Life tables and a physiologically based model application to *Corcyra cephalonica* (Stainton) populations

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Abstract

The rice moth *Corcyra cephalonica* is a harmful insect pest for grains stocked in storage systems. Its infestations represent a serious concern among producers, because of the non-marketability of the products affected by it and subsequent economic losses.

New technologies are improving the supply chain of the stored grains, in line with the integrated pest management framework. However, a prompt control action also requires an in-depth knowledge of insect pests’ biology and their response to environmental parameters. If this information is available, it can also be translated into mathematical language. The modelling of insect pest populations is increasing in utility, particularly if the models are included in decision support systems.

The aim of this work concerns two aspects of a model application and validation. Since physiologically based models require information about interactions between species and environment, *C. cephalonica* individuals were reared at different constant temperatures: 18, 21, 24, 26, 28, 30, 34 and 36 °C. This first part provided
the life tables, whose data were used to estimate the parameters of the Logan, Brière, and Sharpe and De Michele development rate functions.

The second part of the work concerns the application of a physiologically based model described by a first order partial differential equation. The validation of the simulations was conducted with a semi-field experimentation with three repetitions.

Results showed that the life tables are well represented by the Sharpe and De Michele development rate function, and that the physiologically based model proposed is reliable in representing field populations.

KEY WORDS Growth models, Crop protection, Integrated Pest Management, Age-structured models, Generalized Von Foerster’s equation, Rice Moth, Lepidoptera Pyralidae

1. Introduction

Storage is an important stage in the supply chain of cereal grain because it represents a crossing point between the agricultural production stage and the industrial processing stage. Technological innovations have greatly improved storage systems: some relevant examples of enhancements include the loading and unloading phases, transportation across product processing centres and the possibility of controlling the temperature of storage (Atungulu et al., 2019). Technological tools in the storage of cereal grains certainly accelerate industrial times and allow manpower to be conserved (Beta and Ndolo, 2019), but they can also be helpful in controlling the biological adversities to which products are exposed (Johnson, 2020; Qin et al., 2019).

One of the main issues relates to insect pest infestations in warehouses, which can make cereal grains unmarketable (Flinn et al., 2007). Among harmful species, the case of the rice moth Corcyra cephalonica (Stainton) (Lepidoptera: Pyralidae) has caught the attention of the scientific community. In fact, despite its common name associated with rice cultivations, several studies have discussed the ability of C. cephalonica populations to infest other products including corn, sorghum, cocoa, almond, beans and dried fruit (Hashem et al., 2018).

Biological and ecological studies on C. cephalonica were first conducted by Cox et al. (1981) and Osman et al. (1984). The life cycle is composed of egg, six larval instars, pupa and adult stages, with an average duration
of 40 days in optimal temperature conditions (28 – 30 °C). Moreover, the rice moth has shown a high adaptability to develop in different conditions of relative humidity (15 – 90%) and temperature (15 – 37 °C) (Limonta et al., 2009) with no difference in the extent of damages caused. Even if natural populations can be found directly in cultivated fields, most of the damages are reported in storage systems. In fact, the particular conditions in which product stockpiles are kept offer protection and unlimited food to the rice moths, which can reproduce continuously. Accordingly, a prompt control action is required to reduce risks and damages caused by *C. cephalonica* in storage systems.

Despite the different control strategies available in the literature, predictions based on mathematical models represent a powerful tool in an Integrated Pest Management (IPM) framework (Dalal and Singh, 2017). More specifically, forecasts of the population dynamics of insect pests can help farmers and technicians to select the most appropriate control strategy (Rupnik et al., 2019). On the other hand, the development of a reliable model requires a deep knowledge of the species’ biology and of their relationship with environmental parameters. For ectotherm organisms, as well as insects, the average duration of their life cycle is related to environmental parameters, such as temperature or relative humidity (Birch, 1948; Gilbert et al., 2004; Rossini et al., 2019a). However, in the specific case of *C. cephalonica*, the latter is less relevant because stored grain are usually maintained in a dry environment for conservation reasons. As such, temperature is usually the main driving variable, because the majority of storage sites do not have thermal control systems.

