Adaptive movement and spatial scales in advection-dominated systems

Roger M. Nisbet,

Dept of Ecology, Evolution and Marine Biology,

University of California, Santa Barbara.

Based on collaborative work with: Kurt Anderson, Sebastian Diehl, Mark Lewis, Ed McCauley

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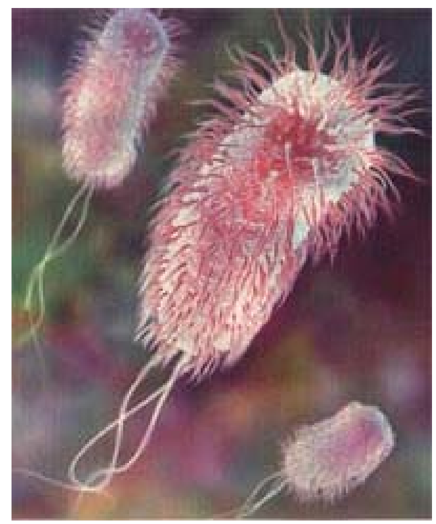
Advection-dominated systems



Representation of an idealized river

Source $\longrightarrow$ Mouth

$x=0$ $\qquad$ $x=L$

Density $\quad N(x, t)$ = number per unit length at location x and time t

Population Dynamics

$$\frac{\partial N(x,t)}{\partial t} = \underbrace{R(x)}_{\text{recruitment}} - \underbrace{e_G(x)\,N(x,t)}_{\text{emigration}} - \underbrace{m(x)\,N(x,t)}_{\text{mortality}} + \underbrace{\int_0^x e_G(y)\,N(y,t)\,h(x-y)\,dy}_{\text{immigration}}$$

Local Population Dynamics

$$\frac{\partial N(x,t)}{\partial t} = R(x) - e_G(x)\,N(x,t) - m(x)\,N(x,t) + \int_0^x e_G(y)\,N(y,t)\,h(x-y)\,dy$$

Spatially homegenous steady state is $\qquad N^* = R^* / m$

Local dynamics have the form $\qquad \frac{dN}{dt} = R + I - (m + e_G)N$

so ***local steady state*** is always given by $\qquad N^* = \frac{R+I}{e_G + m}$

Sensitivity of equilibrium to disturbances

Define ***equilibrium sensitivity***

$$\sigma_R = \frac{\left(\frac{\delta N^*}{N^*}\right)}{\left(\frac{\delta R}{R}\right)} = \frac{d \ln N^*}{d \ln R}$$

(a) If R changes only locally,

$$\sigma_R = \frac{1}{1 + e_G / m}$$

$$= \left(1 + N_J\right)^{-1} \approx N_J{}^{-1}$$

(b) If R changes globally,

$$\sigma_R = 1$$

[Note $N_J = e_G / m$ is the mean number of jumps per lifetime]

Summary of equilibrium sensitivities

Parameter	Local Sensitivity	Global Sensitivity
R	*small*	*large*
m	*small*	*large*
e_G	*large*	*0*

Steady State Response to Spatial Heterogeneity

$$\frac{\partial N(x,t)}{\partial t} = R(x) - e_G(x)\,N(x,t) - m(x)\,N(x,t) + \int_0^x e_G(y)\,N(y,t)\,h(x-y)\,dy$$

Define

$$R(x) = R^*\left(1 + r(x)\right); \qquad m(x) = m^*\left(1 + \mu(x)\right);$$

$$e_G(x) = e_G{}^*\left(1 + \varepsilon(x)\right); \qquad N(x) = N^*\left(1 + n(x)\right)$$

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Substituting and discarding products of small quantities yields a **linear** equation:

$$\boxed{0 = \frac{\partial n}{\partial t} = \overline{m}r(x) - \overline{e}\left(n(x) + \varepsilon(x)\right) + \overline{e}\int_0^x \left(n(u) + \varepsilon(u)\right)h(x-y)dy}$$

Spatial scale and the Laplace transform

Laplace transform of (say) $n(x)$ is defined by:

$$L\left(n(x)\right) \equiv \tilde{n}(s) = \int_0^\infty n(x)\exp(-sx)dx$$

Interpretation: weighted measure with highest weighting to perturbations over a range of order $1/s$.

