



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 for West Nile virus (WNV) vector species, *Culex pipiens* and *Culex restuans*. Temperature-dependent response functions for mosquito development, mortality, and diapause were formulated based on results from available laboratory and field studies. Numerical results compared to observed mosquito trap counts from 2004–2016 demonstrate the ability of our model to predict the observed trend of the mosquito population over a single season in the Peel Region, Ontario. The model has potential to be used as a real-time mosquito abundance forecasting tool with applications in mosquito control programs.

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1. Introduction

Since the first appearance of West Nile virus (WNV) in New York in 1999 (Centers for Disease Control and Prevention CDC, 1999a, 1999b), the mosquito-borne disease has rapidly spread across the North American continent establishing itself as a seasonal endemic infection (Sejvar, 2003; Reisen, 2013). By 2004, WNV had been detected in all states in the continental US; in 2002, the first WNV human infection was reported in southern Ontario, Canada and has since been detected in all provinces except Prince Edward Island and Newfoundland (Infection Prevention and Control Canada, 2017). As there is no vaccine or specific antiviral treatments for WNV infection (Centers for Disease Control and Prevention, 2017), the primary strategy for decreasing the risk of human infection is the implementation of mosquito control methods. In an era of climate change and global warming, it is increasingly important to understand how mosquito population dynamics are affected by changes in climate variables (temperature, precipitation, humidity, and wind) to inform public health policy in the effort to control the disease.

Mosquito population dynamics directly affects the transmission of mosquito-borne diseases such as WNV, Zika, malaria, dengue, and chikungunya (Beck-Johnson et al., 2013; Erickson et al., 2010; Gunaratne et al., 2016; Mordecai et al., 2017; Shaman and Day, 2007). Mosquitoes are exotherms, and thus are highly sensitive to changes in ambient temperature. The effect of temperature on mosquito biology (development, mortality, life-history traits, diapause, and oviposition) has been studied extensively and remains a topic of intense research (Ciota et al., 2014; Eldridge et al., 1976; Kiarie-Makara et al., 2015; Madder et al., 1983; Nasci et al., 2001; Paaijmans and Thomas, 2011; Shelton, 1973; Spielman, 2001). Application of the knowledge gained from these studies in mathematical models enable us to gain a more realistic and qualitative understanding of the relationship between temperature and mosquito biology as well as help to identify the mechanisms that drive their population dynamics.

A substantial number of mathematical and statistical models have been developed to assess the influence of climate variables, such as temperature and precipitation, on the population dynamics and behavior of various mosquito species (Ahumada et al., 2004; Cailly et al., 2012; Cochran and Xu, 2012; Ezanno et al., 2015; Gong et al., 2010; Gu and Novak, 2006; Otero et al., 2006; Tran et al., 2013; Wang et al., 2011; Yoo et al., 2016). Tachiiri et al. (2006) created a raster-based mosquito abundance map for two species, *Culex* (*Cx.*) *tarsalis* and *Cx. pipiens*, which

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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. Spatio-temporal dynamics of mosquito host-seeking behavior were examined in the study by Cummins et al. (2012), where they developed an agent-based/continuum model to explore the effect of behavioral decisions and spatial heterogeneity on the contact rate between mosquito vectors and bird hosts. The study by Gunaratne et al. (2016), used agent-based modeling to describe the population dynamics of Zika vector *Aedes aegypti* subjected to spatial and climatic constraints. Wang et al. (2011) developed a predictive statistical model for mosquito abundance which defined threshold criteria for temperature and precipitation conditions for the population growth of WNV vector species *Cx. pipiens* and *Cx. restuans*. The model developed by Yoo et al. (2016), used harmonic analysis and kernel density estimation as a means of examining the associations with major landscape predictors, including land-use type, population density, and elevation, on the spatial patterns of mosquito abundance.

In the studies that account for temperature, various approaches have been used to model the effect of temperature on the mosquito life cycle. For example, some dynamical models use temperature-dependent development rate functions (Abiodun et al., 2016; Cailly et al., 2012; Lana et al., 2011) to determine the instantaneous rate of development at each time-step. Gu and Novak (2006) developed a stochastic phenological model which calculated probabilities of individuals residing in larval, pupal, and emerging adult stages as a function of temperature. A drawback of using instantaneous rate 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. Some studies also estimate the daily mortality rate of developing mosquitoes based on the ambient temperature for a single day (Ewing et al., 2016; Otero et al., 2006; Shaman et al., 2006; Tachiiri et al., 2006); however, 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 in temperate climates that experience a wide range of diurnal temperature fluctuations.

