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THE INFLUENCE OF BIOLOGICALLY CONDITIONED MEDIA ON THE GROWTH OF A MIXED POPULATION OF *PARAMECIUM CAUDATUM* AND *P. AURELIA*

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(With six Figures in the Text.)

I. INTRODUCTION.

THE displacing of one species by another is apparently connected with the advantages belonging to one of the competitors. In other terms one of them is relatively better adapted to the habitat. The problem of relative adaptation has been recently analysed theoretically by Fisher (4), but in spite of its general interest it has hitherto been very insufficiently investigated on concrete biological examples.

The present paper is an account of the investigation on relative adaptation in two species of Infusoria—*Paramecium caudatum* and *P. aurelia*—under different conditions and at different stages of population growth. The case of two similar species simplifies the analysis of certain general regularities of competition in comparison with the study of similar races belonging to the same species.

Certain interesting observations showing the dependence of the relative adaptation of two species of animals on environmental conditions have recently appeared in ecological literature. For instance, Beauchamp and Ulliyott (3) have shown that when two species of *Planaria* in the English Lake District occur in competition with one another, temperature is the factor which governs the relative success and efficiency of the two species. Timoféeff-Ressovsky (9), dealing with the two species of fruit-fly *Drosophila*, has arrived at the same conclusions. We have studied in this paper the action of biologically conditioned media, containing waste products of the organisms that have lived in them before.

We had to deal with the influence of homotypic and heterotypic conditioning (produced by organisms of the same and of a different species) on the growth of a mixed population. As Woodruff (10) showed in his classical paper, heterotypic conditioning in certain cases has much less influence on the rate of reproduction of Infusoria than homotypic conditioning. In the papers which have appeared since, the question of species specificity of the conditioning has not attracted the attention it deserves—as Allee (1) has

pointed out in his recent review. This author has summarised the literature dealing with this subject (1, 2), and there is no need to repeat it here.

II. METHODS.

Our investigations were carried out in the laboratory. The conditions of the experiments were, however, somewhat complicated, closely approaching those of nature. The nutritive medium was prepared in the following manner: to 500 c.c. of the Osterhout salt solution¹ 2.5 gm. of hay were added, boiled for 30 min., filtered and sterilised. A pure culture of the bacterium *Bacillus proteus* was inoculated and the medium was divided into two parts: one of them being populated by a pure culture of *Paramecium caudatum*, and the other by *P. aurelia*. After the cessation of population growth in both cultures and on their approaching "saturating levels" (about the 11th day at 26° C.), the liquid was carefully freed from Paramecia by filtration, and served as a "biologically conditioned medium" for our experiments. One of these media contained the waste products of *P. caudatum*, and the other those of *P. aurelia*. Into 100 c.c. of such a "biologically conditioned medium" a determined quantity of yeast cells, *Saccharomyces exiguus*, taken up by a platinum loop from the solid medium, was introduced for the nutrition of the Paramecia.

10 c.c. of the liquid were poured into each test-tube and stopped by a cotton-wool plug. On the medium of *Paramecium caudatum* as well as on that of *P. aurelia* three groups of experiments were arranged: (1) the growth of *P. caudatum* in pure culture (initial population 25 individuals per 10 c.c.); (2) the growth of *P. aurelia* in pure culture (inoculation=25); and (3) the growth of a mixed population of *P. caudatum* and *P. aurelia* (inoculation=25+25). The experiments were made in a thermostat at 26° C.

There are two phases in the changes of the population under such conditions: (1) competition between the two species for the utilisation of a certain limited amount of the nutritive substances introduced at the beginning of the experiment. This stage has already been analysed by Gause on yeast cells (6) and on several Protozoa (7, 8). But after the cessation of growth, stage (2) begins: that is the dying out of the population. The investigation of the dynamics of this process has shed some light on certain features of the comparative adaptability of the species studied.

