Chaoborus and fish-mediated influences on *Daphnia longispina* population structure, dynamics and life history strategies

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Summary. This study examined the long term effects of predation by larvae of the midge *Chaoborus* and simulated fish predation on experimental *Daphnia longispina* populations. *Chaoborus* predation, relative to fish predation, led to populations composed of larger individuals as a whole, larger egg-bearing individuals, and a larger primiparous instar. *Daphnia* retained helmets beyond the first instar in response to the presence of *Chaoborus*. Both types of predation, relative to predator-free controls, reduced prey population size and rates of increase, but increased population death rates. The reduction in population size due to predation led to increased resource availability for individuals remaining in the populations and increased individual fecundity in the predation treatments. The differences noted between the *Chaoborus*, fish, and control treatments increased with predation intensity.

Key words: *Daphnia* – *Chaoborus* – Fish – Size-selective – Predation

Predator-induced morphological defenses have been observed among a variety of freshwater zooplankton, including ciliates, rotifers and cladocerans (Gilbert 1966; Kerfoot 1977; Kuhlmann and Heckmann 1985; Stemberger and Gilbert 1987; Stenson 1987). A commonly observed morphological defense for freshwater zooplankton is that of helmet or "neck teeth" induction, which has been observed in *Daphnia* as a response to the predator *Chaoborus*. Studies have documented the occurrence of this response (Krueger and Dodson 1981; Havel 1985; Herbert and Grewe 1985; Vuorinen et al. 1989), the defense it provides (Krueger and Dodson 1981; Havel and Dodson 1984; Mort 1986), the physiological cost (Havel and Dodson 1987; Walls and Ketola 1989;

Riessen and Sprules 1990), and the precursors and generality of this response among different species and clones of *Daphnia* (Havel 1985; Dodson 1988a; Dodson 1989). Studies have also documented *Daphnia* vulnerability (Pastorok 1981; Riessen et al. 1984; Spitze 1985; Riessen et al. 1988) and behavioral adaptations (Dodson 1988b) to *Chaoborus* predation. Despite the considerable attention given to *Chaoborus* predation on *Daphnia*, however, no previous study has looked at such vital processes as long-term predator influences on prey population size (individuals), population size structure, size distribution of the reproductive population, fecundity, size at maturity, and population demographic rates. The absence of such information represents, in my opinion, a major gap in our understanding of *Chaoborus-Daphnia* predator-prey interactions.

Field studies suggest that size-selective predation by fish, relative to that by *Chaoborus*, other invertebrate planktivores, or the absence of fish, depresses cladoceran population size, and shifts populations towards smaller individuals and a smaller size at first reproduction (Gliwicz et al. 1981; Vanni 1987, 1988). The accuracy of all field studies, however, is compromised by differences in such factors as interspecific competition, resource quality and quantity, and temperature between the treatments or study sites compared. Hence, in order to quantify accurately direct long-term predator influences it is necessary to make observations where confounding influences from other zooplankters, differences in resource base, or abiotic factors are controlled or eliminated.

This study examines the influence of size-selective predation (by *Chaoborus* and a procedure designed to simulate fish) on laboratory populations of *Daphnia longispina*. Specifically, these experiments examined the effects of size-selective predation on the numeric response of the population to resource availability, population size distribution, the size distribution of egg-bearing individuals, the size of the primiparous instar, the relationship between individual size and clutch size, morphological responses to predation, and population rates of increase, birth, and death. This study consists of two sets

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of experiments representing different intensities of predation.

Methods

The clone of *Daphnia longispina* (Crustacea: Cladocera) used for these experiments was isolated from Lake Vallentuna and has been maintained in the laboratory. The larvae of the phantom midge *Chaoborus flavicans* were collected from a pond in the vicinity of the Institute of Limnology, Uppsala University, Uppsala, Sweden. Fish predation was simulated using a 700-µm mesh net. It was necessary to simulate fish predation because even one very small fish would immediately consume all *Daphnia* in the experimental populations employed. In the first experiment each treatment had three replicates; each replicate started with 20 *Daphnia*. These daphnids were collected into 9 groups of 20 individuals and randomly assigned to the various treatments. The daphnids were maintained in 2-l flasks and fed the alga *Rhodomonas minuta* at 1- or 2-day intervals. *Rhodomonas* was supplied equally to all replicates and treatments but increasingly with time, i.e. absolute algal loading rates increased with population size; the concentrations are listed in Table 1. The synthetic medium L16 (Lindström 1984), modified with B vitamins and earth extract, was used both for algal culture and the experiments. The experiments were carried out at $15.2 \pm 0.5°$ C (± 1 SD) with a 14L:10D light cycle. The experimental flasks were arranged in a stratified array, i.e. *Chaoborus*1, fish1, predation-free control, *Chaoborus*2, etc. The *Chaoborus* treatments were started with one 2nd-instar *Chaoborus flavicans* per replicate, which developed into a 4th-instar individual by day 30, with an additional 4th-instar *Chaoborus* added on day 40. Fish predation was simulated by pouring 800 ml of each fish treatment replicate through a 700-µm mesh every fourth day. This captured the largest daphnids and allowed the smaller individuals to pass through. No "predation" was imposed on the predator-free controls. The experiment lasted 60 days, with 200-ml samples taken at 10-day intervals. The samples were preserved in a 4% sugar formalin solution and stored in a cold room at 4° C. When enumerating the samples, the total length (excluding helmet) and number of eggs for each individual was recorded. On day 60 all individuals from both predation treatments were preserved and later enumerated, while 400 ml (20%) of the predator-free controls was preserved.

