CONCEPTS & SYNTHESIS

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RESTRICTED MOVEMENT IN STREAM FISH: THE PARADIGM IS INCOMPLETE, NOT LOST

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Abstract. The ''restricted-movement paradigm'' (RMP) states that adult fish in streams are sedentary and spend most of their lives in short (20–50 m) reaches of stream. In mark–recapture studies, however, many fish initially marked are often never recaptured. As well, turnover rates of individuals in the home section (where fish were originally marked) can be high when marked fish moving out are rapidly replaced by unmarked ones. Recent challenges to the RMP have been based on the inference that high turnover indicates high mobility. However, when the home section is small many individuals may leave (high turnover) but not move far away (low displacement). I present two models for the frequency distribution of displacement distances: one represents populations as homogeneous ensembles with a single mobility parameter; the second represents populations as a mixture of stationary and mobile individuals. Both readily distinguish the turnover and displacement components of movement and show that high turnover rate is compatible with low displacement. The models were then fit to dispersal curves for six species of stream salmonids in 27 populations. Empirical estimates of turnover rate were high (median: 0.53), variable among populations (range: 0.15–0.78), but unrelated to displacement distance. Median displacement was <100 m for 24 populations and was typically <50 m. The proportion of mobile individuals was low in most populations (median: 19%) and exceeded 50% in only five of the populations. Brook trout, a species central to studies critical of the RMP, appeared to be exceptionally mobile relative to other salmonids. The compatibility of high turnover rates with short displacement distances and the finding that median displacement was usually limited support the notion that restricted movement is the norm in populations of stream salmonids during nonmigratory periods. However, the finding of considerable intra- and interspecific heterogeneity in the extent of movement underscores the potential importance of the mobile component to population processes. By providing an analytical framework that yields quantitative measures of different components of movement and allows for standardized comparisons, these models can bring needed rigor to analysis and design in movement studies.

Key words: animal movement; dispersal behavior; displacement distance; intrapopulation variation; mark–recapture; models, exponential; restricted-movement paradigm (RMP); salmonid fish; stream habitats; turnover rate.

Introduction

There is growing interest among ecologists in quantifying animal movements and evaluating their biological consequences (Gaines and Bertness 1993, Porter and Dooley 1993, Turchin 1998, Okubo and Levin 2001). For example, knowledge of fish movement in streams contributes to our understanding of energy transfers (Hall 1972), longitudinal size patterns (Hughes and Reynolds 1994), links between ''source'' and ''sink'' populations (Schlosser 1995), colonization of isolated or newly available habitats (Taylor 1997, Lonzarich et al. 1998), and whole-stream patterns of age segregation (Hughes 1998). Stream fishes provide an excellent model system for analyses, because longitudinal movement can be conveniently modeled along a single dimension, reducing model complexity and simplifying parameter estimation. Furthermore, fish can usually be sampled efficiently in streams, and rapid progress is being made due to improvements in tagging and tracking technology, which allow for nondestructive identification of small individuals over many recapture events.

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Traditionally, stream ecologists accepted the notion that adults of resident fish species are sedentary and spend most of their lives within short (20–50 m) stream reaches (Gerking 1959). This notion, termed the ''restricted-movement paradigm'' (RMP), was challenged in a thoughtful and influential review of movement in resident stream salmonids (Gowan et al. 1994). Additional support for this challenge came from a series of recent studies documenting substantial movement of brook trout (*Salvelinus fontinalis*) in high-altitude streams in the Rocky Mountains (Riley et al. 1992, Fausch et al. 1995, Gowan and Fausch 1996*a, b*).

A cornerstone of the critique is that the designs and analyses of many mark–recapture studies supporting the RMP entail potential biases against the detection of movement by not being sensitive to fish movements outside of the study reach (Gowan et al. 1994). Often, a high proportion of recaptured fish are found in the section where they were originally marked (''home section''), but many of the fish initially marked are never recaptured. Turnover rate of individuals (1 − [proportion of marked individuals]) can be high when marked fish moving out of the home section are rapidly replaced by unmarked fish. Therefore, a key assumption of the critique is that high turnover indicates high mobility. However, if the home section is small, many individuals could leave the section (high turnover) but not move far (low displacement); therefore, turnover rate could depend on the ratio of displacement to section length. Clearly, these two components of movement, turnover and displacement, need to be distinguished.

In this paper I introduce two models of movement that can: (1) provide standardized measures of mobility, (2) examine the relationship between turnover and displacement, both theoretically and empirically, and (3) characterize intra-population variation in mobility and analyze its influence on population dispersal. The models are then fit to published data on movement in stream salmonids to quantify turnover rates and displacement distances, as well as intra-population and interspecific variation in mobility under natural or seminatural conditions. Finally, I evaluate the present status of the RMP and identify some of its limitations in light of the main findings: high turnover rates compatible with short displacement distances, limited displacement, and considerable intra- and interspecific heterogeneity in the extent of movement. Although the focus here is on stream salmonids, the group for which data from the literature is most abundant, the RMP applies as well to other stream fishes and has broad implications for their management and conservation (Smithson and Johnston 1999).

Quantitative analyses of fish movement in streams

In a commonly used protocol for studying fish movement, a stream reach is divided into juxtaposed sections of approximately equal length and fish are marked within each section. Displacements are measured as the distance between the midpoint of the section in which a fish was initially captured (the ''home section'') and that in which it was recaptured. Sometimes individual displacements are measured more precisely, but are then grouped into distance classes for analysis. Both procedures generally yield a sharply declining number of recaptures on either side of the home section (e.g., Solomon and Templeton 1976, Heggenes 1988, Heggenes et al. 1991), although data are often presented as distance classes irrespective of direction (Fig. 1). Because studies often deal with multiple home sections, an aggregated distribution of number of recaptures vs. distance class is commonly generated. However, when data are pooled, stream sections near the extremities of the study reach are less well represented than those near the center, which can arbitrarily lower estimates of displacement distance (Stott 1967; also see Porter and Dooley 1993).

