Temperature-driven population abundance model for *Culex pipiens* and *Culex restuans* (Diptera: Culicidae)*

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ABSTRACT We develop a temperature-driven abundance model of ordinary differential equations (ODE) for West Nile vector species, *Culex* (*Cx.*) *pipiens* and *Cx. restuans*. Temperature dependent response functions for mosquito development, mortality, and diapause were formulated based on results from available publications and laboratory studies. Results of model simulations compared to observed mosquito trap counts from 2004-2015 demonstrate the ability of our model to predict the observed trend of the mosquito population in the Peel Region of southern Ontario over a single season. The model could potentially be used as a real-time mosquito abundance forecasting tool with applications in mosquito control programs.

Key words: West Nile virus, Culex, mosquito, abundance, temperature, surveillance, population, trap data, simulations

1. Introduction

Vector-borne diseases account for more than 17% of all infectious diseases worldwide and cause more than 1 million deaths annually (World Health Organization 2014). In particular, mosquito-borne diseases constitute a large portion of these diseases and pose a higher risk to humans due to the availability of breeding sites in close proximity to human settlements. Understanding the relationship between environmental factors and their influence on vector biology is imperative in the fight against vector-borne diseases such as dengue, zika, malaria, and West Nile virus (WNV). Since the first appearance of WNV in New York in 1999 (CDC, 1999a, 1999b), the disease has rapidly spread across the North American continent to establish itself as a seasonal endemic infection. The continued risk to the human population prompted the establishment of annual surveillance programs to monitor virus infection in mosquito populations. In regions where these mosquito-borne diseases are prevalent, the primary strategy for decreasing the risk of human infection is the implementation of mosquito control methods.

The transmission of mosquito-borne pathogens is dependent upon many factors, from weather conditions and available breeding sites to host immunity. Environment factors such as temperature and precipitation have been shown to have significant impact on mosquito biology and consequently the disease transmission dynamics (Bowman et al., 2005; Cailly et al., 2012; Gong et al., 2010; Kunkel et al., 2006). Studies on mosquito development have shown that the surface

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water temperature has significant influence on the rate of development and mortality (Eldridge et al., 1976; Spielman 2001; Shelton 1973; Madder 1983; Rueda et al., 1990; Lounibos et al., 2002; Bayoh and Lindsay 2003; Loetti et al., 2011; Ciota et al., 2014; Jetten and Takken 1994). Understanding the relationship between temperature and mosquito biology is critical to the planning and implementation of mosquito control strategies that can decrease the risk of disease outbreak.

There have been numerous studies that investigate the impact of environmental conditions on mosquito population dynamics (Ahumada et al., 2004; Cailly et al., 2012; Otero et al., 2006; Shaman et al., 2006; Tachiiri et al., 2006; Wang et al., 2011). Tachiiri et al., (2006) created a raster-based mosquito abundance map for two species, *Culex (Cx.) tarsalis* and *Cx. pipiens*, which allowed them to identify areas of greatest potential risk of WNV in British Columbia, Canada. Cailly et al., (2012) developed a generic climate-driven mosquito abundance model that could be run over several years. Their model identified several potential control points in the biological system of mosquitoes that could be used to reduce the risk of mosquito-borne disease outbreak. Otero et al., (2006) developed a temperature driven stochastic population model for the species *Aedes aegypti* and identified temperature and environmental conditions that are needed for the survival of a local population of mosquitoes in a temperate climate.

Various approaches have been used to model the effect of temperature on the different stages of the mosquito life cycle. For example, some ODE models use temperature dependent development rate functions to determine the instantaneous rate of development at any given time (Cailly et al., 2012; Lana et al., 2011). Gu and Novak (2006) developed a stochastic phenological model which calculated temperature dependent probabilities of individuals residing in larval, pupal, and emerging adult stages. A drawback of using these types of functions to model mosquito development is their limitation to capture certain population dynamics such as sudden population increases caused by weather patterns that allow for the simultaneous eclosion of multiple generations. A number of studies also include a temperature dependent mortality function for immature mosquitoes. These functions calculate daily mortality rates based on the temperature experienced by developing mosquitoes on a single day (Otero et al., 2006; Shaman et al., 2006; Tachiiri et al., 2006); however, in a more natural setting, daily temperatures can often fluctuate and immature mosquitoes can survive exposure to high or low temperatures for short periods of time without significant impact on their mortality (Bayoh and Lindsay, 2004). Thus, mortality rates can potentially be overestimated when applied to a location that exhibits a wide range of day to day variability in temperature. In contrast, studies that use constant mortality rates are also subject to diminished model performance when applied to areas that experience large fluctuations in seasonal temperatures. An often neglected but critical factor in mosquito population dynamics is the diapause phenomenon. Environmental conditions trigger a physiological response in developing mosquitoes which enables them to survive harsh winter conditions in a form of metabolic dormancy until more favorable conditions induce their emergence in the following season (Denlinger and Armbruster 2014). Exclusion of this phenomenon may cause an overestimation of the active mosquito population in model simulations during the middle and later months of the mosquito season when diapause destined mosquitoes begin seeking shelter for the upcoming winter months (Gong et al., 2010). Some of the models that do account for diapause consider photoperiod alone to determine the fraction of diapausing mosquitoes (Gong et al., 2010; Cailly et al., 2012) although it has been shown that the proportion of mosquitoes destined for diapause is influenced by temperature (Eldridge 1966; Madder et al., 1983; Spielman 2001).

In this study, we focus on the aspects of mosquito biology that are primarily influenced by temperature: aquatic development, mortality, and diapause. Based on the results of existing studies on the temperature dependence of mosquito biology, we formulate response functions for these key aspects of the mosquito life cycle. These functions are used in a set of coupled differential equations that track mosquitoes throughout their aquatic and adult life. The model is designed to simulate *Cx. pipiens* and *Cx. restuans* population dynamics over a single season. To demonstrate the capacity of our model to describe the observed trend of mosquito abundance in a given area, we apply the model to the Peel Region in southern Ontario using mosquito surveillance data from 2004-2015. Simulation results showed the model could capture the general trend of observed mosquito surveillance data for the majority of years. The proposed model has potential to be used as a real-time mosquito abundance forecasting tool having direct application in mosquito control programs. The model can also be used to study the transmission dynamics of mosquito-borne diseases.

2. Materials and Methods

2.1. Study Area

The Regional Municipality of Peel (also known as Peel Region) is a regional municipality in southern Ontario, Canada, residing on the north shore of Lake Ontario with a total population of 1,296,814 (2011 census) and a total area of 1,246.89 km^2. It consists of three municipalities to the west and northwest of Toronto: the cities of Brampton and Mississauga, and the town of Caledon, as well as portions of the Oak Ridges Moraine and the Niagara Escarpment, 3,270 ha of wetland (2.6% of land area), and 41,329 ha of farmland (33% of land area) (Wang et al., 2011). The four seasons in the region are clearly distinguished. Spring and autumn are transitional seasons with generally mild or cool temperatures with alternating dry and wet periods. Summer runs from June until mid-September with an average monthly temperature of 20°C for the warmest months of July and August. Temperatures during summer can occasionally surpass 32°C.

