

Scale-dependence of movement rates in stream invertebrates

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We used analytical models and random walk simulations in a one-dimensional habitat to study the scale-dependence of migration rates in stream invertebrates. Our models predict that per capita migration rate is inversely proportional to patch length when patches are large compared to the scale of movements. When patches are small the scale-dependence is weaker and primarily determined by the length of individual movements (steps) relative to patch size. Laboratory experiments using isopods (*Asellus aquaticus* L.) and mayfly nymphs (*Baetis* sp.) confirmed that the strength of the scale-dependence decreased with increasing step length.

For the case when step length distributions follow an exponential probability distribution, which is often the case for stream organisms, we provide a simple model that allows the scale-dependence to be predicted from the mean step length. We fitted this model to published field data on drift densities at different downstream distances from a net that blocks the drift from upstream areas. Agreement between model and data was excellent in most cases. We then used already published data on the length of induced drift movements to predict the scale-dependence that was observed in block experiments performed in the same system. Predicted and observed scale-dependence showed very close agreement.

We conclude that our models and published data on drift distances can be used to calculate the expected scale-dependence of per capita emigration rates for a large number of taxa under a wide range of environmental conditions.

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The number of organisms in a patch is determined by within-patch processes, such as birth and mortality, and between-patch processes, such as emigration and immigration. The relative importance of these processes influences a wide range of population and community properties, including short-term dynamics, population persistence, and patterns of biomass accrual at different trophic levels along productivity gradients (Oksanen 1990, Hanski and Gilpin 1997, Thomas and Kunin 1999). It is thus important to understand why and how this balance varies in natural systems. Allometric relationships between animal size, mobility and reproductive rates suggest that, as a coarse generalization, we should expect large animals to be more motile and have

slower vital rates than small animals (Peters 1983). Since predators usually are larger than their prey the influence of between-patch processes is expected to increase as we move upwards in the trophic hierarchy (Holt 1995). Another factor influencing the balance is patch size. Migration per unit patch area is often assumed to decrease with increasing patch size as a result of decreasing edge-to-area ratios (Stamps et al. 1987, Wiens et al. 1993, Englund 1997, Englund and Cooper 2003), while birth and death rates lack this inherent scale-dependence. Empirical studies support this assumption, but the slope of the relationship between per capita migration rates and patch area tend to be shallower than predicted from edge-to-area relationships (Kareiva 1985,

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Bach 1988, Sutcliffe et al. 1997, Petit et al. 2001, Englund and Hambäck 2004).

Our goal in this paper is to study the scale-dependence of emigration rates for stream invertebrates. Movements in this group of organisms are often biased in downstream direction due to the directed water current (Bishop and Hynes 1969, Bird and Hynes 1981). This is most pronounced for movements by drift, when the invertebrates are transported by the water current. To study the scale-dependence of migration rates for this group of organisms we use analytical models and simulations of movements in one-dimensional systems (two-dimensional movements are analyzed in a separate paper (Englund and Hambäck 2004)). The models show that the strength of the scale-dependence is determined by the scale of movements, in particular the length of steps. To test this hypothesis we use indoor channels to examine the scale-dependence of emigration for invertebrates that move with different step lengths. We then demonstrate that step length distributions and thus the scale-dependence of per capita emigration rates can be estimated with high precision from field data on the effect of block nets on downstream drift densities and from studies of drift lengths. This means that published data can be used to calculate the expected scale-dependence of per capita emigration rates for many lotic taxa under a range of environmental conditions.

Modeling results

We study migration in a one-dimensional habitat as an approximation of a stream system where most movements occur in the up-downstream direction and where patch size varies in the same direction. Most stream organisms move both up- and downstream but movements can be biased in downstream direction because individual movements are longer in this direction (McIntosh and Townsend 1998, this study). Thus we first derive modeling results for unbiased bi-directional movements and then examine the effect of letting steps be longer in one direction. As a general model for describing results we use a power model of the form

$$m = cL^{-\beta} \quad (1)$$

where m is per capita emigration rate, L is patch length, c is a constant, and the scaling coefficient β describes the strength of the scale-dependence.

In a first scenario, we analyze the situation when immigration and emigration are unrestricted and the outside and inside densities are at equilibrium. An empirical example may be the system described by Sih et al. (1992) where salamander larvae move in and out of stream pools. Other examples are many field experiments that use cages or channels as experimental arenas (Englund 1993, Cooper et al. 1998, Englund et al.

