditional on availability or the presence of prey, predators, and competitors (Mysterud and Ims 1998; Downes 2001, Godvik et al. 2009). For example, Downes (2001) found that garden skinks (*Lampropholis guichenoti*) basked relatively infrequently in the presence of predator scent, indicating a trade-off for safety over growth, size at maturity, and clutch mass later in life. In the current study, the small sample size for thermal resource selection did not permit the inclusion of additional variables that may identify trade-offs such as those documented in diel vertically migrating organisms (Mehner 2012). Scheuerell and Schindler (2003) provided evidence to suggest that juvenile sockeye minimized the ratio of predation risk to foraging gain while performing diel vertical migration. In Kinbasket Reservoir, optimal temperatures and adequate dissolved oxygen concentrations (>8 mg/L) is apparently not limiting across depths (Bray 2011, 2012; Chapter 3). Bull trout diel vertical migration was hypothesized to result from trade-offs among feeding opportunities, bioenergetics, and predator avoidance (Mehner 2012; Chapter 3), however DVM appears to occur more of a result of diel period rather than temperature, i.e., DVM occurs across a range of temperatures that change little during any given 24 hour period. Given that temperature experience but not depth distribution is the same for large and small bull trout, it follows that smaller individuals are occupying deeper darker water as refuge from conspecific predators that are known for cannibalism under high population densities (Wilhelm et al. 1999; Beauchamp and Van Tassell 2001; Chapter 3). Although their density has not been measured, bull trout are considered abundant in Kinbasket Reservoir (Gutowsky et al. 2011). While the current study presents evidence of thermal resource selection across a thermal gradient, further research should determine how trade-offs influence this apparent selection, e.g., the inclusion of additional covariates such as diel period and body size (Mysterud and Ims 1998; Godvik et al. 2009).

Temperature is commonly used by governments to define habitat suitability for both freshwater and marine fish species (Rosenfeld and Hatfield 2006; Bear et al. 2007; Cheung et al. 2010). As global temperatures continue to rise, shifting thermal regimes and climate patterns are affecting fish behaviour, physiology, and life history (Walther et al. 2002; Munday et al. 2008; Robinson et al. 2009). While it is important to model potential changes in thermal resource availability, the long-term physiological and behavioural impacts of increased temperature requires further investigation in free-ranging fish (Plumb and Blanchfield 2009; Elliot and Elliot 2010; Coutant 2012), particularly given the apparent sensitivity and selectivity of threatened species such as bull trout. Although climate and habitat simulation models are useful tools to project habitat suitability (e.g., Jones et al. 2013), there is real value in acquiring temperature data from wild animals (Cooke et al. 2004). In the current study, adfluvial bull trout exhibited a narrow thermal experience across two years and showed selection for temperatures between approximately 13-15°C during a period when the system contained a thermal gradient (Figure 2.3). Combined with temperature experience data, similar but longer-term investigations could illustrate how bull trout and other thermally sensitive species modify their behavioural in response to their environment, including climate-driven changes in the available thermal regime. It may be unclear exactly how a warming climate will affect the amount of available thermal habitat for cold-water fish (In Plumb and Banchfield 2009); however, climate change will almost certainly influence behavioural thermoregulation (Casselman 2002; Coutant 2012, Wenger et al. 2013). Given that temperature is a resource for pelagic fish and habitat characterization is critical to the successful management of species at risk (Rosenfeld and Hatfeld 2006), free-ranging thermally sensitive fish would be exceptional tools to both identify critical thermal habitat and show how it changes as the climate warms.

Two years of telemetry data illustrated a narrow temperature experience and thermal resource selection in a cold-water stenotherm. Contrary to my hypothesis, there was no appreciable effect of body size on temperature experience in adfluvial bull trout. These results require further investigation, for instance at finer temporal scales and in relation to additional abiotic and biotic covariates (e.g., the presence of predators and prey). While numerous studies have identified the importance of temperature on fish behaviour and metabolism, resource selection has only rarely been examined in fishes across different thermal regimes (Plumb and Blanchfield 2009; Pierce et al. 2013; Goyer et al. 2014). Although not all fishes will be equally affected by climate warming (Somero 2010), many will experience behavioral modifications and physiological impairments resulting from changes to environmental variables such as oxygen and temperature (Pörtner and Knust 2007; Coutant 2012). Thermal experience and thermal resource selection are particularly useful tools for identifying how thermally sensitive and already threatened species might react to climate change. Based on these findings, longer-term field-based data collection on thermal resource selection in thermally sensitive species is a suitable method for projecting the impacts of climate change on cold-water fishes.

Tables

Table 2.1- Model output for the generalized additive mixed models of temperature experience (1) and thermal habitat selection (2). Test statistics are given from the *F*-distribution for the GAMM component and *t*-distribution for the linear-mixed effects components of the model. Random intercept variance in model 1 was 0.21 for fish ID. Random intercept variance for model 2 was 0.35 for fish ID. Values of autocorrelation at lag 1 (φ) for models 1 and 2 were 0.914 and 0.13, respectively.

Model #	**response**	**parameter**	**DF**	**test statistic**	**P-value**
1.	Temperature (°C)	s(Day)	9.0	$F = 10938$	< 0.0001
		TL	149	$t = -0.676$	0.500
		TL:Day	17269	$t = 2.38$	0.017
2.	w_{ij}	s(Day of year): 11-13°C	3.24	$F = 14.71$	< 0.0001
		s(Day of year): 13-15°C	1.00	$F = 16.50$	< 0.001
		Temperature Category	1.00	$t = 5.53$	< 0.0001

Table 2.2- The set of candidate models used to test temperature experience by bull trout across two years (2010-2012). The number of parameters is given by K.

Model Name	Model	K	AIC
M13	$y = s(DAY) + TL + TL{:}DAY$	8	16906.6
M16	$y = s(DAY) + TL + SEX + TL{:}Day$	9	16909.1
M14	$y = s(DAY) + SEX + TL{:}Day$	8	16912.1
M11	$y = s(DAY) + TL$	7	16914.9
M17	$y = s(DAY)$	6	16916.5
M7	$y = s(DAY) + SEX + TL$	8	16917.1
M10	$y = s(DAY) + SEX$	7	16919.2
M0	$y = s(DAY) + SEX + TL + DIEL + TL{:}DAY + DAY{:}SEX + TL{:}DIEL$	12	16921.2
M2	$y = s(DAY) + SEX + TL + DIEL + TL{:}DAY + TL{:}DIEL$	11	16924.1
M1	$y = s(DAY) + SEX + TL + DIEL + TL{:}DAY + DAY{:}SEX$	11	16924.8
M4	$y = s(DAY) + SEX + TL + DIEL + TL{:}DAY$	10	16927.7
M15	$y = s(DAY) + DIEL + TL{:}DAY$	8	16928.1
M5	$y = s(DAY) + SEX + TL + DIEL + TL{:}DIEL$	10	16932.7
M9	$y = s(DAY) + TL + DIEL$	8	16933.6
M12	$y = s(DAY) + DIEL$	7	16935.3
M8	$y = s(DAY) + SEX + DIEL$	8	16938.1
M3	$y = s(DAY) + SEX + TL + DIEL + DAY{:}SEX + TL{:}DIEL$	NA	failed to converge
M6	$y = s(DAY) + SEX + TL + DIEL + DAY{:}SEX$	NA	failed to converge

Table 2.3- Standardized selection index (B_{ij}) and average available thermal habitat (%) in each temperature category. B_{ij} was calculated for individual fish (*j*) per day (*i*) and taken simply as the mean during the study period from 9 August – 24 October, 2010.

Temperature Category (°C)	Mean B_{ij}	SD B_{ij}	- 95% CI	+ 95% CI	n	Zeros (n)	% Avail	SD
5-7	0	0	NA	NA	121	121	30.73	5.37
7-9	0	0	NA	NA	121	121	12.76	7.73
9-11	0.008	0.088	NA	NA	121	120	12.78	7.12
11-13	0.5014	0.4564	0.415	0.588	107	38	25.95	14.15
13-15	0.3162	0.4104	0.169	0.463	30	14	15.65	15.02
15-17	0	0	NA	NA	5	5	2.13	5.46

Figures

Figure 2.1 - Temperature availability (%) for each thermal category (e.g., 5-7°C) between 9 August and 24, October, 2010. Lines of best fit (± 95% confidence limits) are shown to illustrate trends in availability.

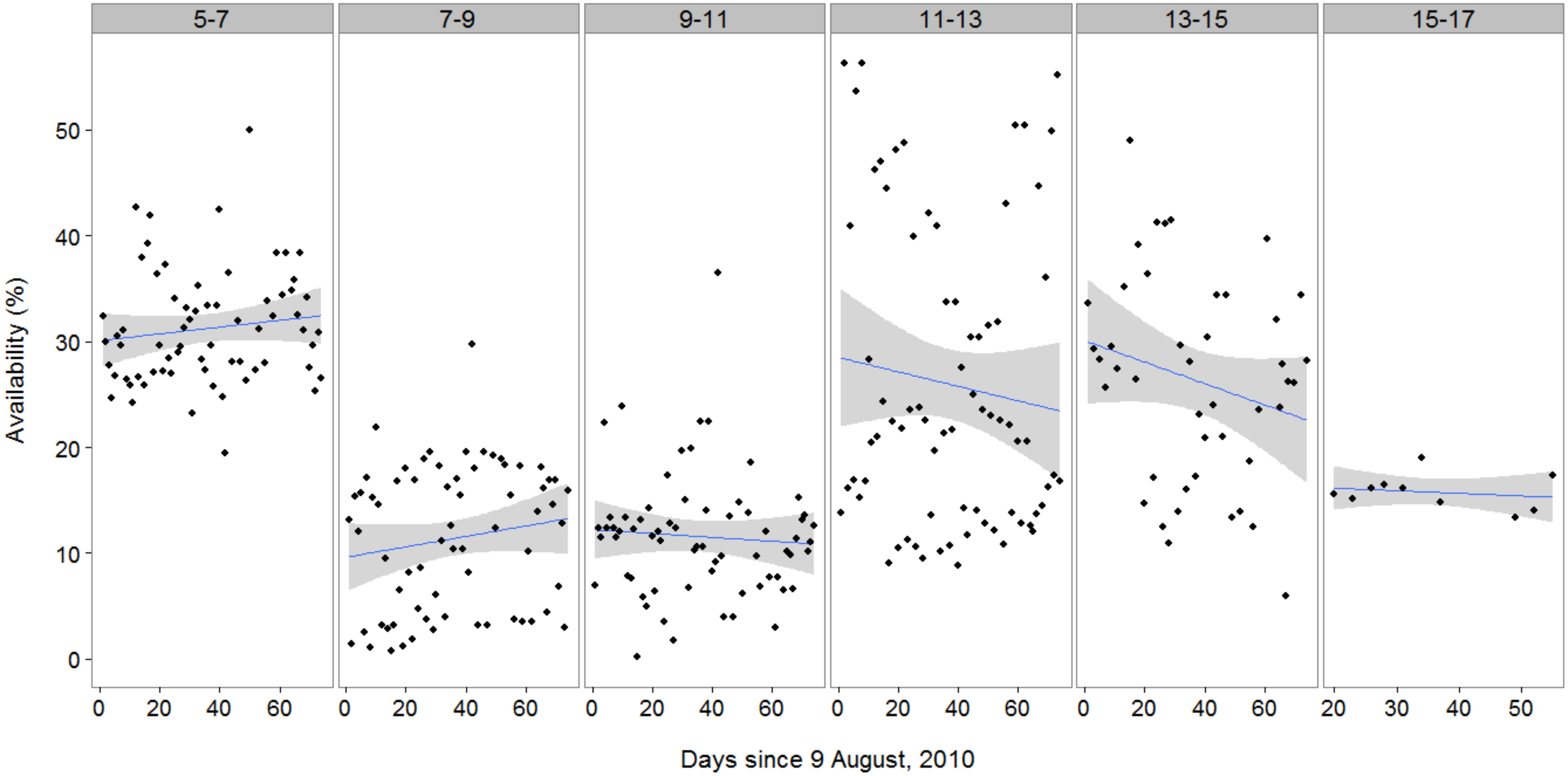


Figure 2.2 - The smoother and 95% point-wise confidence limits from the top model to predict daily bull trout thermal experience across years (2010-2012). The smoother is highly significant ($F = 13388$, $P < 0.0001$) and illustrates seasonal changes across both years. Degrees of freedom are taken from the model hat matrix and given parenthetically in the *y*-axis.

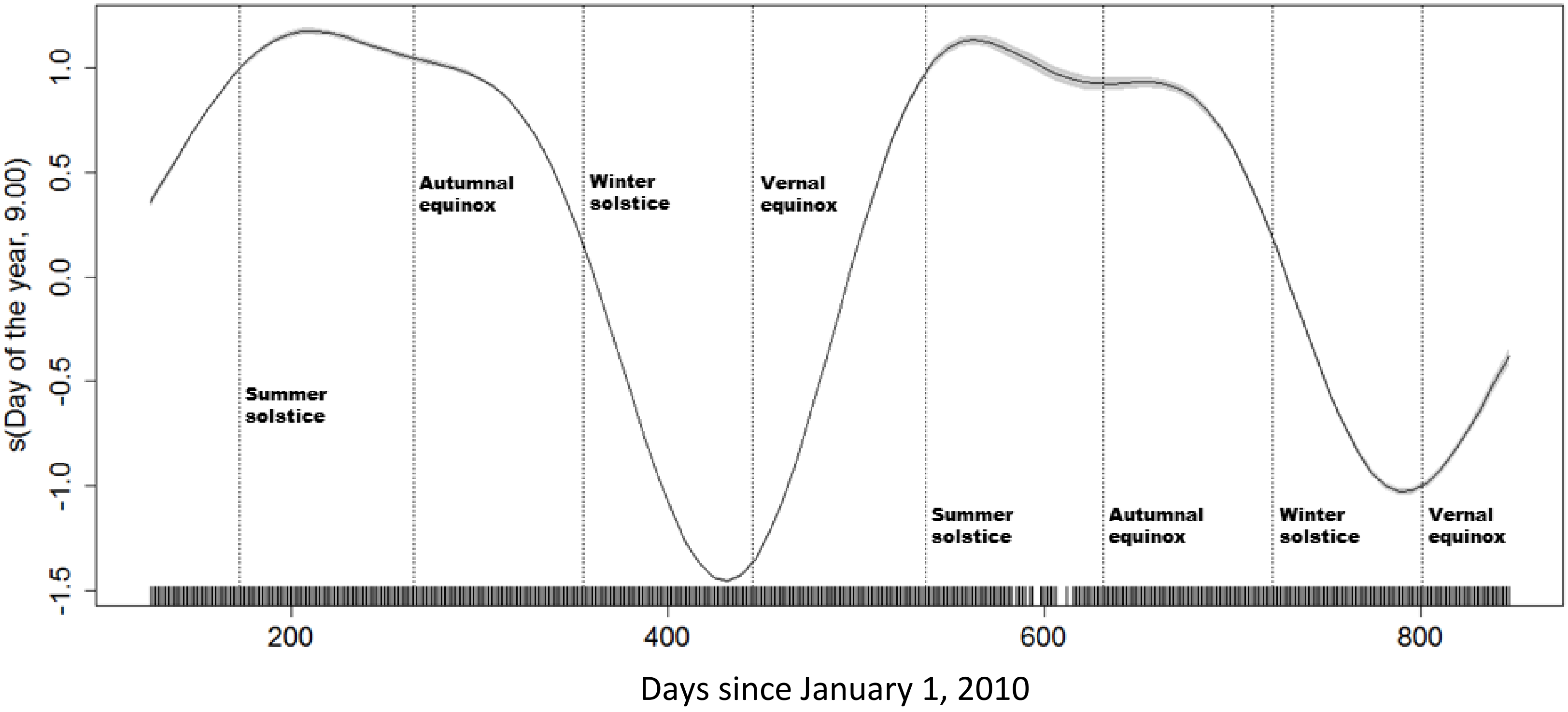


Figure 2.3 - The predicted values (± 95% confidence limits) for bull trout temperature experience in Kinbasket Reservoir from 21 June 2010 to 10 March 2012. The x-axis is days since January 1, 2010. The temperature experience large fish (800 mm TL) are shown as a solid line demarcated by circles whereas small fish (400 mm TL) are shown with a dashed line demarcated by squares. The approximate timing of astronomical seasons is illustrated with vertical dashed lines.

