Assessing brown trout (*Salmo trutta*) spawning movements with multistate capture–recapture models: a case study in a fully controlled Belgian brook

Béatrice M. Frank, Olivier Gimenez, and Philippe V. Baret

Abstract: A multistate capture–recapture model was developed to estimate movements of brown trout (*Salmo trutta*) between a main stem and its headwater tributary and their survival and recapture probabilities in each stream. As all individuals entering or leaving the tributary were captured by trapping, the studied ecological system was fully controlled. The performance of multistate models combining two sources of data (trapping and electrofishing) available for 6 years was first evaluated. Realistic estimates were obtained to infer the average spawning behaviour of trout: (*i*) 58% returned to their original site after spawning, (*ii*) 9% returned to their natal site for reproduction, (*iii*) 55% of the ascending individuals performed natal homing. Because less informative systems are pervading, we eventually assessed the sensitivity of multistate models to the level of trapping data integration. A lack of such data led to an underestimation of movement probabilities, and we found that this effect could be compensated by electrofishing samplings.

Résumé : Un modèle statistique multiétats de capture–recapture a été développé pour estimer les mouvements de truites (*Salmo trutta*) entre le bras principal et l'affluent de tête d'un cours d'eau, ainsi que leurs probabilités de survie et de recapture dans chaque cours d'eau. Le système étudié est entièrement contrôlé car tout individu entrant ou sortant de l'affluent est capturé par piégeage. En premier lieu, la performance de modèles multiétats combinant deux sources de données (piégeage et pêche électrique) provenant d'une étude menée sur 6 ans a été évaluée. Les estimations réalistes obtenues ont ensuite été utilisées pour inférer le comportement reproducteur moyen des truites, à savoir que (*i*) 58 % des individus sont retournés à leur territoire d'origine après leur reproduction dans le ruisseau, (*ii*) 9 % sont retournés à leur lieu de naissance pour frayer, (*iii*) 55 % des truites en montaison ont présenté un comportement de philopatrie natale. Comme les systèmes moins informatifs sont nombreux, nous avons également testé la sensibilité des modèles multiétats au niveau d'intégration des données de piégeage. Un manque de ce type de données a occasionné une sous-estimation des probabilités de mouvement, mais cette dernière a pu être compensée en considérant des données supplémentaires de pêche électrique.

[Traduit par la Rédaction]

Introduction

Migration is a demographic process with a strong impact on population dynamics (Lebreton 1996; Dingle 1996). Indeed, immigration and emigration are two of four factors responsible for changes in the size and the structure of populations through time and space (Townsend et al. 2000), the two other factors being birth and death processes. Movements can also affect genetic differentiation, local adaptation, and evolutionary persistence of populations (Clobert et al. 2001).

Substantial movement in populations of stream-dwelling fish species such as the brown trout (*Salmo trutta*) may occur (Gowan et al. 1994; Gowan and Fausch 1996), although several studies also suggest a high degree of local site fidelity (Bachman 1984; Hesthagen 1988; Carlsson et al. 1999). Between-stream movements are frequent, as brown trout inhabiting complex systems use main streams to grow and mature (Baglinière et al. 1987; Jonsson and Jonsson 1993; Forseth et al. 1999) and first-order streams as spawning grounds and nursery areas (Elliott 1994; Crisp 1996; Armstrong et al. 2003).

To our knowledge, multistate capture–recapture (MSCR) models have never been used to study trout movements between spawning tributaries and the main river and have even rarely been used for other fish species (e.g., Massicotte et al. 2008). Obstacles to the use of MSCR models for fish include the necessity to discriminate between mortality and emigration and to account for temporary emigration. Indeed, emigration cannot be directly estimated in most population studies, and this is accounted for in the estimate of survival, which is consequently underestimated and called "apparent survival" (Olsen

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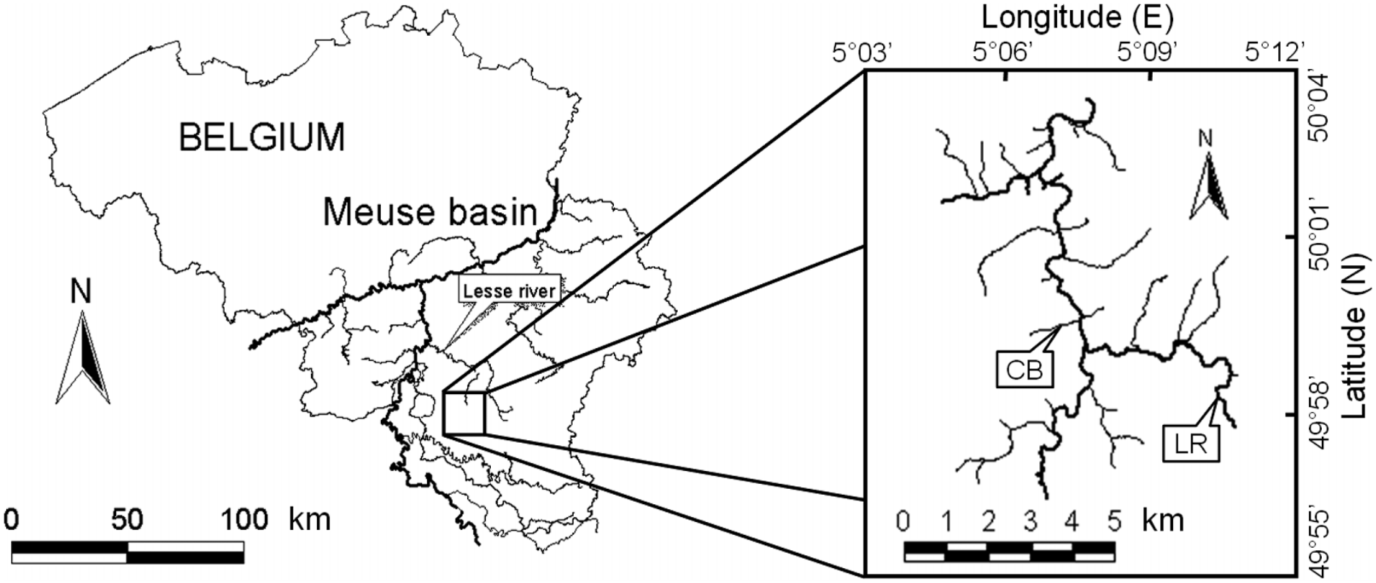
Fig. 1. Situation plan of the Lesse River (LR) in the Meuse basin and position of the Chicheron Brook (CB) in the Lesse basin.



and Vollestad 2001; Fletcher et al. 2002). Furthermore, emigration can be permanent or temporary (see Fujiwara and Caswell 2002), and temporary emigration is often Markovian; the probability of being temporarily absent depends on whether or not an individual was absent during the previous occasion (Schaub et al. 2004). To overcome these difficulties, electrofishing samplings in both streams supplemented by a comprehensive trapping of fish entering or leaving the tributary would be the ideal sampling design. When complete capture of migrants is not possible, extensions of MSCR models have nonetheless been developed to estimate emigration rates (Fujiwara and Caswell 2002; Kendall and Nichols 2002; Schaub et al. 2004). For instance, the model proposed by Horton et al. (2011) separates true survival from permanent emigration using a combination of continuous data from a multiple-antenna array with instantaneous electrofishing live capture–recapture (CR) data.

In the present work, we investigated postspawning homing and natal homing behaviours of brown trout. Postspawning homing is the return of the trout to its original territory once reproduction is complete, while natal homing or natal site fidelity is the propensity of a trout to return to spawn in the stream of its birth (Stuart 1957). We used trapping and electrofishing data from a 6-year CR study of brown trout spawning movements between a headwater tributary and the main river in southern Belgium. This ecological system is fully controlled (i.e., all individuals entering or leaving the tributary are captured in the upstream and downstream traps). Because less informative systems are more common than fully controlled ones, analyses based on different levels of data integration were compared. Performance of MSCR models was evaluated from these comparisons to provide guidance for their future use in fish migration studies.

Radiotelemetry and CR are two complementary methods for studying trout spawning movements. Observations of radio-tagged fish provide fine-resolution estimates of the timing and distance of movements (e.g., Ovidio 1999; Arnekleiv and Rønning 2004; Rustadbakken et al. 2004), while CR methods (see reviews by Schwarz and Seber (1999) and Seber and Schwarz (2002)) allow the study of fish movements at larger spatial and temporal scales (Gresswell and Hendricks 2007). Single-state CR models enable estimating survival and detection (capture) probabilities among individuals, while in MSCR models (Arnason 1972, 1973; Hestbeck et al. 1991), individuals can move between states (e.g., geographical sites, reproductive status, size classes, etc.) and thus have state-specific survival and detection probabilities (see Lebreton et al. (2009) for a review).

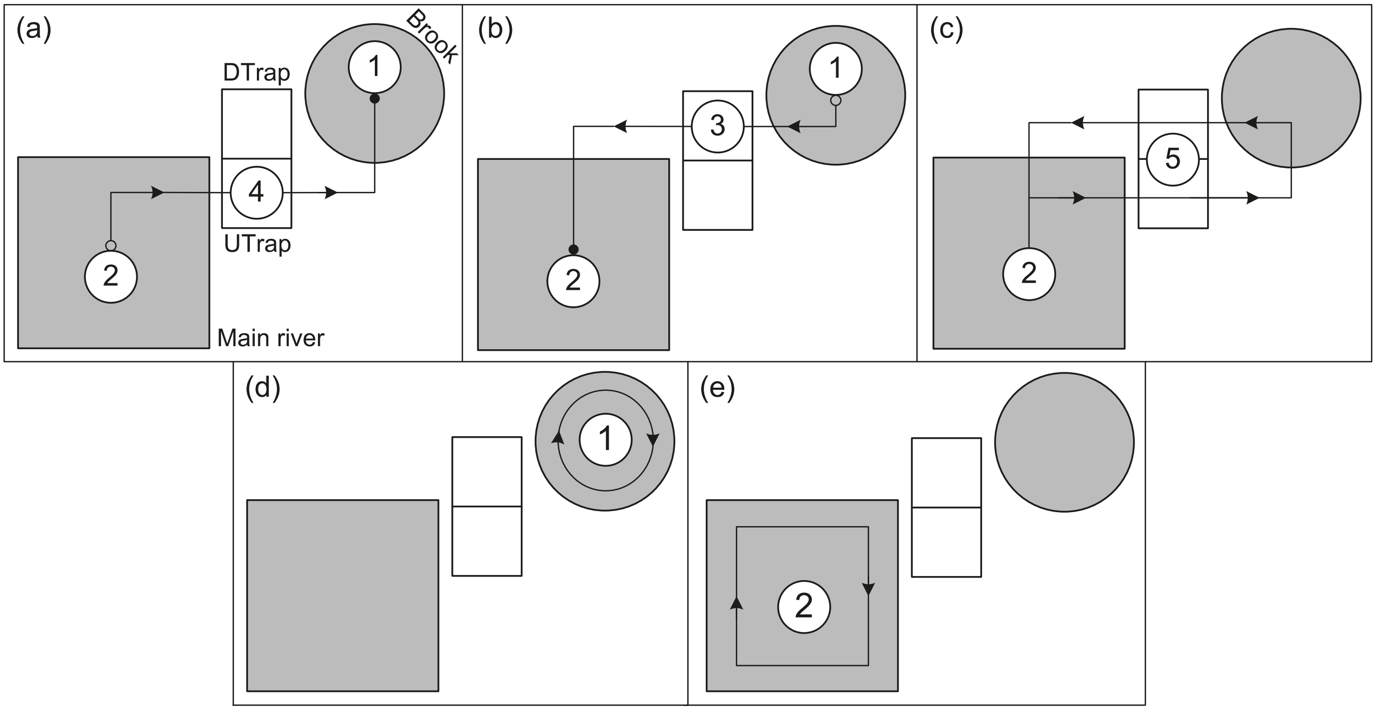
In this paper, two approaches were used to evaluate performance of MSCR models and to infer trout spawning behaviour. On the one hand, a simple analysis of trout movements at the trapping facility was used with two data sets: one including all observations at the traps (full data set), the other including only the half of these observations (reduced data set). On the other hand, MSCR modelling was applied on four individual CR histories: one constructed with all available data for the studied system (total capture histories; i.e., data from the traps and from electrofishing samplings), the others with all electrofishing data and a variable random sample of trapping data (partial capture histories). First, performance of MSCR models and their sensitivity to the level of data integration were evaluated through three questions: (*i*) Were MSCR estimates consistent with true movement observations obtained from the simple analysis? (*ii*) How were they affected by the quantity of trapping data? (*iii*) To what extent can results from a half-efficient trapping facility be improved by an additional source of data (i.e., electrofishing)? Second, trout return rates to their original site after spawning and to their natal site for spawning were computed from results drawn from the simple analysis and MSCR modelling applied to the full data set and to total capture histories, respectively. Then, postspawning and natal homing behaviours were inferred.

Materials and methods

Study area and data

The study was conducted in a small stream network in the Lesse River, a tributary to the Meuse River, which occupies an area of 1343 km^2 and is located in southern Belgium (Fig. 1). The study area consisted of a 1.1 km-long section

Fig. 2. Trout can perform five types of movement: they can move between the main stream and the nursery brook (movement types I (*a*), II (*b*), and III (*c*)) or stay in each stream (types IV (*d*) and V (*e*)). Consequently, trout can be observed at five different locations: in the brook (1), in the main stream (2), at the downstream trap exclusively (3), at the upstream trap exclusively (4), or both at the upstream trap and the downstream trap (5).



of a main stem (Lesse River, LR, fourth-order) with one 1.2 km-long first-order tributary (Chicheron Brook, CB). LR is located at the boundary between the trout and the grayling fish assemblage zones; the stream has a 0.8% slope, is 13 to 27 m wide, has an average depth of 0.5 m, and has a 4 $m^3 \cdot s^{-1}$ average discharge rate. The river flows through a wide forested area and offers excellent water quality. CB has a slope of 4.7%, an average width of 1.4 m, and a depth varying from 2 to 15 cm with several deeper pools. This brook is a well-known area for its spawning grounds and nurseries and is exclusively populated with wild brown trout.

The LR–CB local system was studied for 20 years by Huet and Timmermans (1979) and monitored afterwards for another 30 years. Three types of trout movements were observed between the main stream and the tributary: (*i*) an upstream migration of mature adults from LR to CB for spawning in autumn and winter, (*ii*) the return of these adults to LR after spawning, (*iii*) a downstream migration of fry and juveniles from CB to LR in spring and summer of that same year or the next years. The migration pattern seems to be always the same (Dupont 2009); each winter, 100 to 500 spawners are observed to migrate from LR to CB to spawn, and 300 to 900 young trout swim down to LR during the successive spring and summer. A radiotelemetry study conducted between 2000 and 2004 on 21 spawners of the LR–CB system demonstrated that (*i*) trout always return to their original territory once the reproduction is complete (postspawning homing), (*ii*) trout do not always frequent the same spawning ground and thus can have different reproductive behaviours during their lifetime (Dupont 2004). Earlier, Huet and Timmermans (1979) suggested that the downstream movement of spawners could be determined not only by a tendency to return to the river of departure, but also by a density factor in the brook, which was already inhabited by a resident trout population. Moreover, they found no evidence of natal homing behaviour in the studied system.

