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Movement and early survival of age-0 brown trout

SHANE VATLAND* AND ARNAUD CAUDRON*,†
*UMR CARRTEL – INRA, Université de Savoie, Thonon-les-Bains, France
†Science-Management Interface for Biodiversity Conservation (SCIMABIO Interface), Thonon-les-Bains, France

SUMMARY

1. Complementary data on survival and movement are often missing for early life stages that are logistically challenging to track.
2. Previous studies observed significant declines in the density of age-0 brown trout between summer and autumn in tributaries of Lake Geneva, but the cause of these declines was unknown. We hypothesised that mortality, dispersal within tributaries, early emigration to the lake or a combination of these factors was driving these seasonal declines.
3. To evaluate these hypotheses, we used a combination of electrofishing and PIT-tag mark–recaptures from stationary and portable antennae to quantify summer-to-autumn variation in the abundance, dispersal and emigration of age-0 brown trout.
4. Mortality was the primary cause of the reduction in abundance between summer and autumn. A small proportion (mean = 0.10) of age-0 trout emigrated to Lake Geneva between July and mid-October, while the movement of trout within the study streams was minimal. True survival estimates for this same time period were relatively low at all but one site (mean = 0.63).
5. The seasonal resolution of survival estimates, paired with environmental data, allowed us to develop additional hypotheses on what factors were affecting survival.
6. Understanding animal movement at early life stages can elucidate important aspects of population ecology while concomitantly improving the reliability of demographic data.

Keywords: dispersal, emigration, PIT, *Salmo trutta*, Survival

Introduction

Ecologists, conservation biologists and resource managers frequently use survival data to investigate animal population dynamics (Caughley, 1977; Begon, Mortimer & Thompson, 1996), but such data can be misleading if animal movement is not explicitly considered, especially for highly mobile organisms or life stages. Population-level survival rates are often estimated from changes in local abundance over time, mark–recapture analyses or both. However, immigration and emigration can introduce significant bias to these estimates (Lebreton *et al.*, 1992; Sandercock, 2006; Horton & Letcher, 2008). Numerous analytical frameworks have been developed to incorporate movement data into mark–recapture survival analyses (e.g. Barker, Burnham & White, 2004; Horton & Letcher, 2008; Gilroy *et al.*, 2012), but the use of these techniques is limited relative to the use of apparent survival approaches that do not account for movement bias (Sandercock, 2006). Thus, there is an ongoing need to improve understanding of animal population dynamics by integrating movement and survival data.

Life stage-specific survival estimates are often necessary for evaluating the effects of environmental conditions and biotic interactions on population dynamics (e.g. Gaillard, Festa-Bianchet & Yoccoz, 1998; Dybala *et al.*, 2013), assessing variation in natural mortality among systems (e.g. Elliott, 1993; Lobón-Cerviá, Budy & Mortensen, 2012) and constructing population models to evaluate management strategies (e.g. Hilderbrand, 2003). However, precise and accurate survival and movement data are rarely available for all life stages in a population, and information on critical stages is often missing (e.g. Radchuk, Turlure & Schtickzelle, 2013). This is often true of early life stages because factors such as

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Correspondence: Shane Vatland, UMR CARRTEL – INRA, Université de Savoie, 75 avenue de Corzent, BP 511 F-74203, Thonon-les-Bains, France. E-mail: svatland@gmail.com

small body size and cryptic behaviour can make juveniles logistically challenging to capture and handle safely. Nonetheless, early life stages can drive fluctuations in population abundance, especially for fecund species with limited parental care (e.g. Hilborn *et al.*, 2003). Consequently, there is a need for complementary data on movement and survival for these life stages.

Advances in mark–recapture technology have improved our ability to track individuals of a wide range of sizes and at different spatiotemporal scales (Robinson *et al.*, 2010; Mckenzie *et al.*, 2012). This enables researchers to match the scales of data collection and parameter estimation with the processes hypothesised to drive population patterns (i.e. Cooper *et al.*, 1998). For example, passive integrated transponder (PIT tag) technology, combined with traditional active capture techniques, has increased our understanding of the responses of stream fish populations to variation in environmental conditions across a number of scales (e.g. Berger & Gresswell, 2009). Overall, integrating advances in technology with ecological concepts should improve both the understanding and conservation of animal populations with migratory life stages (Robinson *et al.*, 2010).

The ecology of salmonids is generally well known, but there remains a need for further understanding of juvenile life stages (Elliott, 1994; Jonsson & Jonsson, 2011). These stages are difficult to track because of small body size, heterogeneous environments and ontogenetic shifts in habitat use (e.g. Schlosser, 1991). As a result, data on seasonal movement and survival are rare during the first summer and autumn of life, even for well-studied species such as brown trout *Salmo trutta* (Carlson, Olsen & Vøllestad, 2008). PIT tags small enough for the safe marking of juvenile fish, yet with detection ranges suitable for efficient *in situ* passive recaptures, offer new tools for understanding the movement and survival of these juvenile life stages (e.g. Bowerman & Budy, 2012).

