> Wavetrain Patterns In Cyclic Populations

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This talk can be downloaded from my web site

www.ma.hw.ac.uk/~jas

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Cyclic Predator-Prey Systems What is a Wavetrain? Wavetrains in Ecology

# Cyclic Predator-Prey Systems

The interaction between a predator population and its prey can cause population cycles. This has been modelled extensively using systems of two coupled ODEs:

predators
$$du/dt$$
= $f(u, v)$ prey $dv/dt$ = $g(u, v)$ 



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## Cyclic Predator-Prey Systems

The interaction between a predator population and its prey can cause population cycles. This has been modelled extensively using systems of two coupled ODEs:

predators
$$\partial u/\partial t = f(u, v) + D_u \partial^2 u/\partial x^2$$
prey $\partial v/\partial t = g(u, v) + D_v \partial^2 v/\partial x^2$ 

#### With diffusion, the model predicts wavetrain patterns.

Cyclic Predator-Prey Systems What is a Wavetrain? Wavetrains in Ecology

### What is a Wavetrain?

A wavetrain is a soln of form  $f(x \pm ct)$ , with f(.) periodic.



Jonathan A. Sherratt

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#### Wavetrains in Ecology



Fennoscandian voles *Clethrionomys glareolus* 



Fennoscandia

Ranta & Kaitala: Travelling waves in vole population dynamics. *Nature* 390:456 (1997).

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#### Wavetrains in Ecology





Kielder forest, UK

Field vole Microtus agrestis

Lambin et al: Spatial asynchrony and periodic travelling waves in cyclic populations of field voles. *Proc. R. Soc. Lond.* B 265:1491 (1998).

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#### Wavetrains in Ecology



Charge of Days Charge of Days

Kerloch moor, UK

Red grouse Lagopus lagopus scoticus

Mougeot et al: Experimentally increased aggressiveness reduces population kin structure and subsequent recruitment in red grouse *Lagopus lagopus scoticus. J. Anim. Ecol.* 74:488 (2005).

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### Wavetrains in Ecology





Central European Alps

Larch budmoth Zeiraphera diniana

Bjørnstad et al: Waves of larch budmoth outbreaks in the European Alps. *Science* 298:1020 (2002).

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#### Wavetrains in Ecology



Autumnal moth Epirrita autumnata



Northern Norway

Tenow et al: Waves and synchrony in *Epirrita autumnata/Operophtera brumata* outbreaks I. J. Anim. Ecol. 76:258 (2007).

Wavetrains in Mathematical Models Key Mathematical Questions

# Wavetrains in Mathematical Models

Wavetrain patterns are well studied in reaction-diffusion models:

- in "realistic" ecological models
- in toy models, especially CGLE with real diffusion ("λ-ω systems")

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Wavetrains in Mathematical Models Key Mathematical Questions

## Key Mathematical Questions

#### What are the wavetrain solutions?

General: there is a wavetrain family (1970s)  $\lambda - \omega$ : exact forms for the family (1970s)



Wavetrains in Mathematical Models Key Mathematical Questions

# Key Mathematical Questions

- Which members of the wavetrain family are stable?
  - General: some analytical results (1980s), and detailed numerical results (Rademacher, Sandstede & Scheel 2007; Smith & Sherratt 2007)

 $\lambda$ – $\omega$ : exact condition (1970s)



Wavetrains in Mathematical Models Key Mathematical Questions

# Key Mathematical Questions

- Wavetrain selection by initial / boundary conditions
  - General: wavetrains are generated by invasions (1993), Dirichlet bc's (2002) and Robin bc's (2008)
    - $\lambda-\omega$ : exact solution of the wave selection problem for invasions (1994), Dirichlet bc's (2003) and Robin bc's (2008)



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Open Problem: Wavetrain selection Open Problem: Absolute stability of wavetrains Open Problem: Wavetrains in Other Types of Models Wavetrains in Equations with Non-local Dispersal

#### **Open Problem: Wavetrain selection**

# Open problem: what is the mechanism of wavetrain selection by invasions/bc's?

Recent work: Merchant & Nagata (2010, 2014)



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Recent work: numerical calculation of absolute stability for  $\lambda - \omega$  systems (Smith, Rademacher & Sherratt 2009)



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Recent work: numerical calculation of absolute stability for  $\lambda - \omega$  systems (Smith, Rademacher & Sherratt 2009)



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Open Problem: Absolute stability of wavetrains

Open problem: which members of the wavetrain family are absolutely stable?



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Recent work: numerical calculation of absolute stability for  $\lambda - \omega$  systems (Smith, Rademacher & Sherratt 2009)



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Open Problem: Wavetrains in Other Types of Models

Open problem: understanding wavetrain patterns in ecological models other than reaction-diffusion equations

Recent work: equations with non-local dispersal (Sherratt, SIADS 13: 1517-1541, 2014)

$$\frac{\partial u}{\partial t} = f(u, v) + D \int_{-\infty}^{+\infty} \mathcal{K}(x - y) u(y) \, dy$$
  
$$\frac{\partial v}{\partial t} = g(u, v) + D \int_{-\infty}^{+\infty} \mathcal{K}(x - y) v(y) \, dy$$

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Wavetrains in Equations with Non-local Dispersal

$$\frac{\partial u}{\partial t} = \underbrace{f(u,v)}^{\lambda-\omega} + D \int_{-\infty}^{+\infty} \mathcal{K}(x-y)u(y) \, dy$$
  
$$\frac{\partial v}{\partial t} = g(u,v) + D \int_{-\infty}^{+\infty} \mathcal{K}(x-y)v(y) \, dy$$

For Laplace and Gaussian kernels, wavetrain existence and stability mirrors that for  $\lambda - \omega$  reaction-diffusion eqns

Laplace 
$$K(s) = (1/2a) \exp(-|s|/a)$$
  
Gaussian  $K(s) = (1/a\sqrt{\pi}) \exp(-s^2/a^2)$ 

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Wavetrains in Equations with Non-local Dispersal

$$\frac{\partial u}{\partial t} = \underbrace{f(u,v)}^{\lambda-\omega} + D \int_{-\infty}^{+\infty} \mathcal{K}(x-y)u(y) \, dy$$
  
$$\frac{\partial v}{\partial t} = g(u,v) + D \int_{-\infty}^{+\infty} \mathcal{K}(x-y)v(y) \, dy$$

But in general there are significant differences between wavetrains in the models with non-local dispersal and diffusion. E.g. for the top hat kernel, Eckhaus stability  $\neq$  stability.

Top hat kernel: K(s) = (1/2a) if |s| < a, 0 otherwise

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Wavetrains in Equations with Non-local Dispersal

$$\frac{\partial u}{\partial t} = \frac{\int_{-\infty}^{\lambda - \omega} f(u, v)}{f(u, v)} + D \int_{-\infty}^{+\infty} K(x - y) u(y) \, dy$$
  
$$\frac{\partial v}{\partial t} = g(u, v) + D \int_{-\infty}^{+\infty} K(x - y) v(y) \, dy$$

And for the Cauchy kernel, all non-constant wavetrains are unstable.

Cauchy kernel: 
$$K(s) = \left[\pi a \left(1 + s^2/a^2\right)\right]^{-1}$$

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