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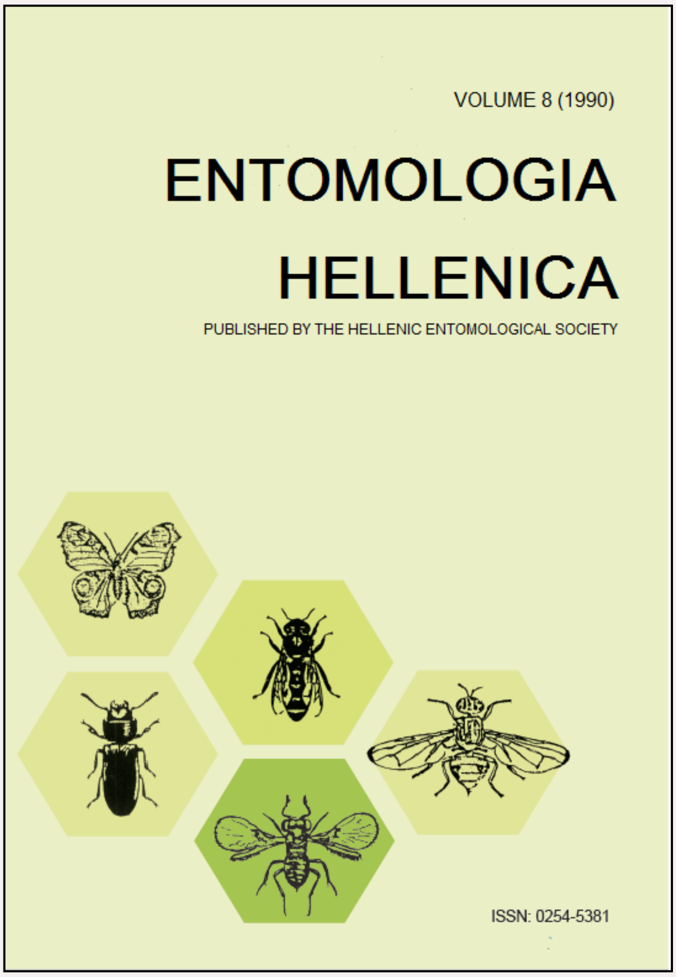

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Population Dynamics of *Saissetia oleae*. I. Assessments of Population and Mortality[1]

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ABSTRACT

The population dynamics of *Saissetia oleae* (Oliv.) (Homoptera-Coccidae) was studied in Corfu during five successive yearly generations (1981-1986). Successive estimates of the population of *S. oleae* were obtained within each of the five yearly generations and survivorship curves were constructed showing the progressive reduction of the living population within each generation and population changes from generation to generation. The calculated mortality rates indicate that the population of *S. oleae* suffers heavy mortality. The major mortality factors were high temperatures during summer, the action of predators, particularly during spring, and mortality of crawlers during summer. Overall survival rate was very low and corresponded to total generation mortality that ranged from 99.693% to 99.987%. It is assumed that variation in the action of mortality factors cause considerable fluctuations of the *S. oleae* population.

Introduction

The olive black scale, *Saissetia oleae* (Oliv.) (Homoptera-Coccidae) is one of the most important pests on olives in Greece and other Mediterranean countries. The biology and phenology of *S. oleae* on olives in Greece has been studied in detail (Argyriou 1963, Viggiani et al. 1975, Stratopoulou and Kapatos 1984) and in Corfu it is mainly univoltine.

Several mortality factors acting upon the stages of *S. oleae* have been recognized (Orphanidis and Kalmoukos 1970, Viggiani et al. 1975, Paraskakis et al. 1980). More emphasis has been given to natural enemies and assessments of their action have been attempted. The evaluation of the mortality factors, however, requires their simultaneous assessment for a number of consecutive generations. Such studies have not been conducted and therefore the accumulated action of the mortality factors and their final effect on the survival rate of *S. oleae* remains unknown.

Within the concept of pest management system on olives it was considered necessary to study in detail the population dynamics of *S. oleae* in Corfu for a number of years (1981-1986) and finally to evaluate the mortality factors and determine their role upon the population system of the coccid. This is the first of a series of publications on the population dynamics of *Saissetia oleae* in which estimates of the population and mortalities for a number of years (1981-1986) are presented and discussed.

