Population dynamics and life history tactics of arthropods from Mediterranean-type ecosystems

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The null hypothesis of this paper is that survival of arthropods under the severe Mediterranean conditions involves specific combinations of conservative and conformist traits. To test this hypothesis a modeling approach employing a Leslie-type matrix model and a fuzzy systems technique for parameter estimation is developed and applied to a model species. The general conclusion is that the results of this paper add support to the null hypothesis, whereas specific conclusions are as follows: 1) matrix models merging demographic and physiological parameters are suitable tools for the simulation of population dynamics of arthropods and further for the discussion of the interplay among life history traits; 2) employing linguistic instead of arithmetic variables, fuzzy approaches allow for the formalization of incomplete and/or missing data exploiting expertise concerning related species; 3) in general, population dynamics of arthropods follow the seasonality of the Mediterranean climate; 4) the basic mechanism underlying skewing phenologies and stochastic equilibrium is identified with the type of temperature dependence of arthropod metabolic activity; 5) under optimal conditions an exponential trend is superimposed on seasonal population dynamics; 6) more realistic conditions involving large-scale random oscillation in temperature in autumn and spring coupled with small-scale temperature oscillation in summer and winter result in stochastic equilibrium; 7) moderate contamination of soil and medium-scale oscillation in temperature result in stable temporal patterns; 8) a sensitivity analysis shows disproportional effect of different demographic parameters on population growth rate. Fecundity of young and middle-aged adults is most important for the rate of population growth, whereas elder animals are considered an important pool for maintenance of the population.

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The study of populations-into-their-environment presupposes that the features of organisms interact with the habitat through an adopted strategy (Southwood 1977, 1988). Consequently, within a habitat-templet context the exploration of organisms' tactics ensuring survival in a given environment requires the consideration of trade-offs between physiological parameters (Q_{10} values, optimal temperature ranges etc), reproductive schedules (e.g. age at maturity, distribution of reproductive effort over age) and demographic variables (e.g. distribution of mortality over age classes). The merit of this approach lies on the fact that it allows for the simultaneous consideration of physiological and demographic variables (Korfiatis and Stamou 1999), which is of special interest for organisms inhabiting severe environments threatening survival such as the Mediterranean (Stamou 1998).

Strong temporal and spatial variation in abiotic variables, usually attaining extreme values encountered in harsh environments, is the very characteristic of Mediterranean habitats. Indeed, temperature and humidity display large diurnal, seasonal and interannual oscillations, whereas small- and large-scale irregularities in the landscape coupled with human impacts such as frequent fire and overgrazing result in habitat fragmentation. Large temporal oscillation in food availability and uneven spatial distribution of limited resources also characterize Mediterranean landscapes (Stamou 1998). To cope with environmental severity, i.e. high summer temperature, desiccation of substrates and varying availability of foods, Mediterranean arthropods might display specific combinations of demographic and metabolic traits.

Many authors (Radea 1989, Asikidis and Stamou 1992, Lymberakis 2003) have investigated the phenology of different arthropod species from different Mediterranean-type ecosystems and showed that changes in population size synchronize with the mid- and long-term oscillations in the environmental variables and display stochastic equilibrium coupled with either right or left skewed phenologies. However, the underlying mechanisms are not known. Moreover, it is not known as to what extent such mechanisms can ensure survival during environmental stress, such as wild fires and soil contamination, recently superimposed to modest human interventions occurring for millenaries in Mediterranean habitats.

Though population dynamics models involving demographic parameters are suitable tools for exploring the complex interplay among different life history traits (McGee and Spencer 2001, Oli and Zinner 2001, Spencer and McGee 2001), numerical simulations usually provide vague approximations to census data (Jensen and Miller 2001). Uncertainties in these simulations stem from imprecise and/or limited data, indirect measurements etc. (Mpimpas et al. 2001). Moreover, additional uncertainty overrides estimations made in Mediterranean habitats consisted of fine-grained mosaics of more or less isolated microsites (Stamou 1998). Thus, even if all information relating to species demography is available, the actual significance of different crisp environmental variables for different demographic parameters under the specific micro-environmental conditions of the Mediterranean mosaic remains uncertain. This uncertainty arises from spatial randomness and is different from that accounted for by stochastic models. To formalize this kind of uncertainty, fuzzy approaches appear more suitable (Bulte and van Kooten 2001). Using fuzzy systems simulation techniques, accounting more for realism and generality (as stated by Levins 1968), proximate solutions relating to the problem of parameter estimation may be obtained.

With above premises in mind the goal of this paper is:

1. To validate the applicability on Mediterranean arthropods of an age structured population dynamics model coupled with a fuzzy technique for treating uncertainties associated with estimations made under Mediterranean conditions.
2. To explore mechanisms allowing arthropods from Mediterranean regions to overcome environmental severity and further to withstand environmental stress (in this paper exemplified by soil contamination).
3. To elucidate the interplay among life history traits leading to skewing phenologies and stochastic equilibrium.

To meet these goals, we focus on the population dynamics of a model species, namely the oribatid mite *Scheloribates latipes* (Koch). This decision grounds upon the consideration that 1) the complexity of oribatids' life history features may stand as an example shaping the strategic response of many other arthropods to the severity of the Mediterranean environments (Stamou 1998), 2) enough field and laboratory data are available for this species, 3) it appears tolerant to modest soil pollution (Stamou and Argyropoulou 1995), 4) it is broadly dispersed within Mediterranean regions, while in most cases it dominates the community of arthropods (Poinsot-Balaguer 1996). In accordance, it is expected that the study of the population dynamics of this model species may exemplify the population dynamics of many other Mediterranean arthropods.

Material and methods

Modelling population dynamics

In this paper the population dynamics of a closed population (i.e. with zero immigration and emigration as well as predation rates) under different circumstances of soil contamination and different temperature regimes was explored. It must be noticed however that, although modeling focuses on a single model species, expertise used for model parameterization combines data referring to many other micro- and macro-arthropods from Mediterranean regions.

