

# Variation and plasticity of biomass allocation in *Daphnia*

L. Y. YAMPOLSKY\* and D. EBERT†‡

Zoologisches Institut, Universität Basel, Rheinsprung 9, CH-4051 Basel, Switzerland

## Summary

1. For organisms with indeterminate growth a trade-off between growth and reproduction is expected. The detection of this trade-off depends not only on the covariance between these two traits, but also on the variation of their sum, the total production (TP = growth + reproduction). The smaller the relative variation in TP, the more likely it is to detect the trade-off. To investigate this trade-off, we studied biomass allocation and variation of 56 clones of *Daphnia magna* from two populations under two food conditions.

2. Broad-sense heritabilities of clutch mass, growth, TP and the allocation ratio ( $R = \text{clutch mass}/\text{TP}$ ) were higher in rich than in poor food conditions. Growth and  $R$  showed no genetic variation at the low food level.

3. No negative correlations were found for the expected trade-off between biomass allocated to reproduction and to growth. Correction for the time period between two reproductive events and for body length, both of which might influence TP, did not influence this result. However, some negative correlations were found between current reproduction and growth during the subsequent instar.

4. Two-way ANOVA with  $R$  as the dependent variable show significant food and population effects for some instars. Including length as a covariable in this two-way ANOVA revealed significant effects for the covariable and for food level in all instars. Population effects and population  $\times$  food interactions were significant in all but two adult instars, indicating that body size does not constrain genetic variation for biomass allocation, and that the food level plays an important role in detecting population effects.

*Key-words:* Genetic correlations, growth, heritability, reproduction, trade-off

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## Introduction

Survival and fecundity are the central traits in life-history evolution, because both contribute directly to fitness. When survival and fecundity are size dependent the effect of reproduction on growth becomes important and trade-offs between growth and reproduction are predicted (Gadgil & Bossert 1970; Stearns 1989; Roff 1992). In reviewing empirical studies, Stearns (1992) concluded that 'the trade-off between growth and reproduction is the best-confirmed broad-sense phenotypic trade-off'. This trade-off has been recorded in all organisms studied with indeterminate growth. However, all attempts to find a negative covariance between growth and reproduction in

*Daphnia* have failed (Bell 1983; Lynch 1989, 1992; Spitze, Burnson & Lynch 1991), although both traits show high levels of phenotypic and genetic variation (e.g. Lynch 1984; Hebert 1987; Yampolsky & Kalabushkin 1991). A possible explanation for this failure is described in the 'Y-model' (van Noordwijk & de Jong 1986; de Jong & van Noordwijk 1992; de Jong 1993). This predicts that the correlation between two traits that rely on the same resource is only negative if the variation of the allocation ratio, i.e. the proportion of biomass invested into reproduction, is relatively greater than the variation of total resource acquisition [see van Noordwijk & de Jong (1986) and Venable (1992) for graphic examples].

In this paper we aim to analyse the trade-off between growth and reproduction in *Daphnia* taking into account the total resource variation and the covariables that might account for an inflation of total resource variance. We further analyse genetic variation and plasticity of the allocation ratio, as this trait might be a key factor in the optimization of growth

Present addresses: \*Institute of General Genetics, Russian Academy of Sciences, Gubkin str.3 GSP-1 V-333, Moscow, Russia and †Centre for Population Biology, Imperial College at Silwood Park, Ascot, Berks SL5 7PY, UK.

‡ To whom reprint requests should be addressed.

**Table 1.** Regression coefficients ( $\pm$ SE) for dry weight-length relationship for newborn and adult *Daphnia magna* in two food concentrations. The regression equations:  $\ln[\text{weight}(\text{mg})] = a + b \times \ln[\text{length}(\text{mm})]$

Food	<i>a</i>	SE	<i>b</i>	SE	<i>r</i> <sup>2</sup>
<i>Neonates</i>					
Low	2.33	(0.068)	3.61	(1.14)	0.62
High	2.62	(0.022)	1.94	(0.20)	0.72
<i>Adults</i>					
Low	2.85	(0.198)	1.69	(0.18)	0.65
High	3.24	(0.107)	1.77	(0.09)	0.86

and reproduction across varying food conditions (Spitze *et al.* 1991; Taylor & Gabriel 1992).

