

UC Santa Barbara

UC Santa Barbara Previously Published Works

Title

Scaling population responses to spatial environmental variability in advection-dominated systems

Permalink

<https://escholarship.org/uc/item/4tt303k7>

Journal

Ecology Letters, 8(9)

ISSN

1461-023X

Authors

Anderson, Kurt E

Nisbet, Roger M

Diehl, Sebastian

et al.

Publication Date

2005-09-01

DOI

10.1111/j.1461-0248.2005.00797.x

Copyright Information

This work is made available under the terms of a Creative Commons Attribution License, available at <https://creativecommons.org/licenses/by/4.0/>

Peer reviewed

LETTER

Scaling population responses to spatial environmental variability in advection-dominated systems

Kurt E. Anderson,^{1*} Roger M. Nisbet,¹ Sebastian Diehl² and Scott D. Cooper¹

¹Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA-93106-9610, USA

²Department Biologie II, Aquatische Ökologie, Ludwig-Maximilians-Universität München, Großhaderner Str. 2, D-82152 Planegg-Martinsried, Germany

*Correspondence: E-mail: k_anders@lifesci.ucsb.edu

Abstract

We model the spatial dynamics of an open population of organisms that disperse solely through advection in order to understand responses to multiscale environmental variability. We show that the distance over which a population responds to a localized perturbation, called the response length, can be characterized as an organisms average lifetime dispersal distance, unless there is strong density-dependence in demographic or dispersal rates. Continuous spatial fluctuations in demographic rates at scales smaller than the response length will be largely averaged in the population distribution, whereas those in per capita emigration rates will be strongly tracked. We illustrate these results using a parameterized example to show how responses to environmental variability may differ in streams with different average current velocities. Our model suggests an approach to linking local dynamics dominated by dispersal processes to larger-scale dynamics dominated by births and deaths.

Keywords

Advection, dispersal, environmental variability, *Leucra nigra*, population dynamics, response to disturbance, spatial scaling, streams and rivers.

Ecology Letters (2005) 8: 933–943

INTRODUCTION

Spatial environmental variability occurs at many spatial scales, and may impact population dynamics differently across those scales (e.g. Wiens 1989; Levin 1992). Because patterns observed at large spatial scales might frequently emerge from and feed back on processes that occur at much smaller scales, spatial ‘scaling’ – the linking of local dynamics to large-scale patterns – has become a major research focus in many fields of ecology. Spatial scaling is particularly central to the study of streams and other advection-dominated systems where the net dispersal of organisms is unidirectional (reviewed in Cooper *et al.* 1997, 1998; Wiens 2002; Englund & Cooper 2003; Gaines *et al.* 2003). Population dynamics in these systems are often inferred from experimental manipulations over small spatial scales (c. 1–10 m²; reviewed in Cooper *et al.* 1998; Englund & Cooper 2003). Such experiments (and related theory) indicate that the observed dynamics are greatly influenced by immigration and emigration processes, obscuring the effects of demographic processes believed to determine dynamics at larger spatial scales (e.g. Cooper *et al.* 1990;

Wooster & Sih 1995; Nisbet *et al.* 1997; Forrester *et al.* 1999; Englund *et al.* 2001). Conversely, descriptive investigations have often found empirical relationships among organism distributions and variation in environmental conditions at a variety of spatial scales (reviewed in Cooper *et al.* 1997; Malmqvist 2002; Woodward & Hildrew 2002), yet these investigations usually lack a mechanistic link to locally observed dynamics.

A major hindrance in understanding spatial scaling in advection-dominated systems is the lack of theory that can link population dynamics observable at small spatial scales with population responses to multiscale environmental variability. Roughgarden (1974) demonstrated that, for systems with random (diffusive) dispersal, spatial patterns in population densities greatly amplify fine scale environmental variability when dispersal is low, with increasing attenuation of this effect as dispersal rates increase. Recent theoretical work establishes that population models with advection typically exhibit very different spatial dynamics than those where dispersal is solely by diffusion (e.g. Ballyk & Smith 1999; Speirs & Gurney 2001; Levine 2003; Lutscher *et al.* 2005; Pachepsky *et al.* 2005). However, none

of these papers have addressed how populations in an advective medium respond to environmental variability.

Here, we analyse a spatially explicit population model that incorporates local recruitment, mortality and dispersal processes to examine population responses to spatial environmental variation across a range of spatial scales. In order to demonstrate key theoretical concepts in a maximally simple context, our primary model assumes open recruitment and no density dependence in any per capita rates. Spatially localized disturbances cause persistent downstream changes in population densities, and the length of this downstream response is shown to be approximately equal to the average distance an individual is expected to disperse downstream during its life-span unless there is strong density-dependence in vital rates. We demonstrate that the downstream response length of the population to local disturbances also determines the population response to spatially continuous environmental variability. Spatial fluctuations in demographic variables at scales smaller than the response length have only weak effects on the spatial population distribution. In contrast, small-scale fluctuations in per capita emigration rates are strongly tracked by the population distribution. The response length therefore yields a measure of the characteristic spatial scale over which population dynamics shift from local dynamics dominated by dispersal processes to larger-scale dynamics dominated by births and deaths. We illustrate these results using data from the stonefly *Leuctra nigra* (Olivier) in Broadstone Stream in southern England and suggest how responses of this organism to environmental variability may differ in streams with different average current velocities.

MODEL DESCRIPTION

Consider an organism that inhabits a one-dimensional habitat such as a stream or coastline. Individuals recruit into the population at rate R (e.g. from an egg bank or an offshore larval pool) and die at specific rate m . We assume that dispersers move unidirectionally with emigrants from a given location being transported downstream and settling over a distribution of downstream locations. This yields the following description of the dynamics of population densities $N(x, t)$ per (individuals length⁻¹) along a continuous one-dimensional spatial environment x ,

$$\frac{\partial N(x, t)}{\partial t} = R(x) - e_0(x)N(x, t) - m(x)N(x, t) + \int_0^x e_0(y)N(y, t)b(x-y)dy. \quad (1)$$

In this continuum representation, individuals recruit, die and emigrate at each point x along a linear habitat at rates $R(x)$ (individual length⁻¹ time⁻¹), $m(x)$ (time⁻¹), and $e_0(x)$ (time⁻¹), respectively. Each point also receives immigrants

from a distribution of upstream positions. The integral in eqn (1) represents the arrival rate of immigrants at location x from all locations y upstream, and involves a probability density $b(x-y)$, known as the dispersal kernel, that specifies the probability that an emigrant from location y settles at location x . A commonly observed dispersal kernel in advection-dominated systems is the exponential distribution (e.g. Waters 1965; Elliott 1971),

$$b(x-y) = \frac{1}{L_D} \exp\left[-\frac{x-y}{L_D}\right], \quad (2)$$

where L_D (D for dispersal) is the average length travelled during a dispersal event.

