CHAPTER 7

Plasticity in filter screen morphology and clearance rate of *Daphnia galeata*, *Daphnia cucullata* and their interspecific hybrids *Daphnia cucullata × galeata*

Sari Repka, Sárka Veselá, Anke Weber and Klaus Schwenk

Abstract
Areas and mesh sizes of filtering structures in *Daphnia galeata*, *D. cucullata* and their interspecific hybrid *D. cucullata × galeata* cultivated at low and high food concentrations were measured. The clearance rates and somatic growth rates of the animals were also determined. When reared at low food concentration, the filtering areas of all taxa were larger. Larger filtering areas resulted also in higher clearance rates. Differences between taxa in both filtering area and clearance rate were caused mainly by interspecific size differences. Hybrids had the largest absolute mesh sizes and the parental species smaller mesh sizes. Hybrids also showed heterosis in somatic growth rate at high food concentration. The differences in mesh size and somatic growth rate contribute to resource partitioning between the taxa and thus to their successful coexistence in lakes.
Introduction

The density and species composition of phytoplankton in lakes vary considerably during the growing season (Sommer et al. 1986). To persist, herbivorous zooplankton must be able to cope with extremely low and extremely high concentrations of food. *Daphnia*, key grazers in many types of lakes, have been shown to possess the ability to increase the area of their food filtering structures in response to food limitation (Koza and Korinek 1985; Korinek et al. 1986; Pop 1991; Lampert 1994; Lampert and Brendelberger 1995). This is effective because the individual filtering efficiency is positively correlated to the filtering area (Egloff and Palmer 1971; Arruda 1983; Stuchlik 1991; Lampert 1994). The mesh size of the filter screens determines the smallest particle that can be captured (Lampert 1987).

The taxa studied here, *Daphnia galeata*, *D. cucullata* and their interspecific hybrids *D. cucullata x galeata* are commonly found in Dutch lakes. They can co-exist or occur solely (Schwenk and Spaak 1995). These taxa belong to the *D. longispina* group in which interspecific hybridisation is common (Wolf and Mort 1986; Wolf 1987; Hebert et al. 1989; Schwenk and Spaak 1995). When coexisting, these taxa may compete for the same food resources.

Although a variety of results have been reported, the mesh sizes of adult *D. cucullata* and adult *D. galeata* most probably differ (Geller and Müller 1981; Brendelberger and Geller 1985). Differentiation in the mesh size of the taxa might facilitate resource partitioning and niche differentiation. Assuming a polygenic basis of traits such as mesh size, interspecific hybrids are expected to harbour intermediate trait values compared to parental species (Falconer 1989). Intermediate trait values for e.g. size at maturity were found for *Daphnia* interspecific hybrids (Weider and Wolf 1991; Weider 1993; Spaak and Hoekstra 1995). It may be that the overlap in the mesh sizes is larger between the parental species and the hybrid than between the parental species. Boersma (1995) reported that both parental species compete with the hybrid but competition between the parentals seemed negligible in the highly eutrophic lake Tjeukemeer.

Theoretically, heterozygous organisms have been indicated to be better buffered against environmental variability (Lemer 1954). In other words, plasticity and developmental instability should increase with increasing homozygozity (Lemer 1954). It is generally assumed that genomic coadaptation and heterozygosity are the two genetic factors that increase developmental stability (Graham and Felley 1985). Developmental instability is defined as phenotypic variation among individuals with identical genotypes living in an uniform environment (Scheiner et al. 1991; Yampolsky and Scheiner 1994). Hybrid populations are therefore thought either to benefit from an increase in heterozygozity or to suffer from disruption of coadaptation, depending on the degree of divergence between hybridising taxa (Harrison 1990). Until recently, it was assumed that, at the level of genetic divergence observed between most naturally hybridising taxa, breakdown in the coadaptation of gene complexes was more important than heterotic effects (Harrison 1990). Therefore we expect the hybrids to be more plastic and developmentally unstable than the parental species. Here we compared phenotypic traits of the parental species *D. cucullata* and *D. galeata* to their interspecific hybrids, *D. cucullata x galeata*, using hybrid clones collected from the field and crossed in the laboratory. The hybrids crossed in the laboratory originate from the same, known, parental clones whereas the parental clones of the field collected hybrids are unknown. Thus we expect the hybrids from the laboratory crossings to exhibit less variation than hybrids collected from the field.