To achieve a discrete-time approximation to the continuous birth, growth and death processes a Leslie-type life stage-structured model was developed (Caswell 1989) and weekly simulations were performed. To account for different rates of demographic parameters of specimens at different ages the demographic vector included 8 life stages; namely egg, larva, protonymph, deutonymph, tritonymh, young mature (aging 0–3 weeks), middle-aged mature (aging 4–21 weeks), and aged mature (> 22 weeks).
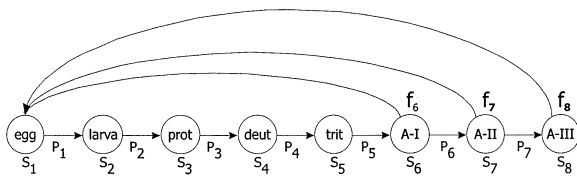
Fig. 1. Life cycle for the model species *S. latipes*. Circles are life stages (egg, larva, protonymph, deutonymph, tritonymph, A-I young adult, A-II middle-aged adult, A-III elder adult. f is fecundity, P_i is development from the stage i to the next stage $i+1$ and S_i is persistence in the stage i.

An age structured life cycle layout for the animal is depicted in Fig. 1. f_i denotes the per capita weekly egg production (rate of fecundity) by adults in age stage i. S_i stands for the probability of a specimen in life stage i to survive and remain in life stage i in the time period t, $t+1$ (persistence; the subscripts t and $t+1$ denote successive weekly steps). Finally, P_i accounts for the probability of a specimen in life stage i at t to survive and hatch into the next life stage during t, $t+1$ (transition). The model shows:

$$N_{t+1} = AN_t$$

where N_{t+1} and N_t are demographic vectors describing the life stage structure of population at time $t+1$ and t correspondingly and A is the projection matrix. The demographic vector shows:

$$N_t = \begin{bmatrix} n_{1,t} \\ n_{2,t} \\ \cdots \\ n_{i,t} \\ \cdots \end{bmatrix}$$

where $n_{i,t}$ stands for the size of the life stage i at time t. Finally, the projection matrix has the form:

$$A_t = \begin{bmatrix} S_{1,t} & 0 & 0 & \cdots & f_{i,t} \\ P_{1,t} & S_{2,t} & 0 & \cdots & 0 \\ 0 & P_{2,t} & S_{3,t} & \cdots & 0 \\ \cdots & \cdots & \cdots & \cdots & \cdots \\ 0 & 0 & 0 & P_{i-1,t} & S_{i,t} \end{bmatrix}$$

Following Hadjibiros (1977) the diagonal and subdiagonal elements of the projection matrix are considered functions of l_i (= duration in weeks of life stage i), and m_i (= weekly rate of mortality of life stage i):

$$S_i = (1 - m_i) \frac{l_i - 1}{l_i} \text{ and } P_i = \frac{1 - m_i}{l_i}$$

Model type

Hadjibiros (1977) tested different versions of a Leslie-type model to simulate population dynamics of oribatid mites and concluded that best simulations are obtained by using linear models. In this vein, Stamou (1981) successfully used a linear model to simulate the population dynamics of the oribatid *Achipteria* cf *italica*. Above considerations are supported by experimental data. Indeed, previous studies referring to oribatids (including *S. latipes*; Asikidis and Stamou 1991), collembolans (Argyropoulou 1993) and diplopods (Iatrou and Stamou 1991) show an uneven distribution of individuals among micro-sites of the fragmented Mediterranean habitats. However, laboratory experiments reveal an Allee-type density dependence of demographic parameters resulting in locally optimal population size (Stamou and Asikidis 1989). Accordingly, density effects on the demographic parameters are not taken into account and a linear version of the model is adopted. Rates of demographic parameters for *S. latipes* are identified with optimal estimates made in standard laboratory conditions (Table 1). As shown, reproductive rate is rather high, adults reach maturity soon after hatching, while mortality of juveniles is greater than that of adults. Furthermore, with many exceptions census data for most sexually reproducing Mediterranean arthropods (Stamou 1998) indicate no bias in sex ratio, therefore only the population dynamics of females is considered in this paper.

The effect of temperature and soil contamination on the demographic parameters

In Greek Mediterranean areas soil moisture has an on/off effect on arthropod survival and correlates mostly with the spatial distribution of animals among favorable and unfavorable micro-sites (Stamou 1998). It follows that above moisture thresholds the demographic parameters are not sensitive to changes in soil moisture, whereas below the thresholds the decline of moisture forces animals to move to favorable micro-

Table 1. Demographic parameters of *S. latipes* estimated at 21°C in laboratory. f denotes fecundity (eggs/female/day), l stands for longevity (in days) and m is weekly mortality (%) (Data from Asikidis 1989).

Life stages	f_i	l_i	m_i
Egg		14.06	2.07
Larva		10.78	5.65
Protonymph		9.00	3.70
Deutonymph		9.44	3.71
Tritonymph		11.17	3.30
Young adult	0.06	3.00	0
Middle-aged adult	0.24	19.00	1.47
Elder adult	0.04	45.00	1.60

sites. Consequently, in this paper moisture effects on demographic parameters are not taken into account. By contrast, seasonally varying temperature has a continuous effect on the development of arthropods' life cycles (Asikidis and Stamou 1992). To describe the relationship between changing temperature and demographic parameters , we refer to Stamou (1986) who stated that a single model can describe temperature dependence of either activity or demographic parameters. To describe the effect of changing temperatures on the metabolic activity of various micro- and macro-arthropods a four-parameter model was used (Argyropoulou and Stamou 1993, Stamou and Iatrou 1993, Stamou et al. 1995, 2000):

$$A = a \{(1 + k e^{-pT})^{-1} - e^{(T - T_l)}\}$$

where A is activity, T is actual temperature, T_l is lethal temperature and k, p are parameters defining the optimal temperature range (plateau) as well as the inflection point of the curve (Stamou et al. 1995). Experimental data concerning the dependence of the demographic parameters of Mediterranean arthropods on temperature are incomplete. However, the above model-type and considerations constitute adequate expertise upon which the generation of linguistic variables employed in fuzzy modeling and relating to temperature dependence of the demographic parameters is grounded (see below).

Another part of expertise relates to the joint effect of temperature and soil contamination on demographic parameters. Earlier studies on various Mediterranean arthropods showed a temperature dependent effect of soil contamination on animals' biological activity. For instance, such effects are studied in the diplopod *Glomeris balcanica* (Stamou et al. 2000). The results of that study showed that although the curve-type remains unchanged, lethal temperature, the length of the optimal range as well as the inflection point of the curve are strongly affected. Available data for various species are limited and concern the respiratory response to changing temperature under laboratory conditions (Stamou et al. 1995) as well as the demographic response and lethal temperatures under different levels of substrate contamination (Stamou and Asikidis 1992). In addition we assume a) a similar response of any parameter of ectotherm organisms to changing temperature as suggested by Stamou (1986) and b) that, as in *G. balcanica*, the type of curves describing temperature dependence of demographic parameters remains unchanged under different regimes of soil contamination. The expected response of demographic parameters to changing temperature under different levels of soil contamination is depicted in Fig. 2a.

