

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

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17

18 ***Abstract***

19

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

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

28 The aim of this work concerns two aspects of a model application and validation. Since physiologically based
29 models require information about interactions between species and environment, *C. cephalonica* individuals
30 were reared at different constant temperatures: 18, 21, 24, 26, 28, 30, 34 and 36 °C. This first part provided

31 the life tables, whose data were used to estimate the parameters of the Logan, Brière, and Sharpe and De
32 Michele development rate functions.

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

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

38

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

41

42 **1. Introduction**

43

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

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

57 Biological and ecological studies on *C. cephalonica* were first conducted by Cox et al. (1981) and Osman et
58 al. (1984). The life cycle is composed of egg, six larval instars, pupa and adult stages, with an average duration

59 of 40 days in optimal temperature conditions (28 – 30 °C). Moreover, the rice moth has shown a high
60 adaptability to develop in different conditions of relative humidity (15 – 90%) and temperature (15 – 37 °C)
61 (Limonta et al., 2009) with no difference in the extent of damages caused. Even if natural populations can be
62 found directly in cultivated fields, most of the damages are reported in storage systems. In fact, the particular
63 conditions in which product stockpiles are kept offer protection and unlimited food to the rice moths, which
64 can reproduce continuously. Accordingly, a prompt control action is required to reduce risks and damages
65 caused by *C. cephalonica* in storage systems.

66 Despite the different control strategies available in the literature, predictions based on mathematical models
67 represent a powerful tool in an Integrated Pest Management (IPM) framework (Dalal and Singh, 2017). More
68 specifically, forecasts of the population dynamics of insect pests can help farmers and technicians to select the
69 most appropriate control strategy (Rupnik et al., 2019). On the other hand, the development of a reliable model
70 requires a deep knowledge of the species' biology and of their relationship with environmental parameters.

71 For ectotherm organisms, as well as insects, the average duration of their life cycle is related to environmental
72 parameters, such as temperature or relative humidity (Birch, 1948; Gilbert et al., 2004; Rossini et al., 2019a).
73 However, in the specific case of *C. cephalonica*, the latter is less relevant because stored grain are usually
74 maintained in a dry environment for conservation reasons. As such, temperature is usually the main driving
75 variable, because the majority of storage sites do not have thermal control systems.

76 As a result, a deeper knowledge of the relationship between *C. cephalonica* and environmental temperature is
77 necessary, and it is also useful to apply physiologically based models to describe the density of its population.
78 Recently, Rossini et al. (2019a) proposed and applied a partial differential equations-based model in other case
79 studies (Rossini et al., 2021, 2020a), in order to represent ectotherm populations developing over time and
80 through their life stages. Subsequently, their model was implemented in a calculation software (Rossini et al.,
81 2020e, 2019b) and supported by a protocol of application (Rossini et al., 2020c).

82 The aim of the present study is the application and validation of the aforementioned physiologically based
83 model to the case study of *C. cephalonica*. The application of the model requires a robust knowledge of the
84 species' response to environmental temperature. For this reason, the first part of the work consisted of a series
85 of constant temperature experimentations rearing at 18, 21, 24, 26, 28, 30, 34 and 36 °C, providing *C.*
86 *cephalonica* life tables. This part of the research completes the previous work of Osman et al. (1984). Life

87 tables were used to estimate the parameters of the Logan, Brière, and Sharpe and De Michele development
 88 rate functions, mathematical expressions that relate the environmental temperature with the speed of growth
 89 of ectotherms. Development rate functions parameters were subsequently included in the physiologically based
 90 model for its validation. The latter, more specifically, was conducted in conditions of varying temperature in
 91 a semi-field environment, by placing a cohort of eggs in Petri dishes and reporting the adults' flight dynamics.

