NRC Research Press

ARTICLE

Distinct diel and seasonal behaviours in rainbow trout detected by fine-scale acoustic telemetry in a lake environment

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Abstract: The fine-scale behavioural activities of rainbow trout (*Oncorhynchus mykiss*) in nature are not well understood, but are of importance for identifying interactions with the ecosystem and of interest to conservationists and recreational anglers. We have undertaken a high-resolution acoustic telemetry study to identify the distinct movement patterns of 30 rainbow trout in a freshwater lake, specifically examining swim speed, area of movement, and site preference in both summer and winter. Activity levels were reduced in winter compared with summer across all fish, but ranking of individuals was consistent. In summer, 16/30 fish displayed diel movement, in which they travelled to a different area of the lake at dawn and returned at dusk, while other fish maintained their site preference regardless of the time of day or swam more randomly throughout the lake. These patterns were minimized in winter, where there was a reduction in cross-lake movement under ice and only 4/30 fish displayed diel movement. Winter conditions may limit the capability (physiological limitations) and (or) motivation (prey availability) for diel behaviours observed in summer.

Résumé : Les activités comportementales à petite échelle des truites arc-en-ciel (*Oncorhynchus mykiss*) en milieu naturel ne sont pas bien comprises, bien qu'elles soient importantes pour cerner les interactions avec l'écosystème et présentent un intérêt pour les agents de protection de la nature et les pêcheurs sportifs. Nous avons entrepris une étude de télémétrie acoustique de haute résolution afin de cerner les différents motifs de déplacement de 30 truites arc-en-ciel dans un lac d'eau douce, en examinant plus particulièrement la vitesse de nage, l'aire couverte par les déplacements et les préférences de sites durant l'été et l'hiver. Les niveaux d'activité étaient plus faibles en hiver qu'en été pour tous les poissons, le rang des spécimens demeurant toutefois le même. En été, 16 des 30 poissons faisaient des déplacements nycthéméraux, se déplaçant vers un secteur différent du lac à l'aube pour revenir à leur point de départ au crépuscule, alors que d'autres poissons demeuraient dans un endroit de prédilection quelle que soit l'heure du jour, ou nageaient de manière plus aléatoire à la grandeur du lac. Ces motifs étaient minimisés en hiver, les déplacements sous la glace à l'échelle du lac étant réduits et seuls 4 des 30 poissons présentant des déplacements nycthéméraux. Les conditions hivernales pourraient limiter la capacité (restrictions physiques) et (ou) la motivation (disponibilité de proies) des poissons à adopter des comportements nycthéméraux observés durant l'été. [Traduit par la Rédaction]

Introduction

Animals utilize a variety of strategies to navigate ecosystems in selective ways to enhance their ability to locate food and avoid predation. While the behavioral ecology of salmonids has been studied by sampling from natural and experimental populations (for example, Werner et al. 1983; Armstrong et al. 2013), observations of fine-scale movements are difficult to monitor in nature, especially in light-poor environments found in temperate climates. Understanding the detailed use of habitats by fishes is vital for assessing how changes in biotic and abiotic conditions can lead to potential resource conflict. Assessing behaviour in laboratory conditions can be performed more easily, but the plasticity of organism response to environmental conditions complicates extrapolation of laboratory data to natural habitats. For example, tank size and shape has been shown to affect fish growth and swimming behaviour among lake trout (*Salvelinus namaycush*) (Ross and Watten 1998) and Atlantic salmon (*Salmo salar*) (Espmark et al. 2017), and genetically engineered salmonids show remarkable plasticity and genotype by environment interaction effects between tank and naturalized stream environments (Devlin et al. 2015). Indeed, certain phenomena such as ice cover, habitat heterogeneity, and prey distribution cannot be accurately recreated in a laboratory setting. Therefore, the observation and measurement of fish activity is ideally done under natural conditions and provides a better understanding of what resources they utilize, what factors may influence behaviour, and how these factors interact in a natural habitat. This information can then be applied to stocking for recreational and commercial fishing purposes, to risk assessments of introduced species or strains, and to conservation and enrichment efforts to counter effects of anthropogenic and natural changes in abiotic parameters such as temperature.

Advances in biotelemetry have facilitated the collection of positional data in aquatic habitats (Hussey et al. 2015), allowing for more detailed analysis of fish habitat use and behaviour throughout the year. Seasonal changes in inland ecosystems affect metabolism, activity, and consumption, both through appetite and prey

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Fig. 1. Map of Gnawed Lake indicating depth, 2D positioning area, locations of hydrophones, assignment of zones, and locations of temperature and light intensity loggers.
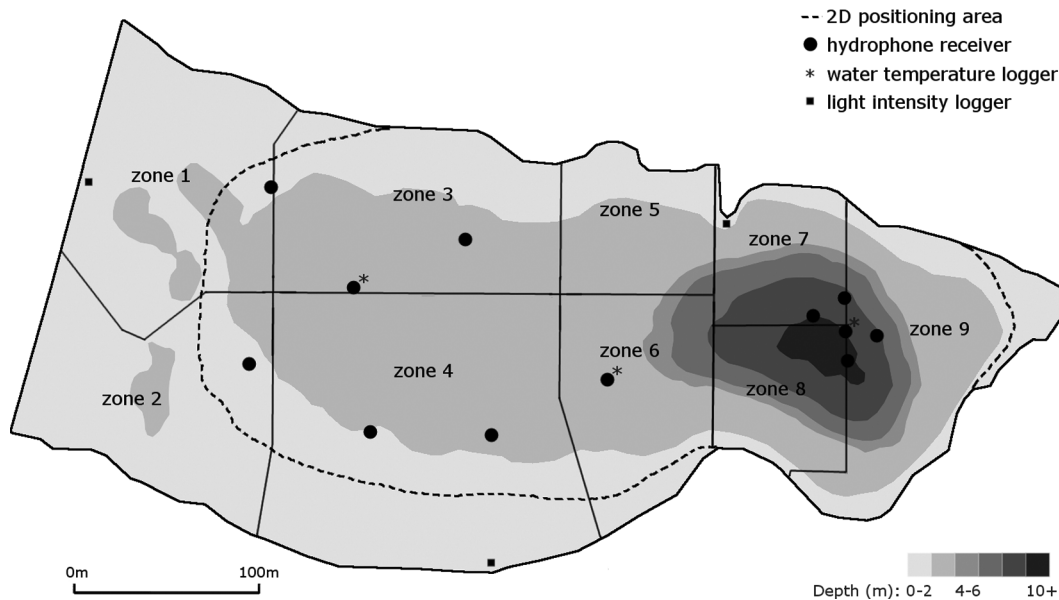
availability. Winter conditions in lake environments are also greatly affected by climate warming (Adrian et al. 2009; Jeppesen et al. 2014), and changes in temperature and ice cover can have cascading effects on fish survival and ecosystem function (Jeppesen et al. 2010; Hedger et al. 2013). Additional studies monitoring under-ice conditions and behaviour will help broaden our base of knowledge and contribute to the prediction and mediation of future changes associated with climate warming. An important aspect of assessing fish behaviour in nature is determining whether fish are randomly distributed throughout a habitat or have preferred areas of occupation and whether these preferences vary depending on the time of day or year. Numerous studies have documented that fish can alter their habitat use in response to varying abiotic and biotic factors, both on a seasonal and diel time scale. For example, the habitat use of lake trout was reduced in winter due to light limitations (Blanchfield et al. 2009), while diel vertical migrations in sockeye salmon (*Oncorhynchus nerka*) (Clark and Levy 1988; Scheuerell and Schindler 2003) and burbot (*Lota lota*) (Cott et al. 2015) appear to result from the interplay of foraging opportunities and predation risk. Identifying which areas fish frequent at different times of day and year can help assess the ecological importance of specific abiotic and biotic features of a habitat and predict shifts in location in response to changing conditions.

Seasonal and diel behavioural variation of salmonids has been studied by sampling from the same population at different times of day or year (Cunjak and Power 1987; Armstrong et al. 2013; Johnson and McKenna 2015), but the role of individual variation cannot be measured in this way. Bolnick et al. (2003) cautions against treating individuals as ecologically equivalent and stresses the importance of identifying and analyzing individual specialization within populations. For example, habitat use has been found to be highly variable among individual lake trout, suggesting alternative foraging strategies within the same population (Morbey et al. 2006), and it has been estimated that 41% of total behavioural variation could be attributed to individual personalities (as opposed to season, body size, or capture location) in a 3-year study of Atlantic cod (*Gadus morhua*) (Villegas-Ríos et al. 2017). The use of acoustic transmitters with uniquely programmed periods (as used in the present study) can allow independent assessment of positional data and comparison of individual behaviours across seasons.

