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Mathematical models for the *Aedes aegypti* dispersal dynamics: travelling waves by wing and wind

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Abstract

Biological invasion is an important area of research in mathematical biology and more so if it concerns species which are vectors for diseases threatening the public health of large populations. That is certainly the case for *Aedes aegypti* and the dengue epidemics in South America. Without the prospect of an effective and cheap vaccine in the near future, any feasible public policy for controlling the dengue epidemics in tropical climates must necessarily include appropriate strategies for minimizing the mosquito population factor. The present paper discusses some mathematical models designed to describe *A. aegypti*'s vital and dispersal dynamics, aiming to highlight practical procedures for the minimization of its impact as a dengue vector. A continuous model including diffusion and advection shows the existence of a stable travelling wave in many situations and a numerical study relates the wavefront speed to a few crucial parameters. Strategies for invasion containment and its prediction based on measurable parameters are analysed.

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1. Introduction

Dengue is a viral disease which is transmitted by arthropods of the species *Aedes aegypti*, a mosquito found throughout the world where a hot and humid climate is predominant (Vasconcelos et al., 1999). The mosquito *A. aegypti* inhabits mainly human

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houses and bites at any time during the day, which makes it a very efficient vector. Infectious individuals, either humans or mosquitoes, can start a dengue epidemic in human populations very quickly when placed in a previously *A. aegypti* infested region (Veronesi, 1991; Ferreira and Yang, 2003; Cummings et al., 2004).

The dengue disease shows only one epidemiological cycle linking the human host and the *A. aegypti* vector. A susceptible female *A. aegypti* is infected by sucking infected human blood, after which follows a short incubation period of approximately eight days. Afterwards the virus begins a replication process inside the mosquito's salivary glands and is ready to infect susceptible humans through any future bite. When an infected mosquito bites a susceptible human the virus is injected into his or her blood stream and begins an incubation period which takes from three to ten days, with an average of five days. After that, a dengue may evolve to a non-symptomatic stage or to a classic set of symptoms which includes fever and Myalgias. Symptoms persist from three to seven days which is also the infectious period. After that the individual develops an specific immunity for a long time (Veronesi, 1991; Gubler, 1998).

In some cases, however, a serious scenario of symptoms shows up, called 'dengue haemorrhagic fever' (DHF), characterized mainly by coagulation problems which may lead to the death of an infected individual.

Dengue is a particularly serious public health problem in Brazil due to favourable climate and environmental conditions for *A. aegypti* population expansion. *A. aegypti* was detected in Brazil for the first time in 1923 and was eradicated by 1955 and re-introduced in 1967. In 1973 it was again considered eradicated but reappeared again in Bahia State in 1976 and in Rio de Janeiro in 1977. Since then, the disease has spread throughout the country, and massive bursts of infections are common during the humid and hot days of every summer. Climate variation caused by the 'El Niño' meteorological phenomenon is believed to be closely correlated with such epidemiological occurrences. In 1998, 537,507 cases of infection were detected in the Public Health System in 24 states, 9 of them being of 'dengue haemorrhagic fever'. Although dengue is not commonly a lethal disease it constitutes a very serious public health problem due to many and varied complications coming from its infection.

Since no vaccine for dengue is expected in the near future, any feasible strategy for controlling its epidemiological dynamics must concentrate efforts on the containment of the *A. aegypti* population, especially when infection is detected (Gubler, 1998). Efficient and practical measures for controlling the *A. aegypti* population are of two different kinds. A classical chemical attack against the mosquito or against its larval form can be made by the use of strong organophosphorates, insecticides and pyrethroids (Fenitrothion, Malathion, Cypermethrin). However, in order to obtain adequate results with such a strategy it is necessary to apply and maintain a high average level of these toxic and expensive chemicals over the entire infested region, mostly occupied by human dwellings as well (Teixeira et al., 2003; Yang et al., 2003). Those conditions make chemical control very difficult from a practical point of view and also dangerous from a public health perspective.

The second kind of strategy emphasizes prevention. For oviposition, female *A. aegypti* mosquitoes need clear and undisturbed water for their larvae to proliferate which is mainly available in unattended containers, either natural ones such as orchids or artificial ones such

as old tyres, flowerpots, empty bottles. So, human-made environmental conditions are the main reasons for *A. aegypti* infestation and, in view of this, the (presumably) most efficient strategy for controlling its proliferation should be a civic attitude of permanent alertness to unattended breeders. Educational programmes run by governmental agencies stating such simple facts are frequently transmitted by the media, especially during the rain season, and are considered to be the safest, cheapest and (theoretically) most efficient strategies for controlling *A. aegypti* infestation. Unfortunately, in practice, community awareness develops slowly and fades away quickly (Ereno, 2003).

Dengue can become endemic in a region infested with an *A. aegypti* population. So, to develop public policies for prevention and strategies for control of this disease it is indispensable to establish a solid and tractable knowledge of the *A. aegypti* population behaviour and dynamics in order to find parameters appropriate for treatment by practical intervention. Mathematical models can provide such knowledge, since they are of necessity simplified descriptions of reality and, if reasonably faithful, they automatically yield the desired control parameters. In this paper we develop mathematical models for the *A. aegypti* spatial population dynamics and show that a feasible strategy can be designed for containing the dispersal by stopping the development of travelling waves (Murray et al., 1986; Murray, 1993; Cummings et al., 2004). Numerical simulations are performed in one dimension and the wave velocity is plotted against some of the biological parameters.

2. The one-dimensional model: travelling waves by wing and wind

Winged female *A. aegypti* in search of human blood or places for oviposition are the main reason for local population dispersal and the slow advance of a mosquito infestation. On the other hand, wind currents may also result in an advection movement of large masses of mosquitoes and consequently cause a quick advance of infestation. Besides this, since the *A. aegypti* is mostly found in urban regions, its movement is also largely influenced by human related activities. Small numbers of mosquitoes are frequently carried by vehicles and, although that might become important if they are infected, we will not take that factor into account. However, large numbers of larvae are frequently carried by unattended water containers, commonly found inside big transportation trucks. That is probably the main cause for the long range advance of an infestation, which can mean thousands of kilometres in just a couple of days. Although this last mechanism certainly occurs in urban areas, its relevance is more significant to the study of inter-city dispersal in a large space scale of continental size. The effect of human transportation networks on dengue propagation was modelled by Takahashi (2004). This paper focuses its attention on an urban scale of space, where a (local) diffusion process due to autonomous and random search movements of winged *A. aegypti* are coupled to a constant advection which may be interpreted as the result of wind transportation. To keep the model tame to simple mathematical techniques the analysis is restricted to the one-dimensional case.

2.1. *Aedes aegypti* population model

To simplify the biological vital dynamics of the *A. aegypti* this model will consider only two sub-populations: the winged form (mature female mosquitoes); and an aquatic

population, which includes eggs, larvae and pupae. The spatial density of the winged *A. aegypti* at point x and time t will be denoted by $\bar{M}(x, t)$ and that only counts the female mosquitoes in fact. The aquatic form will be denoted likewise by $\bar{A}(x, t)$. Let the mortality rate of the mosquitoes and the aquatic forms be respectively $\bar{\mu}_1, \bar{\mu}_2$.

