

Olga Sakwińska

Persistent maternal identity effects on life history traits in *Daphnia*

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Abstract The aim of the present study was to examine the magnitude and persistence of maternal effects in *Daphnia*, in particular maternal identity effects. I studied life history traits of a single clone of *Daphnia galeata* born to 40 different mothers belonging to three age groups. Maternal identity had large effects on offspring traits, that is, identically treated clonal females differed substantially in respect to the traits of their offspring, including size at birth, age at maturity, and number of second generation offspring. The effects of maternal identity on these traits were largely independent of maternally induced differences in offspring size, indicating that maternal effects were mediated through offspring quality. Maternal age also affected offspring traits: older mothers gave birth to larger offspring which matured earlier, were larger and more fecund, and survived better until maturity. Individuals which were larger at birth also had a better chance of survival. Contrary to expectation, I found little evidence that maternal identity or maternal age had any influence on their offsprings' response to fish kairomones.

Keywords *Daphnia galeata* · Plasticity · Fish kairomones · Offspring size · Survival

Introduction

The phenotype of the mother and the environment she experiences can affect her offspring independently of her genotype. Recent work has suggested that such maternal

effects can have important evolutionary implications (Wade 1998; Wolf et al. 1999). Because maternal effects can be molded by natural selection, their sign and magnitude may represent adaptation. In the rich literature on maternal effects (for reviews see Rossiter 1996; Mousseau and Fox 1998) many studies have aimed to show that various aspects of the maternal environment can affect offspring traits, and that such effects may depend on offspring environment, as well as on offspring and mother genotypes.

However, maternal effects are often also detected when the design of the study does not deliberately create variation in the maternal environment, and effort was made to keep the environment constant. Such maternal identity effects considerably complicate experimental designs used to estimate genetic components. This is particularly true for clonal organisms where the methods used with sexual organisms, such as reciprocal crosses or full sib–half sib designs, cannot be applied (Schwaegerle et al. 2000). Usually, independent lines are propagated for several generations in the hope that maternal effects will diminish. However, studies on the persistence and magnitude of maternal identity effects in clonal organisms, and on which traits are affected, are relatively rare (e.g., Lynch 1985; Schwaegerle et al. 2000).

Daphnia is a model organism widely used to address a range of evolutionary and ecological questions, and its clonal mode of reproduction makes the questions related to maternal effects particularly relevant. A variety of studies has explored the effects of different aspects of maternal environment on offspring size at birth, such as quantity (Tessier and Consolatti 1991; Glazier 1992; Guisande and Gliwicz 1992; Ebert 1993; McKee and Ebert 1996; LaMontagne and McCauley 2001) and quality of resources available to the mothers (Brett 1993), as well as the maternal social environment (Cleuvers et al. 1997). The effects on offspring size at birth would be of limited importance if they did not persist long enough to affect offspring survival and fecundity. Maternal effects are often large for traits expressed early in life, but later in life they appear to diminish. Although the consequences of varia-

O. Sakwińska (✉)
Zoology Institute, University of Basel,
Rheinsprung 9,
4051 Basel, Switzerland
e-mail: Olga.Sakwinska@ext.unil.ch
Tel.: +41-21-6462120
Fax: +41-21-6924265

Present address:
O. Sakwińska
Avenue de Floréal 14,
1006 Lausanne, Switzerland

tion in size at birth for the rest of the *Daphnia* life history is well established (Tessier and Consolatti 1989; Ebert 1991, 1994; Barata and Baird 1998; Sakwińska 2002), the persistence of maternal effects and their influence on life history traits expressed later in life have only rarely been studied (Tessier and Consolatti 1989; Boersma 1997). It has been shown that mothers grown at low food levels produce neonates which resist starvation better (Gliwicz and Guisande 1992), and that maternal food supply affected some life history traits of the offspring expressed later in life (Reede 1997).

