The effect of food quantity and food quality on Daphnia: morphology of feeding structures and life history.
Repka, S.H.

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Effects of food type on the life history of *Daphnia* clones from lakes differing in trophic state. II. *Daphnia cucullata* feeding on mixed diets*

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**SUMMARY**

1. The effects of feeding on suboptimal foods were investigated in *Daphnia cucullata* a zooplankton common in many types of lakes. Eleven clones of *D. cucullata* were collected from four lakes of varying trophic levels and fed a high (1 mg C l⁻¹) concentration of one of two diets: (i) a 1:9 mixture of the cryptophyte *Cryptomonas pyrenoidifera* with the green alga *Scenedesmus obliquus*; and (ii) a 1:9 mixture of the cryptophyte *C. pyrenoidifera* with the filamentous cyanobacterium *Oscillatoria limnetica*.

2. As expected, the diet dominated by *Oscillatoria* was found to be significantly poorer compared with the diet dominated by *Scenedesmus*. All *D. cucullata* clones were, however, able to achieve positive population growth rates on both diets, supporting the view that daphnids can grow and reproduce on a diet dominated by filamentous cyanobacteria.

3. Clones originating from different types of lakes differed in their responses to the two diets. On the *Scenedesmus*-dominated diet, clones originating from moderately eutrophic lakes had lower population growth rates than clones from hypertrophic lakes. In contrast, on the *Oscillatoria*-dominated diet, the clones from moderately eutrophic lakes had higher population growth rates than clones from hypertrophic lakes. Contrary to expectation, clones originating from lakes dominated by filamentous cyanobacteria had more difficulty utilizing filamentous cyanobacteria as food than clones from less eutrophic lakes which contain less filamentous cyanobacteria.

4. As the reactions of clones originating from same type of lake resembled each other, it is hypothesized that the life histories of *D. cucullata* populations are locally adapted to environmental factors other than abundance of filamentous cyanobacteria, which are correlated with trophic levels.

**Introduction**

In another paper (Repka, 1997) the life history responses of several *Daphnia galeata* Sars clones were described when fed a diet consisting solely of *Oscillatoria limnetica* or *Scenedesmus obliquus*. In the present study, a smaller *Daphnia* species was used, *Daphnia cucullata* Sars. *Daphnia galeata* and *D. cucullata* coexist in various European lakes and are able to produce interspecific hybrids (Schwenk & Spaak, 1995). Although these two species are so closely related that they can hybridize, they still differ in many respects including morphology, behaviour and life history. For the present study, the most relevant differences can be found in the morphology of the feeding apparatus and life history characters of these two species.

In *Daphnia*, large spherical particles and colonies of cells are kept out of the feeding chamber because their size exceeds the size of the carapace gape. Smaller species of *Daphnia* have a smaller gape between the
edges of the carapace valves and thus, large, potentially harmful particles, like long filaments, are more efficiently kept outside the feeding chamber (Gliwicz, 1980; Gliwicz & Siedlar, 1980). This has been proposed as a mechanism promoting the success of smaller cladocera species in lakes where large inedible algae are abundant (Gliwicz, 1977; Webster & Peters, 1978). The mesh size of the filtering appendages is larger in some smaller species, which makes them less efficient bacteria-feeders than larger species; for example, the mesh size has been reported to be around 0.6 μm in adult D. galeata and around 0.9 μm in adult D. cucullata (Brendelberger & Geller, 1985). In a laboratory life history experiment, the population growth rate, r, for D. cucullata showed less variability in relation to food concentration than that of D. galeata (Boersma & Vijverberg, 1994a). Although at a low food concentration the r of D. cucullata decreased less than that of D. galeata, D. galeata exhibited a higher rate of increase at all food concentrations tested by Boersma & Vijverberg (1994a).