As a result, a deeper knowledge of the relationship between *C. cephalonica* and environmental temperature is necessary, and it is also useful to apply physiologically based models to describe the density of its population. Recently, Rossini et al. (2019a) proposed and applied a partial differential equations-based model in other case studies (Rossini et al., 2021, 2020a), in order to represent ectotherm populations developing over time and through their life stages. Subsequently, their model was implemented in a calculation software (Rossini et al., 2020e, 2019b) and supported by a protocol of application (Rossini et al., 2020c).

The aim of the present study is the application and validation of the aforementioned physiologically based model to the case study of *C. cephalonica*. The application of the model requires a robust knowledge of the species’ response to environmental temperature. For this reason, the first part of the work consisted of a series of constant temperature experimentations rearing at 18, 21, 24, 26, 28, 30, 34 and 36 °C, providing *C. cephalonica* life tables. This part of the research completes the previous work of Osman et al. (1984). Life
tables were used to estimate the parameters of the Logan, Briére, and Sharpe and De Michele development rate functions, mathematical expressions that relate the environmental temperature with the speed of growth of ectotherms. Development rate functions parameters were subsequently included in the physiologically based model for its validation. The latter, more specifically, was conducted in conditions of varying temperature in a semi-field environment, by placing a cohort of eggs in Petri dishes and reporting the adults’ flight dynamics.

2. Materials and methods

2.1. Population density model

The population density model applied to the rice moth consists of a first order partial differential equation, which considers insects’ development through the life stages and over time. These mathematical formulations were first introduced by McKendrick (1926) and Von Foerster (1959), and subsequently revised by several authors over the years (Diekmann et al., 1983; Sinko and Streifer, 1967; Vansickle, 1977) to suit multiple biological contexts. However, in the case of ectotherms, the development through the life stages depends on environmental parameters (Mirhosseini et al., 2017) and more specifically on temperature. Hence, two independent variables have been considered in order to describe insects’ population density: time \( t \), and physiological age \( x \). These concepts were explored by Rossini et al. (2019a, 2020d) when the physiologically-based model applied in the present study was first introduced; this represents a reformulation of the model described by McKendrick (1926) and Von Foerster (1959). In particular, their equation describes a population density \( N(t, x) \) of ectotherms and it has the following mathematical form:

\[
\begin{align*}
\frac{\partial}{\partial t}N(t,x) + \frac{\partial}{\partial x}[G(t,x)N(t,x)] &= -M(t,x)N(t,x) \\
N(t,0) &= \int_{0}^{x_{m}} \beta(t,x')N(t,x') \, dx' \\
N(0,x) &= n_{0}(x)
\end{align*}
\] (1)

The development through the life stages is ruled by the function \( G(t,x) \) known as the ‘generalised development rate function’ and which, in its most general form, considers the dependence on the environmental parameters (usually time-dependent) and on aging. Mortality and birth rates are described by...
\( M(t, x) \) and \( \beta(t, x) \), respectively, while the initial and boundary conditions \( N(0, x) \) and \( N(t, 0) \) represent the initial population profile, and the amount of individuals produced between the ages 0 and \( x_m \), respectively. Hence, biological information within equation (1) are included in the functions \( G(t, x) \), \( M(t, x) \), and \( \beta(t, x) \), which can be considered, in their most general meaning, as sub-models.

However, the application of the model (1) in varying temperature conditions makes the use of numerical solutions essential. This is due to the impossibility of representing the variation of the daily average temperature over the year with an analytical function; hence, this value needs to be recorded by meteorological stations or data loggers directly in the insects’ living environment. This problem was overcome by combining the method of the lines and the Euler’s finite difference method (Bellagamba et al., 1987; Keyfitz and Keyfitz, 1997; Plant and Wilson, 1986; Rossini et al., 2020d, 2020f, 2019a), which led to the following discrete version of the equation (1):

\[
\begin{align*}
N_{i+1}^h &= \frac{i}{h} G^i_h N_{i+1}^h + N_i^h \left[ 1 - 2 \frac{i}{h} G^i_h + \frac{i}{h} G^i_{i+1} - iM^i_h \right] \\
N_0^h &= \sum_{i=0}^{x_m} \beta^i_h N_i^h h \\
N_0^0 &= N_0
\end{align*}
\]