The life cycle of brown trout in Lake Geneva and its tributary streams has been described in numerous studies (Champigneulle *et al.*, 1988, 1990, 1999). Twelve tributaries to Lake Geneva provide critical spawning and juvenile rearing habitat. Artificial and natural barriers limit the extent of this spawning/rearing habitat. Adult brown trout migrate from the lake into these tributaries in the late summer and autumn, and spawning typically occurs between November and February with a median spawning time of mid-December. Hatching and the subsequent emergence of fry occurs between March and May, depending on the time of spawning and water temperature. Juveniles remain in their natal streams from 1–3 years before emigrating to the lake. Overall, the general life history and movement patterns are well known for spawners and fish age-1 and older, although relatively little is known about the ecology of age-0 trout. Previous studies have observed declines in the density of age-0 trout between summer and autumn, but the cause of these declines is unknown (Champigneulle *et al.*, 1999). In this study, we hypothesised that mortality, dispersal within tributaries, early emigration to the lake or a combination of these factors was driving summer-to-autumn declines of age-0 trout. To evaluate these hypotheses, we: (i) monitored the seasonal abundance and density of age-0 brown trout; (ii) evaluated their dispersal within streams and emigration to the lake; (iii) estimated true survival for this summer-to-autumn time period using a combination of abundance and movement data; and (iv) monitored environmental factors potentially driving these patterns in distribution and abundance.

Methods

Study area and fish assemblage

We investigated the movement and survival of age-0 brown trout in the downstream reaches of two tributaries of Lake Geneva, the Redon and Foron de Sciez (Fig. 1), chosen because of the predominance of suitable

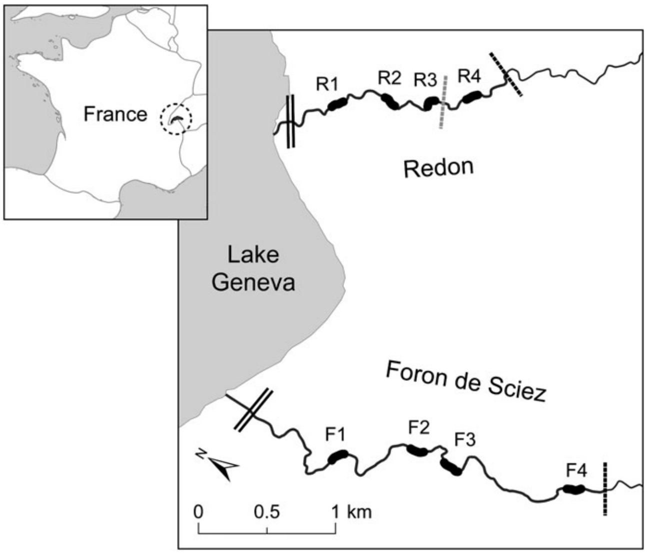

Fig. 1 Density, survival and movement of age-0 brown trout were assessed at four sites each (thick black lines with labels) in two tributaries to Lake Geneva (circled in upper left inset). Barriers to fish (broken black lines) were the upstream limits of the reaches studied, while there was also a partial barrier (grey broken line) in the Redon. PIT-tag antenna arrays (double black lines) monitored emigration of trout to the lake.

spawning and rearing habitat and the availability of past monitoring data on the seasonal density of age-0 fish (Champigneulle *et al.*, 1988, 1990, 1999). Each stream has a partial migration barrier for spawning adults and a complete migration barrier for juveniles at the upstream end of the study area (2.5 km and 4.0 km upstream of the mouth in the Redon and Foron de Sciez, respectively). Mature fish are rarely capable of bypassing these barriers. Note that the upper monitoring site on the Redon is located just above a road crossing and culvert that may also be a partial barrier to fish movement. Channel planform was predominantly pool-riffle sequences. Wetted channel width on the Redon and Foron de Sciez within the study area ranged from *c.* 3–6 and 5–12 m, respectively. Brown trout comprise most of the biomass and numbers of fish in the study area. *Cottus gobio* and *Barbatula barbatula* also occur but at low densities. *Perca fluviatilis* and *Leuciscus cephalus* occasionally occupy sites near the stream mouths.