Specifically, we addressed three questions in this study. Firstly, are there differences in filter screen morphology or plasticity between *D. galeata*, *D. cucullata* and their interspecific hybrid *D. cucullata x galeata*, secondly, are the hybrids more plastic and developmentally unstable than the parental species, and thirdly are the traits of hybrids collected from the field more variable than hybrids crossed in the laboratory?
Materials and methods

*D. galeata*, *D. cucullata* and *D. cucullata × galeata* clones were collected from the Netherlands and from northern Germany (Table 1). The clones were kept in the laboratory under standard conditions. To produce *D. cucullata × galeata* hybrids from known parental species in the laboratory *D. galeata* clone TG100 was used as the father clone and *D. cucullata* clone TC33 as the mother clone (Table 1). To produce males and sexual females the clones were kept in 1 l Erlenmeyer beakers at high densities with a light:dark regime of 16:8 hrs and low food level. Ten males and five to ten sexual females were placed together in 40 ml of 0.45 µm membrane filtered and sterilised Maarsseveen water. The ephippia they produced were collected and kept in + 4° C in the dark for at least 5 months. After this period, the ephippia were transferred to 0.45 µm membrane filtered water supplemented with the green alga *Scenedesmus acutus* as food. The hatching neonates were transferred to larger vessels and clonal cultures were established.

<table>
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<tr>
<th>Species</th>
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To record somatic growth rate, filter screen morphology and clearance rates of *D. cucullata*, *D. galeata* and *D. cucullata × galeata*, two subsequent experiments were performed. In both experiments, the mothers of the experimental animals were reared singly from neonates on a food concentration of 1 mg C l⁻¹ *S. acutus* in 100 ml tubes with 0.45 µm membrane filtered lake Maarsseveen water as the basic medium. In the first experiment, several *D. galeata*, *D. cucullata* and *D. cucullata × galeata* hybrids were used (Table 1). The experimental animals were randomly chosen from the second brood of the mothers. The experimental animals were cultivated in a flow-through system with a flow rate of 500 ml per 24 hrs. The body lengths at birth were measured and the neonates were randomly exposed to two food treatments: low *S. acutus* concentration (0.07 mg C l⁻¹, 4000 cells ml⁻¹) and high *S. acutus* concentration (1 mg C l⁻¹, 59 000 cells ml⁻¹). There were two replicate tubes per series and 5 animals per 50 ml tube. The *Daphnia* were kept in culture until their 2nd adult instar. Two animals from each tube were used for clearance rate measurements and the rest was preserved for filter screen measurements. Afterwards body lengths were measured and the animals were preserved in 4 % sugar formaline (Haney and Hall 1973). The filter screens at the third limb were dissected out of the animal, spread on a microscopic slide with a drop of glycerine and covered with a cover glass. The setae numbers (SN) were counted and filtering areas (FA) were measured with an image analyser to the nearest 0.01 mm².

The clearance rates were measured with the ¹⁴C-tracer technique. To 125 ml of the basic algae medium 1.85 kBq ¹⁴CHCO₃⁻ was added. The algae were grown in a climate chamber for four days. The algal solution was then centrifuged to remove the inorganic nutrient medium and most of the tracer and the pellet was resuspended in 0.45 µm membrane filtered lake water. After sieving over a 33 µm gauze, 0.1 ml algal solution was filtered over 0.45 µm membrane filters. The filters were dried and dissolved in toluene to count ¹⁴C activity in the medium with a scintillation counter. The radioactively labelled suspension of algae was added to the filtered lake water in a concentration of 0.10 mg C l⁻¹ that was used to fill individual tubes (100 ml each).
One ml was filtered through a 0.45 μm membrane filter, rinsed with unlabelled water and dried to determine radioactivity of the experimental suspension. Daphnids in their second adult instar were transferred into individual tubes (100 ml) which contained lake water and 14C-free algae. The daphnids were allowed to adapt to the test concentration (0.10 mg Cl⁻¹) of algae for approximately three hrs. After this the daphnids were transferred to the tubes with labelled algae. To measure the clearance rate, individual daphnids were allowed to feed for 5 min in the water with 14C-labelled algae and then transferred back into the unlabelled water they were kept in previously. Here they were allowed to stay for 1 min in order to rinse the body surface from adhered 14C-containing fluid, and were subsequently transferred into scintillation vials. The scintillation vials containing daphnids for the measurements of clearance rate were dried in an oven at 55 °C. Subsequently, 100 μm of distilled water was added and the well-mixed vials were again dried for at least for 30 min. After the addition of 250 μm soluene the well-mixed vials were again dried (≥ 4 hrs). Finally, 10 ml of toluene scintillation mix were added, the vials well mixed and placed in the scintillation counter to count radioactivity.