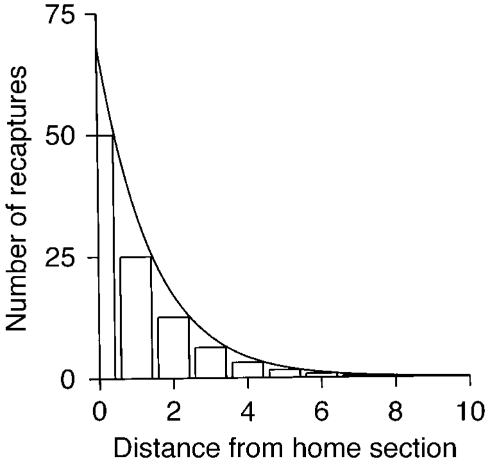


FIG. 1. Representative pattern of decline in number (or density) of recaptures with distance from home section; units for distance from home section are arbitrary. The geometric distribution (bars) generated by the number of individuals recaptured in a series of discrete distance classes (stream sections) can be approximated with a continuous, negative exponential function (curve).

Quantitative analyses of fish movement in streams seldom go beyond presenting the frequency distribution and descriptive statistics of displacement distances and testing some simple hypotheses, such as whether the numbers of fish moving upstream and downstream differ. However, a few studies have used the cumulative frequency distribution of movement distances to estimate the proportion of ''sedentary'' or ''stationary'' individuals (defined operationally as those for which displacement is less than a given distance, X) and ''mobile'' individuals (displacement $>X$) (Solomon and Templeton 1976, Harcup et al. 1984, Hesthagen 1988; other studies reviewed in Gowan et al. [1994]). Nevertheless, because of the paucity of effective analytical tools for analyzing fish movement, Gowan et al. (1994)

noted that additional refinements in quantitative methodology are needed.

Because mark–recapture studies yield data for a number of sections arranged in a defined spatial order, basing inferences on simple ratios, such as the percentage of recaptures made in the home section or the proportion of marked fish that move out of their home section, can discard useful information. A more efficient approach is to model the pattern of decline in the number of recaptures with distance from the home section. When this pattern can be modeled with a simple function, the proportion of individuals that have moved any arbitrary distance away from the home section can be found by integration. Furthermore, if fish movements observed within the study reach can be extrapolated, one can overcome the criticism that mark–recapture studies do not adequately account for movement outside of the study reach.

A simple model accounting for movement, mortality, and sampling efficiency is

$$n(x) = N_0 s \pi f(x) \qquad (1)$$

where $n(x)$ is the density of marked individuals x meters away from the home section, N_0 is the number of individuals marked and released initially in the home section, s is the survivorship over the study period, π is the probability of recapture, and $f(x)$ is a dispersal function describing the decline in density with distance from the home section. $N_0 s \pi$ is the expected number of marked individuals that would be recaptured if the whole domain of dispersal, i.e., the entire length of stream over which individuals actually disperse, were sampled at the end of the study period. This formulation assumes that neither survivorship nor probability of recapture changes with distance from the home section, and that mark loss is negligible.

For relatively homogeneous populations, a one-parameter exponential function,

$$f(x) = \lambda e^{-\lambda x} \qquad (2)$$

provides a useful first approximation to the typical pattern of decline in density of recaptures with distance from home section (Fig. 1). The exponential distribution or its discrete equivalent, the geometric distribution, have been used in numerous studies to model dispersal of terrestrial animals (Porter and Dooley 1993, Turchin 1998). The single parameter λ (m^{-1}) is the inverse of mean displacement distance; higher values of λ are therefore associated with more stationary individuals. The value of λ will not change with distance from the home section and therefore a regression estimate of λ should not be sensitive to the spatial extent of the study (equal to the number of sections times the section length). However, for a population composed of both stationary and mobile components, λ varies with distance from the home section, and thus will be sensitive to spatial extent. In that case, fitting the one-group model can bias the estimates of displacement (Fig. 2); in general, the sign and magnitude of the bias will depend on the spatial extent and population parameters.

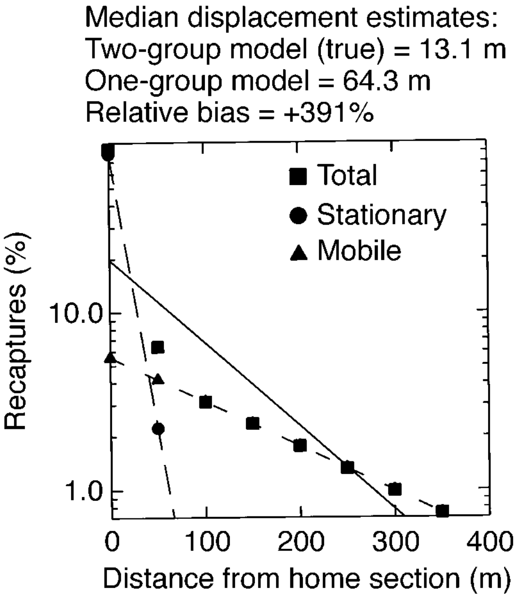


FIG. 2. Simulated data for a population consisting of a mixture of stationary (80%; $\lambda_s = 0.07111$) and mobile (20%; $\lambda_m = 0.00575$) individuals (λ is the inverse of the mean displacement distance). The dashed lines are from linear regressions for the stationary and mobile groups; their respective slopes are λ_s and λ_m. The solid line is from the linear regression for the total population; its slope is the (biased) estimator for the one-group model. (Note the logarithmic y-axis scale.) For this simulation, the relative bias inherent in calculating the median displacement of a two-group population with the one-group model is very large (391%). Note that stationary individuals do not contribute substantially to distance classes beyond 50 m.

For more heterogeneous populations, the distribution of displacement distances can be modeled as a two-group exponential function:

$$f(x) = p\lambda_s e^{-\lambda_s x} + (1 - p)\lambda_m e^{-\lambda_m x} \qquad (3)$$

where λ_s and λ_m correspond to the stationary and mobile components ($\lambda_s > \lambda_m$), p is the proportion of stationary individuals, and $1 - p$ is the proportion of mobile individuals. Note that the term ‘‘stationary’’ refers to individuals with low mobility and not necessarily to immobile individuals. The two-group model assumes that the most likely displacement distance will always be zero, which may not always be appropriate, particularly for the mobile component. Other distributions (e.g., the log-normal or gamma) may be considered when the negative exponential is not an appropriate fit.

To obtain the expected number of individuals recaptured in a given distance class, $N(X_1, X_2)$, the density function $f(x)$ is integrated over the interval (X_1, X_2) covered by the distance class:

TABLE 1. Dispersal functions and derived parameters for the one-group and two-group models.

