

Linking movement and reproductive history of brook trout to assess habitat connectivity in a heterogeneous stream network

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SUMMARY

1. Defining functional connectivity between habitats in spatially heterogeneous landscapes is a particular challenge for small-bodied aquatic species. Traditional approaches (e.g. mark–recapture studies) preclude an assessment of animal movement over the life cycle (birth to reproduction), and movement of individuals may not represent the degree of gene movement for fecund species.
2. We investigated the degree of habitat connectivity (defined as the exchange of individuals and genes between mainstem and tributary habitats) in a stream brook trout (*Salvelinus fontinalis*) population using mark–recapture [passive integrated transponder (PIT) tags], stationary PIT-tag antennae and genetic pedigree data collected over 4 years (3425 marked individuals). We hypothesised that: (i) a combination of these data would reveal higher estimates of animal movement over the life cycle (within a generation), relative to more temporally confined approaches, and (ii) movement estimates of individuals within a generation would differ from between-generation movement of genes because of spatial variation in reproductive success associated with high fecundity of this species.
3. Over half of PIT-tagged fish (juveniles and adults) were recaptured within 20 m during periodic sampling, indicating restricted movement. However, continuous monitoring with stationary PIT-tag antennae revealed distinct peaks in trout movements in June and October–November, and sibship data inferred post-emergence movements of young-of-year trout that were too small to be tagged physically. A combination of these methods showed that a moderate portion of individuals (28–33%) moved between mainstem and tributary habitats over their life cycle.
4. Patterns of reproductive success varied spatially and temporally. The importance of tributaries as spawning habitat was discovered by accounting for reproductive history. When individuals born in the mainstem reproduced successfully, over 50% of their surviving offspring were inferred to have been born in tributaries. This high rate of gene movement to tributaries was cryptic, and it would have been missed by estimates based only on movement of individuals.
5. This study highlighted the importance of characterising animal movement over the life cycle for inferring habitat connectivity accurately. Such movements of individuals can contribute to substantial gene movements in a fecund species characterised by high variation in reproductive success.

Keywords: dispersal, fitness, functional connectivity, gene flow, reproductive success

Introduction

Many animals are found in heterogeneous landscapes where demographic rates (growth, survival and repro-

duction) differ spatially (e.g. Saracco *et al.*, 2010; Rogers, 2011). Animals move to exploit these patchy resources and habitats over a short (e.g. home range) or long time period (e.g. migration) (Schlosser, 1995; Bowler &

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Benton, 2005; Petty & Grossman, 2010). Movement of individuals consequently affects metapopulation dynamics (Hanski, 1998) and gene flow (Bohonak, 1999), highlighting the crucial role that habitat connectivity plays in heterogeneous landscapes. Thus, defining functional habitat connectivity via movement patterns is of great interest to ecologists and conservation biologists.

However, it is challenging to characterise animal movements for small-bodied, cryptic organisms. Following individuals of these species in the field requires tagging and subsequent detection of some kind (e.g. recapture, resightings and telemetry). The minimum body size required for tagging restricts the ability to track individuals during the early stages of their development. A majority of our current understanding of animal movement comes from mark-and-detection field studies based on larger juveniles and adults for stream fish (Albanese, Angermeier & Gowan, 2003; Young, 2011), amphibians (Lowe, 2003; Grant *et al.*, 2010) and insects (Haynes, Diekötter & Crist, 2007; Öckinger & Smith, 2008). Similarly, movements after the last detection of individuals are poorly known, and a key life history event (e.g. reproduction) may be easily overlooked. Restrictions in sampling design lead to biased estimates of animal movements (Gowan *et al.*, 1994; Smith & Green, 2005; Morrissey & Ferguson, 2011; Zimmermann *et al.*, 2011). A study design encompassing movements of all life stages (i.e. birth to reproduction) over a sufficiently large spatial area (relative to the animals' movement capabilities) is required for a complete understanding of animal movements.

Even if animal movement rates are estimated well, they do not necessarily represent the degree of gene movements in the landscape. For example, animal movement is not always related to reproduction (Skorka *et al.*, 2009; Petty *et al.*, 2012), and individuals moving to a 'sink' habitat may experience higher mortality and lower reproductive success (Peery *et al.*, 2010; Rogers, 2011). Thus, assessing reproductive history of individuals is important for improved understanding of habitat connectivity and biological mechanisms that lead to observed spatial population structure. A combination of genetic pedigree analysis (Saenz-Agudelo *et al.*, 2009; Wright *et al.*, 2012) and individual tagging is a promising approach to this challenging issue. Pedigree analysis identifies genealogical relationships among individuals (parents–offspring and siblings). It is suitable for inferring local-scale animal movements because it does not depend upon the presence of spatial population structure (Latch *et al.*, 2006; Saenz-Agudelo *et al.*, 2009). In terms of its application to stream fish, genetic sibship

and parentage analyses have been used to study reproduction and dispersal of brook trout (*Salvelinus fontinalis*) (Hudy *et al.*, 2010; Morrissey & Ferguson, 2011) and brown trout (*Salmo trutta*) (Serbezov *et al.*, 2010; Vøllestad *et al.*, 2012). Pedigree information reveals an individual's reproductive success, as measured by the number of surviving offspring (Thériault, Bernatchez & Dodson, 2007). This is particularly useful for populations of fecund species (e.g. fish), in which individuals may have highly variable reproductive success (Blanchfield, Ridgway & Wilson, 2003; Liu & Ely, 2009).

