

# Encounter Probabilities and Community Structure in Zooplankton: a Mathematical Model

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GERRITSEN, J., AND J. R. STRICKLER. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. *J. Fish. Res. Board Can.* 34: 73-82.

Predator-prey interactions between swimming animals of the zooplankton are studied in a mathematical model. The assumptions are: 1) the animals are points in a 1-m<sup>3</sup> homogeneous space, 2) the animals move at random and are randomly distributed, and 3) the predator animal has an encounter radius given by its sensory system. The mathematics of encounter probabilities are developed for a 3-dimensional space. The results show two optimal strategies: 1) cruising predators which prey upon slow moving animals (herbivores), and 2) ambush (nonmoving) predators which prey upon fast cruising prey. Of the variables used (population densities, speeds of the two animal species, and encounter radius) the encounter radius has the greatest influence on the encounter probabilities. The results suggest a simple community structure and point to the importance of studies on live zooplankton.

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Les auteurs étudient, à l'aide d'un modèle mathématique, les interactions prédateurs-proies entre les animaux pélagiques du zooplancton. Les hypothèses sont les suivantes: 1) les animaux sont des points dans un espace homogène de 1 m<sup>3</sup>, 2) les animaux se déplacent au hasard et sont répartis au hasard et 3) le rayon de rencontre du prédateur est déterminé par son système sensoriel. On établit mathématiquement les probabilités de rencontre dans un espace à trois dimensions. Les résultats indiquent deux stratégies: 1) prédateurs en maraude saisissant des animaux qui se déplacent lentement (herbivores) et 2) prédateurs à l'affût (immobiles) qui se nourrissent de proies nageant rapidement. Parmi les variables utilisées (densités de populations, vitesses de deux espèces d'animaux et rayon de rencontre), le rayon de rencontre est celui qui a la plus grande influence sur les probabilités de rencontre. Les résultats suggèrent une structure de communauté simple et font ressortir l'importance d'études de zooplancton vivant.

Received June 21, 1976

Accepted September 30, 1976

Reçu le 21 juin 1976

Accepté le 30 septembre 1976

PREDATION influences the species composition and abundance of zooplankton in pelagic systems (Brooks and Dodson 1965; Brooks 1968; Dodson 1970, 1974; Confer 1971; Zaret 1972; Steele 1974; Kerfoot 1975). Zooplankton communities have two kinds of predators: other invertebrates and vertebrates. Vertebrate predators have the following characteristics: 1) they are visual predators that select large or otherwise easily visible prey (e.g. Ivlev 1961; Brooks and Dodson 1965; Zaret 1972; Zaret and Kerfoot 1975), 2) they are considerably larger than their planktonic prey,

and 3) they swim much faster than their prey. In contrast, invertebrate predators 1) select mostly small prey due to upper size limits imposed by their grasping appendages (McQueen 1969; Dodson 1970, 1974; Swift and Fedorenko 1975; Kerfoot 1975), 2) use mechanical perception to detect their prey (Horridge and Boulton 1967; Newbury 1972; Strickler 1975a), and 3) are only slightly larger than their prey and are evolutionarily closely related to them.

As the overall effects of predation in zooplankton communities are emerging from these and other studies, and as our knowledge advances on the mechanisms of prey detection in the zooplankton (Strickler 1975a; Zaret and Strickler unpublished data), it is now possible to construct a mathematical model of predator-prey interactions in 3-dimensional space. This will allow us to

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identify the critical factors controlling predation in pelagic communities, to predict evolutionary responses of predators and prey to such interactions, and to predict the role of predation in controlling community structure. This first attempt deals with planktonic communities of low diversity, where the water is well mixed and the animals are widely dispersed, such as in boreal lakes of Canada (Davis 1975). However, due to the abstract nature of the model, it may be applied to other ecosystems.

### Structure of Predation

Predation within an ecosystem can be considered to be the sum of all interactions between single predators and single potential prey animals. A single interaction can result in success or failure for the predator, corresponding to death or escape for the prey.

If we define a successful interaction as one resulting in a meal for the predator, then the rate of successful interactions is the rate of predation. For a given predator or prey, within a certain time interval, there is an associated probability of a successful interaction. To examine this, we dissect predatory interactions further.

A complete predatory interaction can be broken down into a series of chronological events, culminating in ingestion. The number of events is somewhat arbitrary: Edmunds (1974) considers two events, encounter and ingestion. For the purposes of zooplankton predation, we will consider a predatory interaction to consist of four chronological events: 1) the animals must first encounter each other, 2) the predator must recognize the other animal as a potential prey item and attack it, 3) it must capture the prey, and 4) it must successfully ingest the prey. Note that each of the animals can have a set of adaptations to change the probabilities in its favor at each of the four steps.

We define an encounter as an event when a predator and its prey are close enough so that the predator will recognize the other animal 50% of the time. If there is no encounter between predator and prey, there can be no predation. Hence, the rate of encounters will directly affect the subsequent steps, and therefore will affect the amount of food a predator eats. The importance of the encounter rate has been shown in various laboratory studies (Ivlev 1961; Holling 1965, 1966; Ambler and Frost 1974; Salt 1974), where the number of prey eaten per predator was dependent on prey density.