92

93 **2. Materials and methods**

94

95 **2.1. Population density model**

96

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

$$\left\{ \begin{array}{l} \frac{\partial}{\partial t} N(t, x) + \frac{\partial}{\partial x} [G(t, x) N(t, x)] = -M(t, x) N(t, x) \\ N(t, 0) = \int_0^{x_m} \beta(t, x') N(t, x') dx' \\ N(0, x) = n^0(x) \end{array} \right. \quad (1)$$

108 The development through the life stages is ruled by the function $G(t, x)$ known as the 'generalised
 109 development rate function' and which, in its most general form, considers the dependence on the
 110 environmental parameters (usually time-dependent) and on aging. Mortality and birth rates are described by

111 $M(t, x)$ and $\beta(t, x)$, respectively, while the initial and boundary conditions $N(0, x)$ and $N(t, 0)$ represent the
 112 initial population profile, and the amount of individuals produced between the ages 0 and x_m , respectively.
 113 Hence, biological information within equation (1) are included in the functions $G(t, x)$, $M(t, x)$, and $\beta(t, x)$,
 114 which can be considered, in their most general meaning, as sub-models.
 115 However, the application of the model (1) in varying temperature conditions makes the use of numerical
 116 solutions essential. This is due to the impossibility of representing the variation of the daily average
 117 temperature over the year with an analytical function; hence, this value needs to be recorded by meteorological
 118 stations or data loggers directly in the insects' living environment. This problem was overcome by combining
 119 the method of the lines and the Euler's finite difference method (Bellagamba et al., 1987; Keyfitz and Keyfitz,
 120 1997; Plant and Wilson, 1986; Rossini et al., 2020d, 2020f, 2019a), which led to the following discrete version
 121 of the equation (1):

$$\begin{cases} N_h^{i+1} = \frac{i}{h} G_h^i N_{h-1}^i + N_h^i \left[1 - 2 \frac{i}{h} G_h^i + \frac{i}{h} G_{h-1}^i - i M_h^i \right] \\ N_0^i = \sum_{i=0}^{h_m} \beta_h^i N_h^i h \\ N_h^0 = N_0 \end{cases} \quad (2)$$

122 To avoid confusion between continuous and discrete variables, in the numerical scheme (2) discrete age (the
 123 life stage) is represented by h , while i is the time step of the simulation (usually set to one day). The letters N ,
 124 G , M and β conserve the meaning of the functions introduced for the system (1), but in this case they indicate
 125 their respective discrete versions. The numerical scheme (2) was computed with informatic tools based on
 126 C++ programming language and on ROOT's software (Cern 2020) libraries, as reported by Rossini et al.
 127 (2019b, 2020e). The software takes as input the biological parameters of the species (i.e., the development,
 128 mortality and birth rate functions parameters) and the daily average temperatures recorded in the field. The
 129 outputs are the simulated population densities over time for each life stage of the species.

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

133 In the light of these assumptions, further discussion is required for the generalised development rate function
 134 $G(t, x)$, and on how it can be simplified and estimated with experimental data.

135

136 2.2. Development rate functions and life tables

137

138 2.2.1. Development rate functions

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

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

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

- 150 • The Logan development rate function (Logan et al., 1976):

$$G[T(t)] = \psi \left[\exp(\rho T(t)) - \exp\left(\rho T_M - \frac{T_M - T(t)}{\Delta T}\right) \right] \quad (4)$$

151 where ψ and ρ are empirical parameters, T_M is the maximum temperature threshold above which the
152 species theoretically cannot develop, and ΔT is the range of temperature between the maximum of the
153 function, and T_M .

- 154 • The Brière development rate function (Brière et al., 1999):

$$G[T(t)] = aT(t)(T(t) - T_L)(T_M - T(t))^{\frac{1}{m}} \quad (5)$$

155 where a and m are empirical parameters, and T_L and T_M are the lower and upper temperature thresholds
156 for the species, respectively.

- 157 • The Sharpe and De Michele development rate function (Sharpe and DeMichele, 1977):

$$G[T(t)] = \frac{T(t) \cdot \exp\left(A - \frac{B}{T(t)}\right)}{1 + \exp\left(C - \frac{D}{T(t)}\right) + \exp\left(E - \frac{F}{T(t)}\right)} \quad (6)$$

