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The effect of size at birth, maturation threshold and genetic differences on the life-history of *Daphnia magna*

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Summary. Life-history traits of 101 clones from two populations of *Daphnia magna* were measured under controlled environmental conditions in the laboratory. Some individuals had four juvenile instars, others had five. This depended on their length at birth and on the population they came from. Females in the group with five juvenile instars were smaller at birth but larger and older at maturity than those with four juvenile instars. Within groups of females with equal numbers of pre-adult instars (instar groups) age and size at maturity increased with size at birth. This relationship differed significantly among instar groups for both age and size at maturity. Significant differences in age and size at maturity between two populations became non-significant when size at birth was used as a covariable in ANCOVA. Within populations, size at birth depended on the clone and on the parity of the clutch. First-clutch offspring were considerably smaller than those from later clutches. The results suggest that variability in life-history traits is common within and between clones, but that most of this variation can be accounted for by size at birth and the number of pre-adult instars.

Key words: *Daphnia* – Life-history – Genetics – Variation – Maturation

Life-history traits are often assumed to covary with each other in a continuous way (e.g. Schaffer 1974; Gabriel 1982; Stearns and Koella 1986; Lynch 1989). This does not hold for many arthropods, which have a discontinuous rather than a continuous life-history, passing through several instars before maturation. In groups with discrete developmental stages, age and size at maturity are a function of both growth and the number of pre-adult instars. Variation in the number of juvenile instars is known for many arthropods including locusts (Uvarov 1966), spiders (Deevey 1949; Vollrath 1986) and crustaceans (Hartnoll 1985).

In *Daphnia* the number of juvenile instars varies among clones and across environments (Anderson 1932; Green 1954, 1956; Porter et al. 1983; Urabe 1988). Anderson (1932); Anderson and Jenkins (1942); Green (1956); Vuorinen et al. (1989); and Walls and Ketola (1989) showed that differential juvenile growth or small size differences at birth in *Daphnia* can lead to variation in the number of pre-adult instars, which in turn produces considerable variation in other life-history traits.

In organisms where the number of juvenile instars is fixed, size or age at maturity is usually expected to be normally distributed. If the number of pre-adult instars within a given environment varies over a range of only a few instars (Deevey 1949; Anderson 1942; Uvarov 1966), asymmetric bi- or trimodal distributions of many life-history traits may result. Such variation has often been described in *Daphnia*, but the results were not detailed enough to allow predictions, which are the main goal of life-history theory. Thus, it would be helpful to understand the sources of variation in life-history traits in *Daphnia* within one environment.

The goal of this study was to describe and quantify the variation of *Daphnia* life-history traits within a single constant environment. I present evidence that size at birth accounts not only for the number of juvenile instars but also for most life-history variation within groups with equal numbers of juvenile instars. This is important for the prediction of life-history traits and should be included in future models on *Daphnia* life-history evolution. The results also suggest that current models of size-selective predation are not adequate to predict microevolutionary change in the life-history of *Daphnia* populations.

Material and methods

Origin of clones

The 107 clones of *Daphnia magna* Strauss (Cladocera, Crustacea) used in this study originated from two populations in southern

Germany. Ninety-four clones stem from ephippia that were gathered from the sediment of a carp stocking pond (pond number: K2/5) at Ismaning near Munich. This artificial pond has been used to raise carp from mid-April to early November since 1929. Only 2- or 3-year-old carp are kept. From early November until mid-March the pond is completely dry. It has an area of approximately 4 ha, maximum depth 3 m, average depth 1.5 m. Biomass production is supported by inflow of waste water from an urban area. The second set of clones stem from a permanent population near Forchheim (near Freiburg). The Forchheim pond has an area of approximately 0.1 ha, maximum depth 0.6 m, mean depth 0.5 m and was constructed some 30 years ago.

In February 1989 I collected ephippia along the shoreline of the empty carp pond. They were hatched using the method of Schwartz and Hebert (1987). Only clones coming from ephippia where both eggs hatched were used. These clones are probably pairs of full sibs whose quantitative genetics will be published elsewhere. In this study 47 pairs were used.

In May 1989 I collected 14 adult females from the Forchheim population and cloned them in the laboratory. One died before reproduction. Clones from both populations were kept in the laboratory for several generations prior to experimentation.