More generally, five types of trout movements between a first-order tributary and the main stream are observed (Fig. 2; movement types I to V). At the temporal scale, all movement types occur during one given year. They are explained hereafter using brook as a reference. Types I and III involve spawners of the tributary, which in theory immigrate to then emigrate from the brook during the reproduction period. For some of the spawners, the immigration will be permanent because they may die or decide to stay (and die) in the brook (type I); the others will return to the main river after the spawning (postspawning homing hypothesis — verified by radio-tracking) (type III). Movement type II involves fry and juveniles born in the tributary. Some of the young trout swimming downstream from the tributary to the main stem will leave the tributary forever, but some of them will come back during the reproduction period, once mature (natal homing hypothesis). Types IV and V refer to no movement at all; trout stay either in the brook or in the main stream, respectively.

In 2003, an autopowered and self-cleaning trapping facility was build 20 m upstream from the confluence of the tributary to monitor trout movements. Upstream and downstream traps were checked daily. Furthermore, fish were sampled in the two streams on one or two occasions in each year of the study (time period of 6 years, from 6 October 2004 to 9 July 2010). They were captured using standard electrofishing techniques (HERON, 350–450 V DC in LR; DEKA, 250–600 V DC in CB) once a year in LR in autumn (before the spawning migration of mature adults) and twice a year in CB in autumn and in spring (before and after the stay of the adults, respectively). Over the course of the study, 18 sampling occasions were recorded, and each period required 2–3 days to complete. Untagged electrofished trout > 7.5 cm (6 cm since 2007) were marked with passive integrated transponder (PIT; Réseaumatique, Bernay, France) tags following anaesthesia with clove oil. Tag loss was estimated by removing the adipose fin of all tagged trout. Fish captured in the traps undergo the same procedures as those that were electrofished. Trapping efficiency was estimated from inconsistencies in trout capture histories.

For the simple analysis of trout movements, we used observations of 4790 tagged individuals caught at the trapping facility for the full data set (noted FDS) and observations of 2587 individuals for the reduced data set (RDS). This latter number was obtained by taking a random sample of half the size of each set of observations made at the upstream and downstream traps. For the analysis involving MSCR modelling, four individual capture histories were constructed: total capture histories (TCH) that comprise 10 289 trout, including 4028 individuals caught in LR, 3945 individuals caught in CB, and 4790 individuals caught at the trapping facility; partial capture histories (PCH1, PCH2, and PCH3), including the same number of individuals caught in LR and in CB as in TCH, but three-quarters, one-half, and one-quarter of the individuals caught at the trapping facility, respectively. Recaptured fish that died during the capture or marking process were included in the analyses (i.e., 55 individuals out of 10 289).

Simple analysis of trout movements at the trapping facility

After a classification of trout caught at the trapping facility according to their upstream and downstream movements, proportions of trout performing movement types I to III (Fig. 2) were determined for FDS and RDS. Then, trout return rates to their original site after spawning and to their natal site for spawning were computed.

Return rate of spawners to their original location under the postspawning homing hypothesis was computed as the ratio of the number of individuals caught consecutively in the upstream and downstream traps (i.e., movement type III) to the total number of individuals caught in the upstream trap (i.e., types I and III). Some individuals strictly migrating out of the brook (movement type II) will come back, once mature, to the tributary for reproduction. These trout were observed first at the downstream trap and at least several months later at the upstream trap and thus performed movement types II then I or III. It was only possible to determine their total number over the 6 years of the study because both movement types did not occur at the same time. This number of homing individuals was used to compute the global return rate of trout to their natal site for reproduction under the natal homing hypothesis. It is equal to the ratio of the number of homing individuals to the number of individuals observed at the downstream trap exclusively (i.e., movement type II). Furthermore, spawning periods and frequencies for trout assigned to movement types I and III were analysed. We also investigated periods of descent for individuals assigned to movement type II as well as time elapsed between the descent and the first reproduction for homing individuals.

Multistate capture–recapture modelling

Model structure and parameters of interest

A general MSCR model incorporating the biological processes of interest was developed. We considered six states in the model. Five of them are underlying the movement types observed between the headwater spawning tributary CB and the main river LR (Fig. 2): spawners moving from LR to CB (movement type I, state SP1 for “spawner 1”) or moving from LR to LR (type III, state SP2 for “spawner 2”), young trout moving from CB to LR (type II, state YT for “young trout”), non-spawners staying in CB (type IV, state NS1 for “non-spawner 1”) or staying in LR (type V, state NS2 for “non-spawner 2”). The last state corresponds to dead individuals (state D for “dead”).

We considered 12 occasions of capture, two for each year of the study, to separate observations made by electrofishing and by trapping (Fig. 3). At odd occasions (referred to as “A” hereafter), individuals were always captured in state NS1 or NS2 (according to the stream sampled), as electrofishing took place before or after spawning migration of mature adults to CB and the movement of young trout from CB to LR. At even occasions (referred to as “B”), only states YT, SP1, and SP2 are possible for the individuals caught in the trapping facility.

States are related to observations through recapture probabilities. We matched the events of capture histories with the states NS1, NS2, YT, SP1, and SP2 as follows, the notation being 0 when the individual was not captured: (1) NS1 caught by electrofishing in CB but not in the downstream trap, (2) NS2 caught by electrofishing in LR, (3) YT caught exclusively in the downstream trap, (4) SP1 caught exclusively in the upstream trap, (5) SP2 caught consecutively in the upstream and downstream traps. Because electrofishing in CB in the spring overlaps the downstream migration of young trout, a certain number of trout were captured at both events 1 and 3. We assigned these individuals to event 3 (551 trout out of 10 289 for TCH, 428 out of 9726 for PCH1, 293 trout out of 9134 for PCH2, 143 out of 8499 for PCH3). Capture histories were also sorted into two groups, the first one including trout born in CB (i.e., trout captured in state YT) and the second one including trout of unknown origin (i.e., trout never captured in state YT). Examples of capture histories for the two groups are given in Table 1.

In addition to trout recapture probabilities in both streams (R_{CB} and R_{LR}) and in the trapping facility (R_{TF}), we also estimated trout survival probabilities in both streams (S_{CB} and S_{LR}) and the following movement probabilities (Fig. 3): (*i*) $M_{\mathrm{CB\ to\ LR}}$, the probability for a non-spawner of CB to emigrate to LR (i.e., transition from state NS1 to YT), (*ii*) $M_{\mathrm{LR\ to\ CB}}$, the probability for a non-spawner of LR to spawn in CB and to not come back (i.e., transition from state NS2 to SP1), (*iii*) $M_{\mathrm{LR\ to\ LR}}$, the probability for a non-spawner of LR to spawn in CB and to come back (i.e., transition from state NS2 to SP2). From (*i*) we derived M_{CB}, the complementary probability for a non-spawner of CB to stay in CB (i.e., remain in state NS1). From (*ii*) and (*iii*) we derived M_{LR}, the complementary probability for a non-spawner of LR to stay in LR (i.e., remain in state NS2). More details about the structure of the general MSCR model are given in Supplemental Appendix S1[1].

Fig. 3. Conceptual representation of the general multistate capture–recapture model used to infer brown trout spawning behaviour between a headwater tributary (Chicheron Brook, CB, left grey part in the figure) and the main river (Lesse River, LR, right grey part in the figure) in southern Belgium. Trout movements between both streams were monitored by a trapping facility (TF, middle part in the figure). For each year of the study, two capture occasions were considered: individuals were captured by electrofishing in CB or LR at occasions A or caught in TF at occasions B. States and capture events correspond as follows: (1) non-spawners staying in CB (state NS1, movement type IV), (2) non-spawners staying in LR (state NS2, type V), (3) young trout moving from CB to LR (state YT, type II), (4) spawners moving from LR to CB (state SP1, type I), (5) spawners moving from LR to LR (state SP2, type III). Recapture (R), survival (S), and movement (M) probabilities estimated by the model are shown in bold. Recapture probabilities of trout at occasions B in states NS1 and NS2 were set equal to zero, and all survival and movement probabilities between occasions B and A were set equal to one (in italics).

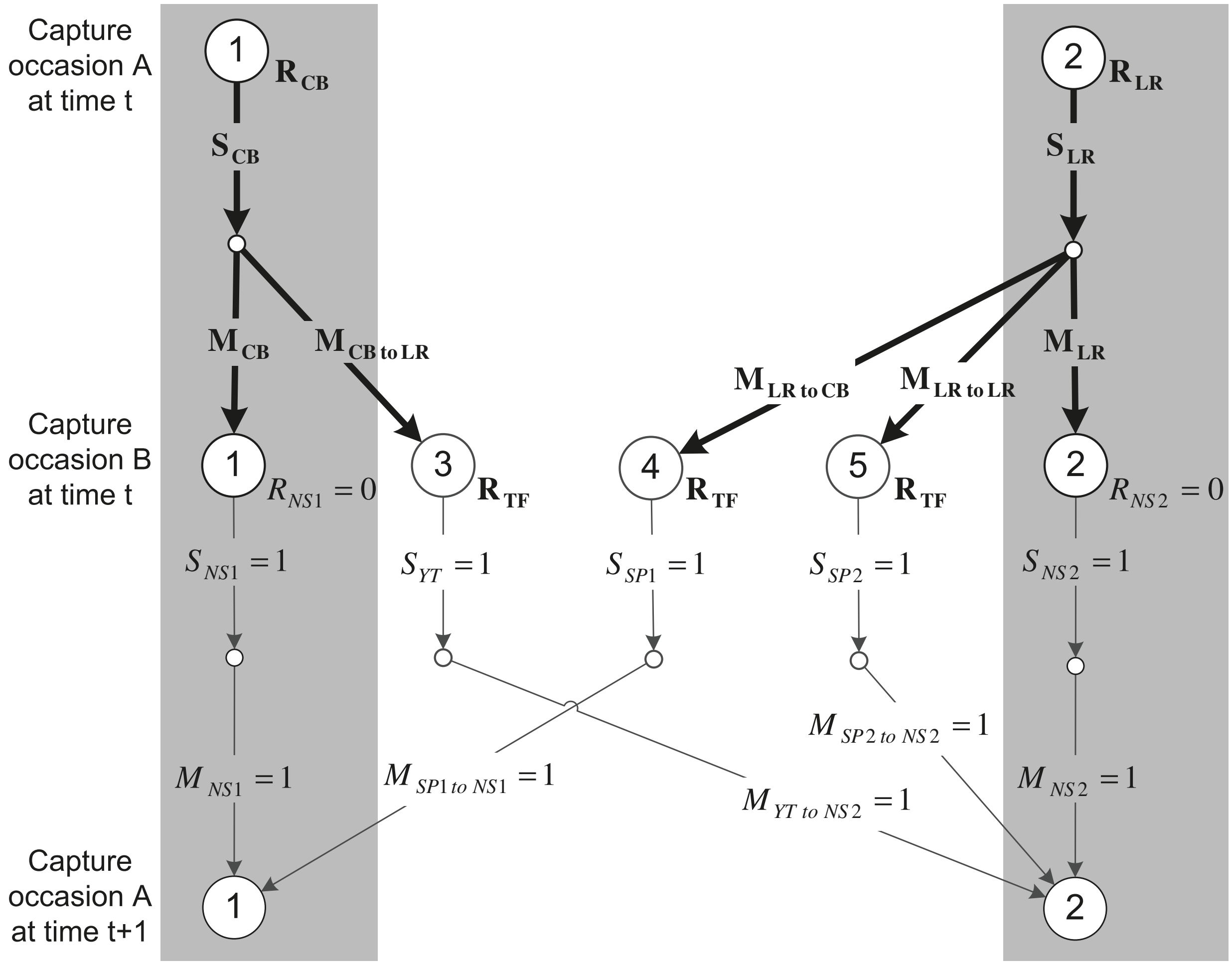


Table 1. Examples of multistate capture histories for the group of trout born in the Chicheron Brook (group 1) and the group of trout of unknown origin (group 2).

Group	History	Events
1	1013	Individual first caught as non-spawner by electrofishing in CB, not caught at the next trapping occasion, recaught as non-spawner by electrofishing in CB, and then recaught as juvenile in the downstream trap
	0324	Individual first caught as juvenile in the downstream trap, caught as non-spawner by electrofishing in LR, and then recaught as spawner in the upstream trap
	1305	Individual first caught as non-spawner by electrofishing in CB, caught as juvenile in the downstream trap, not caught at the next trapping occasion, and then recaught as spawner in both upstream and downstream traps
2	0525	Individual first caught as spawner in both upstream and downstream traps, recaught as non-spawner by electrofishing in LR, and then recaught as spawner in both upstream and downstream traps
	2410	Individual first caught by electrofishing in LR, recaught as spawner in the upstream trap, recaught as non-spawner by electrofishing in CB, and then not recaught at the last trapping occasion
	2504	Individual first caught by electrofishing in LR, recaught as spawner in both upstream and downstream traps, not caught at the next electrofishing occasion, and then recaught as spawner in the upstream trap

Note: CB, Chicheron Brook; LR, Lesse River.

Table 2. Selection results for the 16 multistate capture–recapture models fitted on total capture histories.

Model	Recapture	Survival	Movement	Np	Deviance	QAIC$_c$	Δ_i
1	Time × Group	Time × Group	Time × Group	81	55 640	40 423	0
2	Group	Time × Group	Time × Group	60	55 742	40 455	32
3	Time × Group	Group	Time × Group	67	55 786	40 501	78
4	Group	Group	Time × Group	45	55 896	40 536	113
5	Time × Group	Time × Group	Group	58	56 041	40 667	244
6	Group	Time × Group	Group	36	56 188	40 729	306
7	Time × Group	Group	Group	41	56 199	40 747	324
8	Group	Group	Group	17	56 497	40 914	491
9	Time	Time	Time	43	60 910	44 160	3 737
10	Constant	Time	Time	32	61 094	44 271	3 848
11	Time	Constant	Time	35	61 087	44 272	3 849
12	Constant	Constant	Time	24	61 223	44 349	3 926
13	Time	Time	Constant	30	61 462	44 533	4 110
14	Constant	Time	Constant	19	61 606	44 616	4 192
15	Time	Constant	Constant	21	61 627	44 634	4 211
16	Constant	Constant	Constant	9	61 886	44 798	4 375

Note: Effects considered on recapture, survival, and movement probabilities are shown in the three first columns (group corresponds to trout natal origin). For each model, the number of estimable parameters (Np), the model deviance (Deviance), the modified version of the Akaike information criterion (QAIC$_c$), and the difference in QAIC$_c$ between the model and the most highly ranked model (Δ_i) are given.