158 where A, B, C, D, E, F are parameters related to the enzyme kinetics (Rossini et al., 2019a).
 159 The parameters of equations (4)-(6) were estimated through a non-linear regression using the informatic tools
 160 based on the *Minuit* algorithm included in the ROOT's libraries (Cern 2020; Brun and Rademakers 2007)
 161 presented by Rossini et al. (2019b, 2020e). Moreover, the development rate functions (4)-(6) present a
 162 characteristic increasing-decreasing profile, with a well-defined maximum indicating the optimal temperature
 163 for the development of the species (Rossini et al., 2020e). This important biological information was calculated
 164 for each of the aforementioned development functions. As reported by Rossini et al. (2020e), by setting the
 165 first derivative of the development rate function to zero $\frac{d}{dT(t)}G[T(t)] = 0$, it is possible to obtain the T^* value
 166 for each of the expressions (4)-(6). Since the *Minuit* algorithm also provides the standard errors associated
 167 with the parameters estimated, it is possible to calculate the error associated with the optimal temperature T^* ,
 168 applying the propagation of uncertainty formula. For readers with a particular interest in this topic, the work
 169 of Rossini et al. (2020e) may be helpful for its presentation of the major details.
 170 Once the best fit parameters for the expressions (4)-(6) were obtained, the next step was to evaluate and
 171 determine the most reliable one to use for simulations with equation (1). In pursuit of this part of the study, the
 172 *a priori* analysis described by Rossini et al. (2020c) was applied. In particular, this methodology provides for
 173 an evaluation of the coefficient of determination R^2 , and to a χ^2 -test. The development rate function with the
 174 R^2 closest to 1, and with the higher P -value from χ^2 -test was considered for simulations with the model (1).
 175

176 2.2.2. Stock rearing and egg collection

177 A stock rearing of *C. cephalonica* is maintained since 10 years at DeFENS, Università degli Studi di Milano
 178 "La Statale", at 27 ± 1 °C, 70 ± 5 %RH and photoperiod of 16:8 (light:dark) on a standard diet made of bran
 179 (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
 180 g).
 181 Newly emerged adults were put in a glass jar (Ø 13 cm, height 20 cm, 1.7 L), closed with tulle fixed with
 182 plastic bands, turned upside down on a Petri dish in order to collect eggs. Eggs 0-24 hours old were collected

183 and verified at the stereomicroscope, in order to discharge damaged or irregular eggs. Groups of 100 eggs were
184 reared on the standard diet in Petri dishes (15 cm Ø).

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

187

188 **2.2.3. Life tables**

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

193 For each rearing session, an average number of fifty eggs 0-24 hour old were placed in glass cylinders (Ø 3.8
194 cm, height 2.5 cm) closed with wire net to maintain their individuality. Subsequently, insects grew in the
195 rearing room at a constant temperature (± 1 °C), at 70 ± 5 % of relative humidity and with a photoperiod of
196 16:8 hours (light:dark). The total number of eggs reared for each temperature (summing all the repetitions for
197 each temperature), defined with N_{mit} , is reported in Table 1. Insects were fed with the standard diet described
198 in Section 2.2.2. and inspected once a day to record the current life stage of each specimen. For each
199 temperature, the mean development times of egg, larva (1-6 instar), pupa and egg-adult stages were calculated,
200 with their corresponding standard errors. During the experimentation, only the individuals who emerged after
201 pupation were considered. Hence the standard error was calculated considering the number of adults obtained
202 at each constant temperature of rearing, defined with N_{surv} (Table 1).

203 Although mean development times were calculated for preimaginal stages, the parameters of the expressions
204 (4)-(6) were evaluated only for egg-adult stages. The reason behind this choice is practical: in fact, using a
205 single development rate function instead of one for each preimaginal stage simplifies the application of the
206 numerical scheme (2), without loss of information. For a more accurate estimation of the development rate
207 function parameters, the development times of the 498 adults that emerged from pupation at the various
208 temperatures surveyed were considered. More specifically, each development time was converted into a
209 development rate using the expression (3), and then inputted into the non-linear regression described in Section
210 2.2.1.

