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Behavioral attributes of turbine entrainment risk for adult resident fish revealed by acoustic telemetry and state-space modeling

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Abstract

Background: Fish entrainment through turbine intakes is one of the major issues for operators of hydropower facilities because it causes injury and/or mortality and adversely affects population abundance. Entrainment reduction strategies have been developed based on the behavior of downstream migrating fishes, particularly diadromous species. However, knowledge of the behavior of migratory fishes has very limited application for reducing the entrainment of resident fishes, including several species that represent important recreational and aboriginal fishery resources in reservoirs. In this study, we used fine-scale acoustic telemetry and state-space modeling to investigate behavioral attributes associated with entrainment risk of resident adult bull trout (*Salvelinus confluentus*) in a large hydropower reservoir in British Columbia, Canada.

Results: We found that adult bull trout resided longer in the vicinity of the powerhouse and moved closer to the turbine intakes in the fall and particularly in the winter. Bull trout were more likely to engage in exploratory behavior (characteristic of foraging or reduced activity) during periods when their body temperature was lower or higher than 6°C. We also detected diel changes in behavioral attributes, with bull trout distance to intakes and probability of exploratory behavior slightly increasing at night.

Conclusions: We hypothesize that the exploratory behavior in the forebay is associated with foraging for kokanee (nonanadromous form of *Oncorhynchus nerka*), which have been shown to congregate near the dams of hydropower reservoirs in the winter. Our study findings should be applicable to bull trout populations residing in other reservoirs and indicate that entrainment mitigation (for example, use of deterrent devices) should be focused on the fall and winter. This work also provides a framework for combining acoustic telemetry and state-space models to understand and categorize movement behavior of fish in reservoirs and, more generally, in any environment with fluctuating water levels.

Keywords: Acoustic telemetry, Behavioral ecology, Bull trout, Code division multiple access, Forebay, Hydropower, Movement ecology, State-space model, Turbine entrainment

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Background

One of the major challenges for hydropower operators is determining how to reduce the number of fish that are displaced from reservoirs to downstream waters through turbine intakes—a process termed *entrainment* [1,2]. Entrainment can cause immediate fish mortality in a variety of ways (for example, strike, cavitation, pressure changes [3]) or delayed mortality due to injury and increased susceptibility to predation [1]. In some jurisdictions, there are regulations and guidelines that help reduce entrainment and the impacts that it can have on the abundance of fish populations. For example, resource agencies in the United States have set survival standards for salmonids migrating downstream through hydroelectric facilities in the Columbia River [4]. In Canada, the Fisheries Act prohibits any activity that causes serious harm to fish that are part of, or support, a fishery [5], and national guidelines for managing fish entrainment through turbines and other types of water intake structures are currently in development [6].

Currently, most of the efforts to quantify and reduce entrainment in hydropower facilities have focused on downstream migrating fishes, particularly diadromous species [7-9]. Detailed studies on the behavior of migrants as they enter the forebay (the area directly upstream of the dam) and approach the hydropower facility have informed the design and refinement of guidance systems to direct fish away from turbine intakes and into bypass structures [7,10]. However, because migrants use the water flow as a cue to move past dams [11], knowledge of the movement behavior of downstream migrating fishes has very limited application for understanding and mitigating entrainment of resident fishes (that is, those that do not actively emigrate from reservoirs).

Resident fish can be accidentally entrained in hydropower facilities when using habitats near turbine intakes [11]. Indeed, many technical reports available through hydropower companies and regulatory agencies indicate variable levels of entrainment of resident fish [12-14]. Resident juvenile fish are particularly vulnerable to entrainment [11], but observed rates of entrainment appear to have little impact on populations due to the usual high abundance of juveniles [14]. Entrainment of resident adult fish has the potential for a greater impact on populations because even relatively low levels of entrainment of large, highly fecund females can reduce population growth and long-term viability, particularly in late-maturing species [15]. Important recreational and aboriginal fishery resources in many reservoirs of North America rely on such late-maturing species (for example, walleye, *Sander vitreus*; burbot, *Lota lota*; bull trout *Salvelinus confluentus*), making efforts to reduce entrainment of adult resident fish a crucial factor for future sustainability. Detailed knowledge of

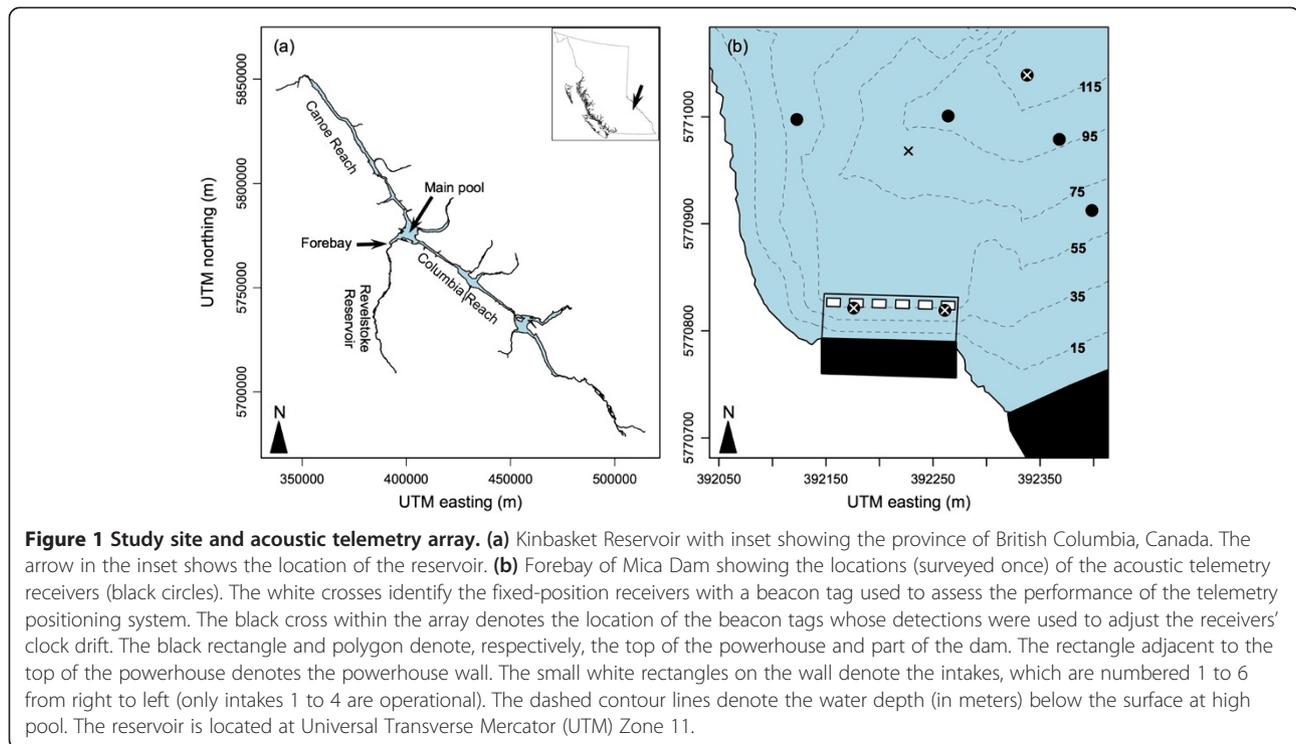
adult resident fish behavior near turbine intakes therefore can help regulators and hydropower operators to identify and implement approaches to reduce entrainment.