The specific rate of maturation of the aquatic form into winged female mosquitoes will be $\bar{\gamma}$, saturated by a term which describes a carrying capacity (\bar{k}_1) related to the amount of ‘findable’ nutrients (human blood, that is): $\bar{\gamma}\bar{A}(x, t) \left(1 - \frac{\bar{M}(x,t)}{\bar{k}_1}\right)$.

Likewise, the rate of oviposition, which is the only source of the aquatic form, by female mosquitoes is proportional to their density but is also regulated by a carrying capacity effect dependent on the occupation of the available breeders: $\bar{r}\bar{M}(x, t) \times \left(1 - \frac{\bar{A}(x,t)}{\bar{k}_2}\right)$.

As already pointed out, we will consider the *A. aegypti* dispersal as the result of a random (and local) flying movement, macroscopically represented by a diffusion process with coefficient \bar{D} , coupled to a wind advection caused by a constant velocity flux \bar{v} . Constant advection can be justified as a ‘bias’ in the transport process caused by a long term geographical direction of the wind, while its random and short term fluctuations are to be included in the diffusion term.

Since we do not take into account human transportation in this model, the aquatic form will be considered as being in a sessile state. In work to be published elsewhere, some of the present authors (LTT and WCFJr) consider the effect of inter-city transportation networks on the geographical dispersal of *A. aegypti* which is the main cause for its spread in the aquatic phase.

Considering the vital dynamics and dispersal process together, an eight-parameter ($\bar{D}, \bar{v}, \bar{\gamma}, \bar{\mu}_1, \bar{\mu}_2, \bar{k}_1, \bar{k}_2, \bar{r}$) mathematical model can be formulated by using two coupled conservation laws as follows:

$$\begin{aligned} \frac{\partial}{\partial t} \bar{M}(x, t) &= \bar{D} \frac{\partial^2}{\partial x^2} \bar{M}(x, t) - \frac{\partial}{\partial x} (\bar{v} \bar{M}(x, t)) \\ &\quad + \bar{\gamma} \bar{A}(x, t) \left(1 - \frac{\bar{M}(x, t)}{\bar{k}_1}\right) - \bar{\mu}_1 \bar{M}(x, t) \\ \frac{\partial}{\partial t} \bar{A}(x, t) &= \bar{r} \left(1 - \frac{\bar{A}(x, t)}{\bar{k}_2}\right) \bar{M}(x, t) - (\bar{\mu}_2 + \bar{\gamma}) \bar{A}(x, t). \end{aligned} \tag{1}$$

Next, to introduce the appropriate scales, we adimensionalize the above system using the following units: \bar{k}_1 for the mosquito population, \bar{k}_2 for the aquatic population, \bar{r}^{-1} for time and $\sqrt{\frac{\bar{D}}{\bar{r}}}$ for space, which gives us the following system of five new non-dimensional parameters ($\mu_1 = \frac{\bar{\mu}_1}{\bar{r}}, \mu_2 = \frac{\bar{\mu}_2}{\bar{r}}, \gamma = \frac{\bar{\gamma}}{\bar{r}}, \nu = \frac{\bar{v}}{\sqrt{\bar{r}\bar{D}}}, k = \frac{\bar{k}_1}{\bar{k}_2}$):

$$\begin{aligned} \frac{\partial}{\partial t} M(x, t) &= \frac{\partial^2}{\partial x^2} M(x, t) - \nu \frac{\partial}{\partial x} M(x, t) \\ &\quad + \frac{\gamma}{k} A(x, t) (1 - M(x, t)) - \mu_1 M(x, t) \\ \frac{\partial}{\partial t} A(x, t) &= k(1 - A(x, t)) M(x, t) - (\mu_2 + \gamma) A(x, t). \end{aligned} \tag{2}$$

Since we intend to analyse this model for invasion processes, the equations are considered in the whole one-dimensional space. In such a case, boundary conditions at infinity are required only for $M(x, t)$ since the second equation is actually an ordinary differential equation and no differentiation of $A(x, t)$ with respect to x occurs within the system. Numerical simulations of the system (2) have used the boundary conditions $M(\pm\infty, t) = \frac{\partial M(\pm\infty, t)}{\partial x} = 0$ which describe a null population and null flux of mosquitoes at distant points at all times. Accordingly, the initial conditions are given by the functions $A_0(x) = A(x, 0)$, $M_0(x) = M(x, 0)$ with compact support, which describe a restricted distribution of population.

Some reaction–diffusion systems such as the one above are notoriously apt to develop attractant (stable) travelling wave solutions which represent the permanent regimes of the dynamical system (Weinberger, 1982; Murray et al., 1986; Volpert and Volpert, 1994; Sandstede, 2002; Lucia et al., 2004). That is, after a quick transient period any sufficiently large initial perturbation will ultimately approximate the travelling wave solution which afterwards becomes the ‘visible dynamics’ of an invasion. We will show that, in fact, for model (2), travelling wave solutions should be expected for a continuous range of velocities. Next, we determine their smallest possible velocity which, for some parabolic equations (Murray, 1993; Volpert and Volpert, 1994; Lucia et al., 2004) as well as in the present case, corresponds to a stable travelling wave.

Such a phenomenon is not rigorously proved in the present paper but will be confirmed by many numerical simulations.

Travelling wave solutions will be searched for in the following form:

$$m(z) = M(x, t), \quad a(z) = A(x, t), \quad z = x - ct, \quad (3)$$

where c is the constant velocity and $m(z)$, $a(z)$ are the wave profiles, all to be determined as usual (Segel, 1980; Murray, 1993). We will look only for profiles representing an invasion process, that is, positive monotonically decreasing functions such that

$$\begin{aligned} \lim_{z \rightarrow -\infty} m(z) &= m^*, & \lim_{z \rightarrow -\infty} a(z) &= a^* \\ \lim_{z \rightarrow +\infty} m(z) &= 0, & \lim_{z \rightarrow +\infty} a(z) &= 0, \end{aligned} \quad (4)$$

where $M_0(x, t) = 0$, $A_0(x, t) = 0$ and $M_1(x, t) = m^*$, $A_1(x, t) = a^*$ are stationary and spatially homogeneous solutions of (2).

The invasion speeds obtained for the two sub-populations are equal and we should expect that from the following biological argument. Suppose that they are distinct, that is, $M(x, t) = m(x - c_1 t)$, $A(x, t) = a(x - c_2 t)$, and, say, $c_1 > c_2$. Then, if we wait long enough there will be some distant interval where the (‘faster’) mosquito population will reach values close to the saturation level with practically no aquatic population for as long as we want. That would contradict the vital dynamics, since in that interval a large population of mosquitoes would lay eggs at an enormous rate because (almost) no saturation effect exists without a sizable aquatic population. A similar argument works if the reverse inequality is proposed. Consequently, from a practical point of view, we should only expect a time delay between the wavefronts and a constant spatial gap, not an expanding one.

