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Studies on the life cycle of *Glomeris balcanica* (Diplopoda, Glomeridae) under laboratory conditions

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With 4 figures

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1. Introduction

Data regarding estimations of demographic parameters in diplopods appear infrequently (SNIDER, 1981a & b). This is due to the fact that culturing of diplopods in the laboratory, especially those with long life cycles appears to be difficult (PEITSALMI, 1981). As a consequence relevant information either dates back to the end of the 19th and the beginning of the 20th century (VOM RATH, 1890; CHALANDE, 1905; VERHOEFF, 1933, 1939), or it refers to species with relatively short life cycles such as julids and polydesmids (STEPHENSON, 1961; BANERJEE, 1970; BLOWER, 1974; KHEIRALLAH, 1978; SNIDER, 1981a & b). As far as glomerids are concerned the only relevant information available is provided by BOCOCK *et al.* (1967) and HEATH *et al.* (1974) who reared *Glomeris marginata* (VILLERS) under laboratory and field conditions. Nevertheless, such information is of prime importance with respect to the understanding of the mechanisms of population development in the field as well as to the general ecology of the species.

In 1984 a project was started to study the activity and dynamics of *Glomeris balcanica* (VERHOEFF, 1906). This diplopod dominates the *Quercus coccifera* L. litter layers at the foot of Mt Hortiatis (Mediterranean Type Ecosystem), about 20 km east from Thessaloniki. Within this framework and in addition to other aspects of the ecology of *G. balcanica,* the animal was reared in the laboratory as well as under semi-natural conditions in an attempt to study its demographic parameters. Our main objective was to find out the extent to which laboratory estimations of these parameters could be applied to field conditions. Additional information on the behaviour of the animal in the cultures is also noted.

2. Materials and methods

To estimate duration of development, specimens of *G. balcanica* were individually reared at room temperature ranging from 20 to 25 °C. Diurnal temperature fluctuations did not exceed ± 1 °C. For the anamorphic stadia as well as for the first two epimorphic stadia (5th and 6th), plastic cylindrical vessels 2.5 cm in diameter were used. Later stadia were reared in bigger vessels (5 cm in diameter). The latter ones were also used for the egg cultures. Plaster of Paris was used as a substrate and was regularly watered to keep the air inside the vessels as close as possible to 100% RH. Food supply was a 9:1 mixture of leaf litter components and humus (SNIDER, 1981a & b). This material was renewed whenever the amount of animal excrement exceeded that of the remaining food, or when development of mycelia became excessive. The cultures were inspected every 3 days and moulting activity, as well as deaths were recorded.

To examine possible density-dependence of the oviposition rate in *G. balcanica* specimens collected in the field during March 1984 were cultured in the laboratory in plastic containers containing 1, 2, 3, 4, 5, 6, 7, 8 pairs of animals. Four replicate cultures were prepared for each population density of animals.

The influence of thermal history on the oviposition rate of *G. balbanica* was estimated in 4 experiments. In the first, the oviposition rate was examined under standard laboratory temperature. During March 1985, 16 pairs of mature males and females were collected in the field, transferred to the laboratory and reared under standard temperature conditions 22 ± 2 °C.

During the 2nd experiment, the relationship of oviposition rate to live mass was also examined. For that purpose the female specimens of *G. balcanica* collected in the field by the end of March 1986 were divided into 6 mass classes: 70–120, 120–160, 160–180, 180–220, 220–260 and 260–310 mg. Male specimens were roughly divided into 6 size classes as well. Cultures were stored outdoors in a shady place where animals could experience diurnal fluctuations of light and temperature (temperature regime 16–29 °C).

In the 3rd and 4th experiment, *G. balcanica* was reared under semi-natural conditions in order to find out whether long-term acclimatization of *G. balcanica* to standard laboratory conditions had any influence on the oviposition rate. In the 3 experiment animals were collected in the field and consequently acclimatized to natural diurnal and seasonal changes of environmental variables; in the 4th animals were acclimatized for about one year to standard laboratory conditions. In both experiments (3rd and 4th), the vessels were buried in the L-F horizons of the *Q. coccifera* organic layers. During the experiments the mean monthly temperature in the field fluctuated between 10–25 °C.