In this study, we investigated fine-scale behavior associated with entrainment risk of adult resident fish in a large hydropower reservoir (Kinbasket Reservoir, British Columbia, Canada, Figure 1). We focused on bull trout (*Salvelinus confluentus*), which is a char native to western Canada and the northwestern United States. Bull trout inhabit cold-water rivers, lakes and reservoirs and exhibit a range of life history forms (resident, fluvial, adfluvial and anadromous) [16]. The species remains active even in water temperatures below 2°C, possesses low thermal optima for growth and is highly sensitive to warm water temperature [17,18]. As a result of climate change, overfishing and habitat loss, as well as fragmentation and degradation, a number of bull trout populations have been listed as threatened in the United States and designated as of special concern or threatened in three of five biogeographic populations in Canada [19,20]. Reservoir populations of bull trout are further impacted by entrainment losses of adults, which occur mostly in the fall and winter and at annual rates ranging from 3.5% to 11.3% [21-23]. Seasonality in entrainment risk is most likely associated with temporal changes in physical (for example, turbine operations, water temperature) and biological (for example, prey distribution) factors affecting behavior and forebay use [11,23].

We applied state-space models to fine-scale acoustic telemetry data to estimate true positions, depth, body temperature and behavioral states of adult bull trout. The resulting estimates were used to investigate the relationship between adult bull trout behavior in the forebay of Kinbasket Reservoir and putative factors influencing their behavior. Behavior was characterized in terms of bull trout residence time and spatial distribution in the forebay, distance to the intakes and two behavioral states based on movement patterns: transiting (fast, directed movement) and exploratory (slow, undirected movement) [24,25]. Specifically, our objectives were to investigate (1) temporal (diel and seasonal) patterns in bull trout behavior; (2) the association between bull trout behavior and physical (that is, turbine operations, reservoir water elevation) and biological (that is, body temperature) factors; and (3) the behavior of fish preceding their entrainment (should entrainment be observed). We synthesized our results to develop an overall characterization of adult bull trout behavior in relation to entrainment risk.

Results

A total of 85 bull trout were tagged, but only 25 individuals were detected in the forebay for a minimum of 30 minutes (see Methods). Twenty-two of these 25 individuals were detected in only one season, and the remaining three



individuals were detected in two seasons. State-space model estimates were obtained for a similar number of individuals across seasons: six individuals in the summer, seven in the fall, seven in the winter and eight in the spring (see examples in Figure 2). However, the total number of positions varied markedly among seasons; they were highest in the winter (8,343, or 51.6% of the total number of 16,184 positions), followed by the fall (5,625, or 34.8%), summer (1,505, or 9.3%) and spring (711, or 4.4%). The median residence time of bull trout in the forebay was 6.3 hours (min–max = 0.6–114.9 hours) in the winter, 2.7 hours (min–max: 1.8–77.8 hours) in the fall, 1.3 hours (min–max: 0.7–16.9 hours) in the summer and 0.7 hours (min–max: 0.5–4.7 hours) in the spring.

The estimated utilization distributions revealed a marked seasonal pattern of space use within the monitored forebay area. In the spring and summer, bull trout used areas away from the powerhouse more intensively, as indicated by the location of the 50% utilization distribution (Figure 3a and b). In the fall, their 50% utilization distribution extended to the powerhouse (Figure 3c) and was located immediately adjacent to it in the winter (Figure 3d).

Model selection indicated strong support for the relationship between mean three-dimensional distance between fish locations and intakes (D_{int}) and season (Table 1). Bull trout were typically 57 to 99 m closer to the intakes in the winter than in any of the other seasons (Figure 4a and b). Visual inspection of the

D_{int} time series for each track and the fish trajectories indicated that none of the tagged bull trout were entrained (data not shown), with the shortest distance estimated between bull trout and intakes being 23 m and occurring in the winter.

Model selection also supported the relationship between D_{int} and time of day (Table 1). However, D_{int} varied by only 20 m over the diel cycle, with slightly reduced D_{int} values occurring between 13:00 and 24:00 (Figure 4c and d). The marginal and conditional R^2 values for the D_{int} models with $\Delta AIC_c < 2$ ranged from 0.22 to 0.23 and 0.31 to 0.32, respectively. None of the models with $\Delta AIC_c < 2$ included operational discharge or reservoir elevation (Table 1).

The estimated probability of being in the exploratory state (P_{exp}) progressively increased from spring to winter and was less variable during the winter than in any of the other seasons (Figure 5a). Model selection, however, did not support the relationship between season and P_{exp} (Table 2). The top-ranked model included only body temperature as a predictor of P_{exp} (Table 2). Bull trout were much less likely to be in the exploratory state when their body temperature was around 6°C, with P_{exp} increasing rapidly when body temperature trended toward lower and higher values (Figure 5b and c). Model selection also supported the relationship between P_{exp} and time of day (Table 2). Bull trout were less likely to be in the exploratory state around 10:00 and slightly more likely to be in the exploratory state between 14:00 and 04:00 (Figure 5d and e).