Substituting Eq. (3) into (2), the following system of ordinary differential equations is obtained:

$$\begin{aligned} \frac{d^2}{dz}m(z) &= (v - c)\frac{d}{dz}m(z) - \frac{\gamma}{k}(1 - m(z))a(z) + \mu_1m(z) \\ \frac{d}{dz}a(z) &= -\frac{k}{c}(1 - a(z))m(z) + \left(\frac{\mu_2 + \gamma}{c}\right)a(z). \end{aligned} \tag{5}$$

The above boundary value problem (4) and (5) can also be written in a dynamical system form as follows:

$$\begin{aligned} m'(z) &= h(z) \\ h'(z) &= (v - c)h(z) - \frac{\gamma}{k}(1 - m(z))a(z) + \mu_1m(z) \\ a'(z) &= -\frac{k}{c}(1 - a(z))m(z) + \left(\frac{\mu_2 + \gamma}{c}\right)a(z), \end{aligned} \tag{6}$$

with the equivalent boundary conditions:

$$\begin{cases} m(-\infty) = m^* \\ h(-\infty) = 0 \\ a(-\infty) = a^* \end{cases} \quad \begin{cases} m(+\infty) = 0 \\ h(+\infty) = 0 \\ a(+\infty) = 0 \end{cases} \tag{7}$$

where $m'(z) = \frac{dm}{dz} = h(z)$ and so on.

The boundary value problem (6) and (7) is defined in the interval $(-\infty, +\infty)$ and so its solutions can be interpreted geometrically as heteroclinic trajectories of the dynamical system (6) in the three-dimensional phase space (m, h, a) linking two different singular points, one of them being necessarily the origin. In fact, $P_0 = (0, 0, 0)$ is a singular point and a second $P_1 = (m^*, 0, a^*)$ is readily found, where

$$a^* = \frac{k\gamma - \mu_1k(\mu_2 + \gamma)}{k\gamma + \gamma(\mu_2 + \gamma)} \quad m^* = \frac{\gamma a^*}{\mu_1k + \gamma a^*}. \tag{8}$$

Since we are only interested in solutions of biological significance, P_1 must be adequately ‘positive’, which means $m^* \geq 0$ and $a^* \geq 0$. These requirements are equivalent to the following mathematical condition:

$$\mu_1 = \frac{\bar{\mu}_1}{\bar{r}} < 1 \quad \text{and} \quad \gamma > \frac{\mu_1\mu_2}{1 - \mu_1} \tag{9}$$

which will be interpreted next as two biological necessary conditions for the existence of the kinds of travelling waves that we are searching for.

The first inequality in (9) is quite obvious and means that the mortality rate $\bar{\mu}_1$ should be less than the maturation rate \bar{r} in dimensional units. The second one can be rewritten in dimensional variables as

$$R_0 = \frac{\bar{\gamma}}{\bar{\gamma} + \bar{\mu}_2} \frac{\bar{r}}{\bar{\mu}_1} > 1 \tag{10}$$

and interpreted from a biological point of view as follows.

Since $\frac{1}{\gamma + \mu_2}$ is the average time of survival of the aquatic *A. aegypti* and $\frac{1}{\gamma}$ is the average time of its existence as such, we can interpret $\frac{\gamma}{\gamma + \mu_2}$ as the probability that an egg will

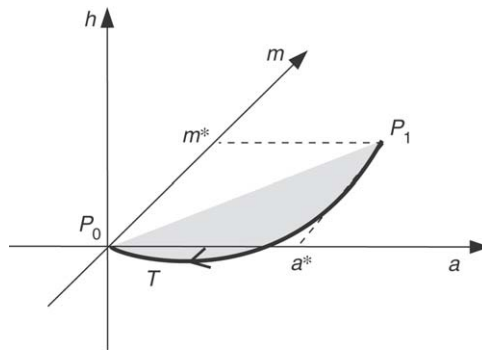


Fig. 1. A trajectory solution in the phase space (m, h, a) from P_1 to P_0 in the P -octant $m \geq 0, h < 0, a \geq 0$.

succeed in becoming a (female) mosquito. On the other hand, $\frac{1}{\mu_1}$ is the average lifetime of a female mosquito and consequently $\frac{r}{\mu_1}$ is the average number of eggs oviposited by each one. So, following epidemiological notation, R_0 will be called the ‘basic reproductive ratio’ and travelling waves will happen only if female mosquitoes produce on average one female mosquito during their whole lives. Of course, that is only a necessary condition because, mathematically, $R_0 > 1$ guarantees just the existence of a non-trivial and ‘positive’ singular point but not yet the existence of a wholly ‘positive’ trajectory linking it to the origin. It must be noted that a biologically acceptable (i.e., a ‘positive’) trajectory should satisfy the following inequalities: $m(z) \geq 0, a(z) \geq 0 \forall z \in (-\infty, +\infty)$ (Fig. 1). From now on we will call the three-dimensional region $m \geq 0, h < 0, a \geq 0$ the P -octant.

So, we will conclude now that $R_0 < 1$ is a sufficient condition for a non-invasive scenario. However, it is reasonable to assume that $R_0 > 1$ might be far from being a sufficient condition for the existence of travelling waves since it has no spatial parameter dependence.

Considering that $R_0 < 1$ is probably too strong a condition for controlling the dispersal of *A. aegypti*, we would like to extend the options for its spatial containment by analysing more closely the case $R_0 > 1$ and, in particular, learning about the wave speed dependence on non-dimensional parameters.

2.2. Travelling waves: their existence and speed dependence on the parameter space

The reaction–diffusion system (2) will be analysed next for the existence of travelling waves of constant speed, as described by (3) and under condition (9).

Let us suppose that the condition (9) for the existence of a singular ‘positive’ point is satisfied. We will use the phase space method to determine the existence of a ‘positive’ solution to the boundary value problem (6) and (7), which means a trajectory from the singular point $P_1 = (m^*, 0, a^*)$ to the origin $P_0 = (0, 0, 0)$ wholly contained in the P -octant. Of course, a necessary condition for the existence of the trajectory solution is that the P_1 must have an unstable (departing) manifold and P_0 a stable (incoming) manifold.

In order to do the required stability analysis, as usual, we linearize the dynamical system (6) and determine the eigenvalues of the Jacobian matrix for each singular point.