1999, Diehl et al. 2001). In a second scenario, we investigate the situation where emigration leads to depletion and where boundaries are absorbing, i.e. emigrants do not return to the patch. This is meant to mimic the way field data are often collected. An example is when drift nets are used to collect animals downstream of a block net (Waters 1965, Elliott 1971, Larkin and McCone 1985).

Unrestricted migration and equilibrium

In this scenario, emigration and immigration are unrestricted and local population densities are roughly constant over time because emigration and immigration balance. Now assume that N_p individuals reside in a one-dimensional patch with length L , i.e. with a density $n_p = N_p/L$, and that the movements of organisms can be described as an uncorrelated random walk. As densities are constant, the per capita emigration rate (m) can be estimated as $m = M/N_p t$ for any time interval t , where N_p is the initial number of individuals in the patch and M is the number of emigrating individuals. A constant density and uncorrelated movements means that the system has no “memory” and its behaviour can be studied over a single time unit. Consider a one-dimensional habitat where organisms move with fixed step lengths (s) at a frequency q . If steps are longer than the patch length ($s > L$) it means that every step taken by an individual in the patch leads to emigration. Thus the per capita emigration (m) rate is given by:

$$m = q \quad \text{if } L < s \quad (2)$$

Next assume that steps are shorter than the patch length. An individual within s length units of a boundary emigrates over that boundary with the probability $q/2$, given that movements occur in both directions with equal probability. The total number of individuals moving over the two boundaries is then $2qs n_p/2$. Dividing by the total number of individuals in the patch ($L n_p$) yields the per capita emigration rate:

$$m = qs/L \quad \text{if } L > s \quad (3)$$

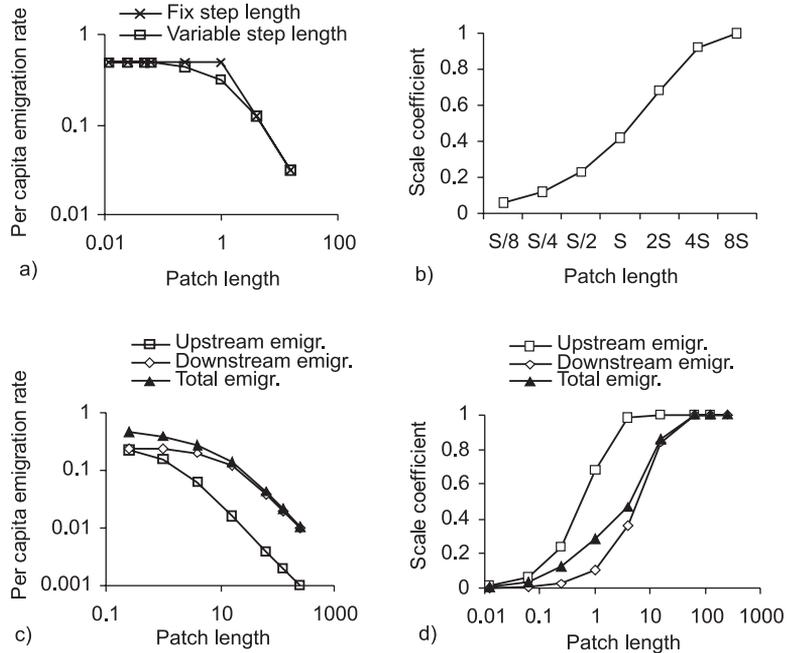
Thus, for large patches, relative to the step length, per capita emigration rates are inversely proportional to patch length, and the scaling coefficient $\beta = 1$ (cf. Eq. 1). For small patches, emigration is independent of patch length and determined by the frequency of moves (Fig. 1a). The transition is abrupt and occurs when step length is equal to patch length ($s = L$). An analogous derivation can be made for immigration. Because the numbers immigrating is a function of the density outside the patch (n_{out}) the per capita emigration rate (i) is given by:

$$i = q n_{out}/n_p \quad \text{if } L < s \quad (4)$$

$$i = q s n_{out}/L n_p \quad \text{if } L > s \quad (5)$$

(notice that when $n_{out} = n_p$ then Eq. 4 and 5 equal Eq. 2

Fig. 1. a) Relationship between per capita emigration rate and patch size in one-dimensional patches under equilibrium conditions (constant density of organisms). The relationships were generated using Eq. 2 and 3 for a fixed step length of one, and Eq. 6 for variable step lengths using a mean step length $\bar{s} = 1$. The frequency of moves (q) was 0.5. b) Scale coefficients (β) predicted by Eq. 8 for different values of the ratio between mean step length and patch length. c) Per capita emigration rate when steps are longer in downstream direction ($\bar{s} = 10$) than in upstream direction ($\bar{s} = 1$). The movement frequency q was 0.25 in each direction. Predictions were generated using Eq. 6. d) Scaling coefficients for the data in Fig. 1c.