For the purposes of this model, we assume zooplankters to be very small animals, randomly

distributed and moving in a large, homogeneous 3-dimensional environment. Within an entire lake or ocean, zooplankters are not randomly distributed (Hutchinson 1967); however, on a scale relevant to a model of predatory dynamics (about 1 m<sup>3</sup> and 1 h), a random distribution may be assumed.

The problem of search and encounter probabilities for randomly moving objects has been addressed by Kohlas (1967) for aircraft of the Swiss Air Force. Kohlas considered the problem of aircraft encounters to be essentially 2-dimensional, and followed the treatment developed by Koopman (1956) for naval operations research. In view of the similarity of the problem, we follow Koopman's reasoning in the development of the encounter model, with the important distinction that we develop here the 3-dimensional case of the problem.

### Model

#### ENCOUNTER RATE

The assumptions of the model are as follows: 1) the animals are considered dimensionless points in space, 2) the animals are randomly distributed, 3) the animals are swimming in random directions, with a uniform probability distribution, 4) the mean swimming speed of each species will be used in the derivation, and 5) predators have an encounter radius,  $R$ , which is assumed constant in all directions.

A logical frame of reference is spherical polar coordinates, with the predator at the origin (Fig. 1). Consider an element of solid angle,  $d\omega$ :

$$d\omega = \sin \theta d\theta d\phi$$

If a single prey swims towards the origin with an unknown track angle,  $\Omega$ , relative to the predator, where the track angle  $\Omega$  is defined as the spherical coordinates  $\theta$  and  $\phi$  of the path of the prey, and  $\Omega$  has a uniform probability over its range (assumption 3), then the probability that  $\Omega$  is in the element  $d\omega$  is proportional to  $d\omega$ :

$$P(\Omega)d\omega = kd\omega = k \sin \theta d\theta d\phi$$

$\Omega$  exists; therefore, the probability that  $\Omega$  occurs within some  $d\omega$  is 1:

$$1 = \int P(\Omega)d\omega = \int_0^{2\pi} \int_0^\pi k \sin \theta d\theta d\phi = 4\pi k$$

Therefore,  $k = 1/4\pi$  and

$$P(\Omega)d\omega = (1/4\pi) \sin \theta d\theta d\phi \quad (1)$$

If there are  $N_H$  uniformly distributed prey per

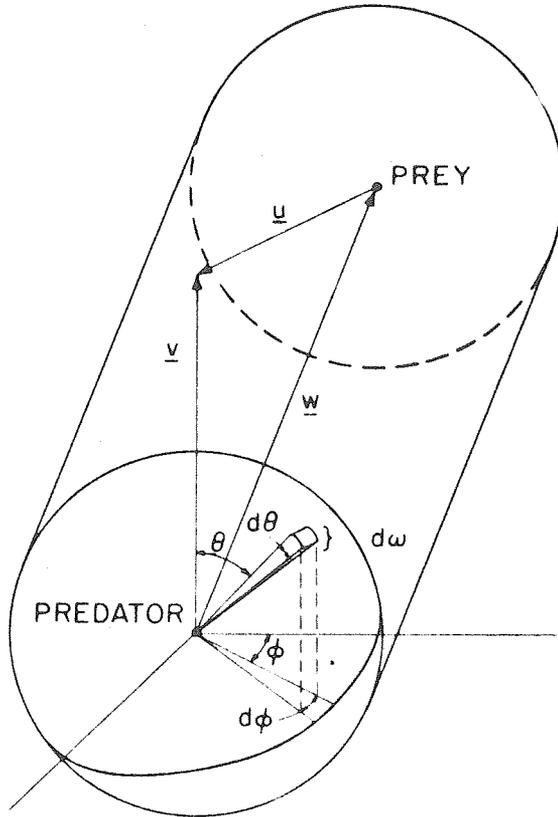


FIG. 1. The encounter sphere of a predator and the volume it sweeps as the predator searches for prey. See text for explanation.

unit volume, the expected number with a track angle in  $d\omega$  is

$$(N_H/4\pi) \sin \theta d\theta d\phi$$

The subscript H refers to prey; the subscript P refers to predators. Thus,  $N_H$  is the density of prey, and  $N_P$  is the density of predators.

Consider a predator with an encounter radius  $R$ , swimming with velocity  $\mathbf{v}$  through the water, and a prey animal swimming with velocity  $\mathbf{u}$ . The magnitudes of the velocity vectors  $\mathbf{v}$  and  $\mathbf{u}$  are the speeds  $v$  and  $u$ . The  $z$ -axis ( $\theta = 0$ ) of the coordinate system lies along vector  $\mathbf{v}$ . The track angle of the prey is the spherical coordinates  $\theta$  and  $\phi$  of the vector  $\mathbf{u}$  with respect to  $\mathbf{v}$ . A prey has a relative velocity  $\mathbf{w}$  with respect to the predator:

$$\mathbf{w} = \mathbf{v} - \mathbf{u} \quad (2)$$

and the relative speed  $w$  is given by the law of cosines:

$$w = \sqrt{u^2 + v^2 - 2uv \cos \theta} \quad (3)$$

To enter the encounter sphere during a time interval  $t$ , a prey animal, at time  $t_0$ , must be in the cylindrical volume that the encounter sphere sweeps with relative velocity  $\mathbf{w}$  during the interval  $t$ . This volume has height  $wt$  and base area  $\pi R^2$ . The number of prey, with a track angle in  $d\omega$ , entering the sphere per unit time is  $\pi R^2 w (N_H/4\pi) \sin \theta d\theta d\phi$ . Integrating over  $\theta$  and  $\phi$  gives  $Z_P$ , the encounter rate of a predator with its prey, or the total number of prey entering the sphere per unit time:

$$Z_P = \frac{\pi R^2 N_H}{4\pi} \int_0^{2\pi} \int_0^\pi w \sin \theta d\theta d\phi$$

$$Z_P = \frac{R^2 N_H}{4} \int_0^{2\pi} \int_0^\pi \sqrt{u^2 + v^2 - 2uv \cos \theta} \sin \theta d\theta d\phi \quad (4)$$

where  $\bar{u}$  is now the mean speed of the prey population, rather than the speed of an individual prey animal.

Evaluating for  $\phi$ :

$$Z_P = \frac{\pi R^2 N_H}{2} \int_0^\pi \sqrt{u^2 + v^2 - 2uv \cos \theta} \sin \theta d\theta$$

and for  $\theta$  gives:

$$Z_P = \frac{\pi R^2 N_H (\bar{u} + v)^3 - |\bar{u} - v|^3}{6 \bar{u}v} \quad (5)$$

Equation (5) reduces to:

$$Z_P = \begin{cases} \frac{\pi R^2 N_H}{3} \left( \frac{\bar{u}^2 + 3v^2}{v} \right) & \text{for } v \geq \bar{u} \\ \frac{\pi R^2 N_H}{3} \left( \frac{v^2 + 3\bar{u}^2}{\bar{u}} \right) & \text{for } \bar{u} \geq v \end{cases} \quad (6)$$

$$(7)$$

Note that (6) and (7) also express  $Z_H$ , the rate of encounter of a prey animal with its predator population, if  $N_H$  is replaced by  $N_P$ , the density of predators, and if  $v$  is replaced by  $\bar{v}$ . The total rate of encounter between predators and prey per unit volume,  $Q$ , is given by multiplying the rate of encounter for a single predator by the density of predators:

$$Q = Z_P N_P \quad (8)$$

We have assumed that using the mean speed of a population in the model gives the same results as if all animals in the population were swimming at exactly the same speed. More precisely, equation (5) must be integrated over  $u$

$$Z_P = \frac{\pi R^2 N_H}{6} \int_0^\pi \sqrt{u^2 + v^2 - 2uv \cos \theta} \sin \theta d\theta$$

$$\times \frac{(u + v)^3 - |u - v|^3}{uv} f(u) du \quad (9)$$

where  $f(u)$  is the probability distribution of  $u$ . This equation is best solved numerically for the individual distribution of  $u$ , because of the absolute value in the integral. Similarly, for  $Q$ , equation (9) must be integrated over  $v$ :

$$Q = \frac{\pi R^2 N_H N_P}{6} \int_0^\infty \int_0^\infty \frac{(u+v)^3 - |u-v|^3}{uv} f(u)g(v) du dv \quad (10)$$

where  $g(v)$  is the probability distribution of  $v$ . For the present we will use the mean speeds in the model, and thus equations (6) and (7) express the basic encounter rate model.

#### ENCOUNTER PROBABILITY

Randomly occurring, independent events over time are Poisson distributed (Fry 1965; Kohlas 1967). The Poisson parameter  $\lambda$  is the rate of encounter multiplied by the time interval under consideration:

$$\lambda_H = Z_H t, \quad \lambda_P = Z_P t$$

The probability of a predator's encountering  $x$  prey animals during time interval  $t$  is then:

$$P(x, t) = e^{-Z_P t} \frac{(Z_P t)^x}{x!} \quad (11)$$

The probability of a prey animal's encountering  $x$  predators is given by replacing  $Z_P$  with  $Z_H$  with equation (11).

#### ENCOUNTER RADIUS

As most zooplankters depend on mechanical signals for information about nearby animals, the encounter radius,  $R$ , is a complex function of many variables and will not be constant under all circumstances. Whether or not an animal detects a disturbance in the water depends on the strength of the disturbance, the distance between the disturbance and the animal, the sensitivity of the animals' receptors, and the relative level of noise (such as turbulence) in the system. An animal that is moving, moreover, creates pressure and shear disturbances in front, in back, and alongside of it (Strickler 1975a, b; Zaret and Strickler unpublished data). These disturbances may combine to reduce the sensitivity of the animal's receptors and to increase the level of noise; moreover, the disturbances should increase with increasing speed, resulting in a reduction of the potential detection radius as a predator swims faster.