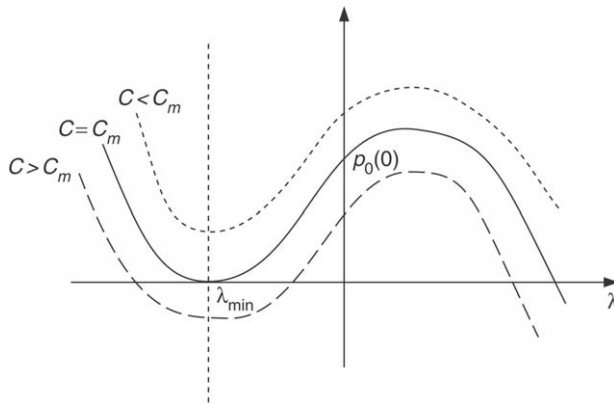


Fig. 2. Graphs of the c -family of polynomials $p_0(\lambda, c)$. In particular we show the graph of the threshold polynomial $p_0(\lambda, c_m)$.

At the origin P_0 the Jacobian matrix is

$$\begin{bmatrix} 0 & 1 & 0 \\ \mu_1 & (v - c) & -\frac{\gamma}{k} \\ -\frac{k}{c} & 0 & \frac{\mu_2 + \gamma}{c} \end{bmatrix},$$

and the corresponding eigenvalues are the roots of the following c -family of λ polynomials:

$$p_0(\lambda, c) = -\lambda^3 + \left[\frac{\mu_2 + \gamma}{c} + (v - c) \right] \lambda^2 + \left[\mu_1 - (v - c) \frac{\mu_2 + \gamma}{c} \right] \lambda - \frac{\mu_2 + \gamma}{c} \mu_1 + \frac{\gamma}{c},$$

where c is the undetermined wave speed.

From (9) we know that $p_0(0, c) = \frac{1}{c}[-(\mu_2 + \gamma)\mu_1 + \gamma] > 0$ and, since $\lim_{\lambda \rightarrow \pm\infty} p_0(\lambda, c) = \mp\infty$, we conclude immediately that each λ -polynomial of this c -family has at least one positive root. This polynomial, in principle, may have either two other real roots or two conjugate complex roots. Complex roots with negative real part might guarantee a solution of the boundary value problem (6) and (7) but the resulting trajectory would arrive at the origin spinning through outside points of the P -octant, which will not produce a biologically acceptable travelling wave. A travelling wave solution would exist only if for a $c \geq 0$ the respective polynomial $p_0(\lambda, c)$ has a negative (real) root.

However, its easy to see that for any $\lambda < 0$ we have $\lim_{c \rightarrow \infty} p_0(\lambda, c) = -\infty$ which means that a real negative λ root of $p_0(\lambda, c)$ will exist if c is chosen sufficiently large. Now, since for any $c > 0$, $p_0(0, c) > 0$, if a polynomial $p_0(\lambda, c)$ has a negative root, it will also have two negative roots. Generic graphs of polynomials of this kind are plotted in Fig. 2.

Let us define the set $C = \{c > 0; p_0(\lambda, c) \text{ has negative roots}\}$. In order to find the stable travelling wave we will have to determine the least value of $c > 0$ for which there is

such a solution, i.e., $\min C$. If there is such a minimum $c_m > 0$, the threshold polynomial $p_0(\lambda, c_m)$ will necessarily have a double root at its local minimum value (Fig. 2).

An interesting remark which might be helpful for visualizing the graphics of the c -family of λ -polynomials $p_0(\lambda, c)$ derives from the following inequality:

$$\begin{aligned} \frac{\partial}{\partial c} p_0(\lambda, c) = & - \left(\frac{\mu_2 + \gamma}{c^2} + 1 \right) \lambda^2 + \left[v \frac{(\mu_2 + \gamma)}{c^2} \right] \lambda \\ & - \frac{1}{c^2} [\gamma - \mu_1(\mu_2 + \gamma)] < 0, \end{aligned}$$

obtained by taking into account condition (9) and fixing any negative value of λ .

The threshold value c_m is the minimum speed c for which there may be a travelling wave or, in other words, $c \geq c_m$ is a *necessary* condition for the existence of a travelling wave solution. Of course we still have to consider conditions on the other stationary point, P_1 , in order to find whether further restriction must be imposed on parameter c .

So, the smaller root $\lambda_-(c)$ of the second-order polynomial $\frac{\partial P_0}{\partial \lambda}(\lambda, c)$ is the one that will eventually characterize the threshold value c_m when it becomes also a root of the third-order polynomial $p_0(\lambda, c)$, which means that we can reduce the above system to one algebraic equation:

$$p_0(\lambda_-(c), c) = 0, \tag{11}$$

whose solution gives us $c_m(\gamma, v, \mu_1, \mu_2)$.

We will not strive for complete algebraic conditions for the existence of a negative root of $p_0(\lambda, c)$, or for explicit formulas for c_m .

Now, turning our attention to the linear stability at the singular point P_1 we analyse the appropriate Jacobian matrix.

It is easily verified by algebraic manipulations that for $c \geq c_m$ the above Jacobian matrix has two positive eigenvalues and consequently the desired unstable manifold is always found; Fig. 3 (Hartman, 1973; Carr, 1981).

Under the above conditions (9), the equilibrium points P_0, P_1 become hyperbolic. Then, well known results from classical dynamical system theory (Hartman, 1973; Carr, 1981) ensure the existence of two invariant analytical manifolds for each point. What concerns us is the existence of an unstable ('departing') manifold at P_1 and a stable ('entering') manifold at P_0 . Using initial value points P_1^θ taken on a tangent line to the unstable manifold from (and close to) P_1 we compute the resulting trajectories until one of them reaches a close enough neighbourhood of the stable manifold at P_0 ; those are taken as approximate solutions to the heteroclinic trajectories; Fig. 3.

The existence of a continuum range of a travelling wave speed poses the immediate question of which, if any, of those solutions might be biologically relevant. The selection for relevance will be dictated by a stability criterion with respect to dynamical system (2) described by partial differential equations. A rigorous mathematical approach to this problem is rather involved (Sandstede, 2002) and falls outside the scope of the present work. However, there is a reasonable intimation from the well known Fisher equation (Murray, 1993) that the minimum speed travelling wave is the attractor solution for localized perturbations. Numerical simulations will later support this hunch for the present case also.

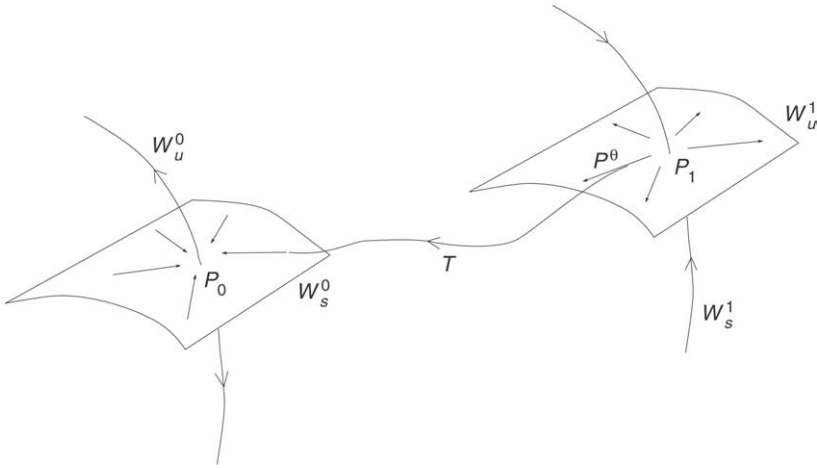


Fig. 3. An illustration of the numerical construction of a heteroclinic trajectory. W_s^i, W_u^i are the stable/unstable invariant manifolds at points P_0 and P_1 , T is the heteroclinic trajectory and $\overline{P_1 P^\theta}$ is the successful eigendirection.