Materials and Methods

a. Study sites and sampling techniques

The study was carried out at seven experimental sites (Klimatia, Sgourades, Kavathates, Garderades, Kontokali, Agios Matheos and Linia) distributed throughout the island and selected to represent a wide range of population densities of *Saissetia oleae*. These sites were free of insecticidal treat-

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ments against all olive-pests except *Dacus oleae* (Gmelin) (Diptera-Tephritidae). The bait spray programme which is carried out for this pest (2-3 bait-sprays during the period from July until September) has possibly affected the natural enemies but not *Saissetia oleae* itself.

Each experimental site was consisted of about 70-150 trees and from each site ten trees (six in 1981/82) were randomly selected for sampling. From each tree 8 samples were taken from two levels and the four quadrants of the tree, and each sample was consisted of one branch of two years growth including the new vegetation. The samples were taken regularly (approximately every month or month and a half according to the season). They were examined under the microscope and all stages of *S. oleae* (living, dead and parasitized) were recorded. Finally, the various estimates of population were expressed as numbers per 100 sampling units. Also, for each site and year the fecundity of healthy females of *S. oleae* and of females parasitized or attacked by the summer female parasites or egg predators were estimated by counting the number of eggs and egg-shells of the females towards the end of the oviposition period (i.e. end of July-beginning August).

b. Estimates of population, mortality and survival rate

Ideally, direct measurements of all mortality factors are required for the study of mortality and survival. This, however, is very difficult for many insects. Particularly for *S. oleae* on olives, estimates of mortality and the cause of death cannot be based with any reliability on dead animals found in samples. Many dead individuals of *S. oleae* are lost during the sampling interval particularly in autumn winter and spring (fall of leaves, rain, wind, predation) and they are not sampled. The most usual alternative would be to calculate the number entering the various stages, based on the living individuals found in the samples and stage duration and then calculate stage mortality. This, however, apart from the additional computational and statistical problems, would create great difficulties in the interpretation of the results due to the very long duration of some stages and because most mortality factors cannot be characterized as stage specific but their action varies according to the season. Therefore, for the better interpretation of the results, population estimates in this study were defined either as number of individuals entering a particular stage (for eggs and first stage larvae present during summer) or as living population at the beginning of a season.

Starting from the initial data a series of successive population estimates within each yearly generation of *S. oleae* was calculated which show the progressive reduction of the living population of *S. oleae* due to mortality, i.e.:

$P_{max} - P_E - P_{L.1} - P_{1/9} - P_{1/12} - P_{1/3} - P_{1/6}$

These population estimates were defined and calculated as follows:

P_{max}: The maximum number of eggs of *S. oleae* expected to have been produced by the females during the oviposition period. P_E: The total number of eggs expected to have been laid by *S. oleae* females after the action of the summer parasites and egg predators has occurred. P_{max} and P_E were calculated by combining the estimates of fecundity with the number of *S. oleae* females estimates to be present at the beginning of the oviposition period (i.e. 1st June) and the percentage parasitism of *S. oleae* females during summer (Stratopoulou and Kapatos 1984, Stratopoulou and Kapatos unpublished). $P_{L.1}$: The population of *S. oleae* successfully established on the leaves and shoots of the tree, i.e. the population of *S. oleae* entered the first larval instar. This estimate was based on the total number of living and dead young stages found to be present on the trees at the beginning of August (end of the oviposition period). It might be possible that this population estimate ($P_{L.1}$) was slightly underestimated because a few individuals of *S. oleae* that died early in the season may had been lost before sampling. This is felt not to present problems in the calculation of mortality. $P_{1/9}$, $P_{1/12}$, $P_{1/3}$, $P_{1/6}$: The living population of *S. oleae* on 1st September, 1st December, 1st March and 1st June (the new offsprings were not considered) respectively. Their calculation was based on the direct estimates of the living population by using the calculated daily survival rate of *S. oleae* for the period between two consecutive sampling dates including the fixed date and finally correcting the initial estimate for the date.

