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Reproductive strategies of two similar *Daphnia* species

BARBARA E. TAYLOR and WILFRIED GABRIEL

With 2 figures and 2 tables in the text

Introduction

Cladocerans, like many other invertebrates, continue to grow after beginning to reproduce, and their reproductive capability increases with size. What are the demographic consequences of this strategy of indeterminate growth? Here we present results of laboratory experiments in which we measured reproductive strategies of two large, similar cladoceran species, *Daphnia pulex* and *D. pulicaria*, under high and moderately limiting food conditions. From the experimental data, we calculated the intrinsic rates of increase r for each reproductive strategy. We also estimated the effect on r of changing the pattern of allocation of biomass to reproduction. The results suggest that the daphnid strategy may represent an evolutionary compromise between strategies that maximize r and strategies that maximize total reproductive output.

Methods

The *Daphnia* were cultured in a flow-through system (a modification of the system described by LAMPERT 1976). Fresh culture medium dripped into the chamber, about 200 ml in volume, at the upper end; old medium and waste material drained out through a mesh screen at the lower end. Culture medium flowed through the chamber at about $1.5 \text{ l} \cdot \text{day}^{-1}$. The chambers were suspended in a water bath kept at 20.0°C . Filtered lake water with *Scenedesmus* grown in chemostat culture was used as the culture medium. Fresh medium was prepared each day.

Daphnia pulicaria and *D. pulex* from laboratory cultures were used for the experiments. Both strains were supplied from the collection of Dr. V. HRBÁČEK in Prague, Czechoslovakia. Neonates (0–18 hrs old) were used to begin the experiments. At the beginning of the reproductive period, each chamber contained about 10 animals. This number decreased during the experiment as animals were removed for dry weight measurements. Animals were counted, measured, and transferred to clean chambers every 2 days. Neonates were counted and discarded at each transfer. Body length was measured to the nearest .04 mm from the top of the head to the base of the tail spine.

Animals were collected for dry weight measurements from the last prereproductive instar (instar P) and each reproductive instar (R1, R2, . . . , Rn). So that the weights of somatic and reproductive tissue could be separated, animals were collected immediately after molting and egg production (in the case of reproductive animals). Animals to be weighed were killed with dilute unbuffered formalin, measured, and rinsed in distilled water. Eggs of ovigerous animals were removed from the brood chamber. Samples were placed in preweighed aluminum boats, dried for 1 hour at 102°C , and stored in a desiccator.

Experiments were run at $1 \text{ mg C} \cdot \text{l}^{-1}$ (*D. pulicaria*, 5 replicate chambers; *D. pulex*, 3 replicates) and $.2 \text{ mg C} \cdot \text{l}^{-1}$ (*D. pulicaria*, 4 replicates; *D. pulex*, 4 replicates). Natural mortality was not significant in these experiments, and none of the experiments was run to the end of the natural lifespan of the animals.

Length-weight regressions (Table 1) were used to estimate biomass at each instar from the length measurements for each experiment. An average egg weight for each experiment was used to estimate reproductive biomass for each instar from the counts of eggs and neonates.

Growth G was estimated by the difference between the average body weights for successive instars. Biomass allocated to reproduction R was estimated by the weight of eggs produced after the

Table 1. Length-weight regressions and egg weights. Best-fitting curve among linear, log-linear, and log-log relations is given. L is length in mm, and W is weight in mg. Sample size for the regression is n, and the correlation coefficient is r. For the egg data, \bar{x} is mean weight per egg in mg, n is the sample size, and s_x is the standard deviation.

Species	Food level $\text{mg C} \cdot \text{l}^{-1}$	Regression equation	n	r	Egg weight		
					\bar{x}	n	s
<i>D. pulicaria</i>	1	$\log W = 2.514 \log L - 5.180$	64	.99	.0028	11	.003
<i>D. pulex</i>	1	$\log W = 1.193 L - 5.581$	29	.99	.0026	12	.002
<i>D. pulicaria</i>	.2	$\log W = 1.628 L - 6.996$	19	.96	.0027	4	.001
<i>D. pulex</i>	.2	$W = .033 L - .039$	24	.91	.0024	4	.001

molt to the following instar. Total biomass production T was estimated by growth G plus reproduction R. The proportion of biomass allocated to reproduction was estimated by R/T .

To analyse the demographic effect of the reproductive strategies, we calculated the intrinsic rate of increase r for each experiment. Assuming that production is a function of body weight, we calculated fecundity schedules and r values for two determinate growth strategies: 1) allocating the total production in instar P and all subsequent instars to reproduction, which results in constant body and clutch size; and 2) allocating the total production in instar P to growth, then allocating the total production to reproduction in all subsequent instars, which results in constant body and clutch size after the 1 instar delay in reproduction. The total number of offspring R_0 was also calculated for each fecundity schedule. Data from 5 reproductive instars were used for each species at $1 \text{ mg C} \cdot \text{l}^{-1}$; data from 4 reproductive instars, for each species at $.2 \text{ mg C} \cdot \text{l}^{-1}$. Increasing the number of instars has a negligible effect on r, but increases R_0 . Survivorship was assumed to be 1 for all calculations.