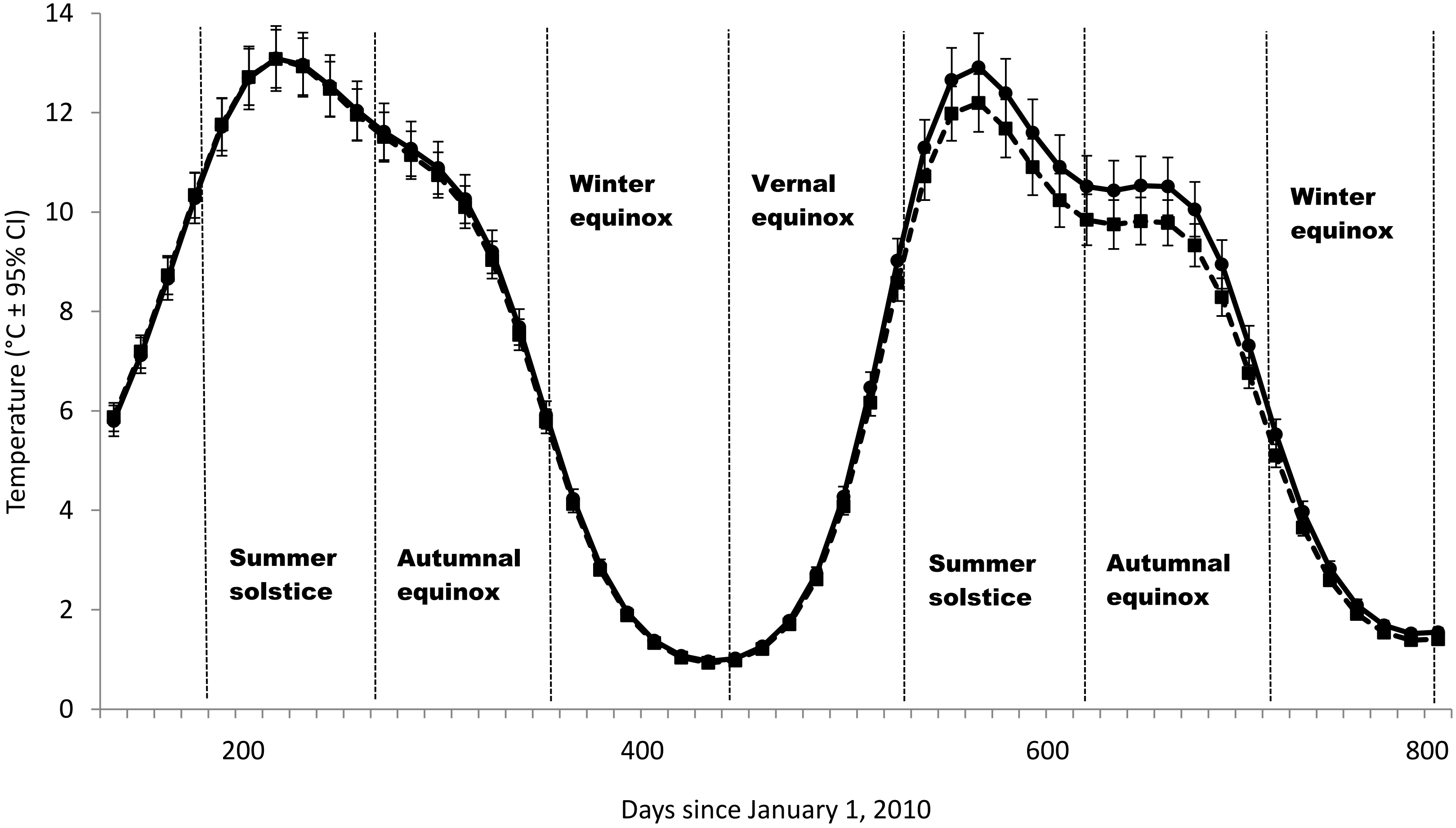
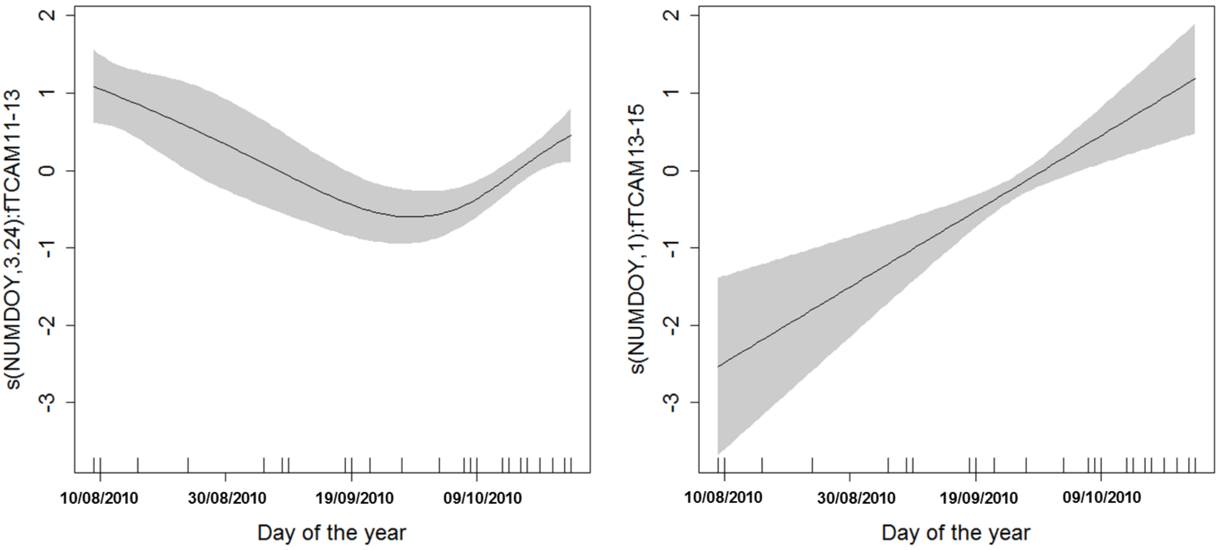


Figure 2.4 - Smoothers and 95% point-wise confidence limits from the model to predict bull trout thermal habitat selection, illustrating the change in thermal habitat availability from 9 August to 24 October, 2010. Over time, thermal habitat availability decreases to a point before increasing for temperatures between 11-13°C (*F* = 14.71, *P* < 0.0001). For temperatures between 13-15°C, availability is predicted to increases over time (*F* = 16.50, *P* < 0.001). Degrees of freedom are taken from the model hat matrix and given parenthetically in the *y*-axis.



Chapter 3: Diel vertical migration hypotheses explain size-dependent behaviour in bull trout

Abstract

In aquatic organisms, 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, I hypothesized that bull trout, a cold-water pelagic-cruising piscivore, will exhibit size-dependent, daily, and seasonal patterns in DVM that are consistent with light levels (proximate trigger) and the feeding opportunities, predator avoidance, and bioenergetics hypotheses. To test these hypotheses, depth-sensing acoustic transmitters were implanted into 187 bull trout (358 - 881 mm total length) that were free-swimming for one year in Kinbasket Reservoir. I found that bull trout were shallowest at night, deepest during the day, and exhibited 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 average depths (~ 15 m) than larger fish (~7 m) regardless of diel period. The results of

this study indicate light as 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.

Introduction

In fishes, DVM is a behaviour that is typically characterized as ascent at dusk and descent at dawn (Neilson and Perry 1990). Linked to a number of processes including thermoregulation (Brill et al. 1999; Cartamil and Lowe 2004; Sims et al. 2006), habitat selection (Pade et al. 2009; Plumb and Blanchfield 2009), and foraging (Sims et al. 2005; Fox and 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 and Adams 2003; Gjelland et al. 2009; Quinn et al. 2012). Although piscivores have been hypothesized to exhibit 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 behavior) thought to be responsible for DVM remains scant and there are 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, 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 behavior 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 be either deeper (Levy 1991) or ascend earlier and descend later (Busch and Mehner 2012) compared with large-sized conspecifics.

In this study I test DVM hypotheses across a wide size range (358 to 881 mm TL) of adfluvial bull trout (*Salvelinus confluentus*) in Kinbasket Reservoir (Figure 1.4). 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 (Levy 1991, Bevelhimer and Adams 1993); 3) exhibit intra- and interspecific competitive behaviour (Beauchamp and Van Tassell 2001; Stewart et al. 2007); and iv) are similar to other cold-water pelagic-cruising predators [e.g., coaster brook charr (*Salvelinus fontinalis*), lake charr (*Salvelinus namaycush*)]. Although not studied in Kinbasket Reservoir, it is well established that kokanee salmon may perform DVM in part to prey on cladocerans that also perform DVM (Bevelhimer and Adams 1993; Ringelberg 1999). Biotelemetry data were used to test hypotheses about DVM in bull trout over an entire year. I 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 et al. 1990), I predicted that individuals 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), 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 and Van Tassell 2001).

Methods

The study location is described in Chapter 1 (Figure 1.4). In addition, VR2W deployment, retrieval, and fish tagging followed similar procedures to those outlined in Chapter 2. Testing my hypotheses for size-dependent DVM across seasons required only a single year of data, thus only data from 2010 – 2011 were analyzed.

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. As described in Chapter 2, detections that occurred within one week following tagging of a particular fish were excluded from the analysis.

Seasons were delineated as: winter (January to March), spring (April to June), summer (July to September), and autumn (October to December). The autumn represented the reproductive period between the first observation of bull trout traversing spawning tributary rapids (personal observation) to the end of the post-spawning period and beginning of the coldest few months of the year (i.e., winter). Since it was impossible to use traditional tools to measure diel patterns of light intensity (e.g., Secchi disk, Wetzel 2001), diel period was divided into day (> local sunrise and < local sunset) and night (> sunset and < sunrise) for a given 24 hour period.

Patterns in DVM were assessed by examining the average depth and absolute maximum change in depth (herein after 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 9 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 reach model convergence in the R statistical environment. 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 between 9 and 19 detections were used to calculate depth and vertical movement for each filtered data point. Based on the time, date, and body size measurement of each detection event, data were categorized into seasons, diel periods, and hour of the day (for examining plots of the observed data). Vertical movement was calculated as the detected absolute maximum change in depth during a detection event and rounded to the nearest integer. Since only larger changes in depth were considered biologically relevant, vertical movement was also assigned a “1” if movement was detected (Δ depth ≥ 0.5 m) and “0” if movement was minimal or not detected (Δ depth < 0.5 m). To first check for continuous hourly patterns of vertical movement, plots of depth and vertical movement from the filtered data were examined and fitted with smoothing functions of the class cyclic penalized cubic regression spline (Wood 2000; Wood 2006). Outliers from the filtered database were identified by examining Cleveland dot plots and model residual plots (Zuur et al. 2009). 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 detections of > 60 m deep (n = 120, < 0.01%) were removed 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 and Bates 2000), diel period and season as fixed factors, and total length as a continuous covariate. The model of depth distribution was used to answer the question: which of the putative factors are correlated with bull trout depth distribution? Vertical activity was modeled to address two questions: (i) which of the putative factors are associated with the likelihood that bull trout change depth, and (ii) when bull trout change depth, which of the putative factors are correlated with the magnitude of the depth change? To answer question (i), a binary response variable (vertical movement = 1, no vertical movement = 0) was modeled as a function of predictor variables (season, diel period, and body size), with individual fish as a random factor. To answer question (ii), the magnitude of vertical activity was estimated 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 Information Criteria (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). Two-way interactions were considered as potentially biologically relevant, however three-way interactions were not considered because they are often difficult to interpret, add unnecessary complexity to models, and add little value to understanding the underlying ecological relationships (Bolker et al. 2009; Zuur 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 moving-average correlation structure to all models (corARMA, Pinheiro and Bates 2000). Q-Q plots and residual plots were used to evaluate normality, heterocedasticity of residuals, and overdispersion (models with Poisson response only). 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. An autocorrelation function (ACF) was used to determine whether the moving-average correlation structure reduced autocorrelation (Pinheiro et al. 2013). In all models the ACF plots showed the correlation structures to reduce autocorrelation. Models were graphically validated following Pinheiro and Bates (2000) and Zuur et al. (2009). Analyses and plots were done in R (version 2.15.3, R Development Core Team 2012) using the packages MASS (Venables and Ripley 2002), nlme (Pinheiro et al. 2013), and ggplot2 (Wickham 2009). Although highly significant P-values were used to determine which model terms were retained, large degrees of freedom warranted that effect sizes and a lack of confidence limit overlap be used to indicate significant differences among groups.

Results

Filtering from the raw dataset (n = 1 309 115 detections) resulted in 27 372 depth observations that were acquired from 171 fish (91% of tagged bull trout). Bull trout size ranged from 358-881 mm TL and was well represented across diel periods and seasons

(Table 3.1). The observed data showed typical DVM patterns where bull trout descended at dawn and ascended at dusk (Figure 3.1). This pattern was least pronounced in the winter and spring and most pronounced in the summer and autumn (Figure 3.1). Vertical activity appeared to increase at sunrise and decrease at sunset and was also observed to vary across seasons (Figure 3.2).

To explain bull trout depth, the model containing all factors and two-way interactions contained the greatest number of highly significant terms (Table 3.2, Figure 3.3). Bull trout were shallower during the night than in the day and depending on season, small bull trout were estimated to be deeper than large bull trout (Figure 3.3). 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 (Figure 3.3). During the winter, summer, and autumn, larger bull trout tended to be shallower 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 a bull trout that was twice as long and detected during the same period was estimated to be almost twice as shallow at 7.8 m [6.4, 9.4, 95% confidence interval]. Overall, a typical bull trout (average TL= 590 mm TL) was deepest during a summer day and shallowest during a winter or spring night (Figure 3.3).

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 (Table 3.2). The model indicated that bull trout were more likely to move vertically during the day in any given season (Figure 3.4). 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 (Table 3.2). For example, the probability that an average size bull trout would change depth during a spring night was 0.492 [0.478, 0.506, 95% confidence interval] whereas the probability of an average bull trout changing depth during a summer day was 0.860 [0.840, 0.880, 95% confidence interval]. A 700 mm bull trout detected during 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: $0.839 \geq 0.804 \geq 0.770$; Figure 3.4).