III. THE INFLUENCE OF BIOLOGICALLY CONDITIONED MEDIA ON COMPETITION FOR COMMON FOOD BETWEEN THE TWO SPECIES.

Table I represents the changes of density in the population per 0.5 c.c. (our counts were usually made on about 0.1 c.c. and then calculated for 0.5 c.c.). Each figure showing the number of individuals represents the mean

¹ NaCl 2.35 gm.; MgCl₂ 0.184 gm.; MgSO₄ 0.089 gm.; KCl 0.050 gm.; CaCl₂ 0.027 gm.; redistilled water up to 100 c.c. This stock solution was diluted by redistilled water 225 times its volume.

value for three cultures. In order to pass from the numbers of individuals to the biomasses (volumes) of our species it is sufficient to multiply the numbers of individuals of the smaller *P. aurelia* by 0.39 (see Gause, (8)).

Table I. *Changes in the density of population*
(numbers of individuals per 0.5 c.c.).

Days	Medium of <i>P. caudatum</i>				Medium of <i>P. aurelia</i>			
	<i>P. c.</i>	<i>P. a.</i>	<i>P. c./P. a.</i>		<i>P. c.</i>	<i>P. a.</i>	<i>P. c./P. a.</i>	
1	3.5	5.5	2.5	4	4	3.5	5.7	4.3
2	28	42	18	48	14.6	24	14.6	41.5
3	70	56	36	80	30.5	66	29	37.4
4	114	228	64	82	61.5	88	59	84
5	132	144	56	82	73.4	108	61.3	93.5
6	130	182	50	184	76	150	61.3	78.7
7	136	222	82	120	86.7	110	61.5	105
8	151.5	220	77	163	87.4	175	60.7	104
9	—	—	—	—	—	—	—	—
10	152	192	78	170	82.6	154	37.4	108
11	86	230	68	124	72	162	38.7	96
12	146	198	62	132	64	126	52	78
13	98	182	28	100	57.5	116	13.3	76
14	50	116	18	134	17.3	166	21.3	88.4
15	38	120	10	134	10	144	4	69.4
16	8	54	2	82	4	108	1	44.6
17	—	42	0	90	—	96	0	68.7
18	—	26	0	16	—	30	0	20
19	—	28	0	14	—	40	0	13.3
20	—	44	0	10	—	16	0	8
21	—	30	0	6	—	18	0	12
22	—	30	0	6	—	14	0	14.6
27	—	52	—	—	—	10	0	12
28	—	56	—	—	—	14	0	12
29	—	28	—	—	—	4	0	3
30	—	26	—	—	—	2	0	5
31	—	20	—	—	—	—	0	6
32	—	10	—	—	—	—	0	9.3
33	—	6	—	—	—	—	0	4
34	—	—	—	—	—	—	0	1

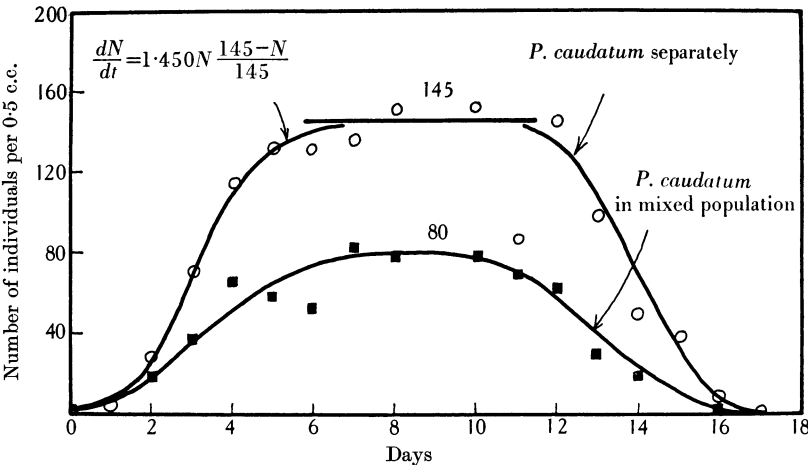


Fig. 1. The growth of *P. caudatum* in pure and mixed populations (medium of *P. caudatum*).

