

Interactive effects of sex and body size on the movement ecology of adfluvial bull trout (*Salvelinus confluentus*)

L.F.G. Gutowsky, P.M. Harrison, E.G. Martins, A. Leake, D.A. Patterson, M. Power, and S.J. Cooke

Abstract: Animal movement occurs as a function of many factors including changing environmental conditions (e.g., seasonality) and the internal state (e.g., phenotypic traits) of the focal organism. Identifying how these factors interact can reveal behavioral patterns that would otherwise go undiscovered. Given a large sample size of individuals ($n = 187$), we used acoustic biotelemetry to examine the spatial ecology of adfluvial bull trout (*Salvelinus confluentus* (Suckley, 1859)) in a large hydropower reservoir in British Columbia, Canada. Dependent variables, including home-range size and lateral movement, were analysed as a function of interactive relationships among seasons (over a 2-year period) and phenotypic traits. Mixed models indicated relationships between home-range size and season, whereas variation in lateral movement was explained by month and a two-way interaction between sex and body size. Large females (765 mm total length) were estimated to move laterally up to five times greater than females half their length, whereas movements between large and small males were not significantly different. This study shows how body size and sex can have a profound and possible interactive effect on animal movement. In addition, the results offer new information on the spatial ecology and conservation of adfluvial bull trout.

Key words: spatial ecology, home range, phenotypic traits, biotelemetry, char.

Résumé : Les déplacements des animaux sont fonction de nombreux facteurs dont des conditions ambiantes changeantes (p. ex. la saisonnalité) et l'état interne (p. ex. des caractères phénotypiques) de l'organisme concerné. La détermination des interactions entre ces facteurs peut révéler des motifs comportementaux qui, autrement, resteraient non décelés. Étant donné un grand échantillon d'individus ($n = 187$), nous avons utilisé la biotélémétrie acoustique pour examiner l'écologie spatiale de truites à tête plate (*Salvelinus confluentus* (Suckley, 1859)) adfluviales dans un grand réservoir hydroélectrique en Colombie-Britannique (Canada). Des variables dépendantes, dont la taille du domaine vital et les déplacements latéraux, ont été analysées en fonction de relations interactives d'une saison à l'autre (sur une période de 2 années) et de caractères phénotypiques. Des modèles mixtes indiquaient des relations entre la taille du domaine vital et la saison, alors que les variations des déplacements latéraux s'expliquaient selon le mois et une interaction bilatérale entre le sexe et la taille du corps. Il a été estimé que les grandes femelles (longueur totale de 765 mm) se déplaçaient latéralement jusqu'à cinq fois plus que les femelles deux fois moins longues, alors qu'il n'y avait pas de différence significative entre les déplacements des grands et petits mâles. L'étude illustre comment la taille du corps et le sexe peuvent exercer un important effet interactif possible sur les déplacements des animaux. Les résultats fournissent en outre de nouveaux renseignements sur l'écologie spatiale et la conservation des truites à tête plate adfluviales. [Traduit par la Rédaction]

Mots-clés : écologie spatiale, domaine vital, caractères phénotypiques, biotélémétrie, omble.

Introduction

Animal movement is a necessary component of wildlife management and is increasingly investigated in the ecological and behavioral sciences (Caro 2007; Holyoak et al. 2008). Identifying behavioral modifications in relation to both phenotypic traits and their interactions with environmental factors provides novel insights into the movement of free-ranging animals (Fryxell et al. 2008; Delgado et al. 2010). Indeed, interactive relationships may illustrate otherwise overlooked patterns in behavior, e.g., movement in the reproductive and nonreproductive periods with respect to sex- and size-based habitat selection (Sims 2005; Barnett et al. 2011; Laidre et al. 2013).

The movement ecology framework (Nathan et al. 2008) has been applied to explain movement in a variety of free-ranging organisms (e.g., bluefin tuna, *Thunnus maccoyii* (Castelnau, 1872); Bestley et al. 2010; elk, *Cervus elaphus* L., 1758; Fryxell et al. 2008); Eurasian Eagle-Owl, *Bubo bubo* (L., 1758); Delgado et al. 2010). Most often, this research focuses on environmental factors and the internal state of the focal individual (Holyoak et al. 2008). Especially for fish and other aquatic ectotherms, optimal environmental conditions (e.g., temperature) for growth, reproductive tissue development, and survival can differ across body sizes and between the sexes (Hanson et al. 2008; Wearmouth and Sims 2008; Elliott and Allonby 2013). Thus for a given phenotype, activity predictably differs according to seasonal changes in the environment. For

Received 22 May 2015. Accepted 19 September 2015.

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example, in broadnose seven-gill sharks (*Notorynchus cepedianus* (Péron, 1807)), 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). Although these effects may be expressed as additive or multiplicative between a phenotypic trait and an environmental factor (e.g., diel period and body size), it is less common to find examples on the interplay between phenotypic traits, i.e., “internal-state dynamics” (sensu Nathan et al. 2008). Once such example is the multiplicative effects of body size and sex on the activity of individual organisms over a range of environmental conditions (e.g., seasons). While such an investigation may illustrate previously undescribed patterns in spatial ecology, there are significant challenges associated with studying free-ranging animals such as fish, which spend their entire lives underwater.

