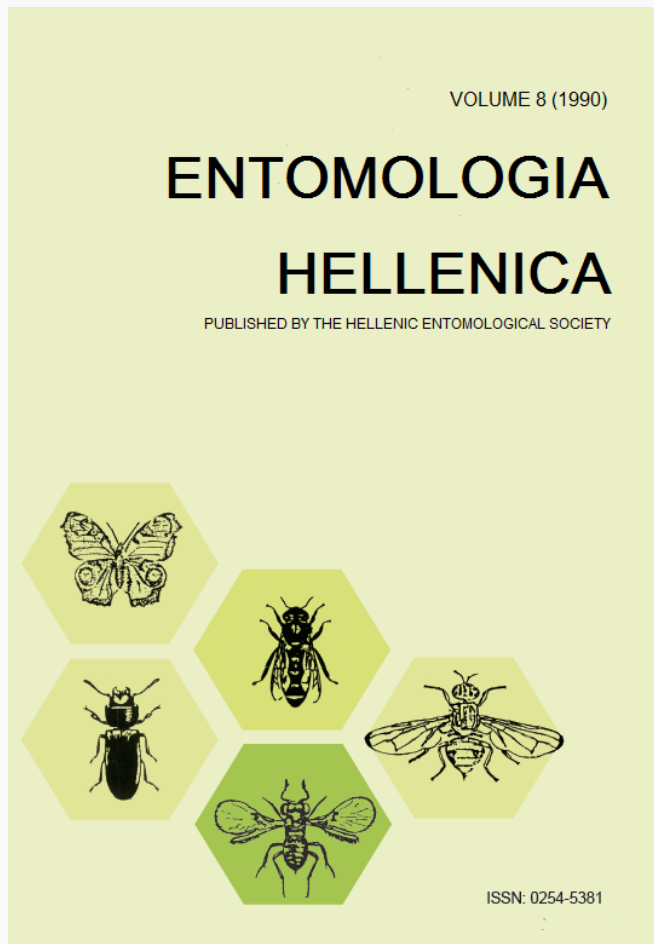


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Population Dynamics of *Saissetia oleae*. II. Life-Tables and Key-Factor Analysis¹

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ABSTRACT

A series of life-tables for the population of *Saissetia oleae* (Oliv.) (Homoptera-Coccidae) during five yearly generations (1981-86) were constructed in Corfu. Key-factor analysis carried out on the life-table data indicated that mortality of young stages during summer, caused mainly by the high temperatures, and mortality during spring, caused mainly by predation, determine total population change within each generation. These two mortality factors are the predominant factors of the population dynamics of *S. oleae* determining population fluctuations. The other mortality factors of the population system of *S. oleae* were less important. Summer parasites and egg predators, in particular, do not play any significant role on the population dynamics of *S. oleae*.

Introduction

The population of *Saissetia oleae* (Oliv.) (Homoptera-Coccidae) is characterized by considerable fluctuations resulting in periodic outbreaks at a local or at a regional base. These outbreaks have been partly related to a reduction in the populations of natural enemies of the coccid caused by intensive applications of insecticides against other pests of olives (Feron and D'Aguilar 1962) but other opinions consider that high temperatures during summer is the mortality factor of *S. oleae* (Orphanidis and Kalmoukos 1970). These opinions, however, are based on indications rather than on precise quantitative information taking into account the total complex of the mortality factors of *S. oleae*.

Life-tables, is a useful tool for analysis of mortality of insect populations (Southwood 1978). Although this technique has been used for many insect populations, for *S. oleae* previous

work comprises only a partial life-table on citrus, of a preliminary stage (Podoler et al. 1979).

Within the concept of pest management system on olives in Corfu it was considered necessary to estimate the population changes of *S. oleae* and to analyse mortality by using the approach of life-tables and key-factor analysis for a better understanding of the population dynamics of this species. In a previous paper estimates of the population and the various mortality factors for five successive yearly generations of *S. oleae* were presented (Stratopoulou and Kapatos 1990). In this paper, life-tables for the five successive generations of *S. oleae* are presented and through a key-factor analysis the factors responsible for the main fluctuations of the populations of *S. oleae* are determined and discussed.

