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Density-dependent predation of *Chaoborus flavicans* on *Daphnia longispina* in a small lake: the effect of prey size

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Abstract

Functional response curves of fourth instar larvae of *Chaoborus flavicans* preying on two size classes of *Daphnia longispina* were examined throughout three summer seasons in a small forest lake. Data for each size class were fitted to Holling's disc equation. The parameters a' (attack rate) and T_h (handling time) were calculated for each prey size from these curves. Attack rate was greater and handling time was shorter for small (0.77 mm) than for large (1.82 mm) *Daphnia*. In 1:1 mixture of these prey size classes the predation rates of *Chaoborus* on small *Daphnia* at prey densities above $20\,l^{-1}$ were greater than predicted from the single size-class experiments. The observed predation rates on large *Daphnia* were lower than predicted at all prey densities. Since both single size-class and two size-class experiments were run during the same period of time the difference in observed and predicted predation rates could not be attributed to seasonal changes in prey preference of *Chaoborus* larvae. In experiments with a concentrated mixture of lake zooplankton (dominated by *D. longispina*) *Chaoborus* preference for *Daphnia* decreased as prey body size increased. There was no obvious correlation between selectivity coefficients and size-frequency distributions of *Daphnia*. When medium-sized *Daphnia* were omitted from calculations the preference of small over large prey did not differ significantly from the predictions of the single size-class model.

Introduction

The larvae of *Chaoborus* are common predators which occur in plankton of various habitats, from shallow ponds to large lakes, particularly when fish populations are not abundant. Even at moderate density, *Chaoborus* can have a significant impact on zooplankton populations and alter the entire community structure (Dodson, 1972; Lynch, 1979; vonEnde & Dempsey, 1981; Nyberg, 1984; Luecke & Litt, 1987; Elser *et al.*, 1987; Black & Hairston, 1988; Vanni, 1988; Hanazato & Yasuno, 1989). Besides its important role in pelagic food webs, *Chaoborus* has been a convenient species with which to investigate the processes of predation, and to analyze the components of feeding behaviour (Swift & Fedorenko, 1975; Giguère *et al.*, 1982; Havel & Dodson, 1984; Moore & Gilbert, 1987; Riessen *et al.*, 1984, 1988), functional responses to various prey (Fedorenko, 1975; Neill, 1978; Smyly, 1980; Vinyard & Menger, 1980; Spitze, 1985; Matveev *et al.*, 1986), and prey selection both in the laboratory (Dodson, 1970; Sprules, 1972; Swüste *et al.*, 1973; Pastorok, 1980, 1981; Walton, 1988; Riessen *et al.*, 1988) and in the field (Lewis, 1977; Kajak & Rybak, 1979; Chimney *et al.*, 1981; Shei *et al.*, 1988; Moore, 1988). The results of these studies provide valuable and extensive information about species-, size-, and density-dependent changes in a predator's feeding rate and prey selectivity. However, these findings have seldom been used to quantify the impact of *Chaoborus* on prey populations in natural or experimental communities. The effect of *Chaoborus* on zooplankton in enclosure and outdoor tank experiments (Vanni, 1988; Hanazato & Yasuno, 1989) has usually been evaluated by analysing prey numerical responses at different predator densities (but see Riessen *et al.*, 1988). The feeding rates and selectivity of *Chaoborus* in the field has been estimated from predator's crop evacuation rates and the average amount of prey in the crop (Neill, 1981).

Although there are some examples in the literature where the functional response of *Chaoborus* has been used to predict *in situ* feeding rates (Fedorenko, 1975; Matveev *et al.*, 1986), the application of this procedure leads to several problems. First, it is difficult to incorporate the effects of diurnal and/or seasonal changes in abiotic conditions, predator age, prey morphology, etc., in laboratory experiments run under constant conditions during a relatively short period of time. Second, it is still unclear whether the information gained from single-prey experiments (with respect to prey size, age or species) is sufficient to allow prediction of predator feeding patterns for mixed prey types (cf. Colton, 1987).