Figs. 1, 2, 3 and 4 show graphically the changes in the populations. One can see that the first stage—growth of the populations—is generally completed

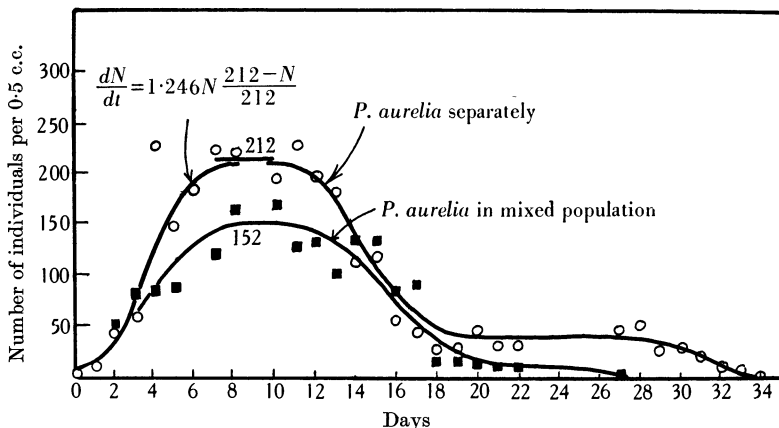


Fig. 2. The growth of *P. aurelia* in pure and mixed populations (medium of *P. caudatum*).

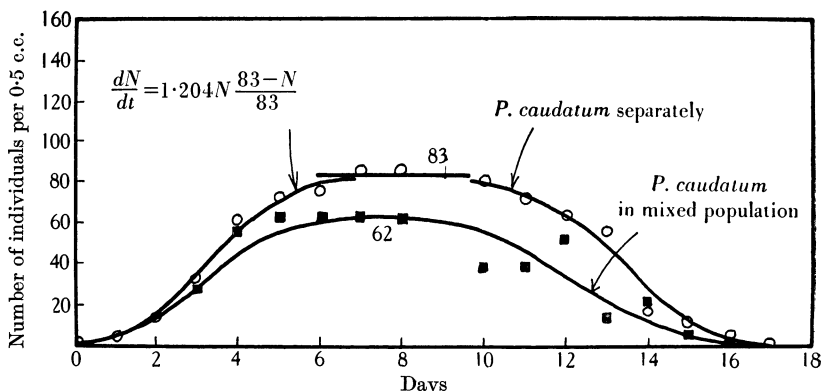


Fig. 3. The growth of *P. caudatum* in pure and mixed populations (medium of *P. aurelia*).

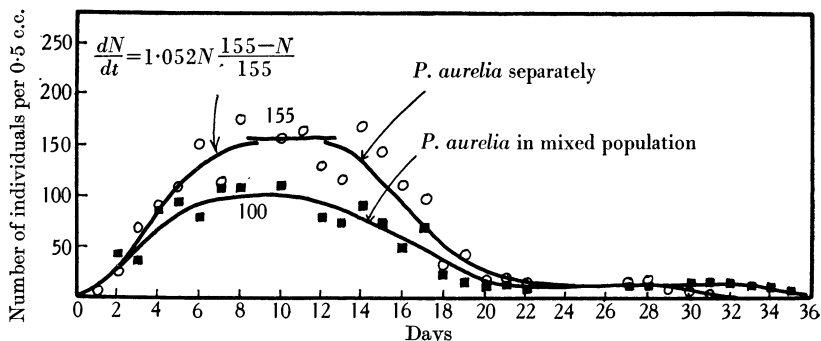


Fig. 4. The growth of *P. aurelia* in pure and mixed populations (medium of *P. aurelia*).

on the seventh day. The maximal level attained remains invariable up to about the tenth day, and decline of the population only begins later on.

Turning our attention to the first stage we may first of all consider the levels of the saturating populations under different conditions (Table II). It is evident that the medium of *P. aurelia* is less favourable for both species. The levels of population of *P. caudatum* (in pure and in mixed cultures) here are, correspondingly, 57·3 and 77·5 per cent., and of *P. aurelia* 73·1 and 65·8 per cent. From the relation between the levels of population of the same species in pure and in mixed culture it is possible to evaluate the degree of the depression of this species due to the other or, in other terms, its energy of competition under given conditions. As Table II shows, *P. caudatum* in a mixed culture on a “homotypic” medium attains 55·2 per cent. of the control, whereas on a “heterotypic” it attains 74·7 per cent. For *P. aurelia* correspondingly we find 64·5 and 71·6 per cent. Therefore our species on a homotypically conditioned medium “of their own” kind appear to be weaker in competition and are more strongly depressed in the struggle for existence.

Table II. *Levels of saturating populations under different conditions (K).*
(Numbers of individuals per 0·5 c.c.)