211

212 **2.3. Experimental design for validation**

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

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

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

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

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

231

232 **2.4. Model validation**

233

234 Simulations were compared with field populations using the *a posteriori* analysis introduced by Rossini et al.
235 (2020c, 2020d, 2020b). This methodology provides for the use of the χ^2 -function as an indicator of the distance
236 between simulations and field data:

$$\chi^2 = \sum_{i=1}^n \frac{(O_i - E_i)^2}{E_i} \quad (7)$$

237 Hence, the n points O_i , corresponding to the experimental population, were compared with their respective
 238 simulated point E_i . In addition, a second indicator of the overlap between simulation and field data is
 239 represented by the R^2 -value (Ikemoto and Kiritani, 2019). The latter can be defined as

$$R^2 = 1 - \frac{\sum_{i=1}^n (O_i - E_i)^2}{\sum_{i=1}^n (O_i - \bar{E}_i)^2} \quad (8)$$

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

241 According to the *a posteriori* analysis, a simulation can be considered reliable if its R^2 -value is close to 1, and
 242 its χ^2 -value (7) is as low as possible.

243

244 3. Results

245 3.1. Development rate functions parameters

246

247 The first results of the present study are the *C. cephalonica* life tables. The average development times
 248 calculated for egg, larva (1-6 instars), pupa and egg-adult stages are listed in Table 1 with their standard errors.
 249 In addition, in Table 1 the total number of eggs reared (N_{init}) and the total number of adults that emerged from
 250 pupation (N_{surv}) for each temperature of rearing are reported.

251

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

Temperature (± 1 °C)	N_{init}	Egg ($\pm SE$) (days)	Larva ($\pm SE$) (days)	Pupa ($\pm SE$) (days)	Egg-Adult ($\pm SE$) (days)	N_{surv}
18	40	8.2 \pm 0.2	25 \pm 5	25 \pm 2	59 \pm 4	7
21	80	8.0 \pm 0.1	44.5 \pm 0.9	21.7 \pm 0.3	74 \pm 1	32
24	140	6.4 \pm 0.1	26.4 \pm 0.2	15.9 \pm 0.2	48.0 \pm 0.2	115
26	160	4.81 \pm 0.08	24.4 \pm 0.4	14.5 \pm 0.3	43.8 \pm 0.6	137
28	70	5.04 \pm 0.03	22.8 \pm 0.4	13.0 \pm 0.3	41.0 \pm 0.4	62
30	180	4.23 \pm 0.06	23.6 \pm 0.5	11.3 \pm 0.2	39.2 \pm 0.6	129

34	40	2.8 ± 0.2	21.0 ± 0.5	10 ± 1	34 ± 1	12
36	40	4 ± 0	53 ± 1	13 ± 3	69 ± 3	4

255

256 The development times of the 498 individuals that were reared and emerged from pupation at the various
 257 temperatures were subsequently converted into rates with the expression (3) and involved in the non-linear
 258 regressions with the expressions (4)-(6). The best fit parameters calculated are listed in Table 2, while Figure
 259 1 shows a graphical representation of the best fit functions.

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

264 In order of reliability, the Brière expression (5) provided $P > 0.999$ from the χ^2 -test, but a higher R^2 -value
 265 than the Logan one. In this case the optimal temperature value calculated was 32.478 ± 0.008 °C.

266

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

Development rate function	Parameter values ($\pm SE$)	χ^2 -value	R^2 -value	Number of degrees of freedom (<i>NDF</i>)
Logan	$\psi = (6.19 \pm 0.03) \cdot 10^{-3}$	0.154	0.815	494
	$\rho = (5.00 \pm 0.01) \cdot 10^{-2}$			
	$T_M = 37.348 \pm 0.008$			
	$\Delta T = 2.00 \pm 0.01$			
Brière	$a = (2.0 \pm 0.3) \cdot 10^{-5}$	0.146	0.949	494
	$T_L = 2.070 \pm 0.009$			
	$T_M = 36.123 \pm 0.009$			
	$m = 3.89 \pm 0.01$			