Given the evidence for maternal effects on size at birth, and the importance of size at birth for life history traits expressed later in life, it is tempting to suggest that all maternal effects are attributable to size at birth, and therefore they could simply and conveniently be measured as maternally induced differences in size at birth. However, it is also possible that the mother influences not only the size, but also the quality of the offspring, which in turn can affect traits expressed later, independently of size at birth.

Size-selective predation exerts strong selection on the *Daphnia* life history, and patterns of variation in life history traits are often interpreted in this context (Brooks and Dodson 1965; Lynch 1980). In the presence of a waterborne cue released by a predator, individuals shift their life history towards earlier maturation at smaller size, an adaptive response to the mortality risk for larger-sized individuals (Stibor 1992; Weider and Pijanowska 1993). A previous study (Sakwińska 2002) suggested that such a response to the fish cue might depend on size at birth. It has been hypothesized that, for a *Daphnia* female, her own age could be an indicator of predation pressure: the fact that an individual survived to an older age signals that predation pressure is low (Lampert 1993). In the same vein, it can be hypothesized that the offspring of older females have less need to respond to fish kairomones.

The main goals of this study are thus:

1. To examine the extent and persistence of maternal effects in *Daphnia*, in particular the effects of maternal identity
2. To establish whether, and to what extent, maternal effects on traits expressed later in life can be independent of size at birth; and
3. To determine whether there are maternal effects on the response to fish kairomones.

Materials and methods

The *Daphnia galeata* clone used in this study was obtained in the spring of 1998 from Lake Constance, Germany, and had been kept in culture for about 2 years before the experiment started. Then, a single individual was isolated to obtain all the animals used in this experiment.

The experimental animals were kept individually in 95 ml medium. The media were refreshed and food (3.5×10^4 cells ml^{-1} of green algae *Scenedesmus*) was added daily. Modified AdaM medium was used (Klüttgen et al. 1994) (modified by using one-twentieth SeO_2 concentration and adding 20% water from a local well). The

water for the fish treatment was obtained by keeping two fish (*Leuciscus leuciscus*, body length 7 cm) in a 10-l aquarium for 24 h: the control treatment received water from an identical aquarium but without fish. Both control and fish water was passed through a 0.2- μm filter before use. The aquaria were cleaned and refilled daily. The fish were fed frozen *Chironomus* larvae every second day in a separate aquarium. The experiment was conducted at 16°C and 16:8 light/dark.

Three siblings were grandmothers of the experimental animals. Mothers of experimental animals belonged to three different age groups. There were 12–16 mothers of the same age. Both grandmothers and mothers were grown in conditions identical to the experimental control, except that water was changed every other day. The oldest mothers produced their third or fourth clutch, the intermediate group produced their second clutch, and the youngest group were primiparous females. From each mother, six offspring (in one case five, and two cases four) were taken and distributed randomly, three each, among fish and control treatment. The animals were less than 24 h old when the experiment started, and they were all born over a period of 3 days.

Every day these animals were checked for molting and body length was measured (from the top of the eye to the base of the tail spine) for each instar. A time-independent measure of juvenile growth, juvenile increment, was calculated following Ebert (1994). Growth increment is the ratio of the body size after the molt to the body size before the molt. The average instar increment for the first three instars was calculated. Size at maturity was the body length of the instar in which eggs appeared in the brood chamber. When the animals started maturing, they were checked every 12 h for the time of appearance of the first eggs in the brood chamber (age at maturity) and time of release of neonates (age at first reproduction). Their offspring from the first and second clutches were counted, and body size was measured for the offspring from the first clutch. These are referred to as second generation offspring. The initial sample size was 236 individuals, originating from 40 mothers of three age groups. Sample size for later traits subsequently decreased due to mortality and some missed observations.

