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

Citation for published version (APA):

General rights
It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations
If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: http://uba.uva.nl/en/contact, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.
CHAPTER 1.

Introduction and outline of the thesis

Scientific background

It is usually assumed that different food resources are nearly identical in nutritional value (Westoby 1978) so that their energy content is decisive for consumers (Schoener 1971, Pyke et al. 1977). However, this assumption is probably not valid for herbivorous organisms. Herbivore food varies more than that of carnivores (Pulliam 1974, Pyke et al. 1977). It has been suggested that herbivores maximize the intake of several nutrients at the same time (Belowsky 1978, Abrams 1987, Tilman 1988). Some recent articles about diet selection have indeed shown that herbivores grew better on a mixture of food types than on any type alone, suggesting that resources can be complementary (Pennings et al. 1993; Gulati and DeMott 1997).

Zooplankton graze mainly on phytoplankton and cyanobacteria, the biochemical composition of which varies greatly. As all organisms, these food types consist mainly of carbohydrates and fat (C), proteins (N) and nucleic acids (P). In addition, other chemical compounds, including a diverse group of secondary metabolites and toxins, are found (e.g. Lewin 1962). There are not only differences in biochemical composition among phytoplankton species, but biochemical composition of same species changes in response to environmental conditions (Wetzel 1982). The literature on food quality for zooplankton growth and reproduction mainly considers two limiting factors, i.e. phosphorus (nucleic acids) and fatty acids (review in: Gulati and DeMott 1997). Generally, the evidence for the first component is stronger than that for the latter. Nevertheless, food components are not mutually exclusive factors but may control the growth of zooplankton in conjunction (Gulati and DeMott 1997).

Seasonal variability in the density and species composition of phytoplankton in freshwater water bodies is large and the algae and cyanobacteria species are variable in size, shape and biochemical composition (Wetzel 1982, Sommer et al. 1986). According to field studies, the C, P and N-contents of a zooplankton species are more constant than that of their phytoplankton food (Andersen and Hessen 1991). Therefore, the food quantity and food quality for the aquatic herbivores vary considerably both spatially and temporally. In order to survive, herbivorous zooplankton must cope with different quantities and qualities of food. A population
can adapt to temporally and spatially variable food resources if genotypic and/or phenotypic variation exists.

The study organism
The central position of the genus *Daphnia* (Crustacea, Cladocera) in the freshwater food webs of the temperate region has attracted interest to its food uptake and utilization. The feeding and nutrition of *Daphnia* are important to both the impacts on bacterial and algal populations and the conversion of food into body mass and eggs. *Daphnia* biomass in its turn is used as food by fish and invertebrate predators (e.g. Reede 1998). *Daphnia*, like insects, shed the old skin (i.e. carapace) by molting in order to grow. At 18 °C, *Daphnia* molts approximately every three days. Depending on the species and growth conditions, it takes 3 to 5 instars to reach maturity. The maximum life-span of a *Daphnia* is 2-3 months.

*Daphnia* commonly reproduce by cyclic parthenogenesis that is characterized by one or more parthenogenetic generations alternating with a sexual generation. Cyclic parthenogenesis gives *Daphnia* the short-term reproductive advantage of parthenogenesis, but also the long-term advantage of sexual reproduction which through recombination of genetic material circumvents the accumulation of slightly deleterious mutations (Maynard Smith 1986). Parthenogenesis of *Daphnia* is not strictly cyclic since under good environmental circumstances several parthenogenetic generations succeed each other until environmental factors determine if males and ameiotic eggs will be produced. Under short day length, food shortage or crowding (Larsson and Hobaek 1988; Larsson 1991), asexual females may produce males and sexual females. Sexual females produce two meiotic eggs that need to be fertilized in order to develop. These sexually produced zygotes, the so-called resting eggs, are protected by a chitin envelope called an ephippium, and will sink to the bottom and hatch later after a diapause. In shallow water-bodies, which freeze completely, or which dry up, the populations can be re-established from resting eggs. Gene flow, especially over long distances, depends on the transport of resting eggs.