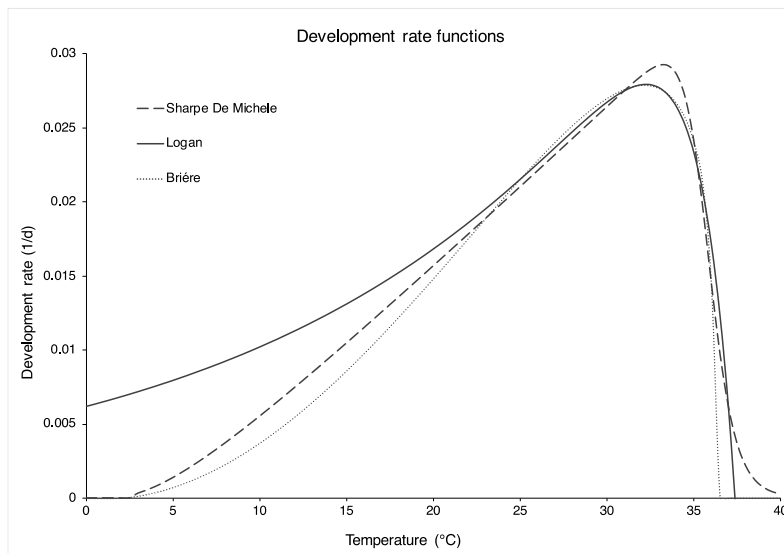
	$A = 28.96 \pm 0.09$			
	$B = -1797 \pm 2$			
Sharpe and De Michele	$C = 35.76 \pm 0.09$	0.200	> 0.999	492
	$D = -1804 \pm 2$			
	$E = 83 \pm 2$			
	$F = -90 \pm 80$			

270

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

274 Additional plots representing the best fit functions listed in Table 2 with the experimental data, or with the
 275 0.95 confidence level, are presented as supplementary material. As stated in Section 2.2.1, the most reliable
 276 development rate function (Sharpe and De Michele) was used for the second part of the present study, the
 277 validation of the equation (1).

278



279

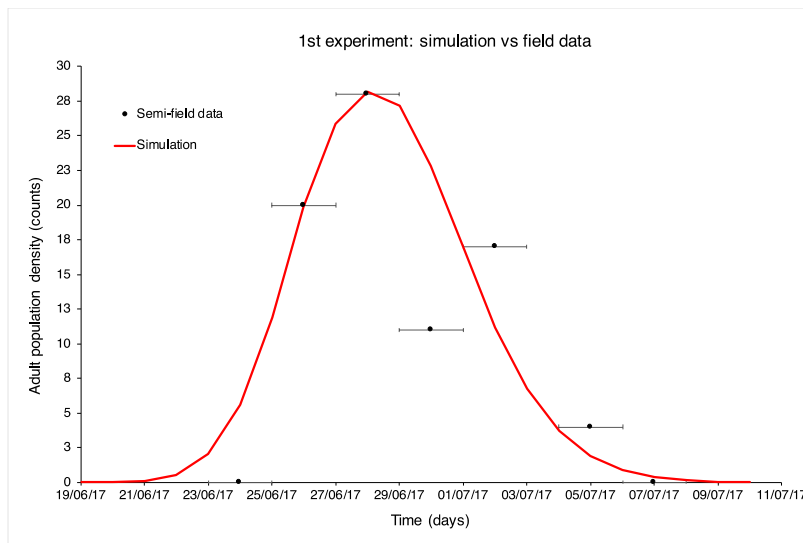
280 Figure 1. Best representing development rate functions for *Coreyra cephalonica* egg-adult stages. The parameters of each
 281 function are reported in Table 2, while additional plots are reported in the supplementary materials.

282

283 3.2. Model validation

284

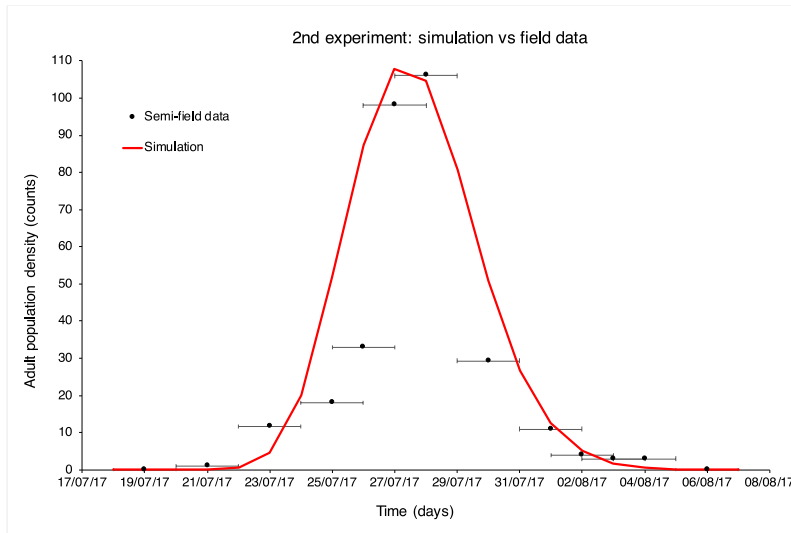
285 The Sharpe and De Michele development rate function (6) was discretised and inserted into the numerical
286 scheme (2) with its best fit parameters. The procedure described in Section 2.1 provided the simulations for
287 each of the three validation experiments. In the three experiments 425, 846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



