Invasion waves in populations with excitable dynamics

J. Brindley[1],*, V.H. Biktashev[2] & M.A. Tsyganov[3]

[1]*Department of Applied Mathematics, University of Leeds, Leeds LS2 9JT, UK;* [2]*Department of Mathematical Sciences, University of Liverpool, Liverpool L69 7ZL, UK;* [3]*Institute of Theoretical and Experimental Biophysics, Puschino, Moscow Region 142290, Russia;* **Author for correspondence (e-mail: amtjb@amsta.leeds.ac.uk)*

Abstract

Whilst the most obvious mechanism for a biological invasion is the occupation of a new territory as a result of direct ingress by individuals of the invading population, a more subtle "invasion" may occur without significant motion of invading individuals if the population dynamics in a predator prey scenario has an "excitable" character. Here, "excitable" means that a local equilibrium state, either of coexistence of predator and prey, or of prey only, may, when disturbed by a small perturbation, switch to a new, essentially invaded state. In an invasion of this type little spatial movement of individuals occurs, but a wave of rapid change of population level nevertheless travels through the invaded territory. In this article we summarise and review recent modelling research which shows that the macroscopic features of these invasion waves depend strongly on the detailed spatial dynamics of the predator–prey relationship; the models assume simple (linear) diffusion and pursuit-evasion, represented by (non-linear) cross-diffusion, as examples. In the context of plankton population dynamics, such waves may be produced by sudden injections of nutrient and consequent rapid increase in plankton populations, brought about, for example, by the upwelling caused by a passing atmospheric low pressure system.

Introduction

Population invasions are often regarded as being caused by the physical invasion of a new territory by individuals of a different species, displacing or annihilating the existing occupants of that territory. A closely similar effect may, however, be achieved with minimal physical movement of individuals if a "wave" of rapid population growth advances into new territory in which a small population already exists; in this case individuals created in the birth rate "explosion" remain essentially where they are born, it is only the birth rate explosion that advances wavelike.

The first necessary requirement for such phenomenology is the ability of the birth rate of the potentially invasive species to increase rapidly in response to some small change in one or more of the existing conditions, for example population density, or some environmental state. Such susceptibility is typical of so-called "excitable" systems, in which a suitable small perturbation to an existing stable equilibrium may provoke a large excursion in the state variables before the system either reverts to its original state, or, in the case of a bistable system, settles down to the alternative equilibrium state.

Excitability has been proposed as a mechanism for the occurrence of plankton blooms (Steele

and Henderson 1992; Truscott and Brindley 1994a, b) in the case where the grazing function (see Equations (3a, b)) takes the Holling Type III form. The robustness of the phenomenology has been demonstrated in extensions to include spatial heterogeneity, (Matthews and Brindley 1997), nutrient feedback loops, (Edwards and Brindley 1999), intratrophic predation (Pitchford and Brindley 1998) and individual physiological variation (Clother and Brindley 1999), and the model forms the basis for the results summarised and reviewed here. Our motivation is the search for better understanding of that part of the oceanic ecological system comprising phytoplankton (and its necessary nutrient and solar radiation inputs), grazing zooplankton, and their predators. These include the larvae of larger fish, for example cod and haddock, in the period before their "recruitment" to adult status. Aside from these obvious implications for the oceanic food chain, whose upper levels provide a very substantial and healthy part of the protein intake of the human race, plankton populations have an important role in the carbon cycle. The skeletons of many species carry with them, mainly in the form of calcium carbonate, a considerable quantity of carbon into the deep ocean, where it is sequestered for thousands of years. Estimates range between 1.5 and 2 gigatons per annum, a substantial fraction of the net input into the biosphere by human consumption of fossil fuels.

A striking feature of plankton populations is their extreme heterogeneity or patchiness. At any one time the population densities of phytoplankton of particular species, and less well documented but presently the subject of intensive worldwide observational and theoretical study through the international GLOBEC programme, their zooplankton grazers and their predators, show large variations in patchy patterns on a great range of scales. At the larger scale of hundreds of kilometres this heterogeneity is often related to physical features of the ocean circulations, for example cold or warm eddies or fronts. At smaller scales, from tens of kilometres down to a few metres, biological influences are progressively more important, even though physical "triggers" may be involved.

The pattern of population behaviour at these scales may be thought of as a succession of local "invasions" and extinctions, creating an ever changing spatio-temporal pattern of great complexity (Biktashev et al. 1998). Whilst some of the phenomenology is clearly linked to the underlying oceanic motion, it is likely that other features, especially those on relatively small spatial scales, are biologically driven. A paradigm problem is that of penetration of an invasion front into a sparsely populated region; a supplementary question, very relevant in the complex patterns of heterogeneity which are observed, is the behaviour of colliding fronts. Both issues depend critically on the form of the population dynamics model assumed, as is demonstrated later in this article. In addition to appropriate local population dynamics, a second requirement for propagation of an invasion front is for a process by which local population changes may have an effect on neighbouring spatial regions. In this way, "news" of the local change and its consequential effect on population is able to penetrate into hitherto unexcited regions, and in suitable circumstances, establish a travelling wave of population growth.

