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AN ATTEMPT TO ESTIMATE PRODUCTION OF A FEW *CARABUS* L. SPECIES (*COL.*, *CARABIDAE*)*

ABSTRACT: Biomass production of four species of *Carabus* was studied. As it appeared, production due to reproduction was an almost constant part (8.7 to 10.8%) of the total production. Production during larval development ranged from 32.7 to 49.7% of production due to growth. Production of a generation per 100 m^2 ranged from 1,017 mg dry weight (*C. nemoralis* Müll). to 1,779 mg dry weight (*C. glabratus* Payk.). A method of approximate estimation of production is presented.

Contents

1. INTRODUCTION

The author's intention was to estimate both production of biomass and the ratio of production due to reproduction to production due to growth, as well as the ratio of production during larval development to production of imagines.

Populations of the four following species were studied: *Carabus arcensis* Hbst., *C. glabratus* Payk., *C. hortensis* L. and *C. nemoralis* Müll. The field investigations were carried out from the 27th of April 1972 until the 30th of August 1973 in two habitats 50 meters apart from one another, and located in the East part of the Kampinos Forest (several kilometers north-west from Warsaw). First of the habitats – designated with the *PQ* symbol – was located in an

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approximately 4 ha rectangular area. In the central part of it a *Pino-Quercetum* association prevailed, and along the longer sides of the rectangle a *Carici elongatae-Alnetum* association was present – being under water from early spring until late autumn. The other habitat – designated with the *TC* symbol – was an islet of 0.15 ha in area covered by an association of *Tilio-Carpinetum*, and completely surrounded by the *Carici elongatae-Alnetum*.

Separate estimates of production in each of the habitats were not the purpose of the study, therefore the entire material sampled has been elaborated in total. Thus, the estimated production of each of the species is the mean value calculated for the both habitats, except for *C. arcensis* – this species inhabited the *PQ* habitat solely, i.e., in the *TC* one, only a few individuals were captured in pitfalls.

2. PARAMETERS

The following parameters which are necessary to estimate production have been previously calculated for the species under study:

a. Egg production per 100 m^2 in the breeding season in 1972 (Tab. I). Both the methods and results were published (G r ü m 1973a).

Tab. I. Egg production in 1972

Species	Number of eggs laid per 100 m^2	Mean dry weight of egg (mg)	Egg production in mg dry weight per 100 m^2
C. arcensis	55.72	2.5	139.3
C. glabratus	29.00	6.6	191.4
C. hortensis	16.01	6.4	102.5
C. nemoralis	16.60	6.0	99.6

b. Duration of separate stages in the life-cycle and the appropriate instantaneous mortality rates. Both the methods and results are given in a separate publication (G r ü m 1975a). Table II shows the results. Duration of the breeding seasons shown there is slightly shorter than in reality, in order to account for adjusting the durations to the periods of acting of the mortality rates appropriate for the breeding seasons. Apart from that, it seems probable that the mortality rates of teneral beetles of *C. arcensis* and *C. nemoralis* were slightly underestimated (G r ü m 1975a).

c. Growth rate of teneral beetles (G r ü m 1973b) and that of larvae of *C. arcensis*, *C. glabratus* and *C. nemoralis* (G r ü m 1975b).

Mean body weight of the Ist instar larvae calculated on the basis of weighing of the larvae captured in pitfalls would be undoubtedly inadequate as a measure of the body weight of the newly hatched Ist instar larvae, because of a time-lapse between hatching and capturing. An approximate body weight of the newly hatched Ist instar larvae was thus calculated on the basis of the weight of the lightest individuals among those captured in pitfalls. An approximate body weight of the newly hatched Ist instar larvae of *C. hortensis* – in the absence of data – was estimated indirectly, i.e., on the assumption that the ratio of the larva weight to the known mean weight of egg of this species was similar to the same ratio calculated for *C. glabratus*. The