2.2. Surveillance Program and Mosquito Data for the Peel Region, Ontario

Mosquito surveillance in southern Ontario was started in 2001 by the Ministry of Health and Long-Term Care (MOHLTC). The Peel Region Health Unit used the Centers for Disease Control (CDC) miniature light trap (Service, 1993) with both CO_2 and light to attract host-seeking adult female mosquitoes. Adult mosquitoes were trapped weekly from mid-June to early October (usually weeks 24-39), and the continuous observation for each trap started in 2004. Traps are set up on one day each week and allowed to collect mosquitoes overnight until the traps are collected the next day. Trapped mosquitoes were identified to species and counted, except for *Cx. pipiens* and *Cx. restuans*, which were combined into one group and counted due to the difficulty in distinguishing the species. Except for year 2002, mosquito abundance in 2003-2015 was measured during a period of active larval control in catch basins and surface water sites (dominated by ditches and culverts or woodland pools). During each mosquito season, there were four rounds of larval mosquito control in non-surveillance based catch basins. Larval control was conducted using either methoprene pellets/briquets or Bacillus sphaericus. However, larviciding in surface water sites was surveillance based and conducted by applying B. sphaericus and Bacillus thuringiensis variety israelensis (Peel Public Health 2009). Larviciding was not done in 2002 (Wang et al., 2011).

As was done in Wang et al. (2011), we used the average mosquito counts from the 30 trap locations to represent the mosquito population at the regional level. For each trap, the original count was smoothed over preceding and succeeding weeks: $W_j = \frac{w_{j-1} + w_j + w_{j+1}}{3}$, where w_j is the original mosquito count in week j, and W_j is its smoothed value for the week that reduces random effects such as moonlight or wind on capture probabilities (Service 1993). Year to year variability exhibited in mosquito trap counts over the same area is likely due to the seasonal fluctuations of temperature and precipitation in the region. Furthermore, during some weeks within a given year certain traps are observed to capture a disproportionate number of mosquitoes relative to other traps in the area. This presents a challenge to modeling population dynamics of mosquitoes for this region and will be considered in the analysis of model performance.

2.3. Temperature Data

Mean daily temperature data for the Peel Region were obtained from Canada's National Climate Archive (www.climate.weatheroffice.gc.ca). Among the three weather stations in Peel Region having temperature records available (Pearson International Airport, Georgetown, and Orangeville), we used the data collected from Pearson International Airport to represent the temperature conditions for the Peel Region as they had no missing data (Wang et al., 2011).

2.4. Mosquito Biology and Related Factors

The mosquito life cycle consists of three successive aquatic juvenile phases (egg, larvae, and pupae) and one aerial adult stage (Fig. 1). Depending on the surface water temperature, it usually takes 1–3 weeks from the time the egg is laid until emergence to the adult stage (Madder 1983; Rueda et al., 1990; Shelton 1973; Spielman 2001). Adult female mosquitoes generally mate within the first few hours of emergence then seek a blood meal to provide a protein source for their eggs. After feeding, the female seeks out a sheltered place to rest for a few days while her eggs develop. Once the eggs are fully developed, the female oviposits her eggs on a raft of 150-350 eggs on the surface of standing water (Madder et al., 1983). The adult female then proceeds to find another blood meal and repeat the gonotrophic cycle (EPA, 2017). During winter months, nulliparous inseminated female mosquitoes can enter into a state of diapause for the duration of the winter until climate conditions are conducive for their re-emergence in the spring. The induction of diapause begins during the mosquito season and depends on the number of daylight hours and temperature experienced by mosquitoes in the fourth larval instar and pupal stages of development (Denlinger and Armbruster, 2014).

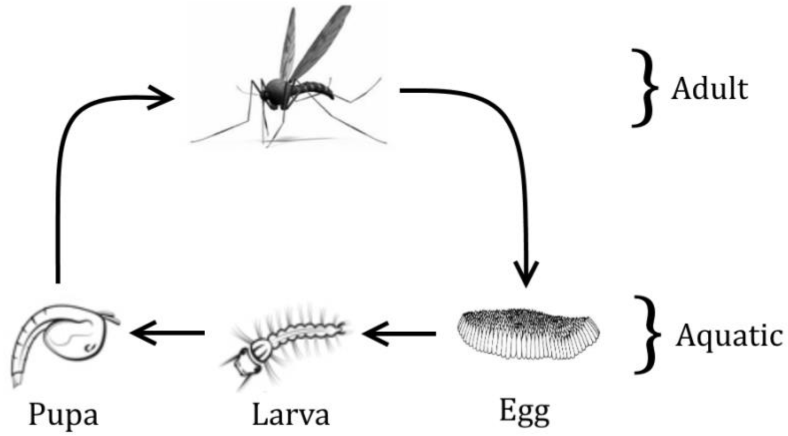

Figure 1 – The mosquito life cycle consists of three aquatic stages and one terrestrial adult stage.

2.5. Modelling *Cx. pipiens* and *Cx. restuans* abundance

We developed a model composed of ODEs to study the impact of temperature on the temporal dynamics of the mosquito population in the Peel region of southern Ontario. The model was designed to encompass both immature and adult stages of mosquitoes by separating the life cycle into two distinct stages: aquatic stage (eggs, larvae, and pupae) and adult stage. Only female mosquitoes will be modelled as male mosquitoes do not take blood meals and are not carriers of WNV. Following the method of Shaman et al., (2006), we assume the mosquito life cycle will proceed continuously. Eggs are deposited directly on breeding waters and immediately proceed through development. The total amount of eggs oviposited in a single day is determined by the total number of adult mosquitoes across all cohorts multiplied by the oviposition rate α. All eggs oviposited on the same day are grouped into the same cohort which are identified and labelled by the day of oviposition. Once a cohort of eggs is oviposited, there is no other recruitment into that cohort population. Aquatic mosquito populations are diminished by a temperature dependent mortality rate and by eclosion. Adult mosquitoes are assumed to live a maximum of ω days after eclosion and are diminished with a temperature dependent mortality rate $\mu_a(T)$. Time t is assumed to be integer-valued with a time-step of 1 day. We assume that mortality occurs at the beginning of each time-step and reproduction occurs at the end of each time-step. Hence, on the day adult mosquitoes reach their maximum lifespan they die without reproducing.

The notation $M_{s,n}(t)$ is used to identify both aquatic and adult mosquito populations at time t and by cohort born on day n. The subscript s indicates the life cycle stage (l = aquatic stage and a = adult stage). The time ranges from the first to last day of the study period $t \in [t_0, t_{end}]$ based on an annual interval of 365 days. Similarly, the discrete cohort index n also ranges from the first to last day of the study period $n \in [t_0, t_{end}]$. Each mosquito cohort is tracked throughout its lifetime through both aquatic and adult stages from oviposition to death, i.e. $M_{a,n}$ represents the female mosquitoes that have eclosed from the corresponding aquatic cohort $M_{l,n}$.

