PRIMARY RESEARCH PAPER



Summer and autumn movement ecology of native brook trout (*Salvelinus fontinalis*) in urban headwater streams of Eastern North America

Lee F. G. Gutowsky Scott G. Blair · Steven J. Cooke · Michael G. Fox

Received: 6 May 2022 / Revised: 20 January 2023 / Accepted: 7 February 2023 / Published online: 6 March 2023 © Crown 2023

Abstract Urban streams are impacted by multiple anthropogenic environmental stressors that exert considerable pressure on resident fish populations. Species such as brook trout (*Salvelinus fontinalis*) are particularly vulnerable because urban environments typically limit the cold oxygenated water required by all life stages. To understand factors associated

Handling editor: Fernando M. Pelicice

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10750-023-05169-8.

L. F. G. Gutowsky (🖂) Fisheries and Oceans Canada, Freshwater Institute, 501 University Avenue, Winnipeg, MB R3T 2N6, Canada e-mail: Lee.Gutowsky@dfo-mpo.gc.ca

L. F. G. Gutowsky · S. G. Blair Environmental and Life Sciences Graduate Program, Trent University, 1600 West Bank Drive, Peterborough, ON K9J 0G2, Canada e-mail: scottblair@trentu.ca

S. J. Cooke

Institute of Environmental and Interdisciplinary Science and Department of Biology, Carleton University, Ottawa, ON K1S 5B6, Canada e-mail: steven.cooke@carleton.ca

M. G. Fox

School of the Environment and Department of Biology, Trent University, 1600 West Bank Drive, Peterborough, ON K9J 0G2, Canada e-mail: mfox@trentu.ca with native brook trout movement in urban streams, we monitored 20 radio-tagged individuals from late summer through the spawning season in autumn, and modelled how movement was influenced by body size and habitat. Tracking occurred in two adjacent streams that differed in forest cover and channelization. In both streams, brook trout mainly travelled upstream, particularly at the onset of the autumn spawning season. Larger individuals exhibited greater movements, and habitat complexity imposed stronger effects in larger individuals. Greater movements were made into locations of shallower depth and lower conductivity, although these factors were conflated with movement into upstream locations. This study addresses a fundamental knowledge gap in urban stream ecology by providing detailed information on the movement of a key indicator species of aquatic ecosystem health.

Introduction

Human alteration of stream habitat negatively affects many native aquatic biota through changes in hydrologic flow regimes (Ward et al., 2015), reductions in water quality from stormwater runoff (Morgan et al., 2012), sedimentation (Curry & MacNeill, 2004), habitat fragmentation (Fagan, 2002), warming of stream temperatures (Wenger et al., 2011), and landscape urbanization (Wheeler et al., 2005) that collectively contribute to the "urban stream syndrome" (Walsh et al., 2005). Habitat loss and habitat fragmentation in particular are major contributors to fish population declines in urban stream habitats (Paul & Meyer, 2001; Urban et al., 2006). The increase of impervious land cover leads to warming of stream temperatures as stormwater runoff enters coldwater streams (Jones et al., 2012; Hasenmueller et al., 2017), which may enhance thermal fragmentation of urban stream habitats and limit coldwater fish populations to smaller groundwater-fed tributaries near the headwaters.

Urban development causes a host of negative effects that degrade natural ecosystem structure and functions vital to sustaining fish populations (Alberti, 2005; Harper & Quigley, 2005). To understand these effects, monitoring strategies, including the use of indicator species, help to define conservation priorities and support urban stream ecosystem management (Ranta et al., 2021; Zerega et al., 2021). For instance, Wallace et al. (2013) explored correlations among urbanization environmental covariates and biotic indices to develop a suite of management recommendations, e.g., road density ≤ 3 km² for brook trout [Salvelinus fontinalis (Mitchill, 1814)] and American brook lamprey [Lethenteron appendix (DeKay, 1842)]. Yet, there remains a need to address specific and fundamental questions about indicator species used in aquatic monitoring (Wenger et al., 2009).

How urbanization affects movement of aquatic organisms and populations both within and beyond urban areas is one of the major questions facing urban ecologists (Wenger et al., 2009). While the attributes and predictors of aquatic organism movement in fluvial environments are generally well defined (Northcote, 1984; Schlosser, 1995; Radinger & Wolter, 2014), empirical research focussed on urban populations is still uncommon. The environmental correlates of urbanization will influence behaviour, particularly in sensitive species, and provide a better understanding of urban stream ecology. In coldwater habitats where conditions favour narrow and specialized thermal niches, brook trout are one of North America's keystone indicators of high-quality habitat (Barton et al., 1985; Steedman, 1988). Brook trout movement is heavily influenced by temperature due to the species' narrow thermal tolerance at all life stages (10–16°C, Coutant 1977). For mature fish, decreasing water temperatures under increasing stream flows is a major trigger for migration to welloxygenated groundwater-fed spawning substrate (Witzel & MacCrimmon, 1983; Hartman & Hakala, 2006). Indeed, movement among groundwater inflows is critical to individual fitness and yearling survival (Power et al., 1999; Borwick et al., 2006; Guillemette et al., 2011). Outside of the reproductive season, moderate changes in water temperature, stream flow, stream morphology and cover are additional environmental covariates that drive brook trout movement in streams (Stranko et al., 2008; McKenna & Johnson, 2011; Lokteff et al., 2013; DeWeber & Wagner, 2015; Goerig et al., 2015).

In the context of urban ecology, research often involves indices of species occurrence on broadspatial scales (e.g., Pépino et al. 2012; Wagner et al. 2013), whereas little is known about individual behaviour (e.g., movement) under the conditions of urbanization. The lack of knowledge on urban brook trout movement patterns puts these populations at risk, as physical and chemical alterations restrict access to preferred habitat. It is essential to understand how brook trout movement in urban streams varies through space and time to protect populations from extirpation. Moreover, as sentinels of environmental change (Power & Power, 1995), tracking brook trout movement is a plausible strategy for monitoring high-quality habitat under disturbance.

In this study, we assess movement patterns in radio-tagged urban brook trout of two streams during approximately a two-month period encompassing their spawning season. We examine factors known to influence brook trout seasonal movement in nonurbanized streams, including body size, habitat complexity and site characteristics (Riley et al., 1992; Curry et al., 2002; Mollenhauer et al., 2013; Goerig et al., 2015). We expected that movement would be affected by body size during the spawning season, as mature, wild brook trout are known to make large upstream migrations in autumn to reach preferable spawning habitat (Mollenhauer et al., 2013). Given that site characteristics such as depth, temperature, and conductivity together influence brook trout abundance in this system (Blair et al. 2021), we tested the effects of these covariates. In addition, larger movements were predicted to occur later in the season and when fish were further from known upstream spawning areas. Finally, we expected that brook trout movement in autumn would be mainly upstream because headwater streams are typically fed by groundwater aquifers, and brook trout are known to select spawning sites in close proximity to these features (Curry & Noakes, 2011; Guillemette et al., 2011).

