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EFFECTS OF FOOD CONCENTRATION ON THE FEEDING OF *DAPHNIA SIMILIS* CLAUS (CRUSTACEA: CLADOCERA)[1]

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Chi-Hsiang Lei, Li-Yung Hsieh and Chao-Kuan Chen (1990) Effects of food concentration on the feeding of *Daphnia similis* Claus (Crustacea: Cladocera). *Bull. Inst. Zool., Academia Sinica* **29**(4): 283-290. Adult females of *Daphnia similis* (mean carapace length, 1.25 mm) without eggs or embryos in brood chamber were subjected to different concentrations (0.028×10^5 to 1.4×10^7 cells/ml) of alga (*Chlorella* sp.) at 25°C, and their filtering and ingestion rates were determined. The rate of filtration decreased whereas the rate of ingestion increased with the increase of algal cell concentrations. The relationship between the filtering rate (F, ml/animal/h) and algal cell concentration (C, 10^5 cells/ml), and between the ingestion rate (I, 10^3 cells/animal/h) and algal cell concentration (C) can be properly described by a power function of $F=0.294\ C^{-0.452}$ and $I=20.26\ C^{0.531}$, respectively.

Key words: *Daphnia similis*, Ingestion rate, Filtering rate, Food concentration effect.

Grazing (feeding) is the main biological process by which zooplankton obtains food from the external environment to provide energy and material necessary for maintenance (metabolism), growth and reproduction. It is also one of the key processes in the ecology of plankton communities. Algal and bacterial production is harvested by grazing (Borsheim and Olsen, 1984; Cushing, 1976; Gliwicz, 1969, 1975; Gulati, 1975; Lampert, 1978; Peterson *et al.*, 1978), and some of the mineral nutrients are recycled through the excretion of grazer (Olsen *et al.*, 1986; Peters, 1975). Therefore, knowledge of zooplankton grazing (or feeding) is vital to understanding production dynamics and interpreting the major flows of energy and matter in aquatic ecosystems and the feeding behavior and activity of zooplankton have been the subject of considerable attention (see reviews by Conover, 1978; Marshall, 1973; Peters, 1984; Raymont, 1983; Rigler, 1971).

Although food concentration has been shown to be an important factor controlling the feeding behavior and activity of planktonic crustaceans (see reviews by Peters, 1984; Rigler, 1971), the response pattern of feeding to varying food concentrations in many species of planktonic crustaceans is still not known. In this study, the filtration and ingestion rates of a common species of Cladocera, *Daphnia similis* Claus in Taiwan were determined at various concentrations of algal cells to see how they respond to varying food concentration.

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MATERIALS AND METHODS

Daphnia used for the experiments were obtained from the stock cultures maintained at the Institute of Zoology, Academia Sinica for more than three months. The stock cultures were initiated with the animals collected from the fish pond in Chu-Pei, and maintained in a growth chamber with temperature controlled at 25°C and light condition regulated at 16L:8D photocycle and 600 lux intensity. Dechlorinated and filtered (Whatman GF/C fiber-glass filter disc) tapwater was used as a culture medium to which cells of *Chlorella* sp. were added in excess of 90,000 cells/ml.

The algae (*Chlorella* sp.) used as food for *Daphnia* culture and in the feeding experiments were cultured with Bold's medium (Nichols and Bold, 1965) at 25°C, 12L:12D photocycle and 2,000 lux intensity. The algal culture at log growth phase was concentrated by centrifugation at 2,900 × g for 2 minutes, and used in feeding *Daphnia* and preparing algal suspensions of different concentrations for feeding experiments.