and 3, as expected). The previous analysis assumed fixed step lengths. Now, we make the analysis more general by assuming variable step lengths. A large number of studies of drift in stream invertebrates show that distributions of step lengths are well approximated by an exponential probability distribution (McLay 1970, Elliott 1971, Allan and Feifarek 1989). Thus we assume that the probability $p(s)$ to choose a step of length s is given by $p(s) = ke^{-ks}$, where k is the inverse of average step length ($1/\bar{s}$). The per capita emigration rate from a patch of length L is then:

$$m = q\bar{s}(1 - e^{-L/\bar{s}})/L \quad (6)$$

and the corresponding model for immigration is:

$$i = q\bar{s}(1 - e^{-L/\bar{s}})n_{out}/Ln_p \quad (7)$$

(for derivation see Appendix). The effect of variable step lengths is to make the transition from scale-dependence to scale-independence more gradual (Fig. 1a). The scale dependence β is the negative of the slope of the relationship between $\ln(m)$ and $\ln(L)$, and can thus be found as:

$$-\frac{\partial \ln(m)}{\partial \ln(L)} = \beta = \frac{e^{L/\bar{s}} - L/\bar{s} - 1}{e^{L/\bar{s}} - 1} \quad (8)$$

Note that L enters in the same way in Eq. 6 and 7, which means that the derivatives for emigration and immigration are identical. Thus we see that the strength of the scale-dependence, as measured by the exponent β , is determined solely by the relation between patch length

and step length (L/\bar{s}). This means that once the mean step length is known, the strength of the scale-dependence can be determined for any patch size (Fig. 1b).

Next we study the situation when the organisms move with longer steps in downstream direction than in upstream direction. The numbers emigrating in one direction is half that predicted by Eq. 6 for the length of the steps taken in that direction. The total emigration rate in both directions is the sum of the rates predicted for long steps in downstream direction and the rate predicted for short steps in the upstream directions. For a bias corresponding to that observed in experiment 1 ($\bar{s}_{down} = 10\bar{s}_{up}$) the downstream emigration rate is much larger than upstream migration except when patches are very small (Fig. 1c). As a consequence, the scale coefficients predicted for total emigration and for downstream movements are approximately equal when the patch is larger than the mean step size (Fig. 1d).

Absorbing edges and depletion

In this scenario we assume that the density of individuals in the patch decreases over time because there is no immigration and emigrants do not return. We have derived analytical diffusion models for this scenario but they were poor approximations when step lengths were large compared to the size of the patch. Thus we studied the scale-dependence of emigration rate by simulating individuals performing a random walk in a one-dimensional habitat.

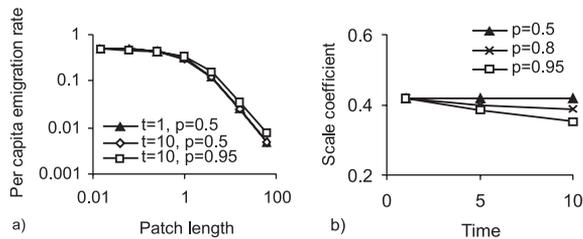


Fig. 2. a) The effect of time and correlation of step directions on per capita emigration rates in patches with absorbing boundaries. The probability that subsequent steps were taken in the same direction (p) was 0.5 or 0.95, duration (t) was 1 or 10 time units, and the frequency of moves (q) was 0.5. The step lengths followed an exponential probability distribution with a mean of one length unit. b) Scaling coefficients (β) estimated from the simulation output in Fig. 2a. We first estimated mean step length by fitting Eq. 6 to simulation output and then used this estimate and Eq. 8 to find the scaling coefficient for the patch length $L = 1$. Parameter values are as in Fig. 2a, except that intermediate values, not shown in Fig. 2a, were included for time (t) and the probability that subsequent steps are taken in the same direction (p).

The results for this scenario are similar to those observed for the equilibrium scenario above (Fig. 2a). The observation period has no effect on the scale-dependence as long as the directions of subsequent steps are uncorrelated (Fig. 2b). A high probability that subsequent steps will be taken in the same direction ($p = 0.95$, in Fig. 2b) means that the scale coefficient is smaller than expected from the mean step length. In essence a high positive correlation between directions of subsequent steps means that the “effective” step length, which predicts the scaling coefficient, is longer than the individual steps taken by the organisms.