In earlier studies, it has been shown that D. galeata, D. cucullata and their interspecific hybrid, D. cucullata × galeata, can achieve positive population growth rates (r) on a diet consisting solely of the filamentous cyanobacterium O. limnetica Lemm. (Repka, 1996; Repka, 1997). The r reached on a diet of filamentous cyanobacteria is, however, markedly lower than on a good quality diet of the green alga Scenedesmus (Repka, 1996; Repka, 1997). In nature, zooplankton are unlikely to encounter a diet consisting of a single species. In this experiment, the aim was to simulate a more natural situation by adding a small amount of good quality food, Cryptomonas pyrenoidifera Geitler, to predominantly S. obliquus Kütz. and O. limnetica diets. All of these algae species are common in West European lakes. Both Scenedesmus and Oscillatoria contain considerable amounts of linolenic acid, but unlike Cryptomonas, lack eicosapentaenoic acid (EPA; Repka, 1997; Weers, Siewertsen & Gulati, 1997). EPA seems to be important for Daphnia growth (Müller-Navarra, 1995) and could nutritionally complement the lack of long-chained polyunsaturated fatty acids (PUFA) in the Scenedesmus and Oscillatoria diets. If adding Cryptomonas to the Oscillatoria diet clearly increased the population growth rate of the herbivore, this would underline the importance of the nutritional inadequacy of Oscillatoria. If not, the decreased manageability of Oscillatoria filaments probably poses the largest problem. On the other hand, if linolenic acid is sufficient for good growth, there should be little difference between the diet with Scenedesmus added and the diet with Cryptomonas added.

The objective of this study was threefold. First, to compare the growth and reproduction of D. cucullata, on a diet dominated by filamentous cyanobacterium with a diet dominated by green algae. Second, to try to distinguish between the roles of manageability and nutritional quality of food, the two most important factors determining the value of non-toxic food particles for Daphnia. Third, to compare the life history responses of clones originating from lakes with varying trophic levels.

**Materials and methods**

As the methods used in the present study and the earlier one were very similar, information about *Daphnia* and algae cultures, experimental design and statistical analyses of the data are not repeated here but given in Repka (1997). Only details about the methods which are specific to the present study are mentioned here.

In the present study, eleven *D. cucullata* clones were used. The clones originated from four lakes located in the Netherlands and northern Germany. Information about the lakes is given in Table 1. Genetic distinctness was examined in German clones by cellulose acetate electrophoresis (Spaak, 1995) and in Dutch clones by polymerase chain reaction (PCR; Schwenk, 1993).

Each of the eleven clones was exposed to two food treatments in a life history experiment. There were ten replicates in each cell, thus the total number of daphnids used in the experiment was 220. The culture medium for the *Daphnia* was filtered (0.45 μm) and

<table>
<thead>
<tr>
<th>Lake</th>
<th>Chlorophyll-a (μg l⁻¹)</th>
<th>Clear-water phase</th>
<th>Clones</th>
</tr>
</thead>
<tbody>
<tr>
<td>Loosdrecht (NL)</td>
<td>200</td>
<td>No</td>
<td>L1, L2</td>
</tr>
<tr>
<td>Breukelevenen (NL)</td>
<td>200</td>
<td>No</td>
<td>Br1, Br2</td>
</tr>
<tr>
<td>Belauerssee (GE)</td>
<td>30-100</td>
<td>Yes</td>
<td>Bet, Be2</td>
</tr>
<tr>
<td>Plüssee (GE)</td>
<td>10-100</td>
<td>Yes</td>
<td>P1, P2, P3, P4</td>
</tr>
</tbody>
</table>
 aged (24 h) Lake Maarsseveen water, supplemented with either a mixture of 0.9 mg C l-1 of S. obliquus (c. 49 500 cells ml-1) and 0.1 mg C l-1 of C. pyrenoidifera (c. 3000 cells ml-1) or a mixture of 0.9 mg C l-1 of O. limnetica (c. 49 320 filaments ml-1) and 0.1 mg C l-1 of Cryptomonas.