Rainbow trout (*Oncorhynchus mykiss*) is a commonly stocked species in the lakes and rivers of North America and around the world for the purposes of recreational fishing, enhancing natural populations, and commercial aquaculture production (Halverson 2008; Bailey and Sumaila 2012). Despite their widespread occurrence, both throughout their natural range and through stocking globally, there exists limited data on variation in seasonal and diel activity of rainbow trout in nature, especially without the effects of interspecific competition. In this study, we examined variation among individual fish in their behaviour and habitat use in a small temperate lake that contained only rainbow trout. We collected fine-scale telemetry data to examine differences in habitat use and behaviour between summer and winter and at different times of day in both seasons.

Methods

Study site

Gnawed Lake is a small engineered lake constructed in 1979 and located in the interior of British Columbia (50.4358°N, 120.9901°W). The lake is approximately 10 ha in area, with a maximum depth of 11 m. While the eastern part of the lake is deep, the rest of the lake is shallow (2–3 m deep), which provides a contrast in available depth strata for fish to occupy (Fig. 1). At an elevation of 1600 m, Gnawed Lake experiences distinct seasons; air temperatures reach 30 °C in the summer with water temperatures exceeding 20 °C at shallow depths, and air temperatures are often below freezing in the winter. Thick (1 m) ice and snow typically cover the lake from late October to mid-May. Located in a remote area on private land, there is minimal human disturbance and no public fishing access, with limited fishing permitted by the owners.

The first recorded stocking of fish into Gnawed Lake was in 1994. Since 2007, the lake has been used for research by FFSBC and has been regularly stocked with various wild-origin triploid strains of rainbow trout (strains carrying three, rather than two, copies of their genome, resulting in sterility), including those originating from Pennask Lake, Blackwater River, and Carp Lake, as well as the triploid Fraser Valley domesticated strain. The estimated density in 2011 was 385 fish·ha^{-1} (Northrup et al. 2012), and as triploid fish are unable to reproduce naturally, it has been stocked annually to maintain the rainbow trout population. Triploid fish are tra-

ditionally stocked in lakes to maintain control of fish density and to avoid introgression between strains, and they are used in this study due to their ecological relevance globally, as well as the individual fish's history in and adaptation to Gnawed Lake.

Fish and surgeries

Rainbow trout were collected from Gnawed Lake via angling by a team of expert volunteer fishers on 2–3 June 2015 and 19 May 2016. Angled fish were transferred in portable aerated tanks within 5 min to an aerated shore tank containing lake water. Surgeries occurred within 15 min and were performed following the procedure for tagging adult salmonids under field conditions outlined in Wagner and Stevens (2000), Ivasauskas et al. (2012), and Rub et al. (2014). Fish were anaesthetized (100 mg·L⁻¹ tricaine methylsulfonate, buffered with a twofold weight of sodium bicarbonate), measured for weight and length, and placed dorsal side down on a surgery table with a moist foam platform. A tube circulating water with 30 mg·L⁻¹ buffered tricaine methylsulfonate was placed in the mouth of the fish to irrigate the gills for the duration of the surgery. A small incision (3 cm) was made along the midventral line anterior to the pelvic girdle, and a uniquely programmed acoustic transmitter was inserted. The incision was closed with continuous horizontal mattress stitches made with 3–0 monofilament absorbable reverse cutting (19 mm) sutures (Ethicon Monocryl). Total surgery time was approximately 2–3 min per fish. Fish were allowed to fully recover (approximately 15 min) in fresh, oxygenated lake water before being returned to the lake. Surgeries were performed by the same individual in both study years. Transmitters (model HTI 795-LY, 307 kHz) were manufactured by Hydroacoustic Technology, Inc., and weighed 11.9 g in air, were 16 mm × 48 mm in dimension, and possessed a 2.5-year battery life with transmitter periods programmed between 3001 and 4681 ms.

A total of 49 triploid fish were tagged in 2015, and 22 were tagged in 2016. Fish ranged 0.58–2.06 kg (mean ± SD, 1.36 ± 0.31 kg) and 34.5–59.0 cm (49.7 ± 4.5 cm), with transmitter weight/fish body weight ratios ranging for all fish from 0.58% to 2.05%. These rainbow trout were stocked as juveniles into Gnawed Lake, and growth data (FFSBC 2012–2014) indicates that all tagged fish were present in the lake for several years prior to tagging, based on their size and fin clip strain identification. While not all strains could be accurately identified due to the presence of many age classes, Pennask Lake and Blackwater River all-female strains made up the majority of tagged fish. All experimental procedures were performed according to Canadian Council for Animal Care guidelines under Animal Use Permit AUP 14-022A2 issued by Fisheries and Oceans Canada Pacific Region Animal Care Committee.

Telemetry system

We deployed 12 stationary hydrophone receivers in Gnawed Lake to maximize the detection area (Fig. 1). Four omnidirectional hydrophones (HTI Model 590, 330° detection range) were placed in the deep area of the lake in a square array that covered 625 m², with two hydrophones near the surface (2 m below water level) and two hydrophones near the lake bottom (1 m above bottom). All four hydrophones were attached to an acoustic tag receiver (ATR, HTI Model 291) by underwater cables and linked to a computer onshore. Six additional omnidirectional hydrophones were placed throughout the rest of the lake (Fig. 1), all 1 m above the lake bottom. These six hydrophones were attached to independent data logger units (HTI Model 395), which save raw acoustic data to an SD card. Two additional directional hydrophones (HTI Model 594, 120° detection range) were placed in the center of the ATR array and in the center of the data logger grid on the lake bottom, both attached to data loggers. Manual GPS locations and an acoustic "ping-around" (as described in Steig et al. 2013) were used to precisely measure the location and relative distances of the stationary hydrophones. Transmitter tows coupled with GPS

Table 1. Temperature and dissolved oxygen presented as averages of manual measurements taken before and after the late summer study period at intervals of 1 m in the eastern end of Gnawed Lake.

Depth (m)	Temperature (°C)	Dissolved oxygen (mg·L⁻¹)
0	12.4	9.6
1	12.4	10.1
2	12.4	10.3
3	12.3	11.4
4	12.3	12.4
5	12.1	12.6
6	12.0	11.7
7	12.0	10.8
8	12.0	6.0
9	11.6	4.5
10	11.1	2.0
11	11.0	1.6

data were used to assess the actualized detection range of each hydrophone. A minimum of three hydrophones must detect the acoustic transmission to position a fish in 2D. Our receiver array did not cover the entire lake, as we could not place hydrophones in certain areas due to depth limitations and the presence of vegetation in shallow areas; however, we were able to position fish throughout most of the lake (65% total area; Fig. 1). Two stationary beacon tags were placed in the lake at the same time the hydrophones were deployed to provide estimates of spatial positioning error. Overall, positioning error was low and slightly lower in the shallow location (mean ± SD, 1.0 ± 0.3 m) compared with the deep location (1.9 ± 0.3 m).

Environmental monitoring

Water temperatures were measured with five data loggers (TidbiT v2, UTBI-001; Fig. 1) at varying depths and manually measured throughout the late summer study periods (Table 1). All loggers recorded temperature data every 15 min from 26 May 2016 to 27 May 2017. Atmospheric light intensity data and air temperature were also collected every 10 min by data loggers (HOBO Pendant, UA-002-64; Fig. 1; Table 2) from 26 May 2016 to 12 December 2016. Monthly benthic invertebrate and zooplankton sampling from July to October yielded high numbers of *Daphnia*, copepods, chironomids, *Gammarus* shrimp, water boatmen, and a variety of freshwater snails (performed by Larratt Aquatic Consulting, Kelowna, British Columbia, Canada). *Daphnia* abundance was high throughout the lake in July and August. Monthly sampling indicated a reduction in *Daphnia* at shallow depths (1–2 m) during September and October, but remained in high proportions in deeper areas of the lake (>3 m). Macrophytes, including *Myriophyllium* spp. and *Chara* spp., were found in shallow areas of the lake throughout the sampling period.

Data processing

The telemetry system collected data throughout 2016, and two 6-day periods were selected for in-depth analysis: 3–8 September (late summer) and 12–17 December (winter). A total of 30 tagged rainbow trout were consistently positioned throughout both of these periods. These fish were 0.78–1.84 kg (mean ± SD, 1.25 ± 0.25 kg) and 38.0–58.0 cm (49.0 ± 3.9 cm). Transmitter weights for this set of fish were 0.65%–1.52% of fish body weight. The telemetry system creates hourly files containing raw acoustic transmitter data coupled with precise time stamps obtained from GPS satellites. Files from each system (ATR and eight data loggers) were merged in MarkTags (HTI, version 6.10) to combine data from all 12 hydrophones into the same hourly files in which transmitter IDs were assigned to acoustic signals. Data were then imported

Table 2. Hourly air temperature and light intensity measurements presented as averages over the late summer study period from two locations at Gnawed Lake.