Experimental investigations of scale dependent emigration

Methods

The scale-dependence of emigration rates was examined in indoor channels (length 3.6 m, width 0.2 m, water depth 0.08 m). Each channel was a closed system, where water was circulated with an electric pump from the downstream end of the channel to the upstream end. As the objective was to study the relationship between movement patterns and migration rates, we set up three experiments using organisms moving with different step length. Mayfly nymphs (*Baetis* sp.) moved with long steps at high current velocity (experiment 1) and intermediate steps at low velocity (experiment 2), while the isopod (*Asellus aquaticus* L.) moved with much smaller steps (experiment 3, Fig. 3).

Experiment 1. The channels had a net in the upstream end preventing larval movement, while water fell over a barrier in the downstream end. Nymphs that swam or drifted over the barrier were caught in a net (mesh 0.5

mm) and were unable to return. Thus the experiment corresponded to the modeling scenario with absorbing edge and depletion. By moving the position of the barrier we created arenas that were 0.4, 0.8, 1.6 and 3.2 m ($N = 16$). Current velocity, measured as cross-section area divided by flow, was 7 cm s^{-1} . When starting an experiment, we turned off pumps and added *Baetis* nymphs at a density of 5 dm^{-2} , and then waited 10 minutes until pumps were turned on again. The number of emigrating larvae was counted after 180 minutes. Movement parameters were determined by direct observations of nymphs within the uppermost 20 cm of 3.2 m arenas to allow drift over several meters. We recorded step length (displacement in up- or downstream direction), movement direction (up- or downstream), and the mode of moving (crawling, swimming or drifting). As nymphs spent most of their time inactive, it was usually obvious when a move started and stopped.

Experiment 2. The current velocity in this experiment was only 2 cm s^{-1} , causing fewer long movements (drift) and more short movements (crawling, Fig. 3b). We delimited experimental arenas by drawing two lines on the bottom of the channel and recorded as emigrants all individuals that left the arena in the downstream direction during 20 minutes. As immigrating individuals replaced emigrants the experiment corresponds to the scenario with equilibrium densities and unrestricted movements. Movement parameters were estimated as in experiment 1. Experimental arenas were 0.2, 0.4, 0.8, and 1.6 m ($N = 48$).

Experiment 3. This experiment was performed as experiment 2, except that we used isopods (*Asellus aquaticus*, density $\approx 5 \text{ dm}^{-2}$) that move with smaller steps than *Baetis* (Fig. 3c). The experiment was run without current, as isopods otherwise aggregated in the up- and downstream ends of the channel. The experimental arenas were 0.4, 0.8, 1.9, and 2.7 m ($N = 36$).

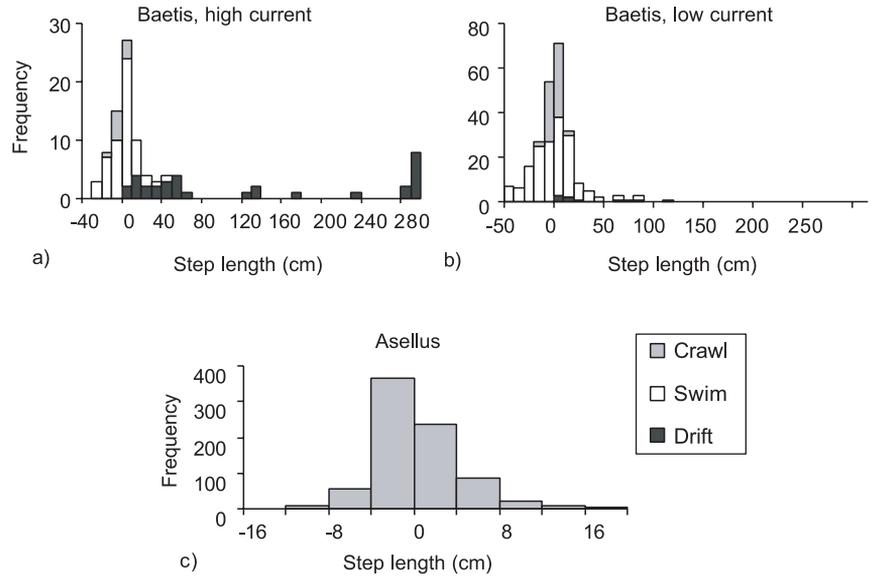
Data analysis

Emigration rates were calculated as $m = M/N_0t$ where M is the number of emigrants and scaling coefficients (β) were determined by regressing $\ln(m)$ on $\ln(\text{arena length})$. For each experiment we calculated the expected relationship between emigration rate and arena length using the mean step length and Eq. 6, or by simulation over a single time step using observed step lengths (Fig. 3). The average scaling coefficient (β) was then estimated by regressing $\ln(m)$ on $\ln(\text{arena length})$.