Biotelemetry and biologging are effective tools for studying free-ranging and cryptic animals such as fish (Cooke et al. 2004; Cagnacci et al. 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 sex, 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).

Bull trout (*Salvelinus confluentus* (Suckley, 1859)) are a glacial relict char that can exist in populations with one of several life-history strategies including resident, fluvial, adfluvial, and anadromous (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. The fitness benefits of an adfluvial life history and the associated foraging strategy of adults in reservoirs, including cannibalism (Beauchamp and Van Tassell 2001), result in a wide range of body sizes including some of the largest attained by the species (up to 100 cm total length (TL); Goetz 1989). Nevertheless, many populations of bull trout are in decline as a result of barriers to migration, habitat degradation, overfishing, and poor water quality (Schmetterling 2003; Johnston et al. 2007; Kiser et al. 2010). Today the species is listed as special concern or threatened in the USA and Canada (U.S. Fish and Wildlife Service 1999; Post et al. 2012). Bull trout are widely considered one of the least understood char and relatively little is known about the spatial ecology of adfluvial populations (Dunham et al. 2008).

Here we investigate correlative factors of movement ecology of adfluvial bull trout across multiple seasons and years in a large hydropower reservoir in British Columbia, Canada. We posited that patterns emerging from the influence of phenotypic traits would (i) demonstrate novel relationships between and among phenotypic traits and environmental factors that affect animal movement, (ii) provide information on the spatial ecology of adfluvial bull trout, and (iii) generate specific information relevant to bull trout in Kinbasket Reservoir where the population is at risk of entrainment (Martins et al. 2013, 2014). We tagged and sexed a wide size range of individuals ($n = 187$, approximately 350–880 mm TL) 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 that both additive and multiplicative effects among phenotypic traits and environmental factors influence home-range size and lateral movement. Given that large-bodied individuals possess the capacity to swim at the highest speeds (Ware 1978; Lightfoot and Jones 1996), body size was predicted to be positively correlated with

both home-range size and lateral movement. Given the species' low thermal optima (Selong et al. 2001), we predicted activity (i.e., lateral movement) to be greatest during cooler periods of the year. Furthermore, given that eggs are more energetically costly to produce than sperm (Gowan and Fausch 1996; Wootton 1998), we expected these costs to be reflected in the activity of bull trout such that large females would possess the largest home ranges and exhibit the greatest movement as a way to locate prey.

Materials and methods

Study location

Kinbasket Reservoir is located in the Kootenay – Rocky Mountain region of British Columbia, Canada (52°8'N, 118°28'W; Fig. 1). The reservoir was formed in 1973 by the construction of Mica Dam (6 km north of Mica Creek town site; Fig. 1) and the subsequent impoundment of four major rivers: the Columbia, Canoe, Wood, and Bush. At high pool during summer and fall, Kinbasket covers at least 425 km², making it among the largest lakes in British Columbia. The reservoir also experiences extreme seasonal fluctuations in water levels (up to 47 m), which may decrease by up to 50% of the maximum surface area during low pool (i.e., during winter). Mean reservoir depth is approximately 57 m, with a maximum of 190 m. In addition to bull trout, Kinbasket contains a number of important recreational fishes including kokanee salmon (*Oncorhynchus nerka* (Walbaum in Arty, 1792)), which is considered the principal prey for bull trout, burbot (*Lota lota* (L., 1758); Harrison et al. 2013), and rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)). Water turbidity and conductivity in the system vary widely due to the many glacial and snowmelt streams that drain into the reservoir. Surface temperatures in Kinbasket range from 2 to 15 °C from April to May and can reach 25 °C in August and September (Bray 2012). In general, both forebay measurements and instantaneous measurements from the reservoir indicate that during summer, temperature profiles are nearly linear from the surface down to the hypolimnion layer (Robertson et al. 2011).