The purposes of this study were: 1) to estimate parameters for functional responses of *Chaoborus* on two size classes of *Daphnia longispina* under summer temperature/light conditions typical of small temperate lakes; 2) to check the applicability of these parameters derived from single size-class experiments to 1:1 mixture of prey size classes; and 3) to compare the feeding rate and prey selectivity predicted by functional responses with those observed for a natural mixture of zooplankton occurring in a small lake dominated by *Daphnia longispina.*

Materials and methods

Feeding experiments using fourth instar larvae of *Chaoborus flavicans* and *Daphnia longispina* as prey were performed during the summer seasons 1986–1988. The experimental organisms were collected with a plankton net from the central part of Lake Maly Okunenok located in S.-W. part of St. Petersburg district, Russia.

Lake Maly Okunenok is a small (2.7 ha) and shallow (max. depth 2.1 m) forest lake. In 1986–1987 the lake contained no fish. In May and June 1988 Lake Maly Okunenok was stocked with carp (*Cyprinus carpio*) fry and larval peled (*Coregonus peled*). The density of *Coregonus* fingerlings was low in comparison with average stocking levels in nursery lakes; the total catch at the end of the season did not exceed 300 fingerlings of approx. 20 g wet weight (A. Jakovlev, pers. comm.). *D. longispina* and *C. flavicans* were the dominant zooplankton species during all three seasons; their densities reached 193 l^{-1} and 1.6 l^{-1}, respectively (Krylov *et al.*, 1992).

Predation rates and prey size selection by *Chaoborus* larvae were tested in three series of experiments: functional response experiments with one and two size-classes of *Daphnia longispina* and experiments with a concentrated mixture of zooplankton from the study lake.

Single size-class experiments were conducted at five different prey densities (10, 25, 50, 100, and 200 liter^{-1}). Widemouth glass bottles (1250 ml in volume) served as experimental containers. A known number of *Daphnia* and 1 to 5 *Chaoborus* larvae freshly collected in the lake before the experiment were pipetted into each container filled with 1000 ml of filtered (40 μm) lake water. Experimental and control (without predators) containers sealed with plastic stoppers were exposed for 24 h on a submerged platform in the littoral zone of the lake. At the end of the experiment the medium was concentrated by filtration, and the animals within the remaining water were transferred to a Bogorov counting chamber, preserved in formalin, and later counted and measured using a binocular microscope.

Prey were selected both by sieving (to separate size classes) and by manually using a binocular microscope (to exclude damaged specimens and females bearing advanced embryos and, thus, to prevent prey reproduction during the experiment). Two prey size classes were used – 'small' and 'large' with mean body lengths (from the top of the head to the base of the tail spine) of 0.770 ± 0.102 mm ($\pm$1SD, $n = 386$) and 1.819 ± 0.163 ($n = 429$), respectively.

Since functional response parameters may depend on the season (Spitze, 1985), the experiments were performed in the following order. Each experiment included a series of 3 to 10 experimental and control bottles with one replication per treatment (prey size/prey density) in random order. This experimental procedure was repeated several times resulting in a set of data with 4 to 8 trials at each prey density using both small and large *Daphnia* distributed randomly throughout the season, and a set of controls. Table 1 illustrates the experimental protocol for one treatment.

The main set of experiments was conducted between July 7 and August 13, 1986. The water temperature in the experimental bottles, incubated in the lake, varied between 17.3 and 26.1 °C (including both daily and seasonal changes). Additional experiments were conducted in 1987 (July 31–August 2; 17.9–20.8 °C) and in 1988 (May 28–June 27; 18.0–26.9 °C).

Although this procedure may increase the inter-trial variance of feeding rates, it permits us to incorporate the effects of seasonal changes in temperature, predator age, prey morphology, etc.

The procedure for experiments with two size classes were similar to those with one size class except that equal numbers of small and large *Daphnia* were presented at 10, 25, 50, and 100 of each size-class per liter (= container).

Recovery of small *Daphnia* in control containers averaged 98.6% ($n = 20$), and of large *Daphnia* 97.4% ($n = 18$). Although in some containers few specimens of both small and large *Daphnia* were get caught in the surface film of water, their numbers were always low. Nonpredatory mortality and reproduction of prey (in controls), and 'wasteful killing' or partial consumption of prey by predators (in experimental containers) also were not significant in these experiments and were ignored. Thus, the difference between the initial and final number of prey in experimental containers after correcting for percent recovery in controls was used to calculate the predation rates.