A vast literature exists of examples of population dynamics in which the information transport process is assumed to be by linear (Fickian) diffusion, and an excellent description of the resulting non-linear waves is given by Murray (1993). Much less widely explored are population waves in which pursuit-evasion strategies by the competing populations, represented by taxis mechanisms (see, e.g., Pedley and Kessler 1990) in which each population responds to gradients of density in the other, play a significant role (Tsyganov et al. 2003, 2004). Examples of both scenarios are presented here, and our purpose in this overview is to expose and discuss the differences, qualitative as well as quantative, in the outcomes of the two modelling approaches. This should suggest crucial observational tests for the validity of models of either type in specific physical and biological contexts.

In the following sections we introduce a mathematical model for population interactions, particularly relevant to plankton and their predators, which admits travelling, wavelike solutions of several kinds, present the results of numerical experiments for various specific forms of the model and, finally, we discuss the results and their ecological significance.

Mathematical model

The most basic dynamical model for the evolution of plankton populations needs to take into account the functional processes of photosynthetic phytoplankton (P) and herbivore zooplankton (Z), together with their interactions. Of the countless desirable improvements to such a model, those involving nutrient or radiation availability for P and higher level predation on Z are perhaps the most important.

The basic models are exemplified by the 2-component systems of Steele and Henderson (1981) and Truscott and Brindley (1994a); more comprehensive examples are those of Fasham (1993) and subsequent co-workers in which nutrients and their recycling are represented in a 7-component system, Edwards and Brindley (1999) in which the sensitivity to higher order predation is explored and Clother and Brindley (1999), which deals with age structured populations. All these models examine the time evolution of spatially homogenous populations. Real populations, as described in the Section Introduction, depart widely from spatial homogeneity on virtually all scales. Despite much research effort over many years (see e.g. Steele 1978; Okubo 1985 for early surveys) there is still much uncertainly over the relative importance of physical effects, e.g. oceanic turbulence (Abraham 1998; Brentnall et al. 2003) and biological mechanisms (Folt and Burns 1999; De Roos et al. 1998) in promoting spatial variations. Undoubtedly both are always important and it is likely that physics dominates the larger and biology the smaller scales; the models we present here call on both. Specifically, we use the approach of Truscott and Brindley (1994a, b), exhibiting "excitable" biology, extended to include spatial effects. Interplay of these effects readily produces patchiness, and more importantly, the possibility of travelling invasive "fronts" of rapid population growth. Both linear diffusion and pursuit-evasion mechanisms may be represented by the general reaction diffusion equation

$$\partial \mathbf{u}/\partial t = f(\mathbf{u}) + \nabla \cdot (\mathbf{D}\nabla \mathbf{u}) \tag{1}$$

where the state vector

$$\mathbf{u} = \begin{bmatrix} P \\ Z \end{bmatrix} \tag{2}$$

and $\mathbf{D}$ is the matrix of diffusivities. The "reaction" terms are

$$f_1(u) = \beta P(1 - P) - ZP^2/(v^2 + P^2) \tag{3a}$$

$$f_2(u) = \gamma\{ZP^2/(v^2 + P^2) - h(Z)\} \tag{3b}$$

Here, P and Z may be thought of as biomass or some equivalent measure of the population magnitudes of phytoplankton and zooplankton. The consumption term is taken in the form of a Holling Type III function. Its suitability in the context has provoked much discussion (Steele and Henderson 1981, 1992); it is at least plausible at the population (though not perhaps the individual) level, especially where some degree of intratrophic predation is present.

External biological effects are represented by the Z-mortality term, $h(Z)$, the form of which has far reaching effects (Steele and Henderson 1992; Edwards and Brindley 1999), as further discussed below. Additionally, the nutrient and radiative inputs are assumed adequate to maintain a constant value for the P growth rate (β). The case in which this growth rate varies seasonally has been considered by Truscott and Brindley (1994a) and Truscott (1995). The physical stirring effects of turbulence are embodied in the diffusion tensor $\mathbf{D}$. For linear diffusion $\mathbf{D}$ has constant diagonal components and non-diagonal components are zero; pursuit-evasion behaviour can be represented by assuming that the non-diagonal components of $\mathbf{D}$ have appropriate dependence on P and Z, corresponding to cross-diffusion (Murray 1993). The precise form of dependence is determined by the swimming motion of the plankton. It is usual to assume that P is totally passive, but the motion of individual zooplankton in their grazing or predatory capacity is undoubtedly significant when considering small scales. In general, we may allot different values to the self-diffusion components to represent different swimming velocities for P & Z; various taxis or pursuit-evasion strategies may be modelled by cross-diffusion components (Tsyganov et al. 2003, 2004). Finally, the

efficiency of conversion of P-biomass into Z-biomass is represented by γ and υ is a half saturation constant. The essence of the behaviour associated with Equations (1–3) is easily understood by reference to the nullclines of the ODEs when diffusion is neglected (Figure 1). Depending on the form of the zooplankton predation function, $h(Z)$, there may be a single stable equilibrium point, as shown in the figure, corresponding to a linear function, which has a vertical straight Z-nullcline; in contrast, for a quadratic $h(Z)$, the Z-nullcline bends over to the right and may intersect the P-nullcline in 3 points, 2 of which are stable.

