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MORTALITY PATTERNS IN CARABID POPULATIONS*

ABSTRACT: Six species of *Carabus* L. and *Pterostichus* Bon. genera, representatives of the spring and the autumn breeders which inhabit woodlands were studied. Instantaneous mortality rates of eggs, larvae, prepupae and pupae as well as beetles were estimated. Larval mortality rates appeared to be much higher than those of eggs, prepupae and pupae. Mortality rates of beetles were always higher in the breeding season than out of the season. A general conclusion is drawn, that the active stages in the life cycle – i.e., stages gaining weight or producing eggs, and thus mobile because of food seeking – are especially susceptible to mortality factors.

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I. INTRODUCTION

Investigations on age-structure and mortality of imagines of *Carabidae* have shown, that during breeding season beetle populations usually consist of two generations (Grüm 1959, Schjøtz-Christensen 1965, 1968, Murdoch 1966, Vlijm, Dijk and Wijmans 1968, Kurka 1972, Dijk 1973, Luff 1973), and the beetle mortality in breeding season is higher than mortality of hibernating beetles (Schjøtz-Christensen 1965, 1968, Luff 1973). There exists an opinion, according to which mortality of beetles is especially high at the end of breeding season (Skuhavy 1959). Data on

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mortality of eggs, larvae, prepupae and pupae are very scarce; the most complete ones were presented by P a a r m a n n (1966): survivorship curves of a few laboratory bred populations were similar to the exponential ones, but in some other populations mortality rates were variable.

The aim of the present paper is to outline an approximate characteristic of mortality rates of a few carabid species inhabiting woodlands, and – beginning with eggs and ending with beetles which reproduce for the second time in their lives – draw the adequate survivorship curves. Six species belonging to two genera (*Carabus arcensis* Hbst., *C. glabratus* Payk., *C. hortensis* L.; *C. nemoralis* Müll., *Pterostichus niger* Schall. and *P. oblongopunctatus* F.) were studied for this purpose. In each of the genera two basic developmental types – i.e., the spring and the autumn breeders (L a r s s o n 1939) – were represented.

Within the study area, the spring breeders – *C. arcensis*, *C. nemoralis* and *P. oblongopunctatus* – deposit their eggs from the end of April till the end of July (G r ü m 1973a), their larval development occurs in summer, and the teneral beetles begin to appear in the late summer (G r ü m 1959, 1973b). The next spring the latter – after having overwintered – start to reproduce for the first time in their lives (G r ü m 1973a), and certain number of them can overwinter again (G r ü m 1962) and probably is able to reproduce for the second time. The autumn breeders – *C. glabratus*, *C. hortensis* and *P. niger* – lay their eggs from June to October (G r ü m 1973a), the larval development occurs in summer, autumn and spring (there is a winter period of hibernation of the larvae), the teneral beetles appear in summer, and immediately start to reproduce (G r ü m 1973a). Part of them hibernates and in the early summer starts to reproduce for the second time (G r ü m 1973a).

The mortality estimates applied in this paper are based on differences in population density (number of individuals per 100 m²) or differences in abundance (number of individuals captured in a constant number of pitfalls). Apart from that, some of the estimates are based on the CMR method. The following values are calculated separately for each of the six species:

1. Cumulative population density of eggs in 1972 (i.e., the sum of numbers of eggs per 100 m² deposited each day in the breeding season).
2. Cumulative population density of teneral beetles originating in the eggs deposited in 1972 (i.e., the sum of numbers of these beetles per 100 m² consecutively hatching).
3. Beetle population density at the beginning of a breeding season.
4. Beetle population density at the end of the season.

Apart from that, the following abundances are calculated:

1. The Ist instar larvae (separately for *C. nemoralis* and *C. glabratus*).
2. The IInd instar larvae (only for *C. nemoralis*).
3. The IIIrd instar larvae (separately for *C. nemoralis* and *C. glabratus*).

2. STUDY AREA AND METHODS OF DATA COLLECTING

The data were sampled in two habitats – about 50 m distant each from the other – located in the east part of the Kampinos Forest (several kilometers north-west from Warsaw) from the 27th of April 1972 till the 30th of August 1973. The first habitat – designated with the PQ symbol – was located in a mixed forest covering an area of about 4 ha, close to rectangle in shape, with *Pino-Quercetum* association predominating in the central part of it, and *Carici elongatae-Alnetum* as well as *Circaeo-Alnetum* associations occurring along the longer sides of the area. The second habitat – TC – covered an islet of *Tilio-Carpinetum* association of about 0.15 ha in area surrounded by the *Carici elongatae-Alnetum*, and isolated from the

neighbouring habitats by high water level all over the year. This made migrations of the studied species in that area difficult or — as in the case of the islet — even impossible. Five of the species inhabited both of the habitats, but one species (*C. arcensis*) occurred only in the *PQ* habitat — thus, all estimates of its population density refer to this habitat.

The method of data collecting is based on isolating small, round sections of the area (G r ü m 1971). Each section (further called “plot”) was fenced with a sheet of plastic dug about 15 cm deep into the ground. The height of the fence was approximately equal to 20 cm above the litter layer. Directly near outside and inside the fence a certain number of pitfalls was placed. Imagines captured in the outside pitfalls of a given plot were marked individually and immediately released in the center of the plot. Thus, only marked beetles were allowed to enter inside. Beetles captured in the inside pitfalls were released outside the fence. Larvae captured inside were immediately released within the plot, and those captured outside were taken out to the laboratory.

Two kinds of plots were in use: small ones — of 3.3 m² in area, equipped with 4 outside and 8 inside pitfalls — for collecting *P. oblongopunctatus*, and big plots — of 33.3 m² in area, equipped with 8 outside and 16 inside pitfalls — which served to collect the remained species. There were totally 7 plots of 3.3 m² and 7 of 33.3 m² in area — four of each size in the *PQ* and three in the *TC* habitat — distributed accordingly to the humidity and shadowness gradient. To collect the beetles and larvae, series of trappings were carried out. Each of them lasted 10 days, and each day the pitfalls were emptied in the morning. The mean interval between the consecutive series of trappings was equal to 4 days.

3. INSTANTANEOUS MORTALITY RATES

3.1. Eggs, larvae, prepupae and pupae

The cumulative densities of the egg populations calculated for the breeding season in 1972 are shown in Table I. The data presented there — i.e., mean values for the *PQ* and the *TC* habitats — have been taken from another paper devoted to estimation of egg production (G r ü m 1973a). Cumulative density of the teneral beetle populations starting to live an active life was estimated by means of counting the unmarked beetles removed from inside of the plots. It was assumed, that in the spring series of trappings in 1972 all the unmarked beetles present inside the plots were removed. Thus, all the unmarked beetles captured inside in the autumn 1972 and in the summer 1973 had to develop from the eggs that had been deposited there in the breeding season in 1972.

