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On Male Reproduction Strategies in *Ommatoiulus sabulosus* (L.) in the Maritime Alps and Provence (France): Juvenile to Adult Maturation Moults

(Myriapoda, Diplopoda)

by

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Abstract: This paper provides information on male juvenile to adult maturation moults (= MMJ) in *Ommatoiulus sabulosus* (L.) in the Maritime Alps and Provence. Five kinds of MMJ variabilities are studied. The notions of poor, good and "explosive" MMJ are dealt with.

1. Introduction:

Little is known about juvenile to adult male maturation moults (= MMJ): FAIRHURST (1974) tried to establish a connection between stadia at which MMJ occur and five different biotopes in Great-Britain. The purpose of this paper is to provide information on male MMJ in *Ommatoiulus sabulosus* (L.) in the Maritime Alps and the Provence (little data — partly erroneous and deficient — has been published on the Mediterranean region by VERHOEFF 1921). At present, this study must be regarded as half complete, the whole investigations on MMJ, periodomorphosis, female strategies and mass migrations being extended over circa 15 - 20 years. Investigations on female strategies in *O. sabulosus* are underway (are females iteroparous, as assumed by the English school or not? If they are, the questions arise: under which conditions and in what proportions?).

2. Methods and Study Sites:

O. sabulosus have been collected by hand. Concerning *O. sabulosus* in the South-East region, the classical sampling methods (plot sampling, pitfall traps) have not been used, being inappropriate and impossible to use (need for live animals, vandalism, etc.) In a given site, the animals were collected in all acessible places (some places were inacessible, for different reasons). The investigated places often constitute day rest sites: on shrub branches, under shrubs, on/in litter. The shrub roots and the soil under the shrub litter are always searched (they are day rest sites as well as moult or hibernation sites). The main shrubs studied were: *Lavandula, Cistus, Euphorbia, Rosmarinus, Juniperus, Genista, Pistacea, Buxus, Quercus.* Animals can also be found under dry cattle dung, compost, piles of decomposed crushed grapes or under heaps of hay and straw. Sometimes they were found in *Pinus* needle litter or in fallen rotten fruit (e.g. figs). Home sites (i.e. where animals were born) as well as migration sites have been studied: during certain months animals leave the bushes and move to grassland (particularly females, for nutritional reasons) or under stones. They have also been collected on walls, trees and bushes (vertical wandering or migration) or on driveways, paths and short grasses — where sheep have grazed (horizontal wandering).

In migration sites and particularly in vertical ones, the number of juvenile males can be biased (the real number of juveniles being higher than in the samples). In other cases, walls can be covered — in daytime, in certain May days — with almost exclusively 5 - 6 RO (= rows of ocelli) juveniles, older individuals being concealed under stones and/or bushes!

Collections were made by the author himself regularly from 1983 to 1990 during the following months: April, May, June, Sept., Oct., Nov. and January. Collections were made by hired locals in some sites during July and August. Over 25.000 individuals have been examined.

The studied coastal area stretched from Antibes to Menton. Concerning the hinterland (i) the "arrière-pays niçois" and the "arrière pays mentonnais" at the East of the Var river and (ii) the Grasse region at the West side were studied. Sites located between Salon-de-Provence and Aix-en-Provence (150 - 200 m alt.) were also investigated. The altitude and the shortest distance from the sea (as the crow flies) will be given for most investigated sites in the Alpes-Maritimes: Cap Martin, sentier Le Corbusier: 10 - 30 m alt., 5 - 20 m; Menton, Borrigo valley: 80 - 120 m alt., 1700 m; Baousset: 160 - 215 m alt., 1500 m; Roquebrune-village: 220 - 250 m alt., 950 m; Monti/S: 250 - 260 m alt., 3200 m; Gorbio: 350 - 380 m alt., 3600 m; Peillon: 350 - 500 m alt., 5400 m; ruines du Château de Drap: 400 - 500 m alt., 4000 m: Ste-Agnès Villette: 410 - 460 m alt., 4800 m; Coaraze: 635 - 650 m alt., 16400 m; Ste-Agnès Righi: 720 -750 m alt., 4400 m; ruines de Châteauneuf: 740 - 749 m alt., 9600 m: Engarvin: 700 - 750 m alt., 19100 m: Col de Braus: 970 - 1020 m alt., 13500 m; Pointe Siricocca: 1020 - 1065 m alt., 5900 m; Rocca spaviera (near the Mont Férion): 1100 - 1250 m alt., 20500 m; Pas de l'Escous (between the Col de l'Orme and the Baisse de la Cabanette): 1100 - 1250 m alt., 19000 m; Peïra-Cava: 1450 - 1480 m alt., 20700 m.