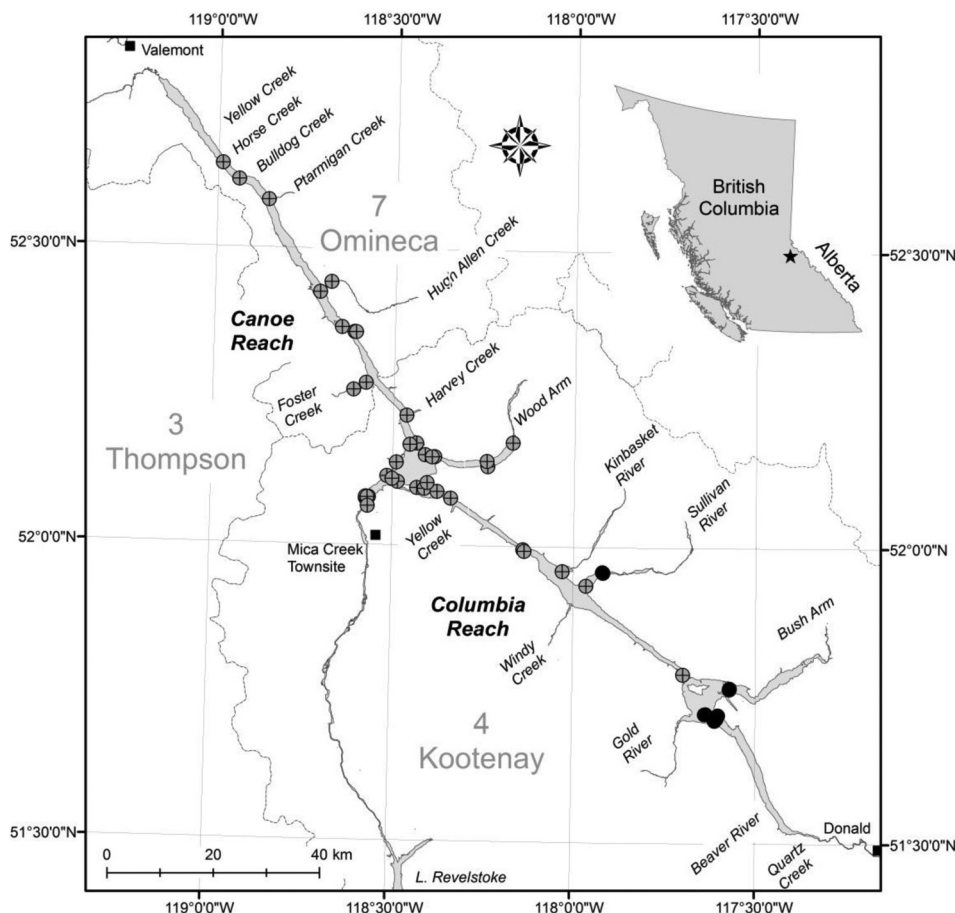
Hydrophone deployment

To track fish, 42 omni-directional VR2W hydrophones (Vemco, Halifax, Nova Scotia, Canada) were deployed in Kinbasket Reservoir between 1 and 5 May 2010 (Fig. 1). In the current study, the detection radius for each hydrophone was approximately 500 m (Shroyer and Logsdon 2009), resulting in an estimated maximum total hydrophone listening area of 33 km² (7.8% of the reservoir area). Hydrophones were placed in locations that 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 <500 m), and the deltas and mouths of known spawning tributaries (Fig. 1). In the spring of 2011, hydrophones were retrieved, downloaded onto a laptop using the program VUE (Vemco, Halifax, Nova Scotia, Canada), and re-deployed at the original location. In the spring of 2012, hydrophones were once again retrieved and the data downloaded. In year 1, no hydrophones were lost. In year 2, 5 of the 42 hydrophones were lost, likely due to unusually low water levels and spring-time ice movement (Fig. 1).

Tagging

Bull trout were sampled from 11 April to 25 May 2010 by trolling throughout the reservoir and near the water surface where the species is commonly found in the spring ($n = 122$; Gutowsky et al. 2011). In summer, bull trout were captured by angling at the mouths of known spawning tributaries (from 18 August to 9 September 2010) where fish congregate prior to upstream migration ($n = 65$). Sampling areas in the summer included tributaries in the Canoe Reach (Yellow, Horse, Bull Dog, and Ptarmigan creeks; $n = 37$; Fig. 1) and tributaries in the Columbia Reach (Beaver River and Quartz Creek; $n = 28$; Fig. 1). Upon capture, fish were placed in a 100 L cooler filled with lake water that was regularly replaced. Bull

Fig. 1. Kinbasket Reservoir in the Kootenay – Rocky Mountain region of British Columbia. Circles represent telemetry hydrophone locations. Grey circles with crosshairs represent hydrophones that collected data for the full 2-year period. Black circles represent hydrophones that were lost in the second year of the study period. Regional boundaries are labelled and shown by a grey dotted line.



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 (as 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 millimetre) was measured prior to surgery. For biotelemetry tag insertion and sexing, a 3 cm long incision was made posterior to the pelvic girdle. Sex was determined by internally examining the gonads (males: small clear to white gonads; females: yellowish gonads containing small to large eggs). A coded acoustic transmitter (model V13 TP; transmissions every 1–3 min) was then inserted into the body cavity. Incisions were closed using three simple interrupted stitches. Postsurgery fish were placed in a recovery bath of fresh water, allowed to fully regain equilibrium, and released.

Data management and filtering

Two years (2010–2012) of biotelemetry data from tagged bull trout were first filtered to remove false detections and incomplete tag-to-hydrophone transmissions. The minimum number of hydrophone detections per individual bull trout was set at two per hydrophone per 24 h period. Since surgical procedures may affect behavior for a short time following surgery (Rogers and White 2007), analyses were only carried out on data collected 7 days after tagging. In addition, detections used were those recorded after the final hydrophone was deployed in May 2010. A final data filter was applied to eliminate estimates from fish that were detected a few times during a season (arbitrarily set to <5 detections/season).