Individuals from the predator-free controls of experiment 1 were used to start experiment 2. Experiment 2 was a repetition of experiment 1 – with 4 replicates per treatment, a start number of 100 individuals per replicate, 400-ml samples, and less intense predation. For this experiment daphnids were split into 60 groups of 20 individuals with 5 groups of 20 daphnids randomly assigned to each replicate. The *Chaoborus* predation treatments were started with one 4th-instar *C. flavicans*, with another 4th-instar individual added on day 30. Fish predation was simulated by pouring 500 ml of each replicate through a 700-µm mesh at 4-day intervals. As in experiment 1, experiment 2 lasted 60 days, with samples collected at 10-day intervals, and the daphnids fed *Rhodomonas* with loading rates equal between treatments and replicates, but increasing with time. The same temperature-controlled room and flask arrangement as for experiment 1 was used. During experiment 2, but not during experiment 1, the *Chaoborus* individuals were rotated between replicates at 10-day intervals. As for experiment 1, the size and number of eggs for each individual was recorded during enumeration.

A morphological response to *Chaoborus* (helmet occurrence) was noted during sample processing for both experiments. The helmeted individuals had pointed helmets of various sizes, while non-helmeted individuals had smooth heads. There was no ambiguity between the two morphotypes. This character was quantified for days 30–60 of experiment 2, when sample sizes were large.

Dynamics between sampling intervals were calculated, i.e., the population after subsample removal at the initial interval was compared against the population before subsample removal at the succeeding interval, so that subsample removal did not influence the

Table 1. The average *Rhodomonas* loading rates, in µg C *Rhodomonas* per *Daphnia* per day

Treatment	Experiment 1 $n = 3$	Experiment 2 $n = 4$
Control (C)	1.29 ± 0.24	0.93 ± 0.05
Chaoborus (Ch)	2.66 ± 0.91	2.16 ± 0.35
"Fish" ("F")	2.19 ± 0.58	1.78 ± 0.15
Significance P		
C vs Ch	0.10	0.001
C vs "F"	0.10	0.0001
Ch vs "F"	>0.10	0.10

Values are averaged (mean ± 1 SD) by replicate, and means compared using a two-tailed t-test

results presented. Subsample removal did influence the absolute number of individuals in the populations and hence the relative algal loading rates (algae per individual), but this had the same effect on all treatments. The plots of number of individuals versus time for the two experiments are based on a three-point running mean. In addition, the population size after subsample removal was equated to that before subsample removal so that the actual dynamics of the populations were shown, as opposed to the effects of subsample removal. The plotting procedure does not present the actual number of individuals in the population; instead it presents the number expected had no subsamples been taken. However, it does show the cumulative effect of predation on population size. This is a very important aspect of predation influences on population dynamics which is generally ignored in short-term studies. The data presented in the figures for size frequency distribution of the population and of egg-bearing individuals, the percentage egg-bearing individuals versus size class, morphological character occurrence versus size class, and clutch size versus individual length were all based on pooled data across dates for each treatment. The population rates of change, birth, and death were based on data pooled by treatment for each sampling date, and were calculated according to Paloheimo (1974). The running mean and data pooling were employed in order to assess general responses, separate from cohort succession, related to the predation treatments.

In cases where sample sizes within replicates were large enough to provide accurate estimates of the population parameter in question, an ANOVA was carried out. This was true for the number of individuals for experiments 1 and 2, population size structure (using three size classes), and helmet occurrence (using four size classes) for population 2. The ANOVA was in all cases carried out on non-smoothed raw data. A two-tailed Smirnov comparison of cumulative frequency distribution (Conover 1980) was used to test for differences in the frequency distributions of the various parameters. A two-tailed F test (Snedecor and Cochran 1980) was used to test for differences in the relationship between clutch size and individual length between the treatments.

The egg development time was determined by observing the time from when eggs were first deposited in the brood pouch to when neonates were released, at 4-h intervals, for 12 separately maintained individuals of the clone of *D. longispina* used for the predation experiments. The egg development time at $15.1 \pm 0.2°$ C was 3.82 ± 0.11 days.

To calibrate the predation treatments it was necessary to determine the number of *Daphnia* eaten per day by *Chaoborus*, the size-selectivity of *Chaoborus* consuming *Daphnia*, and the size-selectivity of the net used to simulate fish predation. The rate of *Daphnia* consumption by 4th-instar *C. flavicans* was estimated by adding 70 *Daphnia* individuals (none with late developmental stage embryos) of various sizes to a 300-ml flask with one prefed *Chaoborus* and observing the number of *Daphnia* present, alive or dead after 24 h; nine treatment and control (no *Chaoborus*) replicates were used. The size selection of *Daphnia* individuals by 4th-instar *C. flavicans*

was assessed by adding 5 *Chaoborus* individuals, with empty crops, to populations of 70 daphnids in 300-ml flasks, incubating in the dark at 15° C for 2–3 h and then examining the daphnids in the crops of the *Chaoborus*, $n = 9$. The total lengths (TL) of the daphnids in the crops were estimated by measuring the postabdomen (PL) and back-calculating total length (TL = 101 μm + 9.0 × PL, $r^2 = 0.96$, SD of residual error = 50 μm, $n = 18$). The size distribution of those daphnids eaten during these experiments was then compared with the size distribution of those daphnids not eaten during these experiments. The capture efficiency of the net used to simulate fish predation was determined by pouring a large population of daphnids through the net and comparing the frequency of individuals, per size class, which did and did not pass through the net. At the end of experiment 2 the population sizes and egg frequencies predicted by subsampling were compared to the actual number of individuals and eggs in the populations in order to determine the magnitude of sampling error.