Predation of *Chaoborus* larvae on concentrated zooplankton from the lake was examined in

Table 1. Predation of fourth instar *Chaoborus* larvae on large (1.82 mm) *Daphnia* at prey density 100 l^{-1} (experimental protocol). PR is predation rate, N_{pred} is the number of *Chaoborus* larvae per jar, N_{prey} is the final number of *Daphnia* per experimental jar. The initial number of prey was always 100 per jar. The mean final number of prey in controls was 97.4 per jar.

Trial no.	Data	Experimental duration, *h*	Temp. °C	N_{pred}	N_{prey}	PR, prey $pred^{-1}\,d^{-1}$
1	July 7, 1986	24	22.4–24.5	3	69	9.47
2	July 27, 1986	24	22.0–26.1	2	82	7.70
3	July 30, 1986	24	21.6–26.1	2	86	5.70
4	July 31, 1987	24	18.0–20.0	4	79	4.60
5	August 2, 1987	19	18.0–19.0	3	86	4.80
6	May 25, 1988	24	18.0–22.1	4	67	7.60
7	June 6, 198	24	20.0–21.5	3	85	4.13
8	June 22, 1988	24.5	19.7–23.0	4	80	4.26

four experiments conducted between June 3 and August 1, 1986 and in one experiment on May 25, 1988. Zooplankton were caught with a modified 8-l Schindler-Patalas trap and poured through a plankton net. Three live plankton samples were rediluted in 10 liters of lake water. Slow continuous mixing of the medium prevented zooplankton aggregation. On the shore one or two equal portions (250 ml each) of the medium were placed in 11 widemouth glass jars (1.25-l in volume). When the second portion was added, the filling order of the jars was reversed to compensate for any biases introduced by possible differences in prey distribution. The remaining volume of the jars was filled with filtered lake water. Ten *Chaoborus* fourth instar larvae freshly collected in the lake were added to each of five jars chosen randomly. The contents of three jars without *Chaoborus* were poured through a mesh filter, preserved in formalin; these 'initial controls' provided estimates of initial prey number. The three remaining jars without *Chaoborus* ('final controls') and five experimental jars were incubated in the littoral zone of the lake for 24 h. At the end of the experiment, prey and predators were preserved in formalin and examined under a binocular microscope.

Daphnia longispina dominated the zooplankton comprising more than 90% of mean total zooplankton biomass. The other organisms were *Asplanchna priodonta*, *Chydorus sphaericus*, naupliar and copepodid stages of cyclopoid copepods (mostly *Mesocyclops leuckarti*), small rotifers and large phytoplankton. For the purposes of this study all prey except *Daphnia* were omitted from subsequent calculations.

In order to assess prey size selection by *Chaoborus*, all *Daphnia* were initially grouped in six size classes (0.53–0.75; 0.78–1.00; 1.03–1.25; 1.28–1.50; 1.53–1.75; and 1.78–2.00 mm). For the purposes of comparison with one- and two size-class experiments *Daphnia* were grouped arbitrarily as small (< 1.03 mm) and large (≥ 1.03 mm). Finally, to obtain discrete size classes which were more similar to those in the single prey experiments, medium-sized prey (1.03–1.25 mm) were omitted from calculations.

Preference was measured using indices α and ε (Chesson, 1983). Index α always sums to 1 over all prey types. 'Neutral' values for the index, which indicate that each prey type is represented in equal proportions in the environment and in the diet of *Chaoborus*, is $1\ \mathrm{m}^{-1}$, where m is the number of prey types. Higher values indicate 'positive' selection, and lower values mean 'negative' selection (avoidance). Index ε was calculated to compare the results of experiments with lake zooplankton where the number of prey size classes varied. Index ε ranges from -1 to $+1$ with 0 representing 'neutral' selection.

The 'disc' equation (Holling, 1959) was chosen as a model of the functional response of *Chaoborus* larvae:

$$\mathrm{PR} = \frac{a'N}{1 + a'T_hN}\ , \tag{1}$$

where PR is predation rate (prey $\mathrm{pred}^{-1}\ \mathrm{d}^{-1}$), N is prey density ($\mathrm{prey\ l}^{-1}$), T_h and a' are coefficients referred to as prey 'handling time' (d) and 'attack rate' ($\mathrm{l\ d}^{-1}$).