Other experimental data (Stamou and Asikidis 1992) showed that the contamination of culture substrate and food affected the relationship of both survivorship and fecundity to age of *S. latipes*. Available data concerned
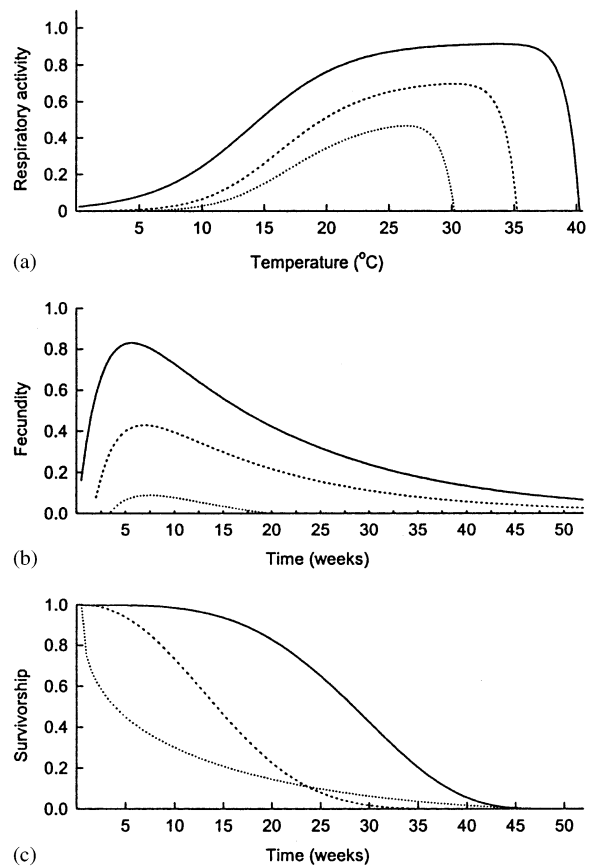

Fig. 2. Effects of (a) temperature on normalized (rescaled in 0, 1) respiratory activity, of (b) the relationship of normalized fecundity to time and of (c) substrate contamination on the relationship of normalized survivorship to time. Continuous line: low pollution level, dashed line: medium pollution level and dotted line: high pollution level.

two levels of substrate contamination and showed strong effects mainly on the mortality of younger specimens. Moreover, accumulation of contaminants resulted in shortening of animals' life span and changes in the type of the survivorship curve. To formalize these data a two-parameter empirical model was used for survivorship:

$$S\% = 100 \left(1 - \left(\frac{t}{100}\right)^a\right)^{1/b}$$

(S% is percentage survivorship, t is time and a, b are parameters accounting for convexity and steepness) and a six-parameter empirical model is used for fecundity:

$$F = a_o\{(1 + a_1 e^{b_1 t})^{-b_2} - c_o e^{c_1 t}\}$$

(F is fecundity rate, t is time and a_0, a_1, b_1, b_2, c_0, c_1, are parameters accounting for elevation, amplitude, convexity and steepness). Changing values of models' parameter families of curves to describe the effect of

contamination on survivorship and fecundity can be obtained (Fig. 2a and c). Above model type and considerations complete the expertise used in fuzzy modeling.

Fuzzy model building

Given incomplete data and over-parameterization of the situation, a fuzzy system approach is undertaken. Fuzzy systems were developed to tackle problems arising within the artificial knowledge framework and aim at the symbolic treatment of human knowledge (Zadeh 1965). The great advantage of fuzzy systems in ecology grounds on the fact that instead of arithmetic they entail linguistic variables with possible value such as "very low temperature", "low", "medium", "high temperature" etc. (Stamou and Stamou 1996). Fuzzy theory claims that words, especially adjectives, are ambiguous with respect to their exact meaning (Terano et al. 1992). The truth of a linguistic variable is a matter of degree. For example, the phrase "very low temperature" is true to some degree for an organism. The lower the temperature the more true the phrase.

Building of fuzzy systems is based upon the definition of the membership function $\mu_A(x)$. X is the reference set termed "universe of discourse" that is the temperature gradient: "very low", "low", "relatively low", "medium", "relatively high", "high", "very high" temperatures, A is a sub-set of X (e.g. high temperature) and x is a given object (e.g. 20°C). Within the fuzzy context a solution of classification problems is achieved by covering the universe of discourse of the input-temperature and the output-demographic parameters with fuzzy sub-sets and by the definition of rules concerning the relation between the input and the output.

Indeed, the membership function $\mu_A(x)$ assigns weights to the object x (e.g. the given temperature of 20°C) that accounts for the "possibility" that this element belongs to the sub-set A (e.g. high temperature). In the case of continuous universe of discourse the form of the sub-set A is:

$$A = \{(x, \mu(x)) : x \in X\}$$

while in case of discrete universe of discourse the sub-set A has the form:

$$A = \mu(x_1)/x_1 + \mu(x_2)/x_2 + \ldots \mu(x_n)/x_n$$

For example the sub-set A = high temperature may obtain the form:

A(high temperature)

$$= 0/0°C + 0/10°C + 0.3/20°C + 1/40°C$$

In Fig. 3 the definition of fuzzy sub-sets in the variable temperature is depicted. From the figure, we can conclude:

- If $x < 10°C$ then $\mu_A(x) = 1$. The conclusion is that x has a very low temperature.
- By analogy if $x > 15°C$ then $\mu_A(x) = 0$ and the conclusion is that x does not have a very low temperature.
- Finally, if $10°C < x < 15°C$ then x has a very low temperature to a degree in [0,1].

Analogous definitions have been made for soil contamination as well as for fecundity, survival and duration of development. However, for the sake of space-saving these definitions are not shown in figures.