Specific data on vegetation, rainfall and temperatures can be found in the excellent paper of LAPRAZ (1984). Typically, the period of maximum rainfall takes place in autumn, the period of maximum dryness in summer. Typically there is more rain in winter than in spring (= type 1). Sometimes the inverse is true (= type 2). In general, in a year, rainfall equals 716 mm rain at Cap Ferrat, 745 at Monaco, 830 at Menton, 863 at Nice, 1029 at Peillon, 1258 at Peïra-Cava. Typically in Nice there are: 336 mm rain in autumn, 239 in winter, 204 in spring and 85 in summer. At Peïra-Cava there are respectively: 447, 299, 302 and 196 (type 2). At 700-800 m alt. there are 7 - 8 days of snow on average a year. Average annual temperatures are: 15.1° C in Menton, 15.5° in Nice. 12° at 840 m alt. (Utelle), 8.4° at Peïra-Cava. Temperatures of the warmest day in July and August are: 26 - 27° in Nice and Menton, 31° at Peillon, 29° at Sospel, 27° at 840 m alt. (Utelle), 24° at Peïra-Cava. Average minimum during the coldest month (January or February) are: 4° in Nice and Menton, 0° at Peillon, −2° at Sospel, 0° at 840 m alt. (Utelle), −4° at Peïra-Cava.

In samples, theoretically only 7 RO and 8 RO adult males can be identified as ad 1, without error. On the other hand, 9 RO and 10 RO adults can theoretically be a mixture of ad 1 and ad 2 of the same generation. In practise, in the investigated sites most ad 2 die by the end of the summer (SAHLI unpubl.). As a result, in autumn, nearly all adult males are ad 1 in nature. The data in the figures are slightly biased: 9 RO and 10 RO males are not rigorously ad 1, they may include a few ad 2.

In most sampling sites, field cultures were made (see SAHLI 1989). It is easy to follow fast growing individuals in wet field and balcony cultures but it is difficult to obtain a slow development (cf. Table 1 a - c), which may be conditioned by dryness and temperature. Concerning dryness, it is difficult to reproduce genuine Mediterranean conditions: one runs the risk of excessive dryness, which is fatal to the animals. (The only method which does maintain true natural conditions is that devised by SAHLI 1989: large rectangular enclosures made of mosquito net tighty covering a bush; but this method is time-consuming and too expensive to be used on a large scale; in addition, as such enclosures cannot be concealed to the eyes, they are not hidden from vandals and meddlers, who are legion).

Table 1: Some possible development types (**a - e**) in males from the same generation in the Mentonnais Hinterland. **a, b, c** minimal development, according to samplings; **d, e** according to field cultures (★ 2 moults a year).

Year	1	2	3	4
a	5 RO	6 RO	7 RO	8 RO
b	6 RO	7 RO	8 RO	9 RO
c	7 RO	8 RO	9 RO	10 RO
d	7 RO ★	9 RO	10 RO	11 RO
e	7 RO ★	9 RO ★	11 RO	12 RO

The surest way of assigning animals to a given generation is to follow a population of a given site regularly — several times a year (and even several times a month) and several consecutive years — from the birth on –, as we did. In addition, it is most useful to have comparison and reference points in numerous other sites, investigated in the same way and particularly in sites inhabited by animals descending from only one generation. Even so, assignation of certain animals to a given generation may be difficult: immigration from a nearby site of animals belonging to another generation (e.g. a younger one) is theoretically possible and cannot be ruled out.

3. Results and Discussion:

First, we will give results concerning several types of variability of male maturation and discuss them one by one as we progress. Then we will tackle problems concerning good and poor MMJ in males.