Let us consider the validity of the above assumption. Mobility of the species under study — except for *P. oblongopunctatus* — was so high that 95% of the beetles marked and recaptured in the same year (Tab. II), in fact were captured inside the plots not later than the 4th day after their releasing (Fig. 1). The percentage of the never recaptured beetles was rather low — from 0.6 to 22.5% (Tab. II) — and positively correlated with the number of days necessary to recapture 95% of the current year recaptured beetles (Fig. 2). Because prolongation of the time-lapse between releasing and recapturing of an individual undoubtedly enhances probability of its death, the mortality of the beetles is regarded as a cause of variable percentage of the never recaptured beetles. Consequently, it seems to be proved that the unmarked beetles were removed from the inside of the plots in the spring 1972, and the applied method of fencing was effective enough to prevent the beetles from migrating.

Tab. I. Instantaneous mortality rates over the period between the MED of eggs and that of teneral beetles

Parameters	Spring breeders			Autumn breeders		
	<i>C. arcensis</i>	<i>C. nemoralis</i>	<i>P. oblongo-punctatus</i>	<i>C. glabratus</i>	<i>C. hortensis</i>	<i>P. niger</i>
Cumulative population density of eggs	55.72	16.60	2228.0	29.00	16.01	144.99
MED of eggs	June 2 1972	May 16 1972	May 24 1972	July 19 1972	August 25 1972	August 10 1972
Cumulative population density of teneral beetles	14.28	5.15	236.0	4.72	4.29	11.16
MED of teneral beetles	August 21 1972	August 10 1972	August 18 1972	July 7 1973	July 18 1973	July 19 1973
Time-lapse between the MED of eggs and that of teneral beetles (days)	80	86	86	353	327	343
Instantaneous mortality rate	0.0170	0.0110	0.0261	0.0051	0.0040	0.0075

Tab. II. Numbers of beetles marked and released within the fence plots in 1972, and then recaptured in 1972 and 1973

Parameters	<i>C. arcensis</i>	<i>C. nemoralis</i>	<i>P. oblongo-punctatus</i>	<i>C. glabratus</i>	<i>C. hortensis</i>	<i>P. niger</i>
Number of marked and released	227*	118*	241*	106	175	267
Number of recaptured in 1972	214	103	174	100	171	244
Number of recaptured in 1973	1	1	13	1	3	1
Percentage of never recaptured	5.3	11.9	22.5	4.8	0.6	8.3

*Except for teneral beetles marked and released in the autumn 1972.

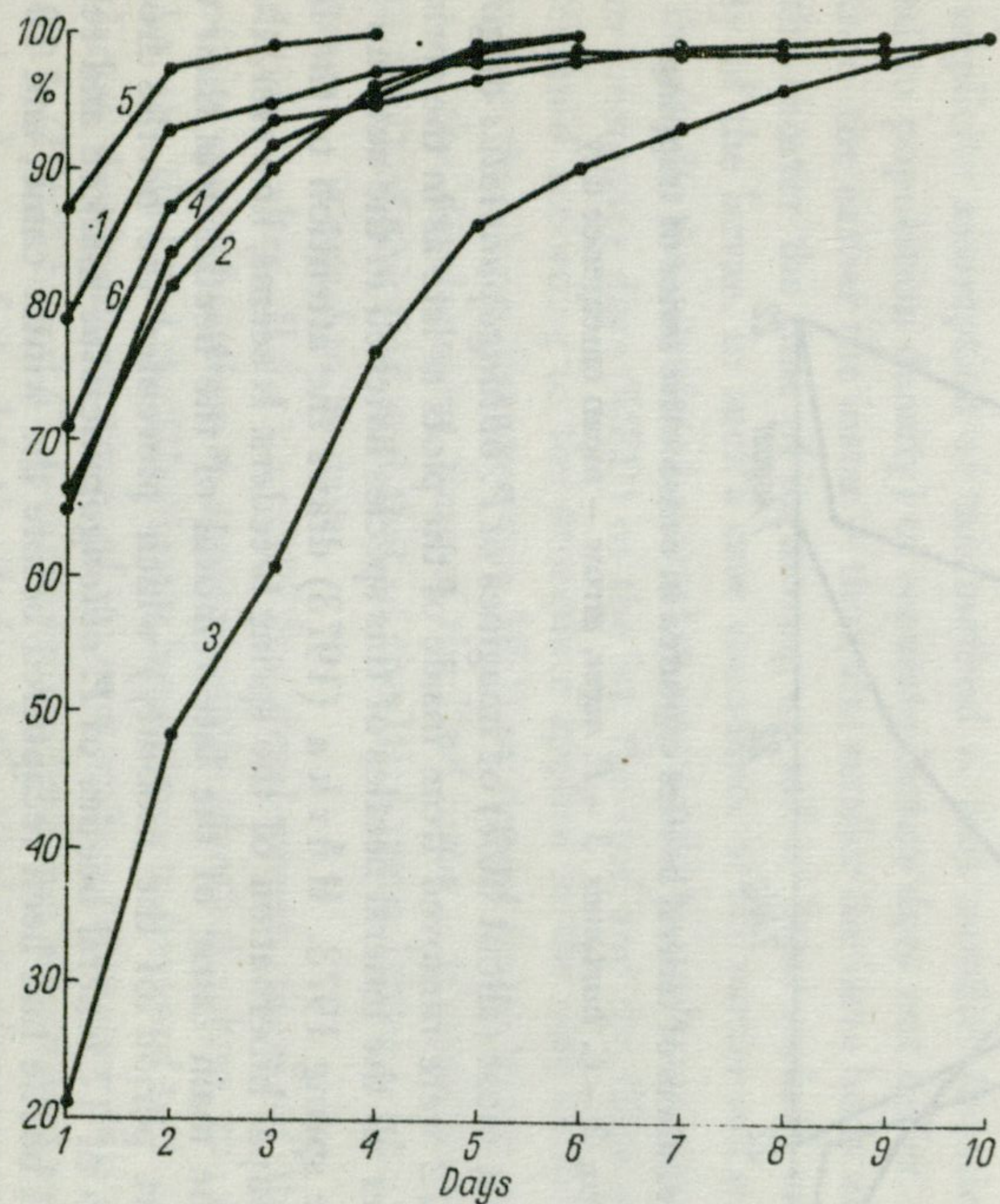


Fig. 1. Cumulative percentage of recaptured individuals belonging to the group recaptured in the year of their releasing, versus number of days from their release

1 - *C. arcensis*, 2 - *C. nemoralis*, 3 - *P. oblongopunctatus*,
4 - *C. glabratus*, 5 - *C. hortensis*, 6 - *P. niger*

