

The interaction of *Chaoborus* size and vertical distribution determines predation effects on *Daphnia*

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SUMMARY

1. Larvae of *Chaoborus*, the phantom midge, are important pelagic planktivores in many freshwater lakes and ponds. The effect of *Chaoborus* on its prey depends on its size, especially mouth gape diameter, and vertical migration pattern, which affects predator–prey spatial overlap. These two features vary considerably in different *Chaoborus* species and instars. In this study, the interacting effects of both *Chaoborus* size and vertical distribution on population growth of *Daphnia pulex* was analysed with a field enclosure experiment and a matrix population model.
2. In the field experiment, *Daphnia* were grown in four replicated treatments that included a control (no *Chaoborus*) and three combinations of instar III and IV *Chaoborus* of two species (*C. trivittatus* and *C. americanus*). Parameters of the matrix model were based on differences between *Chaoborus* species and instars in capture and ingestion of *Daphnia* of differing sizes (prey vulnerability) and in vertical overlap with *Daphnia* in each treatment (density risk).
3. In comparison with the control, the two treatments containing the smaller, migratory *C. americanus* showed a significant effect on *Daphnia* population growth rate, while the treatment containing only the larger, non-migratory *C. trivittatus* did not. The model accurately simulated these effects.
4. A *Daphnia* predation risk model, which uses prey vulnerability and density risk parameters, illustrated the individual and combined effect of the different *Chaoborus* types on *Daphnia*. *Daphnia* have a high prey vulnerability to the large *C. trivittatus*, but overall predation risk was low because of very little overlap. On the contrary, the smaller *C. americanus* affects only a small range of *Daphnia* instars, each with a low vulnerability, yet those instars that were vulnerable had a very high density risk because of an increased overlap.
5. This analysis of *Daphnia* predation risk parameters with coexisting *Chaoborus* species strongly supports an integrated approach using both size and vertical distribution to determine the ultimate predation effect on *Daphnia*.

Keywords: *Chaoborus*, *Daphnia*, morphology, predation risk, vertical migration

Introduction

Predatory freshwater invertebrates, such as *Mysis* (e.g. Nero & Sprules, 1985), *Chaoborus* (e.g. Riessen, O'Brien & Loveless, 1984) and *Bythotrephes* (e.g. Yan, Girard &

Boudreau, 2002) are quite commonly the principal planktivores in pelagic food webs, consuming more zooplankton than do fish, and having large impacts on zooplankton community structure (Lane, 1979; Ramcharan *et al.*, 2001). The success of an invertebrate predator is determined largely by its morphology and behaviour (Greene, 1986). Invertebrate predators are often not much larger than their zooplankton prey; hence, their success in predator–prey encounters

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depends on their size relative to prey, their method of feeding (e.g. ingesting prey whole or in part) (Pastorok, 1981; Greene, 1986), and the morphological defences of the prey (e.g. neck spines) (Havel & Dodson, 1984). Consumption rates are also dependent on frequency of encounter, which, for these small animals, is determined to a great extent by diel changes in their relative vertical distributions. Diel vertical migration (DVM) is a well-studied behaviour of crustacean zooplankton and several of their invertebrate predators (Lampert, 1989). Hence, depending on the migratory behaviour of the predator and prey, spatial overlap can either rise or fall during the day.

Given this functional complexity, predation risk for prey species must be assessed for each macroinvertebrate predator species (Greene, 1986). Holling's (1966) predation model has often been used to predict potential predation effects on a prey population. This model partitions predator-prey encounters into a sequence of conditional probabilities: encounter, attack, capture and ingestion. In terms of comparing predation of particular predators on different prey taxa, the great advantage of this approach is its overt specification of the stages of predation events. Once the stages are identified it becomes clear that differences in predation rates among species may have several different underlying causes. Holling's (1966) model has been applied to a range of predator-prey interactions in freshwater systems, from fish (Wright & O'Brien, 1984), to rotifers and cyclopoids (Williamson, 1993) and to larvae of the phantom midge, *Chaoborus* (Riessen *et al.*, 1984, 1988). Of these applications, only Williamson's embedded Holling's four stages of predator-prey interactions in an integrated model that included overall behaviour of the predator and prey populations. Williamson's (1993) model of overall predation risk incorporated both the Holling fundamentals, i.e. the effect of predator size on its ability to ingest prey (prey vulnerability) and the effect of predator migration on its spatial overlap with prey (density risk).

Chaoborus is a common invertebrate predator in lakes (Wissel, Yan & Ramcharan, 2003), and is a major source of mortality for many zooplankton species, including *Daphnia* (Allan, 1973; Riessen *et al.*, 1984). *Chaoborus* are ambush predators that remain motionless in the water column with the aid of two pairs of tracheal air sacs (Pastorok, 1980a). Therefore, their

encounter rate with prey at any time is determined by their vertical distribution and the vertical distribution and swimming speed of their prey (Pastorok, 1981). *Chaoborus* sense approaching prey with setae that line the length of their body and attack with a striking motion of their prehensile antennae (Pastorok, 1980a). Prey that are no wider than the predator's mouth gape are ingested whole, while larger prey often escape (Swift, 1992).

The different species and the four larval instars of *Chaoborus* vary considerably in their head size and thus mouth gape (Swift, 1992), and in their vertical migration behaviour. Larger *Chaoborus*, such as *C. trivittatus*, have longer heads and wider mouth gapes and therefore are able to ingest larger prey (Fedorenko, 1975). Patterns of DVM are species- and instar-specific, and may also vary among lakes (von Ende, 1975) and over time (Fedorenko & Swift, 1972). It is clear that such differences in *Chaoborus* morphology or migratory behaviour influence their consumption of *Daphnia* (Fedorenko, 1975; Elser *et al.*, 1987; Mackay *et al.*, 1990).

While *Chaoborus*-*Daphnia* interactions have previously been modelled, only prey vulnerability models have been used. These models can only be accurately applied to predictions of *Chaoborus*-*Daphnia* interactions in small systems, such as laboratory aquaria (Pastorok, 1981; Riessen, 1999) or shallow ponds, in which DVM patterns of predator and prey can be ignored (Riessen *et al.*, 1988). These models have been significant in identifying the importance of prey vulnerability to predation risk experienced by *Daphnia*. However, Williamson (1993) suggested that to model predation risk of *Daphnia* in a more natural system, the effect of *Chaoborus* vertical migration patterns on spatial overlap with prey must be considered. This has not as yet been attempted.

The objective of this study was to examine the combined effect of size and vertical distribution differences among *Chaoborus* species and instars on the population growth rate of *Daphnia pulex* (Leydig). This was carried out through both a field enclosure experiment and the development of a matrix population model specific to *D. pulex*. To develop the model, morphological and behavioural parameters of the various *Chaoborus* species and instars were quantified in the field experiment and employed in Williamson's (1993) predation risk model to explore the results of the field study.

