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Short Communication
Temporal pattern of feeding response of *Chaoborus* larvae to starvation

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Abstract. The effect of starvation on the feeding rate of larval *Chaoborus* (Diptera, Chaoboridae) was investigated using *Daphnia rosea* as prey. The starvation period varied from 12 h to 22 days. The starved *Chaoborus* were individually incubated with 10 *Daphnia* under controlled light and temperature conditions. Observations were made on prey mortality every 2 h for the first 12 h and once after 24 h. Feeding rates gradually increased to a maximum between 7 – 11 days of starvation. After this period, feeding rates declined to previous low levels. Generally, feeding rates were significantly higher during the first 2 – 4 h of feeding. Thereafter, feeding rates were lower and exhibited no consistent patterns with length of feeding time.

Introduction

Numerous studies have measured the feeding rate of *Chaoborus*, both in the laboratory (Dodson, 1970; Swüste *et al.*, 1973; Fedorenko, 1975; and others) and *in situ* (Kajak and Ranke-Rybicka, 1970; Fedorenko, 1975). Factors such as temperature (Fedorenko, 1975), prey size (Swift and Fedorenko, 1975; Vinyard and Menger, 1980), and prey density (Fedorenko, 1975; Schiemer *et al.*, 1975; Pastorak, 1980; Vinyard and Menger, 1980) have been demonstrated to influence strongly the predation rate of *Chaoborus*.

However, there is much variation in experimental conditions between investigations. For example, descriptions of the condition of the *Chaoborus* larvae at the start of the experiment vary from 'well fed' (Dodson, 1970), to 'freshly caught' (Fedorenko, 1975), 'caught at 20.00 h' (Schiemer *et al.*, 1975), to 'starved at least 24 h' (Vinyard and Menger, 1980), and 'starved 7 days' (Swüste *et al.*, 1973). Also, duration of feeding experiments range from 3 h (Schiemer *et al.*, 1975) and 6 h (Kajak and Ranke-Rybicka, 1970) to the more frequently used 24-h period (Dodson, 1970; Fedorenko, 1975; Vinyard and Menger, 1980).

In the few studies that have considered the influence of hunger on *Chaoborus* (Pastorak, 1980; Smyly, 1980), there is good evidence that feeding rates may increase as a result of starvation. In this study, we attempt to define more clearly the degree of dependency of feeding rates of *Chaoborus* on the length of starvation period.

Chaoborus americanus larvae were collected from a small pond near Durham, New Hampshire. Larvae of approximately the same size were immediately separated from the samples and kept in 30 μm filtered pond water in 1000-ml beakers. For 24 h prior to the beginning of the starvation period larvae were fed at or above saturation level prey densities ~ 1000 *Daphnia* l^{-1} (Fedorenko, 1973). After pre-feeding, groups of 10 larvae were placed in 200 ml of filtered pond water at 15 ± 1°C and were starved for different lengths of time. Light was held constant at 12 μW cm^{-2}.

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Table I. Effect of starvation on the feeding rates of *Chaoborus* (*Daphnia Chaoborus*$^{-1}$ 2 h^{-1}) at different times during the starvation period. Each value represents a mean of five replicates ± SE.