An often neglected, but important 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 latter half of the mosquito season when diapause destined mosquitoes begin seeking shelter for the upcoming winter months (Gong et al., 2010; Denlinger and Armbruster, 2014). 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); however, there is evidence that temperature influences the proportion of mosquitoes destined for diapause at a given photoperiod (Eldridge, 1966; Madder et al., 1983; Spielman, 2001).



Fig. 1. Map of the Peel Region (shaded grey) and other municipalities in the Greater Toronto Area.

In this study, we focus on the aspects of mosquito biology where temperature has been found to have significant influence: aquatic development, mortality, and diapause. We formulate temperature-dependent response functions for these key aspects of the mosquito life cycle based on the results of available laboratory and entomological field studies. The model is designed to simulate aquatic and adult *Cx. pipiens* and *Cx. restuans* population dynamics over a single season. To demonstrate the capacity of our model to describe the observed dynamics of mosquito abundance in a given area, we apply the model to the Peel Region, Ontario using mosquito surveillance data from 2004–2016. Simulation results showed the model could capture the general trend of observed mosquito surveillance data for most 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 and can also be coupled with epidemiological models to assess the impact of diurnal fluctuations in temperature on the dynamics mosquito-borne disease transmission.

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 with a total population of 1,296,814 and a total area of 1246.89 km² (Canada 2011 census). It consists of three municipalities: the cities of Brampton and Mississauga, and the town of Caledon (Fig. 1). 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. The Peel Region Health Unit used the CDC miniature light trap (Service, 1993) with

both CO₂ 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 (Wang et al., 2011). 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 2003–2016 was measured during a period of active larval control in catch basins and surface water sites. During each mosquito season, there were four rounds of larval mosquito control in non-surveillance based catch basins. Larviciding in surface water sites was surveillance based. 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 for years 2004–2016 (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. 2). 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 et al., 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 (United States Environmental Protection Agency, 2017). During winter months, nulliparous inseminated female mosquitoes can enter 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

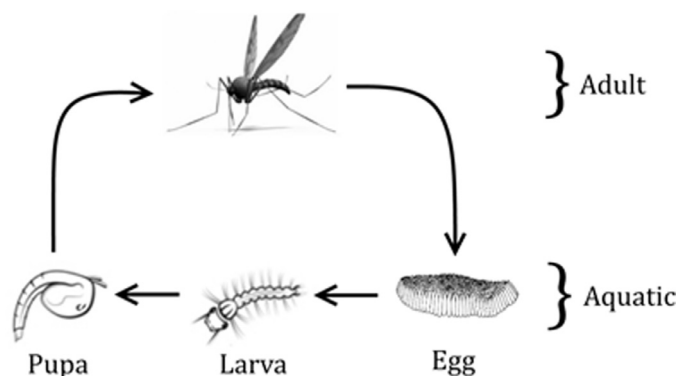


Fig. 2. The mosquito life cycle consists of three aquatic stages and one terrestrial adult stage.

mosquitoes in the fourth larval instar and pupal stages of development (Denlinger and Armbruster, 2014).

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. 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 $t \in [t_0, t_{\text{end}}]$ 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 $n \in [t_0, t_{\text{end}}]$. 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