Table 1

Values for the dimensional parameters in the following unit system: *Space* = $[x]$ = km, *Time* = $[t]$ = one day

D	v	γ	r	k_1	k_2	μ_1	μ_2
1.25×10^{-2}	5.0×10^{-2}	0.2	30	25	100	4.0×10^{-2}	1.0×10^{-2}

Table 2

Values for non-dimensional parameters $v, \gamma, k, \mu_1, \mu_2$ corresponding to Table 1

v	γ	k	μ_1	μ_2
8.164×10^{-2}	2.5×10^{-1}	6.66×10^{-3}	1.33×10^{-3}	3.33×10^{-4}

So, if we are to design any strategy for controlling the *A. aegypti* dispersal based on the above model, the crucial parameter to consider is $c_m = (\gamma, v, \mu_1, \mu_2)$. That is what is done next.

2.3. Numerical simulations

The numerical simulations were run with XPPAUT (Ermentrout, 2002). A numerical example, which is represented by a set of values for the fixed parameters (some of them will vary later), is given by Table 1 (dimensional) and Table 2 (non-dimensional). The values are of the same order as one case given in the literature (Ferreira and Yang, 2003).

The value of $R_0 = 714$ corresponding to the given parameters is very high and so, from a spatially homogeneous model point of view, the propagation would succeed quickly. However, as can be seen from expression (10), R_0 depends only on vital parameters.

So, from now on, all the chances for controlling the *A. aegypti* invasion must rely mainly on the spatial dispersal mechanism, represented by the non-dimensional parameter $\nu = \frac{\bar{v}}{\sqrt{\bar{r}D}}$.

The corresponding equilibrium point for this numerical example is $P_1 = (0.951, 0, 0.971)$. The minimum speed for the existence of travelling waves is $c_m \simeq 0.514$, whose value can be approximately obtained either by solving the corresponding algebraic Eq. (11) or by solving the boundary value problem (4) and (5) or (6) and (7), as shown below.

Numerical simulations of the boundary value problems (4) and (5) or (6) and (7) were performed by using a kind of ‘shooting method’, i.e., by solving Cauchy problems for the system (5) with ‘smart’ initial values P^θ chosen in a neighbourhood of P_1 and in such a way that $P_1 P^\theta$ is an ‘unstable’ eigenvector (Hagstrom and Keller, 1986).

Fig. 4 shows that for $c = 0.38$ there is a heteroclinic trajectory spinning around the origin which indicates that the corresponding polynomial must have two complex roots. Increasing the values of c , we can observe (not shown in the figure) that the spin decreases until $c \simeq 0.52$ when we obtain an almost perfect heteroclinic trajectory wholly inside the P -octant linking P_1 to the origin. It is important to note that for larger values of c we still obtain heteroclinic orbits in the P -octant which are not interesting since they do not yield stable travelling wave solutions, as we already know and will be shown next in the numerical simulations of the reaction–diffusion system (2). Besides, for very large values of c the heteroclinic orbit yields a travelling wave solution of (2) which exhibits densities (of both mosquitoes and the aquatic phase) well beyond the carrying capacity.

As can be seen in Fig. 4, the wavefront for M is detected first, which is biologically expected since only the mosquitoes are capable of moving. However, due to a high oviposition rate and a relatively small maturation rate, the wavefront for A takes over very quickly and reaches the saturation level long before M .

2.4. Indication of the stability of the c_m travelling wave by numerical simulations of the reaction–diffusion model

In order to have a biological use for travelling wave solutions we need to show not only their stability but also that they exhibit a strong attractive behaviour. In that case a travelling wave will represent a permanent regime of the dynamical system in a robust scenario. However, rigorous mathematical treatment of even linear stability of travelling waves is a notoriously difficult problem and estimation of the attractability region, which would be the practical side of this kind of result, is a hopeless task. So, this is where numerical simulation can give us strong support for or evidence against stability arguments. In what follows we show that numerical solutions of the full partial differential reaction–diffusion equations (2) with quite general initial conditions quickly develop into travelling waves with the same velocity c_m as prescribed by the arguments presented in the last section.

The numerical solutions were obtained by using a fourth-order Runge–Kutta method in the second equation for the aquatic phase (actually an ordinary differential equation in time) and a finite-difference approach for the first equation adequately modified in order to take into account advection effects in the spatial variable. A Crank–Nicholson method was used for the semi-discretization of the time variable.

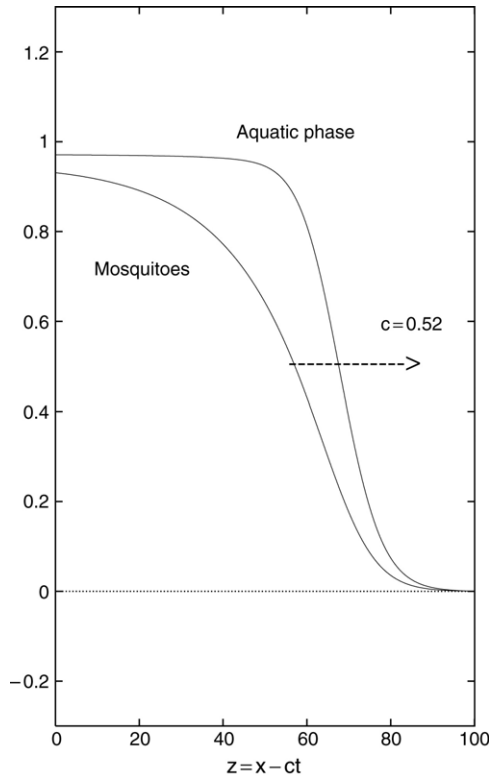


Fig. 4. Front waves for $c = 0.52$.