(2)

To avoid confusion between continuous and discrete variables, in the numerical scheme (2) discrete age (the life stage) is represented by \( h \), while \( i \) is the time step of the simulation (usually set to one day). The letters \( N \), \( G \), \( M \) and \( \beta \) conserve the meaning of the functions introduced for the system (1), but in this case they indicate their respective discrete versions. The numerical scheme (2) was computed with informatic tools based on C++ programming language and on ROOT’s software (Cern 2020) libraries, as reported by Rossini et al. (2019b, 2020e). The software takes as input the biological parameters of the species (i.e., the development, mortality and birth rate functions parameters) and the daily average temperatures recorded in the field. The outputs are the simulated population densities over time for each life stage of the species.

For the purpose of this work, reproduction was not considered, nor was mortality. Simulations were repeated on a daily basis, considering, as the initial condition for the numerical scheme (2), the respective number of eggs laid in each day.

In the light of these assumptions, further discussion is required for the generalised development rate function \( G(t, x) \), and on how it can be simplified and estimated with experimental data.
2.2. Development rate functions and life tables

2.2.1. Development rate functions

The generalised development rate function \( G(t, x) \) introduced in equation (1) describes either the relationship between species and external environment, or intrinsic processes such as aging. However, there is not much information on the latter at the moment, and for this reason it is not opportune to consider, for the present study, the dependence on \( x \) within \( G(t, x) \). Moreover, since \( C. cephalonica \) can develop in a wide range of relative humidity and photoperiod (Russell et al., 2009), without relevant changes in the speed of growth, it is possible to consider only the environmental temperature as main driving variable. As already discussed by other authors, (Quinn, 2017; Severini and Gilioli, 2002) the mean development rate corresponding to a specific temperature \( G[T(t)] \), is defined as the inverse of the mean development time \( D[T(t)] \).

\[
G[T(t)] = \frac{1}{D[T(t)]} \tag{3}
\]

There are several proposals for formulaic representations of the relationship between development rate and temperature (Damos and Savopoulou-Soutani, 2012; Ikemoto and Kiritani, 2019; Mirhosseini et al., 2017), but this study has chosen to consider three of these. These were:

- The Logan development rate function (Logan et al., 1976):
  \[
  G[T(t)] = \psi \left[ \exp(\rho T(t)) - \exp(\rho T_M - \frac{T(t) - T_M}{\Delta T}) \right] \tag{4}
  \]
  where \( \psi \) and \( \rho \) are empirical parameters, \( T_M \) is the maximum temperature threshold above which the species theoretically cannot develop, and \( \Delta T \) is the range of temperature between the maximum of the function, and \( T_M \).

- The Brière development rate function (Brière et al., 1999):
  \[
  G[T(t)] = aT(t)(T(t) - T_L)(T_M - T(t))^m \tag{5}
  \]
  where \( a \) and \( m \) are empirical parameters, and \( T_L \) and \( T_M \) are the lower and upper temperature thresholds for the species, respectively.

- The Sharpe and De Michele development rate function (Sharpe and DeMichele, 1977):
\[ G[T(t)] = \frac{T(t) \cdot \exp\left(\frac{A - B}{T(t)}\right)}{1 + \exp\left(\frac{C - D}{T(t)}\right) + \exp\left(\frac{E - F}{T(t)}\right)} \] (6)

where \( A, B, C, D, E, F \) are parameters related to the enzyme kinetics \( \text{(Rossini et al., 2019a)} \).