Experimental conditions

The *Daphnia* were kept at 15±1° C and 16:8 h light/dark. I used *Ankistrodesmus gracilis* as food. During experiments I added 4×10^4 cells/ml every day to each glass. The water used throughout the experiment came from a small pond in Basel, Switzerland, collected and filtered sterile (0.2 µm, Katadyn filter) within half a day to ensure homogeneous water quality.

During experimentation, water was replaced at the onset of a new generation, on the 5th day of life of each female, and then after each adult moulting.

Experiments

Life-history experiments were conducted from October to December 1989. One reproductive female from each of 107 clones was isolated in a Pulvis 100 ml glass containing 95 ml water. From each mother, I isolated 3 neonates in separate glasses. These constituted the first generation of ($107 \times 3 =$) 321 lines that were kept for three generations under controlled conditions. The second generation started with a newborn from the second clutch of generation one, the third generation with a newborn of the second clutch of generation two. In addition, 64 randomly selected newborns from the first clutch of generation 2 were isolated. All lines were randomized and their locations within the climate chamber were changed daily after feeding. I lost 72 lines in the second generation because male newborns were accidentally isolated. Two females died before maturation. The final data set included 13 Forchheim clones and 88 clones from the carp pond. All females reproduced.

In the third generation all females were checked once a day. I measured the total body length (excluding the spina but including the base of the spina) at birth, at the adolescent instar and at the first four adult instars. Spina length at birth and at the first and fourth adult instar were measured. Times of adult ecdysis were recorded. In cases where daily observation fell in the period between release of young and formation of new eggs, I added 12 h to the time of moulting because this period lasts several hours at 15° C. The number of young in clutches 1–4 and the body length of two neonates from each clutch were recorded. The mean length of the two newborns per clutch was used in the analysis. Fifteen neonates from second-generation mothers were selected for a wide range of sizes at birth (0.73–1.36 mm). They were measured daily until maturity.

Statistical analysis was done with the SAS computer package (SAS Institute Inc, 1985). Genetic and nongenetic correlations were calculated using the variances and covariances from nested ANOVAs. These correlations represent estimates based on broad-sense heritabilities (Falconer 1989).

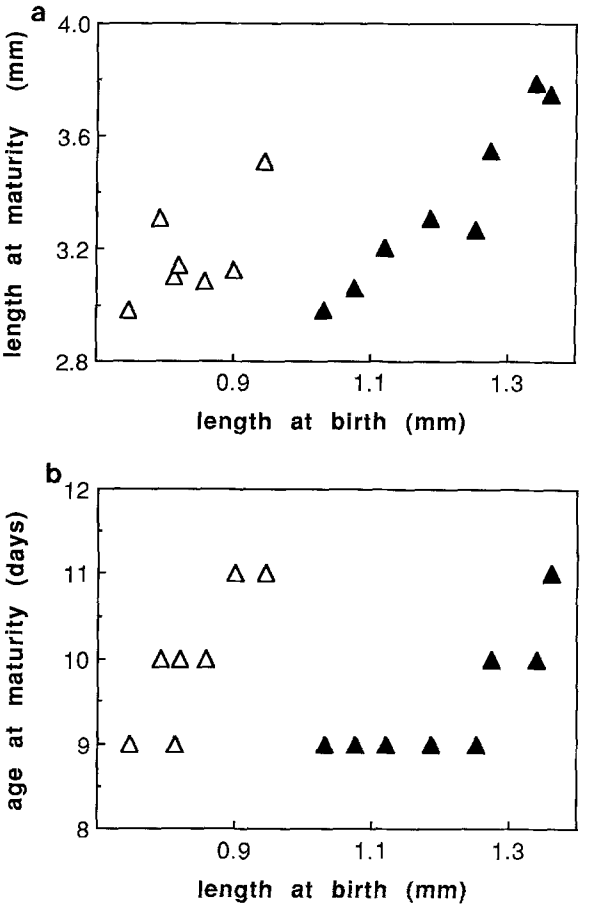

Fig. 1. a Length and **b** age at maturity plotted against the length at birth for 15 females with known number of juvenile instars. *Filled triangles*: daphnids with 4 juvenile instars; *open triangles*: daphnids with 5 juvenile instars

Results

Grouping of data

The 15 females that were measured daily fell into two distinct groups. Those less than 0.98 mm at birth had 5 juvenile instars; larger ones had 4. This had a strong effect on their length and age at maturity (Fig. 1). The clusters on the left in Fig. 1a and b are females with 5 juvenile instars; the clusters on the right are females with 4. I refer to those two groups as "instar groups". The ratio (age at maturity × length at maturity)/(squared size at birth) resulted in two non-overlapping distributions in the two groups (4 juv. instars: 21.86±0.73 (SE), $n=8$; 5 juv. instars: 46.23±1.92, $n=7$). This ratio was used to assign all other females with an unknown number of juvenile instars to the instar groups (4 juv. instars 22.52±0.12, $n=280$; 5 juv. instars 38.09±0.72, $n=43$). All females could be unambiguously assigned to the groups with 4 or 5 juvenile instars (Fig. 2).