Results

Baetis at high current velocity moved with the longest steps (Fig. 3a) and showed the weakest scale-dependence (Fig. 4), while the strongest scale-dependence was observed for *Asellus* that moved with the smallest steps (Fig. 3c, 4). The quantitative agreement between ob-

Fig. 3. Distributions of step lengths for different types of movements in experiments involving mayfly nymphs (*Baetis*) and isopods (*Asellus*). Positive and negative values represent downstream and upstream movements, respectively.



served scale coefficients and those predicted from step sizes was reasonably good, though it may be noted that we overestimated the steepness of the slope in all experiments (Fig. 4b). The predictions generated by simulation was more accurate than those based on Eq. 6, which probably reflects that the step length distribution for *Baetis* deviated from the exponential distribution.

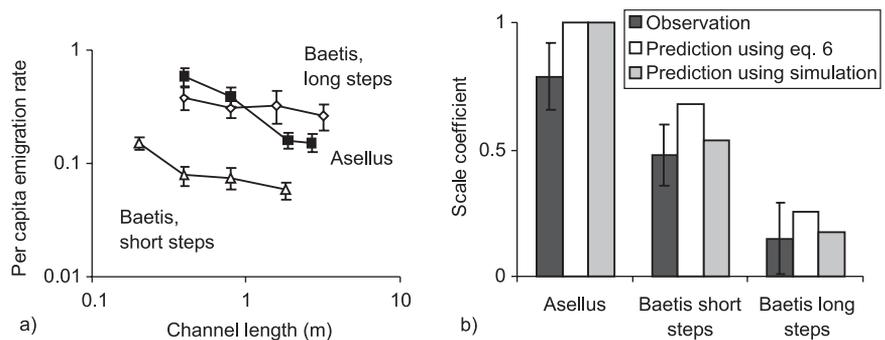
Estimating scale coefficients from published data

In order to broaden our analysis, we located published studies that examined drift movements. The first set of studies had erected block nets that trapped all organisms drifting from upstream areas. Immediately downstream of the block net the drift is very small but it increases as the downstream distance to the block net is increased.

The rate at which the drift increases reflects the length of drift movements, henceforth called the step length. Thus, it is possible to estimate mean step length and the scale coefficient from drift densities at different distances from a block net. Such data are given in Waters (1965), Elliott (1971), and Larkin and McCone (1985). It should be noted that in this context the term “drift movements” can include several types of downstream movements, such as swimming, crawling, and specialized “drift” behaviors.

The number of organisms caught in each drift net was standardized by dividing with the natural unblocked drift and by dividing with the distance between the block net and the drift net. The resulting metric is proportional to the per capita emigration rate from the area between block net and drift net. We fitted Eq. 6 to these data and found excellent agreement in most cases (Fig. 5, Table 1).

Fig. 4. a) Dependence of per capita emigration rates on channel length in laboratory experiments. b) Observed scale coefficients (β) \pm SE for the data in a) and predictions based on the step length distributions in Fig. 3 using either Eq. 6 or simulations.



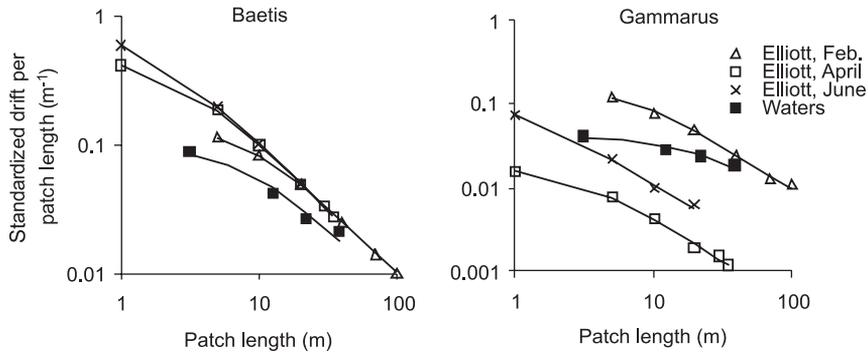


Fig. 5. The figure illustrates the agreement between empirical drift data taken at different distances below a block net and Eq. 6 fitted to the data. Standardized drift rates, indicated by markers, were calculated as the numbers caught in drift nets when the block net was in position divided by the drift when the block net was not in place. Data were taken from Waters (1965) and Elliott (1971). Lines indicate the fitted equations. Regression statistics are given in Table 1.