Days of starvation	*Chaoborus* feeding rate at the end of different 2-h time intervals during the first 12 h of experiment					
	2 h	4 h	6 h	8 h	10 h	12 h
0.5	1.4 ± 0.54	1.2 ± 0.34	0.4 ± 0.22	1.8 ± 0.18	0 ± 0	0.4 ± 0.22
1	0.8 ± 0.33	0.8 ± 0.18	0.6 ± 0.22	0.8 ± 0.33	0.6 ± 0.22	0.2 ± 0.18
2	2.8 ± 0.72	0.6 ± 0.36	0.6 ± 0.22	0.6 ± 0.36	0.6 ± 0.22	1.2 ± 0.66
3	1.8 ± 0.52	1.0 ± 0.28	0.4 ± 0.36	1.0 ± 0.4	0.8 ± 0.33	0.6 ± 0.22
4	2.6 ± 0.61	0.8 ± 0.33	1.0 ± 0.28	0.4 ± 0.22	1.2 ± 0.33	0.4 ± 0.22
5	4.6 ± 0.46	1.0 ± 0.28	0.8 ± 0.33	0.2 ± 0.18	0.2 ± 0.18	0.6 ± 0.36
7	5.2 ± 0.33	2.0 ± 0.28	0.8 ± 0.33	1.4 ± 0.46	0.4 ± 0.36	0.2 ± 0.18
9	2.8 ± 0.72	2.2 ± 0.66	1.0 ± 0.57	0.6 ± 0.36	0.2 ± 0.18	1.6 ± 0.36
11	4.6 ± 0.83	1.8 ± 0.18	1.0 ± 0.40	1.0 ± 0.40	1.6 ± 0.73	0.4 ± 0.22
13	4.0 ± 0.89	1.4 ± 0.61	0.6 ± 0.22	0.4 ± 0.36	0.6 ± 0.36	0.6 ± 0.36
22	2.0 ± 0.57	0.6 ± 0.36	0.6 ± 0.22	0.2 ± 0.18	1.0 ± 0.28	0.4 ± 0.29

Daphnia rosea used in the experiments were taken from a local pond and maintained in laboratory cultures. Although *D. rosea* and *C. americanus* inhabit very similar shallow ponds, they did not co-occur in the ponds used. Feeding experiments were conducted in 100-ml glass beakers containing 50 ml of filtered pond water. Each beaker contained one *Chaoborus* and 10 *Daphnia*. Preliminary experiments showed this was the lowest density at which maximum feeding occurred. Based on the abundance of *D. rosea* in the local ponds, the test density of *Daphnia* is roughly 1 – 2 times the maximum *Daphnia* prey concentrations *Chaoborus* would experience in nature. A total of 11 starvation periods ranging from 12 h to 22 days were tested using five replicates for each period. Observations of prey mortality were made every 2 h for the first 12 h. Eaten prey were replaced after each of these observations. A final count of *Daphnia* was made after 24 h of feeding.

After each experiment, all the *Chaoborus* and *Daphnia* were fixed in 4% formalin. The body length of *Daphnia* (anterior margin of head to base of tailspine) and the head capsule and body length of *Chaoborus* were measured using a dissecting microscope. Total body length measurements of *Chaoborus* larvae were made from the juncture of the prehensile antennae with the head capsule to the posterior end of the last abdominal segment. Head capsule measurements were made from the juncture of the prehensile antennae with the head capsule to the suture separating the latter from the thoracic segments. A scatter diagram of head capsule length versus body length of *Chaoborus* larvae found in the pond and used in the experiments indicated that the larvae were one distinct group, judged to be the fourth instar (La Row and Marzolf, 1970).

Head length of *Chaoborus* for experiments 1 and 2 averaged 1.33 ± 0.03 mm SE and 1.38 ± 0.02 mm SE, respectively. Mean body length was from 9.3 ± 0.01 mm SE and 9.60 ± 0.01 mm SE, respectively. Mean *Daphnia* body lengths for both experiments were 1.37 ± 0.01 mm SE and 1.36 ± 0.01 mm SE, respectively. The ranges of body lengths for both experiments were 1.16 – 1.63 mm and 1.06 – 1.76 mm, respectively. Since *Daphnia* were measured after the feeding experiment, we cannot assess whether *Chaoborus* fed size-selectively. Mean head and body lengths of *Chaoborus*

Table II. Analysis of variance of *Chaoborus* feeding rates (*Daphnia Chaoborus*$^{-1}$ 2 h^{-1}) during the first 12 h of experiment. Treatment is starvation time in days. Differences in means determined with Duncan's Multiple Range Test. Means connected by same lines are not significantly different from each other ($p < 0.05$).