The parameters of equations (4)-(6) were estimated through a non-linear regression using the informatic tools based on the Minuit algorithm included in the ROOT’s libraries \( \text{(Cern 2020; Brun and Rademakers 2007)} \) presented by Rossini et al. \( \text{(2019b, 2020e)} \). Moreover, the development rate functions \( \text{(4)-(6)} \) present a characteristic increasing-decreasing profile, with a well-defined maximum indicating the optimal temperature for the development of the species \( \text{(Rossini et al., 2020e)} \). This important biological information was calculated for each of the aforementioned development functions. As reported by Rossini et al. \( \text{(2020e)} \), by setting the first derivative of the development rate function to zero \( \frac{d}{dT} G[T(t)] = 0 \), it is possible to obtain the \( T^* \) value for each of the expressions \( \text{(4)-(6)} \). Since the Minuit algorithm also provides the standard errors associated with the parameters estimated, it is possible to calculate the error associated with the optimal temperature \( T^* \), applying the propagation of uncertainty formula. For readers with a particular interest in this topic, the work of Rossini et al. \( \text{(2020e)} \) may be helpful for its presentation of the major details.

Once the best fit parameters for the expressions \( \text{(4)-(6)} \) were obtained, the next step was to evaluate and determine the most reliable one to use for simulations with equation \( \text{(1)} \). In pursuit of this part of the study, the \textit{a priori} analysis described by Rossini et al. \( \text{(2020c)} \) was applied. In particular, this methodology provides for an evaluation of the coefficient of determination \( R^2 \), and to a \( \chi^2 \)-test. The development rate function with the \( R^2 \) closest to 1, and with the higher \( P \)-value from \( \chi^2 \)-test was considered for simulations with the model \( \text{(1)} \).

### 2.2.2. Stock rearing and egg collection

A stock rearing of \( C. cephalonica \) is maintained since 10 years at DeFENS, Università degli Studi di Milano “La Statale”, at 27 ± 1 °C, 70 ± 5 %RH and photoperiod of 16:8 (light:dark) on a standard diet made of bran (24.5 g), wheat flour (14 g), corn flour (15 g), wheat germ (9 g), dry yeast (6.5 g), honey (14 g), glycerine (17 g).

Newly emerged adults were put in a glass jar (Ø 13 cm, height 20 cm, 1.7 L), closed with tulle fixed with plastic bands, turned upside down on a Petri dish in order to collect eggs. Eggs 0-24 hours old were collected
and verified at the stereomicroscope, in order to discharge damaged or irregular eggs. Groups of 100 eggs were reared on the standard diet in Petri dishes (15 cm Ø).

This stock rearing ensured a continuous availability of *C. cephalonica* for both the life tables and the model validation purposes detailed below.

### 2.2.3. Life tables

The estimation of the parameters of expressions (4)-(6) requires data about insects’ development times at different constant temperatures, namely, the life tables (Harcourt, 1969). These data were obtained with a series of rearing experimentations in a growth chamber (Piardi mod. CFT600) where cohorts of *C. cephalonica* individuals developed at constant temperatures of 18, 21, 24, 26, 28, 30, 34 and 36 °C.

For each rearing session, an average number of fifty eggs 0-24 hour old were placed in glass cylinders (Ø 3.8 cm, height 2.5 cm) closed with wire net to maintain their individuality. Subsequently, insects grew in the rearing room at a constant temperature (±1 °C), at 70 ± 5 % of relative humidity and with a photoperiod of 16:8 hours (light:dark). The total number of eggs reared for each temperature (summing all the repetitions for each temperature), defined with *N*<sub>init</sub>, is reported in Table 1. Insects were fed with the standard diet described in Section 2.2.2. and inspected once a day to record the current life stage of each specimen. For each temperature, the mean development times of egg, larva (1-6 instar), pupa and egg-adult stages were calculated, with their corresponding standard errors. During the experimentation, only the individuals who emerged after pupation were considered. Hence the standard error was calculated considering the number of adults obtained at each constant temperature of rearing, defined with *N*<sub>surv</sub> (Table 1).

Although mean development times were calculated for preimaginal stages, the parameters of the expressions (4)-(6) were evaluated only for egg-adult stages. The reason behind this choice is practical: in fact, using a single development rate function instead of one for each preimaginal stage simplifies the application of the numerical scheme (2), without loss of information. For a more accurate estimation of the development rate function parameters, the development times of the 498 adults that emerged from pupation at the various temperatures surveyed were considered. More specifically, each development time was converted into a development rate using the expression (3), and then inputted into the non-linear regression described in Section 2.2.1.
2.3. Experimental design for validation

Once the life tables described in Section 2.2.3 were assessed, a second experimentation was conducted involving the validation of the model (1). In particular, the same experiment was repeated three times during the summer of 2017, which consisted of rearing rice moth populations in a semi-field environment located at the DeFENS laboratory, at Università degli Studi di Milano “La Statale”.