Function or parameter	One-group model	Two-group model	Comments
Density function, $f(x)$	$\lambda e^{-\lambda x}$	$p\lambda_s e^{-\lambda_s x} + (1 - p)\lambda_m e^{-\lambda_m x}$	Proportional density (m^{-1}) at point x
Cumulative distribution function, $C(X_1, X_2)$	$e^{-\lambda X_1} - e^{-\lambda X_2}$	$p(e^{-\lambda_s X_1} - e^{-\lambda_s X_2}) + (1 - p)(e^{-\lambda_m X_1} - e^{-\lambda_m X_2})$	Proportion of individuals between points X_1 and X_2 ($X_1 \leq x \leq X_2$)
Median displacement (m)	$\frac{\ln(2)}{\lambda}$	$pe^{-\lambda_s \mathrm{median}} + (1 - p)e^{-\lambda_m \mathrm{median}} = 0.5$	50% of individuals have displacements ≤ median over the study period; no analytical solution for the two-group model, but graphical or numerical solutions are easy to obtain
Mean displacement (m)	$\frac{1}{\lambda}$	$p\frac{1}{\lambda_s} + (1 - p)\frac{1}{\lambda_m}$	Arithmetic mean of displacements
Turnover rate	$e^{-\lambda \mathrm{HSL}} = 0.5^{\mathrm{HSL/median}}$	$pe^{-\lambda_s \mathrm{HSL}} + (1 - p)e^{-\lambda_m \mathrm{HSL}}$	Proportion of individuals moving out of home section over the study period; assumes that all losses are due to emigration ($s\pi = 1$)

Notes: For both models, $n(x) = N_0 s\pi f(x)$, where $n(x)$ is the density of marked individuals x meters away from the home section, N_0 is the number of individuals marked and released initially in the home section, s is the survivorship over the study period, π is the probability of recapture, and $f(x)$ is a dispersal function describing decline in density with distance from the home section. Other symbols and abbreviations: λ, λ_s, and λ_m are displacement parameters (i.e., the inverse of the mean displacement distance; in units of m^{-1}), with subscript s denoting ''stationary'' and subscript m denoting ''mobile''; p = proportion of stationary individuals; $(1 - p)$ = proportion of mobile individuals; HSL = home-section length (in meters).

$$C(X_1, X_2) = \int_{X_1}^{X_2} f(x)\, dx \tag{4}$$

where $C(X_1, X_2)$ represents the proportion of individuals recaptured between the lower (X_1) and upper (X_2) boundaries of the distance class. Thus,

$$N(X_1, X_2) = N_0 s\pi C(X_1, X_2) \tag{5}$$

where the specific form of $C(X_1, X_2)$ differs between the one- and two-group models (Table 1). For a home section of length HSL, $X_1 = 0$ and $X_2 = \mathrm{HSL}$. If interval lengths are constant, $C(X_1, X_2)$ reproduces the geometric distribution $P(i) = q(1 - q)^{i-1}$, where $P(i)$ is the proportion of individuals that move distance i (i is measured in units of section length, i.e., $i = 1$ for the home section), and q is the probability of stopping before moving an additional section length. The link between the exponential and geometric distributions is made explicit by the relationship $q = (1 - e^{-\lambda \mathrm{HSL}})$.

The parameters in Eq. 5 can be estimated by fitting the model to the observed number of recaptures in various distance classes. To avoid bias arising from pooling, the model should be fit to data for individual home sections. Distance classes need not be adjacent or of equal length; thus, study sections can be distributed discontinuously at wide intervals over a long stream reach to ensure adequate spatial coverage. Separate analyses can be done for upstream and downstream movements when recapture frequencies are not distributed symmetrically about the home section.

When no independent estimates are available for N_0, s, and π, only the value of the product $N_0 s\pi$ can be estimated. In mark–recapture studies that use efficient sampling techniques, such as multiple-pass electrofishing, N_0 is known and π can be estimated independently, thus allowing for direct estimation of the survivorship, s. A minimum of two distance classes are required to fit the one-group model, which has two parameters ($N_0 s\pi$ and λ_s), whereas at least four distance classes are required to fit the two-group model (four parameters: $N_0 s\pi$, λ_s, λ_m, and p).

Several useful descriptors of movement, such as mean and median displacement, and turnover rate, can be derived from the parameter estimates for Eq. 5 (Table 1). Median and mean displacement are standardized measures that facilitate comparisons of movement across species and systems. They can also be useful for studying variation within streams, e.g., by performing separate analyses for upstream and downstream movement. The question whether high turnover rate implies high mobility can be muddled by the fact that high turnover may arise purely from in situ mortality or low sampling efficiency even when there is no movement out of the home section. To avoid confounding the effect of mobility with those of mortality and resampling, I calculated turnover rate by assuming that all losses from the home section are due to emigration, i.e., that $s\pi = 1$ (Table 1). This assumption therefore leads to estimating an upper limit to the influence of mobility on turnover rate.

For the one-group case, it is easy to evaluate graphically the effect of mobility on turnover rate (graphical

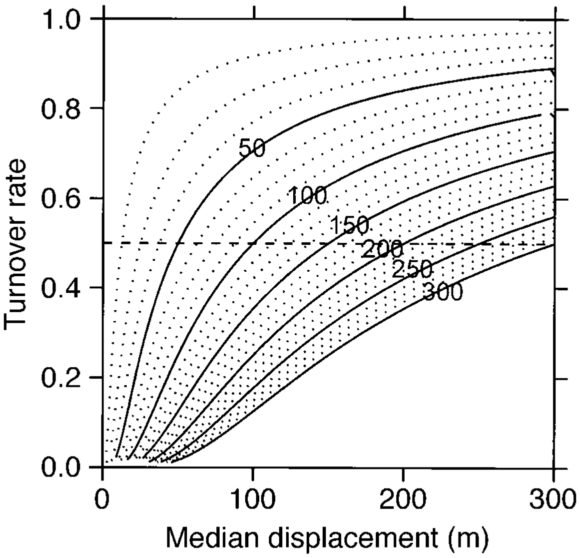


FIG. 3. Relationship among turnover rate, median displacement, and home-section length (HSL) for the one-group model. The curves connect points of equal HSL (numbers accompanying solid curves are in units of meters). The uppermost dotted line corresponds to HSL = 12.5 m.

analysis is more complicated for the two-group formula, which has four parameters: Table 1). The dependence of turnover rate on the ratio of median displacement to home-section length is shown by the following formula:

$$\text{Turnover rate} = e^{-\lambda \mathrm{HSL}} = 0.5^{\mathrm{HSL/median}}. \qquad (6)$$

When the home section is small, high turnover can occur even if movement is limited (Fig. 3). The key empirical question of how turnover rate and median displacement are related in natural populations is addressed below (see *Results* and *Discussion*).

