Modelling the Effect of Temperature on the Seasonal Population Dynamics of Temperate Mosquitoes - Supplementary Material

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S.1   Model derivation

The general formalism of the model is analogous to that described by Nisbet and Gurney (1983) and a full derivation is presented there. Here, we present an overview of the key steps of the derivation which underpins the model we are using.

Let us define a density function $f(a, m, t)$ such that $f(a, m, t)dadm$ represents the number of individuals at time t with age in the infinitesimally range $a \to a + da$ and at a point on some arbitrary development (or maturation) scale in the similarly small range $m \to m + dm$. This gives the following balance equation to describe the processes of ageing, development and death of individuals present in the population at time t

$$\frac{\partial f}{\partial t} = -\frac{\partial f}{\partial a} - \frac{\partial}{\partial m}[gf] - \delta f, \qquad (a > 0) \tag{S.1}$$

in which g and δ (both functions of development, m, and age, a, at time t) represent the development (or growth) and instantaneous per capita death rate of individuals respectively. This equation is solved subject to a renewal condition of the form

$$f(0, m, t) = \int_{a=0}^{\infty} \int_{m=0}^{\infty} \beta(a, m', m, t) f(a, m', t) \, da \, dm'$$

in which $\beta(a, m', m, t)$ represents the per capita rate of production of offspring of development level m at time t by individuals of development level m' and age a. We can simplify these equations by assuming that g, β and δ are independent of age and that all individuals are equally developed at birth (say $m = m_1$). This allows us to rewrite Equation S.1 in terms of a density function $\rho(m, t)$ such that

$$\frac{\partial \rho}{\partial t} = -\frac{\partial}{\partial m}[g\rho] - \delta\rho, \qquad (m > m_1) \tag{S.2}$$

where $\rho(m, t)dm$ represents the number of individuals in the development range $m \to m + dm$ regardless of age. If we denote the total recruitment during the infinitesimal time interval $t \to t + dt$ by $R_1(t)dt$ then we note that these recruits will, at time $t + dt$ be developed in the range $m_1 \to m_1 + dm_1$ where $dm_1 = g(m_1, t)dt$. Since the total number of individuals with masses in that range is $\rho(m_1, t)dm_1$ we have

$$R_1(t)dt = \rho(m_1, t)dm_1 = \rho(m_1, t)g(m_1, t)dt \tag{S.3}$$

meaning

$$g(m_1, t)\rho(m_1, t) = \int_{m_1}^{\infty} \beta(m, t)\rho(m, t)dm$$

is our renewal condition.

By making a few assumptions our equations can be greatly simplified to give the stage-structured form we desire:

- We assume that transitions between stages occur at fixed points of development. We denote the stages as N_i for $i = 1, 2, .., n$ (assuming n stages) with progression from stage $i - 1$ to stage i occurring on achieving development level m_i.

- All individuals within a stage have the same instantaneous growth rates and per capita death rates.

- The adult population has a constant sex ratio and all females have the same fecundity.

This allows us to split the population into subpopulations of the form

$$N_i(t) \equiv \int_{m_1}^{m_{i+1}} \rho(m, t)dm,$$

which change according to

$$\frac{dN_i(t)}{dt} = R_i(t) - M_i(t) - D_i(t) \qquad \text{[recruitment - maturation - deaths]}.$$

Recruitment into stages other than the first occurs solely through maturation and so $R_i(t) = M_{i-1}(t)$ if $i \neq 1$ and $R_i(t) = \sum_{j=1}^{n} \beta_j(t)N_j(t)$ otherwise.

To obtain an explicit expression for the maturation rate, $M_i(t)$, requires that we solve the balance Equation S.2 within the ith age class only subject to the boundary condition in Equation S.3 (slightly modified to apply to the ith age class). This leads us to an expression for maturation out of stage i given by

$$M_i(t) = \frac{g_i(t)}{g_i(t - \tau_i(t))} R_i(t - \tau_i(t))S_i(t)$$

where $S_i(t)$ denotes the probability of survival through class i and $\tau_i(t)$ represents the length of time required for development through class i both at time t. The survival equations are defined as the integral of the sum of all the death rates over the duration of the life stage

$$S_i(t) = \exp\left(-\int_{t-\tau_i(t)}^{t} \delta_i(\psi)d\psi\right) \tag{S.4}$$