In the linear case, though the single equilibrium point attracts all trajectories from any starting conditions, the routes to equilibrium may be very different, some involving a large excursion before returning to equilibrium. Such a large excursion was suggested by Truscott and Brindley (1994a) as an explanation for the rapid rises in populations seen in red tide phenomena, in which large populations of, often toxic, algae occur in estuarial waters with harmful effects, or in blooms in the open ocean caused by seasonal warming or nutrient upwellings.

In the quadratic case, each equilibrium point has its own basin of attraction and a displacement from one may send the system to the other, corresponding to a "permanent" change.

With the addition of spatial variation there enters the possibility of travelling non-linear waves,
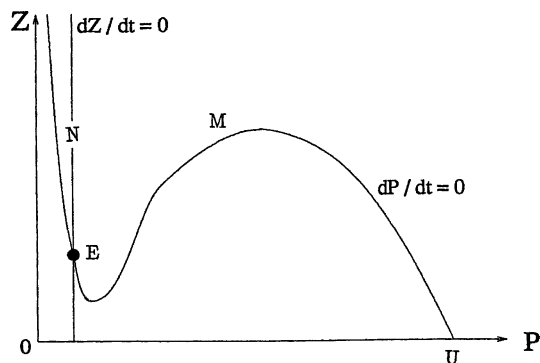

Figure 1. (P, Z) phase plane for Equations (3a, b), showing the P and Z nullclines. Coexisting (stable) equilibrium point denoted be E (P_0, Z_0); unstable equilibrium point by U, at which $Z = 0$. Also shown is a typical trajectory arising from a small perturbation from E.

causing at any one location as they pass either a relatively short lived population "bloom" or, in the case of a bistable situation, a quasi-permanent switch from one equilibrium to another. In the next section we consider several particular examples.

Invasion waves with "excitable" biology

Reaction-diffusion waves

In this case we follow Biktashev and Brindley (2003, 2004) and Brentnall et al. (2003) in choosing the same constant scalar value, **D**, for each diagonal component of D. This is appropriate when the oceanic turbulent diffusion is sufficiently strong that any relative swimming motion of the plankton is negligible. We also neglect any vertical variation and restrict ourselves to 1-dimensional horizontal variation in the x-direction only. Extensions to two horizontal dimensions are considered in Brentnall et al. (2003) and Tsyganov et al. (2003, 2004). Assuming the wave to be initiated at a boundary, and considering a system occupying the region $0 < x < l$, we can recognise two distinct types of waves, supported by differing mechanisms.

The first "invasion" wave is initiated by an injection of Z at the boundary $x = 0$, into a region $x > 0$, in which phytoplankton is at its maximum value and $Z = 0$; in other words, the system is initially at the unstable equilibrium denoted by U in Figure 1. Then, we impose the boundary condition $Z(0_t) = Z_b$, with non-flux conditions in all other cases. There is some evidence that such an invasion of the northern North Sea by copepods of the species *Calanus finmarchicus* takes place when they emerge from a period of winter diapause in the deep waters of the Celtic Channel.

The actual value of Z_b is unimportant for the phenomenology; the only important requirement is a complete absence of Z at $t = 0$.

An example of the wave is shown in Figure 2 (a). The wave is similar to the KPP-Fisher wave (Fisher 1937; Kolmogorov et al. 1937) in that it is a trigger wave from an unstable to a stable equilibrium; it is, however, more complicated, involving at it does two diffusing species. Refer-

ring to Figure 1, the local populations of P and Z, as the wave traverses any point, start near U, then (slowly) progress along the P-nullcline as the predators multiply, reaching a maximum at M before moving rapidly to a point on the P-nullcline near N as the P-population collapses, and finally approaching the stable equilibrium E, along the P-nullcline.

The spatial structure of the wave, associated with this time history at any fixed spatial position, is illustrated in Figure 3a.

The second type of wave an ''excitation'' wave is triggered by an injection of P at $x = 0$ into an initial uniform state of the system at the stable co-existence equilibrium, E.