Any fuzzy system is made up of the fuzzification compartment, the fuzzy knowledge base element, the fuzzy inference mechanism and the defuzzification compartment. Based upon outlined above expertise relating to the effects of temperature and soil contamination on the demography of Mediterranean arthropods, a fuzzy inference base is developed. Fuzzy inference is based upon simple rules contained in the fuzzy knowledge base. For example, the following sentence:

***IF** temperature **IS** low **AND** contamination*

   ***IS** high **THEN** mortality is relatively high*

is such a rule. The structure of the used model is depicted in Fig. 4. Data concerning the level of soil contamination and temperature are the inputs to the fuzzy compartment and the demographic parameters are the outputs. In turn, the latter are the inputs to the compartment in which the compilation of the projection matrix takes place. Then, the demographic vector N_t is multiplied by the projection matrix to produce the demographic vector N_{t+1}.
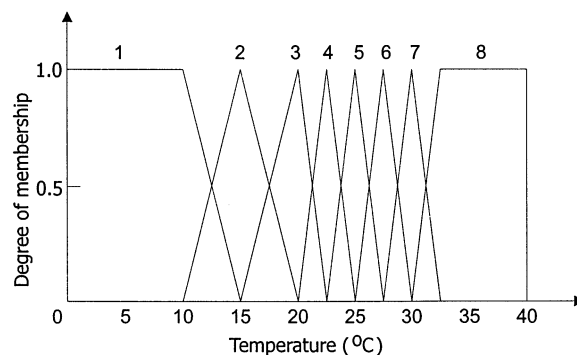

Fig. 3. Definition of fuzzy sub-sets in the variable temperature. 1: very low temperature, 2: low temperature, 3: relatively low temperature, 4: rather low temperature, 5: rather high temperature, 6: relatively high temperature, 7: high temperature and 8: very high temperature.
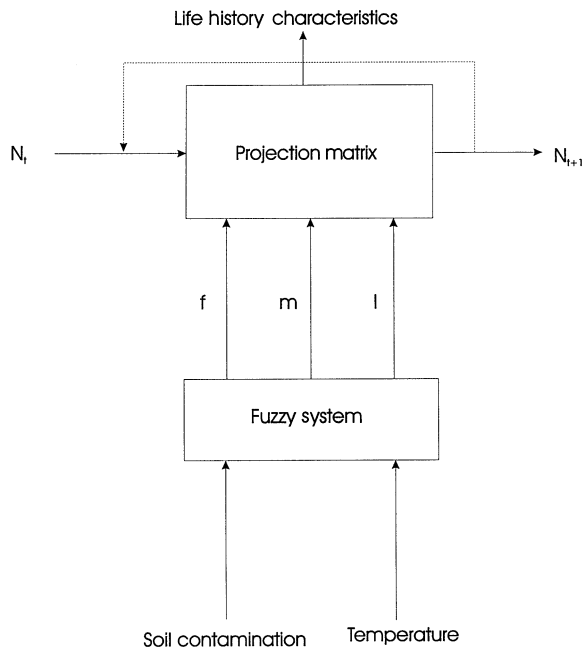
Fig. 4. The structure of the model used for the simulation of the population dynamics of arthropods.

Sensitivity analysis

For constant rates of demographic variables, parameter λ stands for the asymptotic population growth rate. For $\lambda > 1$ the population size increases exponentially, while for $\lambda < 1$ the population declines. Values of λ can be calculated from the dominant eigenvalue of the projection matrix. Following Caswell (1989) the consideration of changes in sensitivity of the population growth rate (λ) to changes in demographic parameters is judged essential for demographic analysis. Bringing forth different aspects of population biology and elucidating the interplay among demographic parameters as well as their relative importance at different times of the life cycle development, this procedure is usually proved fruitful providing insights into population dynamics in the field (Spencer and McGee 2001). To explore the sensitivity of the population growth rate to weekly variations of demographic parameters a simple sensitivity index is estimated:

$$s_{i,t} = ABS \left(\frac{\delta \lambda_t}{\delta D_{i,t}} \right)$$

where $s_{i,t}$ is the sensitivity index, $\delta \lambda_t$ and $\delta D_{i,t}$ are changes in the growth rate and in the demographic parameter D_i estimated at t (McGee and Spencer 2001). D_i stands for f_i, l_i and m_i and sensitivity of the model output for changes in all three demographic parameters has been explored.

Results

For simulation purposes weekly varying rates of demographic parameters are considered and within each year 52 different projection matrices are built to achieve weekly simulations of population dynamics. The response of the demographic parameters to normalized (rescaled in a 0–1 range) changes in temperature and soil contamination are shown in Fig. 5 (A, B, C). Under lower and higher contamination levels slight modifications in curves describing temperature dependence of demographic parameters are depicted, while pronounced differences in these curves correspond to intermediate levels of soil contamination.

Different combinations of temperature and soil contamination regimes are simulated (Table 2). Under conditions of regular seasonal variation in temperature and non-soil contamination (scenario 1) numbers increase exponentially (Fig. 6A, B). A minor peak in population size occurs in winter and a major one in summer. Noticeable is that population size declines slightly in spring. To test the capability of animals to overcome environmental stresses two alternative versions of this scenario are simulated. The first employs a 50% decrease in population size in October and the second a relevant 90% decrease also in October. In the former case population size restores after 10 months (41 weeks) and in the latter it recovers after 2 years (101 weeks).

Population dynamics remain unaffected by weak noise in temperature ($\pm 3°C$) superimposed on sinusoidal oscillation (scenario 2). By contrast, under more realistic Mediterranean conditions (scenario 3) with a large-scale noise ($\pm 10°C$) in autumn and spring and a small-scale noise in summer and winter numbers attain stochastic equilibrium after almost 8 years (Fig. 7).

Low level of soil contamination has no effect on population dynamics (scenario 4), whereas under intermediate levels of soil contamination (scenario 5) population size increases tardily exhibiting strong annual oscillations (Fig. 8). Finally, in circumstances of high level contamination of soils (scenaria 6 and 7) population size declines exponentially (Fig. 9).

The only combination of temperature and soil contamination resulting immediately in stochastic equilibrium is prescribed by scenario 8. A sensitivity analysis for the population growth rate is conducted in that case. Growth rate appears more sensitive to changes in fecundity (Fig. 10b). In summer, fecundity of middle-aged adults is most important, whereas in fall those of young adults is more important. Mortality of young adults is important in the fall, while longevity and mortality of juveniles is of equal although minor importance for changes in population growth rate. It is remarkable that in spring population growth rate appears non-sensitive to changing demographic parameters.