In the second experiment Daphnia for mesh size measurements were reared. The same clones (Table 1), food concentrations and absolute flow rates as in the first experiment were used. This time there were only two replicate Daphnia per tube. The mesh sizes (ME) were measured with electron microscope using the same methods as described in Chapter 6.

In the first experiment, mean somatic growth rate (SGR) per tube was calculated as

\[ SGR= \frac{(\ln SAE-\ln SAB)}{AAT}, \]  

where SAE is size at the end of the experiment, SAB is size at birth and AAT is age at the end of the experiment.

The clearance rate (Re) was calculated according to the formula:

\[ Re = \frac{Ra}{Rt \times (60 \times 24)} \text{ ml/individual/day}, \]  

where Ra= radioactivity of the Daphnia, Rt= radioactivity of the experimental medium (per ml), t= time allowed for consumption (5 min).

After ln-transformation of Re and FA, the data were analysed by analysis of covariance, taking the logarithm of body length as a covariate (Statistical Analysis Systems Institute 1989). SGR, SN and ME were, however, analysed with analysis of variance. In these analyses, D. cucullata, D. galeata, D. cucullata × galeata field hybrids and laboratory hybrids were regarded as separate groups. Tukey's a posteriori test was applied to test differences between these four groups. A sequential Bonferroni procedure (Rice 1989) was used to maintain an experimentwise type 1 error rate of 0.05. Coefficients for developmental instability of filtering area for the different taxa were calculated using a variance partitioning technique (Yampolsky and Scheiner 1994). In short, variance components were estimated with SAS procedure VARCOMP (Statistical Analysis Systems Institute 1989), assuming all main effects random. The residual variance was used as a relative measure of developmental noise. The coefficients of variation for each taxon were calculated as the square root of the variance component divided by the mean of the trait.

Results
The animals cultivated at the low algal concentration exhibited significantly slower somatic growth rate (Table 2). The SGR of the animals cultivated at the low algal concentration was 39 % slower than of those cultivated at the high algal concentration.
Table 2. Results of two-way ANCOVAs and ANOVAs for data sets of two experiments for Daphnia galeata, D. cucullata and D. cucullata × galeata reared at two food concentration. The analysed variables in ANCOVA (corrected for body length) were clearance rate (Re) and filtering area (FA). Setae number (SN), somatic growth rate (SGR) and mesh size (ME) were analysed with ANOVA. Df denotes the degrees of freedom and MS is mean square.

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*: 0.05>p>0.01, **: 0.01>p>0.001, ***: p<0.001.

The SGRs of the taxa responded differently to food limitation as was manifested by a significant interaction between taxa and food concentration (Table 2). Both field and laboratory hybrids were growing faster than the parental species at high food concentration. At low food concentration, the differences in growth between the taxa were not large (Fig. 1).

Filtering area is dependent on body length (Fig. 2) and that can be taken into account in the analysis of covariance. After correcting for body length, the animals cultivated at low food concentration exhibited significantly larger filtering areas than animals cultivated at high food concentration (Table 2, Fig. 2). The taxa also significantly differed in their filtering area (Table 2). The filtering area (corrected for body length) of D. cucullata (adjusted mean ± SE 0.051 ± 0.004 mm²) was the smallest and that of D. galeata the largest (0.065 ± 0.004 mm²). The hybrids had intermediate filtering areas (0.061 ± 0.002 mm² and 0.066 ± 0.002 mm² for field and laboratory hybrids, respectively). Because the taxa × food interaction was not significant (Table 2) the taxa did not differ in the degree of plasticity. The developmental instability in filtering area was the highest for D. cucullata (CV=0.23), the lowest for D. galeata (CV=0.07). The hybrids had intermediate values (CV=0.09 and CV=0.14 for field and laboratory hybrids, respectively).
Clearance rate is also dependent on the size of the animal (Table 2, Fig. 3). The largest taxa, *D. galeata*, filtered more than the smaller taxa. After correcting for body length, the *Daphnia* cultivated at low food concentration exhibited significantly higher clearance rates than the *Daphnia* cultivated at high food concentration (Table 2, Fig. 3). In relation to their body size the taxa filtered at equal efficiency (Table 1).