Analysis of variance and multiple regression for various life history parameters were performed as in Repka (1997). In the present analysis, however, the age at first reproduction and cumulative number of juveniles in the first three adult instars were transformed (y = x^0.7) before performing an analysis of variance to remove a correlation between mean and variance. The body lengths in each instar were analysed with repeated measures ANOVA (Potvin, Lechowicz & Tardif, 1990).

Results
The population growth rate (r) was clearly lower in all clones on an Oscillatoria-dominated diet than on a Scenedesmus-dominated diet. The range of r-values was from 0.04 to 0.15 day-1 on the former diet and from 0.17 to 0.24 day-1 on the latter (Fig. 1). The German clones responded differently to the food types than the Dutch clones. While the German clones were characterized by a moderate r-value on both diets, the reaction of the Dutch clones was more extreme (Fig. 1). In addition to significant differences between the diets and clones, the food × population interaction was significant in population growth rate, r (Table 2).

The cumulative number of neonates in the first three adult instars was comparable to the results for population growth rate. This was expected since the number of neonates is an important constituent in the calculation of r. There were significantly more neonates on the Scenedesmus diet compared with the Oscillatoria diet (Table 2). In general, the German clones from both Plüßsee and Belauersee responded similarly: both exhibited moderate reproduction on the Scenedesmus- and the Oscillatoria-dominated diets. In contrast, the reproduction of the Dutch clones was higher on the Scenedesmus diet but was severely reduced on the Oscillatoria diet (Fig. 2). This was manifested as a significant food × population interaction (Table 2).

Most clones reproduced at an older age when fed Oscillatoria. Summed over all clones, the age at first reproduction ± SE was 8.9 ± 0.2 for Scenedesmus and 9.8 ± 0.2 for Oscillatoria. There were exceptions to this general pattern: both clones from Belauersee started to reproduce earlier on Oscillatoria and the clones from Loosdrecht reproduced at about the same age on both food types. This was the cause of a marginally significant food × population interaction in the ANOVA (Table 2). Most animals matured at the fourth instar, although some animals from both food types matured in the fifth or sixth instar. Thus, although the animals delayed their time to first reproduction on the Oscillatoria diet, the difference in the juvenile period could not be ascribed to a difference in the number of juvenile instars. The mean reproductive instar was 4.30 ± 0.05 for Scenedesmus and 4.50 ± 0.07 for Oscillatoria. The duration of the first instar was increased on average by 20.1%. The durations of other juvenile instars differed less between the diets and there were no diet-dependent differences in the durations of the adult instars.

The animals reproduced at a significantly smaller size on the Oscillatoria diet (0.835 ± 0.006 μm) than on the Scenedesmus diet (0.875 ± 0.008 μm). Populations also differed in their size at first reproduction (Table 2). Clones from Belauersee were the largest and clones from Plüßsee the smallest.
Table 2. Results of a three-way ANOVA on selected life history characteristics of Daphnia cucullata. The effects of food (F), clone (C) and population (P) were analysed on the cumulative number of juveniles from the first three adult instars, the size of the neonates from second adult instar, size at first reproduction and the population growth rate, $r$. MS, mean square