To see how the above effects might change the behavior of the model, appropriate relations were incorporated into a simulation of the model. As a first approximation, the following assumptions were made concerning  $R$ : 1) the size and speed of the prey have no effect on  $R$ , and 2) the predator's encounter radius,  $R$ , decreases exponentially with the predator's speed to a certain minimum, which corresponds to direct contact between the two animals. The following two relations were used:

$$R = c_1 e^{-c_2 v} + c_3 \quad (12)$$

$$R = c_1 e^{-c_2 v^2} + c_3 \quad (13)$$

where  $c_1$  and  $c_2$  are proportionality constants and  $c_3$  is the minimum, direct-contact radius.

#### ENERGETIC EFFICIENCY

For an animal to grow and reproduce, the energy that it obtains from its food must be more than the energy spent to acquire the food. The relative amount of energy available for growth and reproduction may be expressed as the animal's efficiency,  $W$ , defined as the ratio of maximum expected energy gain per unit time, or power input,  $P_i$ , to energy spent per unit time, or power output,  $P_o$ :

$$W = \frac{P_i}{P_o} \quad (14)$$

Seasonal energy storage was ignored to arrive at an animal's average efficiency over its life span.

Power input,  $P_i$ , or food eaten per unit time, was defined as a constant proportion of the encounter rate:

$$P_i = \alpha Z_P \quad (15)$$

where  $\alpha$  represents the proportion of prey encountered that are actually ingested, times the energetic value of the prey. The constant  $\alpha$  expresses the probability of attack, capture, and ingestion, given an encounter, but for the purpose of this model it does not take into account functional responses of predators (Holling 1966).

The power output,  $P_o$ , was defined as the energy spent swimming plus a constant metabolic rate. The drag force on swimming animals of the same size and shape is proportional to the square of the speed (Shapiro 1961; Vlymen 1970), and the power required to swim is thus proportional to the speed cubed (Klyashtorin and Yarzhombek 1973):

$$P_o = \beta v^3 + \gamma \quad (16)$$

TABLE 1. Percent deviation of encounter rates  $Z_p$  and  $Q$  calculated with mean speeds  $\bar{u}$  and  $\bar{v}$  (equations 6, 7, 8) from the correct values of  $Z_p$  and  $Q$  obtained with numerical integration (equations 9 and 10). Right-hand columns give percent deviation. Experimental speed distributions were generated by a pseudorandom number generator.

Case	Predator speed distribution	$\bar{v}$	Prey speed distribution	$\bar{u}$	% deviation	
					$Z_p$	$Q$
$\bar{v} > \bar{u}$	uniform	0.40	uniform	0.10	-0.7	-0.6
	uniform	0.40	normal	0.10	-0.6	-0.5
	normal	0.41	normal	0.10	-0.5	-1.1
	normal	0.41	log-normal	0.11	-1.7	-2.4
	log-normal	0.39	log-normal	0.11	-1.9	-6.5
	log-normal	0.39	uniform	0.10	-0.7	-5.0
$\bar{v} \approx \bar{u}$	uniform	0.39	uniform	0.40	-0.5	-0.8
	uniform	0.39	normal	0.39	-4.0	-4.2
	normal	0.41	normal	0.39	-3.8	-7.1
	normal	0.41	log-normal	0.38	-10.7	-12.7
	log-normal	0.42	log-normal	0.38	-10.7	-16.9
	log-normal	0.42	uniform	0.41	-0.5	-12.2
$\bar{v} < \bar{u}$	uniform	0.10	uniform	0.41	-0.04	-0.6
	uniform	0.10	normal	0.36	-1.8	-2.7
	normal	0.11	normal	0.36	-2.0	-2.5
	normal	0.11	log-normal	0.41	-3.8	-4.3
	log-normal	0.10	log-normal	0.41	-3.7	-5.5
	log-normal	0.10	uniform	0.40	-0.05	-1.9

The constant  $\gamma$  expresses all elements of total metabolism (Kerr 1971a, b) not contributing to growth, reproduction, or capture of prey;  $\beta$  is a constant approximating other variables of the drag function. The proportion of a zooplankter's energy spent swimming is unclear; estimates of energy spent in diurnal vertical migrations range from very low (Hutchinson 1967; Vlymen 1970) to as high as 40% (Klyashtorin and Yarzhombek 1973) or 95% of metabolic rates (Petipa 1966).

## Results and Predictions

### EFFECT OF SPEED DISTRIBUTIONS

Mean swimming speeds were used in the calculations of encounter rates (equations 6, 7, 8), although real zooplankters do not swim at a constant speed. Encounter rates obtained from mean speeds were compared with encounter rates obtained by numerical integrations of equations (9) and (10) (Table 1). Three distribution functions for speeds ( $f(u)$  and  $g(v)$ , equations 9 and 10) were used: uniform, normal and log-normal, and three cases of the relative values of the mean speeds:  $\bar{v} > \bar{u}$ ,  $\bar{v} \approx \bar{u}$ , and  $\bar{v} < \bar{u}$ . Calculations based on mean speeds consistently underestimate encounter rates; the magnitudes of the errors are determined by the speed distributions and by the relative values of the means. Therefore, mean speeds may be used to calculate adequate ap-

proximations of encounter rates in most cases. Correction factors are required only for log-normally distributed speeds.