When bull trout changed depth during a detection period, the model containing all factors and two-way interactions contained the most significant terms (Table 3.2). When bull trout were detected to change depth, highly significant two-way interactions between predictor variables explained the magnitude of the depth change (Figure 3.5). Changes in depth were most pronounced during the day in all seasons and were greater in the day for all but the smallest sized individuals during the summer. The magnitude of depth change was greatest during a spring day (Figure 3.5). 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 for an 800 mm bull trout were twice as great as the depth changes made by 400 mm bull trout (6.56 ≥ 5.25 ≥ 4.20, 95% CI; 800 mm: 12.10 ≥ 9.79 ≥ 7.91, 95% CI; Figure 3.5). In contrast to a spring day, large fish made less drastic depth changes than smaller conspecifics in the night during the autumn (e.g. 400 mm: 5.67 ≥ 4.56 ≥ 3.68, 95% CI; 800 mm: 2.90 ≥ 2.30 ≥ 1.83, 95% CI; Figure 3.5).

Discussion

Depth distribution and vertical movement of piscivorous adfluvial bull trout in Kinbasket Reservoir were related to diel, seasonal, and size related factors which is consistent with the original predictions, i.e., individuals were shallowest at night and deepest during summer. In addition, DVM continued to occur during winter. According to the 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 adfluvial bull trout depth and vertical movement may mask the more extreme behaviours of some individuals (e.g., Mehner and Kasprzak 2011; Busch and Mehner 2012), there was an overall shift in depth and vertical movement in relation to light (Figures 3.1 and 3.2). Bull trout behaviour is consistent with several empirical investigations that have linked DVM to light sensitivity, predator avoidance and foraging efficiency (Levy et al. 1990; Sims et al. 2005; Hrabik et al. 2006; Stockwell et al. 2010). DVM in adfluvial bull trout has not been previously documented but likely 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 and Adams 1993; Scheuerell and Schindler 2003), are found in numerous reservoirs (Crawford and Muir 2008) and are considered the principal prey for bull trout (up to 77% of diet, Steinhart and Wurtsbaugh 1999; RL and L 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 and Wurtsbaugh 1999), in part results from pursuing piscivores (Hrabik et al. 2006). Scheuerell and 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. Juvenile sockeye inhabited 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 and Schindler 2003; Busch and Mehner 2012). Unfortunately, there is little available information on kokanee prey behavior 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 (Figures 3.1 and 3.2).

In most seasons, smaller individuals remained deeper than larger conspecifics (Figure 3.3). There was no difference in depth among sizes in the spring and while the maximum change in depth was not different across sizes during the summer and fall, during day and night small-bodied fish were more likely to be active than larger fish (Figure 3.4). Individual differences in DVM have not been previously identified across body sizes in a piscivore. However, planktivorous fishes are known to exhibit body-size related differences in behaviour that are linked to competitive interactions (Levy 1990; Mehner and Kasprzak 2011). Busch and Meher (2012) found that the timing of ascent or descent in coregonids *spp.* depended on both the time of day and 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. Clear behavioural differences are evident between large and small individuals which has before only been shown in planktivore DVM. However, alternative diel foraging strategies have been shown among species and across sizes (Alanärä, et al. 2001; Harwood et al. 2002). For example, although not specifically linked to DVM, 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 and Brännäs 1997) or may be forced into deeper water by dominant (larger) individuals (McCauley et al. 1977). Competitive interactions, such as those described in McCauley et al. (1977), 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, which are sympatric with bull trout (Bray 2002; Westslope Fisheries 2005), possess a similar temperature for optimal growth (at least for juveniles, 13.1°C, Bear et al. 2007), and may occupy the same lake habitat. In addition, adfluvial rainbow trout migrate into spawning tributaries during the spring. In the spring, the absence of rainbow trout would relieve competitive pressure and allow small-bodied individual bull trout to more frequently inhabit shallow water (Figure 3.3). Bull trout are widely considered aggressive and cannibalistic to the point where cannibalism has been regarded as an important limiting factor of population size (Wilhelm et al. 1999; Beauchamp and Van Tassell 2001). Although anecdotal, while sampling our team observed a larger bull trout attempt to cannibalize a smaller angled bull trout (591 mm TL, L. Gutowsky and P. Harrison, personal observations). I surmise that during most seasons, the presence of both rainbow trout and large-bodied cannibalistic bull trout near the surface has forced small-bodied individuals into deep water refuge (i.e., into an antipredation window). Although there are no depth data for rainbow trout in Kinbasket Reservoir, 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 fall (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 was only 2 m greater than during a winter day (Table 3.1), 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 behavior, 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 (Figure 3.1), all 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 behavior (Kahilainen et al. 2009; Jensen et al. 2011; Mehner 2012). In adfluvial bull trout, several putative factors and their interactions indicated light as a proximate trigger while behaviour among body sizes and seasons provided support for the ultimate causes of DVM. In addition, the results presented here highlight the need to consider animal behaviour hypotheses at the individual level.

Tables

Table 3.1- Summary of the observed data and number and size (mm total length) of adfluvial bull trout detected according to diel period and season in Kinbasket Reservoir.

Season (diel period)	# of bull trout	average size ± SE (mm TL)	size range (mm TL)	Mean observed depth ± SE (m)	Mean of binary response	Mean Δdepth (m)	Count
winter							
day	111	587.3 ± 9.5	358-881	9.7 ± 0.13	0.55	3.6 ± 0.10	3604
night	109	586.2 ± 9.6	358-881	8.2 ± 0.06	0.41	1.0 ± 0.02	7814
spring							
day	116	604.1 ± 8.8	434-881	6.1 ± 0.10	0.57	4.3 ± 0.12	3784
night	99	605.1 ± 9.4	434-881	5.4 ± 0.08	0.34	0.74 ± 0.04	2976
summer							
day	86	613.8 ± 9.8	434-881	13.7 ± 0.16	0.78	5.7 ± 0.10	2969
night	80	615.8 ± 9.9	440-881	12.1 ± 0.17	0.64	2.5 ± 0.09	1863
autumn							
day	106	591.1 ± 9.4	358-881	11.8 ± 0.28	0.69	5.8 ± 0.19	1637
night	101	592.6 ± 9.2	358-826	7.5 ± 0.13	0.52	1.5 ± 0.06	2725

Table 3.2- Generalized linear mixed-effects models (PQL estimation) with coefficient estimates and P-values.

Response	**model**	**parameter**	**value**	**SE**	**DF**	**t-value**	**P-value**
Depth distribution	Poisson GLMM	(Intercept)	2.398	.2469	27190	9.715	<.0001
		Season-summer	1.004	.1563	27190	6.424	<.0001
		Season-autumn	.6986	.1602	27190	4.362	<.0001
		Season-winter	.7510	.1380	27190	5.444	<.0001
		Diel-night	-.4921	.3971	27190	-12.39	<.0001
		Body size	-.0009	.0004	169	-2.190	.0299
		Season-summer: diel-night	.0542	.0173	27190	3.139	.0017
		Season-autumn: diel-night	-.0965	.0198	27190	-4.884	<.0001
		Season-winter: diel-night	.0611	.0159	27190	3.853	.0001
		Diel-night: Body size	.0004	.0001	27190	6.539	<.0001
		Season-summer: Body size	-.0008	.0003	27190	-3.106	.0019
		Season-autumn: Body size	-.0009	.0003	27190	-3.158	.0016
		Season-winter: Body size	-.0007	.0002	27190	-3.264	.0011
Vertical Movement	Binomial GLMM	(Intercept)	-.9082	.5727	27190	-1.586	.1128
		Season-summer	3.782	.8332	27190	4.540	<.0001
		Season-autumn	2.699	.7218	27190	3.739	.0002
		Season-winter	1.023	.5671	27190	1.804	.0712
		Diel-night	.0259	.2672	27190	.0968	.9229
		Body size	-.0034	.0009	169	-3.641	.0015
		Season-summer: diel-night	.3833	.1205	27190	3.179	.0015
		Season-autumn: diel-night	.5483	.1201	27190	4.566	<.0001

		Season-winter: diel-night	.4054	0.093	27190	4.376	<.0001
		Diel-night: Body size	-.0020	.0004	27190	-4.606	<.0001
		Season-summer: Body size	-.0052	.0013	27190	-3.918	.0001
		Season-autumn: Body size	-.0042	.0011	27190	-3.623	.0003
		Season-winter: Body size	-.0017	.0009	27190	-1.848	.0646
Vertical Movement	Poisson GLMM	(Intercept)	1.035	.2922	14269	3.541	.0004
		Season-summer	.9656	.2909	14269	3.319	.0009
		Season-autumn	1.296	.3255	14269	3.981	.0001
		Season-winter	.8530	.2924	14269	2.918	.0035
		Diel-night	-.1474	.1728	14269	-.853	.3937
		Body size	.0016	.0009	168	3.305	.0012
		Season-summer: diel-night	.3385	.0697	14269	4.856	<.0001
		Season-autumn: diel-night	.0185	.0763	14269	.2428	.8082
		Season-winter: diel-night	.0450	.0676	14269	.6658	.5056
		Diel-night: Body size	-.0012	.0003	14269	-4.517	<.0001
		Season-summer: Body size	-.0015	.0005	14269	-3.214	.0013
		Season-autumn: Body size	-.0020	.0005	14269	-3.838	.0001
		Season-winter: Body size	-.0015	.0005	14269	-3.272	.0011

Figures

Figure 3.1 - Observed data [depth (m)] by hour and season. Dashed vertical lines represent the average sunrise or sunset and solid vertical lines represent the minimum and maximum sunset and sunrise for a given period. Smoothing functions are modeled from the expression y = s(hour, by season), where s is the smoothing term of the form cyclic penalized cubic regression spline.

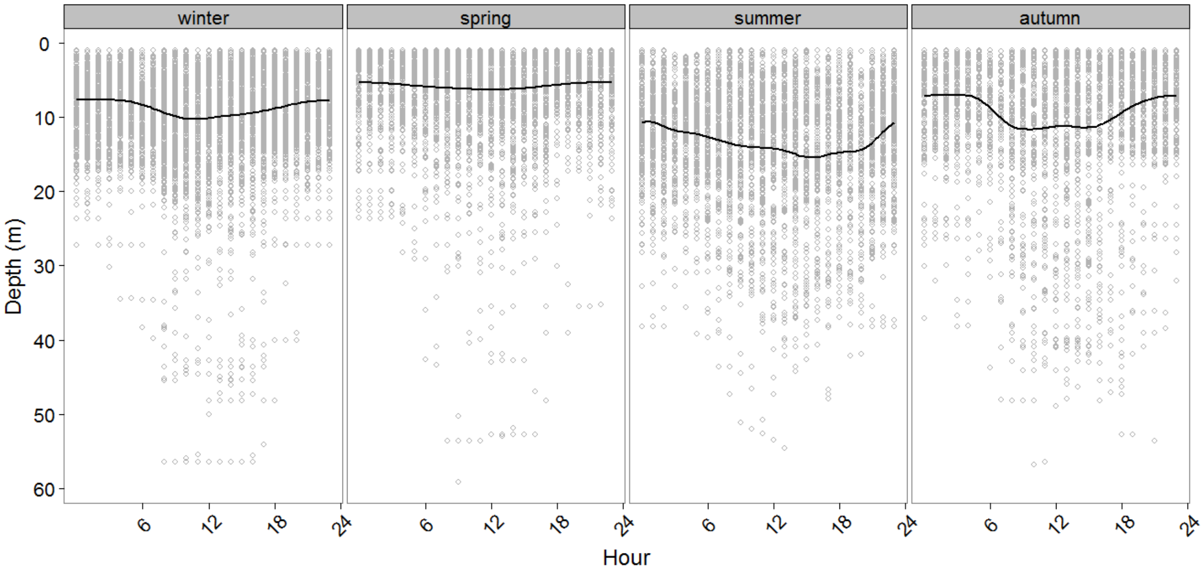


Figure 3.2 - Observed data [Δ depth (m/detection period)] by hour and season. Dashed vertical lines represent the average sunrise or sunset and solid vertical lines represent the minimum and maximum sunset and sunrise for a given period. Smoothing functions are modeled from the expression y = s(hour, by season), where s is the smoothing term of the form cyclic penalized cubic regression spline.

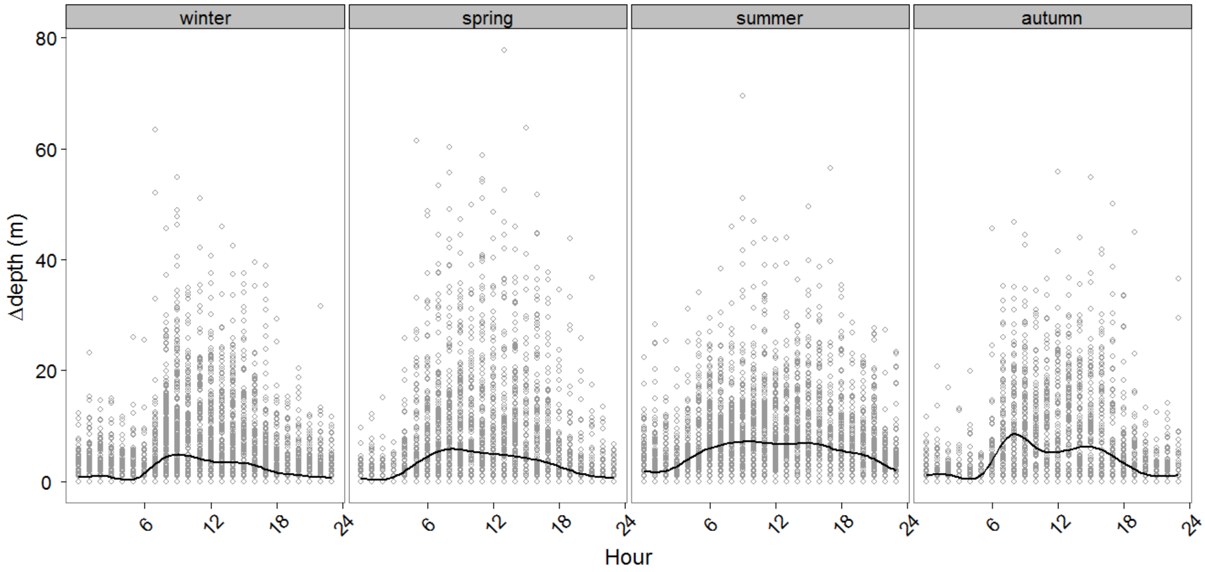


Figure 3.3 - Model estimates of bull trout depth (m) by season, diel period (solid line = night, dotted line = day), and body size (total length (mm)). Shaded regions represent 95% confidence limits for the day (light grey) and night (medium grey). Regions of confidence limit overlap between day and night periods are emphasized in dark grey.