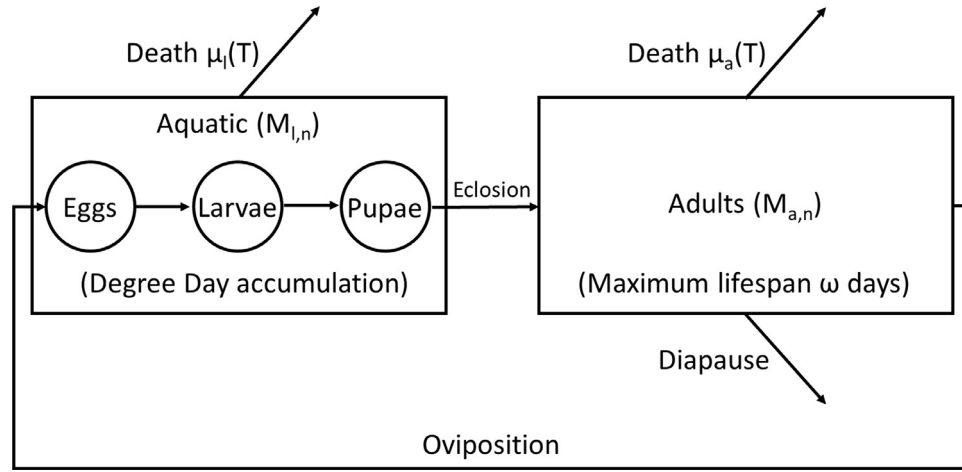


Fig. 3. Model diagram describing the *Cx. pipiens* and *Cx. restuans* life cycle. The number of eggs oviposited into a cohort ($M_{l,n}$) on any day is the total number of adult mosquitoes multiplied by the daily oviposition rate. Once a cohort accumulates enough DDs to complete development, all members of that cohort will simultaneously eclose into adults. Adults lay eggs on a daily basis until they die at most ω days after eclosion.

thermal units above a zero-development threshold temperature.

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

where $T(t)$ is the mean temperature $^{\circ}\text{C}$ 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):

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

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. 3.

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:

$$\frac{dM_{l,n}(t)}{ds} = -\mu_l(T_1(t))M_{l,n}(s), \text{ while } f_n(t) < 1 \text{ and } t \leq s < t+1, \quad (3)$$

$$\frac{dM_{a,n}(t)}{ds} = -\mu_a(T(t))M_{a,n}(s), \quad (4)$$

while $f_n(t) > 1$ and $t \leq s < t+1$,

where $\mu_l(T_1(t))$ is the temperature dependent aquatic mortality rate. Aquatic mortality rates are calculated based on a two-day average daily temperature, denoted $T_1(t)$, 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 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

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

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)).

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

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

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 that 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:

$$M_{a,n}(t) = 0, \text{ if } t - t_n = \omega. \quad (8)$$

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.

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

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	
β	Per capita 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 $T_l(t) \geq T_{op}$	3/1000	–	
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_{De}	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_{De} 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 of days t and $t-1$ used to calculate aquatic mortality $T_l(t) = \frac{T(t) + T(t-1)}{2}$	Variable	°C	[11]
P_n	Photoperiod of the day 4th larval instar begins for a cohort born on day n (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 (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	[1–6], [8], [9]
$\mu_a(T)$	Temperature dependent adult mortality rate	Variable	day ⁻¹	[14]

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)

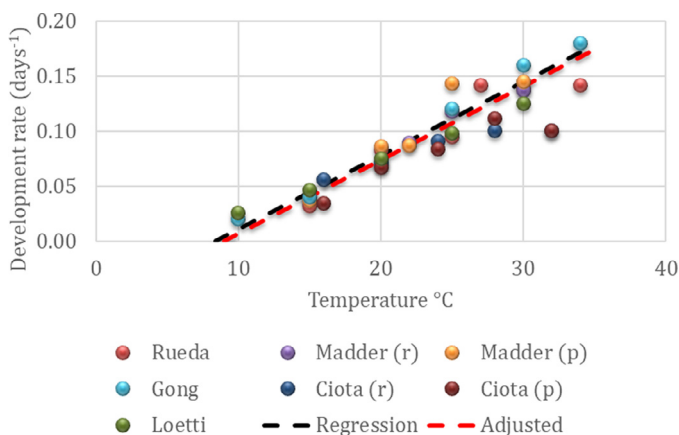


Fig. 4. Comparison of temperature dependent development rates obtained from laboratory studies. The black dashed line represents the linear regression of the collective development rates. The red dashed line represents the adjusted regression line that was locally tuned for the Peel Region, Ontario.

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. 4) in which the linear approximation is valid for the *Cx. pipiens* and *Cx. restuans* species.