One day prior to the experiments, *Daphnia* of similar size (mean carapace length, 1.25 mm) were isolated from the stock cultures, and transferred into separate glass vials (15 ml capacity) containing filtered (0.45 μm Millipore membrane filter) and aerated (24 h) tapwater which had been dechlorinated first (hereafter this water will be referred to as filtered water). Ten animals were placed in each vial, and starved for 24 h to clear their gut of excess food. During the process of starvation the vials with animals were kept in a growth chamber with temperature regulated at 25°C. After 24 h of precondition to the test temperature, 15 *Daphnia* of similar size were first gently picked up with a glass dropper having a wide pore from the vials, rinsed several times with filtered water, and carefully placed into a 60 ml BOD bottle containing test concentration of algal suspension. Concurrently, several control bottles containing the same concentration of algal suspension only were also prepared in the same manner. The experimental and control bottles were then fastened to a wheel in a temperature controlled (25°C) water bath with light turned off, and rotated end-over-end at a speed of 1 rpm to keep algal cells in homogenous suspension. The experiments were carried out in the dark to minimize the change in algal cell concentration owing to multiplication.

After 2 hours of incubation, the bottles were removed from the wheel, and the concentration of algal cell in both control and experimental bottles were determined using a particle analyzer (Elzone 180 XY) with a 95 μm diameter aperture tube. Because pond water must be made saline to conduct electric current, the content of each bottle was diluted with an equal amount of 1% NaCl solution which had been filtered 3 times through a membrane filter with 0.20 μm pore size to get a salinity of 0.5% before counting (Mulligan and Kingsbury, 1968). From the difference in concentration of the algal cell between the mean of controls and each experimental bottle, the filtering rate (F, ml/animal/h) and ingestion rate (I, 10^3 cells/animal/h) were computed by the formulae (Peters, 1984).

$$F = \frac{V(\ln C_0 - \ln C_t)}{NT}$$

and

$$I = \frac{V(C_0 - C_t)}{NT}$$

Where V is the volume of algal suspension in the experimental bottle; N, the number of animals in the experimental bottle; T, the duration (hour) of incubation; C_0 and C_t, the algal cell concentration in the control bottle and experimental bottle, respectively, after 2 hours of incubation.

The measurements of the filtering rate were made at the same time of day (between 11:00 and 13:00 hour) to avoid a possible effect of diurnal rhythm. Algal concentrations from 0.028×10^5 to 1.4×10^7 cells/ml were made by resuspending centrifuged algae in filtered water, and used to determine the effects of food concentration on the filtering and ingestion rates at 25°C in the dark. For this experiment, adult females (mean carapace length, 1.25 mm) without eggs or embryos in the brood chamber and grown at 25°C in the laboratory were used.

RESULTS

At algal concentrations between 0.028×10^5 and 2×10^5 cells/ml filtering rates decreased rapidly with increasing concentration. Above 2×10^5 cells/ml filtering rates continued to decrease gradually with further increases in concentration approaching the abscissa asymptopically (Table 1; Fig. 1). In contrast, ingestion (or feeding) rates increased gradually with increasing the concentration of algae at concentrations between 0.028 $\times 10^5$ and 2×10^5 cells/ml, and then increased rapidly with further increases in concentration of algae (Table 1; Fig. 2).

The relationship between the filtering rate (F, ml/animal/h) and the algal

Table 1
The filtering rate (ml/animal/hr) and ingestion rate (10^3 cells/animal/hr) of adult females of *Daphnia similis* (mean carapace length, 1.25 mm) feeding on different concentrations (10^5 cells/ml) of *Chlorella* sp.

Food conc.	Filtering rate	Ingestion rate
0.028	1.2137	3.47
0.041	0.7705	1.68
0.073	0.8663	3.37
0.145	0.9842	24.95
0.159	0.5728	5.36
0.222	1.3281	17.42
0.246	0.3276	5.48
0.387	0.9400	22.14
0.468	0.6881	18.39
1.531	0.0534	5.81
3.179	0.3781	89.13
18.326	0.0922	109.58
40.923	0.0694	190.40
53.348	0.0190	68.50
136.506	0.0445	366.60

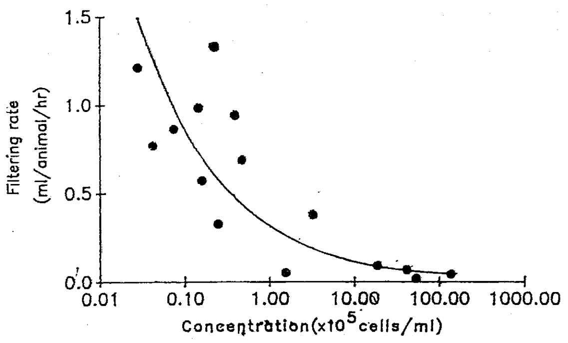

Fig. 1. Filtering rate of adult females of *Daphnis similis* (mean carapace length, 1.25 mm) feeding on different concentrations of *Chlorella* sp.