Hour	Air temperature (°C)	Light intensity (lx)
0000	3.4	0
0100	3.3	0
0200	3.2	0
0300	3.3	0
0400	3.2	0
0500	3.2	0
0600	3.3	908
0700	4.1	7 358
0800	6.9	22 614
0900	9.3	39 812
1000	12.3	56 291
1100	15.0	76 563
1200	13.8	57 025
1300	15.2	78 996
1400	13.8	58 762
1500	14.7	68 047
1600	14.7	59 198
1700	11.5	24 058
1800	9.1	10 846
1900	5.9	1 491
2000	3.8	0
2100	3.3	0
2200	3.0	0
2300	3.1	0

into AcousticTag (HTI, version 6.10) to determine spatial location (X and Y) and were subsequently exported to Excel for analysis. Speeds of sound used for position calculations were 1453.88 m·s^{-1} for summer data and 1404.14 m·s^{-1} for winter data, reflecting differences in water temperature between the two seasons based on readings taken at multiple depths in Gnawed Lake. Total recorded positions for the 30 tracked rainbow trout over the selected 6-day study periods were 1 771 481 in summer and 1 465 057 in winter.

Data analysis

Swim speed was calculated using the difference in time between each acoustic signal ($t_2 - t_1$) and the difference in X and Y positions between the two signals ($x_2 - x_1$ and $y_2 - y_1$). Speed was calculated as follows for each interval: $[(x_2 - x_1)^2 + (y_2 - y_1)^2]^{(1/2)}/(t_2 - t_1)$. The time between pings ($t_2 - t_1$) varied from 3 to 5 s for each fish, depending on the transmitter period. Speeds calculated for intervals in which ($t_2 - t_1$) was greater than 5 s were excluded. These analyses reflect a minimum estimation of speed, as depth was not measured. We calculated a daily average speed for each fish in each season to determine if swim speed was consistent among fish in the population or varied by individual. These averages were then divided by individual body length to adjust for size differences among the tagged fish. Hourly average speeds were calculated in the same way, to test for diel variation in speed. Hourly speeds were pooled into four time periods: dawn, day, dusk, and night. These varied with day length by season, but in both cases dawn and dusk included the hour before and after sunrise and sunset, respectively, while day spanned the remaining hours from sunrise to sunset and night spanned sunset to sunrise. Thus, in addition to 2-hour dawn and dusk periods, there were 12 daytime hours and 8 nighttime hours in late summer and 8 daytime hours and 12 nighttime hours in winter.

We determined space use of tagged rainbow trout using a kernel utilization distribution (KUD), which gives the probability density that an individual is found at a certain point in space

(Worton 1987). Core areas represent 50% of the KUDs and are used to signify areas of high importance, while 95% KUDs are used to calculate home ranges. The home range and core area values were calculated using the "ks" package in the R statistical environment (R Core Team 2017; Duong 2017). Daily averages of these spatial measurements were calculated for individual fish using positions from the entire day, while dawn, day, dusk, and night periods were calculated by averaging the relevant hours. Only fish that had average values for all four time periods in both seasons were included in the diel analysis ($n = 23$). Home range and core area are presented as averages of hourly measurements to compare between seasons.

A qualitative spatial analysis of positional data was made in ArcGIS 10.5 by creating a kernel density map for each time period in both summer and winter. This analysis indicated that use of positional data alone resulted in underrepresentation of fish occupancy in the shallow areas of the lake. Therefore, we included both positional and raw data (see below) to assess location preference quantitatively. We did this by first separating the lake into nine zones (Fig. 1) and calculating the proportion of time each fish was positioned in each zone, on both a daily and an hourly basis. Zones were assigned according to hydrophone detection ranges and approximate ecozones. The proportion of time spent in each zone by hour was averaged over four time periods (dawn, day, dusk, and night), but only day and night were used in this analysis. Since the zones are not equivalent sizes, an initial statistical test was performed to compare the proportion of time fish occupied a zone with the relative area that zone accounted for in the lake. The null hypothesis was rejected in all time periods tested (day and night in both summer and winter; $P < 0.0001$), indicating that fish were not distributed throughout the lake in proportion to zone area. Subsequent statistical analyses were performed to identify zone preferences for individual fish: a two-way ANOVA assessing zone by season and two-way ANOVAs assessing zone by time of day in summer and winter separately. These helped to determine whether all fish frequented the same areas of the lake or individuals possessed some preferences, and if the latter, whether their preferences changed throughout the day. Zone preference analyses were performed in SPSS, and Aitchison's log-ratio transformation (Aitchison 1986; Pawlowsky-Glahn and Buccianti 2011) for compositional data was used throughout.

Raw data inclusion

Fish positions were detected less at night on average (summer: mean ± SD positions per fish per hour; day = 557 ± 25, night = 200 ± 25; t test, $P < 0.0001$; winter: day = 363 ± 25, night = 242 ± 13; t test, $P < 0.0001$) due to their preference for the edges of the lake where there was less hydrophone coverage. However, when a fish was not in range of at least three hydrophones (needed for positioning), it was often possible to determine its approximate area of occupation using raw detection data from individual hydrophones. As all hydrophones had a known detection range determined by transmitter tows, we were able to broadly identify areas of occupation using raw detection data and thus incorporate this information into the zone preference analysis. The number of raw detections that yielded an approximate location over the 6-day study periods were 1 102 181 in summer and 1 055 429 in winter.

Results

Seasonal

Rainbow trout, on average, swam approximately twice as fast in late summer compared with winter (Table 3; paired t test, df = 29, $P < 0.001$). Rainbow trout also occupied larger areas of the lake in summer than winter; average summer home range was nearly two times the average home range in winter (Table 3; paired t test,

Table 3. Mean seasonal activity (range of values in parentheses) of tagged rainbow trout ($n = 30$) in Gnawed Lake and correlation of activity parameters among individuals between seasons.

Variable	Summer	Winter	Spearman R	t	P
Swim speed (bl·s^{-1})*	0.61 (0.23–1.24)	0.34 (0.14–0.70)	0.43	2.52	0.018
Home range (m^2)	13 561 (774–34 087)	7 447 (145–18 683)	0.45	2.69	0.012
Core area (m^2)	2 047 (23–6 341)	840 (34–2 159)	0.48	2.93	0.007

*Body length = bl.

Fig. 2. Home range in dawn, day, dusk, and night periods as described by hourly average extent of movement in (*a*) summer and (*b*) winter. Box limits indicate the 25th and 75th percentiles; whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles (Tukey); outliers are represented by open circles; center lines show the medians; and crosses represent group means ($n = 23$ for all groups).
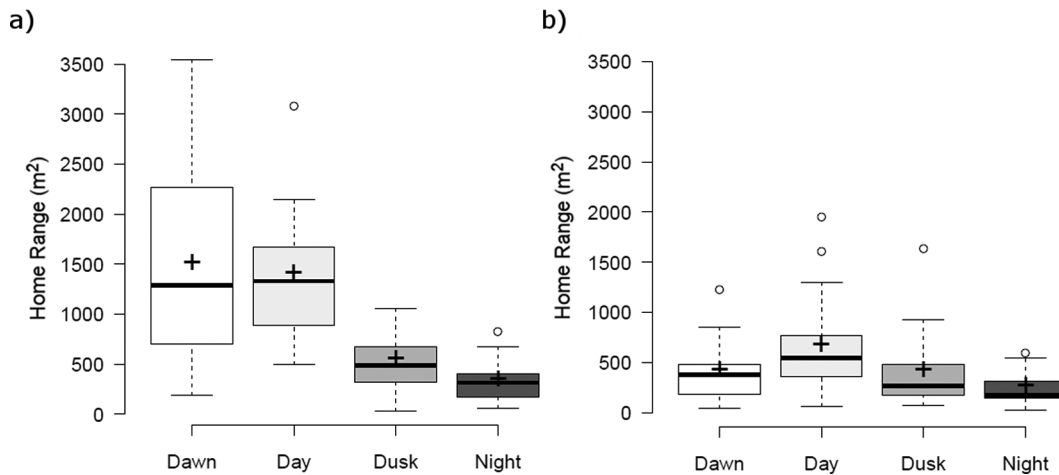
df = 29, $P < 0.001$), while summer core area was more than double the average core area in winter (Table 3; paired t test, df = 29, $P < 0.001$). Ranking of individuals was consistent from summer to winter in all three parameters (Table 3; also refer to the online Supplementary material, Fig. 1[1]; Spearman R, $n = 30$). Hourly home ranges in dawn and day were greater in summer than in winter (ANOVA, $n = 23$, $P < 0.001$ for both comparisons), but dusk and night ranges were not significantly different between seasons (ANOVA, $n = 23$, $P = 0.14$ and 0.28, respectively; Fig. 2). Core areas in the four time periods followed a similar pattern to home ranges.