Equation (1) with the dispersal kernel given by eqn (2) is a special case of a model that describes a population of organisms that can be divided into stationary and mobile states (Lutscher *et al.* 2005), for example, aquatic macro-invertebrates that reside on the benthos and disperse by entry into the water column, or marine invertebrates whose larvae are dispersed in coastal currents. If organisms spend very little time dispersing relative to other processes (an assumption that is valid for many organisms, including those mentioned above), then the two-state model can be collapsed into eqn (1). In this case, the exponential kernel eqn (2) describes a process in which dispersing organisms settle at a constant rate from the dispersal medium which has constant flow speed. The combination of dispersal velocity and settlement rate determine the average dispersal length L_D .

POPULATION RESPONSE TO A LOCALIZED DISTURBANCE

We start by assuming a spatially and temporally constant environment, and deriving the equilibrium response of the population downstream of a persisting disturbance localized at a point x_d . This scenario represents a 'press disturbance' (Bender *et al.* 1984) at x_d and mirrors many natural phenomena that drive local population densities to either increase (e.g. increased recruitment at preferred oviposition sites or decreased mortality in predator refuges) or decrease (e.g. lowered recruitment and increased emigration in small areas of degraded habitat or zero immigration at the upstream boundary of the system).

At locations far downstream from the disturbance, there is an approximate balance of immigration and emigration. At these locations, the equilibrium population density is set by demography alone, and takes the value

$$N_H^* = \frac{R}{m}. \quad (3)$$

Immediately downstream of the disturbance, the equilibrium population decays exponentially towards a constant value,

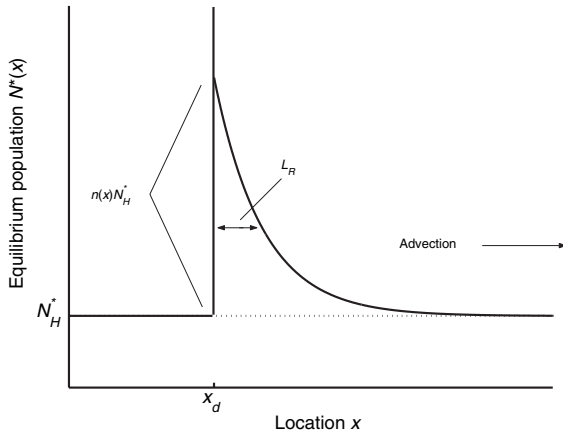


Figure 1 Equilibrium population response to a spatially localized environmental disturbance. Organisms disperse in the direction of advection from left to right. Parameter values are homogenous in space and time with the exception of the localized disturbance, which occurs in this example as a recruitment pulse at x_d . The population exhibits a concomitant spike in density at x_d , but the effect of the disturbance on the population persists well downstream. The magnitude of the population response downstream of the disturbance is given by the difference between the actual equilibrium, $N^*(x)$, and the homogenous space equilibrium, N_H^* . We define the population response in the text as a proportional change in density from the spatially homogenous equilibrium, $N^*(x) = N_H^*(1 + n(x))$. In the example shown, the bracket illustrates the population response $n(x)N_H^*$ immediately downstream of the disturbed site. The response length of the system L_R is the distance required for the population response $n(x)N_H^*$ to decay by a factor of $\exp[-1]$.

regardless of the form of the disturbance itself (Appendix A and Fig. 1). We define the population response by

$$N^*(x) \equiv N_H^*(1 + n(x)),$$

where $n(x)$ is the proportional deviation in population density from its spatial mean value and has the form

$$n(x) \propto \exp\left[-\frac{x - x_d}{L_R}\right], \quad \text{with } L_R = L_D \left(1 + \frac{\bar{e}_0}{\bar{m}}\right). \quad (4)$$

The quantity L_R defined by eqn (4) is hereafter called the ‘response length’ of the system (R for response), and is the distance required for the population response to decay by a factor of $\exp[-1]$ or $\approx 37\%$. It characterizes the average downstream distance over which the population is affected by a spatially localized disturbance.

The formula for the response length L_R admits an intuitive interpretation. The mean time between dispersal events for an individual organism is given by $\tau_E = e_0^{-1}$ and its mean lifetime by $\tau_M = m^{-1}$. This yields

$$L_R = L_D + L_D \frac{\tau_M}{\tau_E} \approx L_D \frac{\tau_M}{\tau_E} \quad \text{if } \tau_M \gg \tau_E. \quad (5)$$

The factor τ_M/τ_E represents the average number of dispersal events that an individual performs during its lifetime. Thus, when the mean dispersal length is small relative to this quantity, the response length of the system is approximately equal to the average distance travelled during an organisms lifetime.

The result in eqn 5 was derived by defining the dispersal kernel $b(x - y)$ as a one-sided exponential distribution. However, the approximation

$$L_R \approx L_D \frac{\tau_M}{\tau_E}$$

holds for any one-sided dispersal kernel whose tail decays exponentially or faster (i.e. it is exponentially bounded), given that the organism disperses many times over its lifespan, $\tau_M \gg \tau_E$ (Appendix A).

Equation 5 requires some modification if the population experiences strong density-dependence in demographic or dispersal rates (Appendix A). In this case, the response length is approximately

$$L_R = L_D \left(1 + \frac{\bar{e}_0 + N_H^* [d\bar{e}_0/dN]_{N=N_H^*}}{\bar{m} + N_H^* [d\bar{m}/dN]_{N=N_H^*} - [d\bar{R}/dN]_{N=N_H^*}} \right), \quad (6)$$

where bars represent the spatial mean values of parameters and the derivatives $[d\bar{R}/dN]_{N=N_H^*}$, $[d\bar{m}/dN]_{N=N_H^*}$ and $[d\bar{e}_0/dN]_{N=N_H^*}$ are measures of the strength of density dependence in recruitment, mortality and per capita emigration rates, respectively, when the population is at its spatially homogeneous equilibrium level. With typical mechanisms of density dependence (e.g. local competition for space or other resources), local increases in population density could inhibit recruitment, increase mortality or increase emigration; i.e. $d\bar{R}/dN < 0$, $d\bar{m}/dN > 0$ and $d\bar{e}_0/dN > 0$. Under these scenarios, organisms dispersing away from a locally disturbed site will reduce the recruitment or increase the mortality of organisms in downstream sites and initiate emigration by other individuals in these sites. Thus density-dependent demographic rates will normally shorten the response length L_R relative to the mean lifetime dispersal distance, while density-dependence in emigration rates will increase it.