In all oviposition cultures semi transparent plastic containers, 9 cm in diameter were used. Plaster of Paris was used as a substrate, while food prepared as described above was offered in large quantities so that the thickness of the organic layer above the plaster substrate would vary between 2.5 and 3.0 cm. The cultures were examined every 15 days in order to minimize disturbance of mating and egg laying activity of the animals. The vessels used in experiments 3 and 4 were modified as described by Frankel (1979) for isopod cultures and 4 males 80–160 mg and 4 females 180–260 mg were introduced in each vessel.

In summary, the effect of thermal history on the oviposition rate of *G. balcanica* was examined in 4 experimental series which differed according to the thermal history of the animals and the temperature regimes provided for oviposition as follows:

Experiment	Rearing temperature	Thermal history of animals
I	Standard laboratory	Acclimatized to field
II	Laboratory (fluctuating)	Acclimatized to field
III	Field (fluctuating)	Acclimatized to field
IV	Field (fluctuating)	Acclimatized to laboratory

3. Results

3.0. General

3.0.1. Mating behaviour

A general description of the sexual behaviour of Opisthandria has been given by Attems (1926). This behaviour has been more accurately described by Haacker (1964) in *G. marginata*. In the present experiment the initial matrimonial "ceremony" performed by the male, as well as copulation, were observed.

3.0.2. Egg protection

In contrast to other diplopods, *Glomeris* lay eggs singly, protected by a well elaborated ovoid capsule made of faecal material. The building of this protective capsule has been described by many authors (e.g. Juberthie-Jupeau, 1967). As regards *G. balcanica*, observations made during our experiments show that the egg-capsule is built as soon as the egg emerges from the vulva, while the female lies with its back on the substrate. The egg is then transferred by the legs down to the anal region where it is placed on a faecal pellet which constitutes the base on which the rest of the capsule is built.

The length of the egg capsule varied between 3 and 4 mm, while the capsule wall was up to one mm thick. The size of the capsule seems to be positively related to the size of the animal, though no systematic measurements were made.

The biological significance of the egg capsule is not yet clarified. Shaw (1966) assumes that the consumption of the capsule material by the larvae of a spirobolid allows the transfer of intestinal flora to the next generation. According to Crawford & Matlack (1979) the importance of the capsule building in the spirobolid *Narceus* is to buffer any relative humidity differences between the air within the capsule and that of the surrounding organic layers. In any case, the capsule appears to be a prerequisite for the oviposition since unprotected eggs have never been recorded in the cultures.

In the cultures the oviposition sites were easily recognized by the large amounts of excrement surrounding the eggs. Generally they were located towards the bottom of the cultures, close to the plaster substrate; possibly due to more favourable humidity conditions. Eggs were laid either singly or in small clumps of 3–5. Egg laying seemed to be positively related to the feeding activity of the animals. However, it was impossible to demonstrate a relationship between these two biotical activities. Such an attempt requires a different experimental approach. In any case our observations are in agreement with those reported by Evans (1911) for Glomeridae and by Shaw (1966) for the spirobolid *Narceus annularis*.

3.0.3. Chamber building

Moulting chambers were recorded only in the laboratory. In the field the animals were observed to moult within cavities, deep in the humus layers. The same behaviour has also been reported by Heath *et al.* (1974), though the last authors have also recorded a few moulting chambers in the field.

Moulting chambers were constructed by using any available material, such as faecal pellets, litter or even plaster of Paris. Old abandoned chambers were used too. Analogous behaviour has been recorded by Snider (1981b) in a polydesmid. In most cases the chambers of *G. balcanica* were made of faecal material moulded using the legs in the anal area.

3.1. Duration of development

In table 1 the results are shown for mean duration of stadia, mean duration of moulting as well as stadia mortality. It should be clarified that moulting time was considered to be either the time spent by the animal in the chamber, or, in cases when a chamber was not built, the time of voluntary starvation, which is related to the moulting behaviour (Halkka, 1958; Bocock & Heath, 1967; Heath *et al.*, 1974).