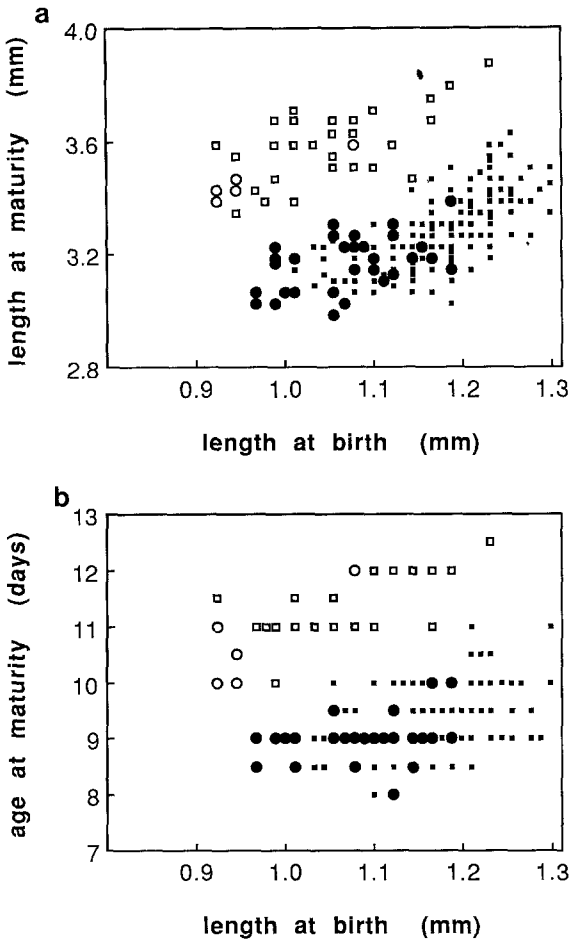

Fig. 2. **a** Length and **b** age at maturity plotted against the length at birth. *Circles*: Forchheim population; *squares*: carp pond population; *open symbols*: daphnids with 5 juvenile instars; *closed symbols*: daphnids with 4 juvenile instars

It was useful to group the females into all 8 possible combinations of: (a) two populations, (b) two instar groups and (c) those females isolated from the first or from the second clutch of their mother. These groups differed in mean length at birth, which was significantly shorter for females from the Forchheim population, for females from first clutches, and for females with 5 juvenile instars (Table 1). I now describe variation in life-histories within and between some of these groups.

Life-history variation among clones

As seen in Figs. 1 and 2, size and age at maturity varied both between and within instar groups. For example, the group with the largest sample size, females from the carp pond population with 4 juvenile instars, isolated from second clutches, still displayed much variation in life-history traits (Table 2). I concentrate on this group for the analysis in this section.

Using one-way ANOVAs, I found significant differences among clones for all traits except developmental time in clutch 1 (Table 2). Developmental times of later clutches, not reported here, did not differ either. This

Table 1. **a** Three-way ANOVA for length at birth with population, number of juvenile instars, and the number of the clutch that females were isolated from as main effects and **b** mean, sample size and S.D. of all groups

a

Source	DF	Type III SS	*F*	*P*
Population	1	0.05399	30.66	0.0001
Instar group	1	0.03169	18.00	0.0001
Clutch number	1	0.15724	89.30	0.0001
Pop × instar	1	0.00059	0.34	0.5602
Pop × clutch	1	0.00005	0.03	0.8660
Instar × clutch	1	0.00168	0.96	0.3288
Pop × instar × clutch	1	0.00074	0.42	0.5172

b

Population	Instar group	Clutch number	*N*	Mean length at birth [mm]	SD
Carp pond	4	1	29	1.07	0.031
	4	2	211	1.19	0.042
	5	1	21	1.01	0.042
	5	2	12	1.13	0.050
Forchheim pond	4	1	10	1.00	0.036
	4	2	26	1.10	0.045
	5	1	4	0.93	0.013
	5	2	1	1.07	–

showed that most life-history traits of *Daphnia magna* are genetically variable. Results from the Forchheim population were similar.