Stream fish have provided important empirical insights into animal movements. In particular, brook trout have played a pivotal role in the development of stream fish movement theory (Gowan *et al.*, 1994; Rodríguez, 2002). They inhabit clear, cold waters in eastern North America, spawning during autumn, preferentially in areas of groundwater upwelling (Curry & Noakes, 1995; Essington, Sorensen & Paron, 1998). Females excavate small depressions on the stream bottom and deposit their eggs in these nests (called 'redds'). Fertilised eggs remain in the substratum for a few months until they emerge from redds in late winter to early spring. Small tributaries are important spawning areas for this species (Petty, Lamothe & Mazik, 2005; Kanno, Vokoun & Letcher, 2011a), but larger individuals prefer pools (deep, slow-moving water) that are typically limited in small tributaries (Petty *et al.*, 2005; Kanno *et al.*, 2012). Stream habitat is also temporally variable due to seasonality (e.g. stream flow) in the temperate region and favourable habitats (e.g. foraging areas) change by space, time and ontogeny for stream fishes (Gowan & Fausch, 2002; Petty & Grossman, 2010; Koizumi, Kanazawa & Tanaka, 2013). As a result, movements are potentially important for brook trout individuals to exploit heterogeneous habitats and maximise fitness. In turn, movement of individuals can be an important mechanism of population persistence in stream salmonids. Habitat fragmentation has been consistently related to local extinction of stream salmonid populations (Morita & Yamamoto, 2002; Letcher *et al.*, 2007).

This study investigated functional habitat connectivity in a headwater population of brook trout by linking movement of individuals and reproductive history (i.e. movement of genes). We used a combination of mark-recapture, stationary antennae and genetic pedigree data from a detailed field study in which nearly 3500 individuals were marked over 4 years. Headwater stream networks provide a favourable setting for an intensive movement study of aquatic organisms. Shallow and

confined waterways allow high probabilities of capture and recapture of individuals. One-dimensional, linear habitats allow the use of stationary antennae for temporally continuous detection of tagged individuals. We tested two hypotheses in this study. First, we hypothesised that a simultaneous use of mark–recapture, stationary antennae and genetic pedigree data would reveal higher estimates of animal movement over the life cycle (i.e. within a generation), relative to more temporally confined approaches (e.g. mark–recapture data alone). Temporal restrictions in a fish's life cycle might result in movement estimates that are low, in a manner similar to the way spatial restrictions in survey areas typically fail to detect long-range movements of stream fish (Gowan *et al.*, 1994). Our second hypothesis was that estimates of movement based on within-generation movement of individuals *versus* between-generation movement of genes would differ for this fecund species, in which reproductive success is habitat dependent. In fecund species, a few individuals that move and reproduce could substantially contribute to spatial population structure. Tributaries are considered important spawning areas for brook trout based on spawning activities (Curry & Noakes, 1995; Essington *et al.*, 1998) and distribution of young-of-year fish (Petty *et al.*, 2005; Kanno *et al.*, 2011a); thus, individuals might achieve greater reproductive success in tributaries. If so, an estimate of between-generation movement of genes from the mainstem to the tributaries could be higher than those of within-generation movement of individuals. Because direct observations of reproduction are extremely difficult for small-bodied aquatic species, individual reproductive histories and between-generation gene movement were inferred based on genetic pedigree analysis.

Methods

Study area

The study was conducted in a stream network in the Connecticut River basin located in western Massachusetts, U.S.A. (Fig. 1). The study area consisted of a 1-km-long third-order mainstem (West Brook, hereafter termed 'WB') and two 0.3-km-long second-order tributaries [OpenLarge (OL) and OpenSmall (OS)]. These three discrete habitats are referred to as streams hereafter. Impassable waterfalls are located at the upstream boundaries of the two tributaries. Fish in the WB have access to the OL and OS, but a perched culvert (0.75 m high) at the confluence of the OS with the WB may hinder the upstream movement of fish, particularly small individu-

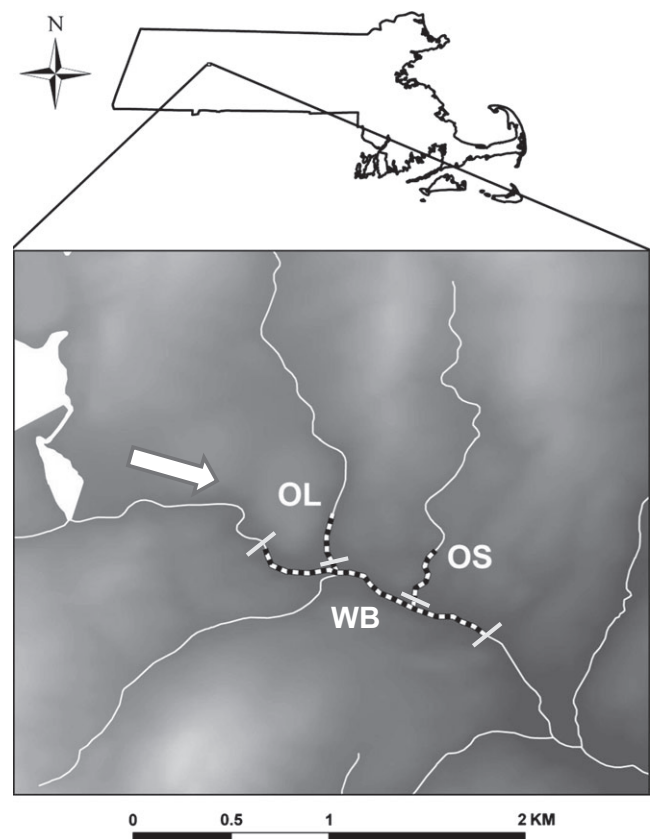


Fig. 1 Map of study stream network in West Brook, Massachusetts, U.S.A. Dashed lines (black and white) represent the study area, and solid, gray lines indicate the locations of stationary antennae. The flow direction is from the west to the east (shown by a white arrow). WB, West Brook mainstem; OL, OpenLarge tributary; and OS, OpenSmall tributary.

als at low-flow conditions. The mean wetted width is 4.5 m in the WB, 3 m in the OL and 2 m in the OS. Rifles with cobble substratum are the dominant habitat type with scattered pools and glides. Brook trout and brown trout reproduce naturally in the study area. Brook trout are common in the WB, OL and OS, but brown trout are mostly restricted to the WB. Brook trout in headwater streams are typically short-lived; most brook trout in the study stream live up to 2–3 years (Xu, Letcher & Nislow, 2010a) and few fish grow > 20 cm in fork length (Fig. 2). Fry stocking of Atlantic salmon (*Salmo salar*) occurred during part of the study period (2002–2004). Blacknose dace (*Rhinichthys atratulus*) is the only other resident fish commonly found in the study area.