Materials and Methods

a. Study sites and sampling procedure

The study sites and sampling techniques were described in the previous paper (Stratopoulou and Kapatos 1990). Briefly, the study was conducted at 7 experimental sites, each of 70-150 olive trees, distributed all over the island. These sites were free of

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insecticidal treatments except the bait spray programme against the olive fly. In each site ten trees were sampled regularly (every month or a month and a half according to the season). From each tree, 8 samples were taken from two levels and four aspects of the tree and each sample was consisted of one branch of two years growth including the new vegetation. The samples were examined and all stages of *S. oleae* found in the samples were recorded. The various population estimates were finally expressed as number of individuals per 100 sampling units. Also, for each site and year, the fecundity of healthy females of *S. oleae* and of *S. oleae* females parasitized or attacked by the summer parasites and egg predators were estimated.

b. Construction of life-tables

The type of life-table adopted in this study was the age-specific (or cohort) life-table (Southwood 1978, Carey 1989) applied to insects with discrete generations and therefore particularly suitable for *S. oleae* which, in Corfu, is mainly univoltine (Argyriou 1963, Stratopoulou and Kapatos 1984). Direct measurements of all mortality factors or

separation of stage mortality into specific mortalities from various causes of death would allow the construction of multiple decrement life-tables and the evaluation of every single mortality factor (Morris 1959, Cameron and Morrison 1977, Carey 1989). However, separation of stage mortality into various causes could not be done in this case, except for the summer parasites and egg predators. In addition, the calculation of mortality per stage creates problems in the interpretation of the results because most mortality factors cannot be characterized as stage specific but their action varies according to the season. Therefore, in this study, a modification of the age-specific life-table was used. The population of *S. oleae* was calculated, from the original data at certain successive points during the generation representing either a particular stage or a particular date, as defined in Table 1.

The total mortality of *S. oleae* within a generation is divided into submortalities or specific mortalities each of which referring to the interval between two successive population estimates and it is defined either as mortality of a particular stage or mortality during a particular period of time (i.e.

TABLE 1. Definition of the calculated population estimates within each yearly generation of *S. oleae*, calculation of the corresponding k-values and sources of mortality for each k-value.

Population estimates	Mortality		
	K-value	Calculation	Sources of mortality
P_{max} Expected maximum number of eggs according to observed fecundity of healthy females	K_1	$\log P_{max} - \log P_E$	Action of summer parasites and egg predators
P_E Total number of eggs produced after the action of summer parasite and egg predators has occurred	K_2	$\log P_E - \log P_{L1}$	"Loss" of crawlers in searching for establishment. Small component regarding adult mortality before the end of oviposition period
P_{L1} Number of individuals of <i>S. oleae</i> entered the first larval instar	K_3	$\log P_{L1} - \log P_{1.9}$	Mortality of young stages during summer, mainly due to high temperatures
$P_{1.9}$ Living population of <i>S. oleae</i> at 1st September	K_4	$\log P_{1.9} - \log P_{1.12}$	Mortality during autumn including parasitism, action of predators and fall of old leaves
$P_{1.12}$ Living population of <i>S. oleae</i> at 1st December	K_5	$\log P_{1.12} - \log P_{1.3}$	Mortality during winter including fall of old leaves and possible action of low temperatures
$P_{1.3}$ Living population of <i>S. oleae</i> at 1st March	K_6	$\log P_{1.3} - \log P_{1.6}$	Mortality during spring including action of predators and parasites
$P_{1.6}$ Number of living females of <i>S. oleae</i> at 1st June			

TABLE 2. Life-table for the population of *S. oleae* at the experimental site of Klimatia during 1981/82.

Population estimate	Number of individuals	log number of individuals	K-values
Pmax	615,600	5.789	0.042
PE	558,144	5.747	0.592
PL.1	142,760	5.155	1.108
P1/9	11,149	4.047	0.290
P1/12	5,720	3.757	0.630
P1/3	1,340	3.127	1.094
P1/6	108	2.033	
Total k			3.756

autumn, winter, spring). Total generation mortality as well as specific mortalities were calculated and expressed as key-values (see Southwood 1978) so that

$$K_T = k_1 + k_2 + k_3 + k_4 + k_5 + k_6$$

A summarized description of the calculation of total and individual k-values and the various sources of mortality are given in Table 1.