3.1. Variability of MMJ the same Year in Different Sites, According to the Life Cycle:

MMJ can take place 1, 2, 3, 4 or 5 years after birth. In other words, some individuals of a given egg deposition become ad 1 after one year (1-year cycle), others after two years (2-year cycle), three (3-year cycle), four (4-year cycle), etc. Let us examine these different cases.

3.1.1. 1-year Cycle:

Relatively few or no ad 1 are produced the first year after birth (they constitute precocious 7 RO ad 1). Two cases will be considered, those of 1984 - 85 and 1987 - 88.

1984 - 85, after a very cold winter (84/85) and a drought year (1985): From 1984's egg depositions, only males from coastal areas such as Baousset, Cap Martin and Menton (Fig. 1) were able to become precocious one-year 7 RO ad 1 in 1985 – a dry year. At Baousset 20 % of the 7 RO males were ad 1. In all other sites (Righi, Peillon, Engarvin, etc.) no 7 RO ad 1 appeared in 1985.

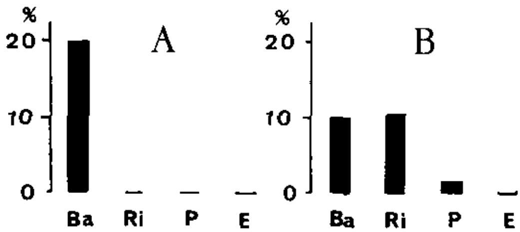

Fig. 1: Frequency of 1-year old ad 1 (black columns), in 4 sites, according to sampling in the autumn of 1985 (A) and 1988 (B). The figure expresses the ratio 7 RO ad 1 males/7 RO males (juveniles + adults). Ba: Baousset (250 ♂ in A, 204 ♂ in B); E: Engarvin (60 ♂, 44 ♂); P: Peillon (148 ♂, 292 ♂); Ri: Ste-Agnès Righi (314 ♂, 94 ♂).

At coastal areas, probably some 7 RO juvenile males have even turned into 8 RO ad 1, one year after the birth, but the 1985's 8 RO ad 1 are perhaps a mixture of ad 1 of two generations: the 1-year generation born in 1984 and the 2-year generation born in 1983 (= overlap of two generations, cf. infra).

1987 - 88, after a normal rainy year (1988): From the 1987 egg depositions, 7 RO ad 1 males appeared in 1988 – among others – at Baousset (10 %), Ste-Agnès Righi (10.6 %) and Peillon (1.3 %) (Fig. 1). In short, under harsh, dry and warm weather conditions as in 1985, 1-year old 7 RO ad 1 males were produced only at coastal sites. At Baousset more 7 RO ad 1 were produced under dry than under "wet" conditions (Fig. 1). Under "wet" conditions as in 1988, few 1-year old 7 RO ad 1 appeared in coastal and near the coast sites facing the sea, even at circa 1050 m altitude (e.g. at Siricocca). But in 1988 no 1-year 7 RO was found in hinterland sites such as the ruins of Châteauneuf, Coaraze, Engarvin, Col de Braus, Pas de l'Escous, etc. In general 1-year old 7 RO ad 1 do not frequently occur in the hinterland (nevertheless, a few were found e.g. in 1987).

3.1.2. 2-year Cycle (1984 - 1986):

Most MMJ occur after 2.3 or 4 years. Concerning the 2-year cycle, we will only take the example of MMJ in 1986, from animals born in 1984. The winter 1984 - 85 was exceptionally cold. 1985 was an exceptionally dry year. April 1986 was a "good" (normal) rainy month. Summer and autumn 1986 were dry. Radioactive rain (Tschernobyl disaster, 26th April, 1986) fell the 4, 5 and 6th of May 1986 over the Mentonnais. Taken as a whole, most successful MMJ of 2-year old males (over 80 % of them) took place in coastal areas and at Peillon (Fig. 2). In the hinterlamd sites, at 750 m elevation, the frequency of MMJ varied between 40 % and 60 % (Fig. 2).