POPULATION RESPONSES TO CONTINUOUS SPATIAL VARIABILITY

We now extend our analyses of the model defined by eqns (1) and (2) to include the effects of continuous spatial environmental variability on the equilibrium spatial population distribution. We initially consider spatial variability in a single parameter, the recruitment rate $R(x)$, which could arise, for example, when egg banks are spatially aggregated

(Peckarsky *et al.* 2000; Lancaster *et al.* 2003; Reich 2004). We then present analogous results for variability in per capita mortality rates and in the parameters that affect dispersal.

We begin by considering the mathematical idealization of periodic cyclic variation in the recruitment rate represented as a simple sinusoid with wavelength L_E (subscript E for environment), i.e.

$$R(x) = \bar{R} \left(1 + a \cos \left(\frac{2\pi x}{L_E} \right) \right), \quad (7)$$

where \bar{R} represents the spatial mean value of the recruitment rate, and the 'amplitude' a is the maximum proportional deviation of the recruitment rate from this mean value. The spatial wavelength L_E characterizes the spatial scale of environmental variation. Although no natural spatial environmental variability is strictly sinusoidal, this starting point is useful as we can use Fourier analysis to represent any arbitrary pattern of spatial variation as a sum of simple sinusoids with different wavelengths L_E (Appendix B).

Figure 2a shows typical steady state responses of the population to sinusoidal spatial variation in recruitment across a range of wavelengths L_E . The population distribution reflects a dampening of recruitment variability when this variability fluctuates over spatial scales that are small relative to the system's response length. In addition, fluctuations in the population distribution are displaced downstream of the driving fluctuations in recruitment because of the effects of advective dispersal. As the spatial scale of recruitment variability increases, it is increasingly reflected in the spatial population distribution, and the downstream displacement of the population becomes small relative to the scale of the spatial fluctuations. This pattern has been observed previously in spatially explicit models, notably by Roughgarden (1974), who used the term 'averaging' to describe the situation where spatial environmental variation is strongly dampened in the population response, and the term 'tracking' for situations where spatial environmental variation is more strongly reflected in the response.

As noted previously, arbitrary patterns of spatial variation can be represented as a sum of simple sinusoids. Figure 2b illustrates how population responses to simple sinusoidal variation can be used to interpret responses to more complex patterns of environmental variability. The pattern of recruitment variation shown in Fig. 2b is a combination of the three sinusoids shown in Fig. 2a. Also shown are the equilibrium spatial responses of two different populations, one whose response length L_R is roughly the same size as the shortest wavelength and one whose response length is longer than all but the largest wavelength. The population with the short-response length tracks the two longer scales of recruitment variability, but strongly averages the shortest scale. In contrast, the

population with the long-response length averages over the smallest scale of recruitment variability, strongly dampens the intermediate scale, and (weakly) tracks only the largest scale. The population responses shown in Fig. 2b thus reveal a central role of the response length in determining population responses to spatial variability in recruitment rates: variability at scales smaller than the response length will be largely averaged by the population distribution, while variability at longer scales will be increasingly tracked. In addition, for those scales of variability in the recruitment distribution that are tracked, the absolute downstream displacement of the population increases with the response length.

The relationship between the spatial scale of recruitment variability, the population response length, and the degree of tracking or averaging exhibited by the population can be demonstrated algebraically. The method is outlined in Appendix B, the result being that if recruitment rates vary according to eqn (7), the equilibrium population distribution

$$N^*(x) = N_{H}^* (1 + n(x))$$

is given by

$$N^*(x) = N_{H}^* \left(1 + b \cos \left(\frac{2\pi(x - L_L)}{L_E} \right) \right), \quad (8)$$