Our simulations showed that estimates of step lengths depend on the time scale of observations if there is a serial correlation between directions of subsequent steps. Because such time dependence would limit the generality of observed relationships we used data in Larkin and McCone (1985) to examine if estimated step lengths change with the time scale of observations. Larkin and McCone examined how drift rates below a block net decreased over four days. We summed the drift over 1, 2, 3, and 4 days, respectively, and estimated mean step length by fitting Eq. 6 to these data. As shown in Fig. 6, there were no detectable effects of time on the estimates of mean step length and thus, on the scaling coefficients.

In a second type of studies drift lengths were estimated by releasing invertebrates at different upstream distances from drift nets. Elliott (1971) used both this technique and block nets in the same system under similar conditions, which allowed us to compare the scaling coefficients estimated with the two methods. For each of

the ten observations listed in Table 1 we predicted the scale-dependence for a patch length equal to the step length estimated from the block experiment. The expected scaling coefficient was $\beta = 0.418$ and the mean of the scaling coefficients predicted from the release-recapture study was $\beta = 0.416$ (SE = 0.016, N = 10). Thus we concluded that the block experiment and the release-recapture study produced indistinguishable estimates of the scaling coefficients.

Discussion

Our analyses suggest simple rules for the dependence of per capita migration rates in stream ecosystems in relation to patch length and individual movement rates (Fig. 1). When patches are large compared to the length of individual movements, only individuals close to the patch edge will emigrate and we should expect the

Table 1. Estimates of mean step length (\bar{S}) from published block net experiments and from experiments where drift was initiated by the experimentalist. Estimates were obtained by fitting Eq. 6 to the data given by the authors. Standard errors are given in parentheses.

Study	Taxa	Scale range (m)	Current velocity (cm/s)	\bar{S} (m) from block exp.	r^2	\bar{S} (m) from induced drift exp.
Waters 1965	<i>Gammarus limneaus</i>	3–38	100	15.3 (2.5)	0.97	
	<i>Baetis vagans</i>			5.0 (0.84)		0.99
Elliott 1971 Feb.	<i>Baetis rhodani</i>	5–100	60	6.0 (0.16)	1.00	5.6 (0.16)
	<i>Ecdyonurus venosus</i>			10.5 (0.3)		10.6 (0.70)
	<i>Gammarus pulex</i>			5.3 (0.37)		5.7 (0.33)
	<i>B. rhodani</i>			1.9 (0.01)		1.9 (0.09)
Elliott 1971 April	<i>E. venosus</i>	1–35	19	2.4 (0.12)	1.00	3.2 (0.66)
	<i>Hydropsyche</i> spp.			5.3 (0.68)		4.2 (0.44)
	<i>G. pulex</i>			2.2 (0.05)		1.9 (0.17)
	<i>B. rhodani</i>			1.2 (0.01)		1.1 (0.08)
Elliott 1971 June	<i>B. scambus</i>	1–20	12	1.8 (0.02)	1.00	
	<i>Ephemera ignita</i>			3.7 (0.28)		3.5 (0.16)
	<i>G. pulex</i>			0.89 (0.07)		1.0 (0.08)
	<i>G. pulex</i>			0.89 (0.07)		1.0 (0.08)
Larkin and McKone 1985	<i>Paraleptophlebia</i> sp.	1–20	–	4.3 (0.99)	0.98	
	<i>Ephemera</i> sp.			0.75 (0.25)		0.98
	<i>Epeorus</i> sp.			0.88 (0.13)		1.00
	<i>Cinygmula</i> sp.			1.6 (0.34)		0.99
	<i>Baetis</i> sp.			0.47 (0.07)		1.00
	<i>Parameletus</i> sp.			2.1 (0.45)		0.99

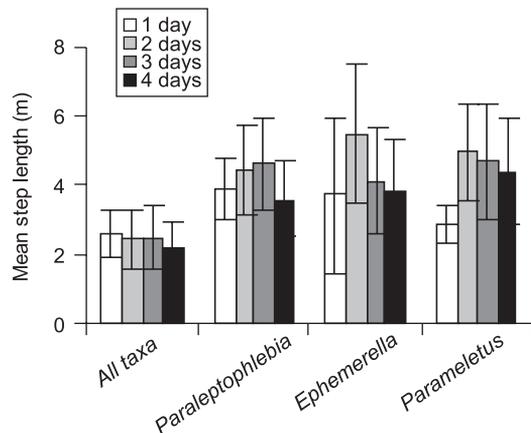


Fig. 6. Effect of sampling period on estimated mean step length for data on the drift downstream of a block net. Data are given in Larkin and McCone (1985). Because sampling period (1, 2, 3 or 4 days) did not affect estimated step length we conclude that

scaling coefficient $\beta = 1$. In a two dimensional system, this prediction corresponds to a scaling coefficient that is completely dependent on the perimeter-to-area ratio (Englund and Hambäck 2004). On the other hand, when patches are small any movement will result in emigration and we should expect the scaling coefficient $\beta = 0$. These predictions are also verified both by own experiments and by published studies, where species differences in the scaling coefficients can be traced to differences in movement characteristics (Figs. 4 and 5).