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>MS</th>
<th>F</th>
<th>P</th>
<th>d.f.</th>
<th>MS</th>
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<th>P</th>
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<tr>
<td>Cumulative number of juveniles</td>
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<td></td>
</tr>
<tr>
<td>F</td>
<td>1</td>
<td>259.03</td>
<td>223.29</td>
<td>0.0001***</td>
<td>1</td>
<td>0.0067</td>
<td>12.88</td>
<td>0.0071**</td>
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<tr>
<td>C(P)</td>
<td>8</td>
<td>4.31</td>
<td>5.06</td>
<td>0.0001***</td>
<td>8</td>
<td>0.0101</td>
<td>2.92</td>
<td>0.0048**</td>
</tr>
<tr>
<td>P</td>
<td>3</td>
<td>12.20</td>
<td>2.83</td>
<td>0.163NS</td>
<td>3</td>
<td>0.0072</td>
<td>7.47</td>
<td>0.0105*</td>
</tr>
<tr>
<td>F × C(P)</td>
<td>8</td>
<td>1.16</td>
<td>1.36</td>
<td>0.216NS</td>
<td>8</td>
<td>0.0005</td>
<td>1.56</td>
<td>0.1405NS</td>
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<tr>
<td>F × P</td>
<td>3</td>
<td>9.06</td>
<td>7.81</td>
<td>0.0092**</td>
<td>3</td>
<td>0.004</td>
<td>0.82</td>
<td>0.5191NS</td>
</tr>
<tr>
<td>Error</td>
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<td>136.15</td>
<td></td>
<td></td>
<td>143</td>
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<td></td>
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</tr>
<tr>
<td>Neonate size (2nd brood)</td>
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<td></td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>F</td>
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<td>15.71</td>
<td>0.0042**</td>
<td>1</td>
<td>0.084</td>
<td>156.57</td>
<td>0.0001**</td>
</tr>
<tr>
<td>C(P)</td>
<td>8</td>
<td>0.012</td>
<td>4.76</td>
<td>0.0001***</td>
<td>8</td>
<td>0.012</td>
<td>3.83</td>
<td>0.0028**</td>
</tr>
<tr>
<td>P</td>
<td>3</td>
<td>0.009</td>
<td>7.35</td>
<td>0.0110*</td>
<td>3</td>
<td>0.0018</td>
<td>1.53</td>
<td>0.2807NS</td>
</tr>
<tr>
<td>F × C(P)</td>
<td>8</td>
<td>0.004</td>
<td>1.57</td>
<td>0.1367NS</td>
<td>8</td>
<td>0.0005</td>
<td>1.73</td>
<td>0.1286NS</td>
</tr>
<tr>
<td>F × P</td>
<td>3</td>
<td>0.002</td>
<td>0.55</td>
<td>0.6630NS</td>
<td>3</td>
<td>0.0051</td>
<td>9.43</td>
<td>0.0053**</td>
</tr>
<tr>
<td>Error</td>
<td>160</td>
<td>0.003</td>
<td></td>
<td></td>
<td>33</td>
<td>0.0003</td>
<td></td>
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<tr>
<td>Size at first reproduction</td>
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<td></td>
</tr>
<tr>
<td>F</td>
<td>1</td>
<td>24.64</td>
<td>18.53</td>
<td>0.0026**</td>
<td>1</td>
<td>0.034</td>
<td>15.57</td>
<td>0.0001**</td>
</tr>
<tr>
<td>C(P)</td>
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<td>1.78</td>
<td>0.0842</td>
<td>8</td>
<td>0.0012</td>
<td>3.83</td>
<td>0.0028**</td>
</tr>
<tr>
<td>P</td>
<td>3</td>
<td>10.50</td>
<td>3.49</td>
<td>0.0700</td>
<td>3</td>
<td>0.0018</td>
<td>1.53</td>
<td>0.2807NS</td>
</tr>
<tr>
<td>F × C(P)</td>
<td>8</td>
<td>1.33</td>
<td>0.80</td>
<td>0.6008NS</td>
<td>8</td>
<td>0.0005</td>
<td>1.73</td>
<td>0.1286NS</td>
</tr>
<tr>
<td>F × P</td>
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<td>3.96</td>
<td>2.98</td>
<td>0.0964</td>
<td>3</td>
<td>0.0001</td>
<td>9.43</td>
<td>0.0053**</td>
</tr>
<tr>
<td>Error</td>
<td>156</td>
<td>1.66</td>
<td></td>
<td></td>
<td>33</td>
<td>0.0003</td>
<td></td>
<td></td>
</tr>
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</table>

NS, non-significant; *0.01 < P < 0.05; **0.0001 < P < 0.01; ***P < 0.0001.