The effects of maternal age and maternal identity on the traits of their offspring were investigated, with maternal age treated as a fixed factor with three levels (age groups), and maternal identity as a random factor nested within maternal age group. Procedure MIXED (SAS 1993) was used to obtain restricted maximum likelihood estimates of variance components for random factors and the ANOVA-based tests of significance for the fixed factors. The analysis of life history traits other than size at birth included a fixed treatment effect and all necessary interactions [i.e., Treatment \times Age group, Treatment \times Mother (Age group)] for the exposure to fish cue, which started shortly after birth.

Results

Maternal effects on size at birth

Older mothers produced larger offspring ($F_{2,39}=13.08$, $P<0.0001$, all three groups differed at $P<0.05$ level according to Tukey's HSD test). The average length ($\pm\text{SE}$) of the offspring born to the youngest mothers (age 1) was 0.568 mm (± 0.002); the intermediate (age 2) 0.580 mm (± 0.003); and the oldest (age 3) 0.607 mm (± 0.002). Variation among mothers within the same age group, i.e., the effect of maternal identity, was highly significant ($Z=4.09$, $P<0.0001$) and accounted for 67% of variation in size at birth (Fig. 1).

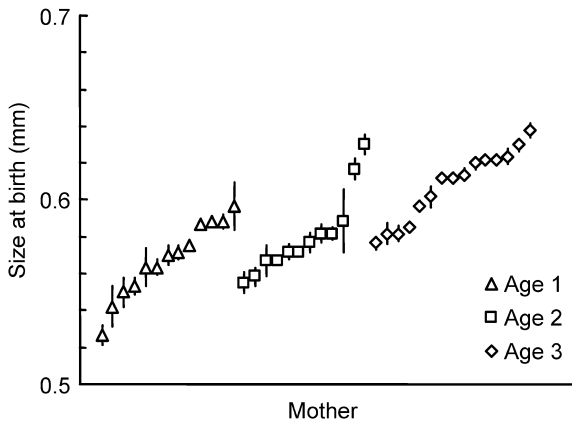


Fig. 1 Size at birth of the individuals born to the mothers of three age groups, where age 1 is the youngest. Mothers are ordered with increasing size of their offspring. Means and SE for six offspring of a single mother are shown

Maternal effects on later life history traits

Maternal age continued to affect the life history traits of the offspring throughout their life. The effect of mother's age on juvenile growth increment was unexpected: the youngest mothers produced offspring with the largest

growth increments, while those of intermediate age produced offspring with the smallest growth increments (Fig. 2; Table 1). Traits expressed later in life were also affected. Older mothers produced offspring who matured earlier, were larger at maturity and produced more second generation offspring (Fig. 2; Table 1). Maternal identity also affected the life history traits of the offspring (accounting for 10–38% of variation), including the number of second generation offspring (20% of variation) (Table 1). Animals in the fish treatment matured earlier, at a smaller size, and produced smaller second generation offspring (Fig. 2), but the juvenile growth increment and early fecundity were unaffected. The interactions Treatment×Age group and Treatment×Mother's identity explained little of the variance and were not significant (Table 1).

Effects due to size at birth

Adding size at birth to the models did not affect the fraction of variation accounted for by maternal identity (Table 2). The effect of maternal age became non-significant for size at maturity and number of second generation offspring. Maternal age remained significant

