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Cohort development models for integrated *Corcyra cephalonica* (Stainton) population management

Abstract - This paper deals with the development of time invariant distributed delay models representing the development of cohorts, i.e. group of individuals born at the same time, that develop under constant temperature, humidity, photoperiod and food conditions. Laboratory cultures of *Corcyra cephalonica* (Stainton) maintained in a rearing room were used for the experiments. Insects were individually reared on a standard diet and on slightly different diets with increased contents of cellulose and carboxymethyl cellulose. The developmental times, the associated variance and the survival of eggs, larvae and pupae were conducted in a thermostatic chamber with 27±1°C, 70±5% R.H. and a photoperiod 16: 8 hours (light: dark). The observations permit the parametrization of three models based on time distributed delays. The first model satisfactorily represents the emergence patterns of adults and could be useful for monitoring activities. The second model adequately represents the dynamics of eggs, larvae and pupae. In an integrated control context, this model could be used to evaluate the effect of mortality factors operating on different life stages and assist in the timing of control operations. In the third model, the development of larvae is represented by a growth based model that is parametrized with data on consumption, egestion, conversion, respiration and weight increase. The model represents not only the development of eggs, larvae and pupae but also daily food consumption and food contamination by faeces and could be used in the design of an Integrated Pest Management (IPM) program.

Riassunto - *Modelli sullo sviluppo di una coorte per la gestione integrata di* Corcyra cephalonica *(Stainton)*

Sono stati sviluppati modelli a ritardo distribuito nel tempo che rappresentano la dinamica di coorti, ovvero di gruppi di individui nati nel medesimo periodo di tempo, con temperatura, umidità, fotoperiodo e cibo costanti. Gli individui di *Corcyra cephalonica* (Stainton) utilizzati nei test provengono da allevamenti in celle climatizzate. Gli insetti sono stati allevati singolarmente su dieta standard e su diete con quantità crescenti di cellulosa o carbossimetilcellulosa. I tempi di sviluppo, la varianza e la sopravvivenza di uova, larve e pupe sono stati osservati in cella termostatata a 27±1°C, 70±5% U.R. e fotoperiodo 16:8 ore (luce:buio). Le osservazioni sono servite per la parametrizzazione di tre modelli basati sul ritardo distribuito di tempo. Il primo modello rappresenta significativamente lo sfarfallamento degli adulti e può essere utilizzato per la gestione delle trappole a feromone e per le operazioni di controllo di questo stadio. Il secondo modello rappresenta adeguatamente la dinamica di uova, larve e pupe. Nell'ambito della gestione integrata, questo modello può essere impiegato per valutare l'effetto della mortalità sui diversi stadi e fornire indicazioni per la scelta del momento degli interventi di controllo. Nel terzo modello lo sviluppo delle larve è rappresentato da un modello basato sulla crescita, parametrizzato con dati sul consumo, la produzione di escrementi, la conversione, la respirazione e l'incremento di peso. Il modello rappresenta non solo il periodo di incubazione delle uova e lo sviluppo di larve e pupe, ma anche il consumo giornaliero di cibo e la contaminazione con escrementi della derrata e può essere utilizzato in un programma di gestione integrata (IPM).

Key words: Rice moth, mathematical models, weight.

INTRODUCTION

Corcyra cephalonica (Stainton), generally known as "Rice moth", is a moth pest of stored rice, sorghum, corn, cocoa, peanuts, almonds, dates, cashews and raisins (Trematerra, 1983; Mbata, 1989; Johnson *et al*, 1992; Locatelli & Limonta, 1998; Harita *et al*., 2000). *C. cephalonica* is able to develop in a wide range of temperature and humidity. In fact, the cycle from egg to adult can be completed between 15 and 35°C and between 15 and 90% relative humidity, and high damage has been reported even under extreme conditions (Parameshwar & Jairao, 1985). These characteristics are important elements for explaining the ubiquitous distribution.