The mean length at birth of all mothers isolated in the second clutch did not differ significantly from the length of their offspring in clutch 2 ($t=1.66$, $P>0.05$), while it differed from the lengths of clutches 1, 3 and 4 (clutch 1: $t=30.59$; clutch 3: $t=13.37$; clutch 4: $t=15.4$; $P<0.0001$ for clutch 1, 3, 4; means in Table 2). Length at birth of mothers isolated from the first clutch did not differ from their offspring of clutch 1 but differed from later clutches. This suggests that under constant environmental conditions, the mean length at birth of a given clutch stayed about the same between generations.

To distinguish between genetic and non-genetic effects of length at birth on other traits, I calculated the total (phenotypic), genetic and environmental (or non-genetic) correlation for length at birth with various life-history traits (Falconer 1989) (Table 3). As expected from Figs. 1 and 2, length and age at maturity are both significantly positively correlated with length at birth. The correlations with body lengths in later instars were significantly positive, but became weaker for older instars. Genetic and non-genetic correlations did not differ much for these traits. Correlations with spina length were generally weak, and only the phenotypic and non-genetic correlations in the spina length at birth were significant. The size of clutch 1 was not significantly correlated with length at birth, but the sizes of clutches 2–4 showed a negative correlation, meaning that larger neonates produced fewer eggs in clutches 2 to 4. Except

Table 2. Means, sample size, coefficient of variation, minimum and maximum values of various life-history traits. Only females from the carp pond population with 4 juvenile instars and isolated from clutch 2 of their mother were included. Asterisks following the mean values indicate significance of clonal differences for that trait. Lengths in mm, ages in days since hatching

Trait	Mean	*n*	C.V.	Minimum	Maximum
Length at birth	1.19***	211	3.6	1.05	1.30
Spina length at birth	0.55*	211	11.3	0.44	1.01
Length of adolescent stage	2.61***	175	4.1	2.34	2.90
Length at maturity	3.31***	211	3.4	3.02	3.63
Spina length at maturity	0.81***	210	11.5	0.48	1.03
Length 4th adult instar	4.05***	201	2.1	3.83	4.27
Spina length 4th adult instar	0.57***	201	17.6	0.37	0.87
Age at maturity	9.37**	211	5.5	8.00	11.00
Age at hatching of clutch 1	14.58*	211	3.3	13.00	16.00
Develop. time clutch 1	5.21	211	7.7	4.00	6.00
Size of clutch 1	12.89***	206	28.1	1.00	21.00
Size of clutch 2	16.78**	196	20.9	6.00	27.00
Size of clutch 3	15.18***	201	22.2	2.00	24.00
Size of clutch 4	10.46***	194	26.6	1.00	21.00
Offspring length clutch 1	1.04*	209	5.3	0.85	1.17
Offspring length clutch 2	1.18***	206	3.4	1.02	1.28
Offspring length clutch 3	1.24***	197	3.0	1.13	1.34
Offspring length clutch 4	1.25***	133	2.8	1.13	1.35

*** $P<0.001$, ** $P<0.001$, * $P<0.05$

for the first clutch, the genetic correlations were more strongly negative than the nongenetic correlations.

In contrast, offspring lengths were all positively correlated with the length at birth of their mother. In all four clutches the genetic correlation was larger than the environmental correlation. This effect increased with clutch number. These results suggest that clutch size and offspring length of later clutches depended more on the genotype than on the environment.

Differences between juvenile instar groups

To compare groups with different numbers of juvenile instars (instar groups), I pooled the females from clutches 1 and 2. This had no effect on the conclusions drawn. From the 273 females from the carp pond population isolated from first and second clutches of their mother, 240 had four juvenile instars and 33 had five. Females maturing in four juvenile instars were larger at birth than those with five juvenile instars (Fig. 3). There is a threshold around 1 mm length at birth at which the life-history of individuals switched. The same was true for the Forchheim population (Fig. 3).