Analysis of variance

Source	SS	DF	MS	F
Total	2.57	54	–	
Starvation	1.53	10	0.15	7.5 $p < 0.05$
Within	1.05	44	0.02	

Treatment (days)	11	7	9	13	5	4	2	3	1/2	22	1
Mean	0.8667	0.8333	0.6999	0.6334	0.6167	0.5333	0.5333	0.4667	0.4336	0.4	0.3167

and mean body lengths of *Daphnia* used in the two experiments were not significantly different. Thus, data from the two experiments were combined for presentation. Duncan's Multiple Range test and analysis of variance were performed on the data.

Experiment 1 included starvation periods of 12 h to 4 days and experiment 2 from 2 to 22 days. The 2-day starvation period was repeated in the second experiment. There were no significant differences ($p > 0.1$) between these two experiments.

A summary of combined data is given in Table I. A comparison of average *Daphnia* mortality during the first 12 h was made for all treatments using analysis of variance (Table II). Although 11-day starved *Chaoborus* ate the greatest number of *Daphnia* during this period, no statistically significant differences were seen among 7, 9 and 11-day starved larvae ($p > 0.05$).

Feeding rates increased gradually with starvation period to a maximum between 7 – 11 days of starvation and thereafter decreased rapidly to approximately the previous low levels (Figure 1). A similar pattern was seen in the second 12 h of feeding. However, predation rates were generally lower during this time, probably caused by the effect of non-replenishment of prey during this time or to satiation of hunger.

The greatest starvation effects seen in the first 12 h began after one day of starvation (Figure 1). Heightened feeding rates in the second 12 h occurred after 4 days of starvation (Figure 1). This suggests that up to 4 days of starvation, the starvation effect can be compensated for within the first 12 h of feeding. Since the feeding rate with no starvation was not measured, it is not known whether the 12 h starvation rates are above satiation feeding rates.

The results in Table I further indicate the higher rates of feeding ($p < 0.1 > 0.05$)

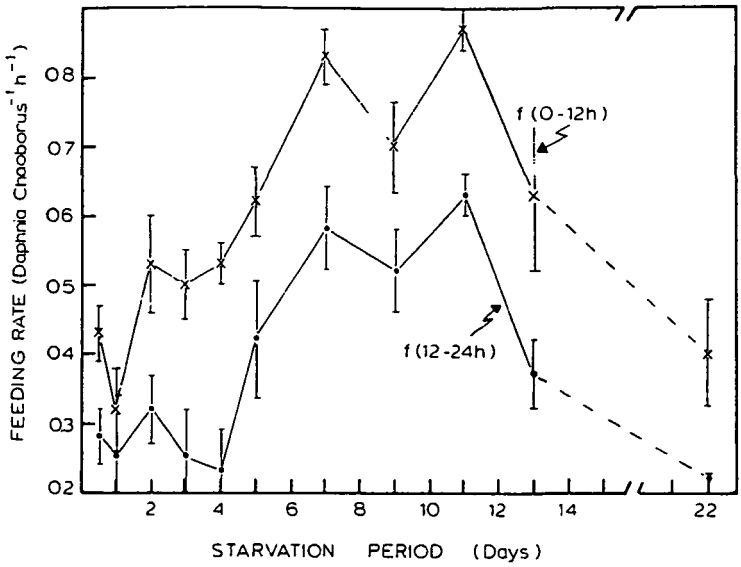

Fig. 1. Effect of starvation period on the feeding rate of *Chaoborus americanus* using *Daphnia rosea* as prey. (×---×) Average feeding rate between 0 – 12 h. Observations were taken every 2 h during this period and prey was replenished at the end of the 2-h periods. (---) Average feeding rate between 12 – 24 h. Single observation was taken at the end of the 24-h period without any replenishment of prey during this period. Mean values ± SE.

generally occurred during the first 2 h of the experiment as compared with subsequent 2-h intervals. This initial increase in the rate of feeding was, however, not observed in the 12-h and 1-day starved larvae. After the first 4 – 6 h the feeding rates are generally lower and not significantly different.

