Synergistic effects of different food species on life-history traits of *Daphnia galeata*

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Key words: *Daphnia*, food quality, life history, standard carbon content

Abstract

In this paper we describe the life history consequences of feeding *Daphnia galeata* with different food types in different concentrations. We fed the animals with four concentrations of two green algae *Scenedesmus obliquus* and *Chlamydomonas globosa*, given separately as well as in a 1:1 mixture. Growth, reproduction and condition of the animals and consequently the intrinsic rate of population increase, \( r \), increased with the concentration of the food for all three experimental series. The life history parameters measured were lowest in the animals raised on *C. globosa*. Animals fed on *S. obliquus* showed higher values for \( r \). We observed a distinct synergistic effect of the two algal species: growth, reproduction, condition and \( r \) were significantly higher for the animals raised on the mixed media as compared to the animals raised on the mono-algal media. We conclude that the two algal species represented complementary food resources.

Introduction

In aquatic communities, filter feeders are among the most generalized herbivores, often ingesting all particles within a given size range. This implies that these animals are faced with a large spectrum of different quality food resources. Since the ability to select for given food types is usually limited, especially in species of the genus *Daphnia* (e.g. Kerfoot & Kirk, 1991), differences in food quality are likely to be of paramount importance for filter feeders.

In ecological studies of *Daphnia*, the effect of food quantity on life history characteristics has been addressed by many workers (e.g. Lampert, 1977; Duncan *et al.*, 1985). Most of these experiments have been carried out with high quality food items, such as Chlorophyceae and Cryptophyceae. Influences of food quality have drawn less attention, although several authors have emphasized the role of differences in quality between algae (e.g. Ahlgren *et al.*, 1990; Lundstedt & Brett, 1991). Most of the investigators compared the quality of Chlorophyceae and/or Cryptophyceae, groups which are usually considered as high quality food, with Cyanobacteria as a low quality resource. Possible toxicity of some Cyanobacteria has also been mentioned as a reason for the lower quality of Cyanobacteria (DeMott *et al.*, 1991). Recently, quality differences within food species as a result of the culturing conditions of the algae have been reported (Müller-Navarra, 1993; Sterner *et al.*, 1993; van Donk & Hessen, 1993).

The effect of mixtures of different food types on life histories of zooplankton has received considerably less attention, although approximately half of the studies reviewed by Vijverberg (1989) on growth and reproduction in zooplankton were carried out with a combination of food types. The differences in the nutritional value of two or more species of algae given separately, versus their value in combination, are not very well studied. Most authors, who have studied the nutritive value of different food species in mixed diets, considered mixtures of palatable and non-edible algae, either to show differences in uptake (Hartmann & Kunkel, 1991) or to investigate inhibitory effects of the ‘inedible’ species, usually blue-greens, on the feeding and growth of the zooplankton (Gliwicz & Lampert, 1990).
We are aware of only a few published works which deal with synergistic effects of different food types fed to herbivorous zooplankton in combination (Jamieson, 1980; Lewis & Maki, 1981; Hanazato & Yasuno, 1984; Roman, 1984; Cowgill et al., 1985; Lundstedt & Brett, 1991; Vanni & Lampert, 1992).

In this paper we present the results of a study on the life history consequences for *Daphnia galeata*, fed with different concentrations of two green algae, *Scenedesmus obliquus*, and *Chlamydomonas globosa*. These were given separately as well as in a 1:1 mixture. Both algal species have been used extensively as food items for *Daphnia* species, and are considered to be high quality food (e.g. Vijverberg, 1989).

**Material and methods**

**Algae**

*Chlamydomonas globosa* and *Scenedesmus obliquus* were cultured axenically in a two-litre flow-through system on a medium as described elsewhere (Boersma & Vijverberg, 1994a). The algae were harvested daily from the overflow bottle of the continuous culture. The culture medium of the algae was removed by centrifuging twice for 20 min at 3000 rpm, and by subsequent washing of the algae with distilled water. The algae were resuspended in 0.45 μm filtered lake water from the Tjeukemeer. The algal density was measured using a haemacytometer, counting a minimum of 500 cells. The carbon content of the algae was measured using a UNICARB carbon analyser (Salonen, 1979). Algal dry weight was established after drying a known volume of a known concentration at 70 °C, and weighing the sample on a microbalance afterwards. Individual cells of *C. globosa* contained 2.52 × 10⁻² ng C. The carbon content of *S. obliquus* cells was 2.30 × 10⁻² ng C cell⁻¹, resulting in carbon to dry weight ratios of 0.53 and 0.50, respectively. *S. obliquus* was usually unicellular. Both algal species had a maximum length of around 15 μm.

**Animals**

*D. galeata* individuals were collected with a 120 μm tow net from the Tjeukemeer, a shallow eutrophic lake in the northern part of the Netherlands. These ‘field’ animals were placed individually in 100 ml test tubes and fed on a 1:1 mixture of *Chlamydomonas globosa* and *Scenedesmus obliquus*. The algal carbon content of this culture medium was 1 mg C l⁻¹. The incubation temperature used was 17.5 °C, and the light-dark period was 16:8 hours. As soon as the ‘field’ animals produced newborns (first generation), the ‘field’ animals were removed. The first generation animals were reared to maturity on the same medium as their mothers. The offspring produced by these animals (second generation) were used for the experiments described below.

**Experimental design**

Different amounts of *Chlamydomonas globosa* and *Scenedesmus obliquus* were added to 0.45 μm filtered Tjeukemeer water to obtain four food levels, with carbon contents of 0.13, 0.25, 0.50 and 2.5 mg C l⁻¹, respectively. Three types of media were prepared: 1) a series of pure *C. globosa* media (CHLAM), 2) a series of *S. obliquus* media (SCENE), and 3) a series of *C. globosa* and *S. obliquus* in a 1:1 mixture (CH_SC). All experiments were carried out at the same time.

The temperature and photoperiod used in the experiments were the same as during the acclimatization period. For each series, 40 second generation neonates were collected within 12 hours of birth, and placed individually in 100 ml test tubes. The animals were selected in such a way that the clonal composition of all series was the same. The animals were examined daily for moulting by inspection of the medium for exuviae. Then they were transferred to clean tubes with fresh medium. To avoid possible increased mortality due to handling we measured two second generation newborn from each brood, which were then discarded.

The rest of the batch was used for the experiments. The time needed to reach maturity and the number of juvenile instars of the animals were recorded. The onset of adulthood is defined as the first appearance of eggs in the brood pouch, although development of the reproductive organs starts earlier. Once the second generation animals reached maturity, the number of eggs they produced was counted and the length of the individuals was recorded for each adult instar. The animals were measured from the upper edge of the eye to the base of the tail spine. The number of offspring produced by the second generation individuals was recorded, their lengths were measured, and subsequently they were removed from the tubes. Growth and reproduction were measured until the animals reached the fourth adult instar, that is approximately 20 days on average. The animals were then discarded, because under natural conditions, judging by the sizes found...