The Oscillatoria-fed animals were always smaller than the Scenedesmus-fed animals (Fig. 3). There were also differences between the populations in growth. The two clones from Belauersee were the largest in every instar (Fig. 3). Furthermore, the clones within the populations differed. These effects were shown by the repeated-measures ANOVA as significant main effects for food, population and clone for sizes at different instars (Table 3). The growth response to the two diets varied widely between clones. The growth of clones P2, P3, P4, L4 and Be2 differed very little between the food types, whereas in other clones the difference was much larger. These differences were manifested as a significant food × clone interaction (Table 3).

The newborn size (from fifth instar of the mother) was also affected by food type (Table 2), but the effect was minor. The mean length of the neonates was 0.417 ± 0.002 µm on the Scenedesmus diet and 0.407 ± 0.003 on the Oscillatoria diet. The populations differed significantly in neonate size; the German clones (0.430 ± 0.004 µm, 0.413 ± 0.002 µm for Belauersee and Plütssee, respectively) being larger than the Dutch clones (0.403 ± 0.003 µm, 0.400 ± 0.005 µm for Breukeleveen and Loosdrecht, respectively). The size of the mother was the most important factor affecting the neonate size (multiple regression, slope = 0.162, P = 0.00000). Larger mothers produced larger juveniles. However, the food type also affected the neonate size, the neonates born on the Oscillatoria diet being smaller (slope = -0.0102, P = 0.02685). In addition, number of neonates in the brood was negatively related to the size of neonates (slope = -0.0015, P = 0.00221).

Discussion

As in earlier studies with daphnids feeding on the filamentous cyanobacterium O. limnetica (Repka, 1996; Repka, 1997), D. cucullata was able to grow and reproduce on a diet dominated by this cyanobacterium. The growth and reproduction were, however, severely decreased compared to a diet dominated by the green algae S. obliquus. EPA contents of the diets were nearly identical and could not account for the observed differences in growth and reproduction. Furthermore, Oscillatoria has a considerable amount of linolenic acid, unlike some other cyanobacteria species like the...
Synechococcus used by DeMott & Müller-Navarra (1997).

In contrast to earlier studies where single-species diets were used (Repka, 1996; Repka, 1997), diets primarily of Oscillatoria and Scenedesmus were supplemented with a good quality food source Cryptomonas. The population growth rate achieved on the diet dominated by Scenedesmus, 0.20 day\(^{-1}\), is higher than that reported for D. cucullata (0.10-0.12 day\(^{-1}\)) in earlier studies (Ebert & Jacobs, 1991; Weider & Wolf, 1991; Boersma & Vijverberg, 1994a; Spaak & Hoekstra, 1995). These differences can be caused by the use of different clones and culturing conditions. The positive effect of Cryptomonas on growth and reproduction of daphnids, as noticed earlier by Ahlgren et al. (1990), may also be responsible for the higher r-values in the present study.

The fatty acid (FA) composition of the strain of C. pyrenoidifera used in this experiment has been reported in Weers et al. (1997) and that of S. obliquus and O. limnetica in Repka (1997). Supplementing the 0.9 mg C I\(^{-1}\) of Oscillatoria or Scenedesmus with 0.1 mg C I\(^{-1}\) of Cryptomonas added c. 2.1 µg C I\(^{-1}\) EPA FA to the diet. Müller-Navarra (1995) found correlations of data from the field EPA to be important to Daphnia performance. She observed Daphnia growth to reach a plateau at a concentration around 0.8 µg C I\(^{-1}\) EPA. Thus, adding 0.1 mg C I\(^{-1}\) Cryptomonas (c. 2.1 µg C I\(^{-1}\) EPA) to the diet of Oscillatoria should be enough to fulfil the Daphnia requirements for EPA even if some Cryptomonas cells were rejected with the filaments.