The total generation mortality of *S. oleae* (M_T) is divided into submortalities (M_1, M_2, M_3, M_4, M_5, M_6) each of which referring to the interval between two consecutive population estimates ($P_{max} - P_E$, $P_E - P_{L.1}$, $P_{L.1} - P_{1/9}$, $P_{1/9} - P_{1/12}$, $P_{1/12} - P_{1/3}$, $P_{1/3} - P_{1/6}$, respectively). These mortalities, which were calculated and expressed as percentages, were defined as follows:

M_1: Reduction in the number of eggs due to the action of the summer female parasites and egg predators, *Metaphycus lounsburyi* How. (Hymenoptera-Encyrtidae), *Scutelista cyanea* Motsch. (Hymenoptera-Pteromalidae) and *Moranila californica* How. (Hymenoptera-Pteromalidae). M_2: This mortality comprises mainly the mortality of crawlers. It comprises also, by its calculation, egg mortality within the female before hatching due to unknown reasons and mortality of the ovipositing females before the end of the oviposition period. These two components of mortality cound not be easily estimated separately but the data from the estimation of potential fecundity of females and the numbers of females found in the samples during summer indicated that they were very low. M_3: Mortality of the established young stages during summer. Because $P_{L.1}$ slightly underestimated the established population, a small part of M_3 has been incorporated in M_2. M_4, M_5, M_6: Mortality during autumn, winter and spring, respectively.

To understand the combined and accumulated action of the mortality factors during the generation, overall survival rate from egg (actually expected number of eggs) to mature female (S) was calculated as the ratio of the survivors to the initial number of eggs. It was finally expressed as number of individuals of *S. oleae*, out of 1,000 eggs that reached the stage of mature female.

Results

Figure 1 shows the successive estimates (average of the seven experimental sites) of the population of *Saissetia oleae* within each of its five successive yearly generations, i.e. 1981/82, 1982/83, 1983/84, 1984/85, 1985/86. As it is seen in these survivorship curves considerable reduction in the living population of *S. oleae* occurs within each generation. Comparison of the corresponding population estimates between generations, e.g. $P_{1/6}$, indicated that the population of *S. oleae* was relatively high in 1981/82 but it declined in 1982/83 and 1983/84. It in-