Data filtering and exploration was conducted using Microsoft Access and the R statistical environment (R Core Development Team 2012).

Analyses

Seasonal spatial distribution

Seasonal spatial distribution was quantified by assessing the percentage of tagged bull trout that visited each hydrophone across Kinbasket Reservoir per season. Percentages were used to account for an uneven total number of individuals detected per season. Because hydrophones were irregularly spaced, the estimates were imported into ArcGIS version 10.1 (Environmental Systems Research Institute (ESRI), Inc., Redlands, California, USA), 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 2003; Hagen-Zanker et al. 2006). Fuzzy Kappa compares the similarity of overlaid map cells and their neighbours where values range between zero (distinct) and one (identical). Mean map similarity was expected to be moderate to high (0.6–0.8; Landis and Koch 1977) between same seasons during the 2-year study period. Statistics were generated using the Map Comparison Kit software version 3.2.3 (Research Institute for Knowledge Systems (RIKS) BV, Maastricht, the Netherlands; available from <http://www.riks.nl/mck/index.php>).

Home-range size

For the analysis of home-range size, we examined the data at the seasonal level where seasons included spring (April–June),

Table 1. Sample size by year, season, sex, and body size (total length (TL)) for the home-range size and lateral movement analyses of adfluvial bull trout (*Salvelinus confluentus*).

Factor	Home range				Lateral movement			
	Count		Range (TL; mm)		Count		Range (TL; mm)	
	Female	Male	Female	Male	Female	Male	Female	Male
Year 1								
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
Year 2								
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

summer (July–September), fall (October–December) and winter (January–March). Seasonal classifications 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 \times year). Home-range size of individual bull trout 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 provide data 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 (Marshall et al. 2011). In the current study, home-range size was calculated as the maximum value that provided estimates for the greatest number of individuals (in this case 90% MCPs). Estimates of MCP home-range size were exported to ArcGIS version 10.1, clipped to a GIS layer of the reservoir, and recalculated in square kilometres. Home-range size was calculated for each individual by season and year.

Lateral movement

Distances between hydrophones were calculated in ArcGIS version 10.1 and used to estimate lateral 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 at unique hydrophones. Since this method almost certainly underestimate distances as time scale is increased and do not account for tortuous movements between hydrophones (Rowcliffe et al. 2012), we generated monthly estimates 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). The minimum number of detections to define a residence event was set at two. Hydrophone residency for a bull trout was assumed to be terminated when approximately 30 min elapsed between detections at the same hydrophone or when the individual was recorded at a different hydrophone. 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

Home-range size and total monthly displacement of bull trout were analysed using a generalized linear mixed-effects model (GLMM) and a generalized additive mixed-effects model (GAMM), respectively. For the analysis of home-range size, we began the model-selection procedure with the full model that included year, season, and sex as categorical factors, body size (TL in millimetres) as the continuous covariate, and all two-way interactions. For the analysis of lateral movement, model selection began with a full model that included month as a cyclic smoothing factor (Wood 2000, 2006) and sex, body size, and the sex \times 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). Rather than transforming the response, which can potentially alter its relationship with predictor variables (Zuur et al. 2009), the model for home-range size included a variance structure that accounted for residual heterogeneity (constant variance structure). Models were fitted to the data using the R packages “nlme” (Pinheiro et al. 2013) and “mgcv” (Wood 2000, 2006). To determine the most parsimonious model for home-range size and lateral movement, backwards model selection was performed using log-likelihood ratio tests using maximum-likelihood estimation where $\alpha = 0.05$. We validated the final models by examining autocorrelation plots and by plotting the residuals against all variables, including those not retained in the final model (Zuur et al. 2009). Final models were updated using restricted maximum-likelihood estimation. The R package “multcomp” was used to examine all pairwise comparisons between the considered categorical factors for home-range size (Hothorn et al. 2008).