The first stadium emerges from the egg capsule about two months after it is deposited. Within this time the egg develops into the 6-legged larva which moults inside the capsule into the first "free" anamorphic stadium. The duration of development of the first 3 "free" anamorphic stadia ranged from 45.36 to 64.06 days, while moulting lasted 10–14 days. Average duration of development of the stadia from the 4th anamorphic to the 10th epimorphic varied between 2.0 and 3.8 months, with an overall mean value of 91.90 ± 4.87 days. In all stadia, with the exception of the 7th, the differences between time of development of males and females were not statistically significant. It is worth noticing that the coefficient of variation (CV%) of the duration of development is generally low although higher in earlier instars than in later ones. Thus an overlap of immatures and pseudomatures in field should not be expected; a fact verified by sensus data (Iatrou, in preparation). The relationship between development time and stadium is shown in fig. 1. Mean moulting time varied between 9.44 and 19.2 days, with an overall mean value of 14.03 ± 0.88 days (C.V. 24.95%). A relationship between moulting time and stadium could not be formulated.

The mortality of the first two life stages of *G. balcanica* (egg, 6-legged larvae) was very high (52.22%). The dissection of the capsules which failed to hatch showed that most of them were infected by hyphae. We cannot tell whether death was caused by the infection. In any case,

Table 1. Mean time of development, mean time of moulting duration and mortality of the developmental stages (up to 10th) of *G. balcanica.*

Stadium		n	Mean duration of development	CV%	Moulting duration	CV%	Mortality [%]
egg and larva		90	64.09 ± 4.05	41.5	–	–	52.22
1st		69	64.06 ± 5.77	52.5	10.85 ± 1.62	39.6	50.72
2nd		32	46.76 ± 3.71	32.7	14.17 ± 1.79	31.1	46.88
3rd		11	45.36 ± 2.65	19.2	12.50 ± 1.28	32.3	–
4th		10	90.00 ± 10.85	38.2	10.44 ± 1.20	34.6	–
5th	♂	7	78.28 ± 13.59	45.9	19.17 ± 4.89	62.6	–
	♀	6	82.33 ± 15.60	46.4	16.66 ± 4.66	48.5	–
6th	♂	9	66.88 ± 3.77	15.1	9.86 ± 1.95	52.2	–
	♀	10	75.85 ± 6.85	26.8	13.77 ± 0.62	13.5	–
7th	♂	10	100.90 ± 13.61	42.7	9.44 ± 1.18	37.5	–
	♀	8	60.25 ± 6.78	31.8	10.14 ± 1.10	28.7	–
8th	♂	9	106.89 ± 11.27	31.6	19.22 ± 2.31	36.0	–
	♀	7	97.57 ± 8.91	24.2	11.71 ± 1.08	24.5	–
9th	♂	7	113.00 ± 8.96	21.0	17.50 ± 3.04	42.6	–
	♀	7	107.43 ± 13.93	34.3	14.00 ± 2.97	56.1	–
10th	♂	6	110.33 ± 8.32	14.3	16.42 ± 4.52	38.5	–
	♀	8	105.00 ± 7.77	12.8	18.67 ± 4.33	40.2	–

* Number of observations (n) and coefficients of variation (CV%) are also given.

according to our own observations, infection of the capsules by hyphae is a common phenomenon in the field; infected eggs were included when estimating natural mortality, although some bias is expected.

Deaths of the 1st and 2nd free anamorphic stadia (50.72 and 46.88%, respectively) were usually recorded while the animals were moulting, especially when animals failed to build a moulting chamber. In the later stadia no mortality was recorded in the laboratory.

3.2. Oviposition rate and population density

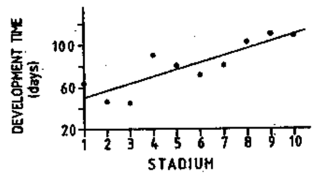
In all densities egg deposition occurred from the last fortnight of May to the first fortnight of August. Density did not affect oviposition temporal pattern. The higher number of deposited eggs per animal per day was recorded during the last fortnight of June and the first fortnight of July.

Population density affects the oviposition rate during the whole oviposition period. In fig. 2 density-dependence of the mean oviposition rate in *G. balcanica* is depicted. The higher number of deposited eggs/female/day have been recorded at density 4, while the overall mean rate 0.57 ± 0.11 eggs/female/day equals to the rate displayed by density 8. The formula suggested by STAMOU & ASIKIDIS (in press) $F = a_0 + a_1 N + a_2 N^{1-b} + a_3 \ln N$, where F = oviposition rate and N = density showed a good fit to the data ($P < 0.01$).