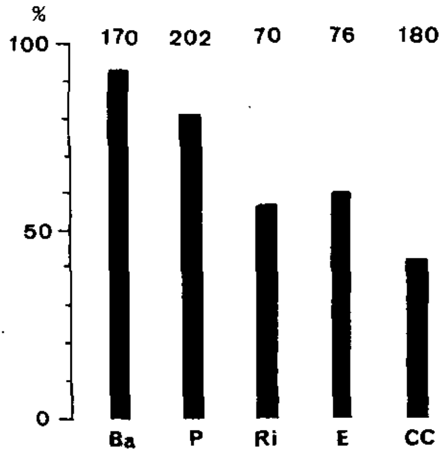

Fig. 2: Frequency of 8 RO + 9 RO adult males (black columns) in 5 sites, according to samplings in autumn 1986. Most (at Baousset) or all (in the 4 other sites) males are 2-year old ad 1 born in 1984. The figure expresses the ratio: 8 + 9 RO adult males/all 8 and 9 RO males (juveniles + adults). The figures above the columns give the number of 8 + 9 RO males collected in each site. Ba Baousset; CC ruines de Châteauneuf; E Engarvin; P Peillon; Ri Ste-Agnès Righi.

Let us examine 9 RO and 8 RO separately. Concerning 9 RO ad 1, many (70 - 98.5 %) 8 RO juveniles turned into 9 RO ad 1 (Fig. 3). Concerning 8 RO ad 1, 66 - 72 % 7 RO juveniles gave 8 RO ad 1 at Baousset and Peillon. At circa 750 m alt., in the hinterland, only few 7 RO juveniles (8 - 17 %) turned into 8 RO ad 1 (Fig. 3).

Fig. 4 shows how males born in autumn 1984 progressed up to 1986. 9 RO juveniles moulted into ad 1 more frequently than 8 RO juveniles (vide infra). Variations exist: the 2-year cycles of males born respectively in 1986 and 1987 are more of less different from the cycle of those born in 1984, chosen as an example. It would be too long to examine these variations in detail. It should be noted that data on a population in a given site a given year cannot be properly generalized or extrapolated to other sites and years (neither past years, nor years ahead).

3.1.3. 3-year Cycle (1986 - 1989):

Figure 3 gives some examples and shows differences according to some sites. It will be noted that MMJ of 2-year-old juveniles were "poor" in the Mentonnais in 1989 – a dry year – compared (a) to the good MMJ of 2-year juveniles in 1986 in some Mentonnais sites (Baousset, Peillon, Fig. 2: MMJ were essentially of the type 2, cf. below), (b) to the good MMJ (essentially of the type 1, cf below) of 3-year old juveniles at Antibes in 1989 (Fig. 5).

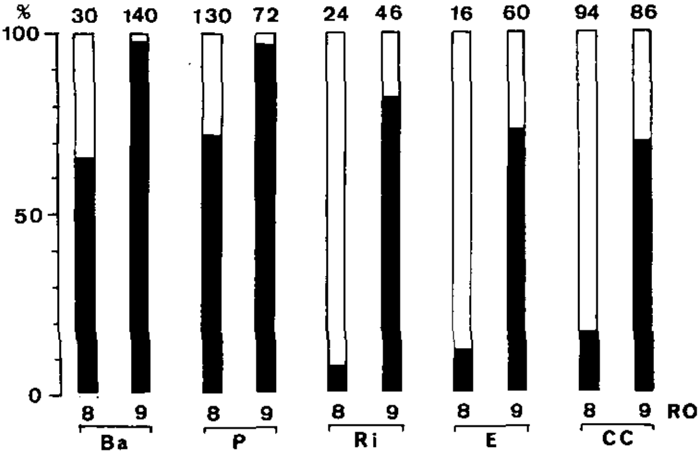

Fig. 3: Respective proportions — stadium by stadium — of adult (black columns) and juveniles (open columns) males at instars 8 (ratio: 8 RO adult ♂/8 RO adult + juvenile ♂) and 9 RO (ratio: 9 RO adult ♂/9 RO adult + juvenile ♂) in 5 sites. After sampling in autumn 1986. All males (except at Baousset, where few 9 RO ad 2 may be mixed with ad 1) are 2-year old ad 1 born in 1984.