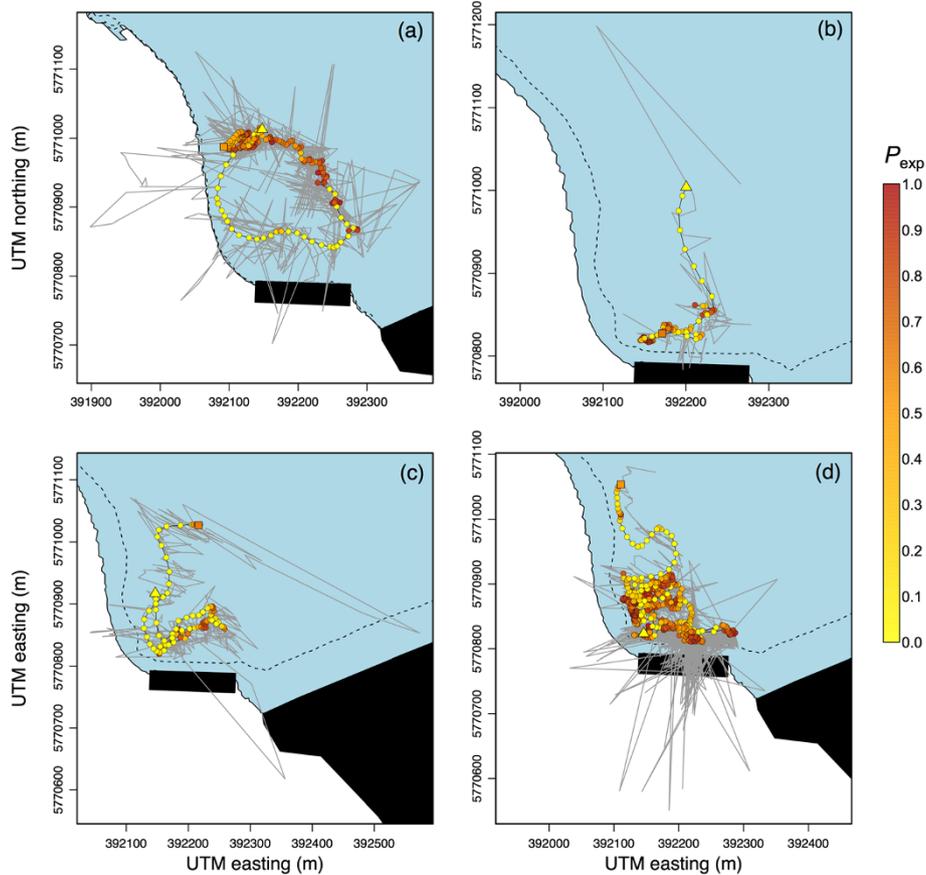


Figure 2 Examples of raw position data and state-space model estimates. In (a) to (d), the solid gray lines denote the raw position data. The filled circles denote the state-space model estimates of true positions and associated probability of being in the exploratory state (P_{exp}). The black rectangle denotes the powerhouse of Mica Dam. The dashed line denotes the waterline at the time the position data were recorded. UTM (Universal Transverse Mercator) Zone 11.

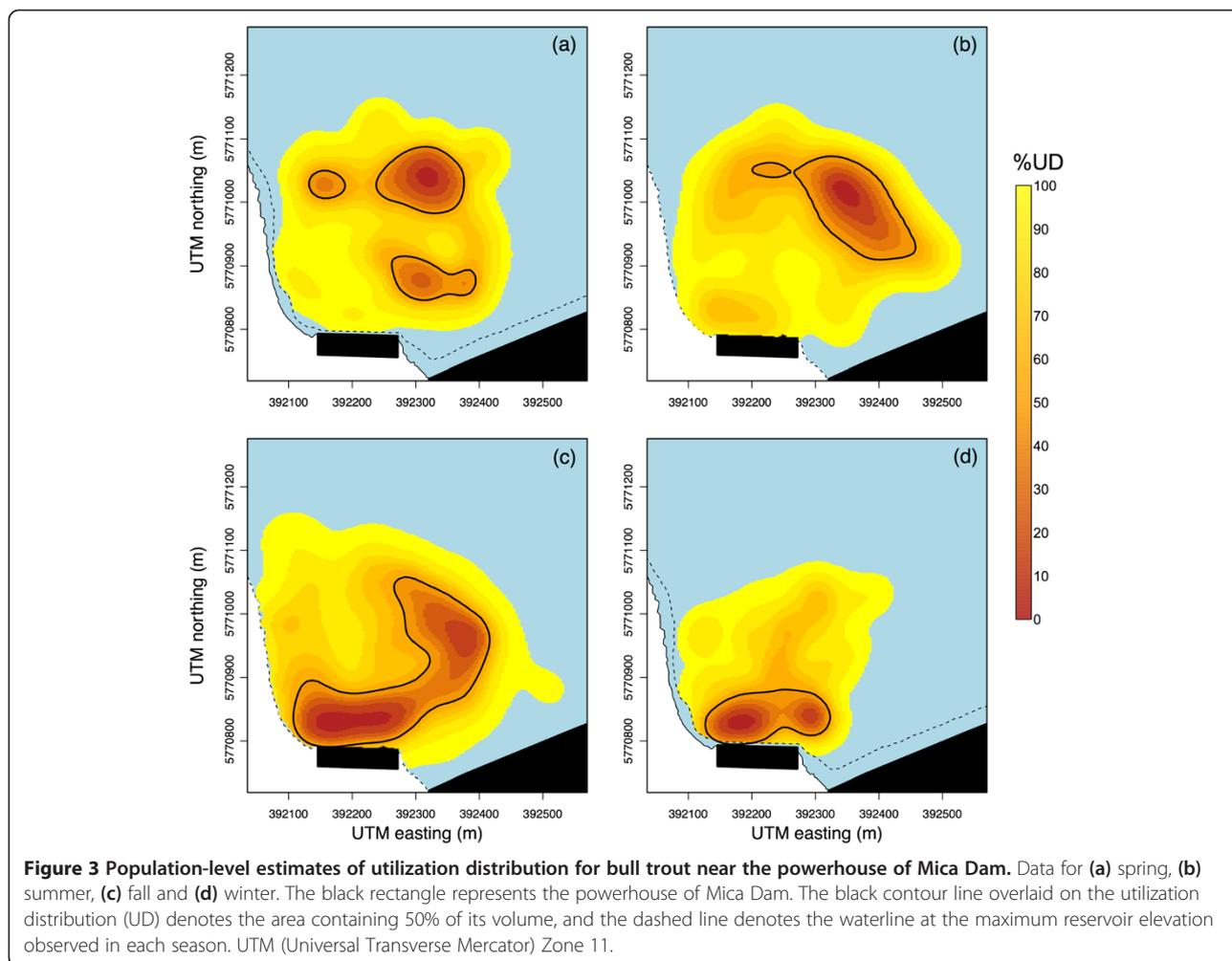
The marginal and conditional R^2 values for the P_{exp} models with $\Delta AIC_c < 2$ ranged from only 0.04 to 0.05 and 0.15 to 0.16, respectively. None of the models with $\Delta AIC_c < 2$ included operational discharge or season (Table 2). Although the model including body temperature and operational discharge had a ΔAIC_c value of virtually 2, the effect of operational discharge was not supported, as its addition resulted in negligible improvement of the model's log-likelihood compared to the model including only body temperature (Table 2).

