

**Predicting Encounter Rates for Zooplankton: A Model Assuming a  
Cylindrical Encounter Field**

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We delimit a cylindrical attack field for a *Chaoborus* larva feeding on zooplankton, and propose a mathematical model to predict encounter rates with prey for this ambush predator. The model is based on the encounter process between a stationary cylinder and spheres moving at constant velocity in random directions. The predictions of the model are corroborated in the laboratory.

*Key words:* zooplankton, encounter model, *Chaoborus*, ambush predator, copepod

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Nous délimitons un champ d'attaque cylindrique chez une larve de *Chaoborus* qui se nourrit de zooplancton, et nous proposons un modèle mathématique qui prédit le taux de rencontre avec des proies pour ce prédateur à l'affût. Le modèle se base sur le processus de rencontre d'un cylindre stationnaire avec des sphères qui se déplacent au hasard et à vitesse constante. Les prédictions du modèle sont supportées par des observations recueillies en laboratoire.

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In coastal lakes and ponds near Vancouver, British Columbia, the 4th instar larva of *Chaoborus trivittatus* feeds primarily on crustacean zooplankton (mainly copepods, Fedorenko 1975; Swift 1976; Giguère 1979); larvae hover in the water and strike at prey that approach closely ( $\leq 3.8$  mm, Giguère and Dill 1979). Because (a) larvae do not pursue or lunge at prey, (b) prey move in more or less unpredictable directions, (c) predator and prey live in a relatively uniform aquatic environment, stochastic collision models could be used to quantify this encounter process accurately. To do so, one must imagine a suitable patch in space within which prey are uniformly or randomly distributed and move in random directions. Prey will encounter a target volume (the ambush predator) according to a function that depends on the size and speed of the prey, and the size and shape of the strike field of the predator.

The objectives of this paper are therefore threefold: first, to delimit the effective strike field of a *Chaoborus* larva; second, propose a mathematical formulation describing the rate at which prey encounter this strike field; and third, to demonstrate the ability of this model to make accurate quantitative predictions by comparing its output to encounter data collected in the laboratory, using copepods as prey.

### Materials and Methods

The configuration of the strike field of a starved 4th instar larva of *Chaoborus* was determined by filming predator-prey interactions at 45–150 frames/s with a Ciné-8 camera (Visual Instrumentation Corp., Burbank, Calif.). Larvae averaging 14.8 mm long (SE = 0.95, based on sample measurement) were starved for at least 1 day, and offered copepod prey (*Diatomus kenai* and *D. leptopus*, 0.9–2.6 mm in length) at 6, 13, and 24°C.

The filming was done from above a small Plexiglas container with about 6–8 mL of lake water. The shortest distance between the prey and the center of the predator at the moment of attack was measured on film perpendicular to the main body axis of the predator (left and right sides were pooled). Because these measurements are of a projection of the position of the prey onto the two-dimensional horizontal plane through the predator, they underestimate true attack distances and are referred to as apparent attack distances.

To test the model predictions, copepods were presented to single *Chaoborus* larvae inside rectangular experimental arenas containing 75 mL of lake water. Predator-prey interactions were observed visually and noted down as a time series with the help of an event recorder. An 'encounter' was scored whenever a part of the body of the prey (excluding antennae) came within 2 mm of the surface of the body of the predator. This included 93% of all attacks observed on high-speed films of predator-prey interactions (see Results below). Note that an encounter is not defined with respect to the sensory apparatus of the predator, but rather with respect to a volume of space within which prey become vulnerable to attack (whether or not prey detection occurred). This definition is simple (a sort of rule of thumb) and easily ascertained with the help of a millimetre grid applied to the bottom of Plexiglas containers. As deciding on an encounter involved judgment on the part of the observer, an initial training period of 33 h was needed until consistent observations were

obtained.