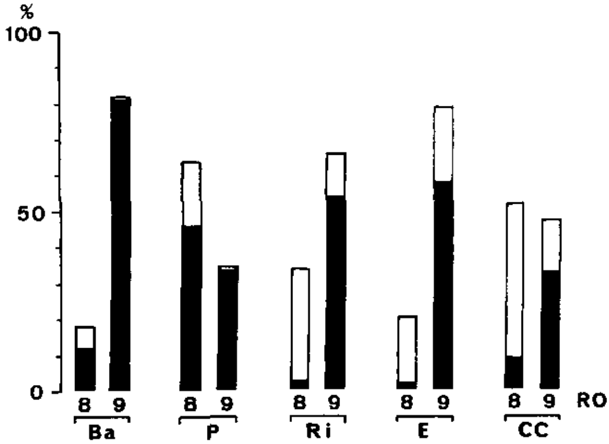

Fig. 4: Frequencies of males (juveniles: open, adult: black columns) respectively at 8 RO (ratio: 8 RO ♂/8+9 RO ♂) and 9 RO (ratio: 9 RO ♂/8 + 9 RO ♂) stadia, which are "coupled stadia" (cf. text). After sampling in autumn 1986. — 8 + 9 RO ♂ = 170 at Ba (Baousset), 202 at P (Peillon), 70 at Ri (Ste-Agnès Righi), 76 at E Engarvin, 180 at CC (ruins of Châteauneuf). The figure shows the progress state of males. The lead of 9 RO males at Baousset will be noted; on the other hand, 8 RO males are in a dominant position at Peillon.

3.1.4. 4-year Cycle (1986 - 1990):

A four-year cycle seems to be typical of *O. sabulosus* living at a certain altitude (1000 m and over) in the hinterland, where even a five-year cycle seems possible. At low altitudes and probably as a result of drought, some males may also need 4 years to become ad 1; e.g. males born in 1986 in the Provence became 10 RO and 11 RO ad 1 in 1990.

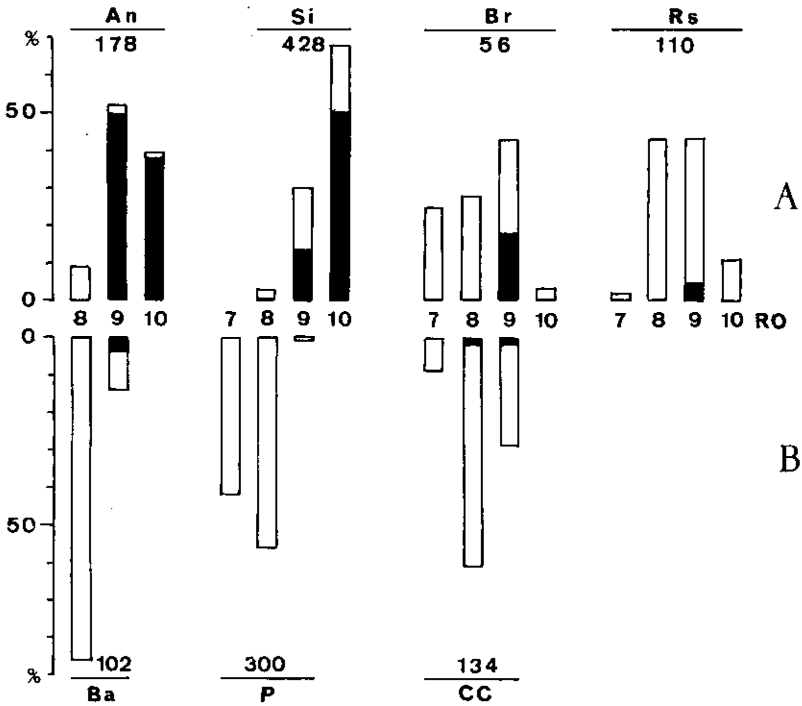

Fig. 5: Percentages of males (juveniles: open, adults: black) at a given stadium. Stadia are "coupled" by 2, 3 or maybe 4. According to sampling in autumn 1989. Comparisons between males presumably born in 1986 (A), thus 3 years after birth and ones born in 1987 (B), thus 2-years after birth. With reserves about 7 RO males (in A) and 9 RO at the ruins de Châteauneuf (in B). An Antibes; Br col de Braus; CC ruins de Châteauneuf; Rs Rocca spaviera; Si Provence.