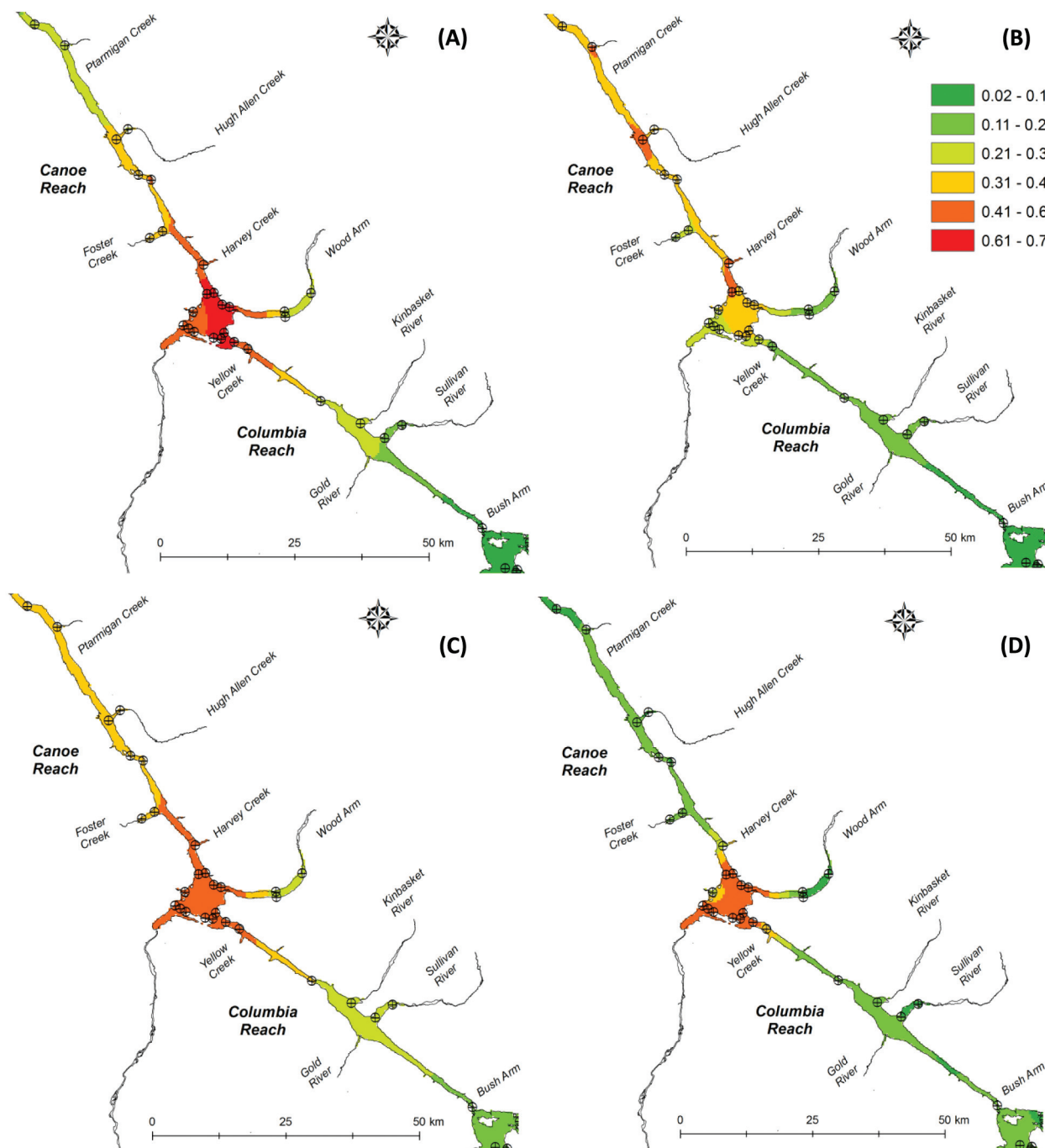
Results

Data were collected from May 2010 to May 2012, yielding 3.5 million detections of bull trout. Body size ranged from 362 to 881 mm TL, with $20.4\% \pm 0.11\%$ (mean \pm SD) more males detected across all seasons and years (Table 1). More than 20 individuals of either sex were available for analysis within any given season over the 2 years (Table 1).

Seasonal spatial distribution

Between the two years, the fuzzy Kappa analyses showed that seasonal-spatial distribution was moderately to highly similar (spring_{Year1&Year2} = 0.741; summer_{Year1&Year2} = 0.744; fall_{Year1&Year2} = 0.754; winter_{Year1&Year2} = 0.58), suggesting that seasonal-spatial distribution of bull trout was consistent across

Fig. 2. Proportion of individual bull trout (*Salvelinus confluentus*) detected in different areas of Kinbasket Reservoir during the spring (A), summer (B), fall (C), and winter (D) of the first year of the study (2010–2011). The total number of individuals detected by season was as follows—spring: $n = 121$; summer: $n = 131$; fall: $n = 156$; winter: $n = 146$. Colour online.



years. Qualitatively, spatial distribution in year 1 varied by season where individuals were largely concentrated in the confluence in spring, becoming increasingly dispersed over summer to the fall, and again concentrated at the confluence during winter (Figs. 2A–2D). Specifically, the greatest proportion of individuals was detected in a relatively small area at the confluence of the Canoe and Columbia reaches during spring (up to 84 tagged individuals in a 45 km² area) and winter (up to 39 individuals in a 68 km² area; Figs. 2A and 2D, respectively). In the summer, the greatest number of individuals (up to 44) was detected in small areas near several named creeks in the Canoe Reach (Fig. 2B). Although the Columbia Reach represented a large portion of the reservoir surface area

during summer (approximately 110 km² 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 (approximately 75 km) from the Canoe Reach south to the Kinbasket River in the Columbia Reach (Fig. 2C). Despite tagging bull trout south of the Bush Arm, few bull trout were detected near the southern end of the Columbia Reach (Sullivan River south to the Bush Arm; Figs. 2A–2D).