Fig. 4 depicts the comparison of 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_{De} . The linear regression estimated a minimum threshold temperature of $T_e = 8.4$ °C, and a total number of degree days to emergence of $T_{De} = 144$ °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 $T_{De} = 149$ °C. The function for the proportion of development on day t is given by

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

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, de-

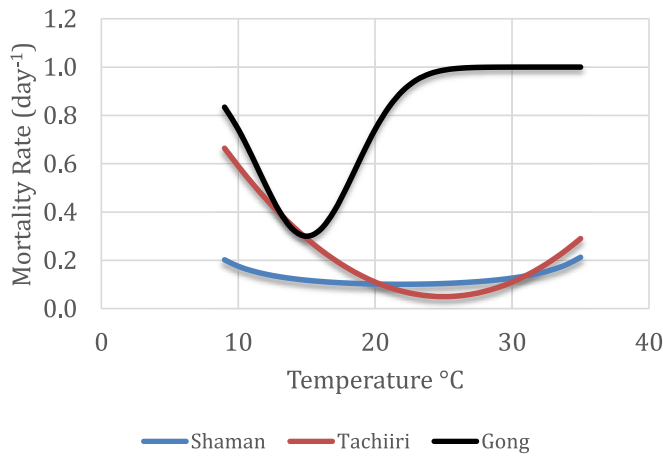


Fig. 5. Comparison of temperature dependent mortality rate functions used in existing studies: Shaman et al., (2006): $\mu = (-4.4 + 1.31T - 0.03T^2)^{-1}$, Tachiiri et al., (2006): $\mu = (0.24(T - 25)^2 + 5) \%$, Gong et al., (2010): $\mu = 1 - 0.7e^{-(\frac{T-25}{10})^2}$.

veloping 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 et al., 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. 5).

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 .

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

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

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

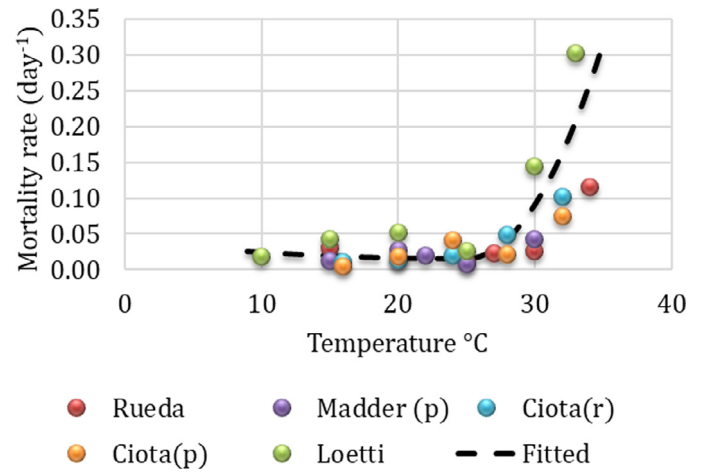


Fig. 6. Comparison of temperature dependent mortality rates (day⁻¹) based on results from available literature. The function (Eq. (11)) used to fit the data points is represented by the black dashed line.

The resulting mortality rates were then plotted (Fig. 6). We assumed the optimal temperature for development to be $T_{op} = 25$ °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} .

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

The resulting mortality rates from each study and the estimated mortality rate function $\mu_l(T_l(t))$ are presented in Fig. 6.

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.

$$\mu_a(T) = 0.000148T^2 - 0.00667T + 0.123 \quad (12)$$

2.6.3. Diapause

To survive unfavorable weather conditions during winter, many mosquito species undergo a hibernation dormancy called diapause (Denlinger and Armbruster, 2014). Depending on the species, most mosquitoes can overwinter in only one stage: egg, larval, or adult (Medlock and Leach, 2015; Vinogradova, 2007). Mosquito species *Cx. pipiens* and *Cx. restuans* 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, 1966; Kunkel et al., 2006; 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, 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

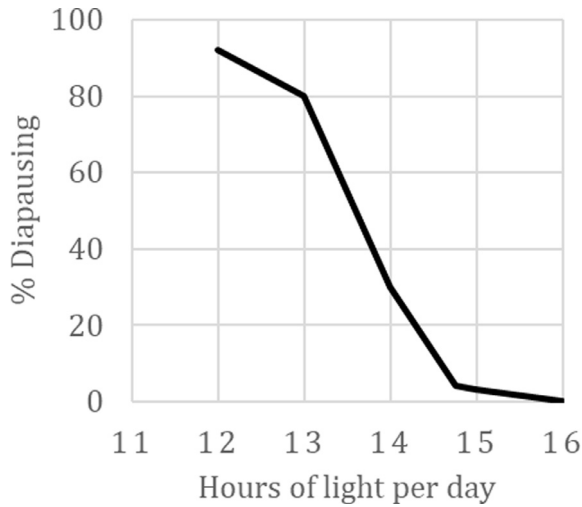


Fig. 7. Effect of photoperiod on the proportion of diapause destined blood-fed female mosquitoes reared at a constant 18 °C (Spielman, 2001).

mosquitoes is almost a linear function of photoperiod at a given temperature (Fig. 7).