### Materials and methods

Forty-six clones of *Daphnia magna* Straus from Forchheim pond in south-west Germany and 10 clones from a carp pond close to Munich, Germany [populations are described in Ebert (1991)] were raised under rich and poor food conditions;  $10^4$  and  $10^5$  *Ankistrodesmus gracilis* cells  $\text{ml}^{-1} \text{day}^{-1}$  at 20 °C. To minimize maternal effects as a result of common environment, for each food level one reproductive female from each of the 56 clones was isolated from the stem cultures. From each of these mothers, we isolated three neonates in separate containers, representing clonal replicates (56 clones  $\times$  3 replicates  $\times$  2 food levels = 336 lines). These 336 females represent the first generation of three generations that were kept under standard conditions. Some lines were lost during these three generations and some females in the third generation died before they reached the seventh adult instar. Measurements were taken only in the third generation. In this generation single females of all lines were checked once a day for exuvia. Times of moulting were recorded and total body length (excluding the spine but including the base of the spine) at birth, at the adolescent instar and at each of the first seven adult instars was measured using a dissecting microscope fitted with an eyepiece. Sizes of clutches 1–6 and the body length of four randomly chosen neonates from each clutch were recorded. Mean neonate length per clutch was used in the analysis. A more detailed description of the experimental conditions and origin of clones is given by Ebert, Yampolsky & Stearns (1993).

To obtain dry weight-length regression at each food concentration we raised females in corresponding conditions, measured and then dried them at 60 °C for 24 h and weighed them to the nearest 5  $\mu\text{g}$  (Table 1). We included only females from which freshly deposited eggs were removed from the brood pouch. Neonates collected during the experiment were

assigned to size groups and 20–100 individuals were measured together. Individuals from both populations were used for the regressions.

The allocation ratio *R* was calculated as the proportion of total biomass (reproduction + growth = TP) invested into reproduction. Clutch mass and growth were estimated for the instar in which the eggs of this clutch were provisioned in the ovaries, i.e. the instar before the eggs were deposited in the brood pouch. The weight of the moult is not included in our growth estimate. Daily investment estimates were calculated by dividing clutch mass and growth by the duration of the instar. Instars with ephippial eggs were excluded from the analysis.

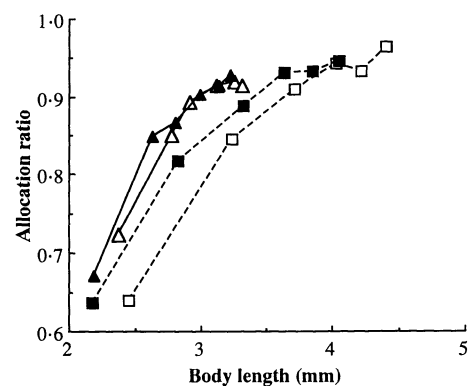
The analysis of covariance was carried out with untransformed allocation ratios and with arcsin-transformed ratios (for linearization of the relation between the ratio and body length, see Fig. 1). Because the deviation from linearity within instars is weak there was no difference in the results. Therefore we present here the ANCOVA for untransformed ratios.

In clonal organisms genetic variance can be estimated from the among-clone variance component. Heritabilities are expressed as percentages of the total phenotypic variance (sum of genetic and non-genetic variance) and thus represent broad-sense heritability (Falconer 1981). For negative genetic variance components (no significant case,  $P > 0.4$ ), heritability was assumed to be zero.

### Results

#### HERITABILITY AND GENETIC COVARIANCES WITH BODY LENGTH

Clutch mass, growth, TP and *R* had lower heritabilities under poor food than under high food conditions, with the highest estimates found for clutch mass and TP in high food and the lowest estimates for growth and *R* in low food. Heritability estimates of TP were more influenced by genetic variation from clutch



**Fig. 1.** Allocation ratio (proportion of biomass invested into reproduction) for each of the first six adult instars plotted against the mean body length of these instars. Forchheim population (filled symbols); carp pond (open symbols). Low food (triangles); high food (squares).