Finally we require an expression for the stage durations, which are defined as the time required for development from development point m_i to m_{i+1} and so can be deduced from the integral constraint

$$m_{i+1} - m_i = \int_{t-\tau_i(t)}^{t} g_i(t')dt'.$$

S.2   Initial History

If we wish to solve the equations from $t = 0$ onwards then we must provide solution values for all points where $t < 0$. For the system of balance equations (Equation 1a) we can state that we have an empty system $(E(t) = L(t) = P(t) = A(t) = 0)$ for $t < 0$. By substituting $A(t) = 0$ into the recruitment and maturation equations (Equation 1b) we quickly see that all recruitment and maturation terms for $t < 0$ are zero.

To determine initial conditions for the delay equations (Equation 1d) is straightforward because the delay depends only on development rate and thus only on temperature. Therefore, by feeding in the temperatures before $t = 0$ the delays can be calculated as normal. Similarly, the histories of the survival equations (Equation 1c) can be calculated through a knowledge of the temperatures before $t = 0$. Since we have stated that there were no larvae present before $t = 0$ there is no predation before this point.

To initiate the system we assume that some innoculation takes place at $t = 0$. This consists of adding I_0 individuals into the adult class ($I_0 = 100$ in this case) (Murdoch et al., 2003). The number of individuals added has not been seen to affect the behaviour of the system past the first full year. As such, simulations were begun on the $1st$ of July and run for 18 months before taking results. When using the North Kent dataset the results of the first year were discarded.

S.3 Delay Equations Derivations

In their paper show the delay equation for each life stage at time, t. However, when coding the model it becomes necessary to reference stage durations at previous points in time by looking back through intermediate stage durations, which are themselves variable. The derivation of the delay which references back through two intermediate life stages is given below i.e. this will give the duration of the egg stage the length of the pupal stage and larval stage ago. This is the procedure required to obtain $\tau_E(t - \tau_P(t) - \tau_L(t - \tau_P(t)))$ where $i = E, i + 1 = L$ and $i + 2 = P$. The derivations of $\tau_E(t - \tau_L(t))$ and $\tau_L(t - \tau_P(t))$ are not presented as they reference through only one delay and so are simplified versions of this derivation.

$$m_{i+1} - m_i = \int_{t-\tau_{i+2}(t)-\tau_{i+1}(t-\tau_{i+2}(t))-\tau_i(t-\tau_{i+2}(t)-\tau_{i+1}(t-\tau_{i+2}(t)))}^{t-\tau_{i+2}(t)-\tau_{i+1}(t-\tau_{i+2}(t))} g_i(\psi)d\psi$$

$$\frac{d(m_{i+1} - m_i)}{dt} = g_i(t - \tau_{i+2}(t) - \tau_{i+1}(t - \tau_{i+2}(t)))\left(1 - \frac{d\tau_{i+2}(t)}{dt} - \frac{d\tau_{i+1}(t - \tau_{i+1}(t))}{dt}\right)$$

$$- g_i(t - \tau_{i+2}(t) - \tau_{i+1}(t - \tau_{i+2}(t)) - \tau_i(t - \tau_{i+2}(t) - \tau_{i+1}(t - \tau_{i+2}(t))))$$

$$\left(1 - \frac{d\tau_{i+2}(t)}{dt} - \frac{d\tau_{i+1}(t - \tau_{i+1}(t))}{dt} - \frac{d\tau_i(t - \tau_{i+2}(t) - \tau_{i+1}(t - \tau_{i+2}(t)))}{dt}\right)$$