Large s	$\leftrightarrow$	small scale
Small s	$\leftrightarrow$	large scale

Solving the linearized equation

$$0 = \frac{\partial n}{\partial t} = \bar{m}r(x) - \bar{e}\left(n(x) + \varepsilon(x)\right) + \bar{e}\int_0^x \left(n(u) + \varepsilon(u)\right) h(x-y)dy$$

Can solve for Laplace transform $\tilde{n}(s)$ with the result

$$\boxed{\begin{gathered}\tilde{n}(s) = T_R(s)\tilde{r}(s) + T_m(s)\tilde{m}(s) + T_e(s)\tilde{\varepsilon}(s) \\ T_R(s) = -T_m(s) = \frac{1}{1 + N_J\left(1 - \tilde{h}(s)\right)}; \qquad T_e(s) = \frac{-N_J\left(1 - \tilde{h}(s)\right)}{1 + N_J\left(1 - \tilde{h}(s)\right)}\end{gathered}}$$

Approximation to Transfer Functions

If s is "small", then

$$\tilde{h}(s) = \int_0^\infty h(s)e^{-sx}dx \approx \int_0^\infty h(s)\left(1 - sx\right)dx = 1 - sL_D$$

with $\quad L_D = \int_0^\infty xh(x)dx$ = mean distance per jump.

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The transfer functions then take familiar forms:

$$T_R(s) = \frac{1}{1 + sN_J L_D} \quad \text{and} \quad T_e(s) = \frac{-sN_J L_D}{1 + sN_J L_D}$$

NOTE: Correction needed at large *s*: depends on kernel

Impulse response function

- ***Impulse response function*** = inverse L.T. of transfer function
- Describes the steady state response to a localized (delta function) perturbation.
- For a perturbation in R at x=0, downstream population density has the form

$$n(x) \propto e^{-x/L_R},$$

- ***Response length*** $L_R = N_J L_D$ = mean displacement in lifetime.
- Note that response to an impulse in emigration rate has a singularity at x=0

Magnitude of Response Length L_R

$$L_R \approx L_D N_J = L_D \frac{e_G}{m}, \quad \text{where} \quad \left.\begin{aligned} L_D &= \text{avg. dispersal length} \\ e_G &= \text{per cap. emigration} \\ m &= \text{per cap. mortality} \end{aligned}\right\}$$