Study design

We used a combination of depletion estimates and mark–'recapture' techniques to evaluate summer-to-autumn patterns in the abundance, movement and survival of age-0 brown trout. Electrofishing depletion estimates were used to quantify the abundance of age-0 trout at four sites in each stream in July and October 2011 and 2012 (Fig. 1). Age-0 trout were implanted with PIT tags during the July sampling. Stream-wide, stationary PIT-tag antennae were installed near the mouth of each stream and operated continuously to monitor any emigration of tagged fish into the lake. We also conducted portable PIT-tag antenna surveys throughout the study area in August and September of each year to evaluate the dispersal of trout within the study area. True survival of age-0 trout from July to October was estimated for each monitoring site and year using a combination of apparent survival (derived from the electrofishing depletion estimates) and movement data collected from the fixed and portable PIT-tag antennae. We began summer electrofishing surveys in early July because age-0 trout were large enough to be captured efficiently by electrofishing and marked with PIT tags [≥55 mm total length (TL)]. Autumn electrofishing occurred in mid-October before a typical, seasonal increase in precipitation and onset of winter. We also monitored a suite of environmental variables to investigate potential factors affecting movement and survival.

Monitoring age-0 trout abundance and density

Age-0 trout abundance was estimated at each monitoring site (R1–R4 in the Redon, F1–F4 in the Foron de Sciez; Fig. 1) in July and October using two- or three-pass electrofishing maximum-likelihood depletion estimates (Carle & Strub, 1978). If the capture probability for age-0 trout was ≤80% after two electrofishing passes, we carried out a third pass to ensure unbiased estimates. Abundance was dividing by stream surface area within respective monitoring sites to estimate density. Age determination for age-0 brown trout is frequently based solely on length frequency distribution. However, in this study, we validated the distinct modes in length frequency distribution between age-0 and age-1 fish by reading scales of a subset of fish of sizes in the range of potential overlap between the two age classes. Correspondingly, scales were collected from fish between 90 and 120 mm TL. Scales were analysed to detect the presence of one annulus ('winter rings') or none, and fish were assigned as age 0 or age 1, respectively. Based on this method, all trout <95 mm TL in July and <105 mm TL in October were considered age-0 fish (see Fig. S1).

Fish marking

Age-0 brown trout ≥55 mm TL captured in July were implanted with glass encapsulated half-duplex (HDX) PIT tags (12 mm × 2.12 mm; 0.10 g; 134.2 kHz; Texas Instruments, Dallas, Texas, U.S.A.). Individual trout <55 mm TL were not marked to avoid potential effects on growth, survival and tag retention (Acolas *et al.*, 2007; Richard *et al.*, 2013), but most trout (81%) were large enough to tag in July (Fig. S1). Prior to PIT tagging, we anaesthetised fish in a solution of clove oil and stream water (*c.* 50 ppm eugenol) and measured TL (nearest mm) and mass (nearest 0.1 g). PIT tags were surgically implanted into the abdominal cavity through a small scalpel incision (*c.* 2–3 mm) near the ventral midline, anterior to the pelvic girdle (Zydlewski *et al.*, 2003). Incisions were not sutured. All PIT-tagged fish were additionally marked with a fin clip unique to that year (adipose or pelvic). Fish were monitored after marking and allowed to recover in a live well in the stream before release. We examined all trout captured in October for the presence of PIT tags and fin clips, allowing for an estimate of tag retention between July and October. Due to the timing and limited availability of newly distributed 12-mm HDX PIT tags in the early summer of 2011: fewer fish were PIT-tagged in 2011 than in 2012; we PIT-tagged fish only in the Redon in 2011; and some fish were captured and tagged directly upstream of monitoring sites in 2011 (Table 1). Non-tagged fish in the Foron in 2011 also provided a comparison for assessing potential tag effects. In 2012, fish were tagged at each monitoring site in both streams. A total of 2814 age-0 trout were PIT-tagged during the study (Table 1).

Emigration

We monitored emigration of PIT-tagged trout from the study streams to Lake Geneva using stationary PIT-tag antenna arrays located near the mouth of each stream (Fig. 1). Two or three flat-panel (swim-over) antennae were used in an array in each stream to verify movement direction and increase overall detection efficiency (e.g. Zydlewski *et al.*, 2006; Connolly *et al.*, 2008). Read range (maximum distance from an antenna that a 12-mm HDX PIT tag was consistently detected when the tag was oriented parallel to the direction of stream flow directly over the antenna wire) was also measured at several locations on each antenna under a range of flow conditions. Based on read range and a simple stage-discharge relationship for each antenna, we estimated a threshold discharge for each stream in which surface water began to exceed the read range of antennae (see Fig. S2). This threshold provided a qualitative tool to evaluate when antennae were at risk of not monitoring the entire water column. We also quantified the detection efficiency of each antenna array using a combination of 'marker' tags (Oregon RFID, Portland, Oregon, U.S.A.) and indirect efficiency estimates, which were based on shared and unique detections among antennae in the same array (Zydlewski *et al.*, 2006). Marker tags were located adjacent to antennae and revealed themselves for detection once every 30 min. Efficiency estimates were also weighted by a moving average of fish detection frequency to account for the potential importance of time-varying emigration patterns (see Supporting Information for further details on efficiency estimates).