Results

The rate at which *Chaoborus* consumed *Daphnia* was found to be 11.5 ± 3.6 daphnids per *Chaoborus* per day. In these treatments 0.3 ± 0.5 daphnids per day died or were killed but not eaten. In control treatments 0.2 ± 0.2 daphnids per day died. The comparison of sizes of *Daphnia* found in *Chaoborus* crops with those available (Fig. 1) indicated that *Chaoborus* may have selected the smallest daphnids, but that size selection by *Chaoborus* was not pronounced until a critical daphnid size of 1700 μm. No daphnids above this size were consumed by *Chaoborus*. This result was confirmed by the visual observation that *Chaoborus* were not able to capture the largest daphnids, although they did attack them. Pastorok (1981) indicated that *C. trivittatus* mainly selected intermediate sized *D. pulicaria*. The differences between selectivities noted by Pastorok and the present study can probably be explained by the differences in *Chaoborus* and *Daphnia* species examined. The net used to simulate fish predation captured very few *Daphnia* individuals at sizes below 1000 μm, and virtually all individuals longer than 1750 μm (Fig. 2).

The error for predictions of population size for individual replicates (absolute value of error in estimate/ correct value) was on average $7.5 \pm 5.9\%$, and was not related to sample size. The error (estimated minus correct value) in estimating population egg frequency was strongly negatively related to sample size. Sample sizes of less than 100 individuals had an average error of 0.082 eggs per individual (range 0.029–0.161), while sample sizes greater than 100 individuals had an average error of 0.011 (range 0.001–0.031). Errors of 0.082 and 0.011 in estimating egg frequency correspond to errors of 0.020 and 0.003, respectively, in estimates of birth and death rates at an egg development time of 3.82 days. As individual estimates of treatment population size were based on 4 replicates, the probable realized error was 3.8% per treatment $(7.5\%/\sqrt{n})$ for estimates of sample size.

Daphnia population density was reduced in the predation treatments (Table 2, and Fig. 3). The differences between the predation treatments and predator-free con-
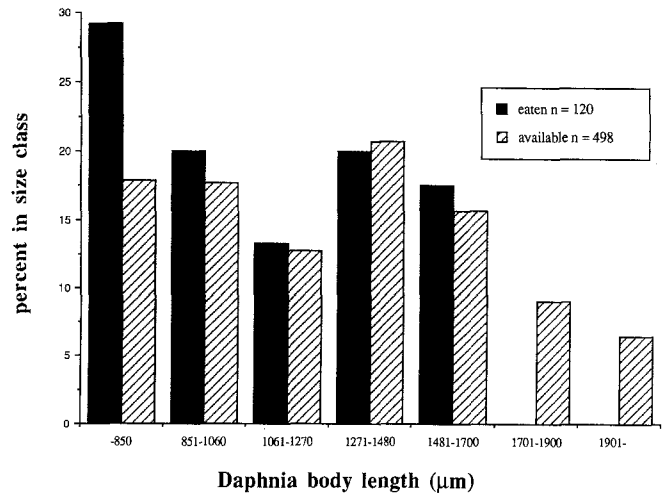

Fig. 1. The size distribution of the *Daphnia* individuals found in *Chaoborus* crops versus that of the *Daphnia* individuals originally available for predation
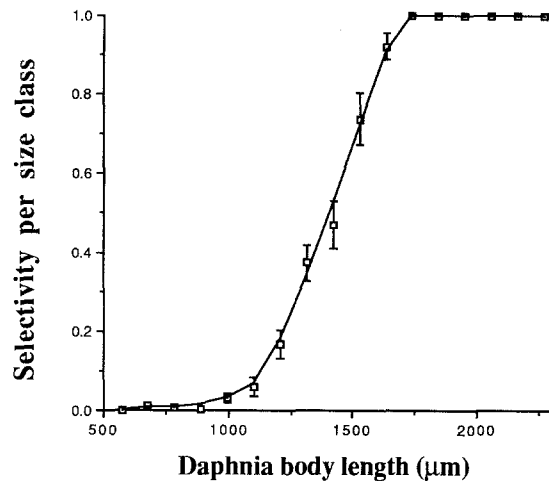

Fig. 2. The selectivity index of the net used to simulate fish predation, 700 μ mesh aperture. The confidence intervals represent ± 1 SD of the binomial distribution

Table 2. Summary of two-way ANOVA of the influence of time and predation treatment on *Daphnia* population size

Source	df	MS	F	P	% Variance
Experiment 1					
Date	5	249799	22.3	0.0001	33.4
Treatment	2	491585	43.9	0.0001	26.3
Interaction	10	110394	9.9	0.0001	29.5
Error	36	11191			10.8
Experiment 2					
Date	5	2083356	83.6	0.0001	53.3
Treatment	2	2367229	94.9	0.0001	24.2
Interaction	10	303193	12.1	0.0001	15.5
Error	54	24924			6.9

