Ecological Modelling 320 (2016) 158–169

Contents lists available at ScienceDirect

Ecological Modelling

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

A model for the interaction of frog population dynamics with *Batrachochytrium dendrobatidis*, *Janthinobacterium lividum* and temperature and its implication for chytridiomycosis management

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ARTICLE INFO

Article history:
Received 19 May 2015
Received in revised form
13 September 2015
Accepted 15 September 2015

Keywords:
Batrachochytrium dendrobatidis
Chytridiomycosis
Frog population
Janthinobacterium lividum
Mathematical modeling
Temperature

ABSTRACT

Chytridiomycosis is an emerging disease caused by the fungal pathogen *Batrachochytrium dendrobatidis* (*Bd*) that poses a serious threat to frog populations worldwide. Several studies have shown that inoculation of bacterial species *Janthinobacterium lividum* (*Jl*) can mitigate the impact of the disease. However, there are many questions regarding this interaction. A mathematical model of a frog population infected with chytridiomycosis is developed to investigate how the inoculation of *Jl* could reduce the impact of *Bd* disease on frogs. The model also illustrates the important role of temperature in disease dynamics. The model simulation results suggest possible control strategies for *Jl* to limit the impact of *Bd* in various scenarios. However, a better knowledge of *Jl* life cycle is needed to fully understand the interaction of *Jl*, *Bd*, temperature and frogs.

1. Introduction

The disease chytridiomycosis poses a serious threat to many frog populations around the world (Berger et al., 1998; Kilpatrick et al., 2010; Stuart et al., 2004; Skerratt et al., 2007). It has infected over 350 species of amphibians and been linked to devastating population declines and extinctions of over 200 species (Fisher et al., 2009; Skerratt et al., 2007; IUCN, 2014). Chytridiomycosis has been detected in 52% of the threatened amphibian species (Commonwealth of Australia, 2006). Chytridiomycosis occurs when the skin of a frog is infected by the chytrid fungus *Batrachochytrium dendrobatidis* (*Bd*) which interferes with normal skin function. Eventually frogs die of cardiac arrest (Pennisi, 2009). Despite much research dedicated toward understanding the natural history of the disease, chytridiomycosis continues to spread (e.g., see http://www.bd-maps.net/). Hence, it is necessary for conservation agencies to devote their research to determining mitigation strategies against chytridiomycosis.

Several studies (Becker et al., 2009; Brucker et al., 2008; Harris et al., 2009) show that a microbial community on amphibian skin, *Janthinobacterium lividum* (*Jl*), can protect amphibians against *Bd*. The proposed mechanism is that the strains of *Jl* that protect frogs from chytridiomycosis produce violacein, a fungicide. However, not all amphibians have these symbiotic bacteria and are thus protected (McKenzie et al., 2012). For example, while *Jl* is not present naturally on the skin of mountain yellow-legged frog (*Rana muscosa*) (Harris et al., 2009), it has been experimentally demonstrated that inoculating frogs of this species with *Jl* protected them from infection with *Bd* (Harris et al., 2009). Thus, inoculation with *Jl* is a promising strategy to control chytridiomycosis (Harris et al., 2009; Lam et al., 2010). While inoculation has been successful with other wildlife diseases (MacInnes et al., 2001; Oral Rabies Vaccination in Raccoons), what might be an effective inoculation strategy for frogs is not well understood. For example, important questions related to inoculation strategies that remain to be answered include: What is the optimal timing of inoculation in order to best control the disease? How frequently should one inoculate? Mathematical modeling is an important tool for testing hypotheses and checking what may happen in various scenarios.

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http://dx.doi.org/10.1016/j.ecolmodel.2015.09.015
0304-3800/