Discussion

Our findings revealed marked seasonal changes in adult bull trout behavior in the forebay of Kinbasket Reservoir, which helps to explain the increased entrainment rates in the fall and winter observed previously [23]. Specifically, we observed increased residence time (see also [23]) and proximity to intakes in the fall and particularly in the winter, as well as slow, undirected movement in the forebay when body temperatures were low (mostly in the winter). Although turbine operations are maximized during the fall

and winter at Mica Dam [26], we did not find any evidence that operational discharge directly influenced adult bull trout behavior in the forebay. This indicates that other factors related to seasons may be associated with the seasonality observed in bull trout behavior.

The forebay of hydropower reservoirs may have high food density for adult bull trout during the late fall and winter. Indeed, kokanee (nonanadromous form of *Oncorhynchus nerka*), one of the main prey for overwintering bull trout [27], congregate near the dams of some hydropower reservoirs in the winter [28,29]. In Revelstoke Reservoir (British Columbia, Canada), the density of kokanee near the dam increases particularly during periods of prolonged turbine operation in the winter, possibly due to advection [29]. Furthermore, kokanee usually occur in habitats with high light intensity during the winter [30,31]. Relatively high light intensity may occur near the powerhouse of hydropower reservoirs in the late fall and winter due to the effect of turbine-induced flows in preventing or inhibiting formation of thick ice cover.



Our finding that P_{exp} increased with decreasing body temperatures provides additional indirect evidence that bull trout may forage near the powerhouse in the late fall and winter. The exploratory behavior is defined by slow movements and frequent turns, which are characteristic movement patterns of animals conducting area-restricted search and foraging [24,32]. Furthermore, the restricted movement of bull trout near the powerhouse is consistent with a sit-and-wait foraging strategy for capturing invertebrates and fish moving with the direction of turbine-induced flows—a behavior similar to that observed in stream-dwelling salmonids (for example, [33,34]). Such a sit-and-wait behavior was observed in adult bull trout preying on sockeye salmon smolts migrating past counting fences in the Chilko River, British Columbia, Canada (N Furey, University of British Columbia, personal communication).

The relationship between P_{exp} and body temperature in bull trout may also reflect the bell-shaped thermal dependency of aerobic scope for activity in fishes [35], though the exact relationship between aerobic scope and

temperature has not yet been examined in bull trout. However, on the basis of the identified relationship between P_{exp} and body temperatures, it is possible that aerobic scope to sustain fast movements (that is, relatively low P_{exp}) is highest around 6°C and decreases as body temperature trends toward 0°C or 12°C, leading to a reduction in swim speeds (that is, relatively high P_{exp}). Alternatively, the increased P_{exp} toward 12°C may be related to a reduction in activity that would facilitate food assimilation and growth at warmer temperatures [36-38].

We also found that bull trout behavior varied slightly on a diel basis. Although diel patterns in activity should be expected to vary seasonally due to changes in the photoperiod [39], we could not evaluate interactions between time of day and season on D_{int} and P_{exp} (see Methods). However, because the majority of our data were recorded in the fall and winter, we believe that the uncovered diel patterns are more representative of bull trout activity in these seasons. The small variation (about 20 m) in D_{int} over the day may be partly associated with bull trout diel vertical migration, which occurs

Table 1 Model selection statistics for models describing mean three-dimensional distance between bull trout locations and intakes (D_{int}) in the forebay of Kinbasket Reservoir^a

Model	AIC _c	ΔAIC _c	wAIC _c	log(L)	K
ssn + $f(tdy)$	11,447.46	0.00	0.65	-5,712.62	11
ssn	11,449.19	1.73	0.27	-5,714.50	10
$f(tdy)$ + ds _g + rel	11,453.59	6.13	0.03	-5,716.70	10
ds _g + rel	11,454.28	6.81	0.02	-5,718.06	9
$f(tdy)$ + ds _g	11,455.11	7.65	0.01	-5,718.48	9
ds _g	11,456.62	9.16	0.01	-5,720.25	8
$f(tdy)$ + rel	11,462.25	14.79	0.00	-5,722.05	9
$f(tdy)$	11,462.54	15.08	0.00	-5,723.21	8
rel	11,466.54	19.07	0.00	-5,725.21	8
No fixed effects	11,467.82	20.36	0.00	-5,726.86	7

^aAIC_c, Bias-corrected Akaike Information Criterion; ΔAIC_c, Difference in bias-corrected Akaike Information Criterion between a given model and the top-ranked model; ds_g, Operational discharge; f , Smoothing function; K, Number of parameters in the models; log(L), Log-likelihood of the models; rel, Reservoir elevation; ssn, Season; tdy, Time of day; wAIC_c, Weight bias-corrected Akaike Information Criterion. All models include fish ID as a random effect. Models are ranked by increasing order of the AIC_c value.

throughout most of the year, including the fall and winter [40]. Bull trout diel vertical migration in winter has been attributed to foraging for kokanee [40], which also exhibit diel vertical migration in that season [31].

Our finding that P_{exp} was higher over most of the night hours (corresponding to fall and winter) may indicate a reduction in bull trout activity when it is dark. However, as mentioned above, the exploratory state may also indicate foraging behavior. Interestingly, the increase in P_{exp} at night coincides with the time that both kokanee and bull trout are located in shallow water [40,41]. Indeed, diel activity of fishes is linked to the activity of their prey [39], and studies conducted on stream-dwelling bull trout during periods of cold water temperature (late fall to early spring) have shown that individuals emerge from cover at night and feed in the dark ([42,43] and N Furey, University of British Columbia, personal communication).