In late summer, tagged rainbow trout favoured zones 4, 5, and 6 (central zones) over at least two other zones ($P < 0.05$), with zones 1 and 2 (shallow water zones) being the least occupied. In winter, zones 4 and 5 were favoured over at least three other zones ($P < 0.05$), with zones 6 and 8 being the least occupied zones. The only significant seasonal change in daily zone preference was that fish spent less time in zone 6 (a transitional zone between deep and shallow ends of the lake) during winter than in late summer ($P < 0.01$). While most fish (22/30 individuals) shifted their zone preference from summer to winter, many maintained one out of two preferred zones, indicating some general site fidelity across seasons. There were few universal trends in zone preference across all tagged fish, as individual diel patterns dominated fish behaviour.

Individual measures of activity were largely reduced in the winter season. Change in individual swim speed from summer to winter varied from −0.9 to +0.2 body lengths (bl)·s^{-1} (Fig. 3a), with an average decrease of 0.3 bl·s^{-1} or 35%. Extent of movement overwhelmingly decreased from summer to winter, with individual change in home range varying from −20 936 m^2 to +3434 m^2 (mean = −6114 m^2; Fig. 3b) and individual change in core area varying from −4537 m^2 to +374 m^2 (mean = −1207 m^2; Fig. 3c).

There was no significant correlation ($P > 0.21$) between individual swim speed and home range or core area size in summer or winter.

Diel

Daytime swim speeds were greater than nighttime speeds regardless of season (0.57 ± 0.29 bl·s^{-1} daytime versus 0.41 ± 0.24 bl·s^{-1} nighttime; ANOVA, $n = 26$, $P = 0.002$), but no significant differences were found between dawn and day or between dusk and night. A frequency histogram of summer swim speeds reveals that faster speeds were observed more frequently during the day, while in winter, the relative frequencies of swim speed were similar regardless of the time of day (Supplemental Fig. 2[1]). In summer, average hourly home ranges during dawn (1485 m^2) and day (1378 m^2) were greater than those for dusk (519 m^2) and night (323 m^2; ANOVA, $n = 23$, $P < 0.001$ for all comparisons; Fig. 2a). In winter, hourly daytime home range (648 m^2) was greater than nighttime home range (241 m^2; ANOVA, $n = 23$, $P < 0.001$; Fig. 2b), but dawn (397 m^2) and dusk (400 m^2) home ranges were not significantly different from other times of day. Core areas followed a similar pattern to home ranges in both seasons.

The spatial use of the lake by fish appeared to differ depending on both season and time of day, as depicted in the qualitative spatial analysis of positional data (Fig. 4). Patterns were more similar among the four time periods in winter compared with summer, where time of day affected the relative density of fish throughout the lake. Kernel density maps show increased movement at dawn during the summer, with greater overall activity than in winter (Figs. 4a, 4e). In both seasons, there were two areas of increased usage during the day (one at each end of the lake) with less movement through the middle of the lake (Figs. 4b, 4f), though these areas were larger in summer than in winter. Activity increased again at dusk, with greater cross-lake movement in

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Fig. 3. Change (winter – summer) in (*a*) swim speed (bl = body length), (*b*) home range, and (*c*) core area of individual fish, arranged from smallest (38 cm) to largest (58 cm) fork length.
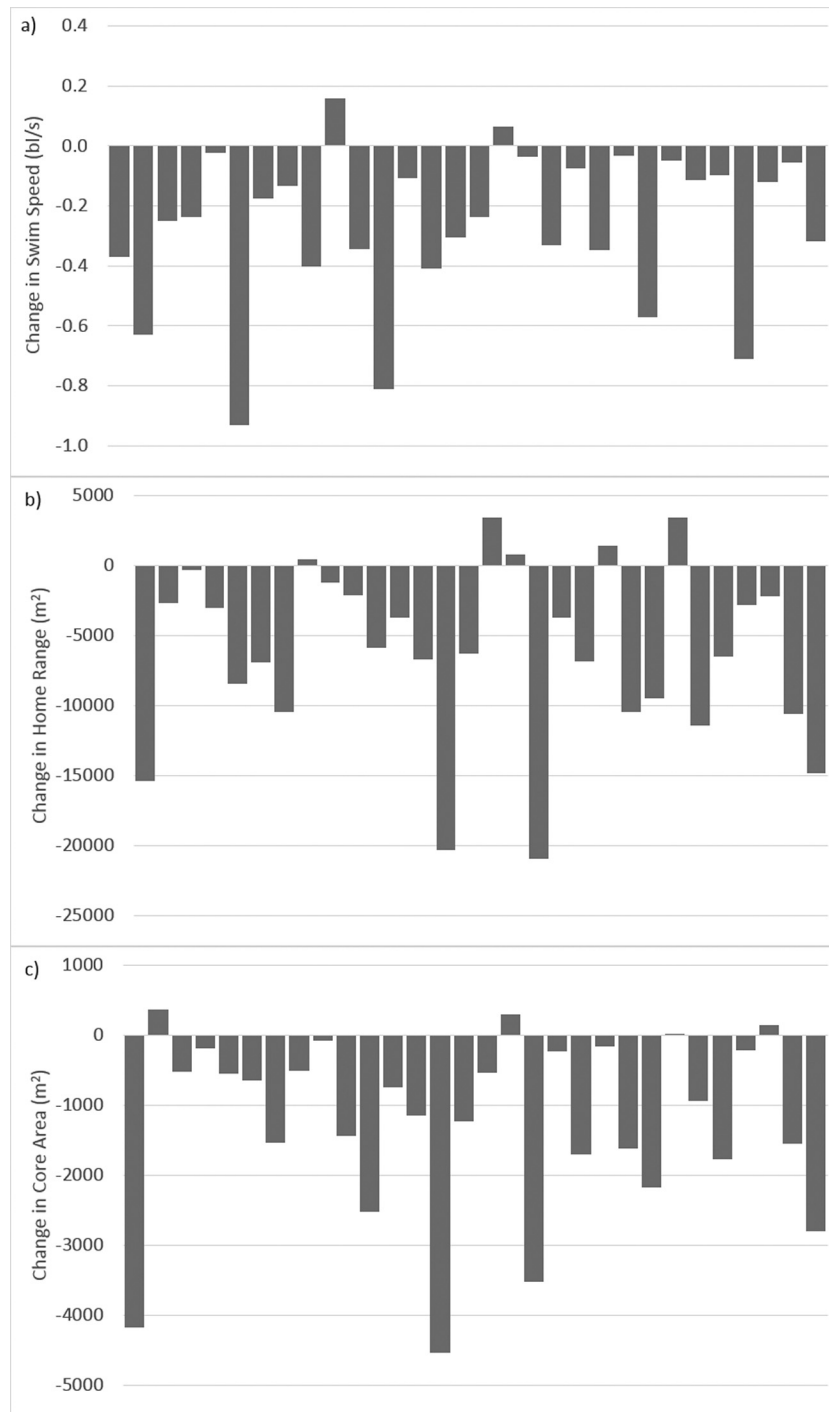

summer only (Figs. 4*c*, 4*g*). Finally, there was a reduction in movement in both seasons at night (Figs. 4*d*, 4*h*), but fish continued to occupy a larger area of the lake in summer compared with winter.

Individual fish showed varied patterns of zone preference, with some occupying certain areas of the lake at specific times of day and some showing more consistent site fidelity. About half of all tagged fish (16/30) had a significant interaction between zone and time of day in summer (Fig. 5*a*). Some fish (4/16) had no significant zone preference during the day, but returned to the same part of the lake at night; others (11/16) had different zone preferences during the day and at night (see Figs. 6, 7, 8, and Supplemental

Video 1[1]); and a single fish had a zone preference during the day and not one at night. For tagged fish that did not have a significant interaction between zone and time of day in summer (14/30), few fish (4/14) showed no preference for any zone in either day or night, while most (10/14) occupied the same areas during both day and night (sometimes one zone, sometimes a combination of two adjacent zones). Thus, approximately one-third of tracked rainbow trout shifted zones predictably from day to night, one-third occupied the same area of the lake regardless of time of day, and the remaining fish had more random patterns of habitat use during summer.