Percentage variance refers to the percentage sum of squares explained by the model
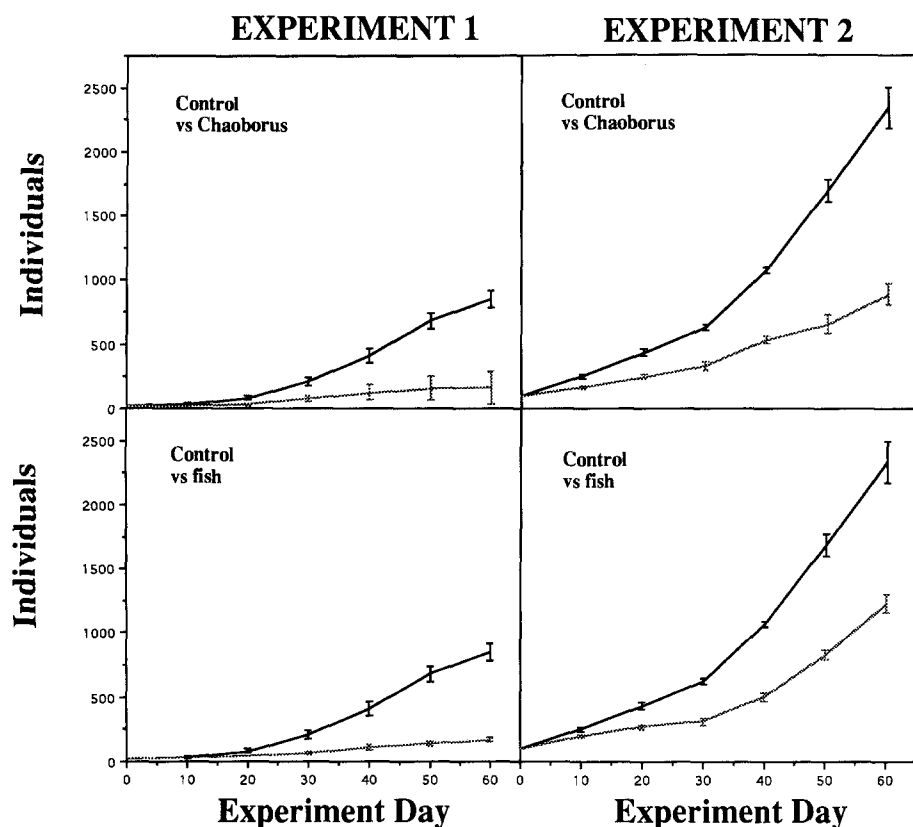
EXPERIMENT 1   EXPERIMENT 2

Fig. 3. Number of *Daphnia* individuals per treatment for the different predation treatments. The plots are of a three-point running mean, with values corrected for subsample removal. The *confidence intervals* are ± 1 SE, *n* = 3, 4 for experiments 1, 2 respectively. The *dark line* represents the control values and the *grey line* represents the respective predation treatments

trols were greater for experiment 1 than for experiment 2. These differences in abundance lead to differences in relative algal loading rates (algae per *Daphnia* individual), as the absolute algal loading rates (algae per replicate) were identical between treatments (Table 1).

Size distribution data were pooled by date and replicate within each treatment (using nine size classes) to produce an "average size distribution". These distributions were usually significantly different but they did have similar overall patterns (Fig. 4). There were no obvious differences in the size of neonates between treatments for these experiments. An ANOVA of the size distribution for individuals for experiment 2 showed strong treatment effects but also showed strong effects of time, which were presumably due to cohort succession and/or extrinsic control of population dynamics, from for example algal loading rates. The large portion of variance unexplained (error) is probably a reflection of the stochasticity of population dynamics, and also the inadequacy of the sample sizes used for providing estimates of population structure (Table 3). The size distributions of egg-bearing individuals in the populations showed patterns similar, but more pronounced, to those of the population as a whole. The fish treatments had more small egg-bearing individuals, while the *Chaoborus* treatments had more large individuals, and the predator-free controls were intermediate (Fig. 5).

A comparison of the relationships between individual length and clutch size showed no significant differences for experiment 1. In experiment 2 both predation treatments had much larger clutch sizes ($P < 0.0001$) for in-

Table 3. Summary of two-way ANOVA of the influence of time and predation treatment on *Daphnia* population size distribution

Source	*df*	MS	*F*	*P*	% Variance
Size	Less than 950 µm				
Date	5	1013	10.9	0.0001	40.7
Treatment	2	866	9.4	0.0003	13.9
Interaction	10	65	0.7	0.7127	5.3
Error	54	92			40.1
Size	950–1600 µm				
Date	5	702	9.8	0.0001	26.3
Treatment	2	2369	33.1	0.0001	35.5
Interaction	10	124	1.7	0.0988	9.2
Error	54	72			29.0
Size	Greater than 1600 µm				
Date	5	214	4.6	0.0013	19.1
Treatment	2	407	8.9	0.0005	14.6
Interaction	10	103	2.2	0.0286	18.4
Error	54	46			44.4