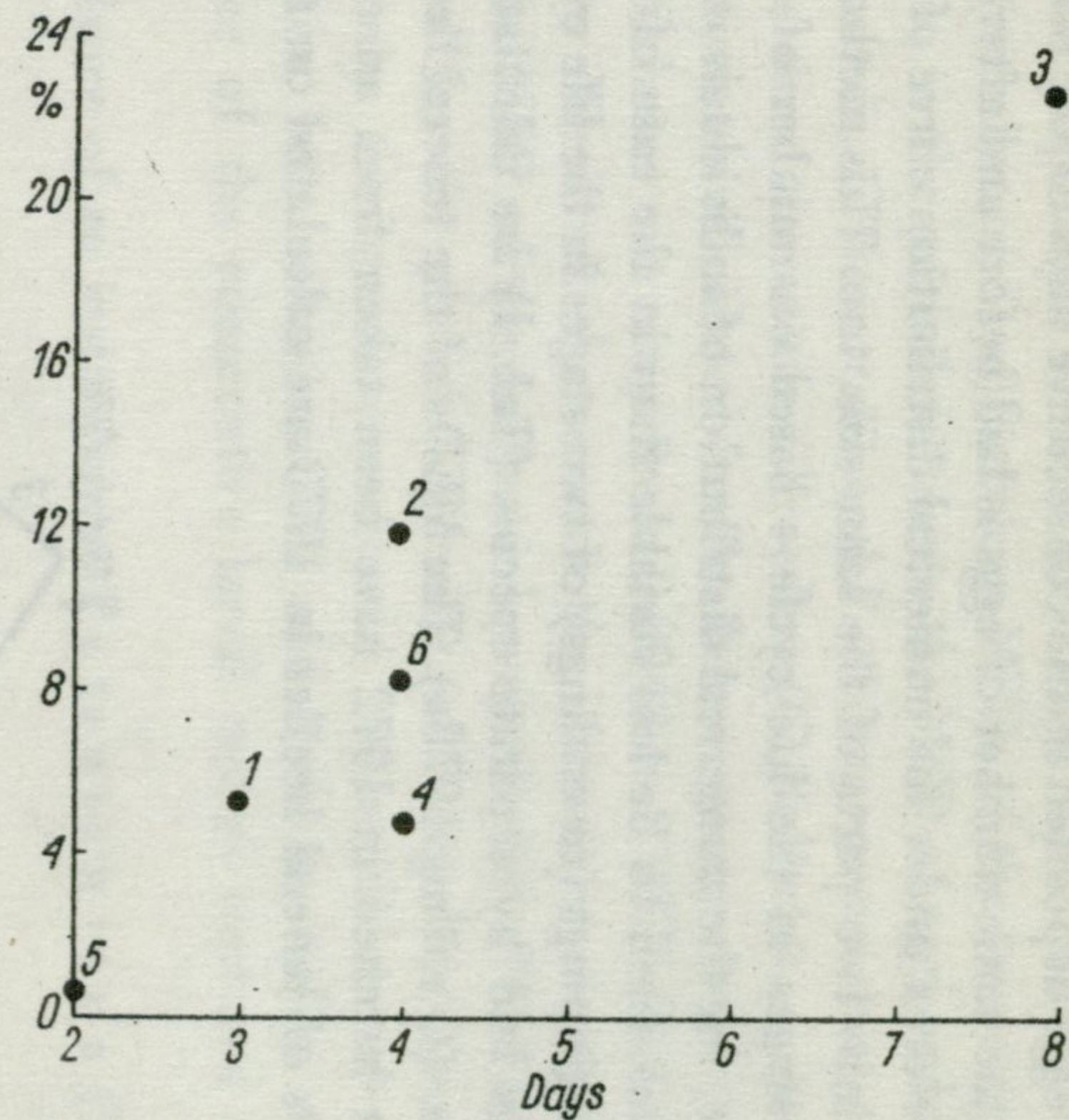


Fig. 2. Percentage of individuals never being recaptured versus number of days necessary to recapture 95% of individuals recaptured in the year of their releasing

1 - *C. arcensis*, 2 - *C. nemoralis*, 3 - *P. oblongopunctatus*,
4 - *C. glabratus*, 5 - *C. hortensis*, 6 - *P. niger*

To estimate time-lapse between egg deposition and teneral beetle emergence the method of mean emergence day (Bujalska, Andrzejewski and Petruszewicz 1968) is applied. In the case of eggs, the mean emergence day – MED – divides the area under the numerical distribution of eggs deposited in the consecutive days of the breeding season into two parts of equal size; thus, the same number of eggs is laid before and after that day. The MED of teneral beetles divides the area under the numerical distribution curve of these beetles removed from inside of the plots into two parts of the same size, too. This method of estimation of the time-lapse between two stages in the life cycle – based on number of days between the two MEDs – has an advantage, for the numerical distribution of individuals is involved there. As the result, the estimated values seem to be less variable than in the case of estimates grounded on comparison of dates of beginnings (or endings) of two stages in the life cycle.

The MEDs of the eggs laid by separate species (Tab. I) are calculated on the basis of the previously published data (Grüm 1973a). The MEDs of the teneral beetles of *C. arcensis* and *P. oblongopunctatus* that hatched in 1972 have been taken from an earlier paper (Grüm 1973b), but all the MEDs of teneral beetles in 1973 are calculated on the grounds of the data presented in Figure 3.