Methods

Field experiment

The experiment was carried out in July 2000 at Costello Lake, Algonquin Park, Ontario, Canada (45°35'N, 78°19'W) over a period of 8 days, which is short enough that environmental conditions did not change significantly, yet long enough for sufficient *Daphnia* population growth to occur. Twelve enclosures, each containing similar initial *Daphnia* densities (Table 1), were randomly assigned to triplicates of four treatments; three predator treatments and a control that contained no *Chaoborus*. In the

predator treatments, we varied the size and distribution of *Chaoborus* by including third and fourth instars of *Chaoborus americanus* (Johannsen), which migrated vertically, and fourth instars of the larger *Chaoborus trivittatus* (Loew), which did not migrate (Fig. 1). The finite population growth rate of *Daphnia*, λ ($=e^r$) was calculated for each enclosure (Gotelli, 1998: eqn. 1.4), using n_0 , the initial *Daphnia* population size on July 22 (day 0), and n_8 , the final count on July 30 (day 8):

$$\lambda = \left(\frac{n_8}{n_0}\right)^{1/8} \tag{1}$$

Table 1 *Daphnia* initial (n_0) and final (n_8) population size and calculated population growth rate (λ) in the enclosures of the 8-day field experiment (Costello Lake, July 2000). Among treatments, average initial counts are not significantly different ($P = 0.239$), while average final counts ($P = 0.017$) and average observed λ ($P = 0.001$) are significantly different (one-way ANOVA).

Treatment	n_0	n_8	λ (day ⁻¹)	Average λ (day ⁻¹)
C (no <i>Chaoborus</i>)	4444	1744	0.89	0.95
	3556	3000	0.98	
	5944	4489	0.97	
T (<i>Chaoborus trivittatus</i>)	5481	1511	0.85	0.87
	4370	822	0.81	
	3067	2156	0.96	
A (<i>Chaoborus americanus</i>)	8815	922	0.75	0.72
	5185	256	0.69	
TA (both <i>Chaoborus</i> species)	6741	100	0.59	0.63
	5778	244	0.67	
	4889	133	0.64	

Three weeks before the experiment began, polyethylene enclosures (1 m in diameter and 8 m long) were assembled and suspended from a wooden frame in Costello Lake. The closed end of each enclosure was reinforced by a cable tie (leaving approximately 7 m depth) and anchored to the lake bottom with a cinder block. The enclosures were each filled with approximately 5500 L of Costello Lake water that was filtered through a 100- μ m mesh sock, which allowed phytoplankton and some rotifers, but not nauplii and juveniles of large zooplankton, to pass through. Approximately 1400 *D. pulex*, cultured from a single clone in 40-L barrels containing well water and the alga *Ankistrodesmus*, were added to each enclosure and left to allow for population growth to occur over the next 18 days. Because the *Daphnia* population increased rapidly, a little more than 50% of each enclosure (3100 L) was filtered with a 130- μ m mesh plankton net 1 week before the experiment began. Five

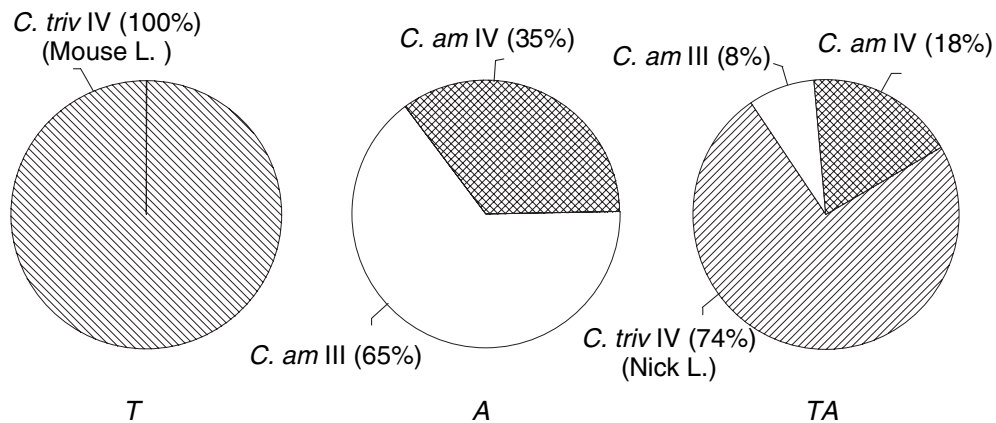


Fig. 1 Relative *Chaoborus* density (N_j) in the three predator treatments for the field enclosure experiment in Costello Lake, July 2000. T = treatment containing *C. trivittatus*; A = treatment containing *C. americanus*; TA = treatment containing both *Chaoborus* species. There was also a control (C), which contained no *Chaoborus*.

hours before the first sampling on day 0, *Chaoborus* were added to each predator enclosure creating an initial density of approximately 1.2 L^{-1} . *Chaoborus* were collected 4 days prior to day 0 from two lakes in south-central Ontario using a 1-m^2 plankton net with coarse mesh (1 mm) that mostly gathered third and fourth instar *Chaoborus*. At that time, there were only fourth instar *C. trivittatus* in Mouse Lake ($45^{\circ}11'N$, $78^{\circ}51'W$), a 9.9-ha lake containing planktivorous fish (Ramcharan *et al.*, 2001). Nick Lake ($45^{\circ}45'N$, $78^{\circ}19'W$), a small, shallow fishless lake in Algonquin Park, was inhabited by two *Chaoborus* species, *C. trivittatus* and *C. americanus*. Fourth instar *C. trivittatus* were situated close to the bottom of the lake, third and fourth instar *C. americanus* were located a couple of meters above the bottom and second instar *Chaoborus* sp. were near the surface. The mixture of *Chaoborus* from Nick Lake was sorted by hand, the smaller and larger *Chaoborus* being separated with a pipette. To determine the quantity of each *Chaoborus* species and instar among treatments, a subsample of individuals from each barrel was measured and identified according to Cook (1956). The coefficient of variation of *Chaoborus* density for these subsamples was $<15\%$. A large hole in one of the enclosures in the treatment with *C. americanus* (treatment A) necessitated its exclusion from the analysis. Before the experiment began, small amounts of phosphorus ($5 \mu\text{g P L}^{-1}$) and nitrogen ($164 \mu\text{g N L}^{-1}$) were added twice (once when *Daphnia* were first added and once 1 week before experiment) to each enclosure to replace nutrients potentially lost by algal sedimentation and periphyton growth, and zooplankton were added to each enclosure to represent a natural community. Zooplankton were collected from the metalimnion of Lake Opeongo, which is connected to Costello Lake, and on the same day were distributed evenly to each enclosure in a density similar to Lake Opeongo. This community was chosen over Costello Lake zooplankton because it does not contain any large invertebrate predators other than *C. punctipennis*, which were absent from the metalimnion during collection, and its *Daphnia* sp. are small and easily distinguishable from our *D. pulex* clone. On day 6, approximately 600 *Chaoborus* were added to each enclosure in the original species and instar mix per treatment to compensate for those removed by prior sampling.