The coefficients T_h and a' were estimated by least sum of squares using iterative (nonlinear) procedure which avoids biases produced by linearizing of Eq. 1 (Bard, 1974).

Predictions about the predation rate of *Chaoborus* on prey size class i in mixed size-class experiments were made substituting the values of T_h and a' obtained from the single size-class experiments into a multiprey version of the 'disc' equation (Murdoch, 1973):

$$\mathrm{PR}_i = \frac{a_i' N_i}{1 + \sum_{i=1}^{m} a_i' T_{hi} N_i}\ , \tag{2}$$

where m is the number of prey size classes. The actual predation rates observed in mixed size-class experiments were compared to these predictions to determine whether Eq. 2 reflects the predator's feeding behaviour in more complex situations.

Results

Functional response curves of fourth instar larvae of *Chaoborus flavicans* preying on small (0.77 mm) and large (1.82 mm) *Daphnia longispina* are shown in Fig. 1. In both series of single size-class experiments, *Chaoborus* exhibited a monotonically decelerating functional response which was described by the 'disc' equation with the following parameters:

Prey size (mm)	a' (l d^{-1})	T_h (d^{-1})
0.77	0.581	0.0178
1.82	0.200	0.1253

The 'attack rate' coefficient (which can also be considered as the maximum volume searched by a predator per unit time) for small *Daphnia* was 2.9 times greater than for large *Daphnia*, while the 'handling time', T_h, for small *Daphnia* (26 min) was considerably less than for large *Daphnia* (3 h). Asymptotical values of maximum predation rate, PR_{∞}, the reciprocal of T_h, were equal to 56.2 and 8.0 prey pred^{-1} d^{-1} for small and large *Daphnia*, respectively. These 'theoretical' maximum predation rates were approx. 1.5 times greater than the actual maximum predation rates, PR_{mx}, observed at the highest prey density (37.2 and 5.7 prey pred^{-1} d^{-1}, respectively).

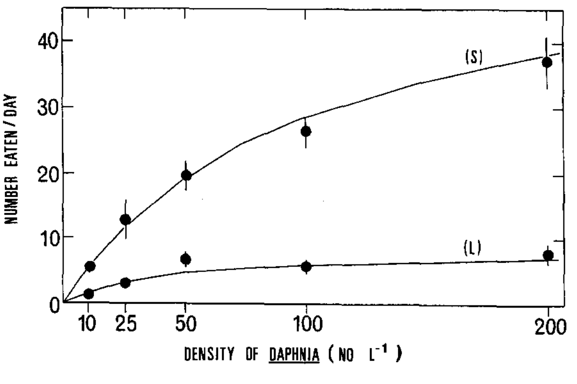

Fig. 1. Functional response curves for fourth instar larvae of *Chaoborus flavicans* preying on small (S) and large (L) *Daphnia longispina* in single size-class experiments derived from the Holling's disc equation fit (see text for parameter values). Vertical bars represent one standard error of the mean.

To test the model, predictions using Eq. 2 based on the values for the parameters of single size-class experiments were compared with actual predation rates of *Chaoborus* larvae on small and large *Daphnia* in 1:1 mixture (Fig. 2).

For total prey densities above 20 l^{-1} the actual feeding rates on small *Daphnia* were greater than predicted, and the actual feeding rates on large *Daphnia* were lower than predicted. For both small and large *Daphnia* 2 out of 4 differences were statistically significant (differences greater than two standard errors of the observed predation rate). At the maximum density tested (200 small and 200 large *Daphnia* per litre) the predation rates of *Chaoborus* larvae on both small and large *Daphnia* decreased (Fig. 2). However, this decrease did not influence the outcome of the

