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Modeling and analysis of a temperature-driven outbreak of waterfowl disease in the Upper Mississippi River

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ABSTRACT

Bithynia tentaculata is an invasive snail that was discovered in the Upper Mississippi River (UMR) in 2002. In addition to being a threat to native benthos, the snail also harbors parasite associated with annual outbreaks of waterfowl mortality in the UMR. Trophic transmission of parasites between snails and birds occurs during seasonal waterfowl migrations, which can depend intimately on temperature. We developed an annual model for waterfowl disease in the UMR where transmission depends on water temperatures gleaned from empirical studies. By running simulations from annual temperature profiles selected randomly from a normal distribution, we quantified the association between the number of infected hosts and annual average temperatures. Model output demonstrated that as annual average temperatures rise, infected host populations initially increase and then decay after temperatures exceed a certain threshold. Results from this work suggest that increasing temperatures in the region may have a negative effect on parasites, decreasing their transmission and reducing infected host populations.
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1. Introduction

Animal populations are continually confronted with seasonal fluctuations which ultimately help to shape biological patterns across natural system. Although the factors underlying seasonality are extensive (rainfall and photoperiod), temperature is widely recognized as a key variable that modulates the expression of animal life-history traits such as growth, reproduction, behavior and immunological function across seasons and over years (Fedorka et al., 2013; Benbellil-Tafoughalta and Koen, 2015; Singh et al., 2015).

More recently, seasonal changes in temperature have been identified as important predictors of disease occurrence within animal populations (Altizer et al., 2006; Leicht et al., 2013). Changing temperatures between seasons and/or years can alter host behaviors (such as migration) leading to variability in contact rates among infected and susceptible hosts thereby shifting infection dynamics (Kuenzi et al., 2007). For example, Studer and Poulin (2012) found that warmer summer temperatures coincided with an influx of host birds into a New Zealand mudflat. This, in turn, corresponded with peak trematode infections in both snail and amphipod hosts within the system. Changing temperatures may also alter host susceptibility through immunological mechanisms. This pattern has been widely reported in ectothermic hosts, and has been recently observed in endothermic hosts as well (Kuenzi et al., 2007; Zhang et al., 2012). Alternatively, temperature may directly influence the parasites themselves which can alter the timing and magnitude of disease. Numerous studies have demonstrated that changing temperature can not only modulate parasite development within hosts, but can also dictate the subsequent infection success of stages released into the surrounding environment (Thieltges and Rick, 2006; Leicht and Seppälä, 2014).

Although temperature-dependent patterns of infection have been empirically identified across a number of host–parasite systems, incorporation of seasonal temperature regimes into wildlife disease models remains relatively rare. Recent studies have incorporated seasonal variation into their models as time-dependent coefficient functions which are often assumed to be sinusoidal (Altizer et al., 2006; Bolzoni et al., 2008; Grassly and Fraser, 2006; Liu et al., 2010; Wesley and Allen, 2009; Zhang et al., 2012). While such models have shown promise in better representing the natural dynamics of both hosts and parasites, their connections to specific drivers of seasonality, such as temperature, remain tenuous. In the

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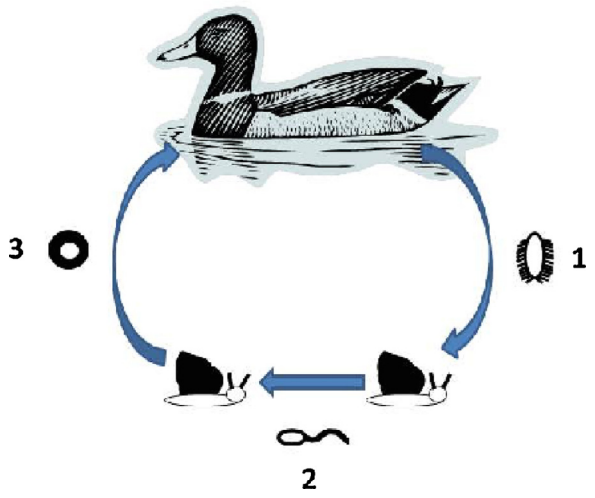

Fig. 1. Established life cycle *S. pseudoglobulus*. Numbers equate to parasite stages: (1) = miracidium; (2) = cercariae; (3) = metacercariae.

cases where temperature is explicitly incorporated into disease models, it either remains constant across seasons/years (Mangal et al., 2008) or is represented as a deterministic function (Ogden et al., 2008; Studer et al., 2013) which negates stochastic temperature changes over time. Stochastic differential-equation disease models have been developed for a number of systems (for example, see Allen, 2008; Andersson and Britton, 2000; Britton, 2010; Keeling and Rohani, 2008); however, few, if any (to our knowledge) have introduced temperature as a stochastic process into the model themselves.