The populations of *C. cephalonica* inhabit often processing departments which provides unlimited quantities of food often at constant temperatures. As a consequence, the dynamics of *C. cephalonica* populations developing under nearly constant condition of temperature, humidity, and photoperiods are mainly driven by food quality and physical as well as chemical control (El-Buzz *et al*., 1974; Cox *et al*., 1981; Trematerra, 1983; Etman *et al*., 1988; Mbata, 1989; Locatelli *et al*., 1990; Yu & Chen, 1991; Johnson *et al*., 1992; Yadav, 1997; Harita *et al*., 2000; Tiwari & Bhatt, 2000; Patel & Patel, 2002; Huang & Subramanyam, 2004; Savoldelli, 2005; Michaelraj & Sharma, 2006). The control can be rationalized by modelling tools that take into account the effect of food quality and management measures on *C. cephalonica* populations developing under given environmental conditions.

The modelling tools developed in this work should contribute to the improvement of Integrated Pest Management (IPM) schemes to efficiently control *C. cephalonica* populations. Of particular interest are modelling tools that enable store managers to forecast population processes such as the emergence patterns of adults. For the timing of control technology applications with differential effects on pest life stages, a modelling tool representing the occurrences of eggs, larvae and pupae may be particularly useful to store managers. In an IPM context, the modelling tools are particularly useful if they represent population development in relation to an economic threshold. In the case of *C. cephalonica*, the damage is due to both food consumed and food contaminated by faeces and silk. Hence, an efficient model should represent the dynamics of larvae as well as the amount of food they consume and the faeces and silk they produce.

The purpose of this paper is to lay the ground for models that forecast the emergence of adults, the dynamics of life stage occurrences, and the dynamics of life stage and damage occurrences. In this paper, the models are constructed for cohorts, i.e. group of individuals born at the same time, that develop under constant temperature, humidity and photoperiod conditions

MATERIAL AND METHODS

Rearing

Laboratory cultures of *Corcyra cephalonica* (Stainton) maintained in a rearing room at 27±1°C, 70±5% R.H. and 16 h of light alternating with 8 h of darkness were used for the experiments. The composition of the standard diet is specified in Table 1.

Experimental conditions

Insects were individually reared on a standard diet and on diets with different contents of cellulose and carboxymethyl cellulose. Each ingredient was ground and used if passed through a 20 mesh sieve. However, soft wheat flour (0), dry yeast, pure cellulose and carboxymethyl cellulose were not ground as they have granulometry inferior to the one required. The percentage amounts of the ingredients are shown in Table 1.

The experiments were carried out in a thermostatic chamber with 27±1°C, 70±5% R.H. and a photoperiod 16:8 hours (light:dark).

Tab. 1 - The ingredients of the food offered to larvae of Corcyra cephalonica *(Stainton) in the different experiments (standard, standard supplemented with 5% carboxymethylcellulose (CMC 5) as well as with 5% (C 5) and 10% (C 10) cellulose).*

Ingredients	**% Diet**			
	Standard	**CMC 5**	**C 5**	**C 10**
Bran	24.5	23	23	22
Wheat flour	14	13	13	12
Corn flour	15	15	15	14
Wheat germ	9	8	8	8
Dry yeast	6.5	6.5	6.5	6
Honey	14	13	13	12.5
Glycerine	17	16.5	16.5	15.5
Carboxymethylcellulose	0	5	0	0
Cellulose	0	0	5	10

Developmental time and survival

The lenght of the immature development was studied on the rearing diet as control and on diets containing none (control), 5% and 10% of cellulose, and none (control), and 5% of carboxymethyl cellulose.

For each diet, the experiment began with 20 insects whose development was followed daily until reaching the adult stage. The experiments were conducted under the above described rearing conditions. The two control experiments and the four different diets result to six groups of data for further analysis.

Food budget for fourth instar larvae

The diet was left for 24 hours in a thermostatic chamber (27±1°C and 70% R.H.) in a thin layer (5 mm) in a Petri dish (15 cm diameter) in order to obtain uniform moisture level. The diet was shaped in spheres of 1cm diameter and weigh. In each dish a sphere of food and groups of ten fourth instar larvae were placed. After 24 hours the group of larvae was weighted in order to evaluate the weight variation. The sphere of food was brushed, in order to eliminate drops and silk, and weighted.

