Population dynamics of gyrrinid beetles*

II. Reproduction

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Summary. Between 1974 and 1983 data concerning egg production and recruitment were obtained by sampling populations of the whirligig water beetle Gyrinus marinus Gyll. All females reproduce, but they differ in the number of eggs laid per oviposition and in the frequency of oviposition. There are two reproducing generations a year, one in spring (April–June) and one in summer (July–August). Females emerging in July and August reproduce immediately after emergence, but at a lower level than the females of the spring generation. In June the egg production of spring females also decreases. No significant differences in egg production occur between populations in different sites or in different years. Individual properties and circumstances of the females probably have a distinct influence on variation in egg production. A female probably oviposits and is fertilized at least once a week. Without fertilization egg production and the viability of the eggs decrease after two weeks. On the average, 60 per cent of the eggs hatch.

Development from egg to teneral takes about 10 weeks in spring and autumn and about six weeks in summer. The hatching and development of eggs laid in April is probably retarded until the half of May. Variation in the length of the developmental period will cause variation in recruitment and in the number of hibernating beetles. Variation in egg viability and in larval and/or pupal development are probably of equal importance to the variation in the numbers of tenerals emerging. The variation in egg production is of no importance.

Recruitment (number of tenerals/female) of the generations reproducing in spring and in summer are independent of each other. Between years the rate of recruitment differs significantly, and probably depends more on environmental conditions such as weather than egg production seems to do.

1. Reproduction consists of (a) the reproductive activities of females and males (fertilization, egg production and egg laying), and (b) development of the eggs until the emergence of tenerals (recruitment). It is frequently supposed that a population reacts to changing circumstances (such as food shortage) by adjusting its egg production, particularly if density-dependent processes have been assumed, which are usually thought to have a regulating effect on population size (e.g. Baars and van Dijk 1984). By means of key factor analyses (Varley and Gradwell 1960; Podoler and Rogers 1975) a number of case studies have shown that the mortality of a stage in the development between egg production and the emergence of adults is a key factor in the population dynamics of the species (e.g. review in Podoler and Rogers 1975).

2. We have carried out measurements and experiments on the reproduction of whirligig beetles (Gyrinus marinus Gyll), to obtain estimates of the relationships between egg production, development and final recruitment. These measurements and experiments are part of a comprehensive study of the population dynamics of whirligig beetles which also includes survival and dispersal. A study of dispersal by flight has already been published (van der Eijk 1983). A study of survival is being published with this paper (van der Eijk 1986).

3. Reproduction of whirligig beetles starts with the laying of eggs under water. After hatching, the larvae grow up under water and pupate outside the water. Each stage in the development from ovocyte to mature adult beetle has its specific growth rate and its own survival chance. The influence of each stage upon the ultimate variation in recruitment is of special interest. For example, if egg production has the greatest influence, the living conditions of the females will probably have a significant influence upon the size of recruitment. But if the conditions for the larvae under water provide the most important factor for the variation in recruitment it may be fairly unimportant to recruitment what happens to the females. We therefore give special attention to variation in egg production and to that in the emergence of tenerals. A full description of reproduction will embrace (a) information about reproductive activities both of females (number of females reproducing, number of ovipositions, number of eggs per oviposition, individual differences) and of males (frequency of fertilizations, influence of fertilization upon egg viability), and (b) information about development from egg to adult (proportion of eggs which hatch, time of development, variation in survival) and about recruitment (number of tenerals per female, per generation, and per month).

Methods

1. As gyrrinid beetles live on the water surface of small water bodies they are convenient subjects for population dynamic field studies. Most of the data were collected from ten populations in the main study-area in the northern part of the
Netherlands near Groningen. These were supplemented with data from other populations within a radius of about 20 km around Groningen. The populations will be indicated by location-symbols and year: for example, Zp-76 and Mp-83 concern populations Zp in 1976 and Mp in 1983 (for the meaning of the location-symbols see map in van der Eijk 1983).