Genotypic and phenotypic variation
In the laboratory, studying clonal organisms like *Daphnia* makes it possible to distinguish between phenotypic and genotypic variation in the traits. *Daphnia* clones can also be crossed in the laboratory making heritability estimates possible (e.g. DeMeester 1991). Phenotypic plasticity is the ability of the organism to produce more than one phenotypic form in response to environmental factors (Bradshaw 1965; West-Eberhard 1989; Scheiner 1993). The phenotype may, for instance, express different morphology, physiology or behavior. Phenotypic plasticity may be adaptive or non-adaptive (Steams 1989). When an organism produces a phenotype that varies as a continuous function of the environment, the relationship is called a reaction norm (Via and Lande 1985; Stearns 1989; Stearns 1992; Via 1994). Phenotypic plasticity is especially common in the plant kingdom (Bradshaw 1965). Among animals, predator-induced defenses in aquatic organisms have received special attention (see reviews in Havel 1987, Harvell 1990). For instance, algae (Hessen and van Donk 1993), protozoans (Kuhlman and Heckmann 1985), bryozoans (Harvell 1986), rotifers (Gilbert 1966), cladocerans (Krueger and Dodson 1981; Hebert and Grewe 1985; Dodson 1988; Grant and Bayly 1981; Machacek 1993), snails (Appleton and Palmer 1988), and fish (Brönmark and Miner 1982) develop alternative, defensive morphologies when predators are present. Both life history and morphology of *Daphnia* exhibit high levels of plasticity. Over the course of a season, the body shape of a single *Daphnia* clone changes within successive generations as a continuous phenotypic response (Jacobs 1987). Thus, phenotypic plasticity enables *Daphnia* individuals to adapt to a changing environment and therefore phenotypic plasticity contributes to the persistence of the population. The question arises as to what extent, besides phenotypic adaptations, also genetical differences in traits are important? Statistically significant differences in many traits of *Daphnia* clones have been reported for several environmental factors. These include: responses to invertebrate predation (Spitze 1992), oxygen stress (Weider and Lampert 1985), susceptibility to toxins of cyanobacteria (Hietala
et al. 1995; Walls et al. 1997), high pH (Vijverberg et al. 1996) and phototactic behavior (DeMeester 1995; van Gool 1998; Reede 1998). Although these trait differences are most likely important under natural conditions, its significance for population persistence has, however, not been verified. In addition to genetic differences in trait means, also plasticity of the traits can vary across genotypes. It has been suggested that plasticity can evolve independent of trait means (Schlichting 1989; Scheiner 1993).

Comparisons of clones originating from different lakes and thus from differing selection regimes, allow the detection of micro-evolutionary changes in the features of the clones. As food environments for Daphnia, highly eutrophic Dutch lakes differ from less eutrophic mesotrophic lakes. Highly eutrophic lakes in the Netherlands are characterized by high seston concentrations during the whole growing season and the seston is generally dominated by cyanobacteria and detritus originating from cyanobacteria (Gons et al. 1992). Mesotrophic lakes, on the other hand, are generally dominated by green algae or flagellates and show clear temporal variations including a 'clear-water phase' due to zooplankton grazing (Sommer et al. 1986). Filamentous cyanobacteria are considered a low quality food for Daphnia (reviewed by de Bernardi and Giussani 1990; Gliwicz 1990). In many Dutch highly eutrophic lakes Daphnia are often abundant, despite the fact that the lakes are dominated by filamentous cyanobacteria (Gulati and Van Liere 1992). Thus it is possible that clones from such lakes have developed adaptations in feeding mechanisms or life history parameters to enable a more efficient utilization of filamentous cyanobacteria as food.

Feeding and life-history of Daphnia

The food filtering apparatus of Daphnia consists of the carapace gape and a feeding chamber with filtering screens at the third and fourth appendage. The carapace gape opening determines the largest size of particle that can be ingested (Burns 1969). If large interfering particles like large algal or cyanobacterial colonies are abundant, the animal can reduce the width of the gape opening (Gliwicz and Siedlar 1980). Reducing the width of gape opening, however, decreases also the feeding rate on edible particles (Gliwicz and Siedlar 1980). Particles that enter the feeding chamber are filtered through the filtering screens that work as a suction-and-pressure pump (Lampert 1987). Particles larger than the mesh sizes of the screens are retained and transported to mouth. Daphnia ingest algae, cyanobacteria, bacteria, protozoa, detritus and silt particles that fall within a size range of c. 0.5 - 40 μm (Burns 1969). The capabilities of Daphnia to discriminate between food particles are limited (DeMott 1986; 1988; Bern 1990a; 1990b). However, if there are too many food particles, or too many unsuitable food particles collected on the filter screens, the screens can be cleaned by rejection movements of the post-abdominal claw (Burns 1968). In some studies, the Daphnia has been shown to select for smaller particles (Meise et al. 1985; Bern 1990b). Bern (1990b) attributed this to selective rejection of larger particles by the post-abdominal claws. Hartman and Kunkel (1991), however, proposed that particle selection by Daphnia is mainly achieved by the varying efficiencies by which particles of varying sizes and shapes are collected, handled and transported. This results in a passive positive selection of small spherical cells and a passive rejection of filaments.

