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

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CHAPTER 8

Concluding remarks

The quantity and quality of edible particles for Daphnia (0.5-40 μm) vary greatly in lakes due to seasonal succession of phytoplankton. Good quality food algae, cryptomonads and green algae, often dominate early in the season. This period is often succeeded by a period of low algal concentrations due to grazing of zooplankton. Relatively grazing resistant, autotrophs, mostly cyanobacteria, dominate after the clear water phase (Sommer et al. 1986). In this study, it was revealed that the filamentous cyanobacterium Oscillatoria limnetica is of low food quality for the Daphnia mainly because of its shape that interferes with the feeding process. In addition, the P-content of Oscillatoria was lower than that of a high quality food source, the green alga Scenedesmus acutus. Polyunsaturated fatty acid (PUFA) contents of O. limnetica, however, did not greatly differ from those of S. acutus and thus are not the reason of the relatively low food quality. Although the potential population growth rate of Daphnia on a diet of O. limnetica is low, it is positive. Thus, Daphnia populations can persist on a diet dominated by filamentous cyanobacteria.

In highly eutrophic lakes, seasonal succession of algae and cyanobacteria is weak. These lakes are dominated by cyanobacteria and their detritus during the growing season. Detritus derived from filamentous cyanobacteria is often more abundant than algae or cyanobacteria in highly eutrophic lakes (Gons et al. 1992). Therefore, it is at least quantitatively an important food source for Daphnia in these lakes. Detritus derived from O. limnetica was clearly of better food quality than live filaments probably due to smaller size and to the bacteria attached to the dead organic material. Abundance of detritus makes highly eutrophic lakes better food environments than previously thought.

I wanted to compare the life-history traits of Daphnia clones collected from highly eutrophic lakes to the life history traits of Daphnia clones collected from mesotrophic lakes. Indeed, when offered S. acutus and O. limnetica as food, a significant proportion of variation in life-history traits of these clones was explained by the lake of origin. The variation could not, however, be explained by historical selection for exploiting different food sources. The growth rates of the larger sized D. galeata clones were more depressed on a diet of Oscillatoria than that of the smaller sized clones. D. cucullata clones from highly eutrophic lakes were doing worse on an Oscillatoria diet than clones from mesotrophic lakes. Thus Daphnia clones from highly eutrophic lakes showing long periods with cyanobacterial abundance were not more efficient in utilising Oscillatoria as food than other clones. One would expect these clones, being constantly faced with high concentrations of filamentous cyanobacterium in their natural habitat, to be adapted. Some genetical variation for utilisation of filamentous Oscillatoria was, however, observed. The clone-specific efficiency to utilise filamentous cyanobacteria as food was indicated to be correlated to body size. The width of carapace gape is related to the size of the animal and would influence the size spectrum of the particles entering the animal. This is crucial for preventing the very long and harmful filaments from entering the feeding chamber (Gliwicz and Siedlar 1982). Differences in width of carapace gape may explain why larger Daphnia species and clones do worse on a diet including filaments than smaller species and clones (Gilbert 1990). Size of the animal, however, is selected also by other in situ factors than just the proportion of filaments in the diet. The size-selective predation on Daphnia and the concentration and quality of food particles in the environment are also of importance. Under low positive size-selective predation by fish, larger Daphnia that can carry more eggs than smaller adults, will have higher fitness. Also under conditions of high negative size-selective predation by invertebrate predators the larger bodied daphnids will have a higher fitness than the smaller bodied daphnids. On the other hand, under
intensive fish predation the smaller individuals have a selective advantage. No quantitative information about the intensity of size-selective predation and the food conditions in the lakes where Daphnia was collected is available. Therefore, it is not possible to explain fully the size composition of Daphnia populations in these lakes.