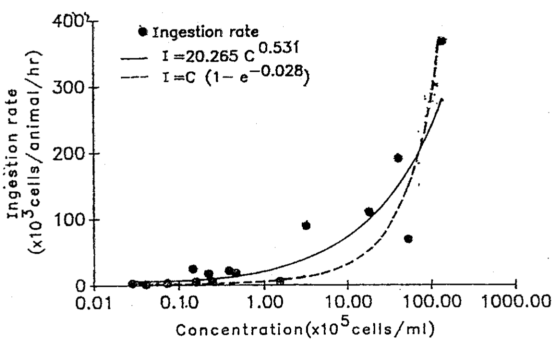

Fig. 2. Ingestion rate of adult females of *Daphnis similis* (mean carapace length, 1.25 mm) feeding on different concentrations of *Chlorella* sp.

concentration (C, 10^5 cells/ml), and between the ingestion rate (I, 10^3 cells/animal/h) and the algal concentration (C) fitted a power function of general type

$$F = a\,C^b \quad \text{and} \quad I = a\,C^b$$

which can be transformed to a linear form by taking the logarithm to the base of 10 of both sides of the equation, yielding

$$\log F = \log a + b \log C$$

and

$$\log I = \log a + b \log C$$

The data of *D. similis* fit these equations for filtering and ingestion rates with a r^2 equal to 0.78 and 0.80 (both significant; $d.f.=13$, $p<0.01$), yielding respectively an equation

$$\log F = -0.532 - 0.452 \log C \quad (\text{or } F = 0.294\,C^{-0.452})$$

and

$$\log I = 1.307 + 0.531 \log C \quad (\text{or } I = 20.26\,C^{0.531})$$

For a comparison, the data of ingestion rates of *D. similis* were also fitted to an equation proposed by Hassell (1978) to express type I functional response of predator to prey density

$$N_a = N_t[1 - \exp(-a'\,T\,P_t)]$$

where N_a is the number of prey eaten, N_t, the prey density; a', the instantaneous search rate; T, the searching time; and P_t, the predator number. In the present study, the above equation was modified as

$$I = C(1 - e^{-a'})$$

where I is the ingestion rate (10^3 cells/animal/h), C the algal concentration (10^5 cells/ml), and a' the constant. The resulting equation is

$$I = C(1 - e^{-0.028})$$

with a r^2 of 0.88. The fitted curves for power function and this equation are shown in Fig. 2.

DISCUSSION

The filtering rate of planktonic crustaceans has been found to vary with food concentration by some investigators (Berner, 1962; Burns, 1966; Chisholm *et al.*, 1975; Kryutchkova and Sladecek, 1969; Marshall and Orr, 1955; McMahon, 1962; McMahon and Rigler, 1963; O'Brien and de Noyelles, 1974; Reeve, 1963; Richman, 1966; Rigler, 1961; Schindler, 1968; this study) but not by others (Fleming, 1939; Fuller, 1937; Gauld, 1951; Harvey, 1942; Lucas, 1936; Richman, 1958; Riley, 1946).