Field sampling

In 2002–2005, fish were sampled in a spatially continuous manner on four occasions per year (spring = late March, summer = June, autumn = late September and

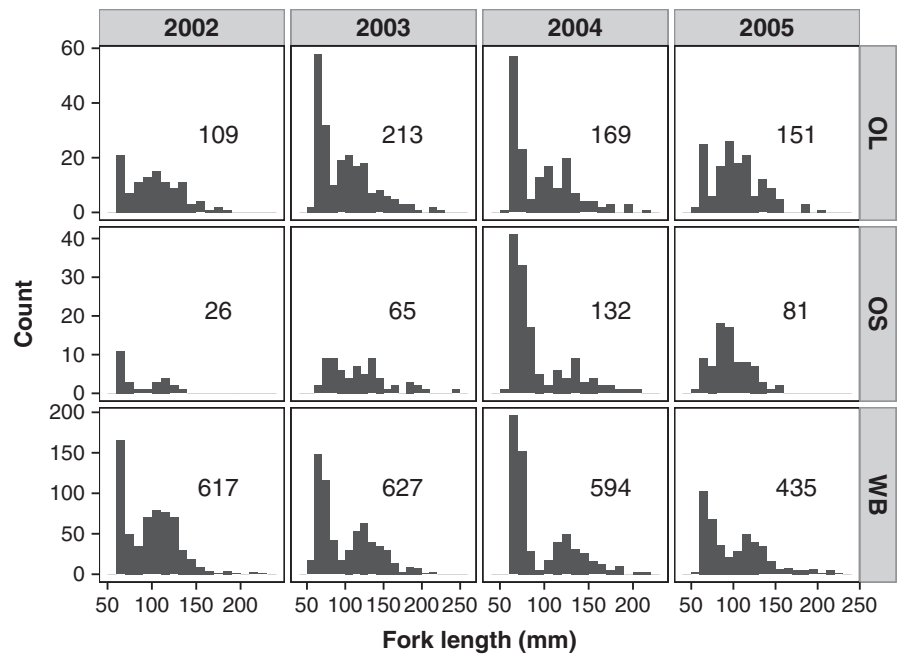


Fig. 2 Autumnal length frequency histograms of brook trout in each stream between 2002 and 2005. The number on each panel indicates total fish count. Note that the y -axis range differs among streams.

winter = early December). The winter sample was partially completed in 2002 after ice build-up precluded fish sampling. In the WB, two-pass backpack electrofishing surveys (300–400 V unpulsed DC current) were conducted on each sampling occasion in 20-m-long fixed sections with block nets. Single-pass electrofishing was carried out without block nets in the OL and OS because of smaller stream size. Detection probability of individuals varied by season, stream and fish size, but it was high (mean = 0.65 in single-pass electrofishing; B.H. Letcher, unpubl. data). Captured fish were measured for fork length (± 1 mm) and weight (± 0.1 g), and their section of capture was recorded. Anal fin clips were taken from captured fish for genetic analysis. Fish exceeding 60 mm in fork length were implanted with 12-mm passive integrated transponder (PIT) tags following anaesthesia. Fish typically attained this body size by their first autumn (age 0). Handled fish were returned to original sections of capture.

A total of four stationary PIT-tag antennae were placed in the study area to detect movements of tagged fish (Fig. 1). An antenna was set up at each tributary confluence (OL and OS) to detect movement between the WB and the two tributaries. An antenna was also placed at the upstream and downstream boundaries of the WB. Individuals that were detected at the two WB antennae and that were not recaptured subsequently were considered permanent emigrants from the study area. Stationary antennae became operational in July 2003; thus, movement of individuals (within-generation movement) was inferred based on data collected during 2003–2005,

while movement of genes (between-generation movement) was inferred using the 2002–2005 data. Antennae were placed over a stream channel (i.e. bank to bank) to maximise detection of tagged fish, and previous studies showed that antenna detection probability of passing individuals was high (80–100%) in our study system (Zydlewski *et al.*, 2006; Horton, Dubreuil & Letcher, 2007).

Genotyping and pedigree analysis

All populations were genotyped at 12 microsatellite loci [*SfoB52*, *SfoC24*, *SfoC38*, *Sfo86*, *SfoC88*, *SfoC113*, *SfoC115*, *SfoC129*, *SfoD75*, *SfoD91a*, *SfoD100* (King *et al.*, 2012) and *SsaD237* (King, Eackles & Letcher, 2005)] following protocols for DNA extraction and amplification detailed in King *et al.* (2005). Loci were electrophoresed on either an ABI Prism 3100-Avant or an ABI Prism 3130xl genetic analyser (Applied Biosystems Inc., Foster City, CA, U.S.A.), and alleles were hand-scored using GENEMAPPER version 3.2 and PEAK SCANNER version 1.0 software (Applied Biosystems Inc.). Reconstruction of full-sibling families and parentage assignment are described in Letcher, Coombs & Nislow (2011).

Movement of individuals and genes

We were primarily interested in assessing habitat connectivity and movement among streams (WB, OL and OS). Mark–recapture data were also used to summarise movement distance at the spatial resolution of 20-m

stream sections. Movement distance was calculated between successive recapture occasions, as well as distance moved between first and last capture occasions. Direction of movement (up- or downstream) was not assessed because directionality could not be assigned for some movement patterns in the stream channel network (e.g. movement between tributaries).