METHODS

I collected 27 data sets describing frequency distributions of movement distance for six salmonid species: brook trout (*Salvelinus fontinalis*), Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), cutthroat trout (*Oncorhynchus clarki*), Gila trout (*Salmo gilae*), and rainbow trout (*Oncorhynchus mykiss*). The data originated from 17 studies conducted in seven countries (Table 2).

Total study duration was between 1 d and 1 yr for 24 of the data sets, and >1 yr for 3 data sets. Sampling schedules were of two different types: some studies tallied distances covered by individuals marked in an initial session and subsequently recaptured in a single session, whereas others pooled distances for all individuals marked and recaptured over multiple sampling sessions. For the latter data sets, study duration was adjusted to reflect more accurately the mean time between release and recapture of marked fish (Table 2). The spatial extent covered by the stream sections, measured as the maximum value of the distribution of displacement distances (the range of the x-axis in Fig. 1), varied substantially among data sets, from 12 to >67 500 m (Table 2).

All data sets reported the number of recaptures in at least four distance classes (median = 6; range = 4–21). Prior to analysis, recaptures expressed as percentages or proportions in each distance class were transformed to number of individuals per class. In most studies, section lengths were equal for all distance classes, but some studies used section lengths that increased systematically with distance from the home section. When exact section lengths were not given but sections were of comparable length, all sections were assigned the mean length reported by the authors. A few studies reported recaptures in open distance intervals at the end of the study reaches (reported as ‘‘distance ≥ X m’’, with no upper boundary); data from those intervals were excluded from analysis. Excluding these data reduced sample size but should not alter parameter estimates if fish movements are generally predictable from observations within the study reach. In a minority of studies, authors pooled the recapture data to generate an aggregated frequency distribution of recaptures vs. distance class. Only rarely (Allen 1951, Harcup et al. 1984) were the data adjusted to compensate for potential bias arising from pooling (see *Introduction: Quantitative analyses*. . .). Analytical procedures to estimate the magnitude of bias and adjust for bias in pooled data may sometimes be useful, but because bias in pooled data sets appeared to be small (see *Results*, below), I used data as presented in the original papers.

Parameter estimates for Eq. 5 were obtained by minimizing $\mathcal{L}$, the sum of negative log-likelihoods over all data points (nonlinear estimation module, SYSTAT program version 9 [SPSS 1999]). Independent estimates of N_0 (the number of individuals initially marked and released in the home section), s (survivorship over the study period), and π (probability of recapture), were not available for most data sets, and therefore their product was estimated as an aggregated parameter. Model fit was checked graphically for systematic deviations from predicted values. Errors were assumed to be distributed log-normally because the variance and mean showed a strong positive relationship in the untransformed data; use of a logarithmic scale stabilized the variance and rendered the distribution of residuals approximately normal in most cases. The Akaike information criterion (AIC), an information-theoretic measure that ranks models based on the support they receive from the data, was calculated for each model as: AIC = $2\mathcal{L}^* + 2K$ (Burnham and Anderson 1992). In this equation, $\mathcal{L}^*$ is the minimum value of the sum of negative log-likelihoods, evaluated at the best choice of parameters for the model, and K is the number of estimable parameters in the model, including the structural parameters and the variance. Median displace-

TABLE 2. Parameter estimates (λ, λ_s, λ_m, p) and fit (R^2) of the one-group and two-group models for the distribution of displacement distances in stream salmonids.

	Data-set information					
Data set	Species	Country	Data source	Study duration‡ (d)	Spatial extent (m)	HSL (m)
1	Atlantic salmon	Canada	Dussault (1995: Fig. 5, p. 49)	28	125	12.5
2		Scotland	García de Leañiz (1989: Fig. 2: immature parr)	175	20	2
3		Norway	Hesthagen (1988: Fig. 3, September)	37	346	20.6
4		Canada	M. A. Rodríguez and R. Larivière (*unpublished data*)	42	125	11.2
5	Brook trout	Canada	Dussault (1995: Fig. 5, p. 49)	28	125	12.5
6		United States	Fausch et al. (1995: Fig. 4)	365	1 350	50
7		United States	Shetter (1968: Table 1: last entry)	180	17 699	150
8	Brown trout	New Zealand	Allen (1951: Table 25)	160	229	15.25
9		Wales	Harcup et al. (1984: Fig. 2c)	21	430	10
10		Wales	Harcup et al. (1984: Fig. 2a)	14	210	10
10‖		Wales	Harcup et al. (1984: Fig. 2a)	14	210	10
11		Wales	Harcup et al. (1984: Fig. 2c)	14	210	10
12		Norway	Heggenes (1988: Fig. 2)	91.5	780	30
13		Norway	Hesthagen (1988: Fig. 3: September)	37	346	20.6
14		United States	Mense (1975: Table 7)	80.5	732	61
15		United States	Shetter (1968: Table 3: last entry)	180	67 578	152.5
16		England	Solomon and Templeton (1976: Fig. 8a)	122	2 900	100
17		New Zealand	Burnet (1969: Table 1: South Branch)	365	2 000	100
18		New Zealand	Burnet (1969: Table 1: Doyleston Drain)	187.5	1 098	183
19	Cutthroat trout	Canada	Heggenes et al. (1991: Fig. 3)	122	300	5
20		United States	Bjornn and Mallet (1964: Table 2)	365	33 789	1609
21	Gila trout	United States	Rinne (1982: Table 1: McKnight, 3 months)	91.5	4 000	10
22		United States	Rinne (1982: Table 1: South Diamond)	244	1 250	10
23		United States	Rinne (1982: Table 1: Main Diamond)	244	1 250	10
24	Rainbow trout	United States	Bjornn and Mallet (1964: Table 2: 3rd entry)	91.5	33 789	1609
25		United States	Bjornn and Mallet (1964: Table 2)	365	33 789	1609
26		United States	Chapman and Bjornn (1969: Fig. 5: morning-evening)	1	12	3
27		United States	Edmundson et al. (1968: Table 1: last entry)	12.5	12	3

Note: Home-section length (HSL) can be used in combination with parameter estimates to obtain all derived parameters in Table 1.