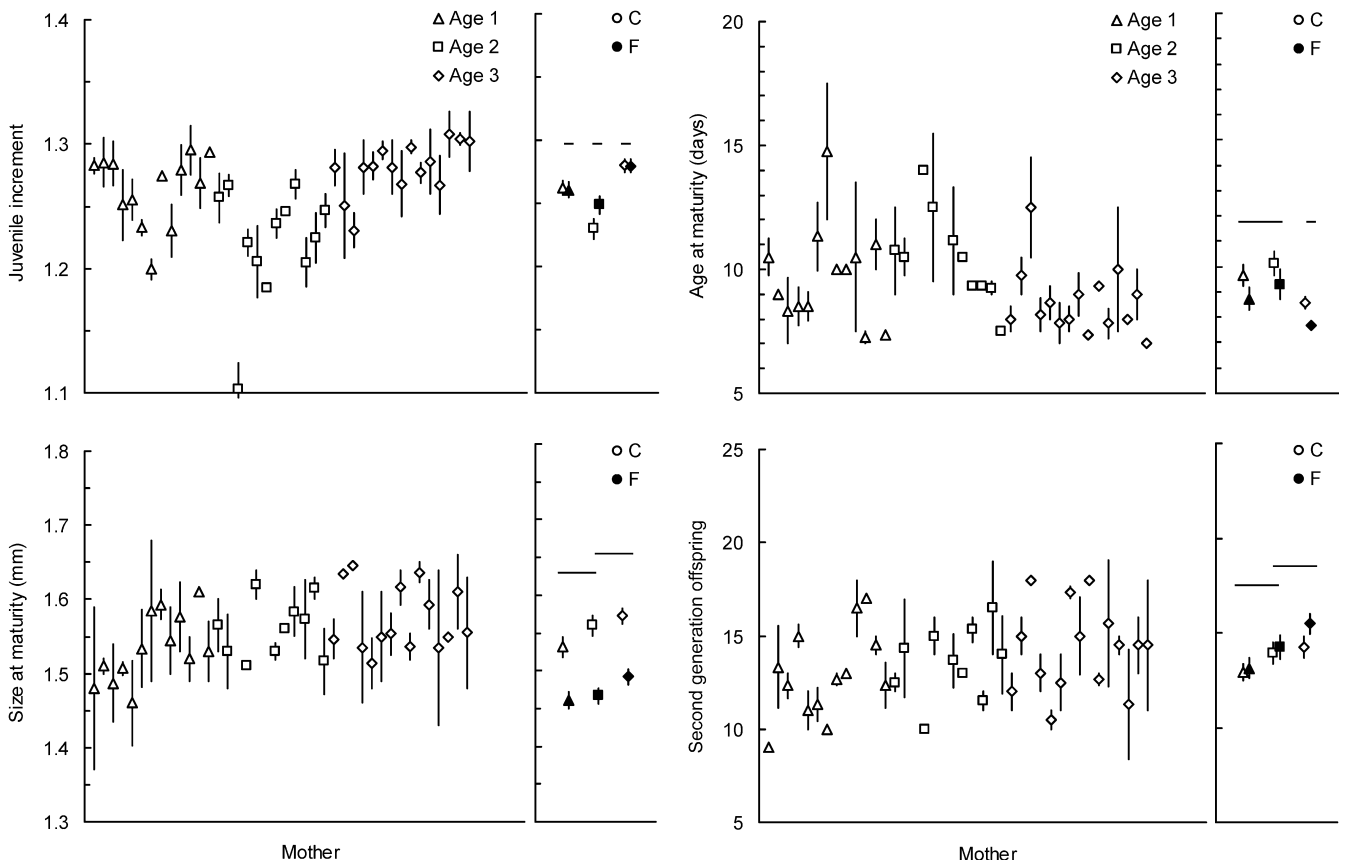


Fig. 2 Life history traits (juvenile increment, size and age at maturity, and second generation offspring number) of the offspring as the function of their mother's age and the fish kairomone treatment (age 1 is the youngest). *Left panels:* Means and SE for three offspring of a single individual. Only offspring from the

control treatment are plotted. *Right panels:* Means and SE for three maternal age groups and two treatment groups. The offspring are ordered in the same way as in Fig. 1, i.e., with increasing size at birth. *Horizontal bars* join age groups which are not significantly different from each other according to Tukey's HSD test at $P < 0.05$