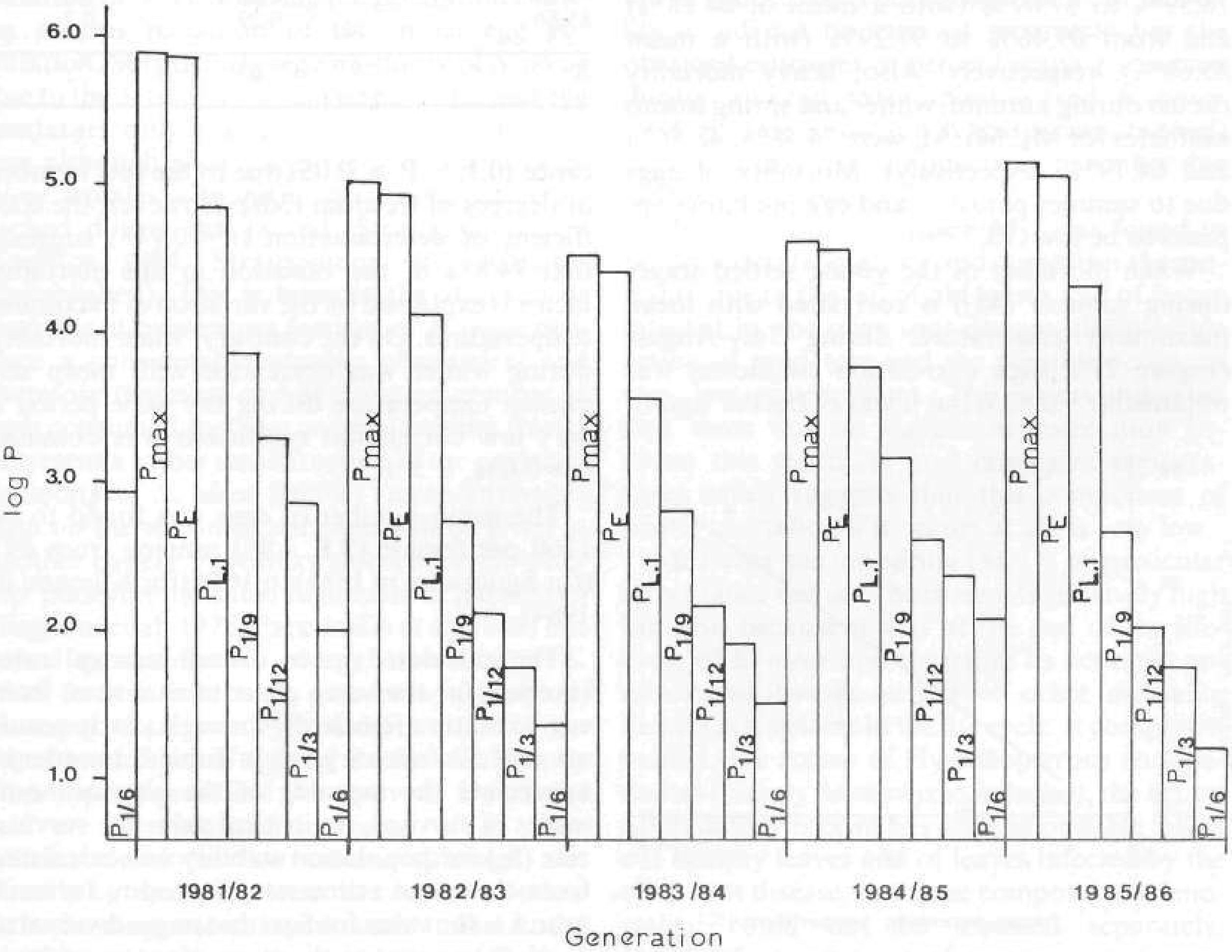

FIG. 1. Successive estimates of the population of *S. oleae* (average of seven experimental sites) within each of five yearly generations (1981/82, 1982/83, 1983/84, 1984/85, 1985/86) in Corfu.

TABLE 1. Mean percentages of mortality (average of seven experimental sites) due to the action of the recognized mortality factors within each of five yearly generations of *S. oleae* in Corfu.

Year	M_1	M_2	M_3	M_4	M_5	M_6
1981/82	6.89	86.86	90.15	76.20	59.26	81.35
1982/83	13.85	87.07	92.73	74.66	49.17	61.73
1983/84	13.14	84.76	78.80	75.81	48.76	63.42
1984/85	8.45	84.32	69.46	73.83	44.44	52.96
1985/86	11.50	78.39	97.29	72.40	41.17	64.51
$\bar{X}$	10.77	84.28	85.68	74.48	48.56	64.79

creased again in 1984/85, apparently due to higher survival, but heavy mortality within the 1985/86 generation resulted in a serious decline of the population.

Table 1 gives the estimated mean percentages of mortality (average of the seven experimental sites) for the five yearly generations of *S. oleae*. The heavier mortality factors appear to be mortality of crawlers (M_2) and young settled stages during summer (M_3). They ranged from 78.39% to 87.07% (with a mean of 84.28%) and from 69.46% to 97.29% (with a mean 85.68%), respectively. Also, heavy mortality occurs during autumn, winter and spring (mean estimates for M_4, M_5, M_6 were 74.48%, 48.56% and 64.79%, respectively). Mortality of eggs due to summer parasites and egg predators appears to be low (10,77%).

When mortality of the young settled stages during summer (M_3) is correlated with mean maximum temperature during July-August (Figure 2) a high correlation coefficient was obtained ($r = 0.865$) but it was of border significance ($0.1 > P > 0.05$) due to the low number of degrees of freedom (3df). However, the coefficient of determination ($r^2 = 0.748$) suggests that 74.8% of the variation in this mortality factor is explained by the variation of maximum temperatures. On the contrary, when mortality during winter was correlated with mean minimum temperature during the same period a very low correlation coefficient was obtained ($r = 0.038$, $P > 0.1$).