For aquatic development, the model employs the concept of degree days (DD) to track the physiological age of developing mosquitoes. This method of tracking temperature dependent development has been applied in a variety of ways in existing models (Craig et al., 1999; Jetten and Takken 1994; Tachiiri et al., 2006). Degree days are calculated (Eq. 1) by measuring the accumulated thermal units above a zero-development threshold temperature.

$$DD(t) = \begin{cases} 0, & if\ T(t) \leq T_e, \\ T(t) - T_e, & if\ T(t) > T_e, \end{cases} \tag{1}$$

where $T(t)$ is the mean temperature °C on day t. The parameter T_e is the minimum temperature threshold below which development is halted. The total number of DDs required for a cohort of larva to be fully developed into adults is denoted by T_{DDe}. Empirical functions that describe the relationship of temperature and development time generally take the following form (Craig et al., 1999):

$$df_n(t) = \frac{max\ (T(t)-T_e, 0)}{T_{DDe}} = \frac{DD(t)}{T_{DDe}}, \tag{2}$$

where $df_n(t)$ is the proportion of T_{DDe} accumulated on day t by a cohort born on day n. The function $f_n(t) = \sum_{k=n}^{t} df_n(k)$, tracks the cumulative development of each cohort. When a cohort accumulates a sufficient number of DDs, the cohort will eclose into adults (Eqs. 6 and 7). The day of eclosion, denoted t_n, for a cohort born on day n is given by $t_n = t$ when $f_n(t) \geq 1 > f_n(t-1)$. A model diagram of the mosquito life cycle is depicted in Fig. 2.

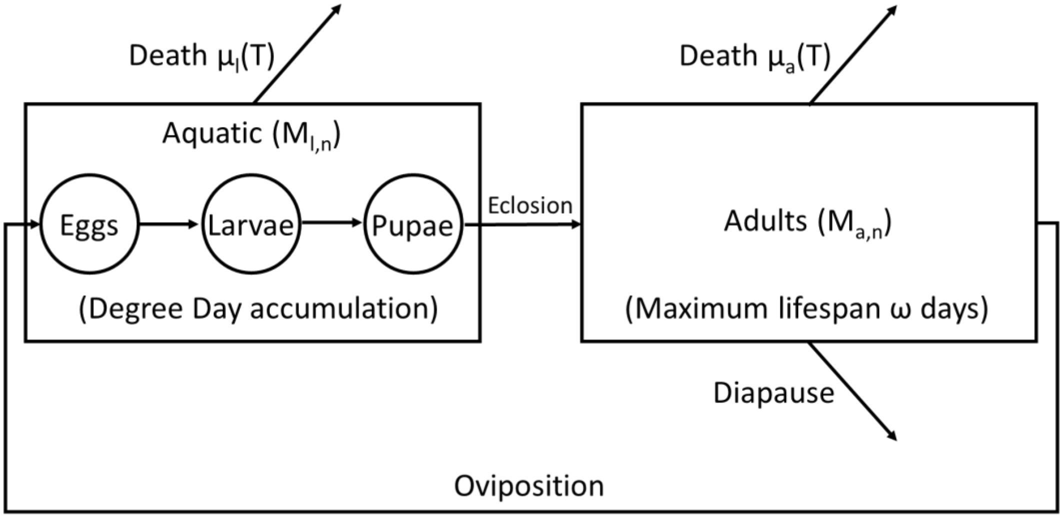

Figure 2 - Model diagram describing the *Cx. pipiens* and *Cx. restuans* life cycle. The number of eggs oviposited into a cohort ($M_{l,n}$) on any day is the total number of adult mosquitoes multiplied by the daily oviposition rate. Once a cohort accumulates enough DDs to complete development, all members of that cohort will simultaneously eclose into adults. Adults lay eggs on a daily basis until they die at most ω days after eclosion.

The model is composed of a system of multiple coupled ODEs to track population cohorts born on any given day throughout the study period. The ODE system for each cohort is given below:

$$\frac{dM_{l,n}(t)}{ds} = -\mu_l\big(T_l(t)\big)M_{l,n}(s), \qquad while\ \ f_n(t) < 1\ and\ t \leq s < t+1, \tag{3}$$

$$\frac{dM_{a,n}(t)}{ds} = -\mu_a\big(T(t)\big)M_{a,n}(s), \qquad while\ \ f_n(t) > 1\ and\ t \le s < t+1, \tag{4}$$

where $\mu_l(T_l(t))$ is the temperature dependent aquatic mortality rate. Aquatic mortality rates are calculated based on a two-day average daily temperature, denoted $T_l(t)$, to reduce the impact of daily temperature fluctuations on the survival of developing mosquitoes.

Boundary conditions defining critical events such as oviposition, eclosion, and maximum adult lifespan are defined by the following.

Oviposition:

The number of eggs oviposited on any day *t* equals the total number of adults that are at least one day old (since eclosion) on that day multiplied by the oviposition rate α. Adults that reach their maximum lifespan die on that day before reproducing. The number of eggs oviposited on day *t* is

$$M_{l,t}(t) = \ \alpha \sum_{n=t_0}^{t-2} M_{a,n}(t). \tag{5}$$

Eclosion:

Upon eclosion, the variable tracking a cohort of aquatic mosquitoes will equal zero (Eq. 6) and the active host-seeking proportion of emerging adults will be initiated (Eq. 7).

$$M_{l,n}(t) = 0, \qquad \text{when } t = t_n, \tag{6}$$

$$M_{a,n}(t) = e^{-\mu_l(T)}\gamma_n(T_n,P_n)M_{l,n}(t-1), \qquad \text{when } t = t_n, \tag{7}$$

where the function $\gamma_n(T_n,P_n)$ represents the proportion of non-diapausing emerging adult female mosquitoes. Function arguments T_n and P_n represent the temperature and photoperiod developing mosquitoes experience during the final 20% of aquatic development, respectively. Formulation of the function $\gamma_n(T_n,P_n)$ is explained in detail in Section 2.6.3.

Adult Lifespan:

All remaining adults in a cohort die before reproducing ω days after eclosion:

$$M_{a,n}(t) = 0, \qquad if\ \ t - n - \tau_n = \omega, \tag{8}$$

where $\tau_n = t_n - n$ is the total number of days to complete development for the cohort born on day n.

2.6. Model Functions and Parameters

Temperature dependent response functions for aquatic development, mortality, and diapause were developed a priori and locally tuned for *Culex* mosquitoes in the study area. Model parameters were based on the most relevant data from existing literature. Definition, value, and dimension of model parameters and variables are given in Tables 1 and 2, respectively.