The numbers of setae in the filter screens were not significantly affected by the food conditions (Table 2, Fig. 4). There were, however, differences between the taxa. *D. cucullata* had significantly lowest number of setae and *D. galeata* the highest. The values for the hybrids did not significantly differ from those of the parentals but were intermediate (Fig. 4).

The animals reared at the two food concentrations did not differ in mesh size (Table 2). The taxa, however, exhibited significantly different mesh sizes (Table 2). The filter screens of the hybrids had the largest meshes (mean ± SE 0.51 ± 0.03 µm and 0.49 ± 0.02 µm for field and laboratory hybrids, respectively). *Daphnia cucullata* (0.44 ±0.02 µm) and *D. galeata* (0.45 ± 0.02 µm) exhibited smaller mesh sizes.
Figure 4. Setae number of *Daphnia cucullata* (CUC), *Daphnia galeata* (GAL) and *D. cucullata × galeata* collected from the field (FCG) and *D. cucullata × galeata* from laboratory crosses (LCG) when reared under low and high concentrations of *Scenedesmus acutus*.

**Discussion**

*Daphnia* reared at low food concentration exhibited larger filter screen area than *Daphnia* reared at high food concentration. This is in accordance with earlier work (Koza and Korinek 1985; Korinek et al. 1986; Pop 1991; Lampert 1994; Lampert and Brendelberger 1996; Chapter 6). The larger filtering areas of the animals cultivated at low food level also translated into higher clearance rates. Earlier, it has been shown that area of the filtering screens and clearance rate are positively correlated in *Daphnia* (Egloff and Palmer 1971; Arruda 1983; Stuchlík 1991; Lampert 1994). In the present study, clearance rates were measured at a food concentration below the Incipient Limiting Level (0.10 mg C l⁻¹) to be able to measure close to maximal clearance rates. It was hypothesised that the advantages of a larger filter screen are evident at low food concentrations when the animal has to increase filtering effort. Generally, the clearance rates measured in this experiment were slightly higher than those reported in the literature for *D. galeata* and *D. cucullata* (see Lampert 1987 for a review). This may well result from the low algal concentration used during clearance rate measurements.

The body size of the animal was the most important factor explaining variance in clearance rate and filtering area indicating that both these features are functions of body size. Thus the largest taxon, *D. galeata*, exhibited the highest absolute filtering rate and the largest filtering area. As the smallest taxon *D. cucullata* exhibited the lowest filtering rate and the smallest filtering area. The filtering areas of the hybrids were intermediate to the parentals. Generally, the filtering areas of *D. galeata* and *D. cucullata* were in the same range as reported earlier (Brendelberger and Geller 1985; Lampert 1994).

To compare the relative filtering areas and clearance rates of the taxa these features can be statistically corrected for the body size by ANCOVA. Even after correcting for body size, the filtering areas of *D. cucullata* were smaller than that of *D. galeata*. After correcting for body size, there were, however, no differences between the taxa in clearance rate. *D. cucullata* can thus maintain relative clearance rates comparable to *D. galeata* and the hybrids even if the relative filtering area of this taxon is smaller.