On the standard diet only, the food budget was studied for fourth instar larvae which are relatively resistant to starvation. Immediately after molting, the insects were separated into groups of ten individuals. To obtain the weight increase, the fresh weight of six groups was measured on an analytical balance (Sartorius CP64, OIML E2) before and after a 24 hours feeding period. For three groups, the amount of fresh food consumed during this 24 hours interval was measured. Also for three groups, we measured the fresh weight of faeces produced during a 72 hours starvation period that succeeded the 24 hours feeding period.

Cohort models

Adult emergence (model A)

We use the Erlang function because it adequately represents the output of a stochastic development process and has widely been used in phenological research and population dynamics (Welch *et al.*, 1984; Severini *et al.*, 1988; Baumgärtner & Baronio, 1989; Gutierrez, 1996; Alilla *et al.*, 2005).

Adult emergence can be represented by eq. A3 of Vansickle (1977) who described the effect of a proportional loss (attrition) *AR* on probability density functions *y(t)* as

$$y(t) = \left[\frac{k}{DEL}\right]^{k} \frac{t^{(k-1)}}{(k-1)!} \exp\left[-\left(AR + \frac{k}{DEL}\right)t\right] \quad [1]$$

with *DEL*= mean transit or developmental time in our work. *DEL* [days], *k*=number of substages, and *AR* [proportion per day] can be obtained from the observations on individual cohorts with survivorship ε and observed developmental time u by

$$k = \frac{u^2}{s^2} \qquad [2]$$

$$DEL = u\,\varepsilon^{-\frac{1}{k}} \qquad [3]$$

$$AR = \ln(\varepsilon)/DEL \qquad [4]$$

Equation [4] is valid for k→∞ and hence, used as an approximation in the case under study. The emergence patters of adults, on the standard diet 1, relative to a cohort of size 1 with ε=0.8, *DEL*=54.0 and *k*=43 is represented in Fig. 2a. Predicted *versus* observed emergence rates of all experiments are depicted in Fig. 2b. The estimates for the parameters are given in Tab. 3.

Development model (model B)

Vansickle (1977) represents the dynamics of a cohort through a series of cascaded delay substages (i=1, 2, ..k) by

$$\frac{dr_i(t)}{dt} = \frac{k}{DEL}\left[r_{i-1}(t) - r_i(t)\left(1 + AR(t)\frac{DEL}{k}\right)\right] \quad [5]$$

where $r_i(t)$ =flow rates out of the *i-th* stage, $r_0(t)=x(t)$=input, and $r_k(t)$=output. In the case under study, the mortality affects young larvae. In the delay process, they are assumed to occupy the substages ($8<i<15$), which represent the degree of stochasticity of the process rather than biological development periods. In fact, young larvae are found in an age group that has completed between 19% and 45% of the total immature development. Hence AR is modified according to $AR_i = 1\text{n}(\varepsilon) / DEL$ for ($8<i<15$) and AR_i=0 otherwise. To obtain the number n_i of individuals in the *i-th* stage, Manetsch (1976) and Vansickle (1977) compute $n_i(t)=r_i(t)\, DEL / k$. The estimates for the parameters are given in Tab. 3. Figure 3 represents the dynamics of eggs, larvae and pupae belonging to a cohort of size 1 with ε = 0.8 and *DEL*=54.03 passing through *k*=43 cascaded delay substages. Predicted *versus* observed emergence rates of all experiments are depicted in Fig. 3b.

Growth-based model (model C)

An Integrated Pest Management (IPM) system should take into account the damage due to feeding and food contamination. This can be done by developing a biophysical model in the context of the supply/demand concept (Gutierrez, 1996) or the metabolic theory of ecology (Brown *et al*., 2004). According to Hilbert (1995), the developmental rates ($r=1/DEL$) can be expressed as a function of food assimiliation, respiration and weight change. For larvae developing at the standard temperature of 27°C with unlimited food supply and exponential growth we obtain

$$r = \frac{c\,(1-\phi)\,(1-\varphi) - R}{\ln\left[\frac{W_f}{W_0}\right]} \quad [6]$$