**Table 2.** Broad-sense heritability estimates for clutch mass (CM), growth (G), TP and *R* (CM/TP), and genetic correlations of these four traits with body length during egg production. Phenotypic and environmental correlations were omitted as they are very similar to the genetic correlations. The row with instar 1–6 gives the average of the six instars

Food/instar	Broad-sense heritability (%)				Genetic correlation with length			
	CM	G	TP	<i>R</i>	CM	G	TP	<i>R</i>
Low 1	21	0	12	11	0.39**	−0.30*	0.23	0.62***
2	27**	13	27**	7	0.09	−0.21	0.04	0.28
3	20*	0	19*	7	0.28	−0.30*	0.22	0.51***
4	24**	0	23*	0	−0.04	−0.43**	−0.09	0.34*
5	13	5	16	0	0.02	−0.17	−0.04	0.11
6	0	0	0	0	0.04	−0.32*	0.02	0.20
1–6	17	3	16	4	0.13	−0.29	0.06	0.34
High 1	41***	32**	44***	39***	0.62***	0.67***	0.69***	0.32*
2	40***	11	37***	30***	0.48***	0.07	0.44*	0.55***
3	38***	19*	38***	10	0.72***	0.33*	0.70***	0.46***
4	47***	19*	43***	37***	0.83***	−0.08	0.79***	0.54***
5	34***	7	36***	16	0.60***	0.17	0.58***	0.17
6	53***	9	51***	11	0.27	−0.24	0.24	0.33*
1–6	42	16	41	24	0.59	0.15	0.57	0.39

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

mass than from growth. The low genetic variation of growth appears to have little influence on the genetic variation of TP.

As variation in TP is known to be correlated with body length in *Daphnia*, we calculated genetic correlations of body length with our four production traits (Table 2). Correlations with clutch mass and TP were around zero in low food conditions and positive in high food conditions. In contrast growth showed mainly negative correlations in low food, and no correlations in high food conditions. *R* had positive genetic correlations with body length in both food levels, underlining the importance of body length in analysing the allocation trade-offs.

#### CORRELATIONS BETWEEN GROWTH AND REPRODUCTION

Correlations of biomass invested into reproduction and growth were mostly positive (Table 3). As the duration of an instar might influence biomass production during this instar we also used daily investment rates for the trade-off analysis. These estimates produced similar, but even more positive results (Table 3).

A trade-off might be found between the investment in the clutch produced in a certain instar and growth during the previous or subsequent instar. Correlation coefficients were around zero between current reproduction and previous growth (phenotypic, mean 0.13, range 0.0 to 0.23; genetic, mean 0.20, range −0.23 to 0.56; environmental, mean 0.07, range −0.29 to 0.32). However, some negative correlations were found between current reproduction and growth in the following instar (Table 3).

Because body length was strongly positively correlated with TP under high food conditions, we corrected for the effect of body length on the allocation trade-offs, by using partial correlations (Table 3). However, there was no change in the trade-off correlation coefficient in either food level.

#### POPULATION EFFECTS

An alternative way of analysing the allocation trade-off is to compare the allocation ratio between populations. Table 4a shows the results of two-way ANOVA for *R*, with food and population as main effects and clones nested within populations. The population effect was significant in the first, third and fourth adult instar, while the food effect was significant in all but the second and fifth instar. A clone effect was found for the first adult instar.

As shown for other cladocerans (e.g. Taylor 1985; Urabe 1988; Lynch 1989), *R* increased within and across each instar with body length (Table 2, Fig. 1). Therefore, we repeated the analysis of variance with body length as a covariable (Table 4b). Under low food conditions, animals of equal size invested more into reproduction than under high food conditions (Fig. 1, Table 4b), although the highest absolute values of *R* of both populations are observed under high food conditions. Significant population effects were found in four instars; however, the significant population × food interactions indicate that population effects vary with food. Population effects were in general more pronounced under high food conditions, with females from the Forchheim population having higher *R* values for a given body length (Fig. 1). In contrast to the ANOVA (Table 4a), the analysis of

**Table 3.** Phenotypic (p), genetic (g) and environmental (e) correlations between biomass investment into reproduction and growth of the 46 Forchheim clones. Analysis is performed by correlating clutch mass with growth in the same and in the subsequent instar. Correlations are calculated using instar-wise investment and daily investment rates. For partial correlations body length during egg provisioning was controlled for and instar-wise data were used. The results for the carp pond population showed the same results as the 46 Forchheim clones and are therefore omitted here