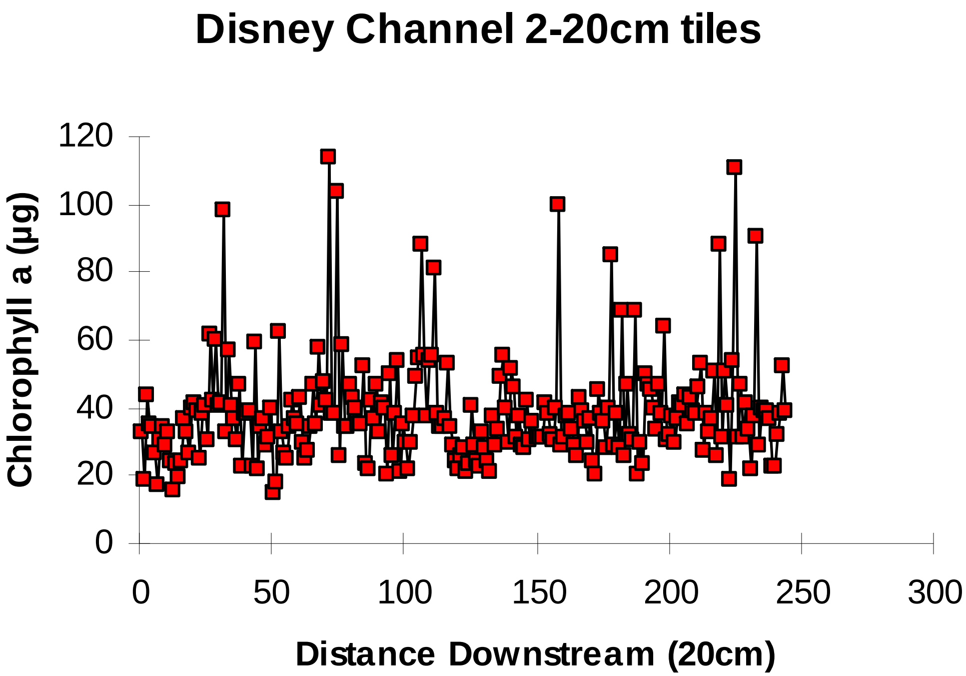
Examples of long (km) response lengths

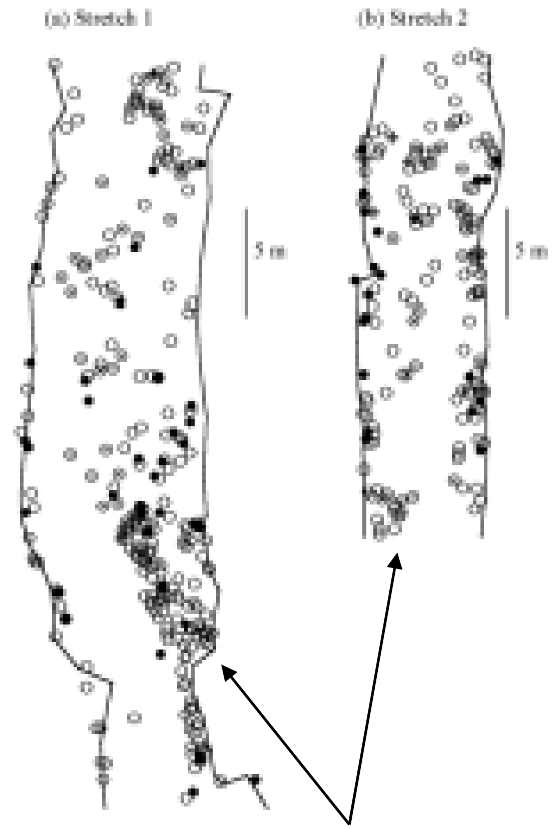
– *Baetis* in Kuparak River
  $\Rightarrow L_R \approx$ **2 km**
- *Gammarus* in Lake District
  $\Rightarrow L_R \approx$ **1.5 km**
- Coastal fish near Diablo Canyon Power Plant (CA)
- $\Rightarrow L_R \approx$ **5 km**
- Stoneflies in Broadstone Creek (England)
- $\Rightarrow L_R \approx$ **0.13-7.6 km**

-Examples of short (m) response lengths

- Many inverts in Convict Creeek (CA)
  $\Rightarrow L_R \approx$ **1-200 km**

Spatially extended variability

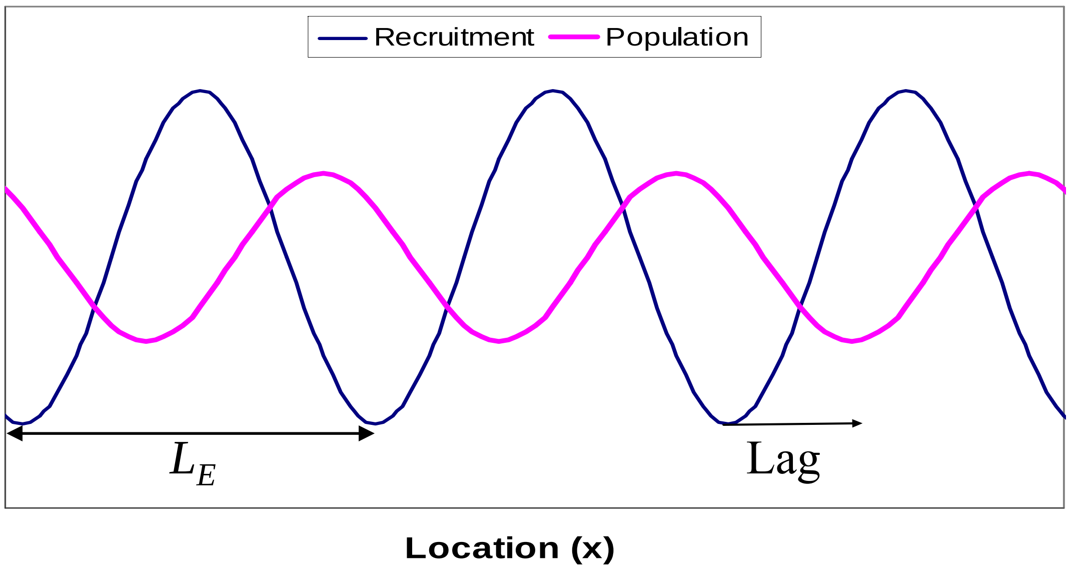




Egg clusters

Steady state response to spatially extended environmental perturbations

Assume spatial variation in recruitment, $R(x)$ represented as sum of *sinusoids* of wavelength L_E