We estimated the probability of age-0 trout emigration (E) occurring between population monitoring in July and October for each site (i) and year (j) using the following equation:

$$E_{i,j} = \frac{D_{i,j}\,(2 - \text{efficiency}_{i,j})}{T_{i,j} * \text{retention}}$$

where D is the number of detected PIT tags at an antenna array; efficiency is the estimated detection efficiency of the antenna array; T is the number of fish PIT tagged in July; retention is the probability of fish retaining PIT tags from July to October. Data from fish recaptured in the October electrofishing were pooled among sites and years to provide a sufficient sample size for estimating tag retention. It was not possible to estimate directly the emigration of age-0 trout in the Foron de Sciez in 2011 because no fish were PIT-tagged there that year. Emigration estimates for R1 and R4 in 2011 were calculated from fish marked immediately upstream of the respective sites (Table 1). Confidence intervals for emigration rates were estimated using the Wilson-Score method for single proportions (Newcombe, 1998; Hintze, 2009).

Dispersal

We conducted spatially continuous portable PIT-tag antenna surveys throughout the study area in August and September of each year to evaluate the dispersal of trout within each stream. We determined the number of portable antennae according to the width of the stream. In each survey, a group of three (on the Redon) or four (on the Foron de Sciez) operators walked in an upstream direction searching the entire channel width for PIT-tagged fish. Each surveyor used a pole antenna with a detection range of *c.* 40 cm (for a 12-mm HDX PIT tag),

Table 1 Number of age-0 brown trout implanted with 12-mm PIT tags in the Redon and Foron de Sciez

		Number of PIT-tagged age-0 trout					
Stream	Year	Site 1	Site 2	Site 3	Site 4	Other	Total
Redon	2011	114*	53	50	87*	63†	367
	2012	323	264	299	282	–	1168
Foron de Sciez	2012	309	190	360	420	–	1279

Marking occurred between 4–22 July 2011 and 11–18 July 2012. A grand total of 2814 age-0 trout were marked. Sites 1–4 correspond to R1–R4 and F1–F4, as labelled in the study area map (Fig. 1).

*Fish were marked directly upstream of the respective sites.

†Data from these fish were used in the dispersal analysis but not in the site-specific emigration analysis.

and each pole antenna was equipped with a data logger that was time-synchronised with a single GPS (Garmin GPSmap 62s, WAAS-enabled, approximate accuracy <10 m). The GPS was carried by one of the crew members, and a track recorded location coordinates every second during surveys. Notes were taken to identify detections that occurred out of the water or in very shallow water with little possibility of fish presence; these detections were excluded from dispersal analyses.

Initial detections of PIT tags within each survey were joined with GPS coordinates using common time stamps. These detection coordinates and the original tagging sites were then linear-referenced to a routed stream line (ArcMap 10.0, ESRI, Redlands, California, U.S.A.), resulting in one-dimensional stream location values for tagging and relocation. The location value at the mouth of each stream was zero and accumulated upstream. Release locations of tagged fish were estimated to be at the mid-point of electrofishing sites, but fish were released throughout the electrofishing sites. Average length of monitoring sites was 113 m (SD = 12), so uncertainty of release locations was *c.* ± 56.5 m.

Dispersal was quantified as the difference between original tagging location and portable antenna relocation. We used a logistic regression to evaluate the relationship between fish emigration and dispersal, because we hypothesised that fish dispersing greater distances downstream had a higher probability of emigrating. Patterns in dispersal and emigration were similar among streams, years and survey months, so all surveys were combined in the logistic regression analysis. As an additional source of information on dispersal, we also evaluated the original tagging site of all PIT-tagged fish recaptured during the October electrofishing.

Survival analysis

We estimated apparent survival as the proportional change in local abundance at each site (*i*) and year (*j*) using the following equation:

$$\text{Apparent survival}_{i,j} = \frac{\text{October abundance}_{i,j}}{\text{July abundance}_{i,j}}$$

In this case, apparent survival is the proportion of animals that stay in the sampling site or that move into the sample site and remain alive. Apparent-survival confidence limits were estimated using the confidence limits of the abundance estimates. We also estimated true survival to account for the potential bias of fish emigrating from the study area. Site- and year-specific true survival estimates were calculated as the sum of emigration and apparent survival for corresponding site and year combinations. These true survival estimates assume emigrating fish are alive and survive over this July-to-October time period. Confidence intervals from apparent survival and emigration estimates were accumulated in the true survival confidence limits. We assumed dispersal within the study area (fish moving into monitoring sites or fish moving out of monitoring sites but remaining in the stream) would not bias apparent or true survival estimates.