Table 2 gives, as an example, the life table of the *S. oleae* population in one of the experimental sites (Klimatia) for the year 1981/82. The first column indicates the stage of *S. oleae* or the time of the year the population estimate refers to. The second and third columns give the population estimates expressed both as numbers and log numbers. The fourth column gives the corresponding mortalities expressed as k-value. Also, total mortality (K_T) is given at the bottom of this column. It can be seen, in this particular life-table, that mortality of the young stages during summer (k_3) and mortality during spring (k_6) contributed the highest proportion to the total K. Such life-tables were constructed for each experimental site and year, i.e. a total of 35 life-tables.

Life-tables is apparently a useful method for describing mortality. The great usefulness of this technique, however, lies on the possibility to investigate the role of each mortality factor in determining population fluctuations, i.e. to recognize the key-factor of the population system. This is done by carrying out further analysis on the life-table data.

Analysis of Life-Table Data

a. Key-factor analysis

The recognition of the key-factor for the main fluctuations of the population can be done by visual correlation (Varley and Cradwell 1960). The various k-values from the life-table data are plotted against generations and the morta-

lities whose k-values are mostly correlated with total K are considered to be the key-factors.

Figure 1 shows the individual k-values and total K plotted against generations in one of the experimental sites (Klimatia). It can be easily seen that during a period of five generations (five years) mortality of the young stages during summer (k_3) and mortality of the advanced stages during spring (k_6) are mostly correlated visually with the total change of the population within each generation (Total K.). This means that variation in K_T from generation to generation is mostly explained by the variation

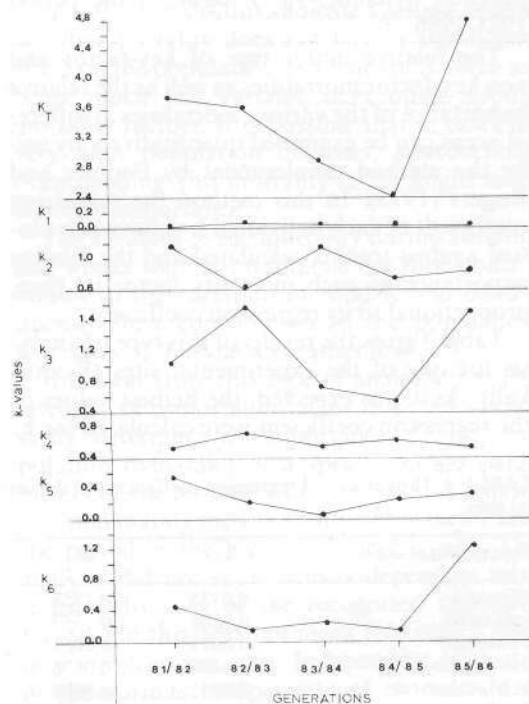


FIG. 1. Individual key-values and total K at the experimental site of Kontokali.

the other experimental sites. These are summarized in Table 4 which gives the regression coefficients of the various mortality-factors plotted against total K. Although the relative importance of the various mortality-factors changes from site to site, a general tendency is observed. In most of the cases, k_3 and k_6 were the key-factors; k_3 was the highest contributor to the variations of total K in 5 sites and in only one site its regression coefficient was very low (Kavathates); k_6 was the predominant mortality factor in one site (Kavathates), but in three experimental sites its regression coefficient was relatively low; k_1 was constantly the lowest contributor to changes in total K and in most of the cases it had a slightly negative regression coefficient. The contribution of k_2 , k_4 and k_5 to variations in total mortality was not significant although their mean values were relatively high (Figure 2).

b. Density-dependence of mortality factors

The next step of analysis of life-table data is to investigate the relationship of the intensity of various mortality factors with the size of the population of the stage on which they act. Because independent measurements of mortality could not be done in this study as required for demonstration of density dependence, the various k-values were tested, indicatively, for density dependence by following the procedure described in Southwood (1978) (ch. 10.4). In this method, the log numbers of the population entering the stage (or the season) are plotted against the survivors and vice versa. The calculated pairs of regression coefficients for any pair of population estimates were not statistically different from 1 and therefore, according to the method, there are no indications for density dependence of the various k-values.