Home-range size

Backwards model selection indicated that only season was significant for predicting the 90% MCP home-range size of bull trout

Table 2. Summary of the importance of individual terms, including a variance structure (var) for the GLMM on home-range size of adfluvial bull trout (*Salvelinus confluentus*).

Model	Model term	t	L ratio	df	P
GLMM: home-range size	Intercept	16.2			<0.0001
	Season		52.6	3	<0.0001
	(var)		53.3	3	<0.0001
GAMM: movement	Intercept	1.64			0.139
	TL		22.2	2	<0.0001
	Sex		10.2	2	0.007
	Sex × TL		7.05	1	0.008

Note: GLMM, generalized linear mixed-effects model; GAMM, generalized additive mixed-effects model; TL, total length.

(L ratio, $L_{[1]} = 52.6$, $P < 0.0001$; Table 2). In the spring and fall, individuals were estimated to occupy a 90% MCP home range of approximately 50 km², respectively. In the summer and winter, 90% MCP home-range size was estimated to cover an area approximately 30% smaller than that of the spring and fall (Fig. 3). Home-range size was similar between winter and summer ($z = 0.6$, $P > 0.05$) and spring and fall ($z = 0.05$, $P > 0.05$), whereas all other comparisons of seasonal home-range sizes were significantly different (in all cases, $P < 0.01$; Fig. 3).

Lateral movement

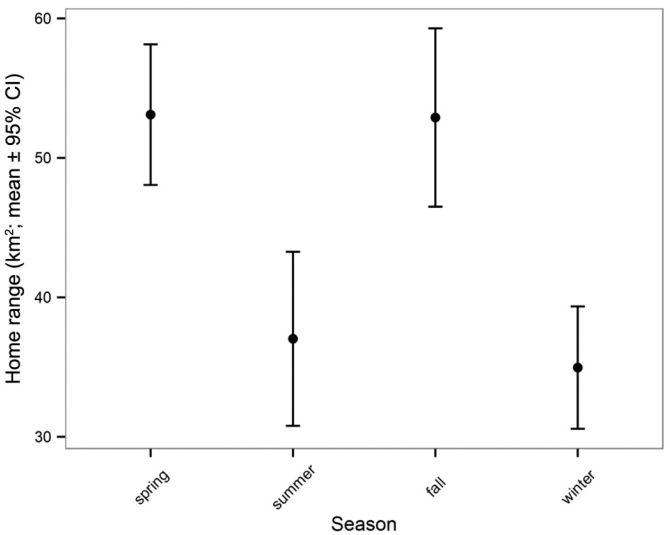
The full model was the most parsimonious model to explain total monthly displacement (km) in adfluvial bull trout (Table 2). The smoothing term, coded as a numerical variable, was significant and showed patterns in total monthly displacement across 2 years for male and female bull trout (male: $t_{[6,8]} = 8.6$, $P < 0.0001$; female: $t_{[12,3]} = 8.3$, $P < 0.0001$). On average, large fish (765 mm TL) were predicted to move greater distances than small fish (400 mm TL) in a given month; however, the difference was significant only among females (Fig. 4, Table 2). For females during a given month, large fish were predicted to move as much as five times farther than smaller conspecifics (Fig. 4). The predicted trend in movement indicated that lateral movement was greatest in the spring (May through June) and fall (October through December), while exhibiting the least lateral movement during the winter months (January through March). Although patterns remained consistent across seasons for the 2 years, the amplitude of these patterns across years was higher in the fall months for year 1 than in year 2, both for males and females (Fig. 4). The mean (\pm SD) differences in predicted monthly movement between years for the months of August through December were 14.9 ± 7.3 km for small males, 23.1 ± 5.7 km for small females, 15.0 ± 7.3 km for large males, and 23.1 ± 5.7 km for large females.

Discussion

Movement of adfluvial bull trout was dependent on the environmental conditions present across seasons and a multiplicative relationship between sex and body size. While our general hypothesis was correct, all of our predictions were not, i.e., sex and body size did not explain both home-range size and movement (Table 2). The interaction between sex and body size illustrates the importance of investigating multiplicative relationships between phenotypic traits or environmental factors on animal movement. Although movement patterns are largely descriptive in nature, they nonetheless provide insights into the mechanisms that shape animal movement and, more specifically, here generate new information about an endangered and vulnerable species of freshwater fish (Dunham et al. 2008).