	In the pure culture (a)	In the mixed culture (b)	(b) as % of (a)
I. Medium of <i>P. caudatum</i>			
(1) <i>P. caudatum</i>	145	80	55·2
(2) <i>P. aurelia</i>	212	152	71·6
II. Medium of <i>P. aurelia</i>			
(1) <i>P. caudatum</i>	83	62	74·7
(2) <i>P. aurelia</i>	155	100	64·5

The latter question deserved further analysis. We therefore passed on from the numbers of individuals to their biomasses (as indicated above), and the calculated characteristics of population growth are given in Table III. Here we find the levels of saturating populations expressed in units of biomass (*K*) as well as the coefficients of multiplication (*b*). These coefficients characterise the rate of potential geometric increase of the population in the absence of any limitation as to the means of subsistence (conditions approximately fulfilled at the beginning of growth). They show an increase per unit of biomass per day; and a description of the method of calculation of these coefficients may be found in (5) and (6).

Table III. *Characteristics of the growth of populations expressed in units of biomass* (*P. caudatum* = 1, *P. aurelia* = 0·39).

	<i>b</i>	<i>K</i>	Coefficients of the struggle for existence
I. Medium of <i>P. caudatum</i>			
(1) <i>P. caudatum</i> separately	1·450	145	$\alpha = 2·12$ (<i>P. a.</i> \rightarrow <i>P. c.</i>)
(2) <i>P. aurelia</i> separately	0·486	83	$\beta = 0·11$ (<i>P. c.</i> \rightarrow <i>P. a.</i>)
II. Medium of <i>P. aurelia</i>			
(1) <i>P. caudatum</i> separately	1·204	83	$\alpha = 0·63$ (<i>P. a.</i> \rightarrow <i>P. c.</i>)
(2) <i>P. aurelia</i> separately	0·411	60	$\beta = 0·20$ (<i>P. c.</i> \rightarrow <i>P. a.</i>)

Comparing the superiority of one species over another under different conditions, we note that *in coefficients of geometric increase P. caudatum* exceeds

P. aurelia on the medium "of its own" 2.98 times, and on the "strange" medium 2.93; in maximal biomasses correspondingly 1.75 and 1.38. The superiority of *P. caudatum* over *P. aurelia* is therefore more clearly apparent on homotypic (in this case generally less toxic) medium. In spite of this *P. caudatum* in competition with *P. aurelia* is relatively more depressed just on "its own" medium. We may thus see that in the complicated situation of these experiments the superiority of one species over another in competition does not simply reflect the properties of these species taken independently, but that it essentially depends on the processes of their interaction.

To clarify this point we can calculate the coefficients of the struggle for existence from the equation

$$\left. \begin{aligned} \frac{dN_1}{dt} &= b_1 N_1 \frac{K_1 - N_1 - \alpha N_2}{K_1} \\ \frac{dN_2}{dt} &= b_2 N_2 \frac{K_2 - N_2 - \beta N_1}{K_2} \end{aligned} \right\}.$$

It has been pointed out by Gause (6) that the coefficient of the struggle for existence α measures the degree of decrease of the unused opportunity for growth of the first species by a unit of biomass of another species (N_2) in relation to the action of its own unit of biomass (N_1). If, for instance, α is equal to 2, it means that every individual (in case of an equality of biomasses) of the second species occupies in the microcosm the place of two individuals of the first species.

The values of the coefficients of the struggle for existence (Table III) show clearly that the superiority of *P. caudatum* over *P. aurelia* in the coefficient of geometric increase on a "homotypic" medium is entirely absorbed by a strong inhibitory action of *P. aurelia* on *P. caudatum* ($\alpha = 2.12$), and in this way results in a depression of the latter species.

We can note that under other conditions of cultivation (8) *P. aurelia* possesses a larger coefficient of geometric increase than *P. caudatum*¹. It has been shown by Gause (7, 8) that, if the food resources of the microcosm are maintained at a certain level and if the density of population fluctuates (rarefaction and subsequent growth up to a saturating level), the species possessing a greater coefficient of multiplication drives its competitor entirely out of the microcosm. Since under some conditions *P. aurelia* possesses a larger coefficient of increase, whereas under others *P. caudatum* has the advantage, it is evident that the ecological situation may completely reverse the direction of the change in the mixed population.