Prey were divided visually into four approximate size (length) categories (I, 1.0–1.29 mm; II, 1.3–1.59 mm; III, 1.6–1.89 mm; IV, 2.0–2.29 mm). All prey size categories were presented at two densities (three and six prey/arena) at 13 and 24°C (unless otherwise indicated). The experiments were carried out for 24–36 min and at a light intensity of 1600 lx.

Two separate tests were carried out: (1) the frequency of encounters per minute in 24 consecutive 1-min intervals was compared to that expected from a Poisson distribution (Sokal and Rohlf 1969) to determine whether 'encounters' were distributed randomly over time (13°C and six prey/arena). Goodness of fit was checked with the Kolmogorov-Smirnov test (Siegel 1956); (2) encounter data were compared to predicted values derived from our mathematical model.

### The Strike Field of a *Chaoborus* Larva

Apparent attack distances did not vary significantly between temperature treatments (ANOVA,  $P = 0.36$ ), and the data were pooled. Prey size was regressed on attack distance but the coefficient of determination was not significant ( $P = 0.62$ ). We grouped observations at 2-mm intervals along the larval body (the first and last intervals are open) and plotted all cases where apparent attack distance was  $> 1$  mm (Fig. 1). In this way, biases due to the effect of the contour of the body of the larva on apparent attack distances were eliminated. It was then possible to carry out statistical comparisons for data collected towards the outside of the attack field of the larva and determine the configuration of this field.

The mean values from the seven different regions did not vary significantly (ANOVA,  $P = 0.64$ ) suggesting that *Chaoborus* attacks at comparable distances along the entire body. Attack frequencies showed a marked decrease at distances greater than 2.2 mm from the longitudinal axis of the body of the larva (Table 1); this may represent a threshold value set by physiological and morphological limitations of the capture mechanism (personal observations suggest that larvae can detect prey at much greater distances). As visual observations in the laboratory indicate that a larva will attack prey above or below its body as well as to the side (except for dead spaces directly behind, directly in front, and just above its head), this threshold value determines a roughly cylindrical effective strike field for the *Chaoborus* larva. This is represented by the hatched line in Fig. 1. It includes 93% of all attacks observed on high-speed films in the laboratory. The dotted line (drawn 2 mm away from the surface of the body of the predator) also includes 93% of all attacks recorded on film. The latter definition was most practical to collect visual observations of predator-prey interactions in the laboratory, and was used in testing the model.

### Designing the Encounter Model

#### ASSUMPTIONS OF THE MODEL

We will consider the encounter process between a stationary cylinder and spheres which are randomly distributed and move at constant velocity in random directions. First we examine the plausibility of these assumptions:

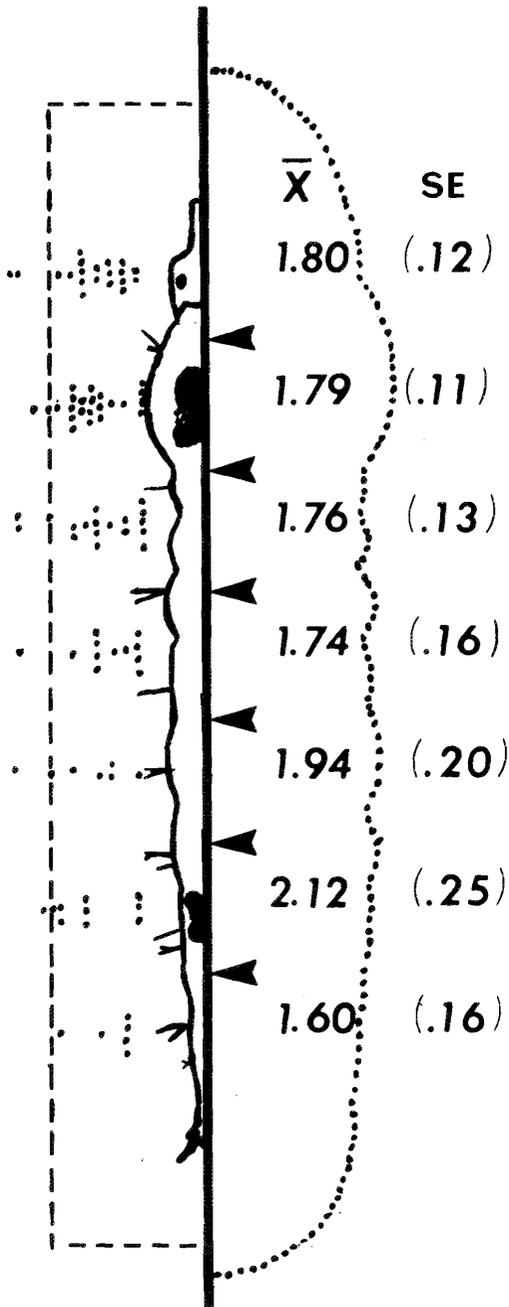


FIG. 1. Position of copepods (projected onto the horizontal plane through the predator when filmed from above) at the moment of attack by the 4th instar larva of *C. trivittatus*. The data (left and right sides pooled) are grouped at 2-mm intervals (between arrows) along the larval body. Apparent attack distance is measured perpendicularly from the long body axis to the nearest position of the prey at the time of attack. Only values  $>1$  mm have been considered. The means are given for each interval (with standard errors). The hatched and dotted lines circumscribe areas which include about 93% of all observations.

*The predator is stationary* — Whether the movements of the larva will affect predicted rates of encounter will depend

TABLE 1. Frequency of attack on copepods by the 4th instar larva of *C. trivittatus* as a function of apparent attack distance (see Fig. 1).

Apparent attack distance (mm)	No. of observations
0.00–0.20	29
0.21–0.40	12
0.41–0.60	17
0.61–0.80	19
0.81–1.00	15
1.01–1.20	27
1.21–1.40	17
1.41–1.60	9
1.61–1.80	11
1.81–2.00	4
2.01–2.20	13
2.21–2.40	4
2.41–2.60	1
2.61–2.80	1
2.81–3.00	3
3.01–3.20	2
3.21–3.40	0
3.41–3.60	0
3.61–3.80	0
3.81–4.00	2

on the amount and rate of displacement. Observations in the laboratory suggest that 4th instar larvae of *Chaoborus* do not 'search' or 'stalk' extensively and that relatively low speeds ( $<1$  mm/s; Pastorok 1978; Gerritsen 1980; Giguère personal observation) are involved. These are small relative to the speed of the prey (Swift and Fedorenko 1975), and Gerritsen (1980) has shown that the greater of two speeds (viz. predator and prey) has the stronger effect in determining encounter rates.

*Prey are spherical* — While this approximation appears reasonable for copepods swimming in straight path segments (see below), prey of different shapes may not be so easily incorporated into the model. It is difficult to determine the equivalent spherical size of prey over a wide range of prey size or length. One factor mitigates this problem. Prey swimming speeds are often strongly positively correlated with prey size (Eq. 5 below; Swift and Fedorenko 1975), and the model should be most responsive to changes in swimming speed of prey as prey size increases, as long as the prey are considerably smaller than the predator. Small errors in estimating the effective size of prey will then be negligible by comparison.

*Prey swim at constant speed and in random directions* — Movement patterns of copepods include rolls, loops, sudden jumps, sprints for fast escape, chases related to sexual behavior, etc. Based on observations in the laboratory, their predominant locomotory behavior consists of relatively slow displacements along straight path segments (while 'filter-feeding') interspersed with sudden jumps or changes of direction of short duration. This would result in a log-normal speed distribution, and cause at most a 3–4% error in calculating encounter rates (Gerritsen and Strickler 1977). As this pattern of behavior generally involves movement at constant speed and frequent changes in swimming direction, it should result in prey approaching the strike field of the predator from random (or unpredictable) directions.