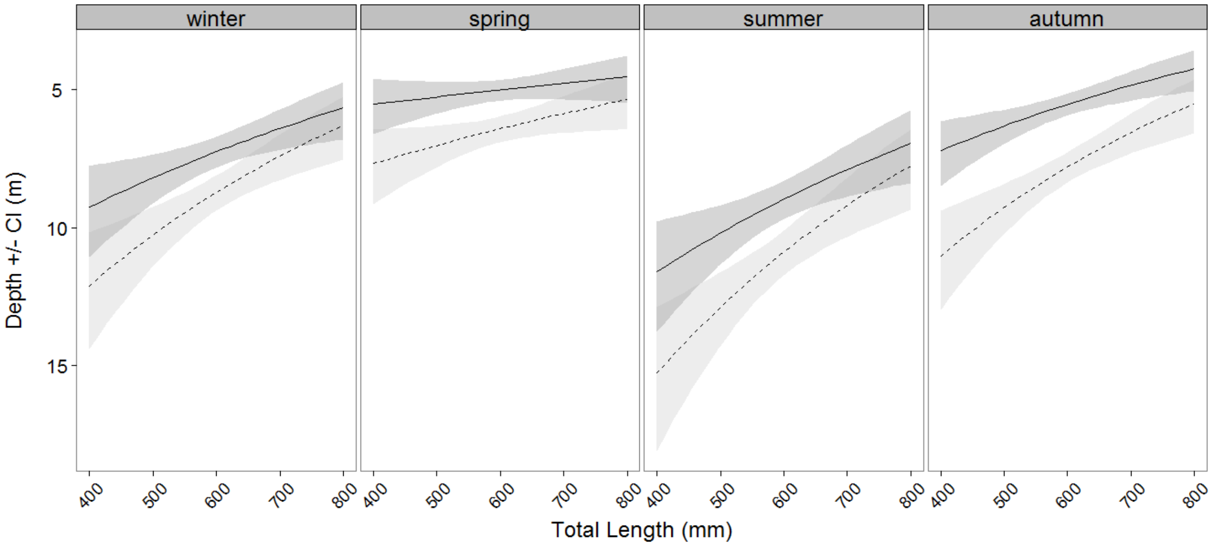


Figure 3.4 - Model estimates of the probability that bull trout change depth by season, diel period (solid line = night, dotted line = day), and body size (total length (mm)). Shaded regions represent 95% confidence limits for the day (light grey) and night (medium grey). Regions of confidence limit overlap between day and night periods are emphasized in dark grey.

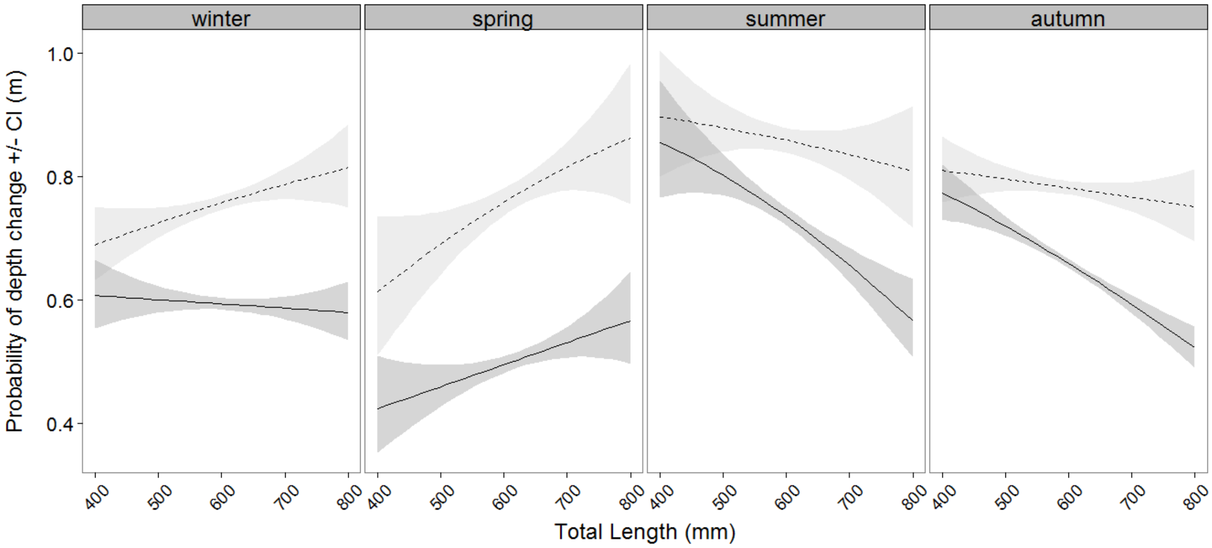
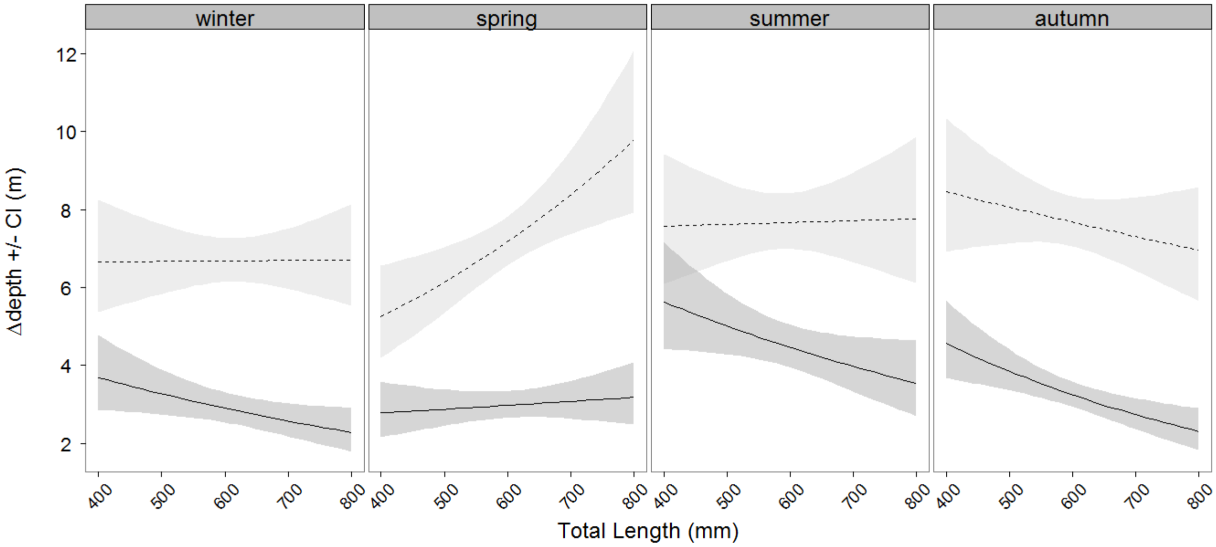


Figure 3.5 - Model estimates of change in depth for bull trout by season, diel period (solid line = night, dotted line = day), and body size (total length (mm)). Shaded regions represent 95% confidence limits for the day (light grey) and night (medium grey). Regions of confidence limit overlap between day and night periods are emphasized in dark grey.



Chapter 4: Sex and body size influences on the movement ecology of bull trout

Abstract

Animal movement occurs as a function of many factors including changing environmental conditions (e.g., seasonality) and the internal state of the focal organism (e.g., phenotypic traits). Identifying how these factors interact can reveal behavioral patterns that would otherwise go undiscovered, especially for cryptic free-ranging animals such as fish. From 2010 to 2012, I used acoustic biotelemetry to examine spatial distribution, home range size, and total monthly displacement of 187 tagged adfluvial adult bull trout in relation to several putative factors (year, season, month, body size, sex, and interactions) in Kinbasket Reservoir. Given the wide range of body sizes, large number of males and females, and two-year monitoring period, I aimed to reveal how the movement of tagged fish was related to body size, sex, time of year, and possible two-way interactions among these variables. Mixed models indicated home range size was best predicted by body size and season; total monthly displacement was predicted by month and a two-way interaction between sex and body size. Generally, bull trout aggregated in a centralized location during winter when individuals occupied relatively small home ranges (< 25 km^2) and had small total monthly displacements. Conversely, the fall was characterized by a broad distribution of individuals, relatively large home ranges (> 35 km^2), and large total monthly displacements. Bull trout were found to rarely use the southern portion of the reservoir and the relatively aggregated distribution near the hydro dam during winter further explains why bull trout entrainment risk is highest during that period. Large females (~800 mm total length) had a total monthly

displacement of up to five times greater than females half their length whereas movements between large and small males were not significantly different. Sex- and body-size related differences in activity are attributed to greater reproductive energy demands and resultant higher activity budgets of large females. This study illustrates size- and sex related differences in activity outside of the reproductive season and offers insights for the conservation of bull trout, which are imperiled throughout their range.

Introduction

Animal movement is defined as a change in the spatial location of an individual in time (Nathan et al. 2008). Baseline movement data are a necessary component of wildlife management (Caro 2007) and animal movement is increasingly investigated in the ecological and behavioral science literature (Holyoak et al. 2008). While simply following the movement paths of an animal can illustrate important ecological information, analyzing the contribution of additional covariates, such as body size and sex, can help elucidate otherwise overlooked patterns in behavior, such as movement in the reproductive and non-reproductive periods (Barnett et al. 2011), sex- and size-based habitat selection (Sims 2005; Laidre et al. 2013), and the consequences of intra- and interspecific competition (Essington et al. 2000). Furthermore, internal-state factor interactions are analogous to internal-state dynamics; a rarely discussed aspect of the movement ecology framework (Nathan et al. 2008). Investigating behavioral modifications in relation to phenotypic traits, internal-state factor interactions, and their interactions with environment factors can be highly informative (e.g., Fryxell et al. 2008; Delgado et al. 2010).

In freshwater and marine fishes, a number of examples exist where movement patterns can be explained according to phenotype and environmental conditions (Hanson et al. 2008; Wearmouth and Sims 2008). In Trinidadian guppies (*Poecilia reticulata*), experiments have illustrated that predation risk largely drives sexual segregation between habitats with differing degrees of predation pressure and harassment by the opposite sex (Croft et al. 2004, 2006). In broadnose seven-gill sharks (*Notorynchus cepedianus*), males and females exhibit substantial differences in the seasonal timing of migration and total distance travelled (Barnett et al. 2011). During diel vertical migration, body-size can have a considerable influence on the timing and range of movement in both prey and predator fishes (Busch and Mehner 2012). In addition, phenotypic traits are increasingly recognized as important factors to consider for conservation (e.g., Wearmouth and Sims 2008). However, simply investigating how movement differs among body sizes or between sexes is challenging, particularly when studying free-ranging animals with large home ranges.

Biotelemetry and biologging are effective methods to overcome the challenges of studying free-ranging animals and make inferences about populations (Cooke et al. 2004; Rutz and Hays 2009; Cagnacci et al. 2010; Hebblewhite and Haydon 2010). Often, high equipment costs restrict biotelemetry studies to small sample sizes across a small size range of individuals (to reduce possible unexplained variation associated with body size on the response) while sex is indeterminable (e.g., species lack secondary sexual characteristics) or simply ignored as a factor (Hanson et al. 2008). However, with a large enough sample size and the ability to determine the sex of individuals, biotelemetry can be used to estimate the influence of phenotypic traits on movement and behavior in wild populations of fish (Eckert et al. 2008; Wearmouth and Sims 2008).

Here I use biotelemetry to investigate correlative factors of adfluvial bull trout spatial ecology across multiple seasons in Kinbasket Reservoir. My central hypothesis was that biotic factors are important determinants of seasonal home range size and movement. I posited that patterns emerging from the influence of phenotypic traits would provide insights into the movement ecology of free-ranging fishes, information on the spatial ecology of adfluvial bull trout, and specific information relevant to bull trout in Kinbasket Reservoir where the population is at risk of entrainment (Martins et al. 2013, 2014). For this study I tagged a wide size range (~350-880 mm total length, Figure 1.2) of individuals with acoustic biotelemetry transmitters and collected data from these animals after they travelled among an array of 42 biotelemetry receivers from 2010 to 2012. Mixed modelling and model selection were used to test the hypothesis about home range size and horizontal movement (measured as total monthly displacement) in relation to sex, body size, and time of year (season or month). Given that large bodied individuals possess the capacity to swim at the highest speeds (Brett 1965; Ware 1987; Lightfoot and Jones 1996), body size was predicted to be positively correlated with both home range size and total monthly displacement. Given the species' sensitivity to water temperature (Selong et al. 2001), bull trout were predicted to have the smallest home ranges during the warmest and coldest periods of the year, i.e., summer and winter. Reproductive migrations and their preference for cool water were expected to result in large home ranges and greater total monthly displacement in the fall months (Barnett and Paige 2013). Given that egg development is energetically costly compared with the cost of producing sperm and a larger body size requires more energy intake (Gowan and Fausch 1996, Wootton 1998), I predicted large females would possess the largest home range sizes and perform the greatest horizontal movement over the study period.

Methods

The study was conducted in Kinbasket Reservoir which is described in Chapter 1 (Figure 1.4). As described in Chapter 2, data were collected using a 42 omni-directional VR2W receiver array that was originally deployed in the spring of 2010. Receivers were retrieved, downloaded, and redeployed in the spring of 2011. Receivers were retrieved again in the spring of 2012 and removed from the reservoir. Bull trout tagging procedures are described in Chapter 2. To reiterate from the methods section in Chapter 2, no receivers were lost in year one whereas in year two, five of the 42 receivers were lost.

Data management and filtering

Data were treated in the same way as in Chapter 2, where false detections and incomplete tag-to-receiver transmissions were removed prior to analysis. Again, the minimum number of receiver detections per individual bull trout was set at two per receiver per 24 hour period. In addition, detections used were those recorded after the final receiver was deployed in May, 2010. A final data filter was applied to eliminate estimates from fish that were detected few times during a season (arbitrarily set to < 5 detections/season). Data filtering and exploration were conducted using Microsoft Access and the R statistical environment (R Development Core Team 2012).

Analyses

Seasonal spatial distribution

Seasonal spatial distribution was quantified by assessing the percentage of tagged bull trout that visited each receiver across Kinbasket Reservoir per season. Percentages were used to account for an uneven total number of individuals detected per season. Because receivers were irregularly spaced, the estimates were imported into ArcGIS 10.1 (Environmental Systems Research Institute, Redlands, CA), interpolated by ordinary kriging, and clipped to a GIS layer of Kinbasket Reservoir. Similarities in the resultant distribution maps were assessed using the fuzzy Kappa statistic (Hagen-Zanker et al. 2006; Hagen 2003). Fuzzy Kappa compares the similarity of overlaid map cells and their neighbours where values range between zero (distinct) and one (identical). Average map similarity was expected to be moderate to high (0.6-0.8; Landis and Koch 1977) between same seasons during the two year study period. Statistics were generated using the Map Comparison Kit software v3.2.3 (http://www.riks.nl/mck/index.php; Maastricht, The Netherlands).

Home range size

For the analysis of home range size, data were examined at the seasonal level where seasons included: spring (April-June), summer (July-September), fall (October-December) and winter (January-March). Seasonal classifications roughly correspond to biologically meaningful periods for adfluvial bull trout, e.g., the fall is associated with both reproductive migrations and spawning in lake tributaries (Nitychoruk et al. 2013). The year variable was defined based on monitoring year (i.e., first monitoring year: May 2010 to April 2011; second monitoring year: May 2011 to April 2012). This classification ensured that each year contained four seasons which facilitated analyses with factor interactions (e.g., season x year). Individual bull trout home range size was calculated as the 90% minimum convex polygons (MCP) from the R package “adehabitatHR” (Calenge 2006). A minimum number of detections at multiple receivers are required to calculate MCPs for an individual, thus a biologically meaningful broad-temporal classification (i.e., season) ensured that a variety of individuals (i.e., wide range of sizes) would be available for statistical analysis. Although other methods could be used (e.g., kernel Brownian bridges, Calenge 2006), MCPs are a simple and commonly used method for estimating animal home range from acoustic telemetry data (IUNC 1994; Marshell et al. 2011). In the current study, home range size was calculated as the maximum MCP (%) that provided estimates for the greatest number of individuals (in this case 90% MCPs). MCP home range size estimates were exported to ArcGIS 10.1, clipped to a Geographic Information Systems (GIS) layer of the reservoir, and recalculated in km^2. Home range size was calculated for each individual by season and year.

