Nonlinear Analysis: Real World Applications 14 (2013) 495–506

Contents lists available at SciVerse ScienceDirect

Nonlinear Analysis: Real World Applications

journal homepage: www.elsevier.com/locate/nonrwa

Traveling waves in discrete models of biological populations with sessile stages☆

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ARTICLE INFO

Article history:
Received 21 October 2011
Accepted 7 July 2012

Keywords:
Discrete model
Spreading speed
Traveling wave
Stage structure
Delay effect

ABSTRACT

A common approach to describing invasions of non-native species into previously unoccupied habitat is to consider the speed of population expansion and the existence of traveling waves. Typical existence theorems for traveling waves require some compactness properties of the next-generation operator. Many realistic modeling assumptions, however, give rise to non-compact operators; for example the occurrence of sessile stages during the life cycle of an individual. Recent results have extended the existence theory of traveling waves to a large class of weakly compact operators, but conditions can be difficult to check and not easily accessible to theoretical ecologists. In this paper, we give a new proof for the existence of traveling waves in a large class of equations where the next generation operator is not compact, but rather the sum of an integral operator and a contraction. We illustrate our proof with a model for the dispersal of a plant species with a seed-bank and a model for dispersal of stream insects with larval stages.

1. Introduction

Invasions of non-native organisms into novel territory can cause huge economic loss, and they pose a great global challenge to the maintenance of biodiversity. For example, while the mountain pine beetle continues to threaten forests across Western North America, the Emerald Ash Borer is spreading from its North American introduction site in Michigan to 14 other states and to Canada, destroying Ash trees along the way. Mathematical modeling of biological invasions is of crucial importance, given the spatial and temporal scales involved. The first models date back to Fisher [1] and Skellam [2]; current theory continues to challenge mathematicians and ecologists alike [3–7].

Mathematical models for biological invasions are typically written as reaction–diffusion equations or, more recently, as integrodifference and integrodifferential equations. Since the seminal work of Weinberger [8], questions about the existence of a spreading speed (see definition below) and traveling waves are studied using a recursion of the form

$$u_{n+1} = Q[u_n], \quad n \in \mathbb{N}, \tag{1.1}$$

where u_n represents the density of the population in the habitat, which we assume to be $\mathbb{R}$, at time $n \in \mathbb{N}$. (The extension to planar waves in higher dimensions is straight forward.) Integrodifference equations naturally come in this form, whereas for continuous-time equations, one considers the time-one map.

☆ The paper was written after short visits of the first author to the University of West Georgia and the second author to the University of Ottawa. The authors gratefully acknowledge travel support from the MITACS network on "Biological Invasions and Dispersal".

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1468-1218/$ – see front matter
doi:10.1016/j.nonrwa.2012.07.011

The equations we consider in this work are formulated in discrete time since natural annual variation often imposes clearly distinct seasons of growth and spread of individuals. In the simplest case, the "next-generation operator" Q is typically of the form

$$Q[u](x) = \int_{\mathbb{R}} K(x-y)f(u(y))dy, \tag{1.2}$$

where the "kernel" K is the density of a probability measure on $\mathbb{R}$, and f is a *scalar* function that characterizes the growth of the population in the absence of spatial movement. An example for such a function is the scaled Beverton–Holt function

$$f(u) = \frac{ru}{1+(r-1)u}, \tag{1.3}$$

where $r > 1$ is a constant, known as the intrinsic rate of growth at low population density. When the species under consideration exhibits a more complicated life cycle then model formulation is more difficult, for example, stage structured models may result [9]. We give a detailed derivation of two particular models in Section 2, but first we explain the background of past mathematical results and challenges.

The pioneering works by Aronson–Weinberger [10,11] and Weinberger [8,12] establish the existence of an asymptotic spreading speed and of traveling waves for Eq. (1.1) and its continuous-time analogue. Lui and, more recently, Liang and Zhao extended many of these results to monotone systems of such equations [13–16]. An excellent recent overview is given by Zhao; see [17].

It is well known that Eq. (1.1) has an asymptotic spreading speed, c^*, if the fecundity function f is nondecreasing [8,12,14], and if some fairly mild conditions on Q are satisfied. The most important of these conditions being that the moment generating function of the kernel K exists in some interval around zero. This speed c^* can be characterized as the lowest speed of a family of non-constant traveling wave solutions of (1.1). Moreover, c^* can be expressed explicitly by a simple formula if additional conditions on f hold (see [18,19,12,8]). In order to prove the existence of traveling waves, however, one typically requires that the operator Q be compact [15,8], or weakly compact [16, condition (A3)]. The existence of traveling waves is much harder to show when the next-generation operator is not weakly compact. For the case of weak compactness we refer the reader to [20] and the general theory in [16]. Finite-dimensional cooperative systems of integrodifference equations were studied by Lui [13,14], Weinberger, Li and Lewis [21–23] and Liang and Zhao [15,16]. Again, the existence of a spreading speed is often guaranteed under fairly mild conditions on the operator Q, but the existence of traveling waves requires that operator to be weakly compact.

A number of scenarios give rise to a non-compact next-generation operator Q. For example, Volkov and Lui considered growth and spread of a population where a fraction of individuals is sedentary and does not move in space [20]. They studied the equation

$$u_{n+1}(x) = Q_g[u_n](x) = (1-g)\int_{\mathbb{R}^d} K(x-y)f(u_n(y))dy + gf(u_n(x)). \tag{1.4}$$

In this case, $g \in [0, 1]$ is the (constant) probability that an individual does not move from one time step to the next. For $g > 0$, the operator Q_g, as an operator acting in a subspace of the space of continuous functions, is not compact. The existence of an asymptotic spreading speed still follows from the general theory by Weinberger [12]. Volkov and Lui proved also the existence of traveling waves for this model. The case where g depends on the density of the population, that is, g is a function of u_n, was considered in [24]. For specifically chosen functions f, g, K a traveling wave was calculated explicitly, but the general theory remains wide open. Even the existence of a spreading speed is not clear in the general case. Note that, under the condition that the kernel K be continuous, the next generation operator determined by (1.4) satisfies the weak compactness condition (A3) in [16], so the general theory of [16] is applicable. In some cases, the operator Q is compact even if the kernel K is not continuous, for example the top-hat kernel with mean dispersal distance β, that is, $K(x) = \chi[-2\beta, 2\beta](x)/(4\beta)$. A model for structured populations with non-dispersing stages was formulated by Neubert and Caswell [9], but the existence of traveling waves was not discussed.

In this work, we prove the existence of traveling waves for a class of structured population models where the next-generation operator is not compact. We give two examples of how such operators arise in the next section. We give details of our proof for a particular example of a population with two stages in Section 3. The general case follows; we include it in our discussion. Before we start, we would like to point out that our idea and methods of proof are quite different and much less technical than the theory developed by Liang and Zhao [16], in particular, the conditions and results formulated here, see Section 2.5, are much more accessible to theoretical ecologists.

2. Models and assumptions

2.1. Plants with seed-bank

We consider an annual plant species whose seeds may stay dormant in the soil for several years (seed bank) before they germinate and grow. This delayed germination is crucial for the species to survive in unpredictable environments [25]. Seeds can remain dormant in the soil for decades, and the density in a seed bank can be as high as hundreds of seeds per square meter [26]. Germination probabilities may depend on the age of the seed in a seed bank. Rees and Long found that