*Prey are randomly distributed within a patch* — This condition might hold for a small patch (see Discussion). To test the model, however, the tendency of predator and prey to aggregate near water-Plexiglas interfaces must be accounted for. Giguère (1981) showed that the extent to which predator and prey aggregate near Plexiglas walls in the arenas is nearly compensated for by the fact that a wall prevents prey from approaching a predator from a particular direction. He derived a simple correction factor (1.035) for these arenas, and we therefore multiplied the encounter data by this factor.

#### THE MATHEMATICAL DERIVATION

We will derive a general formulation of the encounter problem for a stationary cylinder of length  $L$  and radius  $R$ , and spheres of radius  $r$  which are uniformly distributed and move at constant velocity in random directions. From Gerritsen and Strickler's (1977) eq. 7, we find that the rate of encounter ( $E$ ) between prey (considered as dimensionless points in space) and a motionless predator with a spherical encounter field (radius  $R$ ) is:

$$(1) \quad E = n\bar{s} \pi R^2$$

where  $\bar{s}$  represents the average speed of the prey and  $n$  the density of the prey. The term  $\pi R^2$  is the cross-sectional area of the encounter field of the predator. However, the cylindrical encounter field of *Chaoborus* will present a different cross-sectional area depending upon the prey's position relative to the predator. Thus we replace  $\pi R^2$  by the average cross-sectional area ( $\bar{A}$ ) of a cylinder of length  $L$  and radius  $R'$ , to which hemispherical ends were added (Fig. 2). Notice that spherical prey with radius ( $r$ ) are now considered dimensionless, their size being included in that of the strike field of the predator, i.e.  $R' = R + r$ . The average cross-sectional area is then the area of a circle,  $\pi R'^2$ , plus the average area of a rectangle,  $\pi(R'L/2)$ . The appropriate encounter formula then becomes:

$$(2) \quad E = n\bar{s} \pi \left( \frac{R'L}{2} + R'^2 \right).$$

This expression can be simplified further. Let  $L_t$  be the total length of the encounter field, such that  $L = L_t - 2R'$ , and substitute in Eq. 2. Then,

$$(3) \quad E = n\bar{s} \pi \left( \frac{R'L_t}{2} \right).$$

#### MODEL PARAMETERS

To compare the output of the model to encounter data collected in the laboratory, we must choose appropriate parameter values for the model. The characteristic dimensions of the cylinder representing the strike field of the predator can be established as  $L_t = 18$  mm and  $R = 2.2$  mm (see Fig. 1 and Table 1).

The diameter of the spheres ( $d$ ) was set equal to the maximum width ( $mw$ ) of a copepod measured in the cephalic area under a binocular microscope. For *D. kenai* and *D. leptopus*,

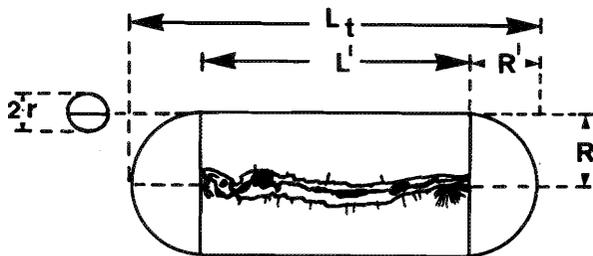


FIG. 2. Side view of a cylinder of length  $L$  and radius  $R'$ . These dimensions are that of the strike field of the predator augmented by the radius ( $r$ ) of the prey.  $L_t$  represents the total length of the cylinder after hemispherical ends of radius  $R'$  are added. The solution of the encounter problem requires an estimate of the average cross-sectional area ( $\bar{A}$ ) of this cylinder. See text for explanation.