		Same instar			Subsequent instar		
		Instar-wise	Daily	Partial	Instar-wise	Daily	Partial
<i>Low food</i>							
1	p	0.30***	0.54***	0.54***	-0.20*	-0.17	-0.26**
	g	0.24	0.51***		-0.19	-0.13	
	e	0.35**	0.58***		-0.23	-0.20	
2	p	0.61***	0.62***	0.66***	-0.43***	-0.35**	-0.45***
	g	0.71***	0.71***		-0.50***	-0.46**	
	e	0.52***	0.56***		-0.39***	-0.28*	
3	p	0.25**	0.25**	0.43***	-0.18*	-0.17	-0.11
	g	0.24	0.23		-0.07	-0.07	
	e	0.25*	0.27*		-0.26**	-0.24*	
4	p	0.34***	0.38***	0.35***	0.00	-0.01	-0.01
	g	0.40***	0.44**		0.06	0.06	
	e	0.34**	0.34**		-0.04	-0.07	
5	p	0.30***	0.40***	0.31***	0.10	0.07	0.09
	g	0.44*	0.53***		-0.02	0.03	
	e	0.22	0.29*		0.13	0.10	
6	p	0.34**	0.36**	0.37***	-0.02	-0.05	-0.02
	g	0.32*	0.41**		0.18	0.06	
	e	0.35**	0.33**		-0.13	-0.13	
<i>High food</i>							
1	p	0.43***	0.72***	0.28***	-0.04	-0.13	-0.10
	g	0.55***	0.72***		0.14	-0.12	
	e	0.26*	0.72***		-0.27*	-0.14	
2	p	0.60***	0.72***	0.64***	-0.01	0.02	-0.03
	g	0.62***	0.75***		0.21	0.13	
	e	0.58***	0.69***		-0.25*	-0.11	
3	p	0.36***	0.39***	0.51***	-0.05	-0.04	-0.07
	g	0.45***	0.42**		-0.02	-0.04	
	e	0.27*	0.36**		-0.07	-0.03	
4	p	0.32***	0.43***	0.53***	-0.01	-0.09	-0.06
	g	0.21*	0.29*		0.22	0.17	
	e	0.47***	0.58***		-0.24	-0.30*	
5	p	0.20*	0.35***	0.31***	0.01	-0.09	0.04
	g	0.30***	0.41**		-0.01	-0.08	
	e	0.10	0.28*		0.04	-0.11	
6	p	0.05	0.18	0.13	-0.04	-0.11	-0.03
	g	0.03	0.09		0.14	-0.08	
	e	0.09	0.28*		-0.22	-0.32*	

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

covariance revealed not only significant food  $\times$  population, but also significant food  $\times$  clone interactions in four of the six instars (Table 4b). Clone effects were weak and only found in the first adult instar in both types of analysis.

## Discussion

The predicted trade-off between simultaneous investment in growth and reproduction was not found. Correlation coefficients in both food levels were mostly positive (Table 3), supporting earlier results by Lynch (1989, 1992) and Spitze *et al.* (1991).

One proximate cause for a positive allocation trade-off coefficient is high variance in total production (see van Noordwijk & de Jong 1986; de Jong & van Noordwijk 1992). We controlled two possible sources for this variation, body length and instar duration, but failed in both cases to detect the predicted negative covariances. For the trade-off between offspring size and number, Ebert (1993) found negative coefficients after correction for body length.

In our analysis we assumed that energy allocation to growth and reproduction happens simultaneously and that an instar is the appropriate time unit. However, recent studies on the pathway and timing of

**Table 4.** Analysis of variance for the effects of food (F), population (P), and clone (C) on the allocation ratio. Food and population are fixed effects and clone is a random effect nested within populations. (a) ANOVA and (b) ANCOVA with length (*L*) at egg production used as covariable. Only *F*-values and significance are given

		Instar					
	df	1	2	3	4	5	6
F	1	52.59***	6.38*	10.46**	28.98***	3.19	27.80***
P	1	7.06*	2.62	14.83***	5.00*	0.0	0.01
F×P	1	6.77*	5.50*	0.01	0.03	1.08	6.78*
C(P)	54	1.69*	1.01	0.75	0.73	0.73	1.25
F×C(P)	1	4.48*	3.36	0.01	0.02	0.98	7.05*
MS error		3.032	2.186	1.521	1.183	1.796	1.870
<i>r</i> <sup>2</sup>		0.63	0.50	0.46	0.52	0.38	0.46