Movement among streams (WB, OL and OS) was assessed using movement rates of individuals (three methods: within-generation movement of individuals) and accounting for reproductive history (two methods: between-generation movement of genes). An array of methods was employed because an assessment of habitat connectivity may depend upon what life stages of individuals were tracked and because it may differ between direct field observations and indirect genetic methods (Wilson, Hutchings & Ferguson, 2004; Morrissey & Ferguson, 2011). Three methods based on the movement rates of individuals differed in temporal resolution (continuous versus periodic) and extent (across life stages) (Fig. 3); they were hereafter termed 'mark-recapture (MR) method', 'mark-recapture and antenna (MR-ANT) method' and 'mark-recapture, antenna and genetic sibship (MR-ANT-SIB) method'. Two methods based on reproductive history (between-generation movement of genes) compared the emergence stream of a parent to that of its offspring (Fig. 3); one method weighted gene movements by accounting for variation in reproductive success ['weighted parentage-sibship (PAR-SIB-weighted) method'] and the other did not ['unweighted parentage-sibship (PAR-SIB-un-

weighted) method']. Each method is described in detail below.

The MR method is the most traditional approach in animal movement studies and it assessed movements of individuals based on consecutive recaptures. This method had the most limited temporal resolution and coverage because it was periodic (seasonal) and because individuals could only be followed after tagging and with recapture events. An individual was considered to have moved between streams if the fish was recaptured at least once in a different stream other than its original capture. For example, an individual originally captured in the WB and then recaptured at least once in the OL was considered to have moved from the WB to the OL. An individual whose capture-recapture events took place all in the WB was considered to have stayed within the WB (regardless of the 20-m section within which the fish was located). This principle also applies to the MR-ANT and MR-ANT-SIB methods.

The MR-ANT method included stationary antenna data, in addition to mark-recapture data. This method tracked movements of tagged individuals continuously over time and it could also include movement data after last recaptures of individuals (Fig. 3). Stationary antennae were particularly useful for identifying the time of the year when tagged individuals moved most commonly. The MR-ANT method included all tagged individuals, including those that were never recaptured, because all tagged individuals were susceptible to antenna detections. We were primarily interested in movements among streams, but the two antennae at the

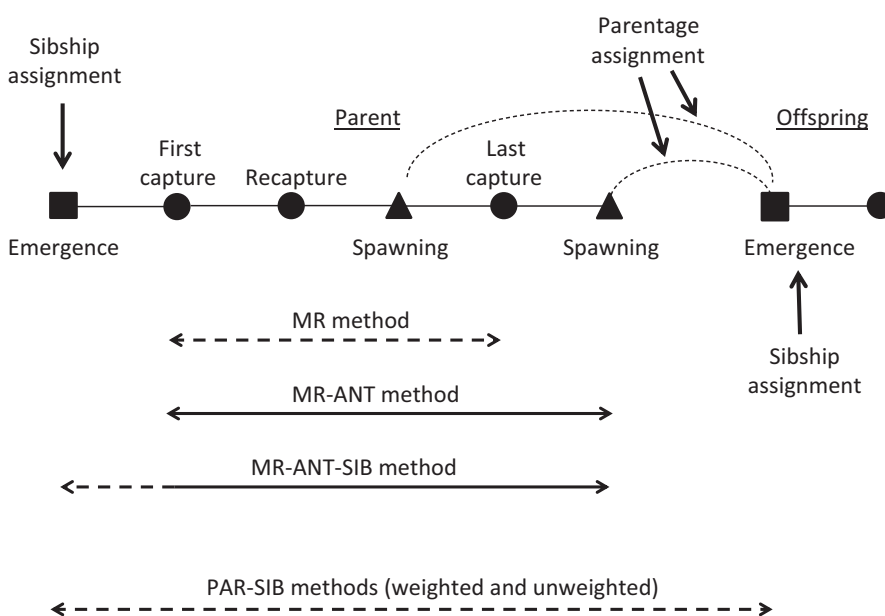


Fig. 3 Schematic description of methods used to estimate within-generation movement of individuals (MR, MR-ANT, MR-ANT-SIB methods) and between-generation movement of genes (PAR-SIB-unweighted and weighted methods). MR method, mark-recapture method; MR-ANT method, mark-recapture and antenna method; MR-ANT-SIB method, mark-recapture, antenna and sibship method; PAR-SIB-unweighted method, parentage-sibship unweighted method; PAR-SIB-weighted method, parentage-sibship weighted method. Filled arrows indicate that movements could be detected continuously over time by stationary antennae. Note that brook trout are iteroparous and may spawn before and after last capture of individuals.

up- and downstream ends of WB also served to identify permanent emigrants from the study area. A low rate of permanent emigration can indicate the adequacy of the spatial extent of study areas for characterising animal movements (Gowan *et al.*, 1994).

The MR-ANT-SIB method further extended the temporal coverage of trout movement by including information on where young fish emerged from redds. This method included the degree of post-emergence movement (before tagging) in our measurement of movement (Fig. 3). The stream in which more than half of fullsib family members were captured initially was considered the emergence stream. We assumed that all members of a fullsib family emerged from a single redd. Emergence locations were determined for fullsib families with at least three individuals because our previous study showed that this was the smallest fullsib family size for which family members and their parents were assigned reliably (>90% accuracy rates) using the same set of microsatellite loci (Letcher *et al.*, 2011). Also, spatial patterns of reproduction were assessed yearly by the density (count/100 m) of fullsib families (≥ 3 individuals) in each stream.

The PAR-SIB-weighted and unweighted methods compared the emergence stream of a parent to that of its offspring (Fig. 3). The two methods were applied only to pairs of parents and offspring, both of which had a fullsib family size of at least three individuals. The two methods differed in whether or not they accounted for variation in reproductive success, as measured by the number of surviving offspring (i.e. fullsib family size of offspring). For example, if a parent born in the WB reproduced successfully in the OL and its fullsib family size was five, the PAR-SIB-weighted method quantified that the gene movement established five new individuals in the OL, but the PAR-SIB-unweighted method considered that a single individual moved and transmitted its genes. In other words, gene movements were weighted by the reproductive success of the parents in the former method. In both cases, our estimates of gene movements differed from traditional estimates of gene flow (m) in population genetics (i.e. number of immigrants in the receiving subpopulation) because our level of resolution is the family in contrast to the population.