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). However, similar to conspecifics with a fluvial life history (Schoby and Keeley 2011), body size was not a significant predictor of home-range size

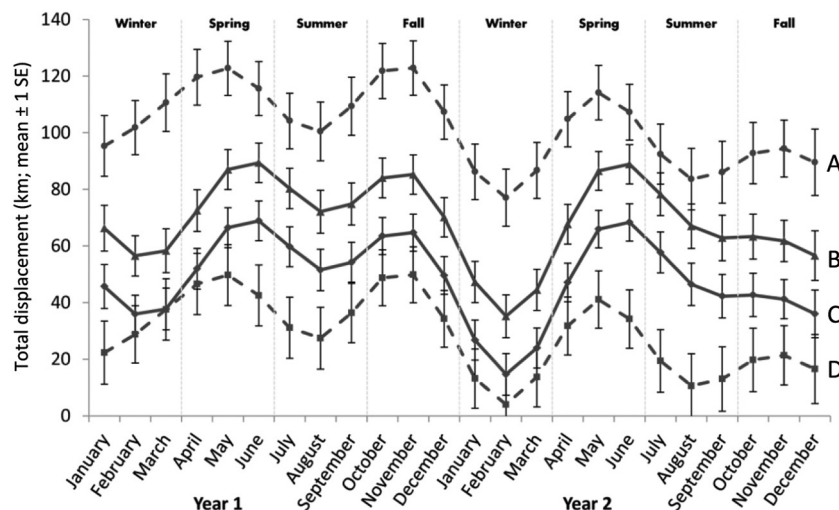
Fig. 3. Generalized linear mixed-effects model (GLMM) predictions of home range (km²; mean \pm 95% CI) of adfluvial bull trout (*Salvelinus confluentus*) by season in Kinbasket Reservoir, British Columbia.



of adfluvial bull trout. Although the exact mechanism remains uninvestigated, it is possible that the distribution and abundance of food resources may not necessitate larger home ranges for large individuals (i.e., optimal foraging theory; Pyke 1984). As with body size, sex was not a significant predictor of home-range size (Table 2, Fig. 4). Home-range size is not always different between the sexes (Norman and Jones 1984), and the relationships between sex, body size, home range, and movement tend not to be universal among fishes (Croft et al. 2003).

The multiplicative relationship between sex and body size of adfluvial bull trout is an example of internal-state dynamics (Nathan et al. 2008). Although body size is a phenotypic trait that also explains how an animal moves, many animals recognize their body size relative to conspecifics and react to environmental stimuli accordingly. There are adaptive consequences for sex- and size-based differences in behavior or activity and such relationships are common in aquatic vertebrates, e.g., sexual-size dimorphism related to growth and behavior both during and outside of the breeding season (Henderson et al. 2003; Rennie et al. 2008; Nitychoruk et al. 2013). For adfluvial bull trout, differences in activity related to sex and body size likely have important consequences for growth and maturation. 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 with 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 total monthly displacement was explained by a body size and sex interaction where large females moved significantly farther than small individuals of the same sex, but large and small males performed similar movements (Table 2, Fig. 4). In fish, sex-based differences in activity are relatively common (Wearmouth and Sims 2008). For example, similarly-sized male and female small-spotted catshark (*Scyliorhinus canicula* (L., 1758)) have been shown to differ in activity, where females exhibit more intense foraging behavior than males (Kimber et al. 2009). Compared with similarly-sized males, the relatively high activity in large-sized females may be due to the greater energy requirements for reproductive tissue development including egg production (Hendry and Berg 1999; Kimber et al. 2009; Yong and Grober 2014). Body size is positively correlated with foraging time when large preys 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

Fig. 4. Predicted lateral movements (km; mean \pm 1 SE) of large female (765 mm total length (TL); dashed line with round markers; A), small female (400 mm TL; dashed line with square markers; D), large male (solid line with triangle markers; B), and small male (solid line with diamond markers; C) bull trout (*Salvelinus confluentus*) across 2 years in Kinbasket Reservoir, British Columbia.



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 Anholt 1993). Although large males may prefer larger prey than smaller individuals of the same sex, the difference in activity here is marginal (Fig. 4). To meet the energetic requirements associated with female reproduction, large mature females may spend more time foraging, in their home range, while searching for rare but optimally-sized prey. The benefits could include increased encounters with optimally-sized prey (Werner and Anholt 1993), better body condition (Nitychoruk et al. 2013), and increased energy for reproductive tissue development in females. However, the mechanisms that explain the movement patterns of male and female adfluvial bull trout remain to be explicitly tested.

Seasonal changes in the movement ecology of adfluvial bull trout

Adfluvial bull trout are in good overall condition in the spring (Nitychoruk et al. 2013), thus the wide distribution seen in the current study, large home-range sizes, and relatively high activity of individual bull trout may be attributed to feeding opportunities and the activity and distribution of prey. Concurrent with several other studies (Fraley and Shepard 1989; DuPont et al. 2007), individuals were concentrated in the confluence in winter (Fig. 2D). The congregation of bull trout likely results from a combination of factors including relatively high flow, high nitrate, low conductivity, and high water clarity in the confluence compared with other areas of the reservoir (Bray 2012). Kokanee are a preferred food source for bull trout during spring (Beauchamp and Van Tassell 2001) and we expect that the abiotic characteristics of a river confluence (e.g., nutrients, primary production) attract both numbers of kokanee and actively foraging bull trout.