The model we use makes no assumptions about how patches differ from surrounding habitat. Also, the field data supporting the model were collected in arbitrary patches defined by the observer. However, real organisms often live in patches with detectable boundaries that signal changes in important environmental conditions. Whether or not our results apply to such patches is ultimately an empirical question. We can, however, provide theoretical arguments suggesting that this may indeed be the case. First, in Englund and Hambäck (2004) we investigated the scale dependence in two-dimensional systems using either a simple diffusion model or simulation models of more realistic scenarios, e.g. when the organisms detect the patch boundary and adjust their behavior when close to the boundary, and when mortality or movement rates are different inside and outside patch boundaries. The results showed that the diffusion model, which made no biological assumptions about patches, gave similar results as the more realistic models. Second, in models with more biological detail, it is often assumed that organisms decide whether to emigrate or not when they encounter the boundary (Stamps et al. 1987, Hjermmann 2000). This scenario, which seems realistic for organisms with good perceptive capabilities, can be modeled using the

step size model used in this paper (Englund and Hambäck 2004). The step size then corresponds to the distance from the boundary at which the decision is taken.

A more detailed description of how the scaling coefficient decreases with decreasing patch size requires a description of the frequency distribution of the step lengths. If the step lengths follow an exponential probability distribution, which is often the case for stream invertebrates (Elliott 1971, Larkin and McCone 1985), the scale-dependence is fully specified by the mean step length and either Eq. 8 or Fig. 1b can be used to translate the mean step size to a scaling coefficient. Empirical estimates of step lengths have been obtained in laboratory studies by direct observations of individual movements (McIntosh and Townsend 1998, this study) and in the field by measuring how the numbers caught in drift nets decline with the downstream distance from a release point (Elliott 1971, Lancaster et al. 1995). Since the organism caught in the field studies may take several steps, rather than a single step, before being caught in the drift nets it is important to ask how this may influence our estimates of mean step length. Our simulation show that step length estimates are time independent, and thus independent of how many steps that are taken, as long as the directions of subsequent steps (down stream or upstream) are uncorrelated. However, if there is such a correlation it means that the estimated mean step size is shorter than the "effective" step size that govern the scale-dependence observed over longer time scales (Fig. 2). As a consequence the scale-dependence may be overestimated. However, serial correlations usually decay if the time scale of observation is increased (i.e. the grain is increased, Turchin 1998, The fact that Elliott's observations of distances drifted by invertebrates released into the water column agreed with the step lengths estimated from the blocking experiments (Table 1), suggests that there was no serial correlation at time scales larger than those of the drift distance experiment (observation periods varied between 1–71 minutes, Malcolm Elliott, pers. comm.). The lack of a significant time effect in the data collected by Larkin and McCone (1985) also indicate that serial correlations was not a problem (Fig. 6). In our laboratory experiments the observations of moves were done with much higher resolution (~ 1 sec). We consistently predicted higher scaling coefficients than was observed, which may reflect that the directions of subsequent steps were correlated at this short time scale.

Several authors have found that drift lengths are under behavioral control (Elliott 1971, Campbell 1985, Allan and Feifarek 1989). Thus we may expect that individuals that are forced to drift return faster to the substrate than individuals that drift voluntarily. However, estimated step lengths did not differ between the experiment where

invertebrates were released in the water column and the blocking experiment where drift was natural (Table 1). This is encouraging because it means that a rather large literature on the length of induced drift movements can be used when predicting the scale-dependence of emigration rate. These studies show that the relationship between mean step length and current velocity is often approximately linear, (Elliott 1971, 2002, Allan and Feifarek 1989) or described by a power function (Larkin and McCone 1985, Lancaster et al. 1995). Other hydrodynamic variables, such as the fraction of dead zones and hydraulic roughness, also affect mean step length (Lancaster et al. 1995, Holomuzki and Van Loan 2002). There are large differences between species, between size classes within species, and between functional feeding groups (Larkin and McCone 1985, Malmqvist and Sjöström 1987, Allan and Feifarek 1989, Ledger et al. 2002). No or weak effects have been found for season, time of the day, hunger levels, presence of predatory fish, and whether released individuals were caught in drift or in the benthos (Elliott 1971, Allan and Feifarek 1989, McIntosh and Townsend 1998). Thus, there is a wealth of information about environmental factors that may affect mean step lengths for different species.