Fig. 4. Kernel density of rainbow trout summer positions in Gnawed Lake during (*a*) dawn, (*b*) day, (*c*) dusk, and (*d*) night and winter positions during (*e*) dawn, (*f*) day, (*g*) dusk, and (*h*) night. An output cell size of 0.1 m was used with 10 naturally spaced categories from least to most dense within a time period as determined by ArcGIS. Dashed line indicates positioning area. Light blue lake background indicates the absence of positional data.
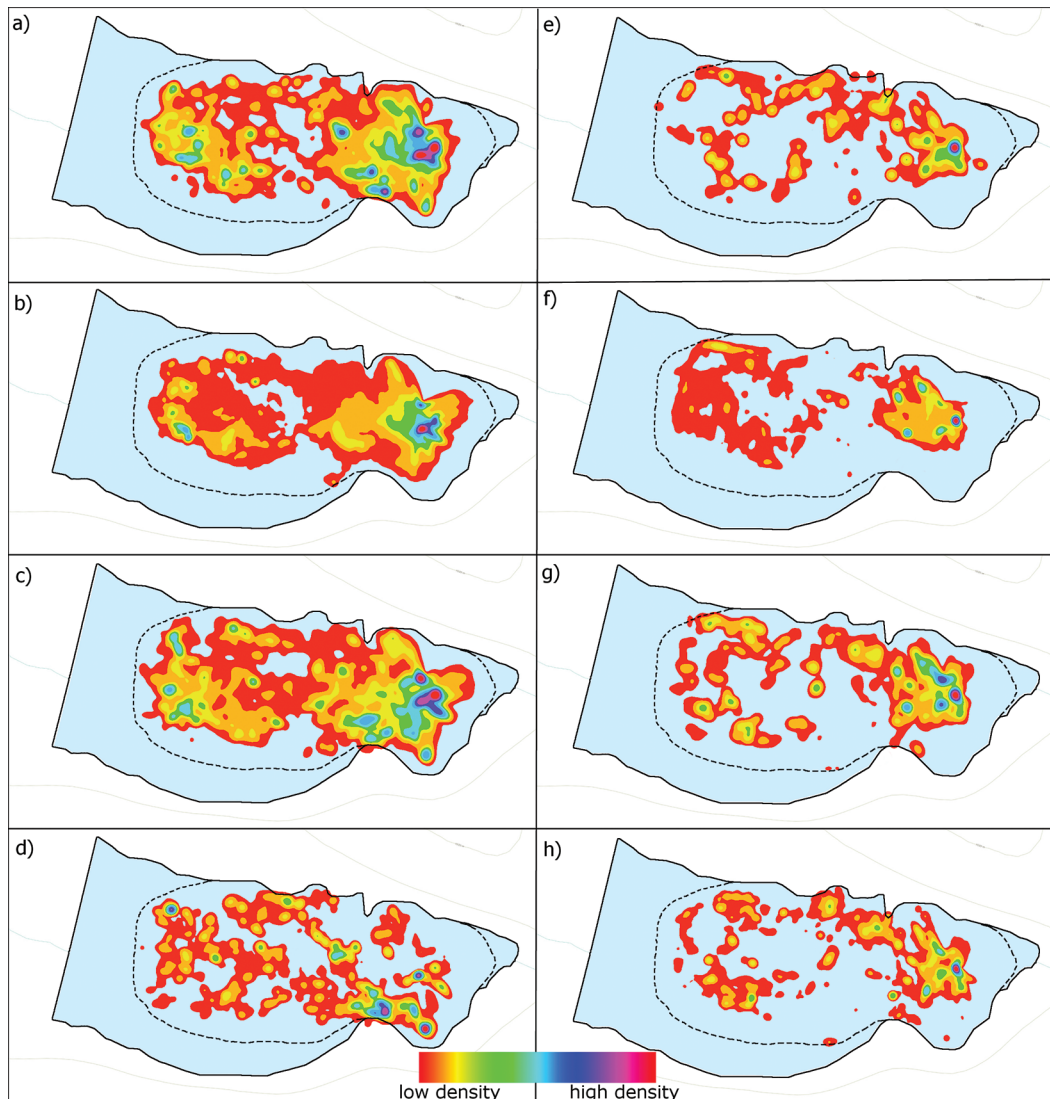
Patterns of zone preference by rainbow trout differed from summer to winter. In winter, most fish (26/30) did not have a significant interaction between zone and time of day (Fig. 5*b*). Many of these fish (16/26) preferred the same zone(s) regardless of the time of day (see Figs. 9, 10, 11, and Supplemental Video 2[1]), while others (10/26) had no significant preference either day or night. Only four fish had a significant interaction between zone and time of day, and all shifted their zones reliably from day to night. Therefore, the number of rainbow trout without any zone preference increased in winter, as well as the number of fish who occupied the same area regardless of the time of day.

Discussion

Seasonal behaviours

Rainbow trout in Gnawed Lake were found to display a large range of individual swim speeds in both summer (0.23–1.24 bl·s⁻¹) and winter (0.13–0.70 bl·s⁻¹). Previous studies of lake salmonids implanted with ultrasonic transmitters have yielded similar, but often lower, swim speed estimates. Warner and Quinn (1995) found average speed in adult rainbow trout to be 0.3 bl·s⁻¹, with

individual speeds ranging from 0.1 to 0.6 bl·s⁻¹ over the study period. Schulz and Berg (1992) measured a similar range of speeds in brown trout (*Salmo trutta*), with short-term speeds up to 2 bl·s⁻¹, while Nowak and Quinn (2002) estimated 0.49 bl·s⁻¹ swim speed in cutthroat trout (*Oncorhynchus clarkii*). More recently, three-dimensional swim speeds of two Biwa salmon (*Oncorhynchus rhodurus*) were estimated to be 0.9 and 1.3 bl·s⁻¹ over several hours (Kamimura and Mitsunaga 2014). These previous studies, while very informative, collected acoustic data through manual tracking, which often limits the number of fish that can be tracked and the times at which data collection can occur (both daily and seasonally). By collecting data on all 30 fish remotely and continuously, we were able in the present study to compare swimming and other parameters between seasons and times of day, as well as identify differences between individuals that reflect intracohort behavioural variation.

The present study found an overall reduction in the extent of movement of rainbow trout during winter, with both measures (home range and core area) having a significantly lower group average as well as a smaller range of individual values in winter.

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Fig. 5. Numbers of individual rainbow trout displaying certain diel patterns in zone preference observed in Gnawed Lake in (*a*) late summer and (*b*) winter.
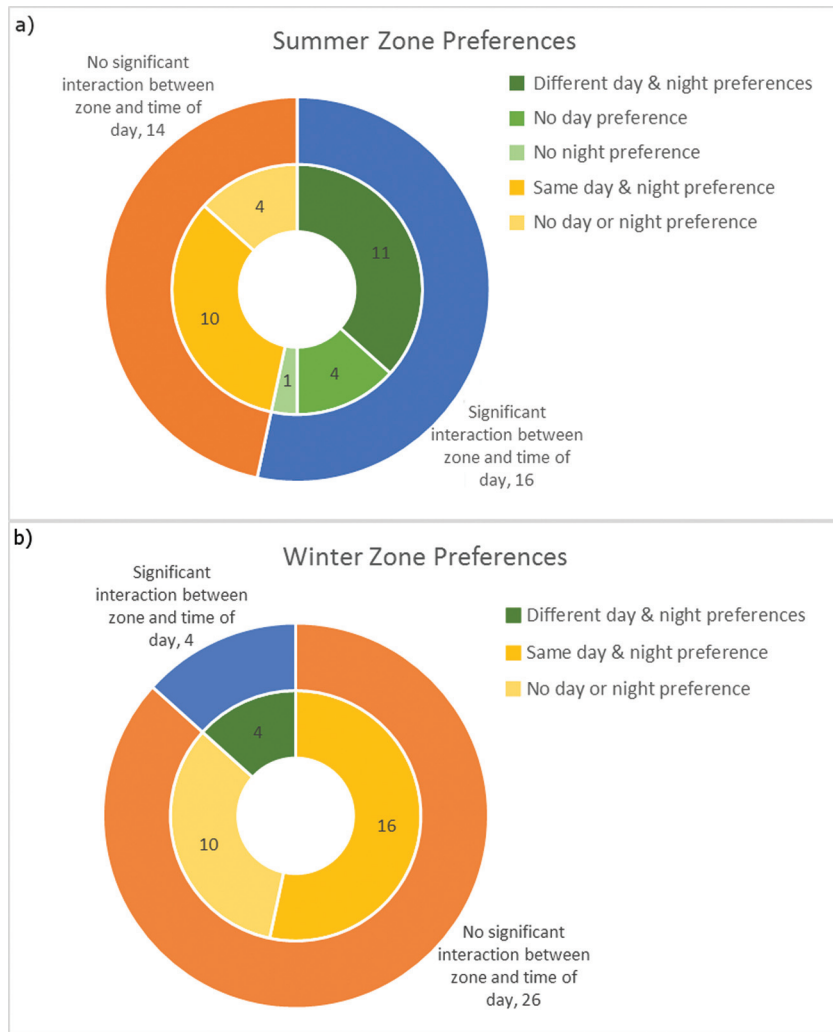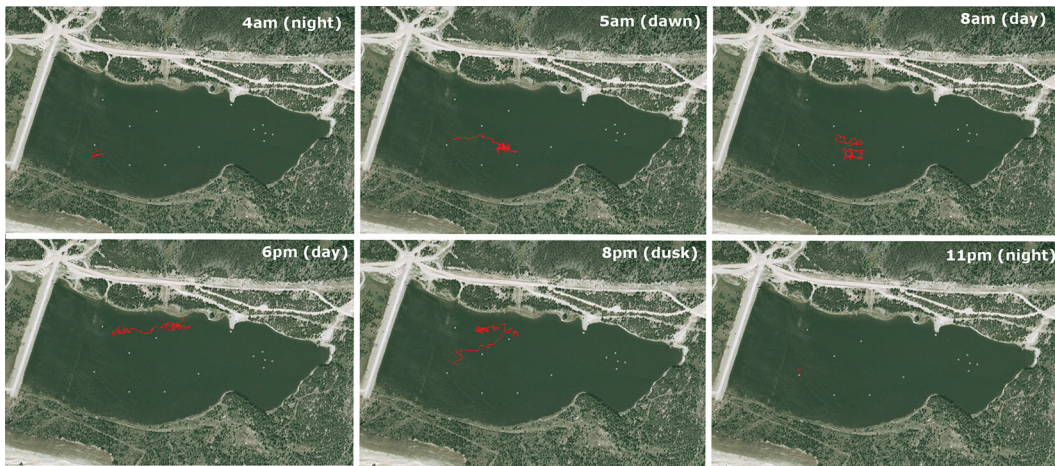