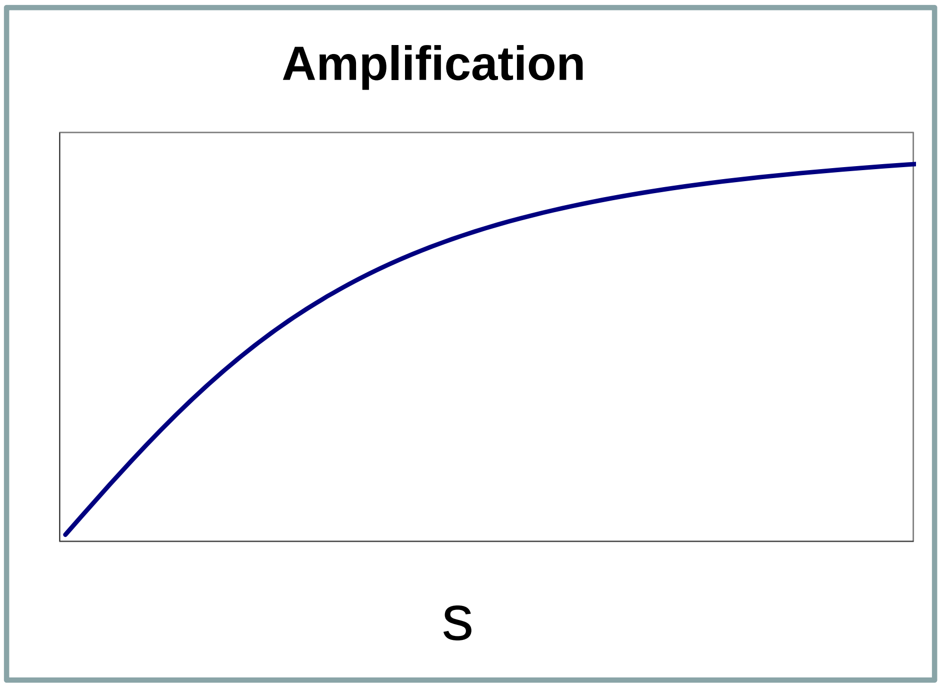


$$\textbf{Amplification} = \frac{\text{amplidude of population variation}}{\text{amplitude of recrutiment variation}}$$

<u>"Tracking" and "averaging" changes in emigration rate</u>

Amplification and downstream lag are calculated by setting

$s = i2\pi / L_E$ in transfer functions



Population distribution:

- "<u>averages</u>" large scale (small s) disturbances
- "<u>tracks</u>" small scale disturbances
- "large" means much greater than L_R

Spatio-temporal dynamics

Transient Dynamics are a key component of many advective systems

Measures of transient response for non-spatial systems include:

