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Spawning-related movements in a salmonid appear timed to reduce exposure to visually oriented predators

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Animals often exhibit extensive flexibility in movement behaviours on a range of temporal and spatial scales in response to cues that reliably predict fitness outcomes. The annual timing of movements between distinct habitats can be crucial, particularly in seasonal environments with narrow ecological windows of opportunity. In polygamous species, sexual selection may further shape sex-specific phenology and movement behaviours. Here, we characterized seasonal, daily and diel movement patterns in adult brown trout, *Salmo trutta*, between a lake feeding habitat and two spawning streams in northwestern Ireland, using passive integrated transponder (PIT) telemetry. Antennae positioned at the inflow and outflow of the lake were used to monitor movements of 197 lake-tagged adults between lake and stream habitats. Across 2 years in both streams, movements were overwhelmingly nocturnal and exhibited distinct seasonality, with a peak in daily detections close to the winter solstice. In both streams, seasonal movement activity of males began and peaked before that of females (protandry). Daily detection probabilities for both sexes increased as the moon waned (decreasing lunar illumination) and as river depth increased, the latter being associated with reduced water clarity. These findings are consistent with fish favouring movement between fluvial and lacustrine habitats when light (both solar and lunar) or hydrological conditions decrease their exposure to visually oriented predators. The observed protandry also suggests a role for intrasexual male competition, whereby earlier male arrival could increase mating opportunities.

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Many species exploit different habitats at various life stages, and such ontogenetic niche shifts are particularly prevalent in size-structured populations of insects and fish (Claessen & Dieckmann, 2002; Werner & Gilliam, 1984). Different habitats can yield contrasting opportunities for growth, reproduction and survival, which may vary with respect to season and the age, maturity or size of an animal. However, movement between habitats often incurs a significantly elevated risk of mortality (Lind & Cresswell, 2006) that may vary temporally (Flávio, Kennedy, Ensing, Jepsen, & Aarestrup, 2019; Jonsson, Jonsson, & Jonsson, 2017; Schwinn, Aarestrup, Baktoft, & Koed, 2017). Thus, the timing of movements is associated with varying fitness trade-offs. In areas with distinct seasonal variation, selection tends to promote movement from one habitat to another during an annual period when conditions in the destination habitat are generally favourable for a particular activity such as feeding or reproduction (Åkesson et al., 2017). At a finer temporal scale, selection may promote movement at specific times within the broader migratory period when environmental conditions facilitate the safe passage of migrants.

In areas with pronounced seasonality, species' endogenous circannual rhythms are often 'entrained' by the cyclical signal of photoperiod, which in turn regulates their seasonal timing at a coarse scale (McCormick, 2012; McNamara, Barta, Klaassen, & Bauer, 2011; Åkesson et al., 2017). This allows the synchronization of key life history events such as maturation, migration and

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reproduction with their long-term average optimum timing (Foster, Ebling, & Claypool, 1988; Gwinner, 1989; Robart, McGuire, & Watts, 2018; Walton, Weil, & Nelson, 2011). Additionally, photoperiodic transitions between darkness and light provide daily signals for entraining circadian rhythms (Hammerschlag et al., 2017; Metcalfe, Fraser, & Burns, 1998). However, variation in other environmental factors such as temperature, tide or rainfall that reliably predict fitness outcomes can provide additional nonphotoperiodic signals that allow the timing of behaviours to be fine-tuned within a particular year, season or even day (McNamara et al., 2011; Visser & Both, 2005).

Transitional areas between habitats often represent survival bottlenecks for migratory species, as migrants contend with novel abiotic or biotic challenges such as unfamiliar predators (Aldvén, Hedger, Økland, Rivinoja, & Höjesjö, 2015; Dieperink, Pedersen, & Pedersen, 2001; Kennedy, Rosell, Millane, Doherty, & Allen, 2018). For example, predation rates among marine turtle hatchlings may exceed 85% as they move the short distance from nesting beach to open water (Whelan & Wyneken, 2007). Many predatory species congregate in such transitional areas at specific times in order to intercept migrating individuals (Bentley et al., 2014; Esbérard & Vrcibradic, 2007; Meyer, 2017). Although predation rates can be exceptionally high during these brief transitional periods, predator efficiency and associated predation rates are often strongly influenced by environmental conditions at the time of migrant passage (Clark & Furey, 2016; McLennan, Rush, Mckelvey, & Metcalfe, 2018). Where predators rely on vision, ambient light levels and environmental clarity will play synergistic roles in determining the distances from which prey are detectable. In response, many prey species limit certain behaviours to times when light levels are low. For example, numerous avian species that are primarily diurnal limit their migratory movements to the hours between sunset and sunrise (Chernetsov, 2006; Zehnder, Akesson, Liechti, & Bruderer, 2001; Åkesson, Alerstam, & Hedenström, 1996). Similarly, diel vertical migrations allow zooplankton to descend from their nocturnal feeding areas near the surface to deeper refuge areas before daylight exposes them to visually oriented predators (Lampart, 1989; Ohman, 1990).

Light intensity at night, however, is variable and strongly influenced by the lunar cycle (Dawson, 1919; Krisciunas & Schaefer, 1991). Some species of nocturnal rodents have been found to reduce or cease their foraging activity in exposed areas around the full moon and increase such activity around the new moon, probably as a response to nocturnal avian predation (Kotler, Brown, & Hasson, 1991; Lockard & Owings, 1974; Morrison, 1978). Additionally, visibility in aquatic environments can vary significantly for a given input of lunar or solar light intensity. Such variation in visibility can be particularly pronounced in rain-fed fluvial habitats where it tends to be associated with variation in water height and turbidity (Doyle et al., 2019). As the height of a river or stream rises, increased turbidity, combined with a less confined habitat, may reduce the likelihood of migrants being detected by predators.

In salmonid fishes, migrations between natal streams and more productive feeding areas such as lakes or oceans facilitate continued growth and increased fecundity while reducing the influence of density-dependent pressures on vital rates (Arostegui & Quinn, 2019; Ferguson, Reed, Cross, McGinnity, & Prodöhl, 2019; Jonsson & Jonsson, 2011; Nevoux et al., 2019). However, these migrations frequently incur severe mortality costs, often driven by greatly elevated predation rates in transitional habitats such as estuaries (Aldvén et al., 2015; Dieperink et al., 2001), lakes (Olsson, Greenberg, & Eklöv, 2011; Schwinn et al., 2017) and river-to-lake confluences (Kennedy et al., 2018). Thus, there may be strong selection for mature lake-feeding salmonids to limit their pre- and postspawning movements between lake habitat and natal streams to periods when environmental conditions reduce predation risk. Previous studies indicate that the behavioural responses of salmonids to temporal variation in environmental conditions can vary markedly among populations (García-Vega, Sanz-Ronda, & Fuentes-Pérez, 2017; Hellawell, Leatham, & Williams, 1974; Jonsson, 1991; Jonsson & Jonsson, 2002; Moore et al., 2012; Ovidio, 1999; Ovidio, Baras, Goffaux, Birtles, & Philippart, 1998; Rustadbakken et al., 2004; Santos, Ferreira, Godinho, & Bochechas, 2002), suggesting that local adaptations underpin these responses. As such, investigation into the proximate environmental drivers of native salmonid movements in relatively pristine habitats may provide broad insights into the ultimate causes of these behavioural responses.

Across animal taxa, males and females display differing reproductive migratory phenologies. Early arrival at breeding areas relative to the opposite sex can confer contrasting benefits or costs on males and females. These can depend on factors such as physiology (sexual dimorphism), mating system (i.e. monogamous, polyandrous, polygynous etc.), forms of intersexual selection and intrasexual competition, demographics, breeding habitat type and availability as well as any differential in mortality risk associated with habitat or sex (Morbey & Ydenberg, 2001). Protogyny, the early arrival of females relative to males, is generally limited to polyandrous species in which females compete for breeding territory or mates (Rappole, 2013). Protandry, the early arrival of males relative to females, is more common and is generally associated with polygynous species (Morbey & Ydenberg, 2001). Brown trout, *Salmo trutta*, represent a particularly interesting species for investigating such sex-based differences in reproductive migratory phenology due to their restricted breeding season, polygamous mating systems (including polygyny and polyandry), often high migrant and spawning mortality and the frequently limited availability of spawning habitat (Gauthey et al., 2015; Montgomery, Beamer, Pess, & Quinn, 1999; Morbey, 2002; Nevoux et al., 2019; Serbezov, Bernatchez, Olsen, & Vollestad, 2010; Tappel & Bjornn, 1983).

The aim of this study was to use passive integrated transponder (PIT) telemetry to investigate associations between the timing of spawning-related movement of male and female brown trout (between a lake and two spawning streams) and environmental variables that were expected to influence the visibility of migrants to predators. We first investigated whether movement patterns displayed a distinct diel signal associated with periods of light or darkness. Second, we investigated whether variation in river height and/or moon phase were associated with variation in daily movement patterns and whether these effects were additive or nonadditive. Third, we assessed whether males and females displayed differing migratory phenology patterns and, if so, whether these differences were consistent with either protandry or protogyny.