3.3. Oviposition rate and thermal history

In fig. 3 the fluctuations of the mean monthly rate of oviposition as well as those of the percentage of the number of moulting animals in the four experiments are depicted.

Egg-deposition in the field (E III) occurs during the period from April to July followed by the moulting period which lasts until October. The same sequence occurs in all 4 experiments, although differences regarding the duration of the periods and the intensity of events could be noted. Animals acclimatized for about one year to laboratory conditions, ovipositing in the field (fig. 3 EIV), and



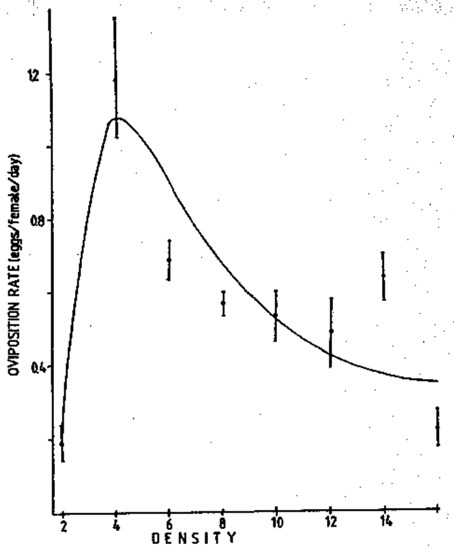


Fig. 1. Linear relationship of stadium duration (D) to stadium (S) developed for the "free" anamorphic and the younger epimorphic stadia of *G. balcanica.* ($D = 6.58\ S + 43.70$, $r = 0.85$)

Fig. 2. The effect of density (N) on the oviposition rate (F) of *G. balcanica.* The equation $F = 3.18 + 0.11\ N - 14.34\ N^{-2.8} - 1.62 \ln N$ was fitted to data.

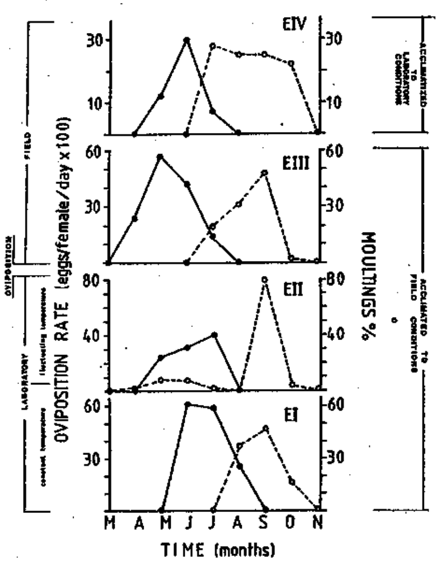
those collected in the field and reared under fluctuating temperatures in the laboratory (fig. 3 EII), have a shorter oviposition period (May–July) than the ones acclimatized to field conditions and reared in the field (fig. 3 EIII). The specimens acclimatized to field conditions – reared under standard laboratory conditions (fig. 3 EI), have a short oviposition period, which also begins one month later. These animals have the highest overall mean oviposition rate whereas the animals acclimatized to standard laboratory conditions (E IV) have the lowest (0.16 eggs/♀/day). Field specimens (E III) and those ovipositing under fluctuating temperature in the laboratory (E II) display comparable overall mean oviposition rates (0.34 and 0.31 eggs/♀/day, respectively). One way analysis of variance showed that the above differences were significant ($P < 0.05$), while a further L.S.D.-test showed the difference to be due to the low value resulting from experiment IV.

Most animals, except those of the experiment IV moult during August–September. The latter appear to moult from July to October.

3.4. Oviposition and live mass

In table 2 the results are shown for oviposition rate in relation to live mass of *G. balcanica.* Mean oviposition rate varies from 0.15 to 0.38 eggs/♀/day with an overall mean value of 0.27 eggs/♀/day. The mass class 160–180 mg appears to be the most reproductively active one, although one way analysis of variance showed that the recorded differences were not significant ($P > 0.05$).