Goodness-of-fit test, model selection, and inferences

The fit of the general MSCR model was assessed using goodness of fit procedures (Pradel et al. 2005) implemented in U-CARE (Choquet et al. 2009*a*). We used modified versions of TCH and PCH in which each occasion A was pooled with the subsequent occasion B (event 3 was then converted to event 1, and events 4 and 5 were converted to event 2) and in which individuals from the two groups were treated separately. A global test was obtained by adding the individual X^2 values and their respective degrees of freedom. The variance inflation factor ($\hat{c}$) was then calculated as the ratio of the global X^2 value to the total number of degrees of freedom and applied in model selection to correct for overdispersion (see Supplemental Appendix S2[1] for more details about goodness of fit tests). Program E-SURGE (Choquet et al. 2009*b*) was used to perform the MSCR analyses.

We constructed a set of 16 models (Table 2), each representing a different combination of four effects (i.e., constant, time, group, time × group) on each of the three parameters (recapture, survival, movement). The group effect allows discrimination of trout born in CB from trout of unknown origin. These models fitted on TCH were compared with the modified version of the Akaike information criterion (QAIC$_c$; Burnham and Anderson 2002). Four of the models were used to evaluate performance of MSCR models and to infer trout spawning behaviour: (*i*) two models considering all trout of the LR–CB system (i.e., no group effect) and all parameters varying with time or held constant (models 9 and 16 in Table 2), (*ii*) two models including time-dependent and time-independent effects in interaction with a group effect for recapture, survival, and movement parameters (models 1 and 8). Time-dependent models allowed us to obtain estimates for each separated year, while time-independent models gave estimates over all years 2004–2010 (models 1 and 9 vs. models 8 and 16). Results for the year 2009–2010 were not considered because of parameter redundancy (i.e., the last survival probability and the last recapture probability cannot be separately estimated; Gimenez et al. 2003). We used the following notation: considering TCH, estimates obtained from models 9 and 16 were affixed with a prime symbol (′) to be distinguished from models 1 and 8 estimates (no prime symbol); for PCH1, PCH2, and PCH3, estimates obtained from models 9 and 16 were affixed with superscripts 1, 2, and 3, respectively.

Parameter estimates derived from models 9 and 16 applied to TCH and PCH, and results obtained from the simple analyses performed on FDS and RDS were used to evaluate performance of MSCR models. As a prerequisite, MSCR estimates derived from TCH and PCH2 were used to calculate proportions of individuals performing movement types I to III: ratio of $M'_{\mathrm{LR\,to\,CB}}$ to the sum of $M'_{\mathrm{CB\,to\,LR}}$, $M'_{\mathrm{LR\,to\,CB}}$, and $M'_{\mathrm{LR\,to\,LR}}$ for type I; ratio of $M'_{\mathrm{CB\,to\,LR}}$ to the sum of $M'_{\mathrm{CB\,to\,LR}}$, $M'_{\mathrm{LR\,to\,CB}}$, and $M'_{\mathrm{LR\,to\,LR}}$ for type II; and ratio of $M'_{\mathrm{LR\,to\,LR}}$ to the sum of $M'_{\mathrm{CB\,to\,LR}}$, $M'_{\mathrm{LR\,to\,CB}}$, and $M'_{\mathrm{LR\,to\,LR}}$ for type III. Then, three comparisons were performed: (C1) individual movement proportions from the FDS analysis were compared with those obtained from MSCR estimates derived from TCH to determine if they were consistent, (C2) TCH estimates were compared with those derived from PCH1, PCH2, and PCH3 to assess the sensitivity of MSCR models to the efficiency of the trapping facility, (C3) movement proportions from the FDS analysis were compared with those obtained from (*i*) the RDS analysis and (*ii*) estimates derived from PCH2 to determine if considering an additional source of data could be a solution when only limited trapping data are available.

Models 1, 8, 9, and 16 applied to TCH were used to infer trout spawning behaviour. Trout return rates to their original site after spawning were calculated from models 9 and 16 estimates by the ratio of $M'_{\mathrm{LR\,to\,LR}}$ to the sum of $M'_{\mathrm{LR\,to\,CB}}$ and $M'_{\mathrm{LR\,to\,LR}}$. Trout return rates to their natal site were obtained from models 1 and 8 estimates as the sum of $M_{\mathrm{LR\,to\,CB}}$ and

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[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/f2012-041.

Table 3. Number (and associated percentage) of tagged individuals performing various movement types during the 6 years of the study (full data set).

Type	2004–2005	2005–2006	2006–2007	2007–2008	2008–2009	2009–2010	2004–2010
I	50 (7)	109 (18)	105 (15)	102 (7)	92 (8)	99 (21)	232 (5)
II	591 (78)	460 (76)	498 (70)	1167 (84)	1012 (89)	326 (70)	4229 (88)
III	117 (15)	36 (6)	111 (15)	120 (9)	32 (3)	43 (9)	329 (7)
III / (I+III)	— (70)	— (25)	— (51)	— (54)	— (26)	— (30)	— (59)

Note: Movement types are as follows: I, strict immigration; II, strict emigration; III, immigration then emigration; III / (I+III), return rate of spawners to their original site after reproduction. The last column presents results over the years 2004–2010.

$M_{\mathrm{LR\ to\ LR}}$. In contrast with models 9 and 16, models 1 and 8 include a group effect, and only estimates obtained for the group of trout born in CB were needed to compute natal site return rates.

Results

Tag loss and trapping facility efficiency

PIT tag loss was estimated to be 2% in TCH (225 individuals out of 10 289), and half of the loss was observed on trout captured at the trapping facility. These fish were retagged before being released.

The efficiency of the trapping facility was equal to 98.14% on average. It was estimated from inconsistencies observed in TCH: 57 individuals were electrofished at least once in both streams but were never caught by trapping, 20 individuals were caught in CB then directly in the upstream trap, and 12 individuals were caught in the upstream trap then directly in LR. The catch efficiency was computed as the ratio of the number of trout that had left or entered the brook out of control (89 individuals) to the total number of individuals caught at the trapping facility over all years 2004–2010 (4790 individuals). All these leaks took place during the year 2005–2006, as fish moving downstream were "jumping" over the traps. Wooden screens were placed to prevent this problem.

Simple analysis of trout movements at the trapping facility

Proportions of trout performing movement types I to III and the annual return rates of adults to their location of origin after the reproduction period were computed from observations at the trapping facility. Results obtained from FDS reflect true movements of trout owing to the high capture efficiency in the traps (Table 3). The same analysis was performed on RDS; results are presented in Supplemental Appendix S3[1].

Over the years 2004–2010, 561 spawners were observed in the upstream trap, and 329 were caught consecutively in the upstream and downstream traps. Thus, 59% of the spawners survived the reproduction period and returned to the main stream. We obtained a similar result over the years 2004–2008 (i.e., 60%; data not shown). Fluctuations were observed among years with the highest return rate during 2004–2005 (70%) and with the lowest return rate during 2005–2006, 2008–2009, and 2009–2010 (25%, 26%, and 30%, respectively). Rates during 2006–2007 and 2007–2008 were similar to the observed global rate (51% and 54%, respectively). We observed 311 homing individuals (i.e., performing movement types II then I or III) over the 6 years of the study. We calculated that 7% of these trout returned to spawn in the brook in which they were born.

The spawning period occurs mainly from November to January (97%) and more rarely in February and early March (3%). For trout assigned to movement types I and III, spawning frequencies were observed as follows: 85% of the trout (478 individuals) spawned only once, 14% (78) twice, and 1% (5) three times. Emigration of young trout to the main stream occurs mainly from March to September (89%) and more rarely from November to February (11%). Among the 311 individuals showing a homing behaviour, half (159 trout, 51%) waited until the following year to spawn in the brook, and one-third waited 1 more year (96 trout, 31%). In 15% of the cases (47 trout), spawning occurred the same year of the descent of the individual to the main stream. Trout waiting more than 2 years before reproducing were rare (9 trout, 3%).

Goodness of fit and multistate model selection

The general MSCR model applied separately to trout born in CB and trout from unknown origin was rejected for all capture histories (TCH: $X^2 = 74.629$, df = 54, $p = 0.033$; PCH1: $X^2 = 96.416$, df = 69, $p = 0.016$; PCH2: $X^2 = 109.271$, df = 68, $p = 0.001$; PCH3: $X^2 = 119.919$, df = 72, $p = 0.000$). Two out of five test components, the trap-dependence (M.ITEC) and transience (3G.SR) tests, were significant for TCH and contributed the most to the JMV model rejection (see Supplemental Appendix S2[1]). This means that the fact that a trout has already been caught could have an influence on its behaviour and that all individuals do not have the same probability of subsequent recapture. To improve the fitting of data, we used the calculated values of the variance inflation factor $\widehat{c}$ in the analyses (1.382 for TCH; 1.397 for PCH1; 1.607 for PCH2; 1.666 for PCH3).

The 16 models fitted on TCH were compared according to $\mathrm{QAIC_c}$ (Table 2). The best supported model was the time-dependent model with a group effect (model 1; $\Delta_i = 0$); all parameters differed according to trout natal origin and varied over time. A huge discrepancy was found at the boundary between models considering a group effect at least on one parameter (models 1 to 8) and models without a group effect (models 9 to 16) (Δ_i between models 8 and 9 = 3245). Models 10 and 11 showed a $\Delta_i < 1$, meaning that considering both survival and movement time-dependent or both recapture and movement time-dependent was equivalent. Considering recapture or survival time-independent was best supported by the data than considering both recapture and survival time-independent, the worst of all being to not consider a time effect for movement.

Trout spawning behaviour

Estimates derived from four MSCR models were used to infer trout spawning behaviour: (*i*) two time-independent and

Table 4. Survival (S'), recapture (R'), and movement (M') estimates with 95% confidence intervals, derived from the time-dependent model (separated years, model 9 in Table 2) and the time-independent model (years 2004–2010, model 16) applied to total capture histories and considering all trout of the LR–CB system.

Probability	2004–2005	2005–2006	2006–2007	2007–2008	2008–2009	2004–2010
S'_{CB}	0.78 (0.70–0.84)	0.52 (0.46–0.57)	0.56 (0.50–0.62)	0.49 (0.45–0.54)	0.62 (0.50–0.72)	0.51 (0.49–0.53)
S'_{LR}	0.55 (0.50–0.60)	0.44 (0.39–0.48)	0.61 (0.55–0.66)	0.68 (0.61–0.75)	0.88 (0.68–0.97)	0.56 (0.54–0.58)
R'_{CB}	1.00 (1.00–1.00)	0.59 (0.50–0.68)	0.40 (0.33–0.48)	0.58 (0.50–0.66)	0.53 (0.45–0.60)	0.49 (0.45–0.52)
R'_{LR}	1.00 (1.00–1.00)	0.35 (0.32–0.39)	0.36 (0.33–0.40)	0.35 (0.32–0.38)	0.27 (0.24–0.29)	0.30 (0.29–0.32)
R'_{TF}	1.00 (1.00–1.00)	0.95 (0.90–0.97)	1.00 (1.00–1.00)	0.99 (0.94–1.00)	0.99 (0.88–1.00)	0.97 (0.94–0.98)
$M'_{\mathrm{LR\ to\ CB}}$	0.04 (0.03–0.07)	0.11 (0.08–0.14)	0.05 (0.04–0.07)	0.05 (0.04–0.07)	0.03 (0.02–0.04)	0.05 (0.05–0.06)
$M'_{\mathrm{CB\ to\ LR}}$	0.60 (0.53–0.67)	0.60 (0.53–0.66)	0.34 (0.29–0.41)	0.48 (0.43–0.53)	0.36 (0.29–0.44)	0.44 (0.42–0.47)
$M'_{\mathrm{LR\ to\ LR}}$	0.96 (0.93–0.97)	0.04 (0.03–0.06)	0.11 (0.09–0.14)	0.11 (0.09–0.14)	0.01 (0.01–0.02)	0.07 (0.06–0.08)
M'_{CB}	0.40 (0.33–0.47)	0.40 (0.34–0.47)	0.66 (0.60–0.71)	0.52 (0.47–0.57)	0.64 (0.56–0.71)	0.56 (0.53–0.58)
M'_{LR}	0.00 (0.00–0.00)	0.85 (0.81–0.88)	0.84 (0.80–0.87)	0.84 (0.81–0.86)	0.96 (0.94–0.97)	0.88 (0.87–0.89)

Note: CB, Chicheron Brook; LR, Lesse River; TF, trapping facility.

Table 5. Survival (S), recapture (R), and movement (M) estimates with 95% confidence intervals, derived from the time-dependent model (separated years, model 1 in Table 2) and the time-independent model (years 2004–2010, model 8) applied to total capture histories and considering only the group of trout born in the Chicheron Brook.