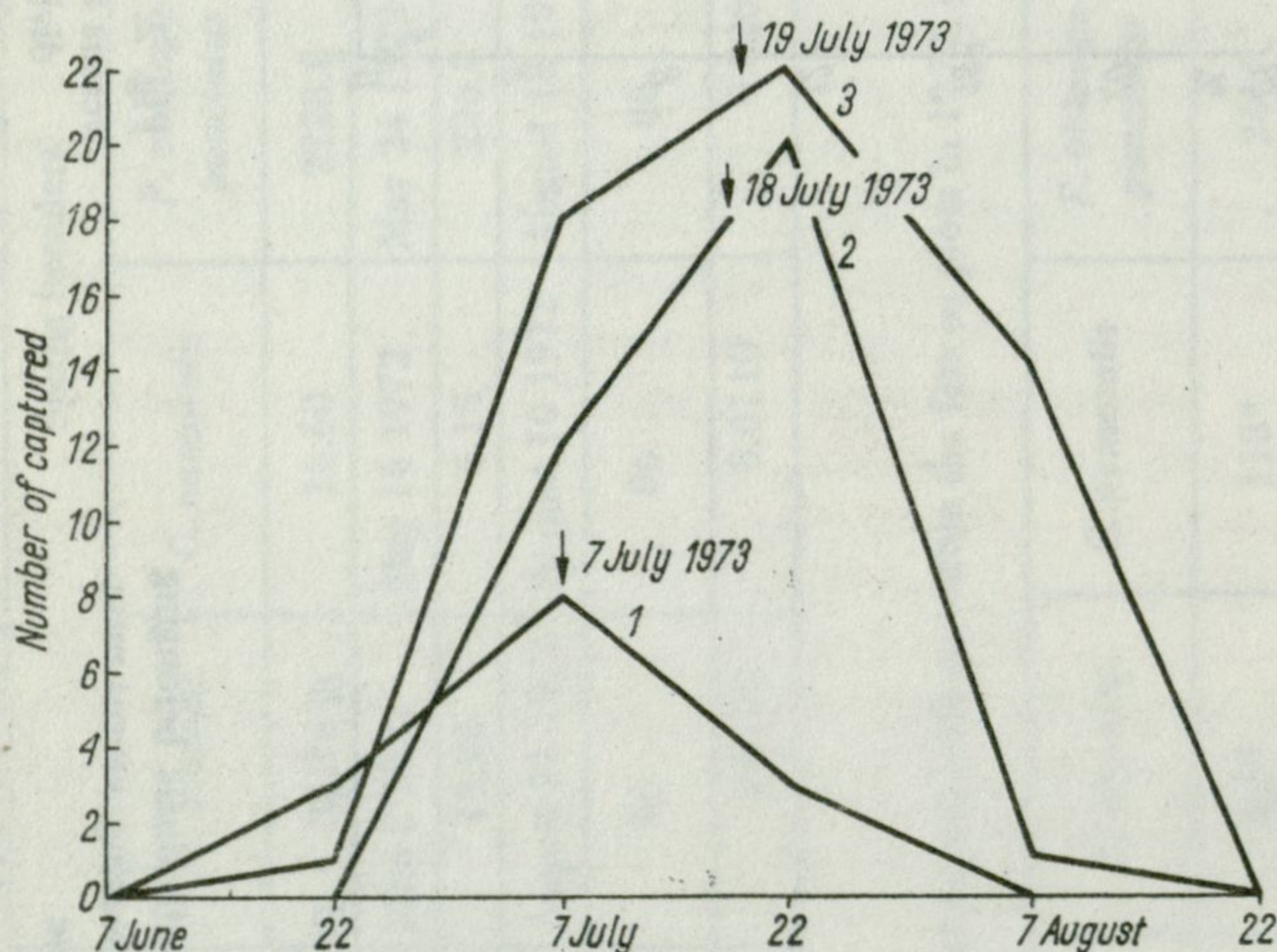


Fig. 3. Changes in numbers of teneral beetles captured in consecutive series of trappings

1 – *C. glabratus*, 2 – *C. hortensis* 3 – *P. niger*, arrow – mean emergence day

It should be added, that most (about 60%) of imagines of *P. oblongopunctatus* originating in the eggs deposited in 1972 were removed from inside of the plots as late as in the spring 1973. A question arises, whether all the teneral beetles of this species hatched in the autumn 1972, or a part of them did in the spring 1973. Hůrka (1973) draws the attention to the fact, that there is a possibility of pupal hibernation of the spring breeders. It seems, however, that in the above mentioned case the main cause of the late removal of the beetles was their very low mobility (or a very short period of the mobility) which prevented the beetles from being recaptured: from a group of 17 teneral beetles of *P. oblongopunctatus* marked and released in the autumn 1972, only 1 beetle had been recaptured before the winter came, and 10 of them were recaptured in the spring 1973.

Accepting a tentative assumption that the survivorship curve is similar to the exponential one, the instantaneous mortality rate is calculated:

$$\mu = \frac{\ln \bar{n}_0 - \ln \bar{n}_t}{T}$$

where: \bar{n}_0 – cumulative population density of 0 stage, \bar{n}_t – cumulative population density of t stage, T – time-lapse (number of days) between MEDs of the two stages.

As the results show, in the periods between the MED of eggs and that of teneral beetles, the spring breeders (*C. arcensis*, *C. nemoralis* and *P. oblongopunctatus*) are characterized by much higher mortality rates than the autumn breeders (*C. glabratus*, *C. hortensis* and *P. niger*). The instantaneous mortality rates calculated for the former group range from 0.0110 to 0.0261, and those calculated for the latter one range from 0.0040 to 0.0075 (Tab. I).

The next step is to check whether or not the instantaneous mortality rates in larval development (i.e., from the MED of the 1st instar larvae till that of the IIIrd instar ones) are similar to the rates calculated for the period beginning with egg deposition and ending with teneral beetle appearance. Only the most numerous captured larvae – that is *C. nemoralis* and *C. glabratus* – are taken into consideration, and their mortality estimates are founded on decrease in abundance of the consecutive larval instars captured in a constant number of pitfalls.

To estimate abundance of an instar larvae Petruszewicz's (1966) equation is applied:

$$N = \frac{\bar{N} T}{\tau}$$

where: \bar{N} – mean number of an instar larvae captured within the whole their appearance period, T – number of days their appearance lasts, τ – mean developmental time of the instar (in days).

An implicate assumption of this method is, that mobility (a ratio of number of individuals captured to population density) of separate instars does not differ. It may be supposed, however, that the earlier the instar – thus, the smaller the larva body and more exposed to drying out – the shorter the time of its moving on soil or litter surface, and consequently the lower mobility of the larvae. In such a case abundance of the earlier instars could be underestimated, and as the result, the calculated mortality rate could be underestimated, too.

Mean emergence days (MED) of the 1st, the IIrd and the IIIrd instar larvae of *C. nemoralis* are calculated according to the procedure applied in the case of teneral beetles (Fig. 4). As it appears, the time-lapse between the MED of the 1st instar larvae and that of the IIrd instar ones – i.e., the development time of the IIrd instar – is equal to 12 days, and the time-lapse between MED of the IIrd and that of the IIIrd instar larvae – i.e., the time of the IIIrd instar development – is equal to 16 days.

Accepting – after Hůrka (1973) – development times of the 1st and the IIrd instar larvae of the spring breeders as approximately identical values, the relative development times of the 1st, the IIrd and the IIIrd instar larvae have to be equal to 1 – 1 – 1.3, respectively. The entire larval development time of *C. nemoralis* – estimated this way – equals 40 days – Sturani (1962) found 47 days (including prepupa) in constant temperature 18°C – and the relative abundances of the 1st, the IIrd and the IIIrd instar larvae equal 457.5, 320.0 and 218.7 individuals, respectively.