### EFFECT OF SPEED

The encounter rate for predators or prey,  $Z$  (equations 6 and 7), is an increasing function of four independent variables:  $N_{II}$  or  $N_p$ ,  $R$ ,  $v$ , and  $u$ . The four independent variables are by definition positive and the first partial derivatives of  $Z$  are positive; hence,  $Z$  is an increasing function. This indicates that predators may increase their encounter rate with prey by increasing their encounter radius or their speed, and, conversely, that prey may decrease their encounter rate by decreasing their speed or the predator's encounter radius.

If predators and prey have different mean speeds, the greater of the two speeds has the greatest effect on the encounter rate (Fig. 2 and 3). This effect is also apparent from equations (6) and (7) and from the partial derivatives of  $Z$  with respect to  $u$  and  $v$ . When the speed of a prey animal is less than that of its predator, a further decrease in speed does not give as great a decrease in encounter rate or encounter probability. If an animal swims very slowly, it will also have a lower rate of encounter with its own food and with potential mates; therefore, a prey animal is expected to have a slower cruising speed

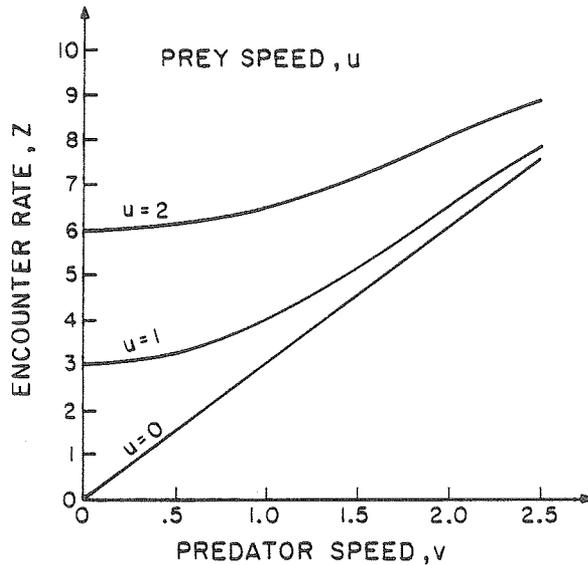


FIG. 2. The encounter rate,  $Z$ , as a function of predator speed,  $v$ , for three different prey speeds,  $u$ .  $R = 1$ ,  $N_H = 1$ . Note that when  $u = 0$ , the encounter rate is linear with  $v$ , and when  $u > 0$ , the encounter rate approaches this line asymptotically. All variables are nondimensional to show the behavior of the model (the same in Fig. 2-6).

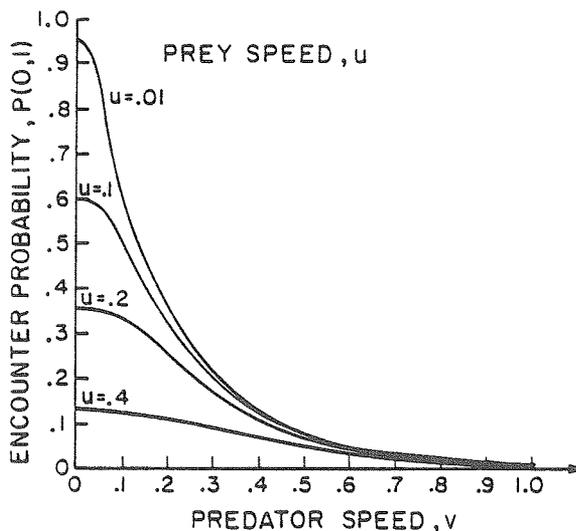


FIG. 3. Poisson probabilities of no encounter [ $P(0,1)$  equation 11,  $x = 0$ ,  $t = 1$ ] as a function of predator speed,  $v$ , for different prey speeds,  $u$ . Encounter radius  $R = 0.3$ , prey density  $N_H = 5$ . Optimal probabilities for predators are lower, and optimal probabilities for prey are higher. Note the sharp decline in the probability of no encounter when prey speeds are low, and the relatively slower decline when prey speeds are higher.

than its major swimming predator, but this speed should not be zero. Conversely, if a predator is slower than its prey, an increase in the predator's speed gives only a slight increase in the encounter rate. Substantial increases in encounter rate will occur only if the predator's speed is as great or greater than that of the prey.

#### EFFECT OF ENCOUNTER RADIUS

The highest-order variable in equations (6) and (7) is the encounter radius,  $R$ ; hence, an increase in  $R$  should produce the greatest relative increase in the encounter rate and encounter probability (Fig. 4). A slight increase in  $R$  results in a considerable decrease in the probability of no encounter (Fig. 4A), while an increase in  $v$  has a smaller effect (Fig. 4B).

When equation (13) is included in the model, there are two predator speeds that result in maximum encounter rates, one at low prey speeds, the other at higher prey speeds (Fig. 5). This relation is sensitive to the values of the constants  $c_1$ ,  $c_2$ , and  $c_3$  (equation 13); if  $c_1$  is small or if  $c_3$  is large, the encounter rate increases with increasing  $v$ . Equation (12) gives a similar figure, but it is much more sensitive to the values of the constants. These results emphasize the close relationship between the performance of the sensory system and the ability of a predator to capture prey.