Total monthly displacement

Distances between receivers were calculated in ArcGIS 10.1 and used to estimate horizontal movement or, more accurately, the detected (i.e., minimum) total displacement for each bull trout by month. Estimates based on this method are dependent on the total number of detections. Since estimates almost certainly underestimate distances as time scale is increased and do not account for tortuous movements between receivers (Yamanaka and Richards 1993; Rowcliffe et al. 2012), monthly estimates were generated to reduce the step size (Nathan et al. 2008) and examine total displacement at a scale finer than season and year. Total monthly displacement was calculated using the R package "V-Track" which is designed for calculating animal movement from biotelemetry data (Campbell et al. 2012). To define residency at a receiver, the minimum number of detections was set at two. Receiver residency for a bull trout was assumed to be terminated when approximately 30 minutes elapsed between detections at the same receiver or when the individual was recorded at a different receiver. The sum of the detected monthly displacement by each bull trout was calculated for each month (excluding April, 2010) for two years (n = 23).

Statistical modelling procedures

Bull trout home range size and total monthly displacement were analysed using a GLMM and a GAMM, respectively. For the analysis of home range size, the model selection procedure began with the full model that included year, season, and sex as categorical factors, body size [total length (TL) in mm] as the continuous covariate, and all two-way interactions. For the analysis of total monthly displacement, the model selection procedure began with a full model that included month as a cyclic smoothing function (Wood 2006, 2011) and sex, body size, and the sex x body size interaction. Both models included fish ID as a random factor. Data exploration was performed using standard tools including Cleveland dot plots (to identify outliers) and box and whisker plots (to identify relationships between continuous and categorical variables) (Zuur et al. 2009). Home range size was $\log_{10}$ transformed to obtain normality. In addition, models included a variance structure to incorporate heterogeneity in the categorical predictors (Zuur et al. 2009). Models were fitted to the data using the R packages “nlme” (Pinheiro et al. 2013) and “mgcv” (Wood 2006, 2011). To determine the most parsimonious model for home range size, backwards model selection was performed using log-likelihood ratio tests at $\alpha = 0.05$. The final models were validated by examining autocorrelation plots and by plotting the residuals against all variables, including those not retained in the final model (Zuur et al. 2009). The R package “multcomp” was used to examine all pair-wise comparisons between the considered categorical factors for home range size (Hothorn et al. 2008).

Results

Data were logged on the telemetry receivers from May 2010 to May 2012, yielding approximately 3.5 million bull trout detections. Body size ranged from 358 mm TL to 881 mm TL with more males detected across all seasons and years (Table 4.1). More than 20 individuals of each sex were available for analysis within any given season over the two years (Table 4.1).

Seasonal spatial distribution

Between the two years, the fuzzy Kappa analyses showed that seasonal-spatial distribution was moderately to highly similar (spring $_{\text{Yr1\&Yr2}}$ = 0.741; summer $_{\text{Yr1\&Yr2}}$ = 0.744; fall $_{\text{Yr1\&Yr2}}$ = 0.754; winter $_{\text{Yr1\&Yr2}}$ = 0.58). Qualitatively, spatial distribution in year one varied by season with the greatest proportion of individuals detected in a relatively small area at the confluence of the Canoe and Columbia reaches during winter and spring (up to 84 tagged individuals in a 45 km^2 area) and winter (up to 39 individuals in a 68 km^2 area, Figure 4.1). In the summer, the greatest number of individuals (up to 44) was detected in small areas near several named creeks in the Canoe Reach (Figure 4.1 ii). Although the Columbia Reach represented a large portion of the reservoir surface area during summer (~110 km^2 or 26%), relatively few individuals (up to 16) were detected here. During the fall, relatively large proportions (21-60%) of bull trout were detected over a long stretch of the reservoir (~75 km) from the Canoe Reach south to the Kinbasket River in the Columbia Reach (Figure 4.1 iii)). Despite tagging bull trout south of the Bush Arm, the southern end of the Columbia Reach (Sullivan River south to the Bush Arm) remained one of the least visited areas for bull trout across all seasons (Figure 4.1).

Home range size

Backwards-model selection indicated that season x year (*L*-ratio = 11.6, df = 7, P = 0.11) and sex x body size (*L*-ratio = 1.44, df = 1, P = 0.23) did not significantly predict adfluvial bull trout 90% MCP home range size (km^2). The most parsimonious model of bull trout home range size contained season and body size with no interactions (Table 4.2). Home range size was similar between winter and summer (z = 0.1, P = 0.99) and spring and fall ($z = 2.5$, $P > 0.05$) whereas all other seasonal home range size comparisons were significantly different (in all cases, $P < 0.01$). Large bull trout (765 mm TL) occupied the largest home range during the spring [mean: 46.0 km^2, 34.4, 61.6, 95% confidence interval], whereas the smallest home ranges were estimated for small bull trout (470 mm TL) during the summer and winter [mean$_{\text{summer}}$: 13.6 km^2, 10.0, 18.4, 95% confidence interval, and mean$_{\text{winter}}$: 13.4 km^2, 9.6, 18.6, 95% confidence interval, Figure 4.2].

Total monthly displacement

According to backwards model selection, the full model was the best model to explain total monthly displacement (km) in bull trout (Table 4.2). The smoothing term, coded as a numerical variable, was significant and showed patterns in total monthly displacement across two years for male and female bull trout (♂: $t = 8.6_{6.8}$, $P < 0.0001$; ♀: $t = 8.3_{12.3}$, $P < 0.0001$, $R^2 = 8.7\%$, Figure 4.3). On average, large fish (800 mm TL) moved greater distances than small fish (400 mm TL) in a given month; however the difference was significant only among females (Figure 4.4). For females during a given month, large fish were predicted to move as much as five times further than smaller conspecifics (Figure 4.4). The predicted trend in movement indicated that total displacement was greatest in the spring (May through June) and fall (October through December) while the least total displacement occurred during the winter months (January through March). Although patterns remained consistent across seasons for the two years, the amplitude of these patterns across years was higher in the fall months for year one than in year two, both for males and females (Figure 4.4). The average differences in predicted monthly movement between years for the months of August through December were 14.9 km ± 7.3 SD for small males, 23.1 km ± 5.7 SD for small females, 15.0 km ± 7.3 SD for large males, and 23.1 km ± 5.7 SD for large females.

Discussion

Biotic factors, namely sex and body size, were significant predictors of adfluvial bull trout movement, however these factors did not explain home range size (Table 4.2). In addition, there was a sex x body size interaction to explain horizontal movement over time (Figure 4.4). This interaction is an overt example of internal-state dynamics from the movement ecology framework (Nathan et al. 2008). The majority of work on organismal movement simply documents movement or describes how it was influenced by the environment (Holyoak et al. 2008). However, movement derives from a number of co-occurring causes and mechanisms (Bennetts and Kitchens 2000; Long et al. 2008; Mehner 2012), which may be further complicated by relationships within, for example, the internal state of an organism. As illustrated here in adfluvial bull trout and in a number of other species (e.g., bluefin tuna, *Thunnus maccoyii*; Bestley et al. 2010, elk, *Cervus elaphus*, Fryxell et al. 2008, eagle owls, *Bubo bubo*, Delgado et al. 2010), putative factors corresponding to the internal state and external factors predict where, when and how often organisms move (Nathan et al. 2008).

Periodic changes in the abiotic and biotic environment (e.g., temperature) can have a predictable set of outcomes for the behavior of ectotherms (e.g., Sims et al. 2001; Morley et al. 2007; Kearney et al. 2009). Given that temperature is the master controlling factor of fish physiology and behavior (Brett 1971), yearly, seasonal, and monthly differences in temperature can have a significant influence on activity (Arendt et al. 2001; Bestley et al. 2010). Behavior in free-ranging fish is commonly explained by seasonally fluctuating environmental factors such as periodic changes in temperature (Sims et al. 2004), light (Schruell and Schindler 2003), and dissolved oxygen (Moreley et al. 2007). In addition, it is increasingly apparent that fish movement can be context- (Dingemanse et al. 2010; Sih et al. 2012) or personality-dependent. For example, reef populations of golden-lined rabbit fish (*Siganus lineatus*) exhibit a different diel foraging strategy than a population from a boulder-shoreline site (Fox and Bellwood 2011). In Kinbasket Reservoir, individually tagged burbot were found to exhibit seasonally-dependent movement that was repeatable for individuals independent of body size, e.g., individuals that moved long distances in summer also did so during winter (Harrison et al. In Press).

Given that forage fish are generally less abundant in the spring compared to the previous fall (Sogard 1997; Suski and Ridgeway 2009), the wide distribution, large home range sizes, and relatively high activity of individual bull trout may be attributed to the distribution of their prey (Figures 4.3 and 4.4). Adfluvial bull trout perform DVM and exhibit their deepest swimming depths during summer, probably in response to warmer surface temperatures (Chapter 3). Light attenuates quickly with depth and if large horizontal movements do not result in increased encounters with prey, bull trout may continue performing DVM to hunt during summer (i.e., when the reservoir develops a thermal gradient, Bray 2012; Chapters 2 and 3) while only maintaining small home ranges and embarking on limited horizontal movements. It is reasonable to predict that the limited movement observed in summer is, in part, explained by bioenergetic requirements of bull trout and the distribution of kokanee salmon prey which perform diel vertical migration (Bevelhimer and Adams 1993; Vogel and Beauchamp 1999). In fall, the high percentage of individuals detected across much of the reservoir, the large total monthly displacement, and large home ranges (Figure 4.1, iii) are most easily explained as a response to cooling water temperatures (i.e., bioenergetics efficiency), the reproductive migratory behavior of prey (feeding opportunity hypothesis, Olmsted et al. 2001), and the fall reproductive migratory behavior of bull trout which is an adaptation of charr and based on environmental cues (e.g., temperature and solar radiation, Dingle 1996). Home range size and displacement were minimal in winter, likely to conserve energy while continuing to vertically migrate and feed on kokanee (Beauchamp and Van Tassell 2001; Helland et al. 2011; Chapter 3).

Body size is a well-known predictor of home range size in mammals, birds, reptiles, and for some species of fish (Reiss 1988; Minns 1995; Haskell et al. 2002; Eckert et al. 2008). Large bull trout had the largest home ranges (~ 45.5 km^2 during spring), a pattern that corroborates with the positive relationship found between body size and total monthly displacement (Figure 4.4). To my knowledge these are the first data to describe adfluvial bull trout home range size. Unlike for adfluvial bull trout, fluvial conspecifics have been shown to possess small home ranges with no effect of body size (Schoby and Keeley 2011). It is likely that the distribution and abundance of food resources in some bull trout rivers may not necessitate larger home ranges for large individuals (i.e., optimal foraging theory, Werner and Hall 1974; Pyke 1984). Although kokanee salmon are abundant in Kinbasket Reservoir, the larger size classes are rare and dispersed (Sebastian and Johner 2011). However, contrary to my prediction, sex was not a significant predictor of home range size (Table 4.2). Home range size is not always different between the sexes (Norman and Jones 1984), and the relationships among sex, body size, home range and movement tend not to be universal among fishes (Croft et al. 2003). The simplest interpretation of this relationship is that compared to male bull trout, the average female moves more frequently within their home range. However, this relationship is further complicated by the sex x body size interaction predicted in horizontal movement.

Sexual-size dimorphism has consequences related to growth, activity, and behavior both during and outside of the breeding season (e.g., Henderson et al. 2003; Rennie et al. 2008; Nitychoruk et al. 2013). For example, Nitychoruk et al. (2013) found seasonal and sex-related differences in body condition where the summer body condition of adfluvial bull trout was relatively poor compared to that of the spring but that females during the fall possessed better body condition than males during the same season. In the current study, the magnitude of the total horizontal displacement was explained by a body size x sex interaction in which only large females moved significantly farther than small individuals of the same sex (Table 4.3; Figure 4.4). It should be noted, however, that only a small amount of the variation was explained by the smoother for month (R^2 = 8.7%). Bahr and Shrimpton (2004) also reported a large variance in monthly movement for bull trout across tributary systems in the Morice River watershed system, BC. Nevertheless, assuming the relationship is biologically significant despite a low R^2, one possible explanation for the body size x sex interaction is an extension of the activity budget hypothesis which has mainly been used to predict sexual segregation in sexually size-dimorphic ungulates and marine animals including fish (Ruckstuhl 2007; Wearmouth and Sims 2008). The hypothesis suggests that sexually size-dimorphic species exhibit sex-based differences in energetic requirements, digestive efficiencies and possibly also movement rates which result in the formation of single-sex groups (Rennie et al. 2008; Wearmouth and Sims 2008). However, sex-based differences in activity can also exist independent of body size. For example, similarly sized male and female small-spotted catshark (*Scyliorhinus canicula*) have been shown to differ in activity, where females exhibit more intense foraging behavior compared with males (Kimber et al. 2009). It is reasonable to suggest that compared to similarly-sized males, the relatively high activity in large-sized females is related to more intense foraging behaviour to accumulate the greater energy required for female reproductive tissue development (Hendry and Berg 1999; Kimber et al. 2009; Yong and Grober 2014).

Body size is positively correlated with foraging time when large prey are rare and given that gamete production is more costly for females than for males, females should be foraging-time maximizers whereas male fish should theoretically minimize foraging time (Schoener 1969; Hoffman 1983). In addition, the risk of predation for the largest fish is probably minimal, thus increased activity would not result in a high cost to survival (Werner and Anhold 1993). Although large males may prefer larger prey than smaller individuals of the same sex, the difference in horizontal movement here is marginal (Figure 4.4). To meet the energetic requirements associated with female reproduction, large mature females may spend more time foraging while searching for rare but optimally sized prey. While increased movement may be energetically costly and risky (Werner and Anhold 1993), the benefits could include increased encounters with optimally-sized prey (Werner and Hall 1974), better body condition (Nitychoruk et al. 2013), and increased energy for reproductive tissue development in females. Again however, the adjusted R^2 for the smoother is low, although not necessarily for biological studies (Møller and Jennions 2002), and my predictions remain to be tested together in the field.

Despite their conservation status, relatively little is known about bull trout spatial ecology in reservoir systems where this species is widely found. Overall, the data collected here in Kinbasket Reservoir were highly informative both as a means to investigate hypotheses related to movement in free-ranging organisms and provide information for the conservation of bull trout, which are imperiled throughout most of their range. For example, winter activity has been shown to occur in other lacustrine bull trout populations (Salow and Hostettler 2004; Dare 2006) and the spatial distribution in Kinbasket Reservoir illustrates why entrainment risk is highest during this season (Martins et al. 2013, 2014). Despite tagging 15% of the sample from tributaries at southern part of the system, bull trout rarely used this location outside of the reproductive period (Figure 4.1). The results from this research chapter could be useful for fisheries managers who are considering mitigation or compensatory activities (e.g., spawning site restoration) to offset entrainment-related losses (Martins et al. 2013).