The areas of filter screens grow with the size of the daphnid, thus growing after every molt. At high food concentrations, the filtering area increases at a slower rate than at low food levels. Consequently, animals growing on high food concentrations exhibit smaller filtering area in relation to body size than animals growing on low food levels. Larger filtering area is advantageous at limiting food concentrations because filtering area is positively correlated to filtering rate (Egloff and Palmer 1971; Arruda 1983; Stuchlik 1991; Lampert 1994). In order to increase clearance rate, larger screens are hydrodynamically less costly than an increase in the appendage beat rate of smaller screens (Lampert and Brendelberger 1996). However, an intriguing question is: why do animals have smaller filtering area at high food concentration? The energetical cost of building larger filtering screens probably is not substantial and under non-limiting food concentrations slight extra costs can easily be compensated. The explanation for why a smaller filtering area is
advantageous at high food concentration probably lies elsewhere. At extremely high food concentrations (> 6 mg C l\(^{-1}\)), *Daphnia* may collect more food than can be ingested per unit time, which will lead to an increase of rejection movements, and thus to a decrease of net energy intake. Decreased growth and reproduction rates at food concentrations above 6 mg C l\(^{-1}\) have been observed (Porter et al. 1982; Porter et al. 1983). Thus, at high food concentrations smaller filtering screens that collect less food would actually increase net energy intake.

Plastic responses to environmental quality requires the presence of reliable signals that can be detected by the organisms (Harvell 1990; Aphalo and Ballare 1995). What is the cue for *Daphnia* about the ambient food concentrations? *Daphnia* might be able to detect directly the amount of particles in the water or may sense its gut fullness giving an indication of the particle concentration. It is known that *Daphnia* adjusts its filtering rate to the prevailing food concentration (Lampert 1987). Food concentrations might, however, fluctuate too rapidly to be a reliable cue. At a time scale of a few days (roughly equivalent to molting interval), food concentrations translate into the physiological condition of the animals that might also be used as a cue for the morphological response.

Clearance rate (synonyms: filtering rate and grazing rate) describes the volume of water theoretically swept clear from particles by the filtering screens. Filtering rate is constant and maximal below a certain food concentration, the Incipient Limiting Level (ILL), but decreases above this level (Lampert 1987). The ingestion rate (synonym: feeding rate) is the amount of food that enters the gut in a unit of time. Below the ILL, the ingestion rate increases proportional to the food concentration and above ILL reaches a plateau (Lampert 1987). Assimilation is the second step in the process of energy uptake. Assimilation includes all the ingested material absorbed through the wall of the intestine. Net production of an organism is the total amount of food assimilated minus the metabolic costs (respiration). Net production is also the sum of somatic growth and reproduction.

Life history traits and trade-offs between traits are important for the performance of *Daphnia* under varying food regimes. Organisms allocate energy to reproduction in such a way that the sum of present and future reproduction is maximized (Williams 1966; Schaffer 1974; Roff 1992; Stearns 1992). A set of life history traits that is advantageous at high food concentration may not be advantageous at low concentrations or low qualities of food. Most life-history traits show plasticity in response to environmental alterations during development (Caswell 1983). Under limiting food concentrations, reduced somatic growth rate and reduced reproduction rate and delay in the onset of reproduction have been observed in *Daphnia* (Threlkeld 1976; Lynch 1989; McCauley et al. 1990; Lynch 1992; Boersma and Vijverberg 1994). It has been proposed that the evolution of *Daphnia* life histories is governed by the size at first reproduction which affects, for instance, the extent of susceptibility to size-selective predation by fish and invertebrates (Lynch 1980; Lynch 1984; Lynch et al. 1986).