† Ellipses (···) denote ''not applicable''; n.c. indicates that parameter estimates were highly unstable or did not converge.

‡ Adjusted when necessary to reflect more accurately the mean time between release and recapture (see *Methods*).

§ The difference in Akaike's information criterion (ΔAIC) for the two models is given also; all ΔAIC values are positive, indicating support for the two-group model over the one-group model.

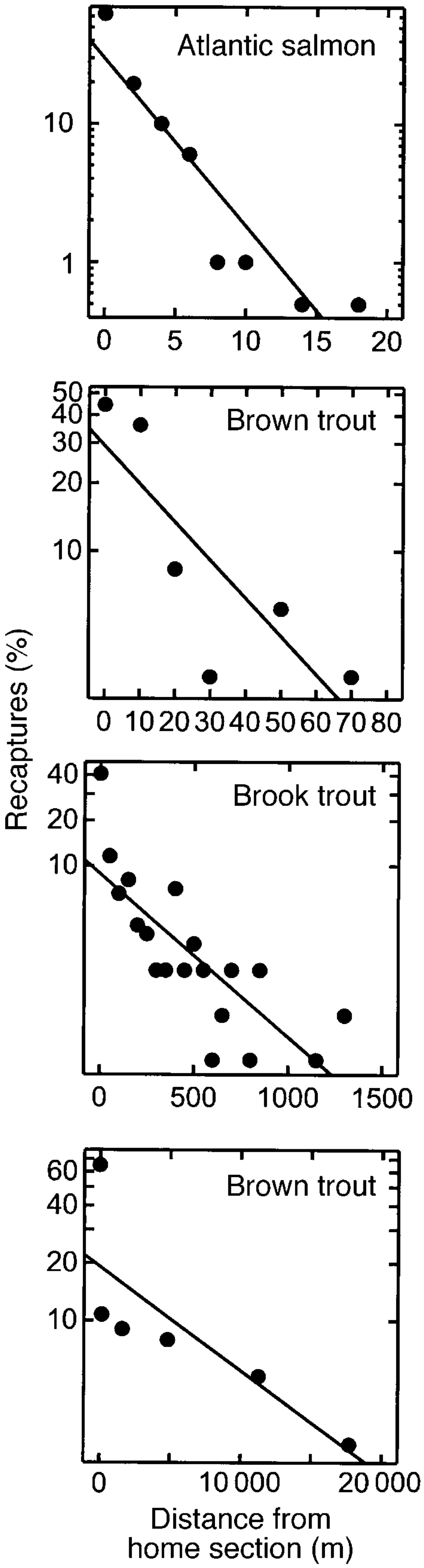
‖ Data set 10 with one outlier excluded (see *Methods*).

¶ Value fixed rather than estimated directly (see *Methods*).

TABLE 2. Extended.

Parameter estimates and fit†						Difference between models, ΔAIC§
One-group model		Two-group model				
λ (m^{-1})	R^2	λ_s (m^{-1})	λ_m (m^{-1})	p	R^2	
0.02881	···	n.c.	n.c.	n.c.	n.c.	
0.28407	0.862	n.c	n.c	n.c	n.c	
0.03452	0.840	0.08888	0.01211	0.646	0.982	27.15
0.05128	···	n.c.	n.c.	n.c.	n.c.	
0.02417	···	n.c.	n.c.	n.c.	n.c.	
0.00251	0.618	0.01767	0.00155	0.460	0.774	5.95
0.00059	0.586	0.01028	0.00037	0.842	0.935	6.16
0.01511	0.607	0.12500	0.00351	0.403	0.952	8.65
0.02129	0.472	0.14575	0.00211	0.811	0.932	26.64
0.01967	0.429	n.c.	n.c.	n.c.	n.c.	
0.04952	0.948	0.10271	0.03358	0.559	0.978	1.96
0.03870	0.681	n.c.	n.c.	n.c.	n.c.	
0.00845	0.568	n.c.	n.c.	n.c.	n.c.	
0.04675	0.731	0.22355¶	0.00519	0.740	0.983	25.79
0.00759	0.903	0.07549¶	0.00605	0.391	0.982	9.89
0.00013	0.650	0.01722	0.00014	0.691	0.979	23.33
0.00384	0.581	0.01822	0.00057	0.775	0.939	9.53
0.00238	0.646	0.01100	0.00057	0.806	0.989	37.39
0.00412	0.910	0.02516¶	0.00341	0.407	0.950	1.07
0.03142	0.609	0.16625	0.00665	0.658	0.905	25.68
n.c.	n.c.	0.00286¶	0.00005	0.243	0.928	15.25
0.02457	0.937	n.c.	n.c.	n.c.	n.c.	
n.c.	n.c.	0.04884	0.00241	0.643	0.997	32.33
0.03839	0.719	n.c.	n.c.	n.c.	n.c.	
0.00023	0.419	0.00286¶	0.00014	0.817	0.929	8.92
0.00018	0.495	1.01000	0.00013	0.515	0.998	23.71
0.33801	0.937	n.c.	n.c.	n.c.	n.c.	
0.20885	0.858	n.c.	n.c.	n.c.	n.c.	

ment and turnover rate were obtained for each data set with either the one-group model or the two-group model; model choice was based on the difference in AIC between the two models. The R^2 of observed and predicted values (Kvålseth 1985) was used as a descriptive measure of model fit except for three studies in which data were given for individual home sections rather than in pooled form (Table 2: data sets 1, 4, and 5), because the value calculated was not comparable to the values calculated for pooled data.



In one case (Table 2: data set 10), an extreme outlier was generated by five individuals, out of a total of 110 recaptures. Parameter estimates were therefore obtained once for the full data set and again after excluding the outlying point (Table 2: data set 10a); only the later estimates were retained for subsequent analysis. For five of the data sets (Table 2: data sets 13, 14, 18, 20, and 24) stable estimates were obtained for all parameters except λ_s, which could fluctuate broadly without affecting the model estimates for the remaining parameters. Estimates of λ_s for these data sets presumably were unstable because individuals from the stationary group rarely moved beyond the first distance class (i.e., out of their home section). Under such circumstances, the regression line is steep and the slope λ_s cannot be uniquely determined. To generate estimates of median displacement and turnover rate for these five data sets, λ_s was arbitrarily fixed to a value implying that not more than 1% of individuals in the stationary group had moved out of their home section at the end of the study period.