In the hinterland, in spite of MMJ variations, 4-year old males can all reach the same stadia, whatever the sites they lived in. Compared with coastal animals, hinterland ones present a slight delay, in the sense that they comprise more belated 4-year old 9 RO males and also a few 4-year old (?) 8 RO males, which do not seem to be found in coastal areas. In brief, only few or no MMJ take place after one year, depending on the site and the weather. Good MMJ can take place either 2, 3, or 4 years after birth.

3.1.5. Generation Overlaps:

As Table 1 shows, there are animals with the same number of RO which can belong to 2, 3, nay 4-year old generations. 7 RO males can belong to 3 generations. In the hinterland, 8 RO males can belong to the 2, 3 or 4-year old generation. Moreover at coastal areas, some fast growing 8 RO individuals are probably 1-year old.

Generation overlaps can occur among individuals from different sites (Fig. 5). They can even occur between animals living in the same site: (a) if migrating or wandering animals belonging to another generation colonize the already inhabited site (such a colonization is theoretically possible) or (b) when in the same site egg deposition occurs in two consecutive years: fast growing individuals born a given year being able to catch up with slow growing ones born one previous year. Assignations of animals to a given generation is generally a very difficult task, which can be fraught with pitfalls (cf. 2.). It is important to know that overlaps between generations can exist, which should prompt myriapodologists to be more prudent and less hasty in their judgement in the future.

3.2. Variability of MMJ of the same Site and Year Acccording to the Period of the Year:

According to the present study, in the Mediterranean region, MMJ can take place at three periods of the year: Type 1, at the beginning of the spring. In this case MMJ are the first moults of the year after the hibernation (juveniles to ad 1 moults occuring, say, March-April); Type 2a, during May and June. First juvenile to juvenile moults take place at the beginning of spring (as in type 1), then, MMJ take place in May-June. Thus the successions are the following: juvenile – juvenile – ad 1 (MMJ are the second moults of the year); Type 2b, during July and August. MMJ are either the second or rarely the third moult of the year (juvenile – juvenile – juvenile – ad 1).

Type 1, manifest by numerous ad 1 at the beginning of the spring, has been observed in the field at Rocca spaviera in spring of 1985 and 1990, at the Col de Braus (1990), in the ruins of Châteauneuf (1990) and also at low altitude at Antibes (1989, 1990) and in Provence (1989, 1990). Apart from some hinterland areas (1000 m and more), in most studied sites in the Mentonnais, typically only few ad 1 could be observed at the beginning of the spring (in other words, only few ad 1 belonged to the type 1). This type seems to depend – at least partly – on the age of the juveniles. In 1985, at Rocca spaviera, virtually all juvenile males turned into ad 1, in one year. But MMJ of the type 1 can be spread over 2 years (CAT strategy, SAHLI 1989): at Antibes and in Provence, a part of 1986 born juveniles became type 1 ad 1 in the spring of 1989, the other part type 1 ad 1 in spring 1990.

Type 2 was much more common than type 1 in most Mentonnais sites, from 1984 to 1990. Type 2a was the most common type in 1986 cultures. Type 2b seems to be less frequent at least in cultures. Type 2 may be in correlation with weather conditions.

3.3. Variability of MMJ in the same Generation, in the same Site and the same Year in Connection with the Stadia:

Figure 3 - 5 show that the number of MMJ can vary with the stadium. The cases of Ste- Agnès-*Righi, Engarvin, ruins of Châteauneuf at stadia 8 and 9 RO are particularly eloquent.* A given year after birth, animals of the same generation belong to 2 stadia (stadia 8 and 9 RO, Fig. 4), 3 or perhaps 4 stadia (7 RO, 8 RO, 9 RO, 10 RO in Fig. 5), two of them being often predominant. One may speak of "coupled" stadia (= stadia which coexist in a given year or season, in animals from the same generation).