The initial state is given by

$$P(x,0) = P_0, Z(x,0) = Z_0 \qquad (4)$$

where P_0, Z_0 satisfy

$$0 = \beta P_0(1 - P_0) - Z_0 P_0^2/(v^2 + P_0^2) \qquad (5)$$

$$0 = Z_0 P_0^2/(v^2 + P_0^2) - h(Z_0)$$

with non-flux boundary conditions in all other cases. Such a scenario may occur when a sudden injection of nutrient, caused for example by upwelling on the passage of an atmospheric low pressure system, leads to a rapid local increase of P from P_0 to P_b. Again the precise value of P_b is not important to the qualitative nature of the re-

sponse provided that it exceeds some threshold; essentially the local displacement from the equilibrium point E must carry the system beyond the middle branch of the P-nullcline in Figure 1.

An example of this wave is shown in Figure 2b. It is notable that its propagation speed is much greater than that of the ''invasion wave'' described above. This is because its propagation is determined essentially by the interaction between diffusion and non-linear local dynamics of the P population rather than that of the Z population, which changes only slightly through the wave. Diffusive influx of prey triggers the prey-escape mechanism, in which the prey multiply much faster than the predators and grow virtually unchecked until reaching the carrying capacity of the habitat. Between the front and the back of the invading wave the prey and predators are in quasi-equilibrium (local conditions remaining close to the P-nullcline of Figure 1), the predators slowly multiplying and consuming the prey before, ultimately, the predator population is no longer sustainable and both populations return rapidly to the stable equilibrium E. Note that qualitatively similar behaviour may be triggered by a reduction in the predator population from its equilibrium value Z_0, as may occur, for example, when a copepod (Z) population is preyed upon by fish larvae. Finally, since each of these waves leaves the final state of the system at the equilibrium E, it is clear that a
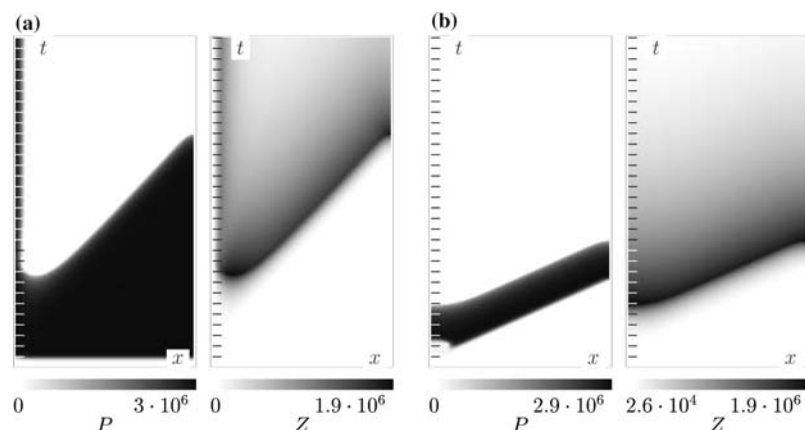

Figure 2. Time-space density plots for phytoplankton (left panel) and zooplankton (right panel) for (a) an invasion wave, as described in the text, and (b) an ''excitation'' wave. Space is horizontal and time vertical: for compatibility with the value of **D**, taken from Okubo (1980), the total width corresponds to 100 km, and each tick on the time axis to 10 days.
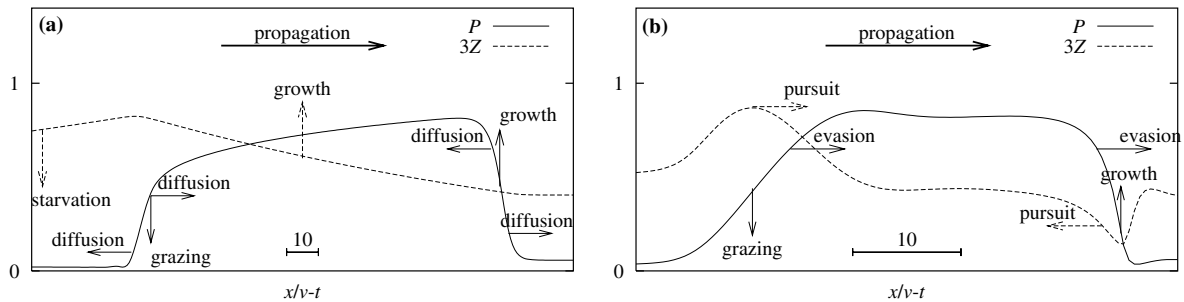
Figure 3. Schematic of the main factors affecting the dynamics of an "excitation" front in (a) a reaction-diffusion system (for D = 0.04, $h_+ = h_- = 0$), and (b) a reaction-taxis system (D = 0, $h_+ = 1$, $h_- = 1$). These include prey dynamics (growth and decrease due to grazing pressure) in both (a) and (b), diffusion of prey in (a), and taxis (pursuit by predators and evasion by prey) in (b). Solid curve denotes P, broken curve denotes Z. Arrows denote direction of movement relative to the travelling wave.

collision of two such waves annihilates both (see Figure 5a).