RESULTS

In all cases where parameter estimates could be obtained for both models (17 of 27 data sets), the AIC (Akaike information criterion) supported the two-group model as the best (Table 2). In these data sets, points for distance class zero (individuals that remained in the home section) had consistently large deviations from the regression line for the one-group model (see examples in Fig. 4), suggesting that these populations were composed of a mixture of stationary and mobile individuals. Fitting the two-group model eliminated this pattern in the residuals. However, for 10 data sets, the two-group model failed to converge (Table 2: n.c. entries), probably because it was overfitted, i.e., the populations were homogeneous and thus required only one mobility parameter. For these data sets there was no evidence of systematic deviations of residuals about the regression line for the one-group model (see examples in Fig. 4). Accordingly, the one-group model was retained as the best model in these cases. For most data sets, satisfactory fit, as revealed by graphical examination and R^2, was attained with the best model (Table 2).

Further evidence for lack of fit of the one-group model to various data sets came from a comparison of the actual number of individuals recaptured with the es-

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FIG. 4. Examples of fit of the one-group model (regression line) to four selected data sets. From top to bottom: data sets 2, 11, 6, and 15 (see Table 2). The one-group model provided adequate fit for data sets 2 and 11, but not for data sets 6 and 15, in which distance class zero (individuals that remained in the home section) deviates notably from the regression line. Note that scales for the *x*-axes differ greatly among data sets; *y*-axis scales are logarithmic.

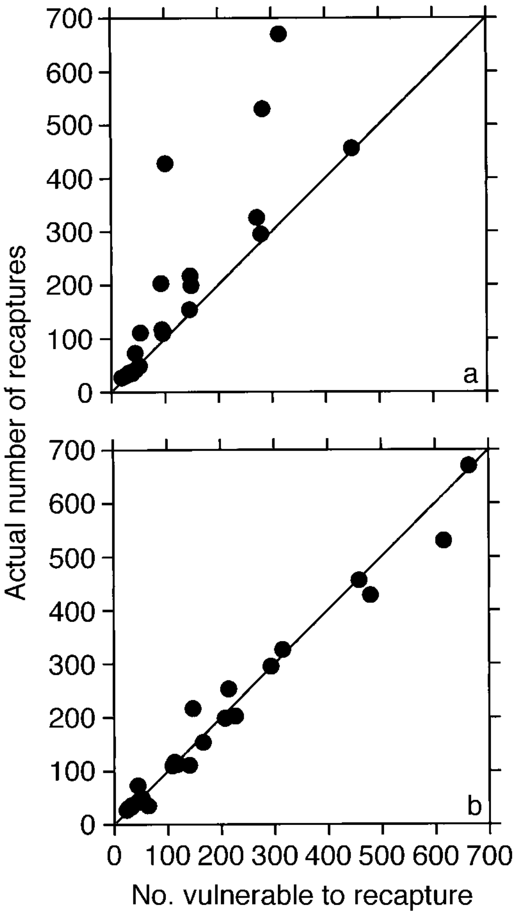

FIG. 5. Actual number of fish recaptured vs. estimated number of fish vulnerable to recapture ($N_0 s\pi$; see Eq. 1). (a) Estimates for $N_0 s\pi$ from the one-group model. (b) Estimates for $N_0 s\pi$ from the best-fitting (one-group or two-group) model. Actual and estimated values match exactly along the 1:1 line.

timate of $N_0 s\pi$, the expected number of individuals vulnerable to recapture (see Eq. 1). Indiscriminate application of the one-group model to all data sets tended to underestimate this value, sometimes badly. In contrast, use of the appropriate (one-group or two-group) model yielded close agreement between the expected and actual number of recaptures (Fig. 5).

Using the best-fitting model, the median of median displacements for the 27 salmonid populations was 27.7 m. Median displacement was <50 m for 17 populations and <100 m for 24 populations (Fig. 6). Median displacement had extreme values for two populations in one study (data sets 20: 8295 m, cutthroat trout, and 24: 322 m, stocked rainbow trout). However, the extreme value for cutthroat trout likely was a consequence of spawning migrations, and seasonal or interannual movements (Bjornn and Mallet 1964). Median displacement did not differ significantly between pooled (median: 50.9 m, range: 4.9–85.3 m; $n = 7$ data sets) and unpooled (median: 25.9 m, range: 2.1–8295 m; $n = 20$ data sets) data (Mann-Whitney U test, $P = 0.70$). Turnover rates were high (median: 0.53), variable among populations (range: 0.15–0.78), and unrelated to displacement distance (Fig. 6).

Median displacement appeared to differ interspecifically (Fig. 7), although most species were represented by few data points. For five of the six species included in this study, the median of median displacement was <51 m. Striking differences in median displacement were apparent between the stationary (median: 17.9 m; range: 0.7–20.6 m) and mobile (median: 328.5 m; range: 242.4–13 862.9 m) components. Most populations appeared to be composed of a majority of stationary individuals (median p [proportion of stationary individuals]: 0.81) (Fig. 8), with the mobile proportion exceeding 50% in only 5 of the 27 populations.

Median displacement was positively related to spatial extent ($ln(y) = 0.121 + 0.479\ ln(x)$; $P = 0.005$) and study duration ($ln(y) = 0.466 + 0.659\ ln(x)$; $P = 0.0002$) in simple bivariate regressions ($n = 27$ data sets). However, spatial extent and study duration were themselves positively correlated $r = 0.66$; $P = 0.002$). Joint analysis of all variables by multiple regression: $ln(\text{median displacement}) = -0.236 + 0.399\ ln(\text{spatial extent}) + 0.207\ ln(\text{study duration})$, showed that median displacement was significantly related to spatial extent ($P = 0.014$) but not to study duration ($P = 0.429$) ($R^2 = 0.44$; model $P = 0.001$). The expected median displacements for studies differing maximally in spatial extent were 3.7 m for a spatial extent of 12 m and 232.3 m for a spatial extent of 67 578 m. These values were highly sensitive to inclusion of a data set for