Methods

Study area

This study was conducted in Harper Creek (44°16′20.1″N; 78°21′16.1″W), a coldwater stream with two branches located in Peterborough, Ontario, Canada (Fig. 1). Harper Creek is fed by groundwater upwellings via seeps and springs located near its

headwaters. The stream flows into Byersville Creek, a tributary of the Otonabee River. There is a steep waterfall located at the base of the Harper North branch, which potentially inhibits fish movement from the south branch into the north branch. The Harper North and South branches are approximately 1.2 km and 3.2 km long, respectively, and share a 1.9 km² catchment with a naturally vegetated forest located in Harper Park.

The study area is surrounded by developed land, including many major city roadways, housing developments, and shopping centres, and both branches of Harper Creek receive urban stormwater runoff. Harper North is the smaller of the two branches, and its midsection has been channelized along an industrial road with almost no riparian buffer and several in-stream culverts. Harper South maintains a relatively unmodified channel morphology with greater groundwater inflows, and

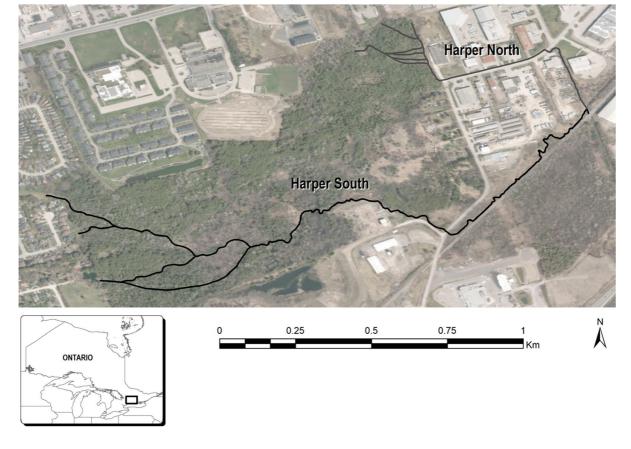


Fig. 1 Study area including Harper Creek North (grey) and South (black) in the city of Peterborough, Southwestern Ontario, Canada (inset map)

contains more fish cover (undercut banks, in-stream woody debris, forested ~50% forested canopy cover; see Blair et al., 2021). Harper South contains only one in-stream culvert with a relatively low gradient, while Harper North contains 10 in-stream culverts with steeper gradients and greater stream velocity, on average. Despite these surrounding urban influences, both branches contain some of the few self-sustaining wild brook trout populations, free of hatchery stocking, within an urban area in southern Ontario (Otonabee Conservation Authority, 2013, 2015).

Radiotelemetry

We used backpack electrofishing (Smith-Root LR-24 electrofisher; Pulsed DC, 150 V, 60 Hz) to capture brook trout from August 23 to August 25, 2017. Twenty brook trout > 165 mm FL were randomly selected from a pail for surgical implementation Lotek NanoTag series digitally encoded of radio transmitters (NTC-3-2, 1.1 g, 110-day life expectancy; Lotek Wireless, Newmarket, Ontario) pre-programmed with a 12-h on/off feature to extend battery life (active during daylight; 7:00-19:00 h). Six brook trout were tagged in Harper North and 14 were tagged in Harper South, the sample sizes being proportional to stream length.

We attempted to tag fish large enough for a 1.1 g transmitter to not exceed 2% of the fish's body mass (> 165 mm fork length (FL) and 55 g; see Online Resource 1) to reduce potential impacts on swimming performance, behaviour, and predation avoidance (Adams et al., 1998). While the 2% rule could not always be followed due to the small body size of the fish in these streams, a tag mass of up to 12% of fish body mass has been shown to not adversely affect physiological performance of stream salmonids when the tag antenna is shorter than the fish (Brown et al., 1999). In the current study, transmitters did not exceed 3.6% of body mass and all radio-tag antennas were trimmed to the base of the caudal fin.

Prior to surgery, brook trout were anesthetized using a solution comprised of 3–5 drops of clove oil in 1 l of stream water (Anderson et al., 1997). Individuals were measured in the field (FL; nearest mm), and wet weight (g) was determined using an Acculab V-200 precision electronic scale. Radiotagged fish were assumed to be age-1 or older and sexually mature, however live determination of sex was not possible. Following surgery and weighing, fish were placed in a recovery pail for at least 10 min before being released to their original location of capture.

The Harper Creek tributaries were visited twice weekly from August 29 and November 8, 2017 to track tagged fish movement with a handheld radio receiver (Lotek SRX600 Telemetry Receiver) using the gain reduction method (Sullivan et al., 2019). Continuous environmental variables collected at the location of each resighting were stream depth (mm), temperature (°C), dissolved oxygen concentration (mg/l), and conductivity (us/cm). These variables were collected as a single mid-depth measurement using their respective probes (YSI Model 55 dissolved oxygen-temperature meter, YSI Model 30 conductivity meter). Unfortunately, a failed YSI oxygen probe inhibited our ability to assess dissolved oxygen concentration as part of this study. Habitat variables at the relocation site were categorized as one or a combination of pool, riffle, undercut, and logjam.

Fish locations were collected and recorded using the "*Collector for ArcGIS*" smartphone application (ESRI, Redlands CA; GPS accuracy~1–3 m). Distance moved by brook trout estimated with ArcMap (ArcGIS 10.4, ERSI 2016) using the "*Network Analyst*" tool. Movements were assigned a stream flow direction of positive (upstream) or negative (downstream). Total movement was defined as the sum of the absolute values of all recorded movements by an individual, and net movement was defined as the stream distance of an individual's position between the first and last sighting. The greatest distance moved from a tagging location was defined irrespective of stream flow direction.

Statistical analysis

A preliminary analysis of movement distances indicated that 66% of relocations were within 0–3 m of previous relocation sites (mean= 0.35 ± 0.67 m SD, Fig. 2A), which corresponded approximately to the accuracy of our GPS. The remaining 34% of relocations varied from 3 to 922 m from the capture site or previous relocation site (mean=92.7 m±177.5 m SD). The pattern of high site fidelity with occasional greater movements led us to formulate a response variable based on these two

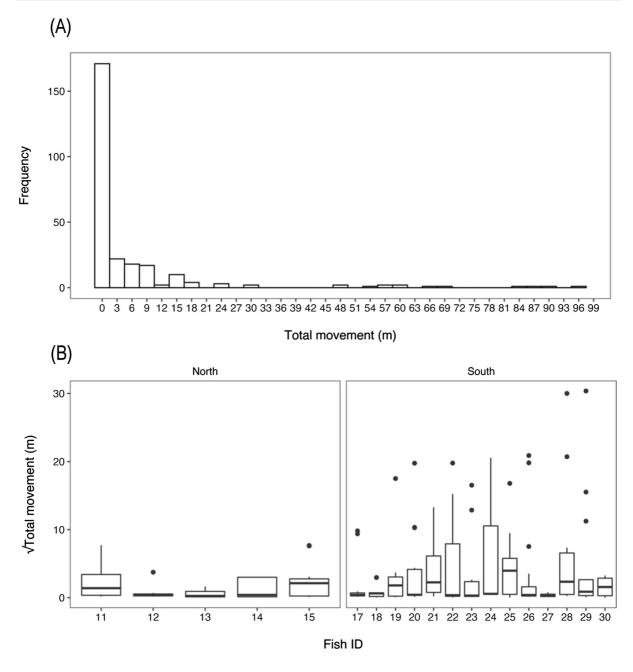


Fig. 2 Frequency of movements by all brook trout radio-tagged and relocated in the Harper Creek North and South (A). Box plot showing the square-root of total movement (m) by individual radio-tagged brook trout (B)