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 et al. (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 h, 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

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

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. Since the variation in photoperiod for the same day each year is negligible, we use a periodic sine function to estimate the number of daylight hours each day.

$$P_k = 3.257 \sin(0.017(k + 0.8\tau_k - 81)) + 12.186, \quad k = 1, 2, \dots, 365 \quad (14)$$

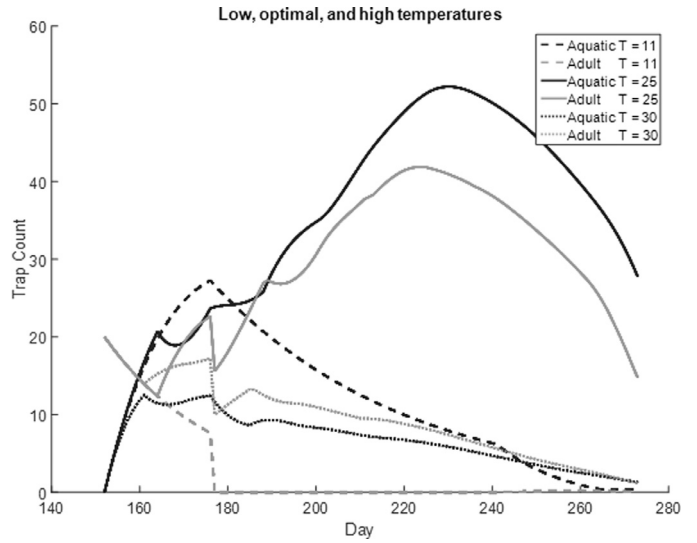


Fig. 8. Time series simulation at constant temperatures of $T = 11$ °C, $T = 25$ °C, and $T = 30$ °C.

The function was formulated based on average photoperiodic values obtained from a table containing the observed number of daylight hours for each day in the city of Toronto, Ontario for years 2004–2016 (The United States Naval Observatory, 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 years 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 specified temperature scenarios and observed temperature data as model input. As constructed, the model is deterministic and there is no stochasticity in model output. As constructed, the model is deterministic and there is no stochasticity in model output.

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 (Fig. 8), 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

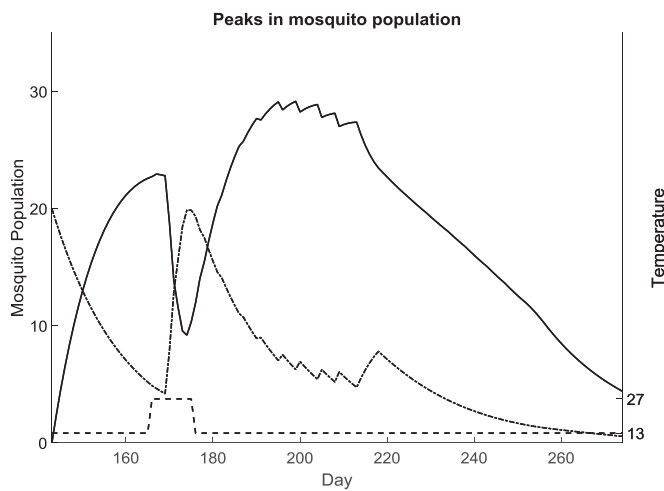


Fig. 9. Temperature pattern (dashed line, right axis) causing a peak in the adult mosquito population (dot-dashed line, left axis). Aquatic population depicted by the solid line on the left axis.

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 (Fig. 9). Finally, we apply the model to the Peel region, southern Ontario using observed temperature data for years 2004–2016 (Fig. 10).

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. Fig. 8 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.

While a variety of weather conditions may cause these sudden increases in the mosquito population, we present one plausible scenario that demonstrates how certain temperature patterns can produce a sudden increase in the mosquito population (Fig. 9). 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. Cohorts oviposited during the cooler period prior to the sudden rise in temperature accumulate 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 during the period of cooler temperatures, causing a sharp increase in the mosquito population on day 176.