#### EFFICIENCY

Within the framework of the encounter model, we would like to know the variables, for a predator, giving maximum efficiency in the utilization of a food resource. We assume that over evolutionary time, natural selection perpetuates those predators that catch the most food relative to their swimming power output. The efficiency includes the effect of increasing drag force as an animal increases its cruising speed (equations 14, 15, and 16). Two types of predators have optimal efficiency under these conditions (Fig. 6): stationary, or ambush, predators are most efficient at utilizing fast prey (curve of  $u = 2.0$ , Fig. 6), and cruising predators are most efficient at utilizing slow prey (curve of  $u = 0$ , Fig. 6). As an animal swims faster, its drag force increases, and it must expend more energy to overcome drag. Consequently, a faster animal encounters more prey (Fig. 2 and 3), but it uses more energy. To be energetically efficient, it must catch prey in proportion to the exponentially increasing energy expenditure. The effect becomes strong at high speeds (Fig. 6, right-hand side), where the energy

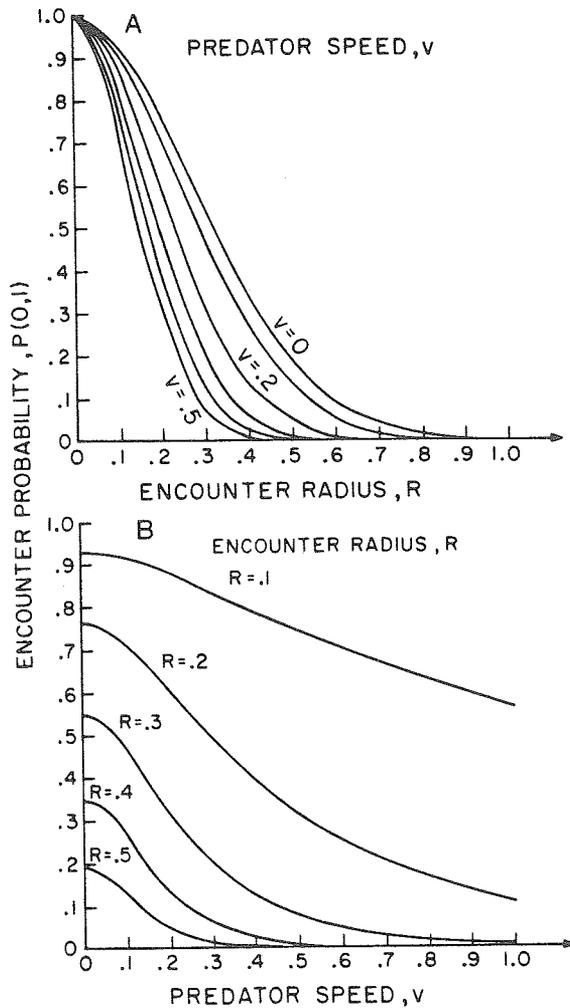


FIG. 4. Poisson probability of no encounter [ $P(0,1)$ , equation 11,  $x = 0$ ,  $t = 1$ ], A, (upper graph) as a function of encounter radius  $R$  for different predator speeds  $v$ , B, as a function of predator speed  $v$  for different encounter radii,  $R$ . Prey speed  $u = 0.1$ , prey density  $N_{II} = 5$ . A and B are orthogonal views of the same 3-dimensional surface.

intake is no longer proportional to the energy expenditure, and as a result efficiency declines. If prey are fast moving, efficiency declines immediately, and an ambush predator is most efficient. In the case of very slow moving prey, the encounter rate increases faster than energy expenditure as a predator swims faster, up to an optimum, moderate speed.

The constants  $\alpha$ ,  $\beta$ , and  $\gamma$  have no effect on the basic shapes of the curves (Fig. 6), but they do

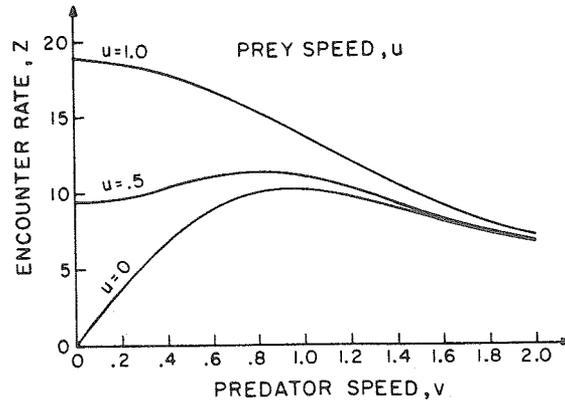


FIG. 5. Encounter rate,  $Z$ , as a function of predator speed,  $v$ , for different prey speeds  $u$ , when encounter radius,  $R$ , declines with increasing predator speed (equation 13).  $N_{II} = 0.67$ .