dividuals of a given length relative to the predator-free controls, suggesting that the control treatments were more food-limited than the predation treatments. For experiment 2 the *Chaoborus* treatment had a significantly ($P < 0.001$) higher slope than did the fish treatment, but because the fish treatment had a higher intercept than the *Chaoborus* treatment the relationship between clutch size and individual length actually predicted larger clutch sizes for the fish treatments (Fig. 6). Due to differences
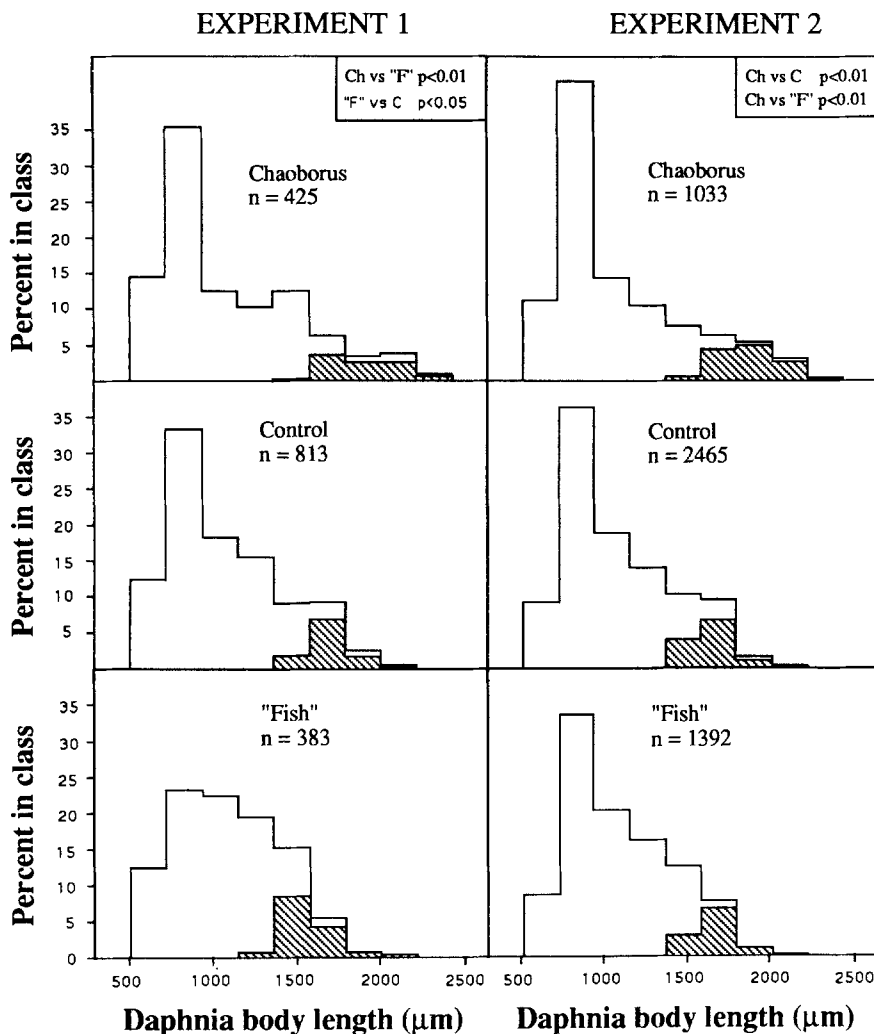
EXPERIMENT 1   EXPERIMENT 2

Fig. 4. Size frequency distributions of *Daphnia* in the different predation treatments. The *hatched areas* represent egg-bearing individuals

Table 4. Summary of three-way ANOVA of the influence of time, size and treatment on individual probability of individual *Daphnia* having a helmet

Source	df	MS	F	P	% Variance
Date (D)	2	1350	21.5	0.0001	1.6
Treatment (T)	2	11541	183.2	0.0001	13.6
Interaction (D × T)	4	13	0.2	0.9376	0.0
Size[1] (S)	3	38237	606.9	0.0001	67.7
Interaction (S × D)	6	299	4.8	0.0002	1.1
Interaction (S × T)	6	3358	53.3	0.0001	11.9
Interaction (S × D × T)	12	11	0.2	0.9992	0.1
Error	108	63			4.0

[1] The observations were divided into four size classes, less than 850, 851–1270, 1271–1700, and greater than 1701 μm

in the size distribution of egg-bearing individuals between these treatments, however, there was only a small overlap on the *x*-axis of this regression. An examination of the percentage of egg-bearing individuals per size class indicates that the fish treatments had their primiparous instar at a smaller size than the *Chaoborus* treatments (Fig. 7).

The percentage occurrence of helmets was quite different between the treatments. All treatments had a similar high occurrence of helmets in the smallest size class. The *Chaoborus* treatment had a much higher occurrence of helmets at other size classes relative to both the fish treatment and predator-free controls. Independent of treatment type, the occurrence of helmets was strongly associated with size, with smaller individuals having higher rates of helmet occurrence than larger individuals (Table 4, and Fig. 8).

There were also differences between treatments for population rates of increase and death. The predator-free controls had higher rates of increase and lower death rates relative to the predation treatments (Table 5). However, as the demographic rate estimates of this study are based on 10-day sampling intervals, they may only reflect the actual dynamics of the populations poorly.

Discussion

This experiment showed that predation depressed population standing crop, individuals per population, relative to the predator-free populations. This has been noted in
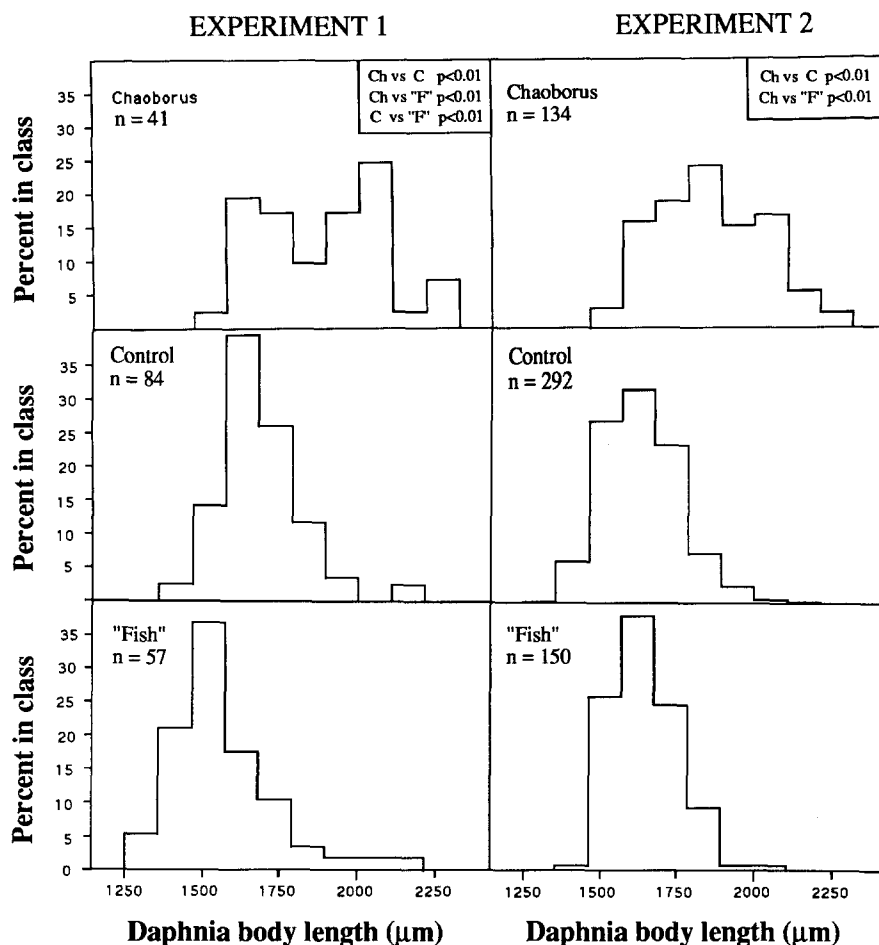
EXPERIMENT 1   EXPERIMENT 2