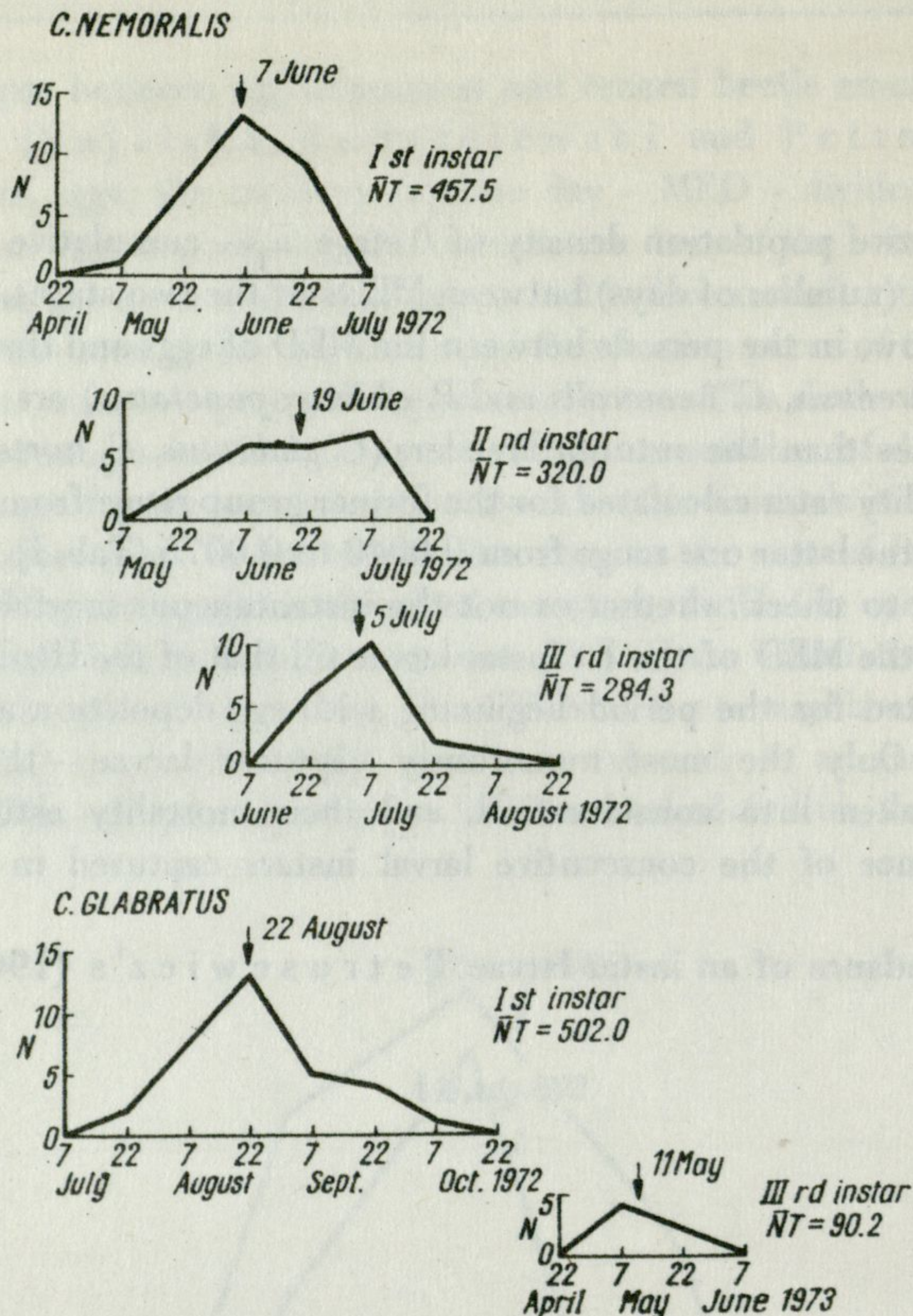


Fig. 4. Changes in numbers of larvae captured in consecutive series of trappings

N – number of captured, arrow – mean emergence day

On this basis, instantaneous mortality rates during the development time of the IInd and the IIIrd instar larvae of *C. nemoralis* are estimated: 0.0300 for the IInd and 0.0254 for the IIIrd instar. The mean value of the *C. nemoralis* larva mortality rate – 0.0273 – is much higher than the mean value calculated for the period from egg deposition till teneral beetle appearance of this species (Tab. I).

On the assumption that the mortality rate in the entire period of larval development of *C. nemoralis* was equal to 0.0273, the population density of this species – in accordance with the exponential equation $N_t = N_0 e^{-\mu t}$ – would have to decrease from 16.60 individuals (eggs) per 100 m² to 5.57 individuals per 100 m² in 40 days. Because the cumulative population density of teneral beetles of this species was equal to 5.15 individuals per 100 m², the instantaneous mortality rate in the remaining 46 days (egg incubation, prepupation and pupation) had to be equal to 0.0017.

Mortality of *C. glabratus* larvae is estimated on the grounds of comparison of the Ist and the IIIrd instar larva abundances (only 2 larvae of the IInd instar were captured in the late autumn 1972). The mean emergence days of these instar larvae are calculated (Fig. 4), and it is assumed that the development time of the IIIrd instar larvae is as much as 1.3 times longer than that of the Ist instar larvae. Thus, applying the equation $N = \frac{\bar{N}T}{\tau}$, the relative abundances of the Ist and the IIIrd instar larvae are calculated (502.0 and 69.3 individuals, respectively) as well as the

instantaneous mortality rate (0.0075). The mortality rate of *C. glabratus* larvae appears to be lower than that of *C. nemoralis* larvae, nevertheless, it is higher than the mortality rate in the period from egg deposition till teneral beetle appearance of *C. glabratus* (Tab. I). Estimating the whole larval development time of *C. glabratus* (including hibernation) as being equal to 250 days, and the appropriate instantaneous mortality rate as the above, this species population density decreases during the larval development so much, that the mortality in the period of egg incubation, prepupation and pupation seems to be close to 0.

Consequently, it seems very probable that both in the case of the spring breeders (*C. nemoralis*) and the autumn breeders (*C. glabratus*), the instantaneous mortality rates of larvae are much higher than those of eggs, prepupae and pupae.

3.2. Beetles

Estimates of population density of beetles — except for teneral ones — are based on number of individuals entering a plot, and their mean time of stay there:

$$\bar{n} = \frac{N_i}{T} \bar{t} \frac{100}{p}$$

where: N_i — number of individuals captured in the outside pitfalls of a plot in a series of trappings, T — number of days the series lasts, \bar{t} — mean individual time of stay inside the plot (in days), p — area of the plot (in m^2). The detailed discussion of this method was presented in an earlier paper (Grüm 1971). The results of the calculations are shown in Table III — it contains only that part of the collected material which is necessary to describe the decrease of the beetle population densities.

Instantaneous mortality rates are calculated for the following periods in the life-cycle of beetles of the spring breeders:

a. From the MED of teneral beetles till the beginning of their first breeding season. This way the mortality rate during the first hibernation is estimated — the estimation being founded on difference in cumulative population density of the teneral beetles developing from the eggs deposited in 1972 (Tab. I), and population density of the same generation in the first decade of May 1973 (Tab. III). In May 1973 the spring breeder populations consisted of individuals originating in the eggs deposited in 1972 as well as in the previous years. However, the individuals originating in the eggs that had been deposited before 1972, were not numerous in May 1973 — this question will be explained later — and therefore could not influence the mortality estimates much.

b. In the first breeding season: the estimates of mortality are founded on difference between population density in the first decade of May (ripe eggs present in ovaries) and population density in the last decade of June [the June estimates were carried out in the period shortly after the occurrence of maximum number of ripe eggs per female (Grüm 1973a)]. The estimates of beetle population density both in May and June are the mean values for 1972 and 1973.

c. From the end of the first breeding season till the beginning of the second breeding season, i.e., during the second hibernation. The mortality estimates are based on difference in numbers of individuals marked and released inside the plots but not recaptured in the year of their

Tab. III. Estimates of beetle population density.