Invasion waves with pursuit-evasion dynamics

Though the assumption of (equal) linear diffusion may be adequate to model the behaviour of phytoplankton and small zooplankton in the ocean, where the turbulent diffusion velocities are expected to dominate any individual motion relative to the surrounding fluid, it is increasingly inadequate for larger species of zooplankton, or for fish larvae, whose individual motion is no longer negligible. When such motion is not random but has some preferred direction in response to an external stimulus it is usually described as taxis. Representation of taxis at the population scale requires equations different from (1) above, and their solutions are less well studied than those of "pure" reaction diffusion type (but see, e.g. Murray 1993; Berezovskaya and Karev 1999). Here we consider a system in which the spatial evolution is governed by three processes, positive taxis of predators up the gradient of prey (pursuit), and negative taxis of prey down the gradient of predators (evasion), yielding "cross-diffusion" terms (Murray 1993), together with random motion of both species (diffusion). To conform with earlier sections, we continue to use the symbols P for prey and Z for predators, though plankton comprises neither the only nor even perhaps the most appropriate example of this behaviour. Again we restrict ourselves to one spatial dimension.

The equations studied are then

$$\partial P/\partial t = f_1(P, Z) + D\nabla^2 P + h_-\nabla(P\nabla Z) \quad (6a)$$

$$\partial Z/\partial t = f_2(P, Z) + D\nabla^2 Z - h_+\nabla(Z\nabla P) \quad (6b)$$

As before, we use Holling type III forms for the predation functions, f_1 and f_2, defined in (3a,b), and we assume a linear mortality function $h(Z) = Z$.

These equations have been shown (Tsyganov et al. 2003) to admit travelling wave solutions, dependent on the taxis terms for their existence, which have properties quite different from those found in the earlier reaction-diffusion system described by Equations (1–3). The contrasting mechanisms are illustrated schematically in Figure 3. Various cases are illustrated in Figure 4, all triggered by a local increase in P from the stable equilibrium values (P_0, Z_0) of the ODE system, defined by Equations (5). It is clear that the taxis terms significantly alter the shape of the wave profile, especially when the pursuit parameter, h_+, is relatively large; in such cases the long "plateau" at high P values is lost and the wave is narrow and sharply pointed.

We can suggest a qualitative explanation of this wave shape change as follows. Ahead of the wave the system is at its stable equilibrium. Consider a local increase of the prey density P above its equilibrium value. The resulting flux of predators to the area, described by the taxis term with coefficient h_+, will deplete the density of predators in surrounding areas and the equilibrium conditions will be violated, permitting
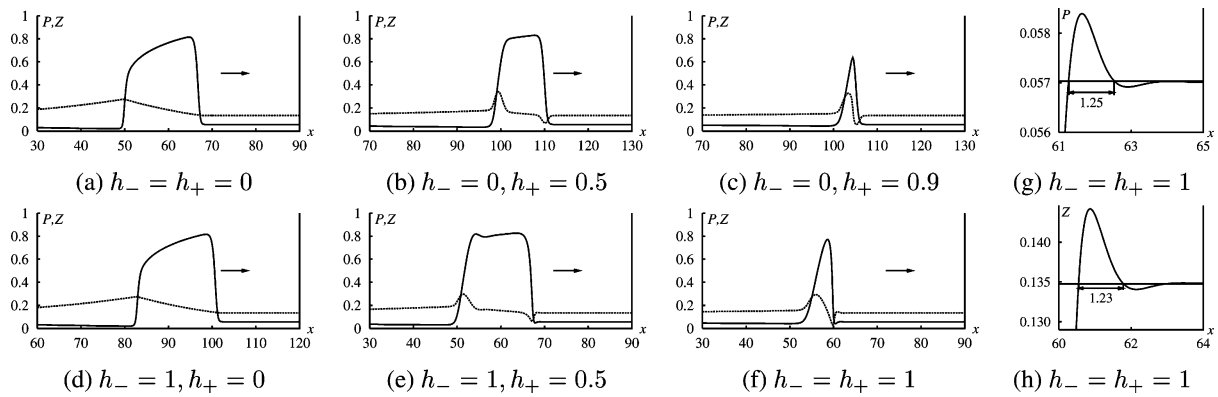
Figure 4. Wave profiles for taxis waves with D = 0.04 and different taxis coefficients. Solid curve denotes P, broken curve denotes Z, direction of motion indicated by arrow. The different shapes of the profiles are evidence of the relative dominance of the different propagation mechanisms involved. Note (in 4(g, h)) the oscillatory onset of the wave front when both $h_+ > 0$ and $h_- > 0$.
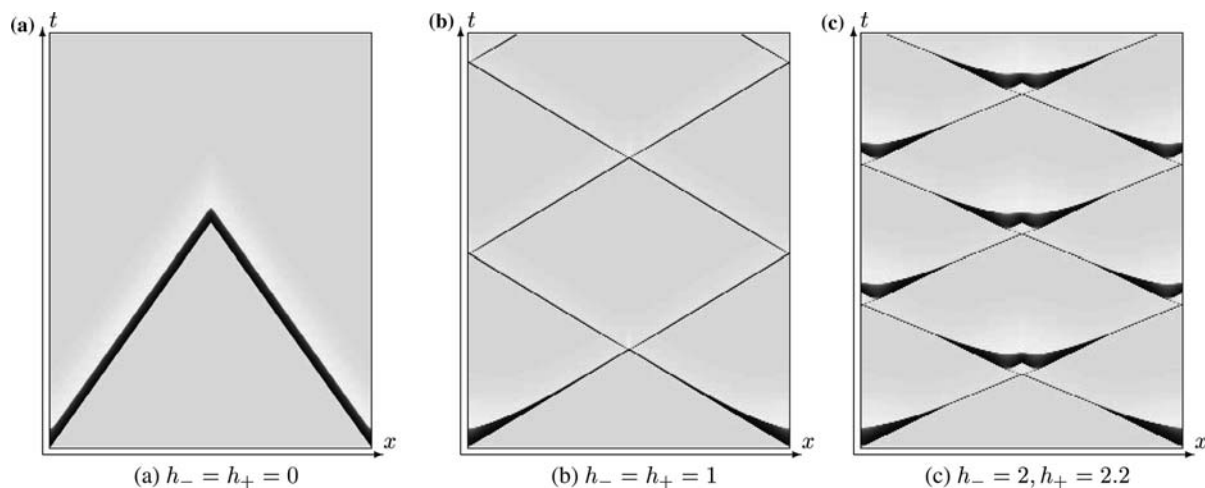