295

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

298

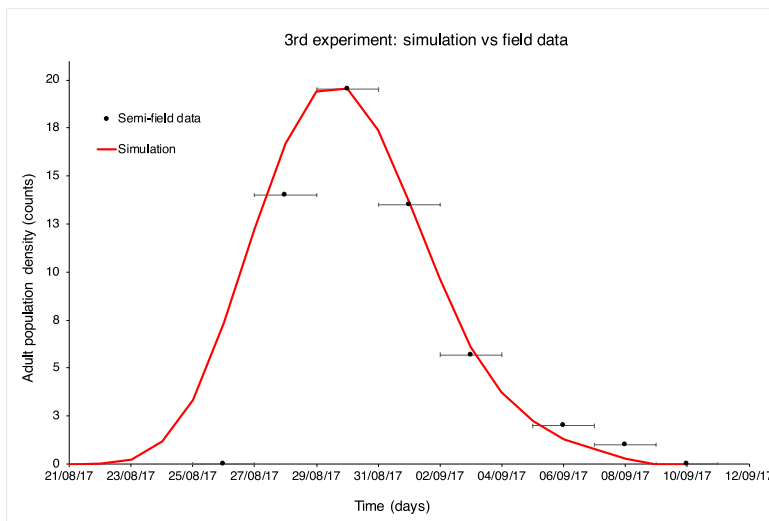


299

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

302

303



304

305 Figure 4. Comparison between *Corcyra cephalonica* population retrieved from semi-field (dots) data and its simulation
 306 (continuous line).

307

308 The overall superimposition between field data and simulation was evaluated using the *a posteriori* analysis,
309 as stated in Section 2.4. χ^2 and R^2 values calculated with the expressions (7) and (8) are listed in Table 3.

310

311 Table 3. χ^2 and R^2 values comparing simulated and field populations for each repeated experiment.

Experiment	χ^2 -value	R^2 -value
1 st validation	7.404	0.823
2 nd validation	53.695	0.992
3 rd validation	2.900	0.981

312

313 4. Discussion and conclusions

314

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

327 The first information derives from the upper and lower thermal thresholds above and below which species
328 development is theoretically not possible, respectively. This aspect is highlighted by the Brière expression:
329 referring to the threshold values (Table 2), it is possible to say that the rice moth is capable of surviving and
330 developing at both low and high temperatures, in line with the results obtained by Cox et al. (1981) and Osman
331 et al. (1984). The knowledge of the threshold values, however, can support the scientific community that is

332 working on alternative control strategies (Nasr et al., 2015) based, for example, on thermal heating with radio
333 frequencies (Yang et al., 2015) or thermal cooling of the stored grains. On the basis of our results, thermal
334 treatments in grain storage silos have to cool below T_L , and heat above T_M in order to be most effective. The
335 latter value is also reported by the Logan expression, and even though there is a small difference between the
336 T_M values of Logan and Brière, on the whole they indicate a similar upper threshold. However, the Logan
337 offers additional biological information, enclosed to ΔT . To be specific, this parameter expresses the response
338 of the species to high temperatures, quantifying the width of the range of abrupt collapse after the maximum
339 of the development rate function (and hence of the optimal temperature). This information is helpful, again, to
340 set opportune control actions for heating the silos: the temperature setting, in fact, is usually based on the
341 concept of “maximum efficiency with minimum costs”. The knowledge of ΔT may be beneficial in this sense,
342 because it can be taken into account in cost-benefit analyses (Pappalardo et al., 2017).