For the mosquito population, an initial condition of a box type

$$M(x, t) = \begin{cases} 0, & |x| > 1 \\ M_0, & |x| \leq 1 \end{cases}$$

and Neumann null boundary conditions

$$\frac{\partial M}{\partial x}(\pm L, t) = 0, \quad t > 0$$

were used, while for the aquatic phase, both the initial and Dirichlet boundary conditions were taken as null:

$$A(x, t) = 0, \quad A(\pm L, t) = 0.$$

In Fig. 5 the spatial graphs of a typical solution for many values of time clearly show a very quick approach to a travelling wave solution. This limit behaviour was always found for different values M_0 and L of the initial and boundary conditions, which supports the conclusion that the travelling wave solution is in fact a very attractive solution. Biologically, that means that invasive processes are typical phenomena for the *A. aegypti* population dynamics. The speed of the limit travelling wave is 0.32 km day^{-1}

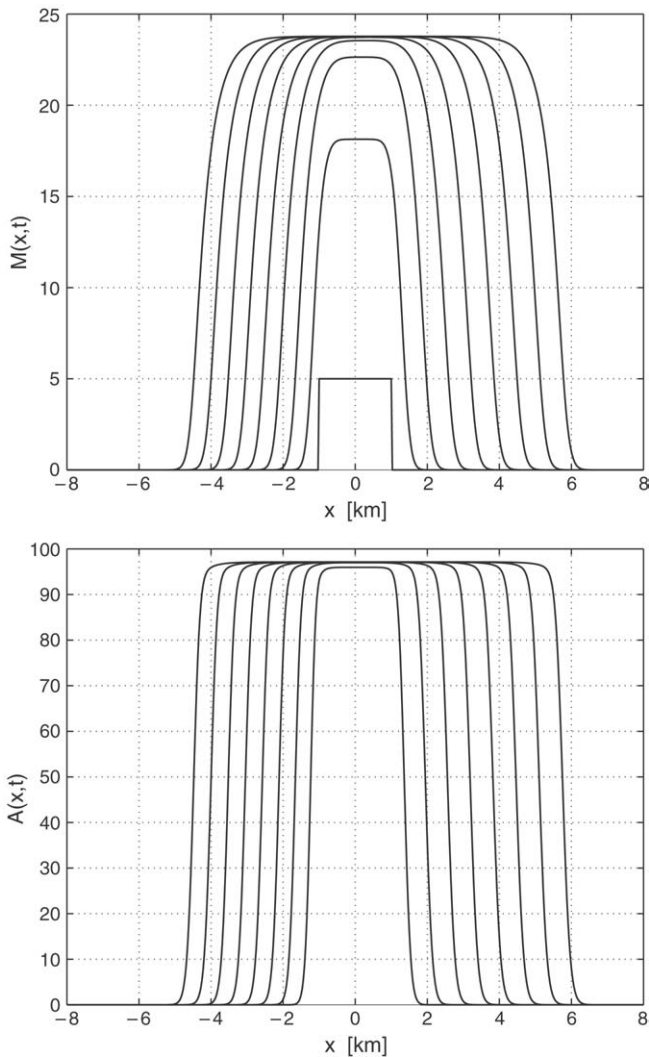


Fig. 5. Graphs of $M(x, t)$ and $A(x, t)$ with respect to the spatial variable x for fixed values of time: $t = 0, 2, 4, 6, 8, 10, 12, 14, 16$ days. The right downstream wavefront is faster moving than the left upstream wavefront.

which closely agrees with the non-dimensional $c_m = 0.514$ obtained from the arguments presented in the last section.

Once $c_m(\gamma, \nu, \mu_1, \mu_2)$ is confirmed as the vital parameter for the invasion phenomenon, the next step must be to analyse the strategies for stopping the wave process or, in other words, to determine the range of values for the non-dimensional parameters $\gamma, \nu, \mu_1, \mu_2$ which may bring the value of $c_m(\gamma, \nu, \mu_1, \mu_2)$ as close as possible to zero.

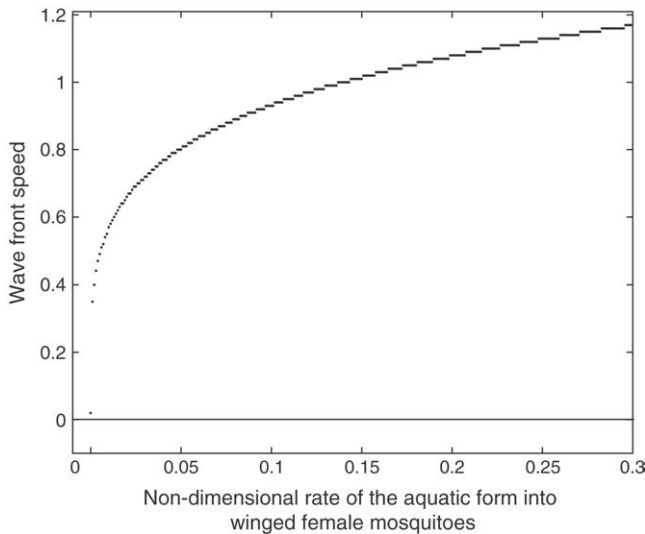


Fig. 6. Variation of $c_m(\gamma, \nu, \mu_1, \mu_2)$ with respect to the parameter γ , when ν, μ_1, μ_2 are fixed as in Table 2.

In the first place we will analyse its dependence on vital parameters γ, μ_1, μ_2 and later that on the movement behaviour parameter ν .

The non-dimensional parameter $\gamma = \frac{\bar{\nu}}{\bar{r}}$ is the ratio of two time units, the average time for one oviposition $\frac{1}{\bar{r}}$ and the average time taken for the aquatic form to mature, $\frac{1}{\bar{\nu}}$. Fig. 6 shows an expected monotonically increasing dependence of c_m with respect to the parameter γ , when ν, μ_1, μ_2 are fixed as in Table 2, and also shows a saturation effect for large values of γ . A complete stop strategy with this parameter is unreasonable from a practical point of view since substantial decrease in c_m is only attained by bringing γ very close to zero; for relatively small values of γ (≈ 0.05) the wave speed still remains too high (≈ 0.8).

Fig. 7 shows that an application of insecticide against the winged (mosquito) phase is much more effective as an infestation containment strategy than insecticide application against its aquatic phase. This should not be surprising, since the winged form is the one responsible for the *A. aegypti* movement. However, as can be seen from the same figure, a saturation effect is very apparent and massive insecticide application to increase the mosquito mortality rate beyond 0.25 will show very little improvement in wave speed reduction.

Insecticide application against the aquatic form is not very effective for wave control, as can be seen from Fig. 8. However, if a chemical attack against the winged form ($\mu_1 \gg 1$) is coupled with the elimination of infested water-holding containers ($k \gg 1$), the results are surprisingly effective, as shown in Fig. 9.

Public education campaigns and debris removal should result in reduction of *A. aegypti* breeders and consequently in a decrease of the (dimensional) carrying capacity (k_2) for the aquatic form. Since the (dimensional) carrying capacity for mosquitoes (k_1) depends only on human population density, which is hardly controllable, the non-chemical strategy can

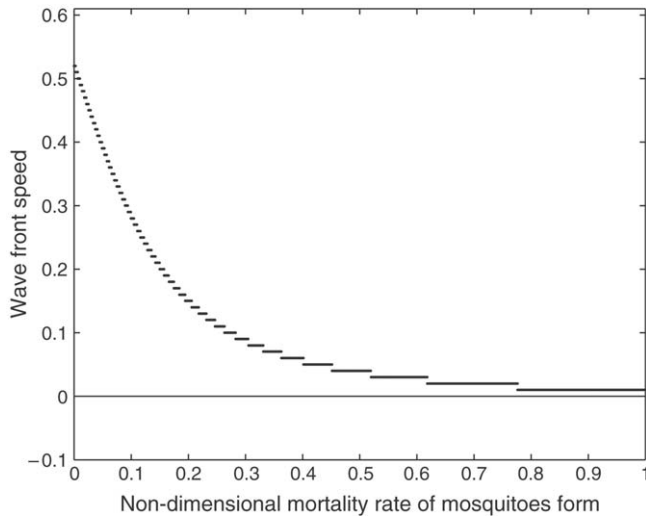


Fig. 7. The dependence of c_m on μ_1 ; all the remaining parameters have fixed values as given by Table 2.