Table 1 The effects of maternal age (Age), maternal identity nested within maternal age [Mother (Age)] and fish cue treatment on life history traits of the offspring. Fish cue treatment was applied only to the offspring immediately after their birth. Maternal identity and its interaction with fish kairomone treatment were random factors, the other effects were treated as fixed. For fixed factors, nominator *df* is

always 2 for Age and Age×Treatment interaction, and 1 for Treatment; denominator *df* is 35. For random factors, restricted maximum likelihood estimates of variance components are given. *P*-values for random factors are based on the *Z* test. They are not available (*na*) if variance estimate=0

Trait	Source	Variance estimate	Ratio	<i>F</i>	<i>P</i>
Juvenile growth increment	Mother (Age)	5.6×10^{-4}	0.38	–	0.0016
	Age	–	–	9.09	0.0006
	Treatment	–	–	1.18	0.29
	Age×Treatment	–	–	2.02	0.15
	Mother×Treatment (Age)	0	0	–	na
	Residual	9.2×10^{-4}	0.62		
Size at maturity	Mother (Age)	4.09×10^{-4}	0.10	–	0.22
	Age	–	–	3.71	0.03
	Treatment	–	–	80.04	<0.0001
	Age×Treatment	–	–	0.48	0.62
	Mother×Treatment (Age)	0.67×10^{-4}	0.02	–	0.88
	Residual	36.9×10^{-4}	0.88		
Age at maturity	Mother (Age)	2.11	0.38	–	0.049
	Age	–	–	4.79	0.015
	Treatment	–	–	15.66	0.0004
	Age×Treatment	–	–	0.35	0.71
	Mother×Treatment (Age)	0	0	–	na
	Residual	3.40	0.62		
Second generation offspring in the clutches 1–2	Mother (Age)	1.95	0.20	–	0.049
	Age	–	–	0.57	0.042
	Treatment	–	–	2.34	0.14
	Age×Treatment	–	–	0.93	0.41
	Mother×Treatment (Age)	0.27	0.03	–	0.76
	Residual	7.44	0.77		
Second generation offspring size clutch 1	Mother (Age)	4.6×10^{-5}	0.11	–	0.12
	Age	–	–	0.57	0.57
	Treatment	–	–	83.60	<0.0001
	Age×Treatment	–	–	0.56	0.58
	Mother×Treatment (Age)	0	0	–	na
	Residual	35.6×10^{-5}	0.89		

for juvenile increment and age at maturity (Table 2). Animals which were larger at birth were also larger at maturity, they matured earlier, and had more second generation offspring. Size at birth had no effect on juvenile growth increment nor second generation offspring size (Table 2). All interactions including the size at birth were not significant ($P > 0.18$) and their removal from the models did not change any of the results.

Maternal effects on survival

Overall survival rate was 86%. The effects of fish kairomone treatment, maternal age, and size at birth on survival until maturity were analyzed with logistic regression using the program LogXact (1999). The overall model was highly significant (likelihood ratio=162; $df=5$; $P < 0.0001$). Mother's age had a large effect on survival;

oldest mothers gave birth to best-surviving offspring (exact likelihood ratio=12.8; $P < 0.002$). Treatment had no effect on survival (exact likelihood ratio=2.10; $P=0.17$). Survival increased with size at birth (exact likelihood ratio=4.44; $P < 0.04$), (Fig. 3). Including the effect of maternal identity in this analysis (as a factor nested within mother's age) was not possible because maximum likelihood analysis models did not converge, and the required exact computations were too large.