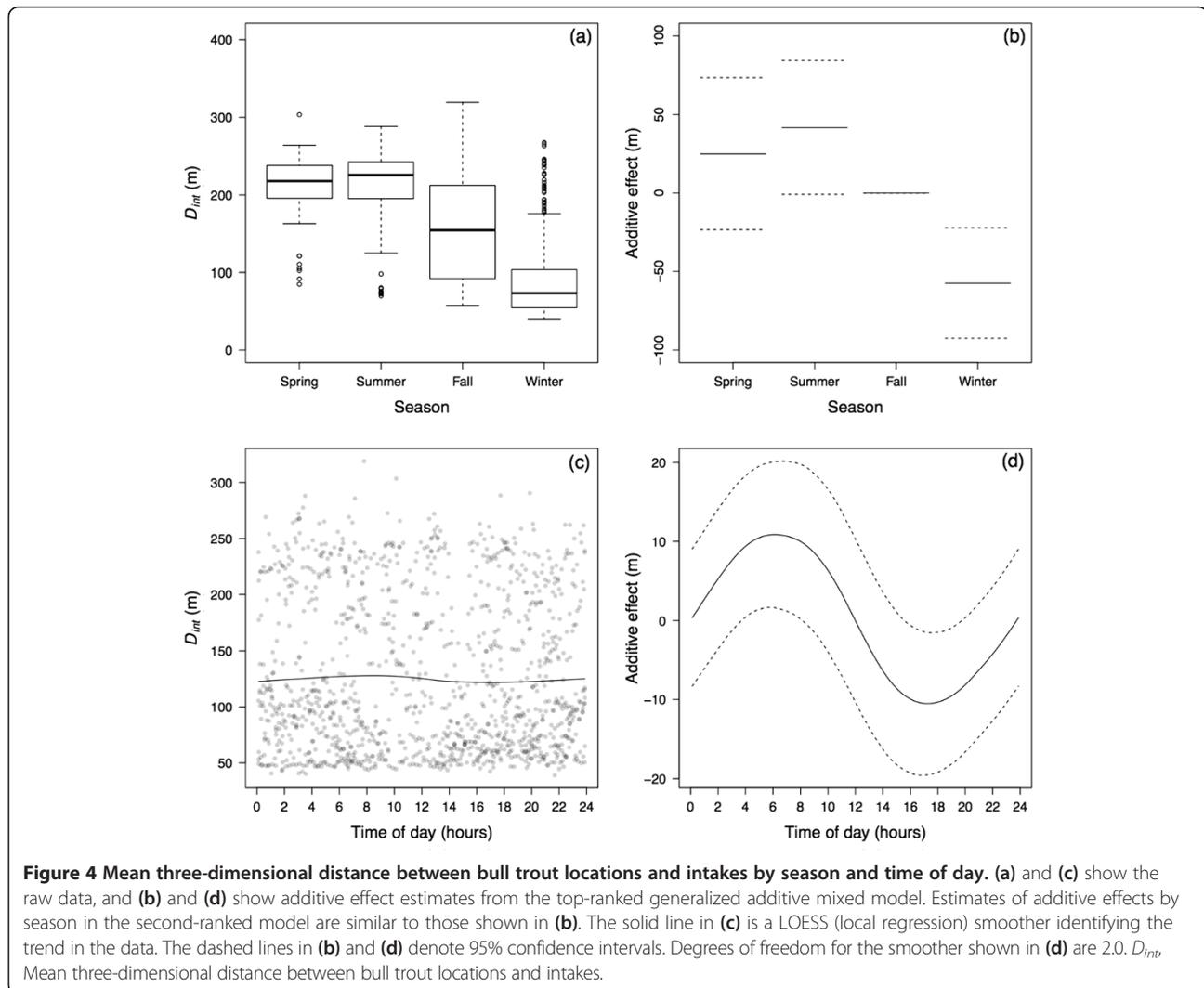
Although we were able to detect relationships between bull trout D_{int} and P_{exp} and time of day, season and body temperature, a large proportion of the variability in our data (as measured by conditional R^2) could not be explained by our predictor variables and individual random effects, particularly in the P_{exp} model. The low ability of our models to explain the variability in the data is partly related to the stochastic component that underlies animal movements [44]. Furthermore, animal movement results from complex interactions between an individual's internal state and environmental conditions [45], which can change at fine spatiotemporal scales. For example, turbine operations generate complex water

flows over three-dimensional space in the forebay of hydropower reservoirs [46]. It is possible that bull trout moving in such an environment respond to fine spatiotemporal changes in flow properties (for example, velocity, turbulence, flow direction) that are not detected by relating behavior to total operational discharge. Indeed, the spatiotemporal variability in the characteristics of water and air flow helps to explain the trajectory of animals moving in fluids, though most work done to date has been focused on migrating animals [10,47,48].

We did not detect bull trout approaching or moving into the intakes in this study, though adult bull trout entrainment is known to occur through Mica Dam in the fall and winter [23]. The closest distance we detected bull trout from an intake was 23 m—a distance where water velocities are <0.2 m/s during turbine operations [49]. We do not consider these velocities challenging for adult bull trout, because even juvenile bull trout (11 to 19 cm) have mean critical swimming speeds >0.48 m/s and critical swim speed is positively correlated with body length [50]. Bull trout may have avoided approaching the flow field near the turbine intakes of Mica Dam, but we cannot exclude the possibility that our telemetry system was unable to position fish at distances <23 m from the intakes during turbine operations. Evidence for this was observed in our assessment of the telemetry system performance in positioning the receiver beacon tags (Additional file 1). During the fall and winter, the median efficiency of the telemetry system in positioning the receiver beacon tags located on the powerhouse wall was nearly 0%, with efficiency decreasing with total operational discharge. In contrast, median efficiency in the fall and winter was 16% and 73%, respectively, for the receiver beacon tag located about 275 m from the powerhouse and did not decrease with increases in operational discharge. The low efficiency in positioning the receiver beacon tags, and possibly fish, near the intakes during turbine operations may be related to reduced propagation and/or integrity of the acoustic signal in the accelerating flow field close to the intakes [51].