METHODS

Study Area, Fish Sampling and Behaviour Monitoring

Study area

The Burrishoole catchment is a complex freshwater system in the northwest of Ireland that drains an area of approximately 83 km^2. Human density in the area is low and the river system is minimally affected by water extraction or pollution. A series of streams and rivers link three main lakes, the most elevated and northerly of which is Bunaveela Lough (54°01′18″N, 9°32′43″W). The maximum depth in Bunaveela Lough is 23 m and the surface area is approximately 46 ha. The lake contains native populations of brown trout, Arctic char, *Salvelinus alpinus*, Atlantic salmon, *Salmo salar*, and European eel, *Anguilla anguilla*. The Fiddaunveela

(hereafter 'the inflow') is the only stream that flows into the lake and the Goulaun (hereafter 'the outflow') is the only outflowing stream (Fig. 1). The inflow rises in the steep hills to the southeast of Bunaveela Lough, flowing for approximately 2 km before joining the lake. The outflow meanders to the southwest for approximately 10 km prior to joining the larger (410 ha) Lough Feeagh, increasing in width and depth as it gets further from Bunaveela. During low rainfall periods, most sections of the inflow become shallow and provide limited sheltering habitat for mature-sized salmonids. The water level in the inflow rises and falls rapidly, often within hours of the commencement and cessation of rainfall, whereas the regulating influence of the lake causes fluctuations in the height of the upper outflow to be somewhat more gradual. Both streams are oligotrophic and poorly buffered (for hydrological parameters see Appendix Table A1), while small sandstone and limestone deposits help to buffer areas of Bunaveela Lough (Whelan, Poole, McGinnity, Rogan, & Cotter, 1998). Long-term electrofishing records (2005–2018) show that, outside of winter spawning months, less than 1% of trout sampled in the inflow ($N = 1136$) or upper outflow ($N = 877$) had a fork length (FL) exceeding 165 mm (see Appendix Fig. A1), our conservative threshold FL for designating maturity status (details in Appendix). In contrast, more than a quarter of the trout sampled by small mesh beach seine in Bunaveela Lough between 1991 and 2018 ($N = 3176$) exceeded 165 mm, indicating that the lake provides a richer feeding habitat, possibly with less exposure to predators, where migrants from the streams can attain greater size and fecundity prior to spawning.

Sampling

Between October 2016 and October 2018, seine netting (9 mm half mesh) was used on six dates to capture trout in littoral areas along the southeastern shore of Bunaveela Lough (Appendix Table A2). Five hundred trout were captured and anaesthetized in pH-buffered tricaine methanesulphonate (80 mg/litre) before weights (to 0.1 g) and lengths (FL to 1 mm) were measured. A tissue sample (ca. 2 mm^2) was extracted from the tail of each fish and preserved in ethanol (95%) for genetic sex determination (see methods in the Appendix). Trout with an FL exceeding 70 mm ($N = 456$) were tagged with 12 mm passive integrated transponder (PIT) tags. A needle inserted to one side of the mid-ventral line (slightly beyond the tips of the pleural ribs) and just beyond the tip of the pectoral fin was used to implant tags into the peritoneal body cavity. After tagging, anaesthetized trout were transferred to oxygenated freshwater tanks and observed until they regained their equilibrium and began to swim actively, whereupon they were released back into the lake.

Ethical Note

We adhered to the ASAB/ABS guidelines for the treatment of animals in behavioural research throughout this project. We conducted all aspects of sampling and tagging in accord with S.I. No.123/2014 Animal Health and Welfare (operations and procedures) Regulations 2014 and with approval of the Marine Institute animal welfare committee (MI Establishment Authorisation No:

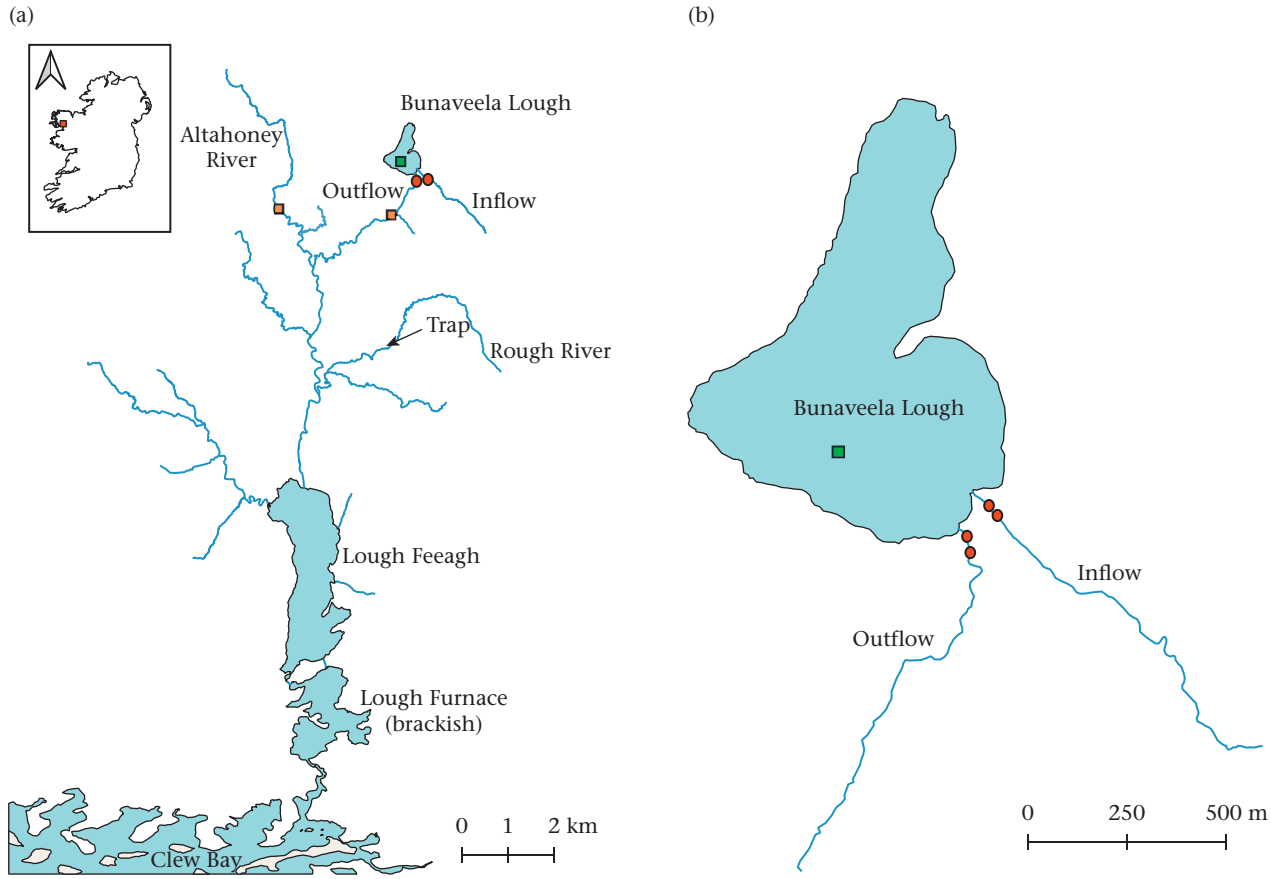


Figure 1. Map of (a) the Burrishoole Catchment and (b) Bunaveela Lough. PIT antennae locations are shown as red circles. Water level logger locations are shown as orange squares. Water temperature logger location is shown as a green square.

AE19121) and the Health Professional Regulatory Authority (HPRA). Procedures for inducing anaesthesia were appropriate for salmonids (Popovic et al., 2012) and full recovery was ensured prior to release. Tagging was carried out by personnel with appropriate training and Individual Authorisations under Scientific Animal Protection Legislation (HPRA).

Monitoring Behaviour: PIT Telemetry

Between August and September 2017, we constructed and installed an array of four cross-channel, pass-through PIT antennae in the upper Burrishoole catchment (Fig. 1.). These PIT antennae record the time and date that PIT-tagged animals pass antenna locations, allowing individual-based movement patterns to be investigated. We installed two antennae in the upper outflow, 15 m and 30 m downstream of Bunaveela Lough, and two antennae in the lower inflow, 75 m and 85 m upstream from Bunaveela Lough (Fig. 1). Each antenna spanned the full depth and width of the channel at its location except during very high flow events. To guarantee that all antennae remained well beyond the edge of lacustrine habitat during the highest water levels, the upper outflow antennae were relocated to 40 m and 60 m downstream of the lake between the first and second spawning periods. We used a test tag to assess the performance of each antenna every 10–14 days and soon after all high flow events. On four occasions during the two spawning periods antennae in the inflow or upper outflow were found to be damaged by flotsam and were not capable of detecting tags. On each occasion we completed necessary antenna repairs within 48 h of damage occurring, ensuring that antennae functioned efficiently throughout most of the study period. As there was evidence that some tagged trout passed antennae without being detected, directionality of movements (away from the lake or towards it) could not be confidently determined for the majority of PIT-tag detections.