The enclosures were sampled on days 0, 4, and 8. On each visit, Secchi depth was measured in all

enclosures as well as in the lake. The average Secchi depth was not significantly different among treatments (e.g. ANOVA of day 4, $P = 0.47$), and increased slightly on each sampling date in both the enclosures (from 3.1 m on day 0 to 3.5 m on day 8), and the lake (from 3.0 to 3.5 m). On day 4, temperature and dissolved oxygen profiles were determined with a temperature and oxygen probe (YSI 50B; Yellow Springs Instruments, Yellow Springs, OH, U.S.A.). Each enclosure was thermally stratified, and both temperature ($P = 0.26$) and oxygen ($P = 0.40$) in each stratum were shown to be similar among treatments (MANOVA, Wilks λ). Chlorophyll *a* concentration was measured 3 days after the end of the experiment with a fluorometer (Turner 10AU005; Turner Designs, Sunnyvale, CA, U.S.A.). Average chlorophyll *a* concentration of $<30\text{-}\mu\text{m}$ algae was low in both the epilimnion ($4.4 \mu\text{g L}^{-1}$) and the hypolimnion ($2.77 \mu\text{g L}^{-1}$) despite previous nutrient additions, and there was no significant difference in either of these layers among treatments (MANOVA, Wilks λ $P = 0.16$).

On day 0 and 8, *Daphnia* were collected from each enclosure by filtering approximately 495 L with a 30-cm diameter, 130- μm mesh plankton net pulled from near the bottom of the enclosure to the surface. The samples were preserved in 6% formaldehyde with sucrose (Haney & Hall, 1973). To determine the vertical distribution of *Chaoborus* and *Daphnia*, each 1-m stratum of the enclosures was sampled with a 30-cm diameter, 130- μm mesh plankton closing net on day 4 from 10:00 hours to 11:45 hours and again that evening from 00:00 hours to 02:00 hours. The shallowest samples were collected first in order to minimise mixing within the enclosure. When counting the plankton, *Chaoborus* were first removed from all sample types and sorted by species and instar according to Cook (1956) and Fedorenko & Swift (1972). To determine n_0 and n_8 for eqn. 1, day 0 and 8 samples containing <300 individuals of *D. pulex* were counted completely and the rest were subsampled. Each *Daphnia* counted was magnified onto a video screen from a Wild M5 stereomicroscope (E. Leitz Inc., Rockleigh, NJ, U.S.A.) and measured with electronic calipers (Sprules, Holtby & Griggs, 1981) from the top of the head to the base of the tail spine. Clutch size was also recorded. In all day and night samples from day 4, juvenile and adult *Daphnia* were counted using a Wild M5 stereomicroscope.

All statistical analysis was performed with S-PLUS Version 6.0.2. We first verified homogeneity of variance for each test performed using a Levene's test. For comparisons among observed *Daphnia* growth rates in treatments, we used ANOVA tests and both two-sided *t*-tests and Tukey's multiple comparisons were used for between treatment comparisons.

Matrix population model

A stage-classified matrix population model for *Daphnia* was developed in *Mathematica* 4.0 (Wolfram, 1999) following the methods outlined in Riessen (1999) and Caswell (2001). The life cycle of *Daphnia* is well suited to a matrix model because of its discrete stages (instars) (Taylor, 1980). This model predicts the finite population growth rate of *Daphnia*, λ ($=e^r$), for each treatment. It consists of a vector of instar densities and a square projection matrix in which the elements are the instar-specific probabilities of survival (P_i), growth (G_i) and fecundity (F_i). After every 1-day time step, a proportion of individuals will survive and either remain in instar i (P_i), or grow into instar $i + 1$ (G_i), and a proportion of adult *Daphnia* in instar i will release neonates (F_i). P_i and G_i are both functions of instar survival, σ_i , and instar growth, γ_i (Caswell, 2001: eqns 6.97 and 6.98).

It is in σ_i where the effect of predator differences will be most apparent in the model. σ_i depends on B_i , the probability of survival because of factors other than predation (background mortality), which is the same in all treatments, and C_{ij} , the probability of survival with each different predator type j present (Riessen, 1999):

$$\sigma_i = B_i \prod_{j=1}^4 C_{ij} \quad (2)$$

By using Holling's (1966) model, predation by each type of *Chaoborus* can be broken down into a series of conditional probabilities allowing C_{ij} to incorporate the unique morphology and vertical distribution of *Chaoborus*. Thus for *Daphnia* instar i , the series of events are the probability of encounter, $P(E)_{ij}$, the probability that the *Chaoborus* attacks (strikes) at a *Daphnia* once encountered, $P(A)$, and the strike efficiency, S_{ij} , i.e. the proportion of strikes that lead to a successful ingestion for *Chaoborus* (Riessen, 1999):

$$C_{ij} = 1 - [P(E)_{ij} \times P(A) \times S_{ij}] \quad (3)$$

Given encounter, $P(A)$ is assumed to be constant for all predators (Riessen, 1999), while S_{ij} is unique for each predator and decreases with *Daphnia* instar body length, L_i , as larger *Daphnia* are more difficult for this gape-limited predator to ingest (Pastorok, 1981). $P(E)_{ij}$, in a 1-s interval, follows the Poisson distribution (Gerritsen & Strickler, 1977; Riessen, 1992):

$$P(E)_{ij} = 1 - e^{-\varepsilon_i \times N_j \times O_{ij}} \quad (4)$$

A 1-s interval was chosen because the probability of multiple encounters within this time period is negligible (Riessen, 1992). As in Riessen (1992: eqn. 1), $P(E)_{ij}$ is a function of predator density (N_j) and encounter rate (ε_i), which increases with larger and faster *Daphnia*. However, this encounter probability differs from Riessen's (1992) model in that it also incorporates *Chaoborus* migratory behaviour by the use of an overlap index, O_{ij} , that, when multiplied by the predator density, creates an effective predator density (density risk), DR_{ij} (Williamson, 1993):

$$DR_{ij} = N_j \times O_{ij} \quad (5)$$

Vertical migration patterns that segregate *Chaoborus* and *Daphnia* produce values of $O_{ij} < 1$, while those that increase spatial overlap result in $O_{ij} > 1$. If either predator or prey is uniformly distributed, $O_{ij} = 1$ and density risk is simply the actual predator density (Williamson, 1993).

Daphnia instar duration varies slightly among the treatments as instar duration is primarily a function of water temperature (Bottrell, 1975) and each predator combination affected *Daphnia* vertical distribution differently in the thermally stratified enclosures (Fig. 2). We use Caswell's (2001: eqn. 6.114) variable instar duration, a function that includes *Daphnia* mean instar duration (D_i^M) and its variance (D_i^V), along with the temperature experienced by *Daphnia* in the various treatments, to estimate these values.