Figure 5. Space-time density plots showing interaction of waves in (a) purely diffusive and (b) taxis cases. The purely diffusive waves annihilate each other on collision; the waves with taxis included penetrate through each other (b), and may show evidence of splitting (c).

increase of prey, followed by influx of predators, and the same sequence of events will occur progressively at each point in the spatial (x) direction, constituting a travelling wave in the population pattern. No diffusion of either predators or prey is required; the phenomenon requires only the presence of taxis terms in Equations (6). Just as in the purely diffusive system considered earlier, the excitable nature of the kinetics leads to a strong local increase in the prey population through the "prey escape" phenomenon (prey multiply more rapidly than predators).

The wave propagation speed depends strongly on the values of h_+ and h_-. For "reasonable" values, it is higher than the pure reaction-diffusion wave, as is clear from Figures 5 and 6.

Moreover a striking difference between taxis waves and diffusion waves is seen when two waves collide. Over an extensive range of parameter values (Figure 7), the taxis waves display a quasi-soliton behaviour; instead of annihilating each other they penetrate through each other (or reflect, since the waves are indistinguishable).

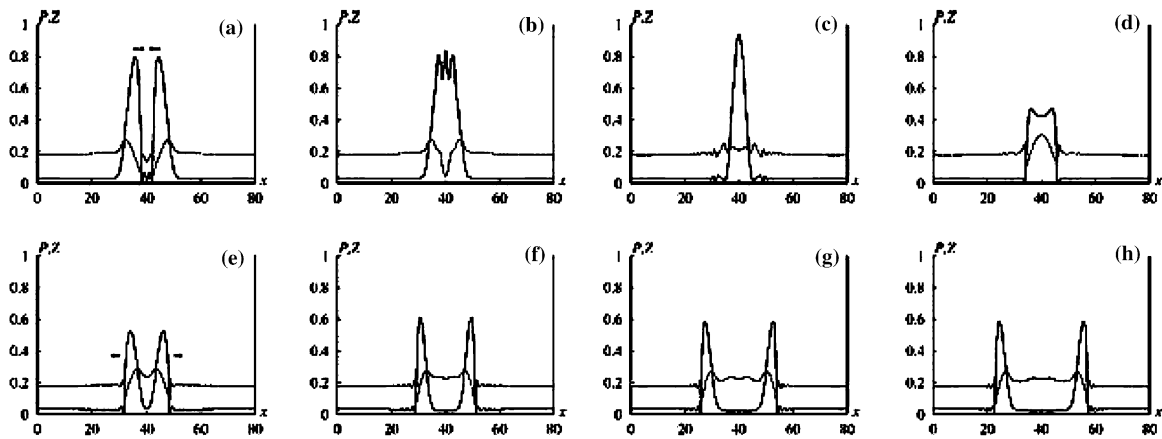The mechanism of quasi-soliton interaction is fully discussed in Tsyganov et al. (2004), but the