- **Resilience**
- **Reactivity**
- **Amplification envelope**

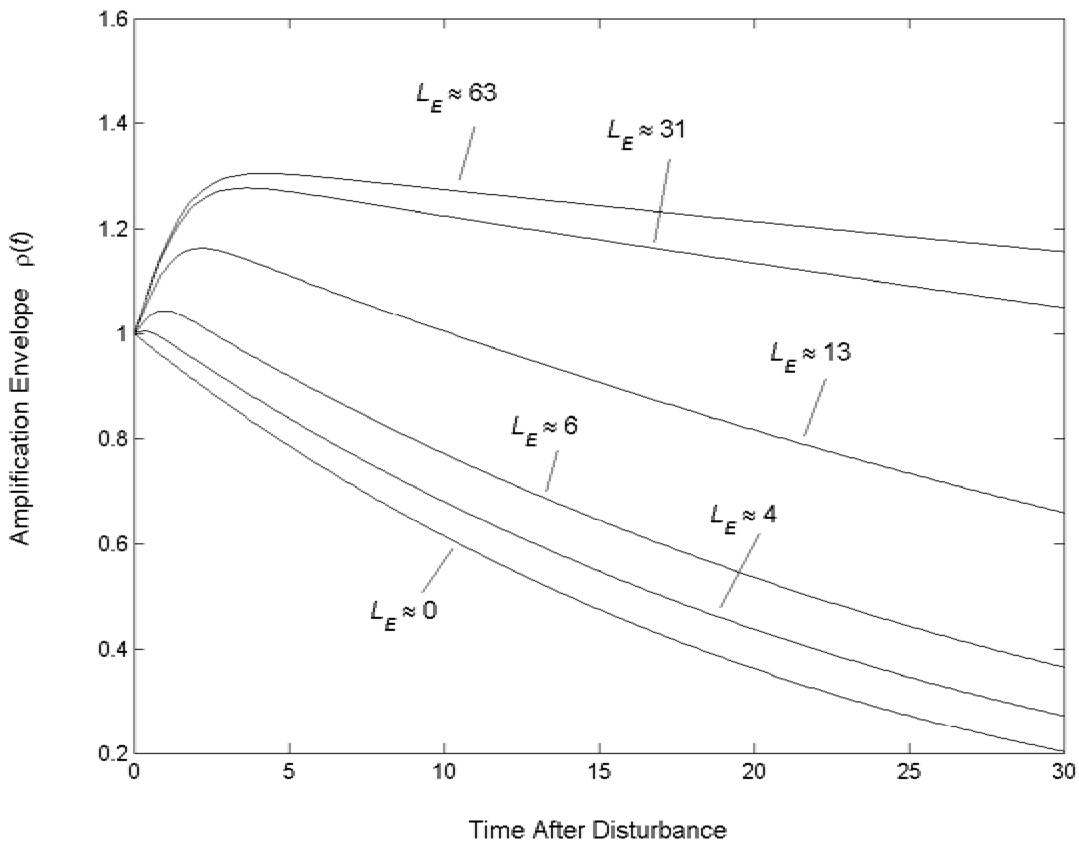
For ODE system of form $\frac{d\mathbf{x}}{dt} = \mathbf{J}\mathbf{x}$:

- Resilience from leading eigenvalue of $\mathbf{J}$.
- Reactivity from leading eigenvalue of $\mathbf{H} = \frac{1}{2}\left(\mathbf{J} + \mathbf{J}^{T}\right)$
- Amplification envelope from matrix norm of $\exp(\mathbf{J}t)$

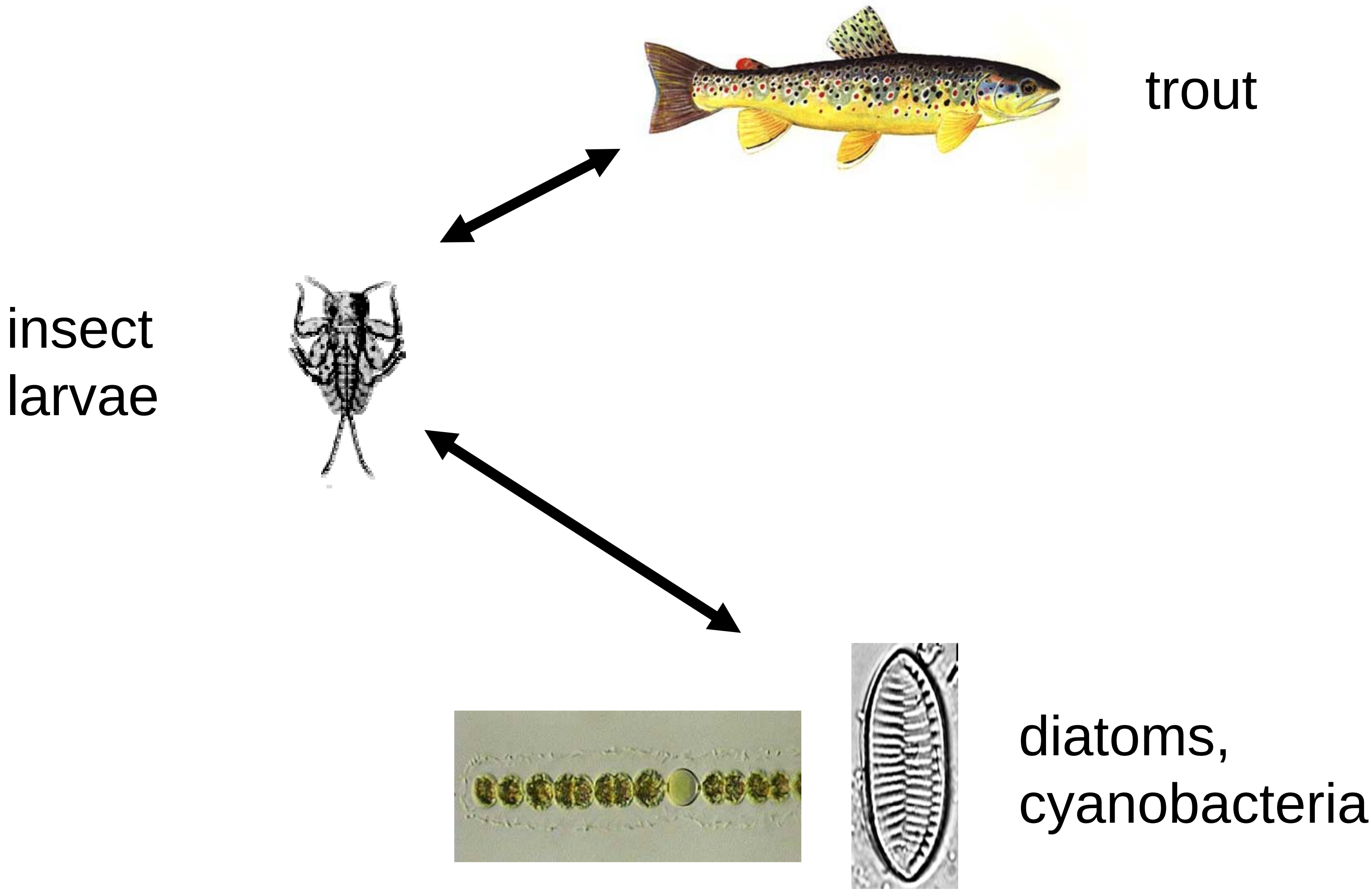
In advective systems, these calculations can be performed on the Laplace or Fourier transformed equations, thereby relating transient response to spatial scale.