Fig. 5. Size frequency distributions of the egg-bearing *Daphnia* individuals in the different predation treatments

Table 5. Population demographic rates, increase (*r*), birth (*b*), and death (*d*), for the experimental *Daphnia* populations

Treatment	Experiment 1	Experiment 2		
	r	*r*	*b*	*d*
Control	0.068 ± 0.025	0.053 ± 0.022	0.071 ± 0.015	0.019 ± 0.012
Chaoborus	0.032 ± 0.028	0.035 ± 0.012	0.102 ± 0.020	0.067 ± 0.027
"Fish"	0.036 ± 0.015	0.043 ± 0.017	0.086 ± 0.022	0.044 ± 0.032
Significance *P*				
C vs Ch	0.012	0.039	0.096	0.006
C vs "F"	0.036	0.125	0.236	0.016

Values are for predation treatment by date, $n = 6$. The means (± 1 SD) were compared using a paired two-tailed *t*-test. The birth and death rates were not calculated for experiment 1 as the samples sizes were too small

other laboratory studies of predation on daphnid populations (Slobodkin and Richman 1956; de Bernardi 1981). The reduction in population size due to predation introduced an important indirect influence of predation. The predation treatments had lower intraspecific competition, i.e. more algae per individual in each population, which strongly influenced population reproductive parameters (discussed later).

Size-selective predation caused shifts in the population size distribution. Simulated fish predation led to an accumulation of intermediate individuals, because larger individuals were more likely to be preyed upon and were

more likely to have been exposed to predation events more than once. Conversely, *Chaoborus* predation led to a suppression of intermediate individuals and increased representation of the smallest and largest daphnids. The increased representation of large individuals follows from *Chaoborus* not being able to capture daphnids larger than 1700 μm. The increased representation of the smallest daphnids is more complicated as this group was if anything selected by *Chaoborus* relative to intermediate sized individuals. While *Chaoborus* may have preferred the smallest daphnids, these individuals are only 1–2 days old and have been exposed to *Chaoborus* predation for
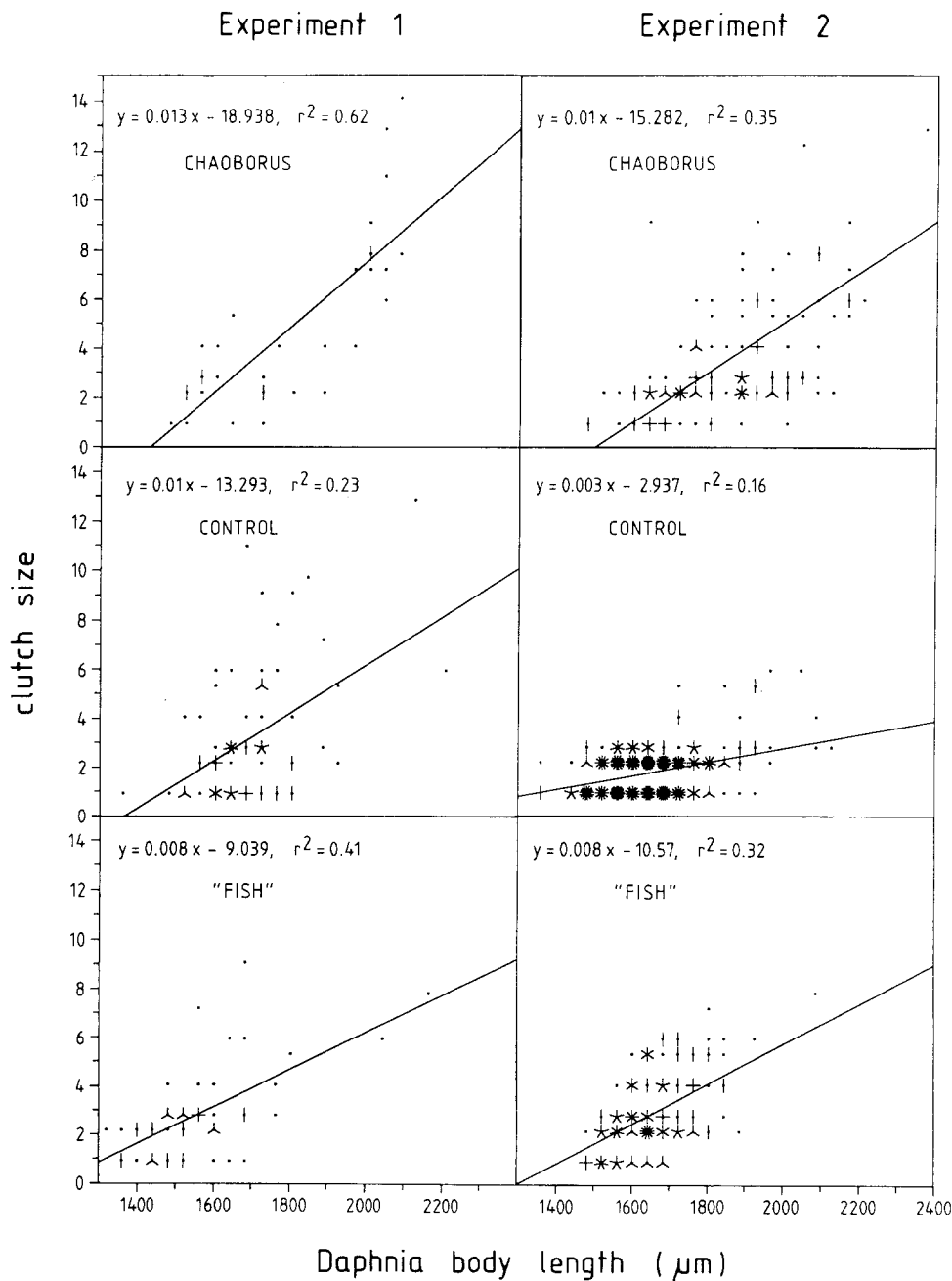
Experiment 1   Experiment 2