Discussion

The analysis of the life-table data indicated that among the various k-values constituting the total mortality, k_3 and k_6 were of determinative importance in explaining population changes of *S. oleae*, i.e. they were the key-factors of population dynamics of *S. oleae*:

k_3 expresses the mortality of the young stages (mainly L₁) during summer and it had been found that this mortality is strongly correlated with maximum temperature during July-August (Stratopoulou and Kapatos 1990). It is,

therefore, concluded that variation during summer explain, to a certain extent, population fluctuations of *S. oleae*.

k_6 expresses mortality during spring which is mainly caused by the action of two predatory coccinellids (Viggiani et al. 1975) and the internal parasite on the third larval instar, *Metaphycus helvolus* (Compere) (Hymenoptera-Encyrtidae). Variation in the intensity of this mortality factors may be caused by a number of factors including the air bait sprays against the olive fly, carried out in the island since 1979, the effect of which on the population of these natural enemies may be different from year to year. Also, the population of the predatory coccinellids may fluctuate considerably from place to place and from year to year due to the polyphagous habits of these species.

k_1 expresses the reduction in the number of eggs of *S. oleae* females due to the action of *M. lounsburyi*, *S. cyanea* and *M. californica*. It was found to have very low values and because of that to be the lowest contributor to the variation of total mortality.

k_2 expresses mainly the mortality of crawlers in searching for establishment. The high k-values of this mortality indicate a strong action but this mortality does not have a significant effect on the population dynamics of *S. oleae* as being much less variable than other strong mortality factors. It is possible that in cases of very high population densities, approaching overcrowding, this mortality factor might have different importance.

The k-values of the mortality during autumn and winter were not negligible but their contribution to the variation of total K and consequently their contribution to the population dynamics of *S. oleae* was rather low.

It is clear from this type of analysis that the intensity of a mortality factor does not necessarily determine its importance on the population dynamics of a species. Other parameters of the mortality factors are also important and mainly the variability of the factor and the period in the life-cycle where it acts. The analysis did not show density-dependent relationship for any of the recognized mortality factors but this does not mean that such a relationship does not exist. Independent estimates of the various components of mortality and precise studies on individual cohorts (Southwood 1978) are required to demonstrate density-dependence.

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KEY WORDS: *Saissetia oleae*, Olive black scale, Population dynamics, Life-tables

Δυναμική του Πληθυσμού του *Saissetia oleae*. II. Πίνακες Θνησιμότητας και Ανάλυση για Προσδιορισμό Διαταρακτικών Παραγόντων (Key-Factor)

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ΠΕΡΙΛΗΨΗ

Μια σειρά από πίνακες θνησιμότητας (life-tables) για τον πληθυσμό του λεκανίου της ελιάς στην Κέρκυρα κατασκευάστηκαν για μια περίοδο πέντε ετήσιων γενιών (1981-86) σε επτά πειραματικούς ελαιώνες. Οι πίνακες θνησιμότητας αυτοί δείχνουν την εξέλιξη του πληθυσμού του λεκανίου από γενιά σε γενιά και τη φυσική του μείωση μέσα σε κάθε γενιά. Ανάλυση των στοιχείων των πινάκων θνησιμότητας (key-factor analysis) έδειξε ότι οι βασικοί διαταρακτικοί παράγοντες του πληθυσμού του λεκανίου είναι η θνησιμότητα των νεαρών σταδίων το καλοκαίρι, που οφείλεται κυρίως στις υψηλές θερμοκρασίες, και η θνησιμότητα στη διάρκεια της άνοιξης που προκαλείται κυρίως από τα αρπακτικά και κατά δεύτερο λόγο από το παράσιτο *Metaphycus helvolus*. Η διακύμανση των παραγόντων αυτών από γενιά σε γενιά είναι αυτή που κυρίως προκαλεί τις εξάρσεις και τις υφέσεις του πληθυσμού του λεκανίου. Οι άλλοι παράγοντες θνησιμότητας αν και μειώνουν τον πληθυσμό του λεκανίου δεν προκαλούν σε μεγάλο βαθμό πληθυσμιακές διακυμάνσεις. Ιδιαίτερα η δράση των ωοφάγων αρπακτικών το καλοκαίρι παίζει ασημαντό ρόλο στη δυναμική του πληθυσμού του λεκανίου.