In each of the three different replications of the validation, 20 males and 20 females of *C. cephalonica* adults were placed in a cage (dimensions of 1x1x1 m) protected with an anti-aphid net to avoid the dispersal of individuals. Eggs, laid by the females after the coupling, were collected daily from the cage until all adults were alive. The eggs of the day were subsequently clustered in Petri dishes and their development was observed every two days.

As for the rearing described in Section 2.2.3, insects in this case were also fed with a standard diet but developed in varying temperature conditions.

During the investigations, a data logger (Cryopak mod. Mini TH) recorded the environmental temperature with a frequency of 1 acquisition/hour. Then, the 24 values acquired each day were used to calculate the daily average temperature value needed as input for the model (1).

Adults’ flight dynamics were ascertained every two days by inspecting the Petri dishes, where the daily eggs have been placed after their collection from the cages, counting and removing the new individuals. Considering the sampling range, an error of ±1 day, corresponding to the half of the time occurring between two inspections, was associated with experimental data.

2.4. Model validation

Simulations were compared with field populations using the *a posteriori* analysis introduced by Rossini et al. (2020c, 2020d, 2020b). This methodology provides for the use of the $\chi^2$-function as an indicator of the distance between simulations and field data:

$$\chi^2 = \sum_{i=1}^{n} \frac{(O_i - E_i)^2}{E_i}$$
Hence, the \( n \) points \( O_i \), corresponding to the experimental population, were compared with their respective simulated point \( E_i \). In addition, a second indicator of the overlap between simulation and field data is represented by the \( R^2 \)-value (Ikemoto and Kiritani, 2019). The latter can be defined as

\[
R^2 = 1 - \frac{\sum_{i=1}^{n}(O_i - E_i)^2}{\sum_{i=1}^{n}(O_i - \bar{E}_i)^2}
\]  

(8)

where \( n \), \( O_i \) and \( E_i \) have the same meaning described for the expression (7).

According to the \textit{a posteriori} analysis, a simulation can be considered reliable if its \( R^2 \)-value is close to 1, and its \( \chi^2 \)-value (7) is as low as possible.

3. Results

3.1. Development rate functions parameters

The first results of the present study are the \textit{C. cephalonica} life tables. The average development times calculated for egg, larva (1-6 instars), pupa and egg-adult stages are listed in Table 1 with their standard errors.

In addition, in Table 1 the total number of eggs reared (\( N_{\text{init}} \)) and the total number of adults that emerged from pupation (\( N_{\text{surv}} \)) for each temperature of rearing are reported.

Table 1. \textit{Coreyra cephalonica} life tables. The mean development time and their standard errors (\( \pm SE \)) are reported for: egg, larva (1-6 instars), pupa and egg-adult stages. \( N_{\text{init}} \) indicates the total number of individuals placed into the growth chamber, while \( N_{\text{surv}} \) indicates the total number of adults that emerged from pupation.