(A)

(B)
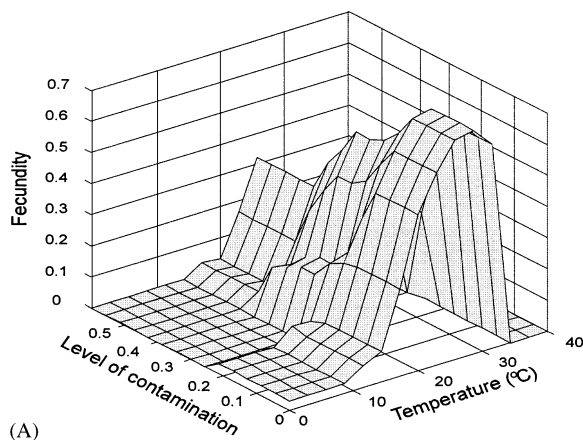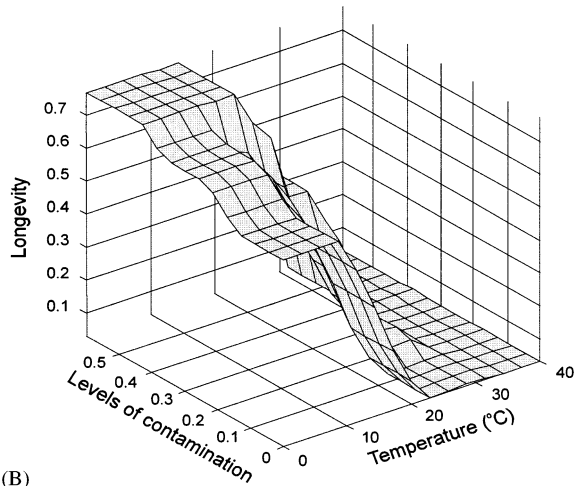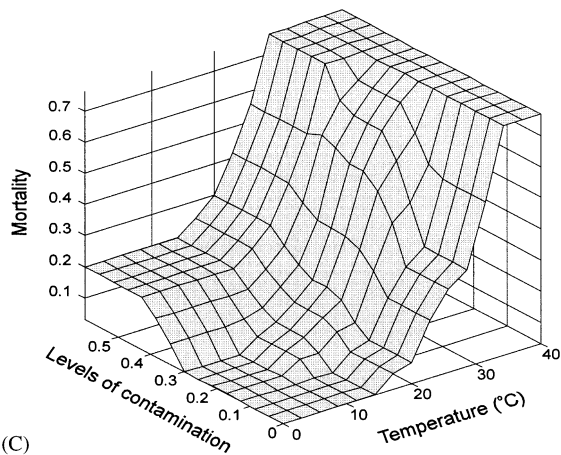
Fig. 5. Normalized (rescaled in a 0–1 range) response of the demographic parameters (A: fecundity, B: longevity, C: mortality) to changing temperature and level of soil contamination.

(C)

In Fig. 11 stochastic equilibrium of the population size is depicted. Simulation results in conjunction with sensitivity analysis provide with a layout of *S. latipes* life cycle development consistent with census data (Sta-

mou and Sgardelis 1989, Stamou and Asikidis 1992). Extremely high recruitment occurs in early summer and again in late fall. During the same period important peaks occur in sensitivity of growth rate to middle-aged adults' fecundity and young adults' fecundity, respectively. Released animals develop rapidly to sexual maturity and flushes of juveniles occurring in summer and winter characterize the population dynamics of this species. Development of juveniles into adults lasts for about three months in summer and about four months in winter. Peaks in the corresponding sensitivity graphs occur in early and late fall. Adults last for longer periods in the field and reproduce by late fall and late spring. Peaks in the sensitivity of growth rate to adult mortality forego valleys in numbers. Noticeable is also that oscillation in adult numbers reduces with age. Finally, although of minor importance, sensitivity of population growth rate to changing parameters relating to long-lasting elder adults is noticeable.

Discussion

In this paper, a general age-structured Leslie-model is developed. To test its applicability, the model is used to simulate the population dynamics of the model species *S. latipes*. The development of such a model requires extensive use of age-specific demographic data, which in most cases are incomplete. To overcome shortage in data availability a fuzzy systems approach is adopted and following Mpimpas et al. (2001) only the range and the most confident values of the input variables are taken into consideration.

In response to one of the aims of this paper it must be noticed that the application of this procedure provides satisfactory outputs. Indeed, the complexity of the system is simplified, as the most difficult task – model parameterization – was carried out qualitatively employing linguistic variables and rules. Moreover, this approach generates more realistic descriptions of the population dynamics of arthropods, while by modifying rules and the initial values of the demographic parameters and demographic vectors, the method can easily be fitted to different organisms inhabiting different biotopes. Evidently, increased realism and generality (sensu Levins 1968) counterbalance possible reduction in the accuracy of the model outcomes.

In general, population dynamics of Mediterranean soil arthropods parallel seasonal fluctuations of climatic variables and most species display skewing phenologies (Sgardelis et al. 1993). As mentioned above, our model is based on the assumption that 1) *S. latipes* is a model species and 2) its population dynamics is representative of non-symmetric phenologies. Simulation results seem to confirm these assumptions. To compile the projection matrix information relating to population dynam-

Table 2. Population dynamics of the model species *S. latipes* under different combinations of temperature regimes and levels of soil contamination.

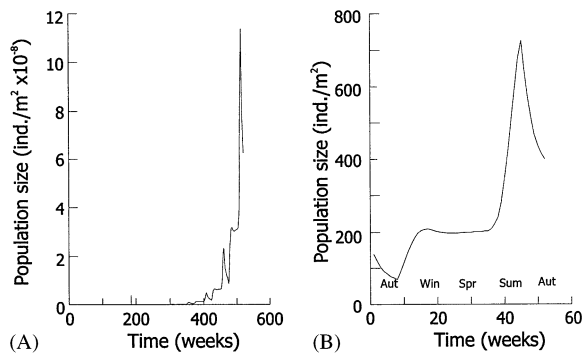| Temperature regimes	Soil contamination levels	Population dynamics
1. Sinusoidal oscillation with T = 52	No	Exponential growth
2. Sinusoidal oscillation with T = 52 plus ± 3°C noise throughout the year	No	Exponential growth
3. Sinusoidal oscillation with T = 52, plus ± 10°C noise in spring and autumn and ± 3°C noise in summer and winter	No	Long-term stochastic equilibrium
4. Sinusoidal oscillation with T = 52	Low level of soil contamination	Exponential growth
5. Sinusoidal oscillation with T = 52	Intermediate level of soil contamination	Strong annual oscillation
6. Sinusoidal oscillation with T = 52	High level of soil contamination	Exponential decline
7. Sinusoidal oscillation with T = 52	High level of soil contamination only during winter	Exponential decline
8. Sinusoidal oscillation with T = 52 plus ± 5°C noise throughout year	Intermediate level of soil contamination	Stochastic equilibrium