**Hybridization in Daphnia**

The taxa studied here, *Daphnia galeata*, *D. cucullata*, and their interspecific hybrid *D. cucullata x galeata*, form the majority of *Daphnia* occurring in the Dutch lakes (Schwenk and Spaak 1995). Recent works on these taxa have concentrated on the evolutionary genetics and ecology (Boersma 1994; Spaak 1994; Schwenk 1997). The ecological characteristics of the hybrids are important in explaining their maintenance in the field. How do they find a suitable niche? To what extent do they compete with the parental species? How do the traits of the parental species express themselves in the hybrids? Often the trait values of the hybrids are intermediate to the parental species as expected from polygenic inheritance. In accordance, traits like size at first reproduction of *D. cucullata x galeata* hybrids are intermediate to the parents (Weider and Wolf 1991; Weider 1993; Spaak and Hoekstra 1995). In other taxa, hybrids can also be superior (Bulger and Schultz 1979) or inferior (Barton and Hewitt 1985) to the parental species in resource utilization.

The success of the *D. cucullata x galeata* hybrids has been explained by the 'temporal hybrid superiority hypothesis' (Spaak 1994). The hybrids can combine useful characters of the parentals, namely high population growth rate, \( r \), and
juvenile growth rate as in *D. galeata*, or long spines and small size at first reproduction as in *D. cucullata*. The combination of high *r* and small body size may give the hybrid a higher fitness in the field during fish predation. On the other hand, long spines and high juvenile growth rate may give the hybrid an advantage under relatively high fish predation. The performance of these taxa differs also under variable food concentrations (Boersma and Vrijenhoek 1994). At high food concentrations, the hybrids will have a selective advantage over the parentals (Boersma and Vrijenhoek 1994). From field studies Boersma (1995) further concluded that both parental species competed for the resources with the hybrid but their competition with each other was negligible. Mesh size or other morphological characters of the filtering apparatus can shed more light to the resource utilization of the taxa.

**Outline of the thesis**

The aim of this thesis was to study traits of *Daphnia galeata*, *D. cucullata* and their interspecific hybrid, *D. cucullata × galeata*, that are relevant for food utilization. Such traits include the morphology of the feeding apparatus, size of the animal and life history traits. Another objective was to quantify genetical differences and phenotypic plasticity of such traits under variable food conditions. The thesis is subdivided into eight chapters, including this introduction (Chapter 1).

The second chapter contains the results of an experiment studying the influence of food quality on growth and reproduction of *D. galeata*, *D. cucullata* and their interspecific hybrid *D. cucullata × galeata*. Food quality is represented by two commonly occurring, but contrasting food sources, the green alga *Scenedesmus* and the filamentous cyanobacterium *Oscillatoria*.

The third and the fourth chapter deal with the results of two experiments comparing *D. galeata* and *D. cucullata* clones originating from lakes of contrasting productivity. Here, intraspecific variations of life history traits of the *Daphnia* species as related to *Scenedesmus* and *Oscillatoria* diets are estimated. Also the fatty acids contents of the diets were determined because of their presumed importance in *Daphnia* nutrition.

The fifth chapter contains the results of experiments in which *D. galeata* was fed on detritus derived from the filamentous cyanobacterium *Oscillatoria*. The food quality of detritus as reflected in growth and reproduction of *Daphnia*, was compared with live *Oscillatoria* filaments and *Scenedesmus*. Biochemical parameters (N, P, protein, carbohydrates and lipids) of these food types, thought to be important in *Daphnia* nutrition, were also determined.

The sixth chapter quantifies the plasticity and genetic variation of the filtering apparatus of *D. galeata* reared at two concentrations of *Scenedesmus*. The responses of several *Daphnia* clones from contrasting environments were compared. The question as to what acts as an indication of food conditions for the *Daphnia*, food density or its physical condition, was also addressed.

Chapter seven deals with morphology and plasticity of the filtering apparatus of the co-occurring taxa *D. galeata*, *D. cucullata* and their interspecific hybrid *D. cucullata × galeata*. Filter screen parameters and somatic growth rates of the animals were determined at two food concentrations. The responses of hybrids originating from laboratory crossings and collected from the field were compared to further study trait variation within the hybrid taxa.

Chapter eight summarizes the most important results of the research presented in this thesis and gives concluding remarks.
References