$y = 0.013x - 18.938, \quad r^2 = 0.62$

CHAOBORUS

$y = 0.01x - 15.282, \quad r^2 = 0.35$

CHAOBORUS

$y = 0.01x - 13.293, \quad r^2 = 0.23$

CONTROL

$y = 0.003x - 2.937, \quad r^2 = 0.16$

CONTROL

$y = 0.008x - 9.039, \quad r^2 = 0.41$

"FISH"

$y = 0.008x - 10.57, \quad r^2 = 0.32$

"FISH"

clutch size

Daphnia body length (μm)

Fig. 6. Individual length versus clutch size regressions for *Daphnia* in the different predation treatments. Each *dot* represents one observation, *arms form dots* represent additional observations

only a short time. Intermediate-sized individuals are older and have been exposed to *Chaoborus* predation for longer. The probability that an individual will succumb to predation, and fail to represent its size class, is due to an interaction between selectivity and accumulated exposure to predation. High birth rates also contributed to the increased representation of small individuals in the *Chaoborus* treatments. While the kinetics of birth rate alone, as exemplified by Leslie matrices, will affect population structure the results of this study suggests this influence is not particularly important relative to predation influences in the present experiments. The two treatments with the most similar birth rates, fish and *Chaoborus* predation, had the most divergent size structures, while the treatment with the most divergent birth rate,

predator-free control, had a size structure which was clearly intermediate between the other treatments. The size distribution of the egg-bearing individuals was more strongly affected by selective predation than was the size distribution of the population as a whole. This was because large size offered a refuge from *Chaoborus* predation, while fish predation fell most heavily on the largest individuals.

There were large differences in the individual length versus clutch size relationship between the predation and predator-free treatments, for experiment 2. The differences between the *Chaoborus* and fish treatments were statistically significant but they were not large. These results indicate that intraspecific competition was more intense in the predator-free control than in the predation
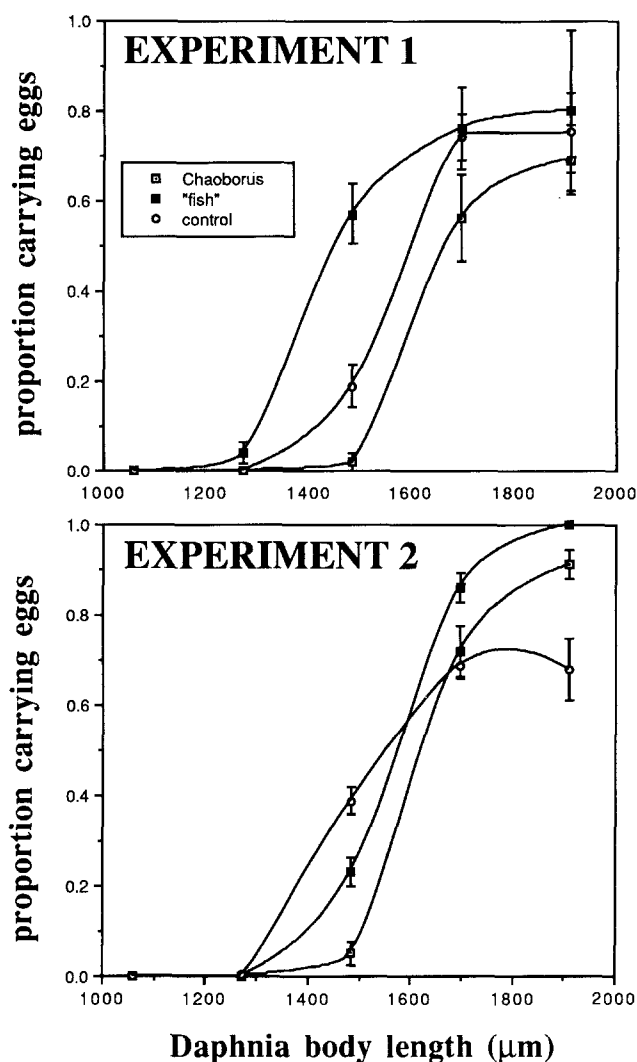
Fig. 7. Proportion of egg-bearing *Daphnia* individuals per size class for the different predation treatments. The confidence intervals are ± 1 SD of the binomial distribution
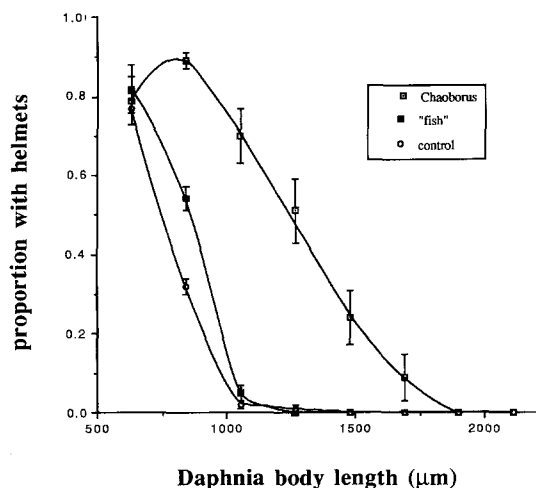