Species	Date	Mean density and standard deviation	Description of the time-moment
<i>C. arcensis</i>	May 7, 1973	9.22 ± 0.97	beginning of the breeding season in 1973
	May 7	10.12 ± 0.71	beginning of the breeding season (mean for 1972 and 1973)
	June 22	2.57 ± 0.23	end of the breeding season (mean for 1972 and 1973)
<i>C. nemoralis</i>	May 7, 1973	4.96 ± 0.49	beginning of the breeding season in 1973
	May 7	4.27 ± 0.30	beginning of the breeding season (mean for 1972 and 1973)
	June 7	1.63 ± 0.12	end of the breeding season (mean for 1972 and 1973)
<i>P. oblongo-punctatus</i>	May 7, 1973	168.1 ± 18.2	beginning of the breeding season in 1973
	May 7	139.5 ± 9.2	beginning of the breeding season (mean for 1972 and 1973)
	June 22	20.5 ± 1.65	end of the breeding season (mean for 1972 and 1973)
<i>C. glabratus</i>	June 27, 1972	3.43	beginning of the first breeding season
	August 22, 1972	1.06 ± 0.12	end of the first breeding season
	June 7, 1973	0.69 ± 0.08	beginning of the second breeding season
	June 22, 1973	0.55 ± 0.07	end of the second breeding season
<i>C. hortensis</i>	July 8, 1972	4.29	beginning of the first breeding season
	Sept. 9, 1972	1.41 ± 0.12	end of the first breeding season
	June 7, 1973	0.62 ± 0.07	beginning of the second breeding season
	June 22, 1973	0.12 ± 0.02	end of the second breeding season
<i>P. niger</i>	July 9, 1972	7.27	beginning of the first breeding season
	Sept. 7, 1972	1.39 ± 0.15	end of the first breeding season
	June 7, 1973	1.13 ± 0.13	beginning of the second breeding season
	June 22, 1973	1.03 ± 0.11	end of the second breeding season

releasing (1972), and numbers of the same individuals recaptured in the next breeding season, i.e., 1973 (Tab. II).

The instantaneous mortality rates of the autumn breeders are calculated for the following periods in the life-cycle of imagines:

a. In the first breeding season. The difference is taken into account between: cumulative population density of the teneral beetles originating in the eggs deposited in 1971 (Tab. III) – those beetles took part in reproduction shortly after hatching in July or August 1972 (Grüm 1973a) – and population density of the same generation at the end of summer or beginning of autumn 1972 (depending on the species involved), i.e., shortly after the peak of mean number of ripe eggs per female. It seems, that percentage of overwintering beetles is rather small at that period of year, and therefore can not influence much the mortality estimates.

b. In the first hibernation. Comparison of the beetle population density at the end of summer or beginning of autumn 1972 to the beetle population density in the first decade of

June 1973 (Tab. III) makes it possible to estimate mortality rate of the same generation during winter period.

c. In the second breeding season. The mortality rate estimation is based on difference in the beetle population densities measured in the first and the third decades of June 1973 (Tab. III). In the third decade of June the overwintered females contained ripe eggs in their ovaries (Grüm 1973a).

The instantaneous mortality rates — shown in Table IV — change greatly in the distinguished periods of the life-cycle. In the first period of the spring breeder life — i.e., the first hibernation — the rates are very low, ranging in limits from 0.0001 to 0.0017. It seems worth-while to point out, that slightly higher values have been calculated on the basis of individual marking. In the autumn 1972 a certain number of marked beetles was left inside the plots: 5 individuals of *C. arcensis* and 16 of *P. oblongopunctatus* as well as 13 beetles of *C. nemoralis* (in between the 7th and the 22nd of September). Till the 7th of May 1973 survived: 2 beetles of *C. arcensis*, 7 of *C. nemoralis* and 10 of *P. oblongopunctatus*. This way calculated rates are as follows: 0.0041, 0.0029 and 0.0024, respectively, for the above mentioned species.

Tab. IV. Instantaneous mortality rates of beetles

Species	Period	Mortality rate
<i>C. arcensis</i>	from the MED of teneral beetles till the beginning of the first breeding season, i.e., the first hibernation	0.0017
	in the first breeding season	0.0298
	from the end of the first breeding season till the second breeding season	0.0054
<i>C. nemoralis</i>	from the MED of teneral beetles till the beginning of the first breeding season, i.e. the first hibernation	0.0001
	in the first breeding season	0.0311
	from the end of the first breeding season till the second breeding season	0.0080
<i>P. oblongopunctatus</i>	from the MED of teneral beetles till the beginning of the first breeding season, i.e. the first hibernation	0.0013
	in the first breeding season	0.0416
	from the end of the first breeding season till the second breeding season	0.0054
<i>C. glabratus</i>	in the first breeding season	0.0209
	from the end of the first to the beginning of the second breeding season	0.0015
	in the second breeding season	0.0151
<i>C. hortensis</i>	in the first breeding season	0.0182
	from the end of the first till the beginning of the second breeding season	0.0030
	in the second breeding season	0.1094
<i>P. niger</i>	in the first breeding season	0.0286
	from the end of the first to the beginning of the second breeding season	0.0007
	in the second breeding season	0.0062

The mortality rates in the breeding season appear to be much higher: from 0.0298 to 0.0416 (Tab. IV). The mortality rates calculated for the second hibernation range from 0.0054 to 0.0080. This means they are rather similar to those in the first hibernation.

The rates calculated for the autumn breeders observe the following pattern. In the first breeding season they are high (from 0.0182 to 0.0286) and similar to those of the reproducing spring breeders (Tab. IV). In the beetle hibernation period the rates are relatively low (from 0.0007 to 0.0030) and close to winter mortality rates of the spring breeders (Tab. IV). In the second breeding season the mortality rates of the autumn breeders seem to be high again (from 0.0062 to 0.1094).

4. SURVIVORSHIP CURVES

Taking into consideration the number of days the distinguished stage in the life-cycle lasts and the appropriate instantaneous mortality rate, the survivorship curves are drawn in terms of percentage of the number of eggs per 100 m² deposited in 1972. The survivorship curves for *C. arcensis*, *C. hortensis*, *P. niger* and *P. oblongopunctatus* in the period from the MED of eggs till the MED of teneral beetles are calculated indirectly — namely an assumption is made that the curves drawn for *C. nemoralis* and *C. glabratus* represent the model curves for the spring and the autumn breeders in this period.

From the data previously described it is concluded that number of days the first three distinguished developmental stages last are as follows in the case of the *C. nemoralis* population: 10 days of egg incubation (this is the result of simple subtraction: number of days between the MED of eggs and that of the first instar larvae minus development time of the 1st instar), 40 days of larval development (the 1st instar — 12 days, the 2nd — 12 days and the 3rd — 16 days), and about 36 days of pupation and prepupation. Taking into regard the appropriate instantaneous mortality rates (0.0017 for incubation, 0.0273 for larval development and 0.0017 for the latter period), the survivorship curve is characterized by the following losses (assuming the entire loss during egg incubation, larval development and both prepupation and pupation is equal to 100%): 2.4% loss in the egg incubation, 94.8% in the larval development, and 2.8% in the last 36 days.

The collected data allow us to estimate roughly number of days the consecutive development stages of *C. glabratus* last. Namely, it has been found that from the MED of eggs till that of the first instar larvae 65 days passed, and from this till that of the 3rd instar larvae 231 days passed. The time-lapse between the MED of the 3rd instar and that of the teneral beetles equalled 57 days. According to Hůrka's (1973) statement that the ratio of number of days of egg incubation to that of the 1st instar larva development in the case of the autumn breeders (including *C. glabratus*) is 1 : 1.7, the calculated egg incubation period of *C. glabratus* had to last 24 days. Thus, the development time of all three larval instars — including winter hibernation — was equal to 255 days (the 1st instar larvae — 41 days). Because the instantaneous mortality rates calculated for the egg incubation, larval development and the period of both prepupation and pupation are equal to 0.0001, 0.0075 and 0.0001, respectively, the entire loss of these stages is approximately distributed as follows: 0.1% in egg incubation, 99.8% in larval development, and the final 0.1% in prepupation and pupation.