Fig. 6. Example of diel movement in summer. Each dot represents a position calculated in AcousticTag from data collected from three or more hydrophones, and all positions from the same hour are presented on the map together. Shown here, a fish starts in zone 5 at night, travels to zone 7 at dawn, forages in zones 7, 8, and 9 during the day, and returns to zone 5 at dusk. [Colour online.]
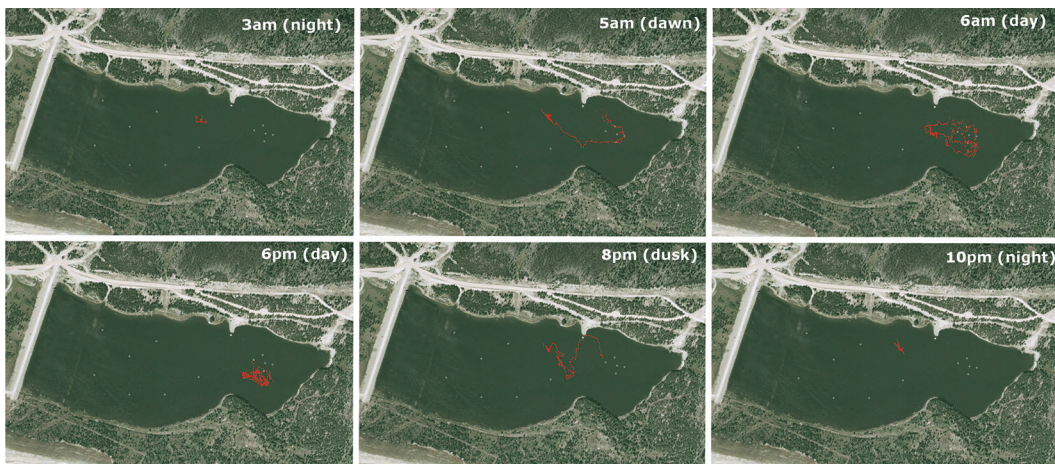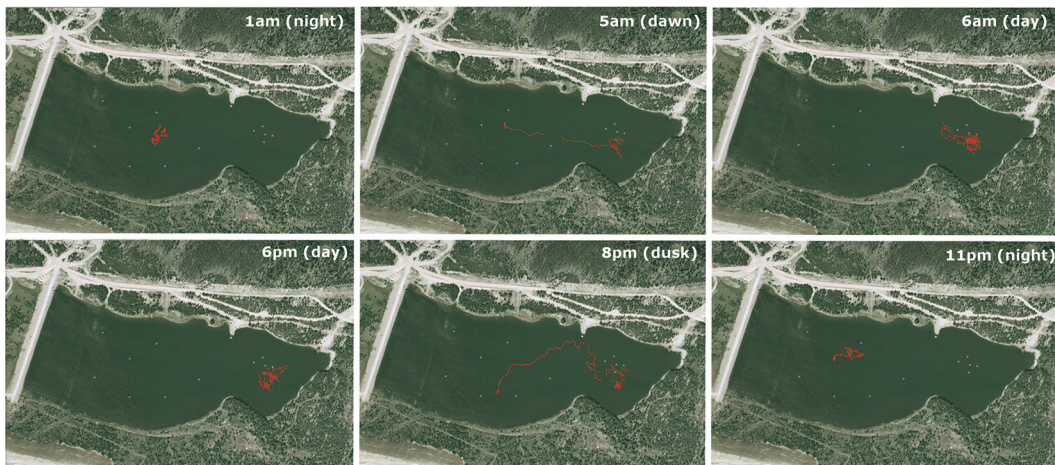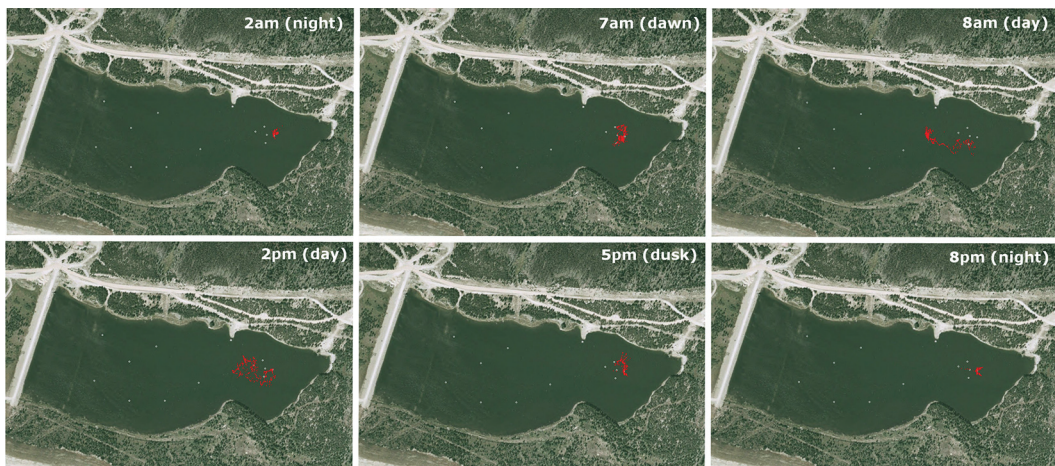
Fig. 7. Example of diel movement in summer. Each dot represents a position calculated in AcousticTag from data collected from three or more hydrophones, and all positions from the same hour are presented on the map together. Shown here, a fish starts in zone 2 at night, travels to zone 4 at dawn, forages in zones 3 and 4 during the day, and returns to zone 2 at dusk. [Colour online.]
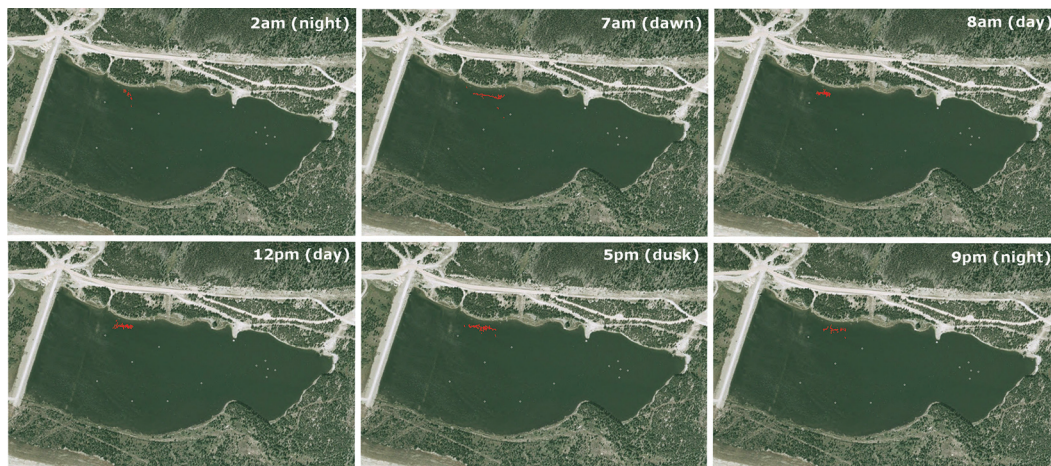

Fig. 8. Example of diel movement in summer. Each dot represents a position calculated in AcousticTag from data collected from three or more hydrophones, and all positions from the same hour are presented on the map together. Shown here, a fish starts in zones 3 and 4 at night, travels to zone 8 at dawn, forages in zones 7, 8, and 9 during the day, and returns to zone 3 (via zone 4) at dusk. [Colour online.]