where c=food consumption [mg mg-1], ϕ=proportion of food egested, φ=proportion of food not converted into body mass, R=respiration [mg mg^{-1}], W_f=final weight [mg], W_0=initial weight [mg]. Broglia (2007) provided estimates for R, ϕ, φ, while c is derived from the thesis of De Angelis (2009). The estimates of the parameters are given in Tab. 3. For each day, eqn.[5] allows the computation of individuals in each delay substage, while the assumed exponential growth rate and the constant initial and final weights, permit the computation of individual weights in each substage. The product of numbers and weights, multiplied by c, can be summed up for all the i=1.2, ..32 larval stages to yield the daily amount of food consumed. When multiplied by ϕ, the sum yields the daily amount of faeces produced. In this model we disregard the amount of silk produced. To obtain the total amount of food consumed and faeces produced by a cohort, the daily amounts are summed until completion of the larval development.

Fig. 4 depicts the dynamics of eggs, larvae and pupae as well as the daily food consumption and faeces production.

RESULTS

Table 2 shows the observed developmental time, the associated variance and the survival of the combined immature life stages. The analysis of variance and the Chi^2 – test, using the R2.6.0 software, show no significant differences in developmental times and survivorships among the diets at P<0.01 l.

Tab. 2 - Immature developmental time (days) at 27°C of Corcyra cephalonica *(Stainton) cohorts fed with standard diets and diets modified by the addition of carboxymethylcellulose and cellulose.*

Diets	**N**	**Observed mean developmental time**	**Observed variance**	**Range**	**Observed survival**
Standard 1	16	53.8	30.20	48-69	0.8
CMC 5	12	50.9	13.53	45-57	0.6
Standard 2	12	52.7	17.33	48-60	0.6
C 5	11	49.8	47.56	43-67	0.55
C 10	13	51.2	16.35	48-62	0.65

Table 3 lists the estimates of the parameters of model A, B and C. When reared on the standard diet 1, the survival is relatively high (0.8) resulting to a *DEL*=54.04 for *k*=43. (Eq. 3). Noteworthy, the proportions of egested food (ϕ) and not converted food (φ) are low indicating that the food made available in this study is efficiently assimilated. The respiration rate *R* represents the loss in body weight per mg body eight at 27°C of starving larvae. Since it has been re-calculated from the Broglia's (2007) data, a small correction of the conversion ratio $\varphi = 0.7421$ reported in his thesis was necessary. We furthermore take into account more accurate measurements of initial and final weights than available to Broglia (2007).

Tab. 3 - Estimates for the parameters of the three models described in the text (DEL refers to the duration of all immature life stages, W_o and W_f are the initial and final weights of larvae, the duration of eggs and pupae are given in parenthesis, the estimates are valid for 27°C.

k	DEL	ε	c	ϕ	φ	R	W_0	W_f
43	54.04 (3.0, 9.0)	0.8	0.3551	0.0251	0.6799	0.0613	0.03	45.13

Adult emergence (Model A)

An Erlang shape parameter *k*=96 is obtained for the cohort developing on standard diet 1 (Tab. 2). Fig. 1a, however, shows that the Erlang function with *k*=43 produces an emergence pattern that closely corresponds to the observations. The reduction of substages increases the efficiency of the computations but may cause the negligible differences at the beginning and towards the end of the emergence period (Fig. 1B). The difference is particularly visible for the beginning of the flight in Fig.1B. The extension of the flight period is in agreement with Manetsch (1976) and Vansickle (1977) who both analyzed the influence of *k* on the Erlang probability distribution.

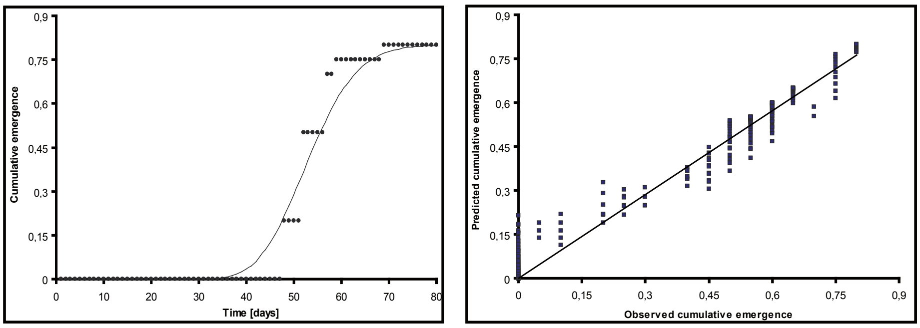

Fig 1 - Observed and predicted adult *Corcyra cephalonica* (Stainton) emergence patterns for cohort developing on the standard 1 (Table 2) (Fig. 1A, filled quadrates represent the observed cumulative adult emergence, solid line represent the calculated cumulative adult emergence patterns), and predicted versus observed adult emergence patterns of all the 5 cohorts at 27°C (Fig. 1B). The predictions are based on equation [1].