The number of setae in the filter screens is specific for the examined taxa. This trait seems to be fixed within the taxon and does not show phenotypic plasticity. At low food concentrations, filtering area grows by growth of the setae not by producing more setae (Pop 1991). The filtering screens of *D. galeata* consisted of higher number of setae than those of *D. cucullata* or the hybrids. The filtering screens of *D. cucullata* had the lowest number of setae. The mesh sizes were not related to the size of the animals. *D. cucullata*, the smallest taxon and *D. galeata* the largest taxon exhibited almost identical mesh sizes. The hybrids exhibited slightly larger mesh sizes than the parental species. The mesh size was not statistically corrected for the body length because the absolute mesh sizes are relevant for resource partitioning in lakes. Earlier, Geller and Müller (1981)
reported for adult *D. cucullata* mesh sizes in the range of 0.23-0.45 μm and for adult *D. galeata* 0.32-1.0 μm. In a later study, however, *D. cucullata* was found to have larger meshes (0.63-0.88 μm vs 0.25-0.62 μm) than *D. galeata* (Brendelberger and Geller 1985). As discussed in Brendelberger and Geller (1985), the observed differences between studies may be accounted for by different habitats from which the specimens were collected. Food regime may also affect the mesh size. *D. magna* and *D. pulex* cultivated at low food concentration exhibited smaller mesh sizes than those cultivated at high food concentration (Lampert and Brendelberger 1996). We cultivated all the taxa in controlled laboratory conditions. In this study, the mesh sizes of *D. galeata, D. cucullata* and *D. cucullata* × *galeata* were not affected by the food concentrations at which the animals were cultivated. In accordance, in an earlier study with *D. galeata* the mesh size neither responded to the food concentrations (Chapter 6).

Differences in mesh sizes and SGR of the taxa indicate resource partitioning among them. This may, among other factors (Spaak 1994), account for the successful coexistence of the *D. cucullata* × *galeata* hybrid with its parental species. The competition in the field is assumed to be more severe among parental species and the hybrid than between the parental species (Boersma 1995). Our results on mesh sizes of these taxa do not, however, explain the apparent lack of competition between the parental species noticed by Boersma (1995). The mean mesh sizes of *D. cucullata* and *D. galeata* were nearly identical (0.44 vs 0.45 μm). The mesh sizes of the hybrids were larger than this. Mesh sizes of all the taxa are small enough to collect most algae and cyanobacteria. However, the smaller meshes of the parental species enable more efficient feeding on bacteria which may be important when algal food is limiting. Since water flows easier through a larger filter mesh, a filter screen with a larger mesh size is energetically less costly (Lampert and Brendelberger 1996). This might partly explain why *D. cucullata* × *galeata* hybrids at high food concentration exhibited the highest somatic growth rate of the taxa.

Spaak (1994) attributed the successful coexistence of the hybrid to its relatively high population growth rate, \( r \), and efficient avoidance of fish predation. In addition, also differences in resource utilisation contribute to the coexistence of the taxa. The somatic growth rate of the hybrids showed heterosis at high food concentrations that gives them an advantage. Somatic growth rate is a component of population growth rate and has been used to predict population growth rate (Lampert and Trubetskova 1996).

The degree of filter screen plasticity did not differ among the taxa. *D. cucullata* was developmentally more unstable than the other two taxa. In earlier empirical studies both animal and plant hybrids have shown greater variability and less developmental stability than their parental populations (Strauss 1987; Ross and Robertson 1990; Graham and Felley 1985; Leary et al. 1985). Probably phenotypic plasticity and developmental stability are not tightly related to the heterozygozity of a hybrid taxon due to disruption of coadapted loci.

The field and laboratory hybrids did not differ in any of the measured parameters. Although field and laboratory hybrids differed in their origin, they showed a high level of similarity in the traits measured in this study. Because the field hybrids originated from the same lake and were collected at the same time, they have encountered the same selective factors. Therefore, one would expect them to show less variation than hybrids collected from different lakes or at different times. Because laboratory hybrids in this study shared the same parental clones they should show less variation than hybrids with more diverse origin. In particular the heterotic effects in SGR and ME in field and laboratory hybrids indicate which traits facilitate coexistence with parental taxa.

To conclude, phenotypic plasticity in filtering area enabled higher clearance rates in low food adapted *D. galeata, D. cucullata* and their interspecific hybrid *D. cucullata* × *galeata*. In relation to the body length, the clearance rates of the taxa were similar. At high food concentrations, the hybrids might have an advantage over the parental species as indicated by the highest somatic growth rates. The larger mesh size of the hybrids allows niche segregation and may contribute to the successful coexistence of the hybrid with its parental species. The differences among the taxa may contribute to the seasonal succession observed in the lakes.
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References