Fig. 6. Development of population size under regular seasonal variation in temperature and non soil contamination (scenario 1). (A) development of population size over 10 years and (B) development of population size over 1 year. Aut: autumn, Win: winter, Spr: spring, Sum: summer.
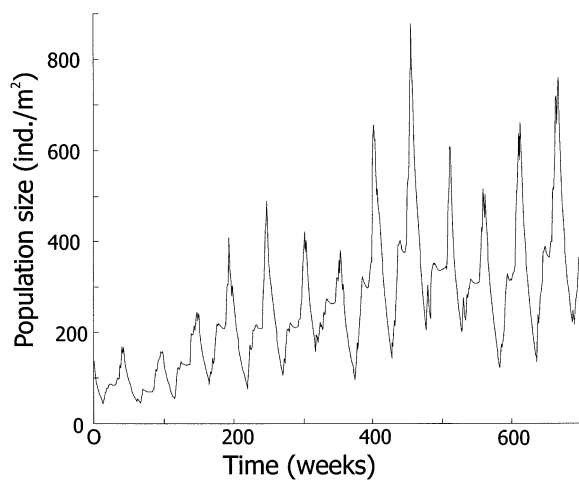
ics of different arthropods from various Mediterranean-type ecosystems being merged, this model gives reasonable projections of the population dynamics of *S. latipes* consistent with earlier studies (Stamou and Sgardelis 1989, Asikidis and Stamou 1992). Model outcomes describe juvenile flushes occurring in summer-early fall well and provide interpretation with respect to as yet unexplained peaks in juvenile graphs occurring in early winter. Moreover, rapid recovering after environmental stress showed in this paper is in accordance with results referring to the effect of wild fires on the population dynamics of many arthropods from Mediterranean-type ecosystems (Sgardelis and Margaris 1993).

Critical values of demographic parameters were identified with estimations made under optimal conditions

Fig. 7. Development of population size under conditions of large-scale noise (± 10°C) in autumn and spring and small-scale noise in summer and winter added on seasonally varying temperature (scenario 3).
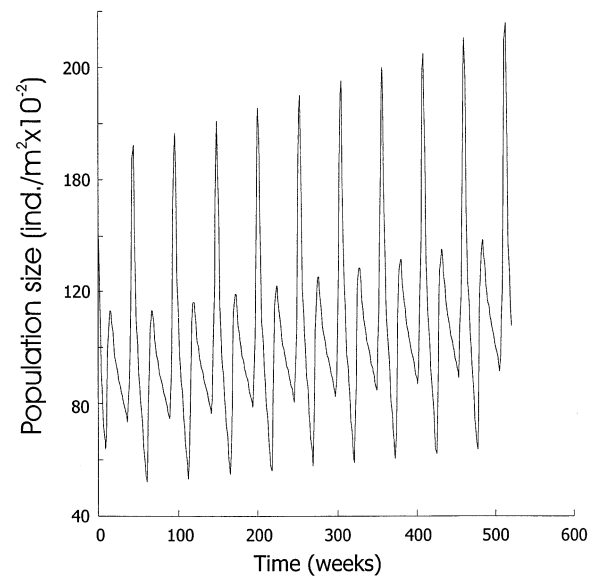

Fig. 8. Development of population size under conditions of intermediate levels of soil contamination (scenario 5).
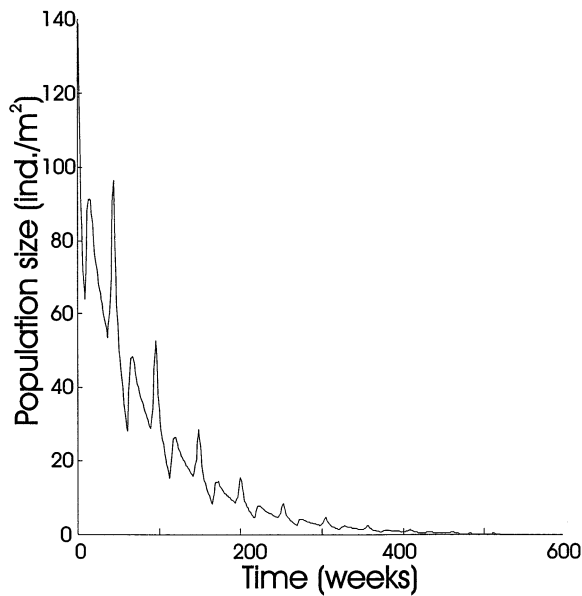
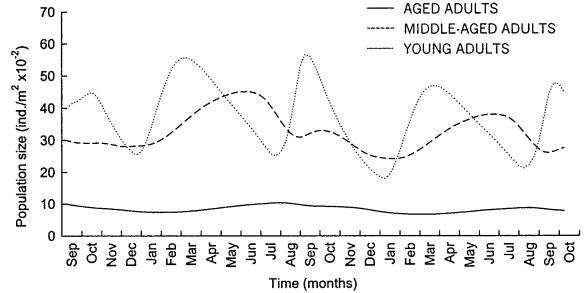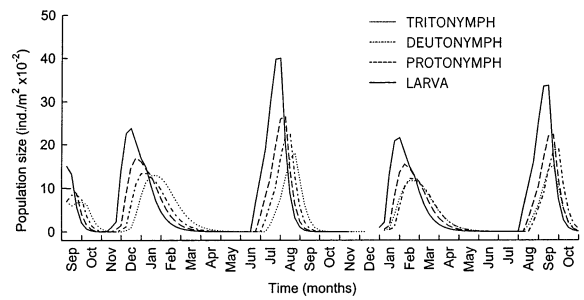Fig. 9. Development of population size under conditions of high levels of soil contamination (scenario 6).