Conclusions

Our findings indicate that increased entrainment risk of adult bull trout in the fall and winter is related to a combination of maximization of turbine operations in these seasons with concomitant changes in behavioral attributes, such as increased residence and proximity of bull trout to the intakes (presumably for foraging on kokanee) and reduced movement (perhaps limiting escape responses to accelerating water flow) during periods of cold water temperatures. Therefore, it would be prudent to explore mitigation measures, such as operating deterrent devices (for example, strobe lights, sound, screens), to prevent bull trout from approaching and becoming entrained



at hydropower intakes during the fall and winter. These approaches would likely benefit other resident fishes (for example, kokanee) at risk of and impacted by entrainment, but would be especially important for bull trout, given that the viability of their populations can be substantially reduced by losses of adults [16,52]. The results of this study also show how acoustic telemetry and state-space models can be combined to understand and categorize fish behavior in reservoirs and, more generally, in other environments with fluctuating water levels.

Methods

Study site

This study was conducted in Kinbasket Reservoir (52°8' N, 118°28' W), which is located in the Kootenay Mountain Region of British Columbia, Canada, and was formed by the impoundment of the Canoe and Columbia Rivers with the construction of the Mica Dam in 1973 (Figure 1a). The reservoir is large (43,200 ha), snowmelt-fed and

oligotrophic, with steep, rocky shorelines, sand, rock and mud substrates. At its highest elevation (high pool, 755 m), the reservoir has a mean depth of 57 m and maximum depth of about 190 m [53]. Surface water temperatures in the reservoir range from 2°C to 15°C in early spring, with summer surface temperatures typically between 12°C and 18°C [54]. From midsummer to early fall, a linear thermal gradient is usually formed in the reservoir, with temperatures decreasing to 4°C at 60 m [55].

The powerhouse at Mica Dam currently consists of four Francis-type turbines, each with a rated maximum discharge of 283 m³/s and capacity of 465 MW [26]. The top of the turbine intakes is located at a depth of about 56 m during high pool. Turbine operation is markedly seasonal, with drawdown starting in late summer or early fall and lasting until early or midspring [26]. As a result of the spring freshet and drawdown, the water surface elevation of the reservoir (hereafter *reservoir elevation*) varies seasonally by as much as 47 m. The

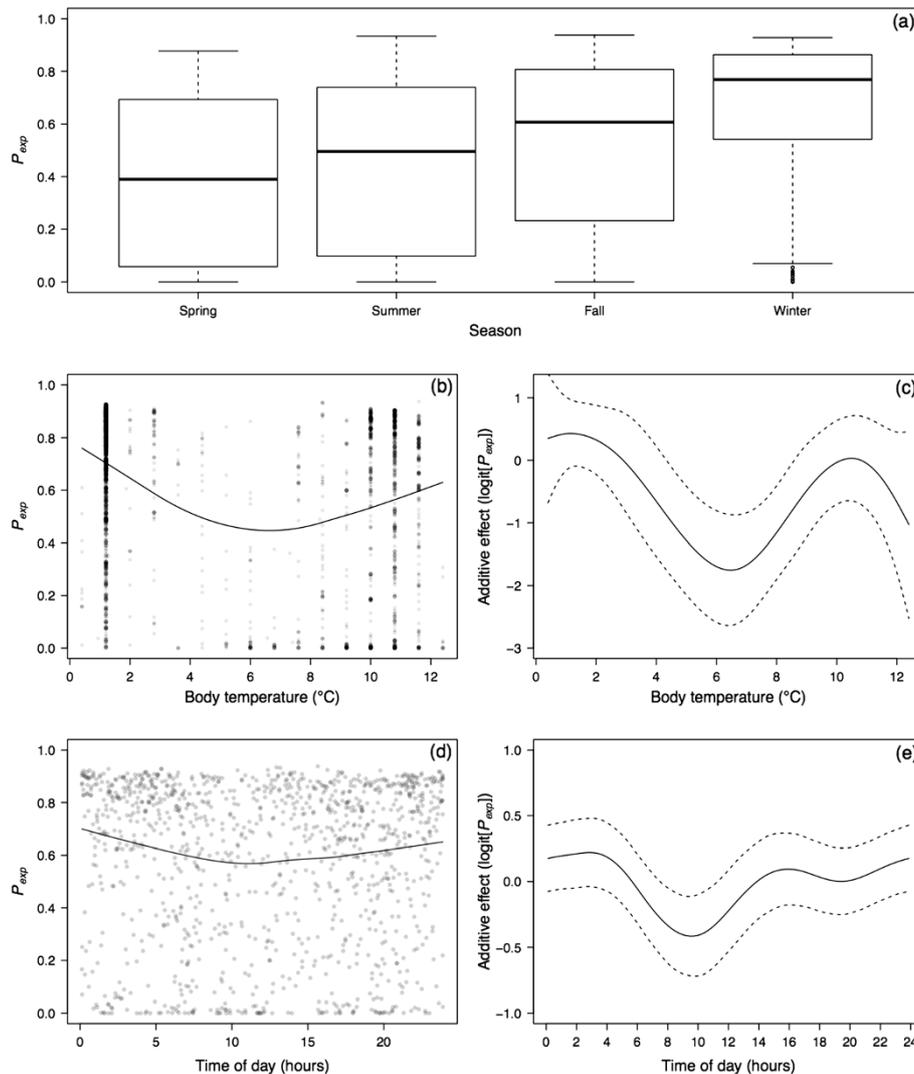


Figure 5 Probability of being in the exploratory state for bull trout by season, body temperature and time of day. (a), (b) and (d) show the raw data, and (c) and (e) show additive effect estimates on the logit scale. The additive effect estimate shown in (c) is from the top-ranked model and is similar to the one estimated by the second-ranked model. The additive effect estimate shown in (e) is from the second-ranked model, as the top-ranked model did not include time of day. The solid lines in (b) and (d) are LOESS (local regression) smoothers identifying the trend in the data. The dashed lines in (c) and (e) denote 95% confidence intervals. Degrees of freedom for the smoothers shown in (c) and (e) are 4.4 and 3.5, respectively. P_{exp} , Probability of being in the exploratory state.

reservoir reaches its lowest elevation (low pool) in the early or midspring and its highest elevation (high pool) by late summer or early fall [26]. The lowest reservoir elevation during our study was about 722 m (top of turbine intakes at a depth of 23 m).