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>( N_{\text{init}} )</th>
<th>Egg (( \pm SE )) (days)</th>
<th>Larva (( \pm SE )) (days)</th>
<th>Pupa (( \pm SE )) (days)</th>
<th>Egg-Adult (( \pm SE )) (days)</th>
<th>( N_{\text{surv}} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>18</td>
<td>40</td>
<td>8.2 ± 0.2</td>
<td>25 ± 5</td>
<td>25 ± 2</td>
<td>59 ± 4</td>
<td>7</td>
</tr>
<tr>
<td>21</td>
<td>80</td>
<td>8.0 ± 0.1</td>
<td>44.5 ± 0.9</td>
<td>21.7 ± 0.3</td>
<td>74 ± 1</td>
<td>32</td>
</tr>
<tr>
<td>24</td>
<td>140</td>
<td>6.4 ± 0.1</td>
<td>26.4 ± 0.2</td>
<td>15.9 ± 0.2</td>
<td>48.0 ± 0.2</td>
<td>115</td>
</tr>
<tr>
<td>26</td>
<td>160</td>
<td>4.81 ± 0.08</td>
<td>24.4 ± 0.4</td>
<td>14.5 ± 0.3</td>
<td>43.8 ± 0.6</td>
<td>137</td>
</tr>
<tr>
<td>28</td>
<td>70</td>
<td>5.04 ± 0.03</td>
<td>22.8 ± 0.4</td>
<td>13.0 ± 0.3</td>
<td>41.0 ± 0.4</td>
<td>62</td>
</tr>
<tr>
<td>30</td>
<td>180</td>
<td>4.23 ± 0.06</td>
<td>23.6 ± 0.5</td>
<td>11.3 ± 0.2</td>
<td>39.2 ± 0.6</td>
<td>129</td>
</tr>
</tbody>
</table>
The development times of the 498 individuals that were reared and emerged from pupation at the various temperatures were subsequently converted into rates with the expression (3) and involved in the non-linear regressions with the expressions (4)-(6). The best fit parameters calculated are listed in Table 2, while Figure 1 shows a graphical representation of the best fit functions.

According to the *a priori* analysis described in Section 2.2.1, the Logan expression was shown to be less reliable in describing experimental data. Although $\chi^2$-test reported $P > 0.999$, the $R^2$-value is lower than that for the Briére and Sharpe and De Michele expressions (Table 2). The optimal temperature value for rice moths’ development provided by the Logan function (4) was calculated to be $32.22 \pm 0.02 \, ^\circ C$.

In order of reliability, the Briére expression (5) provided $P > 0.999$ from the $\chi^2$-test, but a higher $R^2$-value than the Logan one. In this case the optimal temperature value calculated was $32.478 \pm 0.008 \, ^\circ C$.

Table 2. Development rate function parameters and their standard errors. These best fit functions, graphically represented in Figure 1, are related to the egg-adult stages. For each expression the $\chi^2$ and $R^2$ values are also reported, as well as the number of degrees of freedom considered for the $\chi^2$-test.

<table>
<thead>
<tr>
<th>Development rate function</th>
<th>Parameter values ($\pm SE$)</th>
<th>$\chi^2$-value</th>
<th>$R^2$-value</th>
<th>Number of degrees of freedom (NDF)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Logan</td>
<td>$\psi = (6.19 \pm 0.03) \cdot 10^{-3}$</td>
<td>0.154</td>
<td>0.815</td>
<td>494</td>
</tr>
<tr>
<td></td>
<td>$\rho = (5.00 \pm 0.01) \cdot 10^{-2}$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$T_M = 37.348 \pm 0.008$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$\Delta T = 2.00 \pm 0.01$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Briére</td>
<td>$a = (2.0 \pm 0.3) \cdot 10^{-5}$</td>
<td>0.146</td>
<td>0.949</td>
<td>494</td>
</tr>
<tr>
<td></td>
<td>$T_L = 2.070 \pm 0.009$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$T_M = 36.123 \pm 0.009$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$m = 3.89 \pm 0.01$</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
\[ A = 28.96 \pm 0.09 \]
\[ B = -1797 \pm 2 \]
\[ C = 35.76 \pm 0.09 \]
\[ D = -1804 \pm 2 \]
\[ E = 83 \pm 2 \]
\[ F = -90 \pm 80 \]

The Sharpe and De Michele development rate function (6) was shown to be the most reliable in representing the life tables. In fact, the \( \chi^2 \)-test provided \( P > 0.999 \), but the \( R^2 \)-value was the highest (Table 2). The optimal temperature value for this expression was calculated to be \( 33 \pm 1 \) °C.

Additional plots representing the best fit functions listed in Table 2 with the experimental data, or with the 0.95 confidence level, are presented as supplementary material. As stated in Section 2.2.1, the most reliable development rate function (Sharpe and De Michele) was used for the second part of the present study, the validation of the equation (1).