Development model (model B)

Figure 2A depicts the passage of a cohort, fed with the standard diet, with size 1 through egg, larval and pupal stages. The close agreement predicted *versus* observed adult emergence demonstrates the satisfactory predictive capabilities of the model.

Growth-based model(model C)

Figure 4 depicts the predicted development of a cohort of size 1 through the egg, larval and pupal stages. It also shows the daily amount of food consumed and faeces produced. Because of the efficient assimilation and the relatively low respiration rate, a calculated amount of 64.56 mg is required to produce a larvae with a final weight of 45.13 mg (Tab. 2). This means that the damage, expressed in food eaten and food contaminated by faeces per individual is relatively low.

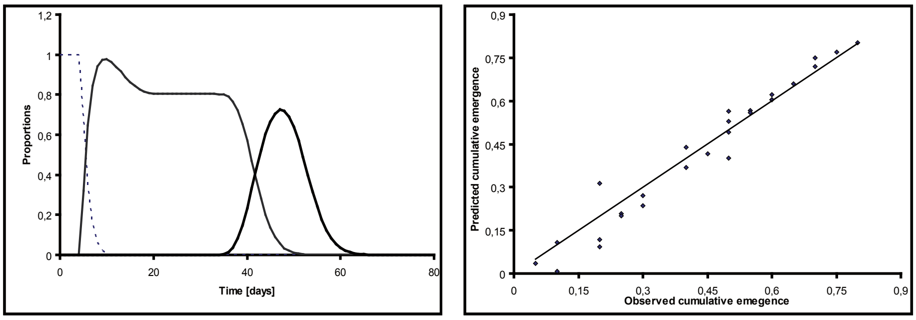

Fig. 2 - Dynamics of the cohort of *Corcyra cephalonica* (Stainton) developing on standard diet 1 (Tab. 2) with eggs (dotted line), larvae (solid line) and pupae (dashed and dotted line) in relation to an input of 1 (Fig. 2A), and observed versus predicted cumulative adult emergence in all experiments carried out at 27° C (Fig. 2B). The predictions are based on equation [5].

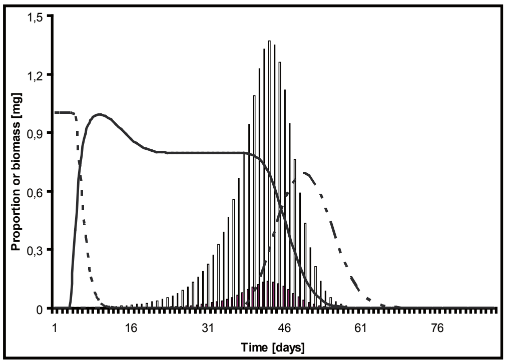

Fig. 4. Dynamics of cohorts of eggs (dashed line), larvae (solid line) and pupae (dashed and dotted lines) of *Corcyra cephalonica* (Stainton) and the damage produced (empty bars represent the daily food consumption rates divided by 4, and filled bars represent the daily faeces production).

DISCUSSION AND CONCLUDING REMARKS

On the different diets, the postembryonic development lasted between 49.82 until 53.75 days. This range falls into the range of values (46.5–77 days) obtained by Kamel & Hassanein (1967) who reared *C. cephalonica* on different food types at 25.5°C and 75% R.H. Possibly, the diet responsible for the developmental time of 77 days is of lower quality than the diets used in our study. Etman *et al*. (1988), however, observed a shorter development period on whole wheat flour with added yeast at a temperature and a relative humidity close to the ones of our study. Mean developmental time was also shorter in the study of Subramanyam and Hagstrum (1993) (27° C, 40.14 days). On the contrary, Haritha *et al*. (2000) observed a mean development of 65.08 days on ground peanuts. Possibly, groundnuts are a lower quality food than the diets used here. The different strains of insects used in these studies may also contribute to these differences.