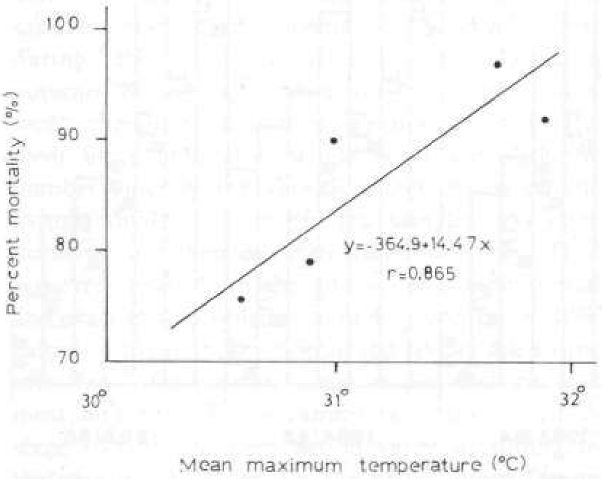

FIG. 2. The correlation of percent mortality of the established young stages of *S. oleae* during summer (M_3) with the mean maximum temperatures during July-August.

TABLE 2. The calculated overall survival rate (S), i.e. number of individuals out of 1,000 eggs that reach the stage of mature female, and the critical value of survival rate (S_c), according to the observed fecundity, for population stability, i.e. one mature female results again in one mature female in the next generation.

Year	S	S_c
81/82	0.13	0.8
82/83	0.34	0.9
83/84	1.33	0.8
84/85	3.07	0.8
85/86	0.29	0.7
$\bar{X}$	1.03	

The mean number of eggs was found to be 1260 per female (S.E. = 45) ranging from 691 (for Sgourades in 1981) to 1614 (for Klimatia in 1984).

The calculated mean overall survival rates (average for the seven experimental sites) from egg to mature female (S) for each yearly generation of *S. oleae* are given in Table 2. In order to appreciate the meaning of the obtained estimates of survival, the critical value for survival rate (S_c) for population stability was calculated from the mean estimate of fecundity for each year, i.e. the value for S so that one individual of *S. oleae* survives to the stage of mature female from the eggs produced by one female.

Heavy mortality during the 1981/82 generation of *S. oleae* resulted in very low survival rate. Only 0.13 individuals reached the stage of mature female out of 1,000 eggs and this indicated a population decline of 6.15 times (0.8/0.13). In the following years, overall survival rates were higher. The highest estimate was obtained in 1984/85 season (3.07). In 1985/86 season, overall survival rate was again very low (0.29).

Discussion

The population of *Saissetia oleae* is often characterized by considerable fluctuations resulting in periodic outbreaks. The analysis of the results obtained in this study indicate that these population fluctuations are caused by considerable variation in the survival rate from generation to generation that reflects the combined variation of the individual mortality factors.

Several mortality factors act upon the population of *S. oleae* during the generation causing serious reduction of the initial egg population. Surprisingly, egg mortality of *S. oleae* due to the action of the female parasites and egg predators during summer was relatively very low although a considerable proportion of *S. oleae* females is found to be parasitized or attacked during this period (Stratopoulou and Kapatos 1984, Stratopoulou and Kapatos unpublished). This is because the attacked or parasitized ovipositing females of *S. oleae* produce a considerable number of crawlers and therefore the more or less constant number of eggs consumed by these natural enemies finally represent a rather small fraction of the potential fecundity of *S. oleae* females (more analytical data on the action of parasites will be given in another paper). Previous evidence for the summer parasites indicated high rates of parasitism (Viggiani et al. 1975, Paraskakis et al. 1980) but actual measurements of egg mortality of *S. oleae* in the field have not been attempted. However, data given by Mendel et al. (1984) on the consumption of eggs of *S. oleae* females by *Scutelista cyanea* and *Metaphycus lounsburyi* and on the potential fecundity of *S. oleae* females developed on citrus, although not directly comparable, seem to confirm the low estimate of egg mortality obtained in this study.

After egg hatching, the population of *S. oleae* suffers heavy mortality. A high proportion of the emerged crawlers is lost in seeking for establishment in suitable positions. It is assumed that this mortality may be even higher in cases of very high populations in which overcrowding occurs. In such cases, which did not happen in this study, the mortality of crawlers may act in a density dependent manner.

After establishment, the population of *S. oleae*, being mainly in the first larval instar, suffers heavy mortality. The analysis of the results indicated that this mortality is, mainly, caused by the high temperatures or other factors (relative humidity, host plant condition) related to high temperatures and constitute a serious limiting factor of the *S. oleae* populations.