Parameter estimation

The model parameters were estimated from the literature, laboratory observations, and/or the field experiment. The parameters that did differ among treatments were ones concerning the different predator types, S_{ij} and O_{ij} , and instar duration, D_i^M and D_i^V :

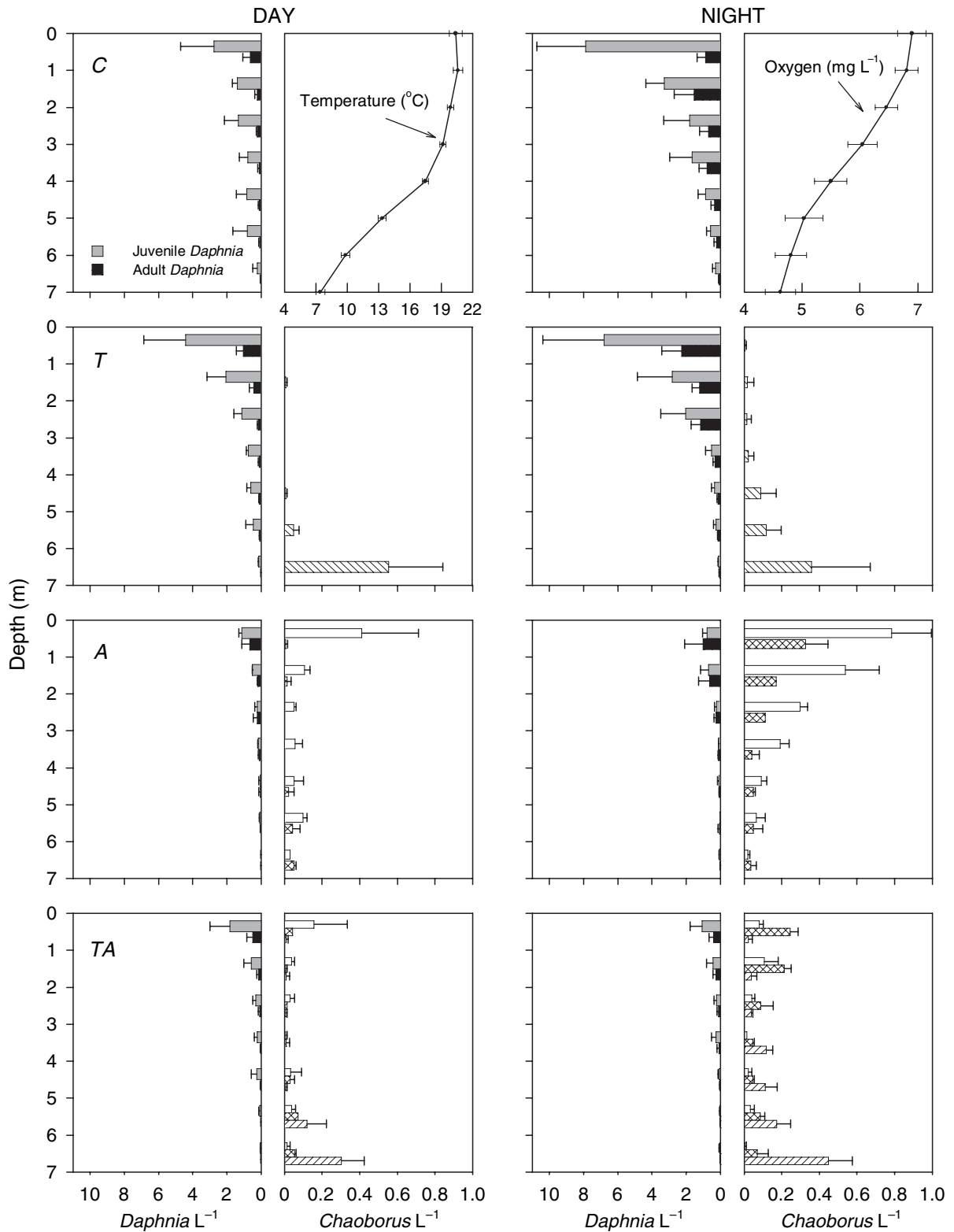


Fig. 2 *Daphnia* and *Chaoborus* average vertical density for day and night on day 4 of the field enclosure experiment in Costello Lake. *Chaoborus* type and composition per treatment are shown in Fig. 1. Because there were no *Chaoborus* in the control, these panels are used to show average temperature and oxygen profiles. All error bars represent standard deviation.

Strike efficiency. S_{ij} (in eqn. 3) is a linear function of L_i and predator mouth gape size (Swift, 1992). It is also influenced by the antipredator formation of neck teeth on juvenile *Daphnia*, which reduces the probability of successful ingestion by *Chaoborus* by making these *Daphnia* more difficult to handle and ingest (Havel & Dodson, 1984). S_{ij} was determined through laboratory observations of *Chaoborus* feeding on various sizes of *Daphnia* (following the methods outlined in Riessen (1999)) during the summer of 2001 with animals identical to those from the field experiment (Table 2). Observations of strikes and ingestions of *C. americanus* III and IV were made with five *Daphnia* size classes and of *C. trivittatus* IV with nine *Daphnia* size classes in an 8-cm³ glass cube filled with 400 mL of well water. Between 30 and 111 strikes were observed per predator for each prey size class. *Chaoborus* were held in small aquaria and isolated and starved for 1–4 days before use. After a *Chaoborus* had been used once for each prey size class, it was preserved and later measured (Table 2). None of the *Daphnia* used in the laboratory observations developed neck teeth, while the majority of second and third instar *Daphnia* in the field experiment did develop them; therefore, we reduced S_{ij} by 50% for these instars following Riessen (1999).

Overlap index. Day and night overlap indices, O_{ij} (in eqn. 4), of juvenile and adult *Daphnia* with each predator were calculated per treatment using average *Chaoborus* and *Daphnia* densities from day 4 of the field experiment (Williamson, 1993: eqn. 6). In the model simulations, 'day' O_{ij} is used for two-thirds of a 24 h cycle, and 'night' O_{ij} is used for the other third. This 16 : 8 photoperiod was estimated from 26 July 2000 (day 4) for the same latitude as Costello Lake.