3.2. Numerical simulations vs surveillance data

The model was applied to the Peel Region of southern Ontario. Simulations were run once for each year from 2004–2016 using observed temperature data (Fig. 10). 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 gonotrophic 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. The initial number of mosquitoes was then incremented by 1 and the simulation was repeated. 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.

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

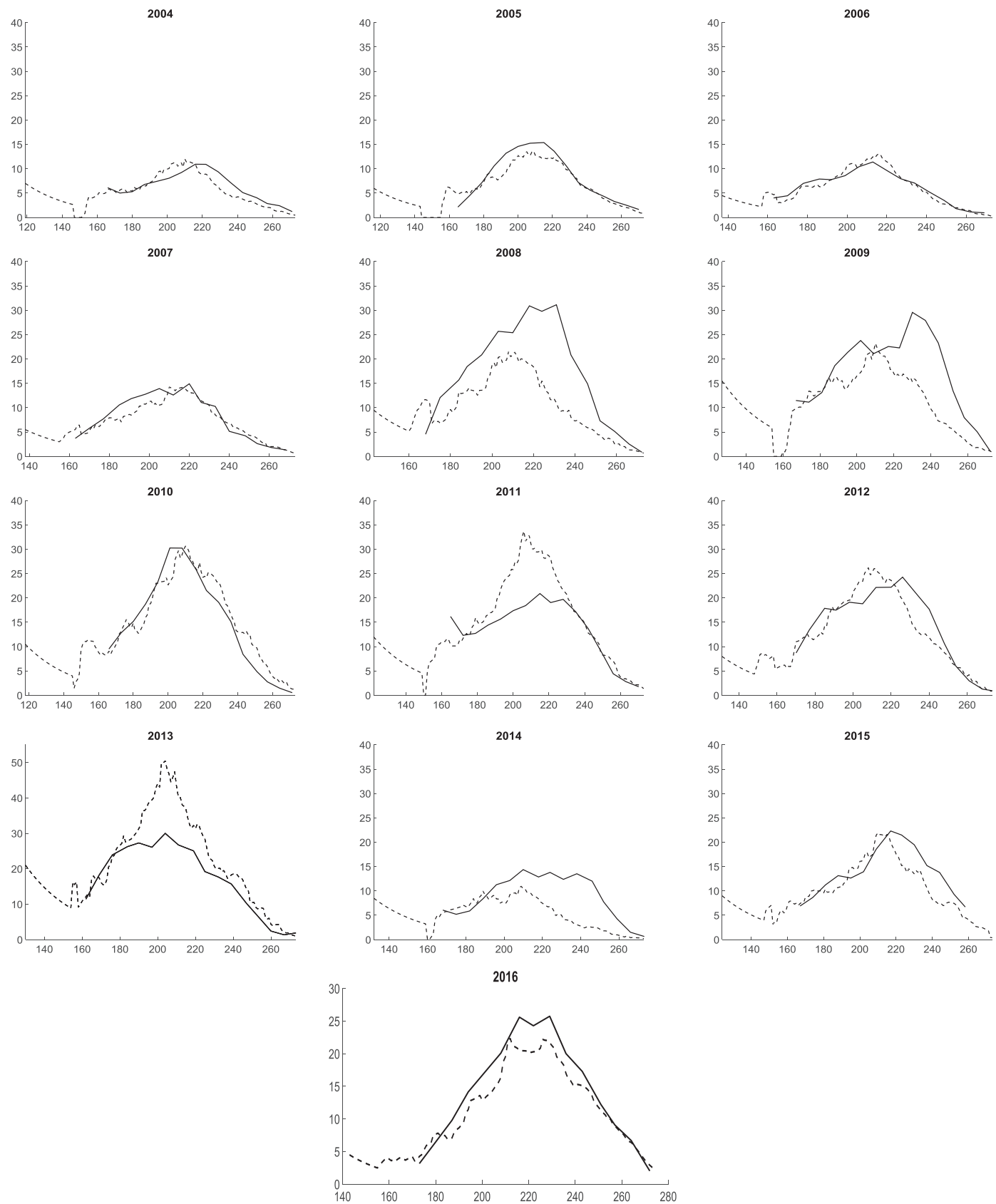


Fig. 10. Comparison of simulated trap counts (dashed line) vs observed surveillance data (solid line) for years 2004–2016.

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 (Caillly et al., 2012; Tachiiri et al., 2006) since each stage may have varying responses to temperature.

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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