Results

A total of 3425 unique individuals were captured and marked during 2003–2005. Forty-six percentage of marked individuals (1584 individuals) were recaptured at least once, and individuals were recaptured up to

nine times. Five hundred and eighty-eight individuals were recorded on either the OL antenna, the OS antenna or both. About 6% (190 individuals) of marked individuals were considered permanent emigrants from the study area (i.e. individuals had an antenna hit either at the upstream or downstream boundary of the WB and were never captured again), indicating sufficient spatial coverage of this study relative to individual movement patterns.

The study population was characterised by high variation in reproductive success. A total of 1274 fullsib families were identified, and approximately two-thirds (826 families) were composed of one or two individuals (Fig. 4). However, occasional very large-sized fullsib families were identified with the largest five families consisting of 64 individuals (spawning inferred in the WB), 41 individuals (OS), 32 individuals (OS), 31 individuals (WB) and 31 individuals (WB). F_{ST} values, a measure of population differentiation between streams, were low (<0.05) when all individuals were used for analysis (Table 1). The highest F_{ST} value was 0.13 for young-of-year trout between the OL and OS in 2003, which probably reflected family-level effects (i.e. spatial aggregation of fullsib individuals at an early age).

Movement of individuals and genes

Mark-recapture data suggested that many individuals stayed close to their previous capture sections, while fewer moved longer distances (Fig. 5). Approximately 70% (1984 observations) of a total of 2856 observations based on consecutive recapture occasions were in the same, or immediately adjacent, sections (movement

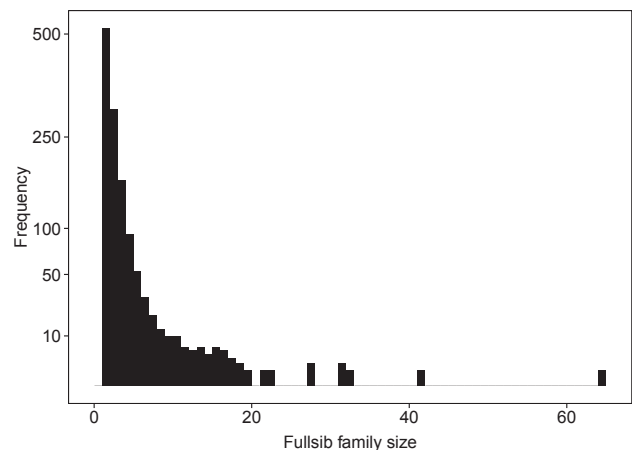


Fig. 4 Frequency distributions of inferred fullsib family sizes in the study area (all streams combined). Values on the y-axis are square-root transformed.

Table 1 F_{ST} values between streams (WB, OL and OS) between 2002 and 2005. F_{ST} values were calculated based on autumn samples for over-yearlings (age 1 and older), young-of-year (YOY) individuals (age 0), and all individuals combined. Sample size for each stream is shown above matrices

Study period(year)	Over-yearlings			YOY			All individuals					
	WB	OL	OS	WB	OL	OS	WB	OL	OS			
2002		304	57	8		136	16	0		440	73	8
		WB	OL	OS		WB	OL	OS		WB	OL	OS
	WB	0	0.02	0.00	WB	0	0.07	–	WB	0	0.03	0.00
	OL	0.02	0	0.06	OL	0.07	0	–	OL	0.03	0	0.04
	OS	0.00	0.06	0	OS	–	–	0	OS	0.00	0.04	0
2003		222	95	34		231	99	23		453	194	57
		WB	OL	OS		WB	OL	OS		WB	OL	OS
	WB	0	0.03	0.01	WB	0	0.01	0.11	WB	0	0.02	0.03
	OL	0.03	0	0.03	OL	0.01	0	0.13	OL	0.02	0	0.04
	OS	0.01	0.03	0	OS	0.11	0.13	0	OS	0.03	0.04	0
2004		139	71	32		60	48	66		199	119	98
		WB	OL	OS		WB	OL	OS		WB	OL	OS
	WB	0	0.02	0.03	WB	0	0.03	0.02	WB	0	0.03	0.02
	OL	0.02	0	0.06	OL	0.03	0	0.05	OL	0.03	0	0.04
	OS	0.03	0.06	0	OS	0.02	0.05	0	OS	0.02	0.04	0
2005		136	100	53		106	15	11		242	115	64
		WB	OL	OS		WB	OL	OS		WB	OL	OS
	WB	0	0.02	0.02	WB	0	0.04	0.01	WB	0	0.02	0.02
	OL	0.02	0	0.05	OL	0.04	0	0.07	OL	0.02	0	0.04
	OS	0.02	0.05	0	OS	0.01	0.07	0	OS	0.02	0.04	0

distance: ± 20 m) (Fig. 5a). Patterns of trout movement were nearly identical when movement distances were compared between the first and last capture occasions (Fig. 5b). Of a total of 1584 recaptured individuals, 983 individuals (62%) were found in the same, or immediately adjacent, sections between the first and last capture occasions. The maximum movement distance observed was 820 m in both approaches; the maximum possible movement distance detectable within the study area was 920 m.