Average instar duration and its variance. D_i^M and D_i^Y were estimated for juveniles and adults in each treatment using temperature values and *Daphnia* day and night densities from day 4. To calculate adult instar duration, we used a curvilinear relationship between temperature (T , °C) and egg-development duration (D , day) of daphnids (Bottrell *et al.*, 1976: Table XIII), as this is roughly equivalent to adult instar duration (Bottrell, 1975). For both day and night, instar duration for each 1-m stratum of the enclosures was weighted by the *Daphnia* density in the corresponding stratum, and averaged over the entire enclosure. The values of D_i^M and D_i^Y were calculated for an entire day with the average day and night instar durations and a photoperiod of 16 : 8 (estimated from day 4 for the same latitude as Costello Lake). The values of D_i^M and D_i^Y were calculated similarly for juveniles with one exception: the relationship between juvenile instar duration and temperature was assumed to be 45% of adult instar duration based on the difference found by Riessen (1999: Table 1) between juveniles and adults at 20 °C. *Chaoborus*-induced development of neck teeth lengthens development time (Riessen & Sprules, 1990); therefore, instar duration for juveniles was increased by 12% and for adults by 3% in predator treatments, following Riessen (1999).

The following parameters were common to all treatments, as abiotic factors and food levels were not significantly different:

Instar fecundity. F_i is the product of instar egg ratios (f_i) and the proportion of individuals growing into instar $i + 1$ (G_i). f_i was calculated by averaging clutch sizes for each *Daphnia* instar found in the field experiment. As *D. pulex* are typically primiparous in the fifth instar, f_1 to f_4 is zero. There were insufficient

Table 2 *Chaoborus* head capsule size (HCS) and corresponding *Daphnia* size (L_i) at which they can no longer be ingested by each *Chaoborus*. This size is determined from strike efficiency (S_{ij}) trials, and is equal to the *Daphnia* size at which S_{ij} is zero (the intercept on the x -axis in Fig. 3a). Average *Chaoborus* HCS are shown (with their standard deviation) from the field enclosure experiment in 2000 and the S_{ij} trials in 2001 (n = number of *Chaoborus* measured).

	Field experiment		S_{ij} trials		Zero S_{ij}
	n	Avg HCS (mm)	n	Avg HCS (mm)	L_i (mm)
Mouse Lake <i>C. trivittatus</i> IV	33	1.853 ± 0.09	55	1.838 ± 0.09	2.42
Nick Lake <i>C. trivittatus</i> IV	49	1.822 ± 0.14	14	1.807 ± 0.13	2.40
Nick Lake <i>C. americanus</i> IV	33	1.500 ± 0.15	7	1.500 ± 0.12	1.89
Nick Lake <i>C. americanus</i> III	4	0.960 ± 0.08	52	0.970 ± 0.07	1.65

individuals in instar 10 to instar 22 to calculate f_{10} to f_{22} separately, and therefore individuals were grouped from instars 10–14 and 15–22. These two groups were deemed necessary, as the increase in egg ratio after instar 10 was not constant.

Background survival. B_i (in eqn. 2), is obtained from the *D. pulex* life table data of Riessen & Sprules (1990; Fig. 2), which uses a natural food environment.

Probability of attack. $P(A)$, from eqn. 3, is taken to be a constant value of 0.727 for all *Daphnia* instars (Riessen, 1999). Assuming that the enclosure conditions are a low food environment for *Chaoborus*, encounter with prey will be infrequent and will not be governed by its hunger level (Pastorok, 1980b; Riessen *et al.*, 1984).

Daphnia instar body length. L_i was estimated from a size-frequency distribution of juvenile *Daphnia* instars from the field experiment in conjunction with a model of growth between instars for juvenile and adult *D. pulex* living under low food conditions (H.P. Riessen, unpublished data). In this growth model, each juvenile instar increases in body length by 22%, while the subsequent rate of increase of adult instars progressively decreases (as *Daphnia* contribute more energy to reproduction) from 16% between instars 4–5 to only 2% per instar beyond instar 12. The resultant L_i ranged from 0.65-mm for first instars to 2.46-mm for instar 22.

Encounter rate. ε_i (in eqn. 4) is a linear function adopted from Pastorok (1981) that was converted to a per second rate for the matrix model following Riessen (1992).

Model simulations

Simulations of the matrix model were run for the control and the three predator treatments at predator densities ranging from 0.2 to 0.7 L⁻¹, in increments of 0.1 L⁻¹, which encompasses the range of densities possible during the experiment. On day 8, the measured density of *Chaoborus* in the water column of the enclosures ranged from 0.2 to 0.6 L⁻¹, but this is a difficult variable to measure because of possible net avoidance by *Chaoborus* in the water column and the inability to sample near the bottom of the enclosures. As we were unable to determine if *Chaoborus* mortality

occurred, we used a range of predator densities for the model simulations.

Results

Daphnia population dynamics

Daphnia population growth rates differed among the four treatments of the field experiment (Table 1). Two of the three predator treatments, A and TA, had a substantial impact on the *Daphnia* population. *Daphnia* densities in the treatment containing 65% third instar and 35% fourth instar *C. americanus* (A) and in the treatment containing 74% *C. trivittatus* IV and 26% *C. americanus* III and IV (TA) were significantly lower than in the control (A, $t = 5.12$, $P = 0.014$; TA, $t = -8.47$, $P = 0.001$). However, predation effects in these two treatments did not differ from one another ($t = 2.17$, $P = 0.119$). In contrast, in the treatment consisting of 100% *C. trivittatus* IV (T) the effect on *Daphnia* densities was not distinguishable from the control ($t = 1.39$, $P = 0.238$). *Daphnia* population growth rate (λ) was <1 in all enclosures (Table 1) because of low fecundity. Average egg ratios for instars 5–9 were 0.03, 0.26, 0.47, 1.00, and 0.98, respectively, while the value for instars 10–14 combined was 1.34, and for instars 15–22 combined was 3.28.

Predation parameters

For each of the four *Chaoborus* categories, strike efficiency (S_{ij}) declined with increasing *Daphnia* body length up to a size at which *Daphnia* were too large for successful ingestion (Fig. 3a). Strike efficiency regressions for *C. trivittatus* IV from Mouse and Nick Lake had similar slopes and intercepts. Therefore, only three distinct strike efficiency patterns were observed (Fig. 3a) with slopes that were not significantly different ($F = 0.22$, $P \gg 0.1$) but intercepts that were noticeably different. *C. trivittatus* IV from Mouse and Nick Lake had a larger head capsule than *C. americanus* III and IV, and therefore consistently had a greater strike efficiency and could ingest larger *Daphnia* (Table 2). Both strike efficiency and encounter rate are functions of the relative body size of *Chaoborus* and *Daphnia* instar body length (L_i), but with opposite trends (Pastorok, 1981). Hence, their product, prey vulnerability (PV_{ij}), is a parabolic-shaped curve, the peak of which corresponds to the most