Table 1: Definitions, values, dimensions, and sources of model parameters

Parameter	**Description**	**Value (Range)**	**Dimension**	**Source**
t	Time-step of 1 day (integer-valued)	$t \in [t_0, t_{end}]$	day	
n	Cohort index and day of oviposition	$n \in [t_0, t_{end}]$	day	
α	Oviposition rate	0.125 (0.036–42.5)	day^{-1}	[5]
μ_{op}	Aquatic mortality rate at optimal temperature of development T_{op}	0.015	day^{-1}	[1-4], [6-9]
ω	Lifespan of adult mosquito	28	day	[5]
m_{14}	Slope of diapause function $\gamma_n(T_n,P_n)$ for 14 daylight hours	0.0375	-	[1]
$m_{14.75}$	Slope of diapause function $\gamma_n(T_n,P_n)$ for 14.75 daylight hours	0.05625	-	[1]
a	Scale factor for $\mu_l(T)$ when $T_l(t) < T_{op}$	1/25,000	-	
b	Scale factor for $\mu_l(T)$ when $T_l(t) \geq T_{op}$	3/1,000	-	
T_e	Minimum temperature at which larva can develop	9	°C	[1-4], [6-8]
T_{op}	Optimal temperature for development	25	°C	[1], [4], [6], [7], [9]
T_{DDe}	Number of DDs required to complete aquatic stage of development	149	°C	[3], [6-8]

Sources: [1] Madder et al., 1983 [2] Tachiiri et al., 2006 [3] Jetten and Takken, 1994 [4] Rueda et al., 1990 [5] Wonham et al., 2004 [6] Bayoh and Lindsay, 2004 [7] Loetti et al., 2011 [8] Gong et al., 2010 [9] Ciota et al., 2014

Table 2: Definitions, values, dimensions, and sources of model variables

Variable	Description	Value (Range)	Dimension	Source
$DD(t)$	Amount of degree days accumulated on day t.	Variable	°C	
$df_n(t)$	Proportion of T_{DDe} accumulated on day *t* by a cohort born on day *n*.	Variable	-	[7]
$f_n(t)$	Cumulative development time of a cohort born on day *n* up to time *t*.	Variable	-	[7]
t_k	The day of eclosion for a cohort born on day k i.e. $t_k = t$ when $f_k(t) \geq 1 > f_k(t-1)$	Variable	day	
τ_n	Total number of days to complete development for a cohort born on day *n*.	Variable	day	
$T_l(t)$	Two-day mean temperature used to calculate aquatic mortality $T_l(t) = \frac{T(t)+T(t-1)}{2}$	Variable	°C	
P_n	Photoperiod of the day 4th larval instar begins for a cohort born on day *n* to determine the induction of diapause (4th larval instar assumed to begin when 80% of aquatic development is complete).	Variable (12-14.75)	hours	[1], [10], [12], [13]
T_n	Mean daily temperature while in 4th larval instar and pupal stages of development for a cohort born on day *n* to determine the incidence or rate of diapause (4th larval instar assumed to begin when 80% of aquatic development is complete).	Variable	°C	[1], [10], [12], [13]
$\gamma_n(T_n,P_n)$	Proportion of non-diapausing adult female mosquitoes at time of eclosion	Variable (0-1)	-	[1], [10], [12], [13]
$\mu_l(T)$	Temperature dependent aquatic mortality rate	Variable	day^{-1}	[1-4], [5], [6], [8], [9]
$\mu_a(T)$	Temperature dependent adult mortality rate	Variable	day^{-1}	[14]
$T_l(t)$	Two day mean temperature of days *t* and *t*-1 for the purpose of calculating temperature dependent aquatic mortality rate on day *t*.	Variable	°C	[11]

Sources: [1] Madder et al., 1983 [2] Tachiiri et al., 2006 [3] Jetten and Takken 1994 [4] Rueda et al., 1990 [5] Bayoh and Lindsay 2004 [6] Loetti et al., 2011 [7] Craig et al., 1999 [8] Gong et al., 2010 [9] Ciota et al., 2014 [10] Eldrige 1966 [11] Canada's National Climate Archive [12] Spielman 2001 [13] Edillo et al., 2009 [14] Cailly et al., 2012

2.6.1. Aquatic Development

There are several commonly used functions of temperature to model development rates for a variety of animals and insects, e.g. Logan, Holling, Briere, Lactin, Sharpe de Michelle, and Degree Days. Of those mentioned above, the Degree Day model is the only linear function. We chose the linear Degree Day model as it provides a straightforward and accessible method of estimating development rates. Although in some cases the linear model may tend to underestimate development rates at low temperatures and overestimate development rates at high temperatures, the mean daily temperatures in the Peel Region over the study period (June-September) generally range from 17°C to 22°C (Canada's National Climate Archive) which is well within the temperature range of 15°C-30°C (Fig. 3) in which the linear approximation is valid for the *Cx. pipiens* and *Cx. restuans* species.

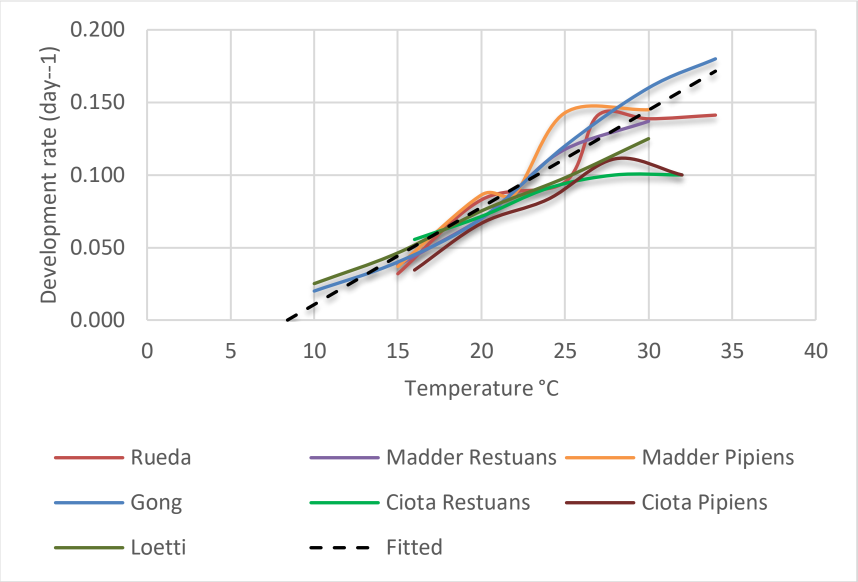

Figure 3 – Temperature dependent development rates for aquatic stage mosquitoes according to laboratory studies. The dashed black line shows the linear regression estimate of the zero-development threshold temperature, T_e=8.4°C. The dashed red line shows the adjusted regression line that was locally tuned for the Peel Region in southern Ontario where T_e=9°C. The equation for the development rate per day is $\boldsymbol{df_n(t)} = \frac{\boldsymbol{max(T(t)}-9,0)}{149}$.