Maternal effects on plasticity

No interactions between fish kairomone treatment and mother's age and identity in any of the measured traits were detected. Similarly, no interactions between size at birth and the fish kairomone treatment were significant. However, because an earlier study (Sakwińska 2002)

Table 2 The analysis of covariance for life history traits of the offspring of maternal age (Age), maternal identity nested within maternal age [Mother (Age)], fish cue treatment, and size at birth (a covariate). Fish cue treatment was applied only to the offspring

immediately after their birth. *P*-values for random factors are based on the Wald *Z* test. They are not available (*na*) if variance estimate=0

Trait	Source	Variance estimate	Ratio	<i>df</i>	<i>F</i>	<i>P</i>
Juvenile growth increment	Mother (Age)	5.64×10^{-4}	0.38	–	–	0.028
	Age	–	–	2, 37	8.38	0.001
	Treatment	–	–	1, 172	2.45	0.12
	Size at birth	–	–	1, 172	0.08	0.78
	Age×Treatment	–	–	2, 172	2.29	0.11
	Residual	9.17×10^{-4}	0.62	–	–	–
Size at maturity	Mother (Age)	3.70×10^{-4}	0.09	–	–	0.18
	Age	–	–	2, 37	0.14	0.87
	Treatment	–	–	1, 150	81.9	<0.0001
	Size at birth	–	–	1, 150	11.4	0.0009
	Age×Treatment	–	–	2, 150	0.22	0.80
	Residual	35.5×10^{-4}	0.91	–	–	–
Age at maturity	Mother (Age)	1.75	0.34	–	–	0.0099
	Age	–	–	2, 37	3.09	0.057
	Treatment	–	–	1, 159	17.0	0.0001
	Size at birth	–	–	1, 159	6.04	0.015
	Age×Treatment	–	–	2, 159	0.56	0.57
	Residual	3.41	0.66	–	–	–
Second generation offspring in the clutches 1–2	Mother (Age)	1.76	0.20	–	–	0.03
	Age	–	–	2, 37	0.04	0.96
	Treatment	–	–	1, 144	4.11	0.045
	Size at birth	–	–	1, 144	21.8	<0.0001
	Age×Treatment	–	–	2, 144	1.49	0.23
	Residual	6.86	0.80	–	–	–
Second generation offspring size clutch 1	Mother (Age)	5.09×10^{-5}	0.13	–	–	0.10
	Age	–	–	2, 37	0.51	0.61
	Treatment	–	–	1, 154	82.7	<0.0001
	Size at birth	–	–	1, 154	0.83	0.36
	Age×Treatment	–	–	2, 154	0.47	0.63
	Residual	35.4×10^{-5}	0.87	–	–	–

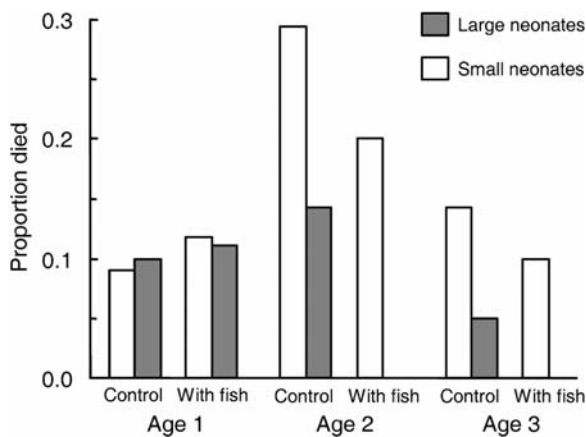


Fig. 3 Survival until maturity for individuals born to mothers of different ages (age 1 is the youngest), growing in control and fish treatments. For illustrative purposes, the animals were divided into two groups: those which at birth were smaller or equal to 0.58 mm, and those which were larger

suggested that size at birth can have nonlinear effects on plasticity of size at maturity, the additional analysis of plasticity was carried out. Plasticity values for each mother were calculated by subtracting the average trait values for three offspring in the fish treatment from the average values in the control treatment. This resulted in a single value of plasticity for each trait and each mother. The plasticity data were analyzed using one-way ANOVA with size at birth, and square of size at birth treated as covariates. There appeared to be weak nonlinear relationship between size at birth and plasticity of size at maturity [plasticity = $-9.16 + (31.3 \times \text{size-at-birth}) - (26.5 \times \text{size-at-birth}^2)$], with offspring from intermediately sized clutches showing the greatest plasticity. However, this relationship appeared to be due to few data points representing very small sizes at birth and negative values of plasticity (Table 3).