Environmental Data

Throughout the study period, a thermistor chain (HOBO Tidbit v2) recorded the water temperature profile of Bunaveela Lough, while an OTT Orpheus Mini Water Level Logger recorded river height in the Altahoney, a tributary of the upper outflow (Fig. 1). In both cases, measurements were taken at 15 min. intervals. A second water level logger operated in the upper outflow (1120 m downstream of Bunaveela Lough) throughout the 2017–2018 spawning period but was damaged by a flood in February 2018. Concurrent data from the two water level loggers collected over 140 days reveal a strong linear relationship between daily mean water heights in the upper outflow and the Altahoney ($R^2 = 0.81$). Additionally, rainfall patterns in the inflow and Altahoney drainage areas, which are less than 2 km apart and occupy similar elevations, are very similar (B. Doyle, personal communication; Fairman, Schultz, Kirshbaum, Gray, & Barrett, 2017). Thus, the Altahoney water height data were used as proxies for stream height in the inflow and upper outflow in statistical analyses. The daily water level and water temperature data used in our analyses represent the maximum and mean values, respectively, that were recorded within a given 24 h period. By using mean daily water level values, discrepancies between the rate of water height fluctuations among the three streams should be mitigated.

Measured Altahoney water levels ranged from 0.36 m to 1.54 m (mean = 0.65 m) during the 2017–2018 spawning period and from 0.32 m to 1.50 m (mean = 0.61 m) during the 2018–2019 spawning period. Lake temperature at 1 m below the surface ranged from 3.77 °C to 11.07 °C (mean = 6.75 °C) during the 2017–2018 spawning period and from 5.73 °C to 9.06 °C (mean = 7.39 °C) during the 2018–2019 spawning period. Mean lake temperature in the 10 days preceding the winter solstice was 5.32 °C in 2017 and 6.73 °C in 2018. The daily timing of sunrise and sunset for the Burrishoole catchment as well as moon phase data are based on data from the United States Naval Observatory (USNO) for 54°01′18″N, 9°32′43″W. Moon phase is treated as a continuous numerical variable between one (full moon) and zero (new moon). Photoperiod refers to the proportion of the 24 h day that falls between sunrise and sunset and had a range of 0.307–0.373 in both spawning periods (mean = 0.331). Preliminary investigation of PIT-derived data indicated the majority of detections during the spawning period occurred at night. To avoid splitting discrete nocturnal activity periods at midnight into two separate dates, detection data and environmental data used in our analyses were adjusted so that each 24 h period began at 1200 rather than at 2400.

Investigating Diel Movement Patterns

All behavioural analyses were conducted using R v3.6.1 (R Core Team, 2019) and were restricted to the core spawning migration period (defined as beginning on 1 November and ending on 31 January) and to the movements of fish that were deemed to be mature (see methods in the Appendix, Appendix Fig. A2 and Table A3 for further details). To investigate diel movement patterns, all detection timing data were converted to circular format and analyses were carried out with the circular package in R (Agostinelli & Lund, 2017). Kuiper's one-sample test of uniformity on the circle was used to assess whether detection rates in each stream and each spawning period varied throughout the 24 h day. Diel detection patterns were also assessed for normality using a Watson's goodness-of-fit test for the von Mises distribution (a circular analogue to a Gaussian distribution). Additionally, the proportion of nocturnal (occurring after sunset and before sunrise) and diurnal (occurring after sunrise and before sunset) detections in each stream in each spawning period were calculated using daily photoperiod data.

Effects of Sex and Environmental Variables

We used a binomial generalized linear mixed model (GLMM), with a logit link function, to explore the extent to which the daily probability of detecting mature-sized lake-tagged trout at the inflow or outflow antennae was associated with four continuous (Day, Day^2, MoonPhase and RiverHeight) and three categorical (Sex, Stream and Year) explanatory variables, as well as two-way interactions chosen a priori on biological grounds (see below). As such, these analyses focused on the probability of fish being detected on a given day based on variation in these explanatory variables, rather than focusing on daily variation in the diel distribution of detections. Models were built with the glmmTMB function in the glmmTMB R package (Brooks et al., 2017).

Our response variable was Bernoulli distributed, whereby, for any given date, unique mature fish that were detected in the focal stream (either inflow or outflow) were designated '1', while all mature fish that were not detected in that stream (but were detected in that stream on at least one other occasion during a spawning period) were designated '0'. We included a RiverHeight*MoonPhase interaction because moon phase (lunar light level) and river height (turbidity) were predicted to play synergistic roles in determining the visibility of nocturnal migrants to predators. Owing to differences in flow direction and availability of shelter habitat between the inflow and outflow, combined with evidence of weak genetic differentiation between the groups of trout that spawn in them (Finlay et al., 2020), we predicted that behavioural responses to environmental cues in each stream might

differ, and therefore we included two-way interactions between Stream (a two-level categorical variable corresponding with 'inflow' and 'outflow') and both MoonPhase and RiverHeight. We also included two-way interactions between Sex and MoonPhase, Sex and RiverHeight and Sex and Day under the expectation that males and females might exhibit differing migratory phenologies (i.e. protandry or protogyny) or behavioural responses to stochastic environmental cues. TagNumber (the individual PIT tag ID of each fish) was included as a random effect (intercept) in our models to account for repeated measures of individual fish throughout the study period, while Year was treated as a two-level fixed effect corresponding to the 2017–2018 and 2018–2019 spawning periods.

Prior to model fitting, we used the scale function in R to mean-centre and scale all continuous main effects to standard deviation units and we quantified collinearity among all fixed effects by Pearson's R using the cor.test function in R. Additionally, the variance inflation factors (VIFs) of all fixed effects were calculated with the check_collinearity function in the performance R package (Lüdecke, Makowski, & Waggoner, 2019). We used the DHARMa package (Hartig, 2019) to plot fitted values versus simulated (scaled) residuals to test for heteroscedasticity and violations of linearity assumptions, and we used the acf function in the stats R package to identify residual temporal autocorrelation. The conditional and marginal R^2 of the model were estimated using the r.squaredGLMM function in the MuMIn R package (Barton, 2019). Using our model, we employed the ggPredict function in the ggeffects R package (Lüdecke, 2018) to plot predicted relationships of interest.

To further investigate sex-based variation in spawning phenology, the first, last and median detection dates, as well as the total number of detection dates and the mean number of detections per detection date were calculated for each fish in each stream (and in both streams combined) in each spawning period. These data were used to summarize overall and sex-specific detection patterns in both streams for both spawning periods (Table 1). Mann–Whitney tests were used to test for sex-based differences in the first detection date and the number of dates during which individual fish were detected in each stream in each spawning period.

RESULTS

Tag Detections

Our growth rate estimates (see methods in the Appendix for details) indicate that 243 of the trout we had previously tagged in Bunaveela Lough exceeded 165 mm in length (our designated threshold for maturity) by the 2017–2018 spawning season while 450 of the lake-tagged trout were of mature size by the 2018–2019 spawning period. Over the two spawning periods, our fluvial antennae detected 197 trout that were designated as mature at the time of detection, producing more than 100 000 detections. Of these fish, 106 were detected in the 2017–2018 spawning period (56 in the inflow, 86 in the outflow and 36 in both), 116 were detected during the 2018–2019 spawning period (51 in the inflow, 89 in the outflow and 24 in both) and 25 were detected in both spawning periods. Sex was confidently determined for 441 of the 456 trout that were PIT tagged in Bunaveela Lough during the study period, identifying 190 males (43.1%) and 251 females (56.9%). Over the two spawning periods, 80 mature females and 110 mature males were detected on our fluvial antennae, including 11 individuals of each sex that were detected in both spawning periods. Seven trout of unconfirmed sex were also detected (three in both spawning periods) but these individuals were excluded from the GLMM.

Table 1
Summary of individually based detection data split by sex, stream and spawning period

Group	2017-2018 Spawning Period						2018-2019 Spawning Period					
	N	First detection	Last detection	Median detection	No. of days	Detections per day	*N*	First detection	Last detection	Median detection	No. of days	Detections per day
Inflow (all fish)	56	04 Dec ±15.8	18 Dec ±15.1	11 Dec ±13.8	4.1 ±4.4	3.1	51	27 Nov ±16.5	08 Dec ± 15.9	03 Dec ±14.9	2.9 ±2.8	3.1
Outflow (all Fish)	86	29 Nov ±22.8	25 Dec ±25.6	12 Dec ±20.3	12.6 ±14.1	34.9	89	29 Nov ±23.6	18 Dec ± 22.7	08 Dec ±2.4	6.6 ±6.3	7.9
Outflow earlier		**4.0**	**−8.0**	**−2.0**				**−2.00**	**−10.0**	**−5.0**		
Male (both streams)*	62	24 Nov ±22.0	26-Dec ±25.9	10 Dec ±20.0	15.3 ±15.2	29.2	59	19 Nov ±18.3	08 Dec ±20.1	29 Nov ±18.2	8.0 ±7.5	8.7
Female (both Streams)*	40	05 Dec ±21.3	25 Dec ±23.2	15 Dec ±19.9	7.3 ±7.2	11.3	51	06 Dec ±21.6	24 Dec ±19.3	15 Dec ±18.2	4.8 ±3.5	3.2
Male earlier		**12.2**	**−0.1**	**6.1**				**16.3**	**15.7**	**16.0**		
Inflow male	37	01 Dec ±14.4	15 Dec ±14.2	08 Dec ±12.5	4.4 ±4.7	3.3	24	21 Nov ±13.9	03 Dec ± 15.1	27 Dec ±13.3	3.8 ±2.8	3.5
Inflow female	17	11 Dec ±16.9	25 Dec ±15.4	18 Dec ±14.6	3.3 ±2.54	2.7	23	05 Dec ±16.4	15 Dec ± 14.6	10 Dec ±14.0	2.5 ±1.6	2.6
Inflow male earlier		**9.9**	**10.3**	**10.1**				**13.6**	**12.1**	**12.8**		
Outflow male	47	25 Nov ±23.2	29 Dec ±26.3	12 Dec ±20.2	17.2 ±16.3	49.5	47	22 Nov ±20.3	11 Dec ±21.6	01 Dec ±19.7	8.2 ±7.5	11.3
Outflow female	35	05 Dec ±21.3	23 Dec ±23.6	14 Dec ±20.2	6.9 ±7.4	15.4	37	07 Dec ±23.2	26 Dec ± 20.9	16 Dec ±19.6	5.0 ±3.7	3.5
Outflow male earlier		**10.8**	**−5.7**	**2.6**				**14.8**	**15.3**	**15.0**		
Total (all fish)*	106	28 Nov ±22.2	25 Dec ±24.5	12 Dec ±19.9	12.1 ±13.1	25.8	116	27 Nov ±21.3	16 Dec ±21.8	06 Dec ±19.7	6.5 ±6.2	6.2