Fig. 9. Example of diel movement in winter. Each dot represents a position calculated in AcousticTag from data collected from three or more hydrophones, and all positions from the same hour are presented on the map together. Shown here, a fish displays minimal movement in zone 4 throughout the day. [Colour online.]

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Fig. 10. Example of diel movement in winter. Each dot represents a position calculated in AcousticTag from data collected from three or more hydrophones, and all positions from the same hour are presented on the map together. Shown here, a fish displays minimal movement in zone 3 throughout the day. [Colour online.]

Fig. 11. Example of diel movement in winter. Each dot represents a position calculated in AcousticTag from data collected from three or more hydrophones, and all positions from the same hour are presented on the map together. Shown here, a fish displays minimal movement in zones 7, 8, and 9 throughout the day. [Colour online.]
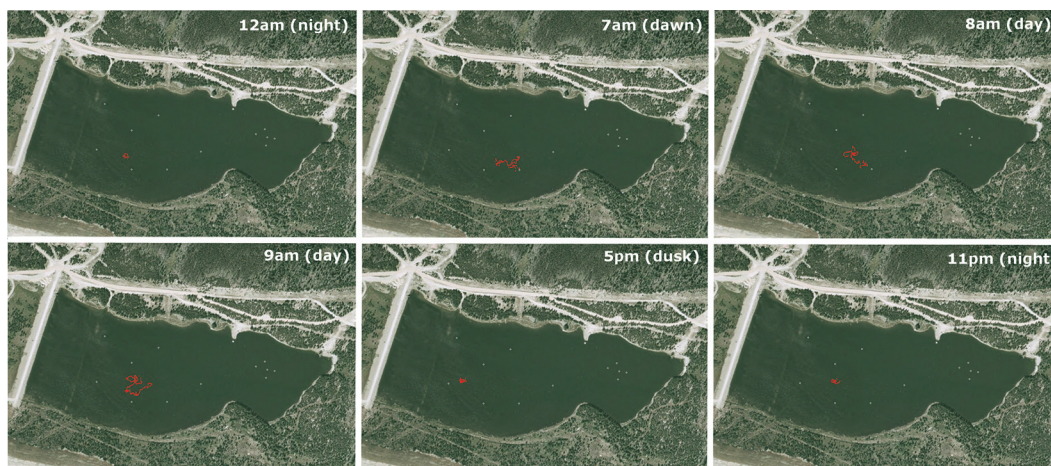
Blanchfield et al. (2009) found that lake trout home ranges were three times greater, and core areas of use were four times greater, in summer than winter, while core areas represented about one-tenth of home range in both seasons. Our data are consistent with these observations, even though Gnawed Lake is almost three times smaller than Lake 373 of the Experimental Lakes Area where the study was performed (area = 10 ha compared with 27.3 ha). Both individual home range and core area were slightly more than four times greater on average in summer than in winter, and core area made up 14% of home range in summer and 12% in winter in our study. Intuitively, home ranges and core areas may be expected to increase in times of food shortage. However, a decrease in area use by fish in winter could be attributed to a lower metabolic rate, as well as the increased cost of foraging in cold water.

It is also likely that physiological limitations can affect swim speeds, which could explain in part the average decrease of 35% in individual swim speeds observed from summer to winter. While no previous studies have measured fine-scale swim speed of the same fish in both summer and winter in nature, this is well-predicted by lab studies measuring swim speed under both warm and cold conditions; Webb (1978) found the maximum velocity of juvenile rainbow trout increased with temperature almost two-fold (from 0.99 to 1.71 m·s⁻¹) from 5 to 15 °C, remaining constant

thereafter up to 25 °C. Jain and Farrell (2003) similarly found U_{crit} to increase linearly among adult rainbow trout from 5 to 17 °C. While colder conditions physiologically limit swim speeds, it also makes ecological sense that rainbow trout would reduce overall swim speed to conserve energy in winter when prey availability is low. We found a significant correlation between individual swim speeds in summer and winter, indicating that faster individuals in summer were also faster in winter, despite a decrease in swim speed overall. These data suggest that fish can possess individual movement traits that are maintained among environmental conditions, at least in the limited scope of this study. Similarly, Taylor and Cooke (2014) found that interindividual variation in movement behaviours was repeatable in bull trout (*Salvelinus confluentus*) on both a diel and seasonal time scale. Determining whether these observations could reflect different evolved foraging strategies, innate genetic differences affecting metabolism and general activity levels, or are learned differences that are retained between seasons will require additional investigation.

We observed large variation in individual home range and core area, particularly in summer. One possible explanation for this could be dominance hierarchy within the population. Höjesjö et al. (2007) found that dominant brown trout individuals moved longer distances and had larger home ranges on average than subordinate fish. The maximum swim speeds we observed in sum-

mer would allow the average fish to cover more than 1 km of two-dimensional distance per hour, but actual distance travelled was much lower. The individual with the largest home range in summer (34 088 m²) only covered approximately one-third of the total lake area (one-half of total area available for positioning), suggesting that even in this small lake, fish are focusing their foraging and exploratory efforts on specific areas, or potentially developing territories, as in juvenile rainbow trout (Wood et al. 2012). This is supported by the zone preference analysis, which indicated only 4/30 fish showed no preference for any zone in summer — the remaining 26 fish either stayed in the same zone consistently or showed some discernable pattern of diel movement. Some fish may be able to behaviourally dominate other fish for access to profitable areas or have improved ability to efficiently identify and consume prey through familiar surroundings and development of search images for specific prey types. In addition, fish that shifted their zone from day to night would naturally cover more lake area than those staying in the same zone, which would also account for the reduced variation in range measurements in winter when fewer fish displayed diel movement. Similar to swim speed, fish that explored larger areas of the lake in late summer continued to do so in winter. However, there was no correlation between individual swim speeds and home range or core area in either season, indicating that faster individuals did not occupy greater areas of the lake.

Dawn and day ranges in summer were significantly larger than dawn and day ranges in winter, but there was no difference between dusk and night ranges from summer to winter, indicating there was a similar amount of fish movement at night that was unaffected by seasonal changes. The ranges observed during dusk and night may reflect a minimum for resting fish activity; regardless of season, fish are maintaining their positions in the lake with few cross-lake movements. While a reduction in range at night has been previously observed in rainbow trout (Warner and Quinn 1995) and brown trout (Hojesjo et al. 2007), consistency between seasons has not been measured. In winter, we observed a slight peak in rainbow trout movement during the day, but no significant increase at dawn as there is in summer. It is likely that fish would react to daylight more gradually in winter, as direct light is obscured by ice and snow cover during this period. Blanchfield et al. (2009) found lake trout habitat to be constricted by light levels under ice, while Bass et al. (2014) found European grayling (*Thymallus thymallus*) to display little vertical movement in winter and remain at shallow depths where light intensity was most favorable for foraging. It is likely that the rainbow trout in this study experienced a similar limitation under winter conditions and reduced their movement patterns both vertically and horizontally. As winter temperatures increase due to climate warming, rainbow trout behaviour would be expected to change as well. Climate change models have predicted delayed and shorter periods of ice coverage in temperate lakes (Jansen and Hesslein 2004), which would result in the extension of open-water behaviour into the winter season and could negatively affect juvenile fish survival in natural populations (Hedger et al. 2013).