Figure 3 displays the results of multiple laboratory and field studies on temperature dependent development for *Culex* mosquitoes (Madder et al., 1983; Rueda et al., 1990; Loetti et al., 2011; Gong et al., 2010; Ciota et al., 2014). A linear regression through the data points from the studies was used to estimate parameters T_e and T_{DDe}. The linear regression estimated a minimum threshold temperature of T_e=8.4°C, and a total number of degree days to emergence of T_{DDe} =144°C. Previous studies specific to southern Ontario (Wang et al., 2011) have used a minimum threshold temperature of 9°C. Adjusting the original estimate of the fitted regression line to reflect a minimum threshold temperature of T_e=9°C yields a total number of degree days to emergence of T_{DDe} =149°C. The function for the proportion of development on day *t* is given by

$$df_n(t) = \frac{max\ (T(t)-9,0)}{149}. \tag{9}$$

2.6.2. Mortality

In addition to mosquito development, temperature also has a significant impact in the survival of mosquitoes throughout their life-cycle. Results from a study by Shelton (1973) showed that the temperature associated with the fastest rate of development was generally greater than the temperature at which the survival rate is highest. The effect of temperature on larval mortality is primarily observed at higher temperatures where high development rates are accompanied by high mortality rates (Bayoh and Lindsay, 2004; Jetten and Takken, 1994; Loetti et al., 2011; Madder et al., 1983; Meillon et al., 1967; Rueda et al., 1990). Furthermore, when exposed to higher temperatures for prolonged periods, developing mosquitoes that do survive until adulthood experience adverse effects on their biological development e.g. wing length, follicle length, and adult mass, that decrease the likelihood of survival and successful reproduction (Ciota, 2014). In their natural environment, mosquitoes are not significantly affected by high temperatures when exposed for no more than a few hours during the day (Shelton, 1973). In contrast, colder temperatures closer to the lower development threshold act more as an inhibitor to larval development rather than causing high mortality (Bayoh and Lindsay, 2003). Laboratory studies also show that the optimal temperature of development for Culex mosquitoes ranges between 24-26°C, where a higher rate of development corresponds with a low mortality rate (Madder et al., 1983; Loetti et al., 2011; Rueda et al., 1990; Shelton, 1973).

In practice, some models assume the mortality rate increases as temperature decreases. As a result, the shapes of the mortality curves resemble Gaussian or parabolic functions. For reference, several equations currently used to describe the functional relationship between temperature and mortality for developing mosquitoes are presented (Fig. 4).

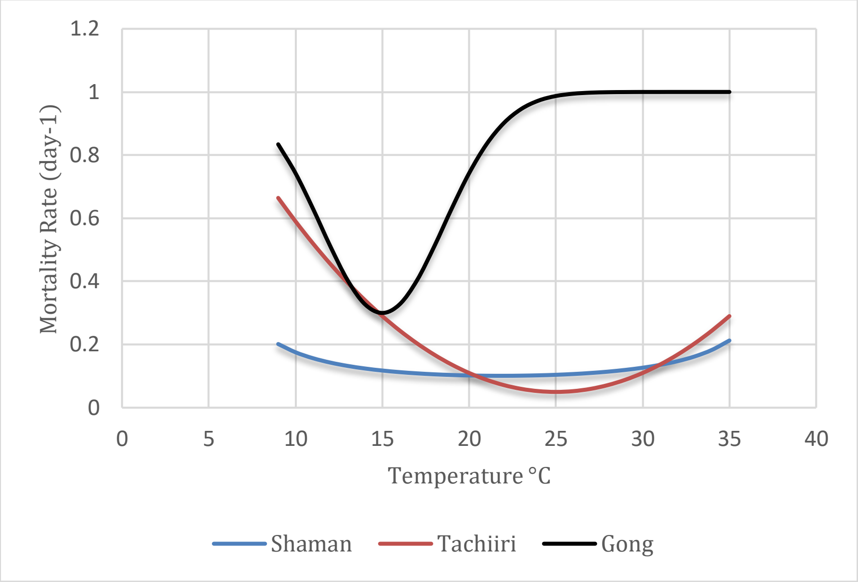

Figure 4 – Temperature dependent mortality rates used in existing studies: Shaman: $\mu=(-4.4+1.31T-0.03T^2)^{-1}$, Tachiiri: $\mu=(0.24(\boldsymbol{T}-\mathbf{25})^2+5)\%$, Gong: $\mu=1-0.7\boldsymbol{e}^{-(\frac{T-15}{5})^2}$ (Shaman et al., 2006; Tachiiri et al., 2006; Gong et al., 2010).

Based on the different responses observed at low and high temperatures, we develop a temperature dependent piecewise parabolic function to model the effect of temperature on developing mosquito mortality. Data obtained from these studies were not originally presented as daily mortality rates. They measured the fraction of individuals that survived the aquatic stage of development when reared at constant temperatures. These survival percentages were converted to daily mortality rates using the exponential model for population dynamics. The number of surviving larvae at time t is denoted by $L(t)$ and the initial number of larvae at the beginning of the experiment is L_0.

$$\frac{dL}{dt} = -\mu L, \text{ with initial condition } L(0) = L_0, \text{ has solution: } \quad L(t)=L_0 e^{-\mu t}$$

Solving for mortality rate μ for every temperature in each experiment yields:

$$\mu = -\frac{1}{t} \ln\left(\frac{L(t)}{L_0}\right), \tag{10}$$

The resulting mortality rates were then plotted (Fig. 5). We assumed the optimal temperature for development to be $T_{op} = 25°\text{C}$ which corresponds with the minimum mortality rate $\mu_{op} = 0.015$ (Madder et al., 1983). For the portion of the piecewise function below T_{op}, we selected the scale factor *a* which yielded the lowest root mean squared error (RMSE) between the estimated function and observed data. The scale factor *b* was determined in the same way for temperatures at and above T_{op}.

$$\mu_l(T_l) = \begin{cases} a(T_l(t) - T_{op})^2 + \mu_{op}, & \text{if } \; T_l(t) < T_{op}, \\ b(T_l(t) - T_{op})^2 + \mu_{op}, & \text{if } \; T_l(t) \geq T_{op}. \end{cases} \tag{11}$$

The resulting mortality rates from each study and the estimated mortality rate function $\mu_l\big(T_l(t)\big)$ are presented in Figure 5.

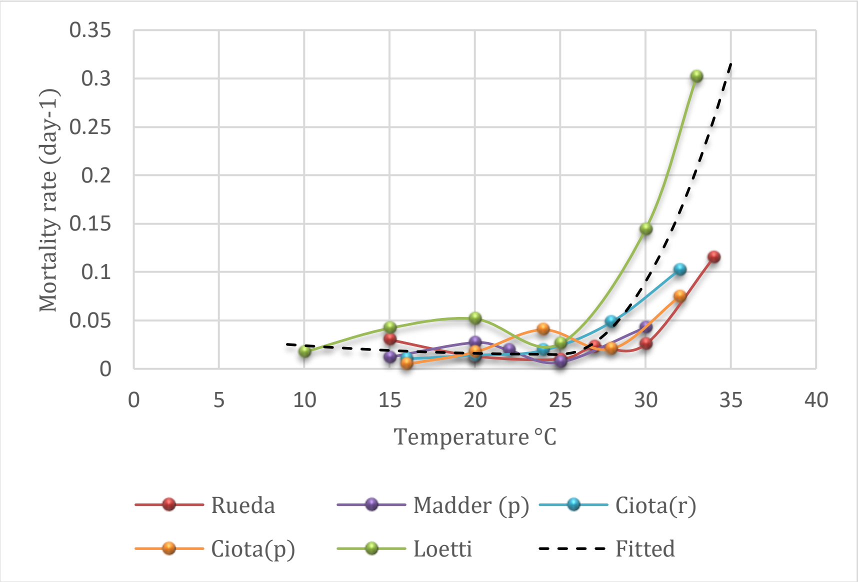

Figure 5 - Temperature dependent daily mortality rates based on results from available literature. The dashed line represents the model function used to fit these data and is given by equation (11).