Table 4 shows the highly significant linear regressions of length at maturity and age at maturity for the two instar groups from the carp pond population.The slopes between groups differed for age but not for length at maturity. However, the intercepts for length at maturity differed significantly. Females with the same length at birth but maturing one instar later were significantly larger and older at maturity (Fig. 2, Table 4). The same positive relations can be seen in Fig. 1 for both instar groups.

The clutch sizes also differed strongly between instar groups (Fig. 4). Clutch size of females with five juvenile instars decreased with increasing clutch number. For those with four it first rose and then fell. The largest difference occurred in the first clutch, (five juvenile instar

Table 3. Phenotypic, genetic, and environmental correlations of length at birth with various life-history traits. Only female from the carp pond population with 4 juvenile instars and isolated from clutch 2 of their mother were included. The mean of two neonates from each clutch per female was used for offspring length

Variable	Phenotypic	*n*	Genetic	*n*	Environmental	*n*
Spina length at birth	0.22**	211	0.16	87	0.29**	124
Length of adolescent stage	0.71***	175	0.74***	81	0.65***	94
Length at maturity	0.60***	211	0.61***	87	0.59***	124
Spina length at maturity	0.03	210	−0.07	87	0.16	123
Length 4th adult instar	0.15*	201	0.17	87	0.10	115
Spina length 4th ad. instar	−0.02	201	−0.05	87	0.05	115
Age at maturity	0.39***	211	0.46***	86	0.30***	125
Age at hatching of clutch 1	0.39***	211	0.51***	87	0.24**	125
Develop. time clutch 1	−0.03	211	0.02	87	−0.08	125
Size of clutch 1	0.13	206	0.06	87	0.22*	119
Size of clutch 2	−0.32***	196	−0.35***	86	−0.28**	111
Size of clutch 3	−0.52***	201	−0.62***	87	−0.35***	115
Size of clutch 4	−0.30***	194	−0.47***	87	−0.07	107
Offspring length clutch 1	0.44***	209	0.47***	87	0.42**	123
Offspring length clutch 2	0.48***	206	0.64***	87	0.26**	120
Offspring length clutch 3	0.49***	197	0.62***	87	0.24*	111
Offspring length clutch 4	0.43***	133	0.56***	70	0.13	64

*** $P<0.001$, ** $P<0.01$, * $P<0.05$

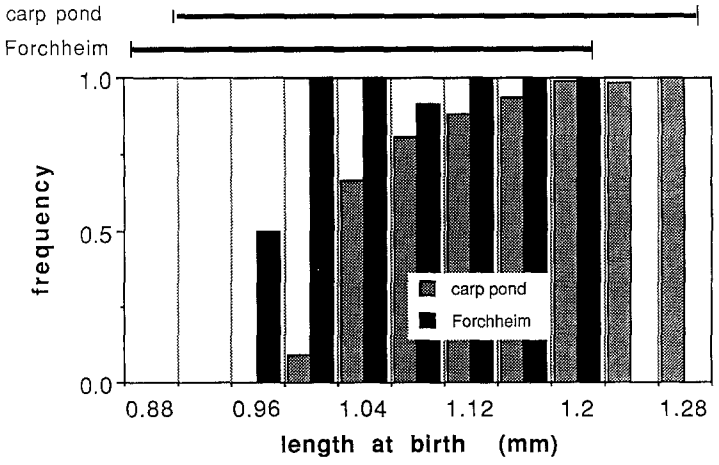

Fig. 3. Proportion of females maturing after 4 juvenile instars in size classes for length at birth. Forchheim population: *black bars* ($n=42$), carp pond population: *grey bars* ($n=273$). Class width = 0.04 mm. The *bars* above the graph represent the ranges of birth lengths for both populations

Table 4. Linear regression of age and length at maturity on length at birth for the two groups with 4 and 5 juvenile instars from the carp pond population. P values indicate significance level of the slope being different from zero. * $P<0.05$, ns $P>0.05$ indicate comparisons between instar groups

Trait	Instar group	n	Slope	(SE)	Intercept	(SE)	r^2	P
Age at maturity	4	240	3.22 *	0.406	5.55	0.475	0.18	<0.0001
	5	33	6.54	0.934	4.37	0.975	0.58	<0.0001
Length at maturity	4	240	1.22 ns	0.079	1.84 *	0.092	0.46	<0.0001
	5	33	0.99	0.210	2.53	0.220	0.38	<0.0001