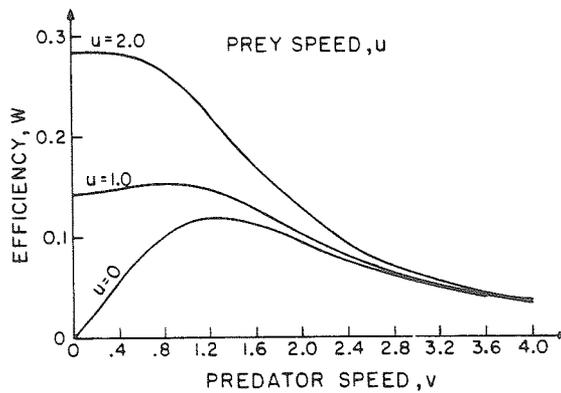


FIG. 6. Predator efficiency,  $W$ , as a function of predator speed  $v$ , for different prey speeds,  $u$ . Efficiency,  $W$ , is power input ( $P_i = \alpha Zv$ , equation 15) divided by power output ( $P_o = \beta v^3 + \gamma$ , equation 16). Prey density  $N_{II} = 1$ ,  $\alpha = 1$ ,  $\beta = 0.5$ ,  $\gamma = 2$ .

affect the scale of the curves.  $\beta$  has the most pronounced effect: a decline in  $\beta$  ( $\beta \rightarrow 0$ ), equivalent to better swimming efficiency, results in a higher efficiency,  $W$ , and a faster optimal cruising speed,  $v$ , on the curve  $u = 0$ . An increase in  $\gamma$  also shifts the maximum on the curve  $u = 0$  to the right, but lowers the value of  $W$ .

Two other results are of note. 1) The curve for  $u = 1.0$  (Fig. 6) has a shoulder as a maximum from  $v = 0$  to  $v = 1.2$ . Any predator speed in this range works with nearly the same efficiency. 2) Figure 6 shows similar results to Fig. 5, where we linked the encounter radius to the speed of the predator. This similarity clearly shows that there are two reasons for the existence of two optimal

predator cruising speeds: 1) higher energetic efficiency, and 2) a better relationship between signals per unit time and the general noise level. This holds for all speeds of the prey.

### Discussion

#### STRATEGIES<sup>2</sup> AND COMMUNITY STRUCTURE

The model clearly predicts two optimal cruising strategies for predators: ambush predation and cruising predation (Fig. 5 and 6), each most efficient at utilizing a certain prey resource. Our model predicts that, in a classic situation of food competition between two predators, each using a different strategy, the swimming behavior of the prey will determine the outcome. Both predators have a higher encounter rate and a greater efficiency with fast prey than with slow prey. However, the ambush predator wins against the cruising predator if the prey is fast moving.

The existence of two discrete types of predator strategies and their specialization on prey with different speeds suggests a mechanism for resource partitioning (MacArthur 1972; Schoener 1974) between the two predator types. However, resource partitioning depends on competitive displacement according to the Gause-Volterra principle (Hutchinson 1958), and the encounter model does not consider (as an input) competition between predators. The model and its predictions are based mainly on physics and probability; thus, the two strategies predicted are not the result of competition. An ambush predator is, in effect, an obligate specialist on fast-moving prey, and will not compete with a predator that uses only slow prey. Cruising predators can be generalists on prey of all speeds, and could switch strategies (Murdoch 1969), thus increasing the probability of competition.

For prey, the best strategy to avoid encounters with predators is to move slowly (Fig. 2 and 3). However, prey animals must also encounter mates and their own food; filter feeders must filter new water, and omnivores must swim to encounter food particles. Very slow animals have a very low probability of encountering ambush predators and a moderate probability of encountering cruising predators. Hence, slow prey need secondary defenses (Edmunds 1974) only for cruising predators. Faster prey animals, however, have high

probabilities of encountering ambush and cruising predators and need secondary defenses for both types of predators.

Considering the strategies and observations above, we may now outline a simple, logical community structure based on speed and trophic level. The primary producers, or phytoplankton in pelagic environments, move passively or very slowly, enough to encounter fresh nutrients (Titman and Kilham 1976). Herbivores grazing on them need some minimum motion to encounter the phytoplankton, but also must swim slowly to avoid encountering their own predators. Filtering currents of planktonic herbivores may serve to increase an animal's encounter rate with phytoplankton. Newton's third law of motion does not allow the animal to remain stationary when it is filtering (special swimming modes may have evolved to counteract this). The slow-swimming herbivores are subject to predation by cruising predators, the first carnivores. The presence of faster-swimming animals now allows the existence of secondary ambush predators, which cannot exist on the slow-swimming herbivores alone. This simple primary structure will increase in complexity as prey species show escape reactions to avoid being captured and predators find alternative food with different behavioral repertoires.