In summary, by pairing biotelemetry data with temporal changes in the environment and phenotypic traits, I found patterns in behavior that would otherwise go unidentified in these free-ranging animals, e.g., internal-state dynamics (Nathan et al. 2008). I have suggested mechanisms that underlie the behaviors, however further investigation is required. Given the sophisticated technology, statistical tools, and software available to study the behavior of wild and cryptic animals such as fish, there are ample opportunities to conduct similar research that could reveal information that is pertinent to behavioral ecology, movement ecology, and species' conservation.

Tables

Table 4.1- Sample size by year, season, sex, and body size for the home range size and horizontal movement analyses of adfluvial bull trout in Kinbasket Reservoir.

	Home range				Horizontal movement			
	Count		Range (TL mm)		Count		Range (TL mm)	
Factor	f	m	f	m	f	m	f	m
2010-2011								
spring	43	66	515-786	434-881	45	71	393-765	434-881
summer	35	48	393-741	440-881	62	84	358-786	434-881
fall	56	73	358-786	434-881	47	71	515-786	434-881
winter	45	65	393-786	362-881	53	75	393-786	362-881
2011-2012								
spring	47	74	451-786	434-881	34	58	445-741	434-881
summer	21	51	467-741	434-881	36	60	465-786	434-881
fall	29	50	515-786	434-881	52	82	445-786	362-881
winter	29	32	515-786	434-881	35	46	501-786	434-881

Table 4.2- Summary of the importance of individual terms, including a variance structure (*var*) for the GLMM on home range size. Residual standard deviation for the random effect in both the GLMM and GAMM were 0.566 and 52.68 respectively.

Model	**model term**	**t-value**	**L-ratio**	**P-value**
GLMM- Home range size	Intercept	4.87		<.0001
	Season		50.5	<.0001
	TL		4.36	0.034
	(*var*)		44.5	<.0001
GAMM- Movement	Intercept	1.64		0.139
	TL		22.2	<.0001
	Sex		10.2	0.007
	Sex x TL		7.05	0.008

Figures

Figure 4.1 - Proportion of individual bull trout detected in different areas of Kinbasket Reservoir during the spring (i), summer (ii), fall (iii), and winter (iv) of the first study year (2010-2011). The total number of individuals detected by season was: spring, n = 121; summer, n = 131; fall, n = 156; winter, n = 146.

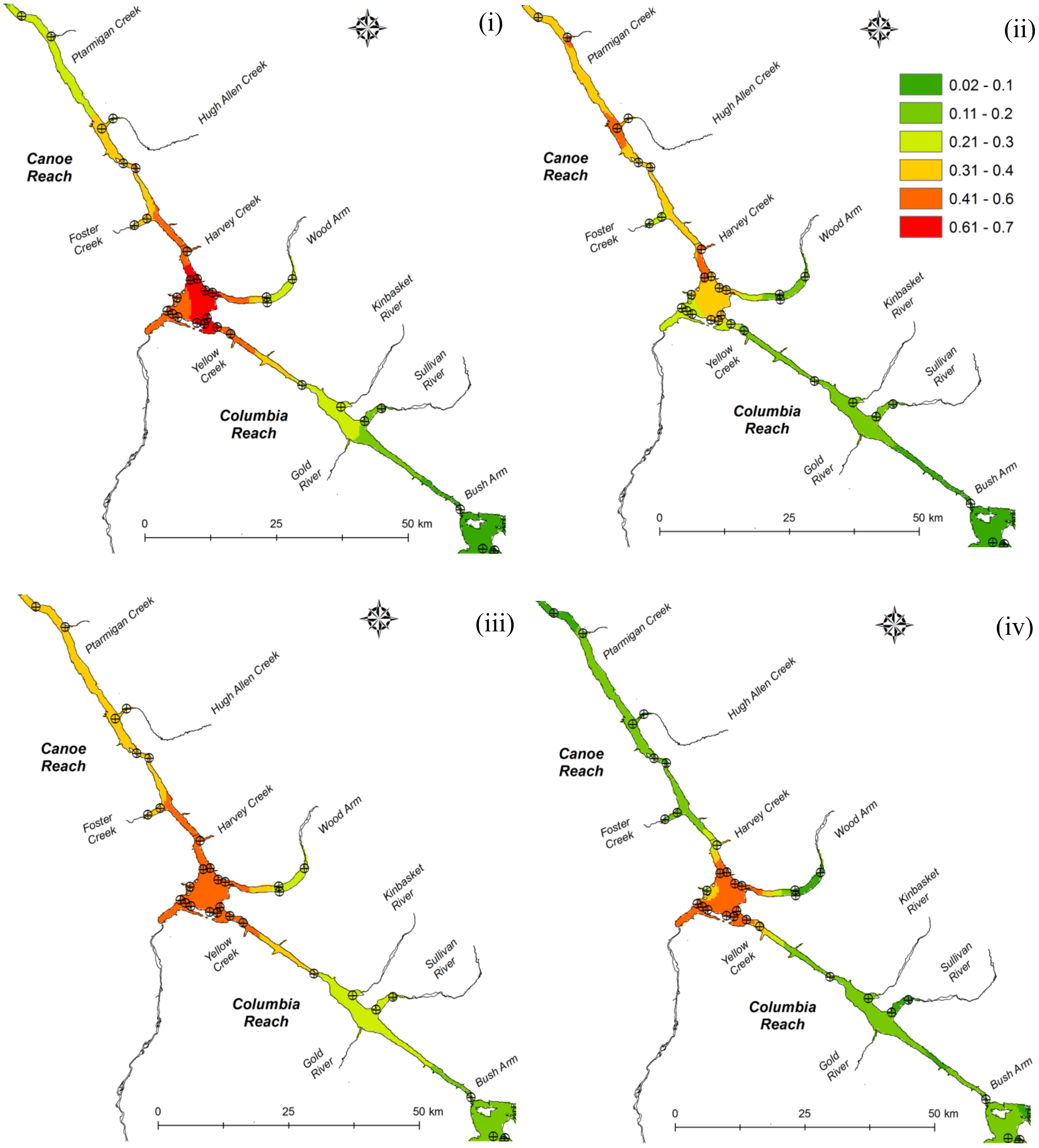


Figure 4.2 - GLMM predictions of adfluvial bull trout home range size (mean km^2 ± 95% confidence limits) by body size (total length, mm) and season in Kinbasket Reservoir, British Columbia.

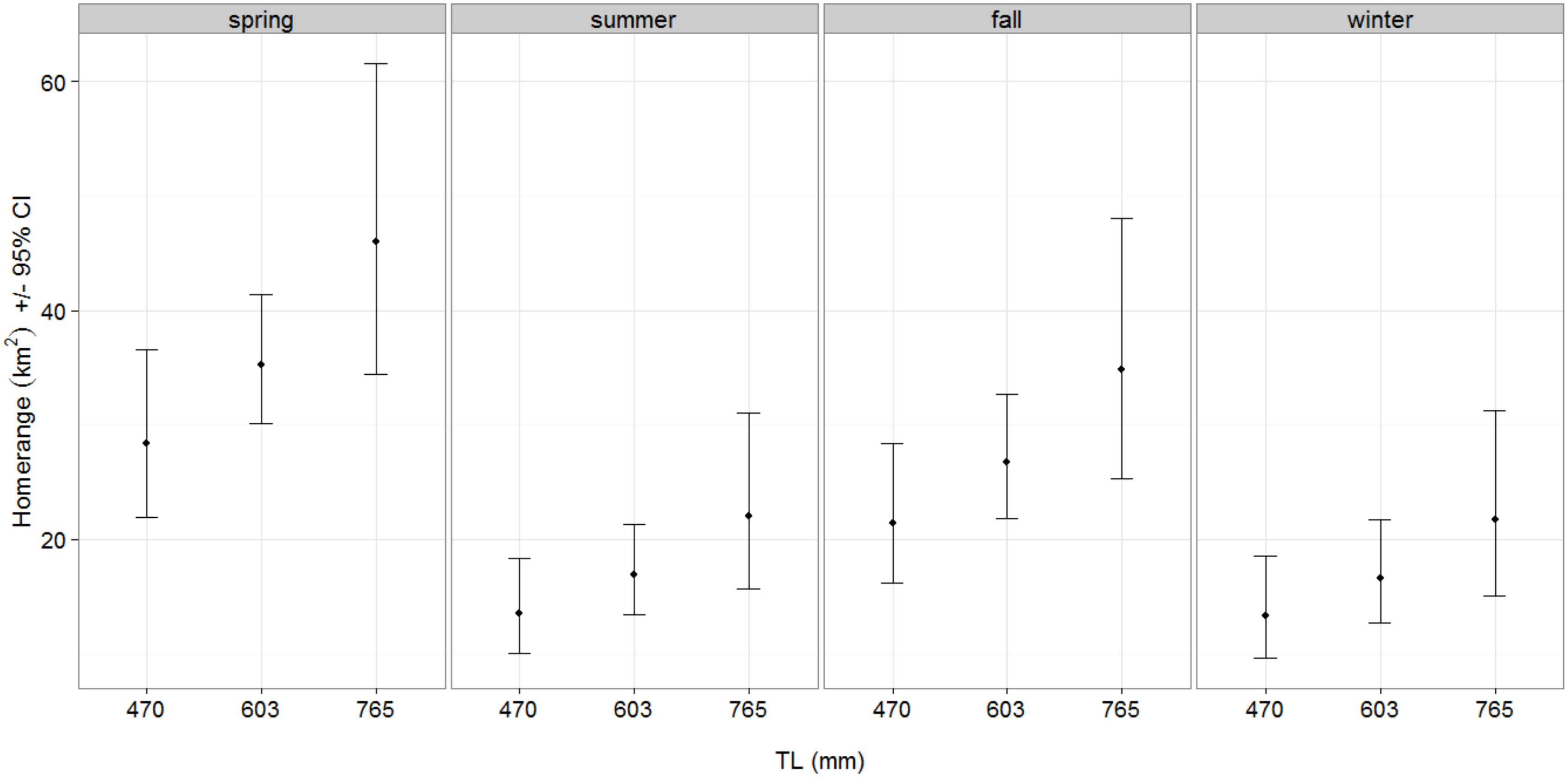


Figure 4.3 - GAMM predictions of the additive effects of male (i) and female (ii) on adfluvial bull trout movement (mean km ± 95% confidence limit) across two years in Kinbasket Reservoir, British Columbia. The approximate significance of the smoother (Month) for males was ($P < 0.0001$) and for females ($P < 0.0001$). Model degrees of freedom, shown in the y-axis titles, are from the hat matrix of the model fit.

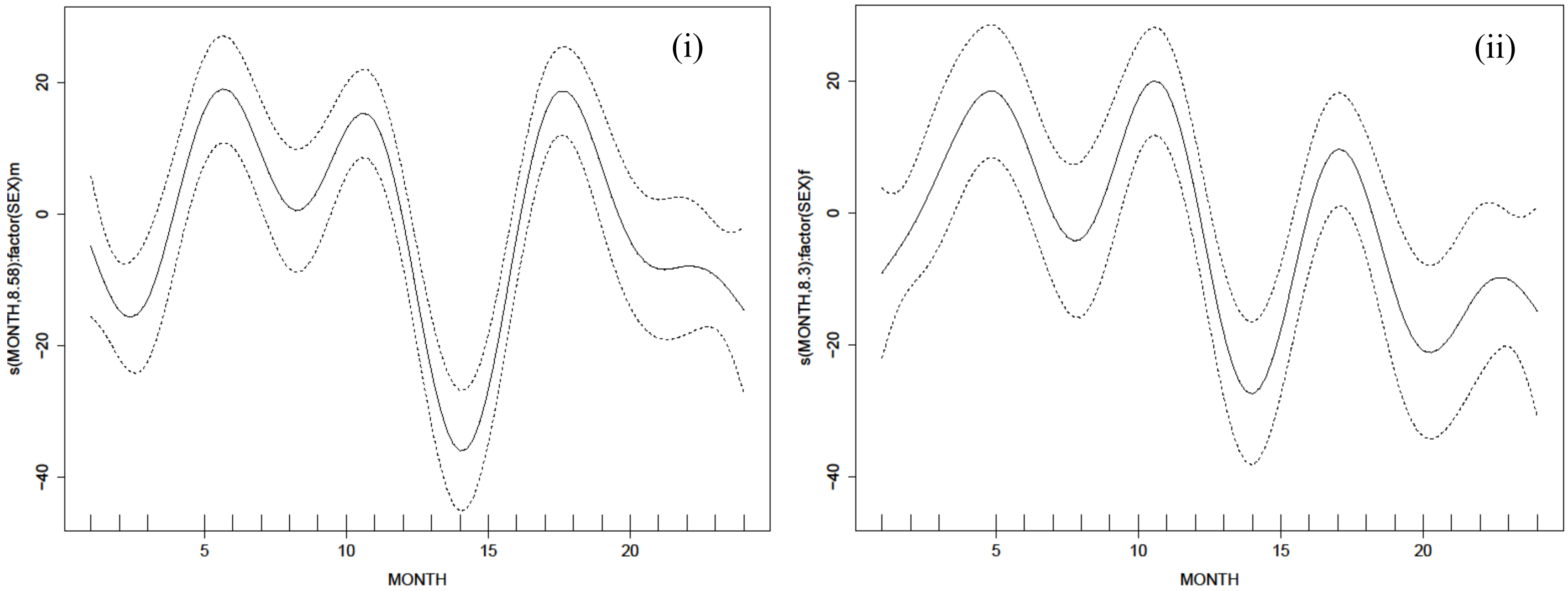
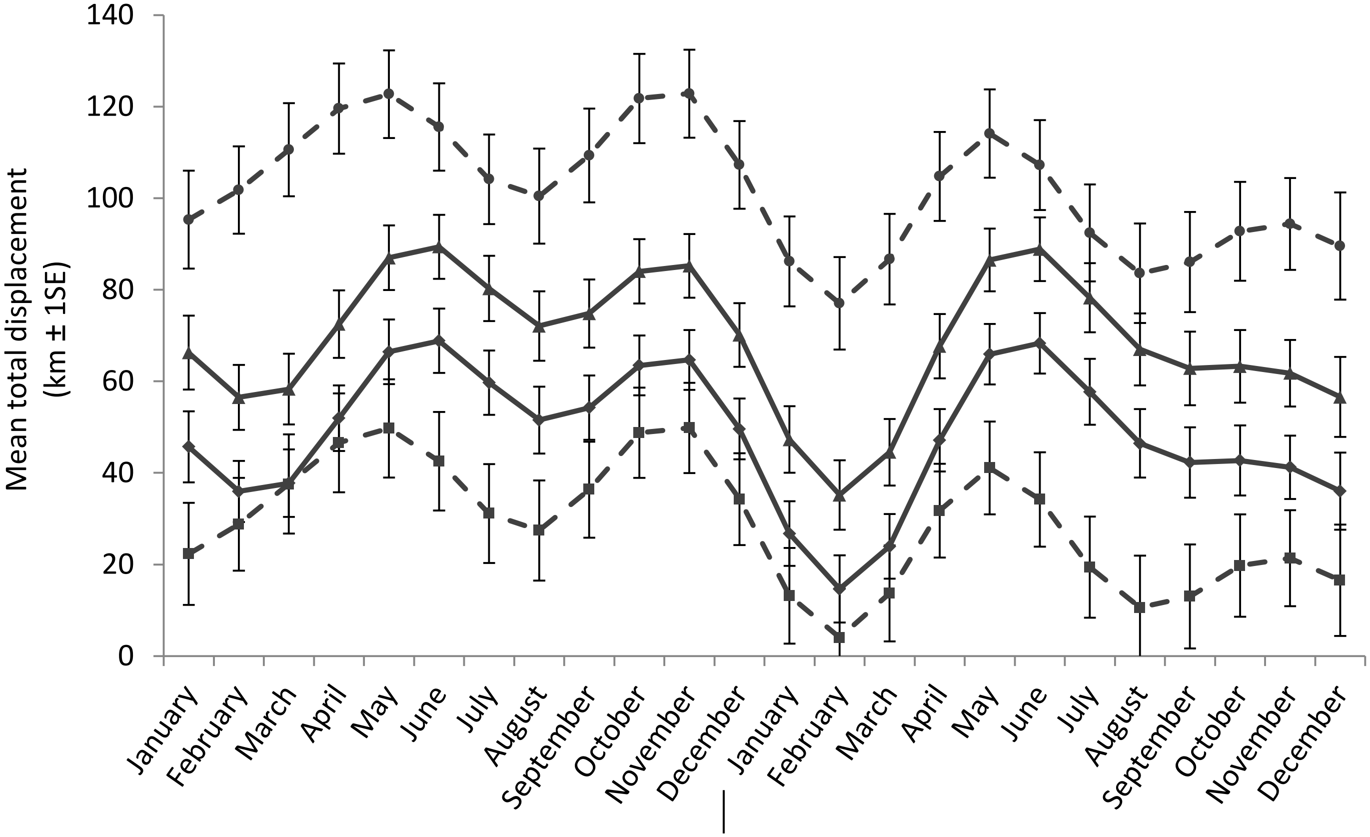


Figure 4.4 - Predicted large (800 mm TL) female (dashed line round marker), small (400 mm TL) female (dashed line square marker), large male (solid line triangle marker), and small male (solid line diamond marker) adfluvial bull trout horizontal movement (mean km ± 1 SE) across two years in Kinbasket Reservoir, British Columbia. For clarity, estimates are shown with standard errors.