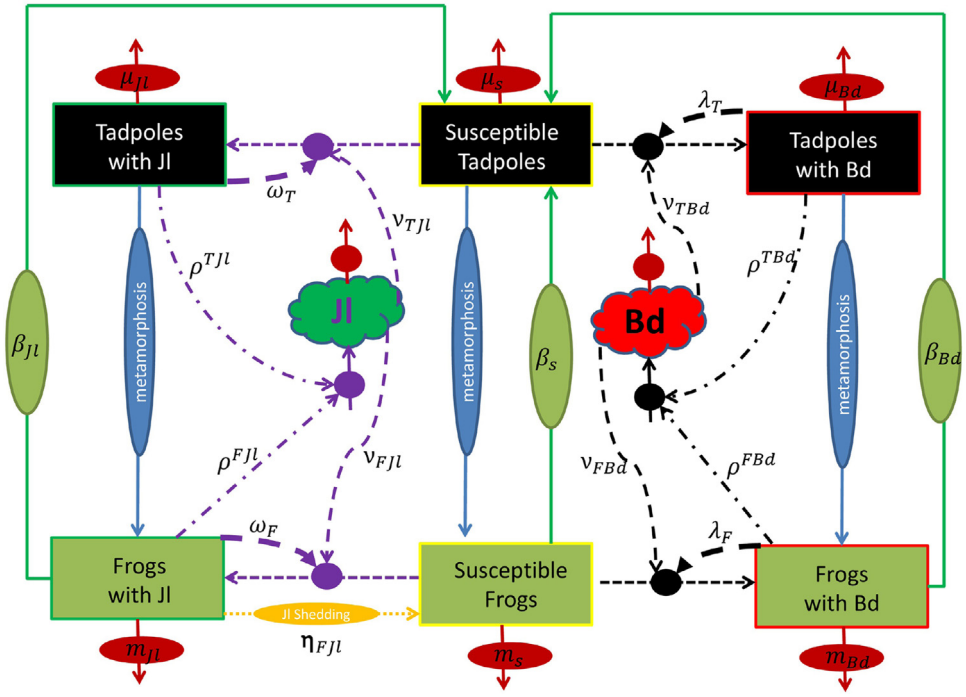

Fig. 1. Flow diagram of the mathematical model. Transmission is simulated among two stages (tadpoles and frogs) with *Bd* fungus and *Jl* bacteria. See text for model equations and Table 1 for model parameter descriptions and units. Solid lines represent vital rates; dashed lines represent transmission rates; dashed–dotted lines represent zoospore release rates; dotted line represents the shedding rate.

In this study, we develop a mathematical model to examine inoculation strategy as it relates to the interaction of *Bd*, *Jl*, temperature and frogs.

Temperature plays an important role in the development of the disease, not just because frog activities such as breeding and hibernation are triggered by temperature, but also because growth rate of *Bd* and its pathogenicity are temperature dependent (Forrest and Schlaepfer, 2011; Kilpatrick et al., 2010). For example, *Bd* grows within a wide temperature range (4–25 ° C), with optimal growth between 17 ° C and 25 ° C (Berger et al., 2005; Piotrowski et al., 2004). *Bd* does not grow well in temperatures above 28 ° C (Piotrowski et al., 2004); 50% of colonies of *Bd* are killed after 8 days at 30 ° C (Piotrowski et al., 2004), and 100% mortality occurred within 96 h at 32 ° C and within 4 h at 37 ° C (Berger, 2001). Therefore, we adopt temperature as an important factor in our model.

The main objectives of this paper are: (i) to develop a mathematical model that can be used to investigate how a variety of factors, including temperature and disease parameters, influence chytridiomycosis, (ii) to use this model to determine an efficient control strategy of the disease under various scenarios, and (iii) to provide insights into how to implement the effective inoculation strategy. We organize this paper as follows: in Section 2 we present the general mathematical model, model parameters utilized in the numerical simulations, temperature profiles and the numerical scheme used to simulate the model. In Section 3 we present the numerical simulation results. Discussion and conclusions are provided in Section 4.

2. Materials and methods

2.1. A mathematical model

We consider a frog population in a single pond and we divide individuals in this population into two stages: frogs and tadpoles. *Bd* fungus is able to infect frogs, as well as tadpoles. Since tadpoles live in water and frogs are amphibious, we assume in the model that the transmission between individuals is within stage only (i.e., frogs only directly infect frogs and tadpoles only directly infect tadpoles). Fig. 1 illustrates the proposed transmission network. Several studies (Carey et al., 2006; Rowley and Alford, 2007) indicate that there are two routes for *Bd* fungus to spread in frog populations:

(i) By exposure to motile zoospores in the environment such as water and moist or wet soil. Some of these zoospores were released from infected tadpoles and frogs.
(ii) By direct skin contact between infected and uninfected individuals of the same life history stage.

In Harris et al. (2009), the symbiont *Jl* was successfully used to inoculate frogs against *Bd* infection. We therefore assume in the model that tadpoles and frogs that are inoculated with *Jl* gain protection from *Bd* infection. We assume that if an individual is infected with *Bd*, it eventually dies of chytridiomycosis. Finally, we assume that *Jl* inoculation only lasts for a limited amount of time before *Jl* is cleared from the skin (Harris et al., 2009), rendering the frog or tadpole susceptible to infection from *Bd* once again.

We divide both tadpole and frog stages into three classes: (i) susceptible individuals, (ii) individuals infected with *Bd*, and (iii) individuals inoculated with *Jl* and thus are protected from *Bd* infection. In Berger et al. (2005), it was found that frogs experienced up to 100% mortality rate when exposed to *Bd* unless inoculated with *Jl*. For this reason and the simplicity of the model, we did not include a recovered class. We assume that tadpoles are structured by age, while frogs are structured by size (body length) (cf. the frog population model in Ackleh et al. (2012) without *Bd*, *Jl*, or temperature).