Rigler (1961) used ^{32}P-labeled yeast to investigate the relation between food concentration and feeding rate of *Daphnia magna*. He suggested that his own results and those of Ryther (1954) and Marshall and Orr (1955) indicated a general phenomenon among filter-feeding crustaceans: below a certain food concentration (critical or incipient limiting concentration) feeding (or ingestion) rate is limited by the ability of the animal to filter water; hence the feeding rate is proportional to food concentration, and filtering rate is constant and maximum. But above the critical concentration, which will vary with the species of crustacean and food organism, feeding rate is limited by the ability of the animal to ingest or digest the filtered food; hence feeding rate is constant and maximum, and filtering rate declines to an asymptote near zero. In marine copepods (*e.g.* see Frost, 1972), freshwater copepods (Richman, 1966) and *Artemia salina* (Reeve, 1963) similar responses have also been found. However, Mullin (1963) and Haq (1967) reported for *Calanus* and *Metridia*, respectively that the ingestion rate increased with increasing food concentration to a maximum level, and then declined with further increases in food concentration; wherease the filtering rate decreased with increasing food concentration in a linear or non-linear fashion depending upon the kind of food used. The filtering rate of *D. similis* in the present study decreased with increasing food concentration as had been found in *Calanus* (Mullin, 1963), *Metridia* (Haq, 1967) and *Pseudocalanus elongatus* (Paffenhoffer and Harris, 1976). However, the rate of ingestion continued to increase with increasing food concentration over the range of concentrations tested, and responded to food concentration changes differently from the patterns reported by other investigators with other crustaceans (Frost, 1972; Haq, 1967; Marshall and Orr, 1955; Mullin, 1963; Reeve, 1963; Richman, 1966; Rigler, 1961; Ryther, 1954). The pattern of the response of the ingestion rate to varying food concentrations in *D. similis* is similar to that found by Paffenhoffer (1971) and Paffenhoffer and Harris (1976) in *Calanus* and *Pseudocalanus*. Clearly, the relationship between food concentration and rates of filtering and ingestion in filter-feeding crustaceans is complex and variable, and more work must be done to clarify it.

The functional response of an organism is the relationship between its ingestion rate and food abundance, and is the end result of its feeding behavior. According to Holling (1959), the functional response of a predator to prey density can be of three types. In type 1, search is random and search rate is constant at all prey densities, leading to a linear increase to the maximum amount of food items taken with increasing density. In type 2, the search rate decreases at higher prey densities, and the curve of prey taken on density becomes convex. In type 3, the curve is sigmoid because not only is there an upper threshold, but also a lower one, beyond both of which the search rate decreases. Type 1 response is supposedly typical of aquatic filter-feeding invertebrates (Hassel, 1978), and has been demonstrated in many species of filter-feeding crustaceans (*e.g.*, Frost, 1972; Marshall and Orr, 1955; Mullin and Brooks, 1970; Reeve, 1963; Richman, 1966). However, type 2 response has also been noted for *Daphnia* (Burns and Rigler, 1967; Porter *et al.*, 1982) and marine copepods (Mayzaud and Poulet, 1978), and type 3 response for calanoid copepods (Adams and Steele, 1966; Corner *et al.*, 1972; Frost, 1975; Reeve and Walter, 1977).

A number of mathematical formulae have been applied to curves which relate feeding rate to food concentration in zooplankton (Downing and Peters, 1980; Frost, 1975; Mayzaud and Poulet, 1978; Mullin *et al.*, 1975; Muck and Lampert, 1980; Porter *et al.*, 1982). However, attempts to distinguish which of these models is best (Corner *et al.*, 1976; Frost, 1972; Mullin *et al.*, 1975) have not been able to identify any one as better than others. The functional response of *D. similis* in the present study does not fit into any one of these three basic types of functional responses proposed by Holling (1959) for predator-prey interaction. However, the relationship between the ingestion rates (I) of *D. similis* and food concentration (C) can be better described by a power function of a general type as $I=20.26\,C^{0.531}$.

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食物濃度對水蚤 (*Daphnia similis* Claus) 攝食之影響

雷 淇 祥　謝 莉 顥　陳 昭 寛

本研究利用不帶卵或胚胎之水蚤雌成蟲（平均背甲長，1.25 mm）在 25°C 及不同綠藻濃度（0.028×10^5～1.4×10^7 cells/ml）下測定其濾水率及攝食率。結果顯示水蚤之濾水率隨綠藻濃度之增加而減小，但攝食率則隨綠藻濃度之增加而增高。濾水率（F, ml/animal/h）與藻細胞濃度（C, 10^5 cells/ml）間，以及攝食率（I, 10^3 cells/animal/h）與藻細胞濃度（C）間之關係可分別適當地以冪函數 $F=0.294\ C^{-0.452}$ 及 $I=20.26\ C^{0.531}$ 表示。