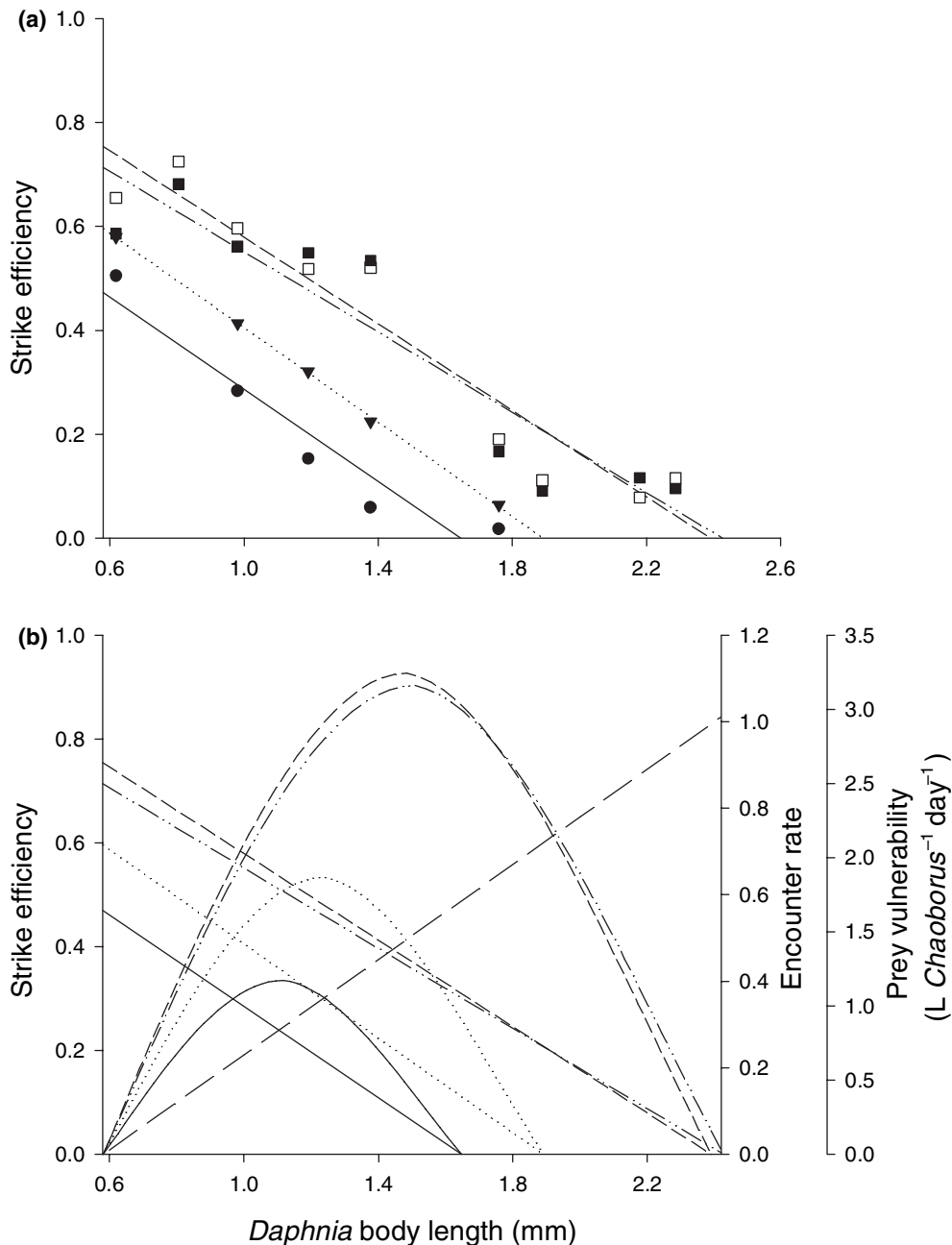


Fig. 3 *Daphnia* vulnerability parameters with the four *Chaoborus* types. (a) Strike efficiency (S_{ij}) determined from laboratory observations for Nick *C. trivittatus* IV (■, - -): $S_{ij} = -0.417L_i + 0.996$ ($r^2 = 0.93$, $P < 0.0005$), Mouse *C. trivittatus* IV (□, - · -): $S_{ij} = -0.387L_i + 0.938$ ($r^2 = 0.88$, $P < 0.0005$), *C. americanus* IV (▼, ····): $S_{ij} = -0.454L_i + 0.860$ ($r^2 = 0.999$, $P < 0.0005$), *C. americanus* III (●, —): $S_{ij} = -0.441L_i + 0.726$ ($r^2 = 0.92$, $P < 0.005$). (b) Prey vulnerability (PV_{ij}). The four decreasing lines are the S_{ij} lines from (a), and the increasing dashed line is the encounter rate function, $\varepsilon_i = 0.55L_i - 0.32$ (Pastorok, 1981). The parabolic-shaped curves represent the corresponding *Daphnia* vulnerability with each *Chaoborus* type, which is the product of S_{ij} and ε_i .

vulnerable *Daphnia* size for each *Chaoborus* (Fig. 3b; Pastorok, 1981). While Pastorok defined PV_{ij} as a product of ε_i and S_{ij} , we use Williamson's (1993) version, which is scaled by including the constant $P(A)$, the probability of attack:

$$PV_{ij} = \varepsilon_i \times P(A) \times S_{ij} \tag{6}$$

For the three distinct strike efficiency functions observed with *Chaoborus* in this study, three prey vulnerability curves exist (Fig. 3b). For *C. trivittatus*

IV, the most vulnerable *Daphnia* size was 1.50 mm, which is the same maximum vulnerability found by Pastorok (1981) for *C. trivittatus* IV feeding on *D. pulicaria*. The 1.24-mm *Daphnia* were most vulnerable to *C. americanus* IV, while 1.12-mm *Daphnia* exhibited maximum vulnerability to *C. americanus* III. In addition, *C. trivittatus* IV affected a greater range of *Daphnia* instars than did the two *C. americanus* instars.

The overlap index, O_{ij} , is a reflection of the vertical distribution of *Daphnia* and *Chaoborus* within each treatment. In A and TA, *C. americanus* III were near the surface day and night, overlapping with *Daphnia*, and *C. americanus* IV migrated to the surface at night, resulting in values of $O_{ij} > 1$ for both (Fig. 4a). On the contrary, *Daphnia* overlap indices were $\ll 1$ with *C. trivittatus* IV in TA and T. During the day, *C. trivittatus* IV stayed near the bottom of the enclosures, although in TA it had a slightly greater presence a couple of meters above the bottom compared with T (Fig. 2). This increased the overlap of *C. trivittatus* in TA by a small amount. Because of their high overlap with

Daphnia, *C. americanus* III and IV in A inflicted the largest density risk; however, DR_{ij} from these two *Chaoborus* was much lower in TA because of their low densities in this treatment (Fig. 4b). *C. trivittatus* in TA had only 74% of the density of *C. trivittatus* in T, yet it had a greater DR_{ij} because of a slightly increased overlap with *Daphnia*.