Probability	2004–2005	2005–2006	2006–2007	2007–2008	2008–2009	2004–2010
S_{CB}	1.00 (1.00–1.00)	1.00 (1.00–1.00)	0.92 (0.85–0.96)	0.98 (0.94–0.99)	0.91 (0.85–0.95)	0.95 (0.93–0.96)
S_{LR}	0.50 (0.50–0.50)	0.45 (0.36–0.53)	0.54 (0.45–0.62)	0.73 (0.61–0.82)	0.70 (0.57–0.81)	0.59 (0.55–0.62)
R_{CB}	1.00 (1.00–1.00)	1.00 (1.00–1.00)	0.18 (0.05–0.48)	0.62 (0.38–0.81)	0.39 (0.27–0.53)	0.33 (0.25–0.41)
R_{LR}	1.00 (1.00–1.00)	0.22 (0.18–0.26)	0.25 (0.21–0.29)	0.25 (0.21–0.29)	0.23 (0.20–0.25)	0.22 (0.21–0.24)
R_{TF}	1.00 (1.00–1.00)	1.00 (1.00–1.00)	1.00 (1.00–1.00)	1.00 (1.00–1.00)	1.00 (1.00–1.00)	1.00 (1.00–1.00)
$M_{\mathrm{LR\ to\ CB}}$	0.33 (0.33–0.33)	0.06 (0.03–0.10)	0.03 (0.01–0.06)	0.05 (0.03–0.07)	0.04 (0.03–0.06)	0.04 (0.04–0.05)
$M_{\mathrm{CB\ to\ LR}}$	0.97 (0.92–0.99)	0.99 (0.96–1.00)	0.91 (0.85–0.95)	0.89 (0.84–0.92)	0.91 (0.85–0.95)	0.91 (0.89–0.93)
$M_{\mathrm{LR\ to\ LR}}$	0.33 (0.33–0.33)	0.01 (0.00–0.04)	0.11 (0.08–0.16)	0.12 (0.09–0.15)	0.02 (0.01–0.03)	0.05 (0.05–0.07)
M_{CB}	0.03 (0.01–0.08)	0.01 (0.00–0.04)	0.09 (0.05–0.15)	0.11 (0.08–0.16)	0.09 (0.05–0.15)	0.09 (0.07–0.11)
M_{LR}	0.33 (0.33–0.33)	0.93 (0.88–0.96)	0.86 (0.81–0.90)	0.84 (0.79–0.87)	0.94 (0.92–0.96)	0.90 (0.89–0.91)

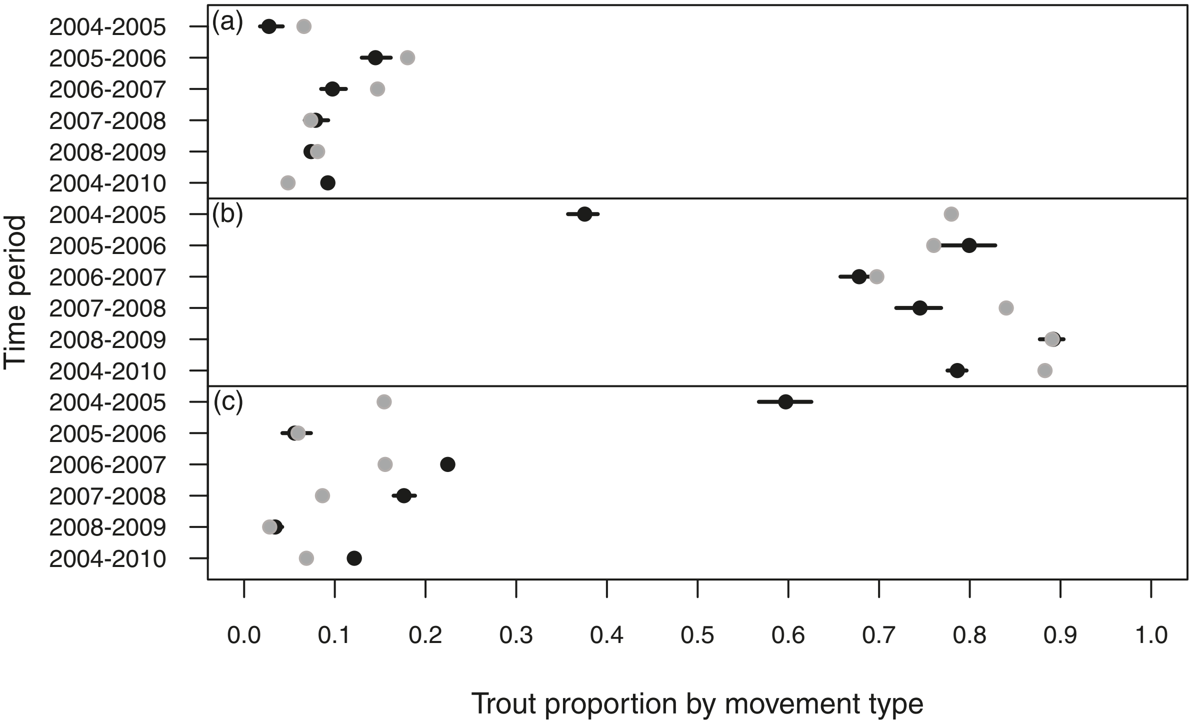
Note: CB, Chicheron Brook; LR, Lesse River; TF, trapping facility.

time-dependent models considering all trout of the LR–CB system, (*ii*) two time-independent and time-dependent models considering only the group of trout born in CB. Survival, recapture, and movement probabilities estimated by the four models applied to TCH were analysed, and results are presented in Tables 4 and 5 (see also Supplemental Appendix S4[1]). Trout return rates to their original site after spawning and to their natal site for spawning were computed from estimates derived from models 9 and 16 and from models 1 and 8, respectively. Results obtained from models applied to PCH were not discussed here given the degradation of information they contain, but the raw estimates are available in Supplemental Appendix S4[1].

Trout survival probabilities in both streams (S'_{CB} and S'_{LR}) over all years 2004–2010 were estimated equal to 0.51 and 0.56, respectively (Table 4). Small variations occurred over years, and we observed a survival higher in CB than in LR during 2004–2006, but the reverse during 2006–2009. On average, recapture probabilities of trout in CB ($R'_{\mathrm{CB}} = 0.49$) were slightly greater than those estimated for trout in LR ($R'_{\mathrm{LR}} = 0.30$). Small variations occurred over years but the trend stays identical. Recapture probabilities of SP1, SP2, and YT in the traps (R'_{TF}) were all estimated nearly equal to unity by the time-independent model. Estimates for separated years given by the time-dependent model were all equal to or higher than 0.95. The probability for a trout in LR to move upstream for spawning can be computed by the sum of the probability for a non-spawner of LR to spawn in CB and to not come back ($M'_{\mathrm{LR\ to\ CB}}$) and the probability that it does come back ($M'_{\mathrm{LR\ to\ LR}}$); over all years, 12% of the trout moved upstream for spawning. The probability that the trout returns to its place of origin was observed to be lower during 2005–2006 and 2008–2009 while being higher during 2006–2008. $M'_{\mathrm{LR\ to\ CB}}$ and $M'_{\mathrm{LR\ to\ LR}}$ are associated with trout movement types I and III, respectively (Fig. 2). The probability that a young trout migrates from CB to LR was equal to 0.44 when considering over all years ($M'_{\mathrm{CB\ to\ LR}}$; movement type II in Fig. 2), and small variations occurred for each separated year. Spawner return rate to their original site after reproduction was found to equal 0.58 on average. Fluctuations occurred over years, with higher values during 2004–2005, 2006–2007, and 2007–2008 (0.96, 0.69, and 0.69, respectively) and lower values during 2005–2006 and 2008–2009 (0.27 and 0.25, respectively).

A trout of LR born in CB has a probability to spawn in CB and to not come back ($M_{\mathrm{LR\ to\ CB}}$) equal to 0.04, and the probability that it returns to its place of origin ($M_{\mathrm{LR\ to\ LR}}$) was estimated equal to 0.05 over all years 2004–2010 (Table 5). This latter probability was observed to be lower for years 2005–2006 and 2008–2009 but higher during 2006–2008. In LR, the recapture probability of a trout born in CB (R_{LR}) was estimated equal to 0.22 on average. Comparatively, recapture probability for this group of trout in CB was greater ($R_{\mathrm{CB}} = 0.33$). Recapture probabilities of trout at the trapping facility

Fig. 4. Proportions of individuals performing movement types I (*a*), II (*b*), and III (*c*) computed from the full data set of observations at the trapping facility (grey circles) compared with those derived from multistate capture–recapture models 9 and 16 applied to total capture histories (black circles). 95% confidence intervals are displayed for each estimate (no intervals were available for computed values).



(R_{TF}) were estimated equal to unity by both time-independent and time-dependent models. It was expected because only trout captured in state YT at the downstream trap were considered. For the same reason, survival probabilities in CB (S_{CB}) were all estimated nearly equal to unity, the probability that a trout born in CB emigrates to LR was estimated very high ($M_{CB\text{ to }LR}$), and values for parameters M_{CB} and M_{LR} were estimated very low and very high, respectively. These two latter movement probabilities are linked to trout movement types IV and V (Fig. 2) (i.e., they correspond to the probability for a trout born in CB to stay in CB and in LR, respectively). Trout return rate to their natal site for spawning was found equal to 0.09 over all years 2004–2010. Considering separated years, values did not fluctuate much (2005–2006: 0.07; 2006–2007: 0.14; 2007–2008: 0.17; 2008–2009: 0.06). The value for the year 2004–2005 was not computed, as the estimates were obviously incorrect.

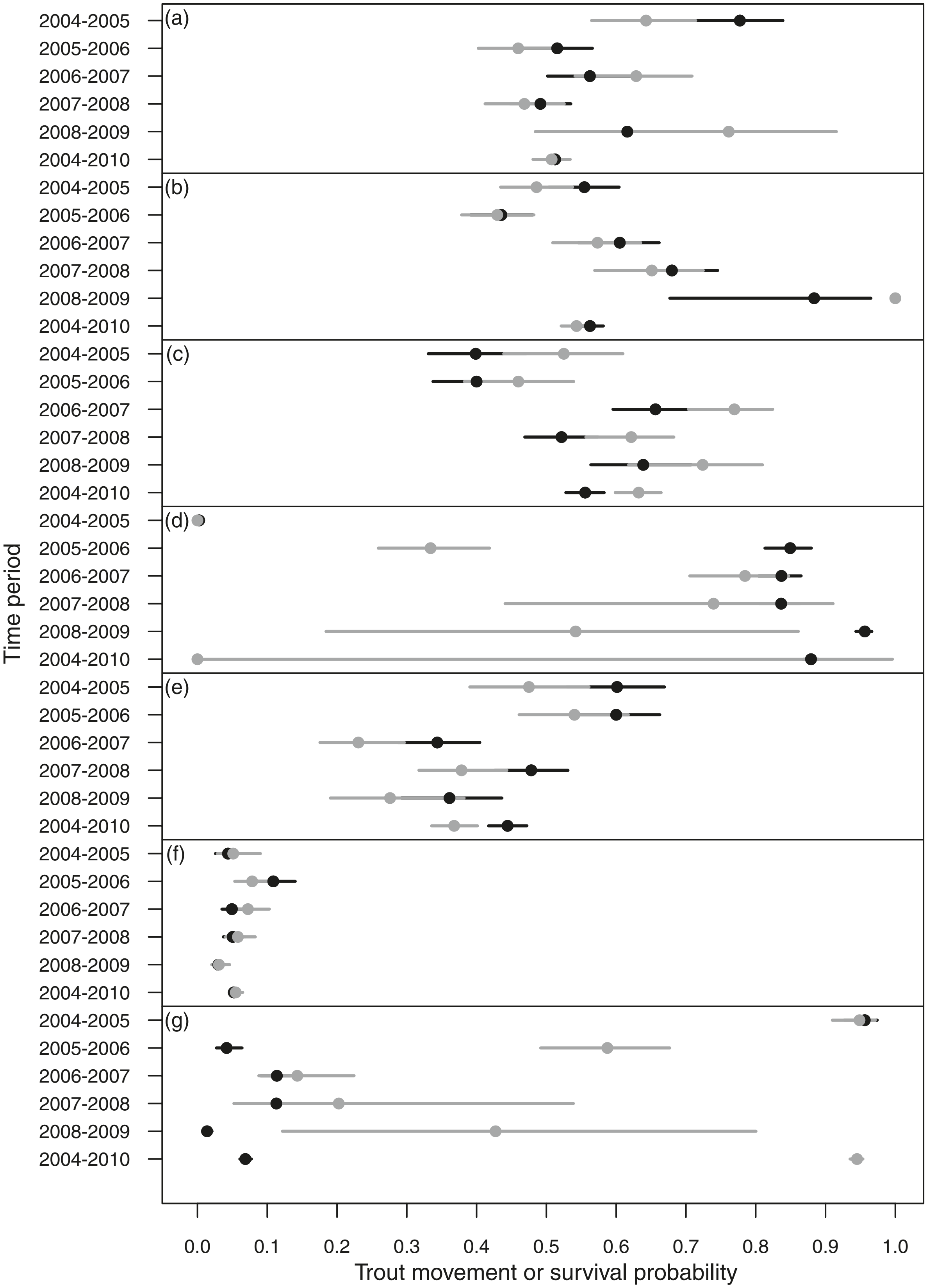
Performance of MSCR models

Proportions of individuals performing movement types I, II, and III (Fig. 2) computed from the simple analysis of FDS were first compared with those derived from MSCR models 9 and 16 (Table 2) applied to TCH (comparison C1). Then, differences between survival and movement parameter estimates derived from the same models applied to TCH, PCH1, PCH2, and PCH3 were examined (C2). Eventually, FDS results were compared with those obtained from RDS and PCH2 (C3).

Results of the C1 comparison were visualized (Fig. 4) and allowed us to determine if estimates from MSCR models were consistent with true movement observations. Indeed, results from the simple analysis of FDS reflected true movements of trout and not estimates, because the capture efficiency in the traps is almost 100%. Considering movement type I, differences between estimated and computed values were all below 6%. One value out of six was overestimated (years 2004–2010) by models applied to TCH, but two were consistent (years 2007–2008 and 2008–2009); other values were all underestimated. For values linked to movement type II, one out of six was overestimated (year 2005–2006) by models, but two were consistent (years 2006–2007 and 2008–2009); other values were all underestimated. Differences between estimated and computed values were all below 10%, excepted for the year 2004–2005 (40%). Two of the six values associated with movement type III were consistent (years 2005–2006 and 2008–2009), and other values were all overestimated by models. Differences between estimated and computed values were all below 9%, excepted for the year 2004–2005 (44%). Overall, six values were comparable for each proportion of individuals performing movement types I to III; two of them were consistent while the others were either underestimated or overestimated by MSCR models. If results obtained for the year 2004–2005 are discarded, discrepancies between estimated and computed values were all below 10%.

The sensitivity of MSCR models to the efficiency of the trapping facility was assessed by the C2 comparison, in which survival and movement probabilities derived from TCH were compared with those from PCH1, PCH2, and PCH3 (TCH and PCH2 comparison is shown in Fig. 5 as an example). The following effects were observed. First, trout survival probabilities were most of the time underestimated when considering PCH. The discrepancy between TCH and PCH estimates was, however, smaller for LR than for CB.

Fig. 5. Comparison between trout survival and movement probabilities estimated by the time-dependent multistate capture–recapture model (separated years, model 9 in Table 2) and the time-independent model (years 2004–2010, model 16) applied to total capture histories 2 (black circles) and to partial capture histories (grey circles): (*a*) trout survival in the Chicheron Brook (CB), (*b*) survival in the Lesse River (LR), (*c*) stay in CB, (*d*) stay in LR, (*e*) movement from CB to LR, (*f*) movement from LR to CB, and (*g*) movement from LR to LR. 95% confidence intervals are also displayed.



Second, an overestimation was observed for trout probabilities to stay in CB (associated with movement type IV) when considering PCH. On the contrary, an underestimation was observed for probabilities to stay in LR (type V) when considering PCH. Discrepancies between TCH and PCH estimates over all years 2004–2010 were rather large. Third, young trout movement probabilities from CB to LR (type II) were underestimated, while movement probabilities for spawning in CB and coming back (type III) were overestimated when considering PCH. Surprisingly, TCH and PCH estimates of spawning movement probabilities to CB (type I) were all in accordance. In general, observed over- or underestimations were better with PCH1 and worse with PCH3. Discrepancies between TCH and PCH survival estimates and those associated with movement types II and IV were weak (i.e., below 7% for PCH1; 15% for PCH2; 23% for PCH3) and even weaker for type I (i.e., below 6% for PCH1, PCH2, and PCH3). Large discrepancies were observed for probabilities linked to movement types III and V (i.e., around 88% for PCH1, PCH2, and PCH3). Furthermore, probabilities associated with types I, III, and V were not correlated with the quantity of trapping data.