Movement rates of individuals inferred among streams differed with the method used to quantify them (Table 2). As hypothesised (Hypothesis 1), higher rates of movements were consistently detected when individuals were tracked for longer time periods (MR-ANT-SIB method > MR-ANT method > MR method). Regardless of the method, emigration rates from the OS were higher than those from the WB and OL. Based on the MR method, trout typically remained within the stream of original capture, with 6–7% of individuals initially captured in WB and OL emigrating. Trout initially captured in the OS tributary moved more frequently (19%). The addition of stationary antenna data (the MR-ANT method) revealed higher movement rates from the WB (16%), OL (20%) and OS (28%), relative to the MR

method. Antenna hits at the OL and OS had distinct peaks in June and October–November (Fig. 6). The latter period coincided with the spawning period of brook trout. The MR-ANT-SIB method revealed even higher movement rates among streams; as many as 33% of individuals born in the OS were considered to have emigrated (28% from the WB, and 29% from the OL; Table 2). Movements between tributaries were rare or absent using any of the three methods to infer within-generation movement of individuals.

Our second hypothesis (within-generation movement \neq between-generation movement) was supported by movement patterns from the mainstem, but not by those from the tributaries (OL and OS). This result indicated the importance of tributary habitat for reproduction. We identified 50 parents that were born in the WB and successfully reproduced with at least three surviving offspring. Thirty-eight percentage (19 individuals) of these parents reproduced in the tributaries (PAR-SIB-unweighted method) (Table 2). When variation of reproductive success was accounted for (PAR-SIB-weighted method), 53% of offspring (188 of 354 offspring) derived from the 50 parents were inferred to have been born in tributaries (Table 2), indicating that parents who were born in the WB and reproduced in the tributaries had

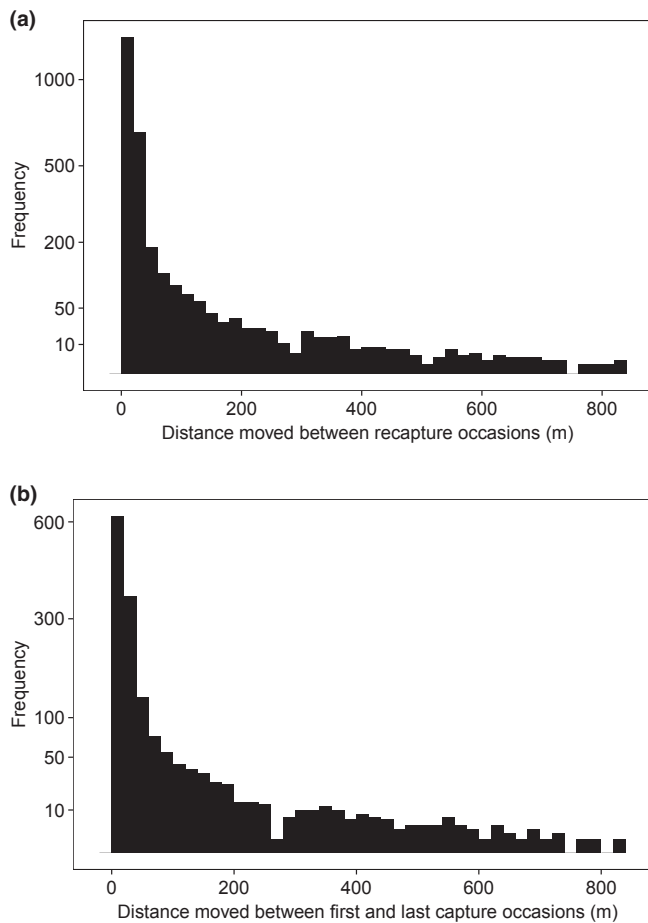


Fig. 5 Frequency distributions of movement distance between consecutive recapture occasions (a) and between first and last capture occasions (b). Values on the y-axis are square-root transformed.

higher reproductive success than those who were born in the WB and reproduced in the WB. This estimate of gene movement from the WB was cryptic, and it was much higher than any of the three methods that estimated movement rates of individuals (7–28%: Table 2).

Furthermore, gene movement from the WB to the OS varied yearly. Sixty-five per cent (80 of 123 offspring) of observed gene movement in the PAR-SIB-weighted method occurred in one year (2004 cohort) with a three-fold higher mean stream flow during the autumnal spawning period in 2003 ($0.31 \text{ m}^3 \text{ s}^{-1}$) compared to other spawning years ($0.10 \text{ m}^3 \text{ s}^{-1}$ in 2002 and $0.09 \text{ m}^3 \text{ s}^{-1}$ in 2004) [see Xu *et al.* (2010a) for the flow estimation method]. Just four parents were responsible for gene movement from the WB to the OS in this particular year, and two of them had large fullsib family sizes of offspring (41 and 27 individuals). Autumnal trout counts in the OS ranged from 26 to 132 individuals (Fig. 2), thus

Table 2 Movement rates of individuals and genes among streams. MR method, mark–recapture method; MR-ANT method, mark–recapture and antenna method; MR-ANT-SIB method, mark–recapture, antenna and sibship method; PAR-SIB-unweighted method, unweighted parentage-sibship method; PAR-SIB-weighted method, weighted parentage-sibship method. Zero values with an underline are true zero values, and others are small values above 0 (<0.005)

	Sample size (N)	From WB			
		To WB	To OL	To OS	To both tribs
Movement of individuals					
MR method	980	0.93	0.05	0.02	0
MR-ANT method	2334	0.84	0.11	0.03	0.02
MR-ANT-SIB method	818	0.72	0.21	0.05	0.02
Movement of genes					
PAR-SIB-unweighted method	50	0.62	0.20	0.18	NA
PAR-SIB-weighted method	354	0.47	0.18	0.35	NA
	Sample size (N)	From OL			
		To WB	To OL	To OS	
Movement of individuals					
MR method	353	0.06	0.94	<u>0</u>	
MR-ANT method	679	0.19	0.80	<u>0</u>	
MR-ANT-SIB method	347	0.28	0.71	0	
Movement of genes					
PAR-SIB-unweighted method	8	0.13	0.88	<u>0</u>	
PAR-SIB-weighted method	47	0.06	0.94	<u>0</u>	
	Sample size (N)	From OS			
		To WB	To OL	To OS	
Movement of individuals					
MR method	251	0.16	0.03	0.81	
MR-ANT method	412	0.21	0.07	0.72	
MR-ANT-SIB method	295	0.25	0.07	0.67	
Movement of genes					
PAR-SIB-unweighted method	11	0.27	<u>0</u>	0.73	
PAR-SIB-weighted method	75	0.12	<u>0</u>	0.88	

the observed gene movement signified a major contribution in the receiving OS population.