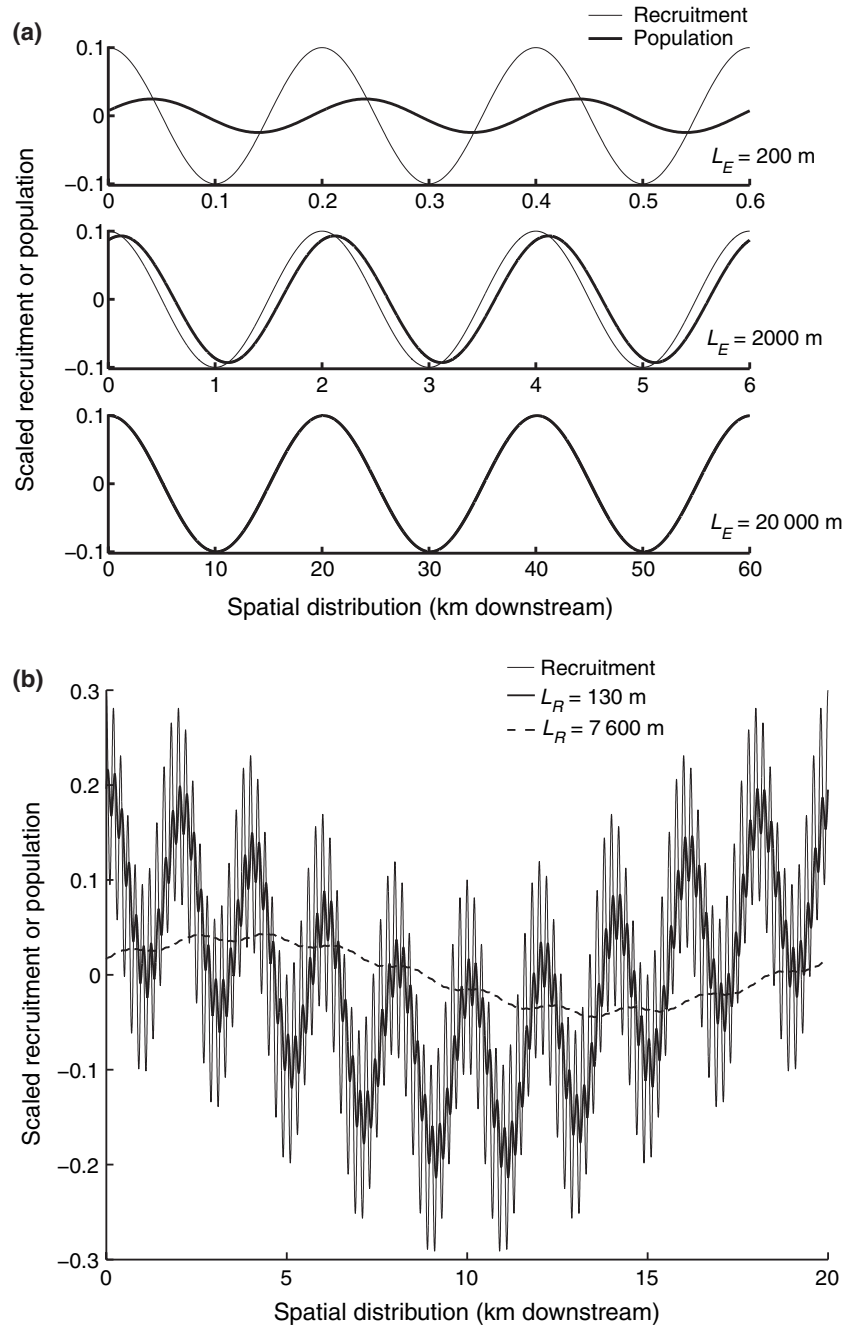
where

$$\frac{b}{a} = \sqrt{\frac{L_E^2 + 4\pi^2 L_D^2}{L_E^2 + 4\pi^2 L_R^2}} \quad \text{and} \quad L_L = \frac{L_E}{2\pi} \tan^{-1} \left(\frac{2\pi L_E (L_R - L_D)}{(L_E^2 + 4\pi^2 L_D L_R)} \right). \quad (9)$$

The ratio b/a is the ratio of the proportional amplitudes of recruitment and population variability at each wavelength L_E . This ratio yields a measure of the degree that spatial environmental variability is reflected in the population response. The length that the population is displaced downstream because of the effects of advection is given by L_L (L for lag). Just as any arbitrary pattern of spatial recruitment variability can be represented by a sum of sinusoids with different wavelengths L_E , the spatial population response to such a pattern is a sum of population responses to each component wavelength (Fig. 2b).

Figure 3a presents the ratio of proportional amplitudes b/a of eqn (9) over a range of spatial scales of recruitment variability. To emphasize the role of the response length L_R in determining the population response, the wavelength of recruitment variability is presented in units scaled by the response length. As also revealed in Fig. 2a,b, the effects of recruitment variability on population density are strongly damped at scales of recruitment variability smaller than the response length. At these small scales of variability, the ratio of proportional amplitudes is approximately the average dispersal length divided by the response length, indicating

Figure 2 General features of spatial population responses to sinusoidally varying recruitment rates. (a) For ease of presentation, population densities and recruitment rates are expressed as proportions of their spatial mean values (\bar{R} and N_{H}^*) and are rescaled to possess spatial mean values of zero [scaled recruitment = $(R(x) - \bar{R})/\bar{R}$, scaled population density = $(N^*(x) - N_{H}^*)/N_{H}^*$]. The amplitudes of pictured fluctuations are thus equal to the proportional amplitudes a in eqn (7) for the recruitment rate and b in eqn (8) for the population density respectively. Distributions are shown plotted over a distance scale that corresponds to three times the given wavelength of recruitment variability, L_E . Very large-scale variability, where $L_E = 20\,000$ m, is tracked by the population response. The population increasingly averages smaller scale variability, $L_E = 2000$ m and $L_E = 200$ m. Qualitative patterns presented are consistent across parameter space; values used here are $e_0 = 0.29 \text{ day}^{-1}$, $m = 0.00414 \text{ day}^{-1}$, $L_D = 1.8$ m, yielding a response length $L_R = 130$ m. See the Discussion and Appendix D for sources of parameter values. (b) Relative degrees of tracking and averaging change with different response lengths. The pattern of recruitment variability pictured is the sum of the three sinusoids pictured in (a). Also shown are the scaled responses to recruitment variability by two hypothetical populations. One population possesses a response length $L_R = 130$ m as in (a). A second population possesses a much larger response length $L_R = 7600$ m.



that the dampening effect is stronger the more times an organism is expected to disperse during its lifetime. As the scale of recruitment variability increases, the degree to which the population tracks this variability increases monotonically towards one at a rate determined by the response length. Spatial fluctuations in recruitment with wavelengths much larger than the response length imply that population densities are very similar among neighbouring localities. Consequently, immigration and emigration rates are approximately in balance and the local population density

is determined by demography alone, $N^*(x) \approx R(x)m^{-1}$ (Appendix B).

The downstream shift L_L of population density relative to recruitment variability approaches zero at scales of variability smaller than the response length, and approaches its maximum value with increasingly large scales of variability (Fig. 3b). From eqn (9), this maximum displacement is $L_R - L_D$, implying that very-large scale fluctuations in recruitment drive fluctuations in population densities that occur downstream at the distance which an individual