The temperature dependent adult mortality rate function $\mu_a(T)$ was derived from Shaman et al., 2006 and adapted to *Culex* mosquitoes in southern Ontario.

$$\mu_a(T) = 0.000148T^2 - 0.00667T + 0.123 \tag{12}$$

2.6.3. Diapause

To survive unfavorable weather conditions during winter, many mosquito species undergo a hibernal dormancy called diapause (Denlinger and Armbruster, 2014). Depending on the species, most mosquitoes can overwinter in only one stage: egg, larval, or adult (Vinogradova, 2007). *Cx pipiens* and *Cx. restuans* mosquitoes diapause as adults. The primary environmental signal responsible for the induction of diapause is photoperiod (Eldridge, 1966). Photoperiod is defined as the interval in a 24-hour period during which a plant or animal is exposed to light, i.e., the number of daylight hours. Once the photoperiod falls below a photosensitive threshold a proportion of developing mosquitoes will undergo physiological and behavioral changes that equip them to survive the duration of winter (Eldridge et al., 1966; Spielman 2001; Vinogradova 2007). Diapause destined females begin to seek shelter soon after eclosion after mating and prior to taking a blood meal. While photoperiod is responsible for determining the induction of diapause, temperature has been shown to enhance the photoperiodic response by generating a higher incidence of diapause destined mosquitoes as temperature decreases (Eldridge et al., 1966; Madder et al., 1983). For *Cx. pipiens* and *Cx. restuans* mosquitoes the photosensitive stages most influenced by temperature are the fourth larval instar and pupal stages of development (Spielman and Wong, 1973). The study by Spielman (2001) found that the proportion of diapause destined mosquitoes is almost a linear function of photoperiod at a given temperature (Fig. 6).

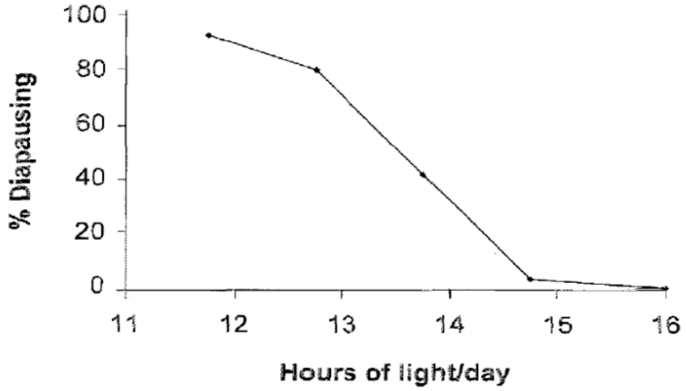

Figure 6 – Effect of photoperiod and temperature 18°C on diapause of blood-fed female mosquitoes reared under diapause inducing conditions (Spielman, 2001).

Exclusion of the effect of diapause can lead to an overestimation of the mosquito population late in the season when there should typically be a decline in the active host-seeking female mosquito population (Gong et al., 2010). Based on data obtained from Madder (1983), we developed a function (Eq. 13) that includes both temperature and photoperiod to estimate the proportion of non-diapausing adult female mosquitoes. In the region of study, the photoperiod corresponding to the observed disappearance of mosquitoes in late September to early October is approximately 12 daylight hours. The maximum photoperiod in the same region in any year is approximately 15.5 daylight hours which occurs in late June. We assumed a photoperiodic threshold of 14.75 daylight hours for the induction of diapause and a minimum photoperiod of 12 hours, below which all mosquitoes are assumed to diapause upon eclosion regardless of temperature. To be consistent with the degree day function for aquatic development (Eq. 1), we assume a lower temperature threshold of 9°C. For each photoperiod, a linear regression using 9°C as a fixed intercept was performed to estimate the proportion of non-diapausing mosquitoes within a range of temperatures. Based on these assumptions the function for non-diapausing mosquitoes is given by

$$\gamma_n(T_n, P_n) = \begin{cases} 1 & if \quad 14.75 < P_n \\ \left[m_{14} + (m_{14.75} - m_{14})\frac{P_n - 14}{0.75}\right](T_n - T_e) & if \quad 14 < P_n \leq 14.75 \\ \left[m_{14}\frac{P_n}{14}\right](T_n - T_e) & if \quad 12 < P_n \leq 14 \end{cases} \tag{13}$$

where m_p is the slope of the function $\gamma_n(T_n, p)$ for the photoperiod indicated by the subscript p (Table 1). The photosensitive stages of aquatic development are assumed to begin when $f_n(t) \geq 0.8 > f_n(t-1)$, i.e., when 80% of development is complete. The average of the mean daily temperatures during the final 20% of development is given by the variable T_n. The variable P_n represents the photoperiod for the day that the cohort completes 80% of development. The photoperiod for each cohort born on day n is obtained from a table containing the observed number of daylight hours for each day in the city of Toronto, Ontario for years 2004-2015 (USNO, 2017).

2.6.4. Overwinter Survival

In southern Ontario, mosquitoes spend major segments of the year in a state of diapause due to a long period of cold weather from fall to spring. The success of diapause has a direct effect on the size of the mosquito population the following season (Denlinger and Armbruster, 2014). There are many factors that affect the survival of diapausing mosquitoes such as temperature, precipitation, land cover, geographic location, and type of shelter. Although the overwintering process of various species of mosquitoes in different geographical contexts has been studied, the availability of applicable data is limited due to the complexity of this process. When more data becomes available on the overwintering process we can extend this model to cover multiple successive year to forecast mosquito abundance over longer periods of time.

3. Results

The model was designed so that temperature is the primary driving force behind mosquito population dynamics. Simulations are based on temperature data, observed or specified, as model input. As constructed, the model is deterministic and there is no stochasticity in model output. In Sections 3.1 and 3.2 we present model results based on controlled and observed temperature scenarios.

3.1. Temperature Scenarios

To study the underlying cause behind certain population dynamics observed in surveillance data (low/high mortality and population spikes) we test the model under controlled temperature scenarios. In the first scenario, we run the model at three constant temperatures to see how prolonged exposure to temperatures near the lower and upper temperature thresholds affect the mosquito population compared with the model when run at the optimal temperature for development T_{op}=25°C. In the second scenario we investigate how observed surveillance data often exhibits sharp increases in trap counts from one week to the next. We present one possible temperature pattern that replicates this type of behavior in Figure 8. Finally, we apply the model to the Peel region in southern Ontario using observed temperature data for years 2004-2015 (Fig. 9).