As shown in fig. 4 oviposition lasted from early May to the end of July. Temporal patterns among age classes were not similar. Younger animals laid most eggs during the first fortnight of July, that is towards the end of the oviposition period, whereas the older ones deposited eggs



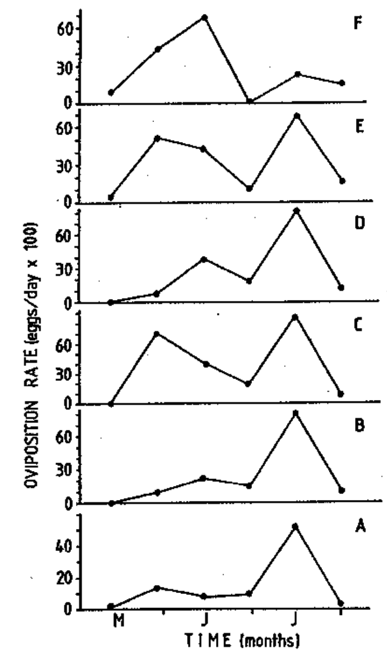


Fig. 3. Mean monthly oviposition rate and percentage of moulting animals in four different experimental series (EI-EIV) in *G. balcanica*. ———: Oviposition rate, ---------: Percentage of moulting animals

Fig. 4. Instead of (eggs/day × 100) read (eggs/female/day × 100). Fluctuation of the oviposition rate of the 6 mass classes of *G. balcanica*. A: 70–120, B: 140–180, C: 160–180, D: 180–220, E: 220–260 and F: 260–310 mg.

Table 2. Mean oviposition rate (eggs/female/day) of mass classes in *G. balcanica*.

Mass [mg] classes	70–120	140–160	160–180	180–220	220–260	260–310
Oviposition rate	.15 ± .08	.23 ± .12	.38 ± .14	.26 ± .12	.33 ± .10	.27 ± .10

during the last fortnight of May and the first one of June. Intermediate age classes display two maximum values of oviposition rate in the beginning and the end of the whole period.

4. Discussion

The results of our experiment show that the duration of anamorphosis in *G. balcanica* lasted for about nine months, while epimorphosis up to the 10th stadium lasted for 18 months. This means that maturation time in *G. balcanica* is about 2.5 years since specimens become mature when reaching the 10–13th stadium. In this study the onset of maturation has only been defined approximately since specimens obtained during this experiment, and belonging to younger epimorphic stadia

(10–13th), did not lay eggs in cultures. This may be a consequence of the long term acclimatization. Conversely, females collected in the field which weighed 70–120 mg, and were assigned to 10–13th stadia (IATROU & STAMOU, 1989a), were fertile in the laboratory. According to BLOWER & GABBUTT (1964) and FAIRHURST (1974), maturation in diplopods does not depend on stadium. It could be correlated with annual and seasonal cycles rather than with the number of moultings (DAVID, 1982). Field data (in preparation) showed that the sexually mature sub-population is renewed every 3 years. It seems likely that the maturation time of *G. balcanica* in the field is related to the 3 year temperature pattern outlined for the district of Thessaloniki (BORA-SEDA, 1980). We conclude that it appears ecologically meaningless to accurately estimate maturation time of the millipedes in the laboratory.

The duration of moulting was estimated by HALKKA (1958) to last for about 2–3 weeks, while BOCOCK (1963) (according to HEATH *et al.*, 1974) estimated moulting to last for about 22 days in *G. marginata*. The overall mean duration of moulting estimated for the stadia of *G. balcanica* varied between 10 and 20 days. This is slightly lower than the estimations made by the above authors. Furthermore, and contrary to the case of *Polydesmus inconstans* (LATZEL) (SNIDER, 1981a), no correlations were recorded between duration of moulting and stadium.

The oviposition rate in *G. balcanica* was found to be density dependent. Density-dependence falls in the "Allee type" category of FUJITA (1954). To our knowledge it is the first time that such a phenomenon is reported for Glomeridae. Although the functioning of the "Allee effect" is of great importance in relation to population regulation in the field, it was not further examined.

Estimations of fecundity rates for *G. balcanica* reared under standard laboratory conditions are comparable with the values obtained for *G. marginata* by HEATH *et al.* (1974). The oviposition temporal pattern outlined for *G. balcanica* is also analogous with the one given by the above authors for *G. marginata*.