movement types. Therefore, movement was coded as a binary response and modelled as a function of covariates hypothesized to affect the probability that brook trout would move ≥ 3 m between relocations. The model was parameterized using integrated nested Laplace approximation in the R-INLA package (Rue et al., 2009; Martins et al., 2013). In addition to computing Bayesian approximations for latent Gaussian models, R-INLA can integrate random effects, splines, and correlated random walks that fit well to animal movement data (Jonsen, 2016; Muff et al., 2020). The probability of movement ≥ 3 m was expected to vary with body size (Curry et al., 2002), habitat complexity (Sweka & Hartman, 2006), the interaction between body size and habitat complexity (Petty et al., 2012), and environmental variables including depth, temperature, conductivity, distance upstream from the mouth, and day of the study. Habitat complexity was classified simply as either moderate (one physical habitat feature; pool, logjam, or undercut) or complex (two or more habitat features previously listed; logjam pool, or undercut pool with a logjam). Relocations to sites with no physical habitat features were relatively rare (n=8) and were therefore excluded from the habitat analysis. The habitat category used was that which the fish moved to in a given interval. Continuous environmental variables and day of the study (day 1-78) were standardized (i.e., mean of zero and unit standard deviation) and partitioned each into equally spaced bins to apply a second-order random walk (Codling et al., 2008; Lindgren & Rue, 2008). Random walks of the second-order are well defined for regularly spaced data and frequently used for smoothing in statistics (Green & Silverman, 1993; Lindgren & Rue, 2008). The estimated variance (σ) for a random walk can be taken to represent smoothness and fit, where smaller values of σ are smoother trends and better fits (Zuur et al., 2017). For the current model, a random intercept for fish ID was added to account for individual-level variability. The model took the form:

 $Y_{Xij} \sim B(\pi_{Xij}),$

$$E(Y_{Xij}) = \pi_{Xij},$$

 $var(Y_{Xij}) = \pi_{Xij} \times (1 - \pi_{Xij}),$

 $logit(\pi_{Xij}) = \beta_1 + \beta_2 \times habitat_{Xij} + \beta_3 \times length_{Xij} + \beta_4$ $\times habitat_{Xij} \times length_{Xij} + a_i + \mu_X + \varepsilon_{ij},$

 $a_i \sim N(0, \sigma_{FISH}^2),$

 $\mu_X = \mu_{X-1} + v_X,$

$$\mu_X - (2 \times \mu_{X-1} - \mu_{X-2}) = v_X,$$

$$v_{\boldsymbol{X}} \sim N(0, \sigma_{v}^{2}),$$
 $\varepsilon \sim N(0, \sigma_{\varepsilon}^{2}),$

where Y_{Xij} is binomial distributed with an expected mean probability π_{Xij} and variance $\pi_{Xij} \times (1 - \pi_{Xij}) \cdot Y_{Xij}$ is 1 if a large movement (≥ 3 m) is recorded from brook trout *i* at observation *j*, and 0 otherwise. π_{Xij} is modelled as a function of the fixed effects including the intercept β_{1-4} , random intercept a_i , trend defined in a random walk μ_X , and noise ϵ_{ij} using the logistic link function. The random intercept a_i is assumed to be normally distributed with a mean of 0 and σ_{FISH}^2 . The random walk μ_X is modelled as the trend from the previous observation plus independent, identical, and normal distributed noise v_X . For brevity, the subscript *X* represents a list of covariates including depth, temperature, conductivity, distance upstream, and day of study.

Data exploration and analyses were performed in the R statistical environment (R Core Team, 2020; Online Resources 2–6). Due to suspected predation early in the study, two fish (#s 16 and 24) were excluded from the analysis. As a result of the limited number of individuals (n=6), small range of body sizes, and environmental conditions in Harper North, stream was not included as a term. Strong collinearity ($|r| \ge 0.7$) was checked in pair-wise tests of the independent variables where none met the threshold (Dormann et al., 2012; Online Resource 3). The model was evaluated through inspection of the residuals against all terms, including those excluded from the model (Zuur et al., 2010; Online Resource 6).

Results

Tagged brook trout were small-bodied (mean=168 mm FL±23 SD) and for the most part displayed short movements (mean: 31 m, median: 0.37) between biweekly relocations in the Harper Creek watershed (Table 1). All but one of the tagged brook trout relocated at least 10 times. Movement was heavily bimodal, with the majority occurring in a 3 m area (Fig. 2A). Harper North fish displayed shorter mean and median total movements (mean: 5.2 m±12.1 SD, median: 0.27 m, range:

Table 1 Summary statistics for tagged brook trout in theHarper Creek urban stream network (n = 19)

Statistic	Mean	St. Dev	Median	Min	Max
FL (mm)	168.4	22.70	163.0	145.0	227.0
Wet wt (g)	57.42	28.00	45.32	30.18	124.8
Imovementl (m)	30.76	103.6	0.368	0	921.8
Net movement (m)	11.30	107.5	0.094	- 392.8	921.8
Depth (cm)	31.80	15.59	29.50	50	69
Temperature (°C)	11.86	1.887	12.10	7.100	18.90
Conductivity (µs/ cm)	518.5	71.82	521.0	265.0	757.0

0.002–59.7 m) compared to those in Harper South (mean: 40 m±119 SD, median: 0.39 m, range: 0–921.8 m; Fig. 2B). The larger movements of the tagged Harper South individuals mostly occurred during two time periods: late summer–early autumn (20 Aug.–7 Sept.) and mid-autumn (3–28 Oct.), around the time when redds were beginning to appear (Figs. 3 and 4). Approximately 85% of biweekly movements of individuals tagged in both branches were in an upstream direction. Two spatio-temporal patterns were predominant over the course of the study: individuals that exhibited little net or total movement (n=9, including all from Harper North),

and individuals that moved > 500 m upstream before or during the spawning period and were still upstream at the end of the study (n=4). The remaining individuals either moved upstream and back, downstream and back, or downstream and remained downstream (Fig. 4, Online Resource 7). Total movement varied by individual, with six brook trout travelling less than 100 m during the study, and three Harper South individuals moving 1 km or more (Figs. 4, Online Resource 7). Detailed information on individual fish movements is presented in Online Resource 1.