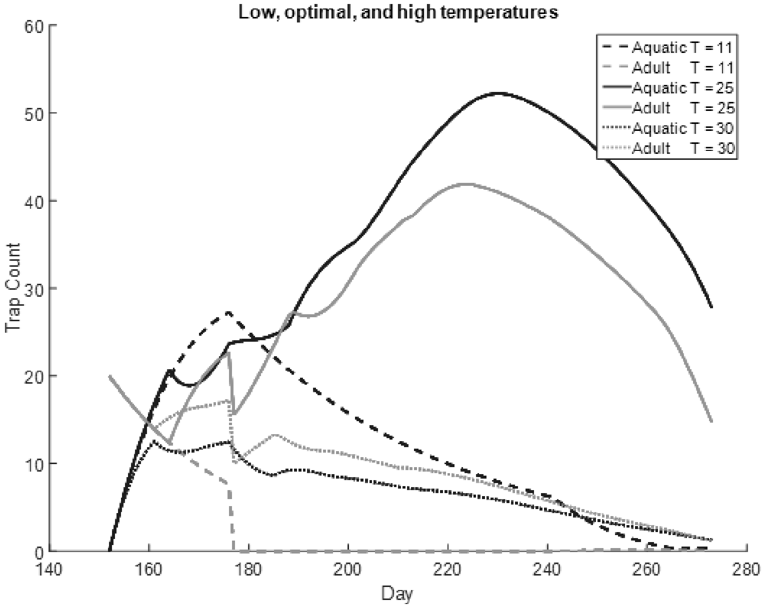

Figure 7 - Time series simulation at constant temperatures of T=11°C, T=25°C, and T=30°C.

Development and mortality rates of aquatic stage mosquitoes are dependent upon the temperature experienced during the aquatic stage. As previously mentioned, lower temperatures act more as an inhibitor to development and do not significantly affect mortality while temperatures near the upper temperature threshold cause a higher rate of mortality offsetting a higher rate of development. Figure 7 depicts simulation results of the model run at three constant temperatures 11°C, 25°C, and 30°C. For simulations run near the lower and upper threshold temperatures of 11°C and 30°C, the model performs as expected. At T=11°C, cohorts in the aquatic stage (black dashed lines) are unable to accumulate enough DDs to complete development before the end of the simulation. Consequently, there are no eclosions to increase the adult mosquito population (grey dashed lines) for the entire duration of the simulation. Near the upper temperature threshold at T=30°C a considerably shorter development time of 9 days is offset by the high mortality rate for developing mosquitoes. Hence both the aquatic (black dotted lines) and adult populations (grey dotted lines), experience a gradual decline in population until the end of the simulation. At the optimal temperature of development T_{op}=25°C the mosquito population achieves a maximum on approximately day 230 (mid-August) after which the population begins to decline due to the effect of diapause.

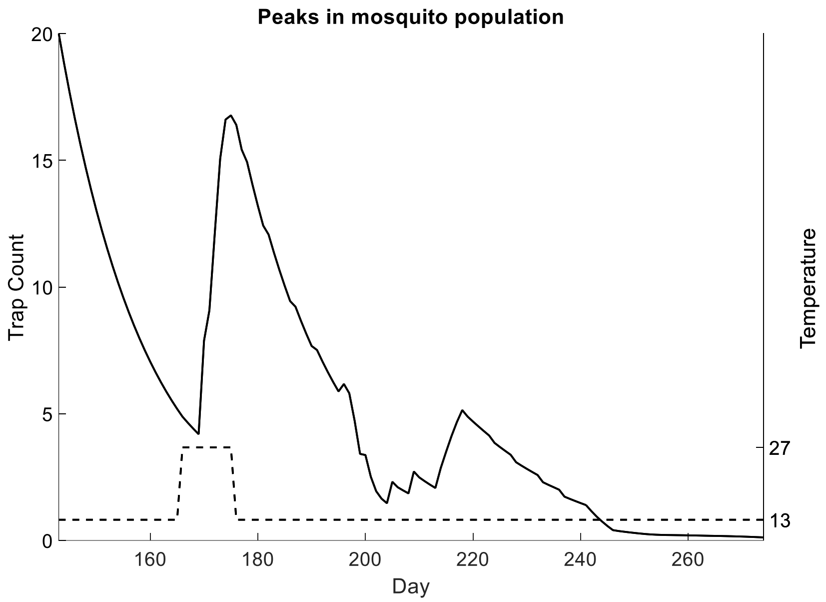

Figure 8 – Temperature pattern (dashed line, right axis) causing a peak in the mosquito trap count (solid line, left axis).

Surveillance data can sometimes exhibit sudden increases or peaks in the trap counts that can be caused by a number factors. In Figure 8, we present one plausible scenario that demonstrates how certain temperature patterns can produce a sudden increase in the mosquito population. In this scenario a period of cooler daily temperatures followed by a sudden and significant rise in temperature for several days causes multiple cohorts of larvae to eclose in rapid succession over a short period of time. Different cohorts oviposited during the cooler period prior to the sudden rise in temperature are accumulating small amounts of DDs each day. A sudden rise in temperature lasting for several days essentially synchronizes the time of eclosion of multiple cohorts that were oviposited on different days, causing a sharp increase in the mosquito population occurring on day 176.

3.2. Initial Conditions and Simulations

The model was applied to the Peel Region of southern Ontario. Simulations were run once for each year from 2004-2015 using observed temperature data (Fig. 9). Model performance was assessed based on the correlation between model outputs and mosquito surveillance data, the latter being the only quantitative data we have concerning the total mosquito population. Due to a lack of data on the overwintering process, we were required to estimate the initial conditions for the start date and number of adult female mosquitoes for each year. Based on the results of Shelton (1973), we assume that a seven-day average daily temperature above 14°C is sufficient to break hibernation and initiate the gonotropic cycle of overwintering adult female mosquitoes. Using this criterion, simulation start times began as early as day 112 (first week of May) up to day 150 (last week of May). All simulations were ended on day 274 (approximately September 30th) corresponding with the disappearance of mosquitoes and the last week of surveillance in the Peel region. Once the start date for each year was determined, initial values for adult mosquitoes were then estimated by first running a simulation for a given year with an initial value of adult mosquitoes set equal to 1. Initial values were then incremented by 1 and the simulation was repeated with the new initial value. For each simulation the root mean squared error (RMSE) of simulation vs observed surveillance data for the first 3 weeks was recorded. The initial value was then selected from the simulation run that yielded the lowest RMSE for the first 3 weeks of the study period for that year.