Environmental monitoring

We monitored a suite of environmental variables that could potentially affect survival and movement patterns in the study area. Temperature loggers were secured in areas of continuously flowing water within each monitoring site and recorded stream temperature hourly from July through October. Hourly discharge data were collected from a gauging station located mid-study area in the Foron de Sciez and at the upstream end of the study area in the Redon. Water quality (temperature, dissolved oxygen concentration, specific conductivity and pH) was also measured every six hours using a Hydrolab MS5 sonde (Hach Environmental) in the Redon at site R1.

Results

Variation in July–October age-0 trout densities

In 2011 and 2012, age-0 trout densities declined between July and October at all sites, except at R4 where densities remained stable between seasons (Fig. 2). The mean decline in density between July and October at sites F1–F4 and R1–R3 was 64% (8% SD) and 51% (5% SD), respectively. At site R4, density estimates for July and October of the same year remained within 95% confidence intervals of each other. Density estimates (no. 100 m^{-2}) varied considerably among sites and averaged 101 (SD = 69) and 48 (SD = 38) in July and October, respectively. Density was generally greater in the Redon than the Foron de Sciez, with the exception of site R4 in 2011. Overall, density was slightly lower in 2012 than in 2011, but this pattern was not consistent for all sites.

Emigration from the study streams

The proportion of marked trout that were detected at stationary PIT-tag antennae between July and October electrofishing was relatively low for all monitored sites in 2011 and 2012 (mean = 0.08, SD = 0.05, n = 12), but

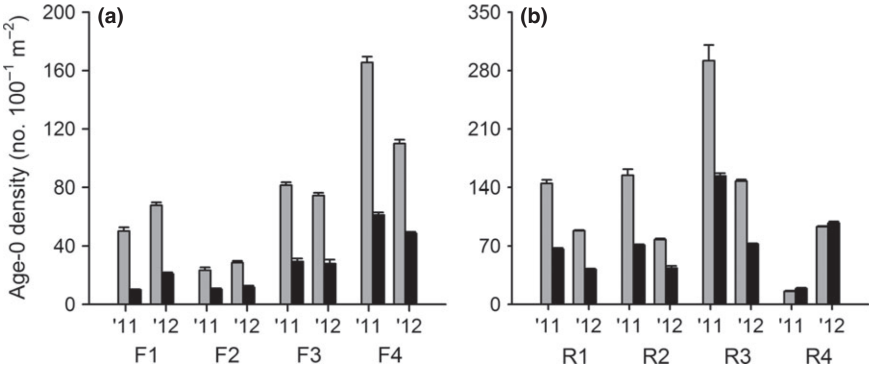

Fig. 2 Mean density (± 95% CL) for age-0 trout in 2011 and 2012 at monitoring sites in the (a) Foron de Sciez and (b) Redon. Grey and black bars represent July and October surveys, respectively. Some error bars are not visible because of their small size. Note difference in *y*-axes.

timing and magnitude of emigration varied among sites (Fig. 3). Fish marked at sites closer to the mouth tended to emigrate sooner than fish marked at sites further upstream. The proportion of fish marked at site R4 that were detected at the stationary antennae was lower than the proportion detected from each other site by the end of October in 2011 and 2012 (Fig. 3).

Estimates of emigration between July and October electrofishing surveys (mean = 0.10, SD = 0.07, *n* = 12) were similar to the proportion of tagged fish detected at the stationary antennae, for tag retention and fixed antenna efficiency were both high. Tag retention from July to October was 94%, while retention rate was positively correlated with fish length (see Supporting Information Fig. S3). Estimates of the efficiency of fixed antennae were also high (mean 91%; SD = 0.06; *n* = 3). Despite efforts to complete electrofishing surveys as quickly as possible, emigration patterns were changing during the October surveys. For example, emigration at site F4 in 2012 was only 2% at the time of October electrofishing, but 1 week later it was 11%. However, we accounted for this potentially confounding factor using site- and date-specific emigration estimates in the survival analysis.

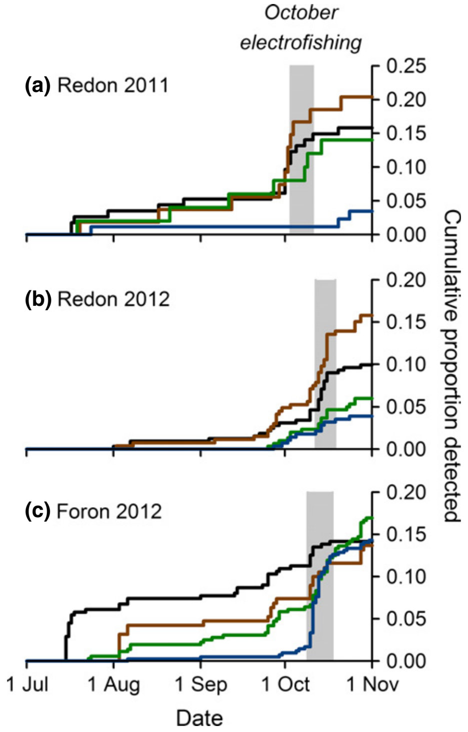

Fig. 3 Cumulative proportion of tagged age-0 brown trout detected at stationary PIT antennae over time (daily increments) in (a, b) the Redon in 2011 and 2012, respectively, and (c) the Foron in 2012. Proportions equal number of trout detected divided by number marked in respective sites within each stream (black, site 1; brown, site 2; green, site 3; blue, site 4).