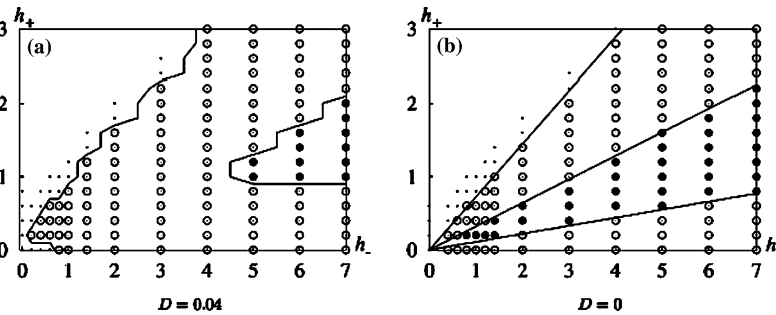*Figure 6.* Soliton tnteraction for D = 0, h_+ = 1, h_- = 5. Equal time intervals between frames.

Figure 7. Parameter regions correspondig to different regimes of taxis waves for γ = 0.016. Solid circles indicate quasi-soliton behaviour, hollow circles non-soliton behaviour. Dots indicate no stable propagation of waves.

essence is that the oscillating precursor of the taxis wave guarantees a departure from the stable equilibrium state ahead of the wave. This is sufficient, for suitable values of h_+ and h_-, to destabilise the configuration and recreate front structures on the margins of the collision zone, which advance as new, or reflected, waves. Diffusion acts to inhibit this behaviour, as shown in Figure 7, but does not destroy it completely if the taxis terms are sufficiently strong.

Discussion

We have described a range of phenomenology associated with travelling waves in a predator–prey system with excitable local dynamics, and with either or both of diffusion and taxis characterising the spatial dynamics of the populations. It appears that direct invasion by a predator of an initially predator-free region can lead to the establishment of a steadily propagating wave, whose speed of progress is limited by the relatively slow growth rate of the predator population. Behind the invasion wave the system reaches an equilibrium state (the point E in Figure 1). Our results here relate to a system having diffusion only; very similar behaviour occurs when some taxis is present, and results for a range of values of some of the parameters are presented in Tsyganov et al. (2004).

Richer behaviour is observed with excitation waves, i.e. waves in which the prey population first increases from its equilibrium state by the well known prey escape mechanism. Predator population growth follows and a long interval of large P is finally ended as predation increases sufficiently to return the system to stable equilibrium. Such behaviour is usually expected to be stimulated by a local injection of P, at a boundary

or at an interior point, though other disturbances from equilibrium of a spatially uniform system at the point E in Figure 1 may bring about similar results.

The character of these excitation waves is strongly dependent on the relative importance of diffusion and taxis in the motion of the populations. In particular, when the taxis of one population takes the form of a response to gradients in the other, as in a pursuit-evasion relationship, the wave forms and speeds, and also the interaction properties, may be very different from the more familiar travelling waves in reaction-diffusion systems.

The ecological significance of travelling fronts in population dynamics has stimulated a huge literature ever since the classic results of Fisher (1937) and Kolmogorov et al. (1937). In the context of biological invasions, the book by Shigesada and Kawasaki (1997), and papers by Sherratt et al.(1995), Owen and Lewis (2001), Petrovskii and Shigesada (2001), and Fagan et al. (2002) exemplify the breadth and depth of recent activity. The extent of clear observational and experimental evidence to support or discount these mainly theoretical approaches is so far disappointingly small as far as animal populations are concerned, though examples from the plant world (Kuznetsov et al. 1994; Fagan and Bishop 2000) display, respectively, evidence of the role of cross-diffusion in the propagation of forest boundaries and of the effects of predation on invasion waves. Also soliton-like interaction of bacterial population taxis waves has been observed *in vitro* (Tsyganov et al. 1993).

The current international GLOBEC programme and its various associated national research efforts, such as the UK Marine Productivity initiative, should go some way to remedying this deficiency, at least for the lower, planktonic, levels of the oceanic web. A particular issue here is the extreme patchiness exhibited on a vast range of scales by the plankton populations, and its effect on productivity throughout the oceanic food chain. The extent to which this is due to biological or physical effects is a matter of much current interest and concern, though, as mentioned earlier, it seems likely that physics dominates on the larger, and biology on the smaller, scales. The results presented above sug-

gest the idea of a constant formation of travelling fronts which are then destroyed by the straining motions of oceanic turbulence. Simple models of this process (Biktashev et al. 1998) yield, on the large scale, a statistically steady state somewhat different from that suggested by Abraham (1998). Crucial observations are awaited.

A rather different example of the potential significance of invasion waves has been suggested by Biktashev and Brindley (2004). They propose that propagating "blooms" of phytoplankton, stimulating rises in the zooplankton population, may be important to the life cycles of higher levels of the ocean web, specifically by influencing the location and timing of spawning by cod and haddock to ensure optimal feeding conditions for their larvae, a major predator of zooplankton. Again we await observational evidence.