Results of the C3 comparison allowed us to evaluate the effects of combining two sources of data when the efficiency of the trapping facility was reduced to 50% (RDS). The purpose was to determine if results were improved or not by the presence of electrofishing data. When comparing results from the simple analysis applied on FDS and RDS, all differences were below 8.1% for all movement types. Yet, it appears that they were on average higher for movement types I and III. The comparison of FDS and PCH2 results showed that all differences were below 17% for types I and III (excepted for type III during year 2004–2005, for which it was 30%) and between 47% and 86% for type II. These differences were compared between them to quantify the expected improvement. For type I, we found no change over all years 2004–2010 (values between –2% and 7%), except for a small improvement for year 2005–2006 (14%). The same result was obtained for type III, with values between 1% and 7% when considering over all years and a small improvement for the year 2004–2005 (22%). Considering movement type II, high improvements were observed with values between 45% and 85% for separated years and 84% over all years 2004–2010.

Discussion

In this paper, we first evaluated performance of MSCR models and their sensitivity to the level of data integration. On the one hand, MSCR estimates were consistent with true movement observations at the trapping facility, as we found only a low error (10%) when they were compared. Besides, their narrow confidence intervals gave evidence of their accuracy. We concluded that MSCR estimates can be safely used to infer trout spawning behaviour. On the other hand, we quantified the extent to which estimates of MSCR models were inaccurate or biased when they were applied to partial capture histories, constructed by varying the sample size of the trapping data. We also determined if considering an additional source of data could be a solution for ecological systems where only limited trapping data are available. Results showed that two trout movement probabilities were the most sensitive: (*i*) the probability for a trout to stay in LR and (*ii*) the probability for a trout to spawn in CB and to come back. These probabilities were underestimated by 88% because some trout that were captured exclusively at the downstream trap were not detected afterwards. We also found that results of young trout downstream movement probability were improved by 85% when electrofishing data were combined with data from a half-efficient trapping facility.

The second objective of the paper was to study the role of CB as spawning ground and nursery area for brown trout. We used results drawn from two different approaches to investigate their spawning behaviour: (*i*) a simple analysis of the full data set of movement observations at the trapping facility and (*ii*) MSCR modelling applied to total capture histories. Comparing results obtained for the same hydrological system over the years 1957–1969 by Huet and Timmermans (1979), mean numbers derived from the simple analysis are all in the same ranges. Indeed, on average and over the years 2004–2010, 169 adults migrated from LR to CB to spawn (respective extremes: 124 and 222), 77 adults returned to LR after spawning (extremes: 32 and 120), and 819 juveniles (i.e., 676 tagged plus 143 untagged fish; extremes: 328 and 1311) moved from CB to LR. In the study conducted by Huet and Timmermans (1979), these numbers were 242 upspawners (extremes: 83 and 530), 150 downspawners (extremes: 70 and 201), 464 juveniles (extremes: 286 and 1007), respectively. Likewise, current spawning and downstream migration periods are roughly identical to those observed 50 years ago.

The simple analysis also revealed that 85% of the adults spawn in the brook only once in their lifetime and that 59% of them returned to the main stream after the reproduction period. The return rate computed from MSCR model estimates was equal to 58% and higher during 2006–2007 (70%) and 2007–2008 (69%). All these results are in accordance with those previously obtained by Huet and Timmermans (1979). Indeed, they found a return rate of spawners equal to 62% on average (extremes: 38% and 84%). Survival rate of trout in the brook (the probability of the fish surviving and remaining in the brook) was estimated equal to 51%. If we extrapolate this finding and consider that half of the upswimming spawners died during their stay in the brook, post-spawning homing behaviour appears exclusive, as originally hypothesized by Dupont (2004); if they had survived, all the spawners would have returned to their original territory. It seems likely that this high mortality is due to predation by herons (E. Dupont, Earth and Life Institute, Université catholique de Louvain, Croix du Sud 2 Box L7.05.14, 1348 Louvain-la-Neuve, Belgium, personal communication, 2011). Spawning movements between the main stream and the brook are influenced by the year period and appear limited by high flow and probably also water temperature (Huet and Timmermans 1979). In fact, a recent study showed that the upstream migration of spawners to CB is mainly driven by environmental conditions such as water level (B.M. Frank, E. Dupont, P.V. Baret, and B. Jonsson, unpublished data).

Estimates from MSCR models revealed that a young trout has a probability of 44% to migrate from the brook to the main stream, with fluctuations over years between 34% and 60%. Analysis of observations at the downstream trap showed that years 2007–2008 and 2008–2009 were exceptional, with twice as many individuals emigrating downstream compared with the other years. This movement could be explained by the rising of waters in the spring (Ovidio et al. 1998), as well as by density-dependent mechanisms, such as territorial competition or limited food availability (Milner et al. 2003). Besides, Huet and Timmermans (1979) suggested that juvenile downstream migration is mainly driven by water temperature. They observed that the movement usually begins when the temperature in the brook is above 10 °C. Return rates of trout to their natal site for spawning were low (computed and estimated values were all below 18%). Comparatively, in France, Baglinière et al. (1987) reported that 22% of the spawners moving from the Scorff River to a nursery stream were young trout that had previously emigrated from this stream. This finding can be explained by the fact that this movement takes at least 2 years and trout have to survive until then. Indeed, 82% of the individuals were observed to return to their natal brook the second and third year after their downstream migration, suggesting that they took advantage of this richer feeding area to grow and mature (Baglinière et al. 1987; Jonsson and Jonsson 1993). These results are in agreement with the hypothesis that this downstream movement can be voluntary and advantageous and is thus not entirely driven by density-dependent population regulation (Jonsson and Gravem 1985; Steingrímsson and Grant 2003). Moreover, recent results support the assumption that the tendency for juveniles to emigrate from nursery brooks is both density- and climate-dependent (B.M. Frank, E. Dupont, P.V. Baret, and B. Jonsson, unpublished data). Previous studies found that brown trout preferentially spawn in first-order streams because they seem to be more advantageous for reproduction and for juvenile growth (Baglinière and Maisse 1990; Armstrong et al. 2003). The strong homing instinct of the trout is also a factor to consider (Elliott 1994; Laikre 1999). Among the 561 spawners observed in the upstream trap over the years 2004–2010, 311 had already been captured as juveniles in the downstream trap (i.e., homing individuals). The percentage of ascending trout performing natal homing is thus equal to 55%, and this finding is in disagreement with the opinion expressed by Huet and Timmermans (1979).

Additional results about survival and recapture probabilities were found with MSCR modelling. On average, trout survival was equal to 54% in both streams, but we observed survival rates, respectively, 19% and 27% higher in the main river than in the brook in 2007–2008 and 2008–2009. These results are explained by the high emigration rate of trout to the main stream observed for both years. Also, a 2% rate of tag loss was observed, and this could lead to an underestimation of survival, as previously shown for Atlantic salmon (*Salmo salar*) (Sigourney et al. 2005). Estimates of trout recapture probabilities in the tributary were always greater than in the main river, considering either over all years (49% vs. 30%) or each separated year. As electrofishing sampling techniques are size-selective (Bohlin et al. 1989; Dolan and Miranda 2003), recapture efficiency should be higher in the main stream, which is mainly inhabited by adults. However, catchability is also dependent of the physical characteristics of the sampling site (e.g., stream width, depth, substrate, water velocity). Indeed, the electrofishing efficiency is known to decrease with increasing river width (Kennedy and Strange 1981), and this could explain why trout were easier to catch in the small CB than in the larger LR. Another hypothesis is that the catchability difference could simply be due to the electrofishing equipment used (i.e., a mobile system for CB vs. a stationary one for LR).

Advantages of MSCR modelling over the simple analysis of trout movements, or over the kind of study conducted by Huet and Timmermans (1979), are twofold. First, it has allowed uncertainty on parameters to be quantified via confidence intervals. The combination of data collected from multiple sources in capture–recapture models is a way to increase the precision of estimates, to control for bias in parameter estimations, and to produce additional estimates. Second, MSCR models have brought additional biological knowledge on the hydrological system. More particularly, trout survival and recapture probabilities were estimated for both streams. Furthermore, we demonstrated that postspawning homing and natal homing were frequent behaviours for the trout of the studied system.

The approaches presented here can be adapted to other animal migration studies with similar sampling design (e.g., fish, amphibians). The MSCR model could be extended by including abiotic factors (i.e., covariates; see Pollock 2002; Lebreton 2006) such as temperature or water level to address additional questions about the interaction of migrating animals with their environment.

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Supplemental materials for Frank et al. CJFAS

Supplemental Appendix S1 - Mathematical formulation and instructions for implementing the multistate capture-recapture models in program E-SURGE

At each sampling occasion A (i.e., by electrofishing), an individual may be non-spawner in the brook (state NS1), non-spawner in the main river (state NS2) or dead (state D). The following observations may be made: 1 (if caught NS1), 2 (if caught NS2) and 0 (if not caught). At each sampling occasion B (i.e. by trapping), an individual may be young trout migrating out of the brook (state YT), spawner moving from the main river to the brook but not coming back (state SP1), spawner moving from the main river to the brook and coming back (state SP2) or dead (state D). The following observations may be made: 3 (if caught YT), 4 (if caught SP1), 5 (if caught SP2) and 0 (if not caught).

We defined the initial state vector (**p**), the transition matrix (which is decomposed into two matrices: survival matrix **S** and movement matrix **M**) and the event matrix (**R**):

$$\mathbf{p} = \begin{pmatrix} p_1 & p_2 & p_3 & p_4 & 1 - p_1 - p_2 - p_3 - p_4 & 0 \end{pmatrix}$$

$$\mathbf{S} = \begin{pmatrix} S_1 & 0 & 0 & 0 & 0 & 1 - S_1 \\ 0 & S_2 & 0 & 0 & 0 & 1 - S_2 \\ 0 & 0 & S_3 & 0 & 0 & 1 - S_3 \\ 0 & 0 & 0 & S_3 & 0 & 1 - S_3 \\ 0 & 0 & 0 & 0 & S_3 & 1 - S_3 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}$$

$$\mathbf{M} = \begin{pmatrix} 1 - M_1 & 0 & M_1 & 0 & 0 & 0 \\ 0 & 1 - M_2 - M_3 & 0 & M_2 & M_3 & 0 \\ 0 & M_4 & 1 - M_4 & 0 & 0 & 0 \\ M_4 & 0 & 0 & 1 - M_4 & 0 & 0 \\ 0 & M_4 & 0 & 0 & 1 - M_4 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}$$

$$\mathbf{R} = \begin{pmatrix} 1 - R_1 & R_1 & 0 & 0 & 0 & 0 \\ 1 - R_2 & 0 & R_2 & 0 & 0 & 0 \\ 1 - R_3 & 0 & 0 & R_3 & 0 & 0 \\ 1 - R_3 & 0 & 0 & 0 & R_3 & 0 \\ 1 - R_3 & 0 & 0 & 0 & 0 & R_3 \\ 1 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}$$

Columns of matrices **p**, **S** and **M** correspond respectively to state NS1, NS2, YT, SP1, SP2 and D. Columns of the matrix **R** correspond to the observations 'not caught', 'caught as NS1', 'caught as NS2', 'caught as YT', 'caught as SP1' and 'caught as SP2'. Rows of matrices **R**, **S** and **M** correspond respectively to state NS1, NS2, YT, SP1, SP2 and D. According to the occasion considered, some probabilities were set equal in order to simplify the parameter fixation with the IVFV interface (see later). For instance, recapture probabilities of individuals caught in states YT, SP1 and SP2 were all equal to R_3, and this parameter was fixed to 0 at occasions A.

Multistate capture-recapture models (see Lebreton et al., 2009, for a recent review) can be implemented in program E-SURGE (Choquet et al., 2009*b*), which is freely downloadable at `http://www.cefe.cnrs.fr/biom/En/softwares.htm`. The first step is to load the data into the program and specify the number of groups (2 here), states (6 here), events (6 here), age classes (2 here) and covariate (0 here). Then, the model specification procedure is decomposed into (i) implementing the basic structural form of the matrices using the GEPAT interface, (ii) setting linear model of each parameter using the GEMACO interface and (iii) fixing initial parameters using the IVFV interface.

Matrices **p**, **S**, **M** and **R** introduced above are specified as follows in the GEPAT module ('*' entries denote the complement of the sum of positive rows entries, and '-' entries denote zero):

```
%%%% Initial state %%%%%%
1
1 5 IS
p p p p *
%%%% Transition %%%%%%
2
6 6 S
f - - - - *
- f - - - *
- - f - - *
- - - f - *
- - - - f *
- - - - - *

6 6 M
* - y - - -
- * - y y -
- y * - - -
y - - * - -
- y - - * -
- - - - - *
%%%% Event %%%%%%
1
6 6 R
* b - - - -
* - b - - -
* - - b - -
* - - - b -
```

```
* - - - - b
* - - - - -
```

In the GEMACO interface (Choquet, 2008), the general structure of the model is constrained in order to fit the desired model. Predefined shortcuts are used to specify which parameters are time-constant, time-specific or state-specific (e.g., ‘i’ denotes constancy, ‘t’ means time effect, ‘g’ denotes a group effect, ‘f’ and ‘to’ mean that parameters are not equal in each matrix row and column, respectively). For the events, the first capture occasions are distinguished from the following ones using the shortcuts ‘firste’ and ‘nexte’, because the capture history of individuals is conditional on being caught in the first period and the following recapture probabilities depend on the state and the time occasions. The phrases used to construct the four models are presented in Table S1.1.

In the IVFV interface, the following constraints should be set before running the models. At occasions A (i.e., 1, 3, 5, 7, 9, 11), beta values associated with survival parameter S_3 and first capture parameters R_1 and R_2 should be constrained to 1, and movement parameter M_4 and recapture parameter R_3 for first and next periods to 0. At occasions B (i.e., 2, 4, 6, 8, 10, 12), beta values associated with survival parameters S_1, S_2 and S_3 as well as movement parameter M_4 and first capture parameter R_3 should be constrained to 1, and movement parameters M_1, M_2 and M_3 as well as recapture parameters R_1 and R_2 for first and next periods to 0.

Table S1.1: GEMACO sentences used to construct the four multistate models.