Unlike in other systems (e.g., Lake Billy, Oregon, USA) where adult adfluvial bull trout are only found in the river during summer (Beauchamp and Van Tassell 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 lateral movements during approximately the same time frame (Figs. 2B, 4). Additionally, adfluvial bull trout exhibit their deepest swimming depths during summer, probably in response to above-optimal surface water temperatures and intense solar radiation (Gutowsky et al. 2013). Light attenuates quickly with depth and if large lateral movements do not result in

increased encounters with prey, bull trout likely continue to perform diel vertical migration to forage during summer (i.e., when the reservoir develops a thermal gradient; Bray 2012; Gutowsky et al. 2013) while only maintaining small home ranges and embarking on limited lateral movements. It is reasonable to predict that the limited movement observed in summer is, in part, explained by the bioenergetic requirements of bull trout, light sensitivity, and the distribution of kokanee salmon prey which also 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 and the large lateral movements and home ranges (Fig. 2C) are most easily explained as a response to cooling water temperatures, the reproductive migratory behavior of prey (feeding opportunity hypothesis; Olmsted et al. 2001), and the fall reproductive migratory behavior of bull trout that is an adaptation of char and based on environmental cues (e.g., temperature; Dingle 1996). Indeed, home-range size and lateral movement was greatest during the fall, presumably because at least some of the tagged individuals had migrated into tributaries to reach spawning grounds and because cooling water temperatures resulted in increased activity (Fig. 4). Kokanee 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 Tassell 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). Whereas the summer is a period of relative inactivity for adfluvial bull trout, movement significantly increases during the fall (DuPont et al. 2007). This remains true for bull trout in both lakes and rivers (Bahr and Shrimpton 2004).

Although home-range size and lateral movement were minimal in winter, patterns differed little from the summer (Figs. 3, 4). Winter activity has been shown in bull trout in Arrowrock Reservoir, Idaho, USA (Salow and Hostettler 2004; Dare 2006), a small alpine lake in the Canadian Rocky Mountains (Wilhelm et al. 1999), and in a study of activity and entrainment of bull trout in Kinbasket Reservoir (Martins et al. 2014). In winter, most bull trout in Kinbasket experienced the coldest water temperatures of the year and performed vertical movement behaviors in an area that spanned the confluence into both Columbia and Canoe rivers (Fig. 2D; Gutowsky et al. 2013). 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 Tassell 2001). This activity, both on a vertical and on a horizontal plane, and congregation near the hydro dam forebay partly explains the relatively high likelihood of entrainment in Kinbasket Reservoir during the winter (Martins et al. 2013, 2014).

Conservation implications

Despite the species' conservation status as threatened or special concern (U.S. Fish and Wildlife Service 1999; Post et al. 2012), relatively little is known about the spatial ecology of adfluvial bull trout in reservoir systems. Data collected in Kinbasket Reservoir were informative both as a way to investigate factors related to movement in free-ranging organisms and to provide information for conservation of bull trout. For example, winter activity has been shown in other lacustrine populations of bull trout (Salow and Hostettler 2004; Dare 2006). Moderate swimming activity and relatively high forebay use are both plausible explanations for the winter entrainment that occurs at the Mica Dam (Martins et al. 2013, 2014). Entrainment can lead to injury and mortality, significant losses to fish populations, and reduced fisheries productivity. Currently, the U.S. Environmental Protection Agency 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-sized intakes (Chen and LeBlanc 2013). By examining the spatial distribution and movement ecology of individuals, such work can identify patterns and help direct management activities. For instance, despite tagging 15% of the sample from tributaries at the southern extent of the system, bull trout rarely used this area outside of the reproductive period (Figs. 2A–2D). Should compensatory (e.g., spawning-site restoration) measures take place to offset entrainment-related losses (Martins et al. 2013), such results could be useful for determining where management activities may be most effective.

In summary, by pairing biotelemetry data with temporal changes in the environment and phenotypic traits, we found patterns in behavior that would otherwise go unidentified. Similar to most empirical research on wild fish, the mechanisms that underlie movement patterns remain unproven. Nevertheless, a large data set with both males and females illustrated a novel relationship between sex and body size that may also occur in other organisms. In addition, the results provided new information about an imperilled freshwater species.

Acknowledgements

We thank S. Landsman, J. Thiem, J. Nitychoruk, M. Taylor, J. Molina, J. Hills, G. Crossin, T. Nettles, and K. Bray. We also thank our guide J. Tippe and our hosts at the Mica town site and the Kinbasket Lake Resort. We are grateful to N. Burnett for calculating the distances between hydrophones. We also thank the BC Ministry of Environment for issuing the necessary permits to carry out this study. This work was supported by BC Hydro, the Natural Sciences and Engineering Research Council of Canada (through NSERC HydroNet, grant number CRDPJ 387271-09), and Fisheries and Oceans Canada (through the Centre of Expertise on Hydropower Impacts of Fish). S.J.C. is supported by the Canada Research Chairs Program. S.J.C. and M.P. are supported by the NSERC Discovery Grant program.

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