Diel behaviours

Several studies have found faster swim speeds and higher activity levels during daylight hours in rainbow trout (Warner and Quinn 1995; James and Kelso 1995; Young et al. 1997) and other salmonids (Schulz and Berg 1992; Baldwin et al. 2002). This observation is often connected to foraging behaviour; peak salmonid feeding has been observed at either dawn and dusk (Jobling et al. 1995) or at dusk only (Beauchamp 1990; Johnson and McKenna 2015), with little to no feeding after twilight (Angradi and Griffith 1990). Rainbow trout behaviour has been contrasted with both brown trout (Young et al. 1997) and cutthroat trout (Nowak and Quinn 2002) under natural sympatric conditions, with rainbow trout displaying increased diurnal activity in both cases. While we

did not observe any significant differences in dawn or dusk speeds, average daytime speed was faster than nighttime speed in both seasons, which is likely connected with reduced feeding and foraging at night. Rainbow trout also showed a difference in the distribution of swimming speeds, which varied by time of day and season. In summer, the greatest proportion of high-speed movements was detected during the day relative to other periods, with dawn and dusk also showing an increase relative to night. Whether such high-speed movements reflect predatory activity on prey, responses to predators, or behavioural interactions among individuals is not known. What is apparent is that fish spend a large portion of their day swimming at slow speeds, with faster swimming occurring periodically throughout the day. Such behavioural activity is reduced, but not eliminated, at night and in winter. Similarly, dawn and day home ranges were greater than dusk and night ranges in summer, and these hours of increased activity correspond to increasing levels of light intensity (Table 2). Fish activity increases at dawn corresponding with sunrise and the first detection of sunlight, but it is not affected by level of sunlight thereafter. This is consistent with observations that rainbow trout feeding is triggered by a threshold level of low light (Johnson et al. 2016) and is also consistent with literature indicating that a relatively low level of light (100 lx) is required for visually foraging salmonids to attain maximum reaction distance for zooplankton (Henderson and Northcote 1985; Baldwin et al. 2002).

Significant variation in diel activity patterns has been found within single populations of salmonids (Reebs 2002; Breau et al. 2007; Roy et al. 2013), and Hyatt (1980) found rainbow trout to be more active during the day than at night, but not strictly nocturnal, diurnal, or crepuscular. In the present study, dawn home ranges in particular show increased variability among individuals compared with other time periods in summer (Fig. 3a), suggesting that some fish are exploring more of the lake than others in these hours. This is evident in the density map showing fish movement during dawn (Fig. 4a), in which the middle of the lake is used as a travel corridor. Fish that shift zones from night to day would be doing so in these 2 hours, while fish that did not have an interaction between time of day and zone preference would not produce larger range measurements at dawn. Thus, increased variability in home range at dawn reflects the variability of foraging strategies within the population. The night density map (Fig. 4d) shows more isolated hot spots, where fish are settling overnight with minimal movement. This corresponds to both the reduced speed and reduced extent of movement that this study identified at night and further shows the nonrandom use of lake habitats. Such behavior may indicate fish are travelling to optimal conditions throughout the day and night to maximize fitness. While it would be of considerable interest to couple observations of the behavior of individual fish with their stomach contents, recovery of tagged fish was not sufficient in the current experiment to allow such analyses.

Beauchamp (1990) found that juvenile rainbow trout in Lake Washington ate primarily *Daphnia*, while adult individuals ate *Daphnia* during the day and smaller fish at dusk. Gnawed Lake does not have natural recruitment or stocking of smaller fish species, but does harbor a large population of *Daphnia*. It is likely *Daphnia* would remain a primary food source for many of the adult rainbow trout in this study and yield increased daytime activity. Stomach contents taken from four untagged adult rainbow trout caught in Gnawed Lake in mid-September confirm that *Daphnia* made up a large proportion of prey items (Michael Ohata, photos taken 17 September 2016). While *Daphnia* represented a high proportion of total zooplankton in all areas of the lake during July and August, it decreased in the shallow areas of the lake in September and October. This is consistent with the observation that *Daphnia* are more abundant during the warmer summer months than in fall and winter, as was also found in an analysis of sockeye salmon stomach contents in Lake Washington (Eggers 1982). *Daphnia*

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abundance remained high through September and October in only the deep areas of the lake, which could have driven the diel foraging pattern seen among some individuals in late summer. Fish that did not display diel movement involving the eastern end of the lake (zones 7, 8, and 9) may have utilized different food sources in their respective areas of the lake; a priority for future research should be more strongly tying fish behaviour to environmental factors, including variation in prey availability.

It has been shown under experimental lab conditions that dominant fish spend more time in open areas, are more active swimmers, and are more likely to trigger self-feeding; however, such fish do not capture more food resources or have increased growth rates compared with subordinate individuals (Chen et al. 2002; Sneddon 2003). These studies suggest that in order for both phenotypes to exist, it is unlikely that one is significantly more advantageous than the other. However, Armstrong et al. (2013) found that stream-dwelling coho salmon (Oncorhynchus kisutch) that foraged in cold water and digested in warm water (termed "diel movers") grew significantly faster than fish with other behaviours. A similar process may explain the behaviour of fish that shifted zones from day to night in the present study; the eastern end of the lake is significantly deeper, and in summer, colder water can be found at lower depths compared with the surface of the lake, along with different zooplankton profiles. The difference between these two findings highlights the importance of performing behavioural experiments in nature. Gnawed Lake is a heterogeneous landscape of both abiotic and biotic factors, and bolder individuals are more likely to explore greater areas of the lake, with a higher possibility of being able to exploit better resources than their timid counterparts (Metcalfe 1986). As in the study by Armstrong et al. (2013), there was a variety of foraging strategies observed in Gnawed Lake, indicating that the interplay of prey availability, predation risk, and abiotic factors at different times of day influenced the behaviours of fish in different ways.

The temperature disparity between shallow and deep areas of the lake was much lower in winter than in summer in the present study, as there was similarly cold water throughout the lake under ice, and consequently less diel movement was observed. Few fish had a statistically significant interaction between time of day and zone preference in winter — 4/30 fish compared with 16/30 fish in summer. Most fish adopted a local movement strategy in winter, in which they occupied a slightly larger area of the lake during the day but stayed within the same part of the lake as at night, instead of traveling to a different zone as many did in summer. Kernel density maps in winter show that fish maintain their 2D positions in the lake more reliably throughout the day, which is consistent with the quantitative statistical analyses that indicated lower occupation of the central, transitional zones of the lake. Watz et al. (2015) found that stream-dwelling brown trout swam more actively throughout the water column and spent more time foraging in winter, as the presence of surface ice reduced predation risk. We did not observe this phenomenon in Gnawed Lake, suggesting that any advantage gained by reduced predation was outweighed by the disadvantages of frequent or long-distance movement in cold water. Additionally, shallow water zones 1 and 2 that were avoided in summer (likely due to high water temperatures) were more frequently occupied in winter. Owing to more uniform abiotic conditions and reduced prey availability, fish displayed less diel movement, which resulted in less observed activity in the transitional zones between the shallow and deep ends of the lake. Most fish also minimized their individual patterns in favour of reduced speed and range, resulting in less individual variation among these parameters in winter.

Giller and Greenberg (2015) defined brown trout as either "movers" or "stayers" in a stream study, and we similarly identified two predominant types of movement in Gnawed Lake in late summer: fish whose position in the lake varied with time of day and fish whose position remained consistent regardless of the time of day.

This behaviour is further specialized by individual site preference; not all fish frequented the same areas of the lake at a given time of day, specifically at night. Fish that shifted zones often repeatedly returned to a specific area of the lake at night (see Supplemental Video 1[1]), separate from other tracked fish. Morbey et al. (2006) found that while habitat use was highly variable among lake trout, individual behaviour was remarkably consistent between two consecutive summers, providing evidence of repeatable behaviour on the individual level when faced with similar environmental conditions. Studies have found resting metabolic rate to be repeatable and correlated with individual behavioral output and productivity, indicating that some individuals may be predisposed to be more active (Biro and Stamps 2010). This would result in faster swim speeds and larger home ranges and could explain the correlation between these factors across seasons in this study. Bioenergetic analysis incorporating individual diet and movement patterns will help to assess this theory further.

The analysis of 3D positioning data would help to support the diel movement theories discussed in this study. Unfortunately, the bathymetry of Gnawed Lake did not allow for accurate 3D positioning with the described hydroacoustic configuration. In addition, identifying the strain of individuals may reveal a genetic component to individual behaviour that this study overlooks. Further research into the effects of ploidy on behaviour could also reveal potential differences. While triploid and diploid fish are highly similar on a whole-animal level, with no differences in critical swimming speed, oxygen consumption, or energy utilization under normal conditions (Benfey 1999), triploid salmonids have been found to have a reduced tolerance for high temperatures and hypoxic conditions due to limitations of their cardiovascular system compared with diploids (Verhille et al. 2013; Sambraus et al. 2017). These differences may mean that certain behaviours observed in triploid fish, particularly under warmer conditions, do not occur in wild diploid populations. However, given that triploid rainbow trout are extensively stocked in lakes and river, these findings are still of importance, especially in the context of climate warming. More research is needed comparing triploid and diploid behaviour in nature under a variety of environmental conditions to characterize fully the distinction between the two. The present study does reveal significant individual variation in swim speed, extent of movement, and diel patterns among triploid rainbow trout in summer and winter and proposes mechanisms by which fish may be influenced in this particular environmental setting. These data are of value by providing a baseline of behaviour and niche utilization to which findings from introduced species and strains, or altered environmental conditions, can be compared and used in management decisions for the protection and utilization of trout in small lake environments.

Acknowledgements

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