Effect	Phrases
A. Initial State IS	
constant	i
B. Event R	
constant	firste.[f(1)&f(2)+f(3)&f(4)&f(5)].t(1 3 5 7 9 11)
	+firste.[f(1)&f(2)+f(3)&f(4)&f(5)].t(2 4 6 8 10 12)
	+nexte.[f(1)+f(2)+f(3)&f(4)&f(5)].t(3 5 7 9 11)
	+nexte.[f(1)&f(2)+f(3)&f(4)&f(5)].t(4 6 8 10 12)
time	firste.[f(1)&f(2)+f(3)&f(4)&f(5)].t(1 3 5 7 9 11)
	+firste.[f(1)&f(2)+f(3)&f(4)&f(5)].t(2 4 6 8 10 12)
	+nexte.[f(1)+f(2)+f(3)&f(4)&f(5)].t(3, 5, 7, 9, 11)
	+nexte.[f(1)&f(2)+f(3)&f(4)&f(5)].t(4, 6, 8, 10, 12)
constant × group	firste.[f(1)&f(2)+f(3)&f(4)&f(5)].t(1 3 5 7 9 11)
	+firste.[f(1)&f(2)+f(3)&f(4)&f(5)].t(2 4 6 8 10 12)
	+nexte.[f(1)+f(2)+f(3)&f(4)&f(5)].t(3 5 7 9 11).g
	+nexte.[f(1)&f(2)+f(3)&f(4)&f(5)].t(4 6 8 10 12).g
time × group	firste.[f(1)&f(2)+f(3)&f(4)&f(5)].t(1 3 5 7 9 11)
	+firste.[f(1)&f(2)+f(3)&f(4)&f(5)].t(2 4 6 8 10 12)
	+nexte.[f(1)+f(2)+f(3)&f(4)&f(5)].t(3, 5, 7, 9, 11).g
	+nexte.[f(1)&f(2)+f(3)&f(4)&f(5)].t(4, 6, 8, 10, 12).g
C. Transition S - Step 1	
constant	[f(1)+f(2)+f(3)&f(4)&f(5)].t(1 3 5 7 9 11)
	+[f(1)&f(2)&f(3)&f(4)&f(5)].t(2 4 6 8 10 12)
time	[f(1)+f(2)+f(3)&f(4)&f(5)].t(1, 3, 5, 7, 9, 11)
	+[f(1)&f(2)&f(3)&f(4)&f(5)].t(2 4 6 8 10 12)
constant × group	[f(1)+f(2)+f(3)&f(4)&f(5)].t(1 3 5 7 9 11).g
	+[f(1)&f(2)&f(3)&f(4)&f(5)].t(2 4 6 8 10 12)
time × group	[f(1)+f(2)+f(3)&f(4)&f(5)].t(1, 3, 5, 7, 9, 11).g
	+[f(1)&f(2)&f(3)&f(4)&f(5)].t(2 4 6 8 10 12)
D. Transition M - Step 2	
constant	[f(1).to(3)+f(2).to(4)+f(2).to(5)+f(3 4 5)].t(1 3 5 7 9 11)
	+[f(1).to(3)&f(2).to(4)&f(2).to(5)+f(3 4 5)].t(2 4 6 8 10 12)
time	[f(1).to(3)+f(2).to(4)+f(2).to(5)+f(3 4 5)].t(1, 3, 5, 7, 9, 11)
	+[f(1).to(3)&f(2).to(4)&f(2).to(5)+f(3 4 5)].t(2, 4, 6, 8, 10, 12)
constant × group	[f(1).to(3)+f(2).to(4)+f(2).to(5)+f(3 4 5)].t(1 3 5 7 9 11).g
	+[f(1).to(3)&f(2).to(4)&f(2).to(5)+f(3 4 5)].t(2 4 6 8 10 12)
time × group	[f(1).to(3)+f(2).to(4)+f(2).to(5)+f(3 4 5)].t(1, 3, 5, 7, 9, 11).g
	+[f(1).to(3)&f(2).to(4)&f(2).to(5)+f(3 4 5)].t(2, 4, 6, 8, 10, 12)

Supplemental Appendix S2 - Goodness of fit test for the Jolly-Move model applied to total and partial capture histories

Goodness of fit (GoF) tests are used to measure the adequacy between the data and the various assumptions underlying the statistical models. The lack of fit of a model is approximated by the variance inflation factor: $\hat{c} \cong \frac{\text{Dev}}{\text{df}}$, where Dev is the deviance of the model and df is the number of degrees of freedom of the model. The deviance is equal to $-2\ ln$ Likelihood.

Two general models are used for GoF tests: the Cormack-Jolly-Seber (CJS; Cormack, 1964; Jolly, 1965; Seber, 1965) model and variants for single-state data, and the Jolly-Move (JMV; Brownie et al., 1993) model and variants for multistate data (Pradel et al., 2005). If the general model fits the data, the value of the deviance of this model is equal to the number of degrees of freedom and $\hat{c}$ value equals 1. When the $\hat{c}$ value of a model is greater than 1, it means that the model is not properly fitted to the data. There are two reasons for this (Burnham and Anderson, 2002; Choquet et al., 2009*a*): (1) the model structure is not suitable for the data, for example because one of the assumptions underlying the capture-recapture method was not respected; (2) the sample variance exceeds the theoretical variance, i.e., the data show an extra binomial variation (overdispersion). In the first case, the model is biologically unrealistic and has simply to be corrected, then the $\hat{c}$ of the new obtained model is checked. In the second case, the cause is purely statistical and the only solution is to take into account the noise, by using the $\hat{c}$ value to calculate the QAIC of the model.

Results of goodness of fit tests for the JMV model applied to total and partial capture histories 1, 2 and 3 are presented in Table S2.1.

Table S2.1: Goodness of fit test for (a) total capture histories, (b) partial capture histories 1, (c) partial capture histories 2 and (d) partial capture histories 3 calculated by adding the individual X^2 values and degrees of freedom (df) for each group (individuals born in CB and of unknown origin). The variance inflation factor ($\hat{c}$), computed as the ratio of X^2 to df, is given for each test component and for the global test.

(a) Total capture histories

Test component	X^2	**p**	**df**	$\hat{c}$
WBWA	0.000	1.000	3	0.000
3G.SR	33.387	0.001	12	2.782
3G.SM	21.919	0.857	30	0.731
M.ITEC	18.488	0.005	6	3.081
M.LTEC	0.835	0.841	3	0.278
TOTAL	74.629	0.033	54	1.382

(b) Partial capture histories 1

Test component	X^2	**p**	**df**	$\hat{c}$
WBWA	1.519	0.823	4	0.380
3G.SR	27.972	0.014	14	1.998
3G.SM	58.445	0.023	39	1.499
M.ITEC	4.432	0.816	8	0.554
M.LTEC	4.048	0.400	4	1.012
TOTAL	96.416	0.016	69	1.397

(c) Partial capture histories 2

Test component	X^2	**p**	**df**	$\hat{c}$
WBWA	5.031	0.540	6	0.839
3G.SR	31.814	0.004	14	2.272
3G.SM	50.271	0.088	38	1.323
M.ITEC	20.830	0.004	7	2.976
M.LTEC	1.325	0.723	3	0.442
TOTAL	109.271	0.001	68	1.607

(d) Partial capture histories 3

Test component	X^2	**p**	**df**	$\hat{c}$
WBWA	14.554	0.042	7	2.079
3G.SR	28.423	0.019	15	1.895
3G.SM	63.009	0.012	40	1.575
M.ITEC	11.363	0.124	7	1.623
M.LTEC	2.572	0.462	3	0.857
TOTAL	119.919	0.000	72	1.666

Supplemental Appendix S3 - Simple analysis of trout movements at the trapping facility applied to the reduced data set

Proportions of trout performing movement types I to III and the annual return rates of adults to their location of origin after the reproduction period were computed from the reduced data set (Table S3.1).

Table S3.1: Number (and associated percentage) of individuals performing the following movement types during the six years of the study (reduced data set): (I) strict immigration, (II) strict emigration, (III) immigration then emigration; and spawner return rates to their original-site after reproduction (III / (I+III)). The last column presents results over the years 2004-2010.

Type	2004-2005	2005-2006	2006-2007	2007-2008	2008-2009	2009-2010	2004-2010
I	55 (13)	64 (20)	82 (21)	76 (11)	55 (9)	57 (25)	248 (10)
II	340 (79)	240 (77)	266 (69)	592 (85)	539 (90)	159 (70)	2300 (89)
III	33 (8)	9 (3)	36 (9)	25 (4)	5 (1)	12 (5)	39 (2)
III / (I+III)	38	12	31	25	8	17	14

Supplemental Appendix S4 - Parameters estimates from multistate capture-recapture models applied to total and partial capture histories

In total, ten parameters were estimated by multistate capture-recapture (MSCR) models applied to total capture histories: trout recapture probabilities in both streams, the Chicheron brook (CB) and the Lesse river (LR) (R_{CB} and R_{LR}) as well as at the trapping facility (R_{TF}), trout survival probabilities in both streams (S_{CB} and S_{LR}), trout probabilities to stay in both streams (M_{CB} and M_{LR}), young trout movement probability to emigrate out of CB to LR ($M_{CB\ to\ LR}$), movement probabilities for spawners of LR to go reproduce in CB and to not come back or to come back ($M_{LR\ to\ CB}$ and $M_{LR\ to\ LR}$). Estimates obtained from models 1 and 8 are shown in Table S4.1 and those from models 9 and 16 in Table S4.2.

For the three partial capture histories, the number of parameters is twelve in each case because recapture parameter R_{TF} is split into three to take into account the states of individuals caught in the traps (YT, young trout migrating out of the brook; SP1, spawner moving from the main river to the brook but not coming back; SP2, spawner moving from the main river to the brook and coming back): $R_{TF\ as\ YT}$, $R_{TF\ as\ SP1}$ and $R_{TF\ as\ SP2}$. Tables S4.3, S4.4 and S4.5 show estimates obtained from models 9 and 16.

Table S4.1: Survival (S), recapture (R) and movement (M) estimates from (a) time-independent and (b-f) time-dependent models with group effect applied to total capture histories with lower (CI-) and upper (CI+) 95% confidence intervals and standard error (SE). Superscripts *a* and *b* stand for the group of trout born in the brook and the group of unknown origin trout, respectively.

(a) 2004-2010

Parameter	Estimate	CI-	CI+	SE
S^{a}_{CB}	0.9459	0.9273	0.9599	0.0082
S^{a}_{LR}	0.5883	0.5537	0.6221	0.0175
R^{a}_{CB}	0.3255	0.2522	0.4084	0.0401
R^{a}_{LR}	0.2213	0.2080	0.2353	0.0070
R^{a}_{TF}	1.0000	1.0000	1.0000	0.0000
M^{a}_{CB}	0.0869	0.0685	0.1097	0.0104
M^{a}_{LR}	0.9005	0.8858	0.9136	0.0071
$M^{a}_{CB\ to\ LR}$	0.9131	0.8903	0.9315	0.0104
$M^{a}_{LR\ to\ CB}$	0.0447	0.0369	0.0542	0.0044
$M^{a}_{LR\ to\ LR}$	0.0548	0.0458	0.0653	0.0049
S^{b}_{CB}	0.4396	0.4037	0.4762	0.0185
S^{b}_{LR}	0.4990	0.4772	0.5208	0.0111
R^{b}_{CB}	0.3948	0.3526	0.4387	0.0220
R^{b}_{LR}	0.6104	0.5773	0.6425	0.0167
R^{b}_{TF}	0.6300	0.4866	0.7536	0.0697
M^{b}_{CB}	0.9904	0.9829	0.9947	0.0029
M^{b}_{LR}	0.7591	0.7074	0.8041	0.0247
$M^{b}_{CB\ to\ LR}$	0.0096	0.0053	0.0171	0.0029
$M^{b}_{LR\ to\ CB}$	0.0874	0.0720	0.1057	0.0085
$M^{b}_{LR\ to\ LR}$	0.1535	0.1176	0.1980	0.0204

(b) 2004-2005

Parameter	Estimate	CI-	CI+	SE
S^{a}_{CB}	1.0000	1.0000	1.0000	0.0000
S^{a}_{LR}	0.5000	0.5000	0.5000	0.0000
R^{a}_{CB}	1.0000	1.0000	1.0000	0.0000
R^{a}_{LR}	1.0000	1.0000	1.0000	0.0000
R^{a}_{TF}	1.0000	1.0000	1.0000	0.0000
M^{a}_{CB}	0.0272	0.0086	0.0825	0.0158
M^{a}_{LR}	0.3333	0.3333	0.3333	0.0000
$M^{a}_{CB\ to\ LR}$	0.9728	0.9175	0.9914	0.0158
$M^{a}_{LR\ to\ CB}$	0.3333	0.3333	0.3333	0.0000
$M^{a}_{LR\ to\ LR}$	0.3333	0.3333	0.3333	0.0000
S^{b}_{CB}	0.5176	0.4281	0.6059	0.0458
S^{b}_{LR}	0.4974	0.4518	0.5430	0.0233
R^{b}_{CB}	1.0000	1.0000	1.0000	0.0000
R^{b}_{LR}	1.0000	1.0000	1.0000	0.0000
R^{b}_{TF}	1.0000	1.0000	1.0000	0.0000
M^{b}_{CB}	0.9826	0.9161	0.9966	0.0143
M^{b}_{LR}	0.0000	0.0000	0.0000	0.0000
$M^{b}_{CB\ to\ LR}$	0.0174	0.0034	0.0839	0.0143
$M^{b}_{LR\ to\ CB}$	0.0526	0.0312	0.0875	0.0139
$M^{b}_{LR\ to\ LR}$	0.9474	0.9125	0.9688	0.0139

(c) 2005-2006

Parameter	Estimate	CI-	CI+	SE
S^{a}_{CB}	1.0000	1.0000	1.0000	0.0000
S^{a}_{LR}	0.4457	0.3603	0.5344	0.0449
R^{a}_{CB}	1.0000	1.0000	1.0000	0.0000
R^{a}_{LR}	0.2175	0.1810	0.2591	0.0199
R^{a}_{TF}	1.0000	1.0000	1.0000	0.0000
M^{a}_{CB}	0.0083	0.0016	0.0410	0.0068
M^{a}_{LR}	0.9319	0.8835	0.9611	0.0191
$M^{a}_{CB\ to\ LR}$	0.9917	0.9590	0.9984	0.0068
$M^{a}_{LR\ to\ CB}$	0.0568	0.0308	0.1022	0.0174
$M^{a}_{LR\ to\ LR}$	0.0114	0.0030	0.0423	0.0077
S^{b}_{CB}	0.3763	0.2980	0.4618	0.0421
S^{b}_{LR}	0.4062	0.3631	0.4506	0.0224
R^{b}_{CB}	0.5485	0.4518	0.6417	0.0490
R^{b}_{LR}	0.5893	0.5310	0.6451	0.0292
R^{b}_{TF}	0.9396	0.7484	0.9879	0.0479
M^{b}_{CB}	0.9897	0.9481	0.9980	0.0086
M^{b}_{LR}	0.7707	0.7145	0.8187	0.0266
$M^{b}_{CB\ to\ LR}$	0.0103	0.0020	0.0519	0.0086
$M^{b}_{LR\ to\ CB}$	0.1606	0.1214	0.2094	0.0224
$M^{b}_{LR\ to\ LR}$	0.0687	0.0435	0.1067	0.0158