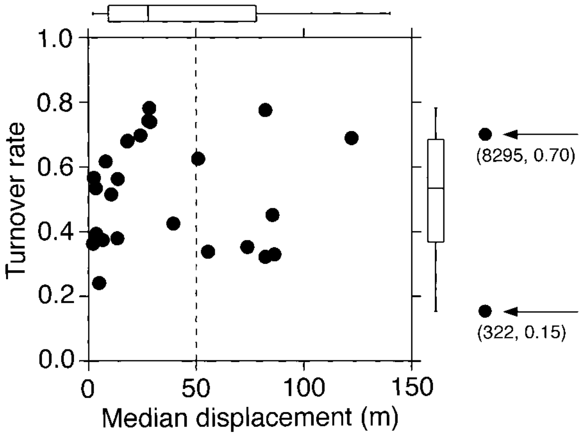

FIG. 6. Turnover rate vs. median displacement in stream salmonid populations (27 data sets). Tukey box plots summarize the marginal distribution for each variable: the center line in the box marks the median; the length of the box gives the interquartile range, between the 25th and 75th percentiles; and the whiskers show the range of data values that fall within 1.5 interquartile ranges of either quartile. The displacement value commonly used as an upper limit defining restricted movement (50 m: dashed line) is provided for reference. Arrows indicate two points with extreme values for median displacement (coordinates in parentheses).

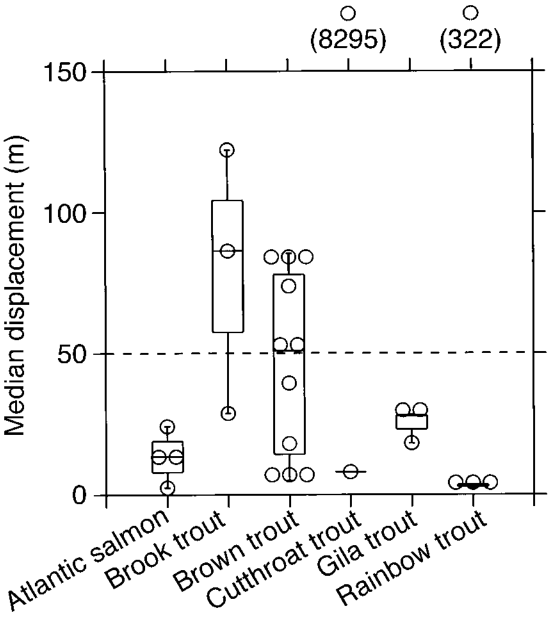

FIG. 7. Combined box–dot plot of displacement distances for six salmonid species, showing the median, quartiles, and whiskers (see Fig. 6), as well as individual values (dots) for displacement distance. The displacement value commonly used as an upper limit defining restricted movement (50 m: dashed line) is provided for reference. Two points with extreme values for displacement (in parentheses) are represented on top of the plot.

cutthroat trout, which was a regression outlier (Studentized residual = 3.9) and possibly a biological outlier as well (data set 20; see above); exclusion of those data changed the aforementioned expected median displacements to 5.1 m and 116.0 m, respectively.

DISCUSSION

This study provides theoretical and empirical evidence that high turnover rates in mark-recapture studies are compatible with short displacement distances. Median displacement in the majority of populations examined fell within the movement range (20–50 m) generally associated with restricted movement, and all but one of the nonmigratory populations had median displacement smaller than 100 m. These results support the conventional notion that restricted movement is the norm in populations of stream salmonids during nonmigratory periods. However, the results also point to considerable intra- and interspecific heterogeneity in the extent of movement. In particular, displacement of mobile individuals (median = 328.5 m) was high relative to expected displacement under the restricted-movement paradigm (RMP) and 18 times higher than displacement of stationary individuals (17.9 m). Although stationary individuals predominated in most studies, the proportion of individuals in the stationary and mobile categories varied considerably among studies.

Categorization of individuals as stationary or mobile, while providing a useful statistical description of within-population heterogeneity, need not imply the existence of two morphs with different rates of displacement (McLaughlin et al. 1992). A priori, it could be equally plausible to assume that populations consist of either a mixture of two morphs, with persistently stationary or mobile individuals in proportions p and q respectively, or a homogeneous group of individuals, each with constant probability p of staying and q of moving over a given time interval. However, the sparse evidence available appears to favor the former alternative. In mark–recapture studies that followed individuals over more than two time periods, movement behavior of an individual between two consecutive sampling periods was influenced by its behavior in preceding periods, indicating persistence of individual differences (brown trout, Harcup et al. 1984: Fig. 4; cutthroat trout, Heggenes et al. 1991: Fig. 4; chinook salmon, *Oncorhynchus tshawytscha,* Bradford and Taylor 1997; see also McLaughlin et al. 1999). Data from field studies relying on passive integrated transponder tags, an increasingly widespread technology that allows for repeated sampling and identification of individuals, should help resolve this issue.

A related question is whether movement patterns of stationary and mobile individuals at the spatial scales examined in the present study (tens to thousands of meters) can be derived simply from movement patterns driven by behavioral processes at the microspace (several meters), such as feeding and agonistic interactions. Direct observations of short-term movement in streams have shown that salmonid fish can adopt alternative foraging and social tactics that are associated with differing mobilities (Grant and Noakes 1988). Other studies also have found that dominant fish are more sedentary and territorial within a local habitat than sub-

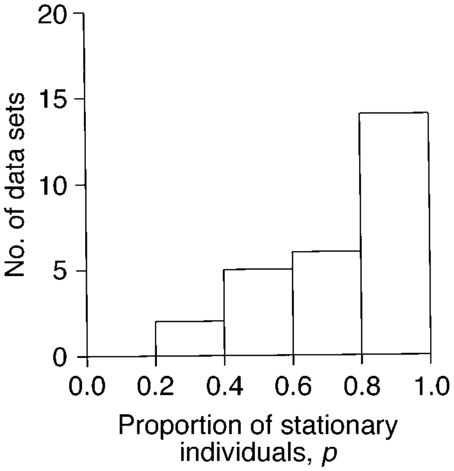

FIG. 8. Histogram for p, the proportion of stationary individuals in stream salmonid populations (27 data sets). The y-axis gives the number of data sets per vertical bar.

ordinate fish (Mason and Chapman 1965, Puckett and Dill 1985, Nakano 1995). It remains to be determined whether stationary and mobile individuals in mark–recapture studies correspond to different behavioral or social groups in observational studies.