2. In the field the eggs are laid on submersed water plants, but the number of eggs produced per female can easily be measured by putting single females in tubes or petri-dishes with moistened toilet paper for 24 h. The ripe eggs will then be laid in rows on the paper. When the paper on which the eggs are laid is kept moist, the eyes of the embryos become visible through the thin egg scale and it is possible to ascertain the number of viable eggs after five days at room temperature.

Young females start oviposition about 10 days after emergence. Unless otherwise stated we used only females with hardened elytra (females older than two weeks) in the experiments.

From population Zp-76 10 to 20 females of each sample taken in April until June were kept in formalin and later dissected to count the numbers of eggs in the ovaries.

By repeatedly measuring the egg production of the same individually-marked females from populations Zp-76 and Mp-83 the egg production of individual females was estimated during the reproduction season. (The technique of individual marking is described in van der Eijk 1983.) In this way it was possible to estimate the rate of egg production in the ovaries, the frequency of ovipositions and the frequency of fertilizations per female.

3. If a female was fertilized before she was captured a spermatophore was also left on the paper. After 20 June 1983 all males were removed from population Mp-83 to trace the influence of both the frequency of copulations and of the duration of the effect of a single fertilization on egg production and on the viability of the eggs laid.

4. Recruitment is estimated by the percentage of 'very soft' beetles (teneral) in the samples. After a beetle has emerged, it takes one to several weeks before the hardening of the cuticula, especially of the elytra, is completed. Until five to seven days after emergence the beetles can be distinguished from previously emerged teneals.

5. Time will be indicated by numbered weeks. In each year the same seven days bear the same number. In this way data of different years are directly comparable (i.e. 1 April always is the last day of week 13, etc.).

6. Variation in the data is expressed as the variation coefficient \( V = \text{standard deviation/mean value} \). Variation coefficients in time sequences (data of the same population in different years) will be indicated as \( V_t \), and in space sequences (data of different populations in the same period) by \( V_p \).

7. Statistical tests used are all referred to Sachs 1983. Unfortunately different authors use different symbols in the same tests. The tests and the symbols used in this paper are as follows: \( t \)-test, parameter \( t \); Mann-Whitney U-test: \( U \), for large samples normally distributed parameter \( z \); Kruskall-Wallis H-test: \( H, z \); correlation test: \( r \) or \( z \); Spearman correlation test: \( r, z \); Chi-square test: \( \chi^2 \); Anovar: \( F \); Wilcoxon paired signed-rank test: \( R, z \); Fisher-test: \( z \). If possible the normally distributed parameter \( z \) is used, because of the comparability of different tests and its independence of the size of the samples.

**Fig. 1.** Mean number of eggs per female per week. *: mean number of eggs found in the ovaries of a female; †: mean number of eggs laid in one oviposition

**Results**

**A. Egg production**

Egg production will first be considered at population level and then at individual level (per female). Finally the influence of fertilization upon egg production will be discussed.

**A.1. Egg production per generation.** 1. Egg production starts after hibernation in April and continues until mid-August. About the end of June the first young beetles emerge. These beetles start to reproduce within two weeks. The offspring of this generation emerges from early September until hibernation at the end of October. The successive reproducing generations only partly overlap (about 25 per cent in summer and about 2 per cent in spring).

As long as a female is alive she produces eggs, until about the last week of August (week 35). Females caught on the first day of activity already have many developing oocytes. It takes several weeks before all females are reproducing, and the number of ripe eggs in the ovaries increases until the second half of May (weeks 19-22, see Fig. 1).

During the period for which both measurements are available the number of eggs laid per female is correlated with the number of eggs in the ovaries (1976, weeks 16-24, comparing the regression coefficients of the time sequences of eggs laid and eggs in ovaries: \( t = 0.84, df = 404, P > 0.05 \)). But the number of eggs laid per week is significantly higher than the weekly number of eggs in the ovaries (Mann-Whitney U-tests per week: all tests \( P < 0.02 \)). After week 22 (early June) the number of eggs laid decreases significantly with time (Spearman test \( r = -0.819, n = 41, P < 0.001 \)). Females of the summer generation start oviposition about ten days after emergence, but their egg production is lower than that of females of the spring generation (Mann-Whit-