By comparing the results of D. cucullata growing on a sole diet of Oscillatoria and Oscillatoria mixed with Cryptomonas, it is possible to draw conclusions about the relative importance of manageability and biochemical constitution in determining the food value of Oscillatoria to D. cucullata. On a sole diet of 1.0 mg C I\(^{-1}\) Oscillatoria, the cumulative amount of neonates produced in three adult instars was 5.0 ± 1.0 (Repka, 1996). In the present study, on a mixture of 0.9 mg C I\(^{-1}\) Oscillatoria and 0.1 mg C I\(^{-1}\) Cryptomonas, it was 5.7 ± 0.2. Both these values were significantly lower than those achieved on a good quality diet in this experiment, 12.9 ± 0.5 neonates. Different clones were used in the two experiments but environmental factors like temperature and photoperiod were kept...
the same. Thus, it was concluded that adding a low amount of Cryptomonas and slightly decreasing the amount of filaments did not considerably improve the diet of Oscillatoria for D. cucullata. Probably the biochemical inadequacy, namely FA composition, is of minor importance compared to manageability in decreasing the growth and reproduction of D. cucullata on a diet of Oscillatoria.

The performance of smaller species of cladocera seem to be less affected by filaments than that of larger species (Webster & Peters, 1978; Porter & McDonough, 1984; Hawkins & Lambert, 1989). If the slighter effects of filaments on growth and reproduction of smaller species are due to the narrower carapace gape opening protecting them from the harmful effects of long filaments, as suggested by Gliwicz (1980) and Gliwicz & Siedlar (1980), or other differences between the species is yet unclear. That other differences between the species might also be involved is supported by the observation that D. cucullata was characterized by lower and more constant r-values when fed on low quantities of good quality food compared to a larger species, D. galeata (Boersma & Vijverberg, 1994a). D. galeata had a clearly higher r-value on high food concentration but was more severely affected by resource limitation. Still, the r of D. galeata remained higher than the r of D. cucullata (Boersma & Vijverberg, 1994a). These results are comparable to results obtained on D. galeata and D. cucullata feeding on Scenedesmus and Oscillatoria diets (Repka, 1996; Repka, 1997). The differing effects of resource limitation on the r of D. galeata and D. cucullata noticed by Boersma & Vijverberg (1994a) cannot be caused by interspecific differences in carapace gape, because the food species (Scenedesmus and Chlamydomonas) used in their experiments were in suitable size ranges to be easily grazed upon by both Daphnia species.

There was a difference produced between the two diets on juvenile instar durations. The duration of the first juvenile instar was greatly increased on the Oscillatoria diet. In contrast to D. galeata (Repka, 1997), there were no differences in the number of juvenile instars. Boersma & Vijverberg (1994a) also noticed an increase in the duration and number of juvenile instars in D. cucullata under resource limitation.

Neonate size was influenced by maternal length, food quality and the number of neonates. As in earlier studies with Daphnia (Green, 1956; Gliwicz & Guisande, 1992; Ebert, 1993), maternal size was positively correlated to neonate size. After controlling for the mother size, the neonates were born smaller on the diet dominated by Oscillatoria. There was also a negative relationship between number and size of neonates. Negative correlations between offspring size and number in cladocera have more often been found under poor or intermediate food conditions than under rich conditions (see review in Ebert, 1993).

Within-species variation in reaction to these two diets was clear. Similar to results with D. galeata (Repka, 1997), the D. cucullata clones originating from the same lake resembled each other in their reactions. In many temperate lakes, a clear-water phase with very low algal densities is observed in late spring as a consequence of zooplankton grazing (Sommer et al., 1986). In some highly eutrophic Dutch lakes, however, clear-water periods are not observed but the lakes are dominated by filamentous cyanobacteria during the whole growing season (van Donk et al., 1990; Lammens et al., 1992). This has led to the hypothesis that predation is a more important factor regulating popula-

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Table 3 Results of a repeated-measures ANOVA on a life history experiment of Daphnia cucullata. The effects of food (F), clone (C) and population (P) were investigated on the sizes in instars (1-7). Instar (I) was used as a blocking factor. MS, mean square