The probability of brook trout movement ≥ 3 m differed according to habitat complexity and body size (Table 2). Habitat complexity was associated with movement in larger brook trout (~200 mm FL) more so than in smaller individuals (Fig. 5). In larger individuals, movements ≥ 3 m were more frequent to less complex habitats than to more complex habitats. For example, probability was 0.32 (0.18–0.48, 95% credible interval) that a 160 mm FL brook trout would move ≥ 3 m to moderately complex habitat, whereas a 220 mm FL fish had a 0.88 (68–98 CI, 95% credible interval) probability of moving ≥ 3 m to the same habitat. No change in body size resulted in a change in the probability of a large movement into complex habitat (Table 2, Fig. 5). While the overall variation in total movement was considerable

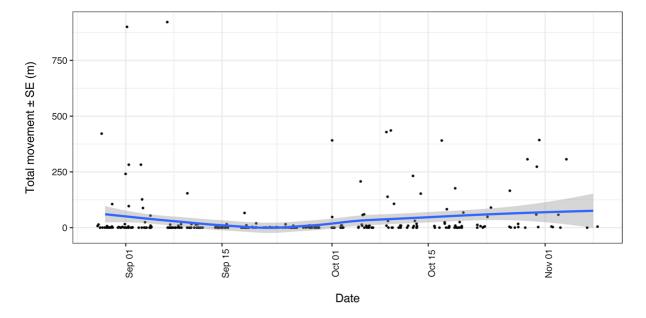


Fig. 3 Total movement (m) of radio-tagged brook trout by relocation date for in the Harper Creek urban stream network. The blue line is a loess smoother \pm SE (shaded grey area)

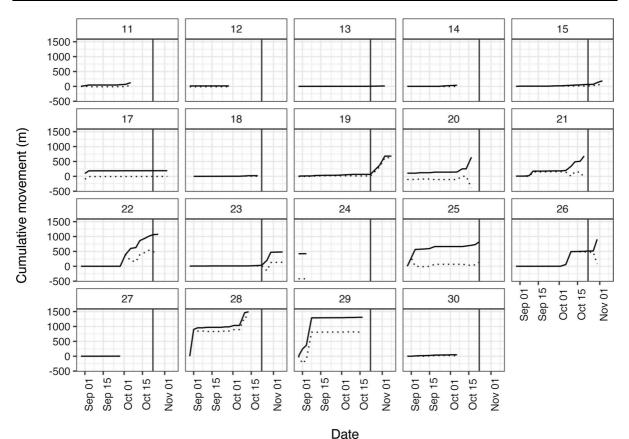


Fig. 4 Cumulative total movement (solid line) and cumulative net movement (dotted line) of radio-tagged brook trout in the Harper Creek urban stream network. The more positive

Table 2 Fixed effects estimates of the model to estimate the probability of brook trout total movement ≥ 3 m in the Harper Creek urban stream network

Term	Mean	2.5% CI	97.5% CI
y-intercept	- 0.36	- 1.05	0.33
FL	1.14	0.56	1.78
Habitat-complex	- 0.46	- 1.22	0.30
Habitat-complex \times FL	- 0.98	- 1.67	- 0.35

(Table 1), the random intercept indicated little variation in the probability of movements ≥ 3 m among individual fish compared with the variance of continuous covariates (Table 3). The smoothest trends and best fits were estimated for depth, temperature, and conductivity whereas probabilities for movements ≥ 3 m were more erratic for day of the study and distance upstream (Fig. 5). Juio

numbers on the *y*-axis indicate upstream travel; more negative numbers denote downstream travel. The vertical solid line marks the date when the first redd was observed in the system

Temperature and day of the study illustrated similar trends that coincide with their moderate to strong collinearly (|r|=0.6, Fig. 5 and Online Resource 2). Patterns in the correlated random walks showed that brook trout tended to make fewer large movements to sites with greater water depth and higher conductivity, whereas water temperature showed no evident effect on the probability of large movements (Fig. 5). Large movement decreased considerably as brook trout were located greater than 1400 m upstream; an estimate that applies only to the longer Harper South reach (Fig. 5). As expected, large movements became increasingly common later in the season (Figs. 3, 4 and 5).

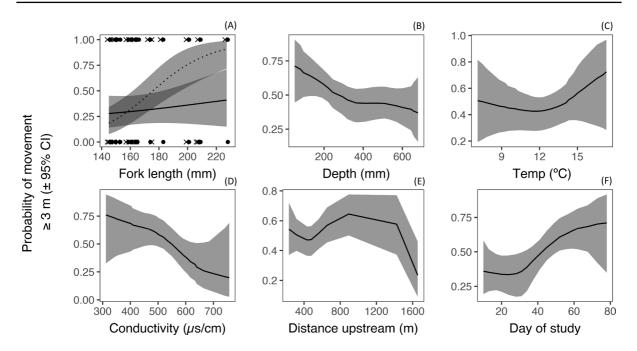


Fig. 5 The estimated relationship between body size and habitat complexity of the site travelled to on the probability of movement $\geq 3 \text{ m} (\pm 95\% \text{ CI})$ by radio-tagged brook trout in the Harper Creek urban stream network (A). Complex habitat

 Table 3 Posterior mean value of the variance for model hyperparameters

Hyperparameter	σ
Random intercept—Fish ID	0.01
Depth	0.20
Temperature	0.26
Conductivity	0.27
Distance upstream	0.66
DOS	0.37

Fish ID was a random intercept and all other terms correlated random walks

DOS Day of study

Discussion

Movement patterns

We observed brief but large upstream movements by mature brook trout, most of which occurred just prior to or during the spawning season. Movement appeared to be greater for larger-sized fish that also originated closer to the creek mouth in summer, supporting the assertion that movement would depend

is marked by a circle and solid line, whereas moderate habitat is marked by an X and dashed line. The effect of continuous covariates, estimated by correlated random walks, on the probability of movement \geq 3 m (\pm 95% CI, **B–F**)

on body size when reproductive fish were migratory. The high percentage of upstream movements during the study upheld the expectation that movement in autumn would be mainly in an upstream direction. The majority of large spawning individuals were located further downstream in summer (Fig. 3), which further underscores the demographic, spatial, and temporal patterns and requirements of urban brook trout (Blair et al., 2021). It follows that complex habitat requirements and connectivity be maintained for the persistence of such populations (Letcher et al., 2007).

Given that groundwater inflows were identified in the upper portion of Harper North and the central and upper portions of Harper South (S. McCallum, unpublished data), it is plausible that large brook trout (n=3) located near the mouth of the Harper South tributary during summer were preparing to migrate upstream towards groundwater inflows. Brook trout spawning is supported by the presence of groundwater aquifers (Kanno et al., 2015) that provide critical habitat (e.g., coarse substrate for cover, high dissolved oxygen, consistent temperatures) for egg incubation and fry survival (Blanchfield and Ridgway, 1997; Power et al., 1999; Borwick et al., 2006; Curry and Noakes, 2011; Guillemette et al., 2011). Increased movement during autumn has been demonstrated in several brook trout populations inhabiting less urbanized areas (Curry et al. 2002; Mollenhauer et al. 2013; Davis et al. 2015) and previous work in the current study system indicates reproductive timing coincides with the relatively large movements in adult brook trout observed here (Blair et al., 2021). Radiotagged brook trout clearly showed that larger ($\geq 3 \text{ m}$) relatively rare movements were more likely late in the season and less likely if fish were occupying far upstream habitat (Fig. 5). Harper Creek is among the first locations where brook trout movements have been linked to reproduction in a highly urbanized setting. While these patterns were expected given the population is native and reproductive (Blair et al., 2021), the migratory timing and spawning areas uncovered by telemetry can be used to steer conservation initiatives, e.g., designation of fish sanctuaries or critical habitat.