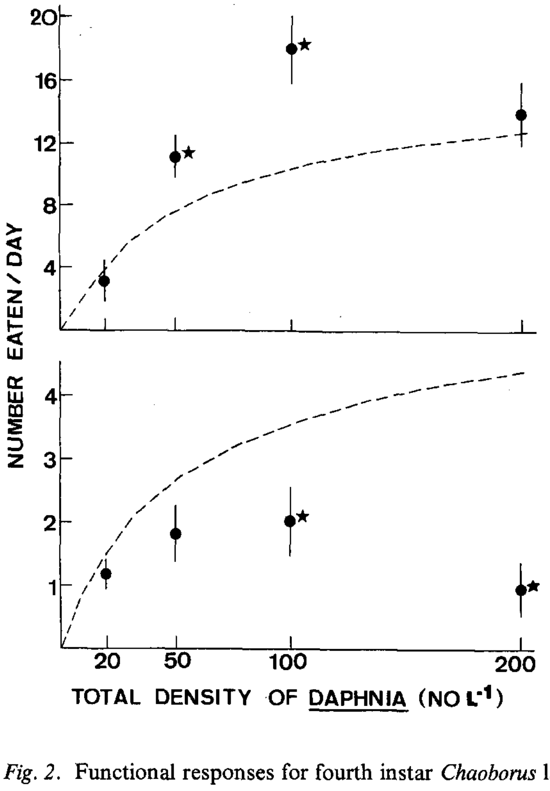

Fig. 2. Functional responses for fourth instar *Chaoborus* larvae preying upon small *Daphnia* (upper panel) and large *Daphnia* (lower panel) in a 1:1 mixture of these prey. Dotted curves represent predictions using Eq. 2 based on parameters values for the single size-class experiments. Symbols represent the means (± 1 SE) for the observed predation rates at each density of prey. '★' indicates that results differ significantly from predictions.

overall comparison of the predicted and observed predation rates in two size-class experiments.

The results of experiments with the concentrated mixture of lake zooplankton are summarized in Fig. 3. The preference of *Chaoborus* larvae tended to decrease as the size of *Daphnia* increased in all experiments. There was no obvious correlation between selectivity coefficients and the initial size-frequency distributions of *Daphnia* (Fig. 3: upper right panels). The intercept of size-selection curves (i.e. neutral selection) fell between 0.96 and 1.24 mm (mean 1.08 mm); *Daphnia* smaller than 1 mm were positively, and *Daphnia* larger than 1 mm negatively selected by *Chaoborus* larvae.

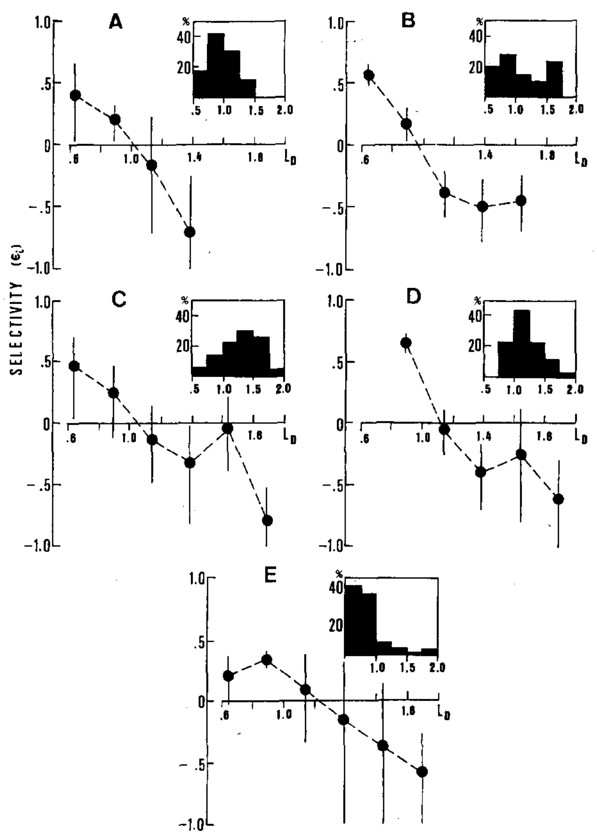

Fig. 3. Size-selection of *Daphnia* by *Chaoborus* larvae in experiments with a concentrated mixture of lake zooplankton. Mean ε_i values, with vertical bars representing 95% confidence intervals. L_D – *Daphnia* body length (mm). Upper right panels: mean size-frequency distributions of *Daphnia* in control jars. A – exp. 1, June 3–4, 1986; mean total number of *Daphnia* per control jar (TD) 407 ± 23 (± 1 SD). B – exp. 2, July 3–4, 1986; TD = 128 ± 11. C – exp. 3, July 13–14, 1986; TD = 140 ± 23. D – exp. 4, August 1–2, 1986; TD = 457 ± 15. E – exp. 5, May 25–26, 1988; TD = 329 ± 42.