Since the start and end points of each life stage are fixed we have that $\frac{d(m_{i+1}-m_i)}{dt} = 0$ so

$$1 - \frac{d\tau_{i+2}(t)}{dt} - \frac{d\tau_{i+1}(t - \tau_{i+1}(t))}{dt} - \frac{d\tau_i(t - \tau_{i+2}(t) - \tau_{i+1}(t - \tau_{i+2}(t)))}{dt}$$

$$= \frac{g_i(t - \tau_{i+2}(t) - \tau_{i+1}(t - \tau_{i+2}(t)))}{g_i(t - \tau_{i+2}(t) - \tau_{i+1}(t - \tau_{i+2}(t)) - \tau_i(t - \tau_{i+2}(t) - \tau_{i+1}(t - \tau_{i+2}(t))))}$$

$$\left(1 - \frac{d\tau_{i+2}(t)}{dt} - \frac{d\tau_{i+1}(t - \tau_{i+1}(t))}{dt}\right)$$

$$\frac{d\tau_i(t - \tau_{i+2} - \tau_{i+1}(t - \tau_{i+2}(t)))}{dt}$$

$$= \left(1 - \frac{d\tau_{i+2}(t)}{dt} - \frac{d\tau_{i+1}(t - \tau_{i+1}(t))}{dt}\right)$$

$$\left(1 - \frac{g_i(t - \tau_{i+2}(t) - \tau_{i+1}(t - \tau_{i+2}(t)))}{g_i(t - \tau_{i+2}(t) - \tau_{i+1}(t - \tau_{i+2}(t)) - \tau_i(t - \tau_{i+2}(t) - \tau_{i+1}(t - \tau_{i+2}(t))))}\right)$$

S.4 Functional forms and parametrisation

S.4.1 Development rates

Growth rates for the immature stages were modelled using a power function, which mirrors the form used by Beck-Johnson et al. (2013) for *Anopheles* and gives development rates which increase with temperature (Figure S.1)

$$g_i(t) = \begin{cases} \alpha_i T(t)^{\beta_i}, & T(t) > \left(\frac{b_m}{\alpha_i}\right)^{\frac{1}{\beta_i}}, \\ b_m, & \text{otherwise} \end{cases} \tag{S.5}$$

Here $i = E, L, P$ correspond to the egg, larval and pupal stages respectively. At this stage, daily average water temperature was assumed to be equal to air temperature due to the lack of available information on water temperatures. The functional forms were chosen to be the same for each life stage as there was good agreement with the data, however different forms could be chosen in other models if deemed appropriate. It was assumed that the lower threshold of the development rate, b_m, should be set to stop development time dropping below 60 days ($b_m = \frac{1}{60}(days^{-1})$ Almirón and Brewer (1996)). The exact value chosen for b_m is unlikely to influence model output because only development rates outwith predicted thermal development thresholds (approximately $10 - 34\,°C$ Almirón and Brewer (1996); Loetti et al. (2011)) are notably affected by this restriction. Beyond these thresholds, mortality is expected to occur before development completes.
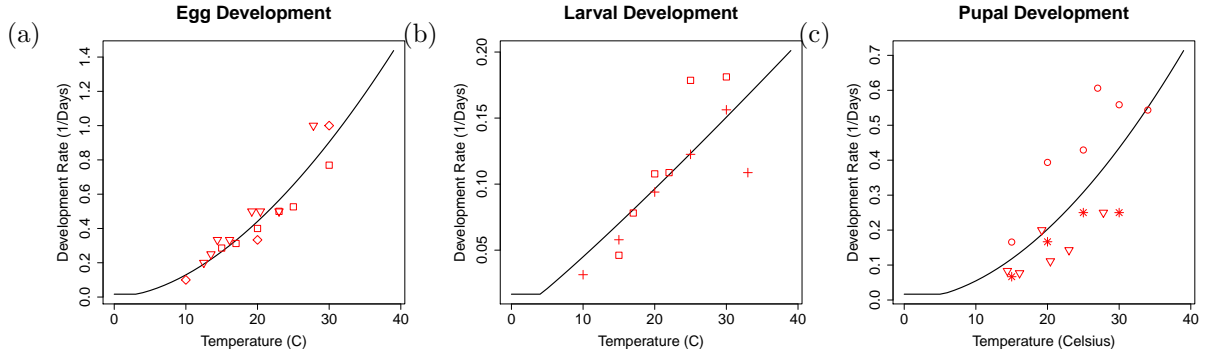