Harper South is more than twice as long as Harper North, and the total distance that fish could travel upstream in the latter is limited (Fig. 1). Furthermore, given the shallow, narrow channels and rapid baseflow of the headwaters of Harper North (Blair et al., 2021), these areas are suboptimal for brook trout spawning. The ditched area where trout were found both before and after the spawning season had been previously re-aligned and recontoured, with the addition of coarse substrate, cobbles and riffle/pool features, rendering the area more suitable than the headwaters for spawning. This was likely the major reason why brook trout in Harper North did not follow the pattern of upstream movement shown by those in Harper South. Given our telemetry findings, environmental disturbance in Harper North could have serious consequences because (1) brook trout of all age-classes are located in a relatively small section of creek with limited areas to disperse and (2) there are no suitable alternative spawning grounds.

In-stream road culverts are known to fragment habitat by inhibiting upstream movement of brook trout. For example, Goerig et al. (2015) found that the probability of culvert passage success by brook trout decreased with steeper culvert slopes, higher stream velocities, and water temperatures exceeding 15° C. Motivation to ascend culverts is further complicated by seasonal timing (i.e., spawning period), body size, diel period, and culvert design (Norman et al., 2009; Goerig and Castro-Santos, 2017). We were unable to statistically compare streams due to sample size restrictions (e.g., limited size ranges in Harper North), however temperature did not appear to be a limiting factor to movement, particularly in Harper South where temperature reached at least 18°C (Online Resource 5). The effects of temperature on brook trout movement has been shown to differ among populations and between individuals (Petty et al., 2012). Based on weekly radiotelemetry tracking, movement by individuals in Harper North was mostly within the stream reach between and rarely upstream through a culvert. Similar to the findings of Goerig and Castro-Santos (2017), the only movements through culverts were documented during the spawning season. Given that only adults moved through the culvert during the spawning season, Harper North may also have restricted connectivity for smaller subadult brook trout.

The occurrence of two distinctive movement patterns in tagged individuals suggests the possibility of "stayers" and "movers" in the population. This type of behavioural pattern has been previously noted in juvenile brook trout (Grant & Noakes, 1987a), and more generally associated with behavioural syndromes (Fraser et al., 2001). The dichotomy of "movers" and "stayers" has also been demonstrated in smallerscale foraging movements by recently emerged brook trout (Mclaughlin et al., 1992), as a response to altered flow conditions (Boavida et al., 2017), and in the context of invasive fishes expanding their geographic range (Myles-Gonzalez et al., 2015, and references therein). However, the complexity of migratory behaviour demonstrated in other salmonids underscores the fallacy of simplifying movement into two categories (Beddow et al., 1998; Rustadbakken et al., 2004; Dodson et al., 2013). Moreover, given the largest individuals tended to be those with the greatest movement, it remains possible that such an apparent behavioural syndrome is actually a function of size and maturity of brook trout in the current study. It stands that more work is needed to determine how personality influences movement relative to other factors in the urban environment.

Relationship of movement to habitat factors and habitat complexity

The analysis of habitat showed fewer movements ≥ 3 m were made to sites with greater water depth and higher conductivity. In addition, such movements were more frequent in habitats with fewer complex features like pools, logjams and undercut banks, but only in the larger radio-tagged brook trout. These effects were likely driven by a few individuals in Harper South that showed major upstream movement during the spawning season, as their position at the outset of the study was in the lower portion of the stream, which contained deeper water with higher conductivity as a result of stormwater inputs (Blair et al., 2021). Young-of-year brook trout have been suggested to avoid risky foraging behaviour as a trade-off for fast growth (Grant and Noakes, 1987b), however the risk of moving into relatively open cover is likely worth the reward for adult brook trout compelled to migrate for reproduction. Many intrinsic and extrinsic factors influence how salmonids use in-stream habitat [e.g., territoriality (Elliott 1990), food availability (Ovidio et al., 2002), diel period (Ovidio et al. 2002; Boavida et al. 2017)] and a thorough evaluation of these in tandem with factors such as stormwater runoff, sedimentation, and habitat fragmentation is required to fully evaluate drivers of fish habitat use in urban environments.

Predation of radio-tagged trout

Movement increases the risk of exposure to predators, especially where riparian canopy cover is limited (Bentley et al., 2014; Penaluna et al., 2016). In our study, predation was noted in Harper South mainly in the downstream reaches with little canopy cover. Several cases of predation were confirmed by field observations, including radio-tag signals transmitted from a great blue heron (Ardea herodias Linnaeus, 1758), recovered tags in a regurgitation pellet, and tags found among bird faeces (Online Resource 1). Heron commonly predate brook trout (Glahn et al., 1999; Pépino et al., 2015) and reportedly prefer to consume individuals varying from 8 to 23 cm in length (Alexander, 1977). Documented predation of brook trout in our study was greatest at the onset of the spawning season when tagged fish began making large upstream movements, as well as during the spawning period when on multiple occasions a heron was observed stalking shallow riffles. While anecdotal, the impacts of predation may be considerable depending on the season, environmental conditions, and habitat. In addition, avian predators reduce the likelihood of risky feeding behaviour, therefore imposing sub-lethal effects on the population (Allouche & Gaudin, 2001). Other tagged brook trout may have suffered natural mortality and were subsequently removed from the study area by scavenger species (Muhametsafina et al., 2014), further contributing to the premature disappearance of radio-tagged brook trout during our study. In subsequent studies, internally fixed antenna may render tagged fish less conspicuous and serve to minimize perceived predation risk.

Summary and management implications

We assessed overall patterns in brook trout movements and how these varied in an urban environment. A follow-up study, including a larger sample of radio-tagged individuals, is needed to further assess how the associated factors of urbanization influence pre- to post-spawn movement patterns. The rate of predation by blue herons was high, and should be studied to understand the extent to which urbanization mediates avian predation on fish such as brook trout. The system also supports a recreational fishery, as observed in the field (S. Blair, personal observation). However, the population-level impacts of brook trout catch and harvest by anglers is unknown.

The urban syndrome challenges coldwater fishes with stressors associated with water quality, habitat fragmentation, increasing water temperature, and urban development (Taylor & Stefan, 2009; Rocco et al., 2016). For instance, impassable culverts reduce the capacity for migration while channelization and the removal of riparian vegetation increase exposure to predators. While urbanization is generally understood to reduce fish habitat, relatively little is known about the movement ecology of sensitive species in urban environments. Localized patterns in behaviour will increasingly be valuable to characterize as urban environments are further developed and encroach into natural spaces. Such knowledge has the potential to inform mitigation and restoration strategies needed to sustain brook trout and other fishes in urban streams.