Predicted *Daphnia* growth rates

Daphnia population growth rates predicted by the model for each treatment closely approximated the corresponding observed *Daphnia* growth rates (Fig. 5). The order of the predicted *Daphnia* population growth rates for the four treatments remained the same for each predator density (from 0.2 to 0.7 L⁻¹) used in the model simulations: C > T > TA > A. The range of predicted values for the treatment containing 100% *C. trivittatus* IV (T) were similar to the observed *Daphnia* growth rates and, in both cases, this treatment was always most similar to the control, thus consistently

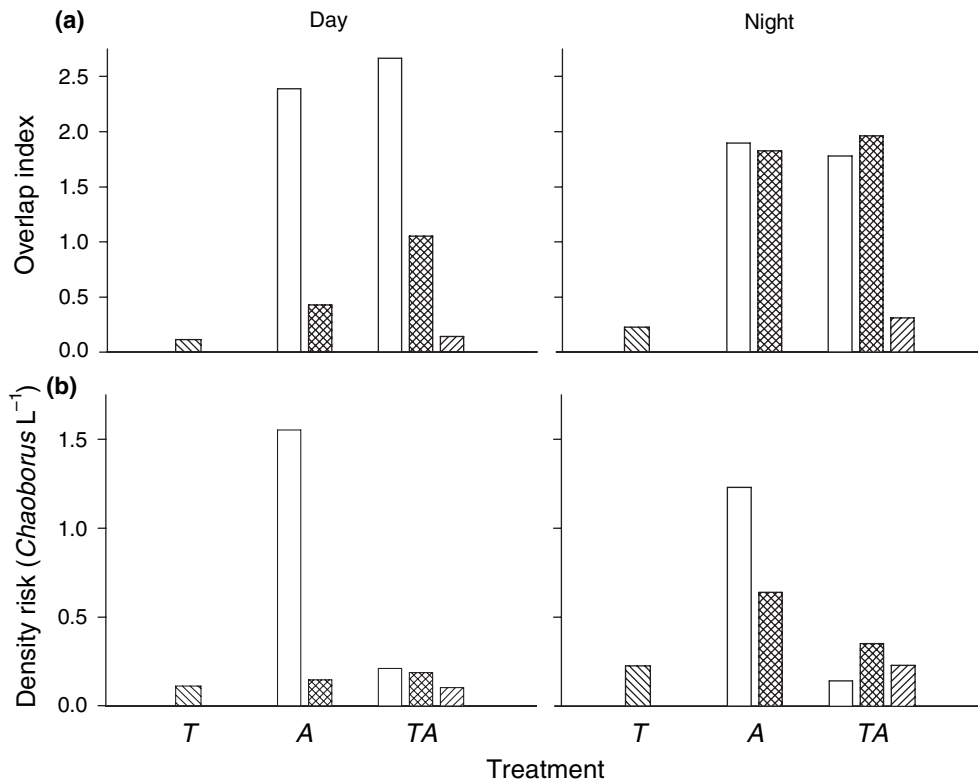


Fig. 4 Adult *Daphnia* density risk parameters with the four *Chaoborus* types in the three predator treatments. The parameters for juveniles show similar trends and therefore are not shown here. (a) Day and night overlap indices, O_{ij} . (b) Relative day and night density risk, DR_{ij} , which is the product of O_{ij} and relative predator density, N_j . N_j in each treatment is shown in Fig. 1.

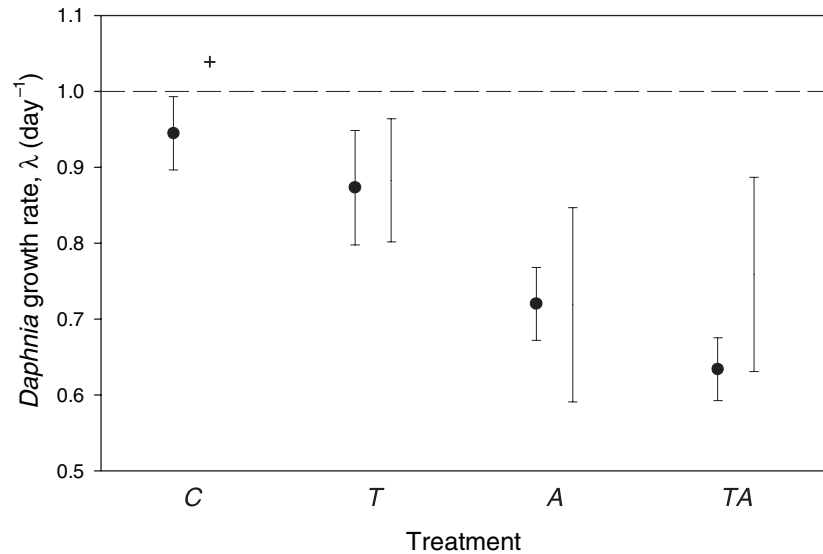


Fig. 5 Observed and predicted *Daphnia* population growth rate (λ) per treatment (defined in Fig. 1). The average observed λ (●) are shown with standard deviation. The corresponding vertical bar to the right of each observed λ is the range of predicted λ for predator densities 0.2–0.7 L⁻¹, and for the control the predicted λ is represented by (+). The dotted line is at $\lambda = 1$, which represents no population increase or decrease.

having the least effect on the *Daphnia* population in comparison with the other predator treatments. The treatments containing Nick Lake *Chaoborus* (A and TA) were predicted to have much lower *Daphnia* population growth rates than the control, as was observed in the field results. The simulations of A and TA growth rates were similar and the effect of these two treatments was not significantly different in the field experiment, suggesting that they had a similar effect on *Daphnia* population growth. However, the model predicts that the effect of A is slightly greater than that of TA, which is the opposite of the observed population growth rates. In addition, the range of predicted values for the treatments was slightly greater than the observed values, except in A.

Discussion

Our matrix model successfully predicted changes in *Daphnia* population growth using instar-specific probabilities of *Daphnia* survival because of the morphology and vertical distribution of each *Chaoborus* present, as well as other *Daphnia* instar-specific probabilities of growth and fecundity. No previous model has had such demographic and ecological realism. However, the complexity of the model required us to employ some parameters from the literature (e.g. background survival). While the use of these parameters might have produced some biased predictions, they would have had the same influence on predictions in each treatment. Furthermore, any

such biases would appear to have a modest influence, as the simulations of the predators' effect on *Daphnia* population growth were qualitatively similar to the growth rates observed in the experiments.