Figure S.1: **Immature development:** The plots show curves fitted to data from the literature about the relationship between temperature and development rate of eggs (a) Madder et al. (1983); Becker et al. (2010); Jobling (1938); Shriver and Bickley (1964), larvae (b) Madder et al. (1983); Rueda et al. (1990); Olejníček and Gelbic (2000); Loetti et al. (2011); Almirón and Brewer (1996) and pupae (c) Rueda et al. (1990); Jobling (1938); Vinogradova (2000). Symbols represent the data source as follows: Madder et al. (1983) - □, Becker et al. (2010) - ◇, Jobling (1938) - ▽, Shriver and Bickley (1964) - ⊠, Rueda et al. (1990) - ◯, Olejníček and Gelbic (2000) - △, Loetti et al. (2011) - +, Almirón and Brewer (1996) - ×, Vinogradova (2000) - ✳. The different coloured data points represent the (sub)species: *Cx. pipiens* (red), *Cx. quinquefasciatus* (teal) and *Cx. molestus* (black).

S.4.2 Death rates

Death rates for the immature stages were modelled using a modified Gaussian functional form

$$\delta_i(t) = \begin{cases} \nu_{0i} \exp\left(\left(\frac{T(t)-\nu_{1i}}{\nu_{2i}}\right)^2\right), & \nu_{1i} + \frac{\nu_{2i}}{2}\ln\left(\frac{b_{di}}{\nu_{0i}}\right) < T(t) < \nu_{1i} - \frac{\nu_{2i}}{2}\ln\left(\frac{b_{di}}{\nu_{0i}}\right), \\ b_{di}, & \text{otherwise}, \end{cases} \tag{S.6}$$

for $i = E, L, P$, which leads to expected survival times following a bell-shaped curve centred at ν_{1i} and bounded to be greater than or equal to $\frac{1}{b_{di}}$ (Figure S.2). The choice of a modified Gaussian form again mimics that chosen by Beck-Johnson et al (2013) Beck-Johnson et al. (2013) and leads to high death rates beyond the developmental thresholds previously discussed. Larvae and pupae were assumed to have the same temperature-dependent death rate because the vast majority of the literature presented survival percentages from egg hatch until adult emergence. There is a lot of variability in the mortality data obtained from the literature, which is not accounted for when we try and fit a function with temperature as the only explanatory variable (Figure S.2). Couret et al. (2014) showed that temperature, larval diet, and density, and their interaction all affected development rates of the immature stages of *Aedes aegypti*. It was shown by Lyimo et al. (1992) that rearing temperature and larval density had a complex series of effects on larval survival, age at pupation, and adult size of *Anopheles gambiae*. Colless and Chellapah (1960) showed that increased body size led to increased egg raft size in two colonies of *Ae. aegypti* and it was shown by Ishii (1963) that increased larval density slowed the development of *Cx. pipiens* larvae. As such, we will not be able to capture all variability in mortality rates using temperature as the only explanatory variable. We use this modified Gaussian function as an approximation for our model and the need for inclusion of a wider range of environmental variables is considered in the discussion. With an unbounded death rate we encountered difficulties with the DDE solver code because the survival values became infinitesimally small. As such, an upper limit of b_{di} was imposed on the death rate (Figure S.2). This limit was chosen such that the minimum expected lifespan was one day because all functions in the model are parametrised on a daily time scale. Upon varying this threshold within a range of values for which the DDE solver code worked we saw no change in results, because development times are all greater than one day.
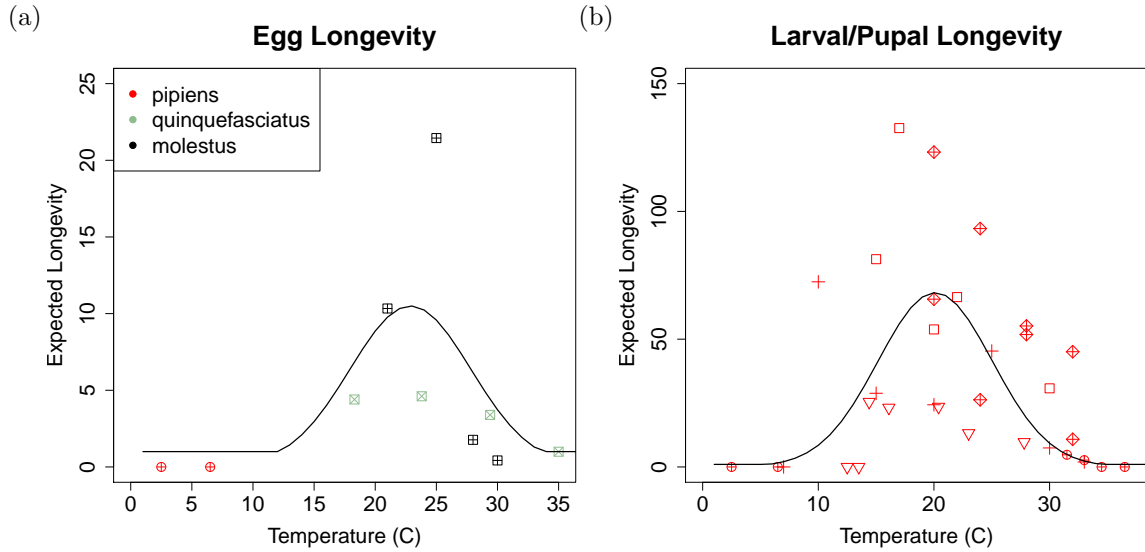
(a)   (b)