Figure 1. Best representing development rate functions for Corecyra cephalonica egg-adult stages. The parameters of each function are reported in Table 2, while additional plots are reported in the supplementary materials.
3.2. Model validation

The Sharpe and De Michele development rate function \( (6) \) was discretised and inserted into the numerical scheme \( (2) \) with its best fit parameters. The procedure described in Section 2.1 provided the simulations for each of the three validation experiments. In the three experiments 425, 846 and 513 eggs, respectively, were collected in the cages, and represented the initial cohort of the three populations simulated in the validation experiments. Simulation and field data from the first experiment are reported in Figure 2. In particular, both the simulation and field data assessed a maximum peak on 28th June. Proceeding by order, the results of the second validation experiment are reported in Figure 3. In this case, the maximum peak of the field population occurred on 28th July, while the simulation indicated a forecast on 27th July. The results of the third and last validation experiment are represented in Figure 4. As assessed for the first validation experiment, both the simulation and field data indicated a maximum peak on the same day, 30th August.

Figure 2. Comparison between *Corcyra cephalonica* population retrieved from semi-field (dots) data and its simulation (continuous line).
Figure 3. Comparison between *Coreyra cephalonica* population retrieved from semi-field (dots) data and its simulation (continuous line).

Figure 4. Comparison between *Coreyra cephalonica* population retrieved from semi-field (dots) data and its simulation (continuous line).
The overall superimposition between field data and simulation was evaluated using the \textit{a posteriori} analysis, as stated in Section 2.4. $\chi^2$ and $R^2$ values calculated with the expressions (7) and (8) are listed in Table 3.

Table 3. $\chi^2$ and $R^2$ values comparing simulated and field populations for each repeated experiment.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>$\chi^2$-value</th>
<th>$R^2$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st validation</td>
<td>7.404</td>
<td>0.823</td>
</tr>
<tr>
<td>2nd validation</td>
<td>53.695</td>
<td>0.992</td>
</tr>
<tr>
<td>3rd validation</td>
<td>2.900</td>
<td>0.981</td>
</tr>
</tbody>
</table>

4. Discussion and conclusions

The life tables presented as the first results of this study provide important information about the biology of the rice moth. Among the values acquired, an unexpected result was obtained in the larval development times at 21°C. In fact, in this case the larval development was highly delayed when compared to the other temperatures; values of this type are to be expected for experimentations close to the thermal thresholds. This unexpected average value at 21°C, however, did not compromise the overall estimation of the development rate functions parameters. In fact, using the total of 498 data acquired, the non-linear regression was made more reliable and less influenced by data not apparently in line with the others. On the whole Logan, Brière, and Sharpe and De Michele development rate functions were assessed for their reliability in representing the life tables’ data, and this is underlined by the $P$-values that resulted from the $\chi^2$-test. Hence, although the \textit{a priori} analysis elected the Sharpe and De Michele as the most reliable development rate function to use within equation (1), the Logan and Brière functions also contributed to extend the pool of information about the biology of the rice moth.

The first information derives from the upper and lower thermal thresholds above and below which species development is theoretically not possible, respectively. This aspect is highlighted by the Brière expression: referring to the threshold values (Table 2), it is possible to say that the rice moth is capable of surviving and developing at both low and high temperatures, in line with the results obtained by Cox et al. (1981) and Osman et al. (1984). The knowledge of the threshold values, however, can support the scientific community that is
working on alternative control strategies (Nasr et al., 2015) based, for example, on thermal heating with radio
frequencies (Yang et al., 2015) or thermal cooling of the stored grains. On the basis of our results, thermal
treatments in grain storage silos have to cool below $T_L$, and heat above $T_M$ in order to be most effective. The
latter value is also reported by the Logan expression, and even though there is a small difference between the
$T_M$ values of Logan and Brière, on the whole they indicate a similar upper threshold. However, the Logan
offers additional biological information, enclosed to $\Delta T$. To be specific, this parameter expresses the response
of the species to high temperatures, quantifying the width of the range of abrupt collapse after the maximum
of the development rate function (and hence of the optimal temperature). This information is helpful, again, to
set opportune control actions for heating the silos: the temperature setting, in fact, is usually based on the
concept of “maximum efficiency with minimum costs”. The knowledge of $\Delta T$ may be beneficial in this sense,
because it can be taken into account in cost-benefit analyses (Pappalardo et al., 2017).