Funding This work was supported by an Ontario Graduate Scholarship (OGS) to SGB and a National Science and Engineering Council Discovery Grant to MGF, as well as funding from the Ontario Federation of Anglers and Hunters (OFAH) and 20 public donors to the Fund and Follow a Fish program via the Peterborough Field Naturalists (PFN), which subsidized the cost of the radio-tags. We thank J. Cotton, S. Degasparro, J. Gobin, T. Liang, S. McCallum, A. Myette, P. Silk, and M. Wheeler for field assistance during electrofishing and radiotelemetry events, as well as comments from D. Beresford which greatly improved an earlier version of this manuscript.

Data availability The authors confirm that data supporting the findings of this study will be made available upon reasonable request.

Declarations

Conflict of interest There are no competing interests to declare.

Ethical approval All work has been performed with the approval of the Trent University Animal Care Committee (Protocol #24839).

References

- Adams, N. S., D. W. Rondorf, S. D. Evans & J. E. Kelly, 1998. Effects of surgically and gastrically implanted radio transmitters on growth and feeding behavior of juvenile chinook salmon. Canadian Journal of Fisheries and Aquatic Sciences 55: 781–787.
- Alberti, M., 2005. The Effects of Urban Patterns on Ecosystem Function. International Regional Science Review, Sage Publications, Thousand Oaks:, 168–192. https://doi.org/ 10.1177/0160017605275160.
- Alexander, G. R., 1977. Diet of vertebrate predators on trout waters in north central lower Michigan. Michigan Academician 10: 181–195.
- Allouche, S. & P. Gaudin, 2001. Effects of avian predation threat, water flow and cover on growth and habitat use by chub, *Leuciscus cephalus*, in an experimental stream. Oikos 94: 481–492. https://doi.org/10.1034/j.1600-0706. 2001.940310.x.
- Anderson, W. G., R. S. McKinley & M. Colavecchia, 1997. The use of clove oil as an anesthetic for rainbow trout and its effects on swimming performance. North American Journal of Fisheries Management 17: 301–307.
- Barton, D. R., W. D. Taylor & R. M. Biette, 1985. Dimensions of Riparian buffer strips required to maintain Trout habitat in Southern Ontario streams. North American Journal of

Fisheries Management 5: 364–378. https://doi.org/10. 1577/1548-8659(1985)5%3C364:DORBSR%3E2.0.CO;2.

- Beddow, T. A., C. Deary & R. S. McKinley, 1998. Migratory and reproductive activity of radio-tagged Arctic char (*Salvelinus alpinus* L.) in northern Labrador. Hydrobiologia 371: 249–262.
- Bentley, K. T., D. E. Schindler, T. J. Cline, J. B. Armstrong, D. Macias, L. R. Ciepiela & R. Hilborn, 2014. Predator avoidance during reproduction: Diel movements by spawning sockeye salmon between stream and lake habitats. Journal of Animal Ecology 83: 1478–1489.
- Blair, S. G., L. F. G. Gutowsky & M. G. Fox, 2021. Factors affecting seasonal habitat use of native brook trout (*Salvelinus fontinalis*) in urban headwater streams. Ecology of Freshwater Fish 30: 490–502. https://doi. org/10.1111/eff.12599.
- Blanchfield, P. J. & M. S. Ridgway, 1997. Reproductive timing and use of redd sites by lake-spawning brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences 54: 747–756.
- Boavida, I., A. Harby, K. D. Clarke & J. Heggenes, 2017. Move or stay: habitat use and movements by Atlantic salmon parr (*Salmo salar*) during induced rapid flow variations. Hydrobiologia 785: 261–275.
- Borwick, J., J. Buttle & M. S. Ridgway, 2006. A topographic index approach for identifying groundwater habitat of young-of-year brook trout (*Salvelinus fontinalis*) in the land-lake ecotone. Canadian Journal of Fisheries and Aquatic Sciences 63: 239–253.
- Brown, R., S. J. Cooke, G. Anderson & R. S. McKinley, 1999. Evidence to challenge the "2% rule" for biotelemetry. North American Journal of Fisheries Management 19: 867–871. https://doi.org/10.1577/ 1548-8675(1999)019%3C0867:ETCTRF%3E2.0.CO;2.
- Codling, E. A., M. J. Plank & S. Benhamou, 2008. Random walk models in biology. Journal of the Royal Society Interface 5: 813–834. https://doi.org/10.1098/rsif.2008. 0014.
- Coutant, C. C., 1977. Compilation of temperature preference data. Journal of the Fisheries Research Board of Canada 34: 739–745.
- Curry, R. A. & W. S. MacNeill, 2004. Population-level responses to sediment during early life inbrook trout. Journal of the North American Benthological Society 23: 140–150.
- Curry, R. A. & D. L. G. Noakes, 2011. Groundwater and the selection of spawning sites by brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences 52: 1733–1740.
- Curry, R. A., D. Sparks, J. Van De Sande & J. van de Sande, 2002. Spatial and temporal movements of a Riverine Brook Trout population. Transactions of the American Fisheries Society 131: 551–560. https://doi.org/10.1577/ 1548-8659(2002)131%3C0551:SATMOA%3E2.0.CO;2.
- Davis, L. A., T. Wagner & M. L. Bartron, 2015. Spatial and temporal movement dynamics of brook *Salvelinus fontinalis* and brown trout *Salmo trutta*. Environmental Biology of Fishes 98: 2049–2065.
- DeWeber, J. T. & T. Wagner, 2015. Predicting Brook Trout occurrence in stream reaches throughout their native

range in the Eastern United States. Transactions of the American Fisheries Society 144: 11–24.

- Dodson, J. J., N. Aubin-Horth, V. Thériault & D. J. Páez, 2013. The evolutionary ecology of alternative migratory tactics in salmonid fishes. Biological Reviews 88: 602– 625. https://doi.org/10.1111/brv.12019.
- Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, C. Mcclean, P. E. Osborne, B. Reineking, B. Schröder, A. K. Skidmore, D. Zurell & S. Lautenbach, 2012. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36: 027–046. https://doi.org/10. 1111/j.1600-0587.2012.07348.x.
- Elliott, J. M., 1990. Mechanisms responsible for population regulation in young migratory trout, Salmo trutta. III. The role of territorial behaviour. The Journal of Animal Ecology 59: 808–818.
- Fagan, W. F., 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. Ecology 83: 3243–3249.
- Fraser, D. F., J. F. Gilliam, M. J. Daley, A. N. Le & G. T. Skalski, 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. American Naturalist 158: 124–135. https:// doi.org/10.1086/321307.
- Glahn, J. F., T. Tomsa & K. J. Preusser, 1999. Impact of great blue heron predation at trout-rearing facilities in the northeastern United States. North American Journal of Aquaculture American Fisheries Society 61: 349–354.
- Goerig, E. & T. Castro-Santos, 2017. Is motivation important to brook trout passage through culverts? Canadian Journal of Fisheries and Aquatic Sciences 74: 885–893.
- Goerig, E., T. Castro-Santos & N. É. Bergeron, 2015. Brook trout passage performance through culverts. Canadian Journal of Fisheries and Aquatic Sciences 73: 94–104.
- Grant, J. W. A. & D. L. G. Noakes, 1987a. Movers and Stayers: foraging tactics of Young-of-the-Year Brook Charr, *Salvelinus fontinalis*. The Journal of Animal Ecology 56: 1001–1013.
- Grant, J. W. A. & D. L. G. Noakes, 1987b. Escape behaviour and use of cover by Young-of-the-Year Brook Trout, *Salvelinus fontinalis*. Canadian Journal of Fisheries and Aquatic Sciences 44: 1390–1396. https://doi.org/10.1139/ f87-167.
- Green, P. J. & B. W. Silverman, 1993. Nonparametric Regression and Generalized Linear Models, Chapman and Hall/CRC, Boca Raton:
- Guillemette, F., C. Vallée, A. Bertolo & P. Magnan, 2011. The evolution of redd site selection in brook charr in different environments: same cue, same benefit for fitness*. Freshwater Biology 56: 1017–1029.
- Harper, D. J. & J. T. Quigley, 2005. No net loss of fish habitat: a review and analysis of habitat compensation in Canada. Environmental Management 36: 343–355. https://doi.org/ 10.1007/s00267-004-0114-x.
- Hasenmueller, E. A., Criss, R. E., Winston, W. E., & A. R. Shaughnessy, 2017. Stream hydrology and geochemistry along a rural to urban land use gradient. Applied Geochemistry 83: 136–149. https://doi.org/10.1016/j. apgeochem.2016.12.010.