Spatio-temporal dynamics

Amplification envelope related to response length



Biotic interactions and the response length



Impacts of biotic interactions on the response length L_R

Let rates depend on an abiotic factor $A(x)$ and a biotic factor $B(x)$

Define $A(x) = \bar{A}(1 + \alpha(x);\quad B(x) = \bar{B}\left(1 + \beta(x)\right)$

Then $\tilde{n}(s) = T_A(s)\tilde{\alpha}(s) + T_B(s)\tilde{\beta}(s)$

with $$T_A(s) = \frac{(\sigma_{RA} - \sigma_{mA}) - s\sigma_{eA} JL_D}{1 + sJL_D} \quad \text{and} \quad T_B(s) = \frac{(\sigma_{RB} - \sigma_{mB}) - s\sigma_{eB} JL_D}{1 + sJL_D}.$$

where σ's are sensitivities.

NEED TO SPECIFY RELATIONSHIP BETWEEN *B*(*x*) and *N*(*x*)

Direct Density Dependence

Set $B(x) = N(x)$ implying $\tilde{\beta}(s) = \tilde{n}(s)$.

Then $$\tilde{n}(s) = \frac{T_A(s)}{1 - T_B(s)}\tilde{\alpha}(s) = \frac{\sigma_{RA} - \sigma_{mA} - sJL_D\sigma_{eA}}{\left(1 - \sigma_{RN} + \sigma_{mN}\right) + sJL_D\left(1 + \sigma_{eN}\right)}\tilde{\alpha}(s) \;.$$

Same form as before, but change in the response length:

$$L_R = JL_D\frac{1 - \sigma_{RN} + \sigma_{mN}}{1 + \sigma_{eN}}$$

Commonly $\sigma_{eN} > 0$, so density-dependent dispersal reduces response length

Interactions via a (not quite) Ideal Free Predator

Assumes the predator's diffusivity, D, is a decreasing function of local prey density.

$$\frac{\partial P}{\partial t} = \frac{\partial^2}{\partial x^2}\Big(D\big(N(x)\big)P(x)\Big) \quad \text{with } \frac{dD}{dN} < 0 .$$

Can show: $$L_R = JL_D \frac{\left(1+\sigma_{DN}\sigma_{eP}\right)}{\left(1+\sigma_{DN}\sigma_{mP}\right)} .$$

Density-independent predation implies $\sigma_{mP} = 1$.

Response length increased if $\sigma_{eP} > 1$ "fleeing"

decreased if inequality reversed "hiding"

On-going work – benthic inverts in Merced River

- Evaluate response length concept through simulations with “pseudo” 3-D river model
- Parameters (except one) estimated for *Baetis*
- Model transient response to floods
- Model food delivery for young salmon