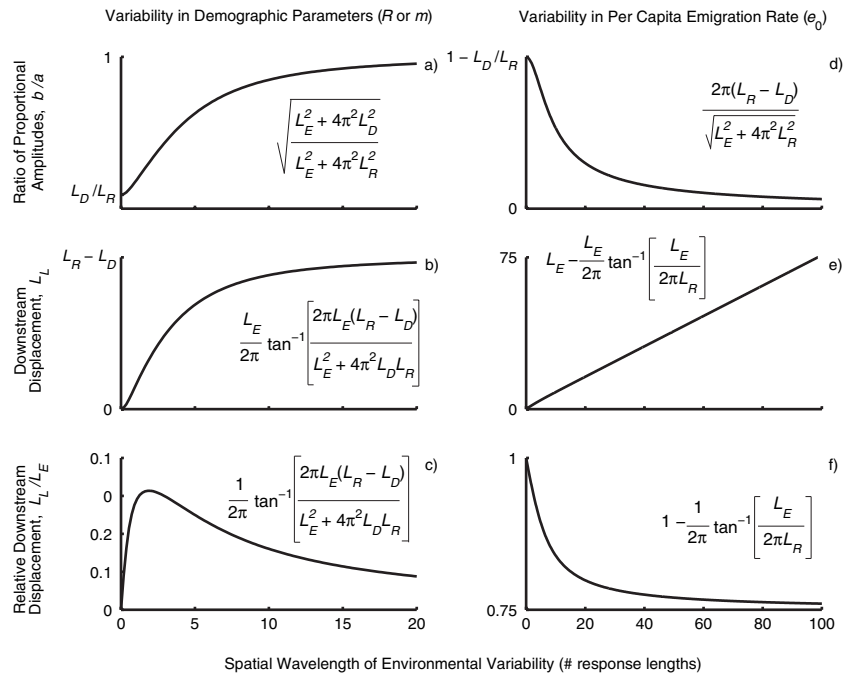


Figure 3 The ratio of proportional amplitudes (b/a), the downstream displacement (L_L), and the relative displacement (L_L/L_E) of component wavelengths of the spatial population distribution relative to component wavelengths L_E of the distribution of environmental variability. The distance units shown on the horizontal axes scale the wavelengths of environmental variability relative to the response length of the population. Equations appearing in each subpanel are those used to generate the respective plots. (a) The population tracks small wavelength variability in demographic parameters (i.e. recruitment R or mortality m) at a minimum level of L_D/L_R . The ratio of proportional amplitudes eventually approaches one over larger wavelengths L_E . (b) The downstream displacement between demographic and population variability also increases in magnitude over larger wavelengths L_E , eventually becoming approximately one response length L_R in distance. (c) The relative downstream displacement shows its largest value at intermediate scales of variability. It eventually approaches zero, causing demographic and population variability to appear in phase despite being separated by approximately a response length. (d) In contrast with (a), the population exhibits the greatest tracking of variability in the per capita emigration rate, e_0 , at small wavelengths. (e) Over all but the smallest wavelengths, the downstream displacement between environmental variation in e_0 and population variability possesses a constant slope of 3/4. (f) For most wavelengths, the population will thus be displaced downstream at a distance that is $c.$ 3/4 of the wavelength of fluctuations. Parameters used in the above example are $e_0 = 0.1 \text{ t}^{-1}$, $m = 0.01 \text{ t}^{-1}$, $L_D = 0.091$ units length, yielding a response length $L_R = 1.0$ units length. In cases where the parameter value varies, the value given above is used as the spatial average.

organism is expected to disperse over its lifetime. Because the downstream displacement asymptotes, it becomes very small relative to the scale of recruitment variability (Fig. 3c). Large scale fluctuations in both recruitment variability and population density appear 'in phase' (Fig. 2a, bottom panel), even though, in practice, they are separated by a constant value $L_R - L_D$.

It is possible to relate spatial variation in per capita mortality and emigration rates (m and e_0) to the spatial population distribution across scales using formulae similar to those in eqn (9). To obtain these, however, requires local linearization of the spatially variable parameter and population terms in eqn (1) about their spatially homogeneous steady states (Appendices B and C). The relative amplitude and downstream displacement of population density in response to spatial variability in per capita

mortality rates at different wavelengths are given by the same formulae in eqn (9). Thus, population responses to spatial variability in any demographic parameter are very similar. A crucial qualitative difference is that peaks in recruitment cause peaks in population density, whereas peaks in per capita mortality rates cause troughs in population densities, both of which are displaced downstream by a distance L_L .

Similar to the effects of spatial variation in mortality rates, peaks in the spatial distribution of per capita emigration rates produce troughs in population density. Otherwise, population responses to spatial variability in dispersal parameters possess qualitatively different properties than responses to demographic variability discussed above. We show in Appendix C that, for population responses to spatially variable per capita emigration rates e_0 , the ratio of

proportional amplitudes and downstream displacement are given by

$$\frac{b}{a} = \frac{2\pi(L_R - L_D)}{\sqrt{L_E^2 + 4\pi^2 L_R^2}} \quad \text{and} \quad L_L = L_E - \frac{L_E}{2\pi} \tan^{-1}\left(\frac{L_E}{2\pi L_R}\right). \quad (10)$$

Similar to the responses to demographic variability (eqn 8), the population responses to spatial variability in per capita emigration rates are largely determined by the response length L_R . However, the population responses in eqn (10) differ from those in eqn (9) in two important ways (Fig. 3d,e). First, the population distribution will most strongly track variability in per capita emigration rates over the smallest spatial scales, where the impacts of dispersal processes are most strongly felt by the population. In contrast to population responses to demographic variability, a lower ratio of L_D to L_R yields stronger population responses to very small scale variability in emigration rates. When the scale of variability in the per capita emigration rate becomes very large, immigration and emigration tend to locally balance, causing the population response to tend towards zero. Thus, the population will almost completely average very large-scale fluctuations in per capita emigration rates, and increasingly track smaller ones. Second, the downstream displacement between population densities and variability in per capita emigration rates is a distance that is $c. 3/4$ of the wavelength of variability L_E for most spatial scales (Fig. 3e,f). It is only for very small scales of variability that the displacement distance deviates from this pattern.

We noted earlier that the average dispersal distance L_D can be interpreted as representing the combined effects of dispersal velocity and settling rate. Calculating the response to spatial variation in these quantities is most conveniently achieved by using the two-state model from which eqn (1) was derived (Lutscher *et al.* 2005). Using these equations, we show in Appendix C that the population responses to spatially variable average dispersal lengths are solely determined by higher-order interactions and are approximately zero in the limiting situations for which eqn (1) holds.

Populations with density dependence respond to continuous variability in demographic or emigration parameters in ways that are qualitatively similar to those shown in Fig. 3. These responses are still largely dictated by the response length L_R , but density dependence may alter the response length as in eqn (6). Populations with density dependent rates therefore transition from averaging environmental variability to tracking it over different spatial scales than similar populations exhibiting no density dependence. Furthermore, while scale invariant effects of density dependence will alter minimum and maximum

proportional tracking, these quantities will still be largely determined by the ratio of L_D to L_R .

DISCUSSION

We have analysed a strategic, spatially explicit model describing population responses to spatial environmental variability in advection-dominated systems. Our results illustrate a means of connecting local population dynamics that are readily inferred in experimental settings to larger scale population patterns. A key property of the model is that the response length of a population to a localized disturbance determines, to a large degree, the intensity and pattern of spatial population responses to continuous spatial variation in environmental variables. This property holds true under both density-independent and -dependent scenarios. When spatial environmental fluctuations are at scales much smaller than the response length, the amplitude of spatial population fluctuations is largely determined by the ratio of the average dispersal length to the response length, regardless of whether environmental variability affects demographic or dispersal parameters. The exception is variability in L_D , which has very little impact at any scale. As the spatial scale of environmental fluctuations increases, variability in demographic parameters are increasingly reflected in the population distribution while that in per capita emigration rates is increasingly averaged out. Thus, the response length yields a measure of the characteristic spatial scale over which population dynamics shift from local-scale dynamics dominated by dispersal processes to larger-scale dynamics dominated by births and deaths.