According to PROSSER (1973) and NEWELL *et al.* (1974), the response of poikilotherms to temperature changes depends on the temperature regime experienced by the animals in the past. Furthermore, CLOUDSLEY-THOMSON (1953), emphasized the importance of fluctuating temperatures for the success of culturing the diplopod species *Orthomorpha gracilis* (C. L. KOCH) and *Blaniulus guttulatus* (BOSC.). The author pointed out that constant temperature depresses activity. On the other hand, SNIDER (1981b), did not record significant differences in the fecundity rates estimated for *P. inconstans* specimens acclimatized to standard temperature conditions and for specimens brought in from the field. In the case of *G. balcanica* short-term culturing to standard laboratory conditions did not affect oviposition rate (E I), whereas long-term culturing seemed to depress oviposition rate by a factor of 1.5 and to have an irreversible effect on it (E IV), also altering oviposition and moulting temporal pattern.

Oviposition rate recorded in field specimens maintained under fluctuating temperatures (E II & E III), were not significantly different. As a consequence, the overall mean oviposition rate obtained from these two experimental series could be used for a rough estimation of its fecundity in the field. Thus, 764.0 eggs $m^{-2} a^{-1}$ should be deposited in the field. Taking into consideration mortality rates, from these eggs only 365.0 could develop into the 1st stadium, 179.9 into the 2nd and 99.6 into the 3rd. These estimations are comparable with the maximum densities determined for these stadia in the field 381.1, 130.8 and 42.2 individuals m^{-2} respectively (in preparation). From these data we could infer that estimates of the oviposition and mortality rates made under laboratory conditions on short-term acclimatized specimens could be used for a rough estimation of relevant rates in the field.

The results of the present study show that brood protection, density dependence, relatively low reproductive potential, low mortality of the later instars, long generation time, long life span and iteroparity are the features of the life cycle development of *G. balcanica* in laboratory. Taking into account these bionomic characteristics we suggest that *G. balcanica* is located on the K side of the r-K continuum (PIANKA, 1970; SOUTHWOOD, 1976). On the other hand, contrary to the typical K-strategists, *G. balcanica* has short reproduction and growth phases. These latter features, in combination with the low values of the coefficients of variation of the life stages duration, are of particular interest with respect to the dominance of this species in an extremely fluctuating, though predictable environment (IATROU & STAMOU, 1989a; IATROU, in prep.). Indeed, these characteristics do not allow populations to attain stable age structure in the field and to enable the whole population to regulate its size. In fact, population dynamics of *G. balcanica* in Hortiatis displays a 3 year temporal pattern which seems to be adjusted with a 3 to 4 year temperature and precipitation pattern (BORA-SEDA, 1980; IATROU, in prep.).

It seems to us that *G. balcanica* living in a very heterogenous habitat does not only face dispersal hazards but time heterogeneity as well. From this point of view iteroparity could be considered not only as an adaptation to space heterogeneity (BLOWER, 1969) but also as an adaptation to the temporal pattern of temperature and precipitation. In diplopods with low reproductive potential (such as *G. balcanica*) iteroparity would facilitate a more or less even allocation of the energy available for reproduction among the age classes of the population.

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The demographic parameters of *G. balcanica* dominating *Q. coccifera* litter layers in a mediterranean-type ecosystem (Greece) were estimated under standard laboratory and semi-natural conditions. In general, qualitative observations concerning mating behaviour, egg protection and chamber building are in agreement with reports for other diplopods. Estimations regarding development up to the 10th stadium were made. Developmental time of the free anamorphic and younger epimorphic stadia increased linearly with stadium. Mean moulting time was 14.03 days while maturation time was 2.5 years. Egg and larva as well as the two first anamorphic stadia display high mortality, whereas no mortality was recorded for the later instars of *G. balcanica*. Oviposition rates were observed to be density-dependent. Egg deposition lasts for 4 months, from April to July followed by a moulting period lasting from July to October. Dependence of oviposition rates on live mass could not be detected. In contrast to short term culturing, long term culturing under standard laboratory conditions influenced both rate and temporal patterns of oviposition and moulting. The life-history strategy of *G. balcanica* is discussed.

Key words: Diplopoda, *Glomeris balcanica*, culturing, demographic parameters, density-dependence, life history strategies.

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