Similar mixture models for populations comprising two distinct subpopulations of differing mobility have been used previously in studies of insect movement (Dobzhansky and Wright 1943, Inoue 1978). Instead of assigning specific mobility parameters to each subpopulation, however, an alternative modeling strategy would allow for continuous variation in the displacement parameter λ. Within-population variation in mobility would then be characterized by a frequency distribution rather than by differences among two or more discrete subpopulations. However, only 3–4 parameters can probably be estimated suitably by fitting a model to the distribution of dispersal distances (Turchin 1998); it may thus be difficult to find models that include continuous variation in λ without being overfitted. Because the relationship between log-recaptures and distance was either linear or bilinear with an inflection point, it is probably not necessary to invoke more than two subpopulations for stream salmonids.

The models provided useful quantitative measures of population mobility and of intrapopulation variation in mobility and its influence on population dispersal. When the aim is to characterize population mobility, it seems preferable to use the median displacement derived from exponential models rather than the mean home range, an individual-based measure of mobility currently in wide use, because the latter measure does not account for mobile individuals that do not have a home range. For populations composed of a mixture of stationary and mobile individuals, the function relating turnover to distance from the origin (Table 1) can have a sharp ‘‘elbow’’ that leads to large changes in the estimate of median displacement with small changes in *p* (Fig. 9). The elbow arises because population turnover declines rapidly as small increases in distance encompass movements of most stationary individuals, but further decline in turnover with distance is determined mainly by mobile individuals and thus is slower. In such cases, reporting median displacement separately for the stationary and mobile components may be more informative and robust than a single median displacement.

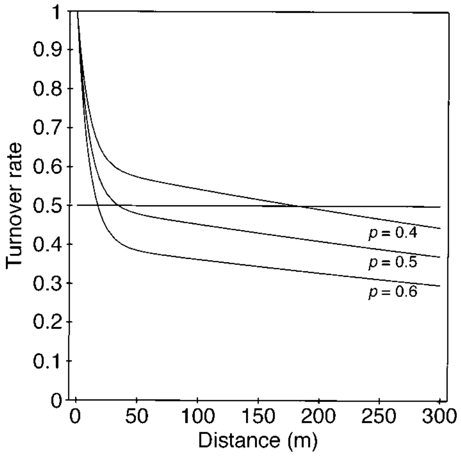

FIG. 9. Simulated data illustrating changes in median displacement with *p*, the proportion of stationary individuals, for three populations comprised of stationary and mobile components ($p = 0.4$, 0.5, and 0.6; $\lambda_s = 0.1$ and $\lambda_m = 0.001$ [λ = the inverse of the mean displacement distance] for the three populations). The curves give turnover rate as a function of distance to the origin. Median displacement is obtained by projecting onto the *x*-axis the intersection of the curve with the horizontal line at turnover = 0.5.

Spatial extent in mark–recapture studies must be large enough to properly characterize the displacements of the mobile component; otherwise, parameter estimates may be inaccurate even when the two-group model is used. Because the expected number of recaptures is given by the integral of the density function (Eq. 1) over the whole domain of dispersal, the observed agreement between expected and actual number of recaptures (Fig. 5) suggests that sampling protocols in these studies effectively covered the entire range over which marked fish dispersed during the study. The increase of ~110 m in median displacement as spatial extent increased from 12 to 67 500 m seems moderate considering that spatial extent and maximum potential displacement can vary jointly simply because both are physically constrained by stream length, particularly in smaller streams.

Although limited, the interspecific comparison of displacement distances in this study (Fig. 7) illustrates well the potential of this approach to eventually yield standardized comparisons of movement among different populations (including stocked vs. natural fish in the same stream), species, or localities. Brook trout, a species that has been the focus of many studies critical of the RMP (Riley et al. 1992, Fausch et al. 1995, Gowan and Fausch 1996*a*, *b*), appears to be highly mobile relative to other salmonid species; it may thus constitute an exception.

The exponential models presented here provide measures of mobility (e.g., λ), that are standardized to a common unit (m^{-1}), thus allowing one to account for differences in spatial extent among studies. However, variation in study duration and resampling schedules (single vs. multiple resampling) is less amenable to analysis with these models because the displacement parameter λ may depend on study duration even if movement behavior is constant. Alternative quantitative models that explicitly incorporate temporal dynamics (e.g., Markov chains, advection–diffusion equations) can provide instantaneous rates of mobility independent of study duration. Although these approaches have been best developed for insect populations (Okubo 1980, Turchin 1998), several studies illustrate their applicability in studies of fish movement

(Hilborn 1990, Zabel and Anderson 1997, Sibert et al. 1999, Skalski and Gilliam 2000). The apparent lack of dependence of displacement distance on study duration may seem surprising given the predictions of simple diffusion models (Turchin 1998). Nevertheless, both diffusion models and empirical data show that for animals that initially disperse rapidly, but then remain within a limited region, squared net displacement in mark–recapture experiments can quickly attain a plateau (Okubo 1980). Stream salmonids may exhibit this behavior because they are often associated with a home range or territory; therefore, most sampling intervals were likely longer than the period of initial dispersal of marked individuals.

Simple quantitative models, in combination with appropriate marking and recapture designs, can bring needed rigor to the analysis of movement and population dynamics in stream fish. In particular, population losses can be better understood by distinguishing emigration from in situ mortality. Model-based estimates of emigration from a stream reach can be readily tested by comparison with recaptures of marked fish in two-way traps or weirs set at various points of the reach (Hall 1972, Schlosser 1995, Gowan and Fausch 1996*b*). Further work, involving field tests and quantitative simulations, is required to test the sensitivity and accuracy of model estimates and determine how to select effectively the HSL (home-section length) and spatial extent when designing a study. Also needed are alternative estimation approaches suitable for count data, such as generalized linear models with Poisson errors, for situations in which log-transformation does not fulfill statistical assumptions.

In its original version, the RMP appears to be incomplete because it fails to recognize the ubiquity of the mobile component and its potential contribution to population processes. However, critics of the RMP may have overemphasized turnover rate and the proportional representation of the mobile component. Concentrating on whether or not stream salmonids conform to the RMP will likely be less profitable than investigating how variation in mobility responds to ecological influences, such as environmental fluctuations or intraspecific and interspecific competition, and the evolutionary correlates of this variation as concerns phenotypic plasticity, adaptive value, intrapopulation variation, and their implications for genetic differentiation. Developing suitable quantitative descriptors of mobility is a prerequisite for this task.

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