Figure S.2: **Immature longevity:** Relationship temperature and expected longevity (reciprocal of the death rate) of eggs (a) Shriver and Bickley (1964); Oda et al. (1980); Farid (1948) and larvae/pupae (b) Madder et al. (1983); Rueda et al. (1990); Olejnícek and Gelbic (2000); Loetti et al. (2011); Ciota et al. (2014); Vinogradova (2000); Jobling (1938); Farid (1948). Symbols represent the data source as follows: Madder et al. (1983) - □, Jobling (1938) - ▽, Shriver and Bickley (1964) - ⊠, Rueda et al. (1990) - ◯, Olejnícek and Gelbic (2000) - △, Loetti et al. (2011) - +, Vinogradova (2000) - ✳, Oda et al. (1980) - ⊞, Farid (1948) - ⊕, Ciota et al. (2014) - ⊕. The different coloured data points represent the (sub)species: *Cx. pipiens* (red), *Cx. quinquefasciatus* (real) and *Cx. molestus* (black).

Adult death rates were modelled using a power function which was constrained below some threshold value (Figure S.3 (a))

$$\delta_A(t) = \begin{cases} \alpha_A T(t)^{\beta_A}, & T(t) > \left(\frac{b_{da}}{\alpha_A}\right)^{\frac{1}{\beta_A}} \\ b_{da}, & \text{otherwise} \end{cases} . \tag{S.7}$$

The death rate was constrained not to drop below a base death rate of b_{da} otherwise diapausing adults experience essentially zero mortality, which is unrealistic. This overwinter survival rate was chosen to give percentage survival of roughly 10% depending on the length of the winter period, which falls within the range observed by Sulaiman and Service (1983). The value chosen was also consistent with some of the observations by Bailey et al. (1982), though they saw substantial variation between death rates of different groups and increasing death rates as diapause progressed, which we have not incorporated here. At this stage, any relationship between humidity and adult mortality has also not been considered.
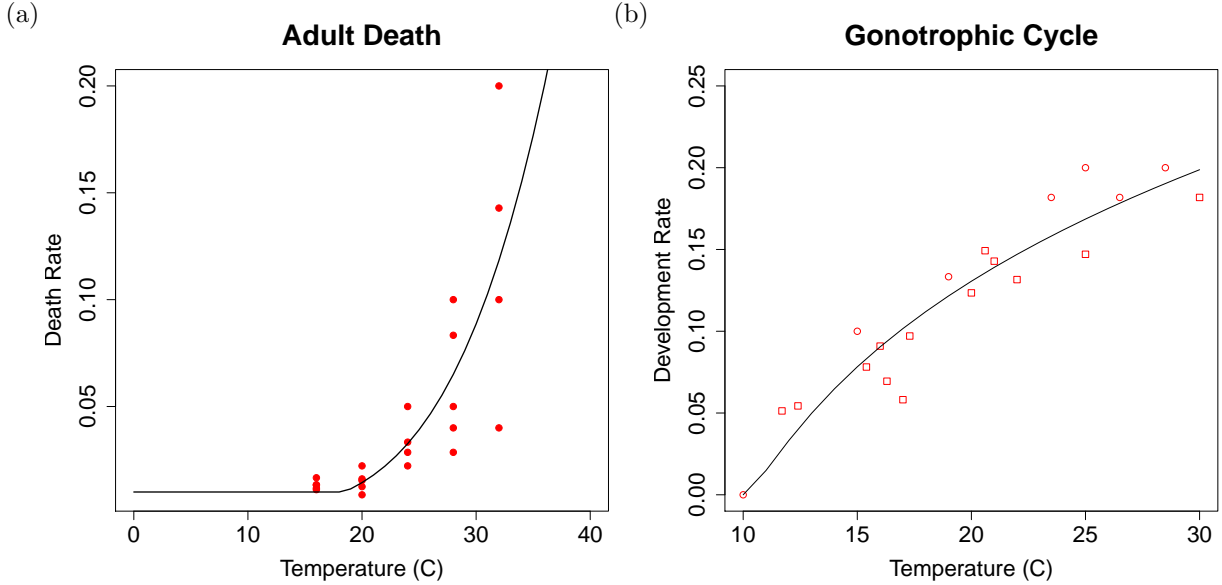
(a)