Dispersal within the study streams

Dispersal of age-0 trout within each study stream was limited. Portable antenna surveys were relatively

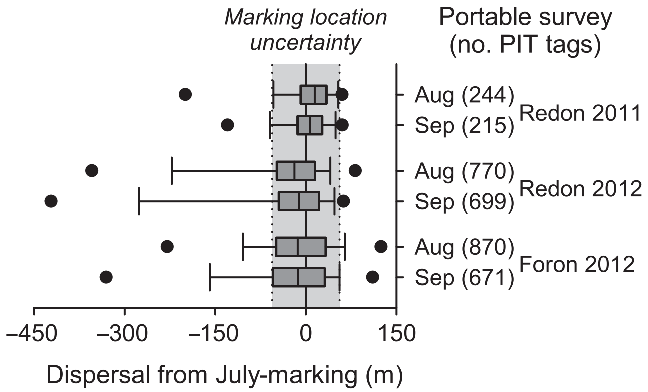

Fig. 4 Dispersal of age-0 trout from original tagging location as determined by relocation during spatially continuous portable PIT-tag antenna surveys in August and September of each year (number of detected fish in parentheses). Negative dispersal represents fish located downstream of tagging location, and positive values represent upstream dispersal. Uncertainty of tagging location was *c.* ± 56.5 m (grey area). Box and whisker plots display the 10th and 90th percentiles as line ends, 25th and 75th percentiles as boxes, 50th percentile as a vertical line in the box, and 5th and 95th percentiles as black dots.

efficient at locating PIT-tagged fish, and fewer than 2% of portable antenna detections were removed from the dispersal analysis because they were identified as lost or shed tags. Most (79%) of all tags implanted in fish were detected at least once in August or September in the same year as tagging; 83% and 81% of tags relocated in August and September, respectively, were found within 100 m of their release location. If fish dispersed within the stream, it was usually downstream (Fig. 4), and the probability of fish emigrating was positively correlated with dispersal (i.e. the further fish moved downstream the more likely they would emigrate; Fig. 5). Dispersal patterns were similar throughout the study area, and we observed no pattern of fish moving disproportionately either to or from particular areas of the streams. We also observed high site fidelity in active recaptures, because more than 95% of tagged trout that were recaptured in October electrofishing surveys were tagged and recaptured at the same site.

Survival analysis

The average true survival from July to October for all sites and years, excluding site R4, was 0.56 (SD = 0.08, *n* = 10, range = 0.45–0.68; Fig. 6). Survival at site R4 in 2011 and 2012 was much higher than at all other sites. Survival rates between July and October were similar between years at each monitoring site. Differences between apparent and true survival estimates varied depending on emigration estimates.

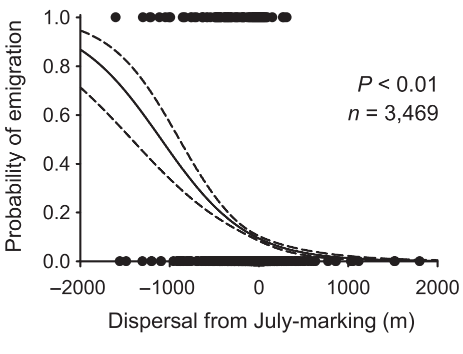

Fig. 5 Probability of emigration versus dispersal (m) from July-marking location. Emigration and dispersal were determined from fixed and portable PIT-tag antenna detections, respectively. PIT-tagged fish were considered as emigrating if detected at a stationary PIT-tag antenna prior to completion of October electrofishing in the same year as tagging. Patterns in dispersal and emigration were similar among streams, years and survey months, so all were combined in this figure and logistic regression (solid black line). Dashed black lines represent 95% prediction limits for logistic regression.

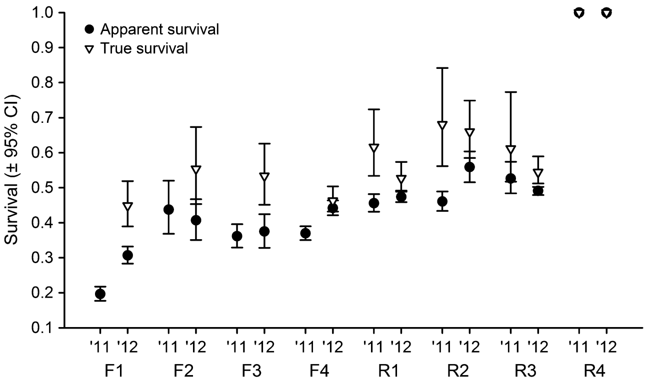

Fig. 6 Apparent and true survival estimates (± 95% CL) from July to October for age-0 brown trout at monitoring sites in 2011 and 2012**.** Apparent survival was estimated from change in abundance at monitoring sites. True survival was estimated from apparent survival and emigration of fish from the study area.