¹ This takes place in media containing pathogenic bacteria, *Bacillus pyocyaneus*, and is apparently connected with the resistance of *P. aurelia* to an accumulation of their waste products (see section IV).

IV. THE INFLUENCE OF BIOLOGICALLY CONDITIONED MEDIA
ON THE DECLINE OF POPULATIONS.

Figs. 1, 2, 3 and 4 represent also the dying out of population. For the analysis of this process we have taken the level of the saturating population

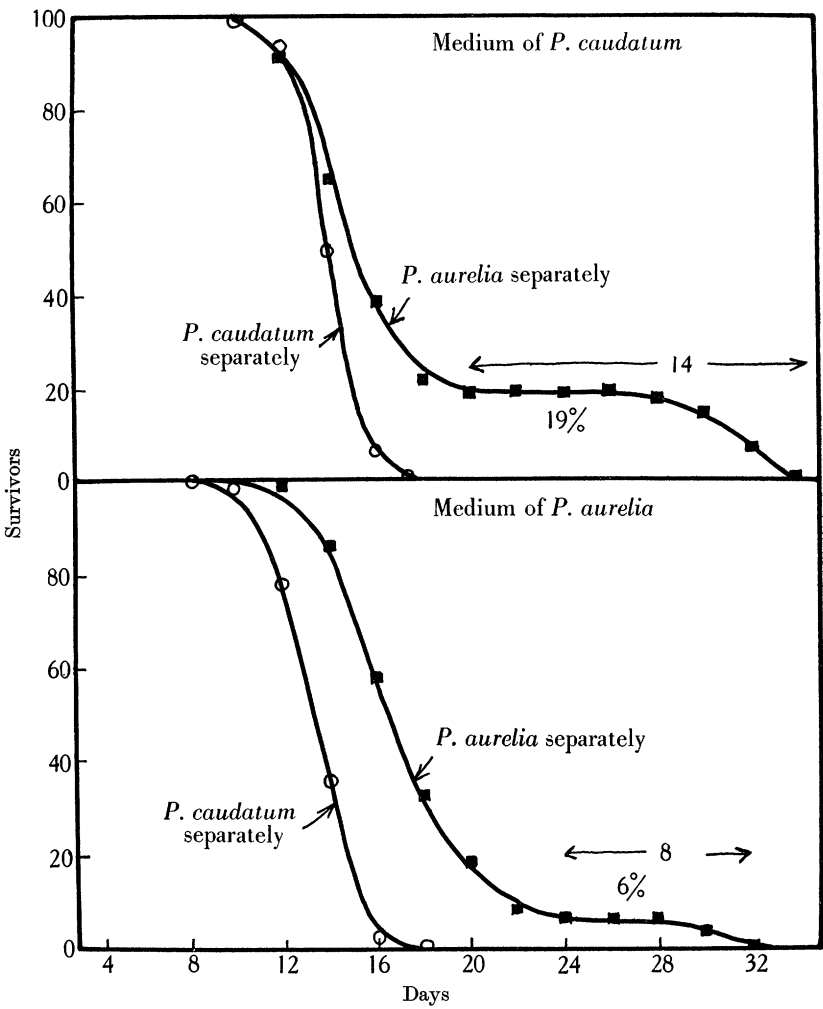


Fig. 5. The relative curves of decline of *P. caudatum* and *P. aurelia* in pure populations.

for 100 in all the cases, and the corresponding relative curves of decline may be found in Figs. 5 and 6.

The analysis of the curves of decline shows the existence of an essential difference between *P. caudatum* and *P. aurelia*. The population of *P. caudatum* dies out rapidly and disappears entirely on the eighteenth day. The rate of

the decline varies of course under different conditions, but these differences are small. Another state of affairs is found in *P. aurelia*. When about 90 per cent. of the population has already perished, the remainder (the experiments were made with pure cultures!) adapt themselves to the rather unfavourable