In contrast, little gene movement was recorded from the tributaries (OL and OS) to the mainstem (WB). A total of 19 parents born in the tributaries reproduced with at least three surviving offspring (eight in the OL and 11 in the OS), and a majority of reproduction (15 parents) took place in the tributaries (Table 2). In the PAR-SIB-weighted method, eight parents born in OL were paired with a total of 47 surviving offspring and 94% of surviving offspring were inferred to have origi-

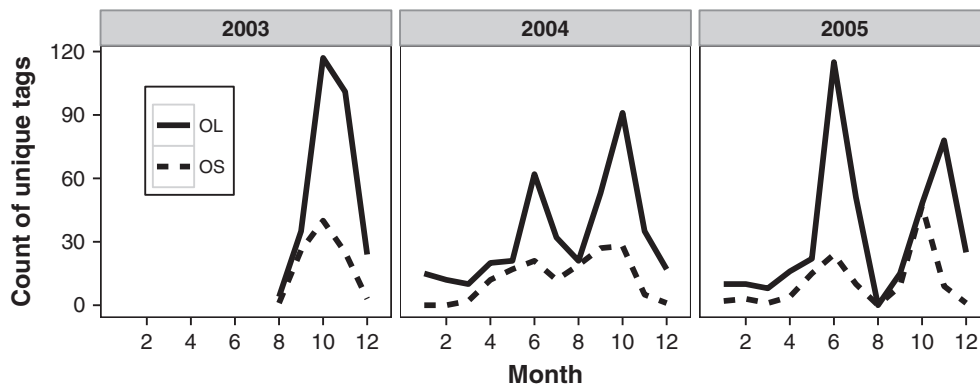


Fig. 6 Monthly tributary antenna hits of unique individuals. Stationary antennae were installed in July 2003.

Table 3 Density (count per 100 m) of large fullsib families (≥ 3 individuals) inferred to have originated in each stream

Cohort year	Stream		
	WB	OL	OS
2002	3.1	4.3	1.7
2003	6.7	7.0	0.7
2004	3.5	8.3	5.0
2005	2.6	1.7	3.3

nated in OL. Similarly, for 11 parents that were born in OS and successfully reproduced, 88% of their 75 offspring were inferred to have been born in OS.

Finally, the density of large fullsib families differed spatially and yearly (Table 3). Reproduction in OS was not common in some years (2002–2003 cohorts). Similar to the pattern observed in gene movements from WB to OS, spawning in OS was most common in a high-flow year (2004 cohort), and this was the only year in which the density of large fullsib families was higher in both tributaries (OL and OS) than in WB.

Discussion

We documented how individuals and genes moved in a heterogeneous riverscape, in which reproductive patterns differed spatially and temporally. A combination of mark–recapture, stationary antennae and sibship assignment demonstrated that around a third of individuals (28–33%) moved between mainstem and tributary habitats within a generation. Such movements of individuals contributed to substantial gene movements from the mainstem to tributaries between generations, due to high fecundity and high variation in reproductive success.

Our first hypothesis was well supported in the West Brook system. In this study, the conclusion of trout

movements depended critically on how long individuals were tracked over time (or what life stages were tracked). In the mainstem and tributaries alike, higher movement rates were detected when individuals were tracked over longer time periods (MR-ANT-SIB method > MR-ANT method > MR method). Based on mark–recapture data alone, more than half of brook trout individuals remained in the original capture sections or immediately adjacent sections (<20 m). The mark–recapture data echo the ‘restricted movement paradigm’ of adult stream fishes (Gerking, 1959; Gowan *et al.*, 1994; Skalski & Gilliam, 2000; Rodríguez, 2002), which states that movement of resident (non-anadromous) fish is generally restricted within a meso-habitat type (e.g. a pool) or stream reach (<10s metres). However, continuous monitoring by antennae and inferences of early dispersal by sibship documented additional movements in our study. These findings are analogous to the challenge posed by Gowan *et al.* (1994) against the restricted movement paradigm prevailing at that time. They argued that long-range movement is more detectable when fish sampling covers longer stream reaches. Similarly, our method extended the temporal extent of investigation by following individuals over longer time periods than traditional approaches allow. An appropriate study design, both spatially and temporally, is a key consideration in movement studies. Even for a well-studied species like brook trout, our understanding of movement ecology of aquatic species has been primarily limited to larger juveniles and adults for which tagging is feasible (Gowan *et al.*, 1994; Pépino, Rodríguez & Magnan, 2012).

Our intensive field sampling targeted the study stream network of 1.6 km over several years (this sampling is still ongoing) and included four electrofishing sampling occasions per year and individual tagging of all captured fish >60 mm in fork length. However, the

mark–recapture method alone was not able to reveal the full extent of individual movements, and antenna and sibship data extended our understanding of trout movements. Continuous monitoring via stationary antennae recorded the distinct peaks in movements in June and October–November. Brook trout movement during the autumn spawning season has been documented in other populations (D'Amelio *et al.*, 2008; Kanno *et al.*, 2011a). The frequent movement in June might be caused by an increase in stream temperature and a decrease in stream flow, which are typical in the study region. In addition, sibship data identified post-emergence movements of young-of-year brook trout. Young-of-year salmonids may engage in downstream movements (Morrissey & Ferguson, 2011; Young, 2011) or remain close to redds (Steingrímsson & Grant, 2003; Einum & Nislow, 2005; Vøllestad *et al.*, 2012). Young-of-year brook trout are sedentary, particularly in small headwater systems, and this is why spatial clusters of young-of-year brook individuals can be used to assign natal streams in this study. Similarly, Hudy *et al.* (2010) found that spatial distributions of young-of-year fullsibs in a Virginia stream were spatially clustered, enabling them to estimate their redd locations. Spatial clusters of some fullsib families were still observable for older individuals of brook trout (mostly age 1+) in Connecticut headwater streams (Kanno, Vokoun & Letcher, 2011b).