Central to our hypothesized community structure is the relationship between cruising speed and efficiency. We have not assigned units to the speeds in our simulations, as we are only interested in the general behavior of the model. The predator and prey cruising speeds in Fig. 6 are in the same, nondimensional units. The value of the optimal speed of a cruising predator will be determined by the values of the constants  $\beta$  and  $\gamma$  in the expression of power output (equation 16). Swimming efficiency, approximated by  $\beta$ , is a complex function involving hydrodynamic efficiency, propulsion efficiency, and muscular efficiency. A decrease in  $\beta$  (i.e. greater swimming efficiency) results in an increase in the optimum speed for cruising predators. In other words, more efficient swimmers will have a higher optimal cruising speed as cruising predators. Fish are more efficient swimmers than zooplankton (Schmidt-Nielsen 1972); therefore, planktivorous fish will have a higher encounter rate than zooplankton.

There are abundant examples in the literature of ambush and cruising predators. Some examples of ambush predators are chaetognaths (Horridge and Boulton 1967), corals preying on passing zooplankton (Porter 1974), and midge larvae preying on herbivorous and predatory zooplankton (Swift and Fedorenko 1975). Cruising predators are also found: many predaceous copepods,

<sup>2</sup>We recognize that the word "strategy" is anthropomorphic, and we use it here merely to facilitate communication. What is implied is that natural selection has perpetuated species which interact in their ecological theater in a nearly optimal manner (with so-called "strategies") to maximize their fitness (Hutchinson 1965).

such as *Cyclops* sp. and *Epischura* sp., cruise much faster than similar-sized herbivorous zooplankters (Gerritsen unpublished data). The best example is the specialization on prey by ambush and cruising predators, described by Anderson (1974), in which two ambush predators, a floating ctenophore species and a chaetognath species, fed primarily on actively swimming copepods, while a cruising ctenophore species fed on slowly drifting copepods.

#### STABILITY AND LIMITATIONS OF THE MODEL

It is necessary to analyze the stability and the applicability of the model as the variables and constants change. The model is most sensitive to changes in the encounter radius (Fig. 4 and 5). The values of the constants  $c_1$ ,  $c_2$ , and  $c_3$  (equations 12 and 13), greatly influence the behavior of the model when it incorporates the assumption of reduced encounter radius with increasing predator speed (Fig. 5). The size of the encounter radius is actually a complex interaction involving predator speed, prey speed, and prey size (Zaret and Strickler unpublished data) and the encounter radius varies considerably with these three variables. This variability of the encounter radius will influence strategies available to predator and prey. Therefore, the behavior of predators' encounter radii under different conditions must first be known before more accurate modifications of the encounter model can be made.

Two assumptions central to the derivation of the model are those of random direction of motion and random distribution of planktonic animals within space. The assumptions seem reasonable within the limits, though they are slightly biased by the behavior of different zooplankters to sink rather than swim down (Strickler 1970). This fact indicates the need for further investigation.

The behavior of the predator-prey system will change when there is a high probability of more than one prey simultaneously in the encounter field of a predator. In this case, the predator has a choice of prey to attack, and the probabilities of attacking each prey are no longer constant, nor are they independent of each other. Note that this does not change the encounter rate, nor the encounter probabilities, but it does change the probabilities of attack. For simultaneous choice to occur either a predator must have a large encounter radius, or the density of prey must be high. If a large invertebrate predator 1 cm long has an encounter radius of 2 cm, its encounter sphere has a volume of about 30 ml. For there to be a high probability of more than one prey in the sphere, the density of prey must

be more than 33 animals/l. This is a high figure, but is within the range observed for freshwater zooplankton (Davis 1975). Smaller predators, such as predatory copepods, have a much smaller encounter radius of about 0.5 cm (Gerritsen, in prep.), requiring an exceedingly high prey density of over 2000 animals/l for a similar effect. We see, then, that as encounter radius increases, the opportunity for choice increases. This is, in fact, the case for planktivorous fish which have a large encounter radius because they are visual predators, and when presented with a choice, they should select the most appealing (e.g. largest) prey (O'Brien et al. 1977).

The encounter model and its predictions are characteristic of any 3-dimensional predator-prey system that satisfies the constraints and assumptions of the model. The model is not derived from characteristics of planktonic animals, but rather from inherent characteristics of predator-prey interactions in 3-dimensional fluid environments. Essential to the model is a homogeneous environment, such that the probabilities of attack, capture, and ingestion remain constant over space at a given time. These probabilities must be constant regardless of where the interaction takes place (within the 1 m<sup>3</sup> for zooplankton). Therefore, neither predator nor prey can have a refuge or hiding place determined by the structure of the environment. Without additional assumptions the model as developed here would not apply to terrestrial or benthic ecosystems where prey have cover (e.g. foliage or rocks). In addition to most pelagic predator-prey systems, the model would apply to some aerial interactions, notably bats and birds preying on insects on the wing.

#### Acknowledgments

Three distinguished scientists gave us support and encouragement at crucial times: Professors W. T. Edmondson, G. E. Hutchinson, and O. M. Phillips. We thank them for their assistance. We also thank Drs R. J. Conover, J. B. C. Jackson, W. C. Kerfoot, K. G. Porter, J. R. Powell, and Mr R. Zaret for editing and suggestions. We acknowledge financial support of NSF (Grant DEB76-02096), the Baltimore Gas and Electric Company, and Sigma Xi. Last but not least we thank the blackflies and mosquitoes that make Newfoundland inland waters uninhabitable and pristine environments.

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