At equal age, males with a higher RO number (e.g. 9 RO) become adults in a higher number than juveniles with lower RO number (e.g. 8 RO, Fig. 3). In other words, among juveniles of a same generation, those which possess the highest RO number become adults, a given year, in a higher number than the other juveniles. This rule – which can present exceptions (Fig. 5) – is valid for both MMJ of type 1 (*1990* observations) and MMJ of type 2 (Fig. 3, 6). Males of a same generation are split up, a given year or season, into ones which become ad 1 and ones which stay juveniles: MMJ are spread over time (= CAT strategy).

3.4. Experimental Variability of MMJ of the same Culture, related to the Home Sites of Juveniles:

Animals stemming from several sites of the Mentonnais were reared, after collection, in field cultures in the Borrigo valley of Menton, under wet conditions. Furthermore animals from Engarvin were reared (a) at the Borrigo valley under wet conditions, (b) at Engarvin under very dry field conditions. The results are summarized in Fig. 6.

In spite of the very wet culture conditions at the Borrigo valley (in the home sites, the second half of May, June and July were relatively dry) and in spite of the low altitude of the cultures in the

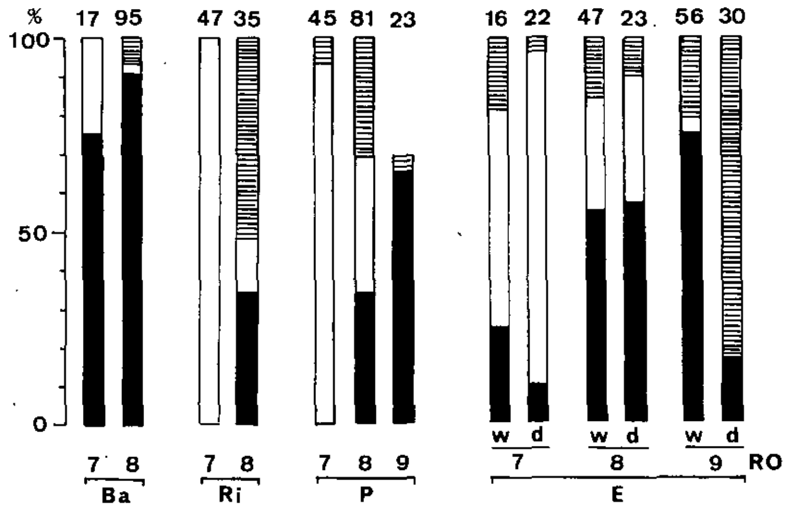

Fig. 6: Respective proportions — stadium by stadium — of ad 1 (black columns: juvenile to adult moult) and juveniles (open columns: juvenile to juvenile moult) males, obtained in cultures from reared 7, 8 and 9 RO juveniles collected at 4 sites. Juveniles which did not moult in cultures: striped columns. — In 9 RO males from Peillon, 30 % of individuals died. w: wet culture conditions; d: dry culture conditions.

Borrigo valley, the numbers of MMJ in males from Baousset, Ste- Agnès-Righi, Engarvin were comparable to the numbers of MMJ in their respective home sites. In these cases, humidity had no special effect and animals appeared as if they were "marked" by their origins or at least by the time spent previously in the home sites. Concerning Peillon, the absence of MMJ in 7 RO juvenile cultures is not understandable and 9 RO ad 1 are curiously less numerous in cultures than in the home site.

Concerning Engarvin, drought had an influence in 7 RO and 9 RO stadia, but, paradoxically, not in the 8 RO stadium. 6 RO to 7 RO moults in 1-year old coastal individuals apart (cf. 3.1.1.), drought typically hinders the moults (cf. SAHLI 1990) in general and the MMJ in particular.