As our models have strong empirical support we believe that they can be useful tools for design and interpretation of empirical research and for theory development. It is often found that predator impacts on prey densities reflect prey movements rather than consumption by predators (Cooper et al. 1990, Sih and Wooster 1994, Englund and Olsson 1996, Englund et al. 2001). A shift from movement control to consumption control is expected if the experimental scale is increased and this shift can cause observed predator impacts to be scale dependent (Englund 1997). Our results show that the mean step size of prey organisms provides information about the scale range at which we should expect the role of movements to decline, and thus, about the scale range over which we should expect predator impact to be scale dependent. Most published experiments have used arenas in the range 0.3–1 m (Englund et al. 1999). Table 1 shows that mean step length was longer than 1 m in most cases, which indicates that the scale-dependence of migration rates is weak within this range. Thus we should not expect that variation between these studies in observed predator impact is caused by scale effects on migration rates. For example, at a current velocity of 60 cm s^{-1} *Baetis rhodani* has a mean step size of 6 m, which means that the scale-dependence is expected to be weak for arenas up to 3 m ($\beta < 0.2$) and that strong scale-dependence should occur for arenas larger than 17 m ($\beta > 0.8$). Thus, in this case we expect that experiments demonstrating effects of consumption must be larger than 10–20 m. However, a more precise prediction

requires knowledge about the absolute levels of migration and predation.

Our findings can also be useful for theory development, as Eq. 6 and 7 can readily be incorporated in spatially explicit models (Heino and Hanski 2001) of migration rates in stream organisms. Many stream organisms that lack a terrestrial phase are likely to form spatially structured populations where drift between sub-populations are dynamically important (Fagan 2002). Models of such systems should ideally incorporate a realistic representation of how migration rates scale with the size of patches. The importance of this point is emphasized by a recent study demonstrating that extinction risks due to habitat loss could be severely underestimated if this scale dependencies are ignored (Kindvall and Petersson 2000).

In summary we have derived models describing how per capita migration rates scale with patch size for stream insects. The models have unusually strong empirical support suggesting that they can be useful tools for the design and interpretation of field studies and when developing models of spatially structured populations in streams.

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Appendix

Migration rates when step lengths are variable

Assume that an individual takes a step of length s with the probability:

$$p(s) = ke^{-ks} \quad (A1)$$

In one-dimensional habitats of length L , a step taken at a distance x from one boundary will result in emigration across that boundary with probability:

$$p_{em(x)} = \frac{1}{2} \int_x^{\infty} ke^{-ks} ds = \frac{1}{2} e^{-kx} \quad (A2)$$

If individuals are uniformly distributed in the patch the total number of individuals emigrating per time unit over the two boundaries is:

$$M = \frac{1}{2} qn_p 2 \int_0^L e^{-kx} dx = qn_p (1 - e^{-kL})/k \quad (A3)$$

where q is the probability of moving per time unit and n_p is the density of organisms in the patch. The per capita emigration rate (m) is found by dividing by the total number in the patch (Ln_p), i.e.:

$$m = M/Ln_p = q(1 - e^{-kL})/kL \quad (A4)$$

The mean of the step length distribution (\bar{s}) specified by equation (A1) is $\bar{s} = 1/k$. Substituting this expression into Eq. (A4) yields the emigration rate:

$$m = q\bar{s}(1 - e^{-L/\bar{s}})/L \quad (\text{Eq. 6 in text})$$

For immigrants the probability p_x that a step taken at a distance x from one of the boundaries will result in

immigration into a habitat with length L is:

$$P_{im(x)} = \frac{1}{2} \int_x^{x+L} k e^{-ks} ds = \frac{1}{2} (-e^{-k(x+L)} + e^{-kx}) \quad (A5)$$

If individuals are uniformly distributed throughout the habitat the numbers immigrating (I) into the habitat over the closest boundary is:

$$I = \frac{1}{2} q n_{out} \int_0^{\infty} -e^{-k(x+L)} + e^{-kx} dx$$

$$= q n_{out} (1 - e^{-kL}) / 2k \quad (A6)$$

After summing for the two boundaries, dividing with the numbers in the patch (Ln_p), and substituting $\bar{s} = 1/k$, the per capita immigration rate (i) is given by:

$$i = q n_{out} \bar{s} (1 - e^{-L/\bar{s}}) / Ln_p \quad (\text{Eq. 7 in text})$$