Results

Both *Daphnia pulicaria* and *D. pulex* at both food concentrations continued to grow for the duration of the experiments (Fig. 1). Reproductive output increased substantially

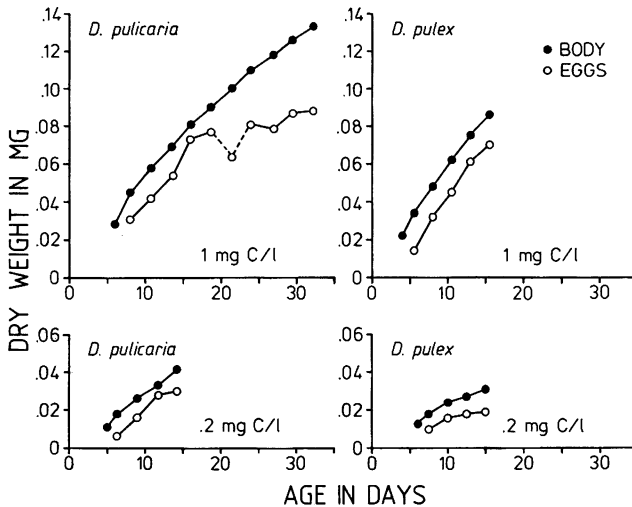


Fig. 1. Body weight and egg weight. Body weight is measured at the beginning of the instar.

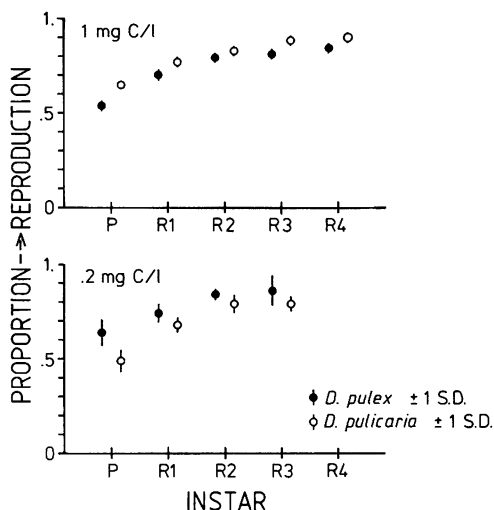


Fig. 2. Proportion of production allocated to reproduction.

Table 2. Values of r and R_0 .

Species	Food level $\text{mg C} \cdot \text{l}^{-1}$	Indeterminate growth		Determinate growth			
		r	R_0	1) no delay		2) delay	
				r	R_0	r	R_0
<i>D. pulex</i>	1	.300	98.7	.315	84.5	.296	121.6
<i>D. pulex</i>	1	.346	77.8	.353	50.0	.345	89.2
<i>D. pulex</i>	.2	.251	29.8	.248	19.6	.261	36.6
<i>D. pulex</i>	.2	.232	23.0	.242	22.4	.223	25.5

in the earlier reproductive instars. At $.2 \text{ mg C} \cdot \text{l}^{-1}$ both species began to reproduce at much smaller body weights. *Daphnia pulex* delayed reproduction for several days at the lower food concentration, but *D. pulex* reproduced slightly earlier.

The reproductive strategies, as measured by the proportion of biomass allocated to reproduction at each instar, were very similar between species and food concentrations (Fig. 2). The general pattern shows moderate investment in reproduction at the last pre-reproductive instar P. This investment increases significantly in the subsequent 2 instars and remains fairly constant after instar R2. Values for instars R4 through R9 (not shown) for *D. pulex* range from .86 to .93.

At $1 \text{ mg C} \cdot \text{l}^{-1}$ the shorter juvenile period gives *D. pulex* a higher r value than *D. pulex*, although *D. pulex* has higher fecundity at each instar (Table 2). At $.2 \text{ mg C} \cdot \text{l}^{-1}$ both higher fecundity and a shorter juvenile period contribute to the higher r value for *D. pulex*.

The r calculations also show that in each case one of the determinate growth strategies gives a higher r value than the value calculated from the experimental data, which represent the natural strategy of indeterminate growth. For *D. pulex* at $1 \text{ mg C} \cdot \text{l}^{-1}$ and for *D. pulex* at both food concentrations, determinate growth strategy 1 (no delay in reproduction) gives the highest r values. For *D. pulex* at $.2 \text{ mg C} \cdot \text{l}^{-1}$, determinate growth strategy 2 (1 instar delay in reproduction) gives the highest r value. In all cases R_0

values are lowest for determinate growth strategy 1, higher for the natural indeterminate growth strategy, and highest for determinate growth strategy 2. These values underestimate R_0 for the natural lifespan of the animal, but show the same rank order as values calculated from longer sequences of data.

Discussion

The relatively higher intrinsic rates of increase for *Daphnia pulex* at the high food concentration and for *D. pulicaria* at the moderate food concentration are consistent with the results of HRBÁČEK (1977). According to his interpretation, *D. pulex* is more "r-selected", and *D. pulicaria* is more "k-selected". The similarities of allocation of biomass to growth and reproduction in these two species suggest that the differences in r values are not caused by differences in this component of the reproductive strategy. The differences lie in the age and size at the beginning of the reproductive period and in the relations between production and body size.

Under constant environmental conditions, the reproductive strategy that maximizes r , within the constraints imposed by physiology and morphology, will be the optimal strategy. Under other conditions, maximizing r may not be optimal. For example, when the growing season is limited and the population does not reach stable age distribution, a strategy that maximizes the total reproductive output R_0 may be better (see GABRIEL 1982).

For both species at both food concentrations, determinate growth strategies estimated from the production data produced higher values of r than did the experimentally measured strategies of indeterminate growth, suggesting that indeterminate growth does not maximize r . However, the r values for indeterminate growth are only slightly lower than the values for the best determinate growth strategies, and the R_0 values for indeterminate growth are higher, excepting the case of *D. pulicaria* at $.2 \text{ mg C} \cdot \text{l}^{-1}$. We speculate that the indeterminate growth strategy may be an evolutionary compromise: at a low cost, in terms of the reduction in r , the animal substantially increases the total number of young produced. The advantage of this compromise may be substantial, given the strong seasonality of many of the environments where cladocerans are found.

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