Fig. 11. Development of population size under conditions of intermediate levels of soil contamination and $\pm 5°C$ noise added on seasonally varying temperature (scenario 8).
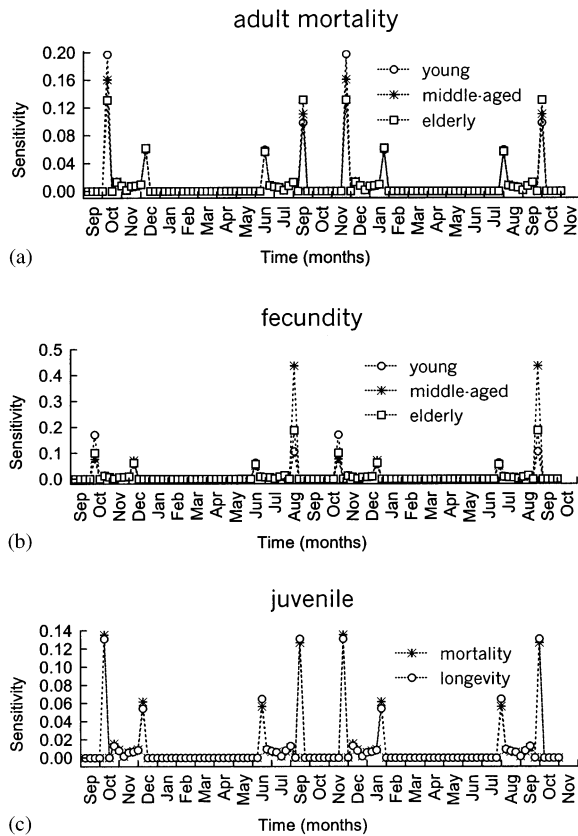

Fig. 10. Sensitivity of the population growth rate to stage specific parameters ((a) adult mortality, (b) adult fecundity and (c) juvenile mortality and longevity) over time for the model.

in the laboratory. Employing laboratory estimation of demographic parameters, the population size expands under regular oscillation in field temperature though skewing seasonality is superimposed on the exponential curve (scenario 1). As mentioned above, seasonal variation of population size is consistent with census data for many species. Inducing seasonal specific demographic rates, changing temperature forces populations to follow the seasonality of the Mediterranean climate. However, the exponential trend is not supported by census data. Considering more realistic situations, i.e. large random oscillations in temperature during spring and autumn and moderate random oscillations in winter and summer (scenario 3), which is more consistent with actual Mediterranean circumstances, the model generates stochastic equilibrium.

To interpret skewing phenologies and stochastic equilibrium we again raise the assumption of similar response of either metabolism or demography to changing thermal regimes. Laboratory data show rapid metabolic response even to slight changes in temperature and stimulation of activity by fluctuating temperature (Stamou et al. 1995) driving an analogous demographic response. Hence, skewed seasonal phenologies result from the immediate response of animals to seasonally varying temperature coupled with non-symmetric dependence of demographic parameters on temperature.

The results of this paper show that if large stochasticity in spring and autumn is added to seasonally oscillating temperature, then expanding dynamics is

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supplanted by balancing population size. This can be explained considering the skewing response of animals' metabolism to changing temperature. Indeed, as shown in Fig. 2 the large temperature range 20–38°C is the optimal plateau. Within this temperature range activity is independent of temperature. On the contrary, in the range 5–20°C metabolic activity depends strongly on changing temperature. In Mediterranean fields arthropods experience an average temperature of about 20°C (range of variation 10–30°C). Peaks of randomly varying temperature fall in the optimal range therefore have no effect on animals' metabolism. By contrast, valleys with a temperature fall in the range 10–20°C result in a significant decline of activity. Consequently random increases in temperature have no effect on demographic parameters, whereas random temperature decreases restrain population growth during these periods, finally leading to stochastic equilibrium. So, we conclude that the mechanism devising both skewing phenologies and stochastic equilibrium in Mediterranean arthropods relates to the type of temperature dependence of their metabolic activity.

Another task of this paper concerns the importance of different demographic parameters for population dynamics. To meet this point, an analysis of sensitivity of population growth rate to changes in demographic variables was conducted (Caswell and Trevisan 1994, Oli and Zinner 2001). Sensitivity analysis reveals seasonally disproportional importance of different parameters for the rate of population increase and major peaks in sensitivity graphs occur in fall. Fecundity has the largest potential influence on population growth rate. Wider temperature noise in autumn than in spring can be considered the most important factor for balancing size, and therefore affects fecundity the most. It is noticeable also that numbers of elder adults display smooth seasonal fluctuations although changes in their mortality and fecundity are relatively important for the entire population. It seems plausible that long lasting elder adults can be considered as a constantly present population reserve contributing significantly to the persistence of *S. latipes*, a suggestion reported also for other species by Stamou and Sgardelis (1989).

The assessment of the effect of soil contamination on population dynamics is based on the assumption that temperature dictates the type of demographic response, whereas soil contamination decides its magnitude (Stamou et al. 2000). Matching of simulation results generated in this paper with census data (Stamou and Argyropoulou 1995) substantiate this assumption. Like many other oribatids and collembolans, *S. latipes* appears modestly tolerant to soil contamination and it justifies its broad dispersion in moderately contaminated habitats. The following suggestions add support to this conclusion: a) only in moderately contaminated soils and under conditions of moderate temperature noise (±5°C) added on regular temperature oscillation

a stable seasonal pattern is attained. As mentioned above such a temperature regime drives restrained population growth. Moreover, b) Siepel (1994) claims that in polluted areas the accumulation of contaminants is a constantly present dominant environmental factor creating constant microenvironments. In these environments food specialists such as *S. latipes* may establish (Stamou 1998). Furthermore, c) Stamou and Stamou (1996) considering data provided by Stamou and Asikidis (1992) concluded that in moderately contaminated areas contaminants drive a fair decline in demographic rates and a gentle shortening of life span and optimal temperature range of arthropods. Above three considerations explain the stabilizing effect of moderate pollution for modestly resistant food specialists.

To sum up, conservative traits such as long lasting adulthood, ontogenetic cost put mainly on juveniles and reduced adult mortality coupled with conformist characteristics such as relatively high reproductive rate, uneven distribution of reproductive effort, rapid development of juveniles into adult and precocity shape the life history tactics of Mediterranean arthropods. Coexistence of conservative and conformist characteristics is assigned to many micro- and macro-arthropods from Mediterranean regions (Stamou et al. 1993, Stamou 1998). Conservative characteristics appear adaptive for the persistence of animals under extreme conditions, as well as under conditions of environmental stress, such as soil contamination. In addition, conformist characteristics force population size to conform to the seasonality of the Mediterranean environment.

References

Argyropoulou, M. D. 1993. Dynamics and activity of collembolan in the soil sub-system of an evergreen-sclerophyllous formation in Mt. Hortiatis. – PhD Thesis, Univ. Thessaloniki (in Greek with an English summary).

Argyropoulou, M. D. and Stamou, G. P. 1993. Respiratory activity of the collembolan *Onychiurus meridiatus*. – J. Insect Physiol. 39: 217–222.

Asikidis, M. D. 1989. Dynamics and activity of oribatid mites (Acari: Cryptostigmata) in an evergreen-sclerophyllous formation (Hortiatis). – PhD thesis, Univ. Thessaloniki (in Greek with an English summary).