The second result of the present work concerns, on the other hand, the validation of the model (1), applied in
conditions of varying temperature in a semi-field environment. These assessments increase the reliability of
the model presented by Rossini et al. (2019a). More specifically, the $R^2$ values close to 1 suggest that
simulations respond to the experimental data trend, but a numerical indication of the overlapping is provided
by the $\chi^2$-values. However, a difference between two high numbers may provide a higher $\chi^2$, reason for which
the a posteriori analysis introduced by Rossini et al. (2021, 2020c, 2020a) considers both $\chi^2$ and $R^2$.
Overall, this study has provided rather important biological information about the rice moth, which will be a
helpful tool for an IPM framework. Preventive actions to control infestations in stored grain, indeed, are
commonly based on active ingredients which are potentially harmful to the health of consumers and
environment, such as fumigants (Yang et al., 2015). The immediate disadvantage of the infestations by C.
cephalonica (and by other insect pests) in the storage sites, would be the non-marketability of products.
However, storage systems also have certain advantages, if supported by modern technologies. A predictive
model based on the environmental temperature, external or internal to the silos, can provide indications about
the risk of infestation. Hence, in an IPM framework, a decision support system based on the tools presented
and applied in this study can be of great assistance to technicians, in order to reduce the amount of active
ingredients required and thus lower production costs. On the basis of the foreseen pest population density, with
a subdivision in life stages, an action threshold may be defined for each infestation level. The model
predictions, in this sense, are helpful to minimize the use of conventional agrochemicals, restricting their use only when it is strictly necessary. An optimised control, for instance, may encourage the alternation of conventional agrochemicals with natural active ingredients extracted from plants, and that may be effective only on particular stages and at low population densities. Indeed, Mathew and Padmanabhan (2015) studied the properties of essential oils of *Origanum majorana* L. on the egg laying and hatchability of species, while Allotey and Azalekor (2000) investigated the insecticidal properties of *Citrus sinensis* (L.) Osbeck, *Chromolaena odorata* (L.) King & Rob, and *Eichhornia crassipes* (Mart.) Solms.

Moreover, the knowledge of the population trends, on the basis of the thermal conditions in the storage system, can be helpful for the management of alternative control methods, such as the use of natural enemies. Natural control methods can be offered by insect enemies belonging to the genera *Trichogramma* and *Bracon* [Bhandari et al., 2014]. These valuable candidates may be involved in a biological control program, but one of the major difficulties is that their efficiency as pest management tools strongly depends on the time of release. Accordingly, a delayed release of natural enemies would not provide the expected result, and in this case a forecasting model could be of fundamental importance. An ideal application, in fact, provides for a double simulation using the model (1) to represent the population density of the rice moth and of its selected natural enemy. This is possible because the application of the model (1) provides for the estimation of the development rate functions parameters, which is made possible only using life tables data. Hence, once a valuable candidate is chosen among those proposed by Bhandari et al. (2014) or Nasr et al. (2015), a series of constant temperature rearing would enable their development rate function parameters to be estimated. Furthermore, life tables in this case can provide the parasitization or predation rate, an additional and helpful set of information, which can be included in the mortality rate function of the rice moth.

To control the rice moth, it also may be helpful to find, because predictions can indicate if the treatment is necessary, and when the most susceptible life stage to control will occur.

The results obtained in this work, hence, lay the foundations of the mathematical description of *C. cephalonica* populations, providing a key element in the development of decision support system tools aimed to control the species in warehouses. Further developments of the model should be directed on the side of optimization algorithms, besides to include mortality and fertility. The idea beyond this study, in fact, is to adjust the simulations on the basis of monitoring data provided, for instance, by automated systems based on the near
infrared spectroscopy (Johnson, 2020). One of the criticalities in applying the model (1), in fact, is the estimation of the population abundance depending, mainly, on the distribution of the individuals into the life stages at time zero. A continuous set of data about the “past and the present” situation in the warehouses, flanked to optimization algorithms may be used to update frequently the model response in order to obtain the most reliable prediction, and a more reliable decision support system tool.

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