Acknowledgements

References

Abraham ER (1998) The generation of plant patchiness by turbulent stirring. Nature 391: 577–580

Berezovskaya FS and Karev GP (1999) Bifurcation of travelling waves in population taxis models. Physics-Uspekhi 169: 1011–1024

Biktashev VN and Brindley J (2004) Phytoplankton blooms and fish recruitment rate: effects of spatial distribution. Bulletin of Mathematical Biology 66: 233–259

Biktashev VN, Holden AV, Tsyganov MA, Brindley J and Hill NA (1998) Excitation wave breaking in excitable media with linear shear flow. Physical Review Letters 81: 2815–2819

Biktashev VN, Brindley J, Holden AV and Tsyganov MA (2004) Pursuit-evasion predator-prey waves in two spatial dimensions. Chaos 14(4), 1–7

Brentnall SJ, Richards KJ, Brindley J and Murphy E (2003) Plankton patchiness and its effect on larger-scale productivity. Journal of Plankton Research 25: 121–140

Cannas SA, Marco DE and Paez SA (2003) Modelling biological invasions: species traits, species interactions and habitat heterogeneity. Mathematical Biosciences 183: 93–110

Clother R and Brindley J (1999) Excitability of an age-structured population. Journal of Mathematical Biology 39: 377–420

De Roos AM, McCawley E and Wilson WG (1998) Pattern formation and the scale of interaction between predators and their prey. Theor. Pop. Biol. 52: 108–130

Edwards AM and Brindley J (1999) Zooplankton mortality and the dynamical behaviour of plankton population models. Bulletin of Mathematical Biology 61: 303–339

Fagan WF and Bishop JG (2000) Trophic interactions during primary succession: herbivores slow a plant reinvasion at Mount St. Helens. The American Naturalist 155: 238–251

Fagan WF, Lewis MA, Neubert MG and Driessche van den P (2002) Invasion theory and biological control. Ecology Letters 5: 148–157

Fasham MJR (1993) Modelling the marine biota. In: Heimann M (ed) The Global Carbon Cycle, pp 457–504. Springer-Verlag, NATO

Fisher RA (1937) The wave of advance of advantageous genes. Philosophical Transactions of the Royal Society of London Series B, Biological Sciences 7: 355–369

Folt CL and Burns CW (1999) Biological drivers of zooplankton patchiness. Trends in Ecology & Evolution 14: 300–305

Kolmogorov A, Petrovsky I and Piskunov NS (1937) Etude de l'equation de la diffusion avec croissance de la quantite de matiere et son application a une probleme biologique. Moscow Univ. Bull. Math. 1: 1–25

Kuznetsov YA, Antonovsky Y, Biktashev VN and Aponina EA (1994) A cross-diffusion model of forest boundary dynamics. Journal of Mathematical Biology 32: 219

Matthews L and Brindley J (1997) Patchiness in plankton populations. Dyn. Stab. Syst. 12: 39–59

Murray JD (1993) Mathematical Biology (2nd edition). Springer, Berlin,

Okubo A (1980) Diffusion and Ecological Problems. Mathematical Models. Springer, Berlin,

Owen MR and Lewis MA (2001) How predation can slow, stop or reverse a prey invasion. Bulletin of Mathematical Biology 63: 655–684

Petrovskii SV and Shigesada N (2001) Some exact solutions of a generalised Fisher equation related to the problem of biological invasion. Mathematical Bioscience 172: 73–94

Pitchford JW and Brindley J (1998) Intratrophic predation in simple predator–prey models. Bulletin of Mathematical Biology 60: 937–953

Sherratt JA, Lewis MA and Fowler AC (1995) Ecological chaos in the wake of invasion. Proceedings of the National Academy of Sciences USA 92: 2524–2528

Shigesada N and Kawasaki K (1997) Biological Invasions: Theory and Practice. Oxford University Press

Steele JH (1978) Some comments on plankton patches. In: Steele JH (ed) Spatial Patterns in Plankton Communities, pp 1–20. Plenum Press, New York

Steele JH and Henderson EW (1981) A simple plankton model. The American Naturalist 117: 676–691

Steele JH and Henderson EW (1992) The role of predation in plankton models. Journal of Plankton Research 14: 157–172

Truscott JE and Brindley J (1994a) Ocean plankton populations as excitable media. Bulletin of Mathematical Biology 56: 981–998

Truscott JE and Brindley J (1994b) Equilibria, stability and excitability in a general class of plankton population models. Philosophical Transactions of the Royal Society of London 347: 703–718

Tsyganov MA, Brindley J, Holden AV and Biktashev VN (2003) Quasi-soliton interaction of pursuit-evasion waves in a predator–prey system. Physical Revier Letters 91: 218102

Tsyganov MA, Brindley J, Holden AV and Biktashev VN (2004) Properties of population taxis waves in a predator prey system with pursuit and evasion. Physica D 197: 18–33