Table 3 The results of an ANCOVA (quadratic regression model) on plasticity in size at maturity. Maternal age is the main effect, and size at birth and square of size at birth are covariates. Plasticity of size at maturity is the difference in size at maturity between average values of three siblings, one group raised in control, the other in the fish treatment

Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Age	2	0.0006	0.15	0.86
Size at birth	1	0.0165	4.06	0.052
Size at birth \times size at birth	1	0.0164	4.03	0.053
Error	33	0.0041		

Discussion

In clonal organisms the effects of maternal identity on offspring traits (also called intergenerational environmental effects; Schwaegerle et al. 2000) have been only rarely investigated despite their potential evolutionary importance (Schwaegerle et al. 2000) as well as practical concerns for experimental design (Lynch and Walsh 1998, p. 593). Here, I found that maternal identity strongly contributed to variation in life history traits of the offspring. Although this effect appeared to diminish with age of the offspring, maternal identity affected traits which largely determine early fitness, e.g., age at maturity, and early fecundity. The fact that maternal effects can be detected is not surprising. Many earlier studies have described the effect of maternal environment on offspring phenotype. What is more remarkable is, firstly, the great range of phenotypes produced by a single phenotype: for example, the siblings' average size at birth varied from 0.53 to 0.64 mm. Secondly, the mothers differed considerably in some aspects of their phenotype, not because they experienced different experimental treatments but, on the contrary, despite having been grown in the identical environment.

Even though the effect of mother identity on offspring traits has been described before (Lynch 1985), in experimental studies on *Daphnia* life history it is often assumed that growing the animals in a defined environment for a generation diminishes maternal effects to negligible levels. This is clearly not the case and it should be taken into account in experimental design whenever genetic differences are investigated. This means that each experimental animal should have a separate mother and preferably also grandmother, although in many studies this has not been made clear in the publication. For example, in the present study, although the effect on second generation offspring size at birth was no longer significant ($P=0.1$), the estimated variance contribution was still 0.11. If such an effect were ignored, the genetic variance component would be inflated by the same amount, which would constitute a considerable error.

Although the effects of mother identity have largely been neglected, the influence of maternal size on offspring traits has often been investigated (e.g., Lampert 1993), although only seldom has the attempt been made to distinguish the effect of maternal age and size, which are

strongly correlated in *Daphnia* (the animals continue to grow after maturity; Glazier 1992; Ebert 1993). In this study, there was undoubtedly some variation in size among mothers of the same age, but I made no attempt to correlate that variation with the traits of their offspring. Although the question of whether mother size has an effect on offspring traits is certainly important for a number of issues, what needs to be emphasized here is that identically treated clonal females differed among themselves in respect to their offspring traits.

I found that older mothers produced larger offspring, which is consistent with earlier studies (Glazier 1992; Ebert 1993; Lampert 1993; McKee and Ebert 1996; Boersma 1997). My results are also in agreement with a few studies which investigated maternal influence on later traits (Lampert 1993; Boersma 1997). Offspring from older mothers were larger and younger at maturity, and they had more second generation offspring. It is worth mentioning that it is usually considered that older mothers produced less fit offspring (e.g., Hercus and Hoffmann 2000; Kern et al. 2001; reviewed in Fox and Czesak 2000) which has been interpreted as the manifestation of aging. However, these findings could hardly be considered contradictory to those reported here: this study, as well as earlier studies on *Daphnia* mentioned above, did not include a range of maternal ages where senescent decline in reproductive value could be expected to occur. Individuals were usually followed for at most six consecutive clutches, perhaps 20 days. In *Daphnia*, the decline of reproductive value only occurs later (Dudycha and Tessier 1999). The well-known fact that in *Daphnia* primiparous females appear to produce substandard offspring (Ebert 1991; Glazier 1992; Lampert 1993), is probably due to very strong selection on early fecundity, at the expense of offspring quality (Boersma 1997).