343 The second result of the present work concerns, on the other hand, the validation of the model (1), applied in
344 conditions of varying temperature in a semi-field environment. These assessments increase the reliability of
345 the model presented by Rossini et al. (2019a). More specifically, the R^2 values close to 1 suggest that
346 simulations respond to the experimental data trend, but a numerical indication of the overlapping is provided
347 by the χ^2 -values. However, a difference between two high numbers may provide a higher χ^2 , reason for which
348 the *a posteriori* analysis introduced by Rossini et al. (2021, 2020c, 2020a) considers both χ^2 and R^2 .

349 Overall, this study has provided rather important biological information about the rice moth, which will be a
350 helpful tool for an IPM framework. Preventive actions to control infestations in stored grain, indeed, are
351 commonly based on active ingredients which are potentially harmful to the health of consumers and
352 environment, such as fumigants (Yang et al., 2015). The immediate disadvantage of the infestations by *C.*
353 *cephalonica* (and by other insect pests) in the storage sites, would be the non-marketability of products.
354 However, storage systems also have certain advantages, if supported by modern technologies. A predictive
355 model based on the environmental temperature, external or internal to the silos, can provide indications about
356 the risk of infestation. Hence, in an IPM framework, a decision support system based on the tools presented
357 and applied in this study can be of great assistance to technicians, in order to reduce the amount of active
358 ingredients required and thus lower production costs. On the basis of the foreseen pest population density, with
359 a subdivision in life stages, an action threshold may be defined for each infestation level. The model

360 predictions, in this sense, are helpful to minimize the use of conventional agrochemicals, restricting their use
361 only when it is strictly necessary. An optimised control, for instance, may encourage the alternation of
362 conventional agrochemicals with natural active ingredients extracted from plants, and that may be effective
363 only on particular stages and at low population densities. Indeed, Mathew and Padmanabhan (2015) studied
364 the properties of essential oils of *Origanum majorana* L. on the egg laying and hatchability of species, while
365 Allotey and Azalekor (2000) investigated the insecticidal properties of *Citrus sinensis* (L.) Osbeck,
366 *Chromolaena odorata* (L.) King & Rob, and *Eichhornia crassipes* (Mart.) Solms.

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

381 ~~T~~to control the rice moth. I, also, may be helpful to findte, because predictions can indicate if the treatment is
382 necessary, and when the most susceptible life stage to control will occur.

383 The results obtained in this work, hence, lay the foundations of the mathematical description of *C. cephalonica*
384 populations, providing a key element in the development of decision support system tools aimed to control the
385 species in warehouses. Further developments of the model should be directed on the side of optimization
386 algorithms, besides to include mortality and fertility. The idea beyond this study, in fact, is to adjust the
387 simulations on the basis of monitoring data provided, for instance, by automated systems based on the near

Commentato [L1]: Manca il riferimento bibliografico. L'autore parla di parassitoidi specifici per *Corcyra* per la lotta biologica a questo insetto?

Commentato [LR2R1]: Sì, l'autore nell'introduzione fa riferimento a tutta una serie di possibili controlli biologici per l'insetto

Commentato [L3]: Il riferimento bibliografico è ancora valido? Non siamo riuscite a trovare il lavoro

Commentato [L4]: Ci spiace ma questo paragrafo è molto discutibile, per il motivo riportato nella nota sottostante. Di conseguenza è meglio eliminarlo.

388 infrared spectroscopy (Johnson, 2020). One of the criticalities in applying the model (1), in fact, is the
389 estimation of the population abundance depending, mainly, on the distribution of the individuals into the life
390 stages at time zero. A continuous set of data about the “past and the present” situation in the warehouses,
391 flanked to optimization algorithms may be used to update frequently the model response in order to obtain the
392 most reliable prediction, and a more reliable decision support system tool.

393

394 **Acknowledgement**

395

396 The authors are grateful to the anonymous reviewers for their comments and suggestions, which have been
397 greatly helpful for the improvement of this manuscript. The research was carried out in the framework of the
398 MIUR (Ministry for Education, University and Research) initiative “Department of Excellence” (Law
399 232/2016).

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