Chapter 5: General Discussion

Adfluvial bull trout selected their thermal habitat as environmental temperature availability changed, and phenotypic traits and environmental factors interacted to explain the size (e.g., home range), shape (e.g., horizontal movement), and direction (e.g., diel vertical migration) of adfluvial bull trout movement in Kinbasket Reservoir. To synthesize all of these findings, I will use the movement ecology framework and the current literature on bull trout behaviour and movement. I will also discuss biotelemetry, mixed-modelling, the implications for bull trout conservation, and several research opportunities.

There are five basic questions in the movement ecology framework: (*i*) *why move*? (*ii*) *how to move*? (*iii*) *where and when to move?* and (*iv*) *what are the ecological and evolutionary consequences of movement* (Figure 1.1)? The acoustic telemetry system and modern statistical techniques (discussed later) were appropriate methods for addressing these questions and by collecting data on phenotypic traits and environmental data, I could directly examine how the internal state, motion capacity, and navigation capacity interacted with external factors to produce and influence movement. For example, putative internal and external factors made it possible to hypothesize about proximate drivers and ultimate causes responsible for diel vertical migration (Chapter 3). In the following subsection I will discuss each component of the movement ecology framework as it relates to the finding of my three research chapters.

The internal state

The internal state addresses the question, "*why move*?" and there are both proximate and ultimate payoffs for choosing to move (Nathan et al. 2008). Thermal resource selection, diel vertical migration, and homerange size were each affected by variables that represented the internal state of tagged bull trout (i.e., phenotypic traits, Delgado et al. 2010). Larger individuals were predicted to experience slightly but not significantly warmer temperatures than smaller conspecifics (coefficients not shown but see Table 2.1 and 2.2), swim at the shallowest depths, and possess larger home ranges. In addition, larger females were predicted to move greater distances than smaller females. According to these results, the choice to move is related to environmental temperature and phenotypic traits. Indeed, the choice whether to move is possibly also related to the distribution of predators and prey which individuals may choose to avoid or pursue based on their internal state (e.g., body size). Additionally, larger individuals are at a decreased risk of predation due to gape limitations of piscivorous predators (Wootton 1998), although as discussed in Chapter 2, swimming at a particular depth does not directly show that predation risk/feeding opportunities are the mechanisms that drive such behaviour. Such a study would require a different approach (discussed later in the mixed-modelling and future research opportunities sections). The interaction between body size and sex illustrates internal-state dynamics across changing environmental conditions, e.g., seasons (Nathan et al. 2008, Figure 1.1). This aspect of the movement ecology framework is rarely discussed in the movement ecology literature. As with diel vertical migration hypotheses, no single hypothesis/variable is sufficient to predict behaviour. Instead, movement paths are generated from a dynamic interplay of variables that include external factors, the internal state, the capacity to move, and the navigation capacity (Nathan et al. 2008; Holyoak et al. 2008).

Motion capacity

The question of "*how to move*?" is largely related to the internal state and external factors that drive how an organism moves. For instance, movement rate is influenced by the internal state (body size) and external factors (competitors, in Chapter 3). In Chapter 4, home range size could be predicted by the internal state, navigation capacity, and the external factors that underlie seasonal change. Horizontal distance moved was also shown to differ seasonally and by the internal state and motion capacity, seasonal change (external environment and navigation capacity), and phenotypic traits. Describing how an organism moves (e.g., rate, magnitude, dispersal) in relation to, for example, external factors is the most commonly made link in the movement ecology literature (Holyoak et al. 2008). Not surprisingly, the link between motion capacity (e.g., home range size) and the environment was common among my work in Kinbasket and among other research on adfluvial bull trout movement (e.g., Brenkman et al. 2001; Wissmar and Craig 2004; Watry and Scarneccia 2008; DuPont et al. 2011). For example, depending on sex and body size, bull trout were estimated to make monthly movement ranging from approximately 5-120 km/month (Figure 4.4). While their methods to calculate monthly movement were different, Bahr and Shrimpton (2004) estimated a similar though slightly smaller range of monthly distances moved (i.e., ~ 0-75 km/month) by bull trout in the

Morice River watershed in BC. Again, these estimates are completely dependent on the step size (Rowcliffe et al. 2012) and I would suggest bull trout likely move far greater distances, perhaps an order of magnitude, than estimated from the Kinbasket system.

Speaking strictly in terms of the biomechanical aspect of movement (e.g., Dickinson et al. 2000), bull trout use body caudal fin propulsion and a sub-carangiform swimming mode (Sfakiotakis et al. 1999). Currently, literature on wild bull trout swimming performance is limited to a small number of lab studies (Mesa et al. 2004; Mesa et al. 2008). Additional data from the V-Track (Campbell et al. 2012) R package used in Chapter 3 estimated that bull trout rate of movement between telemetry receivers ranged between approximately 0.0001 m/s and 1.46 m/s. Given that these estimates are based only on Euclidean distances and the time taken by a bull trout to appear at one receiver from another, I chose not to include or model these data. Although some of these values may be accurate approximations of wild bull trout swimming behaviour, whether swimming performance was sustained, prolonged, or burst (Beamish 1978; Plaut 2001), there is no way of knowing *where and when* fish made linear movements between receivers. Here, values at the lower end suggest that bull trout took a curvilinear path before reaching another receiver whereas values at the upper end of the V-Track estimates were similar to slow sprints in this species (Mesa et al. 2008). In 2010, while undertaking a side project on injury and immediate mortality of bull trout captured in the spring troll fishery on Kinbasket Reservoir, fish regularly pursued minnow-plug lures at speeds in excess of 1.5 ms^{-1} (Gutowsky et al. 2011). Interestingly though, “wild” bull trout in the lab will not perform sprints in water temperatures of 6°C (Mesa et al. 2004) yet wild bull trout in Kinbasket were captured by trolling at speed considered "sprints" and at water temperatures of 2°C (Gutowsky et al. 2011). The field-based troll fishery capture data and lab-based bull trout swimming performance data demonstrate that more research is required on bull trout motion capacity.

In addition to locomotion through body-muscle contraction, bull trout may also use their swim bladder to change swimming depth. In fishes, the swim bladder is air-filled sac located in the coelomic cavity below the vertebral column (Holbrook and Perera 2011). Bull trout have swim bladders that are connected to the mouth by the pneumatic duct (i.e., physostomus). This allows for rapid inflation and deflation of the organ. Among its functions, the swimbladder can be used to regulate buoyancy. Holbrook and Perera (2011) suggested that physostomus fish use hydrostatic pressure to determine their depth and, by regulating their swimbladder, remain neutrally buoyant. While little is known about the energetic costs associated with hydrostatic pressure change (Speers-Roesch et al. 2004) or the exact proximate function of swimbladder regulation for DVM (Mehner 2012; Solberg and Kaartvedt 2014), it remains feasible that both swimming and swimbladder regulation are operational modes of bull trout motion capacity.

Navigation capacity

Navigation capacity addresses the questions of *where and when* to move. The choice of when and where to move is based on the goal (e.g., to attain food, mate, hide) and an environmental assessment by the sensory systems (Bleckmann 1986; Dittman and Quinn 1996; Hara and Zielinski 2006). In other words, navigation capacity largely involves input from the internal state and external factors (Figure 1.1). Although sensory mechanisms were not exclusively tested in adfluvial bull trout, the questions of *where and when* to move were integrated and addressed in each research chapter. For example, decreased availability of optimal temperatures for metabolism and growth is likely responsible for changing thermal resource selection over time (Figure 2.4). Location in the water column was related to diel period, season, and body size. Here, bull trout movement largely relates to light levels that change over a 24 hour period. Location in the reservoir (i.e., distribution) also appeared to be related to season and was repeatable across years (Figure 4.1).

Throughout my research chapters, I discussed the likely underlying goals (i.e., of bull trout) that led to the patterns observed in the telemetry data. For instance, bull trout use sensory information from the environment to move to a depth where food is most likely to be obtained (Chapter 3). DVM likely occurs in part because bull trout are visually detecting prey (Henderson and Northcote 1985; Vogel and Beauchamp 1999; Mazur and Beauchamp 2003; Muhlfeld et al. 2003). Additionally, individuals made decisions based on their body size, with the largest individuals inhabiting the shallowest water with presumably the most available light (Figure 3.3). Although reproductive migrations were not observed in this research, individuals likely use water temperature, flow, and chemical cues to commence migration and locate natal spawning grounds (McPhail and Murray 1979; Fraley and Shepard 1989; Lucas and Baras 2000; Hodgson and Quinn 2002). In winter, individuals congregated at the confluence of the Columbia and Canoe Rivers. Here, temperature change and ice cover (e.g., changes in light levels) may have resulted in this behaviour. Again, as indirectly demonstrated in the behaviour of adfluvial bull trout, individuals use sensory input from their environment and input from their internal state (Figure 1.1).

External factors

External factors represent all aspects of the abiotic and biotic environment. External factors play a key role in determining the activity and behaviour of all organisms (Holyoak et al. 2008). Given the apparent importance of temperature to cold-water stenotherms such as bull trout (e.g., Jones et al. 2013), I investigated the relationship between the amount of thermal habitat available and the temperature these animals selected. Adfluvial bull trout did exhibit thermal resource selection as the external temperature changed (Figure 2.4). In Chapter 3, I found that bull trout vertical movement was strongly related to diel period. As with other salmonids (Levy 1990, 1991; Jensen et al. 2006), activity was explained by light levels in the external environment. Additionally, the same environmental variables influence vertical activity in burbot (Harrison et al. 2013). For bull trout, environmental factors (e.g., temperature, landscape features) are often the primary focus of investigations regarding movement (e.g., Swanberg 1997; Bahr and Shrimpton 2004; Muhlfeld and Marotz 2005; Howell et al. 2010). Similarly, external factors were the most commonly investigated variable among our team's research on Kinbasket. In the literature on organismal movement, nearly 2/3 of all research examines external factors only on the occurrence or frequency of movement (Holyoak et al. 2008). As seen here in adfluvial bull trout, external factors, particularly temperature, are important modifiers of ectotherms behaviour (Bardach and Bjorklund 1957; Brett 1971; Wieser 1973; Zug et al. 2001).

The movement path

As demonstrated in the movement ecology literature (e.g., Fryxell et al. 2008; Mandel et al. 2008; Owen-Smith et al. 2010), movement paths are dependent on the scale of study and may be illustrated as steps, phases, and the lifetime track (Nathan et al. 2008). Steps are based on the difference between two points in time given the spatial and temporal scale of the study. Step length for temperature and depth was limited by the transmission rate of the telemetry tags (2-6 minutes), thus the resolution was relatively fine-scale for these studies. On the other hand, the analysis of homerange and horizontal movement required large step lengths that spanned the distance between receivers. For each study, movement-related questions were based largely on the step length and the limitations of the technology.

While some empirical investigations show tracks by individuals (e.g., Bestley et al. 2010), such movement paths are not always illustrated in studies of animal movement (Holyoak et al. 2008). Among studies of adfluvial bull trout movement, actual individual movement paths are not shown. In the Kinbasket system, individual movement paths were not the focus of any investigation, rather questions more commonly involved motion capacity while movement paths were implied and discussed. Indeed, with 187 individuals tagged in Kinbasket and a potential step length of 2-6 minutes for depth and temperature detections across one year or more, it is unreasonable to plot and present all of the individual movement paths. Instead, most of my investigations examined the fish as collective group-level patterns in behaviour and movement that were associated with motion capacity, navigation capacity, internal state, and external factors.

A synthesis of the movement ecology of adfluvial bull trout

Here I synthesize the movement ecology of adfluvial bull trout based on seasonality. Seasonal movement regards questions about when to move while also representing a period of environmental change, i.e., a change in external factors. Season is commonly associated with organismal movement, particularly in fish. For instance, reaction distances for salmonids such as lake trout (*Salvelinus namaycush*), rainbow trout (*Oncorhynchus mykiss*), and cutthroat trout (*Oncorhynchus clarki*) are dependent on light levels, the spectral properties of light, and turbidity (Henderson and Northcote 1985; Vogel and Beauchamp 1999; Wetzel 2001), which are environmental variables that change seasonally. While seasons span several months and as a predictor of movement may only explain a portion of the total variation (e.g., vertical movement, Figures 3.2 and 3.5), seasons represent periods of abiotic and biotic change that are among the most important variables for directing ectotherm behaviour (e.g., Young 1998; Nowak and Quinn 2002; Deutsch et al. 2008). Although the cut-off points for astronomical season does not necessarily correspond to all abiotic and biotic changes, astronomical season was assumed to be a reasonable approximation of biologically significant changes in the environment (Suski and Ridgeway 2009).

Winter

During winter, adfluvial bull trout experienced increasingly cold water up to a minimum average between 1 and 2°C from January to April (Figure 2.3). These patterns were evident in both 2010 and 2011. Despite the low temperatures and perhaps low-light levels due to ice cover (data on ice cover were unavailable), bull trout continued to exhibit diel-related patterns in movement including DVM and vertical movement (Figures 3.1 and 3.4). Patterns in DVM and vertical movement remained size-dependent where larger fish occupied shallower depths and performed greater depth changes. Estimates of winter homerange size were similar to summer estimates (Figure 4.3) while winter movement was low, especially for small males (Figure 4.4). However, large fish, especially females, were estimated to make horizontal movements of at least 80 km/month during the winter (Figure 4.4). Winter activity has also been shown in bull trout in Arrowrock Reservoir, Idaho (Salow and Hostettler 2004; Dare 2006), a small alpine lake in the Canadian Rocky Mountains (Whilhelm et al. 1999), and in a study on bull activity and entrainment in Kinbasket Reservoir (Martins et al. 2014). Most bull trout in Kinbasket experienced cold winter water temperatures and performed vertical movement behaviours in an area that spanned the confluence into both the Columbia and Canoe Rivers (Figure 4.1). Wild adfluvial bull trout do pursue prey in 2°C water (Gutowsky et al. 2011) and likely actively hunt during winter (Wilhelm et al.1999; Beauchamp and Van Tessel 2001). This activity, both on a vertical and horizontal plane, partly explains the relatively high likelihood of entrainment during the winter (Martins et al. 2013).