(b)

Figure S.3: **Adult vital rates:** Temperature-dependent death rate of adults (a) Ciota et al. (2014) and gonotrophic cycle (b) Madder et al. (1983); Vinogradova (2000) (Symbols □ and ○ respectively) fitted to data from the literature. Values for the gonotrophic cycle rate were calculated using the ovarian maturation times as stated in the literature but with 2 days added for locating a blood meal and ovipositing Hartley et al. (2012). All data is from *Cx. pipiens*.

S.4.3 Predation rate

Based on information from the literature we chose to represent the larval death rate due to predation by the Holling type II function Marti et al. (2006); Fischer et al. (2013)

$$\delta_\pi(L(t)) = \frac{p_0 L(t)}{p_1 + L(t)}. \tag{S.8}$$

Predator density is assumed to be constant and the larval density is assumed to be directly proportional to larval numbers. This gives a low death rate when larval density is low because the time the predator spends searching for prey is high. As larval density increases, the search time tends to zero and the death rate is governed by the handling time a predator needs to process each kill. This leads to an upper bound on the number of prey which can be consumed and thus on the death rate, δ_π.

In Equation S.8, p_0 gives the upper limit to which the death rate due to predation tends, as larval density increases. The constant, p_1, gives the number of larvae required for the death rate to reach half of p_0. We were unable to find parameter estimates for p_0 and p_1 due to their sensitivity to predator behaviour Onyeka (1983), habitat size, habitat type Fischer et al. (2013) and oviposition behaviour Angelon and Petranka (2002); Reiskind and Wilson (2004). We therefore performed a sensitivity analysis to understand the impact of variation in these values. This showed that seasonal abundance patterns could be quite sensitive to changes in p_0 below a certain threshold but that p_1 only affected population size. These results are discussed in full in S.5.

S.5 Predation function sensitivity analysis

Simulations showed that variation of p_1, the larval density at which the death rate due to predation reaches half its maximum, only resulted in changes to the absolute abundance without any effect on qualitative behaviour. The upper limit of larval death due to predation, p_0, can have a substantial effect on model behaviour. At low values of p_0 predation alone is insufficient to regulate the population, which exhibits growing oscillations year-on-year. We assume that either such situations do not occur in wild populations or that the population would also be regulated by larval competition at very high densities. Once p_0 becomes large enough to regulate the population we quickly reach a point where further increases only serve to repress population size with little difference in the pattern of seasonal abundance. We chose to study the population for a value of $p_0 = 0.7$ as this was large enough for regulation but not large enough to result in unexpected extinctions.
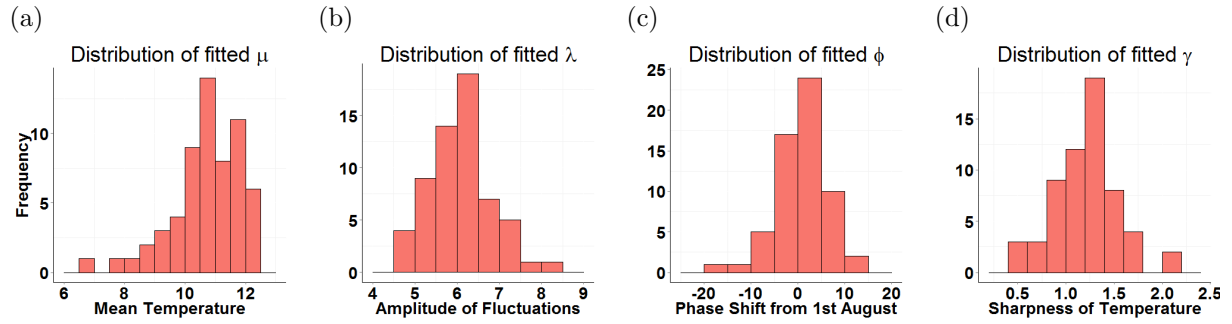
S.6 Range of temperature function parameters