N is the number of fish per group. First detection, Last detection and Median detection are mean dates ± SD (in days) generated from the first, last and median dates on which each fish in each group was detected. No. of days is the mean number of separate dates on which each fish in each group was detected. Detections per day is the mean number of detections generated by each fish in each group on each date that they were detected. Row highlighted in bold designate how much earlier, in days, the named group is compared to the contrasting group. Rows marked with an asterisk use all detection data, regardless of stream. Group names containing '(All fish)' include males, females and individuals for which sex could not be confidently determined. Some individuals were detected in both streams during a single spawning period and some individuals received no sex designation (described in Results), causing the number of fish in group totals to differ from the apparent sum of the fish in their constituent groups.

Characterizing Seasonal Movement Patterns

Daily movement activity, expressed both as the number of mature-sized lake-tagged trout detected by fluvial antennae (Fig. 2) and as the total number of detections generated by such fish (Appendix Fig. A2), rose rapidly in November and peaked around the winter solstice before declining rapidly in January. Activity levels in the inflow fluctuated considerably from day to day, while changes in activity levels in the outflow were generally more gradual. Substantial increases in activity patterns appeared to often coincide with the new moon or with elevated river height (Fig. 2).

Diel Movement Patterns

The distributions of diel detections were nonuniform (Kuiper's test: all $P < 0.01$) and non-von Mises distributed (Watson test: <value nearest to critical in all cases) in both streams and both spawning periods. During the 2017–2018 season, 95.6% and 96.7% of detections from mature-sized trout in the inflow and the upper outflow, respectively, occurred after sunset and before sunrise (Fig. 3). Similarly, during the 2018–2019 season, 88.6% and 92.7% of detections from mature-sized trout in the inflow and the upper outflow, respectively, occurred after sunset and before sunrise.

Effects of Sex and Environmental Variables

All correlations between fixed-effect covariates in our movement probability model were well below $R = 0.7$, and all model parameter VIFs were <10. Model validation confirmed that the model complied with all underlying assumptions, including no evidence of residual temporal autocorrelation.

Detection probability increased as RiverHeight increased and as MoonPhase decreased (Table 2, Fig. 4). A significant two-way interaction effect was found between RiverHeight and MoonPhase ($P < 0.001$), whereby the negative effect of MoonPhase became less pronounced at higher RiverHeight values (Table 2), but this interaction was relatively weak and less pronounced in the inflow river (Fig. 4). Fish detection probabilities were higher overall in the outflow river (Table 2, Fig. 4), but the positive effect of RiverHeight and the negative effect of MoonPhase were both weaker in the outflow river ($P < 0.001$ for both Stream*RiverHeight and Stream*MoonPhase interactions; Table 2, Fig. 4).

There was a significant quadratic effect of Day, with an *n*-shaped curve (Table 2, Fig. 5). The main effect of Day was also significant, indicating that detections did not peak at Day zero, where zero corresponded to the median date (15 December) within the spawning season as Day was mean centred. Detection probability was significantly higher for males than for females, and their detection probabilities peaked significantly earlier (Sex*Day interaction, $P < 0.001$; Table 2, Fig. 5). However, detection probability for males was less strongly associated with water height than that of females (Sex*RiverHeight interaction, $P = 0.044$). The Sex*MoonPhase interaction was not significant ($P = 0.58$). Detection probabilities were significantly higher in the first spawning period than the second (Table 2, Fig. 5). Overall, 44% of the variation

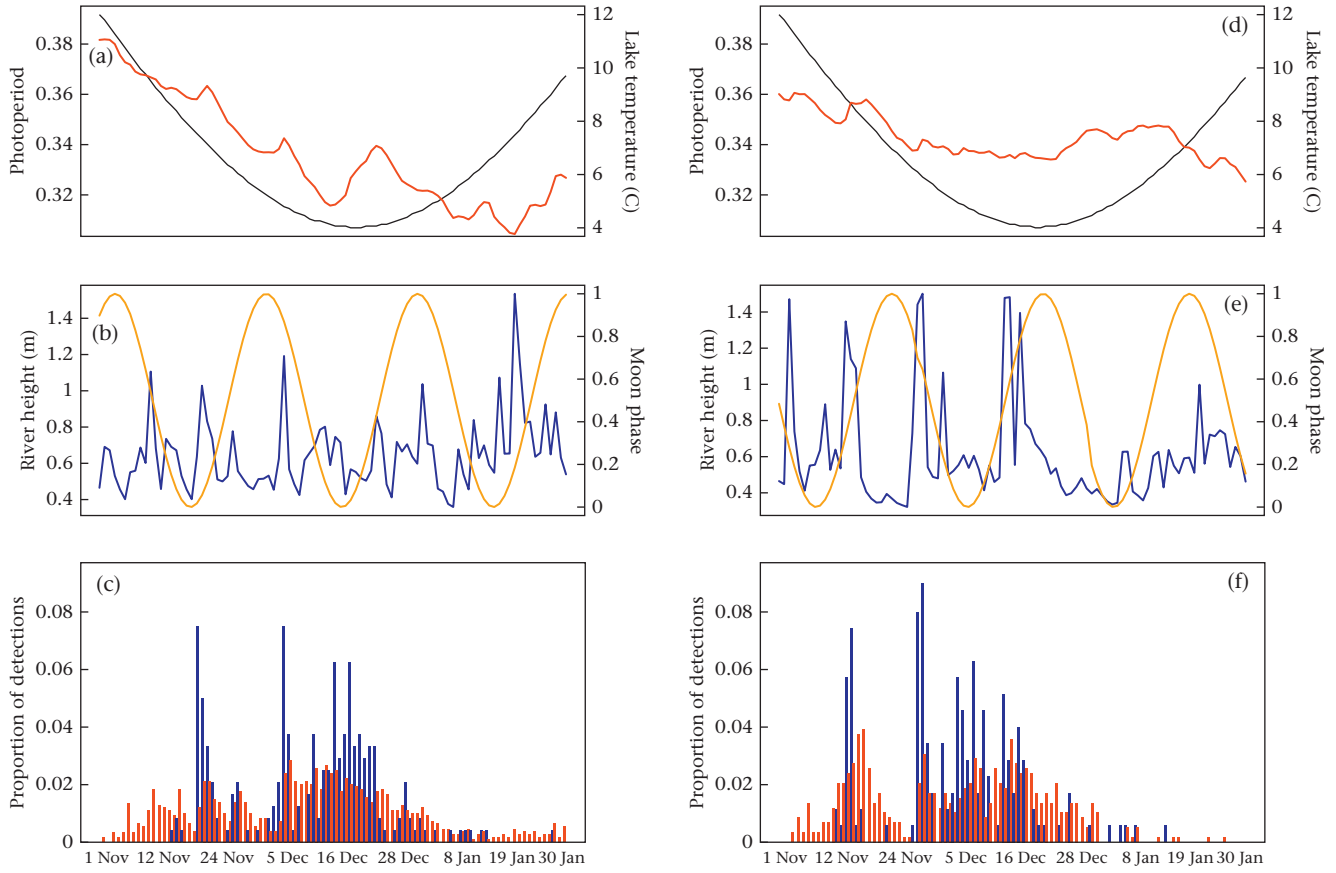


Figure 2. Daily variation in environmental factors and fish numbers in (a, b, c) the 2017–2018 and (d, e, f) the 2018–2019 spawning season. (a, d) Daily variation in photoperiod (black) and lake temperature (red). (b, e) Daily variation in water height in the Altahoney stream (blue) and moon phase (yellow). Full moon = 1, new moon = 0. (c, f) Daily variation in the number of fish detected in the inflow (blue) and outflow (red) streams as a proportion of the total number detected in each stream in the relevant spawning period.