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>MS</th>
<th>F</th>
<th>P</th>
<th>Source</th>
<th>d.f.</th>
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<th>P</th>
</tr>
</thead>
<tbody>
<tr>
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<td></td>
<td></td>
<td></td>
<td>Within-subject effects</td>
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<tr>
<td>F</td>
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<td>36.23</td>
<td>0.0003**</td>
<td>I</td>
<td>1</td>
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<td>12.58</td>
<td>0.0071*</td>
</tr>
<tr>
<td>C(P)</td>
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<td>0.0010**</td>
<td>I × F</td>
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<td>0.0010</td>
<td>2.92</td>
<td>0.0048**</td>
</tr>
<tr>
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</tr>
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<td>0.017</td>
<td>0.91</td>
<td>0.4801NS</td>
<td>I × F × C(P)</td>
<td>3</td>
<td>0.0004</td>
<td>0.82</td>
<td>0.5191NS</td>
</tr>
<tr>
<td>Error</td>
<td>143</td>
<td>0.008</td>
<td></td>
<td></td>
<td>I × F × P</td>
<td>18</td>
<td>0.0002</td>
<td>1.42</td>
<td>0.1678NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Error</td>
<td>858</td>
<td>0.0008</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

NS, non significant; *0.01 < P < 0.05; **0.001 < P < 0.01; ***P < 0.0001.
tions of herbivorous zooplankton than food limitation in these highly eutrophic lakes (Vijverberg & Richter, 1982a, b; Hanazato & Yasuno, 1985; but see Boersma & Vijverberg, 1994b). The task of selecting the lakes from which to collect the clones was not easy. The aim of the present study was to compare hypertrophic Dutch lakes dominated by filamentous cyanobacteria with clear-water phases and less filamentous cyanobacteria. As it was not possible to find such lakes in the Netherlands, two lakes from northern Germany were chosen. The geographical distance could have resulted in other, unknown differences between the populations.

Similarly to the results with *D. galeata*, the clones from two hypertrophic Dutch lakes were not better in utilizing *Oscillatoria* as food than clones from less hypertrophic lakes. The former exhibited high rates of reproduction on the *Scenedesmus* diet, but low rates of reproduction on the *Oscillatoria* diet compared to the latter. Thus, these clones showed smaller differences in growth between the two diets. The lack of a clear-water phase in hypertrophic lakes suggests that the grazers have plenty of food, although of suboptimal quality, during the whole growth period. In these highly eutrophic lakes, the amount of detritus originating from filamentous cyanobacteria can exceed the amount of live filaments (Gons et al., 1992). Detritus may be better food for grazers than live filaments because of reduced size and attached bacteria (Gulati et al., in preparation). As the clones from lakes with clear-water phase are temporarily subjected to more severe food limitation, starvation resistance might be more important to success in these less eutrophic lakes. Although other factors cannot be ruled out, local adaptation to food conditions (food limitation) may play a role in explaining the different reactions of clones from contrasting lakes to the *Oscillatoria* diet. More experimental work in concert with detailed field observations will be necessary to improve our insight into the physiological and genetic basis of the adaptations of herbivorous zooplankton to local food conditions.

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**References**


Ebert D. & Jacobs J. (1991) Differences in life-history and reproduction on the *Oscillatoria* diet compared to the latter. Thus, these clones showed smaller differences in growth between the two diets. The lack of a clear-water phase in hypertrophic lakes suggests that the grazers have plenty of food, although of suboptimal quality, during the whole growth period. In these highly eutrophic lakes, the amount of detritus originating from filamentous cyanobacteria can exceed the amount of live filaments (Gons et al., 1992). Detritus may be better food for grazers than live filaments because of reduced size and attached bacteria (Gulati et al., in preparation). As the clones from lakes with clear-water phase are temporarily subjected to more severe food limitation, starvation resistance might be more important to success in these less eutrophic lakes. Although other factors cannot be ruled out, local adaptation to food conditions (food limitation) may play a role in explaining the different reactions of clones from contrasting lakes to the *Oscillatoria* diet. More experimental work in concert with detailed field observations will be necessary to improve our insight into the physiological and genetic basis of the adaptations of herbivorous zooplankton to local food conditions.

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