There is little information on the effect of a starvation period on feeding rates or feeding patterns of *Chaoborus*. Smyly (1980) found a strong correlation between starvation time and prey consumption by fourth instar *Chaoborus flavicans* (Meigen) when *Ceriodaphnia* were offered as prey, but only weak evidence with other food items including *Daphnia*. In a detailed study using *Daphnia* and *Diaptomus* as prey, Pastorak (1980) observed that *Chaoborus trivittatus* (fourth instar) elevated its initial feeding rate in response to 18-h and 14-day starvation periods, but that this effect persisted for only the first 6 – 8 h of feeding.

In the present study, we found the feeding response of *C. americanus* to starvation to follow three distinct phases. For the first 7 days of starvation, prey consumption showed a nearly linear increase with time. From 7 to 11 days, feeding remained at a plateau of maximum rates. Further starvation depressed feeding rates. Curiously, these depressed feeding rates up to 22 days do not fall below the low starvation rates at 1 – 2 days. This diminished influence of long-term starvation suggests that *Chaoborus* may not simply be in a physiologically weakened state, but rather may reduce their metabolic activity to conserve energy after prolonged starvation.

Also, it is generally seen that following two or more days of starvation the feeding rate is significantly higher ($p < 0.05$) during the first 2 h than in the later periods. After the first 4 h of feeding, the feeding rate is generally low and exhibits no consis-

tent pattern. If the average feeding rate is computed for all starvation periods, excluding the first 4 h of feeding, no pattern between average feeding rate and starvation time is seen. These observations indicate that the effect of starvation on the daily food intake persists only during the first few hours of feeding. However, hunger effects may persist for several days, at least with preferred prey species (Smyly, 1980).

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References

Dodson,S.I. (1970), Complimentary feeding niches sustained by size selective predation. *Limnol. Oceanogr*, **15**, 131-137.

Fedorenko,A.Y. (1973), Predation interactions between zooplankton and two species of *Chaoborus* (Diptera Chaoboridae) in a small coastal lake. M.S Thesis, University of British Columbia, p. 2.

Fedorenko,A.Y. (1975), Instar and species specific diets in two species of *Chaoborus*, *Limnol. Oceanogr.*, **20**, 238-249.

Kaja,Z. and Ranke-Rybicka,B. (1970), Feeding and production efficiency of *Chaoborus flavicans* Meigen (Diptera, Culcidae) larvae in eutrophic and dystrophic lakes. *Pol. Arch. Hydrobiol.*, **17**, 225-232.

La Row,E.S and Marzolf,E.S (1970), Behavioral differences between third and fourth instars of *Chaoborus punctipennis* Say, *Am. Mid. Nat.*, **84**, 428-436

Pastorak,R.A. (1980), The effects of predator hunger and food abundance on prey selection by *Chaoborus* larvae. *Limnol. Oceanogr.*, **25**, 910-921

Schiemer,E.D, Gnaiger,E. and Jantsch,A. (1975), Beobachtungen uber die verteilung, tageszeitliche Wanderungen und Nahrungsaufnahmeraten von *Chaoborus flavicans* (Meigen) im Goggausee, *Carinthia II*, **165**, 184-189.

Smyly,W.J.P. (1980), Food and feeding of aquatic larvae of the midge *Chaoborus flavicans* (Meigen) (Diptera, Chaoboridae) in the laboratory, *Hydrobiologia*, **70**, 179-188.

Swift,M.C. and Fedorenko,A.Y (1975), Some aspects of prey capture by *Chaoborus* larvae. *Limnol. Oceanogr.*, **20(3)**, 418-425

Swüste,H F.J, Cremer,R. and Parma,S (1973), Selective predation by larvae of *Chaoborus flavicans* (Diptera, Chaoboridae), *Verh. Int. Ver. Theor. Angew. Limnol.*, **18**, 1559-1563.

Vinyard,G.L. and Menger,R.A. (1980), *Chaoborus americanus* predation on various zooplankters, functional responses and behavioral observations, *Oecologia*, **45**, 90-93.

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