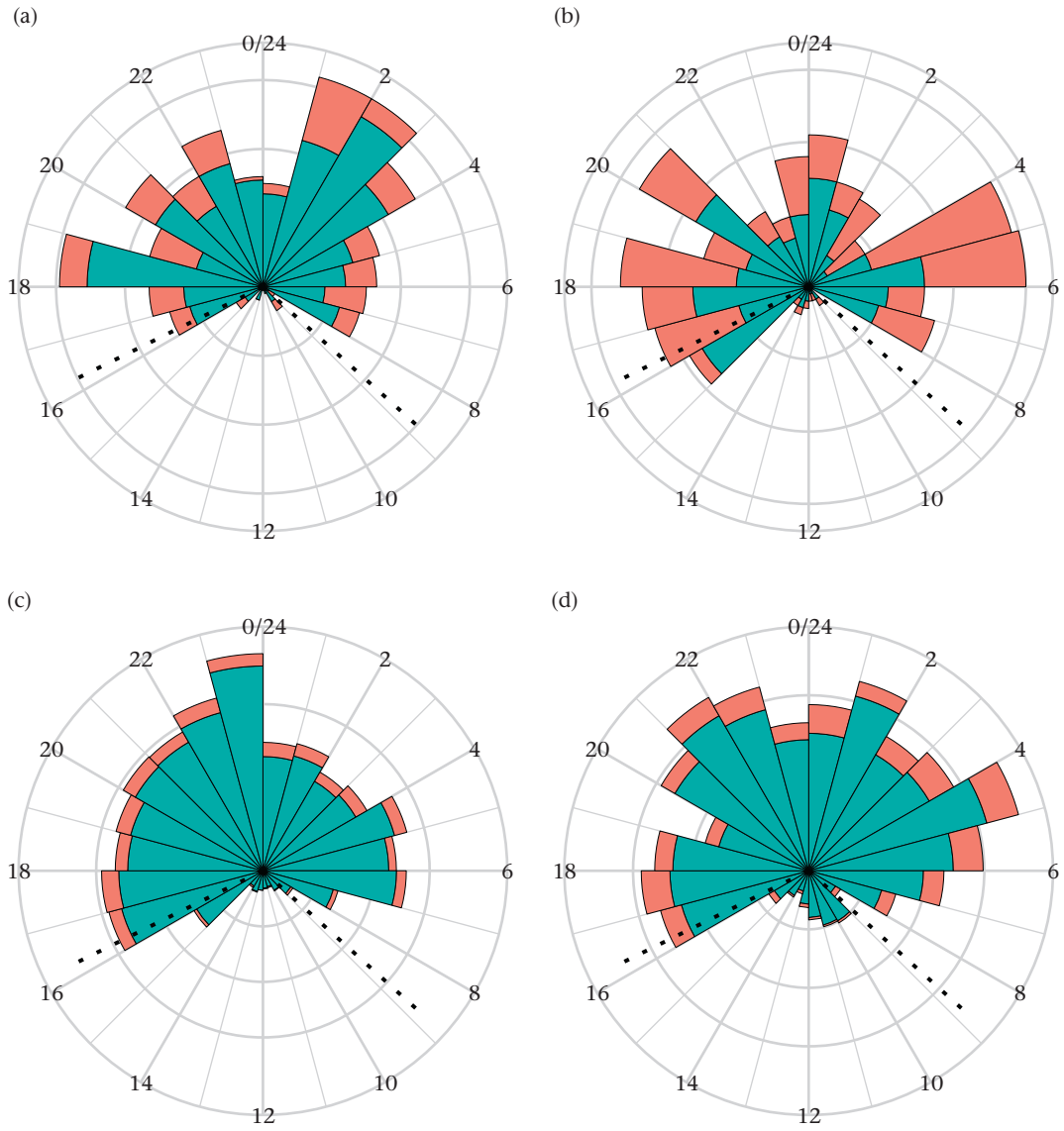


Figure 3. Diel distribution of detections (hourly) from mature male (blue) and female (red) trout recorded on (a, b) the inflow antennae and (c, d) the outflow antennae during (a, c) the 2017–2018 and (b, d) the 2018–2019 spawning period. Male and female bars sum to 100%. The dotted black lines represent sunrise (0852) and sunset (1615) on the median day of each spawning period.

in detection probability was explained by a combination of the fixed and random effects (i.e. conditional R^2) in our GLMM, while fixed effects alone (i.e. marginal R^2) explained 31%. Thus, the random effect of TagNumber accounted for 13% of the overall variation.

Across both streams, the mean first detection date among male migrants was 12 and 16 days earlier than that of female migrants in the 2017–2018 and 2018–2019 spawning periods, respectively, while the mean last detection of males was 0.1 day later and 16 days earlier than that of females (Table 1). The difference between male and female first detection dates was significant in both streams in both study seasons (Mann–Whitney tests: $W = 429.5$–1278, all $P < 0.05$). Individual males were detected in the outflow on significantly more dates than individual females in the first (Mann–Whitney test: $W = 562.5$, $P = 0.014$) but not second (Mann–Whitney test: $W = 690.5$, $P = 0.106$) spawning period, and corresponding sex differences were not significant in the inflow in either spawning period (Mann–Whitney test: $W = 243.5$, $P = 0.66$ and $W = 145.5$, $P = 0.10$). Furthermore, the mean number of detections of males on each date that they were detected in the outflow was 3.2 times higher than that of females in both spawning periods (49.4 versus 15.4 in 2017–2018 and 11.3 versus 3.5 in 2018–2019). In the inflow, the average number of detections per male per 'active' date in 2017–2018 and 2018–2019, respectively, was 1.2 and 1.3 times higher than that of females (3.3 versus 2.7 and 3.5 versus 2.6).

DISCUSSION

This study provides evidence that the timing of spawning-related movements of brown trout between lake habitat and spawning streams is strongly associated with environmental factors that are likely to influence their visibility to potential predators. In both streams and in both spawning periods, the majority (ca. 89–97%) of detections from mature-sized trout were recorded between sunset and sunrise, indicating a strong and consistent reluctance to move through transitional lake-to-river habitat during daylight (Fig. 3). An antenna located in the lower Burrishoole

Table 2
Parameter estimates for the main effects and interaction effects from the binary GLMM, where daily binary detection probability of fish was the response variable

Effect	Estimates	SE	*z*	Odds ratio	5%	95%	*P*
(Intercept)	−3.863	0.137	−28.299	0.021	0.017	0.026	<0.001
RiverHeight	0.629	0.053	11.815	1.875	1.718	2.047	<0.001
MoonPhase	−0.552	0.077	−7.211	0.576	0.508	0.653	<0.001
Stream (Outflow)	1.249	0.086	14.583	3.486	3.028	4.013	<0.001
Sex (Male)	0.424	0.149	2.841	1.528	1.196	1.954	0.005
Year (Second)	−0.688	0.053	−13.028	0.503	0.461	0.548	<0.001
Day	−0.28	0.062	−4.538	0.756	0.683	0.837	<0.001
Day^2	−0.737	0.037	−19.768	0.479	0.450	0.509	<0.001
RiverHeight*MoonPhase	0.108	0.031	3.448	1.114	1.058	1.172	<0.001
RiverHeight*Stream (Outflow)	−0.357	0.049	−7.259	0.700	0.646	0.759	<0.001
MoonPhase*Stream (Outflow)	0.433	0.070	6.189	1.542	1.374	1.730	<0.001
RiverHeight*Sex (Male)	−0.094	0.046	−2.016	0.911	0.844	0.983	0.044
MoonPhase*Sex (Male)	0.032	0.058	0.558	1.033	0.940	1.135	0.577
Sex (Male)*Day	−0.619	0.075	−8.273	0.54	0.476	0.610	<0.001
TagNumber (Random effect)				2.396	2.192	2.644	

All estimates and their standard errors are on the logit scale and therefore correspond to log odds ratios. The odds ratio is also given (exponent of logit-scale parameter estimates), as well as the 5% and 95% confidence intervals around this. The intercept corresponds to mean values on the logit scale for females in the inflow river in the first spawning period (the reference levels for Sex and Stream and Year) when all continuous covariates are set to zero.