Tab. II. Changes of the instantaneous mortality rate (IMR) in the life-cycle

Period	Species							
	C. arcensis		*C. glabratus*		*C. hortensis*		*C. nemoralis*	
	days	IMR	days	IMR	days	IMR	days	IMR
Egg incubation	0 9	0.0020	0 24	0.0001	0 23	0.0001	0 10	0.0017
Larval development	10 46	0.0408	25 279	0.0075	24 278	0.0052	11 50	0.0273
Prepupation and pupation	47 78	0.0020	280 333	0.0001	279 324	0.0001	51 83	0.0017
Beetle gaining weight	79 97	0.0017	334 353	0.0209	325 344	0.0182	84 103	0.0001
Beetle hibernation	98 339	0.0017					104 356	0.0001
First breeding season	340 385	0.0298	354 392	0.0209	345 388	0.0182	357 387	0.0311
Beetle hibernation	386 704	0.0054	393 681	0.0015	389 661	0.0030	388 721	0.0080
Second breeding season	705 750	0.0298	682 696	0.0151	662 676	0.1094	722 752	0.0311
Beetle hibernation			697 986	0.0015	677 946	0.0030		
End of the beetle life	> 751	0.0054	> 987	0.0151	> 947	0.1094	> 753	0.0080

analogy to *C. glabratus* was taken into account for the mean weight of the egg of *C. hortensis* was the less different from that of *C. glabratus*. Table III contains the data on body weight of the newly hatched Ist instar larvae .

Tab. III. Body weight and body weight increase (in mg dry weight) of larvae and teneral beetles

Species	Larvae			Beetles		
	early Ist instar	IIIrd instar	increase	teneral	adult	increase
C. arcensis	2.0	19.1	17.1	19.1*	80.7	71.6
C. glabratus	3.3	39.9	36.6	39.9*	285.2	245.3
C. hortensis	3.2*	28.9*	25.7	28.9*	194.2	165.3
C. nemoralis	3.5	29.5	26.0	29.5*	166.0	136.5

*Approximate value.

Mean body weight of the newly hatched teneral beetles was extrapolated from the data on body weight of the lightest teneral beetles captured in pitfalls and body weight of the fully grown adult beetles; namely, it was assumed that the lightest teneral beetles were captured after 3 days from their hatching, and the rate of their body weight increase was initially exponential. The data on body weight of teneral beetles and fully grown ones, as well as those on duration of body weight increase period were calculated previously (G r ü m 1973b). The approximate body weight of the newly hatched beetles appeared very similar to the mean body weight of the IIIrd instar larvae captured in pitfalls (Fig. 1). Thus, to simplify the production calculations, it was assumed that body weight of the newly hatched teneral beetles equalled body weight of the IIIrd instar larvae (Tab. III).

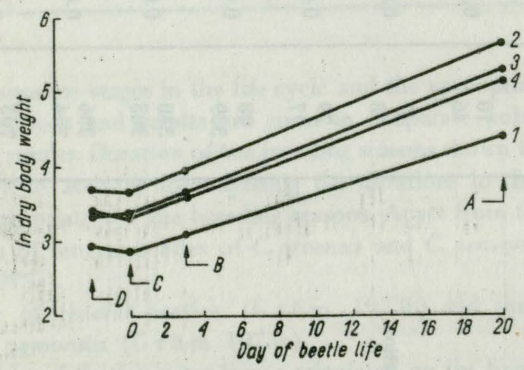

Fig. 1. Body weight increase of newly hatched beetles

1 – *C. arcensis*, *2* – *C. glabratus*, *3* – *C. hortensis*, *4* – *C. nemoralis*, *A* – completion of beetle body weight increase, *B* – first capture, *C* – hatching (extrapolated value), *D* – IIIrd instar

Both production of exuviae and seasonal changes in body weight of adult beetles were not taken into consideration. This caused – of minor importance as it seems – underestimation of the biomass production.

3. PRODUCTION

Having estimated the parameters previously described it was possible to calculate both production of the species generations originating in the eggs laid in 1972, and the components of the production according to the division introduced by Petrusewicz and Macfadyen (1970):

a. Production due to reproduction (P_r), i.e., egg biomass per 100 m^2 deposited in the 1972 breeding season.

b. Production due to body growth (P_g), i.e., production starting with the Ist instar larva growth. P_g is estimated by means of biomass elimination (Tab. IV).

Two components of production due to growth (P_g) are distinguished now:

ba. Larval growth production (P_{gl}), i.e., the sum of biomass eliminated in the period beginning with the Ist instar larva hatching and ending with the teneral beetle hatching, plus biomass of the newly hatched teneral beetles.

bb. Beetle growth production (P_{gi}), i.e., biomass production due to body weight increase of beetles after they have hatched.