Our model was formulated with maximal simplicity in mind, and necessarily, omits obvious features known to occur in many advection-dominated systems such as consumer-resource interactions (e.g. Kohler 1984; Diehl *et al.* 2000; Shurin *et al.* 2002) and temporal environmental variability (e.g. Poff & Ward 1989). However, our methodology can be used to calculate response lengths in models with more complex within- and between-population interactions, and the techniques we employed to determine responses to continuous spatial variability can also be extended to include population responses to combined spatial and temporal environmental variability (Nisbet & Gurney 2003). Populations involved in strong consumer-resource interactions both impact and possess vital rates that respond to the local environment, and will therefore likely respond to environmental variability in a manner similar to our density-dependent model, eqn (6). This implies that consumer-resource systems may possess response lengths that are either elongated or shortened compared with the single-species approximation in eqn (5) depending on the form and strength of interactions among component populations (Anderson 2004).

Despite its simplicity, our model elucidates the key quantities that are likely to influence response lengths, and in turn, population responses to continuous environmental variability. Calculation of the response length for our simple model requires estimation of three parameters: the per capita mortality rate m , the per capita emigration rate e_0 , and the average distance travelled per dispersal event L_D . This highlights the need for field ecologists to carefully quantify both the per capita emigration rates and average dispersal distances of populations in advection-dominated systems. As strong-density dependence may also influence the response length, it is important to quantify key rate processes across a range of population densities.

Per capita emigration rates and many demographic rates are estimable from short-term, small-scale experiments. For example, studies of predator impacts on prey populations typically quantify predator induced changes in per capita emigration rates in addition to consumption rates (Englund *et al.* 2001). In addition, small- and medium-scale experiments can reveal the strength of density-dependent effects on emigration, consumption and recruitment rates (e.g. Kratz 1996; Diehl *et al.* 2000; Hildrew *et al.* 2004). One complication arises in the measurement of emigration rates in small-scale studies. These quantities are typically reported as area-specific emigration rates, calculated as the rate organisms leave an experimental arena. Organisms may experience more than one dispersal event before leaving an experimental arena that is longer than their average dispersal length, creating apparent scale-dependence in observed area-specific emigration rates (Englund & Hambäck 2004). This contrast with the 'true' emigration rates that we assume in our model that refers to the rate of single emigration events and is thus independent of the spatial scale of observation. The true emigration rates can be estimated from area-specific rates, provided there are estimates of average dispersal lengths, by using previously available methods (e.g. Englund *et al.* 2001; Englund & Hambäck 2004).

Average dispersal distances per dispersal event are less commonly reported in the literature than demographic or emigration rates. Existing estimates for macro-invertebrates in streams are on the order of meters to tens of meters (Waters 1965; Elliott 1971; Larkin & McKone 1985), suggesting that the dispersal distributions of these organisms can be assessed using short-term mark-recapture studies (e.g. Elliott 1971). Techniques employing genetic or isotope markers hold the promise of increasing insight into the average dispersal distances of organisms where these distances are large, such as in marine organisms or aquatic bivalves (Palmer *et al.* 1996; Bilton *et al.* 2001). Because the parameters determining the response length for our model are calculated from processes that are quantifiable for many taxa, our results should be readily applicable to, and allow

comparisons of a variety of empirical settings. Even crude estimates of response lengths may provide relative measures for comparing systems.

A common method of testing for scale-dependence influences of the environment on the distribution of benthic organisms in advection-dominated systems is by partitioning variance in both environmental and population measurements among hierarchical sampling regimes (e.g. microhabitat vs. stream reach vs. catchment; see Cooper *et al.* 1997; Mykra *et al.* 2004). Our analyses suggest that these sampling schemes may not effectively characterize scale-dependent environmental influences as the population response to any particular environmental driver should depend on both the factor's spatial mean and the scale over which it varies. For example, if an environmental factor affects demographic rates, our model predicts that the population will respond largely to the spatial mean value of that factor when it varies over small spatial scales. In contrast, if that same environmental factor varies over large spatial scales, the population will exhibit increasing responses to the factor's spatial variance. Even in the latter case, the correlation between environment and population density may be weakened by the downstream displacement of the population response relative to the environmental driver. Population responses to the suite of abiotic and biotic factors comprising the 'habitat template' may thus be more profitably examined by using models similar to ours to link the output of small-scale manipulations with rigorously quantified spatial cross-correlations among system components. The latter requires detailed and extensive data on longitudinal patterns of population abundances and environmental variables (Cooper *et al.* 1997), which, to the best of our knowledge, are currently lacking from the literature.

We now illustrate the application of our theory using parameter estimates from the stonefly *Leuctra nigra* (Plecoptera: Leuctridae; Olivier) residing in Broadstone Stream, a small acidic stream in southeastern England (see Speirs *et al.* 2000 and references therein for details). Details of the parameter estimation and estimated values are provided in Appendix D. Based on experimental evidence, we assume that both per capita emigration rates and average dispersal lengths for *L. nigra* vary positively with average stream velocity, and we assume no density-dependence in any vital rates. For Broadstone Stream, stream velocities typically fall in the range of 0.052–0.24 m s⁻¹, depending on discharge (Winterbottom *et al.* 1997a). Response lengths calculated using this range of velocities are *c.* 130 < L_R < 7600 m. One implication of such long-response lengths is that the localized environmental disturbances will have impacts over long distances downstream. For example, construction of an impoundment that limits dispersal between upstream and downstream habitats will impact downstream population

densities over a scale much larger than the impoundment's physical footprint.