(d) 2006-2007

Parameter	Estimate	CI-	CI+	SE
S^{a}_{CB}	0.9171	0.8523	0.9550	0.0253
S^{a}_{LR}	0.5377	0.4509	0.6223	0.0442
R^{a}_{CB}	0.1765	0.0471	0.4817	0.1088
R^{a}_{LR}	0.2499	0.2124	0.2916	0.0202
R^{a}_{TF}	1.0000	1.0000	1.0000	0.0000
M^{a}_{CB}	0.0859	0.0459	0.1549	0.0268
M^{a}_{LR}	0.8586	0.8084	0.8972	0.0225
$M^{a}_{CB\ to\ LR}$	0.9141	0.8451	0.9541	0.0268
$M^{a}_{LR\ to\ CB}$	0.0278	0.0138	0.0553	0.0099
$M^{a}_{LR\ to\ LR}$	0.1137	0.0797	0.1595	0.0201
S^{b}_{CB}	0.5774	0.4556	0.6903	0.0610
S^{b}_{LR}	0.6341	0.5665	0.6969	0.0334
R^{b}_{CB}	0.3438	0.2716	0.4240	0.0391
R^{b}_{LR}	0.6863	0.6098	0.7539	0.0370
R^{b}_{TF}	0.7034	0.5015	0.8483	0.0913
M^{b}_{CB}	0.9735	0.9411	0.9882	0.0109
M^{b}_{LR}	0.7234	0.6361	0.7964	0.0411
$M^{b}_{CB\ to\ LR}$	0.0265	0.0118	0.0589	0.0109
$M^{b}_{LR\ to\ CB}$	0.0879	0.0594	0.1282	0.0173
$M^{b}_{LR\ to\ LR}$	0.1887	0.1283	0.2689	0.0358

(e) 2007-2008

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^{a}_{CB}	0.9773	0.9425	0.9913	0.0109
S^{a}_{LR}	0.7289	0.6120	0.8209	0.0538
R^{a}_{CB}	0.6211	0.3834	0.8120	0.1164
R^{a}_{LR}	0.2492	0.2149	0.2869	0.0184
R^{a}_{TF}	1.0000	1.0000	1.0000	0.0000
M^{a}_{CB}	0.1138	0.0795	0.1603	0.0204
M^{a}_{LR}	0.8352	0.7922	0.8707	0.0200
$M^{a}_{CB\ to\ LR}$	0.8862	0.8397	0.9205	0.0204
$M^{a}_{LR\ to\ CB}$	0.0473	0.0309	0.0718	0.0102
$M^{a}_{LR\ to\ LR}$	0.1175	0.0887	0.1541	0.0166
S^{b}_{CB}	0.3506	0.2754	0.4341	0.0408
S^{b}_{LR}	0.5293	0.4584	0.5990	0.0361
R^{b}_{CB}	0.4443	0.3559	0.5363	0.0465
R^{b}_{LR}	0.5935	0.5256	0.6580	0.0340
R^{b}_{TF}	0.9272	0.5607	0.9922	0.0792
M^{b}_{CB}	0.9969	0.9695	0.9997	0.0036
M^{b}_{LR}	0.7806	0.7129	0.8360	0.0314
$M^{b}_{CB\ to\ LR}$	0.0031	0.0003	0.0305	0.0036
$M^{b}_{LR\ to\ CB}$	0.0729	0.0466	0.1124	0.0164

(f) 2008-2009

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^{a}_{CB}	0.9113	0.8507	0.9488	0.0243
S^{a}_{LR}	0.6995	0.5662	0.8060	0.0621
R^{a}_{CB}	0.3898	0.2662	0.5294	0.0687
R^{a}_{LR}	0.2253	0.2020	0.2504	0.0124
R^{a}_{TF}	1.0000	1.0000	1.0000	0.0000
M^{a}_{CB}	0.0916	0.0537	0.1520	0.0244
M^{a}_{LR}	0.9392	0.9183	0.9551	0.0093
$M^{a}_{CB\ to\ LR}$	0.9084	0.8480	0.9463	0.0244
$M^{a}_{LR\ to\ CB}$	0.0403	0.0283	0.0570	0.0072
$M^{a}_{LR\ to\ LR}$	0.0205	0.0128	0.0327	0.0049
S^{b}_{CB}	1.0000	0.0000	1.0000	0.0003
S^{b}_{LR}	0.6965	0.3611	0.9031	0.1511
R^{b}_{CB}	0.4599	0.3633	0.5597	0.0507
R^{b}_{LR}	0.5594	0.4788	0.6371	0.0407
R^{b}_{TF}	0.6787	0.3392	0.8968	0.1574
M^{b}_{CB}	0.9976	0.9857	0.9996	0.0022
M^{b}_{LR}	0.9312	0.8655	0.9661	0.0243
$M^{b}_{CB\ to\ LR}$	0.0024	0.0004	0.0143	0.0022
$M^{b}_{LR\ to\ CB}$	0.0501	0.0241	0.1012	0.0184

Table S4.2: Survival (S'), recapture (R') and movement (M') estimates from (a) time-independent and (b-f) time-dependent models without group effect applied to total capture histories with lower (CI-) and upper (CI+) 95% confidence intervals and standard error (SE).

(a) 2004-2010

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S'_{CB}	0.5125	0.4919	0.5331	0.0105
S'_{LR}	0.5625	0.5432	0.5816	0.0098
R'_{CB}	0.4882	0.4519	0.5247	0.0186
R'_{LR}	0.3039	0.2908	0.3173	0.0068
R'_{TF}	0.9669	0.9402	0.9819	0.0101
M'_{CB}	0.5556	0.5279	0.5828	0.0140
M'_{LR}	0.8792	0.8676	0.8899	0.0057
$M'_{CB\ to\ LR}$	0.4444	0.4172	0.4721	0.0140
$M'_{LR\ to\ CB}$	0.0521	0.0458	0.0594	0.0035
$M'_{LR\ to\ LR}$	0.0687	0.0608	0.0774	0.0042

(b) 2004-2005

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S'_{CB}	0.7773	0.7004	0.8389	0.0354
S'_{LR}	0.5545	0.5036	0.6042	0.0257
R'_{CB}	1.0000	1.0000	1.0000	0.0000
R'_{LR}	1.0000	1.0000	1.0000	0.0000
R'_{TF}	1.0000	1.0000	1.0000	0.0000
M'_{CB}	0.3987	0.3308	0.4708	0.0359
M'_{LR}	0.0000	0.0000	0.0000	0.0000
$M'_{CB\ to\ LR}$	0.6013	0.5292	0.6692	0.0359
$M'_{LR\ to\ CB}$	0.0438	0.0259	0.0732	0.0116
$M'_{LR\ to\ LR}$	0.9562	0.9268	0.9741	0.0116

(c) 2005-2006

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S'_{CB}	0.5155	0.4649	0.5659	0.0258
S'_{LR}	0.4355	0.3914	0.4806	0.0228
R'_{CB}	0.5931	0.4977	0.6819	0.0475
R'_{LR}	0.3537	0.3206	0.3881	0.0172
R'_{TF}	0.9470	0.8980	0.9731	0.0181
M'_{CB}	0.4000	0.3375	0.4659	0.0329
M'_{LR}	0.8494	0.8132	0.8797	0.0169
$M'_{CB\ to\ LR}$	0.6000	0.5341	0.6625	0.0329
$M'_{LR\ to\ CB}$	0.1087	0.0837	0.1401	0.0143
$M'_{LR\ to\ LR}$	0.0418	0.0272	0.0639	0.0091

(d) 2006-2007

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S'_{CB}	0.5624	0.5015	0.6214	0.0307
S'_{LR}	0.6052	0.5457	0.6616	0.0297
R'_{CB}	0.4009	0.3271	0.4796	0.0392
R'_{LR}	0.3649	0.3286	0.4027	0.0189
R'_{TF}	1.0000	1.0000	1.0000	0.0000
M'_{CB}	0.6563	0.5954	0.7125	0.0300
M'_{LR}	0.8368	0.8041	0.8650	0.0155
$M'_{CB\ to\ LR}$	0.3437	0.2875	0.4046	0.0300
$M'_{LR\ to\ CB}$	0.0494	0.0351	0.0691	0.0085
$M'_{LR\ to\ LR}$	0.1138	0.0907	0.1418	0.0130

(e) 2007-2008

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S'_{CB}	0.4915	0.4482	0.5350	0.0222
S'_{LR}	0.6799	0.6065	0.7454	0.0356
R'_{CB}	0.5837	0.5031	0.6601	0.0404
R'_{LR}	0.3496	0.3169	0.3837	0.0171
R'_{TF}	0.9899	0.9411	0.9983	0.0093
M'_{CB}	0.5217	0.4691	0.5739	0.0268
M'_{LR}	0.8364	0.8053	0.8633	0.0148
$M'_{CB\ to\ LR}$	0.4783	0.4261	0.5309	0.0268
$M'_{LR\ to\ CB}$	0.0505	0.0371	0.0685	0.0079
$M'_{LR\ to\ LR}$	0.1131	0.0914	0.1392	0.0121

(f) 2008-2009

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S'_{CB}	0.6159	0.5031	0.7174	0.0555
S'_{LR}	0.8837	0.6769	0.9650	0.0676
R'_{CB}	0.5283	0.4537	0.6017	0.0380
R'_{LR}	0.2672	0.2441	0.2916	0.0121
R'_{TF}	0.9857	0.8763	0.9985	0.0164
M'_{CB}	0.6388	0.5637	0.7076	0.0370
M'_{LR}	0.9563	0.9435	0.9663	0.0058
$M'_{CB\ to\ LR}$	0.3612	0.2924	0.4363	0.0370
$M'_{LR\ to\ CB}$	0.0299	0.0221	0.0402	0.0045
$M'_{LR\ to\ LR}$	0.0138	0.0091	0.0209	0.0029

Table S4.3: Survival (S^1), recapture (R^1) and movement (M^1) estimates from (a) time-independent and (b-f) time-dependent models without group effect applied to partial capture histories 1 with lower (CI-) and upper (CI+) 95% confidence intervals and standard error (SE). *YT*, *SP1* and *SP2* notation stand for the following states: young trout migrating out of the brook (CB to LR), spawner moving from the main river to the brook but not coming back (LR to CB), spawner moving from the main river to the brook and coming back (LR to LR), respectively.

(a) 2004-2010

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^1_{CB}	0.5233	0.4976	0.5489	0.0131
S^1_{LR}	0.5573	0.5353	0.5790	0.0112
R^1_{CB}	0.4678	0.4281	0.5080	0.0204
R^1_{LR}	0.3320	0.3154	0.3490	0.0086
$R^1_{TF\ as\ YD}$	0.6948	0.6389	0.7456	0.0273
$R^1_{TF\ as\ SP1}$	0.8560	0.7679	0.9143	0.0368
$R^1_{TF\ as\ SP2}$	0.0457	0.0385	0.0542	0.0040
M^1_{CB}	0.5764	0.5434	0.6086	0.0166
M^1_{LR}	0.0000	0.0000	0.0000	0.0000
$M^1_{CB\ to\ LR}$	0.4236	0.3914	0.4566	0.0166
$M^1_{LR\ to\ CB}$	0.0573	0.0492	0.0667	0.0045
$M^1_{LR\ to\ LR}$	0.9427	0.9333	0.9508	0.0045

(b) 2004-2005

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^1_{CB}	0.7081	0.6254	0.7790	0.0394
S^1_{LR}	0.5186	0.4644	0.5724	0.0277
R^1_{CB}	1.0000	1.0000	1.0000	0.0000
R^1_{LR}	1.0000	1.0000	1.0000	0.0000
$R^1_{TF\ as\ YD}$	1.0000	1.0000	1.0000	0.0000
$R^1_{TF\ as\ SP1}$	1.0000	1.0000	1.0000	0.0000
$R^1_{TF\ as\ SP2}$	1.0000	1.0000	1.0000	0.0000
M^1_{CB}	0.4643	0.3827	0.5479	0.0425
M^1_{LR}	0.0000	0.0000	0.0000	0.0000
$M^1_{CB\ to\ LR}$	0.5357	0.4521	0.6173	0.0425
$M^1_{LR\ to\ CB}$	0.0536	0.0308	0.0919	0.0150
$M^1_{LR\ to\ LR}$	0.9464	0.9081	0.9692	0.0150

(c) 2005-2006

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^1_{CB}	0.4886	0.4304	0.5471	0.0299
S^1_{LR}	0.4357	0.3841	0.4888	0.0268
R^1_{CB}	0.5469	0.4475	0.6428	0.0505
R^1_{LR}	0.4086	0.3667	0.4519	0.0218
$R^1_{TF\ as\ YD}$	0.6421	0.5422	0.7311	0.0487
$R^1_{TF\ as\ SP1}$	0.8854	0.6783	0.9659	0.0672
$R^1_{TF\ as\ SP2}$	0.1497	0.0820	0.2574	0.0440
M^1_{CB}	0.4248	0.3514	0.5017	0.0386
M^1_{LR}	0.7149	0.5986	0.8083	0.0541
$M^1_{CB\ to\ LR}$	0.5752	0.4983	0.6486	0.0386
$M^1_{LR\ to\ CB}$	0.0890	0.0630	0.1243	0.0155
$M^1_{LR\ to\ LR}$	0.1961	0.1119	0.3208	0.0531

(d) 2006-2007

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^1_{CB}	0.6035	0.5264	0.6757	0.0383
S^1_{LR}	0.5797	0.5139	0.6428	0.0331
R^1_{CB}	0.4409	0.3526	0.5330	0.0465
R^1_{LR}	0.3917	0.3471	0.4382	0.0233
$R^1_{TF\ as\ YD}$	0.8328	0.6837	0.9198	0.0593
$R^1_{TF\ as\ SP1}$	0.7978	0.5999	0.9122	0.0797
$R^1_{TF\ as\ SP2}$	0.1836	0.1418	0.2343	0.0236
M^1_{CB}	0.6928	0.6218	0.7558	0.0343
M^1_{LR}	0.4488	0.4044	0.4940	0.0229
$M^1_{CB\ to\ LR}$	0.3072	0.2442	0.3782	0.0343
$M^1_{LR\ to\ CB}$	0.0698	0.0492	0.0981	0.0123
$M^1_{LR\ to\ LR}$	0.4814	0.4249	0.5384	0.0291

(e) 2007-2008

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^1_{CB}	0.5018	0.4467	0.5569	0.0282
S^1_{LR}	0.6737	0.5885	0.7488	0.0412
R^1_{CB}	0.5283	0.4431	0.6119	0.0435
R^1_{LR}	0.3903	0.3490	0.4332	0.0215
$R^1_{TF\ as\ YD}$	0.7790	0.6785	0.8548	0.0451
$R^1_{TF\ as\ SP1}$	1.0000	1.0000	1.0000	0.0000
$R^1_{TF\ as\ SP2}$	0.9997	0.9995	0.9998	0.0001
M^1_{CB}	0.5660	0.5036	0.6264	0.0315
M^1_{LR}	0.8501	0.8149	0.8796	0.0165
$M^1_{CB\ to\ LR}$	0.4340	0.3736	0.4964	0.0315
$M^1_{LR\ to\ CB}$	0.0649	0.0470	0.0891	0.0106
$M^1_{LR\ to\ LR}$	0.0850	0.0639	0.1121	0.0122

(f) 2008-2009

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^1_{CB}	0.6241	0.4753	0.7527	0.0725
S^1_{LR}	0.9228	0.5051	0.9929	0.0895
R^1_{CB}	0.4748	0.3974	0.5535	0.0401
R^1_{LR}	0.2955	0.2661	0.3267	0.0155
$R^1_{TF\ as\ YD}$	0.7321	0.5728	0.8478	0.0713
$R^1_{TF\ as\ SP1}$	0.6976	0.4514	0.8661	0.1110
$R^1_{TF\ as\ SP2}$	0.1041	0.0699	0.1524	0.0208
M^1_{CB}	0.6641	0.5687	0.7478	0.0461
M^1_{LR}	0.8729	0.8310	0.9056	0.0189
$M^1_{CB\ to\ LR}$	0.3359	0.2522	0.4313	0.0461
$M^1_{LR\ to\ CB}$	0.0334	0.0222	0.0500	0.0069
$M^1_{LR\ to\ LR}$	0.0936	0.0643	0.1345	0.0177

Table S4.4: Survival (S^2), recapture (R^2) and movement (M^2) estimates from (a) time-independent and (b-f) time-dependent models without group effect applied to partial capture histories 2 with lower (CI-) and upper (CI+) 95% confidence intervals and standard error (SE). *YT*, *SP1* and *SP2* notation stand for the following states: young trout migrating out of the brook (CB to LR), spawner moving from the main river to the brook but not coming back (LR to CB), spawner moving from the main river to the brook and coming back (LR to LR), respectively.