For the purposes of comparing predictions from the single size-class model, all *Daphnia* were grouped in two size classes: small (< 1 mm) and large (≥ 1 mm). Although the deviations from the predicted values in some experiments were significant, no regular trend was observed (Table 2).

To make the comparison with the single size-class model more accurate, medium-sized *Daphnia* (1.03–1.25 mm) were omitted from further calculations. The new size classes thus obtained were more similar to those in the single prey functional response experiments. The preference of small over large *Daphnia* did not differ significantly from the predictions of the single size-class model at any total prey density tested (Fig. 4).

Discussion

Characteristics of functional response. 'Attack rate' coefficients for small and large *Daphnia longispina* (0.581 and 0.200 l d^{-1}, respectively) fell inside the range reported by Spitze (1985) for fourth instar *Chaoborus americanus* feeding on different-

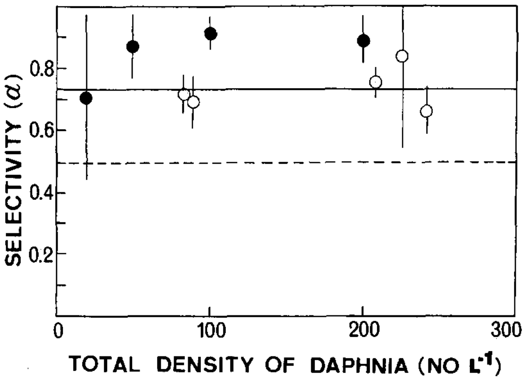

Fig. 4. Selection of small vs. large *Daphnia* by *Chaoborus* larvae in two prey-size experiments (black symbols) and in experiments with lake zooplankton where medium-sized *Daphnia* were excluded (open symbols) plotted against the total density of *Daphnia*. Vertical bars represent 95% confidence intervals. The dashed line represents 'neutral' selection ($\alpha_0 = 0.5$); the solid line, prey selection predicted by the single size-class model ($\alpha_{pr} = 0.734$).

Table 2. Observed (Ob) and predicted (Pr) predation rates of fourth instar *Chaoborus* larvae on small and large *Daphnia* in experiments with a concentrated mixture of lake zooplankton. Values are means of 5 experimental replicates (and 1 SD in parentheses).

	Mean initial density of *Daphnia* (l^{-1})		Predation rate (prey pred^{-1} d^{-1})			
	Small *Daphnia*	Large *Daphnia*	Small *Daphnia*		Large *Daphnia*	
			Pr	Ob	Pr	Ob
1	191.2 (16.58)	136.5 (10.54)	17.0	12.6 (1.10)	3.9	5.0 (2.22)
2	48.3 (3.37)	54.1 (7.93)	8.7	4.8 (0.68)	3.6	2.3 (0.50)
3	20.3 (4.69)	91.5 (14.41)	2.9	1.6 (0.40)	4.7	3.9 (0.81)
4	80.8 (15.84)	284.4 (3.96)	4.3	9.7 (0.75)	5.5	15.2 (3.34)
5	216.5 (28.50)	46.9 (7.37)	25.4	22.8 (0.86)	1.9	3.4 (0.41)

sized *Daphnia pulex* (approx. 0.1–0.7 l d^{-1}). Since 'attack rate' describes the rate of approach to the asymptotic maximum predation rate as prey density increases, and since a' depends on the ability of the predator to search for, to attack, and to ingest prey, it can be used as a simple measure of the predator's efficiency. A 2.4-fold increase in size of *D. longispina* (from 0.77 to 1.82 mm) corresponded with a 2.9-fold decrease (0.581/0.200) in predation efficiency of fourth instar *C. flavicans*. A 2.5-fold increase in size of *D. pulex* (from 0.8 to 2.0 mm) in the experiments of Spitze (1985) corresponded with a 3.1-fold decrease in 'attack rate' coefficients. This comparison suggests that size-selective predation by both *Chaoborus* species on two species of *Daphnia* is similar.