The results obtained show that production of separate species differs (Tab. V): ratio of the highest (*C. glabratus*) to the lowest (*C. hortensis*) production is equal to 1.74 : 1. The components of the production seem to be relatively stable. For instance, the percentage of P_r in P ranges from 8.7 to 10.8%, and that of P_{gl} in P_g changes from 32.7 to 49.7%.

The survivorship curves of the *Carabus* species – and probably those of *Pterostichus* also – have some features in common and independent of the development type (Grüm 1975a). Namely, the mortality rates are low in those periods in the life-cycle in which there is no body weight increase. Contrary to that, high mortality rates accompany the periods of individual body weight increase or egg production. Thus, having at the disposal both the number of eggs deposited in the breeding season and the number of fully grown adult beetles derived from these eggs, it is possible to draw an approximate survivorship curve covering the entire period of individual body weight increase.

The curve of individual body weight increase seems to be of relatively constant shape (Grüm 1975b): body weight of the IIIrd instar larvae ranges from 14 to 24% of the body weight of the fully grown adult beetles.

Taking into regard that both the survivorship and individual growth curves are of relatively constant pattern, and that the percentage of P_r in P is constant, let us consider a method of estimation of production – its value depends on stability of the parameters – based on the following three changeable parameters. Two of them describe mortality throughout the period of individual body weight increase: egg population density and adult beetle population density. The third one – the product of adult beetle population density and their mean body weight – determines biomass per unit of area after completion of the individual body growth.

Evidently, the ratio of the total production (P) to the biomass of the adult beetle population (B_a) is a changeable value depending on mortality in the period until the individual body growth completion. The mortality is defined by the ratio of the egg population density (n_e) to the adult beetle population density (n_a).

If n_e to n_a equals $+\infty$, i e., no individuals have survived until growth completion, then P to B_a equals $+\infty$. On the other hand, if n_e to n_a equals 1, then P to B_a equals 1, for all the individuals have survived until the end of the body weight increase period.

Tab. IV. Biomass elimination in the life-cycle (in mg dry body weight per 100 m^2)

C. arcensis				*C. glabratus*			
day	No. of individuals present	No. of individuals eliminated	biomass elimination	day	No. of individuals present	No. of individuals eliminated	biomass elimination
0	55.72	–	–	0	29.00	–	–
9	54.73	0.99	2.47	24	28.91	0.09	0.59
46	12.09	42.64	449.85	279	4.27	24.64	532.22
78	11.29	0.80	15.28	333	4.24	0.03	1.20
97	10.97	0.32	17.57	353	2.97	1.27	206.44
339	7.27	3.70	298.59	392	1.31	1.66	473.43
385	1.84	5.43	438.20	681	0.85	0.46	131.19
704	0.33	1.51	121.86	696	0.68	0.17	48.48
750	0.08	0.25	20.17	986	0.44	0.24	68.45
> 750	0.00	0.08	6.46	> 986	0.00	0.44	125.49

C. hortensis				*C. nemoralis*			
day	No. of individuals present	No. of individuals eliminated	biomass elimination	day	No. of individuals present	No. of individuals eliminated	biomass elimination
0	16.01	–	–	0	16.60	–	–
23	15.97	0.04	0.26	10	16.32	0.28	1.68
278	4.24	11.73	188.27	50	5.47	10.85	179.02
324	4.22	0.02	0.58	83	5.15	0.32	9.44
344	3.08	1.14	127.17	103	5.14	0.01	0.98
388	1.38	1.70	330.14	356	5.01	0.13	21.58
661	0.61	0.77	149.53	387	1.91	3.10	514.60
676	0.12	0.49	95.16	721	0.13	1.78	295.48
946	0.05	0.07	13.59	752	0.05	0.08	13.28
> 946	0.00	0.05	9.71	> 752	0.00	0.05	8.30

Tab. V. Total biomass production (P) and its elements, calculated in mg dry weight per 100 m^2 per generation

For explanation of the symbols see the text

Species	P_{gl}	P_{gi}	$P_g = P_{gl} + P_{gi}$	$P = P_r + P_g$
C. arcensis	683.2	687.2	1,370.4	1,509.7
C. glabratus	703.2	884.3	1,587.5	1,778.9
C. hortensis	311.1	603.3	914.4	1,016.9
C. nemoralis	342.1	702.3	1,044.4	1,144.0