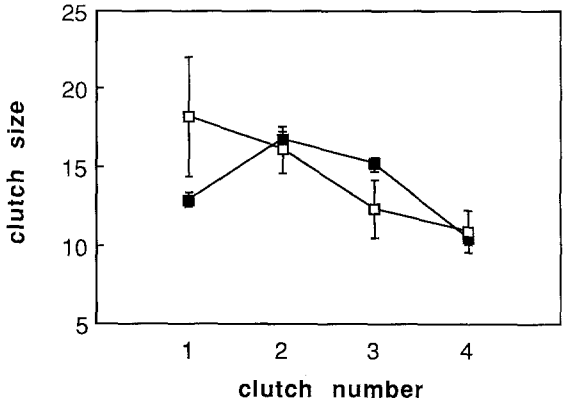

Fig. 4. Clutch size of clutches 1–4 of the carp pond population. *Closed symbols*: 4 juvenile instars; *open symbols*: 5 juvenile instars. *Error bars* indicate 95% confidence limits

females had 30% more eggs), the clutch to which the intrinsic rate of natural increase, r, is most sensitive (Cole 1954; Lewontin 1965). The larger first clutch of females with five juvenile instars may compensate for their delayed maturity.

Differences between populations

With the pooled data of females isolated from clutches 1 and 2, I did a PROBIT analysis for each population to estimate the response thresholds in length at birth above which four juvenile instars and below which five juvenile instars occurred. Lengths at birth were grouped into classes of 0.04 mm (Fig. 3) and log-transformed. The threshold for the carp pond population was higher than for the Forchheim population, but the 95% confidence intervals overlapped slightly (carp pond: threshold 1.02 mm, 95% confidence interval 0.98–1.04; Forchheim: 0.94 mm, 0.71–0.99).

I also used a second approach to compare the size thresholds of the two populations. Of the 107 clones, 30 clones had offspring in both instar groups. To estimate the clonal threshold, I calculated the mid-point between the birth length of the smallest four juvenile instar female and the largest five juvenile instar female of these 30 clones. The means of these clonal threshold estimates differed significantly between the populations (carp pond: 1.08 mm, SE 0.011, $n=26$; Forchheim: 0.99 mm, SE 0.026, $n=4$; $t=2.96$, $P<0.05$), showing that the threshold differed between populations. These threshold estimates were larger than those from the PROBIT analysis, which was most likely an effect of the subsample.

Clutch sizes also differed between the populations (Fig. 5a). Clutchs 2–4 were significantly larger in the Forchheim population, while offspring lengths were significantly smaller in all four clutches (Fig. 5b). It appears that larger offspring were traded-off with smaller clutches.

As shown in Table 1 and Figure 5b, length at birth and length of offspring differed significantly between populations. Life-history traits that are correlated with the length at birth should vary in the same way. This was the case for all traits measured. Traits positively correlated with length at birth (e.g. size at maturity, offspring length of clutches 1–4; Table 3) had lower means in Forchheim clones than in the carp pond clones (Fig. 2a, 5b) and traits negatively correlated with length at birth (Table 3) were larger in the Forchheim clones (e.g. clutch size of clutches 2–4, Fig. 5a). Traits not correlated with size at birth did not differ between the populations (e.g. clutch 1, Fig. 5a).

To analyse birth size further I did two sets of variance analyses with instar group and population as main effects, testing for differences in age and size at maturity:

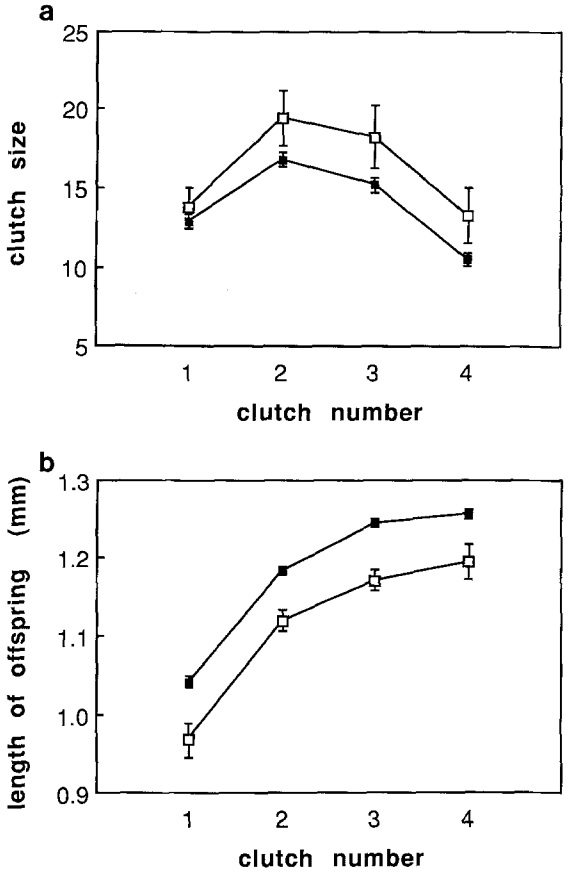

Fig. 5. **a** Clutch size and **b** length of offspring for the carp pond (*closed symbols*) and the Forchheim (*open symbols*) populations. All data from females with 4 juvenile instars. *Error bars* indicate 95% confidence limits. 95% confidence intervals of the carp pond population fall inside the symbols in some cases

one set of ANOVAs and one set of ANCOVAs with length at birth as a covariable. Without the covariable both main effects were highly significant for age and size at maturity (Table 5). With length at birth as a covariable the population effects were no longer significant for age or size at maturity (Table 5). This shows that within each instar group, length at birth was sufficient to characterize and compare both populations.

Discussion

The main results of this study were:

1. There is a threshold size for maturation

Newborns smaller than about 1 mm had one juvenile instar more than larger newborns (Fig. 3). Two other studies report such a threshold. Green (1954) found that larger neonates have fewer juvenile instars. In his study, the threshold size at birth for switching from four to five juvenile instars in *Daphnia magna* was about 0.93 mm. Green (1956) confirmed this result for seven species of *Daphnia*, showing that the mean length at birth was smaller in groups with more pre-adult instars.

Table 5. ANOVA and ANCOVA for age and for size at maturity with instar group and population as main effects. Size at birth was used as covariable in the ANCOVA

Source	*df*	SS	*F*	*P*
Instar group	1	1.28412	96.83	0.0001
Population	1	0.23222	17.51	0.0001
Instar group × population	1	0.00043	0.03	0.8563
Size at maturity: ANCOVA				
Instar group	1	2.36643	285.20	<0.0001
Population	1	0.00139	0.17	0.6826
Instar group × population	1	0.00012	0.01	0.9028
Size at birth	1	1.54718	186.46	0.0001
Age at maturity: ANOVA				
Instar group	1	50.02921	185.49	0.0001
Population	1	3.04077	11.27	0.0009
Instar group × population	1	0.18819	0.70	0.4042
Age at maturity: ANCOVA				
Instar group	1	66.00741	305.24	<0.0001
Population	1	0.07299	0.34	0.5617
Instar group × population	1	0.29059	1.34	0.2473
Size at birth	1	16.78824	77.63	0.0001

For *D. thomsoni* and *D. obtusa* he found three instar groups.

Others have assumed that female *Daphnia* must reach a certain size rather than a certain age or instar before maturation is initiated (Anderson 1932; Hrbackova-Esslova 1962; Taylor 1985; Urabe 1988; Lynch 1989). However, no one has attempted to characterize this threshold or to study its consequences for the life-history.

2. The life-history depends strongly on the number of pre-adult instars

Age, size and clutch size at maturity differed significantly between groups with different numbers of juvenile instars. This caused asymmetrical distributions of these traits. Anderson (1932), Anderson and Jenkins (1942), Green (1956), Ketola and Vuorinen (1989) and Vuorinen et al. (1989) analysed *Daphnia* life-history data separately for different instar groups to circumvent the problem of enlarged variance due to different numbers of juvenile instars. They all found significant differences between life-history traits among instar groups. They agree that it is essential to analyse *Daphnia* life-history data separately for each instar group but found no general pattern to describe the differences between groups.

3. Within groups of equal number of juvenile instars life-history traits can be predicted from the size at birth

Most life-history traits measured in this study were significantly correlated with size at birth (Table 3). Here I want to concentrate on age and size at maturity because of the general importance of these traits. Length at birth was positively correlated with age and with size at matu-

rity within groups with equal numbers of juvenile instars. This correlation may be used to predict age and size at maturity for female daphnids with known length at birth. However, the correlation holds only within instar group. Pooling the data of both instar groups even resulted in a sign change. The correlation between age at maturity and length at birth was 0.38 ($P<0.001$) in the group with four juvenile instars, 0.51 ($P<0.001$) in the group with five juvenile instars, and -0.20 ($P<0.001$) for the pooled data set. The correlations between size at birth and the later life-history were successfully used to predict life-history differences between two populations, with a distinct difference in size at birth (Tables 1 and 5).