Bithynia tentaculata is an invasive aquatic caenogastropod snail that is native to European freshwater systems (Bank, 2004). It was introduced to the Great Lakes in the late 1800s and since that time has spread to a number of freshwater systems throughout the region including the Upper Mississippi River (UMR). This has been a major concern as *B. tenetaculata* has the potential to negatively impact municipal water supplies and aquatic ecosystems (Mills et al., 1993). One of the key factors leading to community-level issues is that *B. tentaculata* harbors trematode parasites (such as *Sphaeridiotrema pseudoglobulus*) that generate pathology and mortality when transmitted to migrating birds, particularly lesser scaup (*Aythya affinis*). Waterfowl ingest the metacercariae while feeding (see Fig. 1). Metacercariae then develop into adult trematodes (flukes) within the infected hosts and produce eggs. Eggs are shed back into the environment via the bird's feces and eventually embryonate and hatch releasing a free-swimming miracidia. The larvae then infect *B. tentaculata* as the first intermediate host in the life cycle reducing snail reproduction within weeks of initial exposure. After a number of weeks, infected snails begin releasing large numbers of the second larval form of the parasite, a free-swimming cercariae (Sandland et al., 2013). Cercariae then infect snails as second-intermediate hosts and encyst as metacercariae (Sandland et al., 2013, 2014). When waterfowl consume infected snails, disease onset is rapid with hemorrhaging, shock, and death occurring within 3–8 days of initial exposure (Sauer et al., 2007).

Numerous waterfowl, including lesser scaup, migrating along the Mississippi River Flyway rely on aquatic snails as a key food source (Thompson, 1973). Consequently, infection and pathology occur during spring and fall migrations along the northern stretches of the Mississippi River. This pattern has been particularly well-documented in Navigation Pool 7 of the UMR which extends from Dresbach, MN upstream to Trempealeau, WI. Since *B. tentaculata*'s discovery in Pool 7 in 2002, a total of 15 bird species have been impacted during spring and fall migrations (Sauer et al., 2007). Reports suggest that thousands of parasite-related deaths annually are further stressing avian populations already in decline (Wilkins et al., 2007). Unfortunately, even though *B. tentaculata* and its parasites are potentially disrupting general ecosystem stability and economics in the upper Midwest of the United States, there is little known about the processes that underlie parasite persistence and waterfowl disease. This lack of knowledge severely limits our ability to (1) understand the interactions among *B. tentaculata*, parasite species, and waterfowl species, and (2) identify points in the parasite life cycles that are most important for their persistence in the UMR.

In this paper, we develop a mathematical model that reflects the transmission dynamics of a trematode species (*S. pseudoglobulus*) associated with waterfowl mortality in the UMR as it cycles through *B. tentaculata* and a common definitive host, the lesser scaup (*A. affinis*). Because interactions among these species vary across seasons (and likely, across years), and that these changes likely correspond with seasonal changes in water temperatures of the Mississippi River, we linked specific model parameters (such as parasite transmission) to water-temperature data collected for the UMR by the U.S. Army Corps of Engineers.

In our model we used Floquet analysis to investigate the stability of periodic solutions corresponding to host population sizes. Floquet analysis is a tool from dynamical systems which is a useful method for studying the effects of temporal variability on ecological systems (Klausmeier, 2008). After numerically (*Mathematica*, Wolfram Research, 2014) locating a point on the limit cycle and determining its period, we tested the stability of the limit cycle by asking if small perturbations away from the cycle grew or shrank over a complete period. This is equivalent to finding the stability of the linear system formed by linearizing the model equations about the limit cycle solution. Stability was identified if the largest eigenvalue of the Jacobian of the Poincare map occured inside the unit circle in the complex plane.

Because a deterministic temperature function can limit our ability to capture the range of seasonal infection patterns in the UMR, we also included random annual temperature values into the model. This approach is rarely considered in models predicting the responses of wildlife disease in the face of global climate change. Repeated model simulations demonstrated a temperature-threshold effect on host infection patterns.

2. Methods

2.1. A year-long transmission cycle

The model presented below reflects general temperature-dependent seasonal patterns (see Fig. 2) exhibited by waterfowl, *B. tentaculata*, and one of its trematode parasites (*S. pseudoglobulus*) in Pool 7 of the UMR. Lesser scaup arrive after ice-off in the spring, remain on the Pool for 3–4 weeks, and then move northwards to their breeding grounds as water temperatures rise. In the fall, the waterfowl return, remain on Pool 7 for 3-4 weeks, and then continue southwards prior to ice-on (US Fish and Wildlife Service Data).

Throughout the year, we assume that parasites exhibit temperature-dependent transmission patterns with no transmission occurring when temperatures either fall above or below specified temperature thresholds. Although specific temperature-dependent patterns of parasite release are not known for *S. pseudoglobulus*, there is substantial empirical evidence from other snail–trematode systems that such responses are common (Schmidt and Fried, 1996; McCarthy, 1999; Thieltges and Rick, 2006; Morley et al., 2010). In these studies, parasite transmission exhibited a consistent parabolic pattern, where parasite transmission was highest at ~20°C and decreased at lower (10–15°C) and

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