It seems, that the survivorship curves of all the six species under study have a few characteristics independent of the species and the development type. Namely, high density decrease of imagines in their breeding season can be observed (Fig. 5). Also, the percentage of individuals

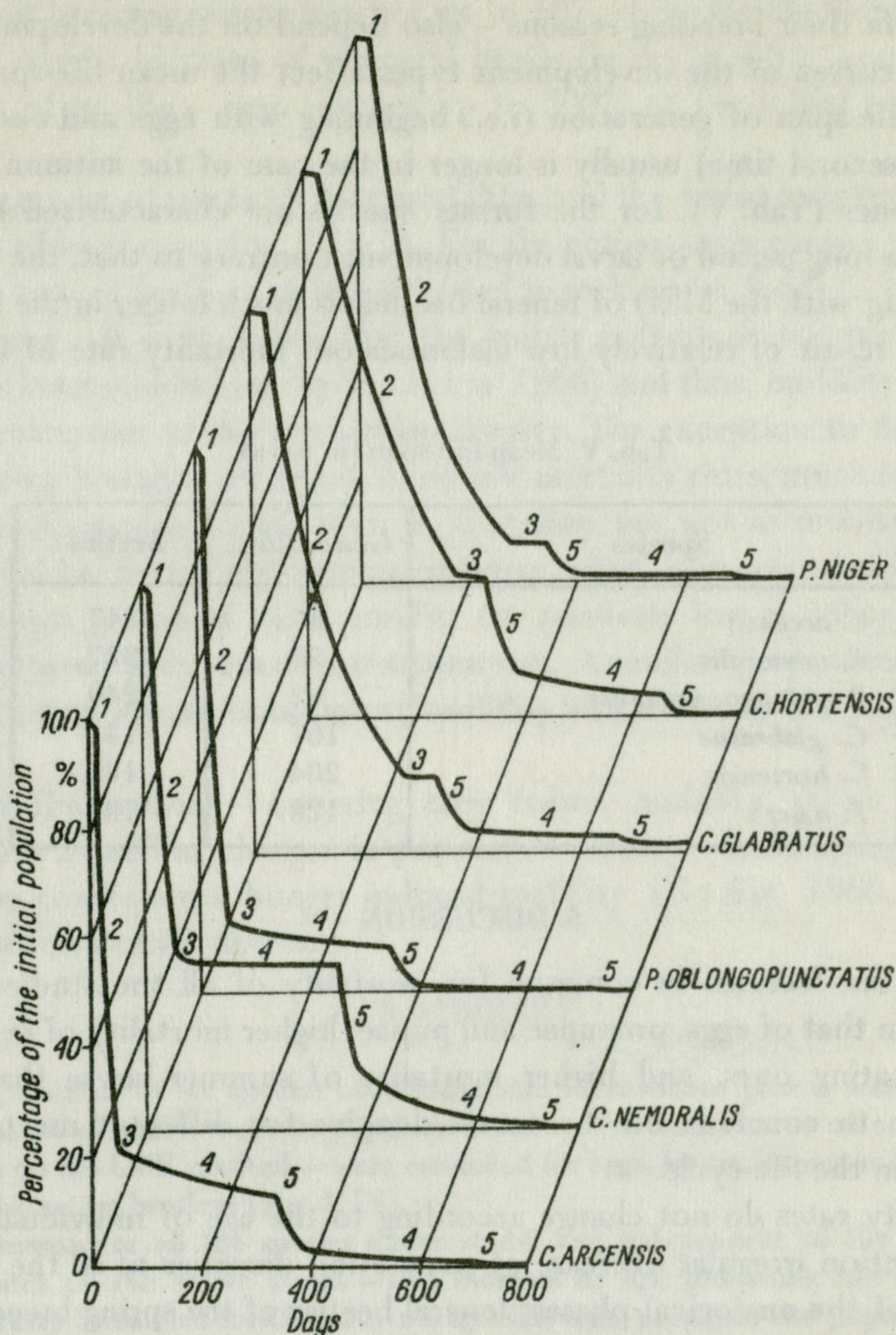


Fig. 5. Survivorship curves

1 – egg incubation, 2 – larval development, 3 – prepupation and pupation, 4 – hibernation of imagines, 5 – breeding season

surviving until the first breeding season varies within similar limits, and independently of the development type: from 8.7 to 30.1% in the case of the spring breeders, and from 7.4 to 26.4% in the case of the autumn breeders. As for the period from the MED of eggs till that of teneral beetles, both in the population of *C. nemoralis* – a representative of the spring breeders – and in that of *C. glabratus* (which represents the autumn breeders), the main decrease of their population densities occurs in the larval development (Fig. 5).

The principal differences between the curves are associated with the development type specificity; populations of the spring breeders – reaching the IIIrd instar larvae after about 50 days from the MED of eggs – are reduced in this period to 13.2–32.9% of the initial population density (eggs). Contrary to that, the autumn breeders have their populations reduced to 7.4–26.5% (the IIIrd instar larvae) after about 280 days from the MED of eggs. Because the imagines of the spring breeders hibernate before attempting at their first breeding season, and – contrary to that – those of the autumn breeders take part in reproduction

immediately after having hatched, the survivorship curves of the imagines – due to relatively high mortality rates in their breeding seasons – also depend on the development type (Fig. 5).

The survivorship curves of the development types affect the mean life-span of the species. Namely, the mean life-span of generation (i.e., beginning with eggs and ending with beetles reproducing for the second time) usually is longer in the case of the autumn breeders than in that of the spring ones (Tab. V), for the former species are characterized by relatively low mortality rates over a long period of larval development. Contrary to that, the mean life-span of beetles (i.e., beginning with the MED of teneral beetles) is much longer in the case of the spring breeders, which is a result of relatively low instantaneous mortality rate of imagines over the long winter period.

Tab. V. Mean life-span (in days)

Species	Generation	Beetles
<i>C. arcensis</i>	85	247
<i>C. nemoralis</i>	150	327
<i>P. oblongopunctatus</i>	62	249
<i>C. glabratus</i>	167	141
<i>C. hortensis</i>	204	103
<i>P. niger</i>	128	103

5. DISCUSSION

On the basis of the features in common for mortality of all the studied species – larval mortality higher than that of eggs, prepupae and pupae, higher mortality of reproducing beetles than that of hibernating ones, and higher mortality of summer larvae than that of winter ones – it is possible to conclude on the causes decisive for different mortality rates in the distinguished stages in the life-cycle.

First, the mortality rates do not change according to the age of individuals. This is evident taking into consideration irregular decrease of population densities of all the species, as well as different mortality of the analogical phases: teneral beetles of the spring breeders, for instance, contrary to that of the autumn breeders, are characterized by relatively low mortality rates.