Capture and tagging

Eighty-five adult bull trout were captured by trolling throughout the Kinbasket Reservoir main pool (Figure 1a) in May 2011. Landed fish were anesthetized using clove oil (40 mg of clove oil/L emulsified in 95% ethanol at a 1:9 ratio), measured for total length (cm) and mass (g) and

surgically tagged [56] with temperature- and depth-sensing acoustic transmitters (models MM-M-16-33-TP and MM-M-16-50-TP, size 16 × 64 to 81 mm; weight in air 27 to 33 g; fixed signal transmission rate 3, 4 or 5 s; temperature accuracy ±0.8°C; depth accuracy ±3.5 m; frequency 76 kHz; battery life 163 to 433 days; Lotek Wireless, Newmarket, ON, Canada). After surgery, fish were placed in a recovery box filled with ambient reservoir water and released at the capture site once they regained equilibrium (recovery typically took 10 to 15 minutes). The median total length and mass of the tagged bull trout were, respectively, 65.9 cm (min–max: 53.4–84.0 cm) and 2,560 g (min–max = 1,280–5,420 g).

Table 2 Model selection statistics for models describing probability of being in the exploratory state (P_{exp}) for adult bull trout in the forebay of Kinbasket Reservoir^a

Model	AIC _c	ΔAIC _c	wAIC _c	log(L)	K
<i>f</i> (btp)	4,273.27	0.00	0.38	-2,127.56	9
<i>f</i> (tdy) + <i>f</i> (btp)	4,273.83	0.56	0.28	-2,126.82	10
<i>f</i> (btp) + dsg	4,275.28	2.00	0.14	-2,127.54	10
<i>f</i> (tdy) + <i>f</i> (btp) + dsg	4,275.83	2.56	0.10	-2,126.80	11
ssn	4,277.89	4.62	0.04	-2,128.85	10
No fixed effects	4,279.26	5.99	0.02	-2,132.58	7
ssn + <i>f</i> (tdy)	4,279.50	6.23	0.02	-2,128.63	11
<i>f</i> (tdy)	4,280.25	6.97	0.01	-2,132.06	8
dsg	4,280.96	7.69	0.01	-2,132.42	8
<i>f</i> (tdy) + dsg	4,281.82	8.55	0.01	-2,131.83	9

^aAIC_c, Bias-corrected Akaike Information Criterion; btp: Body temperature; ΔAIC_c, Difference in bias-corrected Akaike Information Criterion between a given model and the top-ranked model; dsg, Operational discharge; *f*, Smoothing function; K, Number of parameters in the models; log(L), Log-likelihood of the model; ssn, Season; tdy, Time of day; wAIC_c, Weight bias-corrected Akaike Information Criterion. All models include fish ID as a random effect. Models are ranked by increasing order of the AIC_c value.

Permits to capture fish were issued by the British Columbia Ministry of Environment (Permit No. CB-PG10- 61414). Tagging protocols were approved by the Carleton University Animal Care Committee.

Tracking and data processing

An array of seven autonomous acoustic telemetry receivers (model WHS 3150; Lotek Wireless) was used to track the movements of tagged bull trout in the immediate vicinity (approximately 300 m) of the powerhouse. The acoustic receivers employ code division multiple access technology, which enables simultaneous tracking of hundreds of tagged animals on a single frequency without code collision, and they operate efficiently under high ambient noise and multipath [57,58]. Five of the receivers were suspended with aircraft cable attached to the log boom ($n = 4$) and a moored barrel ($n = 1$) located near the powerhouse (Figure 1b). The weight of the receivers (35 kg) and 15 kg of added weight kept the receivers vertically oriented at a fixed depth of 25 m. The other two receivers were deployed on the powerhouse wall approximately 15 m above turbine intakes 1 and 5 (Figure 1b). These receivers were deployed using custom-made carts that were connected with aircraft cable to electric winches located at the top of the powerhouse. The carts were fitted into grooves running down the powerhouse wall to keep the receivers stationary.

One beacon tag (burst rate of 30 s, referred to as a *receiver beacon tag*) was attached to each of three receivers, and two other beacon tags (burst rate of 10 or 20 s, referred to as *nonreceiver beacon tags*) were deployed at a fixed known location within the array (Figure 1b).

The detections of the receiver beacon tags were used to assess the performance of the telemetry positioning system (Additional file 1), and the detections of the nonreceiver beacon tags were used to adjust the receivers' clock drift during data processing.

The detection data were downloaded every 3 to 5 months between May 2011 and October 2012 and used to compute position estimates with ALPS software (Lotek Wireless). Key inputs used for computing fish positions were as follows: the fish and nonreceiver beacon tag detection data; the location of the receivers and nonreceiver beacon tags (surveyed once at the beginning of the study with a differential global positioning system device, model GeoXH handheld GPS; Trimble, Sunnyvale, CA, USA); the depth of the receivers, which was variable only for the ones located on the powerhouse wall, due to changes in reservoir elevation (monitored on-site by BC Hydro, British Columbia, Canada); and the speed of sound in water at a given water temperature. Water temperature was monitored on-site with thermal loggers (model TidbiT v2, accuracy $\pm 0.2^\circ\text{C}$; Onset Computer Corporation, Bourne, MA, USA).

Data analyses

The telemetry positioning system could not resolve estimates for many of the detections and consequently generated tracks with position estimates at irregular time intervals. In addition, a number of estimated positions were obviously erroneous (for example, fish positioned on land or moving at >10 m/s; see examples in Figure 2). Furthermore, preliminary assessments of the system performance to position the receiver beacon tags revealed that position estimates had both systematic and random errors that increased with decreasing numbers of receivers included in the computation of a position estimate (Additional file 1). Indeed, detection efficiency variability associated with a variety of factors (for example, noise from boat traffic, turbines, rain) and positioning errors are common when using automated positioning systems based on acoustic telemetry [58,59].

Rather than using *ad hoc* filters to remove erroneous position estimates, we used state-space models to estimate the true bull trout positions from the observed data. State-space models enable unobserved states (for example, true position, behavioral states) to be estimated from data observed with errors [60,61]. These models have been used successfully to analyze movement data collected over large temporal (hours to days) and spatial (kilometers) scales from marine and terrestrial animals tracked with geolocation devices (for example, [62-64]). Despite the advantages of state-space models, they have rarely been used to deal with the complex error structure observed in fine-scale position data collected by acoustic telemetry (for example, [65]).