The 'handling time' coefficients of *C. flavicans* feeding on small and large *D. longispina* (26 min–3 h) were short as compared with T_h's in experiments with *C. americanus* preying on *D. pulex* (1–10 h: Spitze, 1985). Accordingly, the asymptotic values of the maximum predation rate (PR_{∞}) for both small and large *D. longispina* were considerably higher than PR_{∞} values for similar sized *D. pulex* (Table 3). This difference can be attributed, at least partially, to the greater vulnerability of *D. longispina* to predation by *Chaoborus* larvae. The experiments of Pchelkina (1950) confirm that *Chaoborus* strongly select *D. longispina* over *D. pulex* in a 1:1 mixture of these prey.

High maximum predation rates (PR_{mx}) of *C. flavicans* were consistent with the number of *D. longispina* (19–36 per day) consumed by *Chaoborus* larvae at 24° when prey were abundant (Pchelkina, 1950). They were also comparable with PR_{mx} values of the fourth instar of *C. flavicans* and the third instar of a larger species, *C. trivittatus*, feeding on small cladoceran prey such as *Ceriodaphnia* (Smyly, 1980), *Bosmina* (Matveev *et al.*, 1986), and *Diaphanosoma* (Fedorenko, 1975). Expressed as biomass consumed, PR_{mx} values observed in my experiments fall within the range reported for fourth instar *Chaoborus* larvae (Table 3).

Prey size-selection. In 1:1 mixture of prey size-classes *Chaoborus* showed a greater preference towards the smaller, preferred prey than was predicted from the single size-class experiments. The predation rates on large *Daphnia*, the less preferred prey, were all lower than predicted (Fig. 2). Reynolds & Geddes (1984) observed a similar pattern in feeding behaviour of another invertebrate predator, the notonectid *Anisops deanei* which was fed two size classes of *Daphnia thomsoni*. These findings are inconsistent, however, with the results of the experiments of Spitze (1985) with *Chaoborus americanus* preying on different size classes of *Daphnia pulex*. In his experiments the actual feeding rates on both small and large *Daphnia* were all greater than predicted when two size-class experiments were conducted approximately one month after single size-class experiments. When both single and two size-class experiments were conducted simultaneously, the observed predation rates of *C. americanus* were very similar to predictions of the single-prey

Table 3. Asymptotic values of maximum predation rate (PR_{∞}) and actual maximum predation rates (PR_{mx}) of fourth instar *Chaoborus* larvae on cladocerans in single-prey functional response experiments.

Chaoborus species	Prey species	Prey size (mm)	Temp. (°C)	PR_{∞}		PR_{mx}		Reference
				no d^{-1}	mg d^{-1}	no d^{-1}	mg d^{-1}	
C. americanus	*Moina hutchinsoni*	1.0	14	–	–	10.0	2.79	Vinyard & Menger, 1980[a]
	Daphnia rosea	1.0	14	–	1.11	15.3	0.80	
		1.5	14	–	4.14	12.0	2.12	
		2.0	14	–	7.05	7.7	3.23	
	Daphnia pulex	1.0	14	–	1.52	17.7	0.92	
		1.5	14	–	1.66	7.8	1.38	
		2.0	14	–	2.87	4.0	1.68	
		0.8	15	14.6	0.49	–	–	Spitze, 1985[b]
		1.1	15	9.46	0.90	–	–	
		1.4	15	5.74	1.19	–	–	
		1.7	15	3.50	1.36	–	–	
		2.0	15	2.22	1.47	–	–	
C. flavicans	*Chydorus sphaericus*	0.2	12	–	–	19.0	0.06	Smyly, 1980[c]
	Ceriodaphnia quadrangula	0.4	12	–	–	35.0	0.39	
	Bosmina coregoni	–	17–21	–	–	39.6	–	Matveev *et al.*, 1986[d]
	Daphnia longispina	0.8	17–27	56.2	1.71	37.2	1.13	Present study[e]
	Daphnia longispina	1.8	17–27	8.0	2.94	5.7	2.10	