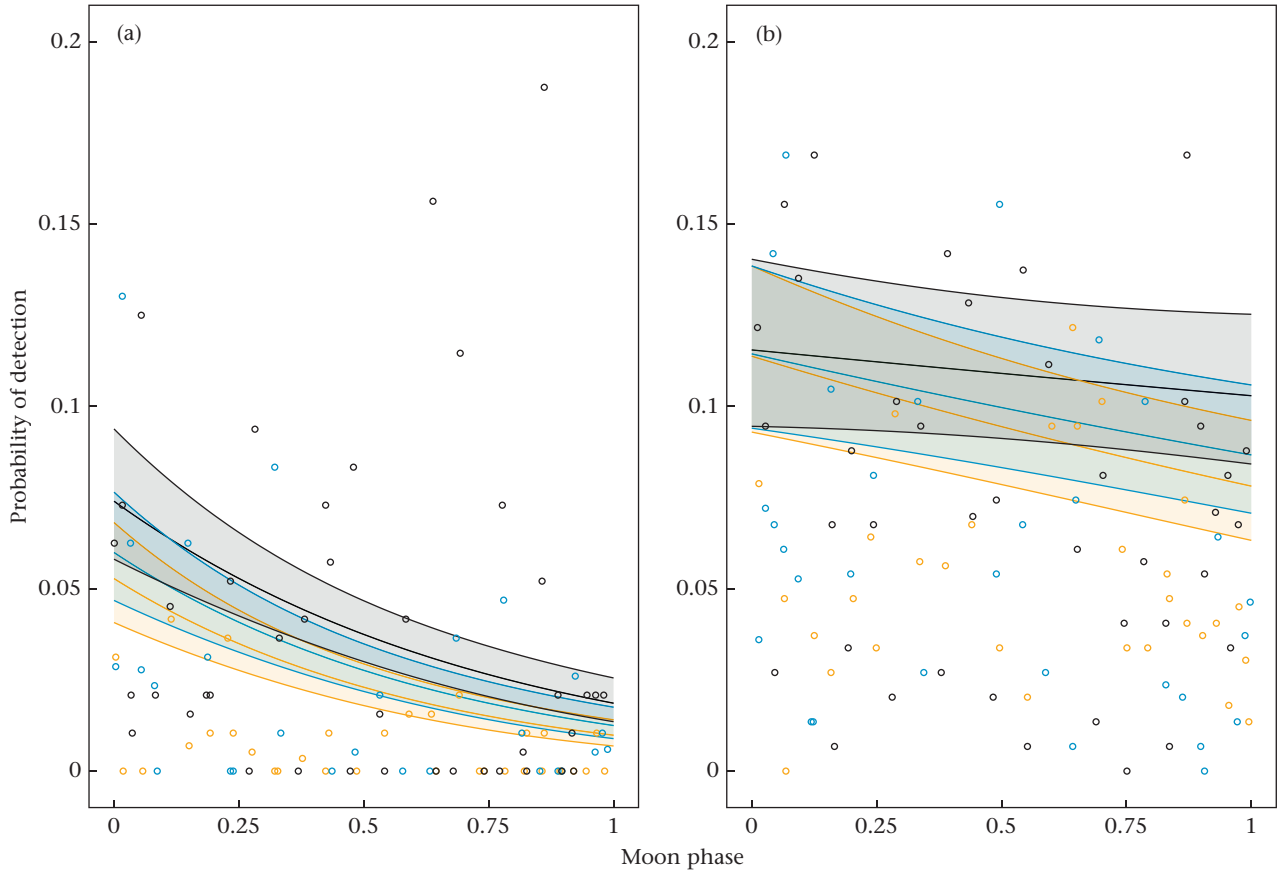


Figure 4. Detection probability of mature trout in (a) the inflow and (b) the outflow in relation to moon phase at low (orange), medium (blue) and high (black) river heights as predicted from the GLMM. Shaded areas represent 95% confidence intervals.

catchment close to the confluence with Lough Feeagh (Fig. 1) recorded a similar (96.9%) nocturnal bias in mature trout movements during the 2018–2019 spawning season (see Appendix for details), suggesting that nocturnal spawning movements through transitional fluvial habitat may be prevalent within the Burrishoole catchment. It is generally believed that nocturnally biased migration in salmonids represents a strategy to minimize migrant visibility and exposure to diurnal predators (Bradford & Higgins, 2001; Fraser, Heggenes, Metcalfe, & Thorpe, 1995; Ibbotson, Beaumont, Pinder, Welton, & Ladle, 2006; Ovidio, Baras, Goffaux, Giroux, & Philippart, 2002; Thorstad et al., 2012; Zavorka, Aldven, Naslund, Hojesjo, & Jonsson, 2016). In support of this, Flávio et al. (2019) found that Atlantic salmon smolts conducting nocturnal movements between fluvial and marine habitats had significantly higher survival than those that moved during the day. While nocturnal spawning migrations are found in some brown trout populations (Moore et al., 2012; Ovidio, 1999; Ovidio et al., 1998; Piecuch, Lojkásek, Lusk, & Marek, 2007) they are not ubiquitous (García-

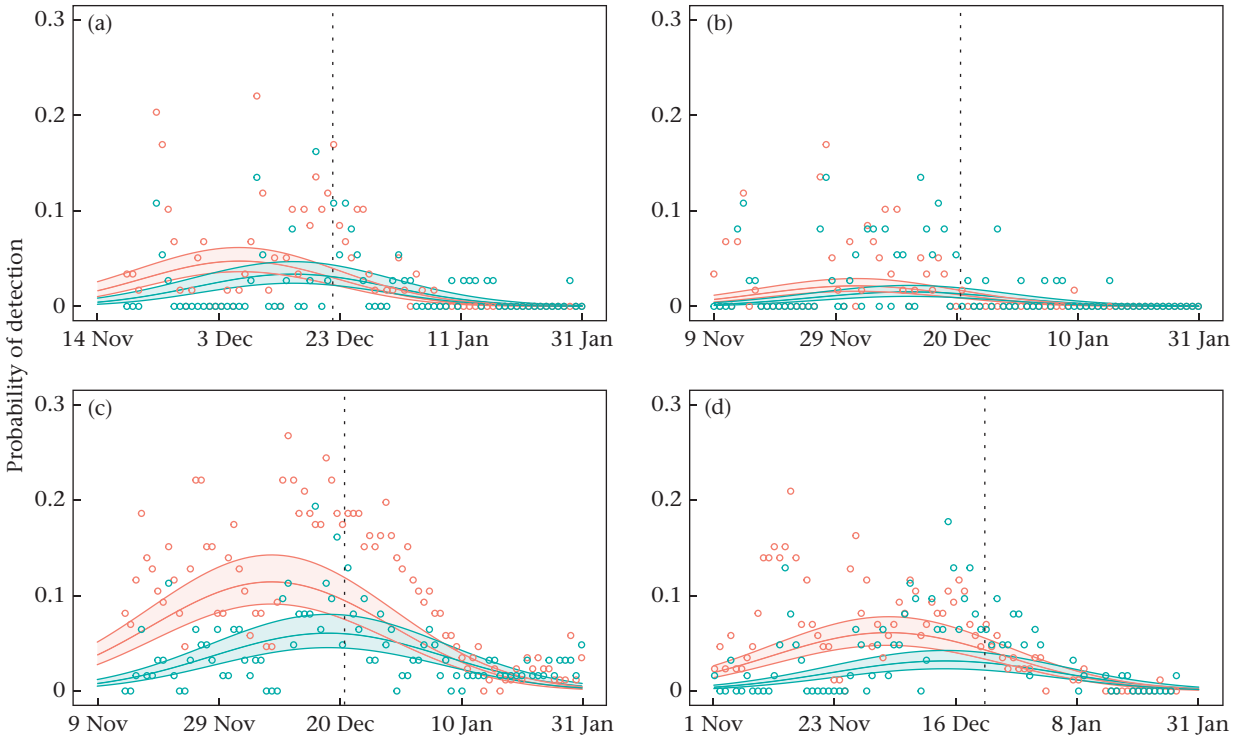


Figure 5. Temporal variation in detection probability of males (red) and females (blue) as predicted from the GLMM. (a, b) The inflow stream and (c, d) the outflow stream during (a, c) the 2017–2018 and (b, d) the 2018–2019 spawning period. Shaded areas are 95% confidence intervals. Vertical dashed lines represent the winter solstice.

Vega et al., 2017; Santos et al., 2002), suggesting that the advantages conferred by this behaviour are context specific. Indeed, some populations appear to alternate between nocturnally and diurnally biased spawning migrations at low and high river heights, respectively (Hellawell et al., 1974; Rustadbakken et al., 2004). For the trout that feed in Bunaveela, moving from a deep lake habitat to shallow stream habitat is likely to alter predation risk and, in particular, increase exposure to grey herons, *Ardea cinerea*, and Eurasian otters, *Lutra lutra*. Previous studies have recorded high predation rates of salmonids during spawning migrations by both otters and herons (Carss, Kruuk, & Conroy, 1990; Pépino, Rodríguez, & Magnan, 2015) and, on numerous occasions during the two spawning periods, herons were observed at dusk hunting in the shallow riffles close to our PIT-antennae where the inflow and outflow connect to the lake (R. Finlay, personal observation). Future work could confirm or refute these conjectures with direct measures of predation risk and relate these to direct measures of ambient light levels, which, for example, could be affected by cloud cover.

Seasonal movements of mature trout in our study peaked close to the winter solstice in both years despite differing prevailing water temperatures (Fig. 2 and Appendix Fig. A2), suggesting that photoperiod plays a dominant role in entraining local spawning phenologies. The unambiguous date signal provided by photoperiodic variation has previously been shown to drive the broad seasonal phasing of reproduction in salmonids, as well as physiological developments associated with sexual maturation (Billard, Reinaud, & Le Brenn, 1981; Bromage, Porter, & Randall, 2001; Pankhurst & King, 2010). Locally adapted responses to photoperiodic variation allow populations to spawn at a time that, on average, maximizes fitness (Foster et al., 1988; Gwinner, 1989; Quinn, Unwin, & Kinnison, 2000; Robart et al., 2018; Walton et al., 2011). Selection for an optimal emergence date of offspring is likely to play a central role in determining the optimal spawning time of the parents, in addition to direct selective pressures on the adults (Crozier et al., 2008). Synchrony with the winter solstice is probably coincidental in our case; that is, in this particular system, reproductive success may on average be highest for fish that undertake spawning movements in mid to late December as spawning during this period is likely to synchronize the timing of fry emergence to coincide with region-specific spring and early summer food abundance.