		Instar					
	df	1	2	3	4	5	6
<i>L</i> (covariable)	1	57.66***	12.36***	144.16***	44.22***	32.09***	27.49***
F	1	90.68***	19.06***	99.63***	24.98***	25.61***	18.19***
P	1	2.80	1.35	14.51***	8.85**	14.76***	12.72***
F×P	1	23.94***	0.07	43.88***	15.64***	14.69***	2.30
C(P)	54	1.65*	0.96	0.88	0.99	1.05	1.33
F×C(P)	1	14.37***	0.04	20.22***	10.24**	12.13**	2.03
MS error		2.235	2.073	0.888	0.813	1.478	1.227
<i>r</i> <sup>2</sup>		0.73	0.53	0.69	0.60	0.47	0.54

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ . MS error multiply by 0.001. The df for the error term ranged from 162 to 206.

biomass allocation to growth and reproduction suggest that these two processes might not be directly linked. The negative trade-off correlation coefficients found between reproduction in the current instar and growth in the following instar indicate a possible time lag between allocation to reproduction and growth. The same results were found by Lynch (1989, 1992) and Spitze *et al.* (1991). *Daphnia* energy allocation models might help to explain this pattern. It is reported that there is only a short time window, about half an instar before egg deposition, during which the decision is made on how much biomass is allocated to a clutch (Bradley, Baird & Calow 1991a; Ebert & Yampolsky 1993). Starvation and refeeding experiments suggest that allocation of assimilated energy to reproduction is direct, while investment in growth seems to be more gradual and at least partially influenced by resources taken from intermediate storage (Bradley, Perrin & Calow 1991b). Earlier models on *Daphnia* energy allocation (Kooijman 1986; McCauley *et al.* 1990a) do not include the possibility of an intermediate storage between energy allocation to growth and reproduction and thus do not allow for a time lag in the allocation trade-off. The model by Bradley *et al.* (1991b) appears to be the most consistent with our results.

#### POPULATION EFFECT ON ENERGY ALLOCATION

Significant differences in energy allocation were found for half of the instars between the two populations (Fig. 1, Table 4). When females of equal length and in equal food conditions are considered, those from the Forchheim population invest at high food level a higher proportion of TP into reproduction than those from the carp pond population. These two populations are characterized by different sizes at birth and at maturity (Ebert 1991), with Forchheim females being generally smaller. Although this size difference might contribute to the population difference in the allocation ratio, correcting for body size did not remove the population effect. Therefore, genetic variation and thus evolutionary change of the food-specific allocation ratio, seems not to be constrained by body size, as suggested by Lynch (1992).

#### FOOD-SPECIFIC ENERGY ALLOCATION

A review of earlier results on the effect of feeding conditions on the allocation ratio reveals no consistent pattern. Taylor's (1985) results on *D. pulex* and *D. pulicaria* agree with the results found here: females of equal body length invest more in reproduction when food is limited. Urabe (1988) and

McCauley, Murdoch & Nisbet (1990b) found the opposite trend for *D. galeata* across three food conditions and *D. pulex* in two food conditions, respectively. Lynch (1989, 1992) found no differences in size-specific biomass allocation across several food levels for *D. pulex*, *D. ambigua* and *Ceriodaphnia quadrangula*. These results may indicate local adaptations of the size-specific allocation ratio, but it is more likely to be a study-specific effect. Trends for food effects found in those studies which tested more than one species or population are highly consistent, while results between studies are inconsistent. Our study revealed consistent food effects for two different populations: Taylor (1985) found consistent food effects for two different species; Lynch (1989, 1992) consistently found no food effect in three cladocerans. It seems unlikely that the species or populations used in these studies had similar adaptive patterns within each of these studies, but different adaptive patterns across studies. We believe that plasticity in the size-specific allocation ratio can be adaptive in cladocerans (Stibor 1992; Taylor & Gabriel 1992), but that experimental methods have contributed more to the observed food-specific allocation patterns than genetic differences.

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