3.5. Variability of MMJ of the same Site, according to the Years:

Contrary to what one might believe, in a given site, MMJ neither occur regularly after a given number of years after birth nor at one given stadium. In Antibes, most larvae born in 1984 gave 8 - 9 RO ad 1 males in 1986, thus 2 years after their birth. On the other hand, only few juvenile males born in Antibes in 1986 turned into (mainly 8 RO) ad 1 in 1988. A good part of juveniles born in 1986 gave 9 - 10 RO ad 1 in 1989, thus 3 years after birth. Males which remained juvenile in 1989 gave 10 - 11 RO ad 1 in 1990, thus 4 years after their birth.

Similar observations could be made for example at Peillon. There were successful MMJ in 1986, 2 years after birth in 1984 (Fig. 4). No MMJ occur in 1989, 2 years after birth in 1987 (Fig. 5).

Differences in maturation in a given site according to the years is an important new fact. Differences are most likely imputable to weather conditions, different according to the years. If many ad 1 males and successful egg depositions both appeared regularly after two years — thus every two years — one would observe situations represented in Tab. 2. A 2-year cycle, regularly repeated over years, would lead to the following 2 combinations: a) many ad 1 and few intercalaries s 1 (years x + 2, x + 4, etc.); b) many intercalaries s 1 and few ad 1 (years x + 1, x + 3, etc.).

Table 2: Possible situations in *Ommatoiulus sabulosus*. S 1 Intercalaries 1.

year x	x + 1	x + 2
many ad 1 ———	many s 1	
few juveniles ———	few ad 1 ———	few s 1
successful egg depositions ———	———	many new ad 1

Such combinations have been admitted by BAKER (1978) in *Ommatoiulus moreleti* (LUCAS). The repeated alternation of the 2 combinations can only exist in repeated constant 2-year cycles. In fact, in the Mediterranean region, as indicated in the present paper, *O. sabulosus* does not develop in a constant way according to a 2-year pattern.

3.6. Notions of good and poor MMJ:

3.6.1. Poor MMJ:

MMJ can be "poor" a given year for two reasons: a) few (or no) juveniles are present in the site a given year, as a result e.g. of a poor egg deposition (e.g. 2 or 3 years before); b) numerous juveniles (e.g. 8 and 9 RO or 9 and 10 RO ones – susceptible of becoming ad 1 in a site x) are present in the site x in a given year but few of them only turn into adults ("poor" MMJ sensu stricto or "unsuccessful" MMJ – the expression "few MMJ" would be better), probably due – at least partly – to poor weather conditions, such as drought.

3.6.2. Good MMJ and explosive MMJ:

When juveniles are numerous and many of them (say over 60 %) turn into ad 1 in a given year, we can speak of "good MMJ" and also of a "good MMJ year". When over 80 % of a given generation (e.g. 2-year 8 RO plus 9 RO juveniles or 3-year 9 RO plus 10 RO ones) turn into ad 1 a given year in a given site – as the result of MMJ of type 1 or/and 2 – we will name this situation an explosive one ("explosive MMJ", "explosive strategy"). Such a situation happened e.g. in Antibes in 1984 and 1986 and at Baousset and Peillon in 1984 and 1986 (Figs 2, 4).

Explosive situations contrast with situations in which MMJ are split up and spread over several times, stadia and years (= CAT strategy): maturation moults of juveniles stemming from the same egg deposition can be spread over four years. To give a rough idea, according to estimates, the following figures can be put forward, as possibilities: 1 % of MMJ the first year after the birth, 33 % the second year, 36 % the third and 30 % the fourth year. Even in case of explosive MMJ, there are always a few juveniles (say 1 - 20 %) which use the CAT strategy. Explosive MMJ appear as extreme cases in which most MMJ (over 80 % of them) concerning animals of a given generation are concentrated in one year, often the second or the third year after birth. In other words, in a given site and for a given generation MMJ can be concentrated in one year or spread over several years, depending on the years.

4. Conclusions:

In the present state of our knowledge, four "factors" seem to play a role in MMJ of *O. sabulosus* in the South of France: a) the site: coastal areas, hinterland, altitudinal and geographical locations (e.g. Mentonnais or Provence); b) the age of the population; c) the stadium (e.g. in coupled stadia); d) the weather conditions (e.g. drought year, normal rainy year). Moreover, MMJ of a given generation can be either concentrated in one year (explosive strategy) or spread over several years (CAT strategy)

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