Treatments consisting of combinations of *Chaoborus* species and instars had diverse effects on a *Daphnia* population (Fig. 5). Treatments TA and T both consisted mainly of large *C. trivittatus*, but they had very different effects on *Daphnia* growth. In contrast, A and TA treatments produced similar reductions in daphnid growth, but they contained very different proportions of larval *Chaoborus*. To explain these results, we employed Williamson's (1993) predation risk model to examine the relative contributions of each *Chaoborus* on *Daphnia* population growth rate. Williamson defined predation risk (PR_{*j*}) as the product of density risk (eqn. 5) and prey vulnerability (eqn. 6). The relative contribution of predation risk from each predator can be illustrated by plotting the average of all instar values of the morphological component, PV_{*j*}, against those of the vertical distribution component averaged over day and night, DR_{*j*} (Fig. 6). Anywhere along a single predation risk isocline, *Chaoborus* inflicts an equal mortality risk on the *Daphnia* population. For example, *C. americanus* III in A and *C. trivittatus* IV in TA have a similar predation risk value (PR = 0.26) despite very different PV_{*j*} and DR_{*j*} values.

The sum of predation risk for each *Chaoborus* in TA and A results in a similar total predation effect (PR_T = 0.4), as was observed in the field experiment. In TA, density risk from each *Chaoborus* made little

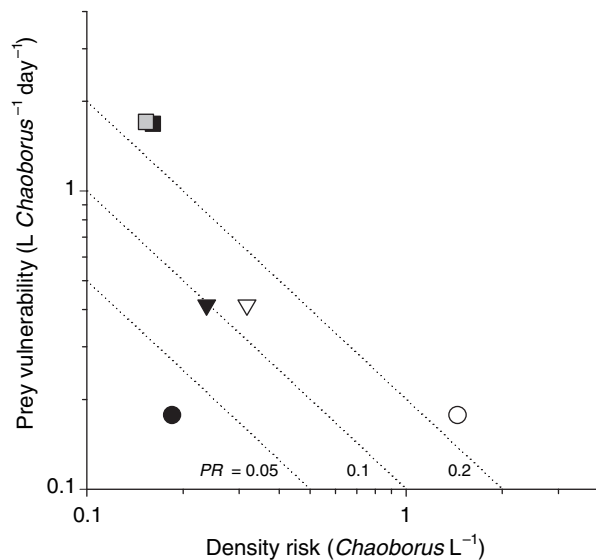


Fig. 6 Relative predation risk for *Daphnia* with each *Chaoborus* in treatment T (grey symbol), TA (black symbols), and A (unfilled symbols) for *C. trivittatus* IV (■, ■), *C. americanus* IV (▼, ▽), and *C. americanus* III (●, ○). Three predation risk (PR) isoclines are illustrated as dotted lines, which are straight because of the logarithmic scale.

contribution to the total predation risk for *Daphnia* (Fig. 6). *Daphnia* risk of predation in TA was largely because of their high average prey vulnerability to *C. trivittatus* IV, with additional predation from *C. americanus* III and IV. On the contrary, in A, most of the predation risk to *Daphnia* was because of its high spatial overlap with *C. americanus* III. This smaller *Chaoborus* only affects a small range of *Daphnia* instars, each with a low vulnerability (Fig. 3b), yet those instars that were vulnerable had a very high density risk. *C. americanus* IV also contribute to the overall predation risk in A.

The predation risk from *C. trivittatus* IV in treatments T and TA is very similar (Fig. 6), despite there being a greater proportion of this *Chaoborus* in treatment T (Fig. 1). This is attributable to the increased overlap in TA of *Daphnia* to *C. trivittatus* (Fig. 4) as well as slightly greater average prey vulnerability (Fig. 3). With the additional predation risk provided by *C. americanus* III and IV, TA has a substantially greater effect on the *Daphnia* population. Thus, regardless of the fact that T contained 100% *C. trivittatus*, which produces a very high prey vulnerability, the overall predation effect in this treatment was low because the distribution of *C. trivittatus* was limited to the bottom of the enclosures

both day and night and encounter with *Daphnia* was extremely rare.

Williamson's (1993) graphical approach aids in the identification of the two key findings of this study. First, it illustrates the interaction of morphology and migratory behaviour in determining predation effect from a single type of *Chaoborus*. For example, *C. trivittatus* IV in TA and *C. americanus* III in A both contributed a similar predation effect on *Daphnia*, yet these two predators differed greatly in morphology and migratory behaviour (Fig. 6). In T, a small predation effect on *Daphnia* was observed not because of small predator size, but because of a lack of spatial overlap of *C. trivittatus* with *Daphnia*. The second important finding is that different combinations of coexisting *Chaoborus* species and instars can have similar (TA and A) or very different (T and TA) effects. As *Chaoborus* density, composition and vertical distribution in a natural system varies seasonally (von Ende, 1975), as well as with vertebrate predators, water colour and water movements (Tsalkitzis *et al.*, 1994; Wissel *et al.*, 2003), many instar and/or species combinations can exist at any time. A model such as ours that has the ability to consider the combinations and variations of predator types simultaneously is required to describe these systems.

Williamson's (1993) predation risk model provides an accurate description of the overall effect of predation by demonstrating how the combination of prey vulnerability and density risk contribute to predation risk. His model can be applied to integrate the individual effects of predator morphology and migratory behaviour for the different *Chaoborus* to understand better its influence on *Daphnia* populations. These analyses indicate that it is not sufficient to consider only the morphological or behavioural characteristics of a predator such as *Chaoborus*. Both morphology and migratory behaviour must be jointly considered to determine the ultimate predation effect.

Our matrix model was reasonably accurate in predicting growth rates of *Daphnia* in summer enclosures in a temperate lake, but extending the model to a larger system will not be a trivial exercise. The parameter inputs are not dynamic as they can be in nature (Caswell, 2001), as seasonal differences in resources would affect *Daphnia* background survival and fecundity parameters, and the density of *Chaoborus* instars. In addition, there are more *Chaoborus* species than we have considered, and strike efficiency

functions do not exist for each of them. Finally, *Chaoborus* are often patchily distributed in nature (Tsalkitzis *et al.*, 1994), making spatial overlap estimates difficult to quantify. Nonetheless, the effort of considering both morphological and distributional characteristics of the predator is critical, given the demonstration that *Chaoborus* are often more important planktivores than fish in lakes (Ramcharan *et al.*, 2001).

Acknowledgments

We thank the personnel at Ontario Ministry of Natural Resources (OMNR) Algonquin and Bancroft units for permitting and facilitating our research. For equipment use, we thank the staff of the OMNR Harkness Laboratory of Fisheries Research and Gary Sprules. We have many to thank for assistance in the set up, sampling and counting of the field experiment, especially Wiebke Böing, Björn Wissel and G. Glen Young, as well as Shannon Allen, Emily Hyfield and Amanda Logue. For helpful advice with the modelling, we thank Robin Sanders and Troy day. We also thank William DeMott, John Havel, J. Dylan Parker, Peter Schulze and Norman Yan for valuable comments on the manuscript. The research was partially funded by Charles Ramcharan with a 'Louisiana Education Quality Support Fund 1999-01-RD-A-13', as well as a Research Incentive Award to HPR from the Research Foundation of SUNY College at Buffalo.

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(Manuscript accepted 17 March 2005)