Size at birth is one of the most important determinants of *Daphnia* life history (Tessier and Consolatti 1989; Ebert 1991; Glazier 1992; Lampert 1993). It has also been known, and was confirmed here, that size at birth was strongly influenced by mother's traits (here age and identity). It would be thus tempting to assume that the maternal effects on traits expressed later in life are mediated through size at birth, being just a simple consequence of maternally induced differences in size at birth. Here, I found that the proportion of variation contributed by the maternal identity remained virtually the same after size at birth was included in the analysis. This demonstrates that the maternal effects on size at birth and later traits were largely independent and implies that maternal effects on offspring quality were not reflected in their size at birth. Maternal effects independent of size at birth are known in other organisms (e.g., McIntyre and Gooding 2000; Schwaegerle et al. 2000). Size at birth and juvenile growth increment showed strong dependence on mother's age and mother's identity, but size at birth had no effect on juvenile increment. In *Daphnia*, the quality of the offspring is likely to be reflected in the juvenile growth increment, which has a considerable impact on later life history (Ebert 1997). Although the effects of mother

identity appeared to be completely independent of offspring size at birth, maternal age effects on some traits were most probably partly mediated through size at birth. The effects of mother's age on size at maturity and early fecundity were no longer significant when size at birth was considered in the models.

The finding that maternal effects are at least partly independent of offspring size at birth has several implications. Clearly, maternal effects cannot be fully estimated by measuring size at birth. It also implies that a rather different effect of size at birth on later traits would be detected, depending on whether offspring from a single mother or a group of offspring from many mothers are considered. If offspring from a single mother were measured, much stronger and more consistent effects of size at birth could be observed. Whenever offspring of different mothers are taken into account, maternal effects that are independent of size at birth can make the effect of size at birth much less clear-cut.

Maternal effects on survival in *Daphnia* have previously only been reported for experiments involving complete starvation (Gliwicz and Guisande 1992). The same is true for the effect of size at birth (Tessier and Consolatti 1989; Glazier 1992). No attempts have been made to distinguish the two effects. Here, I found that survival of the youngest mothers' offspring was considerably lower than that of older ones'. Independently of the effect of mother's age, size at birth also played a role: smaller offspring suffered higher mortality. Many studies of *Daphnia* report intrinsic rates of increase estimated from life table data without taking into account potential differences in survival among experimental groups, setting mortality to zero, and assuming that all observed mortality was due to handling (e.g., Boersma 1997). It is possible that the conviction that all mortality observed in the laboratory studies with *Daphnia* (at least early in life) is due to handling could have led to underreporting observed mortality as any mortality implied bad handling. My results show that mortality varies significantly in the laboratory. Thus, variation in mortality can and should be investigated in laboratory experiments with *Daphnia*.

Contrary to expectations, I found only a weak association between size at birth and plasticity of size at maturity, and no association for any of the other traits. The result seemed to have been due to few data points where offspring were extremely small and they exhibited negative plasticity. That means individuals growing in the fish kairomone treatment were larger at maturity than those growing in the control treatment. Although it is conceivable that the smallest offspring have no need to show strong responses, this was not confirmed by analysis of other traits. It appears more likely that the phenomenon is the manifestation of maladaptedness of extremely small offspring. I found no evidence for any effect of maternal age on response to fish kairomones.

Conclusions

The most important findings of this study are thus:

1. Strong maternal identity effects were found: clonal *Daphnia* females grown in identical environment produced variable offspring.
2. The maternal effects mediated through offspring quality are at least as important as those mediated through offspring size.
3. Intrinsic mortality is an important fitness component that can easily be investigated in laboratory studies with *Daphnia*.
4. No effect of maternal age nor maternal identity on response to fish kairomones was detected.

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