this relates to length ( $l$ ) as follows ( $r^2 = 0.98$ ):

$$(4) \quad mw = 0.3456l^{0.8354}.$$

The speed of copepods (*D. kenai* only) was determined from high-speed films (see Materials and Methods) of individuals traveling along straight path segments. The data were grouped according to prey size at 0.2-mm intervals, and a polynomial equation was fitted by a least-squares method to the mean of each group. Since group sizes were unequal, this was preferred to fitting individual data points. The relationship is ( $r^2 = 0.94$ ):

$$(5) \quad \bar{s} = -0.53 + 2.15l - 0.153l^2.$$

This formula is approximate as it ignores stops and quick bursts of speed exhibited by diaptomid copepods. Nevertheless it represents the overall conditions prevalent in this system and is consistent with the data of Swift and Fedorenko (1975) for the same species.

#### Testing the Model

The agreement of observed encounter frequencies during 1-min intervals with predicted values from a Poisson distribution was good (Kolmogorov-Smirnov,  $P \geq 0.20$ ). However, large copepods (category IV) may have encountered the strike field of the larvae in a somewhat clumped manner. As this could be related to some form of sexual behavior enhanced by the high densities of adult copepods used in these experiments, more data were obtained at low densities (two replicates at 13°C with one, two, and three prey/arena). None of the data ( $P \geq 0.20$ ) indicate that copepods encounter the strike field of a *Chaoborus* larva in a nonrandom fashion over time. Note that although this finding increases the plausibility of our model, it is not a test of the assumption that prey swim in random directions (i.e. this pattern could occur even if prey swim predominantly in one plane).

There were no significant differences between the rate at which prey encountered the strike field of a *Chaoborus* larva at 13 vs. 24°C (two-tailed paired t-test;  $P \geq 0.90$ ). The data therefore were pooled and analyzed in a two-way ANOVA (Sokal and Rohlf 1969). There was no interaction between

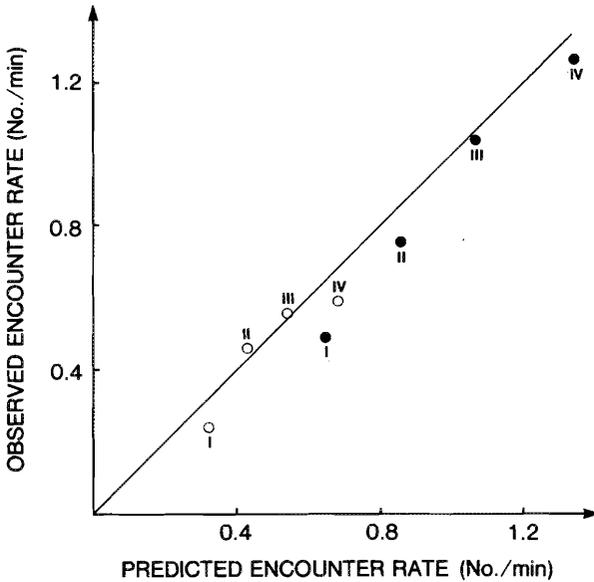


FIG. 3. Graphic representation of observed vs. expected encounter rate values of *Chaoborus*—copepod interactions based on visual data collected in the laboratory and predictions generated from the model, respectively. The line would represent a perfect fit. We show results for copepod size categories I to IV (see Materials and Methods) at two prey densities (open circles: three prey/arena; closed circles: six prey/arena).

prey size and prey density ( $P = 0.28$ ), but there were significant positive effects of prey size ( $P \leq 0.0001$ ) and prey density ( $P = 0.001$ ) on  $E$ . The data were multiplied by 1.035 (see assumption 4 above) and compared to the predictions derived from our model for the same density and prey size categories (Fig. 3). The fit is striking when one considers that the theoretical model was derived independently. The error varied from  $-6.3$  to  $17.2\%$  for categories II, III, and IV, but values as high as  $20.1$  and  $37.0\%$  were obtained for category I. As the latter category was comprised of *D. leptopus*, and Eq. 5 (for copepod speed) applies to *D. kenai* only, the estimates for swimming speed may have been erroneous. We therefore conclude that our model is consistent with laboratory data given proper input parameter values.