Mortality during Autumn (M_4) was found to be relatively high and remarkably constant. It comprises several components of mortality such as the action of high temperatures during September (a situation which is not unusual in Greece), the action of Hymenopterous parasites (*Metaphycus helvolus* etc.) predation and the fall of old leaves. These components of mortality could not be assessed separately but the obtained estimates of percent active parasitism during autumn (Stratopoulou and Kapatos 1984, Stratopoulou and Kapatos unpublished) suggested that the component of mortality due to this factor is low.

Mortality during winter (M_5) was found to be of moderate intensity and comprises the mortality due to the fall of old leaves and of leaves infected by the olive spot disease, the possible action of predators and the possible action of very low temperatures. The results indicated that there was no significant correlation between this mortality and minimum temperatures which suggests that this component of winter mortality, if it occurs at all, is very low.

Mortality during spring (M_6) is of particular importance not only because it is relatively high but also because it acts at the end of the lifecycle of *S. oleae* and therefore its action is not minimized by the action of other mortality factors acting later in the life cycle. It comprises, mainly, the action of Hymenopterous endoparasites (mainly *Metaphycus helvolus*), the action of predatory coccinelids and the possible fall of old healthy leaves and of leaves infected by the olive spot disease, but these components of mortality could not be assessed separately. Independent estimates of percent active parasitism (a parameter which is only of indicative value because it is not an estimate of the total action of parasitism during the whole season) during the course of this study indicated that parasitism during spring although higher than in autumn (Stratopoulou and Kapatos 1984, Stratopoulou and Kapatos unpublished) is not the main component of spring mortality. On the contrary there is the impression that the greater contributor to spring mortality is the action of predators.

The obtained estimates of fecundity are considered rather low compared with data appeared in literature (Argyriou 1963, Podoler et al. 1979). This could be an explanation for the generally low level of the *S. oleae* population in the island during the recent 10-15 years.

The calculated average overall survival rates of *S. oleae* during this study correspond to total mortality that ranged from 99.987% to 99.693%. Overall survival rate for *S. oleae* in citrus has been calculated in Israel (Podoler et al. 1979) for a single year in two different places. Their results (544 females out of 3.225 million eggs that corresponds to 99.983% total mortality and 195 females out of 1.506 million eggs that corresponds to 99.987% total mortality) are remarkably similar with those obtained in this study.

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KEY WORDS: *Saissetia oleae*, Population assessment, *Saissetia oleae* parasites

Δυναμική του Πληθυσμού του *Saissetia oleae*. I. Εκτιμήσεις Πληθυσμού και Θνησιμότητας

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ΠΕΡΙΛΗΨΗ

Η πληθυσμιακή δυναμική του λεκανίου της ελιάς μελετήθηκε στην Κέρκυρα στη διάρκεια των ετών1981-1986. Ο πληθυσμός του λεκανίου εκτιμήθηκε σε διάφορα χρονικά σημεία σε κάθε γενιά και παρουσιάζονται πληθυσμιακές καμπύλες που δείχνουν την προοδευτική μείωση του πληθυσμού του λεκανίου μέσα σε κάθε γενιά και τις μεταβολές του πληθυσμού από γενιά σε γενιά. Ισχυροί παράγοντες θνησιμότητας που δρουν σχεδόν σε όλη τη διάρκεια του βιολογικού κύκλου μειώνουν δραστικά τον αρχικό πληθυσμό του λεκανίου κάθε γενιάς. Οι σημαντικότεροι παράγοντες θνησιμότητας του λεκανίου βρέθηκαν να είναι η θνησιμότητα των νεαρών σταδίων το καλοκαίρι που προκαλείται κυρίως από τις υψηλές θερμοκρασίες και που κυμάνθηκε από 75,70% μέχρι 97,29%, η θνησιμότητα των ερπουσών που κυμάνθηκε από 78,39% μέχρι 87,07% και η θνησιμότητα στη διάρκεια της άνοιξης που κυμάνθηκε από 52,96% μέχρι 81,35%. Το συνολικό ποσοστό επιβίωσης που εκφράζει τη συνδυασμένη δράση όλων των παραγόντων θνησιμότητας βρέθηκε να είναι πολύ χαμηλό και κυμάνθηκε σε όρια που αντιστοιχούν σε συνολική θνησιμότητα από 99,693% μέχρι 99,987%.