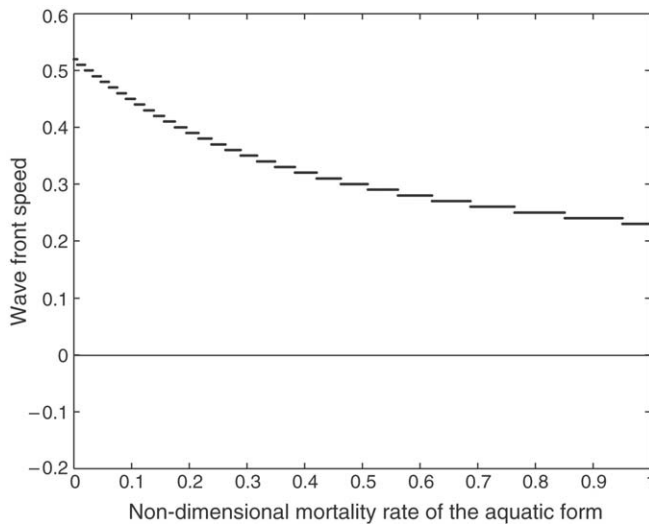


Fig. 8. The dependence of c_m on μ_2 ; all the remaining parameters have fixed values as given by Table 2.

be represented by an increase in the value of the (non-dimensional) parameter $k = \frac{k_1}{k_2}$. Fig. 8 shows that this is a very effective strategy for reduction of the invasive wave speed. However, the practical enforcement of this strategy requires a long period of time and a large workforce, which makes it very difficult to reduce the value of k_2 for an extensive region. So, it is an interesting problem to analyse the travelling wave behaviour in a medium with k_2 varying periodically [see, for example, Pauwelussen (1981),

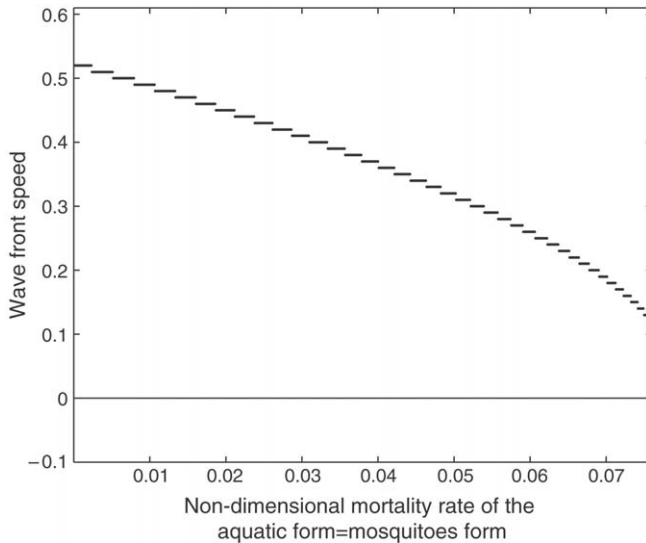


Fig. 9. The dependence of c_m on $\mu = \mu_1 = \mu_2$; all the remaining parameters have fixed values as given by Table 2.

Shigesada and Kawasaki (1997) and Heinze et al. (2001)], in an effort to find an efficient strategy for breeder elimination in just a fraction of the total area based on choosing an appropriate spatial pattern of action. The time dependence of parameter k_2 in specific spots might also provide an efficient strategy for wavefront containment or, rather, represent the influence of an intangible environment (Potapov and Lewis, 2004). The same can be said as regards the insecticide strategy which is notoriously inefficient and noxious to public health when applied to densely populated areas. We will not pursue this matter here.

Control of spatial movement of *A. aegypti* is very difficult from a practical point of view. However, the study of the wavefront speed dependence on advection, i.e., wind transportation, is interesting from a prediction point of view. Fig. 10 shows that the wavefront speed varies linearly with the advection velocity but not in the same way as in the classical Fisher model. Since the advection only carries the winged form, and the mosquitoes need some time to oviposit, the dependence of the wavefront speed in the present model on the advection velocity is not as strong as in Fisher's model.

Up to now we have considered only downstream (positive) wavefront speed. Of course there might be also a wavefront in the upstream direction, as in the case shown by the left side of Fig. 5. In order to find the value of the upstream wavefront speed it is sufficient to keep $v > 0$ and look for solutions of the boundary value problem (4) and (5) for $c < 0$. If non-dimensional parameters take values such as those given by Table 2, we obtain $c_m \simeq -0.40$ (dimensionally $\simeq 0.25 \text{ km day}^{-1}$) for the invasive wave speed in the upstream direction. Note that for $v = 0$, we have $c_m \simeq 0.45$. On the other hand, with $v = 8.16 \times 10^{-2}$ the upstream wave speed is $c_m = 0.40$ while the downstream wave speed is $c_m \simeq 0.52$. So, we conclude that the advection effect on wave speed is stronger in the downstream direction than upstream. Of course, we can expect a sufficiently

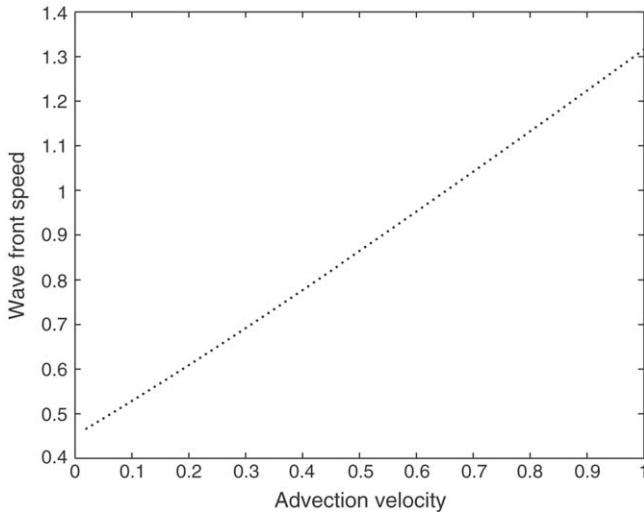


Fig. 10. The dependence of c_m on v ; all the remaining parameters have fixed values as given by Table 2.

strong advection to invert the upstream wave to the downstream direction. Fig. 11 shows the upstream wave speed dependence on the advection velocity, fixing non-dimensional parameters to values such as those given by Table 2. In that case, $v = v_b \simeq 1.95$ is a threshold ('braking') value, after which the upstream wave inverts its direction of propagation. Fig. 12 shows that for an advection velocity close to the braking value and for an initial 'box' distribution of mosquitoes, the solution of the model develops into a travelling wave with only a downstream wavefront; in the upstream direction, and beyond the origin, both the mosquitoes and the aquatic phase populations are swept to extinction.