An additional implication of *L. nigra*'s long calculated response lengths is that they suggest population densities will strongly average the small scale components of variability in demographic parameters. The parameter values used to simulate population responses to variability in recruitment rates in Fig. 2 correspond to those of two hypothetical *L. nigra* populations: one residing in a stream with a constant current velocity of 0.052 m s^{-1} , and one in a stream with a constant velocity of 0.24 m s^{-1} . As noted previously, both populations pictured in Fig. 2b tracks only large-scale variability in $R(x)$, exhibiting averaging over smaller spatial scales, including those over which experiments are typically conducted (noting that distances are plotted over a km scale). These results suggest that recruitment variation over landscape scales – for example, between upstream and downstream reaches – should lead to large amplitude responses in populations that are displaced hundreds to thousands of meters downstream of recruitment sources. Clumped egg banks or other recruitment fluctuations that occur over smaller scales would produce much less dramatic impacts, especially in high velocity streams. Following eqn (9), this does not imply that variable recruitment over small scales will not produce *any* patterns in *L. nigra* densities. Rather, it suggests that population tracking of local scale fluctuations will be very small relative to the average density of the population. Many organisms emigrate from areas of high to low flow in advection-dominated systems (e.g. Lancaster & Hildrew 1993), which could create strong local patterns of co-occurrence between densities and low flow areas possessing low per capita emigration rates. As in our parameterized example, such emigration patterns could also generally weaken associations between densities and areas characterized by high recruitment rates over small scales (e.g. Reich & Downes 2004).

The long-response lengths of *L. nigra* populations stem from the high mean number of estimated dispersal events per *L. nigra* lifetime ($\tau_E = 0.26\text{--}3.5$ days vs. $\tau_M = 242$ days at reasonable stream velocities). Disparities between the time scales of movement and mortality may characterize many aquatic macro-invertebrates, most notably those that are commonly collected drifting in streams. This implies that response lengths for organisms common in the drift will typically be kilometres, rather than meters, in length. For example, Hershey *et al.* (1993) estimated that *Baetis* larvae in the Kuparuk River in Alaska possess a lifetime dispersal distance of *c.* 2 km, while Humphries & Ruxton (2003) estimated that individuals of the amphipod *Gammarus pulex* possess an intragenerational drift distance of *c.* 1.5 km. Equation (5) suggests that lifetime dispersal distances will closely approximate response lengths in these populations.

This contrasts with other organisms that may disperse only one or a few times per average lifespan. For these more sedentary organisms, response lengths will be determined predominantly by the average dispersal distance of a single dispersal bout. Regardless of whether the average dispersal distance per bout is large (e.g. some marine organisms, Kinlan & Gaines 2003; zebra mussels, Stoeckel *et al.* 2004) or small (e.g. caddisfly larvae, Jackson *et al.* 1999), relatively sedentary organisms will possess a high ratio of L_D/L_R . Because these types of organisms will not disperse in response to local environmental conditions at high rates, our theory predicts they should strongly track all scales of spatial variability in demographic processes and very weakly track that affecting per capita emigration rates. Such populations should exhibit very little scale dependence in their responses to environmental variability. Determining the relative time scales over which dispersal and demographic processes operate can provide a starting point for determining which parameters must be most accurately measured to determine population responses to spatial environmental variability across scales.

ACKNOWLEDGEMENTS

The authors would like to thank Mark Lewis, Frithjof Lutscher, Ed McCauley, John Melack, Elizaveta Pachepsky and Keith Taulbee for thoughtful discussions of population dynamics in advective environments. We also thank Bruce Kendall, Elizaveta Pachepsky and Steve Rothstein for helpful comments on earlier drafts of this manuscript. Support for RMN and KEA was provided in part by NSF grant DEB-01-08450, for KEA in part by an NSF Graduate Research Fellowship, for SD in part by DFG grant DI 745/3 and for SDC in part by NSF grant DEB-9407591.

SUPPLEMENTARY MATERIAL

The following supplementary material is available online from <http://www.Blackwell-Synergy.com>:

- Appendix A** Population response to a localized disturbance.
- Appendix B** Equilibrium population responses to spatial environmental variability in parameters describing demography.
- Appendix C** Equilibrium population responses to spatial environmental variability in parameters describing dispersal.
- Appendix D** Additional background on parameter estimation for *Leuctra nigra* in Broadstone Stream.

REFERENCES

- Anderson, K.E. (2004). *The spatial population dynamic consequences of dispersal behavior: case studies in aquatic and terrestrial systems*. PhD Dissertation. University of California, Santa Barbara, CA.