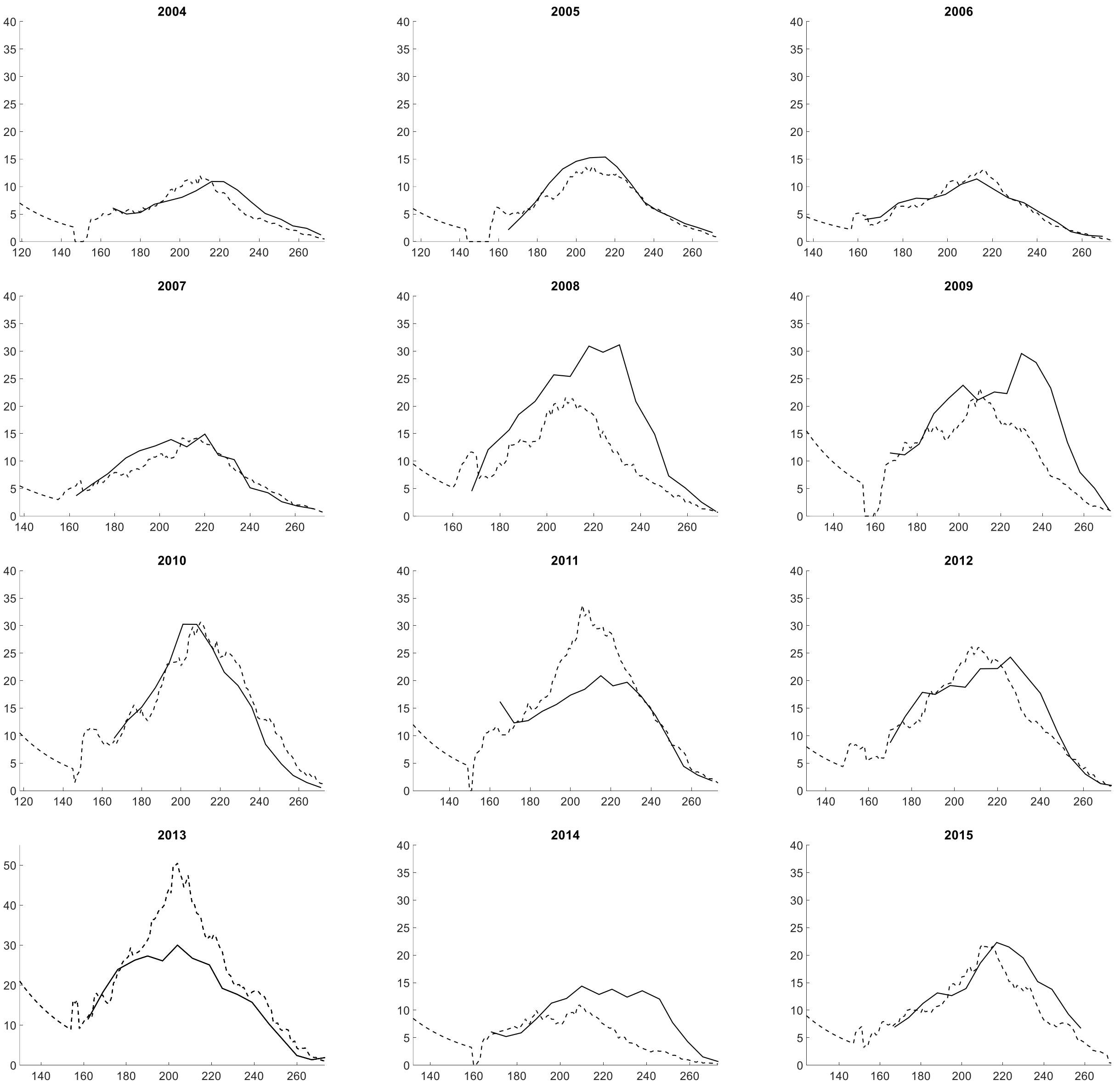

Figure 9 – Comparison of simulated trap counts (dashed line) vs observed surveillance data (solid line) for years 2004-2015.

3.3. Validation

The model adequately simulated the observed trend in the mosquito trap counts except for 2008, 2009, and 2014 where the model underestimated the observed trap counts and overestimated them in 2011 and 2013. As previously mentioned, the differences between model output and observed data may be due to the skewness in the surveillance data caused by a small number of traps capturing a disproportionately large number of mosquitoes relative to other traps in the area during certain weeks. To determine the cause of the disparity in capture amounts among traps requires further investigation and is planned for future modelling initiatives. Model performance during these years may also be due to factors other than temperature such as precipitation, landscape, and wind that may have a strong influence on mosquito population dynamics and capture rates. The study by Wang et al., (2011) demonstrated a correlation of mosquito abundance and the previous 35 days of precipitation. In comparison with the simulation results from their statistical model for years 2004-2009, we observed better overall performance of our model. Since our model is focused solely on the effect of temperature on mosquito abundance, consideration of other factors such as precipitation and land use (spatial) may improve model performance and will be included in future work.

4. Discussion

4.1. Contributions

We developed a temperature driven model of mosquito population dynamics to track the stages and processes in the mosquito life cycle most influenced by temperature. Our model simulates mosquito surveillance data for a single season and was applied to the Peel region of southern Ontario. Although the model was applied to a specific species in a certain geographical area, the structure of the model allows it to be adapted to other species of mosquitoes since the biological processes across different mosquito species are similar. Tuning the model would only require that parameter values and temperature dependent response functions be adapted to fit the species being studied.

The model divides the mosquito life cycle into two separate and distinct compartments where all aquatic stages of development are grouped together in one compartment and the adult stage in another. In this way the amount of accumulated temperature required to complete each stage of aquatic development from egg to pupa is untraceable. However, treating each stage as a separate compartment may provide improved model performance (Cailly et al., 2012; Tachiiri et al., 2006) since each stage can have a different minimum temperature of development.

The use of a degree day function to track the physiological development of aquatic mosquitoes is of primary importance as it enables the model to capture important dynamics such as sudden increases in the mosquito population due to certain temperature patterns. Moreover, modelling development using degree days allows for the addition of a mosquito control feature in the model to reduce the population of developing mosquitoes at specified times which would allow for the study of mosquito control effectiveness on population dynamics. This could be a useful tool in determining the effectiveness and timing of mosquito control measures.

Our results suggest that under certain environment conditions the mosquito population can be adequately predicted using temperature alone. However, the inability of the model to capture the observed dynamics of surveillance data in certain years indicates that additional variables need to be considered to account for the year to year variability in weather and other environmental factors. For example, in 2008 there was above average rainfall during the mosquito season while the daily temperatures remained within the seasonal averages. The abundance of rainfall during this year would have provided an ample amount of breeding sites for mosquitoes which is likely the cause of the model's underestimation of trap counts for this year.

4.2. Future work

Currently, the model is limited to forecasting mosquito abundance over a single season. Extending the study to include a model describing the overwintering process would enable simulations to be run over multiple years with one set of initial conditions for the first year. Then using short-term and long-term temperature forecasts as input in to the model we could potentially forecast mosquito abundance for future years based on a range of climate projections.

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