Figure S.4: Temperature data from the North Kent marshes 1951-2010 was used to investigate typical values for the environmental variation parameters. Histograms of annual fitted values of the parameters are presented (a) mean temperature, μ, (b) amplitude of fluctuations, λ, (c) phase shift presented as +/- days from the 1st of August (the mean date at which the peak occurred), ϕ, (d) sharpness of peak, γ (higher values indicate sharper peaks).

S.7 Table of parameter values

Parameter	Definition	Value	Eqn	Reference
α_E	Fit parameter in egg maturation	2.20×10^{-3} $(days^{-1}\,{}^{\circ}\text{C}^{-\beta_i})$	S.5	Figure S.1 (a)
β_E	Fit parameter in egg maturation	1.77	S.5	Figure S.1 (a)
α_L	Fit parameter in larval maturation	3.57×10^{-3} $(days^{-1}\,{}^{\circ}\text{C}^{-\beta_i})$	S.5	Figure S.1 (b)
β_L	Fit parameter in larval maturation	1.10	S.5	Figure S.1 (b)
α_P	Fit parameter in pupal maturation	7.11×10^{-4} $(days^{-1}\,{}^{\circ}\text{C}^{-\beta_i})$	S.5	Figure S.1 (c)
β_P	Fit parameter in pupal maturation	1.89	S.5	Figure S.1 (c)
ν_{0E}	Baseline egg death rate	0.095 $(days^{-1})$	S.6	Figure S.2 (a)
ν_{1E}	Optimum temperature for egg survival	22.88 °C	S.6	Figure S.2 (a)
ν_{2E}	Width parameter for egg death rate	7 °C	S.6	Estimated from data
ν_{0L},ν_{0P}	Baseline larval/pupal death rate	0.014 $(days^{-1})$	S.6	Figure S.2 (b)
ν_{1E},ν_{1P}	Optimum temperature for larval/pupal survival	20.1 °C	S.6	Figure S.2 (b)
ν_{2E},ν_{2P}	Width parameter for larval/pupal death rate	7 °C	S.6	Estimated from data
α_A	Fit parameter in adult death	2.17×10^{-8} $(days^{-1}\,{}^{\circ}\text{C}^{-\beta_i})$	S.7	Ciota et al. (2014)
β_A	Fit parameter in adult death	4.48	S.7	Ciota et al. (2014)
b_m	Baseline maturation rate	$\frac{1}{60}$ $(days^{-1})$	S.5	Almirón and Brewer (1996) Loetti et al. (2011)
b_{di}	Threshold immature death rate	1 $(days^{-1})$	S.6	Time-scale of model
b_{da}	Baseline adult death rate	0.01 $(days^{-1})$	S.7	Sulaiman and Service (1983)
p_0	Predation upper bound	0.5 $(days^{-1})$	S.8	From simulation
p_1	Predation steepness parameter	100,000 (Larvae)	S.8	From simulation
R	Egg raft size	200 (eggs)	4	Vinogradova (2000)
α_G	Gonotrophic cycle fit parameter	0.122 $(days^{-1})$	3	Figure S.3 (b)
β_G	Gonotrophic cycle fit parameter	1.76	3	Figure S.3 (b)
ξ_S	Spring diapause threshold	14 (hours)	2	Sulaiman and Service (1983)
ξ_A	Autumn diapause threshold	13 (hours)	2	Sulaiman and Service (1983)

Table S.1: Parameter values used for running the model

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