(a) 2004-2010

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^2_{CB}	0.5075	0.4808	0.5341	0.0136
S^2_{LR}	0.5432	0.5212	0.5650	0.0112
R^2_{CB}	0.4750	0.4337	0.5167	0.0212
R^2_{LR}	0.3815	0.3620	0.4014	0.0100
$R^2_{TF\ as\ YT}$	0.5152	0.4611	0.5689	0.0276
$R^2_{TF\ as\ SP1}$	0.8438	0.7442	0.9094	0.0416
$R^2_{TF\ as\ SP2}$	0.0334	0.0270	0.0411	0.0036
M^2_{CB}	0.6322	0.5988	0.6644	0.0168
M^2_{LR}	0.0000	0.0000	0.0000	0.0000
$M^2_{CB\ to\ LR}$	0.3678	0.3356	0.4012	0.0168
$M^2_{LR\ to\ CB}$	0.0549	0.0465	0.0648	0.0047
$M^2_{LR\ to\ LR}$	0.9451	0.9352	0.9535	0.0047

(b) 2004-2005

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^2_{CB}	0.6428	0.5648	0.7139	0.0383
S^2_{LR}	0.4859	0.4344	0.5376	0.0264
R^2_{CB}	1.0000	1.0000	1.0000	0.0000
R^2_{LR}	1.0000	1.0000	1.0000	0.0000
$R^2_{TF\ as\ YT}$	1.0000	1.0000	1.0000	0.0000
$R^2_{TF\ as\ SP1}$	1.0000	1.0000	1.0000	0.0000
$R^2_{TF\ as\ SP2}$	1.0000	1.0000	1.0000	0.0000
M^2_{CB}	0.5250	0.4389	0.6097	0.0440
M^2_{LR}	0.0000	0.0000	0.0000	0.0000
$M^2_{CB\ to\ LR}$	0.4750	0.3903	0.5611	0.0440
$M^2_{LR\ to\ CB}$	0.0513	0.0286	0.0902	0.0151
$M^2_{LR\ to\ LR}$	0.9487	0.9098	0.9714	0.0151

(c) 2005-2006

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^2_{CB}	0.4596	0.4025	0.5177	0.0295
S^2_{LR}	0.4296	0.3785	0.4822	0.0265
R^2_{CB}	0.5708	0.4706	0.6656	0.0504
R^2_{LR}	0.4581	0.4113	0.5057	0.0241
$R^2_{TF\ as\ YT}$	0.5221	0.4229	0.6196	0.0509
$R^2_{TF\ as\ SP1}$	0.8822	0.6365	0.9697	0.0770
$R^2_{TF\ as\ SP2}$	0.0353	0.0180	0.0681	0.0120
M^2_{CB}	0.4598	0.3826	0.5390	0.0402
M^2_{LR}	0.3341	0.2591	0.4186	0.0410
$M^2_{CB\ to\ LR}$	0.5402	0.4610	0.6174	0.0402
$M^2_{LR\ to\ CB}$	0.0784	0.0535	0.1136	0.0151
$M^2_{LR\ to\ LR}$	0.5874	0.4919	0.6768	0.0477

(d) 2006-2007

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^2_{CB}	0.6287	0.5410	0.7087	0.0432
S^2_{LR}	0.5733	0.5091	0.6351	0.0323
R^2_{CB}	0.4776	0.3813	0.5756	0.0502
R^2_{LR}	0.4417	0.3914	0.4933	0.0261
$R^2_{TF\ as\ YT}$	0.7260	0.5632	0.8448	0.0731
$R^2_{TF\ as\ SP1}$	0.7332	0.5224	0.8735	0.0920
$R^2_{TF\ as\ SP2}$	0.5318	0.3239	0.7291	0.1096
M^2_{CB}	0.7694	0.7035	0.8244	0.0309
M^2_{LR}	0.7846	0.7055	0.8470	0.0361
$M^2_{CB\ to\ LR}$	0.2306	0.1756	0.2965	0.0309
$M^2_{LR\ to\ CB}$	0.0723	0.0502	0.1031	0.0133
$M^2_{LR\ to\ LR}$	0.1431	0.0880	0.2244	0.0344

(e) 2007-2008

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^2_{CB}	0.4685	0.4122	0.5256	0.0291
S^2_{LR}	0.6511	0.5693	0.7248	0.0400
R^2_{CB}	0.4954	0.4126	0.5785	0.0427
R^2_{LR}	0.4594	0.4112	0.5083	0.0248
$R^2_{TF\ as\ YT}$	0.5784	0.4779	0.6728	0.0504
$R^2_{TF\ as\ SP1}$	1.0000	1.0000	1.0000	0.0000
$R^2_{TF\ as\ SP2}$	0.3046	0.0714	0.7139	0.1880
M^2_{CB}	0.6216	0.5566	0.6826	0.0323
M^2_{LR}	0.7395	0.4409	0.9108	0.1259
$M^2_{CB\ to\ LR}$	0.3784	0.3174	0.4434	0.0323
$M^2_{LR\ to\ CB}$	0.0580	0.0403	0.0829	0.0107
$M^2_{LR\ to\ LR}$	0.2025	0.0523	0.5386	0.1257

(f) 2008-2009

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^2_{CB}	0.7613	0.4842	0.9155	0.1134
S^2_{LR}	1.0000	1.0000	1.0000	0.0000
R^2_{CB}	0.5083	0.4241	0.5920	0.0432
R^2_{LR}	0.3472	0.3115	0.3846	0.0187
$R^2_{TF\ as\ YT}$	0.4484	0.3278	0.5753	0.0645
$R^2_{TF\ as\ SP1}$	0.7116	0.4567	0.8786	0.1127
$R^2_{TF\ as\ SP2}$	0.0120	0.0037	0.0381	0.0071
M^2_{CB}	0.7240	0.6179	0.8096	0.0493
M^2_{LR}	0.5419	0.1843	0.8610	0.2097
$M^2_{CB\ to\ LR}$	0.2760	0.1904	0.3821	0.0493
$M^2_{LR\ to\ CB}$	0.0308	0.0205	0.0461	0.0064
$M^2_{LR\ to\ LR}$	0.4272	0.1219	0.8003	0.2099

Table S4.5: Survival (S^3), recapture (R^3) and movement (M^3) estimates from (a) time-independent and (b-f) time-dependent models without group effect applied to partial capture histories 3 with lower (CI-) and upper (CI+) 95% confidence intervals and standard error (SE). *YT*, *SP1* and *SP2* notation stand for the following states: young trout migrating out of the brook (CB to LR), spawner moving from the main river to the brook but not coming back (LR to CB), spawner moving from the main river to the brook and coming back (LR to LR), respectively.

(a) 2004-2010

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^3_{CB}	0.4624	0.4377	0.4874	0.0127
S^3_{LR}	0.5173	0.4965	0.5380	0.0106
R^3_{CB}	0.5387	0.4937	0.5830	0.0228
R^3_{LR}	0.4819	0.4583	0.5057	0.0121
$R^3_{TF\ as\ YD}$	0.3794	0.3313	0.4300	0.0253
$R^3_{TF\ as\ SP1}$	0.7175	0.5979	0.8126	0.0554
$R^3_{TF\ as\ SP2}$	0.0153	0.0112	0.0210	0.0025
M^3_{CB}	0.6846	0.6531	0.7145	0.0157
M^3_{LR}	0.0000	0.0000	0.0000	0.0000
$M^3_{CB\ to\ LR}$	0.3154	0.2855	0.3469	0.0157
$M^3_{LR\ to\ CB}$	0.0454	0.0373	0.0551	0.0045
$M^3_{LR\ to\ LR}$	0.9546	0.9449	0.9627	0.0045

(b) 2004-2005

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^3_{CB}	0.5594	0.4908	0.6258	0.0347
S^3_{LR}	0.4324	0.3882	0.4778	0.0229
R^3_{CB}	1.0000	1.0000	1.0000	0.0000
R^3_{LR}	1.0000	1.0000	1.0000	0.0000
$R^3_{TF\ as\ YD}$	1.0000	1.0000	1.0000	0.0000
$R^3_{TF\ as\ SP1}$	1.0000	1.0000	1.0000	0.0000
$R^3_{TF\ as\ SP2}$	1.0000	1.0000	1.0000	0.0000
M^3_{CB}	0.6258	0.5392	0.7050	0.0427
M^3_{LR}	0.0000	0.0000	0.0000	0.0000
$M^3_{CB\ to\ LR}$	0.3742	0.2950	0.4608	0.0427
$M^3_{LR\ to\ CB}$	0.0495	0.0276	0.0873	0.0146
$M^3_{LR\ to\ LR}$	0.9505	0.9127	0.9724	0.0146

(c) 2005-2006

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^3_{CB}	0.3853	0.3355	0.4377	0.0261
S^3_{LR}	0.4224	0.3746	0.4716	0.0248
R^3_{CB}	0.6478	0.5439	0.7393	0.0504
R^3_{LR}	0.5950	0.5409	0.6469	0.0271
$R^3_{TF\ as\ YD}$	0.3703	0.2772	0.4742	0.0509
$R^3_{TF\ as\ SP1}$	0.6739	0.3968	0.8665	0.1283
$R^3_{TF\ as\ SP2}$	0.0201	0.0075	0.0528	0.0100
M^3_{CB}	0.5319	0.4512	0.6110	0.0411
M^3_{LR}	0.1209	0.0024	0.8879	0.2198
$M^3_{CB\ to\ LR}$	0.4681	0.3890	0.5488	0.0411
$M^3_{LR\ to\ CB}$	0.0553	0.0339	0.0890	0.0136
$M^3_{LR\ to\ LR}$	0.8238	0.1917	0.9893	0.2208

(d) 2006-2007

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^3_{CB}	0.6111	0.5295	0.6869	0.0405
S^3_{LR}	0.5859	0.5232	0.6460	0.0315
R^3_{CB}	0.5471	0.4411	0.6489	0.0538
R^3_{LR}	0.5373	0.4805	0.5932	0.0289
$R^3_{TF\ as\ YD}$	0.5148	0.3710	0.6562	0.0748
$R^3_{TF\ as\ SP1}$	0.5409	0.3502	0.7203	0.0991
$R^3_{TF\ as\ SP2}$	0.0865	0.0000	0.9987	0.3621
M^3_{CB}	0.7908	0.7272	0.8428	0.0295
M^3_{LR}	0.4628	0.0000	1.0000	1.9363
$M^3_{CB\ to\ LR}$	0.2092	0.1572	0.2728	0.0295
$M^3_{LR\ to\ CB}$	0.0741	0.0510	0.1064	0.0139
$M^3_{LR\ to\ LR}$	0.4631	0.0000	1.0000	1.9352

(e) 2007-2008

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^3_{CB}	0.4431	0.3894	0.4980	0.0278
S^3_{LR}	0.6062	0.5300	0.6776	0.0379
R^3_{CB}	0.5611	0.4727	0.6458	0.0446
R^3_{LR}	0.5465	0.4902	0.6016	0.0285
$R^3_{TF\ as\ YD}$	0.4618	0.3694	0.5568	0.0484
$R^3_{TF\ as\ SP1}$	1.0000	1.0000	1.0000	0.0000
$R^3_{TF\ as\ SP2}$	0.0398	0.0149	0.1019	0.0196
M^3_{CB}	0.6618	0.5989	0.7194	0.0309
M^3_{LR}	0.3498	0.0559	0.8303	0.2561
$M^3_{CB\ to\ LR}$	0.3382	0.2806	0.4011	0.0309
$M^3_{LR\ to\ CB}$	0.0424	0.0272	0.0655	0.0095
$M^3_{LR\ to\ LR}$	0.6079	0.1579	0.9276	0.2569

(f) 2008-2009

Parameter	**Estimate**	**CI-**	**CI+**	**SE**
S^3_{CB}	0.6787	0.4060	0.8672	0.1255
S^3_{LR}	1.0000	1.0000	1.0000	0.0000
R^3_{CB}	0.5368	0.4491	0.6223	0.0446
R^3_{LR}	0.4261	0.3814	0.4720	0.0232
$R^3_{TF\ as\ YD}$	0.2637	0.1808	0.3674	0.0479
$R^3_{TF\ as\ SP1}$	0.8795	0.3686	0.9892	0.1366
$R^3_{TF\ as\ SP2}$	0.0019	0.0004	0.0077	0.0014
M^3_{CB}	0.7401	0.6187	0.8333	0.0552
M^3_{LR}	0.0657	0.0000	0.9927	0.2370
$M^3_{CB\ to\ LR}$	0.2599	0.1667	0.3813	0.0552
$M^3_{LR\ to\ CB}$	0.0148	0.0089	0.0247	0.0039
$M^3_{LR\ to\ LR}$	0.9194	0.0209	0.9998	0.2374

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