- Ballyk, M. & Smith, H. (1999). A model of microbial growth in a plug flow reactor with wall attachment. *Math. Biosci.*, 158, 95–126.
- Bender, E.A., Case, T.J. & Gilpin, M.E. (1984). Perturbation experiments in community practice: theory and practice. *Ecology*, 65, 1–13.
- Bilton, D.T., Freeland, J.R. & Okamura, B. (2001). Dispersal in freshwater invertebrates. *Ann. Rev. Ecol. Syst.*, 32, 159–181.
- Cooper, S.D., Walde, S.J. & Peckarsky, B.L. (1990). Prey exchange rates and the impact of predators on prey populations in streams. *Ecology*, 71, 1503–1514.
- Cooper, S.D., Barmuta, L., Sarnelle, O., Kratz, K. & Diehl, S. (1997). Quantifying spatial heterogeneity in streams. *J. N. Am. Bent. Soc.*, 16, 174–188.
- Cooper, S.D., Diehl, S., Kratz, K. & Sarnelle, O. (1998). Implications of scale for patterns and processes in stream ecology. *Aust. J. Ecol.*, 23, 27–40.
- Diehl, S., Cooper, S.D., Kratz, K.W., Nisbet, R.M., Roll, S.K., Wiseman, S.W. *et al.* (2000). Effects of multiple, predator-induced behaviors on short-term producer-grazer dynamics in open systems. *Am. Nat.*, 156, 293–313.
- Elliott, J.M. (1971). The distances traveled by drifting invertebrates in a Lake District stream. *Oecologia*, 6, 350–379.
- Englund, G. & Cooper, S.D. (2003). Scale effects and extrapolation in ecological experiments. In: *Advances in Ecological Research*, Vol. 33 (ed. Caswell, H.). Academic Press, San Diego, CA, pp. 161–213.
- Englund, G. & Hambäck, P.A. (2004). Scale dependence of movement rates in stream invertebrates. *Oikos*, 105, 31–40.
- Englund, G., Cooper, S.D. & Sarnelle, O. (2001). The scale-dependence of predator effects on prey densities: a test of theory using stream experiments. *Oikos*, 92, 501–514.
- Forrester, G.E., Dudley, T.L. & Grimm, N.B. (1999). Trophic interactions in open systems: effects of predators and nutrients on stream food chains. *Limnol. Oceanogr.*, 44, 1187–1197.
- Gaines, S.D., Gaylord, B. & Largier, J.L. (2003). Avoiding current oversights in marine reserve design. *Ecol. Appl.*, 13 (Suppl. S), S32–S46.
- Hershey, A.E., Pastor, J., Peterson, B.J. & Kling, G.W. (1993). Stable isotopes resolve the drift paradox for *Baetis* mayflies in an arctic river. *Ecology*, 74, 2315–2325.
- Hildrew, A.G., Woodward, G., Winterbottom, J.H. & Orton, S. (2004). Strong density dependence in a predatory insect: large-scale experiments in a stream. *J. Anim. Ecol.*, 73, 448–458.
- Humphries, S. & Ruxton, G.D. (2003). Estimation of inter-generational drift dispersal distances and mortality risk for aquatic macroinvertebrates. *Limnol. Oceanogr.*, 48, 2117–2124.
- Jackson, J.K., McElravy, E.P. & Resh, V.H. (1999). Long-term movements of self-marked caddisfly larvae (Trichoptera: Sericostomatidae) in a California coastal mountain stream. *Freshw. Biol.*, 42, 525–536.
- Kinlan, B.P. & Gaines, S.D. (2003). Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology*, 84, 2007–2020.
- Kohler, S.L. (1984). Search mechanism of a stream grazer in patchy environments – the role of food abundance. *Oecologia*, 62, 209–218.
- Kratz, K.W. (1996). Effects of stoneflies on local prey populations: mechanisms of impact across prey density. *Ecology*, 77, 1573–1585.
- Lancaster, J. & Hildrew, A.G. (1993). Characterizing in-stream flow refugia. *Can. J. Fish. Aquat. Sci.*, 50, 1663–1675.
- Lancaster, J., Downes, B.J. & Reich, P. (2003). Linking landscape patterns of resource distribution with models of aggregation in ovipositing stream insects. *J. Anim. Ecol.*, 72, 969–978.
- Larkin, P.A. & McKone, D.W. (1985). An evaluation by field experiments of the McLay model of stream drift. *Can. J. Fish. Aquat. Sci.*, 42, 909–918.
- Levin, S.A. (1992). The problem of pattern and scale in ecology. *Ecology*, 73, 1943–1967.
- Levine, J.M. (2003). A patch modeling approach to the community-level consequences of directional dispersal. *Ecology*, 84, 1215–1224.
- Lutscher, F., Pachepsky, E. & Lewis, M.A. (2005). The effect of dispersal patterns on stream populations. *SIAM J. Appl. Math.*, 65, 1305–1327.
- Malmqvist, B. (2002). Aquatic invertebrates in riverine landscapes. *Freshw. Biol.*, 47, 679–694.
- Mykra, H., Heino, J. & Muotka, T. (2004). Variability of lotic macroinvertebrate assemblages and stream habitat characteristics across hierarchical landscape classifications. *Environ. Manage.*, 34, 341–352.
- Nisbet, R.M. & Gurney, W.S.C. (2003). *Modelling Fluctuating Populations*. The Blackburn Press, Caldwell, NJ.
- Nisbet, R.M., Diehl, S., Wilson, W.G., Cooper, S.D., Donalson, D.D. & Kratz, K. (1997). Primary productivity gradients and short-term population dynamics in open systems. *Ecol. Monogr.*, 67, 535–553.
- Pachepsky, E., Lutscher, F., Nisbet, R.M. & Lewis, M.A. (2005). Persistence, spread, and the drift paradox. *Theor. Popul. Biol.*, 67, 61–73.
- Palmer, M.A., Allan, J.D. & Butman, C.A. (1996). Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. *Trends Ecol. Evol.*, 11, 322–326.
- Peckarsky, B.L., Taylor, B.W. & Caudill, C.C. (2000). Hydrologic and behavioral constraints on oviposition of stream insects: implications for adult dispersal. *Oecologia*, 125, 186–200.
- Poff, N.L. & Ward, J.V. (1989). Implications of streamflow variability and predictability for lotic community structure – a regional-analysis of streamflow patterns. *Can. J. Fish. Aquat. Sci.*, 46, 1805–1818.
- Reich, P. (2004). Patterns of composition and abundance in macroinvertebrate egg masses from temperate Australian streams. *Mar. Freshw. Res.*, 55, 39–56.
- Reich, P. & Downes, B.J. (2004). Relating larval distributions to patterns of oviposition: evidence from lotic hydrobiosid caddisflies. *Freshw. Biol.*, 49, 1423–1436.
- Roughgarden, J. (1974). Population-dynamics in a spatially varying environment – how population size tracks spatial variation in carrying capacity. *Am. Nat.*, 108, 649–664.
- Shurin, J.B., Borer, E.T., Seabloom, E.W., Anderson, K., Blanchette, C.A., Broitman, B. *et al.* (2002). A cross-ecosystem comparison of the strength of trophic cascades. *Ecol. Lett.*, 5, 785–791.
- Speirs, D.C. & Gurney, W.S.C. (2001). Population persistence in rivers and estuaries. *Ecology*, 82, 1219–1237.
- Speirs, D.C., Gurney, W.S.C., Hildrew, A.G. & Winterbottom, J.H. (2000). Long-term demographic balance in the Broadstone stream insect community. *J. Anim. Ecol.*, 69, 45–58.

- Stoeckel, J.A., Rehmann, C.R., Schneider, D.W. & Padilla, D.K. (2004). Retention and supply of zebra mussel larvae in a large river system: importance of an upstream lake. *Freshw. Biol.*, 49, 919–930.
- Waters, T.F. (1965). Interpretation of invertebrate drift in streams. *Ecology*, 46, 327–334.
- Wiens, J.A. (1989). Spatial scaling in ecology. *Funct. Ecol.*, 3, 385–397.
- Wiens, J.A. (2002). Riverine landscapes: taking landscape ecology into the water. *Freshw. Biol.*, 47, 501–515.
- Winterbottom, J.H., Orton, S.E., Hildrew, A.G. & Lancaster, J. (1997a). Field experiments of flow refugia in streams. *Freshw. Biol.*, 37, 569–580.
- Winterbottom, J.H., Orton, S.E. & Hildrew, A.G. (1997b). Field experiments on the mobility of benthic invertebrates in a southern English stream. *Freshw. Biol.*, 38, 37–47.
- Woodward, G. & Hildrew, A.G. (2002). Food web structure in riverine landscapes. *Freshw. Biol.*, 47, 679–694.
- Wooster, D.E. & Sih, A. (1995). A review of the drift and activity responses of stream prey to predator presence. *Oikos*, 73, 3–8.

Editor, Michael Hochberg

Manuscript received 17 February 2005

First decision made 25 March 2005

Manuscript accepted 17 May 2005