Although advection by natural causes cannot be controlled, the above discussion may be useful for the prediction of patterns of *A. aegypti* invasion in urban areas exposed to strong and constant winds. Besides this, intervention in the diffusion process, i.e. in the flying movement of the mosquitoes, may also be possible via a spatial strategy such as the one described above (Shigesada and Kawasaki, 1997; Heinze et al., 2001). The treatment of this matter is left to further work.

3. Final comments

Biological invasion is an especially important area of research when it concerns biological vectors of diseases that threaten the public health of large populations. That is certainly the case for *A. aegypti* and the dengue epidemics in South America and South-East Asia (Gubler, 1998; Vasconcelos et al., 1999). Without a vaccine on the horizon, any feasible public policy for controlling the dengue epidemics must take into account appropriate strategies for minimizing the mosquito population factor. Besides this, even when a political will to act on public health problems is shown (which is not as common as it should be), the economic resources available are always very meagre in the infested

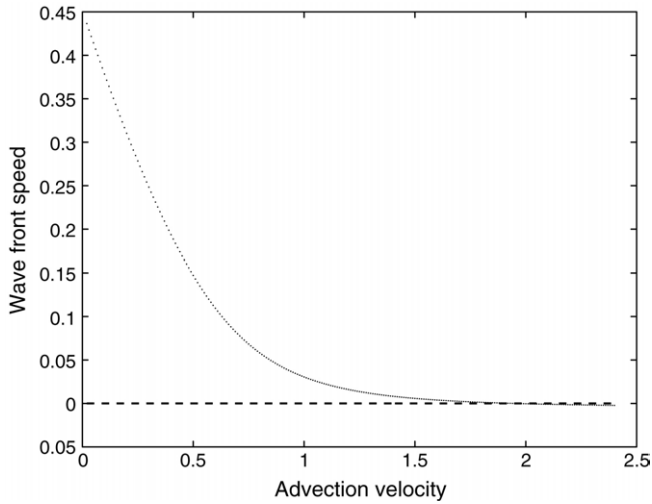


Fig. 11. The upstream wave speed dependence on the advection velocity, fixing all non-dimensional parameters to values such as those given by Table 2. For $v_b \simeq 1.95$ the function ‘slowly’ changes its sign.

countries. So, to guarantee a reasonable impact on public health, prophylactic strategies should rely on the best possible educated guesses and some of them might be significantly helped by the analysis of epidemiological mathematical models.

The present paper focuses its attention on a mathematical model for the population dispersal of *A. aegypti* by considering two coupled sub-populations: the winged female mosquitoes (the effective vector) and an aquatic sub-population which includes the other phases: egg, pupa, larva. The mathematical model consists of two coupled conservation laws, where movement is assumed only for the mosquito sub-population and is described by diffusion–advection processes. Conditions for the existence of travelling waves were analysed and the minimum speed was found, following an assumption that the corresponding wave is the stable one and, consequently, that which might really represent a biological invasion. Numerical simulations with realistic data confirmed that the minimum speed travelling wave does in fact represent a robust scenario for the biological invasion phenomenon, since small and quite general initial perturbations quickly evolve to produce it. Also, the order of magnitude of the invasion speed obtained by the analysis, and corroborated by the simulations, relates well to field observations. All of this gives support to the mathematical model, which can then be analysed for possible strategies for containment and prediction of the *A. aegypti* dispersal process. Some specific situations are analysed, related to the maturation step and the effect of a chemical attack against the winged population, as well as the effect of advection (wind) on the upstream and downstream wavefronts. A chemical attack against the winged form coupled to a reduction of breeders is shown to be a very effective strategy. Some suggestions for the analysis of the mathematical model with respect to reduced and surgical interference in the medium (which are interesting for economical and environmental reasons) are discussed, but their details are left to further work. We hope that this paper will help lead to a better

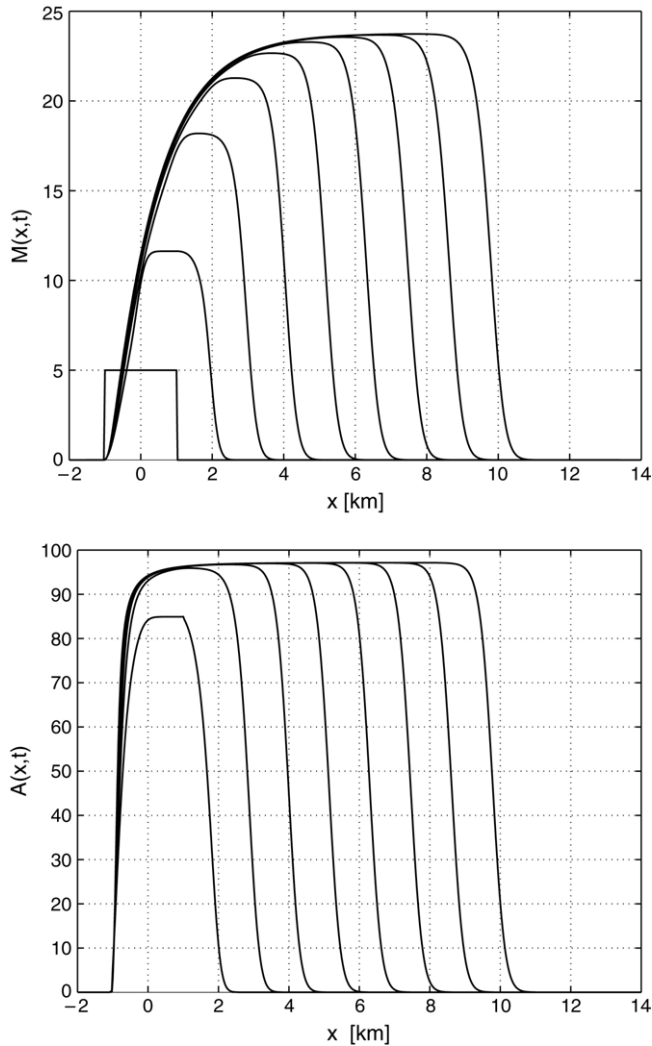


Fig. 12. The development of a travelling wave (top: mosquitoes; bottom: aquatic phase) when the advection velocity is at braking value $v = v_b \simeq 1.95$, obtained by fixing all non-dimensional parameters to values such as those given by Table 2.

understanding of the *A. aegypti* dispersal process and provide new conceptual tools for the advancement of our knowledge of this important subject.

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