Spring

Most adfluvial bull trout were sampled by trolling in the spring when these animals are especially vulnerable to capture but resilient to angling induced stress and immediate mortality (Gutowsky et al. 2011). Given the magnitude of vertical activity (Figure 3.5), large home range sizes (Figure 4.2), and large monthly horizontal movements (Figure 4.4), it appears that adfluvial bull trout are most active during spring. Although bull trout performed vertical migrations in the spring, depth distribution was not related to body size at this time (Figure 3.3). While I attribute this anomaly to the lack of competition during spring, e.g., sympatric adfluvial rainbow trout spawn during spring, additional research is required. More so than winter, individuals were concentrated in the main basin of the reservoir (Fraley and Shepard 1989, DuPont 2011, Figure 4.1). The congregation of bull trout likely results from a combination of factors including relatively high flow, high nitrate, low conductivity, high water clarity in the confluence compared with other areas of the reservoir (Bray 2011, 2012). Based on the large home ranges and extensive horizontal movements in spring, it would appear that individuals patrolled the confluence area at this time. While sampling during spring, our team witnessed sporadic kokanee salmon activity near the surface. Kokanee are a preferred food source for bull trout during spring (Beauchamp and Van Tessel 2001) and I expect that the abiotic characteristics of the confluence are an attractant for numbers of kokanee and bull trout in this reservoir.

Summer

As expected, adfluvial bull trout experienced the warmest temperatures during summer. However, the average temperatures experienced were close to the optimal temperatures for growth and metabolism in juveniles of this species (Figure 2.3). These results are not consistent with the literature that shows final temperature preference should be markedly lower in larger fish (Coutant 1977, Elliott and Allonby 2013 and references therein). Contrary to using free-swimming fish, these studies are lab-based where individuals are not subject to numerous external factors including access to shelter, predators, and dispersed prey (Elliot and Allonby 2013). During summer, small bull trout actually experienced cooler temperatures than larger conspecifics (Chapter 2). This may indicate that adfluvial bull trout are balancing a trade-off between maximum growth efficiency and predation risk depending on body size (Jonsson and Jonsson 2011; Mehner et al. 2013; Chapter 2). As water temperatures began to cool in late-summer to early autumn, bull trout selected water temperatures that were close to the optimal temperatures for juvenile growth (Figure 2.4). Selection for such temperatures continued as the availability of these temperatures declined. In Kinbasket during summer, bull trout were observed to occupy average depths between to 10 and 20 m (Figure 3.1), suggesting that diel vertical migration occurred approximately within the window of selected temperatures and probably light levels. Bull trout made large vertical movements during the summer and, for a given body size, were predicted to occupy some of the deepest water, presumably to avoid intense summer UV light and surface temperatures that were above their apparent temperature preference of approximately 12°C to 13°C (Figure 2.3). Unlike in Lake Billy, Oregon, where adult adfluvial bull trout were only found in the river during summer (Beauchamp and Van Tessel 2001), a large proportion of tagged Kinbasket bull trout (70%, 131/187) were found most evenly distributed across the reservoir where they possessed small home ranges and made small horizontal movements during approximately the same time frame (Figures 4.1 and 4.4). In Kinbasket, at least some individuals certainly spent time in the reservoir during summer where they selected optimal water temperatures and performed DVM within a limited area. In summary, the summer was the period when bull trout experienced the warmest temperatures, occupied deep water, and made limited horizontal movements that were dependent on sex and body size.

Autumn

In autumn, bull trout temperature experience dropped sharply (Figure 2.2) and as the warmest temperatures became less available (Figure 2.1), thermal resource selection increased for this temperature category (Figure 2.4). DVM continued to occur in the autumn when the observed data reflected the most prominent patterns of descent at dawn and ascent at dusk (Figure 3.1). Home range size and horizontal movement were maximized during the autumn, presumably because at least some of the tagged individuals had migrated into tributaries to reach spawning grounds, and because cooling water temperatures led to increased activity (Figures 4.3). Kokanee salmon also spawn during fall and it has been suggested that adfluvial bull trout may move into and out of spawning tributaries to feed (Beauchamp and Van Tessel 2001; Barnett and Paige 2013). The body condition for bull trout in Kinbasket is poor during the late-summer to early autumn (Nitychoruk et al. 2013) and likely declines further after spawning (Mushens and Post 1997; Wilhelm et al. 1999). Whereas the summer is a period of relative inactivity for adfluvial bull trout, movement significantly increases during the autumn (DuPont et al. 2011). This remains true for bull trout in both lakes and rivers (Bahr and Shrimpton 2004). I suspect the increase in activity is likely for reproductive purposes and to build fat stores for the winter. However, these hypotheses remain to be tested.

Biotelemetry and mixed-modelling for movement ecology

Biotelemetry

For the past 50 years biotelemetry has been a useful means of studying the movement of free-ranging organisms (Stasko and Pincock 1977; Kephart 1980; Cooke et al. 2004). For adfluvial bull trout, the characteristics of acoustic biotelemetry, namely its ability to transmit signals in deep water (Heupel et al. 2006), rendered it the best system for recording data on free-ranging individuals in Kinbasket Reservoir. Since the internal application of transmitters required handling individuals, I was able to collect information on phenotypic traits including body size and sex (e.g., Delgado et al. 2010). Once the animal was released, the internal clock of the acoustic biotelemetry system made it possible to align the times of relocations to external factors such the time of day, times for sunset and sunrise, and astronomical season. Then, given the questions and hypotheses, I could then pair explanatory variables (e.g., external factors) with a response variable (e.g., a measure of motion capacity) and use mixed-modeling techniques and model selection as a means to test hypotheses (Anderson et al. 2000).

Mixed-modelling and model selection to analyse movement data from biotelemetry

By collecting data from multiple individuals and analysing data with mixed-modelling techniques, I was able to use biotelemetry to make generalized inferences about adfluvial bull trout (Giuggioli and Bartumeus 2010; Cooke et al. 2004). As discussed in Chapter 4, biotelemetry data are well suited to mixed-modelling because they are easily paired (spatially and temporally) with additional data about the environment and the individual organism. A random intercept for each individual assumes that observations from an individual are more alike to one another than to those from another individual. Random effects have a certain mean and variance that can be included in the model and thus allow for general statements about the group (e.g., population).

Once the appropriate fixed and random components have been identified (i.e., *a priori* hypothesized biologically significant explanatory variables, Anderson et al. 2000), telemetry data can be analysed using a model selection procedure. I used multiple approaches to select the best model to explain adfluvial bull trout movement. For instance, based on model P-values , backwards model selection, or an information theoretic approach. The model selection procedure depends on the initial questions and hypotheses. For example, in Chapter 4 I used backwards model selection to provide the relative contribution of individual terms in the nested models, which was useful for interpreting the biological importance of the hypothesized covariates of these models (Zuur et al. 2009). Temperature experience data (Chapter 2) were analyzed using an information theoretic approach, where all possible models were *a priori* assumed to require a smoothing function for day. Models were then built up to a set of candidate hypotheses (Burnham and Anderson 2002). The information theoretic approach was useful because I was able to evaluate multiple non-nested models, quantify the relative support for multiple models simultaneously, and if necessary, derive predictions that account for model uncertainty using model averaging (Burnham and Anderson 2002; Zuur et al. 2009).

While statistically significant variables may reveal the actual mechanism behind movement, others may only illustrate a weak correlative relationship or be indirect reflections of the actual underlying mechanisms. For example, size-dependence in diel vertical migrations was speculated to be a result of predator-prey interactions that were not measured. By modelling time in Chapter 2 and Chapter 4, I was able to illustrate patterns that reflect the spatial and temporal coordinates of missing covariates, which can also be identified in residual plots (Zuur et al. 2009; Cleasby and Nakagawa 2011; Field et al. 2012). If patterns exist in the residuals, further extensions of modern mixed-modelling packages (e.g., variance structures in nlme, Pinheiro et al. 2013) can be included, e.g., to reduce any bias associated with heterogeneity. Alternatively, residual patterns can indicate missing covariates (Zuur et al. 2009). Bull trout biotelemetry data were often correlated in time or the levels of a particular predictor heterogeneous (e.g., season, Table 4.2) and thus required these extensions to improve model fit and reduce the bias associated with a lack of data independence or heterogeneity. However, the results of a mixed-model are only as good as the data. This was illustrated by the large differences between adjusted R^2 values in Chapter 2 and the model for horizontal movement in Chapter 4. Although I suggest the poor fit by the smoother in Chapter 4 would have likely improved with a smaller step size (e.g. daily rather than monthly measurements of movement), there were too few receivers to generate such estimates. While biological studies commonly report R^2 values ranging from only 2.5-5.4% (Møller and Jennions 2002), the reasons for under fit and over fit data ($R^2 = 1$) should be considered prior to the interpretation of mixed-model results.

Movement ecology and bull trout conservation

In Kinbasket Reservoir, bull trout moved little during winter months and appear to spend much of the winter and spring in the confluence of the Columbia and Canoe Rivers (Figure 4.1). Despite limited activity in winter, the congregation of individuals near the Mica generating station (near Mica Creek Townsite, Figure 4.1) supports Martins et al. (2013, 2014) who demonstrated that winter is the period when bull trout are most vulnerable to turbine entrainment through the Mica Dam (Figure 1.5); a process that can lead to injury and mortality, significant losses to fish populations, and reduced fisheries productivity. Furthermore, bull trout diel vertical migration, which was yet to be described prior to Chapter 3, was supported by Martins et al. (2013) who also found evidence of this behaviour. The results of Chapter 3 are directly relevant to bull trout management as entrainment risk is likely related to swimming depth, time of year, and turbine depth in other reservoir systems. Currently, the US Environmental Protection Agency currently has regulations and guidelines to manage the entrainment of endangered salmonid species in the Columbia River (Skalski et al. 2012). Similarly, Canada is in the process of developing national guidelines to manage the impacts of entrainment of fish at large and medium intakes (Chen and LeBlanc 2013). The current research on Kinbasket adfluvial bull trout movement ecology draws a connection between spatial ecology and the risks of entrainment to bull trout in this system. Our work also provides an example for similar projects in systems across Canada. Here, our team's research on bull trout movement has provided direct and important contributions to the species' conservation, and perhaps to the development of national guidelines on entrainment.

Research opportunities

Measuring temperature was particularly challenging in Kinbasket Reservoir. Water levels fluctuate nearly 50 m during the course of a year (Martins et al. 2013) and thermal loggers could only realistically be tethered to receiver anchor rope and shore structures during low pool. In addition, it was financially unfeasible to attach thermal loggers to every receiver anchor rope. Water temperature could only be calculated at one or two locations in the reservoir and I did not have additional paired data to examine how bull trout might select temperatures based on trade-offs with other factors that occur in pelagic habitat. Based on my current finding, I would hypothesize that temperature and light play the most important roles for determining the depth at which bull trout inhabit.

To ensure the data are continuous, an experiment to test this hypothesis would best be carried out in an environment where receivers have full coverage of the available pelagic habitat for bull trout, e.g., in a small lake (Wilhelm et al. 1999). Full coverage would ensure that multiple individuals were detected during any given sampling interval and that thermal data would be collected in three dimensions. The sampling interval for all data would be hourly, though I would consider examining movement at multiple spatial and temporal scales (Fryxell et al. 2008). In addition, I would hypothesize that lunar period (Gaudreau and Boisclair 2000), body size, and sex may affect movement. Such a study design would provide the opportunity to explore trade-offs that affect movement behaviour at multiple spatial and temporal scales.

Prey distribution was hypothesized to affect the vertical migration of pelagic piscivores, such as bull trout (Chapter 3). Part of the original proposal, resources for kokanee behaviour and entrainment were reallocated to focus on bull trout and burbot research (e.g., Harrison et al. 2013; Martins et al. 2012; Martins et al. 2014). However, kokanee and bull trout movement could be studied simultaneously in Kinbasket. I would recommend a study design that continues to monitor bull trout using acoustic telemetry while acoustic sonar trawls are performed during the day and night to monitor the depth distribution of kokanee. Since sonar can resolve different size classes of fish (Busch and Mehner 2012), it would be possible to perform the first study on size-dependent diel vertical migration simultaneously in predators and prey.

Unlike sex, body size is not fixed in bull trout. However, for modelling purposes, body size was assumed to be fixed for bull trout over the study period. While it may be reasonable to assume that the largest individuals grew little over this period, smaller individuals probably grew faster (Wootton 1998). In addition, there is evidence that males grow marginally faster (1 cm/year) than females (Stelfox 1997). Even moderate changes in total length (e.g., 5 cm/year) for small bull trout could potentially modify behaviour and if the patterns of size-dependent diel vertical migration and movement are true, one would predict these to change according to growth. It is known that compared to insectivorous bull trout, growth is relatively rapid for adfluvial bull trout that feed primarily on kokanee salmon and whitefish (Donald and Alger 1993). If growth rate for adfluvial bull trout in Kinbasket was known, statistical models could include a dynamic measure of body size. However, currently data on bull trout growth rate are lacking for Kinbasket Reservoir. Following methods to investigate growth of free-ranging fish (e.g., Gunckel et al. 2002; Stelfox 1997; Donald et al. 1993), future work could investigate how movement is influenced by body size as it changes across time.

Conclusion

A large number of studies are incorporating a suite of movement ecology components to make inferences about the movement of free-ranging animals (e.g., Fryxell et al. 2008; Maritz 2011; Hansen et al. 2013). Here I used biotelemetry and mixed-modelling of adfluvial bull trout data to explicitly test hypotheses about thermal resource selection, size-dependent diel vertical migration, and body size and sex related influences on movement. The results from my research provided several novel insights into resource selection, DVM, and how phenotypic traits are related to movement. These insights could be applied in other studies and to other species, for instance temperature selection as temperature availability changes is likely illustrated by other temperature-sensitive organisms. Size-dependent DVM probably occurs in a variety of piscivorours fishes. Additionally, research on Kinbasket adfluvial bull trout has added to the growing number of studies that describe movement in this understudied migratory life history form (e.g., Brenkman et al. 2001; Wissmar and Craig 2004; Barnett and Paige 2013) while also providing relevant information for bull trout management and conservation. Specifically, Kinbasket bull trout appear to rarely occupy areas surrounding the Bush Arm (Figure 4.1). Thus efforts to either mitigate or compensate for entrainment related losses ought to focus on locations that are more frequently inhabited by bull trout, for example tributaries of the confluence and Hugh Allen Creek (Figure 4.1). To summarize, the biotelemetry system and study design provided excellent means through which to test hypotheses related to behaviour in free-ranging organisms whereas the movement ecology framework provided a means to synthesize the findings and describe the movement ecology of an important and relatively poorly understood species.

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