Thus, $1 \leqslant \frac{n_e}{n_a} \leqslant +\infty$, and $1 \leqslant \frac{P}{B_a} \leqslant +\infty$

Having compared the data on the ratio of $n_e : n_a$ and that of $P : B_a$ acquired for *C. arcensis*, *C. glabratus*, *C. hortensis* and *C. nemoralis* a relation between both the variable values is calculated (Fig. 2):

$$\frac{P}{B_a} = 0.93 + 0,41 \ln \frac{n_e}{n_a}$$

Thus, production

$$P = B_a \left(0.93 + 0.41 \ln \frac{n_e}{n_a}\right).$$

It is worth-while to mention that $P : B_a$ is an analogical index to $P\ \bar{B}$, i.e., to the biomass turnover. However, $\bar{B}$ – calculated for all the stages in the life-cycle – equals 15 to 50% of B_a. Mean biomass of beetles in the breeding season is more closely related to the B_a (being equal to 41–72% of B_a).

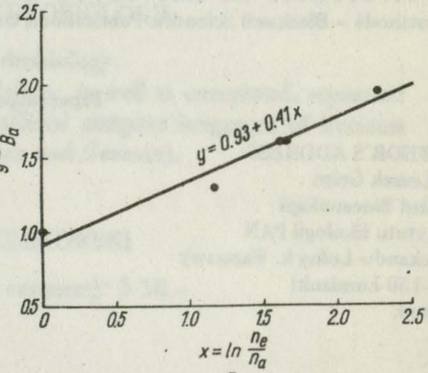

Fig. 2. Relation between $\frac{P}{B_a}$ (ratio of production to biomass of beetles having completed their growth) and $\frac{n_e}{n_a}$ (ratio of egg number to number of the descendant beetles)

4. SUMMARY

On the basis of known parameters – i.e., number of eggs per 100 m^2 deposited in the breeding season, a survivorship curve and an individual body weight increase curve – production of four *Carabus* species has been estimated (Tab. V).

Production due to reproduction (P_r) seems to be a stable part of the total production (P), ranging from 8.7 to 10.8%. Production during larval development (P_{gl}) looks like a more variable part – from 32.7 to 49.7% – of production due to growth (P_g).

The relation between the ratio of production (P) to the biomass of individuals having completed their growth (B_a) and the ratio of number of eggs (n_e) to number of the descendant beetles (n_a) has been found (Fig. 2).

5. POLISH SUMMARY (STRESZCZENIE)

Znając liczbę jaj złożonych w sezonie rozrodczym (w przeliczeniu na 100 m^2) oraz odpowiednie krzywe przeżywania i wzrostu ciężaru osobnika, obliczono produkcję biomasy czterech gatunków z rodzaju *Carabus* (tab. V).

Produkcja jaj (P_r) stanowi – jak się wydaje – mało zmienną część produkcji całkowitej (P), waha się bowiem od 8.7 do 10.8% wartości P. Produkcja podczas rozwoju larwalnego (P_{gl}) jest nieco bardziej zmienna, gdyż stanowi od 32.7 do 49.7% produkcji wynikającej z wzrostu (P_g).

Znaleziono relację między stosunkiem produkcji (P) do biomasy osobników, które zakończyły wzrost (B_a), a stosunkiem liczby złożonych jaj (n_e) do liczby potomnych imagines w momencie zakończenia wzrostu osobniczego (n_a) (fig. 2).

6. REFERENCES

1. Grüm L. 1973a – Egg production of some *Carabidae* species – Bull. Acad. pol. Sci. Cl. II. Sér. Sci. biol. 21: 261–268.
2. Grüm L. 1973b – Weight increase of newly hatched carabid-beetles – Bull. Acad. pol. Sci. Cl. II. Sér. Sci. biol. 21: 499–503.
3. Grüm L. 1975a – Mortality patterns in carabid populations – Ekol. pol. 23: 649–665.
4. Grüm L. 1975b – Growth rate of the *Carabus* L. larvae (*Col.*, *Carabidae*) – Ekol. pol. 23: 667–671.
5. Petrusewicz K., Macfadyen A. 1970 – Productivity of terrestrial animals. Principles and methods – Blackwell Scientific Publications, Oxford-Edinburgh, VII + 190 pp.

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