- Hartman, K. J. & J. P. Hakala, 2006. Relationships between fine sediment and brook trout recruitment in forested headwater streams. Journal of Freshwater Ecology 21: 215–230.
- Jones, M. P., W. F. Hunt & R. J. Winston, 2012. Effect of urban catchment composition on runoff temperature. Journal of Environmental Engineering 138: 1231–1236.
- Jonsen, I., 2016. Joint estimation over multiple individuals improves behavioural state inference from animal movement data. Scientific Reports Nature Publishing Group 6: 1–9.
- Kanno, Y., B. H. Letcher, A. L. Rosner, K. P. O'Neil & K. H. Nislow, 2015. Environmental factors affecting Brook Trout occurrence in headwater stream segments. Transactions of the American Fisheries Society 144: 373–382. https://doi.org/10.1080/00028487.2014. 991446.
- Letcher, B. H., K. H. Nislow, J. A. Coombs, M. J. O'Donnell & T. L. Dubreuil, 2007. Population response to habitat fragmentation in a stream-dwelling brook trout population. PLoS ONE 2: e1139. https://doi.org/10. 1371/journal.pone.0001139.
- Lindgren, F. & H. Rue, 2008. On the second-order random walk model for irregular locations. Scandinavian Journal of Statistics 35: 691–700. https://doi.org/10. 1111/j.1467-9469.2008.00610.x.
- Lokteff, R. L., B. B. Roper & J. M. Wheaton, 2013. Do Beaver Dams impede the movement of Trout? Transactions of the American Fisheries Society 142: 1114–1125. https://doi.org/10.1080/00028487.2013. 797497.
- Martins, T. G., D. Simpson, F. Lindgren & H. Rue, 2013. Bayesian computing with INLA: new features. Computational Statistics and Data Analysis North-Holland 67: 68–83.
- McKenna, J. E. & J. H. Johnson, 2011. Landscape models of Brook Trout abundance and distribution in lotic habitat with field validation. North American Journal of Fisheries Management 31: 742–756. https://doi.org/10. 1080/02755947.2011.593940.
- Mclaughlin, R. L., J. W. A. Grant & D. L. Kramer, 1992. Individual variation and alternative patterns of foraging movements in recently-emerged Brook Charr (*Salvelinus fontinalis*). Behaviour 120: 286–301.
- Mollenhauer, R., T. Wagner, M. V. Kepler & J. A. Sweka, 2013. Fall and early winter movement and habitat use of wild brook trout. Transactions of the American Fisheries Society 142: 1167–1178.
- Morgan, R. P., K. M. Kline, M. J. Kline, S. F. Cushman, M. T. Sell, R. E. Weitzell & J. B. Churchill, 2012. Stream conductivity: relationships to land use, chloride, and fishes in Maryland streams. North American Journal of Fisheries Management 32: 941–952.
- Muff, S., J. Signer & J. Fieberg, 2020. Accounting for individual-specific variation in habitat-selection studies: efficient estimation of mixed-effects models using Bayesian or frequentist computation. Journal of Animal Ecology 89: 80–92. https://doi.org/10.1111/1365-2656. 13087.
- Muhametsafina, A., J. D. Midwood, S. M. Bliss, K. M. Stamplecoskie & S. J. Cooke, 2014. The fate of dead

fish tagged with biotelemetry transmitters in an urban stream. Aquatic Ecology 48: 23–33.

- Myles-Gonzalez, E., G. Burness, S. Yavno, A. Rooke & M. G. Fox, 2015. To boldly go where no goby has gone before: boldness, dispersal tendency, and metabolism at the invasion front. Behavioral Ecology 26: 1083–1090.
- Norman, J. R., M. M. Hagler, M. C. Freeman & B. J. Freeman, 2009. Application of a multistate model to estimate culvert effects on movement of small fishes. Transactions of the American Fisheries Society 138: 826–838.
- Northcote, T. G., 1984. Mechanisms of Fish Migration in Rivers Mechanisms of Migration in Fishes, Springer, Boston:, 317–355. https://doi.org/10.1007/978-1-4613-2763-9_20.
- Otonabee Conservation Authority, 2013. Otonabee Conservation Fisheries Assessment Plan, Final report. Peterborough, Ontario
- Otonabee Conservation Authority, 2015. Otonabee Conservation Fisheries Assessment Project Report for Watercourses in the City of Peterborough, Final Report. Peterboroug, Ontario
- Ovidio, M., E. Baras, D. Goffaux, F. Giroux & J. C. Philippart, 2002. Seasonal variations of activity pattern of brown trout (*Salmo trutta*) in a small stream, as determined by radio-telemetry. Hydrobiologia 470: 195–202. https://doi. org/10.1023/A:1015625500918.
- Paul, M. J., & J. L. Meyer, 2001. Streams in the Urban Landscape. Annual Review of Ecology and Systematics, 32(1): 333–365. https://doi.org/10.1146/annurev.ecolsys. 32.081501.114040.
- Penaluna, B. E., J. B. Dunham & D. L. G. Noakes, 2016. Instream cover and shade mediate avian predation on trout in semi-natural streams. Ecology of Freshwater Fish 25: 405–411.
- Pépino, M., M. A. Rodríguez & P. Magnan, 2012. Impacts of highway crossings on density of brook charr in streams. Journal of Applied Ecology 49: 395–403.
- Pépino, M., M. A. Rodríguez & P. Magnan, 2015. Shifts in movement behavior of spawning fish under risk of predation by land-based consumers. Behavioral Ecology 26: 996–1004.
- Petty, T. J., J. L. Hansbarger, B. M. Huntsman & P. M. Mazik, 2012. Brook trout movement in response to temperature, flow, and thermal refugia within a complex Appalachian riverscape. Transactions of the American Fisheries Society 141: 1060–1073. https://doi.org/10.1080/00028 487.2012.681102.
- Power, M. & G. Power, 1995. A modelling framework for analyzing anthropogenic stresses on brook trout (*Salvelinus fontinalis*) populations. Ecological Modelling 80: 171–185.
- Power, G., R. S. Brown & J. G. Imhof, 1999. Groundwater and fish—insights from northern North America. Hydrological Processes 13: 401–422.
- R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, https://www.r-project.org/.
- Radinger, J. & C. Wolter, 2014. Patterns and predictors of fish dispersal in rivers. Fish and Fisheries 15: 456–473.