The associations we document between daily movement probability and environmental variables (RiverHeight and MoonPhase) indicate that, in addition to photoperiodic responses, brown trout exhibit phenotypic plasticity in movement behaviours that may allow them to balance anticipated benefits of moving on a particular day against perceived mortality risk. Specifically, trout displayed a significant reduction in the frequency of their movements through transitional habitat when stream height was low and when the moon was full (Fig. 4). These patterns were particularly pronounced in the inflow, the shallower of the two streams, which also provides less sheltering habitat than the outflow. While increases in stream height may facilitate the rapid passage of migrants through risky areas such as shallow riffles (Carss et al., 1990), they also provide a less confined habitat in which to avoid predation and tend to be associated with a reduction in migrant visibility through increased water colour (Doyle et al., 2019), depth and turbidity. In keeping with our finding that stream height correlated more strongly with movement in the inflow, previous research indicates that salmonids use increased flow as a cue for upstream migration most frequently in small or shallow streams and rivers (Jonsson, 1991), while in large or deep rivers, increased flow may have a negligible (Hellawell et al., 1974; Rustadbakken et al., 2004), or even negative (Jonsson & Jonsson, 2002) effect on spawning-related migratory activity.

The apparent reluctance of the lake-tagged trout to move through transitional habitat around the full moon reflects previous

observations of trout moving smaller distances during the full than the new moon (Slavik, Horky, Randak, Balvin, & Bíly, 2012; Slavik, Horky, Maciak, Horka, & Langrova, 2018). Analogous patterns of reduced activity or presence within exposed habitats during the full moon have been recorded in terrestrial rodents (Daly, Behrends, Wilson, & Jacobs, 1992; Kotler et al., 1991; Lockard & Owings, 1974), catadromous eels (Poole, Reynolds, & Moriarty, 1990; Sandlund et al., 2017), marine fishes (Hammerschlag et al., 2017), bats (Morrison, 1978), armadillos (Pratas-Santiago, Gonçalves, Nogueira, & Spironello, 2017), ungulates (Palmer, Fieberg, Swanson, Kosmala, & Packer, 2017) and zooplankton (Last et al., 2016). Such 'lunar phobia' is regarded as an evolved response that reduces exposure to visually oriented predators. Nocturnal activity patterns (Cozzi, Broekhuis, McNutt, Turnbull, & Macdonald, 2012), detection range and hunting efficiency (Fraser & Metcalfe, 1997; Metcalfe, Valdimarsson, & Fraser, 1997; Robinson & Tash, 1979) of visually oriented predators tend to decline significantly as lunar illumination levels decrease. Although moving during the new moon is likely to reduce migrant visibility and predation rates, it is also possible that nocturnal spawning during the new moon provides a fitness advantage by reducing egg predation by other fish (Hammerschlag et al., 2017; Šmejkal et al., 2018).

We detected a significant interaction between RiverHeight and MoonPhase, whereby the reduction in movement probabilities at higher values of MoonPhase (fuller moons) was more pronounced when water levels were lower. This interaction makes sense in the context of fish avoiding moving when predation risk is highest, as it suggests that, as the full moon approaches, fish are even more reluctant to move when the water is low and clear with minimal turbidity. However, the effect size was small and was weaker in the inflow stream, so we are reluctant to attach much interpretive weight to this interaction other than to note that it is consistent with our overall conjecture that spawning-related movement decisions may be adapted to reduce predation risk.

Our statistical model and our individual-based summary data (Tables 1 and 2) revealed significant sex-related differences in spawning phenology that were consistent with protandry. In both streams and spawning periods, male detection probability peaked ca. 12–14 days before that of females (Fig. 5) and individual males tended to first move between 10 and 15 days before individual females (Table 1). Protandry has been recorded in both Pacific and Atlantic salmonid species (Esteve, 2005; Jonsson & Jonsson, 2011; Morbey, 2000), although the requirement for iteroparous species, such as brown trout, to preserve sufficient energy to survive spawning may place size-dependent constraints on the magnitude or degree of protandry (Morbey, 2002). Such a trade-off may help explain why Seamons, Bentzen, and Quinn (2004) did not detect protandry in iteroparous steelhead, *Oncorhynchus mykiss*, despite females mating almost exclusively with males that arrived at spawning areas before them.

The mate opportunity hypothesis, whereby earlier arrival of polygynous males at breeding areas increases their opportunity to mate with females, is a plausible explanation for protandry in salmonids, particularly in populations where males reproduce for a longer period than females (Aarestrup & Jepsen, 1998; Anderson, Faulds, Atlas, & Quinn, 2013; Fenkes, Shiels, Fitzpatrick, & Nudds, 2016; Morbey, 2000). However, given that we found limited evidence for a longer reproductive period among males in the focal populations (Table 1), it is also possible that selection on females acts similarly, favouring relatively late arrival in order to ensure that males are present in sufficient numbers to promote intrasexual competition among males while increasing mate choice and decreasing waiting costs for females (Morbey & Ydenberg, 2001). A third potential explanation is that early arriving males enjoy a rank advantage, establishing territorial dominance before the arrival of later males. However, male salmonids tend to roam extensively during spawning while females compete for prime spawning territory (Carss et al., 1990; Nevoux et al., 2019), suggesting that rank advantage mechanisms could also promote early arrival of females.

Individual males were generally more active during the spawning period compared to females, particularly in the outflow stream, as evidenced by a higher mean number of detection days per male and more detections per day (Table 1). Male detection span (i.e. the period between first and last detections) and frequency in the outflow were also substantially higher in the first than the second spawning period. The outflow antennae were positioned closer to the lake in the first period than the second, which may have resulted in increased detections of males conducting short-distance exploratory movements into the outflow in search of females. In contrast with inflowing streams, olfactory cues (i.e. female pheromones) from outflows are unavailable to fish in lakes, requiring males to physically enter outflowing streams to confirm the presence of ripe females.

Salmonids can sometimes shed intraperitoneal PIT tags when spawning (Bateman, Gresswell, & Berger, 2009; Prentice, Flagg, & McCutcheon, 1990), and it has been speculated that such shedding is more common in females. However, the similar span between first and last detection dates of individual males and females in three out of four stream-year combinations (Table 1), coupled with the identical number of males and females that were detected in both spawning seasons (11 of each sex), suggests that tag shedding did not occur more frequently among females.

The male-biased detection frequency patterns found in this study are in keeping with Evan's (1994) observation that male anadromous brown trout will leave and re-enter spawning rivers repeatedly within a spawning season while females generally return rapidly to the ocean after their eggs are laid. Such behavioural differences may increase predation risk for males. Indeed, Carss et al. (1990) observed considerably higher predation by otters on male than female Atlantic salmon during the spawning period and speculated that this male bias was largely due to the vulnerability of males as they move through shallow riffles during their extensive upstream and downstream excursions. The overall lower activity of females than males, in conjunction with evidence of females responding more to variation in stream height (Table 2), is in keeping with Belding's (1934) and Fleming's (1996) assertion that during the spawning season, female salmonids tend to be more risk averse than males. The lack of evidence for equivalent differing responses to moon phase by male and female trout in our current study was somewhat surprising, however.

Conclusions

In this study we have documented pronounced seasonality and sex differences in spawning movement behaviours in brown trout that probably reflect inherited phenology patterns that are cued, at a coarse scale, by photoperiod. At a finer scale, trout appear to move between lacustrine and stream habitats at times that minimize their exposure to visually oriented predators, by moving at night and during darker lunar conditions and higher flows. These findings may be relevant from a conservation perspective, in that climate change or other anthropogenic factors such as artificial light or flow regulation may interfere with the signals fish use to time key transitions between habitats, or lead to mismatches between cue and selective environment, with consequences for fitness.

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Appendix

Defining Spawning Period

On three occasions between June and October 2017 (Appendix Table A2), trout were captured from the eastern shore of Lough Feeagh in the lower section of the Burrishoole catchment (Fig. 1). In addition, a fish trap was operated continuously between December 2016 and March 2019 in the Rough River, a spawning river for trout that feed in Lough Feeagh. Trout caught in Lough Feeagh or the Rough River were scanned with a hand-held PIT reader, measured and visually inspected to determine their state of maturity. As with individuals caught in Bunaveela, we PIT-tagged all trout with an FL > 70 mm ($N = 1913$).

We used a combination of observational data on the maturity status of trout passing through the Rough River fish trap and PIT-derived data on the movement patterns of Bunaveela-tagged 'mature-sized' trout to designate a spawning migration period for Burrishoole trout, beginning on 1 November and ending on 31 January. More than 95% of annual detections from mature-sized trout were recorded on our fluvial antennae and more than 95% of visibly mature ('ripe') trout were caught in the Rough River traps within this period (Fig. A2, Table A3), indicating that movement between lakes and rivers during this time of the year is motivated principally by breeding rather than exploratory foraging.

Designating Mature Length Threshold and Estimating Fish Length

To exclude potentially immature trout from our behavioural analyses, we chose 165 mm as a conservative minimum threshold FL for maturity, as this is roughly one standard deviation below the mean FL of visibly mature (i.e. ripe or spent) brown trout that we captured in the Burrishoole catchment during the study period ($N = 414$, mean ± SD = 201.2 ± 36.5 mm).

Most (87.6%) of the trout from Bunaveela Lough that were tagged during the project were caught on only the original tagging date. Because trout that were detected on antennae during spawning periods had been tagged up to 811 days previously, the FL of tagged individuals in each spawning period was unknown. Individual growth rates in fish populations are strongly influenced by individual size and water temperature (Boltaña et al., 2017; Handeland, Imsland, & Stefansson, 2008; Neuheimer & Taggart, 2007). We therefore used a combination of lake temperature data and individual growth data from 87 individuals that were tagged and recaptured in lake habitat during the project (recapture dates were 15–505 days post-tagging) to calibrate a linear model in R v3.6.1 (R Core Team, 2019) to predict growth per growing degree day (Chezik, Lester, & Venturelli, 2014) as a function of initial FL (full model details and performance indicators presented in Finlay et al., 2020). We used this model in conjunction with lake temperature and tagging FL data to estimate post-tagging growth, and thus the current FL, for each Bunaveela-tagged trout in each spawning period.