### Discussion

We have shown that the *Chaoborus* larva possesses an approximately cylindrical strike field, and have derived a collision model which takes this into consideration. The model predictions agree well with observations collected in the laboratory (i.e. the rate at which copepods approach within 2 mm of the body of the larva). Furthermore, the data indicated a random pattern of distribution of 'encounters' over time when copepods were used as prey. These experimental verifications lend support to the model.

However, the usefulness of the model is limited by our definition of 'encounter,' which does not take into account prey detection by the predator. As we know that (a) prey will pass through the strike field of a larva without being attacked

(Giguère 1981) or possibly even detected, and (b) probabilities of attack are not uniformly distributed within the strike field of the *Chaoborus* larva (more attacks occur near the anterior portion of the body of the larva, Fig. 1), we cannot predict feeding opportunities from a predator's standpoint.

It is possible to determine empirically (through visual observations) what proportion of 'encountered' prey are actually attacked. Giguère (1981), for example, found that about 46% of copepods entering the strike field of the 4th instar larva of *C. trivittatus* are attacked, regardless of prey length (0.9–2.6 mm), prey density (one, three, four, or six prey/arena), or temperature (6, 13, or 24°C). As the proportion of attacks which result in prey capture has also been determined (Swift and Fedorenko 1975; Pastorok 1978; Giguère 1981), laboratory estimates of predation rates can be obtained for this larva.

To determine whether our model can predict *Chaoborus* feeding rates in a natural environment, other factors must be considered.

### PREY MOVEMENTS

For an ambush predator, it is possible to assess the importance of preferential swimming directions by prey (i.e. vertical and horizontal motion) to the encounter process by looking at the symmetry of the strike field of the predator. Giguère (1981) compared the encounter rates for prey which move in a vertical plane (from above and below) to that of prey moving in a horizontal plane, where prey can approach the predator not only from two sides but from the ends as well. He estimated that the encounter rate was  $\sim 20\%$  greater in the latter case than in the former case. Our model would therefore underestimate encounter rate by 10% if prey are migrating vertically in one direction. If copepods move in both planes in various proportions, a smaller difference will result.

### HETEROGENEOUS PREY DISTRIBUTION

A major problem consists of defining an appropriate time scale and patch size while taking into account the tendency of prey to aggregate in specific areas (particularly on a vertical scale). A patch must be sufficiently small to yield a prey distribution that is fairly random, but not so small that a significant number of prey move in and out of it over short periods of time. In other words, one must define an instantaneous rate of encounter for a predator entering a new patch, and apply the model successively as the predator travels from patch to patch over time. The relevant scale of predation dynamics should be determined by potential directional movements of the predator or the prey, e.g. vertical travel.

Fortunately, two factors reduce the problems of applying the model to real situations: (1) predator and prey live in a relatively uniform environment; and (2) larvae attack in response to acoustic stimuli produced by their prey, and the propagation of these signals in water is not altered greatly by biotic or abiotic factors in the environment (in contrast to the situation for visual predators, Giguère 1980, 1981). Thus the model may be used to solve encounter problems for larvae in a natural environment, although this will require extensive knowledge of predator and prey distributions in the field.

The present formula estimates the encounter rate between moving spheres and a stationary cylinder. This approach can be applied to volumes of different shapes (e.g. cone, ellipsoid, etc.). Thus, one can solve encounter problems for other organisms living in a fluid environment. Many predators lie in ambush until the prey comes within a short distance and then launch an attack to subdue it (e.g. chaetognaths, Feigenbaum 1979). The size and shape of their strike field will depend on the anatomy and physiology of the capture mechanism, and non-spherical encounter models will often be necessary.

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