Larvae of C. *cephalonica* are reared on a standard diet (Locatelli & Limonta, 2004) and on diets of slightly reduced quality in relation to the standard diet. With the consideration of a modest change in food quality only, we avoid model development and model parametrization on the basis of the standard diet. Possibly, the exclusive use of a standard diet may have yielded a model that unsatisfactorily performs under practical conditions. To achieve a modest change in food quality and create conditions similar to the ones observed in storage facilities, we added carboxymethilcellulose and varying levels of cellulose to the standard diet. These substances are known to lower the quality and digestibility of food (Martin *et al*., 1991).

Shafer (1983) established an empirical relationship between standard deviations and mean developmental times of a 113 insect and mite species. Accordingly, we expected a variance of 14.69 in relation to the observed mean of 53.8 (Tab. 2). This variance is much smaller than the one obtained in our experiments. Nevertheless, the variance obtained here in relation to the mean (Tab. 2) is considered as high enough as to justify the taking into account of the variability in cohort development (Di Cola *et al*., 1999). Here, this is done by using a time distributed delay model. The selection of a smaller k increases the efficiency of the computations by predicting an emergence patterns that only slightly differs from the observations. The quality of the predictions obtained with k=43 is acceptable for the purpose of this work.

As previously stated, the low egestion and the efficient conversion of food may reflect the high quality of the food under consideration in the study. To reach the observed final weight of 45.13 mg (Tab. 2), a larva consumes a total of 72.62 mg of food and produces a total of 1.82 mg g faeces. The ratio r of biomass produced to biomass consumed (r = 45.13 / 72.62 = 0.62) may be due to the high quality food. For example, Schowalter (2006) reports a ratio r = 0.52 for larvae of the phytophagous Saturniid moth *Hemileuca olivia* (Morr.). For the phloem feeding pea aphid *Acyrthosiphon pisum* Harris, Gutierrez (1996) refers to ratio r=0.486. The respiration R=0.0613mg mg^{-1} (Tab. 2) appears to be relatively high in comparison with the Cereal leaf beetle *Oulema duftschmidi* (Redt.) for which Limonta *et al*. (2009) provide the equation for calculating R=0.0075 at 27 °C. Noteworthy, this value is not the result of measurements but a calibrated value that differs from previously reported value. However, the respiration in our study is similar to the values (R = 0.0708 and R = 0.0729) obtained for larvae of the Ladybird beetle *Coccinella septempunctata* L. reared on two different aphid species at 27°C (Potenza, 2009). We refer to these studies because they use the same method of measuring the weight loss of starving larvae for estimating R.

Model A is able to predict the emergence of adults on the basis of information on preimaginal developmental time, its variance and the combined mortality of immature life stages. In an integrated control context, it could be useful for monitoring activities.

Model B represents the flow of cohort individuals through different life stages and takes into account mortality. The consideration of the adult biology permits the extension of the model to a multi-cohort and multi-generation systems affected by complicated mortality patterns. In an integrated control context, modelling tool B could be used to evaluate the effect of mortality factors operating on different life stages and assist in the timing of control operations.

In model C, developmental rates are related to growth, and the immature development is concluded once a constant final weight has been reached (Hilbert, 1995; Limonta *et al*., 2009). The food budget components (consumption, defaecation, conversion, respiration, weight increase or reproduction) depend on both food quality and quantity as well as on environmental conditions. The model could easily be modified for taking into account these components and predict their influence on development and mortality in the case of multiple cohorts and generations. In this case, the adult biology should be considered in model development. Model C is able to predict the damage resulting from the dynamics of food consumption and contamination by faeces and could be used in an integrated pest management (IPM) program.

The models A, B, C presented here are restricted to immature development, but can easily be extended to include the adult life stage and reproduction. Further model development may lead to the substitution of the time-invariant by a time-varying delay operating under the influence of time varying environmental factors (Vansickle, 1977).

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