Others workers have compared newborn size with maturation size and age or mother age and size with offspring size (Bell 1983; Lynch 1983, 1984; Tessier and Consolatti 1989). The correlations found in their studies in general support the present results, but there are some inconsistencies. These are probably a result of data sets including females with different numbers of pre-adult instars, for which they did not check. Also, clonal differences account for some variance (cf. Tables 2 and 3), and may thus cause inconsistent results. However, a large amount of genetic variance between clones (Table 3; Ebert, unpublished) and populations (Table 5) can nevertheless be attributed to the size at birth which differed between clones and populations (Table 1 and 2). Further data on correlations within instar groups are needed to test how well *Daphnia* life-history can be predicted from the neonate length.

Maturation threshold

Possibly the most important trait in *Daphnia* life-history is the maturation threshold. Having a size just below or above this threshold results in a very different life-history. One more juvenile instar results in larger size at maturity, higher age at maturity and a larger first clutch. Before discussing the relevance of this threshold I want to stress that the size of a late juvenile instar rather than the length at birth may determine the threshold. The size of the pre-adolescent instar (in the case of this study the third or fourth instar) or the adolescent instar itself may be the instar in which maturity is initiated, for ovaries develop and first eggs are produced in the adolescent instar. McCauley et al. (1990) mention that ovaries start to develop by the end of the pre-adolescent instar. However, because length at birth and the body length of later instars are correlated with each other, one may speak of a threshold length at birth. This shortcut does not change the conclusion. The clonal threshold could probably be estimated precisely if all instar lengths were available.

If a later, rather than the first, instar is the stage with the developmental switch, the size at birth may be decoupled from the threshold. If the growth rate (daily biomass production) of early juvenile instars varies between females of equal length at birth, those with a higher growth rate may reach the threshold size sooner and have fewer pre-adult instars than a female with a lower growth rate.

This is strongly supported by the literature: Porter et al. (1983) reported 5.0 ± 0.3 to 8.0 ± 0.3 instars at maturity in *Daphnia magna* over a wide range of food concentrations. The number of pre-adult instars increased as food conditions decreased. Similar results were found by Urabe (1988) for *D. galeata*. Both studies report variation in number of juvenile instars within each food level, suggesting that (1) variability in the number of pre-adult instars is not a special case and (2) daphnids in poor food conditions, which grew slower, had more instars before they reached the length at which maturation was initiated. In other words, decreasing the food concentration only slightly would result in a shift of the threshold length at birth, i.e. a neonate would have to be larger in order to mature after juvenile instars than it would have to be in the higher food concentration.

For the daphnids in this study, the proportion of females with five juvenile instars should increase if the experiments were repeated at a slightly lower food level, which reduces juvenile growth. A further food reduction may cause even more juvenile instars.

There is some evidence that the threshold length at birth may be shifted by chemical substances like the "*Chaoborus* factor". Ketola and Vuorinen (1989) and Vuorinen et al. (1989) showed that the *Chaoborus* factor, which reduced the juvenile growth rate of the daphnids tested, caused a substantial proportion of females to mature one instar later than the control group. The concept of a maturation threshold size seems to hold here too.

In this study, 30 out of 101 clones had females in both instar groups. These clones had extremely large and overlapping ranges for size at maturity. This variability must have consequences for their survival under size-selective predation. Because of (1) the large range of offspring sizes an individual female produces between and within different clutches, (2) the different growth rates these offspring may have in a not completely homogeneous and stable environment, and (3) possible maternal effects on juvenile growth, it is likely that in its natural environment a single clone of *Daphnia* could possibly attain any size at maturity within a certain size range. Under field conditions the clonal mean size at maturity and its distribution would then be unpredictable and possibly there would be no stable correlation between the genotype and its mean size at maturity. In this case size-selective predation would act rather randomly on the genetic structure of a population. This may indicate how clonal diversity within a population can be maintained under size-selective predation. A 'clonal size range for maturity' rather then a fixed clonal size at maturity could possibly be the key factor for explaining phenotypic and genetic diversity within *Daphnia* populations. A computer simulation would help to explore possible outcomes of this question.

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