Secondly, changes in the mortality of the distinguished stages do not seem to depend on the population density of a given stage, because the instantaneous mortality rates do not change regularly, according to the decrease in the density.

Thirdly, influence of weather conditions upon mortality of carabid beetles (Schjøtz-Christensen 1965 and others) does not seem to be directly responsible for different mortality rates of the consecutive stages. For instance, breeding seasons of the spring and the autumn breeders are not simultaneous, nevertheless, the adequate mortality rates of the reproducing beetles are of similar range.

The data collected make it possible to put forward a hypothesis of dependence of mortality of a stage on its activity – measured by body weight increase or egg production of the individual representing the stage – which must be accompanied by seeking for food and moving. This sort of measurement allows us to distinguish between the passive and the active stages. The former consist of incubating eggs, prepupae and pupae, as well as hibernating larvae and beetles. The active stages are represented by non-hibernating larvae and beetles reproducing or increasing in their biomass. The biomass production in the larval development reaches up to 1000–1200% (Grüm 1975). The biomass production of a beetle can be divided into egg production and body weight increase of newly hatched beetles. The egg production (in dry

weight) in the first breeding season reaches up to 50% of the female biomass (Grüm 1973a, 1973b), and the weight increase of a teneral beetle (in dry weight) – occurring mainly in the first three weeks of its life – even reaches up to 500% of the initial body weight (Grüm 1973b).

The passive stages are of relatively low mortality, and the active ones usually (an exception is discussed below) of high mortality (Fig. 5). For the active stages consist of mobile individuals – mobility in the case of beetles can be attributed to seeking for food (Grüm 1966, 1971) or seeking for partners – it is supposed that the mobile individuals are exposed to the predator pressure (as it has been pointed out by Zimka 1966) and thus, mobility plays the rôle of the key-factor in the decrease of the population density. The exception to discuss is, that teneral beetles of the spring breeders are of relatively low mortality rates, much lower than that of the autumn breeders. A possible explanation is, that they are not as mobile and exposed to the predators as teneral beetles of the autumn breeders, which is in accordance with the previously mentioned very short period of their mobility (or relatively low mobility) probably caused by decrease of the autumn daily minimal temperatures. A similar temperature effect is evident in the case of hibernating larvae: ceasation of mobility and relatively low instantaneous mortality rate.

Thus, weather fluctuations – assuming they reduce mobility (Grüm 1959, Briggs 1961 and others) – as well as changes in population density – influencing probability of prey finding and in the consequence hunger induced mobility (Grüm 1966, 1971) – can modify the rate of population density decrease.

6. SUMMARY

Mortality in populations of six species of *Carabus* and *Pterostichus* genera was studied. Instantaneous mortality rates – based on differences in population density (or abundance) of consecutive stages in the life-cycle, as well as on the CMR method – were estimated for eggs, larvae, prepupae and pupae, and both for reproducing and hibernating beetles (Tabs. I, IV).

A feature in common for all the species under study, and independent of the development type, was higher mortality rates of the active stages – i.e., biomass or egg producing like larvae and reproducing beetles – than the rates calculated for the passive stages like eggs, prepupae and pupae, or hibernating beetles and larvae. Thus a hypothesis is put forward, that density decrease of an active stage – the stage consisting of mobile individuals seeking for food or partners – is caused by exposing the mobile individuals to their predator pressure.

On the grounds of the calculated mortality rates, the appropriate survivorship curves were drawn (Fig. 5). The main differences between the curves relied upon the species development type. The spring breeder densities (*C. arcensis*, *C. nemoralis* and *P. oblongopunctatus*) were reduced to 13.2–32.9% of the egg population densities when after 50 days since egg deposition they had reached the IIIrd instar larva. Contrary to that, the autumn breeders (*C. glabratus*, *C. hortensis* and *P. niger*) were reduced to 7.4–26.5% of the initial population density after 280 days since egg deposition, i.e., the day they reached the IIIrd instar larva. In the consequence, different mean life-spans of the species, depending on the development type, were observed. The mean life-span of the spring breeders was usually shorter than that of the autumn ones (Tab. V). On the other hand, the mean life-span of imagines of the spring breeders was longer than that of the autumn breeders (Tab. V), because of hibernation of newly hatched teneral beetles of the former type, and immediate attempting at reproduction of the teneral beetles of the autumn breeders.

7. POLISH SUMMARY (STRESZCZENIE)

Zbadano wskaźniki śmiertelności w populacjach sześciu gatunków z rodzajów *Carabus* i *Pterostichus* zasiedlających siedliska leśne. W oparciu o różnicę w gęstości populacji (lub względnej liczebności), a także i za pomocą metody znakowania, określono wskaźniki śmiertelności jaj, larw, przedpoczwerek i poczwerek oraz imagines w sezonie rozrodczym i zimą (tab. I, IV).

Wspólną i niezależną od typu rozwojowego cechą wszystkich badanych gatunków była wyższa śmiertelność aktywnych stadiów rozwojowych, tj. produkujących jaja, bądź o rosnącym ciężarze ciała – jak larwy i rozmnażające się imagines – niż śmiertelność stadiów pasywnych (nie wykazujących przyrostu ciężaru ciała), takich jak jaja, poczwarki oraz zimujące imagines i larwy. Na tej podstawie wysunięto hipotezę, że intensywna redukcja gęstości populacji stadiów aktywnych – złożonych z osobników poszukujących pożywienia bądź partnera, a więc ruchliwych – jest uzależniona od presji drapieżców.

Korzystając z obliczonych wskaźników śmiertelności, dla każdego gatunku wykreślono przybliżone krzywe przeżywania generacji (fig. 5). Zasadnicze różnice pomiędzy tymi krzywymi są związane z typem rozwojowym gatunku. Gęstość populacji gatunków należących do wiosennego typu rozwojowego (*C. arcensis*, *C. nemoralis* i *P. oblongopunctatus*) była redukowana do 13.2–32.9% gęstości populacji w stadium jaja już po 50 dniach rozwoju, tj. w momencie osiągnięcia przez generację III stadium larwalnego. Natomiast populacje gatunków należących do jesiennego typu rozwojowego (*C. glabratus*, *C. hortensis* i *P. niger*) były redukowane w zbliżonym stopniu (7.4–26.5% gęstości populacji w stadium jaja) dopiero po 280 dniach rozwoju, kiedy to również osiągały etap III stadium larwalnego.

W związku z powyższym średnia długość życia generacji różni się u poszczególnych gatunków: w przypadku gatunków należących do wiosennego typu rozwojowego była ona zwykle krótsza, niż u gatunków reprezentujących typ jesienny (tab. V). Z drugiej strony, średnia długość życia imagines gatunków zaliczanych do wiosennego typu była zawsze dłuższa niż w przypadku reprezentantów typu jesiennego (tab. V), gdyż nowe pokolenie imagines typu wiosennego zimuje przed rozpoczęciem sezonu rozrodczego, a podczas zimowania wskaźnik śmiertelności jest bardzo niski.

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