The bull trout movement data were analyzed using the first-difference correlated random walk model with switch

between behavioral states (DCRWS) developed previously by Jonsen *et al.* [25]. The model enabled us to account for errors in the position estimates and missing data and to estimate the bull trout behavioral state associated with each position. Two behavioral states were estimated: transiting and exploratory. The transiting behavior is characterized by relatively fast moves and persistence in direction, and the exploratory behavior is characterized by relatively slow moves and frequent changes in direction [25].

Bull trout elevations (computed by subtracting fish depth from reservoir elevation) and body temperature data were also modeled using state-space models to account for missing data and errors in sensor readings. Modeling sensor data within the state-space framework enabled us to compare bull trout positions and elevation estimates with bathymetry and reservoir elevation data to create a dynamic, three-dimensional land mask, which informed the models of locations to which bull trout could not move. A Bayesian approach was used to fit the state-space models to the data. Detailed descriptions of the model structure, fitting, performance and parameter estimates are included in Additional file 2. Computer codes used to implement the models, as well as an example data set, are provided in Additional file 3.

Before fitting the models, the tracks were split when the time elapsed between two consecutive observations was greater than 5 minutes. We chose a threshold of 5 minutes to avoid unrealistic movement artifacts, such as looping tracks, which we observed when using time thresholds greater than that. These artifacts arise when the model-interpolated locations are insufficiently constrained by data and are a common outcome when no data are available to inform the DCRWS model with the movement of individuals over a long time interval relative to the model time step [64,66]. From among the resulting tracks, only those that had a minimum duration of 30 minutes were used in the analyses. This filtering did not exclude detections potentially indicating that bull trout were being entrained; only seven excluded detections occurred at a depth <10 m from the top of the turbine intakes and in all cases fish were later detected near (<5 m) the water surface.

In total, the state-space models were fitted to 148 tracks from 25 individuals. The state-space models estimated true position, elevation, body temperature and behavioral state for bull trout at 60-second intervals. This was the smallest time step for which we could adequately fit the models within a reasonable time frame (about 15 days of computing). The proportion of behavioral states estimated as exploratory at each position was computed from 1,000 Markov chain Monte Carlo (MCMC) samples and interpreted as the probability of bull trout being in the exploratory

state (P_{exp}). See Additional file 2 for details on MCMC sampling.

Population-level, season-specific utilization distributions (spring: April through June; summer: July through September; fall: October through December; winter: January through March) were estimated for bull trout using the state-space estimates of true positions. The kernel density estimation method [67] implemented in the R package “adehabitatHR” [68] was used to compute the utilization distributions. The utilization distributions were estimated using 150 positions randomly sampled (with replacement) from each bull trout observed in a season to avoid biases caused by some fish with numerous locations. The utilization distributions gave the probability of encountering a bull trout at a specific location in the forebay. The forebay area most intensively used by bull trout was defined as the area containing 50% of the utilization distribution volume.

Generalized additive mixed models were used to investigate variation in bull trout distance to turbine intakes (mean three-dimensional distance between fish locations and intakes; D_{int}) and P_{exp} as a function of a number of predictor variables [69]. D_{int} was modeled as a function of season, operational discharge (min–max: 0–1,168 m³/s), reservoir elevation (min–max: 726–754 m), and a smoother for time of day (min–max: 0.1–23.99 hours). P_{exp} was modeled as a function of season, operational discharge, and smoothers for time of day and body temperature (min–max: 0.4°C–12.4°C). The analysis was based on logit-transformed P_{exp} values [70].

For both the D_{int} and P_{exp} analyses, models were fitted with all possible combinations of the predictor variables. However, models with season as a predictor variable did not include operational discharge, reservoir elevation (D_{int}) or body temperature (P_{exp}), as these variables were collinear with season (variance inflation factor >5; [71]). The models were fitted only with main effects due to the occurrence of nonpositive definite variance–covariance matrices when interactions were included. The same issue occurred when the individual D_{int} and P_{exp} estimates were used in the analyses, but disappeared when the models were fitted to the median of the variables over 15-minute intervals. Fish identity was used as a random effect. Autocorrelation structures of order 1 were used to account for temporal correlations in the model residuals. A variance structure (implemented using the varIdent function in R package “nlme”; [72]) was used to account for the heteroscedasticity associated with seasons [69].

Model selection was conducted using the bias-corrected Akaike Information Criterion (AIC_c) [73], and models were considered to have strong support from the data when they differed in AIC_c (ΔAIC_c) from the top-ranked model by <2 units [73]. The fit of the selected models was assessed based on marginal and conditional R^2 , which

estimate the proportion of variability explained by fixed effects (marginal) and both fixed and random effects (conditional) [74]. Data exploration and model assessment were conducted using graphical approaches [69,71]. Model fitting and selection were conducted in R 3.0.2 [75] using the packages “mgcv” [76] and “AICcmodavg” [77], respectively.

Additional files

Additional file 1: Assessment of the acoustic telemetry positioning system.

Additional file 2: Description of state-space model structure, fitting, performance and parameter estimates.

Additional file 3: R and JAGS codes for implementing the state-space model and an example data set.

Abbreviations

AIC_c: Bias-corrected Akaike Information Criterion; Δ AIC_c: Difference in bias-corrected Akaike Information Criterion between a given model and the top ranked model; AR1: Autoregressive model of order 1; btp: Body temperature; DCRWS: First-difference correlated random walk model with switch between behavioral states; D_{m3} : Mean three-dimensional distance between fish locations and intakes; dsq: Operational discharge; K: Number of parameters in a model; log(L): Log-likelihood of a model; P_{exp} : Probability of being in the exploratory state; rel: Reservoir elevation; ssn: Season; tdy: Time of day; UTM: Universal Transverse Mercator; wAIC_c: Weight bias-corrected Akaike Information Criterion.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

EGM conducted fieldwork, data management and analyses and drafted the manuscript. LFGG and PMH conducted fieldwork. JEMF and IDJ helped to develop the extended version of the DCRWS state-space model. DZZ, AL, DAP, MP and SJC conceived and designed the study. All authors contributed to the drafting of the manuscript and read and approved the final manuscript.

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