Lower Burrishoole Catchment Antenna

In March 2018 we installed a single additional antenna in the lower outflow, 805 m upstream of Lough Feeagh and 9540 m downstream from Bunaveela Lough (Fig. 1), allowing us to investigate whether diel movement patterns recorded in the inflow and upper outflow were mirrored in the lower catchment. During the 2018–2019 spawning period, 96.9% of detections produced by mature-sized trout on this antenna occurred at night.

Genetic Sex Determination Assays

Genomic DNA was extracted from caudal tissue of all tagged trout using the Promega Wizard SV 96 Genomic DNA Purification System (Promega, Madison, WI, U.S.A.). As described in Finlay et al. (2020) and Keenan et al. (2013), a single sex marker and 18 microsatellite loci were amplified by multiplex PCR (two independent reactions). We determined the genetic sex of each sample depending on whether an amplified DNA fragment of 108 bp was present at the SalmoYF locus (sequence available in GeneBank; P. Prodöhl, unpublished). This DNA fragment is absent from female brown trout and present in males. In cases where this fragment was absent and three or more of the remaining 18 loci had failed to amplify, sex was designated as 'unconfirmed'.

Table A1
Hydrological properties of Bunaveela Lough, the upper outflow and the inflow streams

Site	pH	Conductivity μS/cm	Alkalinity ($CaCO_3$ equivalent mg/litre)	Nitrogen (mg/litre)	Phosphorous (μg/litre)
Bunaveela	7.2	86	33.0	0.657	17.66
Inflow	7.23	116	30.87	0.274	15
Upper outflow	7.05	96.65	10.14	0.238	7

Table A2
Summary of trout that were caught, tagged or recaptured in Bunaveela Lough, Lough Feeagh and the Rough River traps during the project

Date	Site	No. of of seine net hauls	Trout tagged FL>70 mm	Trout FL<70 mm	Trout recaptured (previously tagged)
11 Oct 2016	Bunaveela	5	44	0	0
21 Jun 2017	Bunaveela	5	147	13	1
23 Jun 2017	Feeagh	5	71	0	4
16 Aug 2017	Bunaveela	6	102	16	14
21 Aug 2017	Feeagh	6	52	0	17
26 Oct 2017	Bunaveela	6	91	6	19
27 Oct 2017	Feeagh	6	31	0	12
24 Oct 2018	Bunaveela	4	41	6	10
08 Nov 2018	Bunaveela	3	31	3	10
Daily	Rough River Traps	NA	1759	165	287
	Total	NA	2369	209	374

FL: fork length.

Table A3
Mature-sized trout caught in the Rough River fish trap per month

	N	Not yet ripe	Ripe	Spent
Oct	16	0.750	0.250	0.000
Nov	66	0.182	0.621	0.197
Dec	86	0.047	0.267	0.686
Jan	67	0.075	0.050	0.875
Feb	6	0.000	0.000	1.000

Trout were visually identified as 'ripe' (i.e. ready to breed), 'not yet ripe' (i.e. not displaying any physical characteristics indicative of sexual maturity) and 'spent' (i.e. have finished spawning). Data are for 2017–2019.

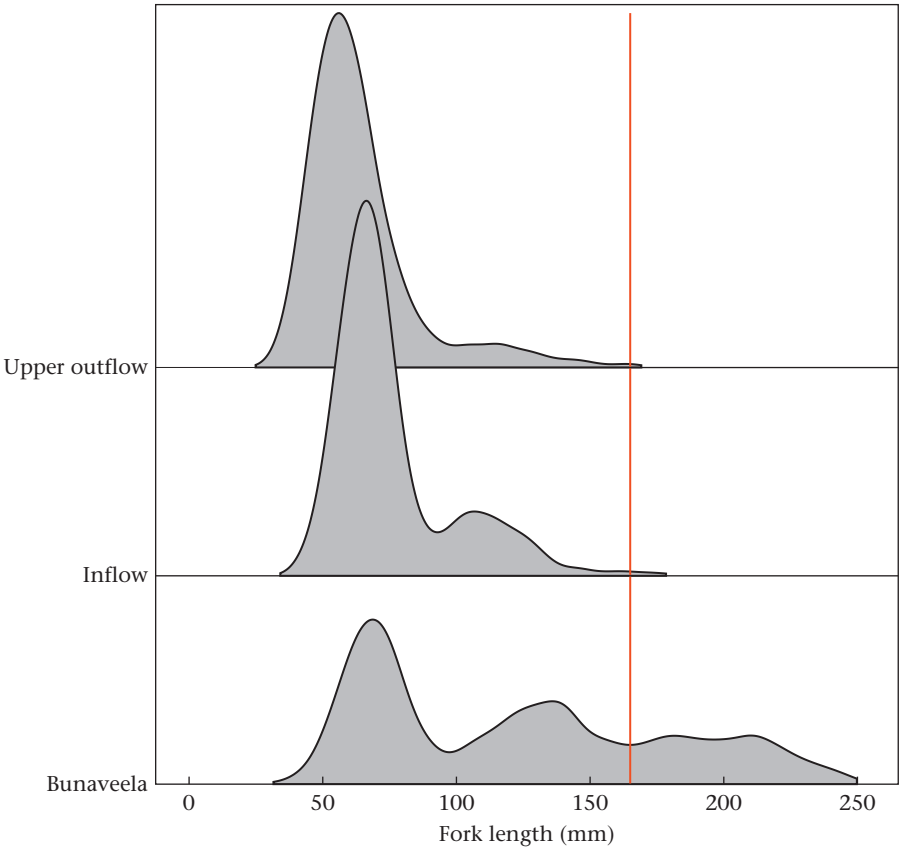


Figure A1. Size distribution (fork length) of trout sampled from June to September in the upper outflow ($N = 1136$) and the inflow ($N = 877$) between 2005 and 2017, and from Bunaveela Lough ($N = 3176$) between 1991 and 2017. The red line at 165 mm represents the threshold length for maturity selected for this study (ca. mean − 1 SD).

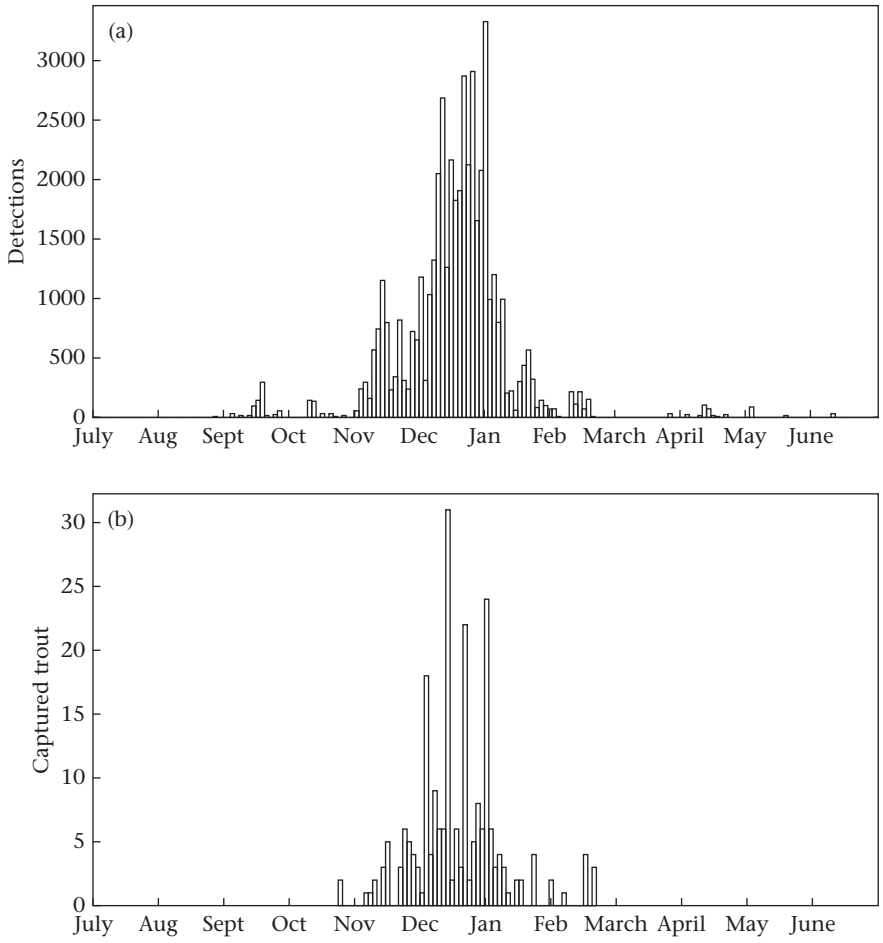


Figure A2. (a) Mature-sized trout detected at the upper outflow antennae (July 2017 to June 2018) and (b) trout identified as mature (either ripe or spent) in the Rough River fish trap (2016–2019).