[a] These values of PR_{∞} were computed by Spitze (1985) as 'prey profitability' (in units of dry weight) and converted to biomass consumed assuming a dry weight/wet weight ratio of 0.10. Data for *M. hutchinsoni*, *D. pulex* and *D. rosea* with body lengths of 1 and 2 mm are from Vinyard & Menger's (1980) Table 2. Data for *D. pulex* and *D. rosea* with a body length of 1.5 mm from their Figure 1 were converted to biomass consumed using length-wet weight regressions in Edmondson & Winberg (1971).

[b] PR_{∞} was computed as $1/T_h$ using length-dry weight and T_h-dry weight regressions in Spitze (1985) and then converted to biomass consumed assuming a dry weight/wet weight ratio of 0.1.

[c] Data from Fig. 1 in Smyly (1980) were converted to biomass consumed using regressions in Balushkina & Winberg (1979).

[d] PR_{mx} at a prey density of approx. 140 prey l^{-1} from Fig. 4 in Matveev *et al.* (1986).

[e] PR_{∞} and PR_{mx} were converted to biomass consumed using length-wet weight regressions in Balushkina & Winberg (1979).

model. Spitze explained the disparity between the two experimental series by possible time-dependent variations of Holling's parameters. However, seasonal factors could not be responsible for the differences between expected and actual feeding rates of *Chaoborus* observed in the present study because both single and two size-class experiments were run concurrently.

Despite differences in absolute and relative abundance of different-sized *Daphnia* in experiments with a concentrated mixture of lake zooplankton, *Chaoborus* larvae exhibited a similar pattern of prey size-selection (Fig. 3). Switching from positive to negative preference occurred at prey size ranging from 0.96 to 1.24 mm; these values were slightly less than 1.3 mm reported by Dodson (1970, 1974) for fourth instar *C. flavicans* and *C. americanus*.

However, the observed predation rates of *Chaoborus* on small and large *Daphnia* in lake zooplankton differed considerably from values predicted using Eq. 2, which either underestimated or overestimated the predation rates on a given size-class of prey. The source of deviation from predictions may have been *Daphnia* of medium size (1.03–1.25 mm). As shown in Fig. 3 (upper right panels) their contribution to total number of prey varied from one experiment to the other. Moreover, their influence on feeding rate of *Chaoborus* could possibly depend on the relative abundance of different size groups among 'medium size-class'.

To test this hypothesis, all medium-sized prey were excluded from calculations. The size classes thus obtained were more similar to those in the single size-class experiments; as a result the preference of small over larger *Daphnia* by *Chaoborus* larvae was very similar to the predictions (Fig. 4).

The results of the present study suggest that the model derived from one size-class experiments failed to predict the observed predation rates of *Chaoborus* in the 1:1 mixture of two prey size classes but accurately predicted the predation rates on *Daphnia* of similar size in lake zooplankton. Natural zooplankton is a more complex environment in comparison with a 1:1 mixture of two size classes of one prey. Alternative prey as well as several other factors may be responsible for the observed difference in predictive ability of the single-prey model. Additional experiments and behavioural observations are required to give a plausible explanation of this discrepancy. However, these results suggest that the outcome of testing of a single-prey model may depend on the type of the test. Care should be taken to make conclusions concerning predator's feeding patterns based on one type of experiments only.

In general, a comparison of the results obtained in single-, two-, and multiprey size situations suggests that some as yet undisclosed mechanisms of feeding behaviour of *Chaoborus* larvae may be important in determining its prey size-preference. A recent review of this problem (Krylov, 1989) has led to two conclusions. First, in almost all cases single-prey experiments allow the prediction of the right order of prey selection by invertebrate predators in prey mixtures, although selectivity coefficients may deviate from predictions. Second, the predictive ability of single-prey models is higher for size- than for species-selection by a predator. The present investigation is consistent with the first conclusion, however, it suggests that even in the case of size-selection the results may depend on the mode of testing the single-prey model (artificial 1:1 mixture vs lake zooplankton). These results indicate that the analysis of predictive ability of single-prey functional response models deserves further consideration.

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