Environmental monitoring

Environmental conditions during the study were suitable for the growth and survival of juvenile brown trout (Crisp, 1996). Temperatures within each stream were slightly lower upstream than downstream, but the mean standard deviation of concurrent hourly temperature measurements during July, August and September was <0.2 °C in the Redon and <0.3 °C in the Foron de Sciez. Foron de Sciez sites were slightly warmer than Redon sites, and stream temperatures were higher in 2012 than in 2011 (see Fig. S4). Over all sites combined, observed stream temperature during July, August and September ranged from 9.7 to 21.3 °C. Mean discharge for the Foron de Sciez from July to October in 2011 and 2012 was 0.18 and 0.29 $m^3\ s^{-1}$, respectively. Discharge for the same time period in the Redon was 0.09 and 0.19 $m^3\ s^{-1}$, respectively. The increase in discharge between 2011 and 2012 was mostly due to a difference in precipitation in October (Fig. S2). Dissolved oxygen ranged between 7.9–10.8 mg L^{-1} (mean = 9.4 mg L^{-1}), pH between 7.6–9.2 (mean = 8.5) and specific conductivity between 390–750 μS cm^{-1} (mean = 680 μS cm^{-1}). Overall, measured environmental variables were considered suitable for juvenile trout throughout the study.

Discussion

We hypothesised that early emigration to Lake Geneva was one of three potential factors driving the change in abundance of age-0 brown trout between July and October. Early downstream emigration of age-0 trout has been documented in some systems, especially when carrying capacity is limited (Thorpe, 1974; Baglinière, Prevost & Maisse, 1994; Matthews *et al.*, 1997). Here we found that 10% of age-0 trout emigrated between July and mid-October, with most doing so in early October. Our data clarified the effect of emigration, even though it was minimal, on seasonal variation in local abundance and allowed us to improve the accuracy and reliability of summer-to-autumn survival estimates. The early downstream emigration of age-0 trout, in addition to the previously documented emigration by older year classes (Champigneulle *et al.*, 1999), also highlights some of the behavioural diversity in this migratory population in Lake Geneva. Further, we were unable to monitor movement of the smallest age-0 trout (<55 mm TL in July), and thus, it is possible that these very smallest fish exhibited different movement patterns than other age-0 trout (e.g. Landergren, 2004).

We found little support for the hypothesis that dispersal within these two tributaries affected summer-to-autumn variation in age-0 brown trout abundance. There was relatively limited movement of age-0 trout within the streams during this study; most (>80%) tagged fish were relocated within 100 m of their original location. Similarly, 74% of age-0 trout moved <10 m, and only 2% moved >250 m, between August and November in a land-locked population of lake-migratory brown trout in Sweden (Olsson & Greenberg, 2004). Sedentary behaviour in juvenile brown trout is common in several systems, and this behaviour can have significant implications for the ecology and evolution of populations, especially in the presence of migration barriers (Northcote, 1992, 2010). Nonetheless, territorial behaviour, such as dispersal due to resource competition, can also occur in juvenile brown trout (Héland, 1999), but we observed no disproportionate movement of trout either to or from certain areas of the stream during this summer-to-autumn period. Environmental factors can also affect the movement patterns of juvenile brown trout (e.g. Arawomo, 1981). In our study, interannual differences in stream discharge may have contributed to the slight differences in instream dispersal between 2011 and 2012 in the Redon. Overall, these movement data still support our assumption that the net gain or loss of individuals due to dispersal within monitoring reaches was negligible, and thus, it did not bias apparent and true survival estimates.

The combination of survival and movement data collected in this study supports the hypothesis that mortality was the main cause of summer-to-autumn variation in the density and abundance of age-0 trout. Survival of brown trout is expected to be low during a critical period of *c.* 2 months following the emergence of juveniles from the substratum, with greater survival in subsequent life stages (Mortensen, 1977; Elliott, 1989, 1993; Crisp, 1993). In this study, all age-0 trout captured in July would have passed this bottleneck following fry emergence. Thus, our results show that survival rates of age-0 trout can also be low for the summer-to-autumn period. It has often been assumed that summer provides suitable conditions and high survival for fry while winter is another survival bottleneck, but there is little empirical support for this assumption (see review in Carlson *et al.*, 2008).