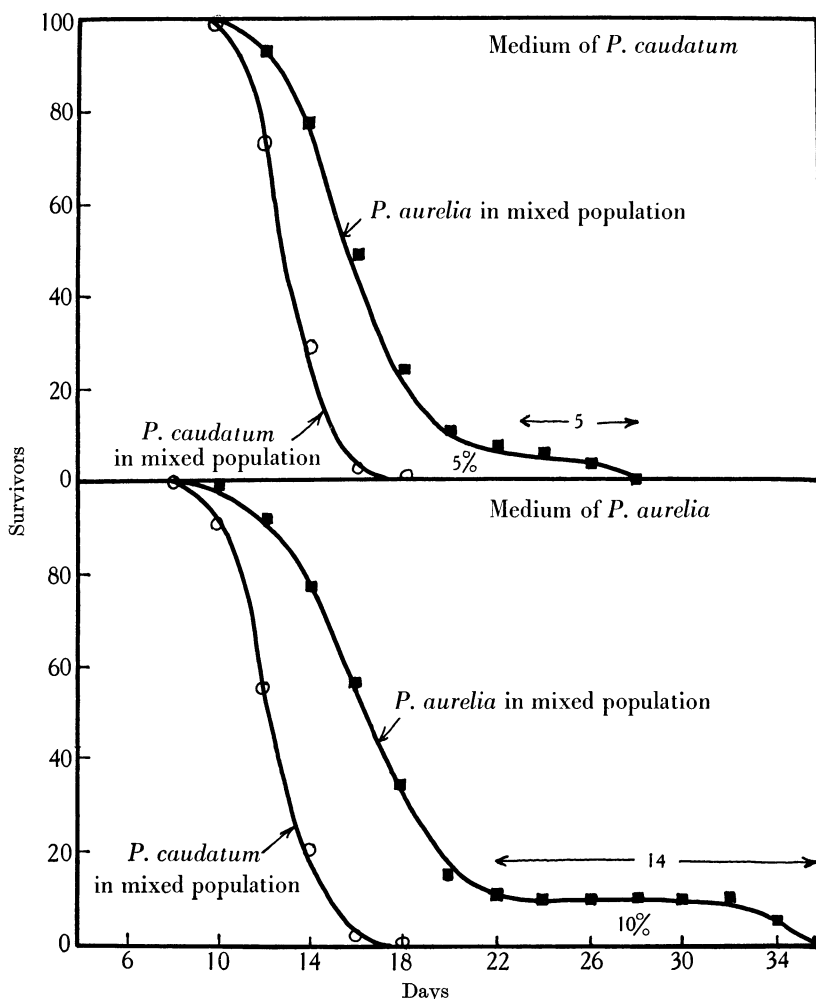


Fig. 6. The relative curves of decline of *P. caudatum* and *P. aurelia* in mixed populations.

conditions and continue to live for a certain time. Later there appears a second cycle of decline sharply separated from the first. The second cycle of decline in *P. aurelia* presents an extraordinary sensitiveness to the homotypic and heterotypic conditioning of the medium:

(1) *P. aurelia* in pure culture on a "homotypic" medium possess a relatively lower level of the second cycle than on a "heterotypic" one (6 per cent.

as compared to 19 per cent., Fig. 5), and it is of shorter duration (8 days instead of 14). The level is here taken in a relative form and is apparently not connected with the lower absolute values of growth on the *P. aurelia* medium. It seems that here the waste products of the species itself are more toxic than those of the other species.

(2) If *P. aurelia* grows on the unfavourable "homotypic" medium, but in presence of *P. caudatum*, the second cycle of decline of *P. aurelia* appears to be more powerful than in a pure culture on the same medium. (The level 10 per cent. as compared to 6 per cent., and the duration of 14 days as compared to 8.) This observation demonstrates directly the weaker toxicity of the heterotypic conditioning for *P. aurelia*.

V. CONCLUSION.

Returning to the problem of the relative adaptation of two species at different stages of population growth we can conclude that *P. caudatum* under the conditions of our experiments has an advantage over *P. aurelia* in the coefficients of geometric increase, whilst *P. aurelia* surpasses *P. caudatum* in its resistance to waste products. (This finds its expression in the values of the coefficients of the struggle for existence and in the presence of two cycles in the dying out of the population.) Therefore, if the decisive factor of competition is a rapid utilisation of the food resources, *P. caudatum* has an advantage over *P. aurelia*; but if the resistance to waste products is the essential point, then *P. aurelia* will take the place of *P. caudatum*.

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