In order to cope with variable food regimes the daphnids have to be plastic. Indeed, all the Daphnia taxa studied exhibited considerable plasticity in filter screen morphology in response to food concentrations. The plasticity probably is adaptive because at low food concentrations filtering rate is increased (Egloff and Palmer 1971; Arruda 1983; Stuchlik 1991; Lampert 1994; Chapter 7). There are usually costs of plasticity because sensory and regulatory mechanisms have to be maintained. Estimating the cost of plasticity is, however, difficult (Dewitt et al. 1998). By feeding the daphnids with food types of varying quality, it was revealed that the individuals use their own nutritional condition as a cue for the filtering area plasticity. Animals in good condition (i.e. high growth rate) exhibited smaller filtering areas in relation to their body length than food limited animals. It was hypothesised that, if plasticity is costly, clones originating from lakes with high particle concentrations during the whole growing season might lose or diminish plasticity. This was, however, not the case. A possible explanation for this phenomenon is that, the phytoplankton of highly eutrophic lakes also vary as food environments for Daphnia although the particle concentrations expressed as carbon remain high during the growing season. Yet, the food quality and thus the condition of Daphnia can be poor in highly eutrophic lakes (Boersma and Vijverberg 1994). Daphnia individuals assess the food availability from their own physical condition and grow larger filtering area when food is limiting. Thus, at times of low food quality (but high quantity) Daphnia from highly eutrophic lakes will exhibit large filter screens. This might not be advantageous for the animal because collecting larger amounts of low quality food (e.g. filaments) does not necessarily improve the condition of the animal. On the contrary, if more postabdominal rejection movements are needed to clean the filtering screens of unwanted particles, energy may even be lost upon feeding. Specific adaptations in filtering screens of Daphnia from highly eutrophic lakes seem, however, not to have evolved. It may be that adaptations are not needed, but some degree of plasticity is in the long run advantageous in both mesotrophic and highly eutrophic lakes. On the other hand, the evolution of filter screen adaptations may be constrained.

In the present study I investigated the abilities of three coexisting Daphnia taxa to utilise food particles of differing quantity and quality. The coexistence of D. cucullata x galeata hybrids with their parental species has been studied earlier by Boersma (1994) and Spaak (1994). Spaak (1994) attributed the successful coexistence of the hybrids to their relatively high potential population growth rate, r, and to their efficient avoidance of fish and invertebrate predation. These traits give the hybrids a temporal advantage in certain conditions, e.g. when both fish and invertebrate predation is intense. The successful coexistence of the hybrids with their parental species is, however, also affected by food conditions. D. cucullata exhibits relatively low and constant potential population growth rate, r, on varying food conditions (Boersma 1994; Chapter 2). Hybrids, however, exhibited the largest variation in potential r and somatic growth rate (Boersma 1994; Chapter 7). The population growth rates and somatic growth rates of the hybrids were the lowest at low food concentrations and the highest at high food concentrations (Boersma 1994, Chapter 7). Thus, hybrids have a selective advantage at high food concentrations. Present study showed that the mesh size of the hybrids' filter screens is larger than that of the parental species and this difference might also facilitate niche segregation of the hybrids and their parentals. The parental species can more readily utilise smaller food particles (bacteria) than the hybrid which is of advantage at limiting food concentrations. However, at non-limiting food concentrations the larger mesh size of the hybrids may be more effective because water flows easier through larger pores. The growth and reproduction of D. cucullata were the least depressed by feeding on low quality food particles, the filamentous cyanobacterium O. limnetica. Thus, D. cucullata will improve its competitive status when filaments are abundant (Chapter 2). In eutrophic lakes, D. galeata and the D. cucullata x galeata hybrids are often dominant in early spring, early summer and autumn. D. cucullata is generally
dominant during a relatively short period in summer (Boersma 1995, Spaak and Hoekstra 1995, Schwenk 1997). Increasing abundance of filamentous cyanobacteria in the diet in this summer period may trigger this seasonal pattern, but also the selective role of increased fish predation may stimulate *D. cucullata* abundance.

*Daphnia* taxa exhibit considerable plasticity in life history traits and filter screen morphology in response to food conditions, but clonal differences in these traits are minor. However, taxa-specific differences in food utilisation can, together with fish predation, explain the seasonal patterns noticed in lakes.
References