Our second hypothesis was supported by data on movement patterns from the mainstem (WB). This study demonstrated that an estimated movement of genes between generations may differ markedly from movement of individuals within a generation for a fecund species. Gene movements were substantial from the mainstem to tributaries (53%) despite moderate movements of individuals (7–28%). This result was due to the high skew in reproductive success; many fullsib families were represented by one or two surviving individuals with occasional very large families (up to 64 individuals) (see also Hudy *et al.*, 2010; Whiteley *et al.*, 2012). For fecund species, a few individuals that move and reproduce successfully can generate considerable gene movement. As an example, four parents born in the WB contributed to 80 offspring born in OS in one particular year. It should be noted that these offspring were those that survived to the minimum capture size by electrofishing and there might have been more individuals earlier. Habitat-dependent reproductive success should be a rule rather than an exception in a spatially heterogeneous landscape. Our study provided an empirical case of a fecund species for which movements of individuals were challenging to observe but reproductive heteroge-

neity among habitats was revealed by genetic pedigree analysis.

Tributaries were important spawning habitats. High gene movement occurred from the mainstem to tributaries when variation in reproductive success was accounted for (53% in the PAR-SIB-weighted method). In addition, when individuals born in tributaries successfully reproduced, most of their surviving offspring were inferred to have been born in tributaries (94% for the OL and 88% for the OS). These results support previous research that identified tributaries as important spawning areas for brook trout (Petty *et al.*, 2005; Borwick, Buttle & Ridgway, 2006). Brook trout prefer to spawn in areas of groundwater upwelling (Curry & Noakes, 1995; Essington *et al.*, 1998), which contributes to spatial variation in temperature among small-sized streams (Santhi *et al.*, 2008). Incubating eggs may be less likely to experience flashy bed-moving flows, and juvenile trout may encounter fewer predators and competitors in tributaries (Petty *et al.*, 2005). It was particularly interesting to find that 65% of gene movement from the WB to the OS occurred in a single year with a high stream flow during the autumnal spawning period. A perched culvert (0.75-m high) at the OS appears to block upstream movements of brook trout under low-flow conditions, and this tributary is characterised predominantly with isolated pools when stream flows are low. Natal homing at the very fine spatial scale has been reported among stream salmonids (Armstrong & Herbert, 1997; Carlsson & Carlsson, 2002). However, brook trout born in the mainstem in our study system may use tributaries opportunistically when they are able to access these habitats.

Although tributaries were important reproductive habitats, it is noteworthy that emigration from tributaries to the mainstem was common. While 7–28% of individuals emigrated from the WB to the tributaries (depending upon the method), 6–29% (OL) and 19–33% (OS) of individuals moved to the WB. Previous research in the West Brook system indicated that the mainstem provides important habitat for adults. Large brook trout individuals are most typically found in pools in the West Brook mainstem (Letcher *et al.*, 2007). Xu, Letcher & Nislow (2010b) found that survival of large trout was reduced during summer low-flow periods in the tributaries, but not in the mainstem. Fecundity increases with body size in fish (Morita *et al.*, 1999; Thériault *et al.*, 2007). Stream salmonids are often territorial and form a dominance hierarchy mediated by body size (Nakano *et al.*, 1998). Thus, attaining larger body size would affect reproductive output directly. Brook trout in this study system may

use movements to exploit spatially heterogeneous habitats (survival and growth in the mainstem and reproduction in the tributaries), which maximises their reproductive fitness. Future research is warranted to investigate whether individual variation in life history and movement patterns affects individual-based fitness.

Some limitations of this study are worth noting. First, estimates of gene movements from the tributaries were based on small sample sizes (e.g. eight parents in the OL and 11 in the OS for the PAR-SIB-unweighted method). Inference of gene movements required at least three fullsib individuals to identify spawning locations reliably. This requirement was not easy to satisfy because fullsib family size was dominated by those with one or two individuals (Fig. 4). This explains why sample sizes for gene movement estimates decreased substantially in comparison with movement of individuals (Table 2). However, the sample size to estimate gene movement from the mainstem was sufficiently large (50 individuals), and thus this limitation should not influence the conclusion that tributaries were important spawning habitats for brook trout. Second, obtaining unbiased estimates of movement is inherently challenging. Gene movement was based on individuals with relatively high reproductive success (i.e. fullsib family size \geq three individuals). When movement affects survival of individuals, mark-recapture methods could either underestimate movement rates (if individuals that move suffer higher mortality rates) or overestimate movement rates (if individuals that move experience higher survival rates). By monitoring movement continuously over time and without relying upon recaptures of individuals, the antenna method might perhaps be the least biased estimate of individual movement in the current study. We recognise that an unknown degree of potential bias exists in our movement estimates, but we also stress that a combination of mark-recapture, antennae and genetic pedigree information provided an unusual opportunity to understand the degree of functional connectivity in the spatially heterogeneous riverscape.

In summary, this study showed a high degree of functional connectivity in a heterogeneous riverscape in which reproductive success was habitat dependent. It highlighted the importance of quantifying gene movements of a fecund species and tracking animal movements during all life stages. An accurate assessment of habitat connectivity is becoming more important as ecologists and conservation biologists attempt to understand the impact of environmental changes on the persistence of spatially structured populations. The high functional habitat connectivity in the study area would make the

brook trout population highly vulnerable to habitat fragmentation; Letcher *et al.* (2007) reported that this metapopulation would go extinct within a few generations in a simulated habitat fragmentation scenario. We suggest that the combination of robust mark-recapture and pedigree data is particularly important for cryptic, highly fecund species whose movements are not directly observable and where reproductive success is variable and habitat dependent.

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