Asikidis, M. D. and Stamou, G. P. 1991. Spatial and temporal patterns of oribatid mite community in en evergreen-sclerophyllous formation (Hortiatis, Greece). – Pedobiologia 35: 53–63.

Asikidis, M. D. and Stamou, G. P. 1992. Phenological patterns of oribatid mites in an evergreen-sclerophylous formation (Hortiatis, Greece). – Pedobiologia 35: 53–63.

Bulte, E. H. and Kooten, G. C. 2001. Harvesting and conserving a species when numbers are low: population viability and gambler's ruin in bioeconomic models. – Ecol. Econom. 37: 87–100.

Caswell, H. 1989. Matrix population models. – Sinauer Ass. Inc.

Caswell, H. and Trevisan, M. C. 1994. Sensitivity analysis of periodic matrix models. – Ecology 75: 1299–1303.

Hadjibiros, K. 1977. Simulation d' un système prédateur-proi à partir d' un model matriciel. – Thése de 3e cycle. Univ. Paris VII.

Iatrou, G. D. and Stamou, G. P. 1991. The life cycle and spatial distribution of *Glomeris balcanica* (Diplopoda, Glomeridae) in an evergreen-sclerophyllous formation in northern Greece. – Pedobiologia 35: 1–10.

Jensen, A. L. and Miller, D. H. 2001. Age structured matrix predation model for the dynamics of wolf and deer populations. – Ecol. Model. 141: 299–305.

Korfiatis, K. J. and Stamou, G. P. 1999. Habitat templets and changing worldview of ecology. – Biol. Philos. 14: 375–393.

Levins, R. 1968. Evolution in changing environments. – Princeton Univ. Press.

Lymberakis, P. 2003. Altitudinal differentiation of the fauna of Lefka Ori, Crete. – PhD Thesis. Univ. Athens (in Greek with an English summary).

McGee, B. L. and Spencer, M. 2001. A field based population model for the sediment toxicity test organism *Leptocheirus plumulosus*: II. Model application. – Mar. Environ. Res. 51: 347–363.

Mpimpas, H., Anagnostopoulos, P. and Ganoulis, J. 2001. Modelling of water pollution in the Thermaikos Gulf with fuzzy parameters. – Ecol. Model. 142: 91–104.

Oli, M. K. and Zinner, B. 2001. Partial life cycle analysis: a model for pre-breeding census data. – Oikos 93: 376–387.

Poinsot-Balaguer, N. 1996. Effect of undergrowth-clearing on evergreen leaf litter decomposition and colonisation by microarthropods. – Pedobiologia 40: 289–301.

Radea, C. 1989. A study of litter decomposition and the community of arthropods in an insular ecosystem of *Pinus halepensis*. – PhD. Thesis, Univ. Athens (in Greek with an English summary).

Sgardelis, S. P. and Margaris, N. S. 1993. Effects of fire on soil microarthropods of a phryganic ecosystem. – Pedobiologia 37: 83–94.

Sgardelis, S. P., Sarkar, S., Asikidis, M. D. et al. 1993. Phenological patterns of soil microarthropods from three climate regions. – Eur. J. Soil Biol. 29: 49–57.

Siepel, H. 1994. Structure and function of soil microarthropod communities. – Thesis Dissertation, Wageningen.

Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies. – J. Anim. Ecol. 46: 337–365.

Southwood, T. R. E. 1988. Tactics, strategies and templets. – Oikos 52: 3–18.

Spencer, M. and McGee, B. L. 2001. A field based population model for the sediment toxicity test organism *Leptocheirus plumulosus*: I Model development. – Mar. Environ. Res. 51: 327–345.

Stamou, G. P. 1981. Population dynamics of *Achipteria* cf *italicus* in the soil subsystem of an oak-wood in Holomon. – PhD. Thesis, Univ. Thessaliniki (in Greek with an English summary).

Stamou, G. P. 1986. Respiration of *Achipteria holomonensis* (Acari: Cryptostigmata). – Oikos 46: 176–184.

Stamou, G. P. 1998. Arthropods of mediterranean-type ecosystems. – Springer-Verlag.

Stamou, G. P. and Asikidis, M. D. 1989. The effect of density on the demographic parameters of two oribatid mites. – Rev. Ecol. Biol. Sol. 26: 321–330.

Stamou, G. P. and Sgardelis, S. P. 1989. Seasonal distribution patterns of oribatid mites (Acari: Cryptostigmata) in a forest ecosystem. – J. Anim. Ecol. 58: 893–904.

Stamou, G. P. and Asikidis, S. P. 1992. The effect of certain biotic factors on the demographic parameters of *Scheloribates* cf *latipes* (Acari: Oribatida). – Pedobiologia 36: 351–358.

Stamou, G. P. and Iatrou, G. D. 1993. Studies on the respiratory metabolism of *Glomeris balcanica* (Diplopoda, Glomeridae). – J. Insect Physiol. 39: 529–535.

Stamou, G. P. and Argyropoulou, M. D. 1995. A preliminary study on the effect of Cu, Pb and Zn contamination of soils on community structure and certain life-history traits of oribatids from urban areas. – Exp. Appl. Acarol. 19: 381–390.

Stamou, G. P. and Stamou, G. B. 1996. Possible application of fuzzy system simulation models for biomonitoring soil pollution in urban areas. – In: van Straalen, N. M. and Krivolutsky, D. A. (eds), Bioindicator systems for soil pollution. Kluwer, pp. 55–65.

Stamou, G. P., Asikidis, M. D., Argyropoulou, M. D. et al. 1993. Ecological time versus standard clock time: the assymetry of phenologies and the life history strategies of some soil arthropods from Mediterranean ecosystems. – Oikos 66: 27–35.

Stamou, G. P., Asikidis, M. D., Argyropoulou, M. D. et al. 1995. Respiratory responses of oribatid mites to temperature changes. – J. Insect Physiol. 41: 229–233.

Stamou, G. P., Karris, G., Tsiafouli, M. A. et al. 2000. The effect of acclimation to constant temperatures, pollution of food by heavy metals and short-term fasting on the metabolic activity of *Glomeris balcanica* (Diplopoda: Glomeridae). – Web Ecology 1: 11–19. On-line serial at < htpp://www.oikos.ekol.lu.se >

Terano, T., Asai, K. and Sugeno, M. 1992. Fuzzy systems theory and applications. – Academic Press.

Zadeh, L. A. 1965. Fuzzy sets. – Information and Control 8: 338–353.