Fig. 8. Proportion of helmeted *Daphnia* individuals per size class in the different predation treatments. The confidence intervals are ± 1 SD of the binomial distribution. The data presented are for observations made on days 40–60 in experiment 2

treatments. The size of the primiparous instar was shifted between treatments with the individuals in the fish treatments attaining maturity at a smaller size than those in the *Chaoborus* treatments. The predator-free controls were intermediate to the predation treatments in experiment 1, but not in experiment 2. The differences between the predation treatments were probably primarily due to direct effects of predation, as opposed to food limitation, as both predation treatments had similar levels of relative *Rhodomonas* loading. Havel and Dodson (1987) have shown that protective spine formation leads to increased time until reaching maturity and smaller size at maturity. Walls and Ketola (1989) found 58%, and Riessen and Sprules (1990) 17%, of individuals in spined morph treatments delayed reproduction one instar relative to individuals in unspined morph treatments. The results of the present study contradict Havel and Dodson's (1987) finding of smaller size at first reproduction. It should be pointed out, however, that in Havel and Dodson's (1987) experiment individuals in *Chaoborus* and *Chaoborus*-free treatments were given equal concentrations of algae. In the present study predation reduced population size hence relaxing intraspecific competition. Reduced resource availability has previously been shown to lead to a smaller size at first reproduction (Brambilla 1980). In fact, in experiment 2 the smallest size at first reproduction was found in the predator-free control, where interspecific competition was most intense. As reproduction in *Daphnia* represents a diversion of energy which could otherwise be utilized for individual growth it would be advantageous from an evolutionary perspective for a *Daphnia* individual exposed to *Chaoborus* predation to channel all its resources into rapid growth until a size safe from *Chaoborus* predation is attained, i.e. 1700 μm. For an individual exposed to fish predation it would be advantageous to reproduce as quickly as possible, before large size increased the probability of being preyed upon. This interpretation is supported by the results of Edley and Law (1988) who selectively culled large or small *Daphnia magna* from six laboratory populations (i.e. three replicates per treatment) over 150 days. In the treatments where large individuals were culled juvenile growth was slow and maturity was reached at a smaller size. In the treatments where small individuals were culled juvenile growth was fast and maturity was reached at a larger size.

Chaoborus predation led to an increased incidence of helmets. There was no notable difference between treatments in the frequency of helmets for the smallest size class, but individuals in the *Chaoborus* treatments were much more likely to retain helmets at larger sizes. Individuals in the fish and predation-free treatments rarely retained helmets beyond the second smallest size class (≈ 700 μm). The incidence of helmeted individuals in the *Chaoborus* treatment had a maximum of approximately 90% at the second smallest size class and successively decreased to 10% at a size class corresponding to the first reproductive instar (≈ 1700 μm) and 0% at larger size classes. Research has shown higher survival rates for individuals bearing spines in the presence of *Chaoborus* predation (Krueger and Dodson 1981; Havel and Dod-

son 1984; Mort 1986) suggesting strong selective pressures for those individuals capable of responding to predation with spines. This is particularly important as all populations in this study contained individuals that did and did not develop or retain helmets. Given a higher mortality of non-helmeted individuals relative to helmeted individuals one could expect a rapid shift towards individuals retaining helmets at larger sizes and particularly those individuals capable of passing this trait on to their offspring. On the other hand, a clear physiological cost of spine formation has been demonstrated (Havel and Dodson 1987; Walls and Ketola 1989; Riessen and Sprules 1990) indicating the maladaptive nature of this morphotype in the absence of *Chaoborus* predation. In an experiment using the same design as the present, but using a population of *D. longispina* isolated from a pond with a very dense population of *C. flavicans,* the daphnids in the *Chaoborus* treatments had a very high frequency of neck teeth (Brett, unpublished data).

The last response to treatment type noted was the differences in population rates of increase and death. The predator-free population had the highest rates of increase and the lowest rates of death. The differences in the rate of increase and death between the predator-free and the predation treatments were a direct result of the imposed predation.

The present study attempts to fill a gap in our present understanding of *Chaoborus-Daphnia* predator-prey interactions. The results of this study confirm and extrapolate on several observations made in field studies indicating that size-selective predation is important in determining cladoceran population structure and dynamics. Particularly the numeric response of the population to resource availability, population size structure, the size structure of the reproductive population, size at maturity, mean clutch size, morphological characteristics, and population rates of increase and death, all appear to be strongly affected by selective predation.

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