Ecology of juvenile salmonids needs further understanding and seasonal data of movement and survival are still lacking (Elliott 1991, Jonsson & Jonsson, 2011). Survival of brown trout can vary throughout the year, and important patterns are often evident at seasonal intervals (Olsen & Vøllestad, 2001; Carlson & Letcher, 2003). Seasonal survival data are rare for age-0 brown trout, and the relative importance of different seasons may vary among streams, populations and cohorts. Seasonal survival data are also extremely useful for forming hypotheses on drivers of population dynamics, for seasonal data often match the scale of predictors and biological responses better than annual data (e.g. Cooper *et al.*, 1998; Berger & Gresswell, 2009). Detailed studies such as this are needed to provide the necessary data for an evidence-based evaluation of seasonal survival patterns in juvenile trout.

Our analysis of movement and survival relied on assumptions regarding the performance of the PIT-tag technology and fish behaviour. For example, stationary PIT-tag antennae were located near the mouth of each stream, but it is possible that fish detected at the arrays, and assumed to be emigrating to the lake, still remained in the short stream section between the antennae and the lake. Regardless, this type of behaviour would not have affected our survival analysis, but it could have created ambiguity in differentiating dispersal and emigration. During portable PIT-tag antenna surveys, it is possible that some tag detections were of individual PIT tags and not PIT-tagged fish, despite efforts to remove non-fish detections from the survey data. Other studies have dealt with this potential problem using field protocols similar to this study (e.g. Berger & Gresswell, 2009; Bowerman & Budy, 2012). However, the relatively high density of PIT-tagged fish in this study, the small size of fish relative to substratum particle sizes, and potentially cryptic behaviour, may have allowed non-fish detections. Nonetheless, these non-fish detections would not have affected our survival analysis, for the portable antenna data were only used to assess dispersal.

Handling and tagging stress can alter behaviour and artificially increase mortality in wild fish (e.g. Hansen, 1988). We did not address this potential bias explicitly in our study design, but several lines of evidence suggest it was not a factor here. First, a recent study (Richard *et al.*, 2013) found no negative effects on growth, survival or tag retention for age-0 brown trout (>55 mm) tagged with 12-mm HDX PIT tags (using the same protocol as this study). These results are consistent with others evaluating tag effects on juvenile brown trout (e.g. Ombredane, Bagliniere & Marchand, 1998; Acolas *et al.*, 2007). Second, no age-0 trout were PIT-tagged in the Foron de Sciez in 2011, yet summer-to-autumn declines in abundance were similar between the Redon and Foron de Sciez in 2011 and between 2011 and 2012 at all sites in the Foron de Sciez. Third, we observed high survival at one site (R4) even though most age-0 trout in the site were PIT-tagged, suggesting no negative effects from handling. For these reasons, we assume that the movement and survival patterns observed in this study were not biased by our handling procedures.

There are a number of factors which may have contributed to the seasonal mortality observed in this study, such as predation by birds and fish, limited food supply, environmental stressors and disease. Bird predation can reduce the density of stream-resident juvenile salmonids (e.g. Wood, 1987), but we did not observe large numbers of avian predators in the study area. Fish predation, though possible, was also unlikely to contribute to mortality because the fish population was comprised of almost entirely non-piscivorous juvenile trout during this time period. Density-dependent competition over limited resources can also reduce survival in age-0 trout (e.g. Cattanéo *et al.*, 2002), but there was no apparent relationship between density and survival in this study. Environmental conditions were generally suitable for age-0 brown trout growth and survival (Crisp, 1996), but temperature in the two streams frequently exceeded 15 °C during the summer. At stream temperatures >15 °C, there is an increased risk of mortality for juvenile salmonids from proliferative kidney disease (PKD; Hedrick, MacConnell & De Kinkelin, 1993; Bettge *et al.*, 2009). Indeed, age-0 trout sampled near the downstream end of the Redon and Foron de Sciez showed a high prevalence of infection by *Tetracapsuloides bryosalmonae*, the causative agent of PKD (unpublished data, H. Schmidt-Posthaus). The combination of pathological evidence and high stream temperature suggests that PKD could be a significant driver of the low summer-to-autumn survival rates in this study, but further investigations are needed to evaluate the potentially dynamic processes driving mortality from PKD.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1 Size distribution of brown trout captured in July and October of 2011 at monitoring sites in the Redon and Foron de Sciez (a–d) and scale-ageing results from a subsample of these trout in July (e) and October (f).

Fig. S2 Hourly discharge (black line) and PIT-tag read range threshold (grey line) by stream and year (a–d).

Fig. S3 Top panel: Proportion of age-0 trout marked in July and recaptured in October of the same year that retained (grey) or lost (black) PIT-tags. Bottom panel: Logistic regression results for the same data.

Fig. S4 Mean hourly stream temperature among monitoring sites in the Foron de Sciez and Redon from 1 July–30 September in 2011 and 2012 (a–d)

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