- Ranta, E., M. R. Vidal-Abarca, A. R. Calapez & M. J. Feio, 2021. Urban stream assessment system (UsAs): an integrative tool to assess biodiversity, ecosystem functions and services. Ecological Indicators 121: 106980.
- Riley, S. C., K. D. Fausch & C. Gowan, 1992. Movement of brook trout (*Salvelinus fontinalis*) in four small subalpine streams in northern Colorado. Ecology of Freshwater Fish 1: 112–122. https://doi.org/10.1111/j.1600-0633.1992. tb00080.x.
- Rocco, R. T., N. E. Jones, & C. Chu, 2016. Past, present, and future summer stream temperature in the Lake Simcoe watershed: brook trout (*Salvelinus fontinalis*) habitat at risk. Climate Change Research Report—Ontario Ministry of Natural Resources and Forestry 2016 No.CCRR-45 pp.iii + 9 pp. ref.3. Peterborough, Ontario, https://www. cabdirect.org/cabdirect/abstract/20173170946.
- Rue, H., S. Martino & N. Chopin, 2009. Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. Journal of the Royal Statistical Society. Series B: Statistical Methodology 71: 319–392. https://doi.org/10.1111/j.1467-9868.2008. 00700.x.
- Rustadbakken, A., J. H. L'Abee-Lund, J. V. Arnekleiv & M. Kraabol, 2004. Reproductive migration of brown trout in a small Norwegian river studied by telemetry. Journal of Fish Biology 64: 2–15. https://doi.org/10.1111/j.1095-8649.2004.00275.x.
- Schlosser, I. J., 1995. Critical landscape attributes that influence fish population dynamics in headwater streams. Hydrobiologia 303: 71–81. https://doi.org/10.1007/BF000 34045.
- Steedman, R. J., 1988. Modification and assessment of an index of biotic integrity to quantify stream quality in southern Ontario. Canadian Journal of Fisheries and Aquatic Sciences 45: 492–501. https://doi.org/10.1139/f88-059.
- Stranko, S. A., R. H. Hilderbrand, R. P. Morgan, M. W. Staley, A. J. Becker, A. Roseberry-Lincoln, E. S. Perry & P. T. Jacobson, 2008. Brook Trout declines with land cover and temperature changes in Maryland. North American Journal of Fisheries Management 28: 1223–1232.
- Sullivan, B. G., S. H. Clarke, D. P. Struthers, M. K. Taylor & S. J. Cooke, 2019. The gain reduction method for manual tracking of radio-tagged fish in streams. Animal Biotelemetry 7: 1–6. https://doi.org/10.1186/ s40317-019-0168-4.
- Sweka, J. A. & K. J. Hartman, 2006. Effects of large woody debris addition on stream habitat and brook trout populations in Appalachian streams. Hydrobiologia 559: 363–378.
- Taylor, C. A. & H. G. Stefan, 2009. Shallow groundwater temperature response to climate change and urbanization. Journal of Hydrology 375: 601–612.
- Urban, M. C., D. K. Skelly, D. Burchsted, W. Price & S. Lowry, 2006. Stream communities across a rural-urban landscape gradient. Diversity and Distributions 12: 337–350.
- Wagner, T., J. T. Deweber, J. Detar & J. A. Sweka, 2013. Landscape-scale evaluation of asymmetric interactions between Brown Trout and Brook Trout using twospecies occupancy models. Transactions of the American Fisheries Society 142: 353–361.

- Wallace, A. M., M. V. Croft-White & J. Moryk, 2013. Are Toronto's streams sick? A look at the fish and benthic invertebrate communities in the Toronto region in relation to the urban stream syndrome. Environmental Monitoring and Assessment 185: 7857–7875. https://doi.org/10.1007/ s10661-013-3140-4.
- Walsh, C. J., A. H. Roy, J. W. Feminella, P. D. Cottingham, P. M. Groffman & R. P. Morgan, 2005. The urban stream syndrome: current knowledge and the search for a cure. Journal of the North American Benthological Society. North American Benthological Society 24: 706–723. https://doi.org/10.1899/04-028.1.
- Ward, E. J., J. H. Anderson, T. J. Beechie, G. R. Pess & M. J. Ford, 2015. Increasing hydrologic variability threatens depleted anadromous fish populations. Global Change Biology 21: 2500–2509.
- Wenger, S. J., A. H. Roy, C. R. Jackson, E. S. Bernhardt, T. L. Carter, S. Filoso, C. A. Gibson, W. C. Hession, S. S. Kaushal, E. Mart, J. L. Meyer, M. A. Palmer, M. J. Paul, A. H. Purcell, A. Ramrez, A. D. Rosemond, K. A. Schofield, E. B. Sudduth & C. J. Walsh, 2009. Twentysix key research questions in urban stream ecology: an assessment of the state of the science. Journal of the North American Benthological Society 28: 1080–1098. https:// doi.org/10.1899/08-186.1.
- Wenger, S. J., D. J. Isaak, C. H. Luce, H. M. Neville, K. D. Fausch, J. B. Dunham, D. C. Dauwalter, M. K. Young, M. M. Elsner, B. E. Rieman, A. F. Hamlet & J. E. Williams, 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. Proceedings of the National Academy of Sciences 108: 14175–14180.

- Wheeler, A. P., P. L. Angermeier & A. E. Rosenberger, 2005. Impacts of new highways and subsequent landscape urbanization on stream habitat and biota. Reviews in Fisheries Science 13: 141–164.
- Witzel, L. D. & H. R. MacCrimmon, 1983. Redd-site selection by brook trout and brown trout in southwestern Ontario streams. Transactions of the American Fisheries Society 112: 760–771.
- Zerega, A., N. E. Simões, & M. J. Feio, 2021. How to improve the biological quality of urban streams? Reviewing the effect of hydromorphological alterations and rehabilitation measures on benthic invertebrates. Water (Switzerland). Multidisciplinary Digital Publishing Institute, 2087, https://www.mdpi.com/2073-4441/13/15/2087/htm.
- Zuur, A. F., E. N. Ieno & C. S. Elphick, 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1: 3–14.
- Zuur, A. F., Ieno, E. N., & A. A. Saveliev, 2017. Beginner's guide to spatial, temporal, and spatial-temporal ecological data analysis with R-INLA Volume I: Using GLM and GLMM. Newburgh, UK: Highland Statistics Ltd. ISBN: 978:1–12.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.